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Terrestrial Biomes and Ecoregions

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Foreword

Angola is globally recognised and envied for the richness of its biomes, ecoregions, fauna and flora. With habitats ranging from the rain forests of Cabinda to the ultra-desert of Namibe, Angola has a greater diversity of ecosystems than any other African country. In contrast to many other African nations, however, Angola has very few academic resources (textbooks, training manuals) to support students and young researchers studying the country's living natural assets—its 'life on land'. Furthermore, most of the books published on Angola's biodiversity are not available in Portuguese. A critical challenge to students and researchers in Angola has been the reality that English is the international language of science.

This barrier to developing a new generation of motivated and skilled researchers and technicians, together with interested citizens, into the fields of biodiversity, conservation and sustainable development, has been recognised by academics both in Angola and Portugal. Encouraged and supported by the respective ministries of science, technology and higher education in both countries, several ambitious initiatives have recently been launched to address this language impediment. In this respect, CIBIO (the Research Centre in Biodiversity and Genetic Resources of the University of Porto) has made a major contribution.

CIBIO's mission is to develop world-class research in the area of biodiversity, advancing knowledge on the origins and maintenance of biodiversity and applying this knowledge to address societal challenges related to climate and land use changes, environmental degradation, the loss and sustainable use of biodiversity and agrobiodiversity and the management, restoration and sustainable use of ecosystems and their services.

Over the past decade, the CIBIO initiatives in Africa have grown rapidly through several collaborative projects. These include the *TwinLabs* Programme, the UNESCO Chair *Life on Land*, and the evolution of CIBIO into a major Centre of Excellence—the BIOPOLIS Association—supported by the European Commission, the Portuguese Ministry of Science, through national and regional funding entities, the universities of Porto and Montpellier and multiple private sector investors.

Throughout this phase of growth, CIBIO has worked closely with its Angolan partners to ensure a strong focus on the country's priority needs in science, technology and higher education.

The first TwinLab was created in October 2012, in Angola, at the Higher Institute of Education Sciences (ISCED) of Lubango, Huíla. Since then, the TwinLabs network has expanded through formal agreements with institutions of higher education in Mozambique, Namibia, South Africa, Zimbabwe and Botswana. Preparatory work is under way for the implementation, among others, of TwinLabs in São Tomé e Príncipe and Guinea-Bissau. The UNESCO Chair *Life on Land* was established in 2017 and the BIOPOLIS Association in 2021.

Results from these initiatives include an encouraging number of new publications, both generalist and technical, that can inspire students and encourage the general public to take an interest in and support the conservation of Angola's biodiversity. These include *Biodiversity of Angola: A Modern Synthesis*; *South West Angola: A Portrait of Land and Life*; *50 Birds of Angola: Rarity and Endemism*; and the present volume, *Biomes and Ecoregions of Angola: An Introduction to Terrestrial Ecology*. Each of these authoritative books, published by CIBIO, is available in free-access e-book format, making them easily accessible to Angolan students. Further, through the UNESCO Chair *Life on Land*, two volumes of the UNESCO *Biodiversity Learning Kits* have been translated into Portuguese and published by CIBIO, in both hardcopy and e-book format. These richly illustrated volumes are of the highest technical quality and provide essential introductions to the biological sciences for secondary and tertiary-level students.

The strong collaboration between the Angolan and Portuguese ministries of science, technology and higher education has been fundamental to the success of these joint initiatives. With the evolution of CIBIO into the new BIOPOLIS Association, it is our firm expectation that our two countries will enjoy the benefits of a new generation of biodiversity scientists ready to meet the developmental needs of our countries. We therefore welcome the publication of the present volume, which will provide the basis for advanced courses in ecology, biodiversity and conservation at Angolan universities. We thank and congratulate CIBIO/BIOPOLIS on yet another outstanding contribution to Angolan biodiversity science and education.

Minister of Higher Education, Science, Technology and Innovation, Angola
Minister of Science, Technology and Higher Education, Portugal

Dr. Rosário Bragança Sambo
Minister of Higher Education, Science,
Technology and Innovation, Angola

Prof. Manuel Frederico Heitor
Minister of Higher Education, Science,
Technology and Innovation, Portugal

Preface

The need for a Portuguese language textbook with a focus on Angolan ecosystems has been recognised by the country's academics and conservation professionals for many years. The present book results from discussions held with Vladimir Russo, Amândio Gomes, Fernanda Lages, Serôdio d'Almeida and Brian Huntley at the launch of *Biodiversity of Angola* in Luanda in April 2019. The event marked the launch of two major books on Angolan biodiversity and regional landscapes, products of the CIBIO *TwinLabs* and UNESCO *Life on Land* initiatives. A primary objective of these projects, conceived and hosted by CIBIO, has been to support the development of facilities and tools for biodiversity research and education in Angola and other Lusophone countries. As Director of CIBIO, I requested the coordinator of the *Biodiversity of Angola* project, Professor Brian Huntley, to prepare a synthesis on the terrestrial ecosystems of the country, as a 'student primer'. This somewhat more comprehensive *Ecology of Angola: Terrestrial Biomes and Ecoregions* is a consequence of our discussions.

This book provides a detailed account of the distribution, structure and functioning of Angolan biomes, ecoregions and ecosystems and the interactions of plant and animal species with their environment. It will serve as a learning resource for use by Angolan students, from undergraduate to postgraduate levels. For the first time in Africa, an ecological textbook has been devoted to a single country, in the national language. The subject matter provides a strong African perspective, using examples of ecological concepts, principles and phenomena drawn from Angolan landscapes, ecosystems and species. Furthermore, the book aims to develop an understanding of the mechanisms determining the dynamics of ecosystems in response to natural and human-driven changes. Such an understanding is essential for the sustainable use and conservation of Angola's natural resources. The book is thus designed to serve not only students and the interested public, but also the key leaders of land use management policy, planning and practice.

The author, Professor Brian Huntley, has been actively involved in the survey and conservation of Angola's ecosystems since 1971. Over the past 50 years, he has been repeatedly called upon by Angolan authorities and academics and international development agencies for advice and mentorship. He has initiated and led several training expeditions for young Angolan ecologists and, most recently, coordinated the compilation and publication of a comprehensive synthesis of knowledge on the country's biodiversity.

Prof. Nuno Ferrand de Almeida
UNESCO *Life on Land* Chair Holder
Director, CIBIO/Associação BIOPOLIS
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Acknowledgements

In preparing a work for use by present and future Angolan ecologists, it was clear that guidance would be needed from colleagues across southern Africa, most especially from Angola. My friends of many years—Serôdio d'Almeida, Vladimir Russo, Amândio Gomes, Pedro Vaz Pinto, Francisco Gonçalves and Martim Melo—were generous in their advice. In developing the structure of the book, ecologists Pedro Beja, William Bond, Chris Hines, John Mendelsohn, Bob Scholes and Thomas Smith gave valuable suggestions.

The rapidly expanding literature on the terrestrial ecology of southern Africa has provided a rich resource on challenging concepts and fascinating evidence, too much to reduce to a single volume. In contrast, published research on Angolan ecosystems remains embryonic, necessitating use of examples of ecological processes and phenomena from neighbouring countries. Here the enthusiastic support from colleagues across the continent and beyond was a source of great encouragement. As the technical content of the chapters evolved, specific material was contributed and the presentations enriched by leading specialists in key fields of research. In particular, the support of the following scientists is greatly appreciated.

- Francois Engelbrecht, Eckhart Freyer, Jasper Knight, Antonio Martins, John Mendelsohn, Roger Swart, John Ward, Mike de Wit (Geology, Geomorphology, Soils, Climate);
- Tristan Charles-Dominique, Gareth Hempson, Marc Stalmans, Brian van Wilgen (Fire and Herbivores);
- William Bond, Chris Hines, Bob Scholes (Ecosystem Processes);
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- Sally Archibald, Amândio Gomes, Francisco Gonçalves, Andre de Kesel, François Malaisse, Rasmus Revermann, Bryan Shorrocks, Izak Smit, Nicola Stevens, Pedro Vaz Pinto, Luis Veríssimo, Paulina Zigelski (Mesic and Arid Savannas);

- Patricia Craven, Joh Henschel, Norbert Juergens, Gert Kruger, Barry Lovegrove, Ernst van Jaarsveld (Namib Desert);
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These colleagues not only contributed original papers, figures and photos, but also reviewed many chapters. Where there are lapses or incorrect interpretations of evidence, the responsibility remains with me. My special thanks go to Nuno Ferrand for initiating the project, and to Christopher Hines and John Mendelsohn for regular discussion. Kenneth L Tinley's unique understanding of African landscapes has guided my approach to ecosystem ecology throughout my career. My wife, Merle, is thanked for her critical editorial support, and for sharing, supporting, enjoying and enduring a half-century of Angolaphilia.

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Portugal

Editorial Notes

Definition of Terms: Important terms and concepts are indicated in bold at their first use, where a brief definition is given. A Glossary of Ecological Terms is provided. *Vernacular terms* (*cacimbo, anhara*, etc.) are indicated by the use of italics.

Common Names: Common names of mammals follow Beja et al. (2019), birds follow Mills & Melo (2013), and reptiles and amphibia follow Marques et al. (2018), where common names of animals or plants are used in a general sense (elephants, acacias), they are not capitalised.

Scientific Names: The scientific, English and Portuguese names of vertebrate species will be found in the above references and in the Appendix. Species names of plants follow Barbosa (1970) and Figueiredo & Smith (2008). The traditional taxonomy of *Acacia* is used rather than *Vachellia* (for species with capitate inflorescences and spinescent stipules) and *Senegalia* (for species with spicate flowers and non-spinescent stipules) (Kyalangalilwa et al. 2013).

Portuguese Terminology: Vegetation types follow Barbosa (1970), but with the use of *Bioma de Florestas Húmidas Guineo-Congolesas, Bioma de Florestas e Prados Afromontanos*, *Bioma de Savanas Mésicas* and *Bioma de Savanas Áridas* for the main biomes and the terms *prados, savanas, bosques, matos* and *florestas* for the main physiognomic types.

Abbreviations: Frequently used abbreviations include Ma for Million Years Ago, C_3, C_4 and CAM for photosynthetic pathways, MAP for mean annual precipitation, MAT for mean annual temperature and ITCZ for intertropical convergence zone.

Photographs: Author credits are given in the captions of contributed photos. The remaining photos are by the author.

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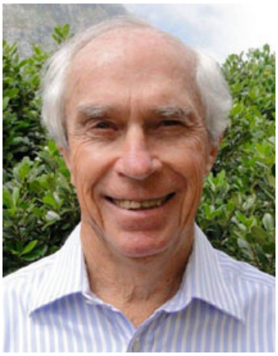
About the Author



Brian John Huntley is an internationally respected conservationist with over 50 years of research and management experience in southern African countries. Following ecological studies in the sub-Antarctic Prince Edward Islands in the 1960s and national park management planning across Angola in the early 1970s, Huntley coordinated biome research programmes across South Africa, before two decades as CEO of the South African National Biodiversity Institute. He has been active in many international conservation organisations. *Ecology of Angola* concludes a trilogy on the conservation history, biodiversity and terrestrial ecology of the country, written since retirement to a village between sea and mountains, near the southernmost tip of Africa. He is currently attached to the Research Centre for Biodiversity and Genetic Resources (CIBIO) at the University of Porto.

Part I
An Introduction to Angola's Biomes and Ecoregions

Context: Angola: An Ecologist's 'Continent in One Country'

Angola occupies only four percent of the terrestrial area of the African continent, yet it possesses the highest number of biomes of any African country. It is second in terms of the number of ecoregions represented within its borders. It has ecosystems as diverse as the rain forests of Maiombe of Cabinda, to the vegetationless dunes of Namibe, and the endless savannas and woodlands of the Cuando Cubango, to the tiny remnant forests of the highest valleys of Mount Moco in Huambo. It is the only home to the most magnificent mammal in the world—the Giant Sable Antelope.

João Manuel Gonçalves Lourenço: His Excellency the President of the Republic of Angola

In the opening paragraph of his Foreword to *Biodiversity of Angola*, President João Lourenço (2019) succinctly encapsulates the magic of Angola's biological and ecological riches. Angola is truly an ecologist's 'continent in one country'. It is the perfect living laboratory for research into the structure and functioning of African ecosystems, be they rain forests, deserts, savannas, montane grasslands or the mangroves that clothe the mouths of the Cuanza and Congo rivers. Nowhere else on the continent can one find such ecological diversity.

This introduction provides a brief outline of what awaits the inquisitive student. It is a snapshot of Angola's biodiversity and ecosystems, sufficient to stimulate interest but without attempting to answer the multitude of questions that arise when scanning the ever-changing landscape. A first step is to recognise the range of biomes that unfolds as one moves from Cabinda to the Cuando Cubango, or from the heights of Morro Moco to the coastal desert of Iona.

Given the central importance of the concepts of biomes and ecoregions in this volume, it is necessary to define these terms at this point.

- A biome is a large unit of structurally and functionally similar habitats which share climates, soils and disturbance factors.
- Biomes, such as equatorial rain forests, tropical savannas, temperate grasslands and deserts, occur on many continents, but often with very different floristic and

faunistic compositions. They are the ecological units which one can recognise in satellite images.

- An ecoregion is a large unit of land or water that contains a distinct assemblage of species, habitats and processes and whose boundaries attempt to depict the original extent of natural communities before major land use change.
- Biomes and ecoregions in turn are assemblages of many ecosystems, themselves comprising multiple species.

The Congo Basin holds the second-largest area of equatorial rain forest on the planet, second only to the Amazon. On the southwestern margin of the Congo Basin lie the Maiombe forests of Cabinda, Gabon and the Republic of the Congo. The Angolan Maiombe has no fewer than 14 primate species, from Gorillas and Chimpanzees to the tiny Talapoin. It has several hundred species of birds and over two thousand species of plants. Antelope includes five species of forest duiker, plus the small, deer-like Chevrotain, Forest Buffalo and Forest Elephant. Its amphibians and reptiles await detailed survey, as do its rich butterfly and dragonfly faunas. Of its ecology, no studies have yet been undertaken. In terms of biological surveys, it is Angola's *terra incognita.*

Southwards from the Maiombe, and running from Cabinda to the Cunene, is the Angolan Escarpment. This major topographic buttress between the coastal lowlands, the Marginal Mountain Chain and the interior high plateau—the planalto—is of special ecological importance. Providing a steep gradient of landscapes and habitats between the arid coast and the moist interior plateau, the Escarpment Zone has long been recognised as a centre of evolution and speciation. With a dense mosaic of forests, thickets, woodlands, savannas and grasslands, the Escarpment has provided a refuge for species from the arid lowlands and moister plateau during the climatic changes of the Pleistocene—the 'Ice Ages' of the Northern Hemisphere that reached tropical Africa as alternating wetter and drier periods.

Rising above the Escarpment are Angola's high peaks—Moco, Mepo and Namba. Here the cooler, moist climate provides conditions for remnant patches of Afromontane forest. This distinctive phytogeographic division extends as an archipelago of forest patches from the Ethiopian Highlands, down the Eastern Arc Mountains of Kenya and Tanzania, along the escarpments of Malawi, Mozambique and South Africa to Cape Town. After a gap of 2000 km across Namibia, Afromontane forests appear again in the highlands of Huíla, Huambo, Benguela and Bié provinces. These remote and highly threatened forest fragments are the habitat of many species of birds, reptiles, amphibia, invertebrates and plants that are endemic to Angola, or have close relatives in other Afromontane ecosystems in eastern, southern and western Africa. They represent what were much more extensive forests during the wetter periods of the Pleistocene. They are appropriately described as providing 'fingerprints of the past'.

The greatest proportion of Angola, over two-thirds of its surface area, is occupied by mesic savannas and woodlands, known internationally as '*miombo*'. This biome covers most of the planalto and the great Congo and Zambezian peneplains—the gently undulating landscapes that extend from the highlands of Malange, Huambo, Benguela and Bié to the Lundas, Moxico and Cuando Cubango. Rainfall is seasonal, falling in the hot summer, with from 650 to 1400 mm per year. Tall woodlands of deciduous trees, typically species of *Brachystegia* and *Julbernardia*, alternate with grassy valleys (*mulolas*) along the drainage lines, with occasional gallery forests (*muxitos*) that occupy moist but well-drained soils. The miombo has its own distinctive fauna, which includes species of antelope such as Giant Sable, Roan Antelope, Puku, Oribi and Lichtenstein's Hartebeest. The soils are nutrient poor, and the grasses are of low quality for herbivores, so these mesic savannas support low mammal biomass. They are shaped by regular bush fires, the great consumer of African savannas.

In the southwest, northwards along the hot, low coastal belt, arid savannas, woodlands and thickets dominate. Here rainfall is highly erratic, ranging from 250 to 650 mm per year. A typical community is that of the tree *Colophospermum mopane* (*mutiati*) that occurs on rich soils of Cunene, Namibe and Benguela provinces. Along the coast, many hardy, drought-resistant woody species of *Acacia*, *Combretum*, *Commiphora*, *Euphorbia* and *Sterculia* are conspicuous. Throughout the arid savannas, from the Cunene to Cabinda, the baobab (*imbondeiro*) *Adansonia digitata*, is the most prominent tree. The shrubs and grasses of arid savannas, occurring on rich soils, are highly nutritious and in past centuries supported large herds of herbivores such as wildebeest, buffalo, zebra, kudu, eland, impala, elephant and black rhino. These herds have been severely reduced, and the herbivore niche has now been filled by cattle and goats.

The ultimate extreme of harsh environmental conditions is to be found in the Namib Desert. From the Namibian border at Foz do Cunene, the Angolan component of this ancient desert extends northwards as a narrow belt, never more than 80 km in breadth, to the Carunjamba River just south of Lucira. While geographers define a desert as an area receiving less than 250 mm rainfall per year, the Namib generally receives less than 150 mm rainfall per year. It is best characterised by plant and animal species and their adaptations for life in hyper-arid conditions, rather than being defined by the rainfall it receives. The gravel plains, calcrete pavements and rocky hills of the Namib are the habitat of *Welwitschia mirabilis*, penetrating inland in places with slightly higher rainfall. Intermontane basins, carrying grasslands and shrub savannas, are occupied by Gemsbok, Springbok and Hartmann's Zebra, with Kirk's Dik-dik, Greater Kudu and rarely, Savanna Elephant and Black Rhino (now extinct) in the wooded hills below the Escarpment. The antelope moves from one area to another according to rainfall patterns, often moving farther inland as food resources are depleted during dry periods. The desert is also home to many specialised reptiles and invertebrates. All species of animal and plants make good use of the fog that moves inland from the cold Benguela Current, in places adding more than five times the moisture received from rainfall, which is often less than 30 mm per year.

Against this background of biome and ecosystem diversity, one can expect high species richness. The Angolan inventory of vascular plants now stands at over 6850 species. Mammals number 291 species, birds 940, reptiles 278 and amphibians 111. Of invertebrate groups, only butterflies (792 species) and dragonflies (260 species) have been surveyed in any detail. Much has still to be learned of the diversity of some taxa, especially invertebrates, but even reptiles and amphibia have species new to science described every year.

While good progress is being made on the inventory of Angola's biodiversity, very few studies, beyond those on Giant Sable and vegetation surveys, have been initiated on the ecology of individual species or ecosystems and nothing on ecosystem processes such as primary production, consumption and decomposition, or on energy, water and nutrient transfers. The opportunities for research are diverse, exciting and ready for action. It is in the new generation of Angolan ecologists that expectations are vested.

Reference

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Chapter 1
Opportunities in and Approaches to the Study of Angolan Ecology

Key Concepts and Questions: This Chapter Explains

- *The critical role of an ecological understanding in achieving the sustainable use of the biosphere.*
- *What we understand by the term ecology, its interdisciplinary scope and the need for an African perspective.*
- *Why spatial and temporal scales and the integration of successive levels of biological organisation need to be studied.*
- *The importance of understanding the processes of evolution and adaptation in shaping the composition of communities.*
- *Why the ecological whole is greater than the sum of its parts.*
- *The basis of research—the scientific method—and its application in ecological studies.*
- *The structure of this book in phased steps of a learning process.*
- *How to use this book in developing knowledge, understanding and a career in ecology.*

Context: Why Ecology? Human–Environment Interactions

This book has a pragmatic purpose. It has been written for Angolan students, young and old, to help them to get to know, understand and value the amazing natural life and landscapes of the country. This book aims to introduce the student to the science and practice of ecology by describing examples of key features and concepts which relate to Angola's terrestrial ecosystems, their structure and functioning. The focus is on providing an enduring understanding of what is special about Angolan ecosystems, in succinct chapters illustrated with easily accessible examples.

Why is an understanding of ecology critical to Angola's sustainable development? The answer is easy to predict if one recognises that Angola's human population has increased from 6.5 million at independence in 1975, to 32.8 million in 2022. At its current rate of growth, the population will surpass 50 million by 2035. At Independence, over 80% of the human population comprised rural communities of

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subsistence farmers, but today 67% of the population lives in cities and towns and only 33% in rural areas. These dramatic demographic changes have had significant and often negative impacts on the natural environment. In urban situations, pollution through injudicious solid waste disposal and erosion through poor storm-water management, are serious problems. In rural areas, the loss of forest and woodland cover (to provide charcoal as the primary domestic energy resource for urban families), extinction of mammal populations (through the bushmeat trade), accelerating soil erosion (through mining operations and unsustainable farming practices) and the transformation of plant communities due to clearance for agriculture or repeated, extensive and uncontrolled bush fires, plus the impacts of invasive plants, accounts for severe loss of the productive potential of landscapes. To these impacts must be added that of global dynamics, most especially the impacts of climate changes. These human–environment interactions are described in a series of Boxes at the end of chapters, demonstrating why an ecological understanding of the structure, functioning and vulnerabilities of the country's ecosystems is so critical to achieving the sustained wellbeing of Angola's people.

1.1 The Science and Practice of Ecology

An ecologist is a person imbued with an insatiable curiosity about the workings of all living things. The great nineteenth-century European explorer-naturalists—Alexander von Humboldt (1769–1859), Charles Darwin (1809–1882) and Alfred Russel Wallace (1823–1913)—were passionate seekers of knowledge, but specifically of explanations as to why certain species were found only in specific regions of the globe and not in others. They were the pioneers of ecology. The term 'ecology' was first described as the study of 'the economy of nature' (Haeckel, 1866) and **ecology** is today defined as 'the scientific study of the distribution and abundance of organisms and the interactions that determine their distribution and abundance'.

An Interdisciplinary Science

In the two centuries of its gestation and development, ecology has become a multi- and **interdisciplinary science**, being undertaken by researchers in fields as diverse as the biochemical reactions within nitrogen-fixing bacteria—to the feeding habits of elephant—to the influence of the Earth's tilted axis on the passage of seasons. Both curiosity-driven and applied interests stimulate ecological studies. The workings of insect pollinators in the fertilization of tropical orchids are as fascinating to one ecologist as the resilience of socio-economic systems to the impacts of global climate change is to another.

Ecology has its early nineteenth century roots in the tropics—through the revolutionary thinking of Humboldt, Darwin and Wallace. The theory of evolution through natural selection is a cornerstone of ecology. Humboldt sought explanations for the distribution of vegetation formations across altitude and climate. Darwin sought understanding by studying smaller and smaller pieces of life's puzzle in a world driven by competition and selection at the species level. Wallace explored life at a planetary scale, in which the world is a web of interdependencies (Flannery, 2010).

Presenting an African Perspective

These broad perspectives were evolved further into specific ecological concepts in the northern temperate latitudes by Andreas Schimper (1856–1901), Arthur Tansley (1871–1955) and Frederick Clements (1874–1945) and others in the early twentieth century. From the 1950s, the science accelerated rapidly in North America and Europe, from where the great majority of concepts and examples quoted in standard textbooks on ecology are drawn. Some concepts developed in temperate latitudes are of limited relevance to tropical African ecosystems, so this volume presents a deliberately **African perspective**. In recent decades there has been a blossoming of ecological research in South and Central America, Australasia and southern Africa. In Angola, important contributions were made by the pioneers of Angolan biodiversity research—Welwitsch (Swinscow, 1972), Anchieta (Andrade, 1985), Gossweiler (Gossweiler & Mendonça, 1939), Jessen (1936), Barbosa (1970), Monteiro (1970) and Machado (1995). Today there is increasing investment in ecological research across Africa, as scientists and governments recognise the important relationship between biodiversity, environmental health and socio-economic development and sustainability.

Scales in Space and Times

Ecology is an integrative science, working at **multiple spatial and temporal scales**, from the individual organism to the biosphere. At the level of the individual plant or animal, ecologists examine how features of morphology, physiology and behaviour determine an individual's ability to **survive, grow and reproduce**. Successive levels of organization—individual, population, community, ecosystem, landscape, ecoregion, biome, biosphere—all work at different spatial and temporal scales, but are closely linked through positive and negative interactions that determine their dynamics.

An Evolutionary Base

Because ecology is fundamentally about the consequences of **natural selection** in the evolution of **adaptations** to the environment, which are based on the differential transfer of genetic material from one generation to the next, the basic unit of ecology is often regarded as the individual. This follows the thinking of Russian/American geneticist Theodosius Dobzhansky (1900–1975) who stated: "Nothing in biology makes sense, except in the light of evolution." (Dobzhansky, 1973). Townsend et al. (2008), in their comprehensive textbook on ecology, added the cautionary note: "But equally, very little in evolution makes sense except in the light of ecology: ecology provides the stage direction through which the 'evolutionary play' is performed. Ecologists and evolutionary biologists need a thorough understanding of each other's disciplines to make sense of key patterns and processes." A further interesting perspective on ecology is that of tropical forest ecologist Whitmore (1998): "Ecology as a science is always seeking for generalizations to make sense of the bewildering diversity of Nature."

Individual and Emergent Properties

Many field and laboratory studies focus at the species level—how a single species interacts with the environment, known as **autecology**. The study of how species interact with each other at the ecosystem level and higher levels of integration—populations or communities—is referred to as **synecology**—which will be the focus of attention in this book. Each successive level of the hierarchy places different demands on the research approach—scales of both time and space are fundamental considerations when planning ecological research. An important concept in ecology is that of the **emergent properties** that can be observed, measured and predicted, operating at different spatial and temporal scales. Emergent properties are usually defined as an **output**, resulting from an interacting set of variables that have a property, not of the individual, but that emerges from the collective interactions of many different individuals within the system. The concept of **the whole being greater than the sum of the parts** is at play. Examples include the **microclimate** created by a community of shady forest trees, the development of **fuel loads** of combustible material by grasses in savanna ecosystems, or the influence on soil physics and chemistry and plant and animal communities by the activities of termite colonies. In short, an emergent property is a property which a complex system has as the outcome of multiple interactions, but a property which the individual members do not have.

Functional Processes

Recognising the importance of **scale** is a fundamental requirement in developing an ecological understanding. Within an **ecosystem** (the living and non-living components of a functioning ecological system) specific **ecosystem processes** such as photosynthesis, energy flows, water and nutrient cycling, growth, reproduction, survival, adaptation and evolution—are operating at timescales from seconds to millions of years. All ecosystems are ultimately interlinked through their **interactions**—such as the exchange of materials and energy—across the scales of biosphere, atmosphere, hydrosphere and geosphere. To understand these multiple scales and intimate linkages, terrestrial ecologists have to collaborate with specialists in the earth, ocean and atmospheric sciences, and from the social sciences and economics.

Earth and Biodiversity Sciences

The world of ecological research thus ranges from '**biodiversity science**', at the level of individuals and populations where competition is emphasised, to the scale of the whole planet, '**earth system science**', where the web of interdependencies is the focus. While many studies relate to reasonably static features—such as the patterns and composition of soils and vegetation—other factors are constantly changing, such as photosynthetic rates, patterns of grazing and browsing, fire frequency and intensity, and predator–prey relationships. Eco-physiological studies might be conducted in laboratories with hourly or daily iterations and timeframes, while ecosystem-level phenomena such as the impacts of fire regimes on ecosystem structure need **long-term field studies** running for many decades. Both laboratory and field **experiments** are needed in the search for the **mechanisms**—the **causation**—of observed patterns.

Stability and Heterogeneity

The importance of scale is also linked to pattern and patchiness in communities and ecosystems, and to the role of **heterogeneity**, the ultimate source of biodiversity richness and of ecosystem resilience. Spatial patchiness (heterogeneity) at different scales enables a system to absorb sudden disturbances. Concepts of scale, patchiness, heterogeneity, redundancy and resilience are fundamental to understanding and effectively managing ecosystems, as demonstrated in the century of research on complex systems such as the Kruger National Park, South Africa, the long-term studies of Serengeti, Tanzania and the 40-year savanna research programme at Lamto, Ivory Coast.

The Scientific Method

Underpinning ecological research is the **scientific method**. From Humboldt's time, this has meant careful and repeated observation and measurement, the definition of questions, the gathering of evidence, the formulation of **hypotheses** that seek to provide answers to questions and predict the outcomes of phenomena, and thereafter the repeated testing of such hypotheses. When successive attempts to disprove a hypothesis fail, it might become a principle. Once accepted by the scientific community, it might be adopted as a theory or ultimately, a **law**. A **theory** is an integrated set of hypotheses that together explain a broader set of observations rather than any single hypothesis. However, a word of caution is needed. In ecology, most hypotheses are best regarded as challenges to tease the mind, to give structure to discussions, to serve as challenges for new research. They should not become ends in themselves. Figure 1.1 presents a simple representation of the scientific method.

Models and Simulations

Because of the complexity of scales and processes, ecologists use **models**—simplified representations of real systems. A model begins with a descriptive statement backed by multiple observations, such as Darwin's theory of evolution. It can be an intuitive and conceptual 'box and arrow' chart, providing a plausible set of linkages between components of an ecosystem, such as simple food webs. More sophisticated models incorporate quantitative data and produce predictive mathematical simulations. Models are most effective when the objective of the model is explicit. They should not be expected to replace focused thinking. All models should help to structure thinking and explanation. As examples cited in many chapters of this book demonstrate, ecology is still **a work in progress**. In essence, ecology is an iterative process of **successive approximation** to the truth, constantly and rigorously seeking to eliminate incorrect interpretations of natural patterns and phenomena and to find conclusions in which we can be confident.

The practice of ecology has advanced from its foundations in natural history curiosity to many disciplines of direct importance to socio-economic development.

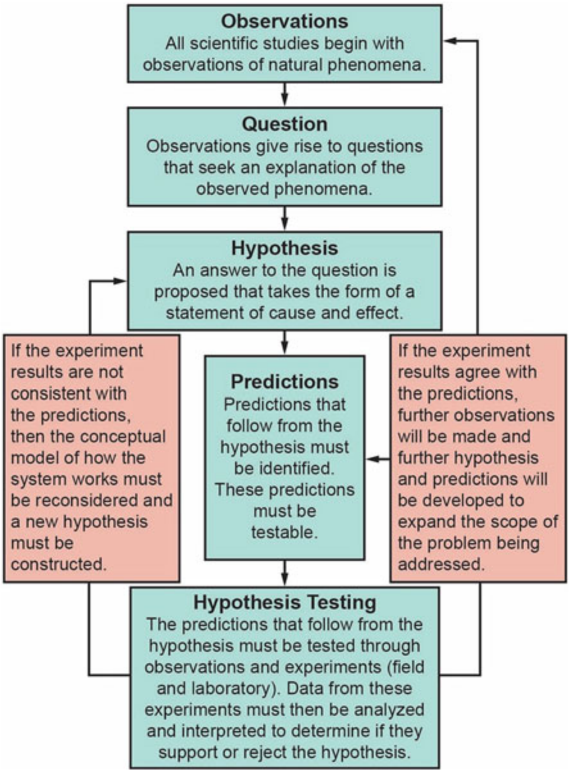

Fig. 1.1 A model of the scientific method. From Smith and Smith (2015) *Elements of Ecology*. (9th Edition). Pearson, Boston

Across the broad fields of the environmental sciences—from impact analysis, land use planning and the management of conservation areas—ecological theory helps identify answers to complex questions. The development of resilient socio-ecological systems, of quantifying the economic value of ecosystem services and improving sustainable resource use and governance rests on sound ecological understanding. Ecology is a field employing thousands of professionals in southern Africa—in conservation area management, agriculture, forestry, marine resource management and environmental policy.

Ecology as a Career

Ecology is a **career opportunity** that requires commitment, passion and an understanding of the essential features, facts and concepts presented in this book. Angola is alive with opportunities for the young ecologist: it is a country with limitless horizons for the enquiring mind.

1.2 The Structure of This Introduction to Terrestrial Ecology

In this book, several interrelated topics and questions are addressed:

- What are the main characteristics of Angola's biomes and ecoregions?
- What physical and biological forces determine the distribution and abundance of species?
- Why do the ecosystems and their constituent species occur where they are found?
- How have plants and animals adapted to specific environmental conditions?
- How do Angolan ecosystems function as integrated and dynamic systems?
- Why is an understanding of ecology critical to Angola's sustainable development?

In addressing these questions, the structure of this book does not follow that of traditional ecology textbooks, which provide stepwise coverage of system organization, from individuals to populations to communities and ecosystems, and interactions from birth, death, competition and predation, and processes such as fluxes of energy and matter through ecosystems. Here the emphasis is on the living environment of Angola, which the student can encounter in the field, ideally in the country's national parks, where examples of the structure and dynamics of ecosystems can be experienced in situ.

Each chapter is headed by a series of statements that focus on the lessons to be learned in the chapter. An introduction to each chapter provides context to the theme, and in some cases, reference is made to the founders of ecological concepts, to provide a historic background to the development of the science of ecology. Complex concepts or unique phenomena are presented in highlights (**Boxes**). The purpose of the Boxes is to provide depth on topics that are essential learning, without interrupting the flow of chapter structure.

More generally, this book follows a series of key questions, as addressed below, ultimately brought together within the biomes and ecoregions of the country. The coverage of topics does not specifically embrace the important discipline of **conservation biology**, for which an excellent reference is available in Wilson and Primack (2019).

What and Where?

Knowing 'what' and 'where' is the first step. The introduction to the biomes, ecoregions and the biodiversity of Angola in Part I serves to demonstrate their richness and the exciting opportunities for further study. A framework of African biomes provides an entry point for the reader to develop a **continental perspective**. Understanding the structure, composition and distribution of ecosystems requires knowledge of many **ecological terms** and **concepts**, a step that at first might seem challenging. Part I therefore introduces basic terms that will be used repeatedly through the book. Ecological terms are merely the tools for communicating consistent messages. Throughout the text, key terms are highlighted in bold, linked to a succinct definition of the term provided in the Glossary of Ecological Terms.

Why?

Following an outline of Angola's biomes and ecoregions, the next step is to build an understanding of the factors and processes that determine the structure and distribution of these complex systems. This is provided in Part II by a review of the **driving forces**—climate, geology, hydrology, soils, fire and herbivory—that determine why species live where they do, and why their distributions are limited to specific conditions for survival, growth and reproduction. These elements are the fundamental tools that an ecologist needs to understand before approaching the living landscape—the ultimate workplace of an ecologist.

How?

With a basic knowledge of the 'what', the 'where' and the 'why' of species and ecosystem distributions and abundance, we can look at questions of 'how'. Part III explores how plants and animals interact within species, between species, and with their environments to form the **patterns** we see in nature. In short, what morphological, physiological and behavioural **adaptations** have evolved to survive and prosper in the diverse landscapes of Angola? General concepts in ecosystem structure, function and dynamics are discussed based on **ecological principles** and illustrated with examples from Angola and other African countries. Building on this knowledge, one can move to the **mechanisms** operating at the ecosystem level. Here we will, for example, look at the processes of energy, water and nutrient pathways though savanna ecosystems, adaptation to aridity within the desert biome, and speciation questions within the forest biome. All processes are determined by basic principles of physics and chemistry, and molded by biological interactions.

Ecological Features of Angolan Biomes and Ecoregions

Part IV provides a more detailed examination of the biomes and ecoregions of Angola, looking more closely not only at their defining features, distribution and structure, but also at the evolution of **patterns and processes**. Unusual features, unique to Angolan or regional landscapes are used to demonstrate the importance of both applied and curiosity-driven research. These include the pattern of soil-vegetation catenas, of termitaria as nutrient hotspots, the possible explanations for 'fairy circles' in the Namib and of 'underground forests' in miombo.

Synopsis: Key Elements of Angolan Terrestrial Ecology

Part V presents a brief synthesis of the main messages that the student should understand and embrace as she or he explores and studies Angola's diverse landscapes. These elements of ecology are the building blocks of the learning process. The evolution of Angola's landscapes, the contemporary drivers of ecosystem structure, function and patterns, and the general theories relevant to conserving Angola's fauna, flora, ecosystems and human life-support systems are outlined.

1.3 How to Use This Book: Interconnections and Recurrent Messages

It is not intended that the full breadth of the science of ecology be covered in this brief synthesis of Angola's biomes and ecoregions and of selected ecological concepts. For a more comprehensive study of ecology, many excellent textbooks are readily available and should be consulted for greater depth (Du Toit et al., 2003; Levin et al., 2012; Owen-Smith, 2021; Shorrocks & Bates, 2015; Smith & Smith, 2015; Townsend et al., 2008; Whitmore, 1998; Wilson & Primack, 2019). For inspiration, young students are encouraged to read biographies of the great pioneers of ecology: Humboldt, Darwin and Wallace (Selsam, 1959; Wallace, 1881; Wulf, 2015). These and many other resources are referenced at the end of each chapter, providing a shortlist of selected textbooks and research papers. Because of the interconnectedness of ecological concepts and processes, cross-referencing will be indicated throughout the book. A major challenge to students is the multitude of terms that need to be understood, and for this reason terms indicated in bold are defined succinctly at first mention and collectively in the Appendix.

Finally, four themes or 'leitmotifs' will become evident in this book and underpin its learning objectives:

- **Ecology is about recognizing patterns and processes** that operate at widely differing scales of time and space.
- **Nothing in biology makes sense except in the light of evolution**. But equally, very little in evolution makes sense except in the light of ecology.
- **Ecological research explores the mechanisms of survival, growth and reproductive output** of organisms in relation to their environment.
- **The whole is greater than the sum of the parts**. Interactions and webs of interdependencies between individuals, species and populations and their environments create emergent properties that define ecosystem structure and function.

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Chapter 2
Biomes: Concepts, Characteristics and Terminology

Key Concepts and Questions: This Chapter Explains

- *How the concepts of biomes, biogeographic realms and centres of endemism are related.*
- *How Africa's biomes are distributed and characterised.*
- *What linkages Angola's biomes have with Africa's centres of plant diversity and endemism.*
- *What key concepts and terms are used to describe the life forms and ecological characteristics of plants and the communities they develop.*
- *How ecological characteristics distinguish savannas from forests.*
- *How plant-available nutrients and plant-available water and disturbance pressures (fire and herbivory) influence the distribution of mesic, arid and mixed savannas and of closed forests.*

Context: The Classification of Biogeographical and Ecological Diversity

> To be meaningful, a classification has to take into account floristic, ecological and physiognomic features, which are difficult to integrate in a single system and even more difficult to portray on a map.
>
> Adams (1996)

Understanding patterns in the distribution and abundance of species and the processes of ecosystem functioning are cornerstones of ecology. In a country as large and diverse as Angola, developing such knowledge is a challenging objective. It can most easily be achieved by proceeding from the general to the specific, scoping down from global to regional to local patterns and processes. Many patterns in nature are hierarchical, functioning at embedded spatial and temporal scales. In Angola, six levels of biotic and habitat organization can be recognised.

B. J. Huntley, *Ecology of Angola*,
https://doi.org/10.1007/978-3-031-18923-4_2

- At the highest conceptual level of pattern are the **biogeographic realms.** Realms reflect global scales of shared evolutionary relationships (**lineages**) of floras and faunas. Eight biogeographic realms are recognised across the globe, of which two—the Palearctic and the Afrotropical—are found in Africa. Angola, together with the rest of Sub-Saharan Africa, falls wholly within the **Afrotropical Realm**.
- Next, and visible from outer space, are the major habitat groups, or ecological formations (biomes). Each **biome** has unique ecological, structural and functional characteristics. Globally, biomes are recognised through their **structure**, not their floras and faunas, which differ from one continent to another (Olson et al. 2001). Six biomes are found in Angola. Where two or more biomes meet**, transitional mosaics** are often found, such as at the broad interface between rain forest and mesic savanna biomes in northern Angola.
- At the continental scale, and within the Afrotropical Realm, nine regional **centres of endemism** are recognised (White, 1971, 1983). Regional centres of endemism indicate **floristic** evolutionary linkages. The floristic composition of a centre of endemism is often unrelated to the ecological structure of the vegetation, which might include grasslands, savannas and forests. Four of Africa's regional centres of endemism are represented in Angola.
- Next are **ecoregions,** large units of land with distinctive assemblages of species, habitats and processes, that serve as useful units for purposes of mapping related ecosystems at a regional rather than a national scale (Burgess et al., 2004). Land use development and management interventions are often taken at this level. Angola has 16 ecoregions, ranging from the tropical rain forests of Cabinda to the hyper-arid desert of the Namib.
- Ecoregions are assembled from the mapped **vegetation types** that represent major groupings of plant communities. Barbosa (1970) described 32 vegetation types in Angola and his account still reflects the current state of knowledge of Angola's vegetation as a whole.
- Finally, and key to characterizing all the above levels of the hierarchy are the **species** of animals and plants that represent a site's species richness, constituting, with its ecosystems and genetic diversity, a country's **biodiversity**.

In this book, the focus will be on the biomes and ecoregions which represent the great biological and ecological diversity in Angola and which demonstrate the impacts of environmental conditions (climate), resources (radiation, landscapes, soils), and disturbances (fire and herbivory) on the patterns of plant and animal distribution and abundance.

2.1 Biodiversity, Biogeography and Centres of Endemism

An important first step in developing an ecological understanding of the environment commences at the species level. Knowing the characteristics, and ideally the recognised scientific names of the species of plants and animals that form a given community or ecosystem, is a key learning objective. Species are the fundamental units of biological diversity, collectively referred to as an area's biodiversity. **Biodiversity** has been defined by the United Nations Convention on Biological Diversity as: 'the variability among living organisms and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems'. The collective term **biota** includes animals, plants and microorganisms.

Analyses of Angola's species distribution and emergent biodiversity patterns have been limited by the lack of accurate and comprehensive geo-referenced data on the fine-scale distribution of its rich biodiversity. However, a synthesis of Angola's biodiversity was recently prepared by teams of experts on major taxonomic groups (Huntley et al., 2019), Table 2.1. The synthesis provides outlines of the biodiversity of all vertebrate and several invertebrate groups, relating these to biogeographic patterns across Africa. Synopses of vertebrate species composition and vegetation types are given in the biome and ecoregional accounts of this chapter, while brief notes on behavioural, physiological and ecological adaptations of selected animal groups are included throughout this volume. Key ecological concepts relating to species richness, endemism and community structure of animal groups are included in Part III.

Biogeographers have studied patterns in the distribution of plant and animal species across Africa for over a century and have proposed many **phytogeographic** (plant) and **zoogeographic** (animal) classification systems. Terms such as **phytochoria** and **zoochoria** are used by some researchers for the units of biogeographic

Table 2.1 Species richness and endemism in Angolan plant and animal groups

Group	Total species	Number of endemic species	% Endemism
Plants	6850	997	14.6
Butterflies and skippers	792	57	7.2
Dragonflies and damselflies	260	16	6.1
Fishes	358	78	21.8
Amphibians	111	21	19.3
Reptiles	278	36	12.9
Birds	940	29	3.1
Mammals	291	12	4.1

(From Huntley et al., 2019)

classification. These have been based on extensive, intuitive field knowledge (e.g. Chapin, 1932; White, 1971, 1983), or advanced statistical analyses of plant and animal distribution records based on specimens held in herbaria and museums (e.g. Linder, 2014; Linder et al., 2012; Rodrigues et al., 2015), or on data from field surveys (Fayolle et al., 2018, Osborne et al. 2018).

As already described, there are successive levels of habitat, floristic and faunistic classification of importance to understanding Angola's terrestrial ecology. At broad scales, centres of endemism and biomes are most commonly used as basic frameworks. There is general consensus on the key patterns of plant distribution across Africa, based on the centres of endemism described in the work of British botanist Frank White (1971, 1983). White (1971) defined a **regional centre of endemism** as an area having more than 50% of its species confined to it, and a total of more than 1000 endemic species. Angola has representatives of four of White's regional centres of endemism:

- **Guineo-Congolian** Regional Centre of Endemism: mosaics of forests, thickets and tall grass savannas;
- **Zambezian** Regional Centre of Endemism: arid and mesic woodlands, savannas, grasslands and thickets;
- **Karoo-Namib** Regional Centre of Endemism: desert, shrublands and arid savannas; and
- **Afromontane** Archipelago-like Regional Centre of Endemism: forests, savannas and grasslands.

White's (1971) centres of endemism and transition zones reflect the floristic composition and relationships that form the basis of the UNESCO Vegetation Map of Africa. The production of the map (White, 1983) drew on the experience of over 100 specialists in the flora and vegetation of Africa, and it remains a primary reference on the subject.

Linder (2014) has used vast herbarium databases to further define African **floras**, with distinct geographic centres, ages of radiation and of speciation rates. Four of these floras are represented in Angola and correspond closely to White's regional centres of endemism. Linder provides a chronology of the evolution of the floras, relevant to understanding the floristic and vegetational history of Angola. He describes a sequential adding of plant families, genera and species to Africa's floral diversity:

- The first tropical angiosperm **lowland forest flora** (Guineo-Congolian) was established by the early Cenozoic, during the Paleocene (66–56 Ma).
- An **arid flora** (Karoo-Namib) appeared from the Eocene (55–34 Ma).
- A tropical **montane flora** (Afromontane) evolved with the volcanic and mountain-building episodes of the Neogene (23–2.6 Ma).
- Finally, a **savanna flora** (Zambezian) was introduced with the development of open grasslands and savannas which replaced earlier floras as the incidence and impact of fires increased in the Miocene (23–5 Ma).

Geological time periods and their ecological importance are described in Chap. 4.

2.2 Biome and Ecoregion Definition and Characterisation

Whilst biogeographic units such as centres of endemism are of great value in explaining the **evolutionary relationships** of the major plant and animal communities, a more useful tool towards understanding **ecological relationships** is the biome concept. Introduced a century ago by the American ecologist Frederick Clements (1916), the **biome** has become widely used to identify the **largest category of habitat** and the associated plant and animal life-forms. Biomes are the large scale units that can be identified in remote-sensing data such as satellite images or aerial photographs—forests, savannas, grasslands and deserts. Plants and animals of individual biomes have physiological processes that are adapted to similar macroclimatic, soil, water and disturbance regimes, and have similar appearance, complexity and functional characteristics. Biomes are most easily recognised by their **physiognomy** (structure of plant life forms) and **phenology** (seasonal growth, flowering and fruiting patterns). Definitions of key structural and functional attributes are provided in Box 2.1.

Both biomes and centres of endemism reflect the long history of their constituent floras, faunas and life forms, and have been described as 'theatres of evolution'. Over the long geological history of the planet, the size and distribution of biomes have ebbed and flowed. While some have gone extinct, others survive to this day. The coal-forming swamps of the Carboniferous geological period (359–299 Ma) are long gone, while swamp-forests that date back to the Miocene (23 Ma) still survive in Borneo. Many families of animals and plants of southern hemisphere biomes have their origins in the super-continent Gondwana. The separation of Gondwana to form South America, Africa, India and Australia resulted in floristic and faunistic fragmentation or **disjunction**, isolation and speciation (known as **vicariance** events). The 'Gondwana' elements of the African biota thus have links going back to the Cretaceous (145–66 Ma). In addition, modern floras include many taxonomic groups that arrived through long-distance trans-oceanic dispersal after the breakup of Gondwana (Pennington et al., 2004). However, much of the fauna and flora we encounter today has evolved more recently, in-situ. Recent global paleoecological models (Allen et al., 2020) suggest that much of the Earth's land surface has experienced at least one biome change over the past 140,000 years. In summary, the biota and biomes of Africa have been in constant flux over geological and evolutionary time scales.

The key determinants of biome distribution, as will be discussed in Part II, are environmental conditions (climate), resources (solar radiation, landscapes and soils) and disturbance (fire and herbivory). It is important to note that biomes are not classified by the **species** of plants (**flora**) or animals (**fauna**) that are found in them. Biomes are characterised by their **structural and functional** attributes reflected in their **vegetation.** Vegetation in turn reflects the **habitat** and its environmental conditions. Thus the term 'savanna biome' is used in Brazil (for *cerrado*), in Angola (for *miombo*) and in Australia (for *mulga*), despite these savannas having no plant species in common. What they have in common, however, are the ecological-evolutionary **functional**

traits. A trait is a morphological, biochemical, physiological, structural and phenological adaption to survive, grow and reproduce. Traits (such as the thick bark of savanna trees) have evolved in response to similar climates, soils and disturbance regimes. The biome concept is defined by the similarity of structure and ecological roles of plants within different environments.

Environmental factors and evolutionary processes select for the best adapted plant **life form** (grass, shrub, tree) and vegetation **physiognomy** (the vertical layering and horizontal spacing of vegetation components. Plant life form and physiognomy characterise different appearance of vegetation (grassland, savanna, thicket, woodland, forest) for a given site (Box 2.2). Climate determines whether the dominant life form of forests, woodlands or savannas (trees) are **evergreen** (retaining leaves for several years in non-seasonal climates such as humid equatorial rain forest) or **deciduous** (in seasonal climates such as tropical savannas where leaves drop and are replaced every year). Disturbance impacts of fire and herbivory are also factors that influence the nature of biomes, especially in Angola, where **fire** and large mammal **herbivores** have contributed to shaping biomes across evolutionary time. Finally, **landscape** (geomorphological) and **edaphic** (soil drainage, texture, nutrient status) factors influence biome characteristics at a local to regional level.

While the biome concept is used to classify major units of habitats, such as the tropical savannas and woodlands that cover approximately 50% of Africa, some biomes, such as the montane grasslands and forests of Angola, are represented by very small, scattered and isolated patches in an archipelago of ‘island relicts’, such as the Afromontane forests of Mount Moco and Mount Namba. Biological attributes, not size, thus determine what is recognised as a biome.

Within each biome, distinctive plant and animal **communities** occupy the different ecological conditions and habitats found across a landscape. Communities can vary in scale from groups of animals or plants in a small wetland pool, a patch of grassland, or an extensive forest. An **ecosystem** was defined by British ecologist Arthur Tansley (1935) as a community of organisms living in conjunction with non-living components of their environment, interacting and functioning as a system.

At continental and regional scales, ecosystems are too numerous and diverse for either mapping or descriptive purposes at those scales, so a more pragmatic category, the ecoregion, has been used to bring an intermediate level of detail within biomes. An **ecoregion** is defined as: “A large unit of land or water that contains a distinct assemblage of species, habitats and processes, and whose boundaries attempt to depict the original extent of natural communities before major land use change.” (Dinerstein et al., 1995). Throughout this book, the use of the term ecoregion will follow this definition. Burgess et al. (2004) defined a total of 119 terrestrial ecoregions for Africa and its islands. It is impressive to note that Angola has not only the largest diversity of biomes, but also the second largest representation of ecoregional diversity found in any African country.

2.3 The Biomes of Africa in Outline

Before examining Angola's biomes, it is important to consider the distribution and characteristics of Africa's biomes as a whole to obtain a perspective of the continent's diversity of landscapes, ecosystems and biodiversity.

Some researchers (Burgess et al., 2004, Mucina & Rutherford, 2006; Olson et al., 2001) follow a strictly structural classification of African biomes. A purely structural approach can mask important ecological relationships (such as the distinction between arid and mesic savannas) while exaggerating others (recognizing edaphic ecosystems such as flooded grasslands as a biome). It is important to note that some traditional European botanists use the term '**dry tropical forests'** for the savanna biomes. Modern ecologists apply the term **tropical savannas** for the *Acacia, Brachystegia, Baikiaea, Colophospermum, Combretum* systems of Africa, and similar biomes in South America and Australia. These 'dry tropical forests' lack many key forest physiognomic features and ecological traits such as closed canopies and the absence of a grass understorey. Furthermore, some units of classification are compromises between ecological reality and the constraints of mapping scale. Taking these factors into consideration, in this account seven African biomes, and two transitional mosaics are recognised (Fig. 2.1; Table 2.2).

In simple terms, the biomes of Africa can be described, and are mapped (Fig. 2.1), as a succession of broad bands of **biomes** and linking transitional **mosaics**. To these may be added the more restricted Mangroves of the tropical coastal estuaries and the Montane Forests and Grasslands of the highlands. Within the Mesic and Arid savannas, locally extensive flooded grasslands and **halophytic** basins occur. From the Equator, the successive bands and transitional mosaics, illustrated in Fig. 2.1, comprise:

- The Guineo-Congolian **Rain Forest Biome** of the Congo Basin and West African lowlands;
- To the north and south of the rain forests lie two belts of **Forest/Savanna Mosaics**—the Guinean and Northern Congolian, and the Southern and Western Congolian Forest/Savanna Transitional Mosaics.
- Beyond these mixed transitional mosaics, to the north are the Sudanian, and to the south the Zambezian **Mesic Savanna Biome** of southern and eastern Africa. Extensive flooded grasslands are found in some river basins within this biome.
- Next, to the north and south of the mesic savannas are representatives of the **Arid Savanna Biome**—the *Acacia* savannas of the Sahel, and the *Acacia/Adansonia/Commiphora* savannas of southern and eastern Africa. Some internal drainage basins within this biome have large halophytic grasslands and shrublands.
- Beyond the Arid Savannas are representatives of the **Desert Biome**—the Sahara in the north and the Namib/Karoo in the south.
- On the tropical coasts of Africa, the **Mangrove Biome** occupies the estuaries of great rivers.

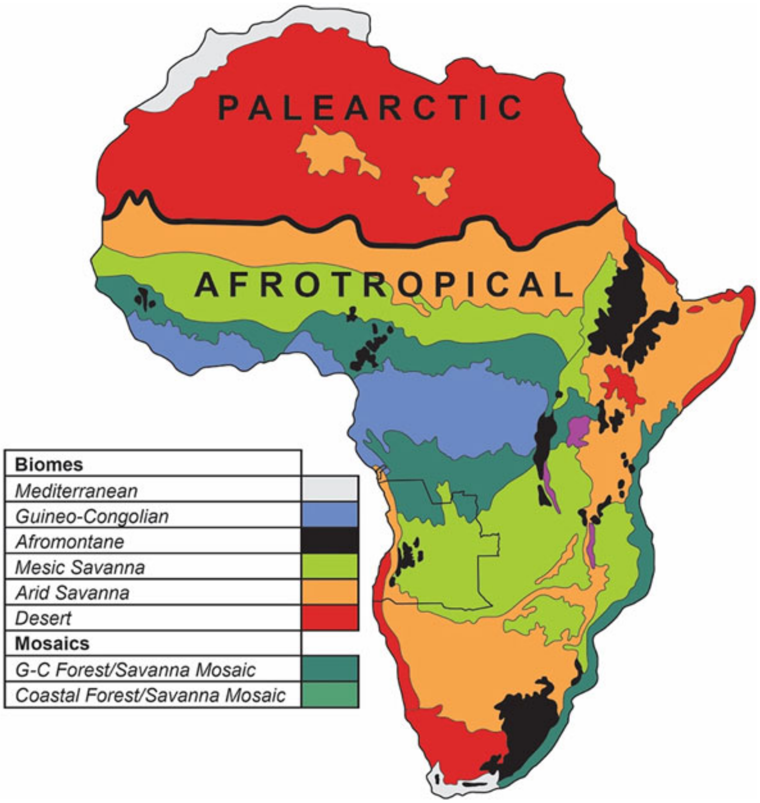


Fig. 2.1 Biogeographic realms, biomes and transitional Mosaics of Africa, redrawn and simplified after White (1983). Mangroves are not mapped

- Along the East African coast, a mosaic of grasslands, savannas and forests form the Indian Ocean Coastal **Forest/Savanna Mosaic**.
- At the northern and southern tips of the continent, examples of the **Mediterranean-Type Biome** are found—the Maquis of North Africa and the Cape Fynbos of South Africa.
- Finally, rising above the lowlands of Africa are the highlands and mountains carrying forests and grasslands of the **Afromontane Biome**.

A Synopsis of the African Biomes and Mosaics

Mediterranean Biome (*Area* 858,000 km^2*, 2.9% of Africa*). The North African Mediterranean Biome, including ***maquis*** and ***garrigue*** is 10 times larger than the South African ***fynbos*** (779,000 v 79,000 km^2. However, the fynbos flora, with over 6000 species and with 70% endemics, is vastly richer than that of the maquis at ca. 2000 species and with few endemics. Diagnostic genera in the North African Mediterranean shrublands and forests include *Quercus, Juniperus, Olea* and *Ceratonia*;

Table 2.2 Estimated area of African biomes and mosaics

Biomes	Area, 1000 Km^2	% Area of Africa
Mediterranean	858	2.9
Guineo-Congolian rain forest	2343	8.0
Afromontane forest and grassland	1271	4.3
Mesic savanna	6177	21.2
Arid savanna	7376	25.3
Desert	8290	28.4
Mangrove	71	0.2
Mosaics		
G-C forest/savanna mosaic	2536	8.7
Coastal forest/savanna mosaic	344	1.1

Based on ecoregional data in Burgess et al. (2004) *Terrestrial ecoregions of Africa and Madagascar—a conservation assessment*. Island Press, Washington DC

and for the South African sclerophyllous shrubland and heathland the characteristic genera include *Protea, Erica* and *Restio.* The key ecological determinants of Mediterranean climate ecosystems are cool wet winters and warm dry summers. Great climatic and physiographic diversity is found in this floristically and ecologically distinctive biome.

Guineo-Congolian Rain Forest Biome (2,343,000 km^2*, 8.0%*). The Guineo-Congolian Rain Forest Biome occurs below 1200 m in West and Central Africa. Rainfall ranges from 1000–2500 mm per annum, with short dry seasons of 1–3 months. The surface areas of the major blocks differ considerably from one to another. The Guinean block covers 559,000 km^2, most of this comprises fragmentary remnants of forest in highly transformed landscapes. The central Congolian block covers 1,794,000 km^2. Much of this is continuous forest but with significant levels of transformation. Diagnostic rain forest tree genera include *Entandrophragma, Gilbertiodendron, Lophira* and *Pentaclethra.*

Mesic Savanna Biome (6,177,000 km^2*, 21.2%*). The mesic savanna blocks lie to the north (2,885,000 km^2) and south (3,292,000 km^2) of the equatorial rain forest blocks, dominated respectively by Sudanian and Zambezian floristic elements. These formations are often referred to as ‘dry tropical forests’ by European botanists. Within the mesic savanna biome several extensive floodplain grasslands (Sudd, Zambezian, Lake Chad) are located, fed by the catchments of the mesic savannas.

The Sudanian Mesic savannas of northern Africa are floristically depauperate compared to the Zambezian Mesic savannas of southern Africa. Further, the Sudanian

Mesic savannas share few species with the Zambezian Mesic savannas, but tree genera such as *Burkea, Isoberlinia, Combretum, Terminalia* and grasses such as *Andropogon, Hyparrhenia, Loudetia* and *Pennisetum* are common to both. *Anogeissus* and *Boswellia* dominate many Sudanian savannas, but do not occur in the Zambezian savannas. The Sudanian Mesic savannas lie at 200–1000 m, receiving from 600–1600 mm rainfall per annum. The transition from Sudanian Mesic savannas to Sahelian *Acacia* Arid savannas is gradual and poorly defined but in general follows the 650 mm isohyet. *Combretum* species are important in the transitions between mesic and arid savanna biomes.

The Southern, Central and East African Mesic savannas lie at 1000–1600 m on the leached soils of cooler plateaus, typically receiving 650–1200 mm rainfall per annum. Miombo ecosystems dominate the southern Mesic savannas, which cover 3,000,000 km^2. Trees of the genera *Brachystegia, Burkea, Julbernardia and Isoberlinia* characterise miombo. Mesic savanna soils are typically nutrient poor and trees are thornless but protected against herbivores by chemical defences. Grasses are productive of biomass but of low nutritional value with the consequence that mammalian herbivore biomass is low. Following extended dry seasons, natural (and increasingly human-mediated) fires, are regular and widespread. Trees, shrubs and grasses have multiple traits that tolerate fire. These savannas are ecologically characterised as Mesic/Dystrophic Savannas. The Mesic savannas feed large floodplain grasslands on the Nile, Niger, Cubango and Zambezi rivers.

Arid Savanna Biome (7,376,000 km^2, *25.3%*). Arid Savannas occur in three main blocks. To the north of the Sudanian Mesic savannas, the Sahel *Acacia* Arid savannas cover 3,108,000 km^2. Semi-arid thorn scrub and savannas on highlands within or adjoining the Sahara Desert cover an additional 469,000 km^2. Spinescent woody genera found across the Sahel include *Acacia, Balanites, Boscia, Commiphora* and *Zizyphus*—all genera common in the eastern and southern African Arid savannas. Within the arid savanna biome, several large internal drainage basins result in extensive salt pans with halophytic vegetation, such as Etosha and Makgadikgadi.

In East Africa, *Acacia-Commiphora* Arid savannas cover 1,633,000 km^2. These include the rich volcanic soils of iconic landscapes such as the Serengeti.

In Southern Africa, Arid savannas cover 2,193,000 km^2. Of this area, 1,326,000 km^2 is dominated by *Acacia, Adansonia, Commiphora* and *Sterculia* savannas. In addition, *Colophospermum* dominates or is a conspicuous feature of savannas, woodlands and shrublands that cover 607,000 km^2 of the region.

Arid savannas occur between sea level and 1200 m, on comparatively nutrient-rich soils of hot valleys and low plateaus, receiving from 250 to 650 mm rainfall per year with dry seasons of up to eight months. The rich soils carry thorny tree species and nutritious grazing. The Arid savannas thus carry a high diversity and biomass of ungulate herbivores whose grazing and browsing activities influence grass and tree demography and dynamics. Fire is less frequent than in Mesic savannas. Ecologically, the Arid savannas are referred to as Arid/Eutrophic Savannas to distinguish them from Mesic/Dystrophic Savannas.

Desert Biome (8,290,000 km^2, *28.4%*). Deserts form the largest biome in Africa, with the Sahara occupying 7,458,000 km^2 of North Africa and the Karoo/Namib 580,000 km^2 of southwestern Africa. Rainfall is erratic and usually less than 50 mm in the Sahara, 150 mm in the Namib and 250 mm per annum in the Karoo. Diagnostic genera for the Namib include *Acanthosicyos, Stipagrostis* and *Welwitschia* and with members of the Mesembryanthemaceae and Asteraceae characterizing the Karoo. The Karoo has over 3000 species of succulent plants, and is recognised as a global floristic 'hotspot'. The geological substrate is highly variable over the vast areas covered by desert, with shallow soils, sands or bare rock exposures.

Mangrove Biome (71,000 km^2, *0.2%*). Examples of this biome are restricted to the mouths, deltas and floodplains of large rivers on the Atlantic and Indian Ocean coasts. At the interface of fresh and saline waters, a limited number of woody and herbaceous genera have adapted to the challenging aquatic environment, including the mangrove genera *Avicennia, Brugueria, Ceriops, Laguncularia, Rhizophora* and *Sonneratia* and the sea-grasses *Halodule* and *Cymodocea.*

Afromontane Biome (1,271,000 km^2, *4.3%*). Most of the Afromontane Biome occurs at altitudes of 1200–2200 m, with important forests in the highlands of Cameroon, Angola, South Africa, Ethiopia and East Africa where the highest peak (Kilimanjaro) reaches 5895 m. The Afromontane grasslands, shrublands and woodlands cover 80% of the biome, with forests and alpine communities in moister and higher areas. Rainfall ranges from 1000–2500 mm per annum. Afromontane forests have a distinctive floristic composition, including diagnostic genera such as *Podocarpus, Olea, Juniperus*, *Apodytes* and *Philippia,* shared across the archipelago-like chain of forests that follow the escarpments and highlands of eastern and southern Africa and the isolated mountains of western Africa.

Guineo-Congolian Forest/Savanna Mosaics (2,536,000 km^2, *8.7%*). Lying between the Guineo-Congolian rain forests and the Sudano-Zambezian mesic savannas is a broad belt of transitional forest/savanna mosaics. Much of the forest/savanna mosaic in West Africa has been highly transformed by agriculture to secondary grasslands and croplands. Fire-adapted tallgrass savannas dominate these mosaics, with rain forests constituting less than 10% of the area.

East African Coastal Forest/Savanna Mosaics (344 km^2, *1.1%*). Along the lowlands and interior escarpment of the East African coast, and extending from Somalia southwards to South Africa, is a band of grasslands, savannas and fragments of moist forests, today largely transformed by human activities, but with a rich flora and fauna. The forests have both Guineo-Congolian and Afromontane elements, while the savannas comprise a mix of both Arid and Mesic Zambezian floristic elements.

2.4 Classification of Angola's Biomes and Ecoregions

Representatives of six of the seven African biomes and one of the mosaics described above are found in Angola. The founders of Angola's vegetation classification and mapping systems, Gossweiler and Mendonça (1939) and Barbosa (1970) respectively described and mapped 19 and 32 main vegetation types, each with many subtypes. Here we will not try to initiate the learning process by describing every vegetation type. Rather, we will focus on the biomes and ecoregions, following the pattern of Africa's biomes described above. Understanding the distribution of vegetation relies on maps, of which the latest covering the vegetation of the whole of Angola is that of Barbosa (1970). More recently, the World Wildlife Fund (WWF) has produced a map of the Ecoregions of Africa (Burgess et al., 2004); updated by Dinerstein et al. (2017) and available at https://ecoregions2017.appspot.com.

For the purpose of delineating the ecoregions of Angola, the WWF map of African biomes and ecoregions has been adapted, but in addition, recognises the distinction of the Arid and Mesic savannas biomes in Fig. 2.2. Furthermore, Angolan ecoregion 12—Coastal Arid Savannas—is recognised as a separate ecoregion. The sharp mapping lines separating the ecoregions are artificial. In reality, Angola's vegetation is an ever-changing continuum of species abundances, densities and physiognomies, with few sharp boundaries. Biomes and ecoregions do not end at a given point, but rather merge in a complex mosaic pattern across their interfaces.

Angola's biomes and their 16 constituent ecoregions will be described in detail in Part IV. These groupings (with ecoregion numbers), plus conservation areas or sites where typical examples can be studied in the field, are listed below. The classification and distribution of Angola's biomes (Fig. 2.2) follows that of African biomes and closely correlates with the regional centres of endemism of White (1971, 1983) reflecting their close evolutionary and ecological relationships. A simplified profile of biome structure is presented in Fig. 2.3.

Angola's biomes, transitional mosaics and escarpment zone, mapped in Fig. 2.2, and with examples of where they may be studied, comprise:

- **I Guineo-Congolian Rain Forest Biome and Forest/Savanna Transitional Mosaic**: (Ecoregions 1–3) Maiombe, Pingano, Cumbira, Lagoa Carumbo
- **II Afromontane Forest and Grassland Biome**: (Ecoregions 4 and 5) Moco, Namba
- **III Mesic Savanna Biome**: (Ecoregions 6–11) Cangandala, Luando, Bicuar, Cameia
- **IV Arid Savanna Biome**: (Ecoregions 12–14) Iona, Namibe, Chimalavera, Quiçama
- **V Namib Desert Biome**: (Ecoregion 15) Iona
- **VI Mangrove Biome**: (Ecoregion 16) Quiçama, Ilha dos Passaros

An idealised profile of vegetation physiognomy along a rainfall gradient is presented in Fig. 2.3, while Fig. 2.4 demarcates the distribution of Angolan biomes and ecoregions, using Barbosa's (1970) vegetation map as a template. The mapped

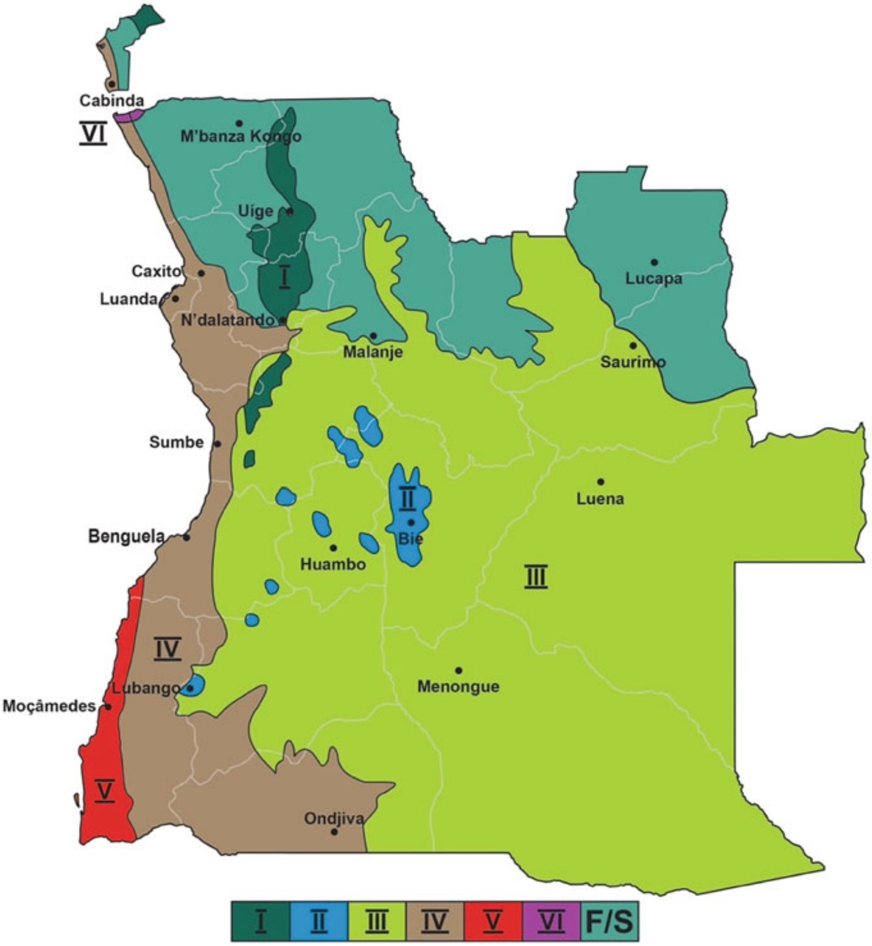


Fig. 2.2 Biomes and mosaics of Angola. I Guineo-Congolian rain forest (dark green); II Afromontane forests and grasslands (blue); III Mesic savanna (yellow-green); IV Arid savanna (brown); V Desert (red); VI Mangrove (purple); F/S Guineo-Congolian rain forest/mesic savanna transitional mosaic (Turquoise)

ecoregions closely follow the concepts of ecoregions as defined in Burgess et al. (2004) and developed further during field surveys in Angola. Table 2.3 provides summarised characteristics of each ecoregion, plus estimates of the area occupied by each as a percentage of Angola's land area. The key plant genera found within the Barbosa vegetation units included in each ecoregion provide an idea of their floristic composition. Chapter 3 provides outlines of the main vegetation types and habitats typically found within each ecoregion, providing context to the detailed account of environmental drivers of pattern, given in Part II.

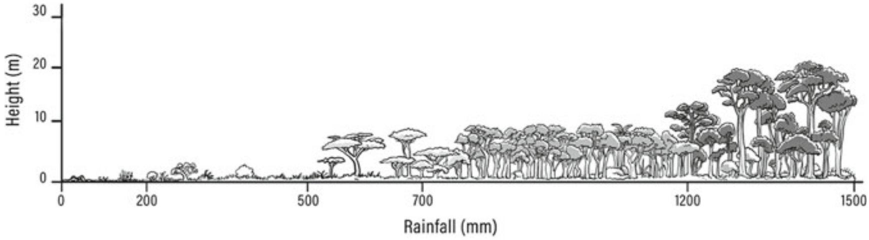


Fig. 2.3 A profile of vegetation physiognomy with increasing rainfall from desert to semi-desert shrublands, to arid and mesic savannas and woodlands, and to closed rain forest. Redrawn after Shorrocks (2007) *The Biology of African Savannahs.* Oxford University Press, Oxford

Box 2.1: Terminology of Structural, Compositional and Functional Attributes

The terminology used in classifying and describing the biomes and ecoregions of Angola can be challenging, as terms used for biogeographic and structural concepts and even terms used in local languages are frequently intermixed in the literature. Some terms, such as savanna, are used both in a strictly structural sense, and also in a broad biome sense, as discussed later (Box 2.2). In order to better understand the identity (structure, composition and physiognomy) of the key vegetation components found in Angola, some definitions of structural terms are essential.

- A **forest** is a plant community with a closed tree **canopy** of touching or interlocking crowns (50% or more, typically above 75% of projected vertical cover) in two or more layers (**strata**) and usually with a shrub and sapling layer and a discontinuous herb layer. Climbers and epiphytes may also be present. In Portuguese literature, the term *floresta densa* is used to distinguish woodlands from closed forest.
- A **thicket** is a very dense, often impenetrable plant community of large **multi-stemmed** shrubs and trees. Climbers can be abundant, but grasses are sparse. Thickets can be evergreen or deciduous, thorny or non-thorny. The terms *balcedo* or *brenha* are used in Portuguese papers for thicket.
- A **woodland** is a stratified plant community with an open tree layer (less than 50% projected canopy cover) with crowns less than one diameter apart or touching, but usually not overlapping. Woody species might be trees or shrubs, usually single-stemmed but occasionally multi-stemmed. Some Portuguese researchers use the terms *floresta clara* or *floresta aberta* for woodland, but the term *mato* is recommended for the savanna woodlands of Angola.
- A **savanna** is a plant community with a discontinuous layer of woody species (trees or shrubs) whose individuals are spaced more than one

crown diameter apart and with a usually dense ground layer of non-woody species of grasses and forbs. Savannas might be dominated by trees (tree savanna—*savana arborizada*) shrubs (shrub savanna—*savana com*

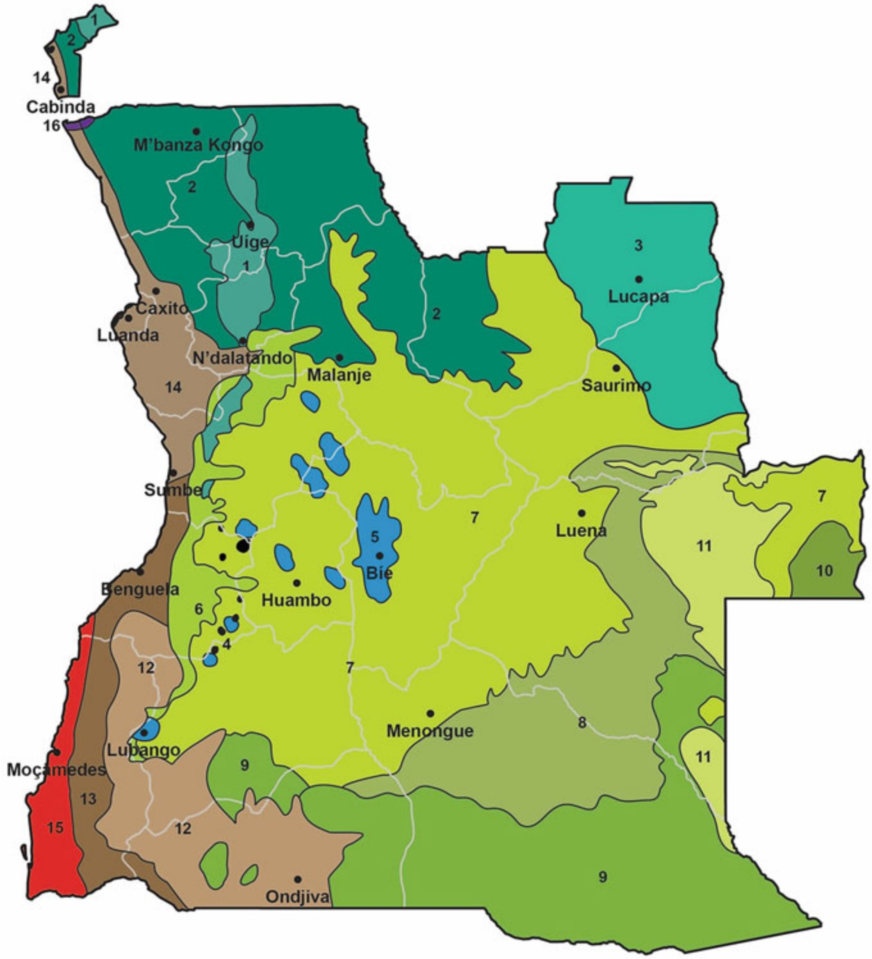


Fig. 2.4 Ecoregions of Angola, modified from Burgess et al. (2004). Boundaries of Ecoregions are based on the delineation of vegetation types by Barbosa (1970). Ecoregion numbers follow Table 2.3. Provincial boundaries are indicated in white

Table 2.3 Biomes and Ecoregions of Angola. (MAP—Mean Annual Precipitation)

Map No.	WWF No.	Biome/ecoregion	Barbosa (1970) vegetation type	Alt range (m)	Station and MAP (mm)	Estimated % cover and area Km^2
I	*Guineo-Congolian rain forest biome and forest/savanna mosaics*					*16.5%*
1	5	Congolian rain forest	Closed forest/savanna mosaic—1, 2, 3 *Gilbertiodendron, Tetraberlinia, Librevillea*	50–2000	Belize 1612	0.3% 3 771
2	63	Western Congolian forest/savanna mosaic	Forest/savanna mosaic—7–10, 13, 14, 26 *Entandrophragma, Erythrina, Annona*	0–1400	Tomboco 893	11.6% 136 183
3	58	Southern Congolian forest/savanna mosaic	Forest/savanna mosaic—8, 12 *Marquesia, Daniellia, Erythrophleum*	800–1000	Dundo 1669	4.6% 54 508
II	*Afromontane forest and grassland biome*					*1.1%*
4	77	Afromontane forest	Relict forests—6 *Podocarpus, Apodytes, Pittosporum, Protea*	1600–2600	Ebo 1177	0.01% 200
5	77	Montane grassland	Highland grasslands—32 *Protea, Monocymbium, Themeda*	1400–2600	Humpata 805	1.1% 12 802
III	*Mesic savanna, woodland and grassland biome*					*68.2%*
6	35	Angolan escarpment savannas	Savanna-woodland, thicket & forest mosaic—5, 18B, 22 *Cochlospermum, Albizia, Celtis, Brachystegia*	500 1200	Gabela 833	5.2% 61 614

(continued)

Table 2.3 (continued)

Map No.	WWF No.	Biome/ecoregion	Barbosa (1970) vegetation type	Alt range (m)	Station and MAP (mm)	Estimated % cover and area Km^2
7	36	Angolan wet miombo woodlands	Woodland—16, 17A, 17B, 18A, 19 *Brachystegia, Julbernardia, Burkea, Guibourtia, Cryptosepalum,*	1100–2000	Huambo 1390	34.8% 408 457
8	42	Angolan dry miombo woodlands	Savanna Woodland—24 *Brachystegia, Burkea, Guibourtia, Julbernardia, Cryptosepalum*	1100–1200	Mavinga 815	10.3% 121 222
9	64	Zambezian *Baikiaea* woodlands	Tree & Shrub Savanna—15, 25 *Baikiaea, Guibouria, Pterocarpus, Combretum, Erythrophleum, Burkea*	1000–1300	Mucusso 774	13.5% 158 390
10	33,39	Zambezian dry evergreen forest	Closed Forest—4 *Cryptosepalum, Brachystegia, Guibourtia, Burkea*	1100–1200	Cazombo 1441	0.05% 646
11	76	Zambezian flooded grasslands	Grasslands—31—*Loudetia, Monocymbium, Tristachya, Parinari*	1000–1100	Luau 1276	4.3% 51 093
IV	*Arid savanna, woodland and thicket biome*					*12.8*
12	34	Angolan mopane woodlands	Woodland—20, 21 *Colophospermum, Croton, Combretum, Acacia,*	500–1200	Chitado 405	6.6% 77 212

(continued)

Table 2.3 (continued)

Map No.	WWF No.	Biome/ecoregion	Barbosa (1970) vegetation type	Alt range (m)	Station and MAP (mm)	Estimated % cover and area Km^2
13	104	Namib savanna woodlands	Shrubland—27 *Acacia, Commiphora, Colophospermum, Rhigosum, Sesamothamnus*	0–800	Bruco 466	3.0% 35 417
14	104/35	Coastal arid savannas	Woodland—11, 23—*Acacia, Adansonia, Sterculia, Euphobia*	0–500	Luanda 405	3.2% 37 200
V	*Desert Biome*					*1.2%*
15	98	Angolan Namib desert	Desert, Shrubland—28, 29 *Welwitschia, Zygophyllum, Stipagrostis, Odyssea*	0–600	Tômbua 15	1.2% 14 479
VI	*Mangrove Biome*					*0.1%*
16	111	Central African mangroves	14A Mangroves—14 *Avicennia, Rhizophora, Raphia, Elaeis*	0–5	Soyo 590	0.1% 1 878

Note In broad terms, closed moist forests (within Ecoregions 1–3) cover less than 1% of Angola while moist tallgrass savannas (forming a transitional mosaic with closed forests in ecoregions 1–3) cover 16%. Mesic savannas (mostly miombo but including flooded grasslands) cover 68%, and Arid savanna 13%. The collective total of mesic savannas (miombo), moist (tallgrass) savannas and arid savannas thus total ca. 97% of the country *arbustos*) or clumps of woody species usually associated with termitaria (clump savanna).

- A **grassland** is a plant community dominated by grasses (tufted, stoloniferous or wiry) and **forbs** (broad-leaved herbaceous, non-graminoid flowering plants), with few if any woody species. Grasslands are termed prados or savana herbácea in Portuguese.

These definitions relate to **physiognomic** structure. They do not describe any **floristic** or **ecological** characteristics that relate to different evolutionary relationships or environmental conditions. With a flora of over 6800 plant species in Angola, it is essential that a small group of **indicator** species, genera or families be used to characterise vegetation types and ecoregions. It is usual to choose indicators that are either dominant in numbers or area occupied within a vegetation type (such as species of *Acacia* or *Brachystegia*) or which through their size are most prominent (such as *Adansonia* or *Baikiaea*) or which are indicators of a particular biome (such as *Podocarpus* in Afromontane forest). Some biomes can be characterised at the level of sub-families of common species such as the Detarioideae (including *Brachystegia,* which characterise the Mesic Savanna Biome) or the *Mimosoideae* (including *Acacia* which characterise the Arid Savanna Biome).

Ecological characteristics are as important as physiognomic and floristic in defining biomes and are influenced by biotic as well as abiotic factors as described below.

Seasonality of temperature and rainfall will determine whether trees lose their leaves annually (**deciduous**) or every few years (**evergreen**). **Light penetration** through the canopy influences grass cover and in turn determines whether fires will enter wooded communities. The combination of soil, water and nutrient conditions often determines whether the woody species have fine pinnate leaves (**microphyllous**) or broad leaves (**mesophyllus**). Soil nutrient availability for plant growth is poor (**dystrophic**) or rich (**eutrophic**). The pH of soils ranges from **acid, neutral** to **alkaline**. The degree of **herbivory** is associated with the dystrophic/eutrophic dichotomy. Rich soils produce nutritious grasses, herbs and woody plants. The plants of eutrophic soils frequently have thorny, spiny or other **defence mechanisms** against browsing. These mechanisms have evolved over millions of years in communities populated by numerous species of large mammal herbivores. Grasses can translocate nutrients from above ground to root systems at the end of summer ('**sour grasses**') or retain nutrients in the foliage into winter ('**sweet grasses**'). Most southern African grasses are physiologically adapted to sunny, warm dry conditions (**C_4 grasses**). Grasses adapted to growing in shaded and cooler, moister conditions, such as forest floors, follow the **C_3 photosynthetic pathway** typical of grasses of temperate climates (Sect. 3.3.2). Many African savanna trees and shrubs have evolved mechanisms to survive regular natural **fires**, such as thick corky bark or the ability to **coppice** (re-sprout) after fires. The extreme of such fire adaption is found in species of **geoxyles**—woody members of dozens of plant families that escape fire damage with roots, trunks and branches below the soil surface. After the passage of fires, geoxyles produce short branchlets which carry leaves, flowers and fruit before grasses emerge and shade them out following the first rains (Box 15.1). Further plant structural and functional adaptations will be described in the detailed accounts of Angolan biomes (Part IV).

Box 2.2: When is a Forest a Forest, and when is a Savanna a Savanna?

Considerable confusion has developed in recent decades regarding the use of the term ‘forest’ and ‘savanna’ by ecologists working in different African countries. In particular, the Food and Agricultural Organization (FAO) of the United Nations has confounded the classification of open and closed vegetation by defining all land with more than 10% tree canopy cover as ‘forest’. The ecological definition used in this book recognises the transition from wooded savannas to closed forests at projected canopy cover of 50%. It is of importance to clarify these concepts before proceeding with the description of Angolan biomes and ecoregions.

Huntley and Walker (1982) defined the tropical savanna biomes of the world on the basis of their co-dominance of trees and a near-continuous layer of **heliophilous** (shade-intolerant) grasses that follow the **C_4 photosynthetic pathway**. The crowns of savanna trees and the canopies of savanna woodlands are more **permeable to light** than those of forests. The grasslands associated with the savanna woodlands support a rich diversity of **forbs** (non-grass herbs) that make up an important component of their botanical diversity. Fires penetrate the woodlands of the savanna biomes, but due to the sparse cover of grasses, are seldom damaging to the fire-tolerant trees and shrubs. Savanna tree saplings are fast growing, rising above the ‘kill-zone’ of fires within a few years. In summary, savanna plants are fire-tolerant but shade-intolerant. Huntley (1982) further recognised two distinctive savanna biomes—**arid/eutrophic** and **mesic/dystrophic**—occupying different landscapes across Africa with distinctive floras and faunas. The two savanna biomes have a similar codominance of trees and grasses responding to periods of soil water stress during the dry season (Table 2.4). The dichotomy in African savanna biomes, and the distinction between closed forests and savannas, is especially important to recognise in Angola, and is outlined below.

Table 2.4 General characteristics of arid/eutrophic, mesic/dystrophic savannas and closed-canopy rain forest biomes of Angola

	Arid/eutrophic savanna	Mesic/dystrophic savanna	Rain forest
% Area of Africa	25%	21%	8.0%
% Area of Angola	13%	68%	<1%
Angolan biome	Arid savanna	Mesic savanna	Guineo-Congolian forest
Typical ecoregion	Coastal arid savanna	Angolan wet miombo	Guineo-Congolian rain forest
Rainfall, mm/yr	250–650	650–1400	1200–1800
Frost	Occasional	Rare	Absent
Dry months	More than 8	Less than 8	1–3
Geology	Sedimentary/basic Igneous	Acid igneous/sedimentary/sands	Mixed
Erosional surface	Recent	African/Post African	Recent
Landscape	Incised valleys, hills	Peneplains, plateaus	Escarpments
Catenal patterns	Frequent	Typical	Rare
Leaching	Low	High	High
Base status	Eutrophic (High CEC)	Dystrophic (Low CEC)	Mesotrophic (medium CEC)
Phosphorus availability	Moderate	low	Moderate
Mycorrhizae	Ectomycorrhiza (ECM)	Endomycorrhiza VAM)	VAM and ECM
Available moisture	Low	High/Moderate	High
Centre of endemism	Zambezian; Karoo/Namib;	Zambezian	Guineo-Congolian
Typical tree genera	*Acacia, Adansonia, Commiphora, Colophospermum*	*Brachystegia, Julbernardia, Baikiaea, Burkea*	*Gilletiodendron, Tetraberlinia, Entandrophragma*
Physiognomy	Grassland, shrubland, thicket, woodland	Grassland, woodland, thicket	Closed Canopy forest
Average tree height	6 m	15 m	30 m

(continued)

Table 2.4 (continued)

	Arid/eutrophic savanna	Mesic/dystrophic savanna	Rain forest
Canopy depth	Shallow, 1–3 m	Shallow, 2–5 m	Deep, 5–10 m
Light penetration	High	High	Weak
Strata	Grass/shrub/tree	Grass/shrub/tree	Multi-strata
Grass genera	C_4 Chloridoid/Aristidoid	C_4 Andropogonoid	C_3 Bambusoid
Tree bark	Thin	Thick	Thin
Underground storage	High	High	Low
Fire frequency	5–50 yr	1–5 yr	Absent/rare
Root suckering	Common	Common	Rare
Spinescence	Abundant	Rare/absent	Rare/absent
Succulents	Frequent	Rare	Absent
Leaf phenology	Deciduous	Deciduous/semi-dec	Semi-deciduous/semi-evergreen
Tree leaf/Leaflet length	Microphyll/fine-leafed (0.1–1 cm)	Mesophyll/broad-leafed (2–10 cm)	Mesophyll (2–20 cm)
Geoxyles	Absent	Common	Absent
Self-pruning	Rare	Common	Frequent
Primary productivity	Low	High	High
Leaf cell M/S ratio	High	Low	Low
Nutrition value	High	Low	Low
Herbivore density	High	Low	Low
Feeding behaviour	Mixed feeders	Bulk feeders	Selective feeders
S. American analog	Chaco	Cerrado	Amazon/Atlantic

Exceptions occur. Transitions between arid and mesic savannas include the *Combretum* savannas of mixed landscapes and soil types. Based on Huntley (1982) and Scholes (1997)

In Africa, the **transition** from the mesic savanna biome to the rain forest biome is characterised by a **mosaic** of forest and savanna communities, each very different in their response to fire, and existing as **bi-stable states**, as described in Sect. 3.2.7. While the transition from Mesic/Dystrophic to Arid/Eutrophic savannas can be gradual and appear as a continuum, the interface between the closed forest and mesic savanna components of the mosaics is very sharp (Fig. 12.5). Because the forest patches are often of limited size and diverse shape, they are seldom mapped as distinct communities, and ecologists tend to designate them as ‘mosaics’ (Barbosa, 1970) or ‘transitions’ (White, 1983). In the map of African biomes (Fig. 2.1) to the north of the Guineo-Congolian Rain Forests, a belt of Guinean forest/savanna mosaics lie between the forest blocks and the Sudanian Savannas. To the south of the Congo Basin, a belt of Guineo-Congolian forest/savanna mosaics separates the forest block from the Mesic Savannas. The sharp lines marking the biome boundaries are artificial. In reality, the boundaries between most biomes are gradual, as rainfall and landscape changes interdigitate.

The characteristics of the two savanna biomes and the closed canopy rain forest biome are summarised in Table 2.4 and described below.

Closed Canopy Forests. The forests of Angola have a continuous and dense tree canopy, with sparse shade-tolerant grasses, herbs and shrubs on the forest floor. Shade-tolerant species are adapted to low-light environments, in contrast to shade-intolerant species, which are adapted to high-light environments. Shade-adapted plants have low photosynthetic, respiratory, metabolic, and growth rates. Sun plants (shade-intolerant) generally have higher photosynthetic, respiratory, and growth rates but lower survival rates under shaded conditions. The closed canopy forests have a distinct flora to that of both arid and mesic savannas. Forest trees and shrubs are fire-intolerant. C_4 grasses are typically very sparse or absent from the forest interior. The few grasses that do occur are shade-tolerant, C_3 species. The low biomass of grasses and herbs on the forest floor and its shaded moist microclimate limits the entry of fire into the forest interior. Where fires do penetrate, during extended dry spells, or where strong winds drive hot fires into the forest, damage and death of tree and understorey species can occur.

In Angola, four distinct closed forest types on well-drained (**terra-firme**) sites can be recognised.

- The most extensive and species-rich closed forests are those of Guineo-Congo floristic affinity (Ecoregions 1, 2 and 3).
- Second, extremely limited areas of Afromontane forests occur on the highest mountains (Ecoregion 4).
- A third forest type, comprising elements of both Guineo-Congolian and Zambezian floras occurs along the foothills of the Angolan Escarpment, as dry deciduous forests within Ecoregions 6 and 14.
- Finally, the evergreen *Cryptosepalum* forests of Moxico (Ecoregion 10) have a closed canopy and many forest traits, and physiognomically meet several forest criteria, but floristically are part of the Mesic Savanna Biome and are placed there in this account.

In addition, two specialised edaphically determined habitats (inland swamps and coastal esturies) support limited areas of closed-canopy swamp forests and mangroves.

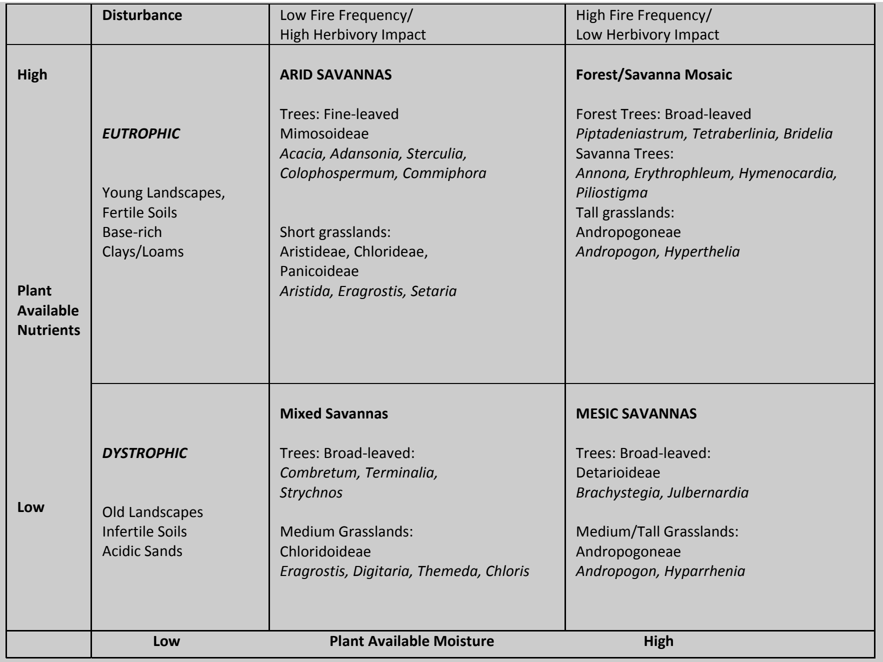
Forest/Savanna Interface. Shade-intolerant savanna species fail to establish under the canopy of forest. In the tall grasslands surrounding forest patches in the Congolian Forest/Savanna mosaic (Ecoregions 2 and 3), fires usually die at the forest margin, unless this has been weakened by logging or other disruptive human activities. Where the forest margin is disturbed, fast-growing **invasive alien species**, such as *Chromolaena odorata* and *Inga vera* out-compete indigenous species and become established. Hot fires in the tall grasslands kill any seedlings of forest species that might have expanded into adjoining grassland. The contrasting influences of fire and shade result in very sharp boundaries between the distinct floras of the two systems of the Forest/Savanna mosaic**,** as discussed in detail in Chaps. 12 and 14.

Mesic Savannas. Across Angola's extensive interior plateau, miombo woodlands, savannas and associated grasslands dominate, occupying 68% of Angola (Ecoregions 6–11). To the north of the miombo, where it transitions into evergreen and semi-deciduous forests of the Congo Basin, a tallgrass savanna, which totals 16% of Angola, forms a mosaic with the forest patches, (Ecoregions 2 and 3). These tall grasslands are highly flammable. The trees and shrubs that are found in the mesic savannas have evolved fire-adaptations such as a thick corky bark that protects the inner cambium or growing tissues of the stems and branches, robust underground storage organs, and the ability to re-sprout after fire from **epicormic** buds that lie under the protective cork bark. The Angolan miombo, and the Congolian Forest/Savanna mosaics occupy leached soils that are poor in nutrients, in areas receiving an annual precipitation exceeding 650 mm. They are Mesic/Dystrophic savannas.

Arid Savannas. In the arid southwest of Angola, and along the arid coastal lowlands, the savannas are distinctive from those of the miombo and the tallgrass savannas of the Congolian Forest/Savanna mosaic. These are the Arid/Eutrophic savannas, which occupy 13% of Angola (Ecoregions 12–14). They lie on richer soils, are subject to soil water stress for up to eight months of the year, are less productive of biomass than the mesic savannas, and as a consequence are less prone to the regular fires that characterise the mesic savannas. Profiles illustrating the contrasts between Mesic/Dystrophic and Arid/Eutrophic savannas are presented in Figs. 2.5 and 2.6. The ecological relationships between the two savanna biomes and of the transitional mixed savannas and forest/savanna mosaics are presented in Fig. 2.7.

Fig. 2.5 Physiognomic profile: Woodland of the Mesic Savanna Biome. Note the near-continuous grass cover under the light canopy of trees. Redrawn after Shorrocks (2007) *The Biology of African Savannahs.* Oxford University Press, Oxford

Fig. 2.6 Physiognomic profile: Arid Savanna Biome. Note continuous grass cover below broken tree and shrub cover. Redrawn after Shorrocks (2007) *The Biology of African Savannahs.* Oxford University Press, Oxfords



	Disturbance	Low Fire Frequency/ High Herbivory Impact	High Fire Frequency/ Low Herbivory Impact
High **Plant Available Nutrients**	***EUTROPHIC*** Young Landscapes, Fertile Soils Base-rich Clays/Loams	**ARID SAVANNAS** Trees: Fine-leaved Mimosoideae *Acacia, Adansonia, Sterculia, Colophospermum, Commiphora* Short grasslands: Aristideae, Chlorideae, Panicoideae *Aristida, Eragrostis, Setaria*	**Forest/Savanna Mosaic** Forest Trees: Broad-leaved *Piptadeniastrum, Tetraberlinia, Bridelia* Savanna Trees: *Annona, Erythrophleum, Hymenocardia, Piliostigma* Tall grasslands: Andropogoneae *Andropogon, Hyperthelia*
Low	***DYSTROPHIC*** Old Landscapes Infertile Soils Acidic Sands	**Mixed Savannas** Trees: Broad-leaved: *Combretum, Terminalia, Strychnos* Medium Grasslands: Chloridoideae *Eragrostis, Digitaria, Themeda, Chloris*	**MESIC SAVANNAS** Trees: Broad-leaved: Detarioideae *Brachystegia, Julbernardia* Medium/Tall Grasslands: Andropogoneae *Andropogon, Hyparrhenia*
	Low	**Plant Available Moisture**	**High**

Fig. 2.7 A generalised model of the savanna types of southern Africa. The environmental space is defined by Plant Available Nutrients (PAN) and Plant Available Moisture (PAM) and by the importance of disturbance by fire and herbivory. Indicator sub-families and genera for dominant trees and grasses are included. Plant Available Moisture integrates rainfall, water infiltration, evapo-transpiration, soil texture and hydrologic regime in a single function. The two extremes of Arid/Eutrophic and Mesic/Dystrophic savannas are often separated by mixed savannas, while the transition from Mesic savannas to Guineo-Congolian forests is occupied by mosaics of forest patches and galleries within a matrix of tallgrass savannas with fire-tolerant trees. After Frost et al. (1986) and Scholes (1997)

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Chapter 3
Profiles of Angola's Biomes and Ecoregions

Key Concepts and Questions: This Chapter Explains

- *How the six African biomes represented in Angola are defined.*
- *Where the biomes are found, and what their landscape and climatic characteristics are.*
- *What the key physiognomic, floristic and faunistic features are of Angola's 16 ecoregions.*

Context: From African Biomes to Angolan Ecoregions

The introductory outlines of Angola's biomes, mosaics and ecoregions presented here form a continuum from the synopses of African biomes and mosaics given in Sect. 2.3, and elaborated in detail in Part IV of this book. Brief outlines of Angola's biomes, mosaics and ecoregions set the stage against which the ecological drivers of such ecosystem diversity are analysed in Part ll. In the ecoregional profiles, reference is made to the WWF Ecoregion numbers (https://ecoregions2017.appspot.com) and the vegetation units in Barbosa (1970), where additional detail might be found.

3.1 Guineo-Congolian Rain Forest Biome and Forest/Savanna Mosaic

Across northern Angola, the rich Guineo-Congolian flora of African rain forests is represented in the moist forests found along the low mountains and escarpments of Cabinda, Zaire, Uíge, Cuanza-Norte, Cuanza-Sul and Malange. The flora penetrates southwards along the Angolan escarpment as isolated fragments in Benguela and Huíla provinces and as gallery forests up the tributaries of the Congo drainage in Malange and Lunda-Norte. Biogeographically important but poorly studied forests also occur along the Quela and Tala Mungongo escarpments on the western margin of the Baixa de Cassange. These fire-sensitive forests form a mosaic within fire-tolerant

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Western and Southern Congolian tall grasslands and savannas as the vegetation transitions into the Zambezian flora of the Mesic Savanna Biome. The Guineo-Congolian Rain Forest Biome (*sensu strictu*) occupies less than 1% of Angola. Far more extensive are the tallgrass savannas of the Congolian Rain Forest/Mesic Savanna Mosaic, that forms a transition between the Guineo-Congolian Rain Forest Biome and the Mesic Savanna Biome. These transitional mosaics (Ecoregions 2 & 3) cover 16% of Angola.

The Maiombe forests are of great importance for the conservation of large mammals, especially for Western Lowland Gorilla, Central Chimpanzee, Forest Elephant and Forest Buffalo. The Maiombe forests are of high conservation priority as home to 14 species of primate, five species of forest duiker and the enigmatic Water Chevrotain.

Ecoregion 1. Guineo-Congolian Rain Forest (*WWF 5; Barbosa 1, 2, 3;* Figs. 3.1 and 3.3). Angola has a rather limited area of closed canopy tropical rain forest (ca. 3500 km^2). These forests occur mostly in Cabinda, where a continuation of the narrow belt of Lower Guinean evergreen to semi-evergreen broadleaf forest extends from central Cameroon to just north of the mouth of the Congo River. Outliers of Guineo-Congolian Rain Forest floristic and faunistic elements follow the Angolan Escarpment in isolated blocks in Cuanza-Sul, and as tiny forest fragments in the seaward-facing ravines of the Serra da Chela. The inland hills of Cabinda form the drier southern limit of the Mayombe forest block, known in Angola as the Maiombe forest. Most of the ecoregion lies on Precambrian rocks, producing cambisols and nitisols. The Alto Maiombe forests of Cabinda receive from 1200 to 1600 mm of rain per annum, with dry spells in July–September and again in January. The canopy of mature forest in Maiombe may reach 60 m height, but generally the canopy is between 30 and 40 m height. Important genera include *Gilbertiodendron, Julbernardia,* and *Tetraberlinia* in climax forest and *Milicia, Musanga, Piptadeniastrum, Ricinodendron* and *Terminalia* in disturbed, secondary forest. The semi-deciduous forests of Zaire, Uíge, Cuanza-Norte (including the large Dembos forest block) and Cuanza-Sul are drier, with from 800 to 1400 mm rainfall per annum. As a whole, the ecoregion has, in African terms, exceptional species richness with many endemic species.

Ecoregions 2 & 3. Western and Southern Congolian Forest/Savanna Mosaics (*WWF 63, 58; Barbosa 7–10, 12–14, 26;* Figs. 3.2, 3.4 and 3.5). These two large blocks (136,000 and 54,000 km^2 in Angola) of mixed forest and tallgrass savannas extend the reach of rain forests as gallery forests in valleys and isolated forest fragments on hillsides and plateaus, southwards from the Congo Basin. Rainfall ranges from 1000 to 1600 mm per annum, with a distinct dry season from May to September. The Guineo-Congolian Rain Forests comprise less than 5% of the landscape of these mosaics, but contribute possibly as much as 80% of the species diversity of these two ecoregions. The major portion (ca. 95%) of these two ecoregions consists of tallgrass savannas which belong, floristically, to the Mesic Savanna Biome. They are therefore mapped as transitional mosaics in Figs. 2.2 and 2.4. Tall grasslands with sparse trees characterise the sandy plateaus between river valleys. Extensive areas of Ecoregion 3, for instance, are treeless grasslands with an abundance of geoxyles

Fig. 3.1 Subsistence farm in Alto Maiombe Forest, Cabinda. Tall trees include forest margin pioneers *Terminalia superba* with erect white trunks, and the branched crowns of *Musanga cecropioides* at left and right of the scene

(Box 14.3) and are known in Lunda-Norte as the *chanas da borracha* due to the abundance of the rubber plant, *Landolphia parvifolia.*

The landscapes of northern Angola range from 1000 to 1500 m in the mountainous regions of Zaire and Uíge, and the high plateau of Malange and the plains of Lunda-Norte. The landscapes descend via a series of valleys to 500 m in the Congo Basin along the Cuango River, and down to sea level at the mouth of the Congo. Soils include ferralsols on Precambrian crystalline rocks in the west, and arenosols of the Kalahari sands in the east. The deeply incised valleys occupied by gallery forest usually lie on exposed Karoo strata and Precambrian rocks.

This very mixed topography carries a rich flora and fauna, where elements of Zambezian and Guineo-Congolian phytogeographic regions meet, and where the fauna of Guineo-Congolian forests interdigitate with those of the Zambezian woodlands, savannas and grasslands of the south and east. Trees of genera such as *Dialium, Daniellia, Cryptosepalum* and *Marquesia* are prominent in woodlands and dry forests of the northeast of Angola. Typical miombo genera such as *Brachystegia,*

Fig. 3.2 Western Congolian Forest/Savanna Mosaic near Camabatela, Cuanza-Norte. Tall grasses of *Hyparrhenia* and *Trachypogon* species, with a fire-tolerant *Hymenocardia acida* in left foreground

Fig. 3.3 Location of Ecoregions: **1** Guineo-Congolian Rain Forest

Fig. 3.4 Location of Ecoregions: **2** Western Congolian Forest/Savanna Mosaic

Julbernardia, Burkea and *Isoberlinia* increase in importance from north to south, but never dominate. The river valleys have tall gallery forests in which species of *Ceiba, Entandrophragma, Milicia, Musanga, Piptadeniastrum, Raphia* and *Xylopia* are found. The grasslands here comprise tall, dense *Andropogon, Hyparrhenia, Loudetia* and *Trachypogon* species, reaching 4 m height, which rapidly develop a high biomass of fuel between frequent, hot fires. The sharp boundary between forest and grassland marks the limit of fire penetration. Indeed, few tree species can survive the regular fires that sweep across these tall grasslands, and those that do survive are well adapted to resprouting. Fire-tolerant woody genera include *Annona, Erythrophleum, Hymenocardia, Piliostigma* and *Strychnos.*

Fig. 3.5 Location of Ecoregions: **3** Southern Congolian Forest/Savanna Mosaic

3.2 Afromontane Forest and Grassland Biome

Angola's most isolated and vulnerable biome comprises two ecoregions. The highest areas of the Angolan plateau and mountains have relatively small areas of Montane Grassland on the Huambo, Huíla, Benguela and Bié highlands, with very small remnants of Afromontane flora in the forests and shrublands along the Marginal Mountain Chain—specifically Mount Moco, Mount Namba and along the Chela Escarpment. They are important centres of biotic richness and endemism, although occupying only 1.1% of the country. Most larger mammals of the biome have been exterminated. The increasing pressures of land transformation for agriculture place the rich avifauna of forest and grassland habitats at risk of local extinction. The avifauna is notable for high levels of endemism and of narrow-range species.

Ecoregion 4. Afromontane Forests (*WWF 77, Barbosa 5, 6;* Figs. 3.6, 3.7 and 3.8). The Afromontane Forests of Angola are the most fragmented and isolated of all representatives of the Afromontane Biome in Africa. With a total area of less than 1000 ha across their entire range in Angola, they occur as small forest patches that are provided some shelter from fire in deep valleys and by rock outcrops. These highland sites receive from 800 to 1600 mm rainfall per annum, with a dry season from June to September. The shallow soils lie on Basement Complex and West Congo crystalline rocks. The weakly stratified forests have a broken canopy of up to 20 m height. Trees include Afromontane genera such as *Apodytes, Cassipourea, Erythroxylum, Halleria, Ilex, Maesa, Myrica, Nuxia, Pittosporum* and *Podocarpus*. The importance of these forests lies in the rich endemic and near-endemic bird species that occur as isolated, disjunct populations, over 2000 km from related species and subspecies elsewhere in the Afromontane forests of eastern, southern and western Africa.

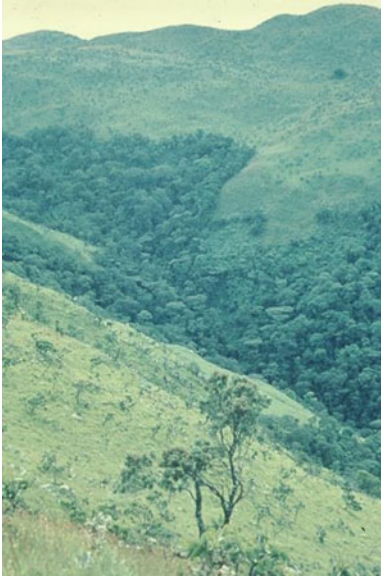

Fig. 3.6 The largest block of forest on Mount Moco, at 2200–2450 m, photographed in 1972. Note the short montane grasslands and shrublands of *Philippia* and *Protea*

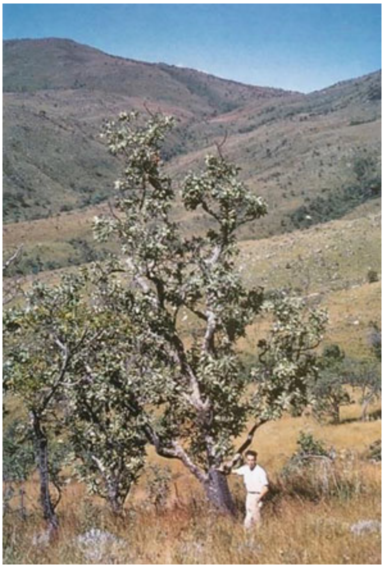

Fig. 3.7 *Protea welwitschii* in the grasslands of Mount Moco. Described as the tallest protea in the world in 1960. *Photo* J. S. Beard. *The proteas of tropical Africa.* Kangaroo Press

Ecoregion 5. Montane Grasslands (*WWF 77, Barbosa 32;* Figs. 3.7, 3.9 and 3.10). The Montane Grasslands of the Angolan Marginal Mountain Chain and Ancient Plateau (Diniz, 2006), extend across the highlands of Cuanza-Sul, Benguela, Huambo, Bié and Huíla. These grasslands await a detailed study of their botanical and faunistic diversity. Lying mostly at from 1500 to 1800 m, the rolling hills rise

Fig. 3.8 Location of Ecoregions: Black dots: **4** Afromontane Forest

to 2620 m on Mount Moco, the highest point in Angola. The underlying geology comprises crystalline rocks producing shallow leptosols, ferralsols and grading into arenosols in the east. These short grasslands cover approximately 1% of Angola. They are important contributors to the 'water towers' of central and southern Africa, feeding the Cuanza, Cubango, Cunene and upper tributaries of the Congo and Zambezi. The seasonally waterlogged soils result in the near absence of trees but an abundance of grass, forb and geophyte species, including many orchids. Better-drained areas have shrubs and low trees, often with the appearance of 'dwarf' miombo (2–5 m height) of *Brachystegia spiciformis, B. floribunda* and *Julbernardia paniculata* especially on shallow rocky soils over quartzites. Seasonally waterlogged sites have extensive areas dominated by 'underground forests' of geoxyles, locally known as *anharas do ongote* (Box 14.3).

3.3 Mesic Savanna Biome

Two savanna biomes are recognised in Africa, the Mesic/Dystrophic and the Arid/Eutrophic savannas, as outlined in Chap. 2 and detailed in Chaps. 14 and 15. Both savanna biomes comprise floras belonging to the most extensive regional centres of endemism in Africa, the Sudanian Centre (north of the Equator) and the Zambezian centre (mostly south of the Equator). The Zambezian flora dominates Angola, occupying over 90% of the country. The Mesic Savanna Biome, typical of the Zambezian centre of endemism, extends over 68% of Angola, predominantly on the interior plateau, above 1000 m, and on freely draining nutrient-poor and acidic (dystrophic) soils. Fire is the key driving force that maintains the mix of grasses and trees that constitute the woodlands, savannas, shrublands and grasslands of the biome. Fire

Fig. 3.9 Location of Ecoregions: Grey shading: **5** Montane Grasslands

Fig. 3.10 Moist Montane short grassland at 2000 m, Humpata, Huíla

prevents the transformation of savanna to closed-canopy forest even where mean annual rainfall is sufficient to support closed rain forest.

Characteristic of central Africa's mesic savannas are the miombo woodlands (known as *mato de panda* in Angola, based on the local name *mupanda* or *m'panda* for *Brachystegia spiciformis*). Miombo trees are distinctive in their shape, usually with relatively short, slender trunks with ascending branches forming a light, shallow and often flat crown. The mesic savannas occupy distinct landscapes. To the west of the central planalto and the Marginal Mountain Chain, the Angolan Escarpment Woodlands form a transition between the highlands and coastal lowlands, following the rolling hills and steep slopes of the Central Escarpment. The most extensive of Angola's 16 ecoregions is the Angolan Wet Miombo that covers the central Angolan plateau. To the southeast of the Wet Miombo is the Dry Miombo beyond which lie

Fig. 3.11 Grey shading: Location of Ecoregions: **6** Angolan Escarpment Savannas

the Zambezian *Baikiaea* Woodlands. A small area of the Central Zambezian Wet Miombo falls within eastern Moxico. Within the geographic embrace of miombo woodlands are two further ecoregions, recognised by Burgess et al. (2004) as falling within distinctive biomes (Flooded Grasslands and Dry Broadleaf Forests), but are treated here as ecoregions within the Mesic Savanna Biome. The vast plains of the Cameia/Bulozi catchment are dominated by Zambezian Flooded Grassland. Dry Broadleaf Forest is represented in Angola by a small extension of the Zambezian Evergreen Dry Forest in eastern Moxico. Collectively, these ecoregions constitute the Mesic Savanna Biome.

The grasslands and open woodlands of the Mesic Savanna Biome originally carried a diverse vertebrate fauna. Large mammal species (now decimated) which had their main distribution in the biome include Lichtenstein's Hartebeest, Roan Antelope, Giant Sable Antelope, Defassa Waterbuck and Puku. Bird species typical of the miombo habitat include Miombo Wren Warbler, Miombo Tit and Miombo Scrub Robin.

Ecoregion 6. Angolan Escarpment Savannas (*WWF 35; Barbosa 18B, 22;* Figs. 3.11, 3.14 and 3.15). South of the Cuanza River and along Angola's Central Escarpment, this narrow band of mixed savannas lies between the arid savannas of the coastal lowlands (Ecoregions 12, 13 and 14) and miombo savannas of the planalto (Ecoregion 7). This mosaic of tall grasslands and woodlands constitutes Angolan Escarpment Savannas which include Barbosa (1970) vegetation types 18B and 22. Barbosa's vegetation type 18B comprises fire-tolerant tall grass (1–3 m height) and short miombo (4–6 m height). Trees include *Brachystegia spiciformis, B. wangermeeana, B. boehmii, B. gossweileri, Burkea africana, Combretum collinum, Cussonia angolensis, Pterocarpus angolensis, Terminalia sericea* and *Uapaca benguelensis.* Grasses are mostly Andropogoneae. Vegetation type 22 lies below Type 18B, on the lower and drier slopes of the Escarpment and above the coastal plain.

Outliers of Guineo-Congolian Forest patches and thickets occur in moist valleys and ravines. Fire-tolerant short trees are scattered within an open savanna of tall grasses. The abundant yellow flowers of *Cochlospermum angolense* makes this tree the most conspicuous characteristic of this vegetation type, together with *Acacia sieberiana, Adansonia digitata, Albizia versicola, Burkea africana, Cussonia angolensis, Piliostigma thonningii, Pterocarpus rotundifolius, Sterculia quinqueloba* and *Terminalia sericea.* Grasses are mainly members of the Andropogoneae (Figs. 3.12, 3.13).

Ecoregion 7. Angolan Wet Miombo Woodlands (*WWF 36, 39; Barbosa 16, 17, 18A;* Figs. 3.12, 3.16 and 3.17). These woodlands, savannas and grasslands typically receive more than 1000 mm rainfall per year and lie at elevations between 900 and 1500 m. The deep, moist soils support a canopy height of 15–25 m. *Brachystegia spiciformis* (*mupanda*) occurs in varying densities and robustness throughout the miombo biome, with other species (*B. floribunda, B. glaberrima, B. longifolia, B. wangermeeana, B. gossweilerii*) at varying densities according to soil characteristics. *Julbernardia paniculata* (*mumue*) is also widespread across the Angolan miombo, together with *Burkea*, *Cryptosepalum, Guibourtia,* and *Pterocarpus.* The wet miombo is a mosaic of woodlands, savannas and grasslands, with a more or less continuous grass cover, always of C_4 grasses, even under a thin cover of the woodland canopy, where the grass biomass might be too sparse to support fire penetration in most seasons. Shrubs and short trees of this miombo include *Diplorhynchus condylocarpon, Baphia massaiensis* and *Copaifera baumiana.* On the edges of drainage-line grasslands (*mulolas, dambos*) species of *Monotes, Protea* and *Uapaca* occur as short trees. Grasses include species of *Andropogon, Digitaria, Elionurus, Eragrostis*, *Hyparrhenia, Loudetia, Monocymbium, Setaria* and with *Panicum* becoming prominent under woodland.

Fig. 3.12 Grey shading: Location of Ecoregions: **7** Angolan Wet Miombo

Fig. 3.13 Grey shading: Location of Ecoregions: **8** Angola Dry Miombo

Ecoregion 8. Angolan Dry Miombo Woodlands (*WWF 42; Barbosa 24;* Figs. 3.13 and 3.18). These woodlands occur on the deep, heavily leached Kalahari sands of southeast Angola, where the gently undulating landscape with broad valleys is drained by the crystal-clear waters of the Longa, Cuito and Cuando basins, descending from 1200 to 1000 m. The deciduous woodland canopies are from 8 to 15 m in height. The floral composition is less rich than the Wet Miombo, with *Brachystegia bakerana* and *Burkea africana* prominent, along with *Julbernardia paniculata, Guibourtia coleosperma, Dialium engleranum, Schinziophyton rautenenii* and *Cryptosepalum exfoliatum.* The catenal series of broad valleys (*mulolas*) between the rises (ancient dunes) are seasonally waterlogged and carry grasslands of *Loudetia, Trachypogon, Eragrostis* and *Monocymbium.* On the open margins of the catenas, communities of 'underground trees' (**geoxyles**) are found and include *Brachystegia russelliae, B. bakerana, Parinari capense* and *Chamaeclitandra henriquesiana.*

Ecoregion 9. Zambezian Baikiaea Woodlands (*WWF 64; Barbosa 15, 25;* Figs. 3.19, 3.22 and 3.23). These woodlands occur at from 1000 to 1300 m, on the leached and nutrient poor Kalahari sands which cover most of the gently undulating landscapes of southeast Angola. Annual rainfall in the Angolan distribution of this central African woodland is 600–750 mm, strongly seasonal, with up to eight dry months. Despite the low rainfall, the deeply rooted *Baikiaea plurijuga* trees (*muiumba* or *mucusse*) can form woodlands of up to 20 m height, usually on the crests of ancient dune fields. While *Baikiaea* is recognised as the indicator species of this ecoregion, it nowhere dominates the canopy nor the biomass. A mosaic of woodland, thicket, savanna and grassland species characterise the ecoregion. Tree genera include *Afzelia, Baikiaea, Burkea, Dialium, Erythrophleum, Guibourtia, Schinziophyton* and *Terminalia* in the woodlands, with dense thornless thickets of coppicing species of *Baphia, Bauhinia, Combretum, Croton, Pteleopsis, Pterocarpus* and *Strychnos* on areas with shallow

Fig. 3.14 Fire-tolerant *Cochlospermum angolense* trees typical of the tall grasslands covering the rolling the hills of the Angolan Escarpment Savannas

Fig. 3.15 Flower of *Cochlospermum angolense* *Photo* Ernst van Jaarsveld

Fig. 3.16 Miombo in the Quibala hills, Cuanza-Sul. *Photo* Antonio Martins

Fig. 3.17 Angolan Wet Miombo Woodland dominated by *Brachystegia* species in Luando Strict Nature Reserve, Malange. African Wild Dogs resting on the road

Fig. 3.18 Miombo woodland with dense grass and forb ground cover. North of Cuvango, Huíla Province. *Photo* Antonio Martins

sands overlying water-impermeable duricrusts. The transition from typical miombo to *Baikiaea* woodlands is at ca. 700 mm annual precipitation (Figs. 3.20, 3.21).

Ecoregion 10. Zambezian Evergreen Dry Forest (*WWF 33; Barbosa 4;* Figs. 3.20, 3.24 and 3.25). This evergreen forest type occurs as small patches within miombo communities over a broad area of eastern Angola (Lunda-Norte, Lunda-Sul, Bié, Cuando Cubango), reaching its greatest extent in the south-eastern border of Moxico with Zambia. This dry forest is best developed where it occurs on deep well-drained Kalahari arenosols with an adequate supply of water in their deeper soils during the dry season. This ecoregion lies at 1100–1200 m. Floristically, Zambezian elements dominate, with some Guineo-Congolian and Afromontane species. The evergreen leguminous tree *Cryptosepalum exfoliatum* dominates, together with *Brachystegia spiciformis, Daniellia alsteeniana, Entandrophragma delevoyi, Guibourtia coleosperma, Erythrophleum africanum, Ochna pulchra*, *Marquesia acuminata, M. macroura* and *Pteleopsis anisoptera.*

While *Cryptosepalum* reaches up to 25 m in height, most of the forest communities are shorter, at 10–15 m. Due to the typically closed canopy the herbaceous layer

Fig. 3.19 Location of Ecoregions: **9** Zambezian *Baikiaea* Woodlands

Fig. 3.20 Location of Ecoregions: **10** Zambezian Evergreen Dry Forest

is sparse and often carries a bed of mosses and liverworts. Lianas and epiphytes, usually uncommon in miombo woodlands, are frequent. Epiphytic pteridophytes of the genera *Polypodium, Platycerium* and *Lycopodium* are abundant in these forests. *Cryptosepalum exfoliatum* is fire-intolerant, although the dense tree canopy, shaded microclimate and sparse forest ground cover normally prevents the entry of fires. However, if subjected to frequent fires, or to shifting cultivation, the forest converts to an open, 'derived' savanna known as *tchirhuto* in Lunda-Norte and *chipya* in Zambia. This stunted savanna/thicket includes most of the fire-tolerant miombo species plus *Aframomum biauriculatum*, *Pteridium aquilinum* and climbers such as *Smilax kraussiana*. It is the least well-studied ecoregion of Angola.

Fig. 3.21 Location of Ecoregions: **11** Zambezian Flooded Grasslands

Fig. 3.22 *Baikiaea* woodland in Bicuar National Park

Ecoregion 11. Zambezian Flooded Grasslands (*WWF 76; Barbosa 31;* Figs. 3.21, 3.26, 3.27, 3.28 and 3.29). The major sources of the waters of the Zambezi River lie in the 'water towers' of the Angolan plateau. A key catchment flows via the Bulozi Floodplain, perhaps the largest ephemeral wetland in Africa (Mendelsohn & Weber, 2015). Half of the floodplain is found in Moxico, the rest in neighbouring Zambia. This vast system of seasonal wetlands, grasslands and fringing miombo savannas and woodlands, and narrow gallery forests, has received very little attention from researchers, despite the teeming game populations that occurred in Cameia

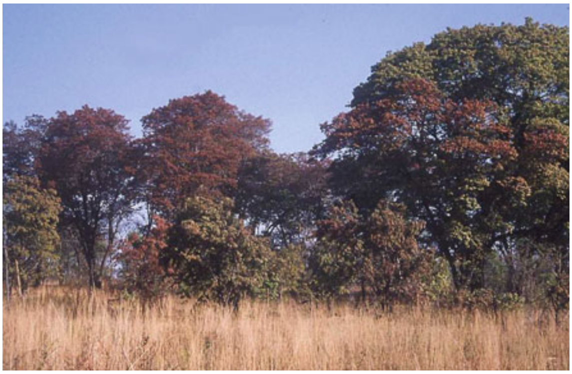

Fig. 3.23 *Guibourtia* community within *Baikiaea* woodland in southern Cuando Cubango. Both woodlands are on deep Kalahari sand

Fig. 3.24 *Cryptosepalum/Marquesia* Dry Forest on deep Kalahari sands, Lunda-Norte

Fig. 3.25 The extensive plains known as *chanas da borracha* of Lunda-Norte*,* with sparse grass cover but abundant geoxyles appearing following fire

National Park during colonial times. Barbosa (1970) devotes less than one page to its vegetation. The floodplains lie at 1000–1100 m, and stretch over 800 km from north to south and 200 km west to east at their widest points. They cover Kalahari sands, with seasonally waterlogged gleysol clays, often with hardpan layers

Fig. 3.26 Floodplain of the Luele River, Lunda-Norte

Fig. 3.27 Lechwe on an old termitarium, Luando floodplain, Luando Strict Nature Reserve, Malange

beneath the surface, making tree growth impossible over much of the area. Fires sweep across the dry grasslands almost every year, further suppressing woody plant growth, other than of the 'underground trees'—the geoxyles. The raised surfaces of termite mounds and fossil sand dunes provide a less challenging substrate for typical miombo trees and shrubs. The grasslands carry a diversity of grass species, dominated by *Loudetia simplex*, along with species of *Acroceras, Arundinella, Bothriochloa, Chloris, Cynodon, Echinochloa, Imperata, Leersia, Oryza, Setaria, Tristachya, Vetiveria* and *Vossia.*

3.4 Arid Savanna Biome

The arid savannas of Angola cover 12.9% of the country and are characterised by low rainfall (less than 650 mm per annum) and richer (eutrophic) soils than the leached, nutrient-poor (dystrophic) ferralsols and arenosols of mesic savannas. The arid savannas of southwestern Africa include large areas of typically dystrophic

Fig. 3.28 Aerial view across the Bulozi Floodplain. *Photo* John Mendelsohn

Fig. 3.29 Marginal woodland and floodplain grassland, Bulozi Floodplain, Moxico. *Photo* John Mendelsohn

Kalahari sand, south of Angola, where they are ephemerally eutrophic when pulses of nutrients are released during rainfall events. The arid savannas typically lie below 1000 m, while the mesic savannas generally lie above 1000 m. In the southwest of Angola, Mopane Woodland occupies richer soils at the base of the Chela Escarpment and along the Cunene River. Here the Zambezian flora mixes with representatives of the **Karoo-Namib flora** within the Namib Savanna Woodland ecoregion that extends northwards along the coast towards Benguela. This arid coastal climate continues under the influence of the Benguela Current as a mosaic of grasslands, savannas, thickets and dry forests as the Coastal Arid Savanna ecoregion to beyond the Congo River, and as a narrow coastal margin in Cabinda.

The arid savannas of Africa typically support high biomasses of herbivores, mostly herding grazers and mixed feeders. In earlier times, large populations of many arid savanna mammal species were recorded in the south and southwest of Angola, especially Common Wildebeest, Cape Buffalo, Common Eland, Greater Kudu, Plains

Zebra, Black Rhino and Savanna Elephant. Bird species typical of the biome include White-tailed Shrike, Monteiro's Hornbill, Benguela Long-tailed Starling and Pririt Batis.

Ecoregion 12. Angolan Mopane Woodlands (*WWF 34, Barbosa 20, 21;* Figs. 3.30 and 3.33). The leguminous tree *Colophospermum mopane* (*mutiati*) occupies much of the lower Cunene valley forming woodlands, savannas and shrublands. Mostly confined to the hot dry valleys of the main drainage basins of southern Africa (Cunene, Zambezi, Luangwa, Limpopo) the species is typically found on heavy clay soils and stony hills in arid savannas receiving less than 650 mm rainfall per annum. Although often found as a single dominant species in woodlands, it also forms mixed communities with species of *Acacia, Adansonia, Albizia, Boscia, Combretum, Commiphora, Sclerocarya* and *Terminalia.* Together with grasses of the genera *Anthephora, Aristida, Cenchrus, Eragrostis* and *Enneapogon*, it provides rich herbage for mammal browsers, grazers and mixed feeders (Figs. 3.31 and 3.32).

Ecoregion 13. Namib Savanna Woodlands (*WWF 104; Barbosa 27;* Figs. 3.31 and 3.34). This ecoregion occupies a narrow belt of coastal lowlands from the Cunene River northwards to Sumbe, wedged between the Angolan Namib Desert and Angolan Mopane Woodland ecoregions. The region has a mix of rolling stony hills and sandy plains, between sea level and 500 m. Rainfall increases from south to north, from 100 to 400 mm. Short trees and shrubs of the genera *Acacia, Balanites, Boscia, Catophractes, Combretum, Maerua, Rhigosum, Sterculia* and *Terminalia* form open savanna, with extensive grasslands of *Aristida, Cenchrus, Enneapogon, Schmidtia, Stipagrostis, Tricholaena* and *Urochloa* species. Succulent herbs, shrubs and trees are common.

Ecoregion 14. Coastal Arid Savannas (*WWF 35; Barbosa 3, 7, 10, 11 and 23;* Figs. 3.32, 3.35 and 3.36). The arid coastal belt from Sumbe northwards to the

Fig. 3.30 Location of Ecoregions: **12** Angolan Mopane Woodlands

Fig. 3.31 Location of Ecoregions: **13** Namib Savanna Woodlands

Congo River comprises marine sediments of sands, marls and limestone, lying from sea-level to 500 m. The influence of the Benguela Current accounts for the low rainfall, mainly below 500 mm per year, across the ecoregion, as explained in Chap. 5. A limited group of tree species, including *Acacia welwitschii, Adansonia digitata, Euphorbia conspicua* and *Sterculia setigera*, plus grasses of the genera *Eragrostis, Digitaria, Heteropogon, Schizachyrium* and *Setaria* characterise the ecoregion's flora. The vegetation is nevertheless very diverse, including extensive monospecific grasslands of *Setaria welwitschii*, open mixed clump savannas, dense low thickets, mixed woodlands, dry forests and gallery forests. The dry deciduous forests of ravines and narrow valleys that skirt the first step of the escarpment have a mix of Zambezian and Guineo-Congolian tree species, forming a closed canopy with little if any understorey strata.

3.5 Namib Desert Biome

A narrow tongue of hyper-arid desert stretches from the Cunene River to the Carunjamba River near Lucira, with a mix of Karoo-Namib and Zambezian floristic elements. Vegetation-less dunes occur along the coast, with gravel plains occupied by dwarf shrublands to the interior, succeeded by ephemeral grasslands on the sandy plains of intermontane basins. The rocky hills to the east have mixed open woodlands and a light cover of grasslands. This biome occupies ca. 0.4% of the country. Despite the challenges of the desert environment, a diverse and specialised fauna (Chap. 11) is to be found in Iona National Park, today under severe human-mediated threat.

Mammals found in the biome include Cape Fox, Meerkat, Aardwolf, Springbok, Kirk's Dik-dik, Gemsbok and Hartmann's Mountain Zebra. Bird species typical of

Fig. 3.32 Location of Ecoregions: **14** Coastal Arid Savannas

Fig. 3.33 Mopane *Colophospermum mopane* woodland in Mupa National Park. *Photo* Francisco Maiato Gonçalves

Fig. 3.34 Mixed commiphora and acacia savanna at the interface between the Namib Savanna Woodlands and Angolan Namib Desert ecoregions, Iona National Park, Namibe. *Photo* Ernst van Jaarsveld

Fig. 3.35 Tall mono-specific *Setaria welwitschii* grasslands on the deep vertic clays of Quiçama inland of Cabo de São Braz

Fig. 3.36 Clump savanna of *Adansonia digitata* and *Euphorbia conspicua* with *Schizachyrium sanguineum, Heteropogon contortus* and *Digitaria milanjiana* grassland, on the sand plateau of Quiçama

the desert include Ostrich, Ruppell's Korhaan, Ludwig's Korhaan and Burchell's Courser.

Ecoregion 15. Angolan Namib Desert (*WWF 98; Barbosa 28 and 29;* Figs. 3.37, 3.38 and 3.39). The Angolan sector of the Namib Desert extends from the Cunene River to the Carunjamba River, forming a narrow (20–80 km) wedge between the Atlantic Ocean and the coastal plains which skirt the Angolan Escarpment. Characterised as a hyper-arid desert, the ecoregion receives less than 150 mm rainfall per annum, with much of the area receiving half of this figure. Mobile dunes and hard calcrete, gypsum and gravel plains lie between the sea and intermittent sandy plains and rocky hills of the interior. The dunes have little if any vegetation. Inland, succulent shrubs, thorny bushes and low trees of *Acacia, Commiphora, Euphorbia, Rhigozum, Sesamothamnus* and *Sterculia* are scattered across a matrix of sparse, short grasses of *Stipagrostis* species. Over much of the desert, the iconic gymnosperm *Welwitschia mirabilis* is common. Despite its aridity, the desert is home to a rich diversity of

Fig. 3.37 Location of Ecoregion 15. Angolan Namib Desert

Fig. 3.38 *Welwitschia mirabilis* on a gravel plain with dead annual grasses and herbs

vertebrate and invertebrate species, these demonstrating complex adaptations to life in an almost waterless environment.

3.6 Mangrove Biome

The mangrove communities of Africa are given biome status by Burgess et al. (2004), as part of the global network of tropical mangroves. The limited area occupied by mangroves and the challenges of the environment account for the very low vertebrate diversity found in the biome, which however includes three crocodile species in

Fig. 3.39 *Euphorbia* and *Commiphora* at the base of a gneiss outcrop, with sparse arid grasslands during an extended dry period. Iona National Park

Cabinda—West African Slender-snouted Crocodile, African Dwarf Crocodile and Nile Crocodile.

Ecoregion 16. Central African Mangroves (*WWF 111; Barbosa 14A;* Figs. 3.40, 3.41 and 3.42). At the mouths of the Congo, Cuanza, Longa and Cuvo rivers, small communities of Central African Mangroves are found. The mangroves form tall (20 m height) forests of *Rhizophora* species along the margins of the major river estuaries, flanked by shorter mangrove communities on mudbanks that occur in embayments and lagoons, where species of *Avicennia* form dense short woodlands. In terms of their flowering plant diversity, mangroves are extremely species poor, with only four mangrove tree species and two seagrass species recorded in the ecoregion. The marine fauna of the ecoregion is rich, as is the avifauna that uses the sandbanks and mudflats of the estuaries and embayments of the ecoregion.

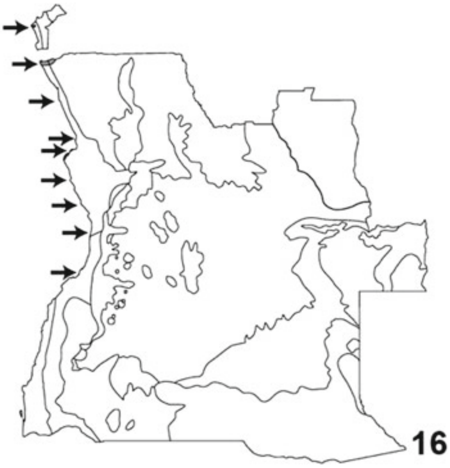

Fig. 3.40 Location of Ecoregion 16: Central African Mangroves. Arrows indicate location of Mangrove communities at mouths of rivers

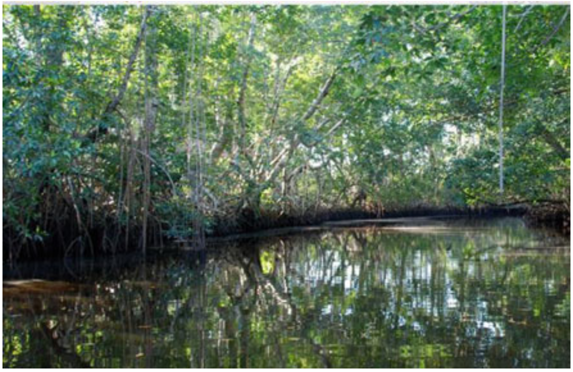

Fig. 3.41 Mangroves at the mouth of the Congo River, Zaire Province. *Photo* Kellie Pendoley

Fig. 3.42 Mangroves at the mouth of the Congo River, Zaire Province. *Photo* Kellie Pendoley

3.7 Angolan Escarpment Zone

Inland of the coastal plain and following the Angolan Escarpment between northern Cabinda and the Cunene River is a complex mix of biome elements, vegetation structure and floristic affinities (Zambezian, Guineo-Congolian and Afromontane). The Angolan Escarpment Zone (AEZ) constitutes a physiographic **Zone** rather than a biogeographic unit. It comprises a mosaic of grasslands, savannas, woodlands, thickets and forests. The Zone includes many endemic plant and animal species that have evolved along the steep gradients of its landscapes. On the Maiombe and Northern Escarpments, Guineo-Congolian Rain Forests (Ecoregion 1) and tallgrass savannas of the Western Congolian Forest/Savanna Mosaic (Ecoregion 2) dominate, while the Angolan Escarpment Savannas (Ecoregion 6, below) occur along the Central Escarpment, comprising mixed grasslands and woodlands of Mesic Savanna elements. The biogeographical and ecological importance of the Angolan Escarpment is discussed in detail in Chap. 18.

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Part II
Determinants of Pattern: Conditions, Resources and Disturbance

Africa, with its highly diverse landscape and intermingled floras, offers an excellent opportunity to disentangle the effects of environmental variables such as topographical complexity, climatic stability, and climatic extremes, from biotic variables such as fire frequency and herbivory.

Linder (2014)

Context: The Driving Forces of Landscape and Ecosystem Patterns

Angola lies between the Equator and the Tropic of Capricorn. It has 1650 km of Atlantic Ocean coastline and extends 1230 km into the interior of central Africa. Within its 1.246 million km^2 territory, it possesses an extraordinary diversity of landscapes, climates and biota. The country's biological richness results from the wide mix of conditions, resources and disturbance regimes that interact at the level of individual organisms, where selection and survival factors operate. Individuals of a particular species mostly occur within breeding communities, with distinct intraspecific or interspecific relationships and interdependencies with other organisms and with their physical environment. Organisms, species, communities and the physical environment together form ecosystems, which are the basic units of ecoregions and biomes.

Change at diverse temporal and spatial scales is a fundamental feature of Africa's ecosystems where habitat patterns might be seemingly monotonous, as in the miombo of the planalto, or ever-changing, as in the fine-scale pattern of vegetation types along the Escarpment. The heterogeneity of Angola's landscapes is reflected in its biodiversity. The interactions between species and environment, in a cycle of constant flux, are the basis for ecosystem resilience. Droughts, floods, fires and herbivory are natural disturbance factors that play essential roles in the regenerative processes within ecosystems, determining the life forms of species and the physiognomy of habitats. As background to describing Angola's floral, vegetation and faunal structure and interactions, one must first examine the key drivers of biotic functions and patterns and define key concepts relating to landscapes, climate, soils, fire and herbivory.

Three components of the environment need to be kept in mind as the drivers of form and function are discussed. The terminology used to describe features of ecosystem dynamics needs definition, and here Frost et al. (1986) are followed.

- **Conditions**: The physico-chemical characteristics of the environment such as temperature and humidity influence the life of organisms, but which cannot be consumed.
- **Resources**: The energy and materials are consumed by organisms and for which they compete with other organisms. Plants, for example, use solar energy, light, carbon dioxide, water and mineral nutrients in the process of photosynthesis, which creates the carbohydrates consumed by herbivores. Herbivores provide food for carnivores, which in turn provide food for decomposer organisms which mineralise organic material, releasing nutrients for uptake by plants and thus continuing the life cycle of ecosystems.
- **Disturbance**: Operating at the ecosystem level, disturbances are often caused by episodic events, such as floods, severe storms, prolonged droughts, severe frosts, excessive herbivory, intense fires or human activities such as deforestation or cultivation. At finer scales, disturbances might operate via ants eating or dispersing seeds, termites building nutrient hotspots, moles burrowing though the soil or elephants breaking down trees. Disturbance might result from one, but more often from a combination or sequence, of several events. In some cases, the events might be of an extreme nature, such as cyclones, floods or fires. In many cases, however, it is the combination (contingency) of relatively small events that are responsible for triggering significant ecosystem processes. Disturbances create opportunities for new individuals of the same or different species to become established within a community. A distinction is made between natural disturbance factors and those caused by human (**anthropogenic**) interventions such as agriculture, land use change, urbanisation and domestic livestock. Unless specifically stated, in this book the term is used for natural disturbances. It is recognised that increasingly, disturbances are the result of human activities. Examples of human–environmental interactions (often with negative outcomes) are provided in boxes.

In addition to the concepts of conditions, resources and disturbance, four further terms relating to ecosystem dynamics must be highlighted.

- **Stress** is used in a physiological sense to describe a constraining environmental influence that restricts the productivity and efficiency of an individual and, by extension, an ecosystem. Such stresses usually operate when an environmental variable, such as temperature, light, water, nutrients or defoliation, deviates from its normal range of values in the system. Stress is seldom accompanied by mortality.
- **Stability** refers to change, of the lack of change, in the variables that define the state of the system. The state of the system is described by properties termed its **state variables**, which include species composition, relative abundances, biomass and productivity. State variables change little in response to outside pressures (stress or disturbance) such as drought, fire and herbivory. If disturbed, state variables return rapidly to their original values. A stable system therefore shows little variability

through time in its state variables. Compositional stability (species composition and abundance) and functional stability (constancy of primary production and primary consumption) can vary independently as stress and disturbance factors fluctuate.

- A **perturbation** is a disturbance that can cause the destabilisation of a system and a change in the state variables.
- **Resilience** is the ability of a system to absorb disturbance and return to its original state following a perturbation, while maintaining its self-organised structure, function and feedback processes (its alternative stable state). **Elasticity** is the speed of the return to the original state.

It must be emphasised that the biomes, ecosystems and constituent biota of Angola are the products of tens of millions of years of evolutionary change. Change is a continual process, happening at widely differing spatial and temporal scales. Ecological studies keep issues of scale in constant focus, looking both at the deep history of evolutionary processes and also at the daily rhythms and interactions of species with their environment and as individuals with one another. Ecologists survey the details of the structure and dynamics of local ecosystems as well as the long history of global patterns of geology, climate and biogeography. Ecology is an integrative science.

Part ll examines the key drivers of the patterns of plant and animal distribution and abundance in Angola, providing answers to such questions as:

- *How do topography, climate and soils interact in determining the patterns of Angola's vegetation?*
- *Why has Angola both rain forest and desert ecosystems?*
- *What accounts for the presence of both forest and savanna under similar rainfall regimes?*
- *How can fire be both a destructive force and at the same time be a primary factor in the maintenance of savanna structure and function?*
- *What roles do herbivores play in shaping the structure of ecosystems?*

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Chapter 4
Landscapes: Geology, Geomorphology and Hydrology

Key Concepts and Questions: This Chapter Explains

- *What accounts for the great diversity in age, structure and properties of the rocks on which the country is built.*
- *What the main geological and rock groups are, and how they are distributed across Angola.*
- *What the country's main landscapes are and where they can be found.*
- *How the landscapes of Angola have been shaped by geological events, erosion by rivers, and the redistribution of loose sediments by wind.*

Context: Angola's Ancient Gondwana Origins

> You have to understand the past to understand the present. (Carl Sagan, 1980)

The biodiversity of Angola and the ecological processes that determine the patterns of distribution and the abundance of its biota have evolved over many hundreds of millions of years, most especially since the formation of the supercontinent **Gondwana**. Familiarity with the deep history of Africa's geological evolution, even at a general level, helps in the understanding of current features and phenomena. The following outline focuses on some key events of the past 550 million years, and defines relevant geological and geomorphological terminology. A summary of geological history and major timelines (Eons, Eras, Periods and Epochs, and the first appearance of major biological groups) is presented in Fig. 4.1. The most ancient rocks in Angola belong to the Precambrian Eon, predating the Phanerozoic.

Angola's landscapes are underpinned by dynamic geological processes which originate within the Earth's **lithosphere**—the topmost layers of the Earth—the **crust** and the uppermost **mantle**. The lithosphere is made up of igneous, sedimentary and metamorphic rocks.

- **Igneous** rocks, formed deep within the crust, include granites and gabbros, which today can be found in many parts of Angola where they have been exposed by erosion. In Angola, they date from 2700 Ma (**Ma = million years ago**).

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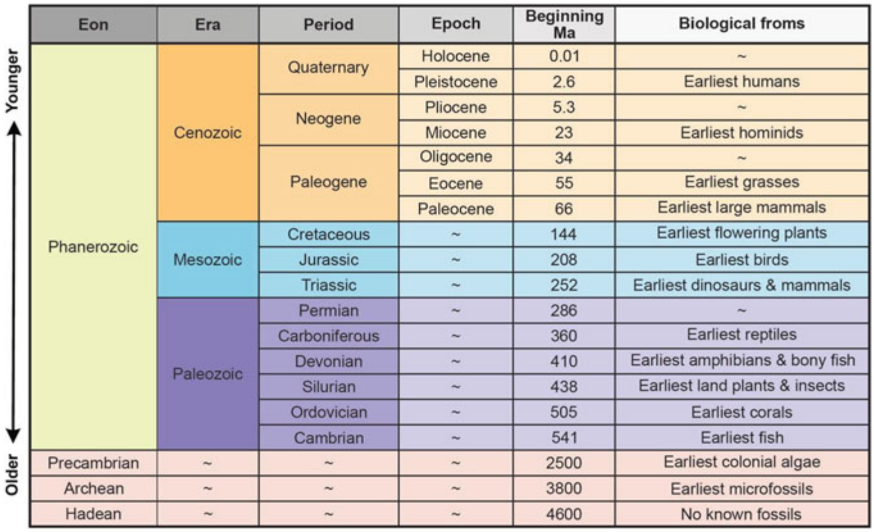

Eon	Era	Period	Epoch	Beginning Ma	Biological froms
Phanerozoic	Cenozoic	Quaternary	Holocene	0.01	~
			Pleistocene	2.6	Earliest humans
		Neogene	Pliocene	5.3	~
			Miocene	23	Earliest hominids
		Paleogene	Oligocene	34	~
			Eocene	55	Earliest grasses
			Paleocene	66	Earliest large mammals
	Mesozoic	Cretaceous	~	144	Earliest flowering plants
		Jurassic	~	208	Earliest birds
		Triassic	~	252	Earliest dinosaurs & mammals
	Paleozoic	Permian	~	286	~
		Carboniferous	~	360	Earliest reptiles
		Devonian	~	410	Earliest amphibians & bony fish
		Silurian	~	438	Earliest land plants & insects
		Ordovician	~	505	Earliest corals
		Cambrian	~	541	Earliest fish
Precambrian	~	~	~	2500	Earliest colonial algae
Archean	~	~	~	3800	Earliest microfossils
Hadean	~	~	~	4600	No known fossils

Fig. 4.1 The geological timescale, referencing the first appearance of major biological groups. Ma (million years ago) indicates the age of first appearance of major plant and animal groups

- **Sedimentary** rocks are formed where eroded materials—gravel, sand and mud—accumulate on the floor of basins (depressions, lakes, oceans) and become cemented over time into conglomerates, sandstones and shales.
- **Metamorphic** rocks are the product of the transformation by heat and pressure of igneous or sedimentary rocks. For example, under such conditions, limestone transforms into marble, shale into schist, granite into gneiss and sandstone into quartzite.

The global lithosphere is divided into seven major **tectonic plates**—vast slabs of solid rock, made up of cratons, mobile belts and basins. Globally, the plates have been displaced from their original positions over periods of hundreds of millions of years by the process of **plate tectonics**. The plates typically conform to each major continent and surrounding oceans. Within the **African Plate**, extensive and stable foundations of the continental lithosphere are known as **cratons**—such as the **Congo Craton** which underpins most of Angola, also known as the **Angolan Shield**. Precambrian Basement Complex rock exposures—such as the granites that are visible over much of Angola—are common and prominent (Fig. 4.2).

Some 550 million years ago, the supercontinent Gondwana was formed through the accretion (joining together) of several ancient plates and cratons. Between 180 and 140 Ma Gondwana started to break up.

- First, around 180 Ma, East Gondwana (Antarctica, India, Australia, Madagascar) split from West Gondwana (Africa and South America).
- By 130 Ma Africa started to break from South America with the formation of the Atlantic Ocean, which was fully established by the late Cretaceous (80 Ma).

Fig. 4.2 Large granite outcrops are a prominent feature of western Angola's landscapes, such as these bornhardt domes in Cuanza-Sul. *Photo* John Mendelsohn

- Much later, by 34 Ma, the separation of Australia from Antarctica and the formation of the Drake passage was completed, events of great significance for Angola, as they resulted in the start of the circumpolar oceanic circulation. During this period, the icing of Antarctica and the aridification of southern Africa was firmly established.
- Around 14 Ma, the Panama Isthmus formed, joining North and South America, and blocking the oceanic circulation from the central Pacific into the Atlantic.
- Between 10 and 7 Ma, the Benguela Current developed along the southwest African coast, bringing cold water northwards and triggering the production of fog along the Namib margin. The patterns of oceans and continents as we know them today had been established.

The tectonic plates are still in motion, moving Africa into Eurasia, and India into Asia, with frequent earthquakes signaling the process.

The Cenozoic Era (66 Ma to present) saw the land surfaces of Africa established, the results of which help in understanding the evolution of Angola's terrestrial ecosystems. Since the start of the breakup of Gondwana the surfaces of the African continent were intermittently uplifted and subsequently eroded downwards to form a mosaic of extensive denudation plains, known as **planation surfaces** and called **peneplains** or **pediplains**. (These generic terms are used interchangeably by geomorphologists. Here preference is given to the Angolan custom of using peneplain). The oldest and most extensive of these are known as the **African** and **Post-African** surfaces. The products of many millions of years of downward (peneplanation) or backward (pediplanation) erosion, these surfaces formed between 85 and 42 Ma (African), 19–15 Ma (Post-African I) and 3–1 Ma (Post-African II), according to the studies of geomorphologists (Knight & Grab, 2018; Partridge & Maud, 1987). Remnants of these surfaces are visible today, most prominently as the **Central African Plateau** which dominates the Angolan planalto and the extensive peneplains of the subcontinent. Many of these surfaces carry sedimentary layers such as in the **Kalahari Basin**, which contains thick layers of windblown and waterborne sediments, and in which

Fig. 4.3 The Angolan Escarpment reaches its most dramatic expression at the Serra da Chela. At 2300 m above sea level, the plateau above the quartzitic scarp face is a remnant of the African Planation Surface

laterite, silcrete and calcrete have formed during long periods of relative tectonic stability and gradually changing climates.

With the splitting of Africa from the other continents, **escarpments** were formed along the coastlines of southern Africa by a process of shoulder uplift along the rifted continental margin and regional elevation of the subcontinent. The face of the **Great Escarpment** of Southern Africa gradually retreated in parallel with the coast. The pace and distance of retreat has varied from place to place, influenced by the prevailing rainfall climate. The escarpments of southern Africa are most prominent in Angola, and along the east coast of South Africa (Fig. 4.3).

Southern Africa experienced a geomorphologically stable period during most of the Cenozoic (from 66 Ma to the present) with only minor and locally enhanced levels of uplift, subsidence and erosion (Fig. 4.4). These erosional periods are believed to be related to **uplift** of the subcontinent. The driving tectonic forces of uplift are known as **mantle swells**. Two of these—the **Mayombe** and **Bié** swells—uplifted the existing Angolan landscape by about 500 m. The Bié swell accounts for the highlands of Angola, which today serve as the ‘water towers’ of southern Africa (Sect. 4.3). Two **subsiding** internal draining (**endorheic**) basins—the older **Congo Basin** and the more recent **Kalahari Basin**—developed and were filled by sediments throughout the Cenozoic. The uppermost and most recently deposited sediments are the Kalahari sands. The **Kalahari sands**, mostly less than 100 m deep but up to 500 m deep, were formed during the past 5 Ma through the deposition of sediments from the water and wind erosion of the Post-African Surface. They cover over 2.5 million km^2—the largest continuous body of sand on Earth (Fig. 4.5).

River incision was accelerated from 34 Ma by a drop in global sea-level of 70 m consequent to the formation of the Antarctic ice sheet, the circum-polar circulation, and the regional increase in elevation of southern Africa on newly forming swells. More recently, erosion cycles of landscapes, following uplift in the **Pliocene** (5.3–2.6 Ma) of from 100 m in the west to 900 m in the east of southern Africa triggered the rejuvenation of river systems. The planation surfaces of this period have been called ‘**Post-African**’ (i.e. formed after the ‘African’ surfaces) by many researchers following the terminology of King (1962). Erosion stripped away much of the African

Fig. 4.4 Map of the Africa's major mantle swells, rifts, escarpments and sedimentary basins. Note the Congo and Kalahari basins and the Mayombe, Bié and Namibian swells. Redrawn and simplified from Knight and Grab (2016) *Quaternary environmental change in southern Africa: physical and human dimensions.* Cambridge University Press, Cambridge

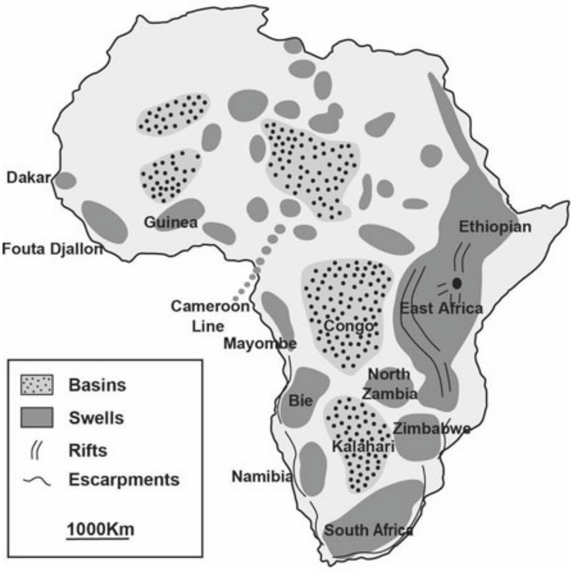

Fig. 4.5 The sluggish Cuchi River feeds the Cubango drainage of the gently undulating landscape (at 1200–1300 m above sea level) of the Post-African Planation Surface, Cuando Cubango. *Photo* Antonio Martins

Surface, but many remnants are preserved to this day where they are capped by resistant **duricrusts**—laterites, silcretes and calcretes (Knight & Grab, 2016).

The mosaic of African and Post-African planation surfaces, with both ancient and more recent tectonic, erosional and depositional sequences, climatic interactions and feedbacks, have created a confusing imprint that only the trained geomorphologist can readily interpret. But these processes provide explanations for many questions of biogeographic and ecological importance, such as river capture, the creation of the Angolan Escarpment, the Kalahari Basin, the deep gorges of the Cunene River and the extensive floodplains of the Zambezi catchment.

Against this brief overview of Africa's landscape evolution, the geology, geomorphology and hydrology of Angola will be described before examining more detailed facets of the soil substrate on which plants grow and animals live.

4.1 Geology: A Brief History of the Earth and of Angola

A necessary first step in learning about the geology of a country such as Angola, and of the planet's evolutionary history, is to become familiar with certain timelines and associated geological layers—the succession of rock formations known as its **stratigraphy**. This is best understood through reference to a geological map of Angola, and the sequence of geological layers laid down during the long history of the Earth (Fig. 4.1). The geological map of Angola (Fig. 4.6) emphasises the four main geological **Eras** of planet Earth—Precambrian (541 Ma and older)—where **Ma = million years ago**, Paleozoic (541–252 Ma), Mesozoic (252–66 Ma) and Cenozoic (66 Ma and younger). A brief synopsis of these Eras, and the geological **Periods** and **Epochs** within them, will provide orientation for the many references to geological terms that appear in this volume.

Precambrian Era

- The **Precambrian Era** is the earliest geological era, dating from the birth of the planet approximately 4600 million years ago to 541 Ma. Very few fossils are known from the Precambrian, of which the first recognizable forms of life—**stromatolites**—date from 3500 Ma. Later examples (1250 Ma) of these fossilised layers of cyanobacteria can be seen at Humpata in Huíla.
- The extended spine of Angola's western escarpment, highlands and plateaus is formed by Precambrian **crystalline rocks** of the Basement Complex and the West Congo System, in addition to scattered outcrops of igneous rocks such as granites, and volcanic rocks such as dolerites. **The Basement Complex** comprises a **lower** series of granites, gneisses, and migmatites and an **upper** series of metamorphosed sediments including schists and quartzites. The terms 'lower' and 'upper' refer to older and younger geological strata respectively. Lying above the Basement Complex is the **West Congo System**, a mobile belt composed of metamorphosed sedimentary rocks of the upper Precambrian. These include limestones, schists, slates and quartzites.

Paleozoic Era

- The Precambrian Era was followed by the **Paleozoic Era** (541–252 Ma). There are few examples in Angola for most of the Paleozoic Era. However, the **Carboniferous Period** ('Age of Amphibians') left its footprint in the glacial valleys and tillites in southwest Angola (Figs. 4.7 and 4.8) and in the Baixa de Cassange. Where they exist in Angola, most of the Paleozoic formations are overlain by

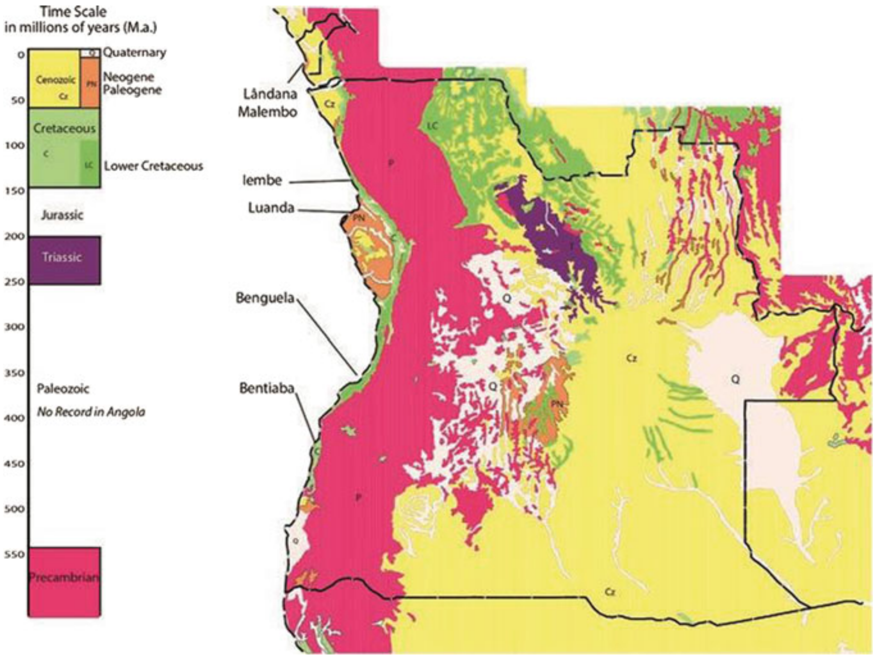

Fig. 4.6 The major geological formations of Angola, with a stratigraphic log indicating the geological periods in which they were formed. Note the importance of the Precambian crystalline rocks of the western spine of Angola, and the extensive cover of Cenozoic Kalahari sands on the eastern half of the country. From Mateus et al. (2019) *Biodiversity of Angola. Science & Conservation: a Modern Synthesis*. Springer Nature, pp 53–78

Kalahari sands. The Paleozoic Era ended with the **Permian Period**, at the conclusion of which there was a mass extinction of 95% of Earth's animal and plant species.

Mesozoic Era

- The **Mesozoic Era** (the 'Age of Reptiles', between 251 and 66 Ma), was introduced by the **Triassic Period.** Dinosaurs were dominant throughout the Mesozoic, and the first birds appeared during the Triassic. Evidence of the Triassic is provided by the continental deposits of sandstones, limestones and shales of the **Karoo Supergroup** that cover the depression of the **Baixa de Cassange**, together with Cretaceous marls, conglomerates and shales.
- Following the Triassic was the Jurassic Period—so far not known in Angola—which was in turn followed by the **Cretaceous** Period (144–66 Ma). The Cretaceous not only saw the appearance of the first **flowering plants**, but also the end of the dinosaurs at its conclusion, which was marked by mass extinctions at 66 Ma. Cretaceous formations in Angola are found as continental fluvial sediments in the interior and marine sediments along its coastal margin, and as crater-fills in extinct Cretaceous volcanoes.

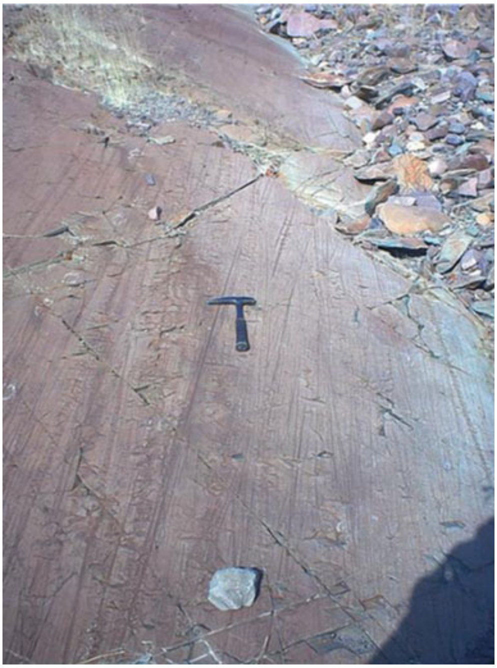

Fig. 4.7 Glacial **striations** (scratches) on the bed of the lower Cunene at Otjiborombonga. The scratches are cut into bedrock by the abrasion of hard rocks held in the base and margins of glaciers during the Carboniferous (300 Ma) as they cut a deep valley into what is now the Cunene Gorge

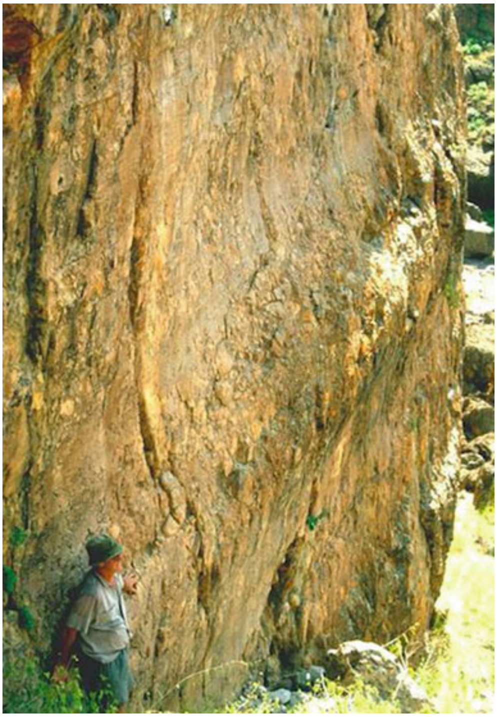

Fig. 4.8 Wall cut by glaciers on conglomerates of the Cunene valley. *Photos* Eckhart Freyer

Cenozoic Era

- The last, (and present) Era is the **Cenozoic**—the 'Age of Mammals'. Geologists recognise three **Periods** and seven **epochs** within the Cenozoic. The terms **Paleogene** and **Neogene** Periods include the five epochs from 66 to 2.6 Ma. The **Miocene** Epoch (from 23–5.3 Ma) witnessed many major climatic, ecological and evolutionary events of great significance to Africa, as outlined in Box 4.1. The last two epochs (**Pleistocene** and **Holocene** 2.6 Ma to present) are referred to as the **Quaternary Period**.
- Five marine **sedimentary basins**—(Cabinda, Zaire, Cuanza, Benguela and Namibe-the *Orla Sedimentar*)—are found along the Angolan coast. The northern basins comprise flat plateaus of red, yellow and grey **Pleistocene** sands (*musseques*) which cover earlier Lower Cretaceous to Miocene sediments of clays, limestones, marls, sandstones and conglomerates while older beds dominate the southern (Benguela and Namibe) basins. These latter sediments include many marine fossils.
- The eastern half of Angola is covered by continental deposits of **Cenozoic Kalahari sands**. Much smaller deposits of **Quaternary** sand are found in the extreme southwest, forming the **mobile dunes** of the Namib Desert. On the western high plateau, Quaternary soils have developed through weathering of the Precambrian substrate. The products of erosion are found as alluvial deposits in the Cuvelai Basin, and in the Zambezi headwaters across the vast Bulozi floodplains of Moxico.

Box 4.1: The Miocene: The Springboard of Africa's Modern Ecosystems

> The Miocene (ca. 23–5.3 Ma) is considered one of the most pivotal periods for tropical Africa, with several climatic, geological and physiographic changes hypothesised to have led to a complex evolution of African biodiversity. Couvreur et al. (2020)

Geological, climatic and evolutionary events during the Miocene Epoch shaped many of the biodiversity patterns and ecological processes that will be discussed in this volume. The Miocene will be referred to frequently in chapters that follow, and it is thus helpful to understand its characteristics and importance.

The Miocene occurred between 23 and 5.3 Ma (Million Years Ago). It was preceded by the Oligocene and followed by the Pliocene, during a period in which the planet was initially warming but thereafter cooling and drying, due to the reduced ability of the cold atmosphere to absorb moisture and form rain. The continents, following the breakup of Gondwana, had drifted close to their current positions. Africa moved up against Arabia for a brief period, allowing Eurasian biota to migrate onto the continent, before separating once again. Geologists and palaeontologists refer to three stratigraphic sub-epochs:

Early Miocene (23–20 Ma), Middle Miocene (20–11 Ma) and Late Miocene (11–5 Ma).

Through the Miocene, important changes in climates occurred.

- During the Middle Miocene, the climate cooled sharply after 14 Ma. The Central African Atlantic Swell uplifted the Mayombe massif and the East African plateau by 1200 m, the latter creating a barrier to the moisture-bearing southeast trade winds, blowing across Africa from the Indian Ocean, and causing the aridification of the Congo Basin and the fragmentation of the rain forest.
- The Antarctic ice sheet, developing since 34 Ma, reached its current extent by 8 Ma in the Late Miocene. The Antarctic Circumpolar Current had already cooled the planet and increased seasonality and aridity. By this time the Namib Desert and the extensive savannas of Africa were well developed.
- The rain forests expanded and the savannas contracted at the end of the Miocene, during a warmer, wetter period in the Early Pliocene (5.3–3.6 Ma) which was soon followed by a cooler, drier period.
- During the Late Pliocene (3.6–2.6 Ma) a further uplift, by 900 m, rejuvenated the Great Escarpment that characterises the geomorphology of western Angola. This had profound influence on the region's biodiversity dynamics during the Pleistocene.
- Hereafter, oscillations of cool dry (glacial) and warmer, wetter periods (interglacials) occurred through the Pleistocene Ice Ages (2.6–0.1 Ma). The impact of these climate changes on the tropical rain forests of Angola will be discussed in Chap. 12.

Of considerable importance to the ecology of Africa was the formation of grasslands during the Miocene. The evolution of silica-rich, fibrous, fire-tolerant grasses, and long-legged herding ungulates (hooved mammals) with high-crowned teeth, was perhaps the key evolutionary/ecological process that shaped modern African ecosystems. Savannas, dominated by water-efficient C_4 grasses (Sect. 10.2), provided the open habitats in which perissodactyls (zebras, rhinos) and artiodactyls (antelope, giraffe) proliferated. Ninety-five percent of modern plants and all modern bird families existed by the end of the Miocene. Apes speciated, and the first bipedal hominins (our ancient ancestors) appeared in Africa at the end of the Epoch. Two key features of Angolan savannas (spiny and thorny trees and shrubs of the arid savannas and the 'underground forests' of the mesic savannas (Chap. 14, Box 14.3), evolved through interactions and coevolutionary processes with the herbivore fauna and fire regimes during the Miocene.

In summary, during the Miocene multiple key events occurred:

- The intensification of the Antarctic ice sheet,
- The reinforcement of the Circumpolar Current,

- The establishment of the Benguela Current,
- The cooling and drying of the planet,
- The creation of the Namib desert,
- The expansion of grasslands and savannas and the contraction of forests,
- The evolution of C_4 grasses and the increasing frequency and intensity of fires, and
- The speciation of herding antelope and of spinescent woody plants, reaching their current importance in ecosystem structure and function.

By the end of the Miocene, savanna landscapes and 95% of modern plant, mammal and bird families had appeared. Africa as we know it had been formed.

4.2 Landscapes, Landscape Ecology and Geomorphology

The general topography of Angola is illustrated in Fig. 4.9. In summary, coastal lowlands lying below 200 m altitude and of 10–150 km breadth occupy 5% of the country's land surface, leading to a stepped and mountainous escarpment rising to 1000 m (23%), and an extensive interior plateau of 1000–1500 m (65%). Seven percent of the country lies above 1500 m, reaching its highest point at 2620 m above sea level on Mount Moco.

The major landscapes of Angola have been categorised and mapped—based on key features of their topography, geomorphology, geology, climate, soils, phytogeography and agro-ecological potential—into 11 'mesological' or landscape units by agronomist Castanheira Diniz (1973, 1991, 2006). Diniz's concept of agro-ecological/mesological units closely corresponds with current perceptions of ecoregions. His thinking reflects what is today called **landscape ecology**, the study of the composition, structure and function of landscapes. Diniz used an interdisciplinary approach, where scales of ecological patterns and processes are integrated with functional utility for human societies and their impacts on the landscape. Important aspects of these 11 broad units (Fig. 4.10) are summarised here, listing the dominant ecoregions found in each landscape type. The economic values of each landscape are illustrated by the agricultural crops that Diniz (1973, 2006) identified as having highest existing or potential productivity within the unit.

1. **Coastal Zone** (*Faixa litoranea*): Angolan Ecoregions 12–14 & 16. This is a mostly continuous coastal peneplain at 10–200 m, broken occasionally by broad river valleys. In places as narrow as 10 km, the coastal belt is mostly of about 40 km width, broadening to 150 km northwards of Sumbe and up the lower Cuanza River. In contrast to the situation on the east coast of Africa at similar latitudes, the Angolan coastline is notable for the absence of coral reefs and coastal dune forests. Long sandbars stretch northwards from rivers

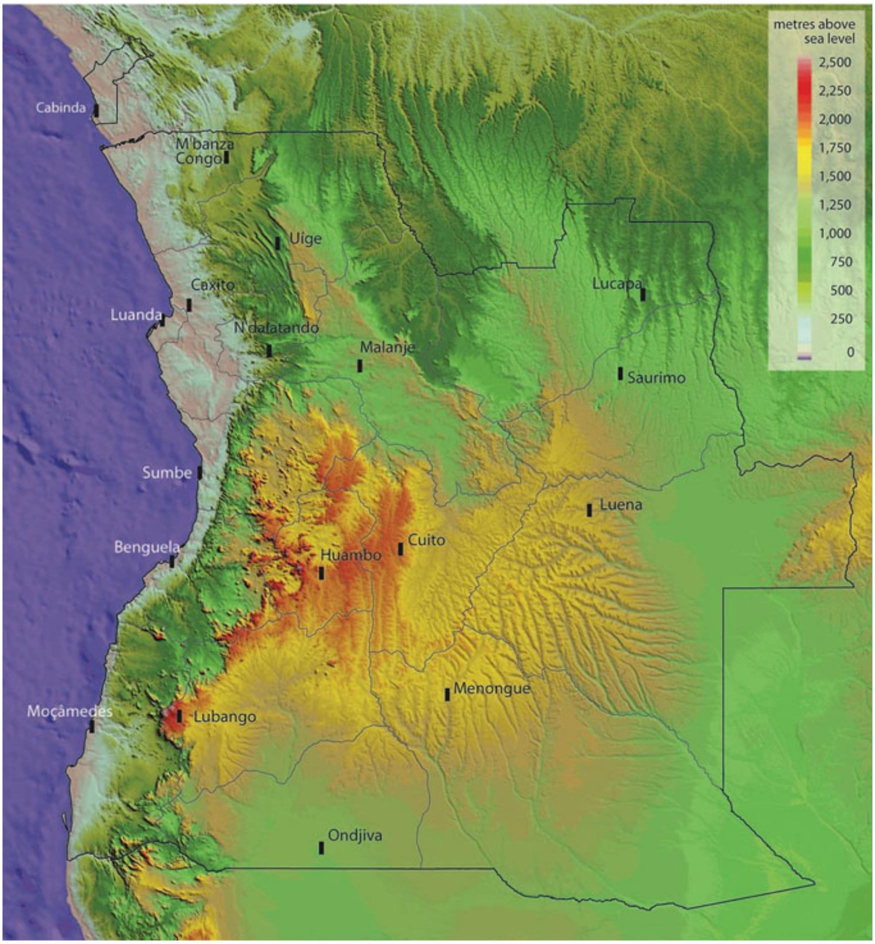

Fig. 4.9 General topography of Angola. From Huntley (2019) *Biodiversity of Angola. Science & Conservation: a Modern Synthesis.* Springer Nature

such as the Cunene and Cuanza. Mudflats and mangroves occur at most river mouths from Lobito northwards, increasing in dimension and diversity towards the Congo. Much of the coast is uplifted, resulting in sharp sea-cliffs of 10–100 m height. Several **inselbergs** (isolated mountains) rise above the coastal peneplain, the most important being **Serra da Neve**, which rises to 2489 m. The coastal plains are composed mostly of fossiliferous marine sediments of the Cabinda, Zaire, Cuanza, Benguela and Namibe sedimentary basins. The northern coastal platforms are covered by deep red Pleistocene sands of former beaches (*terras de musseque*). Lying below the sands, and exposed over large areas, are Cretaceous to Miocene clays, gypsipherous marls, dolomitic limestones and sandstones. Important beds of Cretaceous fossils occur at Bentiaba

Fig. 4.10 The main landscape systems of Angola From Huntley (2019) *Biodiversity of Angola. Science & Conservation: a Modern Synthesis*. Springer Nature

and Iembe, the latter including the sauropod dinosaur *Angolatitan adamastor*. The southernmost segment of the Coastal Belt includes the mobile and mostly vegetationless dunes of the contemporary Namib Desert. The floodplains of coastal rivers provide rich alluvial soils, supporting intensive agriculture. Crops include cotton, bananas, cashew, sugar, manioc, mango and palm oil.

2. **Escarpment Zone** (*Faixa subplanaltica*): Angolan Ecoregion 6. A broad transition belt lies between the coastal plains and the Marginal Mountain Chain and interior plateaus, and is variable in breadth and gradient. Over much of the escarpment, the transition advances up a complex series of steep steps of between 100 and 600 m height. In the south, between Moçâmedes and Lubango, the escarpment of the Serra da Chela is very sharp, rising 1000 m in relief

at Tundavala and Bimbe. The geology of the Escarpment Zone is complex, comprising crystalline rocks of the Precambrian: granites, gneisses, schists, quartzites and amphibolites. The Escarpment Zone (sometimes referred to as the Western Angolan Scarp) includes very hilly country, with mountainous belts in the north, and many inselbergs. The Angolan Escarpment has long been recognised for its biogeographic importance (Chap. 18). Agricultural crops include cotton, pineapples, bananas, robusta coffee, sugar, citrus, beans, sunflower, manioc, mango, millet, palm oil, vegetables, sisal and tobacco.

3. **Marginal Mountain Chain** (*Cadeia Marginal de Montanhas*): Angolan Ecoregions 4 & 5. These mountain lands, at 1800–2620 m, and underlain mostly by Precambrian rocks such as gneiss, granites and migmatites, lie above the Escarpment along the western margin of the extensive interior plateau, and are known as the Benguela, Huambo and Huíla Highlands. The highest peaks rise to 2620 m above sea level at Mount Moco, 2582 m at Serra Mepo and 2420 m at Mount Namba. The mountains are of biogeographic importance for their montane grasslands, with some elements of the Cape flora, and relict patches of Afromontane forests and endemic bird assemblages. Agricultural crops include potato, vegetables and wheat.
4. **Ancient Plateau** (*Planalto Antigo*): Angolan Ecoregions 4–7. This extensive plateau (the ***planalto***) drops eastwards from below the Marginal Mountain Chain and encompasses the headwaters of the Cunene, Cubango, Queve and Cutato rivers, comprising rolling landscapes with wetlands and low ridges with scattered granitic inselbergs. Together with the Marginal Mountains Chain, the planalto represents the highlands of Angola, including large areas of Benguela, Huambo, Huíla and Bié provinces. It drops from 1800 m in the west to 1400 m in central Angola. These flat to gently undulating landscapes, together with the Congo and Zambezian peneplains, are known as the African and Post-African planation surfaces (Feio, 1964; Jessen, 1936; King, 1962), and were thought to have been formed during two periods of continental erosion, between 100 and 45 million years ago (late-Cretaceous to mid-Cenozoic) and 23–7 million years ago (Miocene). Agricultural crops include ground nuts, potato, arabica coffee, citrus, beans, maize and wheat.
5. **Lower Cunene** (*Baixo Cunene*): Angolan Ecoregions 12 & 13. This landscape unit leads imperceptibly down from 1400 m on the 'Ancient Plateau' to the frontier with Namibia at 1000 m. The gentle gradient of the eastern half forms the very clearly defined Cuvelai Basin, which drains as an ephemeral catchment into the Etosha Pan. West of the Cunene the landscape is more broken, with pockets of Kalahari sands between low rocky hills. Agricultural crops include cotton, sorghum, millet, maize and manioc.
6. **Upper Cuanza** (*Alto Cuanza*): Angolan Ecoregion 7. The upper catchments of the Cuanza and its tributary the Luando, at altitudes between 1200 and 1500 m, form a distinct basin of slow drainage feeding extensive wetlands during the summer rains. Agricultural crops include maize, manioc and sugar.
7. **Malange Plateau** (*Planalto de Malange*): Angolan Ecoregion 7. A gently undulating plateau at 1000–1250 m which drops abruptly on its northeastern margin

by some several hundred metres to the Baixa de Cassange and the Cuango drainage. The escarpment ravines hold important moist forest outliers (such as at Tala Mungongo and Quela). To the west, the plateau is drained by rivers flowing to the Atlantic, most spectacularly by a tributary of the Cuanza (the Lucala) that drops over 100 m at the famous Calandula Falls. Agricultural crops include sugar, sunflower, manioc and maize.

8. **Congo Peneplain** (*Peneplanície do Zaire*) Angolan Ecoregions 2 & 3. This is a vast sandy peneplain, drained by the northward flowing tributaries of the Cassai/Congo Basin. The penelain stretches eastwards from the margins of the mountainous northern end of the Escarpment Zone in Uíge, to the extensive *Chanas da Borracha* of the Lundas. These gently dipping plains, mostly at 800–1100 m, are being dissected by the many northward flowing, parallel tributaries of the Congo Basin. The Cuango River, draining the Baixa de Cassange, drops to 500 m at the frontier with the Democratic Republic of Congo. The southern boundary of the Congo peneplain is defined imperceptibly by the watershed between the Zambezi and Congo basins, lying at ca. 1200 m. Agricultural crops include ground nuts, sunflower and manioc. The Cretaceous sediments of many rivers of the Lundas are the source of Angola's rich diamond industry.
9. **Cassange Basin** (*Baixa de Cassange*): Angolan Ecoregion 2. A wide depression, several hundred metres below the surrounding plateaus, is demarcated by abrupt escarpments to the west and the densely dendritic catchment of the Cuango to the northeast. The underlying geology comprises Triassic Karoo Supergroup sediments of limestone, sandstone and conglomerates. Within the Basin, several large tablelands (*mesas*)—remnants of the old erosional (planation) surface—rise above the depression as extensive plateaus. These are flanked by sheer 300 m high escarpments, exemplified by Serra Mbango, which awaits biological survey. Agricultural crops include cotton and manioc.
10. **Zambezi-Cubango Peneplain** (*Peneplanície do Zambeze-Cubango*): Angolan Ecoregions 7–11. This is the vast peneplain draining deep Kalahari sands, with slow-flowing rivers that meander across the gently dipping plateau from 1200 m at the watershed with the Congo Basin, to 1000 m at the frontier with Namibia. The climatic gradient (moist high ground in the north, drier in the south) across the Kalahari sands is reflected in several ecoregions in this geomorphological unit. Within this extensive peneplain, the Bulozi Floodplain occupies an area in excess of 150,000 km^2 in Angola and Zambia. Agricultural crops include manioc, maize and sorghum.
11. **Upper Zambezi Massif** (*Maciço do Alto Zambeze*): Angolan Ecoregion 10. The Calunda Mountains of eastern Moxico, composed of Precambrian schists and norites, dolorites, sandstones and limestones, rise to 1628 m above the Zambezi peneplain which lies at 1150 m. The mountains form a striking contrast to the almost featureless landscape that stretches some 800 km eastwards from Huambo to Calunda. Agricultural crops include maize.

4.3 Hydrology: Wetlands, Water Towers, Rivers, Floodplains and Estuaries

The scientific study of the movement, distribution and management of water is called **hydrology**. Understanding the role of water in ecosystems is paramount, and here one needs to commence at the moment water enters the terrestrial ecosystem from the atmosphere as various forms of precipitation, most commonly as rainfall. Consider the life of a single drop of rain falling onto the high peaks of the Marginal Mountain Chain. The raindrop might simply evaporate off plant and soil surfaces, or join many other drops entering the soil vertically by percolating down to the **water table**, and seeping laterally into a wetland on the mountain slopes and adjoining plains. A **wetland** is a seasonally or permanently waterlogged area, usually dominated by grasses, and often forming a deep organic layer (**peat**), which acts as a sponge, gradually releasing water into streams that become rivers as they descend from the highlands. Much of the Angolan planalto is a great water **sponge**, providing **ecological services** (water storage, filtering and regulating, plus supporting great biological diversity). These planalto sponges are found in the ecoregions described by Diniz (1991), Fig. 4.10—the Ancient Plateau, Malanga Plateau, Upper Cuanza, and the upper reaches of the Congo and Zambezi Peneplains. Here we will first focus on the rivers and their catchment dynamics. Box 4.1 discusses the ecological services provided by the water towers of Angola, and the human–environment interactions that lead to the loss of these services.

Coastal Rivers

Angolan river systems (Fig. 4.11) fall into two categories. First, **coastal rivers** drain the central and western highlands and flow westwards, where they penetrate the steep Angolan Escarpment to the Atlantic Ocean. Most of these coastal rivers are perennial, relatively short and swiftly flowing. They are highly erosive and carry high sediment loads, as in the northwest and westcentral basins. Backward (headward) erosion by some of these coastal rivers has produced minor basins, such as the amphitheatres of the upper Queve and Catumbela rivers. By contrast, the coastal rivers south of Benguela are **ephemeral**, only flowing after high rainfall events in their upper catchments.

The coastal rivers mostly end in broad **floodplains** in their lower reaches, such as those of the Cuanza, Longa and Queve rivers. These floodplains deposit heavy silt loads that form the substrate to densely vegetated and permanently waterlogged **swamps** dominated by papyrus *Cyperus papyrus* and reeds *Phragmites mauritianus*. As the rivers approach the sea, **estuaries** form where the interaction of tidal marine water mixes with the freshwater of the rivers. From Lobito northwards, these estuaries and mudflats are occupied by **mangroves** and **seagrasses**, forming a distinctive biome and ecoregion (Chap. 17).

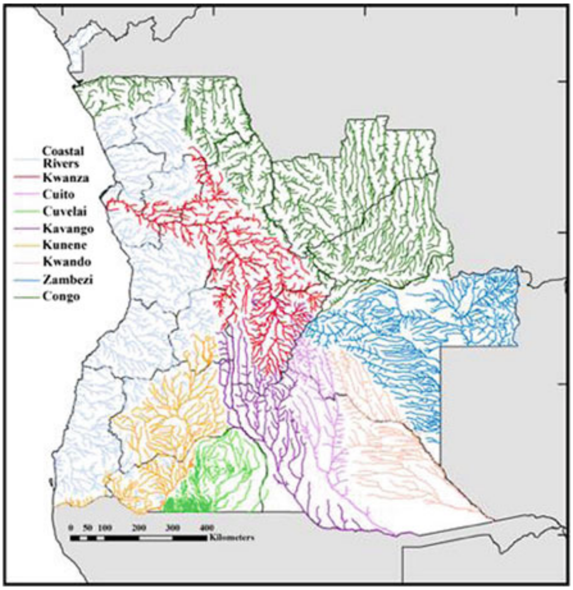

Fig. 4.11 Main hydrographic basins of Angola. From Marques et al. (2018) *Diversity and Distribution of the Amphibians and Reptiles of Angola.* California Academy of Sciences, San Francisco

Rivers Draining the Planalto and Eastern Peneplains

The second major category of river systems is that of the Angolan planalto and the extensive peneplains of eastern Angola. Drained by seven large **hydrological basins**, six of which are transnational, Angola serves as the **'water tower'** for much of southern and central Africa. These water towers comprise the extensive wetlands that occupy the gently rolling plains (*anharas do alto*) and shallow valleys (*mulolas*) of the vast Angolan plateau, characterised by the Montane Grassland (Ecoregion 5) and the Wet Miombo (Ecoregion 7). The grassy sponges and swamps, and deep sands of the plateau, store water through the year, gradually releasing this water into the major river basins. Many of these rivers arise in close proximity on either side of the gently undulating **watershed** between the Cuanza, Cassai (Congo), Lungue-Bungo (Zambezi), Cunene, and the inland-draining (**endorheic**) Cubango (Okavango) basins (Mendelsohn, 2022). The rivers that flow across Kalahari sands are slow moving and, due to the filtering action of the sands, are crystal clear and nutrient poor. Faster moving rivers, such as the Cunene and Cubango, are more erosive and carry higher sediment and silt loads, and richer invertebrate, amphibian and fish biomass due to the higher nutrient content of their water. Between the Cunene and Cubango catchments, a separate ephemeral, endorheic system, the Cuvelai Basin, drains southwards into the Etosha Pan.

The biodiversity conservation value of the Angolan river systems is of great significance, feeding as they do two great wetlands of global importance (Okavango and Etosha), and the still under-researched Bulozi Floodplain of Moxico. The Bulozi is possibly the largest ephemeral floodplain in Africa—800 km from north to south and 200 km from east to west—straddling the Angola/Zambia frontier. Other, smaller floodplains, such as those of the Congo tributaries, are important for the **swamp forests** and **gallery forests** that line their margins, providing biogeographically significant corridors for Guineo-Congolian species penetrating the Zambezian savannas of the miombo. In strong contrast to the moist closed-canopy gallery forests of the perennially fast-flowing Congo tributaries, are the **linear oases** of the Namib. These *Acacia erioloba, Faidherbia albida* and *Ficus sycomorus* woodlands follow the deep sands of ephemeral rivers such as the Curoca, Bero and Bentiaba from the escarpment to the coast. The nutritious foliage and seedpods of these great trees support the penetration of species such as Savanna Elephant, Giraffe and Greater Kudu deep into the Namib Desert.

River Capture

The current landscapes and geomorphology of Angola are the result of hundreds of millions of years of geological dynamics, accompanied by the erosive action of rain, rivers and wind. Major **tectonic** movements of the earth's crust, through faulting and rising or sinking, can result in **river capture**, where one river cuts into the stream of another, rapidly increasing its erosive power. Such tectonic events shaped the course of the Congo, Cuanza, Cunene and Zambezi rivers many millions of years ago, and more recent tectonic events are currently changing the dynamics of the Cassai and Congo basins. The Palaeo-Congo originally drained into a massive lake in the centre of today's DRC, while the Palaeo-Cunene flowed due south to the Etosha Pan in Namibia, which for many millions of years was a major lake. About 30 million years ago the Congo was captured by the incision of a small river cutting eastwards from the present mouth of the Congo. The Cunene was captured by a stream that cut backwards from the coast through an existing, but ancient, Carboniferous (300 Ma) glacial valley, which redirected the river to its current mouth at the Foz do Cunene (Figs. 4.7 and 4.8). Less dramatic examples of river capture, but with great biological consequences, are where tributaries of the Congo and Zambezi systems have cut back into one another, changing the direction and volume of water carried by these river systems and mixing their aquatic faunas. The river captures associated with the Congo, Cuanza, Cubango, Cunene and Zambezi have all been of great biogeographic importance.

Box 4.2: Human–Environment Interactions: Ecosystem Services Provided by Angola's Water Towers

Angola is unusually blessed with abundant freshwater ecosystems: the wetlands, streams, rivers, floodplains and estuaries that fall within the country's seven hydrological basins. The benefits of freshwater systems, essential for human health and wellbeing, and environmental productivity and sustainability, include the four categories of **ecosystem services** recognized by the Millennium Ecosystem Assessment (MEA, 2003):

- Provisioning Services: *the provision of genetic resources, food, fresh water, fish, fuel, fibre, hydropower and other goods*;
- Regulating Services: *carbon sequestration, flood control, water purification, disease regulation, pollination and the maintenance of biodiversity*;
- Supporting Services: *soil formation, nutrient cycling and primary production*;
- Cultural Services: *spiritual, educational, aesthetic, and cultural heritage values as well as recreation and tourism.*

The importance of the highland catchments of Angola, the 'Water Towers' of much of central and southern Africa, can be illustrated by three key national and international roles. First, they provide drinking water for Angola's human population. Second, they provide the latent energy that is captured by hydroelectric power projects for use by Angola and Namibia. Third, they sustain the vast natural ecosystems of Botswana's Okavango Delta, Angola and Zambia's Bulozi Floodplain and Angola and Namibia's Cuvelai Basin. However, the sustainability of these roles is threatened by human activities.

First, the quality of water is being severely eroded by pollution from poorly managed urban wastes, from open cast mining, and from agricultural and industrial chemicals (Mendelsohn, 2019, 2022). Despite the then president's 'Water for All' project, initiated in 2007 to meet Millennium Development Goal 6 for water supply (potable water for 80% of peri-urban and rural communities), the official government assessment indicated that by 2015 only 50% of the target population had been reached. For example, the problem of supplying safe drinking water to Luanda's four million residents of its *musseque* settlements remains acute. Water selling has developed into the largest sub-sector of the city's extensive informal economy, involving extractors, transporters and retailers (Cain & Baptista, 2020). Further, Angola is one of the countries with a high rate of waterborne diseases, due to the scarcity and poor quality of water for human consumption. The watercourses are receptors of many effluents, mainly domestic sewage, due to a precarious or inexistent sanitation system and the small number of water treatment plants (Paca et al., 2019). The consequent pollution accounts for high levels of eutrophication of sections of the main bulk water sources (Bengo, Dande and Cuanza rivers) with growth of invasive aquatic plants such as *Eichhornia crassipes*. Remote rural communities are largely dependent on standpipes fed by boreholes, and pit-toilet sanitation.

Second, the vast river basins and flows of water from the highlands and planalto result in Angola's hydropower potential being among the highest in Africa, estimated at 18,200 MW. The government's stated aim is to substantially grow its hydropower generation capacity from its current levels of around 3590–9000 MW by 2025. Hydropower provides 68% of Angola's electricity needs. Angola's hydropower development has been mainly located on the Cuanza River, with installed capacity from dams at Laúca (2070 MW), Cambambe (960 MW) and Capanda (520 MW). Within Angola, the Cunene River has a small hydropower plant at Matala (40 MW). However, the Cunene, via the storage facilities at the Gove and Calueque dams, feeds the Ruacana hydropower plant (347 MW), situated just south of the Namibian border, and which provides 50% of Namibia's electricity needs. The maintenance of reliable river flows to these hydropower plants through responsible land use in the catchments is thus critical to Angola's socio-economic future. Deforestation of much of the planalto and the combined impacts of shifting cultivation, wild fires and soil erosion are causes of concern.

Third, the water towers of Angola sustain one of the world's most iconic centres of biodiversity—the Okavango Delta, recognised by UNESCO as a World Heritage Site. The whole ecosystem is dependent on the seasonal flows of water from two Angolan rivers—the Cubango and Cuito. The Cubango sends pulses of water downstream each summer, while the Cuito provides a steady flow throughout the year. It is the pulses of water and nutrients that bring abundant life to the dry lands beyond the Delta's permanent swamps. As Mendelsohn et al. (2021) describe, if the pulses of the Cubango are reduced or polluted by upstream developments, the rich biodiversity and related lucrative tourism industry of Botswana will be threatened. Of serious concern is the rapid expansion of commercial agricultural projects along the Cubango, increasing from 300 ha in 2011 to 3100 ha in 2021, with plans to expand the area under irrigation to 221,000 ha in the next decade. Such huge irrigation schemes will drain the Cubango during the dry months, and prevent the pulses of water and nutrients from reaching the Okavango, with potentially catastrophic ecological consequences.

These few examples illustrate the vulnerable interconnections that exist between human wellbeing and environmental sustainability, not only in Angola, but across the region, where water quantity and quality are key determinants of livelihoods and biodiversity.

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Chapter 5
Solar Energy, Temperature and Rainfall

Key Concepts and Questions: This Chapter Explains

- *The nature and source of solar energy and how it is transferred to the planet.*
- *How the Sun's energy, and the Earth's rotation on its axis, create the climate that we experience.*
- *Why seasons are important to the rhythms of life and what drives seasonal patterns.*
- *How solar energy is captured, retained and converted to sustain living organisms through photosynthesis.*
- *How the oceans, atmosphere and land interact to create the climates of Angola.*
- *How the patterns of climate vary across Angola, and what processes account for them.*
- *Why Angola has both rain forest and desert in a single country.*
- *What the El Niño phenomenon is, and how it affects Angolan ecosystems and society.*

Context: Solar Radiation, Weather and Climate

Life on Earth is possible because of the energy it receives from the Sun. Climate, geology, topography, hydrology, soils, fire and herbivory determine the distribution and abundance of plant and animal species and of ecosystem patterns. Of overriding importance driving these interlinked factors is solar radiation which shapes the global patterns of temperature, air pressure and moisture, and of atmospheric and oceanic dynamics. Solar radiation determines the weather and climate experienced at the scale of individual organisms to continental biomes. Most importantly, solar radiation drives photosynthesis, the source of life on Earth.

Angola offers excellent opportunities to examine the influence of climate on ecosystems that range from hyper-arid desert to tropical rain forest. Before focusing on Angola, it is helpful to understand the driving forces of climate at global and regional scales. Solar radiation, the rotation of the Earth on its axis and its annual path around the Sun, result in both long-term cycles and annual seasonality of climate,

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and associated processes of oceanic and atmospheric circulation. These drivers are modulated by latitude, altitude and distance from the ocean to produce the patterns of temperature and rainfall experienced over Angola.

A distinction must be made between the concepts of weather and climate.

- **Weather** is the temperature, humidity, rainfall and wind experienced at a particular place and at a **specific time**, such as a hot, humid summer afternoon in Luanda. Weather refers to local, short-term phenomena.
- **Climate** refers to the long-term **average pattern** of weather at local, regional and global scales, such as the cool desert climate of Tômbua
- or the wet tropical climate of Buco Zau. Climate describes the overall summary of regional weather features. For example, spells of wet weather can be experienced in a dominantly arid climate.

5.1 Where Life Begins: Solar Radiation and Photosynthesis

Solar energy drives the functioning and dynamics of all ecosystems. The first step in understanding the ecology of living organisms is to become familiar with the key life-giving mechanisms, the transfer of **solar energy** from Sun to Earth, and the process of **photosynthesis**.

Energy is emitted from objects as **electromagnetic radiation**. In brief, hot objects emit **shortwave** and cool objects emit **longwave** radiation. The Sun has a surface temperature of 5800 °C and emits shortwave solar radiation to the Earth, some of which is reflected back into the atmosphere. The Earth, with an average temperature of 15 °C emits longwave radiation. The Earth's **energy budget** is the balance between radiant energy that reaches the Earth from the Sun, and that which flows back from Earth into space (Fig. 5.1). The proportion of sunlight that is reflected back into the atmosphere by different land surfaces is called their **albedo**. Light surfaces, like the Namib Desert, have a high albedo, reflecting energy. Dark surfaces, such as the rain forests of Cabinda, have a low albedo, absorbing energy.

The solar energy (shortwave radiation) received at the Earth's surface as **sunlight** is harnessed through the process of **photosynthesis**—a series of biochemical reactions by which atmospheric carbon dioxide and water are transformed by light energy into **carbohydrates** (simple sugars), with **oxygen** released as a by-product. The process occurs within specialised organelles (**chloroplasts**) in the **mesophyll** cells of plant leaves. Basically, six molecules of carbon dioxide and six molecules of water are transformed into one molecule of sugar and six molecules of oxygen ($6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2$). The energy received from the Sun and captured in plants by photosynthesis is stored as carbohydrates and as high-energy molecules (**adenosine triphosphate—ATP**) which carries energy within and across cells.

Gas transfer takes place via the opening and closing of small pores (**stomata**) on the surface of plant leaves. The process is catalysed by a nitrogen-based enzyme, **rubisco** (ribulose biphosphate carboxylase-oxygenase), the most abundant protein on Earth and a major source of nitrogen for herbivores. Photosynthesis requires sunlight

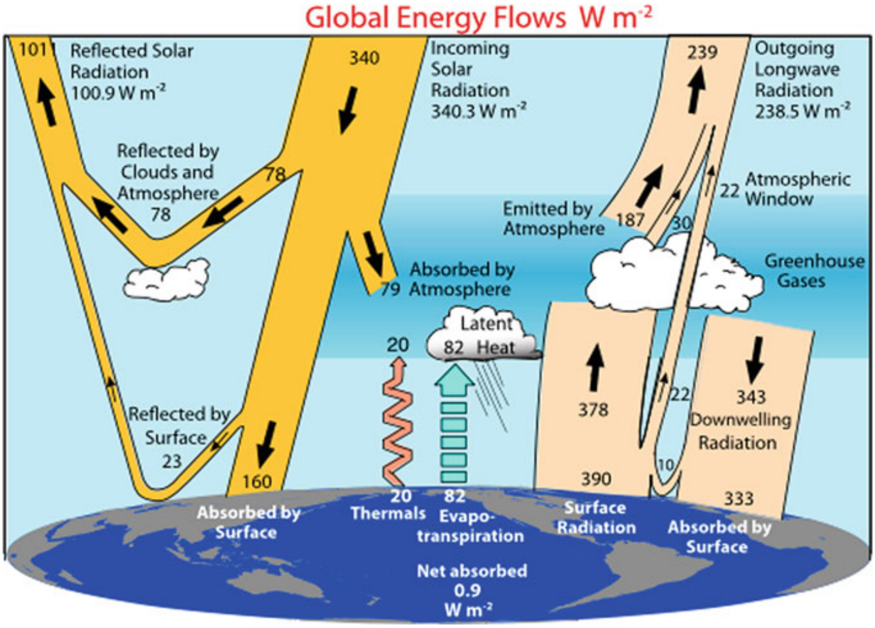

Fig. 5.1 The Earth's energy budget illustrating the main flows of solar radiation and how it is absorbed and reflected by Earth. From Trenberth (2020) *Journal of the Royal Society of New Zealand*, 50:2, 331–347. c The Royal Society of New Zealand

(**photosynthetically active radiation**—PAR) to function. In the absence of PAR (at night) the carbohydrates are used during cellular **respiration**, a chemical reaction which breaks down carbohydrates to form ATP, while releasing carbon dioxide. Respiration is the opposite process to that of photosynthesis, requiring oxygen and releasing carbon dioxide and water ($C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O$). During these processes, while the stomata are open for the exchange of carbon dioxide and oxygen, water is lost from the leaf via **transpiration**. One of the key adaptations to survival in plants is the regulation of gas exchange (and water loss) via the stomata.

The net gain of carbohydrates (sugars and cellulose) formed through photosynthesis, minus the losses through respiration, provide the energy and structural components of plants, which are then available to the rest of the **food chain** that progresses from **primary producers** (plants), to **consumers** (herbivores) to **predators** (carnivores) and ultimately to **decomposers**. The importance of solar energy, water, nutrients (such as nitrogen and phosphorus), rubisco and ATP will become evident in later discussions in **Part III** Chap. 10 on ecosystem processes, and more specifically in Sect. 10.2, which describes the three photosynthetic pathways that have developed in the long history of plant evolution. These different pathways (abbreviated as **C_3, C_4**, and **CAM**) account for the success and diversity of Angola's forest, savanna and desert ecosystems which function under very different climatic regimes.

5.2 Seasonality of Day Length and Temperature

The major climatic patterns of the globe result from a sequence of physical processes triggered by the Earth's rotation on its axis as it progresses on its annual elliptical orbit around the Sun. The Earth's tilt is 23.5° from the perpendicular. Each season results from the relative position of the equator (and any other point on the Earth's surface) relative to the incoming Sun's rays (Fig. 5.2).

The Sun is directly overhead the equator twice per year at midday on the spring and autumnal **equinoxes** (22 September and 21 March) when day and night are of equal length at all points on the planet. As the Earth moves on its orbit around the Sun, the Southern Hemisphere receives an increasing exposure to solar radiation until the Tropic of Capricorn falls directly under the Sun at midday on 22 December, which marks the summer **solstice** (and winter solstice in the Northern Hemisphere). The tilt of the Earth on its axis then accounts for the migration of the overhead Sun northwards, until it is overhead the Tropic of Cancer on 22 June, when the Southern Hemisphere experiences its shortest day of the year on the southern winter solstice. On the Equator, seasonal changes in incoming solar radiation are not great, but at high latitudes, the acute angle at which the Sun's rays reach the Earth's surface, after passing through a broad band of atmosphere, explains the decrease in solar radiation (and hence temperatures) experienced at the poles, and why the poles are covered in ice, while the equatorial regions are mostly covered by forest (Fig. 5.3).

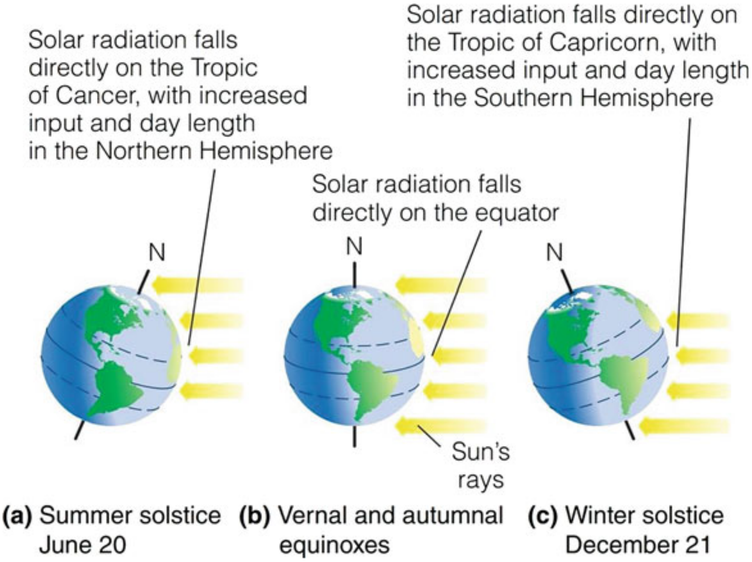

Fig. 5.2 Changes in the concentration of the Sun's rays during the Earth's annual orbit around the Sun. Left: winter solstice 22 June, Sun overhead the Tropic of Cancer. Centre: spring and autumn equinoxes, Sun overhead the Equator. Right: Summer solstice, 22 December, Sun overhead Tropic of Capricorn. From Smith and Smith (2015) *Elements of Ecology*. (9th Edition). Pearson, Boston

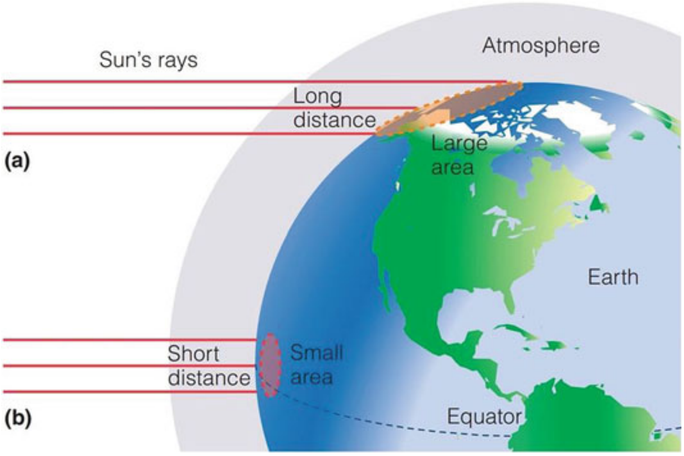

Fig. 5.3 The amount of radiation received at the Earth's surface depends on season and latitude. When the Sun is overhead the Equator, the Sun's rays are concentrated over a small area, while at the high latitudes, it is spread out over a much wider area, with much less radiation and heat being received. From Smith and Smith (2015) *Elements of Ecology*. (9th Edition). Pearson, Boston

In tropical countries, such as Angola, the changes in day length and mean daily temperature are not nearly as noticeable as they are in high latitudes such as northern Europe. In Angola, seasonality of rainfall is much more important for ecological processes than are temperature conditions, where warm wet summers are followed by mild dry winters, regulated by large-scale atmospheric dynamics. The duration of the dry season varies from a few months in the north to eight months in the south, and is a primary factor influencing the structure and functioning of Angola's rain forests, mesic and arid savannas, floodplain grasslands and deserts.

5.3 Large-Scale Drivers of Climate: Oceanic and Atmospheric Circulation

The seasonal differences in the amount of solar radiation received at the equator and the high latitudes are the major drivers of energy, air and moisture circulation around the globe. There is a net surplus of heat from the Equator to the mid-latitudes, and a net deficit over the mid-latitudes to the poles (Fig. 5.4). The reason why the tropics do not become increasingly hotter and the poles increasingly colder is because the atmosphere and ocean currents transfer the surplus heat from the tropics to the poles. The transfer of heat from the Equator to the poles is via **convection**—where there is a transfer of warm equatorial oceanic water and atmospheric air moving towards colder regions.

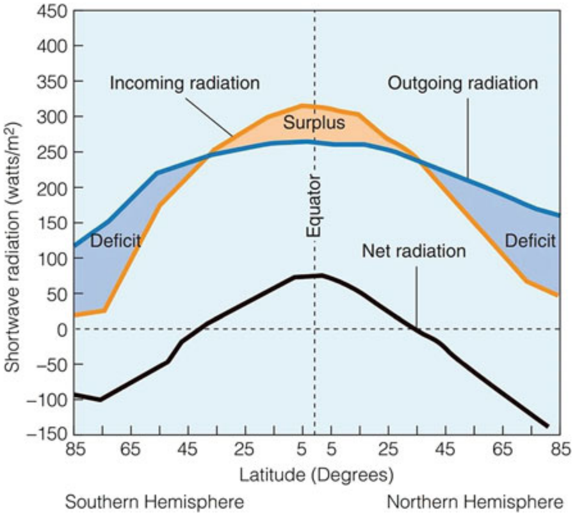

Fig. 5.4 Variation of mean annual incoming shortwave radiation, outgoing longwave radiation, and net radiation as a function of latitude. Note the surplus of incoming radiation over outgoing radiation between the equator and 30°–35° north and south, and the radiation deficit between 35° and the poles. This gradient of net radiation drives the transport of heat from the tropics to the poles through circulation within the atmosphere and the oceans. From (Smith & Smith, 2015) *Elements of Ecology* (9th Edition). Pearson, Boston

These mass movements of energy result in three circulating air systems (cells) over the northern and southern hemispheres, driven by low and high pressure zones of the equatorial and the mid-latitudes (Fig. 5.5). The three large-scale atmospheric circulation 'cells' are known as the Hadley, Ferrel (or Mid-latitude) and Polar cells. The **Hadley** cells are of special importance to Angola and are illustrated in cross-section in Fig. 5.6. The mechanisms of atmospheric circulation are depicted in Figs. 5.4, 5.5 and 5.6. The converging air mass that is warmed over the equatorial regions rises into the lower atmosphere, thereby establishing an area of low pressure at the Earth's surface—the **equatorial low**. This area of low pressure is called the **Intertropical Convergence Zone** (ITCZ). As the altitudinal position of the Sun changes relative to the Equator, the ITCZ moves latitudinally, northwards or southwards, between equinoxes and solstices. The shift in position of the ITCZ produces seasonality in precipitation, reflected in rainy seasons and dry seasons. In Angola, with increasing distance from the Equator, the tropical dry season tends to be longer and the rainfall lower. Understanding the role of the ITCZ and of the Hadley cells is helpful to understanding the climate of Angola. Several features deserve emphasis:

- The **rising**, warm and wet equatorial air along the **ITCZ** is unstable and cools as it rises, causing condensation, saturation, cloud formation and precipitation. This accounts for the high rainfall received across northern Angola.

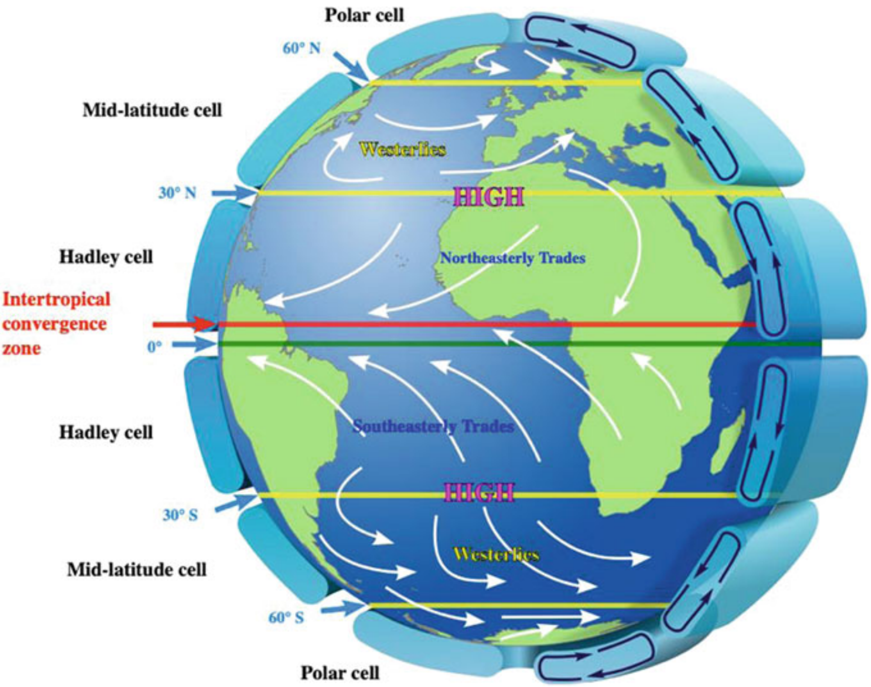

Fig. 5.5 A simplified depiction of large-scale atmospheric circulation on Earth, as at the equinoxes. Note the position of the Hadley cells, the ITCZ and of the Southeasterly Trades. *Source* Wikipedia Commons

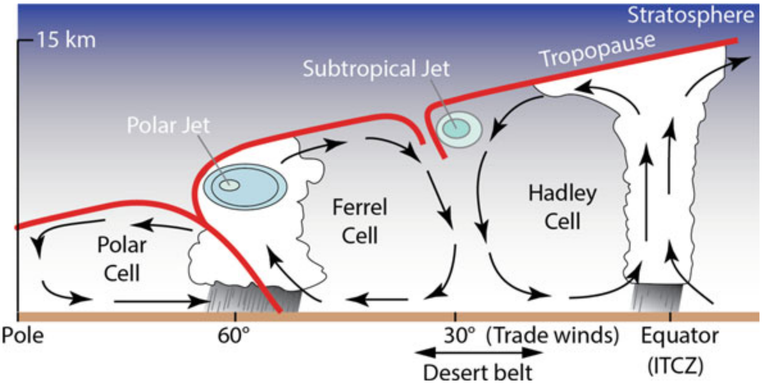

Fig. 5.6 A cross-section of the Hadley, Ferrel and Polar cells in the Southern Hemisphere. Note the position of the ITCZ, Tropopause, Stratosphere, Subtropical and Polar jets, and the descending dry air between the Hadley and Ferrel cells, that cause the desert belt and the Trade winds. From Lovegrove (2021) *The Living Deserts of Southern Africa (2nd Edition).* Penguin Random House. *Artwork* John Warren

- From space, the ITCZ appears as a band of clouds which produce extensive thunderstorms and intense rainfall encircling the globe near the equator, supporting the equatorial **rain forests** of South America, Africa and Southeast Asia.
- The strong precipitation along the ITCZ releases latent heat, driving the air upwards to the **tropopause** at about 15 km above sea level.
- At this altitude, the air is no longer buoyant, and this sub-stratospheric air is forced poleward by the continuing thrust of the rising air below it.
- At about 30°S of the equator, the cool, dry, high altitude air begins to sink and is warmed **adiabatically** by compression from the overlying air. The **subsiding** air forms **subtropical high** pressure zones (also known as **anticyclones**, such as the South Atlantic Anticyclone). The subsiding air is dry and stable, not conducive to forming rainfall.
- At the arid mid-latitudes (ca 30°–35° north and south of the equator), the Sahara and Namib **deserts** and their specialised animals and plants have evolved over many millions of years.
- A key feature of global atmospheric and oceanic circulation patterns is that of the **Coriolis Effect**. As the Earth spins on its axis, the relative ground speed at the Earth's surface increases from the poles to the equator (because of the great differences in the Earth's circumference between low and high latitudes). This phenomenon is known as the Coriolis Effect. As a result, circulating air and water currents are deflected to the right (clockwise) in the Northern Hemisphere and to the left (anticlockwise) in the Southern Hemisphere). These patterns of circulation are best illustrated in global ocean currents (Fig. 5.7).

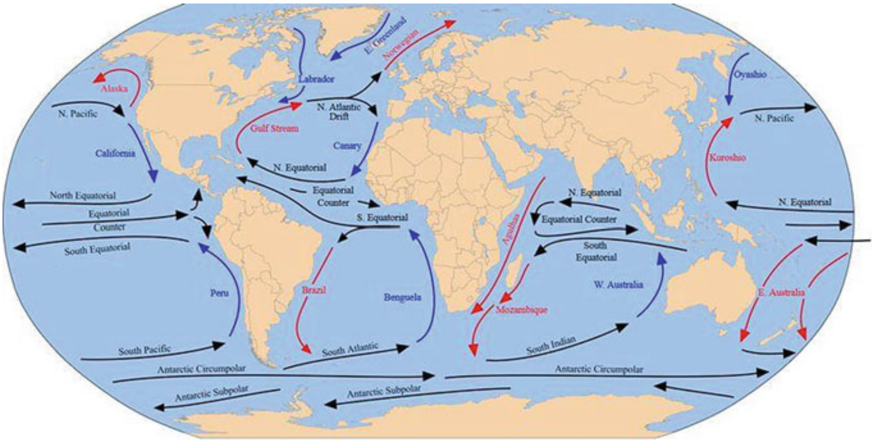

Fig. 5.7 Ocean currents of the world. Blue arrows indicate cold currents, red arrows indicate warm currents. Note how the oceans are connected by currents, how the circulation of currents—clockwise in the Northern Hemisphere, counter-clockwise in the Southern Hemisphere—is influenced by the Coriolis force and by the positions of the continental landmasses. From http://www.coastalwiki.org/wiki/Ocean_circulation

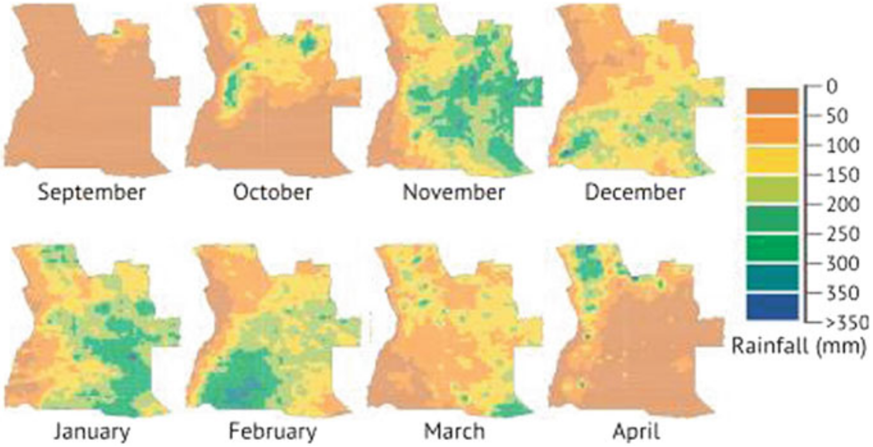

Fig. 5.8 The southwards and northwards movement pattern of rainfall seasonality (highlighted by the green tones) across Angola during 2009/2010, in tandem with the migration of the Intertropical Convergence Zone. From Huntley (2019) *Biodiversity of Angola. Science & Conservation: a Modern Synthesis.* Springer Nature

- Finally, as the summer season approaches, the position of the ITCZ moves southwards across central to southern Africa, moving northwards after the summer equinox (Fig. 5.8).

The pressure differences between the low pressure belt of the wet ITCZ and the high pressure of the dry subtropics results in winds from the south and north converging along the ITCZ. The winds from the northern and southern high pressure zones thus converge towards the low pressure of the ITCZ. These **Trade** winds follow a regular pattern of seasonality. Blowing across the Atlantic and Indian oceans, for instance, they provided the early Portuguese navigators with a reliable guide to crossing the oceans. The mariners had to learn to avoid the notorious region known as the **doldrums,** the low pressure belt of the ITCZ, where the rising hot air results in little surface wind, a serious challenge to sailing ships.

The winds blowing across the oceans generate the major ocean currents. Following the principles of the Coriolis effect, these currents move clockwise in the Northern Hemisphere and anti-clockwise in the Southern Hemisphere, creating **gyres** (like massive whirlpools) bringing cold waters to the equatorial regions and taking warm equatorial waters to the polar regions (see Fig. 5.7). The south-westerlies bring cold Antarctic waters to the southwest African coast and, coupled with the influence of offshore southeast trade winds, cause upwelling (the **Benguela Current**) bringing rich nutrients to the surface, and cool foggy air to the coast of Angola. As we will see in Part IV, Sect. 16.3, the Benguela Current has a profound influence on Angolan ecology.

In Angola, the seasonal migration of the Intertropical Convergence Zone, in response to Earth-Sun dynamics resulting from the tilt of the Earth's axis, can be followed in rainfall patterns and pulses, illustrated in Fig. 5.8. In winter, the high pressure system, lying over central Angola, blocks out the moist tropical air. In summer, the southward movement of the ITCZ brings rain across the country.

5.4 Local Influences: Maritime, Continental, Altitudinal and Aspect

The temperatures experienced on the ground are primarily determined by latitude, seasonality, altitude, aspect and proximity to the ocean. We have already discussed the influence of latitude and seasonality at global scales. At more regional and local scales, land and water surfaces heat and cool at different rates because of differences in their **specific heat**. Water bodies, such as the Atlantic Ocean, require four times more solar energy to raise the temperature by 1 °C than do land surfaces. This difference in the heat balance of water and land has two outcomes:

- The coastal belt of Angola is cooled by its proximity to the ocean (**maritime influence**). Coastal cities experience much less variation in diurnal and seasonal temperatures than do cities in the interior. The mean daily temperature range in Luanda is 7 °C in July, compared with a range of 24 °C in July at Menongue. This is due to the effect of Menongue's distance from the ocean, known as **continentality**.
- In addition, hot air over the coastal plains rises through the day, creating a vacuum that is filled by cooler air drawn off the ocean—experienced as strong **sea breezes** on many summer afternoons along the Angolan coast. This inflow of cool oceanic air as it moves across the Benguela Current also accounts for the presence of the stratus clouds (***cacimbo***) that characterise coastal Angola, and that penetrate many km inland, especially during winter.

The highest mountains of Angola such as Mount Moco (2620 m above sea level) experience a much cooler and wetter climate than the coastal lowlands below them, due partially to the altitudinal decrease in temperature of about 0.6 °C per 100 m. The rainfall gradients are locally accentuated by the **orographic** influence of the sea-facing slopes of the escarpment and the highland mountain massifs. The folded mountain ridges of Cabinda, Zaire and Uíge are effective in catching the rain-bearing winds, with marked differences in annual precipitation being received by the west-facing compared to the east-facing slopes that lie in the **rain-shadow**. The direction a slope faces (**aspect**) is very important in temperate latitudes, and even in the tropics of Angola, the temperature and moisture **microclimate** of south-facing mountain slopes in the highlands of Huambo and Huíla support larger patches of montane forest than do warmer, drier north-facing slopes, where evaporation rates can be up to 50% higher than south-facing sites. Microclimates can also be important for the survival of plants sensitive to **frost**, which is infrequent over most of Angola, but has been recorded where associated with pockets of **cold air drainage** in the valleys of Cunene and Bié. Finckh et al. (2021) propose that frost is the primary causal factor in shaping the treelines of Angolan miombo woodlands and driving the evolution of geoxyles. The hypothesis deserves testing over a wider range of miombo landscapes than the two study sites on which it is based.

5.5 Water Cycle Processes: Precipitation and Evapotranspiration

Precipitation, like temperature, is a key determinant of the distribution and abundance of animal and plant species. **Mean Annual Precipitation** (**MAP**) is influenced by the same mix of factors as is air temperature. Air masses, whether from over the sea or land, carry water vapour with them. Two processes describe the state of water within a given body of air. **Evaporation** is the transformation of water to a gaseous state—**water vapour**. Conversely, **condensation** is the transformation of water vapour to a liquid state—water—or **precipitation** as rain. Each transformation requires equivalent amounts of energy. A simple measure of the amount of water vapour in the air is **relative humidity,** which is scaled from zero to 100%, at which point the air is **saturated.** The capacity of air to hold water vapour increases with increasing temperature. On a cool morning, **dew** might be found on plants, but this rapidly evaporates as the Sun rises and the air temperature increases, simultaneously increasing the water-holding capacity of the air.

Most large-scale studies of climate/vegetation correlations refer to **mean annual temperature** (**MAT**) and **mean annual precipitation** (**MAP**). However, plants grow in response to effective precipitation, not mean annual rainfall, and to potential evapotranspiration, not to relative humidity. **Evapotranspiration** is the combined water loss both from plant surfaces and from the soil. **Potential evapotranspiration** (**PET**) is a measure of the energy available to evaporate water, defined as the amount of water that would evaporate or be transpired from a saturated surface. **Effective precipitation** is MAP minus PET. Effective precipitation is the amount of rainfall that is actually added to the soil, and is hence available for plant growth. Ecological modellers therefore use effective precipitation and potential evapotranspiration as parameters that more closely relate to plant growth than do measurements of rainfall. Over much of southwest Angola, PET exceeds MAP for up to eight months of the year, with effective rainfall ranging from minus 250 to minus 1000 mm per year, accounting for the presence of arid savannas. In Angola, mesic savannas occur where PET exceeds MAP for five months; and moist tallgrass savannas and forest occur where PET exceeds MAP for two months, and where effective annual rainfall can reach 1200 mm.

5.6 Regional Climates of Angola

The basic principles of global climatology, and how they explain regional climates and ecosystem patterns and processes, are nowhere better illustrated than in Angola. Here we illustrate the general principles relative to the climate experienced on the ground.

Latitude

The geographic position of Angola, stretching from near the Equator to close to the Tropic of Capricorn, across 14° of **latitude**, accounts for the overall decrease in solar radiation received and thus influencing the mean annual temperature experienced from north to south. The latitudinal decrease in mean annual temperature is illustrated by data from stations in the hot northwest and northeast (Cabinda: 24.7 °C; Dundo: 24.6 °C), compared with stations in the milder southwest and southeast (Moçâmedes: 20.0 °C; Cuangar: 20.7 °C).

Altitude

Both temperature and precipitation are influenced by **altitude**. The altitudinal decrease in mean annual temperature can be illustrated from sites on the same latitude, but at different altitudes above sea level. From the base of the Chela Escarpment to the highest points at its summit, the mean annual temperature drops as follows:

- Bruco: altitude 699 m, mean annual temperature 23.8 °C;
- Jau: altitude 1700 m, mean annual temperature 18.0 °C; and finally
- Humpata-Zootécnica: altitude 2300 m, mean annual temperature 14.6 °C.

Atmospheric Systems

Of the greatest importance to the rainfall patterns that determine vegetation and habitat structure are the influences of the **atmospheric systems** which dominate central and southern Africa. Angola’s climate is strongly seasonal, with hot wet summers (October to May) and mild to cool dry winters (June to September). As described in Sect. 5.3, the Intertropical Convergence Zone (ITCZ) moves southwards over Angola during summer, and then returns northwards to the Equator as winter approaches. The rainfall season that is triggered when the ITCZ passes across northern Angola from early summer reaches southern Angola in late summer (Fig. 5.8). The changing position of the ITCZ results in two rainfall peaks in northern Angola, and one over the rest of the country as illustrated in the climate diagrams in Fig. 5.9.

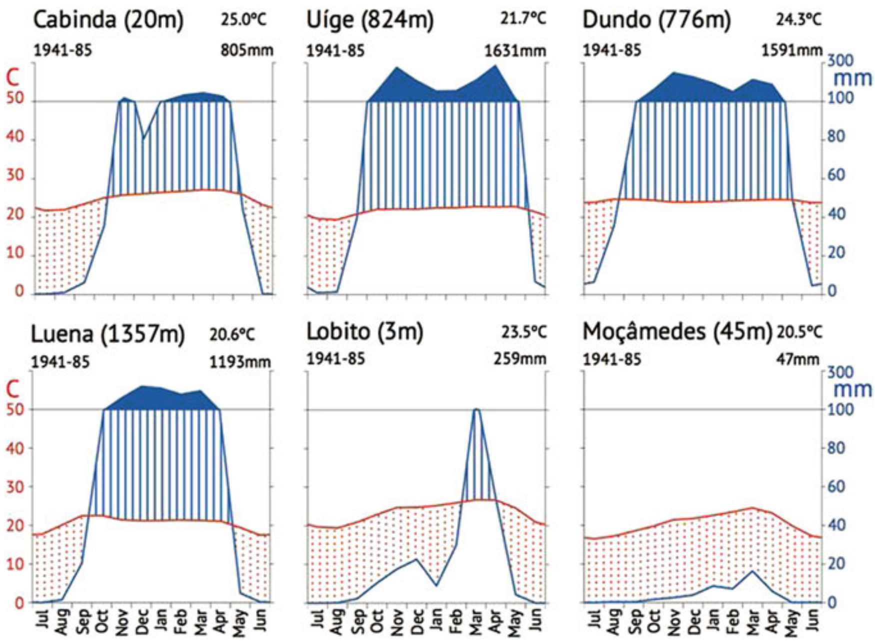

Fig. 5.9 Climate diagrams illustrating rainfall and temperature seasonality and other climatic parameters. Note the weak bimodal rainfall maxima for stations in northern Angola and unimodal maxima in central and southern Angola. The diagrams follow the system of Walter and Lieth (1967). Stipples represent dry periods; vertical stripes represent rainy periods; solid blue represents months with rainfall exceeding 100 mm. From Huntley (2019) *Biodiversity of Angola. Science & Conservation: a Modern Synthesis.* Springer Nature

Moving in tandem with the **low pressure** system of the ITCZ are two subtropical **high-pressure** systems over the Atlantic and over southern Africa. These are the **South Atlantic Anticyclone** and the **Botswana Anticyclone.** These two anticyclones block the southward movement of moist air from the ITCZ during winter (preventing cloud formation). As the high-pressure cells move southwards in summer, the conditions required for cloud formation return. This migration of rainfall systems is clearly illustrated in the series of rainfall maps prepared from weather satellite imagery and presented in Fig. 5.8.

During winter and early summer, the Botswana Anticyclone generates strong **winds** that blow across Angola from east to west. In the southwest, the winds pick up dust from the arid lands and create hot, choking dust storms that feed and sculpture the sand dunes of the Namib. The winter winds are also notorious in Lunda-Norte, where they desiccate the grasslands and promote the spread of extensive fires. In the east, the winds and their sand deposits account for dune formation across the Bulozi Floodplain (Mendelsohn & Weber, 2015).

Benguela Current

While altitude and seasonality determine temperature conditions, an anomaly to this general rule occurs in the coastal belt of Angola, especially in the far south, where the cold, upwelling Benguela Current creates a **temperature inversion** (see Chap. 16, Fig. 16.6). The cold Benguela Current has a stabilizing effect on the lower atmosphere and inhibits the evaporation and upward movement of moist, rain-forming air off the ocean. Its impact extends as far north as Cabinda, where a narrow belt of arid savanna and dry forest, of acacias, sterculias and baobabs, flanks the rain forests of the Maiombe (Chap. 15.3).

Despite the aridity of the coastal zone, the cooling effect of the Benguela Current results in low stratus cloud and fog (***cacimbo***) through much of winter, with heavy dew condensing on vegetation along the coast, even during the driest months of winter. This contributes significantly to the moisture balance of the region. The fog belt is most pronounced between Moçâmedes and Benguela, where epiphytic lichens reach great abundance in an otherwise desert environment. The Benguela Current also results in a gradient of increasing precipitation from south to north and from west to east. The rainfall gradients are locally accentuated by the **orographic** influence of the escarpment and the highland mountain massifs. The sharp relief of the **Angolan Escarpment** creates conditions for orographic rainfall along most of this zone, supporting the ‘coffee forests’ of Seles, Gabela, Cuanza-Norte and Uíge. The distribution of mean annual precipitation across Angola is summarised in Fig. 5.10. Table 5.1 provides summarised climatic data for selected Ecoregions.

Variability

Average measures of climatic parameters, such as mean annual temperature (MAT) and mean annual precipitation (MAP) are often too simplistic to reflect ecological drivers, where extreme but infrequent events, such as frost, might be of great significance. In 1947, for instance, the cotton crop of the Baixa de Cassange, a perennially hot basin in northern Angola, dropped by 70% because of frost damage (Gouveia, 1956). Finckh et al. (2016) recorded 49 frost nights during the winter of 2013, at a highland site subject to cold air drainage near Cusseque. However, Angola’s long-term meteorological records report the absence or very low incidence of frost activity over most of the country. Based on further research, Finckh et al. (2021) propose that frost is the primary causal factor in determining the treelines of Angolan miombo woodlands and of driving the evolution of geoxyles. This interesting hypothesis deserves testing over a wider range of miombo landscapes than the two study sites (Cusseque and Bicuar) on which it was based.

As described in Sect. 5.8, episodic droughts (such as El Niño events) have had devastating impacts on livestock and wildlife populations across southwest Angola. The distribution of mean annual precipitation across Angola is summarised in Fig. 5.10. Table 5.1 provides summarised climatic data for selected Ecoregions.

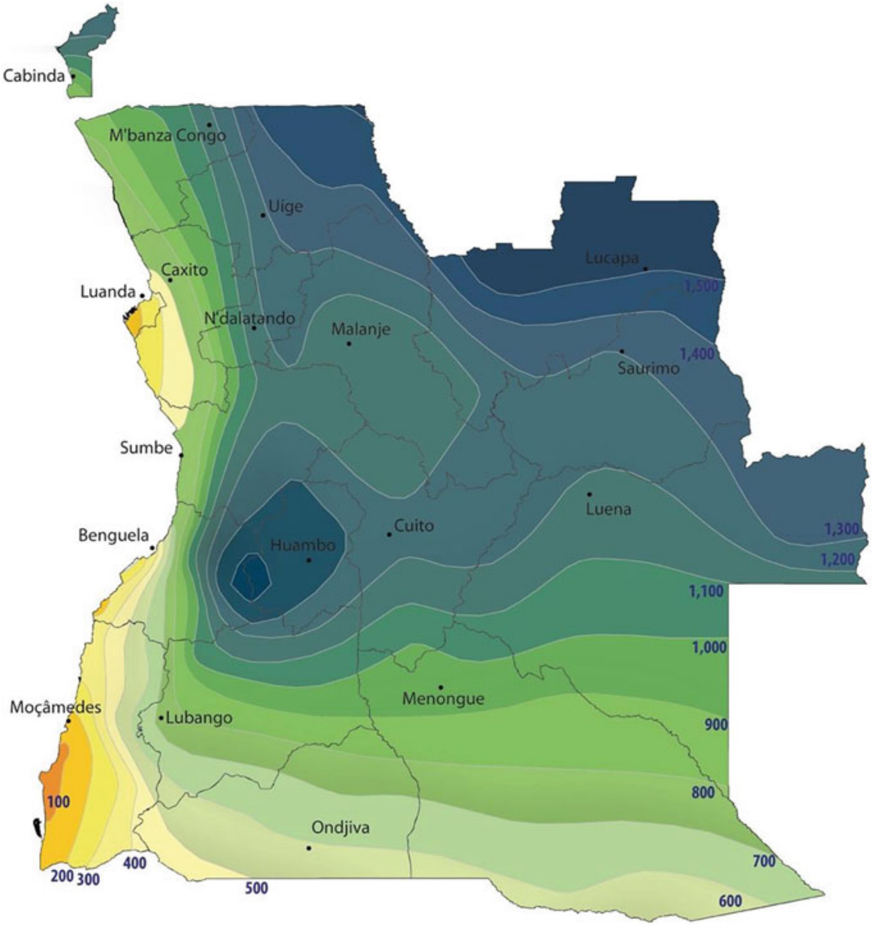

Fig. 5.10 Mean annual precipitation over Angola. From Huntley (2019) *Biodiversity of Angola. Science & Conservation: a Modern Synthesis*. Springer Nature

Like temperature, precipitation in general increases from the poles to the equator, with a dip in the mid-latitudes as described earlier. Rainfall variation is not only spatial, but also temporal. Temporal variations are not only intra-annual, but are also inter-annual, with some years or periods experiencing floods or droughts with exceptionally high or low rainfall and temperature conditions, as illustrated in Fig. 5.25, in Sect. 5.8.

Table 5.1 Summary of climatic data for selected Ecoregions

No.	Ecoregion	Station	Province	Altitude (m)	Mean annual ppt. (mm)	Mean annual temp. (°C)	Mean of hottest month (°C)	Mean of coldest month (°C)
1	Guineo-Congolian Rain Forest	Belize	Cabinda	245	1612	25.2	26.7	22.2
1	Guineo-Congolian Rain Forest	Negage	Uíge	1267	1633	20.6	21.5	19.0
2	Western Congolian Forest/Savanna Mosaic	Sanza Pombo	Uíge	990	1423	24.3	25.5	22.2
3	Southern Congolian Forest/ Savanna Mosaic	Dundo	Lunda-Norte	726	1629	24.6	25.0	23.7
4	Afromontane Forest	Bimbe	Huambo	1777	1541	19.1	20.6	17.8
5	Montane Grassland	Humpata	Huíla	2300	805	14.6	17.2	11.2
6	Angolan Escarpment Savanna	Gabela	Cuanza-Sul	1099	833	19.8	21.6	15.9
7	Angolan Wet Miombo Woodland	Huambo	Huambo	1700	1210	18.8	20.6	15.7
7	Angolan Wet Miombo Woodland	Cuemba	Bié	1300	1476	20.2	22.6	15.2
8	Dry Miombo Woodland	Cuito Cuanavale	C. Cubango	1280	857	21.2	24.3	16.2
9	Zambezian Baikiaea Woodland	Mucusso	C. Cubango	890	774	22.9	26.6	16.0
10	Zambezian Dry Cryptosepalum Forest	Cazombo	Moxico	1180	1441	22.2	24.3	18.8
11	Zambezian Flooded Grasslands	Lumbala Guimbo	Moxico	1131	1126	20.8	23.8	15.1
12	Angolan Mopane Woodland	Chitado	Cunene	1000	405	24.0	27.4	19.2
13	Namib Savanna Woodland	Caraculo	Namibe	440	123	22.9	26.4	17.2
14	Coastal Arid Savanna	Luanda	Bengo	44	405	24.9	27.0	20.1
15	Angolan Namib Desert	Moçâmedes	Namibe	44	37	20.0	24.2	15.5

Data from Silveira (1967) *Climas de Angola.* Serviço Meteorólogico de Angola, Luanda

5.7 Climate as a Determinant of Vegetation Patterns

Global Patterns

Early attempts to understand the global patterns of vegetation (Humboldt & Bonpland, 1805; Schimper, 1903) found a strong correlation between vegetation formations and climate—especially mean annual precipitation (MAP) and mean annual temperature (MAT). Elaborate systems of classifying climate and vegetation were published by the German-Russian climatologist Wladimir Köppen (1900) and American geographers Leslie Holdridge (1947) and Charles Thornthwaite (1948). These scientists mapped the world into regions that were as much a reflection of vegetation pattern as they were of climate. In fact, for many regions where very few climate records were available, vegetation maps were used as a surrogate for climate. Although widely used for many decades, these classifications are less popular today.

In 1975, American ecologist Robert Whittaker plotted biome types (as defined by ecologists) against gradients of MAP and MAT (Fig. 5.11). The results give a generalised model of the relationship, although they omit the importance of disturbance factors such as fire and herbivory, and resource factors such as soils and topography. The Angolan biomes and ecoregions fit well within the patterns presented by Whittaker (1975).

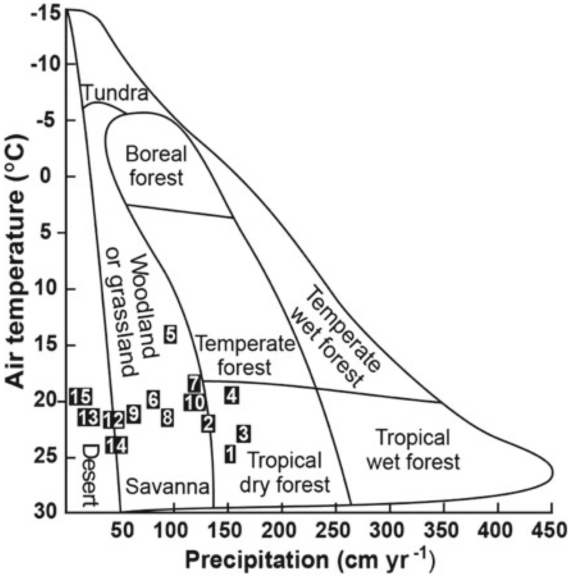

Fig. 5.11 The distribution of global terrestrial biomes in relation to mean annual temperature and precipitation. Numbers within boxes correspond to the MAP and MAT of weather stations within the numbered Angolan ecoregions. The close fit of Angolan biomes and ecoregions with the global model is evident. Redrawn after Whittaker (1975) *Communities and Ecosystems*. McMillan, New York

Continental Patterns

At a continental scale, Angola fits into broader patterns of climate-vegetation relationships. Analyses of climate and tree cover of savanna ecosystems across the globe have revealed that savannas and forests may be alternative stable states in the African tropics (Bond, 2019; Staver et al., 2011) (see Sect. 10.7). Rainfall deterministically results in arid savanna in low rainfall, and rain forest in high rainfall regions. At intermediate rainfall levels, such as between 1200 and 1800 mm in northern Angola, both savanna and forest occur in a mosaic. Tree cover does not increase continuously with rainfall, but is bimodal, with savannas having less than 40–50% and forests more than 75% projected canopy cover (Fig. 5.12). Intermediate levels of tree cover rarely occur.

Above 40–50% canopy cover, shading by tree canopies prevents sufficient photosynthetically active radiation from reaching the ground for C_4 grasses to establish. As a consequence, insufficient grass biomass accumulates to support the hot fires needed to prevent tree saplings from growing to maturity. The canopy cover increases and the feedback enhances canopy density until a new stable state (forest) may be established.

Patterns Across Angola

The strong gradients of mean annual rainfall across Angola are reflected in the distribution of biomes. Nowhere in Angola are radiation and temperature limiting to

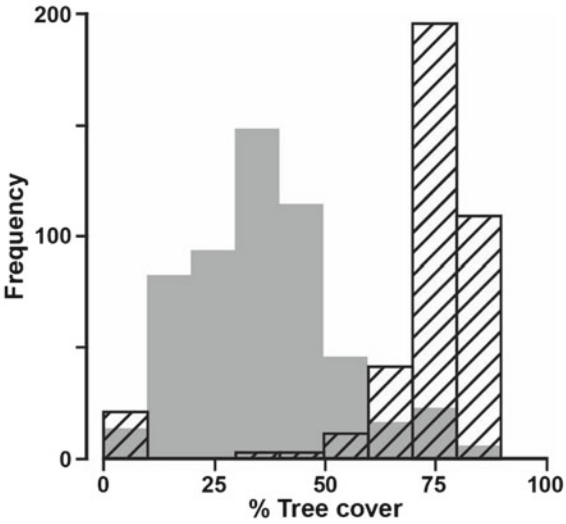

Fig. 5.12 Frequency distributions (y-axis) of the percentage of tree canopy cover (x-axis) in areas of intermediate rainfall (1000–2500 mm MAR) and mild seasonality (dry season <7 months), with fire present (grey bars) and with fire absent (hatched black bars). The canopy cover (0–55%) of fire-tolerant savannas is distinct from fire-intolerant forests (50–90% canopy cover). From Staver et al. (2011) *Science*, 334(6053): 230–2

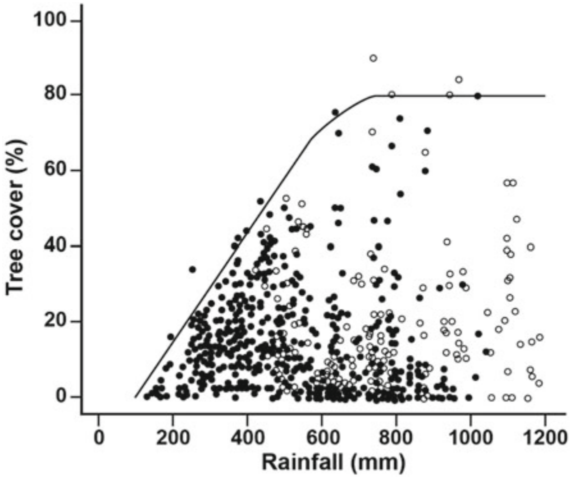

Fig. 5.13 Change in woody cover of African savannas as a function of mean annual rainfall. Below 650 mm MAP, tree cover is limited by rainfall. Above 650 mm MAP, disturbance factors (primarily fire) limit tree cover. Fire frequency indicated by open circles (fire return interval less than 3 yrs); closed circles (return intervals more than 3 yrs). Redrawn from Sankaran et al. (2005) *Nature*, 438: 846–9

tree growth. Rainfall seasonality, however, is a key feature of tropical climates, and in Angola seasonality is strongest in the south and weakest in the north. For most of the country, sufficient rainfall is received for tree growth. Sankaran et al. (2005) used data from over 800 sites across Africa (Fig. 5.13) to demonstrate that the cover of woody plants of savannas is determined by resources (water and nutrients) and disturbance regimes (fire, herbivory). Two patterns were demonstrated:

- At sites with less than 650 mm MAP, maximum tree growth and cover is related linearly to rainfall. Vegetation structure (woody cover) is limited by climate: higher rainfall supports denser maximum tree cover.
- At sites receiving more than 650 mm MAP, structure is determined not by rainfall but by disturbance (fire) that maintains a balance between trees and grasses in a system that is buffered against transition to a closed forest canopy.

These findings, together with similar data-rich studies by Lehmann et al. (2011) of savannas of the southern continents, confirm earlier descriptions of drivers of mesic and arid savannas (Huntley, 1982).

In Angola, in areas receiving more than 1200 mm annual rainfall, closed canopy forests can establish if fire is excluded. However, even in the highest rainfall region, the Maiombe of Cabinda, two to three months without rainfall prevents the total dominance of evergreen trees except along water courses. Semi-deciduous tree species are therefore important components of Angola's moist closed-canopy forests.

Vegetationless dunes, desert grasslands and low shrublands occupy the extremely arid southwest, where trees are rare or absent in areas receiving less than 150 mm

MAP, other than along the ephemeral riverbeds of the Curoca, Bero and Bentiaba, where deep sands retain moisture throughout the year and tall acacia woodlands line the river course. For the remainder of the country, where rainfall ranges from 150 to 1800 mm per annum, three patterns emerge.

- Below ca. 650 mm MAP, arid savannas dominate.
- Above 650 mm MAP, mesic savannas dominate, gradually transitioning into moist savanna/forest mosaics above 1200 mm MAP.
- Above 1400 mm MAP, in the absence of regular fire, moist closed forest will dominate.

Patterns Across Steep Landscape Gradients

One of the world's most striking demonstrations of the influence of macroclimatic factors on vegetation is to be found in southwest Angola. A transect from Humpata in Huíla to Moçâmedes in Namibe, 140 km in distance, provides a classic example of vegetation zonation according to climate (Cardoso et al., 2006; Van Jaarsveld, 2010). The vegetation is best illustrated by a series of photos, from above the Angolan Escarpment at Leba Pass, to the Atlantic Coast (Figs. 5.14, 5.15, 5.16, 5.17, 5.18, 5.19, 5.20).

- The transect begins at 2300 m, at the Zootechnical Research Institute, Humpata, where MAT is 14.6 °C and MAP is 805 mm. Here the vegetation is an open grassland with fragments of Afromontane forest, with species such as *Podocarpus milanjianus, Buxus macowanii, Erythroxylon emarginatum* and *Maytenus acuminata* in ravines protected from frequent fires. Adjoining the grasslands are savannas and woodlands of *Brachystegia spiciformis, Julbernardia paniculata, Burkea africana* and *Ochna pulchra*—a typical mesic/dystrophic savanna.
- At the crest of the Leba Pass, at 1700 m, drier mixed woodlands and thickets, with *Albizia antunesii, Brachylaena huillensis, Combretum apiculatum, Pteleopsis myrtifolia* and *Terminalia sericea*, are dominant.

Fig. 5.14 The zig-zag Leba Pass leading down from the summit of the Chela Escarpment clothed with a dense thicket of *Acacia, Albizia, Commiphora, Spirostachys* and *Terminalia*. *Photo* Ernst van Jaarsveld

Fig. 5.15 Montane Grassland on the Humpata Plateau at 2300 m *Photo* Ernst van Jaarsveld

Fig. 5.16 *Burkea, Brachystegia* Mesic Savanna mixed with Afromontane elements in sheltered valley *Photo* Ernst van Jaarsveld

Fig. 5.17 Succulent caudiciform *Cyphostemma uter*. *Photo* Ernst van Jaarsveld

Fig. 5.18 ‘Dwarf’ baobab *Adansonia digitata* on calcrete pavement of coastal plains, 2 km from the Atlantic Ocean

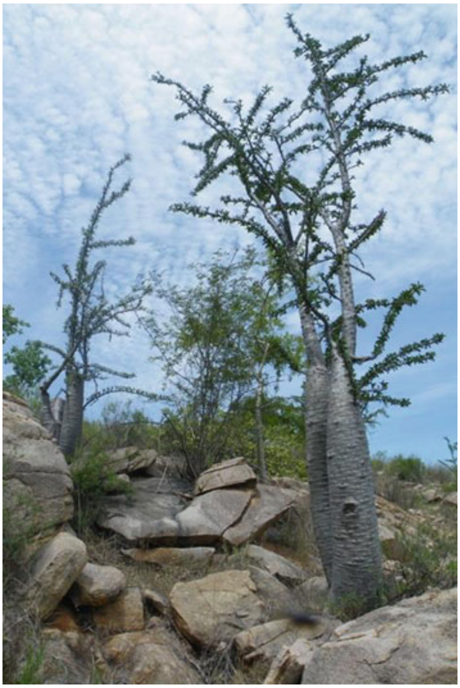

Fig. 5.19 Pachycaul trees of *Pachypodium lealii Photo* Ernst van Jaarsveld

Fig. 5.20 Arid savanna on the margin of the Namib Desert, *Welwitschia* in foreground. *Photo* Ernst van Jaarsveld

- On descending the Escarpment, at 1200 m, one passes into drier woodlands and thickets of *Combretum zeyheri*, *Tarchonanthus camphoratus* and *Ptaeroxylon obliquum*.
- At 850 m *Adansonia digitata* and *Spirostachys africanus* appear.
- At the base of the Escarpment, at 700 m, the MAT increases to 23.8 °C and MAP decreases to 466 mm. The vegetation changes to a *Colophospermum mopane* and *Terminalia prunioides* arid savanna.
- At Caraculo one is already at the margin of the Namib Desert with low *Acacia tortilis*. Here, 50 km from the coast and at 440 m, the MAT is 22.9 °C and the MAP is 123 mm.
- Within 30 km of the Atlantic Ocean, the MAP has dropped to 50 mm. The vegetation transitions into a dwarf shrubland, with ephemeral grasses, tufts of lichen and short succulent (**caduciform**) tree trunks of *Adenium boehmianum*, *Sterculia africana, Catophractes alexandri, Pachypodium lealii, Cyphostemma currorii*, *C. uter* and even dwarf *Adansonia digitata* trees.
- At the coast, 15 m, Moçâmedes has a MAT of 20.0 °C, and a MAP of 37 mm. This is the habitat of *Welwitschia mirabilis*, a true desert ‘miracle plant’ (Box 16.1).

The transect provides the ornithologist with opportunities to see many Angolan bird endemics, from rocky outcrops and scrub at the summit of the Escarpment, where Angola Cave Chat, Swierstra's Francolin, Finsch's Francolin, Angola White-headed Barbet, Angola Slaty Flycatcher, Ludwig's Double-collared Sunbird, Oustalet's Sunbird, Angola Swee Waxbill and Ansorge's Firefinch may appear. As one descends to the base of the Escarpment, Bocage's Akalat, Benguela Long-tailed Starling and Cinderella Waxbill may be found. The altitudinal and climate gradient, reflected by habitat, determines species distribution.

5.8 El Niño, La Niña, Droughts and Floods

Weather patterns are notoriously changeable. Of global importance are the major climatic variations known as **El Niño** or **El Niño-Southern Oscillation** (ENSO), associated with the periodic abnormal warming of the surface waters of the east-central equatorial Pacific and stronger than usual westerly winds, causing a decrease in upwelling of cool water off Peru. This in turn results in the collapse of the normally rich fisheries of the **Humboldt Current**, and in flooding in Peru and Ecuador, as well as in droughts in Indonesia and Australia. A reverse, cool ENSO phase, known as the **La Niña** has opposite effects.

ENSO events occur on average once every four years. In southern Africa, ENSO brings higher temperatures and less rainfall to the region, with negative impacts on agricultural crops and hence on socio-economic conditions. During the 2015/2016 ENSO event, Angola suffered the worst drought in 60 years across the entire country, with the coastal region receiving less than 30% of its normal rainfall (Fig. 5.21).

Droughts and **floods** are not only the result of the El Niño-Southern Oscillation. Change is a constant feature of southern African weather and climate. Over long time scales, exceptional droughts and floods are experienced over southern Africa. Examples include the droughts of 1966, 1971 and more recently, the prolonged drought of 2015–17. Floods occur at frequent intervals. In the Cuvelai Basin, over a period of 64 years, 11 major floods were recorded, while in 21 of the 64 years, there was no surface flow due to abnomally low rainfall (Mendelsohn & Mendelsohn, 2019). The Cunene ran dry at its mouth in 2010, but reached its highest recorded flow in 2011. The Bero and Giraul river floods of 2001 and 2011, which caused severe damage to property and the loss of many lives in Namibe, were triggered by the so-called **Benguela Niño**, when the South Atlantic is warmer than normal and the ITCZ progresses further south, bringing higher than normal rains to the Escarpment and causing flash floods to the lowlands.

Droughts are not only associated with El Niño events. Over southern Africa, drought occurrence is to a large degree associated with multiyear climate variability and follows a cycle of about 18 years in southern Africa (Tyson & Preston-Whyte, 2000). The perceived severity of a drought is also influenced by public opinion. For

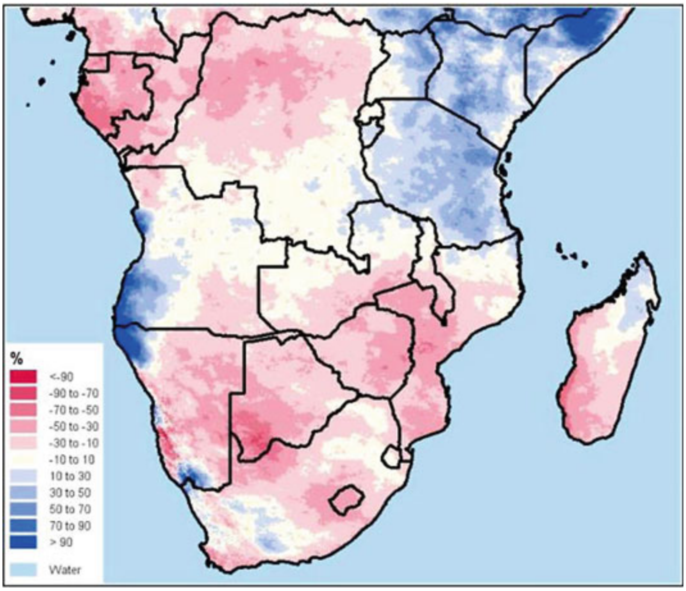

Fig. 5.21 The impact of El Niño on rainfall in southern Africa in the period 1 October 2015 to 11 February 2016. The rainfall for the Angolan coastal region was less than 30% of the long-term average. From Rembold et al. (2016)

much of Africa, rangelands tend to be placed under excessive pressure by pastoralists, and even large national parks are often subject to very high densities of herbivores. The conflation of grazing pressure impacts and perceived drought events is common in media reports. Arid regions are naturally subject to high **coefficients of variation** in inter-annual rainfall. It is often management practices rather than weather that is the driving force. Droughts are less dramatic in their impacts in the mesic savannas of Angola than they are in the arid savannas. Arid savannas reflect event-driven (**stochastic**) rather than **deterministic** ecosystem dynamics (Scholes & Walker, 1993).

In Tsavo National Park, Kenya, and Kruger National Park, South Africa, which have ecosystems very similar to Quiçama National Park and parts of southwest Angola, droughts combined with high herbivore densities have resulted in the massive mortality of both animals and woody plants. In Iona, during 1973, competition between cattle and gemsbok resulted in high mortalities of both**.** In 2009, in sites where boreholes had been provided to supplement water in areas far beyond the normal grazing areas of domestic stock, starving cattle resorted to eating the tough leaves of *Welwitschia mirabilis*, destroying the local populations of these unique desert plants, Fig. 5.22.

Fig. 5.22 Cattle resort to eating the tough leaves of *Welwitschia mirabilis* during a drought in Iona National Park, 2009. *Photo* Bill Branch

In order to distinguish between a perceived drought and an actual extreme climatic event, meteorologists use the **Extreme Climate Index** (ECI). Two statistical components are used to calculate ECI—the Standardised Precipitation Index (SPI) and the Standardised Heatwave Index (SHI). Using the ECI, Malherbe et al. (2020) identified four major drought events in Kruger National Park in the period 1980–2018 (Fig. 5.23). These coincided with El Niño events, and had severe impacts on both vegetation and fauna, influencing forage availability for both grazers and browsers, fuel available for fires, and increased mortalities in buffalo, hippo and other large mammal species. Droughts are sometimes broken by high rainfall episodes, with rapid recovery of annual grasses. The spasm of new plant growth triggers post-drought population **eruptions** (population explosions) such as recorded in rodent and certain bird species such as the nomadic Red-billed Quelea *Quelea quelea*. Coincident with these droughts, Namibia and Angola also suffered severe impacts. However, although dry years were experienced at frequent intervals, only four major extreme droughts were identified within the 40 year period.

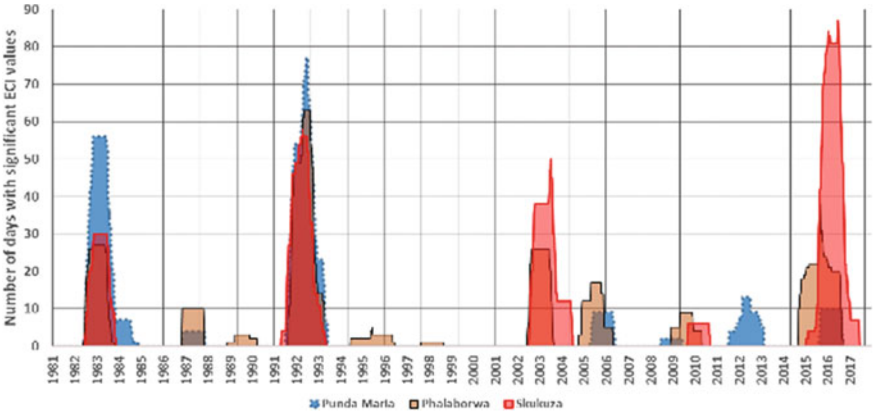

Fig. 5.23 Accumulated number of days within a moving 12-month window, when the Extreme Climate Index exceeded the 90th percentile value for three sites in Kruger National Park. From Malherbe et al. (2020) *African Journal of Range & Forage Science*, 37:1, 1–17

Box 5.1: Human-Environment Interactions: Climate Change and the Impacts of Increasing Atmospheric Carbon Dioxide

The most important and challenging ecological problem of the twenty-first century is that of accelerated global climate change. It is important to recognise that climate change is not a new phenomenon. Major changes in the concentrations of atmospheric oxygen, carbon dioxide and other gases, and the temperature at the Earth's surface, have occurred throughout the hundreds of millions of years since life first appeared on the planet. An example of the extent of climate changes over what is today Angola, is visible in the Cunene valley. During the Permian/Carboniferous period, 300 million years ago, Gondwana was located over the South Pole, and glaciers cut the deep valley of what is now the lower Cunene (Figs. 4.7 and 4.8). Glacial striations can be seen on the rock floor and cliff faces of the river.

Over many millions of years, slight changes in the Earth's tilt, or in its elliptical path around the Sun, result in cycles of climatic conditions that recur at approximately 22,000, 41,000, 100,000 and 413,000 year intervals (**Milankovitch cycles**). These cycles were prominent through the Pleistocene Ice Ages, which will be discussed in Chap. 12 in relation to the biogeography of Angola's rain forests. Global climate change in the twenty-first century, however, is unequivocally due to human activity, in particular the burning of fossil fuels, which release carbon dioxide (CO_2) into the atmosphere (Fig. 5.24). Successive reports by the **Intergovernmental Panel on Climate Change** (IPCC) confirm global trends, which document a human-induced warming of 1.5 °C since pre-industrial times. Projections suggest that warming will grow to 3 °C by 2100. Impacts will differ from one region to another, with the polar regions warming more than the tropics (IPCC, 2019). The speed of change is as alarming as its magnitude. Current rates are 100 times the speed of temperature changes that occurred between the cool and warm periods of the Pleistocene Ice Ages. This has implications for the ability of plants and animals to adapt to rapidly-changing climates and environments.

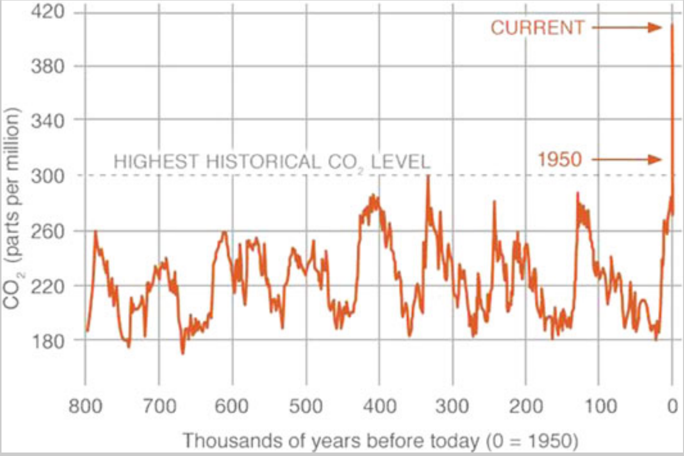

Fig. 5.24 Atmospheric carbon dioxide levels over the past 800,000 years, based on ice core data. From NOAA

The driver of the current pace of climate change is popularly called the **greenhouse effect**. The Earth reflects some of the energy it receives from the Sun back into the lower atmosphere. Here some of the energy is absorbed by **water vapour** and **carbon dioxide** (termed **greenhouse gases)** and some of this energy is once more reflected back to Earth. The greenhouse gases provide a thin envelope around the planet which maintains the Earth's temperature. As a result of this thin but effective shield, the Earth is a much cooler body than the Sun, with an average temperature of only 15 °C. Without the protective envelope of greenhouse gases, the Earth would lose energy and become an icy planet like Mars.

The term 'greenhouse effect' needs explanation. It comes from the similarity in the processes of temperature increase experienced within a nursery **greenhouse**—or a parked car—on a sunny day. In an analogy with the gases that form an envelope around the globe, incoming **shortwave radiation** passes through the glass windows of a greenhouse or a car, but cannot escape because outgoing **longwave radiation** cannot pass through glass. The air temperature within the greenhouse, car, or the Earth's lower atmosphere, rises rapidly. The ecological consequences of **global warming,** and of increasing atmospheric carbon dioxide and other greenhouse gas concentrations which are driving the warming, are of serious global concern.

A recent study (Carvalho et al., 2017) provides the first analysis and comparison of a set of four **Regional Climate Models** (RCMs) that include Angola. Scenarios of future temperature and precipitation anomaly trends, and the frequency and intensity of droughts, are presented for the twenty-first century. Consistent results were found for temperature projections, with an increase of up to 4.9 °C by 2100. The temperature increases are lowest for the northern coastal areas and highest for the southeast of Angola. In contrast to temperature rises, precipitation was projected to fall over the century, with an average of −2% across the country. The strongest change was projected for the southeast, with decreases of as much as −4%. The central coastal region is expected to have a slight increase in precipitation. More recent models for southern Africa (Engelbrecht and Monteiro (2021), Fig. 5.25, suggest even more extreme warming and drying than the projections described by Carvalho et al. (2017).

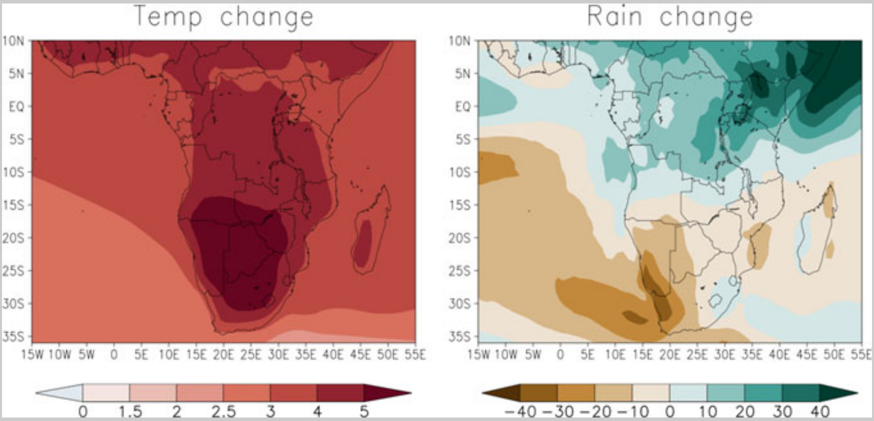

Fig. 5.25 Projected spatial patterns of change in annual average temperature (°C) and annual average precipitation (expressed as a percentage change) for the period 2081–2100 relative to the period 1979–2014, as assessed from the ensemble average of 30 global climate models that contributed to the Coupled Model Intercomparison Project Phase Six under the low mitigation scenario SSP5-8.5. From Engelbrecht and Monteiro (2021). *South African Journal of Science*: 117

The IPCC and RCM projections focus on changes in temperature and precipitation. Of ecological interest is the influence that increases in atmospheric carbon dioxide concentrations will have on photosynthesis and soil water balance. CO_2 concentrations were at 285 parts per million (ppm) in 1850, rising to 300 ppm by 1900 and 410 ppm by 2018. They are projected to reach 700 ppm by 2100. As we will see in Chap. 14, African savannas are dominated by C_4 grasses, and have been so since the C_4 photosynthetic pathway evolved about 30 million years ago, in response to an increasingly arid and low CO_2 environment. Trees, which are C_3 species, will benefit from increasing CO_2 concentrations, and might out-compete C_4 grasses. Some researchers predict a major expansion of forests at the expense of grassy savannas due to the increase in woody C_3 species. Other models suggest that an increase in fires due to global warming will maintain savannas. However, other factors apart from climate also determine the balance between C_3 and C_4 plants and ecosystem composition, including rangeland management practices and agriculture. The future remains uncertain, emphasising the urgency for increased ecological research.

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Chapter 6
Soil, Water and Nutrients

Key Concepts and Questions: This Chapter Explains

- *How soils develop and what their critical roles are as the sources of moisture and nutrients for plants and in turn for animals.*
- *How soils vary in physical and chemical properties and in the vegetation that they support.*
- *How the main soil types are classified and where they occur in Angola.*
- *Why over half of Angola's land surface is covered by infertile Kalahari sands, yet these nutrient-poor soils carry dense grasslands and woodlands.*

Context: Soils, Plant Growth and Soil Types

Soil is the substrate in which plants grow, where water and nutrients are cycled, and where the remains of plants and animals are transformed into their basic elements through the process of decomposition and mineralisation, mediated by fungi and bacteria that live in the soil. An understanding of the processes of soil development, and of the interactions of soil chemistry and physics to yield soil properties, is a necessary basis to answering questions about why plants grow where they do, and what root, stem and shoot structures they develop. This chapter examines the physical and chemical weathering processes, and the mechanisms that determine the availability of water and nutrients to the root hairs and leaf stomata of plants—where the transfers of moisture, nutrients and gases take place.

Soils are typically formed in situ, but in Angola, erosion and transport of soil and mineral particles by water and wind results in the current distribution of vast areas of sand that covers over one half of the country. These are known as the Kalahari sands. Like vegetation, soils have been classified into several dozen main Soil Groups. These serve as points of reference in any discussion of the ecology of Angola's ecosystems, and how they relate to the soils of other regions of Africa and the globe.

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https://doi.org/10.1007/978-3-031-18923-4_6

6.1 Soil Structure

A first step in understanding soils is to examine their **profile**—exposed on a roadside cutting or by digging a soil pit (Fig. 6.1). Soils display a succession of layers, or **horizons**, that might or might not be present in any one soil type. From top to bottom these are the O—**organic horizon**, comprising accumulated organic material; A—**top soil**, with high biological activity, comprising a mix of organic and mineral material; B—**subsoil**, with a concentration of silicate clay, **sesquioxides** (oxides of iron and aluminium) and organic matter; C—the unconsolidated **weathered regolith** extending down to the bedrock. Once a soil pit has been dug, one can sample the horizons and, using simple criteria such as **texture** and **colour**, identify the type, and proceed to analyse the important properties of soil **moisture holding capacity** and **ion-exchange capacity.**

The soil profile is influenced by several processes relating to drainage. **Eluviation** refers to the removal of mineral or organic soil material in suspension or solution from part of, or the whole horizon. **Leaching** refers specifically to removal of nutrients in solution. **Illuviation** is the deposition of soil material removed by percolating water from one part of the soil profile to another. The importance of these processes is discussed in Box 14.1.

Different **soil colours** result from their organic content (black), oxides (red, purple), minerals (white, grey) and drainage (mottled). While colour is useful in soil description, it has little influence on plant growth and survival. However, soil colour can be an excellent indicator of soil drainage which is a major factor influencing vegetation structure and composition in many African landscapes:

- Red soils indicate free drainage.
- Yellow soils indicate slightly impeded drainage, implying more available moisture than red soils, but generally not waterlogged.

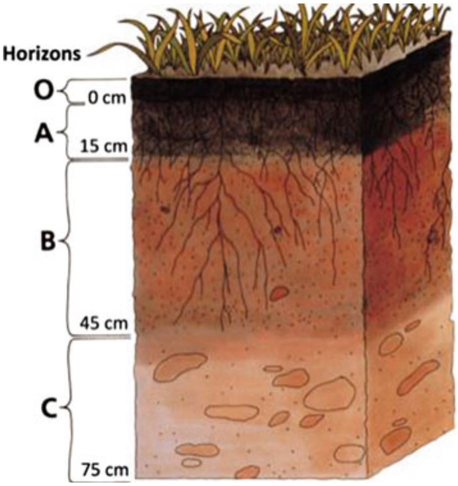


Fig. 6.1 A typical soil profile illustrating the main horizons. O = organic horizon; A = top soil; B = subsoil; C = weathered regolith. Creative Commons Attribution 4.0

- Grey subsoils indicate poor drainage, producing anoxic conditions which limit rooting depth.
- Mottled soils indicate frequently changing depths of a water table with both oxygenated and reduced soil atmospheres.

Soil texture is an important soil characteristic as it influences water flow and nutrient availability. **Soil texture** is defined by the relative proportions by weight of three main constituents—sand, silt and clay. It is the **pore space** within soil that determines the movement of air and water in the soil through its porosity and permeability, and access to these by plant roots. Soils with 50% of their volume as pore space provide optimal conditions for root access to air, water and nutrients. Coarse sandy soils allow rapid water infiltration and drainage, and very fine clayey soils might be poorly aerated and easily compacted. Soil scientists (**pedologists**) use a simple model to classify texture (Fig. 6.2), and a standard **Munsell** chart to describe colour.

A further characteristic of soil structure relates to the type of **clay minerals** found in them. Two types are of particular importance: Shrink/swell clays (2:1 **montmorillonite** or **smectites**), and non-shrink/swell clays (1:1 **kaolin**). The 2:1 and 1:1 sign relates to the atomic structure of their minerals. Kaolin, produced by the chemical weathering of aluminium silicate minerals in moist tropical climates, has low cation-exchange capacity and often has reddish colouration from iron oxides, typical of ferralsols. Montmorillonites develop in more arid climates, have high sodium content, and are dark coloured. On wetting, montmorillonite clays can expand to three times their dry structure, characterising vertisols. This swelling and shrinking limits woody plant growth due to the shearing of roots, and accounts for the extensive

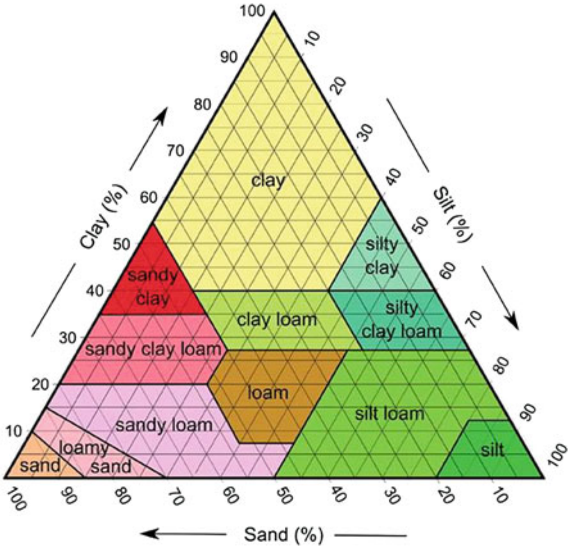


Fig. 6.2 A soil texture chart showing the percentages of clay (less than 0.0002 mm diameter), silt (0.002–0.05 mm) and sand (0.05–2.00 mm) in the basic soil textural classes. For example, a soil with 60% sand, 30% silt and 20% clay would be classified as sandy loam. Creative Commons Attribution 4.0

treeless *Setaria welwitschii* grasslands of the '*terras de Catete*' that occupy much of Quiçama National Park (Figs. 3.35 and 15.11).

6.2 Development of Soil: Weathering and Pedogenesis

Soil is comprised of mineral and organic constituents, water and air. It is the product of the weathering of unconsolidated rocks and minerals, with the addition of nutrients and chemical components derived from organic materials. Soil has been appropriately described as 'the epidermis of the Earth'.

Weathering comprises physical, chemical and biological processes. Five factors influence the weathering of the geological substrate and the development of soil.

- **Parent material**. The weathering of the geological **bedrock** in hot wet climates, such as Angola's, forms **saprolite**. The weathered saprolite layer is referred to as the **regolith**. It can be very shallow or absent as on steep rocky slopes, or up to 100 m in depth on flat relief. Geological substrates determine the mineral constituents from which the soil develops, and the associated soil properties such as soil structure, texture, porosity and permeability. As examples, **granites** produce acidic, low-nutrient soils, while **basalts** produce **basic soils** with higher nutrient status.
- **Climate** is the driving force of most soil formation processes. Across the 1270 km of Angola's latitude, the climate varies dramatically, and therefore the end product of the soil development process is strongly influenced by local temperature and precipitation. The impact of **leaching** of soluble nutrients through the soil is particularly important in the higher rainfall regions of Angola. In general, lower temperatures and drier climates have slower soil development; warmer, wetter climates have faster rates and deeper soil development.
- **Biological composition** of soils, from micro-organisms to the plants and animals occupying the soils, is influenced by and in turn influences the nature of soil developed, particularly in forest/grassland mosaics. Plant roots actively mine soils for phosphorus and can increase weathering rates by an order of magnitude. Vegetation cover also influences weathering rates, with faster rates under forests and slower rates under grassland.
- **Topography** plays a critical role in the movement and nature of soils—from shallow gravels on steep, rapidly eroding mountain slopes—to deep alluvial soils that accumulate on bottomlands and river valleys.
- **Time** is required for the slow physical, chemical and biological processes needed to develop individual soil types. Soils typically require from 2000 to 20,000 years to form, yet a landscape's soil mantle can be swept away within decades by erosion due to injudicious land management.

The products of weathering develop further through soil formation processes (**pedogenesis**) which vary according to substrate, climate, vegetation and hydrology.

Five main soil types, resulting from distinctive pedogenetic processes are recognised in Angola. Some of the terms introduced here are defined in Sect. 6.7.

- **Laterite** soils are common across the **humid tropics** of the world where precipitation exceeds evaporation. Rapid chemical weathering of rocks and minerals results from a hot, wet climate, with leaching of nutrients out of the soils. Lateritic soils are characterised by low organic matter, high **eluviation** and a lack of soil structure. Eluviation is the movement of dissolved mineral and organic material from one layer in a soil profile to another layer. Oxides of iron and aluminium (**sesquioxides**) are not leached, and they accumulate, as displayed by the red colour (through the oxidation of iron) in the **ferrallitic** soils (ferralsols—that include lateritic soils) that dominate much of the Angolan plateau. Over the millions of years in which soils have formed on the extensive planation surfaces of the African plateau, thick hard crusts—**duricrusts**—have formed by chemical processes. These occur at or just below the soil surface and may be from centimetres to several metres thick. Duricrusts are resistant to water penetration because they are **indurated** (resistant to crumbling or powdering). The three most common duricrust types are **laterites, calcretes** and **silcretes**.
- **Calcified** soils occur in semi-arid subtropical climates, where evaporation exceeds precipitation and where the water table fluctuates through the seasons. Evaporation causes an upward movement of dissolved alkaline salts, typically calcium carbonate, from the groundwater. The upward movement is countered by a downward movement as rain water moves the salts down the soil profile. This results in gentle leaching and eluviation, resulting in a light-coloured soil. A **hardpan** or **calcrete** layer may be formed in the subsoil. Calcrete pavements occur across much of the coastal peneplains of Benguela and Namibe provinces. **Silcrete** is formed in a similar manner, when sand and gravel are cemented together by dissolved silica. Silcretes are found in both coastal and interior sandy **arenosols**.
- **Salinised** soils follow the evaporative process described for calcification, but with the salt deposits accumulating on the surface. This typically occurs in arid regions, where evaporation exceeds precipitation, with a negative water balance, especially where internal drainage (**endorheic**) basins receive mineral-rich water, such as Etosha Pan in Namibia. Examples of salinization can be seen at Gunza in Quiçama National Park (Fig. 6.3) and along the Curoca valley in Namibe.
- **Podzol** soils are typically found in the cool, moist climates of temperate zones, where precipitation exceeds evaporation, and where coniferous forests dominate, resulting in acidic, strongly leached soils with a white/grey E horizon and a dark brown B horizon. The accumulation of organic matter creates a strongly acidic soil solution that results in heavy leaching of cations, including the sesquioxides of aluminium and iron, from the topsoil. Podzols typically have a pale grey to white layer in the A horizon with a dark iron-humus (ferrihumic) B horizon. In Angola, podzols occur on the wetlands of cool moist valleys of higher regions of Bié and Huambo.
- **Gley** soils occur in poorly drained, clay-dominated areas such as wetlands and footslopes in areas of high rainfall, where the decomposition of abundant organic

Fig. 6.3 A soil profile at Gunza, Quiçama National Park, illustrating the formation of soils under changing climatic conditions. The upper profile is most probably a Cambisol, formed through colluvial deposits of material washed down from the nearby hills. The white lower profile comprises sodium chloride, rising by capillary action from an adjacent stream during long dry seasons. The deep salt horizon might have accumulated during an arid period of the Pleistocene, with the colluvial horizon forming during a wetter period. *Photo* Antonio Martins

matter is very slow, and organic acids accumulate. Under anaerobic conditions, iron oxides are in their reduced ferrous form which is black (rather than in oxygenated soils with red ferric iron oxide), resulting in black to bluish colouration and a characteristic 'rotten egg' smell. Extensive areas of gleysols occur in the Moxico and Cuando Cubango provinces, such as the Bulozi Floodplain.

6.3 Soil Water Relations

Water Availability

Water is essential for all life on Earth. Too much water, or too little water, can be fatal. Most plants (and animals) are largely composed of water, but even at close to 95% of plant mass, the water within a plant at any time represents a minor fraction of that which passes through the plant during growth, carrying nutrients and providing a moist surface for the transfer of gases in photosynthesis. Carbon dioxide enters a plant through the tiny pores (**stomata**) on leaves, simultaneously allowing moisture and oxygen to escape during the respiration phase of photosynthesis. A fine balance must be reached between gas and moisture exchange processes during transpiration, photosynthesis and respiration. Soil is the medium that holds and makes water available to living organisms.

Rain falling on the soil surface drains through the soil, but much is held against gravity by **capillary forces**. The size and distribution of soil pores determines the passage of rainwater through the soil profile. Penetration by **infiltration** might be rapid in sandy soils, with large pore spaces, but slow in clayey soils. Clay soils have very fine pores and hold much more moisture per unit volume than do sandy soils. However, the higher water content of clay soils does not mean higher water availability to plants. The moisture in clay soils is held tightly by the **surface tension** of the fine grains and by chemical bonding, and it is thus not as accessible to the root hairs of plants as is the moisture in sandy soils. Plants growing on clayey soils can suffer from **physiological drought**, unable to access the moisture which is held tightly by the strong **capillary forces** of the fine clay particles.

Pore Spaces in Clays and Sands

If all pore spaces are filled to overflowing, the soil is **saturated**. If all pore spaces remain full after excess rain has drained off, with **capillary water** being held within the profile by capillary forces, the soil is said to be at **field capacity**—measured as the weight of water held in soil expressed as a percentage of the oven-dried soil weight. As a general rule, pore space increases as soils become finer. Clayey soils, with up to 60% pore space by volume, have higher field capacity than sandy soils, with 30% pore space. Water is lost from the soil profile by gravitational drainage to the **water table**, by the transpiration of growing plants and by evaporation.

Evaporative loss from sandy soils is restricted by its coarse texture, and water below 30 cm depth in sandy soil is reasonably protected from such evaporative loss. In contrast, the higher water-holding capacity of fine textured (clayey) soils results in the water being held nearer the soil surface, which leads to more water being lost from the soil due to evaporation, with less available for plant uptake. Clayey soils are thus generally drier and hold less oxygen than sandy soils. Swelling clays (common in drier climates, such as the '*terras de Catete*' of Quiçama), restrict water infiltration more than the ferralsols of the more humid climate of miombo mesic savannas.

Once capillary water is no longer available to a plant, it has reached its **wilting point**. The difference in the amount of water held in soil at field capacity and wilting point is known as the **plant available water capacity** of the soil. Soil texture thus determines available water capacity. Clays have a higher surface area to volume ratio than do sandy soils, and thus hold moisture more tightly than do sands (Fig. 6.4).

Water Movement from Root Hairs to Leaf Stomata

Within the plant, the water status is expressed in terms of the **turgor** pressure—which is the pressure exerted by the water in the cell against the cell wall. Wilting occurs when the turgor drops in response to dehydration within the plant xylem. Plants must draw water upwards from the soil, via their roots, stems and shoots, to retain turgor. The gradient in water along the soil/plant/atmosphere continuum is measured as **water potential**. In simple terms, if the atmosphere surrounding the plant leaf is saturated (relative humidity 100%) and the soil is at field capacity, the gradient of water potential is zero. If the gradient increases, with water loss via the leaf stomata, a transfer of water will occur along the gradient from the area of higher water potential to the area of lower water potential from soil to root hairs to leaves. As the available water in the soil declines, the water potential gradient between soil/plant/atmosphere increases. Eventually the leaf stomata close until the soil water potential again rises. The ability to maximise photosynthesis while minimising water loss via stomata

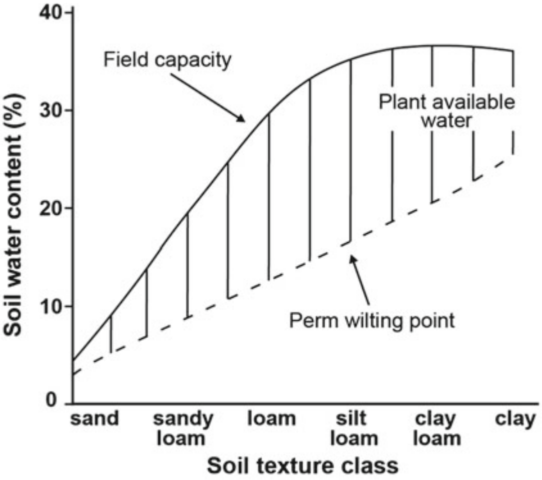


Fig. 6.4 Plant available water of different soils at permanent wilting point and at field capacity. The soils differ in texture from coarse-textured sand to fine-textured clay. Plant available water is defined as the difference between field capacity and wilting point. Both field capacity and wilting point increase from coarse- to fine-textured soils, and the highest available water capacity is in the intermediate-textured soils

(transpiration) varies greatly between plants growing in different environments. The ratio of carbon fixed through photosynthesis to water lost by transpiration is called **water use efficiency**. As described in Sect. 10.2, C4 grasses are more water efficient than are C_3 grasses, accounting for the success of C_4 grasses in seasonally dry tropical savannas.

Responses to Rainfall Seasonality

Available water regulates a plant's access to moisture and nutrients. Seasonality of rainfall is a feature of Angola's climate, and is a key characteristic of deciduousness, whether in the closed forests of the Maiombe or the mesic and arid savannas that make up the major proportion of the country's vegetation. The pattern of hot wet summers and mild dry winters brings with it several months during which the moisture essential for plant growth is limited or even absent in the soil, which might drop below wilting point for extended periods. Furthermore, nutrients cannot be transported in the absence of available water. Trees grow tap roots for accessing water at deep levels, and fine roots close to the soil surface for nutrient uptake. This dimorphic rooting strategy also provides for the use of shallow roots for water uptake in the rain season, and for tap roots to draw on deeper resources during the dry season. As a further conservation strategy, trees in mesic savannas (miombo) conserve nutrients by withdrawing them from their leaves into their terminal branches before leaf fall, which usually occurs before the first rains. In mesic savannas leaf fall is immediately followed by a flush of new leaves, made possible by drawing on water reserves held within the plant, and with the new growth appearing before the rains.

Rainfall Interception

It is important to note that trees, grasses and litter have important impacts on the amount of water reaching the root zone of soils. The process whereby plants redistribute rain falling onto them (through evaporation or stem-flow) is known as **interception**. An example of the effects of interception on the water budget of mesic savanna on sandy soils is drawn from the Savanna Ecosystem Project at Nylsvley (Scholes & Walker, 1993). In this field study, of the total incoming rainfall: 47% evaporated from the soil surface; 36% was lost via transpiration (trees 21%, grass 15%); 15% was lost by evaporation from interception (by trees 6%, grass 3% and litter 7%); and only 1% infiltrated to the water table. No water was lost to runoff on the sandy soils. The study demonstrated that in broadleaf savannas, only one third of incoming rainfall is lost through the plant metabolic processes via transpiration, with the rest lost to evaporation from plant, litter and soil surfaces.

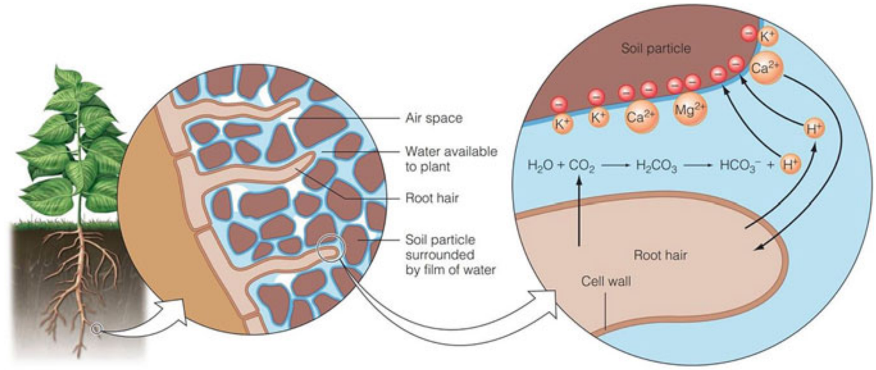
6.4 Soil Chemistry and Nutrient Status

Macro- and Micro-nutrients

The water in soil provides the medium in which chemicals dissolve to form an exchangeable nutrient solution, available for uptake by plants. Both water and mineral-derived nutrients are extracted from soil by the root hairs. Root systems are designed to forage for both water and nutrients according to their distribution in the soil profile. Some nutrients are needed in large amounts. These are called **macronutrients** and include carbon (C), hydrogen (H), oxygen (O)—(the basic constituents of all organic matter), nitrogen (N), calcium (Ca), phosphorus (P), magnesium (Mg), sulphur (S) and potassium (K). Nitrogen is fixed by living organisms from atmospheric nitrogen and is not derived from the geological parent material of soils. **Micronutrients** (trace elements) are needed in very small quantities for plant growth, and include chlorine (Cl), iron (Fe), manganese (Mn), boron (B), copper (Cu), molybdenum (Mo), zinc (Zn) and nickel (Ni). At high concentrations, some micronutrients such as copper and aluminium can be toxic for plant growth.

Ions: Positive Cations and Negative Anions

Nutrients comprise oppositely charged particles known as **ions**: those with a positive charge are **cations** (such as calcium Ca^{2+}, magnesium Mg^{2+}, potassium K^{+}, sodium Na^{+} and ammonium (NH_4^{+}); those with a negative charge are **anions** (chloride Cl^{-}, nitrate NO_3^{-}, phosphate PO_3^{-}, carbonate CO_3^{-} and sulphate SO_4^{-}). These ions bind with negatively and positively charged sites on soil particles, the availability of which is called the **ion exchange capacity**. Negatively charged mineral or organic soil aggregates are called **colloids**. Colloids are the most active constituents of soils and determine the physical and chemical properties of the soil. The total number of negatively charged sites on clay and organic matter particles is referred to as the **cation exchange capacity (CEC)** and the CEC of the soil is closely linked to its



(a) Water film around soil particles **(b)** Cation exchange in soil

Fig. 6.5 The process of cation exchange in soils. Cations occupying the negatively charged particles in the soil are in a state of dynamic equilibrium with similar cations in the soil solution. Cations in the soil solution are continuously being replaced by or exchanged with cations on clay and humus particles. Cations in the soil solution are also taken up by plants and leached to ground and surface waters. From Smith and Smith (2015) *Elements of Ecology* (9th Edition). Pearson, Boston

total clay content. Most soils contain more negatively charged sites than positively charged sites, resulting in anions such as nitrate and phosphate being leached if not absorbed by plants. Like soil texture and water retaining capacity, the CEC is an essential measure of soil agricultural quality. The process of cation exchange in soils is illustrated in Fig. 6.5.

Bases, Base Status and Leaching

The importance of the negatively charged particles is that they prevent **leaching** of positively charged nutrient cations (e.g. calcium, magnesium, potassium and sodium). The cations are collectively known as 'bases' (derived from the base or alkali metals) and are lost from the ecosystem through leaching. The '**base saturation**' is the percentage of the soil cation exchange capacity filled with bases. This measure decreases with increasing rainfall and increasing weathering intensity, thus the soils of arid savannas have a higher base saturation than those of the mesic savannas and forests. In some arid savanna soils, the bases exceed the CEC and the excess of salts can precipitate as calcrete, saline or sodic horizons.

Dystrophic, Mesotrophic and Eutrophic Soils

A general measure of soil nutrient properties is its **base status** (also referred to as the S-value)—essentially the sum of its exchangeable Ca, Mg, Na and K. **Dystrophic** (low base status) soils have a sum of exchangeable (as opposed to soluble) Ca, Mg, Na and K, of below 5 milli-equivalents/100 g clay. These are highly leached soils, such as those of much of the miombo systems (mesic/dystrophic savanna) of Angola's planalto. **Eutrophic** soils have a high base status (exchangeable cations of more than 15 milli-equivalents/100 g clay). Eutrophic soils are typically found in the arid lowlands of southwest Angola and along the coast—the arid/eutrophic savannas. **Mesotrophic** soils have exchange capacities of between 5 and 15 me/100 g clay (MacVicar et al., 1977). Much of the Escarpment has mesotrophic soils, which are good for agricultural production.

Soil pH: Measures of Acidity and Basicity

An important soil characteristic is that of **pH**, a measure of **acidity** or **basicity**, which is controlled by its CEC. Rainwater and acids from organic matter in the soil increase the concentration of hydrogen ions in the soil, and displace other cations such as calcium on the soil exchange sites. Increasing hydrogen ions relative to other cations result in the soil becoming increasingly acidic. Soil pH is defined as the negative logarithm of the hydrogen ion concentration. Soil pH ranges from pH 3 (extremely acid), pH 7 (neutral) to pH 9 (strongly alkaline). Acid soils, such as most of the soils of the Angolan plateau and interior, have high levels of exchangeable aluminium cations, which can reach concentrations toxic to agricultural crops. Aluminium toxicity damages plant root systems, reducing their ability to take up nutrients. Neutral or slightly alkaline soils are developed from limestones, such as those along parts of the coastal belt, where marine sediments of the Cuanza and Benguela basins occupy large areas. Soil acidity has a very strong influence on the species of plants found at any one place, and on the ecological processes involved in shaping Angola's ecosystems.

Mineralisation

Within terrestrial ecosystems, the most important nutrients to plant growth, ecosystem structure and production, are nitrogen and phosphorus. These are found in organic form (as part of carbon-based molecules) in dead plant and animal matter. This bonding with carbon needs to be broken (mineralised) for N and P to be released as inorganic N and P, and thus become available for uptake by organisms in ionic form. **Mineralisation** dominates both the nitrogen and phosphorus cycles in savannas and is in turn controlled by water availability and temperature. Scholes and Walker (1993) consider that the key linkage between rainfall and primary production in savannas such as the broad-leaf *Burkea africana* ecosystem at Nylsvley (which is a species-poor form of miombo) probably operates via the influence of water availability on the nitrogen and phosphorus cycles, which in turn determine the carbon cycle and hence photosynthesis and primary productivity. The interactions between light, water, soil, chemicals, physical properties, plant structure and growth, and the microbial communities that drive mineralisation processes, demonstrate the complexity of even the simplest ecosystem. The role of micro-organisms in the mineralisation process is discussed in Sect. 10.6.

6.5 Soils and Tree Growth

Soils are a fundamental necessity for the growth of all but highly specialised plants such as epiphytes and parasites. Trees require soils deep enough to ensure sufficient root volumes to provide water, nutrients and anchorage. Trees, on average, require a rooting depth of 7.5 m, shrubs require 5.1 m, and grasses 2.6 m. Many Angolan ferralsols have hardpan (**duricrust**) horizons within a metre of the soil surface, which limit the size of trees that can grow on them due to the alternation of waterlogging during the rains and excessive dehydration during the dry season. Some vertisols comprise swelling-shrinking clays which damage tree roots but do not damage the shallow, fibrous roots of grasses. Gleysols are seasonally waterlogged, creating anoxic conditions that prevent tree growth. In areas receiving less than 250 mm annual rainfall, dominated by arid tropical calcisols, water constraints prevent anything more than scattered trees becoming established, except in the deep sands of ephemeral rivers which can support dense groves of tall acacias, figs and tamarisks. But for most Angolan soils, conditions are favourable for tree growth in the absence of recurrent fires. The role of soils in determining the patterns of vegetation in Angola will be discussed more fully in Part IV, specifically in Box 14.1. Most important for Angola's human wellbeing is the maintenance of soil fertility and productive potential. The loss of this potential over much of Angola's most productive land is a cause for serious concern, and a topic that requires fundamental ecological knowledge to reverse. The problems of soil deterioration and land degradation are discussed in Box 6.1.

Box 6.1: Human–Environment Interactions: Livelihoods and Land Degradation

> Almost everything that man eats and wears is derived ultimately from plant food retained in the thin envelope of topsoil … The good health of this layer is therefore of vital importance to the prosperity of mankind. Elspeth Huxley (1937).

Huxley's words, and her description of the problems and processes relating to poor land management, are as pertinent today as they were over 85 years ago. Indeed, the IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security and Greenhouse Gas fluxes in Terrestrial Ecosystems (IPCC, 2019) echo her words.

The IPCC report concludes that land degradation is rampant across Africa, and occurs on 46% of the total land area. Land degradation and climate change reinforce each other, creating serious implications for food security, biodiversity and livelihoods in Africa. The main drivers of land degradation include demographic growth, social displacement due to conflicts, inappropriate soil management, deforestation, shifting cultivation, insecurity of land tenure, and intrinsic features of fragile soils. Further, land use change through clearing of woodlands is a major source of greenhouse gas emissions from both plant biomass and soil organic carbon. All these IPCC conclusions apply to Angola.

Land degradation refers to the loss of the productive capacity of soils characterised by loss of soil fertility, biodiversity and overall deterioration of natural resources. **Soil erosion** is a key component of land degradation, and involves the relocation and loss of soil within or from a field, a decline in organic matter, in soil structure, in nutrient content and in soil fertility. It is one of the greatest threats to the production capacity and sustainability of agriculture and of rural livelihoods. A distinction can be made between **deforestation** (where trees are clear-felled over a given area) and woodland or forest **degradation** (where trees are selectively removed for construction timber, charcoal production or other uses).

Few county-wide studies of land degradation and soil erosion and their socio-economic impacts have been conducted in Angola. However, the use of satellite imagery has made some general measures possible. Schneibel et al. (2018) and Mendelsohn (2019) provide syntheses of available knowledge, and demonstrate the widespread deterioration of forest and woodland cover, and of trends in soil erosion, in Angola. While much of the Huambo, Bié and Huíla planalto was cleared in the colonial era for crop farming, the rate of deforestation has accelerated since independence, especially since the peace accords of 2002, after which many displaced rural people returned to their original homesteads. Most alarming is the finding that woodland cover in Huambo fell from 78% in 2002 to 48% in 2015 (Palacios et al., 2015). Similar trends are being witnessed across northern, central and southeastern provinces.

Small-scale subsistence farming by rural communities is based on the shifting cultivation (slash-and-burn) process. Due to land pressures on the heavily populated planalto, cultivated fields are no longer being given time to recover their nutrient and soil carbon reserves between planting seasons. The change from the tradition of shifting cultivation to semipermanent to permanent rainfed cultivation is contributing to the exhaustion of soil nutrients and decrease in food production potential. Furthermore, regular fires remove the vegetation cover that protects the topsoil from erosion by wind and rain. The result is a rapid loss of food production, loss of cash crop income and heightened levels of rural poverty.

In a detailed time-step analysis of Landsat imagery from 1989–2013, Schneibel et al. (2016) found a steady increase in the area of woodland cleared, mainly for maize production, in central Angola. The reduction of ecosystem services provided by miombo woodland is serious. Schneibel et al. (2016) found that during the period 2009–2013, the removal of 961 000 t of woodland biomass per year resulted in a maize crop of 1240 t per each succeeding year during the production lifetime (4 years) of cultivated fields. The negative trade-off between deforestation and food production, using unsustainable farming methods, is cause for concern.

The general problem of rural land degradation is not as intense as it is in areas of urban settlements, infrastructure developments and opencast mining. Many Angolan cities face regular crises when poor stormwater management results in rapidly growing gullies and canyons. High-density informal settlements (*musseques*) are the most seriously affected by flooding, erosion and landslides. However, the most extreme levels of soil erosion are found in the diamond mining areas of Lunda-Norte, where a century of uncontrolled opencast mining and river diversion has created vast areas of erosion and the annual spillage of millions of tonnes of sand and silt into the Congo tributaries, destroying vulnerable aquatic ecosystems and placing human communities at risk.

The socio-economic consequences of weak legislation, poor land management and a general lack of knowledge and information on the processes of soil conservation and sustainable agriculture amount to a national crisis. They point to the urgent need for agro-ecological research at the landscape level and the training of all users and administrators of Angola's soil resources.

6.6 Soil Classification

Soils, like rocks, plants and animals, have been classified into a hierarchy of types. Soils have been classified on universally agreed criteria into **Forms** and **Series**—vaguely analogous to biological Orders and Families. As is the case with biomes and ecosystems, a somewhat confusing array of terms have been used by pedologists from different countries for similar soils. Fortunately, the Food and Agricultural Organisation (FAO) of the United Nations has developed a standard international soil classification system and a soils map of Africa (Jones et al., 2013). The FAO recognises 32 **Reference Soil Groups** (RSGs) as the highest level of classification. The next level of classification uses a set of principal and supplementary qualifiers. Angola has representatives of 17 RSGs, mapped in Fig. 6.8, and outlined in Box 6.2.

6.7 Key Soil Groups of Angola

The geological history and soil genesis of Angola is complex and interrelated, and as previously described, is influenced by rainfall, drainage, evaporation, wind, and time, as well as ecosystem properties and dynamics. At a regional scale, it is important to recognise the sharp contrasts in age, stratigraphy and composition of the geological structure of Angola, as presented in Chap. 4 on geology and in Fig. 4.6. The predominance of a broad belt of Proterozoic Precambrian (2700–541 Ma) crystalline rock systems along the western margin of the country, with Cenozoic (66 Ma to present) Kalahari sand systems occupying most of the eastern half, is striking. Geology determines the major soil divisions. Over three-quarters of the country is covered by two main soil groups (arenosols and ferralsols), an understanding of which provides an essential introduction to Angolan soil classification.

The characteristics of the FAO Reference Soil Groups of Angola, mapped in Fig. 6.8, are summarised in Box 6.2. A broader profile of the main groups follows.

Arenosols

The main soil group in Angola comprises sandy arenosols (*solos psamíticos*) that cover more than 53% of the country. These sands are dominant features of three major landscapes: the dunes of the Namib Desert; the red 'terras de musseque' of the coastal belt northwards from Sumbe (Fig. 6.6); and the vast Kalahari Basin. The great majority of the arenosols lie to the east of approximately 18° longitude, comprising the **aeolian** (wind deposited) sands of the **Kalahari Basin**—which cover nearly 50% of Angola and which hide nearly all of the underlying geological formations. The Kalahari Basin, extending across 2500 km from the Cape in the south to the Congo Basin in the north, and up to 1500 km in breadth, is reputedly the largest continuous body of sand in the world. The sands of the Kalahari Basin have been deposited by wind and water over the past 66 million years, with the upper layers being of more recent age, perhaps as recent as the last 5–2 Ma. Composed of quartz grains that have very little accumulated organic matter, they are of very low fertility, are acidic and of low water-holding capacity. Waters passing through the vast catchments of the Congo, Cubango and Zambezi basins that drain the Kalahari sands are therefore extremely pure. As nutrient minerals are all concentrated in the humus of the tree and grass rooting zone of the upper 20–50 cm of the soil, removal of the vegetation by cultivation inevitably results in loss of fertility and of ecological and economic value (Ucuassapi & Dias, 2006).

Fig. 6.6 A typical representative of the 'terras de musseque' arenosols of the Luanda Plateau. Note the absence of clear diagnostic horizons in the soil profile *Photo* Antonio Martins

Ferralsols

The higher ground of the western half of Angola (the Ancient Massif) is dominated by the second major soil group, the **ferralsols** (*solos ferralíticos*) derived from underlying crystalline rocks (gneisses, granites, metamorphosed sediments of the Precambrian Basement Complex; and schists, limestones and quartzites of the West Congo System). Ferralsols are deep, infertile and dominated by 'low activity' clays such as **kaolinites** and other aluminium oxides. Ferralsols cover approximately 23% of Angola. The soils are mostly of low water-holding capacity. Ferralsols are usually several meters thick, with diffuse soil horizon boundaries (Fig. 6.7). Quartz is the primary mineral. Most ferralsols are clayey, a consequence of advanced weathering. The presence of micro-aggregates (particles composed of mineral, organic and biotic materials bound together during soil formation) explain the excellent porosity, good permeability and high infiltration rates of ferralsols. Their good permeability and stable microstructure make ferralsols less susceptible to erosion than most other tropical soils. Dissolved minerals are absent and cation retention is weak. Under natural vegetation, some nutrient elements taken up by the roots are eventually returned in leaves and other plant debris falling to the surface. But the bulk of all nutrients taken up is held in the living trees. Thus almost all plant nutrients available in the soil (and living plant roots) are concentrated in the upper 10–50 cm soil layer. While ferralsols have good physical properties, their low natural fertility is a serious challenge

Fig. 6.7 A ferralsol profile illustrating a senile soil, with the presence of pisoliths (concretionary grains), and with a dark laterite formation at the base. Wako Kungo, Cuanza-Sul Province. *Photo* Antonio Martins

to plant nutrition and to crop production in the absence of agricultural fertilisers. The addition of lime is used to raise the pH-value of the surface soil, to combat aluminium toxicity, and to raise the soil cation exchange capacity. Ferralsols are characteristically reddish, orange or yellow (Fig. 6.7) due to oxidation of their high iron and aluminium content, which also accounts for the presence in many areas of **fericrete/laterite** hardpan horizons a metre or two below the surface, impeding root and water penetration and resulting in the formation of extensive areas of laterite.

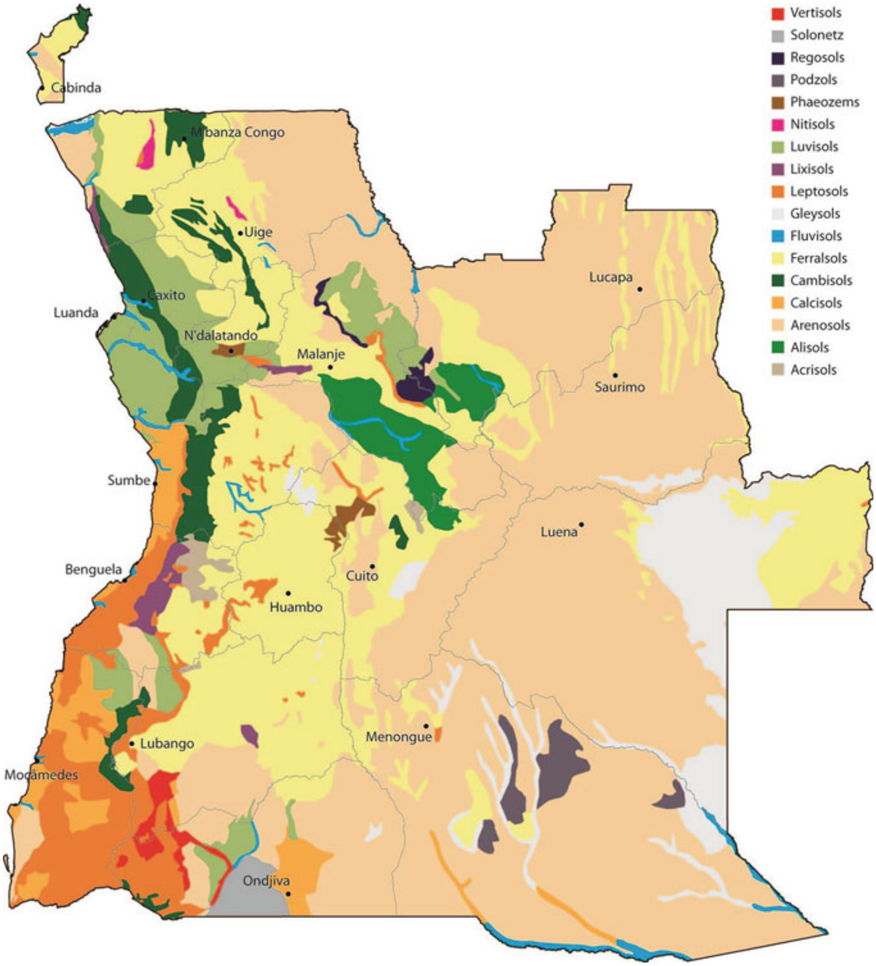


Fig. 6.8 Outline of the main soil types of Angola (from the FAO Soil Map of Africa), illustrating the dominance of arenosols in the eastern half of the country, and ferralsols across the western and central plateau. From Huntley (2019) based on Jones et al. (Eds) (2013). *Soil Atlas of Africa.* European Commission, Publications Office of the European Union, Luxembourg

These two low-fertility soil groups (arenosols and ferralsols) cover over 76% of the country. Thus, despite the adequacy of rainfall over most of Angola, agricultural production faces the challenges of low soil fertility. The soils are acidic and have high levels of silicon which is not a plant nutrient. The natural vegetation types that cover both arenosols and ferralsols—predominantly miombo woodlands—are well adapted to these soil conditions, and the untransformed landscape gives the deceptively misleading appearance of great vitality and luxuriance. These soils dominate the old, leached African Planation Surface of the Central African Plateau, dating from the long period of stability following the breakup of Gondwana. For the rest of Angola, uplift and incision by rivers during the Post-African erosional cycle rejuvenated the soil substrates, producing potentially richer soils, usually in the lower, younger landscapes of hotter, drier valleys. The erosion processes exposed rocks of volcanic origin, such as basalts, gabbros and dolerites which produce soils with the mineral elements that support plant growth, with ’high activity’ clays such as **montmorillonite**. The younger soils are generally of higher nutrient status, but mostly occur in the lower, drier landscapes of Angola and therefore require irrigation for agricultural production.

Leptosols, Calcisols and Cambisols

The remaining 24% of Angola’s soil cover include a wide range of soil types, on specific geological substrates or positions in the landscape. In terms of landcover, the third largest soil group, occupying 6% of Angola, are the shallow leptosols or regosols (*litosolos*) of rocky hills and gravel plains, most extensive in the arid southwest. Other important soil types, described in Box 6.2, include luvisols, calcisols and cambisols (*solos calcários, solos calcialíticos*), which provide fertile loam soils for crops (including the ‘coffee forests’ of the Escarpment Zone); alluvial fluvisols (*solos aluvionais*) in drainage lines with high organic content and high water retaining capacity, suitable for crops if not waterlogged; gleysol clays (*solos hidromórficos*), typically acidic and waterlogged and occasionally very extensive, as on seasonally flooded plains such as the Bulozi Floodplain.

Box 6.2: FAO Reference Soil Groups (RSGs) Represented in Angola

(Portuguese names according to Diniz, 1991).

Leptosols (*Litossolos*). Soils with a very shallow profile depth (indicating little influence of soil-forming processes). They often contain large amounts of gravel. Extensive in southwest arid zone.

Solonetz (*included with Arídicos tropicais*)**.** A dense, strongly structured, clayey soil that has a high proportion of adsorbed Na and in some cases also Mg ions. Solonetz soils that contain free soda (Na_2CO_3) are strongly alkaline (field pH > 8.5). Also known as sodic soils.

Vertisols (*Barros*). These heavy clays are known as *Terras de Catete* in the Sedimentary Basin of the Cuanza, north and south of Luanda. They comprise heavy alkaline or saline shrinking/swelling montmorillonite clays. These soils form wide cracks from the surface downward when they dry out. Extensive areas are found in Quiçama, where they are covered by a tall, dense monospecies grassland of *Setaria welwitschii.*

Gleysols (*Hidromorphícos*). Gleysols cover the extensive Bulozi floodplains of Moxico and other floodplains of Angola's vast network of major rivers. They are much more abundant and widely distributed than the mapped data indicate because they occur as narrow strips at the bottom of the undulating landscapes that cover most of the Angolan interior. Such areas are too narrow to be mapped at national scales. Hydromorphic soils can be saturated for long periods, leading to reducing conditions through oxygen depletion and results in an anaerobic soil. These reduction and oxidation (redox) processes remove iron, leaving the gleyic layer devoid of the brown and red colouration normally derived from iron. The uppermost A horizon layer is rich in organic matter and may be up to 50 cm thick. This upper layer is also relatively fertile and well-suited to small-scale crop production.

Podzols. These infertile soils are usually found in moist temperate regions of the world. In Angola podzols are found in the upper sources of the great river systems on Kalahari sands. These podzols have developed under the influence of acidic humus of high water-table grasslands and wetlands, in Bié, Moxico and Cuando Cubango provinces. The soils have a bleached eluvial horizon and low cation exchange capacity. They typically have sub-surface impermeable laterites formed by the vertical migration of iron and aluminium oxides.

Nitisols (*Paraferralíticos*). Deep, well-drained, red tropical soils predominantly found on level to hilly land under forest or savanna vegetation in Zaire and Uíge. Among the most productive soils of the humid tropics. **Ferralsols** (*Ferralíticos*). The dominant soil group of the western plateau typical of the deep-weathered red and yellow soils of the tropics, with a low base status and kaolin clays and high content of sesquioxides and limited fertility. Laterites are common.

Phaeozems Young soils of wet grasslands within miombo, porous, dark, rich and fertile.

Calcisols (*Calcarios; Arídicos tropicais*). Soils characterised by a layer of translocated calcium carbonate—soft and powdery or hard and cemented. Covering much of the Cuanza Sedimentary Basin, plus the coastal plains and interior of Namibe (often as calcrete pavements, interspersed with gypsum) and lower Cunene, and northwards along the Escarpment. The translocation of calcium carbonate from the surface horizon to an accumulation layer at some depth is the most prominent soil-forming process in Calcisols, and it is common to find the surface horizon wholly or partly de-calcified. Calcisols contain only 1–2% organic matter but are rich in plant nutrients. The pH is near-neutral in the surface soil, but slightly higher at a depth of 80–100 cm where the carbonate content may be up to 25%.

Acrisols. Strongly weathered acid soils with low base saturation, in miombo. These soils generally form on old land surfaces with undulating topography, and in regions with a wet tropical climate. Acrisols are characterised by a dominance of kaolin clays, a general deficiency of base or cation minerals, as well as most other minerals that have been leached away. Exceptions are iron and aluminium. Levels of plant nutrients are low and aluminium toxicity limits plant growth. Some regeneration of Acrisols is possible if fields are used for short periods (one to three years only) and then left fallow for long periods of up to 10 years.

Lixisols (*Fersialíticos*). Soils developed on old landscapes. Their age and kaolin clay mineralogy have led to low to moderate levels of nutrients and high erodibility along the Escarpment. Indurated lateritic layers are frequent. Lixisols are strongly weathered soils in which clay has been washed down from the surface layers to an accumulation horizon at some depth. These soils occur in areas with a warm climate and a pronounced dry season, and are very similar to Acrisols. Lixisols have low levels of available nutrients and low nutrient reserves. However, their chemical properties are generally better than those of Ferralsols and Acrisols because of their higher pH and the absence of severe aluminium toxicity.

Alisols (*Oxissialíticos*). Soils with a low base saturation, highly acidic, poorly drained and prone to aluminium toxicity and water erosion. Alto Cuanza, Bié and Malange.

Luvisols (*Calsialíticos*). Moderately fertile and moderately base-saturated soils of younger landscapes of the Baixa de Cassange.

Cambisols (see Calcisols). Poorly developed young soils of steep slopes of the Escarpment, with moderate to high fertility.

Arenosols (*Psamíticos*) The deep sandy acidic and infertile soils with low organic content that occupy most of eastern Angola on the Kalahari sands, Namibe desert dunes and the red *musseque* sands of the Luanda Plateau.

Fluvisols (*Aluvionais*) The young fertile alluvial soils of mixed sediments of river valleys and well-drained floodplain margins as along the Cuanza, Longa and Luando rivers. Fluvisols form from alluvial sediments of silt and clay deposited by the periodic flooding of floodplains along rivers, and in deltas and alluvial fans and lakes. Permanent or seasonal saturation with water preserves the stratified nature of the original deposits. Over time, the sediments change (or mature), becoming stratified by chemical processes associated by drying (oxidizing) and wetting (reducing). Fluvisols generally have neutral or near-neutral pH values, which do not impair the availability of nutrients.

Regosols (see Leptosols). Weakly developed soils in unconsolidated material of eroding landscapes along escarpments such as that above the Baixa de Cassange.

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Chapter 7
The Ecological Role of Fire

Key Concepts and Questions: This Chapter Explains

- *Why fires are so important in the ecosystem dynamics and structuring of Angola's vegetation.*
- *That fires ignited by lightning are natural and very ancient features of African savannas.*
- *Why fires are considered the greatest consumers of vegetation across African mesic savannas.*
- *Why the grasses of African savannas have been so successful despite hot, dry conditions and repeated fires.*
- *How plants and animals respond both positively and negatively to the impact of fires.*
- *How fires drive the maintenance of alternative stable states between savanna and forest ecosystems.*
- *The importance of an understanding of fire regimes, behaviour and potential impacts as the basis for the development and implementation of fire management systems.*

Context: Fire: Africa's Great Consumer

For the Gondwana continents (South America, Africa, Australia and India) natural fires are the key drivers responsible for shaping savanna ecosystems and limiting the distribution of closed forests. Surprisingly, most textbooks on the fundamentals of ecology have little if anything to say about fire as an ecological driving force, despite the long history of fire research in Africa (Booysen & Tainton, 1984; Phillips, 1931).

In the mesic savannas, fires more than herbivores, are the great consumers of plant biomass. Annually, fires burn over three percent of the vegetated globe. Of this, African savannas contribute 70%. Fires have driven some of the most important ecological adaptations, shaping plant life-forms and animal niche structure. Whole suites of fire adaptations, such as the storage of seed banks in the inflorescenses of proteas and pines (serotiny), the thick corky bark of mesic savanna trees, and the

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evolution of C_4 grasses, owe their existence to regular fires. However, for most of the last two centuries, most northern ecologists have attributed savannas to human-driven fires and land transformation. Many followers of plant succession theory have viewed Africa's savannas as artefacts of human-driven fire and deforestation.

The anthropogenic origin of bushfires is not supported by recent research, as comprehensively and elegantly synthesised by South African ecologist William Bond (2019). Based on ecological, paleoecological, phylogenetic and physiological evidence, it has been demonstrated that savannas and their constituent grasslands and woodlands are both natural and ancient features of tropical landscape dynamics. Most importantly, tropical savannas are shaped by fire, natural and human induced.

7.1 The Ancient History of Fire in Africa

Fire in African ecosystems has long been attributed to the activities of ancient hunter-gatherers, burning the savannas to make hunting more efficient. Africa, recognised as the Cradle of Humankind, has had members of the genus *Homo* present for about 2.6 million years, and modern *H. sapiens* has occupied the African savannas for about 200,000 years. But both fire and savannas were dominant features of the African (and global) landscapes, many millions of years before the evolution of modern humans. Lightning strikes, not humans, have been the principal agent for the ignition of fires across the globe. Lightning is a natural phenomenon, with millions of strikes per day. Most of these do not trigger bushfires, but lightning strikes remain important sources of fire ignition over much of Africa, despite the increasing role of humans in setting fires.

Paleoecological studies of charcoal, fossils and carbon isotopes indicate that fire has been a feature of terrestrial ecosystems for 400 million years, appearing at least 100 million years before the first vertebrate herbivores evolved and 300 million years before early angiosperms emerged from forests into more open habitats (Bond, 2019). The arrival of open savanna ecosystems, characterised by a mixture of trees and grasslands, occurred with the resurgence of fire in the late Miocene (ca. 10 Ma), possibly linked to the increased seasonality of rainfall in the tropics and the increasing dominance of C_4 grasses at that time (Box 4.1). Phylogenetic evidence (Fig. 7.1) points to a sharp increase in fire activity in C_4 grasslands within the last 10 million years (Bond, 2015, 2019) providing evidence of the close links between savannas, fires and C_4 grasses. The incidence of fires in global landscapes has increased through human activities during the Holocene, but as extensive agriculture, grazing and human settlements increased, globally, the actual area burnt per year has decreased over the past 150 years (Marlon et al., 2008). However, the ecological role of fire is a deeply embedded and ancient evolutionary force.

As human populations grow and the demands for resources increase in both industrialised and developing countries, conflicts at the urban/wildland interface are reaching serious proportions, as demonstrated by fire events in Australia, Brazil, California, Portugal, Greece and South Africa. The need to understand fire regimes

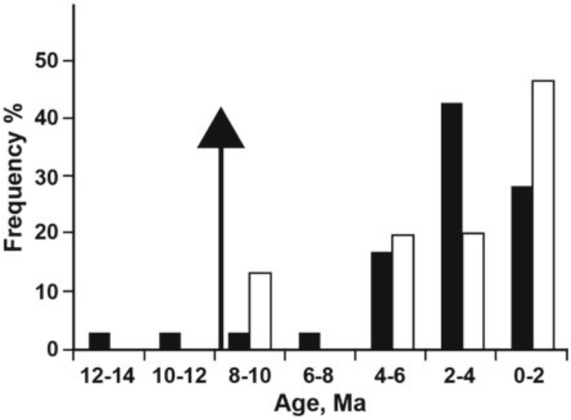

Fig. 7.1 Estimated age and frequency of fire-adapted woody clades from savannas in Africa (black) and Brazil (open). The arrow indicates the surge of fire activity after 10 Ma. After Bond (2015). *Frontiers in Plant Science*, 5, 749. Creative Commons Attribution License (CC BY)

and fire behaviour and to develop fire management strategies has stimulated intensive research programmes on all continents. Fire ecology has become a science in its own right, and southern African workers lead in many aspects of this research (Bond, 2019, and included references). Of particular relevance and value to Angola are the results of long-term fire experiments and fire research projects such as those in Kruger National Park and in Hluhluwe-iMfolozi Park, where for over 60 years, burning trials have been conducted in both arid savanna and mesic savanna (Box 7.1).

The results of both basic and applied research into the role of fire in natural ecosystems have been synthesised within a model (Fig. 7.2) that presents the linkages of biological and geophysical forces and feedbacks over long and short timescales (Archibald et al., 2018). The model provides a useful framework for developing an understanding of the multiple factors involved in fire ecological processes and their evolution, as will be discussed in this chapter.

7.2 Fire Regimes and Pyromes

Fire researchers have recognised distinctive **fire regimes** to describe the repeated patterns of fire at a particular location based on measurable characteristics of individual fires (Bond & Keeley, 2005; Keeley et al., 2012). These characteristics are:

- **Fire frequency** (period of time for plant growth and fuel accumulation between fires),
- **Fire intensity** (rate of energy released by the fire),
- **Fire severity** (the impacts on the affected ecosystems such as biomass consumed, damage to growing points),
- **Fire season** (period of the year during which fires normally occur), and
- **Fire size** (areal extent of fire impact).

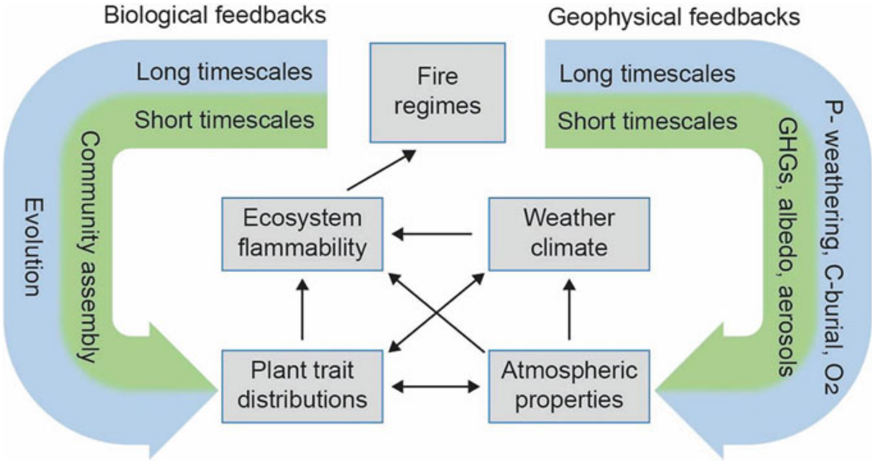

Fig. 7.2 Fire acts through both geophysical processes (exchange of energy and matter between the biosphere and atmosphere) and biological processes (community structure and evolution). Plant innovations that alter the degree to which vegetation is tolerant of fire and the flammability of the vegetation can alter fire regimes, and potentially impact global biogeochemical processes. With both biological and geophysical feedbacks, the type of processes impacted depend on the time scales involved. From Archibald et al. (2018) *Environmental Research Letters*, 13(3):4. Creative Commons Attribution 3.0 Licence

Season, frequency, severity and intensity are interrelated and influence the plant composition (by selecting for fire-tolerant adaptations) and trigger feedbacks between fire and vegetation structure. Fire regimes integrate fire behaviour, climatic, vegetation, faunal and human activities, and are therefore best conceived as emergent properties of a given ecosystem.

In addition to the features of fire regimes, fires are grouped in three **fire types**:

- **Ground fires** (fires that burn in organic layers of the soil, common in the peat of northern **taiga** ecosystems),
- **Crown fires** (fires that burn in the tree canopy, common in Mediterranean-climate shrublands and some confer forests of North America and Eurasia) and,
- **Surface fires** (fires that burn fuels contiguous with the soil). In Angola, surface fires dominate, burning the grass layers below savanna tree canopies with minimal damage to the trees above.

Attempts have recently been made to classify and map fire regimes at a global scale, calling the units **pyromes** (Archibald et al., 2013), analogous to biomes. The system is very generalised, but has some applicability to southern Africa. Three pyromes are important in Angola. The largest, including most of the moist and mesic savannas, are characterised as **FCS** (frequent, cool, small) referring to the high frequency of fires, their low intensity and small patch size. This pyrome is typical of the miombo mesic savannas. The fire patterns of this pyrome have been influenced over the past century by increased shifting cultivation activities. The second pyrome is the **FIL** (frequent, intense, large) which includes the extensive plains of the Lundas and the Cuando Cubango (Fig. 7.3).

The arid savannas of the southwest belong to the **RIL** (rare, intense, large) pyrome which relates to the infrequency of fires, often once in 30 years, due to the low biomass of arid savannas, the infrequency of high rainfall events which provide rapid build-up of grass biomass and carry rare but extensive fires. For most years, low rainfall and high levels of herbivory of the palatable grazing and browse reduce combustible biomass to low levels. After episodic, high rainfall events, biomass in arid savannas

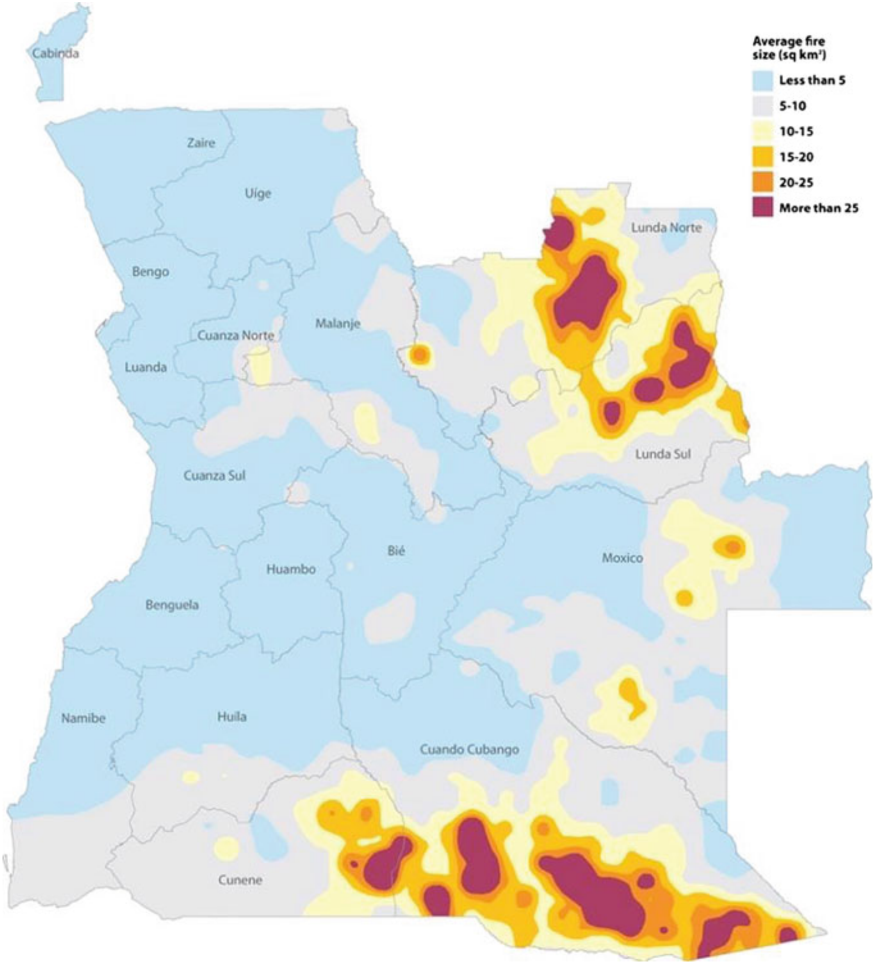

Fig. 7.3 The average size class of fires. Size classes range from less than 5 km^2 (blue) to greater than 25 km^2 (purple). Note the frequent, very large fires in the Lundas and Cuando Cubango. From Mendelsohn (2019) redrawn from Archibald et al. (2010) and data available at http://wamis.meraka.org.za/products/firefrequency-map

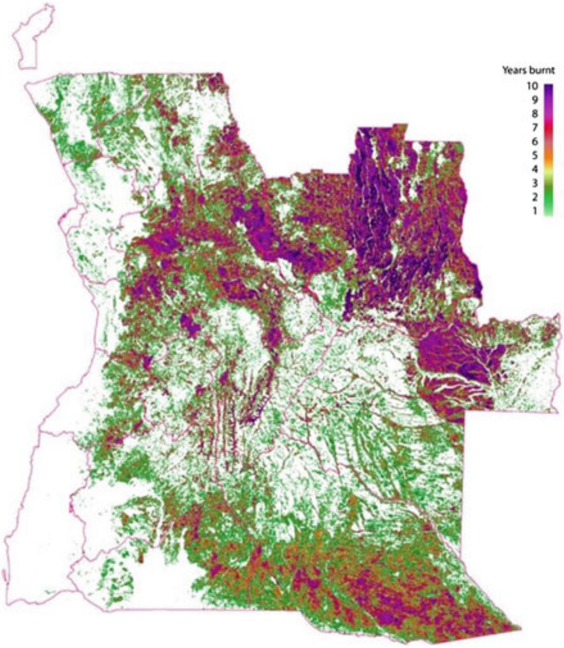

Fig. 7.4 The frequency of fires expressed as the number of years each area of 500 × 500 m burned between 2000 and 2010. Frequency ranges from less than one fire in ten years (white) to fires in every year (purple). Note the absence or low frequency of fires in the coastal belt and arid southwest and the high frequency of fires in Cuanza-Sul, Malange, Lunda-Norte, Lunda-Sul, Moxico and Cuando Cubango provinces. From Mendelsohn (2019) redrawn from Archibald et al. (2010) and data available at http://wamis.meraka.org.za/products/firefrequency-map

increases to the level at which fires can spread over wide areas. In the last century, indigenous herbivores have been replaced by domestic livestock (cattle, sheep and goats) as the main vertebrate consumers of potential fire fuel, with the consequence that RIL fires are very uncommon in heavily grazed Angolan arid savannas (Fig. 7.4). In northern Angola, high rainfall supports dense tall forests that are too wet to burn under normal circumstances (Van Wilgen et al., 1990).

A detailed study of the spatial and temporal trends of fire across Angolan landscapes from 2001 to 2019 (Catarino et al., 2020) showed that ca. 30% of the country's area burned each year, with the highest percentage burnt being in the northeast and southeast, as reported earlier in the studies of Archibald et al. (2010), Fig. 13.3. Increasing frequency of fires followed trends in human population growth and small-scale subsistence agriculture in the miombo ecoregions of central Angola, with the conversion of forests and woodlands into grasslands and shrublands. Catarino et al. (2020) record an increasing incidence of fire across 23% the area of Bicuar National Park between 2001 and 2019.

7.3 Fire Intensity

Fire intensity is a function of fuel load, heat yield and rate of spread. Rate of spread is influenced in turn by wind speed: the stronger the wind, the more intense the fire. The impact on tree recruitment or mortality increases as the grass cover (**fuel load**) accumulates and dries towards the end of winter, due to the decrease in the moisture content of leaves, from 88% in summer to 28% in the late dry season. Fuel load does not build up linearly but increases for the first three to four years post-burn, after which decomposition reduces the rate of increase in combustible material.

Build-up of fuel is rapid on nutrient-poor soils such as those of the Angolan miombo, where grasses are of low palatability and herbivores are scarce. Mesic savannas generally experience low intensity fires once every one to three years, both trees and grasses surviving due to their fire-tolerant adaptations. In arid savannas, grazing and browsing by herbivores removes much of the biomass, and reduces the potential of fires spreading from the point of ignition. Fires are infrequent and usually of low intensity in arid savannas, except after high rainfall events with subsequent rapid fuel accumulation.

Fire intensity is measured in **kW/m**—the energy released at the fire front per unit area as it moves across the landscape. Fires in African miombo and Brazilian cerrado have similar fire intensities, at between 2000 and 15,000 kW/m. Fires of 3000 kW/m are sufficient to result in **top-kill** of 90% of tree saplings of 1 m tall, but only 40% of those 2 m tall. Top-kill is the destruction of the growing tips of young trees, leading to stem death. Trees that survive the top-kill **fire trap** of high intensity fires, which are typical of late winter burns, can grow to maturity. Fire, through its control of tree growth, determines the density of trees in savanna systems. The inability of fire to penetrate closed-canopy forests determines the distribution of savanna or forest in tropical landscapes where climatic conditions do not limit forest growth (Sect. 10.7).

Experience in southern Africa indicates that closed forests are especially vulnerable to damage during firestorms, through the simultaneous combination of three weather factors that increase fire intensity—air temperature above 30 °C, relative humidity below 30%, and a wind speed of over 30 km/h. Such **firestorms** can generate their own weather conditions by creating a convective column of scorching, rising air above the fires (Archibald et al., 2017). The heat and smoke generated by firestorms can be enormous. The local formation of cumulus clouds above the Cuanza floodplain, as heat rises off burning swamplands, and cools and condenses, is a familiar sight in Quiçama National Park during the dry 'fire season'. Similarly, the flamboyant sunsets over Angola during the fire season, created by the scattering of the sun's rays by smoke particulates in the lower atmosphere, are indicative of the vast extent of bush fires (***queimadas***) over the Angolan interior from April to October.

7.4 Fire Season

In Angola, fire seasonality varies from early-season burns (May–June) in the north to late-season (July–September) in the south (Fig. 7.5).

Fire experiments are lacking for Angola, but studies in similar ecosystems in Zambia, Zimbabwe and the Ivory Coast demonstrate the effects on trees of annual fires. Distinct patterns of impact of fires in the early dry season, late dry season, and with total fire exclusion (Fig. 7.6) have been recorded in fire experiments initiated in

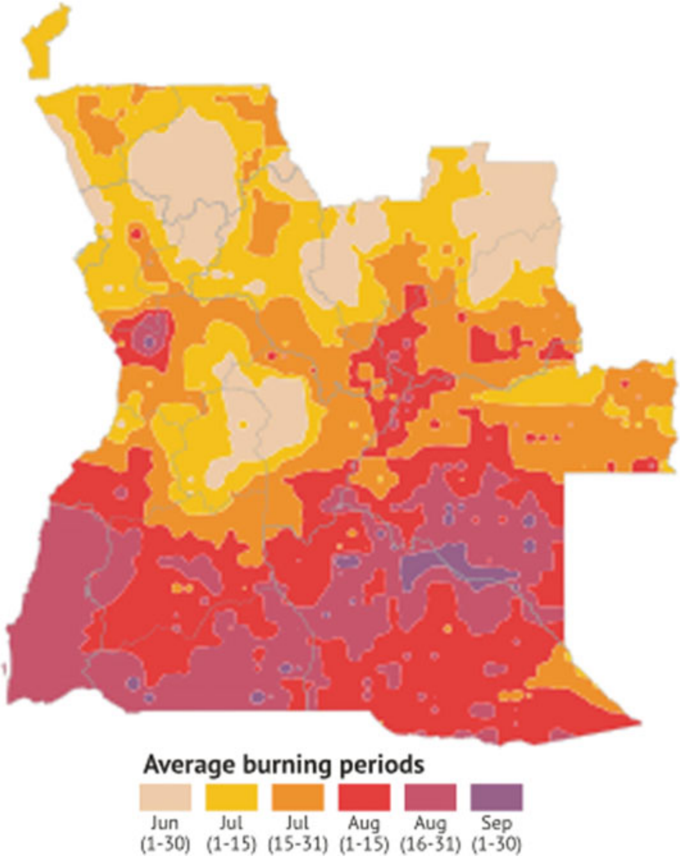

Fig. 7.5 Seasonality of fires in Angola. First early-season fires commence during May in the north (yellow), with late-season fires commencing from July to September in the south (red). From Mendelsohn (2019) redrawn from Archibald et al. (2010) and data available at http://wamis.meraka.org.za/products/firefrequency-map

1936 in the Ivory Coast (Laris & Wardell, 2006). After 60 years, an open savanna had developed on the late season site, where high intensity fires prevented tree growth in all but the most fire-adapted species. On the early season site, where fire intensity was mild, a dense woodland had established, of mixed species more typical of mesic savannas. On the site from which fire had been excluded, a closed canopy of rain forest trees had established. Similar long-term experiments in South Africa found that trends towards forest establishing on sites from which fire was excluded were only observed at sites receiving over 700 mm rainfall per annum (Bond et al., 2003). Fire, herbivory, rainfall and season all interact to determine fire impact.

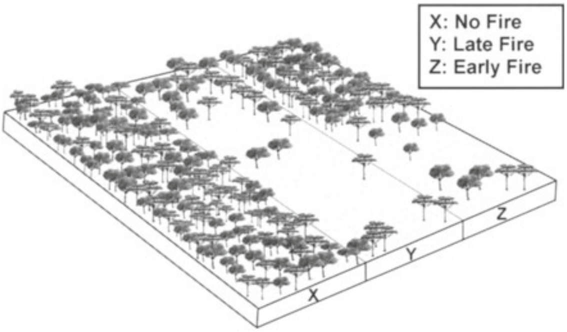

Fig. 7.6 The layout of the burning experiment at Lamto, Ivory Coast. A 'late' fire is more intense than an 'early' fire due to greater biomass accumulation and drier fuel load. Today, the 'no fire' block has returned to a moist forest, the 'late fire' is open savanna. From Laris and Wardell (2006) *Geographical Journal*, 172(4): 271–290, based on Louppe et al. (1995)

7.5 Fire Frequency

Fire-free periods of more than four years are rare in mesic savannas such as the miombo of Angola. Researchers estimate that for mesic savannas, fire-free intervals of nine years might occur once per century. Human activities make such events highly unlikely in Angola. Conversely, in Gabon, attempts to re-establish open savanna communities within forest reserves (to provide open habitats for tourists to view Forest Elephant and Forest Buffalo) have been frustrated by the rapid re-colonisation of sites by forest trees, unless hot dry-season fires are applied annually. Once forests have established in the moist tropics, return to an open savanna is extremely rare without human intervention.

7.6 Impacts of Fire on Soils

Over most of Angola, with the exception of the Congo forests and the arid savanna, fires are a frequent phenomenon. Hot fires often result in the loss of nitrogen, phosphorus and organic carbon, although cooler fires can facilitate the release of nutrients from plant matter into the soil. Loss of nitrogen and sulphur is particularly high (90% and 60% respectively) through **volatilization** (vaporization) when a fire reaches temperatures above 700 °C. Cation loss from volatilization is not as high. Despite these losses, the main effect of fire is a short-term increase in the availability of almost all inorganic nutrients, which are added to the soil as ash.

The passage of heat during a fire also stimulates biological **mineralisation** in the organic layer, due to the increase of pH resulting from the added ash. A nutrient pulse might occur for several months following a fire, with dramatic increases in plant growth rates and higher nitrogen concentration in leaves. Fires can thus favour grasses such *Panicum* species, which have high light and nitrogen requirements, and which are also greatly preferred by grazers. The green flush following fires, and the mineralisation of soil nitrogen and the increase of the protein content of leaves, is attractive to all herbivores, with corresponding movement of grazer populations from unburnt to burnt areas. The nutrient pulse following **slash and burn** agriculture, which lasts for two or three years before the nutrients are exhausted, is the basis for this subsistence farming practice across Africa.

One of the few fire studies conducted in Angola, in open and dense woodland near Savate in Cuando Cubango, found much lower nutrient levels in the open than in the dense woodland soils. This difference was probably a consequence of the open areas being burned often and intensely, while the dense woodlands were seldom burned (Stellmes et al., 2013; Wallenfang et al., 2015).

Fires leave distinctive pale, sandy, and sparsely wooded margins around savanna woodlands in eastern Angola (Fig. 7.7). The processes involved have not been researched. However, several factors might be important. The shading by large trees on the outer margin of wooded clumps might favour short, sparse, shade-tolerant grasses, which form an effective apron as a fire break. A second possibility is that the woodland trees might produce an **allelopathic** chemical substance that suppresses grass growth around their perimeter. Third, the band of sandy soil might result from soil–water processes, such as on the 'seep-line' in the typical catenas of miombo

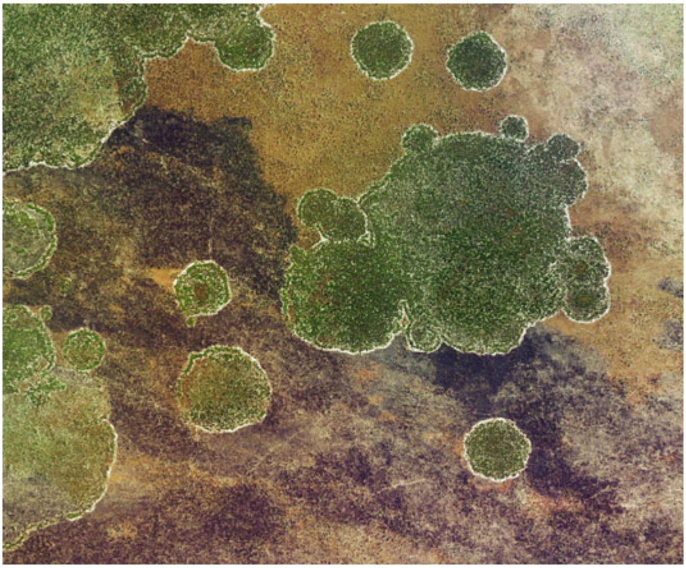

Fig. 7.7 'Fairy forest circles' in Angola. The two circles at the top of the image are each about 700 m in diameter. The bare, whitish rings around the fairy forests and larger rounded blocks of forest are clear of vegetation. The dark area across much of the lower part of the image was recently burnt. The centre of the image is at 15.587 South and 19.3435 East, some 60 km SSE of Cuito Cuanavale. Image from Microsoft's Bing aerial imagery. From Mendelsohn et al. (2022)

ecosystems. Finally, the accumulation of litter around the forest margin promotes slow, smouldering fires that kill plant growth in a narrow belt, depositing a fine ash apron which might also be allelopathic. This is but one of Angola's many ecological phenomena that deserves further research.

7.7 Plant Responses to Fire

Fire is a very strong selective pressure in fire-maintained ecosystems. It is a consumer of vegetable matter and it behaves like a herbivore in that it consumes plant organic compounds and converts them into by-products. But unlike herbivores, fire is an unselective consumer, it is not controlled by predators, nor does fire avoid plant material high in cellulose and lignin nor low in nitrogen. The responses of plants to fire are simple—survival or death. Plants fall into one of two categories—**pyrophilic** (fire-tolerant) or **pyrophobic** (fire-intolerant). The adaptations of plants to fire vary with fire frequency, intensity and season. Grasses, forbs, shrubs and trees respond in different ways to fire, resulting in a gradient of physiognomic structures from open grassland to grasslands with scattered trees and shrubs, to woodlands with open crowns, to closed-canopy forests. Savannas depend on fire for their existence, whereas forests depend on their ability to exclude fire.

To survive recurrent fires, savanna trees have evolved five key adaptations—**thick bark**, deeply embedded **epicormic buds**, underground **lignotubers**, **self-pruning** and **hydraulics**. The first four traits have been known for over a century. These traits protect the tree stems against direct fire damage and allow rapid sprouting of woody shoots after the passage of fires. They also provide underground storage of water and nutrient reserves. Further, by regularly dropping old twigs and branches (**self-pruning**), savanna trees prevent fire from climbing into the tree canopy. Forest trees, however, do not possess such adaptations, and post-fire mortality is very high where fire breaches the forest margin.

Tree mortality following the passage of fire has been attributed to the destruction of the **cambium** (growth tissue) and **xylem** (water transfer tissue) of trees, but South African researchers (Midgley et al., 2011) have suggested that the sudden death of forest trees is caused by '**hydraulic death**'. The heat pulse from a fire causes the blocking (**cavitation**) of xylem vessels by air bubbles—similar to an **embolism** (the blockage of an artery by a blood clot) in humans. Savanna trees have seemingly developed greater resistance to cavitation and suffer lower mortality than forest trees.

A further advantage to tree survival, growth and reproduction in savanna trees is the ability of tree saplings to emerge rapidly above the '**fire-trap'** of repeated fires, typically by reaching over 2 m in height before the next fire season. Below 2 m height, saplings are vulnerable to topkill. The presence of large underground storage organs (lignotubers) plus other fire-resistance adaptations, allows some saplings to survive successive fires until they emerge above the flame zone, especially during extended fire-free periods. An extreme fire adaptation is that of **geoxyles** (also known as geoxylic suffrutices)—trees and shrubs that have very limited aboveground growth except during the immediate post-fire period (Box 14.3).

Among savanna grasses, species of the Andropogoneae (which dominate Angola's moist and mesic savannas) are the 'fire grasses'. These burn regularly, are typically intolerant of shading, and which accumulate tannins, which in turn discourage herbivory and retard decomposition. In summary, the grasses of mesic savannas grow rapidly following a fire, accumulating a fresh load of combustible material that cures rapidly and creates an aerated fuel bed that enables rapid spread. The grasses of arid savannas are less well adapted to fire, but well adapted to grazing.

7.8 Responses of Animals to Fire

Studies on the responses of animals to fire are far less common than studies on the responses of plants. However, comprehensive syntheses of knowledge on animal responses to fire in African ecosystems are provided by Bigalke and Willan (1984), Frost (1984), Smit and Coetsee (2019) and Nieman et al. (2021a). A few generalisations can be made.

Contrary to popular opinion, high rates of mortality are uncommon in most animal groups during fire events. Most animal species respond to fires by avoidance or immediate dispersal. Many insects flee in advance of the flame front, and most vertebrates are able to move faster than fires. Exceptions, such as reptiles, amphibians and small mammals, survive in refuges within the habitat matrix that do not burn. Examples are termitaria, underground rodent holes, bush clumps, rocky outcrops or bare overgrazed patches. Some invertebrates, such as ticks, can sense the volatile substances released by approaching fires, and drop to the ground to take refuge in cracks in the soil surface.

The heat pulse from savanna fires seldom exceeds a few centimetres depth, making escape possible for many soil-dwelling animals (Frost, 1984). Studies in the mesic savannas of Ivory Coast found low mortalities in soil organisms. Insects survived in trees and shrubs above the fire killing zone of ca. 2 m. The majority of mobile insects fled before being consumed by fire, with only 5% of grasshoppers being killed, 7% surviving in situ, and 88% dispersing away from burned areas in the Ivory Coast study (Gillon, 1973).

Fires attract numerous species of birds (storks, kites, hornbills, drongos) to feed on the fleeing insects, causing a higher mortality to their prey than that caused directly by fire. In the short term, rodents and other small mammals disperse from burned areas, as do many larger species, returning once the first shoots of recovering grasses and woody plants appear. For many small mammals, cover and refuge from predators might be more important than food limitations in determining a return to areas recovering after a fire. Ground-nesting birds, such as pipits, larks and plovers generally nest after the fire season.

Following fires, the recovery of the vegetation triggers the return of herbivores, with population density often greatly exceeding pre-fire levels. Fire effects differ in terms of fire intensity, frequency, seasonality and the spatial extent and pattern of burned and unburned areas. Furthermore, the recovery rate of vegetation structure influences the species composition and biomass of the surviving or colonising animal populations. A rapid turnover of animal species often occurs, with the immediate increase of predators (especially insect-feeding birds) during fires, followed by grazers, then browsers, as the grass cover and woody plants recover. Mammal predators take advantage of the high densities of prey species that converge on the rich grazing and browsing available in post-fire areas.

Studies on the behavioural patterns of various small mammals (rodents and shrews) suggest the existence of pre-adaptations for population recovery on burns (Bigalke & Willan, 1984). These include non-territorial sociability, a broad non-specialist feeding niche, nocturnal activity, and tolerance of low cover.

In a synthesis of studies on 51 species of larger mammals (body mass greater than 5 kg) of African savannas and grasslands, Nieman et al. (2021b) found a strong correlation between body size and response to fire. The vast majority of studies were conducted in arid/eutrophic savannas of protected areas such as the Serengeti and Kruger National Park. Grazing species were more likely to respond positively to fire (showing a preference for burned over unburned areas) than browsing species. Very large species of roughage feeders such as buffalo and elephant, were found to be ambivalent in their responses to fire. Nieman et al. (2021b) suggest that smaller-bodied herbivores (5–200 kg) require more energy and nutrients relative to their body mass, and are thus more influenced by the nutrient increases found on recently burned areas. As described in Box 8.1, larger-bodied herbivores have greater gut capacity and retention time, and can thus extract nutrients from lower-quality forage on unburned areas.

Mammals, like other animals, may be killed or injured by fire during the fire event, but otherwise respond by dispersal. Over longer periods, both grazing and browsing herbivores respond by concentrating on burned areas as the regrowth of grasses and woody plants progresses, resulting in changes to the vegetation structure.

Herbivores are attracted to the burned vegetation due to the increased nutritive quality of young regrowth, especially in areas where old, moribund and low-value herbage has accumulated in the absence of fire. Many savanna antelope species drop calves in the late winter following an autumn fire season, benefiting from the increased forage quality for the nutrition needs of rapidly growing calves. Although increased concentrations of game provide greater opportunities for predators, the open habitats following fires also provide greater visibility of predators by their prey. There are clearly trade-offs between advantages and disadvantages for predators and prey.

African mammals appear to be well adapted to fires, and many derive benefits from fires. Despite the expectation that fires could cause high mortalities among mammals, reports on fire-induced mortalities are rare. In an isolated case, following eight fire-free years, an extensive hot fire in Kruger National Park spread over 25% of the Park, and led to death or injury in nine mammal species, including lion, elephant and antelope (Brynard, 1972). In general, mortality in larger mammals is very low, except where barriers, such as rivers or fences, prevent escape to refuges.

Box 7.1 Human–Environment Interactions: Fire Impacts and Ecosystem Management

> Fire is a key driver of natural ecosystems in Africa. However, human activity and climate change have altered fire frequency and severity, with negative consequences for biodiversity conservation. Angola ranks among the countries with the highest fire activity in sub-Saharan Africa. (Catarino et al., 2020)

Wildfires, especially extensive fires that can threaten human settlements and livelihoods, are popularly and justifiably regarded as negative environmental forces. However, natural, lightning-ignited fires have existed on the planet for hundreds of millions of years, reaching their current importance in the savannas of the seasonally dry tropics about ten million years ago. *Homo sapiens* thus evolved in the fire-adapted ecosystems of Africa, and soon learned how to ignite and manage fire as a useful tool. As the 'Cradle of Humankind', it is not surprising that Africa has long been known as the 'fire continent', and today has the highest incidence of fires, natural and anthropogenic, on Earth. At the human–environment nexus, fire is both a useful tool and a dangerous force, depending on how it manifests.

In Angola, the rate of loss of forests and woodlands to charcoal production, and through short-term subsistence agriculture, is among the highest in Africa. Fire is a key element in the land transformation process. A detailed analysis of moderate-resolution imaging spectroradiometer (MODIS) satellite data by Catarino et al. (2020) indicates that annually, up to 30% of the Angolan landscape is burned. The extent and frequency of bush fires varies for one ecoregion to another, but over most of the country, the impacts of fires caused by human activity far exceeds that of natural (lightening ignited) fires. The negative impacts of uncontrolled bush fires are particularly serious along the margins of the isolated remnant patches of Guineo-Congolian, Afromontane and Mangrove forests. These rich centres of biodiversity are critically endangered by repeated fires. Similarly, the extensive mesic savannas of the planalto—the bread-basket for many rural communities—are also under threat over the vast area occupied by the miombo woodlands of central Africa.

The increasing incidence and intensity of fires over much of Angola coincides with the rapid increase in both urban and rural populations since Independence, with human populations increasing from 6.5 million to 32 million between 1975 and 2022. The problem is double edged. The majority of the rapidly increasing urban population cannot afford fossil-fuel based energy sources and are dependent for their domestic needs on charcoal and firewood imported from rural areas. In response to this demand, charcoal has replaced fruit and vegetables as the key cash crop produced by rural communities. Traditional, ecologically sustainable systems of shifting agriculture, where fields were rested after four or five years of cropping, allowing fertility to recover over perhaps 30 years before the next cycle of use, have been abandoned. The notoriously poor soils of the planalto are soon depleted of their nutrients, and new fields cleared through deforestation and fire. Traditional systems have not been replaced by modern systems of fire management.

In some African conservation areas fire has been used to manage ecosystems in favour of selected habitats, rare species or the protection of infrastructure. Modern fire management systems are complex and expensive to implement. They require advanced knowledge of fire behaviour and habitat responses based on many years of research. Few African countries can today afford the investment needed to implement controlled, rotational burns over large areas. For this reason, learning from the experience of other countries, such as Namibia, South Africa, Tanzania and Zimbabwe is the most pragmatic approach. General principles and guidelines for fire management have been developed for the arid and mesic savannas of Kruger National Park, which ecosystems are similar to those in many Angolan national parks. The findings of these studies are of use to fire managers in Angola's protected areas (Archibald et al., 2017; Bond & Van Wilgen, 1996; Govender et al., 2006; Van Wilgen et al., 2007). As a guiding principle, more frequent fires, early in the dry season, and therefore less intense, are recommended for mesic savannas.

It is wise to remember that fire must be respected for both its positive and negative attributes. The words of pioneer African ecologist, John Phillips (1965) "Fire: a good servant but a bad master", are pertinent when considering fire management options.

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Chapter 8
Herbivory: Mammalian Grazers and Browsers

Key Concepts and Questions: This Chapter Explains

- *How soils, climate, fires and mammalian herbivores evolved and interacted to shape Angola's vegetation and animal communities.*
- *Why soils and the nutritional quality of vegetation they carry influence the patterns of herbivore impacts in African ecosystems.*
- *What factors determine the distribution and structure of Angola's mammal herbivore communities.*
- *How the impacts of grazing cattle and browsing goats have replaced those of indigenous herbivores.*

Context: The Coevolution of C_4 Grasses, Savannas, Herbivores and Humans

> Herbivores are a main driver of ecosystem patterns and processes in semi-arid savannas, with their effects clearly observed when they are excluded from landscapes.
>
> (Wigley-Coetsee et al., 2022)

African ecosstems have endured and adapted to at least eight million years of regular fires across the highly flammable C_4 grasslands and fire-tolerant woodlands of its mesic/dystrophic savannas. Its arid/eutrophic savannas have co-evolved in the presence of a rich fauna of mammal herbivores, in particular the antelope that characterise Africa as a wildlife paradise. Climatically, Africa did not experience the dramatic episodes of glaciation that transformed the landscapes of Northern Hemisphere continents during the cold, dry Ice Ages of the Pleistocene. Neither did Africa witness the extinction of megaherbivores that occurred in Australia, the Americas, Madagascar and New Zealand (Owen-Smith, 1987, 2021) over the last 40 thousand years, as *Homo sapiens* the hunter/gatherer expanded across the globe from the savannas of eastern and southern Africa—the Cradle of Humankind. The happy coincidence of the early evolution of *H. sapiens* on the savannas of Africa is possibly the reason why the modern large herbivores of Africa were able to co-evolve with the human species. The mammals could adapt to human hunting pressures over many tens of

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https://doi.org/10.1007/978-3-031-18923-4_8

thousands of years, rather than collapse as they did on the other continents, where the encounter was comparatively rapid.

More recently, during the past 10,000 years, domesticated cattle and goats have been introduced to Africa from Eurasia. Their impact on Africa's rangelands has been dramatic. A synopsis of the role of indigenous mammal herbivores (largely free-roaming) in shaping the vegetation of the savannas, and the changes brought about by the introduction by human societies of domestic grazers and browsers (largely sedentary) to Africa provides insights to the changing patterns of herbivory across the continent.

Herbivores, whether grazers or browsers, have both negative and positive impacts on the plants on which they feed. Herbivores can:

- Stimulate grass growth, or be destructive of plants.
- Contribute to nutrient cycling.
- Maintain or change the relationship between grass and woody plant density.
- Open the canopy of grasses and trees.
- Reduce the rate of fuel accumulation and thus of fire intensity.
- Retard or accelerate the pace of recovery from defoliation.

Herbivores range in size from the smallest invertebrates to the largest of land mammals. In mesic/dystrophic savannas of central and western Africa the biomass of vertebrate herbivores is much lower than in the arid/eutrophic savannas of eastern and southern Africa. In the mesic savannas, earthworms, termites and decomposing microorganisms, together with fire, occupy the role of the large herbivorous mammals of arid savannas. The close evolutionary relationships between herbivores and the plants they depend on and the landscapes they inhabit, account for the diversity of the herbivore communities across Africa.

8.1 The Evolution of African Mammalian Herbivores and of Arid/Eutrophic Savannas

Our understanding of the distribution and density of the African fauna, like that of its flora, has progressed from the oral accounts of traditional communities, and the documented observations of naturalists of the colonial era, to the more objective and data-rich syntheses of the past decades. While the century-old biome concept has recently been widely applied for African vegetation formations (Burgess et al., 2004), new concepts such a pyromes (Archibald et al., 2013) and herbivomes (Hempson et al., 2015a) have been proposed for the collective characteristics of fires and herbivores. These are useful conceptual frameworks, and will help guide an understanding of the role of mammalian herbivores in shaping Angola's biomes.

Plant responses to herbivory have long been recognised, but the distinction between the patterns of response to fires and herbivory in arid/eutrophic and mesic/dystrophic savannas has been blurred by many studies that treat all African

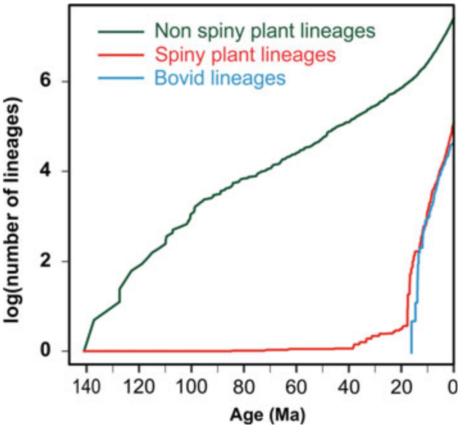

Fig. 8.1 Diversification of spiny plant and bovid (including antelope) lineages in Africa. From Charles-Dominique et al. (2016) *Proceedings of the National Academy of Sciences*, 113(38), E5572–E5579

savannas as a single biome. Recent research by Bond (2019 and references therein) has brought convincing phylogenetic, paleoecological and ecological evidence that informs an understanding of the long history of the distinctive evolutionary pathways of the two African savanna biomes.

The key feature of tropical savannas (their C_4 grasses, evolved in response to fire and seasonal drought) made their appearance ca. 30 Ma, with the rapid expansion to their current prominence dating from ca. 8 Ma. The disjunction between the mammalian herbivore-dominated arid/eutrophic savannas, and fire-dominated mesic/dystrophic savannas (Archibald et al., 2017; Huntley, 1982), might date from the mid-Miocene (ca. 16 Ma). This was when stem spines appeared on woody plants (to reduce browsing) and the diversification of African bovids accelerated (Charles-Dominique et al., 2016; Fig. 8.1). The thornless mesic savannas probably evolved later. They were well established before the origin of geoxylic suffrutices, which are characteristic features of mesic savannas, and which date from the Pliocene, less than 5.3 Ma (Maurin et al., 2014).

Both woody plant **architecture** (spiny/non-spiny) and grass **nutrition quality** (high/low) are key features of different African savannas and their resultant herbivore composition. An important distinction between the grasses of African savannas is the differences in the proportions of their respective investment in metabolic (M) and structural carbohydrate (C) constituents (Bell, 1982). **Metabolic constituents** (proteins and soluble carbohydrates) are what **herbivores** require for growth. **Structural carbohydrate constituents** (cellulose, hemicellulose and lignin) are what **grasses** require for growth. The ratio of M/C determines the value of herbage to herbivores. Plant-available soil nutrients determine the ability of grasses to produce protein, while water limits the total biomass of the end product of grass growth. The consequences of the different soil nutrient conditions in the two savanna biomes are summarised in Table 8.1.

The fire/herbivory interactions in arid and mesic savannas are typical of nature's feedback systems which maintain ecosystem equilibria and include:

Table 8.1 Characteristics of the grass cover of arid/eutrophic and mesic/dystrophic savannas

Arid/eutrophic savannas	Mesic/dystrophic savannas
• Grasses have high nutrition value	• Grasses have low nutrition value
• Low rainfall/low grass biomass	• High rainfall/high grass biomass
• High herbivore biomass controls grass structure	• Low herbivore biomass has low impact on grass cover
• Mixed feeders	• Selective or bulk feeders
• Limited combustible material	• High biomass of combustible fuel
• Infrequent fires	• Frequent fires

- A high proportion of palatable arid savanna grasses being consumed by herbivores, with less fuel for fire;
- A high proportion of unpalatable grasses in mesic savannas, with low levels of herbivory, providing more fuel for fires.

The mechanisms involved in these interactions have been demonstrated in arid and mesic ecosystems of Kruger National Park (Smit & Archibald, 2019) and are relevant to similar systems in Angola. The evolutionary responses of mammalian herbivores to these and other food quality challenges are well illustrated by adaptations of their digestive systems (Box 8.1).

Box 8.1 The Ruminant Gut and Hypsodont Teeth: Succeeding on Low Quality Forage

The most successful mammalian herbivores are the ruminants, which include members of the bovidae, giraffidae and tragulidae. The bovidae include 35 species indigenous to Angola (including, for example, Impala, Springbok, Giant Sable, Greater Kudu and Forest Buffalo), with one species each of giraffe and tragulid. The Angolan Giraffe (*Giraffa giraffa angolensis*) was once the symbol of Mupa National Park, but is now extinct in Angola. The tragulid (Water Chevrotain *Hyemoschus aquaticus*) known from Cabinda and Uíge, is an ancient, ancestral species related to the first small, forest-dwelling ruminants that evolved 50 million years ago. Little is known of the ecology of this elusive mini-ungulate of the Maiombe and Uíge forests. Currently the most numerous ruminants in Angola, and the world, are domestic cattle, sheep and goats, with a massive global population of 3.6 billion, which is orders of magnitude more abundant than indigenous ruminant species.

The rapid speciation of ruminants can be explained by the adaptations to life on the grasslands and open savannas of Africa during the arid Miocene (Chap. 4, Box 4.1). However, the early mammal herbivores faced two challenges. First: the fire-tolerant C_4 grasses that dominate tropical savannas have high **cellulose** and **silica** contents. To digest cellulose a special enzyme, **cellulase**, is needed, but is absent in mammals. Second: the teeth of early mammalian herbivores were rapidly worn down by the gritty grasses. Two evolutionary responses evolved.

- First, mutualistic relationships evolved with **microorganisms** (bacteria, protozoa and fungi) that have cellulases that facilitate digestion in the herbivore stomach. These microorganisms break down the cellulose to fatty acids, proteins and sugars, essential for energy and growth. This mutualism solved the first challenge.
- Second, the problem of gritty grasses was addressed by the evolution of high-crowned (**hypsodont**) teeth covered with enamel—the hardest material in nature—extending past the gum line, greatly reducing wear and tear. These grinding molars were adapted to masticate the coarse grass leaves and stalks, and prepare rough plant material for digestion.

Grasses, in response to grazing by herbivores, evolved **intercalary meristems**. These are the growing points in grass stems and at the base of grass leaves that allow rapid growth after damage, such as that caused by frequent grazing. Grasses also have the meristematic tissue of their main shoots (**tillers**) located at the soil surface (**basal tillering**), providing protection against fire and intense grazing. Most savanna grasses form multi-tiller tussocks, which might live for many decades. Grasses depend on regular defoliation (by grazers or fire) to stimulate growth. Too much grazing and trampling pressure can damage the meristems and cause death. Too little defoliation can result in a dense mat of fire-prone dead grass shading and ultimately killing the grass plant. It has been suggested that fire, grasses (with basal tillering and intercalary meristems), and antelope (with hypsodont dentition and slender, hoof-tipped legs, ideal for fast escape from predators in open grasslands), coevolved during the rapid expansion of savanna through the Miocene/Pliocene (Box 4.1).

It is important to note that the ungulates (hooved mammals) fall into two distinct groups—the even-toed ungulates (**artiodactyles**—pigs, hippopotamus, antelope) and the odd-toed ungulates (**perissodactyles**—zebra, rhinos). Ungulates are furthermore grouped according to two different digestive systems—hindgut fermentation and foregut rumination.

Artiodactyles (with the exception of pigs and hippos) are **ruminants**, which require relatively high-quality food. Perissodactyles are **hindgut fermenters** which can make use of low-quality food. The two digestive systems are illustrated in Fig. 8.2.

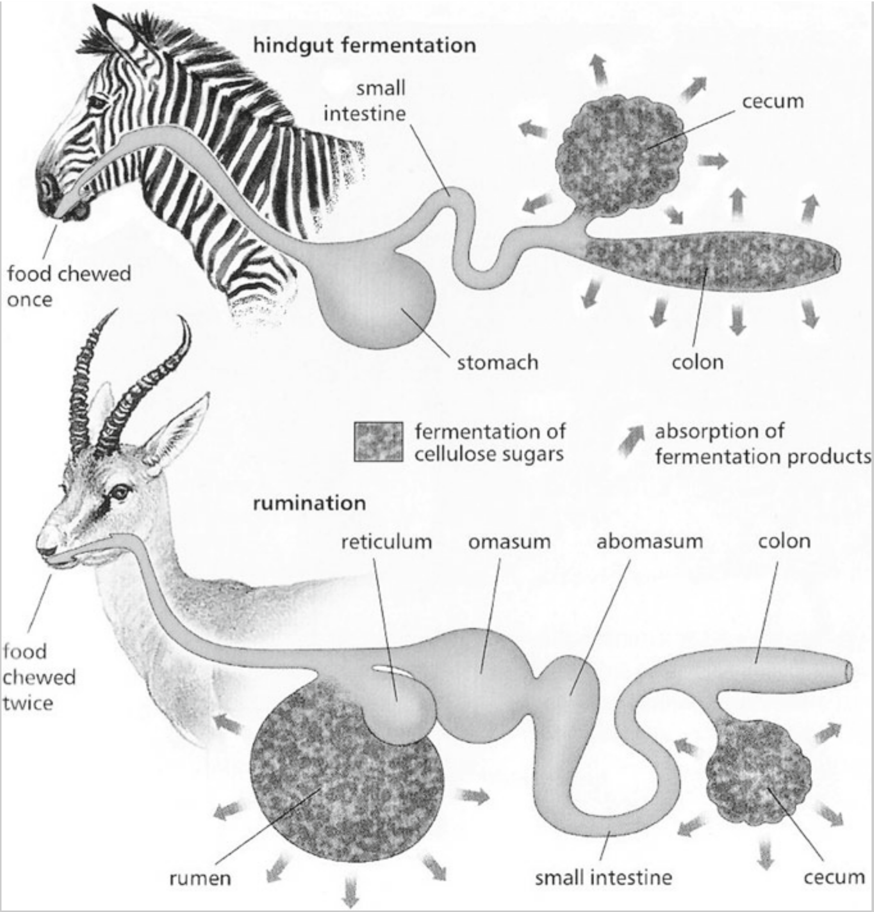

Fig. 8.2 Stylised comparison of hindgut fermentation and rumination digestive systems. From Shorrocks (2007) *The Biology of African Savannahs*. Oxford University Press, Oxford

- In hindgut fermenters (which include elephant as well as zebra and rhino), the food is chewed once and passed to the stomach where it is digested. It then is passed to the caecum and colon, where it is fermented by microorganisms. This process is only 50% effective in digesting cellulose, but because it is a comparatively simple throughput, it is fast, completed in 48 h. The dung of hind-gut digesters is rough, reflecting the poor breakdown of celluloses.
- Ruminants (excluding the primitive Chevrotain) have a four-chambered stomach. Food is consumed, chewed with a mix of saliva, and enters the first chamber—the **rumen**. The rumen acts as a storage compartment, allowing continued processing of food long after it is consumed. The

coarsest parts of the plant material (the **cud** or **bolus**) are then regurgitated back into the mouth where they are once again chewed (chewing the cud) a process known as **rumination**. Passed back to the rumen, it is fermented by microbial activity. This material is then passed to the second chamber—the **reticulum**. Here it is further fermented, and passed to chamber three—the **omasum**, where it is filtered. Hereafter it passes to the fourth chamber, the **abomasum**—the 'true stomach'—and to the **small intestine** and on to the **caecum**, where further digestion and absorption occurs. This complex process takes about 80 h, but is 80% effective in breaking down (**hydrolysing**) the cellulose and other nutrients contained in the rough plant material. The dung of ruminants is consequently fine-grained.

The minimum level of protein required by ruminants to maintain microfloral activity is 6%. Despite the selection of relatively high-quality forage, the slow digestion process of ruminants has a serious constraint. If the protein level drops below 6% (frequent in the mesic/dystrophic savannas of the miombo) the slow processing of their food can lead to the loss of weight and physical condition. Despite the high primary (plant) productivity of low nutrient mesic savannas, they cannot carry a proportionate (herbivore) productivity. In contrast, the arid/eutrophic savannas, with sustained protein content, can carry a much higher ungulate biomass than the mesic savannas.

The coevolution of C_4 grasses, hypsodont teeth and rumination accounts for the success of savanna herbivores across Africa.

8.2 The Herbivomes of Africa

South African ecologist Gareth Hempson and co-workers undertook an ambitious synthesis of the biomass and **functional traits** of 92 species of African mammal herbivores. Together with rainfall, fire regime, biome and soil data they delimited herbivory regimes which, following the language of biomes and pyromes, they called herbivomes (Hempson et al., 2015a). Their five **functional types** (Fig. 8.3) and four **herbivomes**, provide conceptual frameworks that are highly relevant to understanding the distribution patterns of Angola's mammal herbivores. The concept of functional type (or functional trait) is used by ecologists to simplify the structure of communities into manageable units for study and to answer basic questions on their relationships with other species and the environment. All five functional types and four herbivomes are represented in Angola.

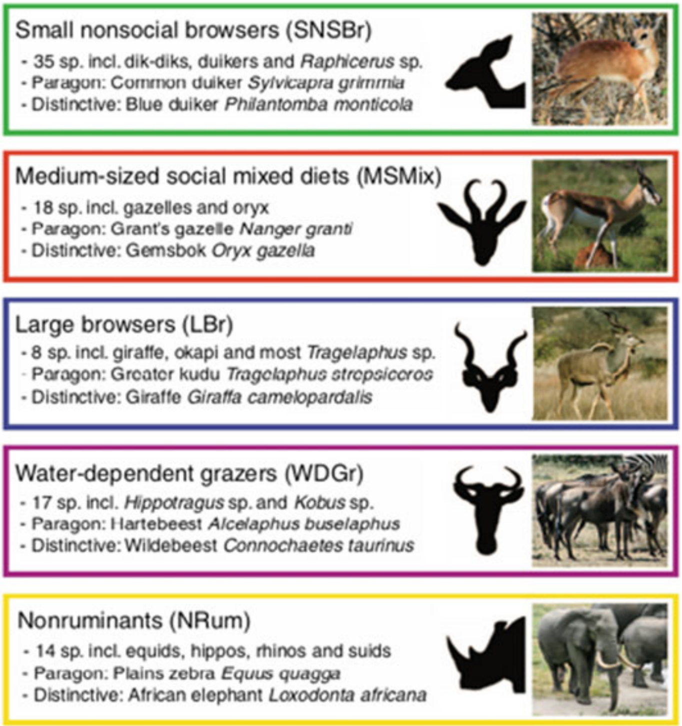

Fig. 8.3 Herbivore functional type classification for African mammals. From Hempson et al., (2015a) *Science*, 350(6264): 1056–61

Functional Types

- The **small, non-social browser** functional type is characteristic of the antelope of the moist closed forests of Cabinda, Zaire, Uíge and Lunda-Norte (Bay Duiker, White-bellied Duiker, Black-fronted Duiker, Blue Duiker; Water Chevrotain). This group of small, non-social browsers also includes the Dik-dik and Steenbok of the arid southwest.
- The **medium-sized, social mixed feeders** are arid savanna species (Springbok, Gemsbok).
- **Large browsers** (Greater Kudu, Giraffe) are also arid savanna species.
- **Water-dependent grazers** include both arid and mesic savanna species (Blue Wildebeest, Sable, Roan, Lechwe, Puku).
- The fifth group includes **the non-ruminants** (Zebra, Black Rhinoceros, Savanna and Forest Elephant) that because of their ability to utilise rough, nutrient-poor herbage are characterised as bulk-feeders.

The distribution of herbivore biomass according to functional type in Africa is overwhelmed by the non-ruminant group, where elephant alone exceed the biomass

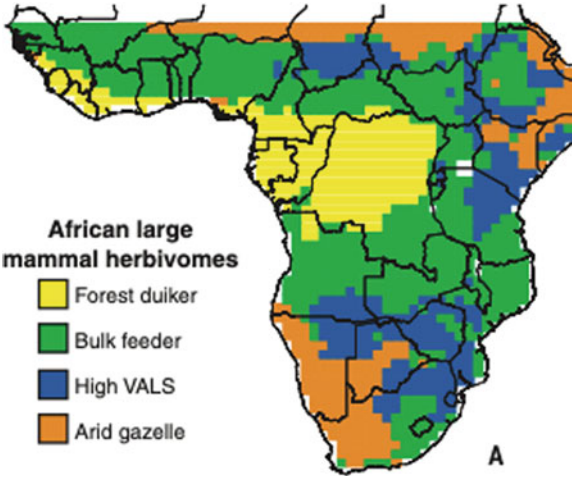

Fig. 8.4 Distribution of African large mammal herbivomes. From Hempson et al., (2015a) *Science*, 350(6264): 1056–61

of all other 91 herbivore species combined (Hempson et al., 2015a). Fritz et al. (2002) demonstrate that the biomass of megaherbivores, in particular elephant, is limited by food quantity, not by food quality, due to their ability to tolerate low quality food in higher rainfall areas with low fertility soils.

Herbivomes

A cluster analysis of the data-set compiled by Hempson and colleagues revealed four **herbivomes** based on functional type, social behaviour and habitat (Fig. 8.4).

- The **'forest duiker' herbivome** fits with the forested habitats of central and west Africa, including northern Angola.
- The **'arid gazelle' herbivome** matched the arid savannas of southwest Africa, the Horn of Africa and the Sahel.
- The third, and largest distinct group is the **'bulk feeder' herbivome**, with distributions fitting with the mesic/dystrophic savannas (including miombo). The bulk feeder herbivome comprises a high proportion of water-dependent non-ruminant grazers, but with elephants making the largest contribution to overall biomass. The habitat of this group is largely confined to low nutrient soils, where grasses are of low nutrition value, produce high biomasses of fuel, and where fire rather than herbivory is the main consumer.
- The fourth grouping is the **'high variety and abundance of larger species' herbivome (VALS)**. This group includes the arid/eutrophic savannas of Africa, especially those of nutrient rich soils and consequently more nutritious herbage.

In southern Africa, this fourth 'VALS' herbivome includes the floodplains and adjoining open savannas of the Cuando Cubango/Okavango, and the arid savannas of Botswana, Zimbabwe and South Africa. In previous centuries it also included the arid coastal zone of Angola, from Namibe to Benguela and even Luanda, where remnants of a once abundant large herbivore fauna survived in Quiçama until the 1970s. In eastern Africa, it includes the basaltic Serengeti Plains. These are the epicenters of antelope diversity and abundance of the world and the sites of major national parks and World Heritage Sites such as Okavango, Kruger, Hwange, Gorongosa, Tsavo and Serengeti.

8.3 Patterns of Impacts of Browsers and Grazers

Africa today retains, at least in effectively managed protected areas, a megafaunal assemblage that resembles that of the Pleistocene. It is an ideal continent on which to study the role of mammal herbivores in ecosystem dynamics, especially in terms of their impacts on nutrient cycling, damage to trees, consumption of buds, seeds and leaves, the dispersal of fruit and the opening up of woodlands by trampling.

Herbivores (specialist consumers) also act as competitors with fire (a generalist consumer) by consuming potentially combustible fuel, thus reducing fire intensity and impact. At high densities, browsers create a distinct browse line in trees and shrubs, at levels proportionate to their reach. If they remove the growing tips of tree saplings, the combined effects of browse and fire will cause mortalities and possibly a change in vegetation structure. Tree saplings have to outpace both the **fire trap** and the **browse trap** to reach maturity (Chap. 10, Fig. 10.14).

In some areas, herbivores might maintain open savanna where the climatic potential is forest, although evidence of such herbivore-mediated controls in high rainfall areas is limited. Herbivore-constrained savanna structure is rare in moist and mesic savannas, which are notorious for their very low herbivore biomass. Conversely, in arid savannas, herbivores exert significant controls on vegetation structure. Megaherbivores (body mass greater than 1000 kg) such as elephant might cause physical damage to large trees, and reduce a tall woodland to a short shrubland. In Kruger National Park, herbivore exclusion over 22 years revealed an 11-fold greater woody canopy cover in areas without herbivores when compared with sites exposed to mammalian herbivores (Asner et al., 2009). The long-term herbivore-exclosure experiments in an arid/eutrophic *Colophospermum* savanna in Kruger National Park (Wigley-Coetsee et al., 2022; Figs. 8.5 and 8.6) demonstrate the impact of elephant on vegetation structure. Similar impacts were not noted in exclosures in mesic/dystrophic savannas with the same elephant densities (Asner & Levick, 2012). Mega-grazers, such as Hippopotamus and White Rhinoceros can also open up dense grass and shrub cover, establishing ‘**grazing lawns**’ (Hempson et al., 2015b). Waldram et al. (2008) describe White Rhinoceros as ecological engineers due to their top-down effects on ecosystem structure, creating a mosaic of fire-free patches of short, nutritious lawns, thereby facilitating the habitat’s use by other herbivore species.

Owen-Smith (1982, 2021) notes the distinction between browsers (which select plant species and plant parts for maximum **energy** gain), and grazers (that focus on plant quality, for maximum **nutrient** gain). Whereas *Colophospermum mopane* (mopane/mutiati) has no structural defences against herbivory, many woody species

Fig. 8.5 Elephant damage to *Colophospermum mopane* arid/eutrophic savanna in Kruger National Park. *Photo* Merle Huntley

Fig. 8.6 Mopane woodland protected from elephants within a large exclosure. *Photo* William Bond

of arid/eutrophic savannas do, such as the spinescent adaptations of genera such as *Acacia, Adenium, Balanites, Capparis, Dichrostachys, Euphorbia, Gymnosporia, Maytenus* and *Zizyphus*. Such defences do not always prevent herbivores from consuming leaves and shoots, but reduce the rate and volumes removed per unit effort. These plants, and the mammals that feed on them, have co-evolved.

Mammals that browse on spiny trees and shrubs have narrower muzzles, longer tongues, and prehensile lips, allowing them to handle thorny plants better than broad-mouthed grazing species. An instructive comparison is that of the two African rhino species. The Black Rhinoceros (also known as the prehensile-lipped rhino) is a browser while the White (or Square-lipped Rhino) is a grazer. The two species have distinctive feeding habits and ecological impacts. Black Rhino consume thorny shrubs, opening up thickets. White Rhino graze grasses into distinctive ‘grazing lawns’, which maintain fire-free areas.

The tallest of antelope, Giraffe, which usually have limited impacts on habitat structure, can exert serious damage to arid savanna species if the density of giraffes exceeds the carrying capacity of the tree community (Bond & Loffell, 2001). After giraffe were introduced into the Etendeka Concession in northwest Namibia, they caused the local suppression of their preferred browse (*Maerua* and *Boscia*) and the disappearance of some bird species (Christopher Hines, pers. comm. 2020). This situation can even arise at low densities of Giraffe (and other herbivores) where low browse availability results from drought or high levels of competition.

While elephants have the physical capacity to transform woodlands to shrublands, so too do porcupines, at the opposite end of the herbivore biomass spectrum. Yeaton (1988) describes a sequence of porcupine damage to the basal bark of *Burkea africana* trees, followed by repeated fire damage to the exposed xylem, and finally the collapse of the trees during windstorms. The process developed over a 20-year sequence of four or five fires, each fire burning deeper into the damaged trunk, and resulting in up to two percent of the large trees being felled per year. In mesic/dystrophic savannas such as those dominated by *Burkea africana*, with low soil nutrient status and very slow tree growth, even a two percent per annum mortality can have significant impact on woodland structure.

Box 8.2 Human–Environment Interactions: The Transformation of Savannas by Domestic Livestock

We live in a world that has been greatly transformed by human activities, especially over the last two centuries of industrialisation (the **Anthropocene**). Such changes were preceded by changes throughout the late Pleistocene—especially over the last 40,000 years—as described in the introduction to this chapter. As human-driven ecological transformations intensify through the Anthropocene, focus has been directed towards the progressive socio-economic impacts of global warming anticipated within the present century (Box 5.1). But in Africa, far more rapid changes have occurred during the past century through distortions to the structure and biomass of herbivores as a result of agriculture, grazing, and deforestation. In a series of studies embracing sub-Saharan Africa, Hempson and colleagues have synthesised a vast data base on the mammalian herbivores (both indigenous wildlife and introduced livestock) of the region (Archibald et al., 2013; Archibald & Hempson, 2016; Hempson et al., 2015a, 2017). These authors have made remarkable and important findings. By comparing geo-referenced current and historic herbivore communities, based on species-level biomass data, with data on fire frequency, herbivore impact and soil characteristics, they demonstrate substantial total mammalian biomass losses in mesic savannas and biomass increases in arid savannas. They relate these changes to a range of environmental pressures (hunting, rainfall, fire and the increase of domestic livestock).

Pastoral traditions with domestic livestock (cattle, sheep, goats) have been practiced across Africa for at least 2000 years, and the numbers of individuals and the total biomass of domestic species now greatly exceed those of indigenous species. Domestic livestock strongly modify ecosystems through effects on fire frequency and intensity, tree cover and nutrient dispersal. Domestic livestock also compete directly with indigenous herbivores for the most nutritious grazing. Livestock biomass currently matches or exceeds past wildlife biomass (excluding elephant) in areas with rainfall up to 1000 mm per year (Hempson et al., 2015a; Fig. 8.7). In areas receiving more than 1000 mm MAP, the biomass of livestock falls below that of former wildlife biomass levels.

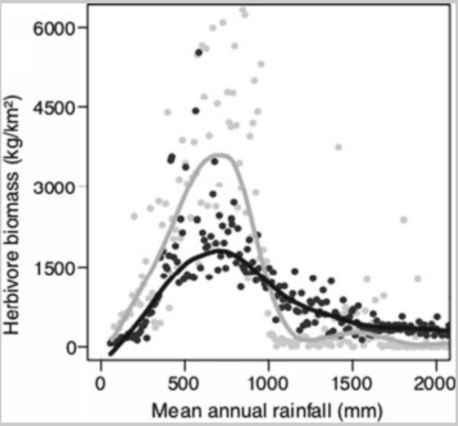

Fig. 8.7 Herbivore biomass in relation to mean annual rainfall. Both reconstructed past indigenous herbivore biomass (excluding elephants)—(black points and line) and present livestock biomass (grey points and line) peak at ca. 650–750 mm mean annual rainfall, where arid/eutrophic savannas and mesic/dystrophic savannas interdigitate. From Hempson et al., (2015a) *Science*, 350(6264): 1056–61

Current domestic livestock populations exceed past wildlife biomass in arid savannas, where the provision of supplementary water and fodder has boosted carrying capacity and removed a key constraint on herbivore numbers—as determined by the interannual variability in water and food availability. Hempson et al. (2017) demonstrate that above a biomass threshold of 1500 kg km^2, herbivores reduce grass accumulation and thus increase fire suppression. This situation is true in Angola, both in arid savannas (Cunene, Namibe, Benguela) and on the margins of mesic savannas (Huíla) where intensive pastoral systems have been developed over the past century. Whereas indigenous mammal numbers fluctuate widely in response to the variability of resources, domestic livestock numbers tend to be pegged to the pastoralist's perception of average conditions defined by traditional stocking rates.

A consequence of heavy grazing, and the reduction of fuel load for fire, is that of thicket formation (**bush-encroachment**) in many parts of southern Africa. Spiny *Acacia* species and *Dichrostachys cinerea* are particularly prone to such thicket formation where fire has been suppressed by overgrazing. However, after episodes of high rainfall and rapid growth of annual grass species, and the accumulation of fuel followed by rare but hot fires, the seeds of *Dichrostachys cinerea* are known to germinate rapidly. Fire is thus both a stimulant of seed germination, and a suppressor of seedling development, interacting in complex ways with herbivores.

In contrast to the arid savannas, over most of the mesic/dystrophic savannas (miombo), past and present livestock biomass remains low due to the nutrient-poor herbage on heavily leached and low nutrient soils, and to the presence of diseases such as trypanosomiasis.

Both Savanna and Forest elephants historically exerted strong impacts on woody vegetation, but the dramatic contraction of elephant range and population sizes over recent decades has resulted in measurable increases in woody cover (Stevens et al., 2016). The change results directly from reduced tree damage by browsing elephants, and indirectly through reduced opening of wooded communities to grass growth and thus increased fire penetration and damage to trees. Conversely, increasing goat populations in arid savannas have suppressed woody plant growth in some areas due to their negative impact on seedling establishment.

Long-term impacts of the distortion of the herbivore profile in Africa have included changes to patterns of nutrient dispersal due to the corralling of livestock at night to protect them against predators. Indigenous herbivores disperse nutrients over a wide area while domestic livestock, though corralling, concentrate nutrients in confined areas. Such nutrient hotspots can have significant effects on ecosystem structure, even at fine spatial scales. In *Burkea africana* mesic/dystrophic savanna at Nylsvley in South Africa, the sites of Middle Iron Age pastoral villages are reflected in pockets of *Acacia tortilis* arid/eutrophic savanna within the broad matrix of mesic/dystrophic *Burkea africana* savanna. The accumulation of nutrients from domestic livestock corralling resulted in a change in soil chemistry and texture, a change in vegetation structure and composition, and a change in bird communities which persisted for hundreds of years after the corrals had been abandoned (Scholes & Walker, 1993). Extended across sub-Saharan Africa, the impacts of such changes in nutrient diffusion (estimated by Hempson et al. (2017) to have been reduced to 5% of past levels) could introduce novel distortions to ecosystem patterns.

Africa is thus unique in its richness of indigenous ungulates, and the close interactions these have with the diversity of biomes, ecoregions and ecosystems that have evolved in parallel for millions of years. The continent is also unique in the extended history of the co-evolution of *Homo sapiens*, the fire-maker and pastoralist, over many tens of thousands of years more than in any other continent.

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Part III
Ecological Concepts and Ecosystem Processes

Context: Concepts, Principles and Laws in Structure, Function and Dynamics

Ecology—'the scientific study of the distribution and abundance of organisms and the interactions that determine their distribution and abundance'—has been an active profession for over a century. A strong body of concepts, principles and laws has been developed on which the science and practice of ecology are founded. In this volume, it is only possible to give meaningful descriptions of a few of the key concepts and principles. Examples of phenomena and relationships from Angolan and other southern African ecosystems will be used to illustrate what are often complex and even contentious ideas. Greater depth is available in the comprehensive textbooks and original research papers listed for further reading and in the bibliography.

As noted in the introduction to this book, ecological systems reflect a hierarchy of levels of organisation, from species, populations and communities, to ecosystems, biomes and the biosphere. For each level of the hierarchy, and for interactions between them, there are guiding concepts and principles, bound by the theory of evolution by natural selection and by the laws of thermodynamics.

In order to focus on concepts and principles relevant to the biomes and ecosystems of Angola, three levels of detail will be presented.

- First, general concepts that are basic to the study of any ecosystem or biome will be outlined. While not exhaustive, they include many of the elements of ecology of with which the student requires familiarity.
- Second, the workings of terrestrial ecosystems will be examined in terms of energy pathways governed by the laws of thermodynamics. Structural/functional interactions and dynamics will be considered at the landscape scale. Studies from the Mesic Savanna Biome and its interface with the Rain Forest Biome will be used as models.
- Third, the multiple ways in which animals and plants have adapted to survive, grow and reproduce in challenging environments will be described, using the Namib Desert Biome as a model to provide insights into the amazing products of evolution by natural selection.

Chapter 9
General Concepts in Ecology

Key Concepts and Questions: This Chapter Explains

- *How ecosystems are structured and function at successive levels within a hierarchy of interactions.*
- *Why evolution by natural selection is a founding principle of biology.*
- *How populations are structured spatially and in terms of age, movement, and life history patterns.*
- *Why species richness, evenness and dominance are key elements of community structure.*
- *How the interrelationships of species within a community create food chains and food webs.*
- *Why a landscape view of community structure is needed to identify patterns and relationships in and between habitats and biota.*
- *How the theories of island biogeography and metapopulations explain the diversity and dynamics of isolated populations.*
- *Why the competitive advantages of certain non-native (invasive) species can exert strongly negative impacts on rural livelihoods.*

Context: Ecological Assembly: Key Levels and Related Terms

Textbooks on the fundamentals of ecology usually follow a logical sequence from the organismic to population to community levels. Thereafter, processes are examined at higher scales of integration such as ecosystem energetics, patterns of distribution and abundance, and the emergent properties of ecosystems. Here we will introduce some of the foundational concepts and principles at these successive levels, and provide selected examples of their characteristics in the chapters that follow. Key terms mentioned in bold print will be discussed in more detail in succeeding chapters. The structure of this outline follows that presented by Smith and Smith (2015) in their excellent volume *Elements of Ecology*.

B. J. Huntley, *Ecology of Angola*,
https://doi.org/10.1007/978-3-031-18923-4_9

Organismic-Level Concepts

As emphasised in the definition of ecology, the science starts at the study of **organisms**, and therefore has to consider both the **genotype** (where **genes** are the units of inheritance in the process of adaptation by natural selection) and the **phenotype** (which is the physical expression of the genotype as molded by the environment). **Adaptation** by natural selection (or other processes such as genetic drift) occurs through the mechanism of **genetic variation** within populations and can result in genetic **differentiation,** and in certain environments the formation of **geographic isolates** and subspecies. Over longer periods, differentiation might lead to the creation of distinct **species**.

Population-Level Concepts

A **population** is a group of individuals of the same species that inhabit a given area. Populations vary in terms of the area encompassing all the individuals of the species, representing their **geographic range**. A species might comprise many, often isolated, populations. These individual populations form part of what is referred to as a **metapopulation** (Sect. 9.7). **Endemic** species and subspecies occupy a defined and limited area, usually referring to a single country or biome, such as Giant Sable of central Angola and *Welwitschia mirabilis* of the Namib Desert. **Ubiquitous** species occur over a wide geographic area, often across many countries and habitats, such as the dominant tree of the miombo, *Brachystegia spiciformis.* The term **dominant** is use both for a species that might, due to its size, abundance or other features, be visibly prominent, or where it is most abundant in numbers of individuals, or dominant in terms of biomass. A population's abundance and distribution within its range provides a measure of density, and the spatial pattern within the range might be **uniform, random or clumped**. While plant populations are fixed where they germinate, root and grow to maturity, most animal species are mobile and might be **migratory** or **nomadic** (as in many birds and some antelope) or the populations might be **sedentary** within a seasonally or permanently defined **home range** and, in many cases, a defended **territory**.

The **structure** of a population usually varies over time, both in sex and in age. An understanding of the **demography** of populations, in terms of rates of birth and death, and the timing of such events within the life history of individuals, is a requirement for the study of the dynamics of populations and communities. The life history characteristics of species can be used to understand how they relate to environmental forces, through what are known as ***r*- and *K*-strategies**.

Within populations of a single species, **intraspecific** interactions include competition for resources, where environmental factors (such as water and light availability, food and shelter resources) might limit growth according to the habitat's **carrying capacity**. Intraspecific competition might result in **self-thinning** within plant populations, as occurs in monospecific stands of trees in miombo woodlands. Self-thinning is the progressive decline in density and increase in biomass (growth) of remaining individuals caused by the combined effects of density-dependent mortality and growth within a population. Within antelope species, territorial behaviour might function as a regulator of population growth.

Community-Level Concepts

The structure of communities is one of the central topics of ecological research. Key measures of community structure are **species richness** and **species evenness**. Related to richness and evenness is the concept of dominance, which can refer to the number or size of individuals of a species. Species which predominate (in number or size) in a community are called **dominants**. In arid savannas, individuals of a single grass species might vastly out-number the scattered trees. Trees such as baobabs, through their size, the shade they cast and the alteration of soil water and nutrients around their base, might dominate both the functioning of the savanna community and the visual appearance of the landscape. Conversely, grasses might overshadow baobab seedlings, or through the accumulation of fuel and a resulting fire, might prevent the growth of baobab seedlings and thus have a dominant role in the life history and demographics of the physically much larger trees. Size or abundance are not the only measures of importance or dominance. **Keystone species** are those that influence community structure and function disproportionally to their size or numbers. For example, porcupines have been shown to influence savanna tree mortality at a level similar to the great 'ecosystem engineers'—elephants.

The concept of structure relates not only to physiognomic form (grassland, savanna, forest) or species composition (floral and faunal) but also to the physiological, morphological and behavioural adaptations that species have evolved to succeed in a particular location along an environmental gradient. The particular set of conditions, resources and adaptations needed to succeed in a particular ecosystem determine the **fundamental niche** of a species. Other factors, such as competition, determine the **realised niche** of a species within the range of conditions within which it can physiologically succeed.

Within communities, **interspecific competition** for resources is defined as a relationship that affects the populations of two or more species adversely. Two main forms of competition are recognised by ecologists. **Interference** or **contest** competition occurs where some individuals—using **direct** threats such as fighting or poisons—access resources while excluding other competitors (some winners, some losers). **Exploitation** or **scramble** competition occurs **indirectly** where the increasing intensity of competition depletes each other's resources. This process reduces growth and reproduction in all individuals in a population (all individuals losing equally) and described in examples in Sect. 9.5.

The concept of interspecific competition is one of the cornerstones of evolutionary ecology, and the subject of many classic studies. The fundamentals were established independently by two mathematicians, the American Alfred Lotka and the Italian Vittora Volterra, in the 1920s. Lotka and Volterra both described four possible outcomes of interspecific competition. The key outcomes of interspecific competition, according to the Lotka-Volterra equations, and as summarised by Smith and Smith (2015), are:

- Species 1 may outcompete species 2;
- Species 2 may outcompete species 1.

Both of these outcomes lead to the **competitive exclusion principle**, which states that two species with exactly the same ecological requirements cannot coexist. The other two outcomes involve coexistence.

- An **unstable equilibrium**, in which the species that was most abundant at the outset usually outcompetes the other.
- A **stable equilibrium**, in which two species coexist but at a lower population level than if each existed without the other.

A further outcome of the Lotka-Volterra models of interspecific competition is that which suggests mutual control between predator and prey populations that oscillate through time. Here another classic study demonstrates the concept—that of the relationship between Snowshoe Hare and Canadian Lynx, described in Sect. 9.6.

One of the important evolutionary consequences of competition is the **coevolution** of often complex structural features such as those that contribute to the successful pollination of plants by insects. Competition for similar resources, such as for soil moisture by trees and grasses, might result in **partitioning** of the use of such resources in space and time (Box 10.1). When a species' niche expands in response to the removal of a competitor, the result is known as **competitive release**. An example of rapid and major changes in herbivore populations, following removal of competitors (other herbivores), and of predators and poachers. This has occurred in the past several decades in Gorongosa National Park, Mozambique, as illustrated in Fig. 9.1. Box 9.1 provides a synopsis of the problem of invasive species in Angola, demonstrating the result of competitive interactions between invasive species and natural communities, mediated by human influences.

Box 9.1 Human–Environment Interactions: Invasive Species Threaten Rural Livelihoods

> Invasive species are among the top threats to biodiversity globally and are reported to be affecting livelihoods in 70% of African countries.
>
> Munyaradzi Makoni (2020).

One of the cornerstones of evolution and ecology is the concept of competition. The equilibrium of natural ecosystems is provided by a dynamic playing field—the demand for resources between competing species reaching a balance until some factor alters the availability of specific resources to the advantage of one of two competing species. Nowhere is the imbalance better illustrated than in the interactions between indigenous (native) species and alien (exotic, non-native) species, occasionally leading to the surge in dominance of the 'invasive' species. Many factors can account for a sudden proliferation of the population of a non-native species. First, the newly arrived species might be free of the factors (predators, competitors, parasites, diseases) that control its

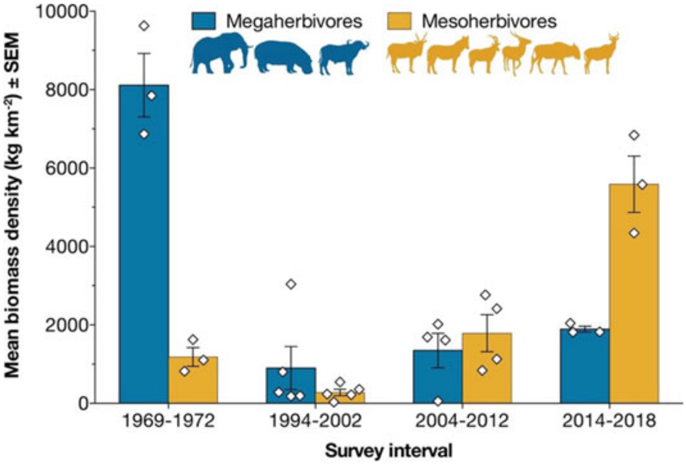

Fig. 9.1 Changes in the structure of herbivore biomass in Gorongosa National Park, Mozambique, following civil war and the reduction of carnivores and mega-herbivores. Mega-herbivores (greater than 600 kg body mass), meso-herbivores (less than 600 kg). From Stalmans et al. (2019) *PLoS ONE* 14 (3): e0212864

abundance in its natural habitat. Second, invasive species usually have high reproductive rates, effective dispersal mechanisms, rapid growth, and broad or generalist niche requirements. Third, human interventions frequently provide ideal conditions for newly arrived species.

During the past few centuries, the role of humans, as agents of long range dispersal (ships, cars, planes) and as transformers of landscapes through agriculture, have accelerated the distribution of species across the globe. The majority of immigrant species die unless supported by human intervention, or survive because they can adapt to their new environment. On average 10% of new arrivals do not survive and reproduce, less than 10% become naturalised. Of these, less than 10% become invasive. But the few species that have become invasive are today threatening sustainable food production, human wellbeing and biodiversity.

Despite the global impacts of invasive species, surprisingly little attention has been given to the problem in Angola. This is in contrast to the situation in Europe, where annual damage worth 12 billion Euros results from invasive species impacts on human health, damaged infrastructure and agricultural losses. In South Africa, with over a century of investment in invasive species research (Moran et al., 2013), such species currently cost the country over US$450 million a year and are responsible for about a quarter of its biodiversity loss.

Several explanations might been offered for the absence of a concerted programme of invasive species management in Angola. These include the lack of information, limited scientific capacity and inadequate technological and financial resources. But a key factor is that despite the five centuries of inter-continental contact and trade between Angolan ports such as Luanda and Benguela with Europe, the Americas and Asia, surprisingly few invasive plants and animals have established themselves in Angola. The country has relatively few aggressive invasive plant species, perhaps less than a dozen, compared with South Africa where 775 invasive species of plant have been identified (Van Wilgen et al., 2020). Yet several invasive plant species are currently spreading rapidly across valuable agricultural land, reducing the production potential of rural communities and threatening rare plant and animal species and biodiversity hotspots. Very limited information is available on invasive animal species, but a rapid survey of invasive plants was undertaken in 2014 (Rejmánek et al., 2016), providing insights into the seriousness of Angola's invasive species problem.

Here the focus is on invasive plants. Three categories of non-native plants with invasion potential are recognised (Pysek et al., 2004):

- Casual alien plants: Non-native plants that may flourish and even reproduce occasionally outside cultivation in an area, but that eventually die out because they do not form self-replacing populations, and rely on repeated introductions for their persistence.
- Naturalized plants: Non-native plants that sustain self-replacing populations without direct intervention by people (or in spite of human intervention) by recruitment from seed or ramets (tillers, tubers, bulbs, fragments, etc.).
- Invasive plants: A subset of naturalized plants that produce reproductive offspring, often in very large numbers, even at considerable distances from the parent plants, and thus have the potential to spread over a large area.

In a 4000 km roadside survey across nine provinces and 13 vegetation types during August 2014, Rejmánek et al. (2016) identified 44 naturalised plant species (excluding crop or horticultural species), of which 19 species were conclusively invasive. Three of these are of immediate concern.

The spiny cactus *Opuntia stricta*, which is rapidly invading the southern escarpment and the lowlands from Dombe Grande to north of Luanda, is listed among the world's 100 worst plant and animal invaders (Lowe et al., 2004). It is an extremely aggressive invader of savannas, and has been the subject of intense control projects in Kruger National Park for over 50 years (Foxcroft et al., 2004). Fortunately, it can be suppressed through inexpensive biological control methods, using the herbivorous insect *Dactylopus opuntiae*. *Opuntia stricta* is invading much of Quiçama National Park, and an urgent response is needed to prevent loss of habitat for the park's wildlife population.

The second most invasive plant species in Angola is another of the world's 100 worst invaders—the triffid weed, *Chromolaena odorata*, which is infesting agricultural lands in the moist forests of Cuanza Norte, Uíge, Zaire and

Malange. This plant spreads through the wind dispersal of its seeds. It is unpalatable to livestock and has no traditional use. It is difficult to control and manual methods need to be supplemented by chemical poisoning. Biological control methods have been used with variable success.

The third invasive species of concern—the fast growing South America tree *Inga vera*—has been invading escarpment forests, notably in Cuanza-Sul, where it was introduced to provide shade in coffee plantations. It rapidly outcompetes indigenous forest trees, and thus threatens the biodiversity of the critically threatened escarpment forest remnants. It is resilient to control by mechanical means as it coppices if not treated with chemicals.

The control of these three species is of the highest priority. But prevention is better than cure, and several species of great concern elsewhere in Africa, but not yet recorded in Angola, should be detected at an early stage and eradicated before they become established. These include *Azolla filiculoides, Broussonetia papyrifera, Clidemia hirta, Parthenium hysterophorus, Rubus rosaefolius,* and *Salvinia molesta.* The planting of highly invasive species, such as the Australian *Acacia mearnsii*—recently planted as a shade tree at Tundavala, Huíla, should be prohibited.

Ecosystem-Level Concepts

The **ecosystem** concept, like that of genes, species, populations and communities, is one of the founding elements of ecology. First defined by Tansley (1935) and elaborated by Odum (1983), the concept encompasses both structural and functional attributes. These attributes include all the organisms in a given area interacting with the physical environment, so that the flow of energy, and cycles of water and nutrients, create a defined trophic structure and biotic diversity. These include the exchange of materials between living (**biotic**) and non-living (**abiotic**) components of the system.

The **trophic** structure of an ecosystem comprises **primary producers** (the autotrophic component, which is dependent on solar energy, water and mineral nutrients, i.e. plants), **primary consumers** (the heterotrophic component, the consumers of plant tissue, i.e. herbivores); and **secondary consumers** (consumers of primary consumers, comprising carnivores and omnivores). Finally, **decomposers**, which mainly include invertebrates and microorganisms (bacteria, protozoa and fungi), break down the dead organic matter (**detritus**) produced by the higher trophic levels, releasing nutrients in a form that can be used by primary producers (Sect. 10.6).

The structure of the interconnections between the different trophic levels is termed a **food web**. Of special interest to conservation biologists are the consequences of any disruption to a food web. This often takes the form of a **trophic cascade**, where a predator reduces the abundance of its prey (herbivores) such that the impact cascades down to the next trophic level (grasses and browse—primary producers) with a rapid increase in the abundance and biomass of the latter. A different trophic dynamic has been recorded in the rapid explosion of the Waterbuck population in Gorongosa National Park, Mozambique, following the extinction of its main predator (lion) and the dramatic reduction of its herbivore competitors (buffalo, elephant, hippo) during the civil war. The Waterbuck (a mesoherbivore) population increased by an order of magnitude to over 55,000 from 1970 to 2020. Lion and other carnivore populations have been supplemented by re-introductions, but in the absence or low biomass of competitors, the waterbuck population continues to increase (Stalmans et al., 2019). The dynamics of herbivore populations affected by war and by the removal of carnivores is well illustrated by the Gorongosa data (Fig. 9.1).

The study of the processes of production, consumption, decomposition and the transfers of energy and materials between trophic levels has become a major branch of ecology, with specialised branches known as **systems ecology** or **ecological energetics**, as will be described in Chap. 10.

Landscape-Level Concepts

At the scale of a country with as much environmental diversity as Angola, details of community structure are often lost in the breadth of seemingly uniform landscapes that stretch from horizon to horizon. A **landscape** is defined by geographers as a part of the Earth's surface that can be viewed from one place. A landscape is usually made up of a collection of landforms such plains, valleys, hills, mountains and plateaus. Ecologists study the spatial patterns in landscapes and the habitats they offer for plants and animals, especially in terms of diversity and heterogeneity. The pioneers of Angolan ecology, from Welwitsch (1859) to Diniz (1973, 2006) took a landscape view of the country's ecosystems. Today, the **patterns** of Angola's landscape diversity are most easily detected with the aid of satellite imagery and drones, but much can be still learned from ground-based observations (Box 14.1).

Throughout this book, pattern is a central theme. It is defined by the spatial arrangement and **connectivity** of patches, large and small, across landscapes. As will be described, these patterns range from the scale of termitaria, to catenal sequences, to the extensive patterns of biomes, pyromes and herbivomes. Connectivity, through **corridors**, and **disjunction** (physical separation) are key features of pattern, and are responsible for the maintenance and creation of biodiversity through speciation and extinction processes. **Boundaries** between the units that create pattern can be diffuse or sharp, usually reflecting underlying environmental gradients, but also resulting from ecological processes. These processes might be immediate, by fire or herbivory, or very slow, as the result of the oscillations of climates and geological and evolutionary processes that cover millions of years. Gradual transitions between landscape units and plant communities are often called **ecotones**. Some ecotonal zones support **edge species** that have very narrow habitat preferences, such as Swierstra's Francolin, that occupies the scrubby margins of Afromontane forests of Mount Moco and Mount Namba.

Pattern and connectivity have become important concepts of conservation science, and have led to classic theories such as those of **island biogeography** and of **metapopulations**, which have direct importance for the understanding of Angola's Afromontane forest remnant patches and of fragmented populations of iconic species such as Giant Sable, Forest Buffalo and Forest Elephant (Sect. 9.7).

9.1 The Evolutionary Basis of Ecology

Overview

The foundations of ecology, and its underpinning by the concept of evolution by natural selection, go back to the writings of Malthus, von Humboldt, Wallace and Darwin. All these scholars were pioneers in the future science of ecology. Foremost of their publications was Darwin's (1859) seminal work *On the Origin of Species* which provided a revolutionary framework for understanding the diversity of life on Earth. A general introduction to the evolutionary basis of ecology is thus an important step in the learning process.

Throughout this book, several recurrent themes will have become familiar to the reader:

- Life on land imposes diverse constraints on organisms. Each environment presents a different set of constraints on processes relating to the **survival, growth, and reproduction** of organisms.
- **Species richness** varies widely across the face of the Earth, yet the set of characteristics that enables an organism to succeed in one environment typically precludes it from doing equally well under a different set of environmental conditions.
- The **theory of natural selection** is arguably the most unifying principle in biology. It provides a basis for understanding the distribution, diversity, and abundance of species, and is an essential point of departure for an understanding of ecology.

It is not intended that a detailed introduction to evolutionary biology and genomics be presented in this introduction to terrestrial ecology. An excellent and concise introduction to the subject of natural selection, adaptation, and evolution is given by Smith and Smith (2015) and is summarised here. It is relevant, however, to note that the modern tools of genomics, especially phylogenetics, have provided new insights into the evolution and age of many features of African ecosystems. These advances are described in relation to spinescent trees and shrubs in savannas (Sect. 8.1), hypsodont teeth in ungulates (Box 8.1), the evolution of C_3 and C_4 grasses (Sect. 10.2), the speciation of Afromontane birds (Box 18.1) and of the underground geoxyles of mesic savannas (Box 15.3).

Natural Selection and Differentiation

Adaptations are those heritable characteristics that enable an organism to survive and reproduce in a given environment. An adaptation is the product of natural selection—a heritable behavioural, morphological or physiological trait that an organism evolves over an extended period of time. **Natural selection** results from the differential fitness of individuals within a population to interactions with their environment. **Fitness** is a measure of the proportional contribution an individual makes towards future generations. In a given environment, some individuals will survive better, reproduce more, and leave more descendants—they will be fitter—than other individuals. The process of change in **heritable characteristics** carried from one generation to the next is called **evolution**. Natural selection and evolution occur within species.

Darwin laid down the key ideas defining the process of natural selection, summarised by Townsend et al. (2008) as follows:

- Individuals that form a population of a species are not identical.
- Some of the variation between individuals is heritable—that is, it has a genetic basis and is therefore capable of being passed down to descendants.
- All populations could grow at a rate that would overwhelm the environment; but in fact, most individuals die before reproduction and most (usually all) reproduce at less than their maximal rate. Hence, for each generation, the individuals in a population are only a subset of those that 'might' have arrived there from the previous generation.
- Different ancestors leave different numbers of descendants (descendants, *not* just offspring): they do not all contribute equally to subsequent generations. Hence, those that contribute most have the greatest influence on the heritable characteristics of subsequent generations.

The units of heredity, passed from parent to offspring, are called **genes**. **Genes** are arranged on **chromosomes**, with the genetic information being carried by molecules of **DNA** (deoxyribonucleic acid). A gene is a stretch of DNA coding for a sequence of **amino acids**. The different forms of a gene are called **alleles**. The pair of alleles present at a given locus defines the **genotype**. The sum of heritable information carried by an individual organism is the **genome**.

A **phenotype** is the physical expression of the genotype. The genotype can give rise to a range of phenotypes under different environmental conditions, a property known as **phenotypic plasticity**. The adaptive characteristics of phenotypes are referred to as **traits**. **Genetic variation** occurs within subpopulations, among subpopulations of the same species, and among different species. The **gene pool** is the sum of genetic variation within all members of a population. Where genetic variation occurs between subpopulations of a given species, it is referred to as **genetic differentiation**. All individuals of a species are part of the species' **metapopulation**, which might comprise many subpopulations, often geographically isolated from one another, as discussed in Sect. 9.7.

The process of **natural selection** acts on the phenotype, and involves altering a heritable characteristic of the genotype within the population and requires that this variation results in differences among individuals. Natural selection eliminates most deleterious genes from the gene pool, leaving behind only genes that enhance an organism's ability to survive and reproduce—which is their 'fitness' as described earlier.

Adaptations can only result from natural selection. Genetic variation can result from **mutations** (heritable changes in a gene or chromosome) or non-random mating. **Non-random mating** is the selection of a mate based on some phenotypic characteristic such as size or colouration. In small populations, non-random (or selective) mating can result in in-breeding between closely related individuals, which in turn can result in the inheritance of deleterious genes. These genes can result in decreased fertility, even death, a consequence known as **in-breeding depression**.

Genetic differentiation provides individuals and populations with the ability to survive and reproduce within a given environment. It also leads to variation in morphological, behavioural and physiological characteristics as a consequence of different selective pressures through natural selection. Species with a wide geographic distribution are exposed to significant environmental gradients. The subtle changes in genotype and phenotype across such gradients is called a **cline**. In Angola, the Forest Buffalo ranges widely across the country, from Quiçama on the coast to Luando in central Angola, to Lunda-Norte in the northeast and to Cabinda in the northwest. Across this geographic range a clear gradient (cline) in horn size and shape, and body mass and colouration is found in the different populations of Forest Buffalo.

Where abrupt changes in the habitat or environment occur, the population might be recognised as an **ecotype**. An ecotype is a population of a species that survives as a distinct group through environmental selection and isolation and that is comparable with a taxonomic subspecies. Clines and ecotypes are common in Angola, given the very sharp environmental gradients that occur, for example, along the Angolan Escarpment. The fragmented Afromontane forests of the Highlands have many examples of **geographic isolates**, where barriers to the free flow of genes within the populations have caused the evolution of **subspecies**, as illustrated in many bird species (Box 18.1).

Speciation

Speciation is the evolutionary process where populations evolve to become distinct species that are reproductively isolated from one another. **Species** can therefore most simply be defined as populations that can potentially breed together and produce **fertile** offspring. The concept is illustrated by the classic study of hybridization in the Cangandala population of Giant Sable. The isolated Cangandala population had been severely reduced, with a small group of females, but no males, surviving the impact of poaching. However, the Giant Sable cows mated with a lone Roan Antelope bull, producing a generation of hybrid, but infertile calves. When a Giant Sable bull was translocated from Luando to Cangandala, the group of cows successfully raised a new generation of fertile Giant Sable calves, saving the population from ultimate extinction through hybridization (Vaz Pinto, 2019).

Speciation may be **allopatric**, where all divergence occurs in subpopulations in **different places**, which is especially likely for island species. **Sympatric** speciation occurs where divergence takes place in subpopulations in the **same place**. It should be noted that the origin of a species, whether allopatric or sympatric, is a process, not an event. Speciation might occur as an isolated process, with few new species being produced. However, under special conditions, best illustrated by Darwin's classic studies of the Galapagos finches, a single species might give rise to multiple species, each exploiting a particular environmental resource or opportunity. This process is called **adaptive radiation**. In Africa, several rapidly radiating taxa in genera such as *Hyperolius* (Reed frogs), *Brachypodion* (Dwarf Chameleons), *Pachydactylus* (Geckos) and Aizoaceae (Mesem succulents) have displayed niche differentiation in response to fine-scale environmental conditions.

It is not only island archipelagos that are characterised by high levels of speciation. The biota of mountain ecosystems can become ecologically isolated from one another during periods of climate change, as described in Box 18.1. The bird faunas of the mountains of the Angolan Escarpment are characterised by high levels of species of very restricted range, with many **endemic** species, which occur nowhere else on Earth.

9.1.1 Species Richness, Evenness and Diversity

One of the central questions in ecology is seemingly quite simple: why do some communities contain more species than others? Before one can answer this question, one must have an objective measure of the number of species in a community—a statistic referred to as its **species richness**. Quantifying species richness is one of the first steps in describing community structure, and is a basic ecological tool. The relationship between species richness and habitat is a consistent feature of ecological patterns, varying according to temporal, edaphic, climatic, biotic and disturbance factors. Equally important is the relationship between species richness and area.

Species Richness

The **species-area relationship** is used in many studies of biodiversity. Counts of the species of a taxonomic group or trophic level present in samples of a habitat generally increase as sample sizes, or replicates, of the sample increase. The most common species usually appear in the first samples, with rarer species appearing as the sample size increases. Empirically, the increase in numbers with increasing sample size follows a mathematical relationship which decelerates as the area increases on **arithmetic axes** and looks like a straight line on **log–log axes** (Fig. 9.2). Plant ecologists often use the **species-area curve** to determine the size of a sample needed to adequately characterise a plant community. Adequacy can be judged as the sample size where the addition of more samples ceases to add significantly more species per work effort. This is where the species-area curve approaches a plateau, where increasing effort is not rewarded by an equivalent increase in information collected. Experience working in different habitats provides guidance on how many samples of what size are needed to characterise the community.

Challenges in quantifying richness come with the identification of species. This is especially difficult in Angola where the fauna and flora are poorly known, particularly within certain taxonomic groups. However, many regional guides to major taxonomic groups are available to assist ecologists to identify organisms to at least the genus level, while several taxa (amphibians, reptiles, birds, butterflies) have detailed accounts of Angolan species.

Species richness and diversity indices vary widely between communities, and thus using the same sample design for grassland, savanna and rain forest habitats would give results that are not logically or statistically comparable. Botanists often use a standardised cluster of samples (**quadrats**) of increasing area to measure species

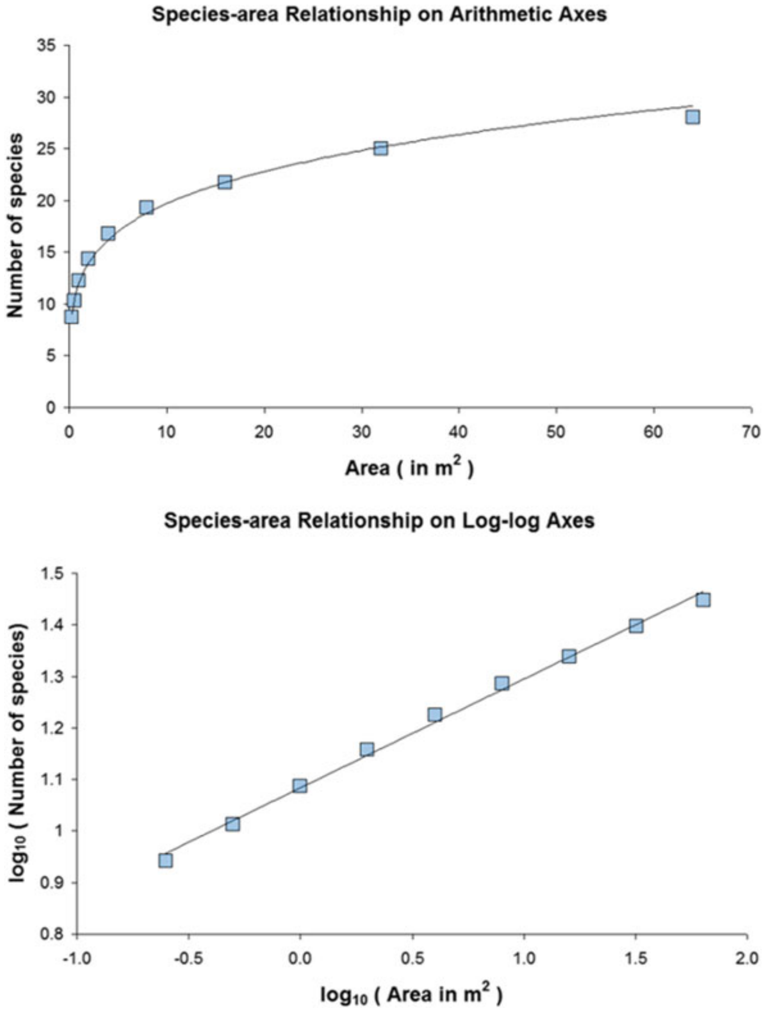

Fig. 9.2 The species-area relationship for a contiguous habitat. Note the different shape of the species-area curves of arithmetic and log–log axes. Creative Commons Attribution 4.0

numbers, growth form, abundance and other characters within the series of subsamples, and repeat the sampling across the landscape. **Abundance** is defined as the total number of individuals in a population. **Population density** is defined as the number of individuals per unit area. This information can thereafter be analysed using various data analysis techniques such as association analysis, principal components analysis and other approaches relevant to the purpose of the study. In practice, one size does not fit all.

Species Richness and Evenness

On its own a measure of species richness provides a good indication of the relative importance of an area for biodiversity—but it is only a list of species and does not provide any insight into how important the area is for different species and in terms of conservation value. Ecologists need some measure to make comparisons between similar habitats and communities, based on more than a simple list of species present. A more meaningful measure is the **diversity index** which combines both species richness and the **evenness** or equitability of the distribution of numbers of individuals among those species (Fig. 9.3). More complex measures of the distribution of species abundance in a community have been developed. The most commonly used index is the **Shannon-Weiner** diversity index which determines, for each species, the proportion of individuals which that species contributes to the total number of individuals in the sample. It gives a measure of the relative dominance, commonness or rarity of one species in relation to others in a community. Such information is important in experimental studies where the impacts of different treatments (fire, fertilization, grazing) are being tracked. Diversity indices also provide an indication of a community's 'health', where high evenness indicates a healthier state than a low diversity index that might be due to dominance of pioneer or invasive species.

Another measure of populations and diversity is that of density—the number of individuals of a species or a taxonomic group per unit area. Estimates of African bird densities indicate that the actual number of birds per km^2 increases following a rainfall gradient and habitat. Brown et al. (1982) gave estimates of 25 birds per km^2 in desert, 125 birds per km^2 in sub-desert shrubland, 1500 birds per km^2 in arid savanna, 3500 birds per km^2 in mesic savanna, 6000 birds per km^2 in forest/savanna mosaics and 8000 birds per km^2 in rain forest.

Alpha, Beta and Gamma Diversity

Species diversity measures differ according to their spatial scale. A count of species (or a taxonomic group) at the scale of communities is called **alpha diversity**. Defining a **community** is a complex task, as the structure and scale of communities vary

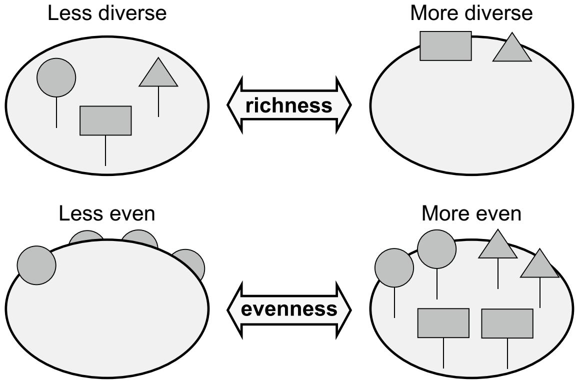

Fig. 9.3 A simplified representation of the difference between species richness and evenness. Each icon represents an individual of one species

considerably from one ecosystem to another. In Quiçama National Park, the *Setaria welwitschii* grasslands, comprising less than a dozen plant species, cover many thousands of hectares in unbroken blocks. In contrast, the species-rich gallery forests of the Muengueje River are confined to a narrow belt of a few metres width and a few km length. Alpha diversity of forests also differ from one continent to another, influenced by tree size and density. A single hectare of rain forest in Peru average as many as 618 trees of greater than 10 cm dbh (**diameter at breast height**); compared with 377 trees per ha in Gabon. Peru has many small tree species, Gabon forests have fewer species of trees, but larger trees per ha. On average, about 200 tree species are found within one ha of Peruvian forest, compared with only 50–75 species in equatorial Africa (Terborgh et al., 2016).

Over larger areas, of mixed habitats and communities, the variation in species composition is called its **beta diversity**. Beta diversity describes the rate at which species composition changes (the species turnover) across a region, or along a gradient or transect. It increases with habitat and environmental **heterogeneity**. Beta diversity is higher in the patchy mosaic of ecosystems on young landscapes of broken relief such as the Angolan Escarpment, and lower on older landscapes such as the African and Post-African peneplains of the interior plateau. Quiçama, which has some 28 plant communities within its 9960 km^2 has a much higher beta diversity than the less heterogenous landscapes of Bicuar National Park of 7900 km^2, as illustrated in the maps presented in Figs. 14.4 and 15.8.

Within tropical rain forests such as the Maiombe of Cabinda, the secondary forests are significantly poorer in species than primary, climax forests. At a landscape scale, however, the mosaic of mature, stable climax forest and disturbed secondary forest has a higher beta diversity than either of these two forest types. The mix of disturbance regimes in communities has led to the **intermediate disturbance hypothesis** (Connell, 1978) which holds that in such communities, the richest diversity is found not in climax forest, nor in secondary forest, but in communities where there is a mix of disturbance levels. In reality, the scale of measurement determines species richness, and in rain forest this is particularly important, as the size of disturbance area, period of recovery, and maturity of climax forest are the key determinants of species richness, as discussed in Sect. 12.4.

At a broader geographic scale, the total number of species across all communities is called **gamma diversity**. The gamma diversity of the Guineo-Congolian rain forests, at ca. 8000 plant species, although much poorer than similar forests of the Neotropics and Indo-Pacific, is nevertheless extremely rich compared with other African biomes (Chap. 12). The richness of rain forests is due to a combination of factors. First, long periods of climatic stability, and the perennial hot, moist climate of tropical evergreen forests, without widespread and lengthy episodes of extinction (such as happened due to glaciation of the northern temperate regions during the Pleistocene), allowed continued accumulation of species. Second, the structure and microclimates below the forest canopy and the temporal niches provided by forest-gap succession, supports a great diversity of life. Third, the interactions of animals and plants strengthens and diversifies the webs of life that characterise tropical rain forests. The gamma diversity of Angola, including representatives of six biomes, is much higher than that of Botswana, which has only three biomes. Namibe province, for example, with only three ecoregions, has a much lower gamma diversity than Huíla province, with seven ecoregions.

9.2 Endemism, Threatened Species and Hotspots

Endemism

Species richness is not the only measure used by biologists and conservationists to compare the importance of biomes, ecoregions and communities. Endemism is a much used metric. An **endemic** species is one that is only found within a defined geographic area, usually an ecosystem, biome or country. **Narrow endemics** are species with a very limited range, usually within a specific habitat or geographic region. **Near-endemics** refers to species that have 70% of their range within one country, such as some species that mostly occur in the Angolan Namib, but also across the border in Namibia. Examples include Black-faced Impala, Angolan Giraffe, Hartlaub's Spurfowl, Cinderella Waxbill and Anchieta's Python. **Paleo-endemics** are species that might have had a wide distribution in much earlier times, but are now restricted to isolated populations, such as certain bird species of the Afromontane forests of Mount Moco. **Neo-endemics** are species that have recently evolved through divergence and reproductive isolation. **Ubiquitous** species are those that occur across a wide range of habitats, landscapes or countries.

Categories of Threat

The science of ecology is the cornerstone of **conservation biology,** the study of the world's biodiversity, the threats to its sustainability, and the prevention of extinction of species, ecosystems and their services to society. Threats to species survival are a key concern of conservation biologists. **Categories of threat** are measures used in conservation assessments of the threat to the survival of individual species. Categories of threat have been standardised by the International Union for the Conservation of Nature (**IUCN**) and are widely applied. In descending order of threat, the IUCN Red List threat categories are as follows (Rodrigues et al., 2006):

- *Extinct*: known only from museum, herbarium or other historical records.
- *Extinct in the Wild*: with the last remaining individuals or populations alive in zoos, aquaria or botanical gardens.
- *Critically Endangered*: if there is considered to be more than a 50% probability of extinction in 10 years or three generations, whichever is longer.
- *Endangered*: if there is more than a 20% chance of extinction in 20 years or five generations.
- *Vulnerable*: if there is a greater than 10% chance of extinction in 100 years—species threatened with global extinction.
- *Near Threatened*: species close to the threatened thresholds, or that would be threatened without ongoing conservation measures.

- *Least Concern*: species evaluated with a lower risk of extinction.
- *Data Deficient*: no assessment is possible because of insufficient data.

The term '**endangered**' is applied to the following categories: extinct in the wild, critically endangered, endangered, and vulnerable. Species falling within these groups are recorded in global or national '**Red Lists'** such as those published by many national conservation agencies. Based on these criteria, the IUCN global Red List includes 36% of tree and shrub, 14% of bird, 27% of mammal, 34% of reptile and 41% of amphibian species currently assessed as being threatened with extinction.

Gap Analysis and Hotspots

Evaluating the level of protection afforded species or habitats at national or global scales (**gap analysis**) has been used for conservation planning and priority setting purposes since the 1970s. In Angola, Huntley (1973, 1974a, 1974b) assessed the conservation status of 80 mammal species and measured the proportion of vegetation types falling within conservation areas, in order to draw attention to priorities for the establishment of new conservation areas. Based on the percentage of Angola's 32 vegetation types falling within conservation areas, Huntley found that only 11 vegetation types were represented within the existing protected area system. Of these vegetation types, the species-poor desert and sub-desert systems, which occupied only 1.1% of the country, had 81% of their area protected. At the opposite extreme, the moist Guineo-Congolian forests and grasslands, occupying 10.2% of the country, and with possibly more than 70% of the country's biological diversity, had 0% of their area within national parks or reserves. A similar situation prevailed for the tiny patches of Afromontane forests. Nearly 50 years after the assessment, the recommendations are currently being implemented (GoA 2018). Since the early measures of gap analysis were tested in Angola, a vibrant science of **systematic conservation planning** has evolved (Margules & Pressey, 2000) and is being implemented in many countries with considerable impact.

At global scale, British conservationist Norman Myers (1988) introduced the concept of biodiversity **hotspots**, using a combination of high species richness, high levels of endemism and high levels of threat. The baseline for a hotspot was set at 1500 endemic plant species, with at least 70% of the region having lost its original habitat. The original global hotspot assessment included 25 sites, increased to 35 in 2004 (Mittermeier et al., 2004). The most significant finding of the assessment was that these 35 sites, covering 15.7% of the Earth's land surface, had already lost 86% of their intact habitat, which by 2004 totalled only 2.3% of the Earth's land surface, while being home to over 50% of the world's endemic plant species.

Triage Approaches

Decisions on what habitats or species to conserve with the limited resources available to governments is a question frequently placed before ecologists. In response, Myers (1979), introduced the **triage** concept to conservation. The term *triage* was used during the First World War (1914–1918) by the French medical corps at the Battle of the Somme and other battle-fields where they were overwhelmed by the numbers of wounded and dying. By assigning degrees of urgency to casualties, they were able to more efficiently and effectively prioritise treatment. Casualties would be divided into three categories:

- Those who are likely to live, regardless of what care they receive
- Those who are likely to die, regardless of what care they receive
- Those for whom immediate care might make a positive difference in outcome.

The concept has been used in recommendations to prioritise the most urgent conservation needs in Angola (Huntley, 2017), but has yet to be tested or implemented. More recently, triage approaches have been used by some medical facilities confronted by the surge in numbers of Covid-19 patients.

9.3 Life History Patterns: *r*- and *K*-Selection Strategies

Great thinkers often think alike. In considering two different species responses to environmental extremes (long-lived and constant; short-lived and unpredictable), two of the great ecological thinkers of the twentieth century, Robert MacArthur of Princeton University and Edward Wilson of Harvard University, USA, developed the concept of ***r*- and *K*-selection** (MacArthur & Wilson, 1967). While there has been much debate on the general application of the system, for our purpose of illustrating patterns in the Namib Desert and other arid zone ecosystems of Angola, the concept of *r*- and *K*- selection in life history strategies is useful, despite its detractors.

The *r-/K-* strategies are based on familiar observations. Reproductive patterns of organisms can be grouped into a few life history categories. These include factors such as the organism's size, rate of growth and of development, the number of progeny it produces, the investment it makes in its progeny, and the stage in its lifetime when it reproduces. The terms *r* is derived from the instantaneous or intrinsic per capita **rate of growth** (*r*). **Carrying capacity** (*K*) is the maximum sustainable population size for the prevailing environment. Carrying capacity is a function of the supply of resources such as food, water and space.

The concept argues that organisms lie somewhere on a continuum or spectrum delimited by two extreme life-history patterns.

- ***r*-selected** species are typically small, have relatively fast growth rates, reproduce at an early age, produce large progeny, and are short-lived. They typically live in unpredictable habitats. In such habitats, resources, often in limited amounts, periodically become available (flood or famine) and the potential for pulses of rapid population growth is enormous. Under these conditions there is little competition, but adult mortalities are high because the resources are short-lived.
- ***K*-selected** organisms are typically larger, develop more slowly, are longer lived, reproduce at an older age, and produce fewer progeny. They live in constant or seasonally predictable habitats. *K*-selected species live at or near the carrying capacity of their habitat. Conditions being constant, the population growth levels

off at carrying capacity in response to competition between organisms for limited resources. Because of stiff competition, the young suffer highest mortalities.

Angolan animals and plants include a mix of *r*- and *K*-strategies. Elephant and rhino are typical *K*-strategists, producing few calves, providing high levels of parental care, maintaining their populations (when in natural systems) at carrying capacity, and being long-lived. The opposite strategy is displayed by annual grasses and herbs. Annual plants often produce vast numbers of seeds with varying germination cues, some germinating after the first rains, but others having germination-inhibiting substances that delay germination for one or two seasons, by which time the inhibiting substances are leached out. The recruitment of new generations is thus spread over several years. This staggering of recruitment allows plants to hedge the bets for success over unpredictable seasons, one of which might be ideal for germination, growth, reproduction and further seed dispersal. This is particularly the case in Namib grasses (typical *r*-strategists), which need at least a 10 mm rainfall event before germinating. In good years, the mass of grass seeds stored in the soil germinate, turning the desert green and then gold as the grasses mature. As the annual grasses die the litter decays and much of this is blown into the dune sea, to form the detritus that is the foundation of dune food webs.

In considering *r*- and *K*-strategies, scale must be considered. As a simple generalisation, *r*- and *K*-selection models are best suited to comparisons of organisms that are functionally or taxonomically similar. An example of a *K*-selected life history is that of the dune-sea dwelling tenebrionid *Onymacris plana*, which lives for more than three years, unusually long for a small beetle. It feeds on the reliable food source of detritus blown into the dunes, and water from the regular morning fog. It breeds throughout the year, producing small batches of eggs. By way of contrast, the much larger, Brown Locust *Locustana pardalina* of Africa's arid zones dies after just two months. In the swarming 'gregaria' phase, Brown Locusts have massive outbreaks numbering many millions, even billions, of locusts. They are the continuing expression of one of the ten biblical plagues—the epitome of *r*-selection.

9.4 The Concepts of the Ecological Niche and the Guild

The Ecological Niche

The ecological niche is a much-used concept in ecology, developed by Hutchinson (1957). An organism's niche describes how and where an organism can live, grow and reproduce, influenced by multiple environmental conditions, resource needs and tolerances. Conditions such as temperature, humidity, pH and wind velocity, together with resources such as space, nutrients, water and shelter determine an organism's habitat and its way of life.

Most species are capable of using much more of an environment's resources than they actually do. Hutchinson described the environmental space where a species could survive and reproduce in the absence of competition from other species, as

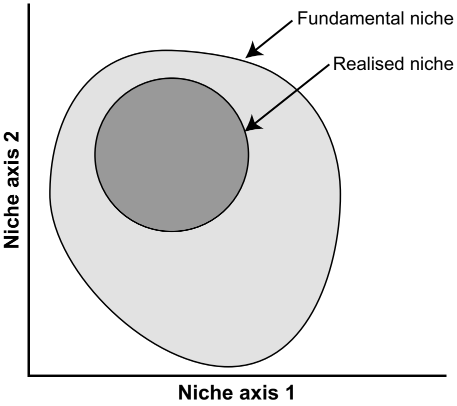

Fig. 9.4 The relationship between a fundamental niche and a realised niche. A species can survive and reproduce within the environmental conditions of its fundamental niche, but competition from other species will reduce the niche to a more limited space of its realised niche

its **fundamental niche**. Competition for resources with other species might restrict the environmental space of a species to what Hutchinson called its **realised niche** (Fig. 9.4). However, not all interspecific interactions are negative. A species' fundamental niche can be expanded where interactions are beneficial for one species but neutral for another (**commensalism**) or where both species benefit (**mutualism**), as discussed in Sect. 9.6.

A species' fundamental niche can also be expanded where there is a shift in the availability of certain resources (food, breeding sites). However, it is clear that within the realised niche, reproductive success is maximised, whereas outside of the realised niche the environmental limiting factors will depress breeding success.

Competitive Exclusion

The niche concept led to the formulation of the competitive exclusion principle, which states that two species cannot occupy exactly the same ecological niche, as discussed previously. However, under certain circumstances, two species competing for similar resources can co-exist in a stable environment through the **partitioning** of their needs in time or space—the differentiation of their realised niches. If there is no differentiation, one species will exclude or eliminate the other, or result in an evolutionary or behavioural shift in the weaker competitor towards a different ecological niche. The complexity of natural communities and interactions and the effects of **stochastic** (random or unpredictable) events create disruptions to competition 'running its course' and competitive exclusion is seldom observed in natural ecosystems. An example of partitioning is provided by the interactions between trees and grasses in savannas. Partitioning of resources can be spatial or temporal of both, as described in Box 10.2. Another example of temporal partitioning is that of diurnal raptors, such as the Black-shouldered Kite and the nocturnal Eagle Owl, both using the same food resource (rodents) but at different times of the day.

Guilds

A concept closely related to the niche is the **guild**. As exemplified in many bird communities, groups of species that use similar resources, or different resources in a similar fashion, are called guilds. Guilds may occupy the same habitat but use different components of the habitat, or different nesting choices. Examples include forest canopy leaf-eaters and forest floor insect scavengers; cavity nesters and nest weavers. In mammals, the term would apply to browsers or grazers in savannas. Some ecologists distinguishing between mega-, meso- and micro-grazers and browsers according to body sizes. Botanists sometimes use the term for different life-forms, such as graminoids, forbs, trees, shrubs, vines, parasites, epiphytes or saprophytes. Increasingly, the concept of **functional traits** has gained greater traction than guilds for such ecological groups. A functional trait is a morphological, biochemical, physiological, structural and phenological adaption to survive, grow and reproduce.

9.5 Herbivory, Predation, Parasitism and Mutualism

The structure and dynamics of communities is largely determined by the relationships between consumers and their food source. The manner in which animals acquire their food (and therefore energy) helps classify them into those that feed exclusively on plants (**herbivores**), exclusively on other animals (**carnivores**), both plants and animals (**omnivores**) and those that feed on the remains of dead animals and plants (**detritivores/decomposers**).

A further system of classifying the relationships between two species is that of the reciprocal effects—neutral, positive or negative—between them. **Predation**, **parasitism**, and **parasitoidism** have positive results for one, and negative consequences for the other organism. **Mutualism** has **positive** effects for both; **competition** has **negative** results for both. **Amensalism** has a negative effect on one, but no effect on the other. **Commensalism** has positive results for one and neutral outcomes for the other where a pair of species are closely associated. The interactions are summarised in Table 9.1.

Herbivores

Herbivory is the consumption of plant materials by animals (herbivores). Some ecologists regard herbivory as a form of predation (the plant being the prey, the animal—from grasshoppers to elephants—being the predator). Here we restrict the term predation to those actions in which animals hunt and consume their prey.

The physical and chemical composition of plants plays a dominant role in determining the acceptability of plants to herbivore consumers. Plants are made up of carbon-based compounds (carbohydrates), mostly in the form of the cellulose and lignin of their cell walls. Most vertebrate herbivores lack the cellulolytic enzymes needed to break down the walls of plant cells to release their metabolic contents,

Table 9.1 Positive (+), negative (−) and neutral (0) interactions between individuals of two species (A and B)

Type of interaction	Species A response	Species B response
Neutral	0	0
Mutualism	+	+
Commensalism	+	0
Competition	–	–
Amensalism	–	0
Predation	+	–
Parasitism	+	−
Parasoidism	+	−

From Smith and Smith (2015) *Elements of Ecology*. (9th Edition). Pearson, Boston

including nitrogen, which is essential in the production of protein. As described in Box 8.1, the role of bacteria is critical in the specialised digestive systems of ruminants. This form of mutualism is known as a **commensal** relationship.

Animal tissues are high in fats and protein, used as structural building blocks. Plants, as described above, are built of carbohydrates. The ratio of carbon to nitrogen is about 50:1 in plants, and 10:1 in animals. The concentration of proteins in the diet of herbivores is highest in the young leaves of grasses and growing tips of tree shoots. The level of protein in plant material declines as the plant parts age and senesce. In savannas, if the protein content of grasses drops below 6%, the condition of the mammalian herbivores feeding on them will decline and survival, growth and reproductive success might be compromised.

The removal by grazing or browsing of photosynthetic tissue (shoots and leaves) from a plant does not necessarily lead to the plant's death. In many cases, especially tropical grasses, defoliation of mature leaves can stimulate new growth and avoid the grass tussock becoming moribund due to shading by old leaves. Plants can also respond to the removal of roots, shoots or fruit by compensatory growth. Repeated defoliation can also trigger a response of increased production of defensive chemicals. Predation-prey relationships have evolved adaptations in the form of **defence mechanisms** in both animals (cryptic colouration, behaviour) and plants (poisons, spines, architecture) and a response from animal predators in terms of hunting techniques, as described in Sect. 11.4.

Predators and Carnivores

Predation is the consumption of all or part of one living organism by another. **Predators** kill their prey, a behaviour that is best characterised by carnivores. Prey choice might vary during the course of a year. Carnivores, unlike herbivores, consume high energy food, and are not faced with the problem of digesting cellulose. Predators such as Lion, Leopard and Cheetah often attack the most vulnerable (weak or old) prey individuals. The impact of predation on prey populations is therefore not necessarily greater than mortality from other causes in the absence of predators. Predators have inherited specific foraging strategies that result in the highest levels of hunting efficiency—behavioural patterns called **optimal foraging strategies.** These provide the best energy and nutrient return on hunting investment (energy gained per unit of energy expended). These strategies include the selection of habitats in which to hide, ambush or search for prey; or decisions on how long to sit and wait, depending on how many competing predators, or alternative prey, are present. A further decision for the predator is what prey is acceptable. Most predators have a fairly wide prey menu, but with preferred species. In productive environments populated with herding antelope, such as nutrient-rich arid savannas, a narrow and specialised diet is feasible for large carnivores, but in low-nutrient mesic savannas, a wide and opportunistic diet is more appropriate. However, studies of large predators such as Lion have revealed unexpected prey items, such as Porcupine, or cases where Honey Badgers attack and eat highly poisonous snakes. In such cases, both prey species can inflict serious injury on the predator.

Generalist predators spend little time searching, but consume low-value prey, while **specialist** predators spend more time and energy targeting high value but less abundant prey. In Angola, despite the decimation of most mammal species over the past 50 years, a very low abundance but widely distributed population of large carnivores (Lion, Leopard, African Wild Dog, Spotted Hyaena) survives. This situation can only exist where these predators have become opportunistic feeders, surviving as metapopulations by active dispersal over extensive hunting areas.

The availability of prey changes with season and patterns of climate from wet to arid periods, with consequent predator–prey **population cycles** or oscillations, often with large fluctuations in predator and prey abundance. Shorrocks (2007) provides a review of predator–prey dynamics in African ecosystems, where the complex interactions between multiple species (of both predators and prey) and rainfall and habitat, make simple generalisations impossible. Such cycles are more typical of strongly seasonal temperate climates. The best known of these are the Snowshoe Hare *Lepus americanus* and Canadian Lynx *Lynx canadensis.* Both hare and lynx populations across the boreal forests of North America follow an approximately 10-year cycle of abundance (Fig. 9.5), suggesting a predator–prey causal relationship. The hare population responds to the availability of food plants (twigs of trees and shrubs) and the predatory pressure of lynx, which in turn responds to hare abundance. The two populations function as a density-dependent regulator on the other. Predators regulate the growth of the prey population by functioning as the driver of density-dependent mortality. The prey population functions as the driver of density-dependent regulation on the birthrate of the predator population. High levels of prey mortality are attributed to the impacts of stress on hare fecundity, exacerbating the direct impacts of predation. However, the highly complex food webs of both predator and prey could provide alternative hypotheses for the synchronicity of the two cycles.

Parasites

Parasites draw on resources directly from their host. One partner draws benefit from the association while the other is harmed, but not necessarily lethally. Parasites include **microparasites** such as bacteria, protozoa and viruses. **Macroparasites**

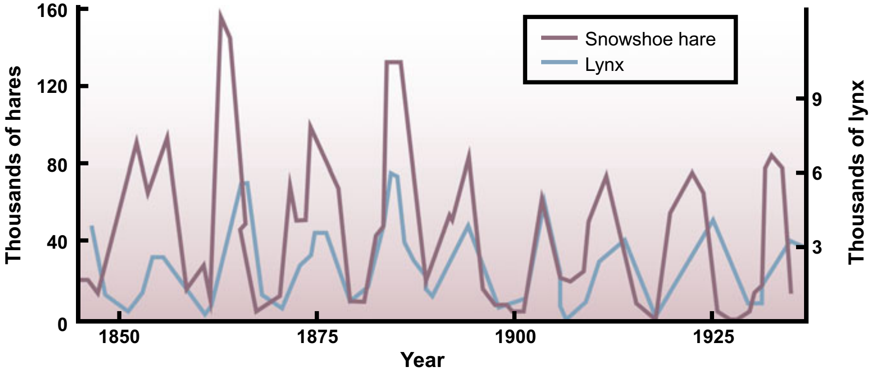

Fig. 9.5 The apparently synchronous oscillations in the abundance of prey (Snowshoe Hare) and predator (Canadian Lynx) as reflected in pelts sold to the Hudson's Bay Company. Redrawn from Townsend, Begon and Harper (2008) *Essentials of Ecology*. Blackwell, Oxford

include worms, lice and ticks. Transmission of parasites between hosts is usually direct, but some parasites have complex life cycles which include other hosts, called **vectors**. While most parasites are non-lethal, with death usually occurring as a result of co-morbidities (such as in the case of the Covid-19 virus), some parasites are highly lethal.

In Africa, the most important microparasitic impact on wildlife populations in recorded history was that of the **rinderpest** (cattle plague) **pandemic** of the 1890s. Rinderpest is a **zoonotic** disease transmitted by the *Morbillivirus* virus. Introduced to Africa from Asia via Eritrea in 1889, within a decade it had swept across Africa, decimating the populations of nearly all even-toed ungulates (cattle, buffaloes and wildebeest). Rinderpest depopulated not only livestock and wildlife, but also the human populations of pastoral communities. Since the eradication of recurrent outbreaks of rinderpest from the Serengeti in the 1960s, the wildebeest population has increased ten-fold. The interactive impacts of rinderpest on herbivore population size and structure, grazing pressure, grass availability, fire frequency, survival and growth to maturity of trees, and the balance between grazers, browsers and carnivores provides the most complex but revealing demonstration of parasite-mediated trophic dynamics in African ecosystems (Sinclair, 2012).

Mutualisms

Mutualisms are associations that are beneficial to both parties. These include the critically important symbiotic relationship (termed **commensalism**) between microorganisms and their hosts in the transfer of nutrients in the specialised digestive systems of ruminants described above and in Box 8.1. In the fog belt of the Namib Desert, mutualisms between algae and fungi produce the diverse lichen flora (Sect. 11.1), while in the rain forests of the Congo Basin and in the arid savannas of the southwest, ant/plant mutualisms provide food and defence for the partners. One of the most important mutualisms in African ecosystems is that of between trees and **nitrogen-fixing** bacteria that form nodules on the infected root hair cells of the host plant. Bacteria receive carbon from the tree in exchange for the nitrogen that they fix and make available to the host plant. A similar association is that of fungal **mycorrhizae** which mobilise nutrients and water in exchange for carbohydrates provided by their hosts, as in the dominant trees of the Angolan miombo (Sect. 10.6; Box 14.2).

9.6 Theories of Island Biogeography and of Metapopulations

The evolutionary dynamics of Guineo-Congolian and Afromontane forests will be described in Chaps. 12 and 13, where the expansion and contraction of these forests over tens of thousands and even millions of years is described. Today, a much more rapid dynamic is at play—the dramatic reduction in the size and stability of Angola's moist forest ecosystems. The ongoing destruction of the isolated forests of the Angolan Highlands and Escarpment is the country's most urgent biodiversity conservation crisis. Furthermore, the fragmentation of once widespread and interconnected populations of large mammals such as Lion, Cheetah, Forest and Cape Buffalo, Giant Sable and Forest and Savanna Elephant has led to their survival in small, isolated and critically threatened populations that are below the viable population size for their survival. These processes can be used to illustrate two of the most influential concepts in ecology—the theories of island biogeography and of metapopulations.

The Theory of Island Biogeography

The vulnerability of Angola's remnant forests is directly related to the size and shape of individual patches and their connectivity with other patches. The endemic bird fauna of Mount Soqui has been eliminated since it was first surveyed in the 1930s. The original forest patches have disappeared. The avifauna of Mount Moco and Cumbira have been seriously reduced since 2000 as their forest margins and interiors are increasingly damaged by fire, wood cutting and agricultural activities (Mills & Dean, 2021). Along the Chela Escarpment, tiny forest remnants are being reduced by fires and charcoal production. Only the forests of the deep ravines of Mount Namba have thus far been free of major damage, due to their larger size and inaccessible location. In addition to their current vulnerability to human activities, Angola's Afromontane forests lie over 1900 km from similar forests on the Cape Peninsula, Mount Cameroon, Ruwenzori and the Eastern Arc Mountains of Tanzania—the ancient links of their faunistic and botanical diversity. The fragmented chain of Guineo-Congolian forests of the Angolan Escarpment are losing their connectivity with similar forests through land transformation around and between them.

In 1967, the American ecologists (Robert MacArthur of Princeton University and Edward O. Wilson of Harvard University) proposed a theory of island biogeography in a classic paper that has strongly influenced thinking and research on the relationships between size, connectivity and patterns of species richness on islands. The theory was built on the observations of early explorer-naturalists who had noted the increase in animal and plant species richness on islands of increasing size. A general pattern emerged of a tenfold increase in island size leading to a doubling of the number of species inhabiting the island. What MacArthur and Wilson (1967) described for islands was a dynamic equilibrium between **survival** of new colonising species and the **extinction** of previously established species on islands dependent on mainland sources of potential immigrant species. As species numbers increase on islands through immigration, competition for resources increases the extinction rate until immigration rate equals extinction rate. The composition of the biota might change through different rates of extinction of immigrants and original populations. Over time, there will be a continual **turnover** of species. For any given island a stable number of species (the **equilibrium species richness**) will ultimately be reached. Larger islands will support more species than smaller islands, and those close to mainland sources will accumulate more species than remote islands (Fig. 9.6).

MacArthur and Wilson's theory can be summarised in the following predictions:

- The number of species on an island should eventually become roughly constant through time.
- This should be a result of a continual *turnover* of species, with some becoming extinct and others immigrating.
- Large islands should support more species than small islands.
- Species number should decline with the increasing remoteness of an island.

The theory does not only apply to oceanic islands. As already discussed, the forests of the Afromontane 'archipelago-like centre of endemism' represent islands

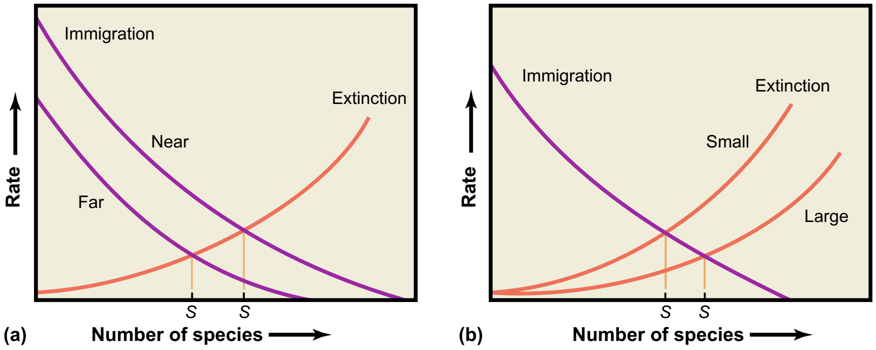

Fig. 9.6 **a** Immigration rates are distance related. Islands near a mainland have a higher immigration rate and associated equilibrium species richness (*S*) than do islands distant from a mainland. **b** Extinction rates relate to area and are higher on small islands than on large ones. The equilibrium number of species varies according to island size, and larger islands have greater equilibrium species richness than do smaller islands. From Smith and Smith (2015) *Elements of Ecology*. (9th Edition). Pearson, Boston

in a sea of grasslands and savannas. The fragmented Guineo-Congolian forests of the Escarpment, and Afromontane forests of the highlands, are islands in rapidly transforming agricultural landscapes. Applying the theory of island biogeography to Angola's remote, isolated Afromontane and Escarpment forests offers special opportunities to explore the evolution of their endemic avifauna, as initiated by Hall (1960) and taken further by Vaz da Silva (2015), as described in Box 18.1. The theory is also of relevance to conservation measures for small populations of critically endangered species, such as Giant Sable. Conservation areas are increasingly isolated from one another due to land transformation through agriculture and urbanisation. Viable breeding populations, within networks of conservation areas linked by corridors, are fundamental to the maintenance of metapopulations, as discussed below.

Metapopulation Theory

A **metapopulation** is a group of spatially separated local populations of the same species which interact at some level. Each of these local subpopulations has a chance of going extinct or being established again through recolonisation. Metapopulation theory was developed by Richard Levins of Harvard University (Levins, 1969) in studies of agricultural pest insects and is now widely applied in the conservation biology of fragmented habitats and populations. In simple terms, it is 'the study of populations of populations and their interactions and dynamics.

The theory differs from that of island biogeography, in that the distinct local populations of a single species are separated, not by uninhabitable oceans of water (or savannas or deserts), but by areas of suitable habitat that are not currently occupied by populations of the species. Further, island biogeography looks at processes of colonization and extinction of many species of a given island or habitat from a large and distinct species pool. Metapopulation studies typically focus on populations of a single species.

Metapopulation theory is applied at the landscape scale, where small local populations within the larger habitat matrix can go extinct through random events (**demographic stochasticity**), including inbreeding depression. The smaller the local population, and the greater the distance between local populations, the greater the chance of extinction. Under natural conditions, members of expanding local populations might immigrate to a suitable but unoccupied habitat and initiate a new local population. Interchanges between local populations through dispersal might occur. Where one population emigrates to a population in decline, it might prevent extinction in the smaller population, a phenomenon known as the '**rescue effect**'. Across the whole metapopulation, some stability is achieved by the balance between extinction and recolonization of local populations. In common with island biogeography theory, the achievement of equilibrium and long-term maintenance of the metapopulation is a function of the influence of patch size and isolation on the processes of colonization and extinction.

In southern Africa, local populations under threat of extinction due to landscape transformation or over-exploitation have been artificially rescued by re-introductions from genetically similar populations within the metapopulation. The application of the concept in the study of fragmented populations of several iconic Angolan species, such as Giant Sable, Forest Buffalo (*pacassa*) and Forest Elephant is particularly appropriate. A classic example of a subpopulation approaching extinction was that of the Cangandala local population of Giant Sable, which had been reduced to a small group of females, hybridizing with a single male Roan Antelope. In an elegant model of conservation biology in action, the Cangandala population was rescued through the removal of the Roan male, and the introduction of Giant Sable males from the closest local population in Luando Strict Nature Reserve (Vaz Pinto, 2019) as described previously.

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Chapter 10
Ecosystem Processes and Dynamics in Mesic Savannas

Key Concepts and Questions: This Chapter Will Explain

- *Why the laws of thermodynamics underpin the processes of energy capture, transfer and loss within ecosystems.*
- *How different photosynthetic pathways have evolved in response to temperate and tropical climates.*
- *How the carbon cycle of a savanna ecosystem is structured.*
- *Why plant biomass production in mesic savannas is higher, but herbivore biomass is lower, than that of arid savannas.*
- *How nutrients are transferred from plants to the soil through decomposition and mineralization processes driven by insects, bacteria and fungi.*
- *Why the rain forests and mesic savannas of Angola can be described as alternative stable states.*
- *How trees and grasses coexist while competing for similar resources.*

Context: An Introduction to Systems Ecology

One of the unifying concepts in ecology is that of food webs, where energy and nutrients are transferred from one trophic (feeding) level to the next (Sect. 10.1). Ecological research has paid much attention to trophic interactions and structures since the concepts were introduced by Elton (1927) in his classic book *Animal Ecology*. The processes were quantified by Lindeman (1942) for aquatic ecosystems, and later championed by American brothers Eugene and Odum (1953), co-founders of modern integrated whole-ecosystem science. Odum (1983) used general systems theory and the laws of thermodynamics to better understand the flows of energy through ecosystems, and to describe them using conceptual and mathematical models.

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Ecosystem Models

Systems ecologists are largely focused on understanding and managing ecosystems. The functioning of ecosystems is defined by the complex relationships and interactions between living organisms and their physical and biological environments, and the influence of human interventions on these relationships. Systems ecologists attempt to view ecosystems holistically and use models to show how the components within the ecosystem relate to one another. This can be done across a wide range of scales, both spatial and temporal. This is called the **systems approach**—the application of which is not limited to ecology, but also widely used in banking, communications, transport and other sectors.

In ecology the interdependent components of a system are linked through the transfers of energy and matter, as all parts are linked together and affect each other. The similarities, efficiencies and challenges associated with these transfers are what define ecosystems in terms of the growth, development, stability and evolution of the organisms in that system. The systems (or **holistic**) approach simultaneously investigates different components at different spatial and temporal scales. It regards the properties and collective interactions of complex systems to be equal to *more* than the sum of their parts. It contrasts with the **reductionist approach**—which considers that complex systems can be reduced to studies of simpler, individual components and to be *equal* to the sum of their parts.

In systems ecology the emphasis is on how the system operates as a whole and how interactions produce **emergent** properties. An example is the influence of a dense canopy of mixed tree species on the shaded microclimate below it—an emergent property contributed by and exploited by many different organisms.

Given the complexity of ecosystems, models are used to enable scientists to investigate and understand the functional linkages and implications of disrupting any of these linkages. A simple model of a system is given in Fig. 10.1.

Ecosystem models are necessarily far more complex, showing many different storages (boxes), flows between them (indicated by arrows) and the processes (e.g.

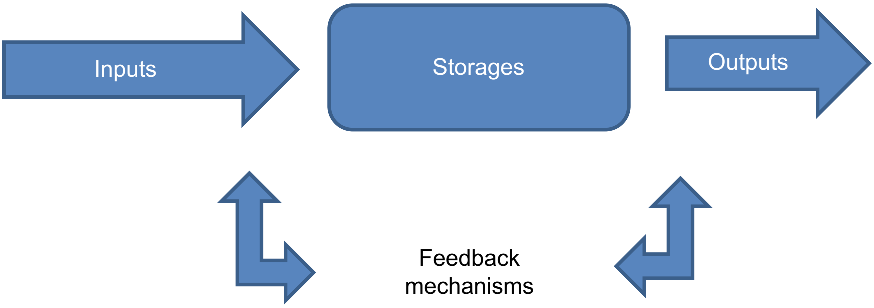

Fig. 10.1 A simple model of a system. Feedback mechanisms include the interactions between components and processes that maintain system stability, or drive change

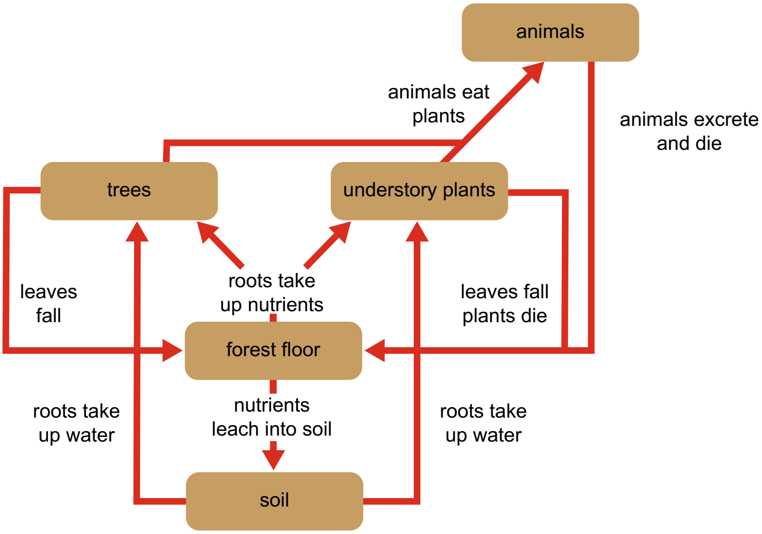

Fig. 10.2 Pathways and pools of materials in a terrestrial ecosystem. The red arrows indicate transfers of energy, nutrients and water between pools

photosynthesis, herbivory, predation, harvesting, migration) defining the nature of the inputs and outputs. Figure 10.2 shows a more complex, but still simple model.

From the above models, it becomes apparent that two basic processes must occur in an ecosystem for organisms to live. These processes are critical to understanding how and why Angolan ecosystems occur where they do, function as they do and why the plants and animals occurring there are highly adapted to prevailing conditions. There have to be **inputs** and **outputs** of energy and matter (chemical elements). All energy enters ecosystems in the form of sunlight, is converted by photosynthesis into plant biomass and is passed along food chains as it is consumed and eventually leaves the system as heat. The behavior of energy in ecosystems (most importantly, the amount and availability) is determined by two laws of thermodynamics—these govern the flow and storage of energy in a system and the ability to do work.

The First and Second Laws of Thermodynamics

Energy exists in two forms: **potential energy** and **kinetic energy**. The **First Law of Thermodynamics** relates to the **conservation** of energy, and states that energy cannot be created or destroyed, but it can be changed (transformed) from one form to another. For example, when wood burns, stored chemical energy is transformed into heat and light. In photosynthesis, the energy of sunlight is harnessed by the chlorophyll within the plant leaf. No energy is gained or lost to the system in the process. The First Law is important in that it allows ecologists to determine energy transformation efficiencies (how much energy is passed along the food chain) and to determine where energy is lost from ecosystems. Energy is used to do work—in growth, movement, reproduction and in the assembly of complex molecules—all which require energy. Although the total amount of energy in a system does not change (the First Law tells us this) the amount of energy available to do the work does change. Energy available to do work declines along the food chain because of inefficient energy conversions—there is always less usable energy at the end of a transformation that at the beginning. Once energy is transformed into heat, it can no longer be used by living organisms to do work or to fuel the synthesis of biomass. The heat is eventually lost to the atmosphere and can never be recycled. Here the second law of thermodynamics comes into play.

The **Second Law of Thermodynamics** refers to the **transfer** of energy, and states that as energy is transformed, there is a loss of that energy (usually through heat loss) —and in natural systems a point is reached where there is no usable energy. The implication of this is that there has to be a constant input of energy for living things to do work. Energy is derived from the Sun, through photosynthesis, where **light energy** is transformed into **chemical energy**. This chemical energy is stored in plant biomass, eaten by herbivores, which in turn are eaten by carnivores. All living organism will eventually die. At each stage of transformation, less and less energy is available (usually only about 10% at each stage is passed on) and all energy is ultimately lost as heat.

Whole Ecosystem Studies in Africa

During the 1960s and 1970s, an ambitious collaborative scientific initiative, known as the **International Biological Programme** (IBP) stimulated a rapid growth in studies of the structure and functioning of whole ecosystems following Odum's **Systems Ecology** approach. The thinking was that questions relating to the management and sustainable use of the world's biomes and ecosystems could be answered through knowledge of the paths, patterns and processes of **energy flows**, and nutrient and water **cycles,** through ecosystems. The common currency for such transfers of energy is **carbon**, with photosynthesis (**primary production**) as the basic measure of energy entering and being assimilated within communities and becoming available to sustain all ecosystem processes. The amount of energy assimilated (using the surrogate measure of carbon) and transferred as energy in the form of **adenosine triphosphate (ATP)** from one **trophic level** to the next, became a principal focus of the IBP. The quantification of the carbon cycle of ecosystems from tropical rain forests to the arctic tundra was a key output of the IBP. The importance of an understanding of the carbon cycle within ecosystems became increasingly relevant as emphasis on the role of CO_2 in **climate change** entered the global environmental policy arena. Carbon also plays a central role in the cycling of other elements such as nitrogen, phosphorus and sulphur, and thus in the growth, survival and reproduction of all organisms in terrestrial ecosystems.

In Africa, two research projects followed the IPB model, the **Lamto Project** in central Ivory Coast and the **Savanna Ecosystem Project** conducted on Nylsvley Nature Reserve in northern South Africa. Both projects have high relevance to the understanding of Angolan mesic savannas. The Lamto Project is located in the transition from Guinean Rain Forest to the Guinean Forest/Savanna Mosaic, similar to much of the tallgrass savannas of northern Angola. Nylsvley is located at the floristically depauperate southern extension of mesic/dystrophic savannas, with a structure and function very similar to that of the dry miombo of Angola. The dominance of trees such as *Burkea africana*, *Ochna pulchra* and *Terminalia sericea* reflect this similarity, as do the leached, infertile and sandy soils of the Nylsvley ecosystem.

The results of the 16-year Savanna Ecosystem Project (1974–1990) were synthesised by Scholes and Walker (1993) and provide a detailed account of the structure and functioning of the *Burkea* savanna. The results of the 30-year Lamto Project have been comprehensively synthesised by Abbadie et al. (2005). The Lamto and Nylsvley syntheses, together with that of Frost (1996) on the miombo of Zambia and Zimbabwe, remain the most important reviews of the subject and form the basis of the present outline. Here we will examine components and interactions in the creation, transfer and cycling of energy and nutrients in mesic/dystrophic savannas as quantified at Nylsvley, also referencing data from miombo sites in Angola, the Democratic Republic of the Congo, Ivory Coast, Zambia and Zimbabwe.

This chapter will commence with an outline of food webs and trophic levels in nature, then follow the pathways of primary production, consumption and decomposition, and conclude with a discussion on concepts of tree-grass dynamics in African savannas.

10.1 Food Chains, Food Webs and Trophic Levels

Before considering the processes of ecosystem energetics and nutrient transfers, an understanding of the framework of ecosystem structures is necessary. The interspecific interactions within ecosystems described earlier—(Sect. 9.6 on herbivory, predation, parasitism, and mutualism)—evolved for the acquisition of energy and nutrients for growth and ultimately, reproduction. These relationships, between the various species in an ecosystem, form **food chains**, and the collective interactions (**links**) form **food webs**. Savanna ecosystems such as those that dominate Angolan landscapes have two food chains—a grazing food chain and a detrital food chain, as illustrated in Fig. 10.3.

The successive levels in a food web are called **trophic levels**. The feeding relationships are classified into **autotrophs** (primary producers—which receive their energy directly from the Sun via photosynthesis) and **heterotrophs** (consumers of plant and animal tissue). **Primary consumers** comprise **herbivores** which feed on plants, **secondary consumers** comprise **carnivores** that feed on herbivores, and **omnivores** that feed on both plants and animals. The relationships are popularly compared to a pyramid. Topping the trophic pyramid are **apex predators**, which feed on lower trophic levels but are not themselves eaten. In addition to the contributors to the pyramid, **decomposers** (detritivores) consume dead organic matter and convert it into energy and nutrients, which become available for plant growth and therefore to the cycling of materials through the ecosystem. The movement of mineral nutrients is cyclic, whereas the movement of energy is unidirectional and noncyclic.

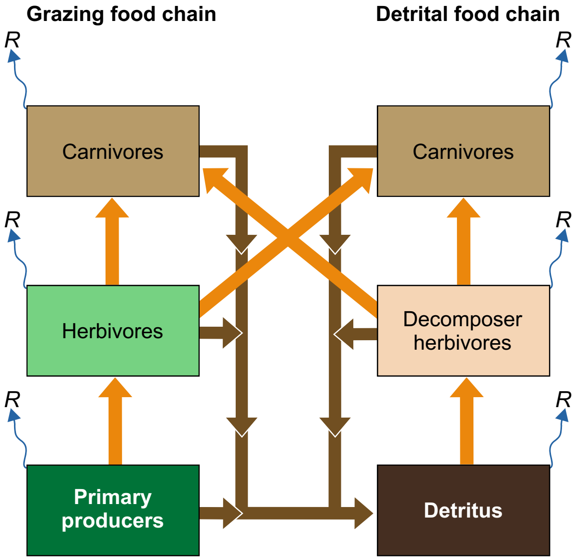

Fig. 10.3 Generalised grazing and detrital food chains. Orange arrows linking trophic levels represent the flow of energy associated with ingestion. The blue arrows represent the loss of energy through respiration (*R*). The brown arrows represent a combination of dead organic matter unconsumed biomass) and waste products (faeces and urine). From Smith and Smith (2015) *Elements of Ecology*. (9th Edition). Pearson, Boston

Once the structure and quantification of food chains has been achieved, an immediate observation will be the rapid loss of energy transferred from one trophic level to the next. In grazing food chains, this is approximately one order of magnitude per step. In crude terms, in a food chain of four levels, for every 1000 kg of grass produced by primary production and consumed by antelope, only about 100 kg of animal tissue is produced, sufficient to support 10 kg first-level predators, and 1 kg of second-level (apex) predators. This explains why there are so few predators compared with herbivores, and why food chains seldom have more than three or four levels.

An important concept relating to food chains and food webs is that of bottom-up and top-down controls. **Bottom-up controls** are those that limit the productivity and abundance of populations in the trophic level above them. Thus grass productivity places limits on the biomass of herbivores that they support, which in turn controls the numbers of predators that feed on them. Conversely, predators can control herbivore population size, which in turn can control grass and tree biomass by defoliation. These are **top-down controls**.

Against this framework of food chains, food webs and trophic levels, the successive steps in the functioning of savanna ecosystems can be summarised, starting with the basis of life on Earth—the capture and synthesis of solar energy, carbon dioxide and water into organic matter through photosynthesis.

10.2 The Photosynthetic Pathways of Angolan Plants

Plants have evolved three photosynthetic pathways (known by the abbreviated forms **C_3, C_4 and CAM**). The earliest pathway, C_3, evolved 2800 Ma in a CO_2-rich atmosphere, while the C_4 pathway evolved much later, about 30 Ma when atmospheric CO_2 had decreased to one eighth of the concentration during the Paleozoic. C_4 grasses dominated open landscapes by 8 Ma. Today, C_4 plants make up less than 3% of the world's flowering plant species, yet because of their high productivity, they account for about 25% of primary productivity on the planet, including such crop species as maize, sugarcane, sorghum and millet (Sage, 2004). Of the 7500 species of C_4 plants, 4500 are grasses. Within the grasslands of the world, C_3 grasses dominate in temperate climates and C_4 grasses are dominant in the open (non-forested) ecosystems of the tropics. Of the world's 16,000 species of CAM plants, most are succulents, adapted to hot, arid climates.

C_3 Photosynthesis

Globally, the most common photosynthetic pathway is C_3, used by more than 95% of plant species (trees, shrubs and herbs), and particularly those grasses that occur in regions of moderate sunlight intensities and temperatures, humid soils and an absence of fires. The term C_3 refers to the fact that the first carbon compound produced during C_3 photosynthesis contains three carbon atoms. The C_3 photosynthetic pathway is less efficient than C_4 in terms of water use and growth, especially in warmer climates and at lower concentrations of atmospheric CO_2. C_3 grasses are rare in Angola. Unlike C_4 grasses, C_3 grasses are tolerant of shading and the few Angolan C_3 grass species such as *Olyra latifolia* are found in the shady environment of forests.

C_4 Photosynthesis

A defining characteristic of tropical savannas is the prominence of fire-tolerant but shade-intolerant C_4 grasses as the dominant ground stratum (Huntley, 1982). Over 95% of Angolan grasses are C_4 species. It is therefore useful to understand what is special about the C_4 photosynthetic pathway as it relates to the success of C_4 grasses in savanna ecosystems.

Over evolutionary time, many plant lineages have evolved specialised anatomical and biochemical mechanisms that have given competitive advantages to plants growing in the tropics, in regions with high temperature and light, with soil moisture limitations, and especially in fire-prone environments such as the savannas (Sage, 2004). The C_4 pathway first evolved in grasses in the Oligocene (about 34–24 Ma) during periods of global cooling, aridification and declining atmospheric CO_2. It is important to note that during the Triassic, Jurassic and Cretaceous periods, atmospheric concentrations of carbon dioxide were four to eight times greater than during the Oligocene and Miocene and through to the present time. During the late Miocene (8–5 Ma), there was a massive increase in the dominance of C_4 over C_3 grasses according to records determined by the carbon isotope ratios of fossil soils. This was the age of speciation of C_4 grasses, the expansion of savannas and, especially in

Africa, the diversification of antelope and other mammal herbivores. The dicotyledons (trees and forbs) evolved the C_4 path later than the grasses, about five million years ago. The C_4 path evolved independently over 45 times, in 19 families of angiosperms, providing a remarkable demonstration of convergent evolution.

At the biochemical level, C_4 plants operate the full C_3 process, but add on an additional layer of metabolism, in effect supplementing rather than replacing the C_3 pathway. The unique leaf anatomy and biochemistry of C_4 plants enables them to concentrate carbon dioxide around the carboxylating enzyme **rubisco**, producing a 4-carbon compound. Further, by suppressing photorespiration, the plant's photosynthetic and water use efficiency is improved. **Photorespiration** is the metabolic process where rubisco takes up oxygen during the day and releases some carbon dioxide, wasting some of the energy produced by photosynthesis. As a result, in high light and temperature environments, by supressing photorespiration, C_4 plants tend to be more competitive and productive than C_3 plants while using less water (Edwards et al., 2010).

CAM Photosynthesis

CAM is the acronym for **Crassulacean Acid Metabolism**, a photosynthetic pathway first discovered in species of the succulent family Crassulaceae. Evolved for life in arid environments, CAM plants have a very interesting adaptation to increase water use efficiency involving closing the leaf stomata during the day, and opening them at night. This behaviour reduces moisture loss by evapotranspiration via the stomata on hot sunny days. CO_2 is collected by opening the stomata at night, when the air is cooler and more humid. The CO_2 is stored overnight as malic acid in vacuoles of the leaf mesophyll cells, and during the day, the malic acid is transferred to the chloroplasts, converted back to CO_2, and used in photosynthesis. In Angola, typical CAM plants include *Euphorbia conspicua* and *Aloe littoralis*, both common along the coast.

10.3 Primary Production in Mesic Savannas

The study of ecosystem energetics has introduced many key terms to the science. As we have seen, photosynthesis is the process of converting carbon dioxide and water into organic compounds using the energy of solar radiation. The result is referred to as **primary production (PP)** and the **rate** is **gross primary productivity (GPP)**. Some energy is lost through **respiration (R)** before storage. The rate of storage of energy after respiration is **net primary productivity (NPP)**. The amount of accumulated organic matter at a given time is called the **standing crop biomass**.

Solar Radiation and Precipitation

Solar radiation drives all life on earth, but only a tiny fraction of incoming radiation is assimilated by terrestrial ecosystems (Sect. 5.1). The solar radiation reaching the upper atmosphere over the tropics is reduced by 40% due to reflection and absorption by clouds. A further 13% is reflected by the canopy of vegetation and soil, while most of the remaining 47% is used up in evaporating the moisture, or warming the surface of the soil and vegetation. Less than 1% of the incoming solar radiation is used in photosynthesis, indicating that primary production is not limited by solar radiation. Water, not energy, is the key constraint on primary production and the carbon flows and nutrient cycles of savannas.

Climate, but specifically mean annual temperature (MAT) and mean annual precipitation (MAP), and soil nutrient status (especially nitrogen, phosphorus and sulphur) determine NPP of Angolan savannas. The relationship between mean annual precipitation and the peak of above ground herbaceous biomass is illustrated in Fig. 10.4. The actual rate of photosynthesis in savannas is controlled by evapotranspiration which is the combined value of plant transpiration and surface evaporation. On soils of similar fertility, the maximum canopy photosynthesis of African savannas has been shown to increase exponentially with mean annual precipitation (Merbold et al., 2009). Primary production also varies through the course of a year. In the tropics, the length of the growing season is determined by rainfall rather than by daylength or temperature. By way of contrast, in temperate regions, day length and temperature are key determinants of plant growth activity.

Quantification of Energy Pools and Fluxes

An early objective of many ecosystem studies was to quantify the flow of energy (using carbon as a surrogate) through the system. In the systems ecology tradition, the quantification of interactions between organisms and the environment is usually presented as **'box and arrow'** models (Fig. 10.5) where boxes represent the **pools** of materials (carbon, nutrients, water) and arrows indicate the direction and quantity

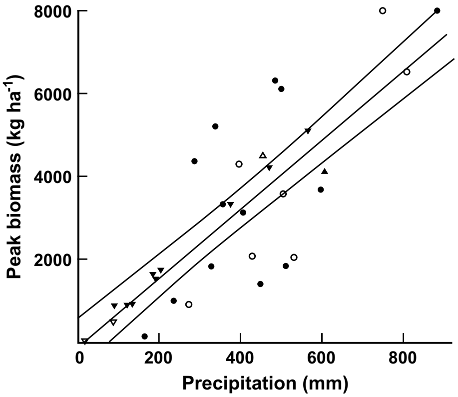

Fig. 10.4 The relationship between mean annual rainfall and peak above-ground herb biomass, for sites in East and southern Africa. (Symbols indicate sample sites across the region). The significant linear regression predicts a biomass increase of approximately 800 kg ha^{-1} for every 100 mm increase of precipitation. From Shorrocks (2007) *The Biology of African Savannahs*. Oxford University Press, Oxford

of transfers (**fluxes**) of energy and matter. Primary production is usually quantified as grams of dry matter (DM) produced by plants per square metre per year (g DM m^{-2} y^{-1}). One gram of dry matter contains about 0.45 g carbon, or 20 kJ of energy. It should be noted that measures of net primary productivity are usually given as grams carbon per square metre per year (g C m^{-2} y^{-1}), or in g dry weight (DW) per square metre per year (g DW m^{-2} y^{-1}) while standing crop biomass is given in Mg ha^{-1}, equivalent to 100 g DW m^{-2}. Comparisons of data sets on primary productivity and biomass should take the large differences between measures of dry matter and carbon into account.

Very few studies of whole ecosystem energy flows have been undertaken in African savannas due to the cost and complexity of such research projects. One such attempt was that of the South African Savanna Ecosystem Project. Figure 10.5 presents the carbon budget for Nylsvley *Burkea africana* savanna woodland, representing mesic/dystrophic savanna at the southern limit of the biome's rainfall and productivity gradient. The total standing biomass for the *Burkea* savanna ranged from 10–35 Mg ha^{-1}, significantly less than that of mature miombo in Angola, which reaches 100 Mg ha^{-1}. For comparison, Rain Forest averages about 440 Mg ha^{-1}, while at the opposite extreme, the standing biomass of desert shrubland is about

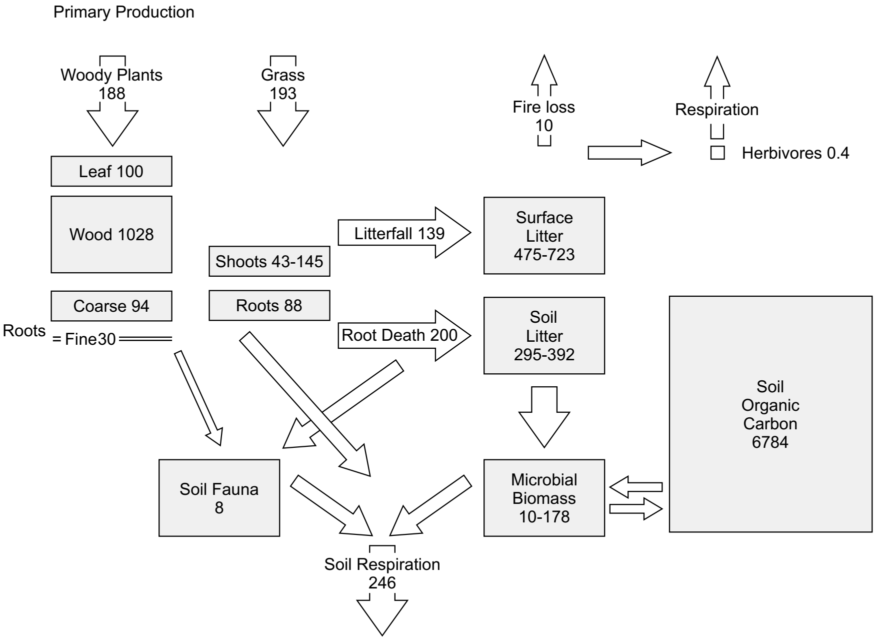

Fig. 10.5 The mean annual carbon cycle in the *Burkea africana* broad-leafed savanna at Nylsvley in northern South Africa. The values in the pools (boxes) are in g C m^{-2}; the fluxes (arrows) are in g C m^{-2} y^{-1}. The total ecosystem carbon stock of 9357 g C m^{-2} includes two-thirds as soil organic carbon. From Scholes and Walker (1993) *An African savanna: synthesis of the Nylsvley study*. Cambridge University Press, Cambridge

7 Mg ha^{-1}. The Nylsvley carbon budget and profile of annual primary production provides an illustration of the components of energy flowing through a woodland and its allocation to different plant parts.

Allocation of Primary Products

In savannas, grasses have a higher relative Net Primary Production than trees. **Relative NPP** is the NPP relative to the standing biomass. This reflects the higher relative growth rate of grasses compared to trees. Tree saplings might allocate 50% of energy to leaves, but as they increase their biomass with age, this might drop to only 5% going to leaves, with the major share of energy going to support structures (stems and branches) and for maintenance (respiration). The allocation of fixed carbon to different plant parts (leaves, shoots, stems, roots) varies considerably in different ecosystems and also in terms of light conditions (full sun or shade). The **root to shoot ratio** (R:S) ranges from 0.2 in tropical rain forest to 1.2 for arid savannas to 4.5 in desert. Rain forests have most of their carbon stock located in their above ground organs, with relatively little below ground in their shallow roots systems. Savannas and especially grasslands have their carbon stores below ground. This gradient relates to declining rainfall, net primary production and standing biomass. As a general observation, as aridity increases, investment in underground storage organs also increases. However, some mesic savannas have 'underground trees' which have extensive lignotubers and branching structures below the soil surface (see Box 14.2). Angolan plant ecologist Amândio Gomes and colleagues found that *Parinari* grassland geoxyles on arenosols had a belowground biomass of 16 Mg ha^{-1} while in *Brachystegia* grasslands on ferralsols the biomass averaged 44 Mg ha^{-1} (Gomes et al., 2021). They found that the below-ground biomass of the geoxyle grasslands almost equalled that of the above-ground biomass of neighbouring miombo woodland.

Net Primary Production in the Nylsvley Burkea *Savanna*

The net annual primary production for the Nylsvley study site was 950 g DW m^{-2} y^{-1}, using about 0.3% of radiant energy received by the ecosystem, with NPP about equally contributed by trees and grasses. The contribution of different plant parts to the total annual primary production of dry matter in the *Burkea africana* savanna (in grams Dry Matter per square metre per year (g DM m^{-2} y^{-1}) was estimated as follows (Scholes & Walker, 1993):

- *Woody plants*—total 468 (wood growth 89; current twigs 27; leaves 156; flowers and fruit 10); coarse roots 11; fine roots 175 g;
- *Herbaceous plants*—total 482 (leaf and culm 157; roots 325).

Grazeable grass production (that available to herbivores) at Nylsvley was 157 g DM m^{-2} y^{-1} of a total grass NPP of 482 g DM m^{-2} y^{-1}.

Basal area of woody plants in the study population (4.2 m^{-2} ha^{-1}) increased at 6% per year. A maximum basal area level of ca. 10 m^{-2} ha^{-1} of trees was measured on an adjoining site that had been protected from fire for 30 years. Here competition with other trees had stabilised the tree growth rate in the absence of fire and other disturbances. Increases in the basal area of mature trees in both Wet and Dry miombo approximates 3% per year, but with several-fold higher total NPP and standing crop biomass than the Nylsvley *Burkea* broadleaf savanna, as discussed below.

Frost (1996) indicates that annual leaf and twig growth in miombo amounts to about 5% of total woody biomass, with young trees adding proportionately more per unit biomass than older trees. Much of this growth is lost annually through litter fall.

10.4 Standing Crop Biomass and Canopy Cover in Mesic Savannas

The above-ground biomass of mature stands of miombo woodland increases following a precipitation gradient from about 20–30 Mg ha^{-1} at Nylsvley to 55 Mg ha^{-1} in Dry Miombo to over 100 Mg ha^{-1} in Wet Miombo. Total biomass of old-growth miombo in Zambia was calculated as 106 Mg ha^{-1}, of which 63% was aboveground and 37% belowground (Chidumayo, 1995; Chidumayo & Frost, 1996). The ratio of aboveground to belowground biomass tends to decrease with decreasing rainfall, due possibly by the need for more extensive water-harvesting root systems in drier sites such as Nylsvley (Frost, 1996).

The total woody plant canopy cover at Nylsvley was 32%, biomass was 16.2 Mg ha^{-1}, with a tree basal area of 4.2 m^{-2} ha^{-1}. Grass canopy cover was 33% and basal cover 5.5% with 1.6 Mg ha^{-1} above ground biomass. The dominance of three tree species (*Burkea africana, Ochna pulchra, Terminalia sericea*) is illustrated by their contributing, collectively, 78% to woody plant biomass, to leaf area index and to primary production.

In the miombo of Shaba, DRC, Malaisse et al. (1975) recorded basal area of trees as 13.5 m^{-2} ha^{-1}, increasing by 2.9% per year. Herbaceous standing crop biomass of grasses and forbs ranges from 1.5 Mg ha^{-1} in Dry Miombo to 3.3 Mg ha^{-1} in Wet Miombo. Grass biomass contributes only 2–5% of total aboveground biomass in woodlands. The biomass of grasses on the moist valley grasslands (locally called *mulolas*, *chanas* or *dambos*) is much higher, in the absence of trees and shrubs.

10.5 Herbivory and Primary Consumption in African Savannas

The next step in the energy budget of savannas will now be considered—the transfer of energy from the primary producer component to the primary consumption component. Measures of biomass (usually live weight) is often used as a surrogate for energy in studies of large mammals. An example of the pathways and partitioning of plant material into the herbivore component at Nylsvley, northern South Africa, is given in Fig. 10.6. Scholes and Walker (1993) synthesised field data from several studies in the Nylsley *Burkea* ~~savanna~~ woodland, which illustrates that most above ground primary production is consumed by decomposers and fire in this mesic/dystrophic system. Herbivores such as Impala use only a small fraction of the primary production component. Most of the material ingested (I) passes out as excretion (E) or respiration (R). Very little goes to production (P). Grasshoppers, although more efficient at assimilating energy than impala, are wasteful feeders, with much of the material removed from plants falling to the ground during feeding.

Relationship Between Mean Annual Precipitation and Herbivore Biomass

Coe et al. (1976) presented a close correlation between mean annual rainfall, predicted primary production, and mammalian herbivore biomass (as a surrogate

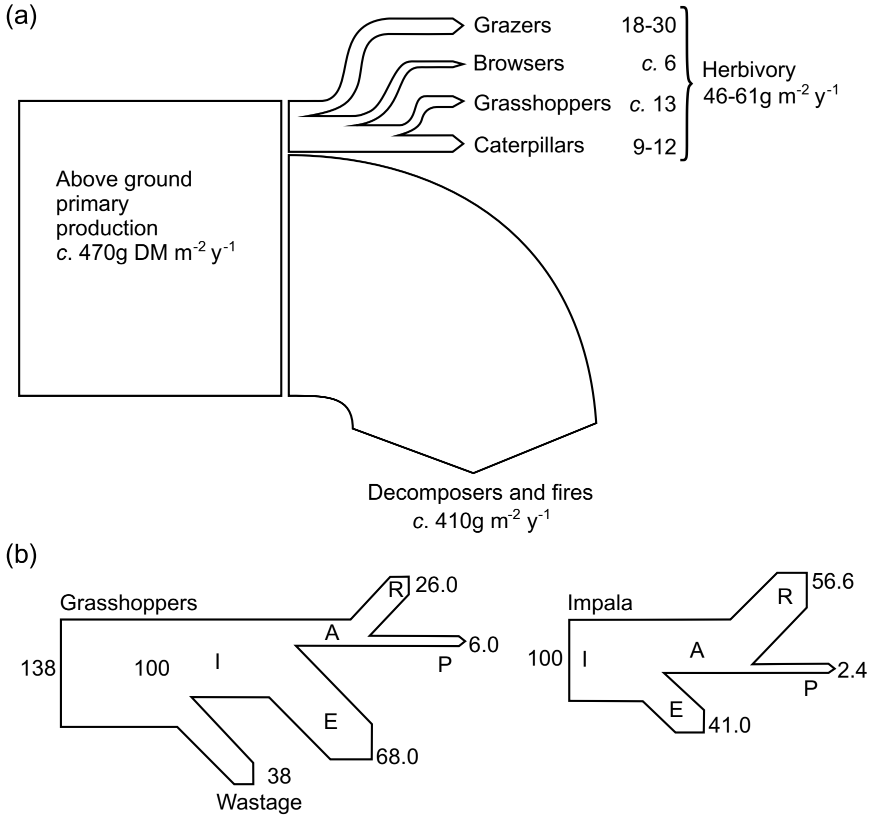

Fig. 10.6 Primary consumption at Nylsvley, a mesic savanna in northern South Africa. **a** Pathways showing the fate of primary production, with the major portion going to decomposition and fires. **b** Partitioning of energy consumption by two herbivores into intake (I), excretion (E), production (P) and respiration (R). The fraction not excreted is assimilated (A), by the digestive system. The ratio of intake to assimilation indicates that grasshoppers (4%) have a higher assimilation efficiency than impala (2.4%). From Scholes and Walker (1993) *An African savanna: synthesis of the Nylsvley study*. Cambridge University Press, Cambridge

for primary consumption) in African savannas. However, this relationship differs between the savannas of high and low nutrient soils (Bell, 1982). The mammal biomass of Africa's arid/eutrophic savannas increases with increasing mean rainfall. In the heavily leached moist/dystrophic miombo ecosystems, at some sites, the higher the rainfall, the lower the mammal biomass (Frost, 1996). The relationship between herbivore biomass (for herbivore species with an adult live mass of more than 15 kg) and mean annual precipitation, in three soil nutrient availability groups has been presented by Fritz and Duncan (1994) for African savannas. They found that for a given rainfall the herbivore biomass on high nutrient soil is significantly greater (2–3 times) than savannas on low nutrient soil (Fig. 10.7). They also found that mammal species richness had a significant but very small effect on the biomass-rainfall relationship, indicating that carrying capacity is limited at the community rather than the species level in African savannas.

Mammals in particular are scarce in miombo, with low biomass and low densities. Several antelope species are endemic to, or have their primary range, in miombo. These include Sable Antelope, Roan Antelope and Lichtenstein's Hartebeest. These are large-bodied, coarse-grass grazers, which are very selective in seeking out herbage at its optimal nutrition stage, or by moving through their home range which includes some diversity of forage through the seasons. Selective feeding in nutrient-poor habitats requires relatively large home ranges, and miombo ungulates occur at low densities, when compared with the large herds of Wildebeest, Zebra, Gemsbok and Springbok in arid savannas. The net result is that the mammal biomass that can be carried by miombo ecosystems, even at high plant biomass, is much less compared to that carried by rich arid/eutrophic savannas such as the acacia savannas and short grasslands of volcanic soils of East Africa.

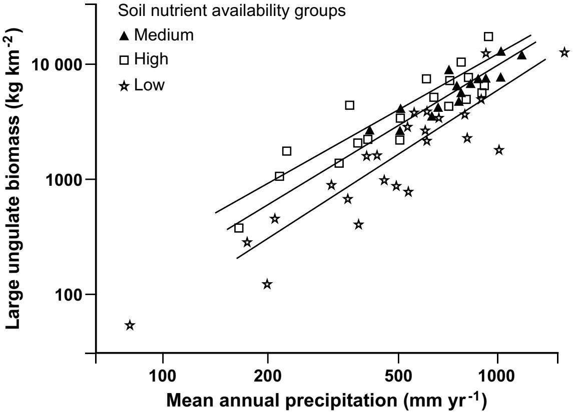

Fig. 10.7 Relationship between mean annual precipitation and large herbivore biomass. Regression lines for soil groups: Top—high nutrients (squares); Middle—medium nutrients (triangles); Bottom—low nutrients (stars). Note that herbivore biomass is 2–3 times higher on high nutrient than on low nutrient soils at the same precipitation level. From Owen-Smith and Danckwertz (1997) In Cowling et al. *Vegetation of Southern Africa.* Cambridge University Press, Cambridge

While the arid/eutrophic savanna grasslands of Serengeti have 50–80% of their annual grass primary production removed by herbivores (McNaughton, 1979), the use in mesic/dystrophic savannas such as miombo probably lies between 5% (Shaba, DRC: Malaisse et al., 1975) and 10% (Nylsvley: Scholes & Walker, 1993). This is a consequence of the low nutrient value and rank nature of miombo grasses, the rapid loss of nutrient status at the onset of the dry season, and the poor browse quality of trees and shrubs. All this relates to the poor nutrient status of miombo soils.

Nutritional Quantity and Quality

The nutritional quality of grasses, measured in terms of nitrogen content (essentially a surrogate for protein content), at ca. 2% N at the early growing season, drops to ca. 0.8% as the young leaves expand, decreasing further to 0.5% during early dry season. Given that the N level required to maintain ungulates on natural range in Africa is 0.8%, it can be recognised that the nutrition value of miombo grasses and woody plants is very poor, accounting for the very low herbivore biomass carried by miombo woodlands. This low herbivore biomass results in less than 2% of available browse in miombo being consumed, as reported from a study in Zimbabwe, and 4% consumed in the *Burkea-Ochna* savanna of northern South Africa (Scholes & Walker, 1993). Even bulk-consumers such as elephant are very selective in their feeding habits in miombo. In Malawi, only 13 out of 35 woody species eaten by elephant were rated as their preferred food.

As a general rule, mammal herbivore productivity in arid/eutrophic savannas is limited by food quantity, which is in turn limited by rainfall, which limits primary productivity. In mesic/dystrophic savannas, primary consumption is limited by food quality, which is limited by soil nutrients. Furthermore, Owen-Smith (1982) recorded that browsers face an **energy** (**quantity**) shortage during the dry season (when many deciduous trees have lost their leaves) while grazers face a **protein** (**quality**) shortage at that time. As a consequence, in miombo, nutrient cycling does not pass through large herbivores, but through two other consumer pathways—fire, as discussed earlier, and termites, as discussed below. In Angola, domestic livestock is most productive in the arid southwest, and almost absent in the north, due not to the quantity of grass, but due to its quality.

Herbivory by Invertebrates

While termites have very visible roles in the miombo decomposer component (Sect. 10.6), the impact of other invertebrates, both as consumers and pollinators, needs mention. In Zimbabwean miombo, invertebrates consumed up to 30 kg ha^{-1}, double the value eaten by mammals (Martin, 1974). In the moist miombo of Shaba, Zaire, lepidopteran larvae were found to feed on 80% out of 159 plant species studied. Selection of plants by moth larvae was very focused for most species. Of 153 lepidopteran species recorded as feeding on miombo trees, 75% fed on only one or two plant species. An exception was noted in the ubiquitous miombo dominants—*Brachystegia spiciformis* and *Julbernardia paniculata*—which hosted 16 and 30 lepidopteran species respectively (Malaisse, 1983). Defoliation of trees by invertebrates occurs during the wet season, and is normally not very conspicuous. However, in some years outbreaks of moth and beetle populations can defoliate broad areas of *B. spiciformis* and *J. paniculata,* their faeces (frass) providing a shower of nutrients to the litter layer and triggering microbial decomposition. At Nylsvley, periodic outbreaks of defoliating caterpillars (*Cirina forda* and *Sphingimorpha chlorea)* removed up to 33% of leaf production of the dominant tree *Burkea africana.*

Assimilation, Production and Consumption Efficiency

Primary consumers (herbivores) vary in efficiency of food use after ingestion. **Assimilation efficiency** is the ratio of assimilation to ingestion. Of the energy assimilated, some goes to respiration and some to production (building new tissue and reproduction). **Production efficiency** is the ratio of consumption to assimilation. Endotherms (mammals, birds) have higher assimilation efficiencies than ectotherms (insects, reptiles), and predators are more efficient than herbivores. Production efficiency is lower in vertebrate endotherms than ectotherms, because endotherms have to expend energy to maintain a constant body temperature. They typically convert only 2–4% of assimilated energy into production. African ungulates are near the bottom of the production efficiency scale, at about 2% (Fig. 10.6b). Most invertebrate ectotherms have low assimilation efficiencies but high production efficiencies, on average around 40%. Measurements for mesic savanna at Lamto, Ivory Coast, found grasshoppers had a production efficiency of 42% (Gillon, 1973). The ratio of ingestion to production at the next-lower trophic level is termed **consumption efficiency**. These ratios are derived from measures of the energy transfers from one trophic level to the next along the food chain, from primary producers (plants) to primary consumers (herbivores) to predators and to detritivores and decomposers.

10.6 Decomposition and Nutrient Cycling

Scholes and Walker (1993) in discussing nutrient cycling in the Nysvley savanna, make the important observation: "Building nutrients into organic molecules is one half of the cycle of life; disassembling the molecules is the equally important other half."

A generalised model of nutrient cycling in woodland ecosystems is presented in Fig. 10.8. Solar radiation drives primary production, synthesizing carbon, water and nutrients into living organic matter. The balance of production after respiration and other metabolic losses is net primary production, represented by the trees, shrubs and grasses of the savanna community. Some nutrients in the vegetation are re-translocated within the canopy. Even before leaves fall to the ground, nutrients are withdrawn from them. The carbon to nitrogen ratio of leaves prior to leaf fall is 50:1, dropping to 20:1 before they enter the litter layer of the woodland floor. Dead leaves, twigs, branches and trunks contribute to the build-up of dead organic matter through litterfall. Decomposer organisms break down and mineralise the organic matter, releasing nutrients which together with atmospheric and soil mineral sources, are incorporated into new plant growth.

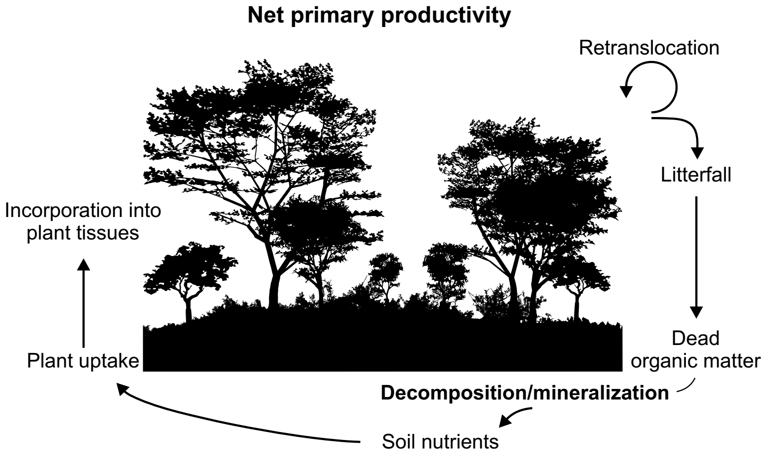

Fig. 10.8 A generalised model of nutrient cycling in a terrestrial ecosystem. Plants take up water and nutrients from the soil, these are used in the process of photosynthesis within tree and grass leaves, some nutrients are retranslocated prior to litterfall, whereafter the accumulated litter is decomposed and mineralised, releasing nutrients for uptake by plant roots. At the ecosysystem level, inputs are also received from the atmosphere (oxygen, nitrogen) and from the weathering of rocks and minerals. Outputs from the ecosystem include nutrients released from the decomposition and mineralization of dead organic matter and from soil nutrients leached from the system. Redrawn after Smith and Smith (2015) *Elements of Ecology* (9th Edition). Pearson, Boston

Nutrient Cycling in Mesic/Dystrophic versus Arid/Eutrophic Savannas

The nutrient cycling processes of mesic/dystrophic and arid/eutrophic savannas differ in fundamental ways. In mesic savannas, it is the rate at which organic compounds can be **disassembled** (releasing nutrients by decomposers) which limits primary production, not the rate at which they can be **assembled** (forming carbon compounds through photosynthesis). These contrasts are summarised in Fig. 10.9, developed as a general model of nutrient cycling (Chapin, 1980). The model can be adapted to summarise the different processes, transfers and feedbacks of nutrient-rich and nutrient-poor ecosystems, such as the mesic/dystrophic and arid/eutrophic savannas of Angola. In short, low nutrient soils result in low rates of net photosynthesis, producing plant tissue of low nutrient content. The litter falling from plants with low nutrient levels result in slow rates of mineralization, and higher rates of immobilisation by the decomposer organisms, thus releasing low amounts of nutrients into the soil for plant uptake. As Smith and Smith (2015) state: “Low nutrient availability begets low nutrient availability (Fig. 10.10).”

Decomposition, Mineralisation and Carbon: Nitrogen Ratios

Organic compounds produced by photosynthesis and held in plant tissues are ultimately consumed by herbivores or become litter, and are gradually transformed into minerals in the process of **decomposition**. The product of the decomposition process is called humus, the main component of **soil organic matter**, which in turn is an

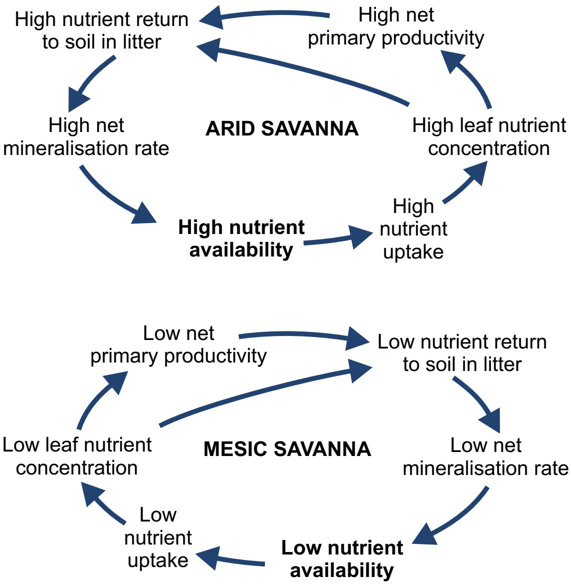

Fig. 10.9 Feedbacks that occur between nutrient availability, net primary productivity, and nutrient release in decomposition for initial conditions of low and high nutrient availability. Adapted from Smith and Smith (2015) *Elements of Ecology* (9th Edition). Pearson, Boston

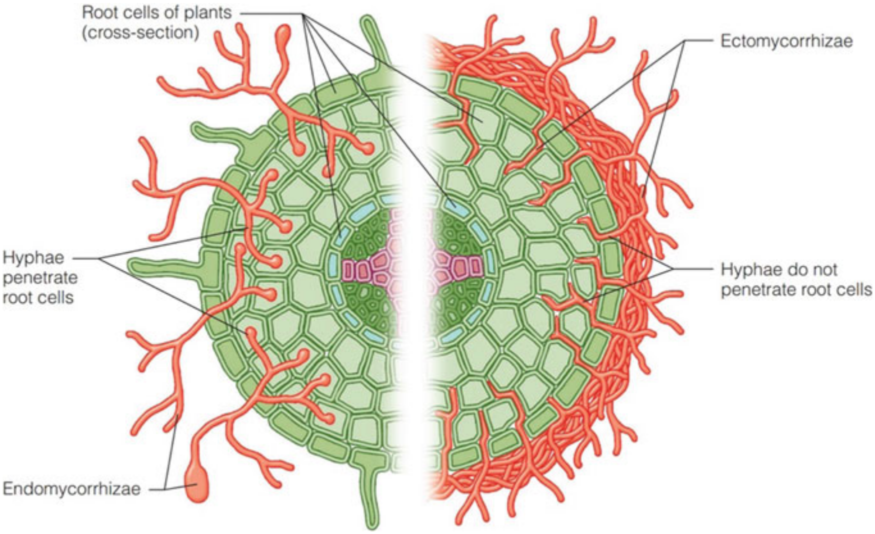

Fig. 10.10 Mycorrhizal structures. Left: Endomycorrhizae grow within tree roots, and fungal hyphae enter the cells. Right: Ectomycorrhizae form a mantle of fungi about the tips of rootlets; their hyphae invade the tissues of rootlets between the cells. From Smith and Smith (2015) *Elements of Ecology* (9th Edition). Pearson, Boston

important constituent of the rooting zone (**rhizosphere**) where most root growth, and water and nutrient uptake, occurs. The chemical bonds holding together organic compounds such as the carbohydrates of leaves and twigs must be broken to release essential macronutrients such as nitrogen, phosphorus and sulphur into their inorganic form, for uptake once again by plants. The process is called **nutrient mineralisation**. Some of the released nutrients are taken up again by decomposer organisms, resulting in **nutrient immobilisation**. A wide range of organisms (decomposers) are involved in the fragmentation, digestion and excretion processes of mineralisation, including termites, woodlice, dung beetles, earthworms, nematodes, bacteria and fungi.

The rate of breaking down organic matter varies according to chemical composition and nutrient content. Glucose and other simple sugars are easily broken down, but cellulose and lignins are more difficult. An important consequence of the decomposition process is the change in the **carbon to nitrogen (C:N) ratio** in soils as decomposition proceeds. As decomposer organisms use up the high energy carbon of litter, there is an increase in the proportion of nitrogen. This nitrogen is incorporated into complex lignin-based compounds and is thus not available to plants. Gradually the quality of the litter is degraded into a form where decomposition proceeds very slowly. As in most biological processes, temperature and moisture influence the rate of microorganism activity and therefore of decomposition. Warm, moist conditions favour microorganism activity; cool, dry conditions do not.

The Role of Fire in Mesic Savanna Nutrient Cycling

It must be remembered that in savannas not all mineralisation occurs through the activity of decomposer organisms. Decomposition includes the microbial oxidation of litter—microbial digestion in the gut of herbivores by microbes (Box 8.1) —or combustion by fire. Fire is a significant contributor to the nutrient cycle of mesic savannas where very little of the products of photosynthesis are consumed by herbivores. At Nylsvley only about 50 g C m^{-2} y^{-1}out of 950 g C m^{-2} y^{-1} primary production is consumed by above-ground herbivores. By far the major portion is transferred directly from the primary producer component to the decomposer component. About 5% is consumed by herbivores, 15% is oxidised by fires, and 80% is broken down by decomposer organisms. Mineralisation rates are fastest by fire, intermediate by passing through a ruminant gut, and slowest by microbial decomposition in the leaf litter layer or soil. Releases of nutrients from decomposing organic material, and the nutrient cycle as a whole, are driven by rainfall and fire and therefore occur as pulsed events, not as smooth and continuous processes.

Decomposition Rates

Litter decay is as much as 90% in the first year in Wet Miombo, where termites account for 40% of litter decay. Decay rates are much slower (40% in the first year) in Dry Miombo, where termites are less active. Litter decomposition in the mesic savanna of Nylsvley is even slower, with a mean turnover time of five years. Termites and ants process less than 5% of this—the major role in decomposition is that of microorganisms. The seasonality of decomposition in mesic savannas is complemented between microorganisms that are active in the warm moist summer and the incidence of fires in the cooler, dry winters.

Mycorrhizal Mutualisms in the Nutrient Cycle

Perhaps the most common, but least recognised, mutualistic interactions in nature are those between mycorrhizas, rhizobia and the roots of vascular plants. Without the nutrient capture and nitrogen-fixing roles of these soil microorganisms, plant life as we know it could not exist. The relationship is so profound that some authors have commented that most higher plants do not have roots: they have mycorrhizae.

Mycorrhizae are mutualisms comprising networks of fungal hyphae that capture nutrients (including phosphorus and nitrogen) from the litter layer and transport these to the roots of plants in exchange for carbon. Three types of mycorrhizae are recognised:

- **Vesicular–arbuscular endomycorrhizae** (VAM: nitrogen-fixing) that are found in over two-thirds of plant species.
- **Ectomycorrhizae** (ECM: non-N-fixing) that are particularly common in nutrient-poor miombo woodlands and are found in 10% of plant species.
- **Ericoid mycorrhizae** found in nutrient-poor heathlands.

The structural distinctions between endo- and ectomycorrhizas are illustrated in The hyphal sheaths surrounding the roots of ectomycorrhizal hosts do not penetrate root cells, while the hyphae of endomycorrhizae penetrate root cells

Endomycorrhizae have tiny, below-ground fruiting bodies. Ectomycorrhizae produce large above-ground fruiting bodies (such as mushrooms, Fig. 10.11), which release vast numbers of wind-borne spores. The mutualistic association of termites and fungi in the decomposition of plant material is especially well illustrated by the association of mycelial gardens of the litter-feeding termite *Macrotermes falciger* and the mushroom *Termitomyces reticulatus* (Fig. 10.12). The association is described in Box 14.2.

A unique feature of miombo woodlands among tropical woodlands and forests is the number of tree species having ectomycorrhizal rather than endomycorrhizal associations. In miombo, the canopy dominants—*Brachystegia, Julbernardia, Isoberlinia, Marquesia, Monotes*—all have non-N-fixing ectomycorrhizas. Endomycorrhiza are associated with *Albizia, Erythrophleum, Pericopsis* and *Pterocarpus,* which also have root nodules of N-fixing rhizobia. Globally, leaves of trees with nitrogen-fixing root nodules (rhizobia) normally have 40% higher N content than non-N-fixing species.

In Angola, ectomycorrhizae might be particularly important in mobilising nutrients (particularly phosphorus) in the inherently nutrient-poor soils of the miombo. Frost (1996) suggested that the success of *Brachystegia* and other detarioid legume species on the infertile soils of the miombo is due to their having extensive ectomycorrhizas. This suggestion is supported by recent studies by Gomes et al. (2021) of the plant functional traits of trees and geoxyles of the very acid (pH 3.3) and very low plant-available phosphorus soils of the Angolan Wet Miombo ecoregion. The study concluded that key traits such as specific leaf area, and leaf phosphorus content,

Fig. 10.11 *Termitomyces titanicus*, the world's largest edible mushroom, symbiotic with *Macrotermes* termites. Mushrooms are a significant food source for rural communities in miombo. *Photo* Pedro Vaz Pinto

were highest in detarioid Fabaceae when compared with other legume lineages. The ectomycorrhizal associations of the dominant Detarioideae trees (e.g. *Brachystegia, Julbernardia*) were found to produce higher nutrient levels than the endomycorrhizae of non-Detarioid and non-Fabaceae trees of miombo landscapes (Gomes et al., 2021).

Rhizobia

While nitrogen is the most abundant constituent of the atmosphere, contributing 79% of atmospheric gases, it is not directly available to plants. Atmospheric nitrogen is broken into a soluble form by lightning, and carried to earth by rain. Nitrogen from the gaseous form is also made available to plants by nitrogen-fixing bacteria of the genus *Rhizobium*. Here it is relevant to emphasise the importance of nitrogen to all living things. Nitrogen is a major part of amino acids, the building blocks of proteins and of nucleic acids such as DNA, which transfers genetic information to subsequent generations. It is a major component of chlorophyll, the substrate for photosynthesis. It is also the key component of adenosine triphosphate (ATP)—the energy-carrying molecule found in the cells of all living organisms.

While the main source of nitrogen is via atmospheric precipitation, the role of nitrogen-fixing bacteria is critical in the nitrogen cycle. In rhizobial mutualisms, soil-living bacteria come into contact with the root hairs of host plants, enter the root

Fig. 10.12 *Termitomyces reticulatus*, cultivated by the termite *Macrotermes falciger* in miombo woodland, DRC. *Photo* Andre De Kesel

hair via an infection thread which stimulates the root cells to divide and to form a nodule. The bacteria have the ability to absorb atmospheric nitrogen and convert it to plant-available nitrogen in the form of ammonia. Rhizobia are mostly associated with members of the legume family Fabaceae.

10.7 Savanna/Forest Dynamics: Fire as the Driver of Alternative Stable States

The Process of Plant Succession

In most of the ecological literature of the twentieth century, especially that of colonial botanists working in Africa, the savanna landscapes of the tropics were considered the result of human influences. The perception was based on prevailing concepts on the processes of vegetation change, where developing communities passed through a series of stages (or **seres**). It was suggested that tropical savannas were **seral** communities, retarded in their development towards a climax forest by human activities, including fire and deforestation. In the early twentieth century, British and American ecologists (Clements, 1916, 1936; Tansley, 1935) had developed the concept of **plant succession**—whereby plants of **pioneer** species colonise open sites (coastal sand dunes, landslides, volcanic lava flows) and gradually build soils and initiate a **primary succession** of simple plant communities.

The process of plant succession results in floristic and structural changes to the community, as richer organic soils, and more moderate microclimates, develop. These **seral stages** support shrubland, then woodland, then forest systems, each forming part of a slowly changing continuum. The **climax community** (forest) was considered the ultimate reflection of vegetation potential within a particular climatic zone. In Clements's view, for each climate, there was a single, stable vegetation state—the climax. Clements likened communities to organisms, each species being part of an integrated, interacting whole. His **organismic community** concept was challenged by another American ecologist, H.A. Gleason. Gleason (1939) considered each species in a community to have independent responses to the environment. The mix of species across a landscape represent a **continuum** of **individualistic** responses, not interdependent clusters. Today, ecologists increasingly view communities as manifesting characteristics of both concepts. Emphasis is now placed on how the adaptations and life history traits of individual species determine species interactions and distribution patterns under changing environmental conditions (Smith & Smith, 2015).

In particular, ecologists working in southern African and Brazilian savannas have challenged the traditional successionist view, demonstrating that very different vegetation states, such as forests and savannas, can share the same landscapes and the same climate. The convergence of ecological characteristics of the cerrados of Brazil and of the mesic savannas of Africa described by Huntley (1982) is well illustrated by their dynamics relative to fire in the maintenance of **alternative stable states**. Indeed, tropical savannas and forests have evolved in parallel over many millions of years, characterised by distinctive physiognomic and floristic structures, endemism and responses to fire. Savannas, such as miombo and cerrado, are not, in the language of twentieth century ecologists, '**early successional**', '**secondary successional'** or '**fire sub-climaxes'**, but are alternative stable states living in a dynamic relationship with adjacent closed forests under the same climate. As has been repeated in previous chapters, savannas are ancient ecosystems—not human-induced artefacts.

Equilibrium, Resilience and Feedbacks

To understand the theory of alternative stable states, it is necessary to introduce the concept of ecosystem equilibrium. Natural ecosystems are considered to be in a state of **equilibrium** when the system may be subject to slight fluctuations of energy and matter but where there are no sudden changes in the system's structure and function. Observed fluctuations tend to occur within defined limits. They are considered to be in a steady-state equilibrium where there are no (or very slow) changes in the long term, even though there are oscillations in the short term (e.g. due to rainfall variability). Systems in a steady state equilibrium usually return to the steady state following a **perturbation** (a disturbance such as a fire or drought). The ability to return to equilibrium after a perturbation is referred to as an ecosystem's **resilience**. The maintenance of a steady state equilibrium is through the mechanisms of feedback loops. There are two types of feedback—negative feedbacks and positive feedbacks. A **negative feedback counteracts** the change in input or impact, tending to **maintain** the system in its current state. A **positive feedback amplifies** the change in input or impact, pushing the system toward a more pronounced change and sometimes leading to another state.

Instability and Tipping Points

Change at geological or evolutionary time scales allows plants and animals to adapt to new conditions, whereas rapid change (such as current global warming) may be too rapid for species to adapt, resulting in declining habitat conditions and ultimately, species extinctions. If a system is altered, with such change leading to additional or accelerated change, the system might move away from its original equilibrium past a **tipping point**. The system will have been pushed towards a new **stable state**. If this happens the system is said to have been subject to **positive feedback**. The feedback is *positive for change* and the system may be considered to be **unstable**. A negative feedback counters any change away from the equilibrium and contributes to system **stability**. Ecosystems that have not been transformed by human activities are normally in a stable equilibrium because of the multiple stabilizing **negative feedback** loops that drive the system back to the steady state equilibrium.

Alternative Stable States

The theory of **alternative stable states** (ASS) suggests that each state is maintained at equilibrium by negative feedbacks. Much of the evidence for the ASS theory comes from tropical savannas. The crux of the ASS theory is that ecosystems can switch to an alternative state through what is termed a **regime shift**. A regime shift might occur when there is a major shock to the system, such as a fire storm penetrating a forest, opening the canopy and allowing fire-tolerant grasses to establish and result in a change from a closed canopy forest to an open canopy savanna. A regime change can also be more gradual, as through longterm fire exclusion in savanna, where forest species gradually establish in the savanna. As the canopy of woodland closes, a moist, cool, forest microclimate develops, where low biomass and low fuel-load of shade-tolerant but fire-intolerant grass and ground cover is established, supressing fire entry.

Hoffmann et al. (2012) present an elegant model of alternative stable states involving the complex interaction of fire, climate and species traits that maintain the structure of cerrado and closed forest in central Brazil. The model is highly relevant to miombo, despite Angola's mesic savanna having a totally different species composition to that of the mesic savannas of the Brazilian cerrado.

Thresholds: Fire-resistance and Fire-suppression

Fire-tolerant (**pyrophilic**) savannas are maintained by fire as grasslands and woodlands, and have done so for millions of years. However, under an unchanging climate, but with the sustained absence of fire, the transition to a different state, such as a fire-intolerant, (**pyrophobic**) forest, is possible. Such regime change results in a mosaic of bi-stable states, such as the moist savanna/forest mosaics of Zaire, Uíge and Malange provinces in the Congo basin (Figs. 2.2 and 12.5). Disturbances such as hot fires along a forest margin, might change the vegetation structure by opening up the canopy and allowing shade-intolerant grasses to establish. But unless followed by successive fires, the forest margin will recover, returning to its former state.

Hoffmann et al. (2012) describe two critical ecological thresholds involved in the resistance to change or the transition of savanna to forest.

- Savanna trees cross the **fire-resistance threshold** once individual trees have accumulated sufficiently thick bark to avoid stem mortality due to fire and to attain sufficient height to escape top-kill by frequent fires. Adaptive traits in plants are critical. Savanna trees accumulate bark thickness faster than do forest trees. They also have other adaptations to fire such as epicormic buds and relatively larger investments in underground storage organs. The open canopy of mesic savannas maintains a light and flammable C_4 grass layer, sufficient to support low intensity fires that do not damage trees, but sufficiently hot to kill the seedlings of fire-intolerant forest species.
- Forest communities cross the **fire-suppression threshold** when they have developed enough canopy cover to suppress fire by excluding shade-intolerant, highly flammable savanna grasses. Forest tree species accumulate leaf area and canopy density more rapidly than savanna trees, thus shading out shade-intolerant savanna grasses, accelerating the transition to forest. The dense forest canopy creates a cooler, more humid microclimate that supports a light, poorly combustible ground cover, including forbs and C_3 grasses.

Regime Shifts and Feedback Mechanisms

In the savanna/forest mosaic example, both states are stable until a particular ecological threshold (such as regular fires or total fire exclusion) is crossed. The passage across the thresholds (tipping points) result in substantial changes in the structure and function of the system. The shift from one regime to another might be sudden, such as when the feedbacks that usually maintain the system are overwhelmed by a firestorm, or gradual, such as the drying out of a wetland and its replacement by a thicket. Evidence for grasslands changing to forests as a consequence of fire exclusion come from many experiments in southern, central and west Africa (Fig. 7.6). Similarly, the conversion of forest into grassland from increased frequency of fires along the forest margin and penetration of fire into forests, has happened in many of the Afromontane forests of Angola. Once the regime shift has occurred, it might take centuries to revert back to a former state.

The interactive geophysical and biological processes and feedbacks that operate within the mesic savannas of Africa are comprehensively synthesised by Archibald et al. (2018) as illustrated in Fig. 7.2. Plants create feedbacks to flammability through their structure and the microclimate that they create. **Flammability** is the property of an ecosystem to ignite and propagate a fire, if a source of ignition is present. Tall, shade-intolerant C_4 grasses of the Andropogoneae dominate the most flammable fire regimes of Angola. In the humid, cool microclimate of forests, C_4 grasses are physiologically incapable of out-competing C_3 shrubs and shade-tolerant, slender C_3 grass species, which produce little flammable material. Most undisturbed closed-canopy forests have very little ground vegetation and thus minimal fuel for combustion, so even when fires penetrate the forest margin, they do not advance very far into the forest. In the arid savannas, the shorter Chloridoid and Aristidoid grasses are palatable to grazing herbivores, and thus do not accumulate much fuel. Mammal grazers and browsers thus regulate vegetation structure. The responses to disturbance pressures, such as fire and herbivory, are evolutionary feedbacks demonstrated by features of plant morphology and physiology, and community emergent properties such as structure and microclimate.

The Influence of Spatial and Temporal Scale

Spatial scale influences the pace of change. A small patch of grassland in the middle of a forest might be too small to be ignited by lightning strikes that are the main trigger for natural fires. In the absence of fire, the fire-suppression threshold will be crossed and forest trees will close over the site, shading out any flammable grass species and thus preventing further fire ignition or spread. At the forest margin, grassland fires normally die as the architecture, microclimate and flammability of the vegetation changes. However, as the ratio of perimeter to surface area increases as forest patch size decreases, smaller forest patches become highly vulnerable to fire. In the mountains of Cuanza-Sul, Bié, Huíla and Huambo, the ratios of forest margins to forest canopy of remaining forest fragments have increased due to human-induced pressures such as frequent fires and timber extraction. Single fire events can now sweep through a forest and eliminate the shade-tolerant grasses, which are rapidly replaced by sun-loving flammable species, resulting in hotter and more damaging fires in following years. The once stable state of forest is then replaced by an alternative stable state of savanna, maintained by fire-resistant grasses, shrubs and trees. Finally, it should be recognised that human-driven disturbances (fire frequency, invasive species, charcoal production, deforestation) have accelerated these processes over much of Angola. The forest patches of the Angolan highlands can well be described as rapidly vanishing forest islands in a sea of grassland fires.

Paleo-ecological Evidence of Regime Change

While field observations of regime changes are difficult because of the long timeframes of the processes, paleo-ecological studies are providing valuable evidence of regime changes of African vegetation. Carbon isotope studies measure the proportions of C_4 grasses and C_3 trees and shrubs found in samples extracted from soil profiles. Studies in southern and western Africa provide evidence of both rapid regime change, and stability, in savanna/forest dynamics. Paleo-ecological evidence indicates that since the end of the last Ice Age, approximately 12,000 years ago, the grasslands of many African savanna ecosystems have persisted against conversion to forest cover (Bond, 2019). In other areas, forests have replaced savannas (Maley et al., 2018). The alternative stable state concept has recently been applied to biogeographical models of Africa's forest and savanna biomes, using extensive site-based lists of tree species (Aleman et al., 2020). The results demonstrate the wide divergence of tree species between the two biomes, but also the broad areas in which both formations occupy similar climates. The forest/savanna transitional mosaics (Ecoregions 2 and 3) at the interface between the Guineo-Congolian Rain Forests and Mesic Savannas of northern Angola represent distinctive alternative stable states that have existed for millennia within the same climatic zone.

Box 10.1 Tree—Grass Coexistence: The 'Savanna Problem'

Savannas are neither grasslands nor forests, but integrated mixes of grass and tree life forms within a co-dominant continuum of both grassland and woodland physiognomies. Both trees and grasses influence and are influenced by the availability of light, water balance, water cycle, primary production and the accumulation of fuel for periodic fires. But how do tropical savannas achieve the coexistence of grasses and trees without one displacing the other? The Venezuelan ecologist Sarmiento (1984) described the phenomenon as the 'savanna problem'. The topic has attracted the attention of many researchers and resulted in numerous papers describing alternative causal mechanisms. Here some of the explanations for tree/grass coexistence will be summarised to provide an introduction to one of the most debated features of savanna ecology.

The first and classic model explaining the relationship between trees and grasses in savannas was that of German ecologist Heinrich Walter (1898–1989). The '**Walter Hypothesis**' was based on field work undertaken in Namibia in the 1930s. The hypothesis presented a vertical niche-partitioning model where grass roots are more successful competitors for water in the surface horizons of soil than are trees (Walter, 1971). In contrast, tree roots access water from both the surface and from the deeper horizons that are inaccessible to grasses. Walter argued that deep-rooted savanna trees can use subsoil water throughout the year, including during the dry season, while grasses use their dense, shallow root system in the topsoil to rapidly take up water after infrequent rainfall events. The two life forms can therefore coexistence at equilibrium. Walter confined his hypothesis to arid savannas. He presciently considered that nutrient-deficient mesic savannas are controlled by biotic and disturbance factors. He also emphasised the important difference in the superior water use efficiency of grasses over trees as the ultimate cause of vertical partitioning.

Walker and Noy-Meir (1982) tested the Walter hypothesis in the *Burkea africana* mesic savanna of Nylsvley and simplified Walter's arid savanna model to a generalised 'two-layer' hypothesis (Fig. 10.13), extending the original arid savanna hypothesis to a mesic savanna at the dry, southern limit of the biome's distribution.

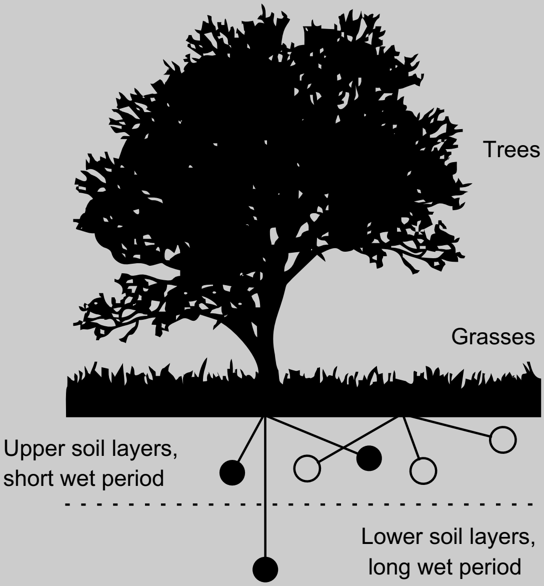

Fig. 10.13 The simplified 'two-layer' model of vertical resource partitioning. Filled circles represent tree roots, open circles grass roots. Note that competition only occurs in the upper soil layer, where water is available for a short period prior to evaporation. Redrawn after Walker and Noy-Meir (1982) *Ecology of tropical savannas*. Springer, Berlin

The 'savanna problem' discussion was taken further by Scholes and Archer (1997) who presented a detailed global review of the complex interactions between trees and grasses in savanna ecosystems. They describe four models: niche separation by depth; niche separation by phenology; spatial separation, and balanced competition.

- **Niche separation** by depth has been discussed above (the Walter hypothesis).
- **Phenological partitioning** can be illustrated in mesic savannas such as Angola's miombo, where trees come into full leaf before the onset of rains, using resources stored since the previous rainfall period. Grasses, however, have very limited water and carbohydrate storage capacities and therefore have to slowly build up photosynthetic capacity as the rain season proceeds. There is thus a clear temporal (phenological) separation in the root and shoot

activity of trees and grasses, the trees using the earliest rains and the grasses only becoming competitive later in the season.

- Besides vertical partitioning in soil and seasonal partitioning in root activity, a third dimension is that of **spatial partitioning** across the savanna landscape. Trees create their own microenvironment of increased fertility and a milder microclimate below their canopies from litter fall and shading. Their roots also expand into the adjacent grassland by up to seven times their canopy radius. Inter-specific as well as intra-specific competition increases as the biomass and density of trees increase, up to a level at which competition between trees limits their density and biomass.
- **Balanced competition** models argue that intra-specific competition for resources is stronger than inter-specific competition. In this case the dominant species becomes self-limiting at a biomass insufficient to eliminate the weaker competitor. In miombo woodlands, certain species tend to dominate over selected areas, with a limit to their density and biomass, and with a sparse under-storey of grasses.

All these mechanisms could lead to stable coexistence between trees and grasses. Scholes and Archer (1997) concluded that no single model can account for the variety of phenomena at all savanna locations. They noted that climate is as important as competition in mediating these interactions.

Building on the discussions of Scholes and Archer (1997), Sankaran et al. (2004) provide a synthesis of hypotheses that seek to explain the coexistence of trees and grasses in savannas drawing on the different processes occurring in arid and mesic savannas. They identify two classes of models: first, competitive interactions that maintain coexistence and second, demographic bottlenecks to tree establishment and persistence in savannas. The competitive interaction models have been discussed above. Here the second approach—**demographic-bottleneck** models—provide another approach to the 'savanna problem'. Here the critical challenge for savanna trees is not on fine-scale effects of resource competition but relates to the recruitment and persistence of trees in the face of climatic variability and/or disturbance (Higgins et al., 2000; Osborne et al., 2018). The emphasis is placed on the success or failure of tree germination, sapling growth and adult tree establishment (Fig. 10.14). Several steps are involved:

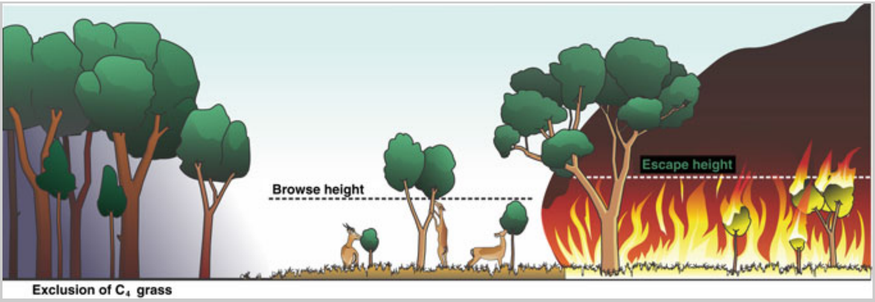

Fig. 10.14 The mechanisms of tree-grass coexistence in savannas. Fire and browsing cause demographic bottlenecks for tree recruitment into the grass layer, leading to the emergence of 'escape heights' in each case. When trees surpass these heights they are no longer suppressed by fire or browsing, and may reach mature sizes. Most C_4 grasses are excluded under closed canopies because they are intolerant of shading, a mechanism which suppresses fires. Each of these feedbacks is positive, leading to the emergence of tipping points beyond which the ecosystem transitions rapidly to an alternative stable state. From Osborne et al. (2018) *New Phytologist*, 220: 10–24

- Tree recruitment in savannas can be slow, due to drought, herbivory and/or fire. Initial recruitment is controlled by rainfall, for successful germination, and for growth to seedling stage.
- Thereafter, fires and herbivory may hold sapling growth below the '**fire escape**' height for many years.
- Fluctuating recruitment and overlapping generations 'store' the reproductive potential of the trees (known as the '**storage effect**') until they can escape above the fire trap and progress to mature adult stature.
- Having established, trees may persist for long periods, until extended droughts, or high rainfall periods followed by intense fires, change the patterns of mortality and regeneration.

Savanna grasses live in a mix of microhabitats, each with differing light, soil nutrient and moisture conditions, and varying degrees of disturbance from mammals and fire. But grasses and forbs, despite their humble stature compared with trees, exert powerful interactions with tree populations. The accumulation of grass biomass, providing fuel for fires, regularly impacts on tree sapling recruitment. But equally, the shading of grasses by trees and suppression of C_4 grass growth and fuel accumulation prevents grass fires from killing the mature trees of woodland. Disturbance from wind, fire, and by burrowing, grazing, browsing or trampling mammals—from porcupines to elephant—results in a non-equilibrium grass-tree situation. Fire prevents woodlands developing into forest and also maintains open grasslands within the savanna matrix. The savanna ecosystem is under continual but subtle change. Individually, disturbance factors such as wind, herbivory and fire might have limited critical impacts, but in combination, the chance occurrence of discrete, often rare events can result in the shift to alternate stable states of savannas as illustrated below (Fig. 10.13).

In recent years, the competition-based hypotheses have lost support to the demographic bottleneck hypotheses. Both approaches await greater clarity on grass demography to conclude the discussions on the 'savanna problem'.

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Chapter 11
Adaptations to Life in the Namib Desert

Key Concepts and Questions: This Chapter Explains

- *Why the physics of water evaporation, and surface area to volume ratios, are important to survival in hot, arid environments.*
- *What adaptations have evolved in plants and animals to increase water capture and reduce water loss in desert environments.*
- *How desert animals regulate temperature to avoid over-heating through morphological, physiological and behavioural adaptations.*
- *What the role of interspecific competition is in securing resources in food-limited environments.*
- *How a diversity of defence mechanisms protects desert plants and animals from predation.*
- *What hypotheses have been proposed by researchers to explain the 'fairy circles' of the Namib.*

Context: The Namib, A Living Museum of Animal and Plant Adaptations to Aridity

The Namib Desert, most comprehensively represented in **Iona National Park**, is a living museum not only of the geological history of Angola, but also of the extraordinary adaptions (the products of natural selection) that have evolved in animals and plants to survive, grow and reproduce under extreme conditions of aridity and temperature. Responses are exhibited in **morphological, behavioural** and **physiological adaptations.** The outcomes of such long evolutionary processes have fascinated ecologists for many decades, and deserts have become centres of research across the world's hyper-arid zones. In Africa, knowledge of desert adaptations is especially advanced for the Namib biota. Research into the ecology and evolution of desert ecosystems has, for more than 70 years, received a world-renown status through international collaboration at the Gobabeb Namib Research Institute at **Gobabeb** in Namibia. The development of **the Iona-Skeleton Coast Transfrontier Conservation Area**, a collaborative project between Angola and Namibia, has as one of its

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https://doi.org/10.1007/978-3-031-18923-4_11

objectives the sharing of scientific knowledge and wildlife management experience. Angolan students have a wonderful opportunity to benefit from this partnership.

The breadth and depth of studies undertaken in the Namib exceed those for any other biome represented in Angola and they provide models for many ecological concepts and principles. Dozens of books, and hundreds of scientific papers have been published on the results of research undertaken at Gobabeb, but only a few examples can be illustrated here, drawing from Barry Lovegrove's excellent synthesis *The Living Deserts of Southern Africa* (Lovegrove, 1993, 2021) and Mary Seely's many publications (Hamilton & Seely, 1976; Seely, 1990; Seely & Hamilton, 1976; Seely & Louw, 1980; Seely & Pallett, 2008).

Five key challenges to survival, growth and reproduction in the desert environment serve as a framework for a summary of adaptions: water, heat, food, competition and reproduction.

To these five challenges, one more can be added: wind. In the Namib, wind accounts for sand-blasting, sand erosion, sand deposition and the transport of nutrients from the interior to the coastal dunes, and of fog from the ocean to the land. Wind is the primary factor involved in the formation and movement of hummocks and dunes, in the transport and burying of detritus and seeds, in wind-chill and even as an acoustic signal influencing the activities of dune beetles that can detect the wind from below the sand (Henschel, pers. comm. 2021).

Although exemplified by adaptations for life in the Namib, these factors all demonstrate general principles for life in terrestrial ecosystems.

11.1 Water: The Currency of Life in Desert Environments

Lovegrove (1993) introduces the concept of water as the 'currency of life' to underpin the essential challenge to survival in hyper-arid environments. But all organisms, from the Equator to the Arctic, must regulate the concentration of their body fluids to avoid fatal biochemical imbalances. Mammals cannot lose more than 10% of their body water without resulting in problems due to excessive concentration levels in their bodily fluids. Plants must maintain their water balance to permit the gas exchanges essential to photosynthesis. Water loss takes place through evaporation at the surfaces of animals and plants. Further, in plants, water is lost by transpiration through plant leaf stomata and in animals, during breathing. The rate of water loss is determined by external temperature and water vapour pressure as described in Sect. 5.5.

A fundamental factor in water loss is that of the **surface area to volume ratio**. Small organisms have a higher surface area to volume ratio than larger organisms. A small desert gerbil, weighing 0.1 kg, evaporates 13% of its body weight per hour—17 times faster than a 500 kg camel (Schmidt-Nielsen, 1985). Many Namib plants—such as species of *Adenia, Commiphora, Cyphostemma, Euphorbia, Hoodia*—adapt a short, stout growth form that reduces the surface/volume ratio—the **cauduciform** or **pachycaul** life form (Fig. 5.19). Many desert succulents follow the CAM photosynthetic pathway, opening their stomata and transpiring during the cool of the night.

Some desert trees, such as *Commiphora anacardiifolia* (Fig. 11.1) and *Cyphostemma currorii* (Fig. 11.2) with succulent trunks, have large, fleshy and deciduous leaves, which maximise photosynthetic activity immediately after rain, rapidly storing both carbohydrates and water, thereby being able to endure long rainless periods. Yet others, such as the mopane *Colophospermum mopane* have paired leaves that close together during the midday heat, reducing exposure to the sun's rays. Within the fog belt, the sand-binding grass *Stipagrostis sabulicola* captures fog droplets on it long leaves, which then slip down to the leaf base or fall to the rooting zone of the grass tussock (Fig. 11.3). Some plants reduce leaf architecture to the extreme, as sharp spines, with photosynthetic tissue embedded in their stems, thorns and flowers, as in *Acanthosicyos horrida*, a spiny shrub of the desert dunes (Fig. 11.4).

Two behavioural responses to water scarcity are found in desert plants. Opportunistic species grow fast after unpredictable rains and complete their life cycle—from germination to flowering to setting seeds—within a few weeks. A different

Fig. 11.1 Large-leaved deciduous trees such as *Commiphora anacardiifolia* succeed in the most arid parts of the Namib by exploiting infrequent rain through rapid photosynthesis via their large leaves

Fig. 11.2 Caduciforms such as *Cyphostemma currorii* store water in their succulent trunks *Photo* Ernst van Jaarsveld

Fig. 11.3 Condensed fog droplets on the leaves of the sand-binding dune grass *Stipagrostis sabulicola* *Photo* Joh Henschel

Fig. 11.4 The melon *Acanthosicyos horrida* has tiny leaves but compensates by having photosynthetic stems, thorns and flowers. Its fruit are a source of food and water for many desert animals. *Photo* Joh Henschel

pattern is found in slow growing and long-lived CAM succulents described above, which can tolerate extended periods of physiological inactivity.

Animals have many adaptations to **reduce water loss** such as the waterproof cuticle of insects, scales in reptiles and the hairy pelage in mammals. Desert reptiles have the lowest water loss rates recorded in animals, about one tenth of that of mammals. Small mammals such as the Namib Golden Mole can regulate their temperature and moisture environment by burrowing under the sand, where they can go into **torpor** while dropping their body temperature. Larger mammals such as springbok make use of the microclimate under shady trees (Fig. 11.5).

The greatest loss of water in animals and plants is during the processes of gas exchange. Animals breath in oxygen and release carbon dioxide; plants take in carbon dioxide during photosynthesis and release oxygen. Section 10.2 describes how grasses and succulents use water efficient C_4 and CAM pathways to reduce water loss during photosynthesis. The gas exchange gateways in plants (**stomata**) have an analogue in insect **spiracles**—an example of the **convergent evolution** of functional adaptations to similar environmental challenges, but within species of very different ancestry. One of the most enigmatic of Namib insects, the flightless

Fig. 11.5 Springbok escaping midday heat under the shade of a mopane (mutiati) *Colophospermum mopane*. *Note* The horizontal browse-line along the lowest branches of the tree

tenebrionid beetles of the genus *Onymacris*, have fused elytra (the wing covers that open during flight in normal beetles) and which cover the abdominal spiracles. The 'cap' over the spiracles maintains a high humidity, with gas exchange being reduced to a single outlet near the anus. The opening is normally kept closed, except when briefly opened to ventilate the chamber (Fig. 11.6). This adaption for greater water economy came at a cost—the ability to fly.

A regular loss of water in all animals is that which occurs when waste products—faeces or urine—are excreted. These contain energy-rich molecules, CO_2, water and a toxic waste product—**ammonia**. Animals must excrete ammonia in its various forms as rapidly and efficiently as possible. The process requires water. Many desert mammals have specialised kidneys which reduce the volume of water needed in the excretion process by creating a very **concentrated urine**. Short-tailed Gerbils achieve a urine concentration 14 times higher than their blood concentration. It is not

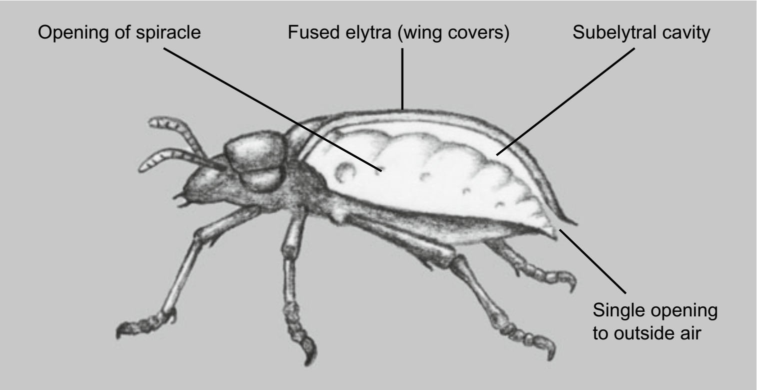

Fig. 11.6 A profile of a typical tenebrionid beetle showing part of the fused elytra, cut away to reveal the sub-elytral cavity into which the abdominal spiracles open for gas exchange. Redrawn from Lovegrove (1993) *The Living Deserts of Southern Africa*. Fernwood Press

only small rodents that must achieve water use efficiency in their bodily functions. The smallest antelope in southern Africa, Kirk's Dik-dik (which was once common in the arid savanna of Iona) has a urine concentration 11 times that of blood. Like Steenbok, also once common in Iona, Dik-dik live independent of any free water sources, selectively feeding on shrubs and grasses at the time of their highest moisture content.

Improving mechanisms of **water capture** is as important to desert biota as their ability to use water efficiently. The coastal Namib, within the zone receiving the cool foggy weather under the influence of the Benguela Current, has many examples of adaptations for effective water capture. Inland of the fog belt, clear, calm nights cause the rapid loss of desert heat, cooling and condensing the air and producing morning dew, a further source of moisture in a region of very limited, unpredictable rainfall. Gemsbok in Iona may be found grazing at night, when the moisture content of the grass *Stipagrostis uniplumis* is 26%, far higher than its midday level of only 9%.

In a narrow margin along the Atlantic coast, **lichens** are unusually common. These cover rocks, sands, shrubs and trees, or simply roll freely over the ground. Lichen are exceptionally well adapted to climatic extremes, reaching their highest diversity and abundance in ecosystems as different as the Namib Desert and the Arctic Tundra. Lichen is a composite organism of algae and fungi forming a **mutualistic relationship**, with different properties to those of the component organisms. Lichens come in many forms, colours and sizes. In the Angolan Namib, especially along the coast between Moçâmedes and Benguela, they are found in foliose, fruticose and crustose forms. During most of the day, they are inactive, presenting the appearance of dead litter. Overnight, they absorb moisture from the fog, initially metabolise using stored energy, and as the sun rises, using solar radiation to photosynthesise in the short time before they once again dehydrate.

Some algal species live entirely below the quartz pebbles that can be found on the gravel plains in many areas of the Namib. The algae utilise the moisture accumulated below the stones, and the light that penetrates the translucent quartz, to photosynthesise. This strange flora is remarkably rich, with over 20 species of green algae and 50 species of diatoms being recorded in the Namib. As Lovegrove (1993) describes, each quartz pebble supports its own **food chain**, with desert arthropods and even snails living off the algae, and desert lizards eating the insects. The organisms that live under these quartz stones are known as **hypolith** communities.

Some Namib plants **capture moisture** from fog directly—their leaves and stalks act as traps down which moisture droplets flow to their roots. Water is also collected by the extensive shallow root systems of the dune grass *Stipagrostis sabulicola* which occupies the bottom of dune slip faces, stabilizing sand movement (Fig. 11.3).

Among desert animals, the Namib **tenebrionid beetle** *Onymacris unguicularis* achieved scientific stardom status in 1976 with cover-page publications in the world's two leading research journals, *Nature* and *Science*. Papers by American researchers Bill Hamilton and Mary Seely (Hamilton & Seely, 1976; Seely & Hamilton, 1976) described studies on the tenebrionid beetles' '**fog basking**' and '**sand trenching'** behaviour. These diurnal flightless dune-dwellers spend the daylight hours foraging for organic litter, retiring at night under a few centimetres of sand of a dune slip-face.

With the cool early morning sunrise, the beetles emerge, climb to the top of the dune crest and take up a headstanding stance. Incoming fog collects on the beetles' shining black backs (the fused elytra previously mentioned), and then rolls down the elytra to be imbibed orally. The beetles increase their body water by up to 34% in this manner. The survival value of this practice is significant. *Onymacris unguicularis* (and *O. bicolor* of Angola, Fig. 11.7) endure long rainless periods through this behavioural adaptation. Populations of other tenebrionid species, lacking this water source, are decimated in such dry spells. Another tenebrionid beetle, the nocturnal *Lepidochora discoidalis*, makes shallow trenches in the sand of sea-facing dunes, trapping fog moisture as a ready source for drinking.

One of the most active carnivores of the Namib, the Brown Hyaena, survives because it is an opportunistic and omnivorous feeder—finding dead seals on the Atlantic shores or dead Gemsbok in the interior. It also feeds voraciously on melons *Citrullus lanatus* and cucumber *Acanthosicyos naundianus*, perhaps more for their water content (up to 90%) than for any nutritional value.

One of the many remarkable research findings in the arid savannas and deserts of southern Africa was that of **water transport** by Burchell's Sandgrouse. South African ornithologist Gordon Maclean found that these desert dwellers often nest up to 60 km from the nearest water source. The **precocial** chicks can run about from the day of hatching, feeding themselves on grass seeds, with their parents not contributing to their feeding. But the chicks are still unable to fly. The male adult flies up to 60 km to the closest water source, soaks his highly absorbent ventral feathers in the pool, collecting up water and flying back to the nest. The water-absorbent feathers are held close to the belly, preventing loss by evaporation during the flight home. Here the young chicks take the still wet feathers in their beaks and strip the water from them.

A common water economy strategy of desert plants is **water storage** in underground bulbs, tubers or aboveground succulent leaves and trunks. **Geophytes** (plants with underground bulbs or rhizomes) are highly sought after by Desert Molerats. They are also excavated by Gemsbok, Porcupine and even small carnivores such as Black-backed Jackal.

Fig. 11.7 The Namib tenebrionid beetle *Onymacris bicolor*, on the dunes at Foz do Cunene. *Photo* Joh Henschel

Water storage is a key property of **pachycauls**, (Fig. 5.19). Pachycauls are especially frequent inland of Lucira, where species of *Commiphora, Cyphostemma, Moringa, Pachypodium* and *Sesamothamnus*, display this growth form. Even more common in the Namib is that of stem and leaf succulence found in many species of *Aloe, Ceraria, Crassula, Euphorbia, Haworthia, Hoodia, Huernia, Sansevieria* and *Stapelia*. The **succulent life form** has evolved independently in many dozens of plant families, but nowhere as abundantly as in the Aizoaceae of the arid zone of southern Africa, where over 35% of the world's succulents are found.

11.2 Adaptations to the Heat of the Desert

A characteristic of desert climates is their clear skies and dry atmosphere, with rapid heating during the day and cooling at night. The surface temperature of Namib desert sands can rise to 75 °C during a summer day, and fall below zero on a winter night. The wide seasonal and diurnal temperature changes are among the many challenges for organisms, which mostly have narrow temperature bands within which to function optimally. Temperature regulation is a critical adaptation in such environments.

A primary physical force in nature is the **cooling power of evaporation**. When water evaporates, the high amount of energy required to break the hydrogen bonds between water molecules is removed from the evaporating surface, resulting in a decrease in surface temperature. Evaporation is triggered by various actions: plants transpire, mammals sweat or pant, birds cool by **gular fluttering**—the rapid oscillation of the floor of their open mouth. Each process is costly in terms of water economy, so many other adaptations have evolved to achieve water efficiency while keeping temperature under control.

Temperature regulation (**thermoregulation**) in animals falls into two types. **Ectotherms** tolerate relatively wide temperature fluctuations and therefore sacrifice the ability to function optimally at all times. Ectotherms include insects, reptiles and amphibians. Their heat is derived from outside sources. Most ectotherms use the sun to warm them to their optimum operational temperatures and regulate energy expenditure. They cannot move about at will as in flying birds or highly mobile mammals. They may either become too hot or too cold, and therefore have to exploit a range of adaptations as described below.

Endotherms can generate heat within their bodies and thus maintain and control a fairly constant body temperature at all times. They can therefore function optimally when and where they choose. Endotherms include mammals and birds. Mammals regulate their temperature between 34 and 38 °C, and birds between 39 and 42 °C. Under cold ambient conditions, their temperature is raised by burning energy until a peak metabolic rate is reached. If the ambient temperature continues to fall, the animal might experience **hypothermia** and possibly die. In hot conditions, cooling is achieved by sweating and evaporation, but this has limits above which the body temperature rises, enters **hyperthemia** (42 °C in mammals, 45 °C in birds) and dies. Despite these constraints, mammals and birds have the freedom to choose where to live and be active, making them the most thermally efficient creatures on Earth (Lovegrove, 2019).

Animals have two options to deal with deviations from the optimal body temperature—**conform** (ectotherms) or **regulate** (endotherms). Temperature regulation in endotherms can be compared with that of an air-conditioner. A balanced body temperature is achieved through homeostasis. **Homeostasis** is the mechanism by which body temperature is regulated to the desired state (the **set point)** while the external temperature changes. Homeostasis provides a good model of the concept of **negative feedbacks**. The feedback loop includes four steps—the **variable** (body temperature), the **receptor** (nerves, acting like a thermometer), the **integrator** (the brain, acting like the thermostat of an air-conditioner), and the **effector** (brown fat, muscles—acting like the air-conditioner). If the external temperature increases above the set point, the receptor sends a message to the brain which in turn triggers an action—such as sweating, shivering and non-shivering heat production in brown fat—that reduces or increases the body temperature. This feedback system regulates the body temperature to its optimum level.

Some animals, especially those regularly exposed to cold nights and winter temperatures, can temporarily revert from endotherm to heterotherm characteristics—undergoing rapid changes in their body temperatures. This can take the form of short-term **torpor** or longer-term **hibernation**. There are few examples in Angola, but one—the White-backed Mousebird from the Cunene valley—goes into torpor at night, dropping body temperature from 40 to 26 °C, with a corresponding temporary reduction in metabolic rate and oxygen consumption. The small arid zone insectivore, Bushveld Sengi (also known as an elephant shrew because of its long nose) is also known to undergo torpor on cold nights.

Plants are more tolerant of body temperature changes, and some succulents can survive temperatures ranging from −16 to 68 °C. Plants have many adaptations to reduce heat stress, such as those cited with regard to water economy. Succulents such as *Euphorbia virosa* have thorny and deeply fluted stems, scattering radiation and thus shading half of the stem, thus minimising heat loading.

A second physical factor that strongly influences adaptations to heat is called the **boundary layer**. The boundary layer above the soil (or around a leaf) is a thin zone of calm air that influences how quickly energy (or gas) is exchanged between the soil or leaf surface and surrounding air. The gradient of heat above a sand or rock surface is very steep in the first few millimetres, as is the temperature decrease with depth below the sand surface, factors that are exploited by some desert insects and reptiles.The beetle *Stenicara phalangium* has the longest legs in any beetle and walks about as if on stilts, keeping its body above the temperature boundary layer of the desert gravel surface of their habitat. The sand dwelling Shovel-snouted Lizard has a remarkable behavioural adaptation to hot sand. It alternates lifting back and front legs, and even using its tail as a lever, to do a dance on the sand, keeping its body above the hottest levels of the boundary layer. The Shovel-snouted Lizard also has the ability to dive under the sand and burrow down to cooler levels, thus escaping the surface heat.

While endotherms have the ability to regulate their temperatures, this comes at a cost, especially for small mammals and birds, with large surface area to volume ratios. While surface coverings (fur and feathers) can moderate heat accumulation or loss, many **behavioural adaptations** make it easier to maintain a stable body temperature. Most small desert mammals, such as gerbils, are nocturnal and during the day, retreat to burrows, thus escaping the midday heat of summer or the cold of winter nights. Ground squirrels use their bushy tails as umbrellas to provide shade as they forage and feed. Springbok and Steenbok seek out shady trees, Gemsbok climb to the crest of dunes to catch cooling breezes. When grazing, many mammals such as Springbok face towards the sun to reduce the profile of their body exposed to the sun's rays, thus reducing heat absorption while simultaneously lowering their visibility to predators.

Sweating alone might dehydrate desert mammals in the absence of other heat-reducing systems. In response, a remarkable vascular anatomy and response physiology has evolved in Gemsbok and several other desert antelope to help survive the dehydrating heat of summer. The system known as **selective brain cooling**. To reduce water use, Gemsbok can stop their normal sweating behaviour on very hot days, gradually storing heat, with the body temperature rising to as much as 43 °C. If blood at this temperature were to be fed directly to the brain, death would result. A choice must be made between water-expensive sweating or temperature-threatening increases in body temperature. The delicate balance between sweating and allowing body temperature to rise is governed by the **hypothalamus**, which monitors both temperature and blood concentration, triggering responses to over-heating and dehydration.

Gemsbok and other antelope can allow their body temperatures to rise, while their brain temperature is kept within functional limits through the **carotid rete system** (Fig. 11.8). Arterial blood first passes through a network of intermingled venous and arterial blood vessels (the carotid rete) which act as a '**blood-flow radiator**', before reaching the brain. The radiator mechanism is simple and efficient. When a Gemsbok becomes hot and dehydrated, it starts to pant. The temperature of the venous blood in its nasal sinuses drops due to evaporative cooling. Hot, freshly oxygenated arterial blood from the lungs passes through the rete and is cooled by transferring heat to the colder venous blood. Through this 'counter-current heat exchange' blood passing through the carotid artery falls to 40 °C before it reaches the brain. The difference between 40 and 43 °C is the difference between life and death. It also is the difference between extreme dehydration and survival through water use efficiency, accounting for Gemsbok (and Springbok and other several other ungulates) prospering in Iona National Park even without access to open water sources.

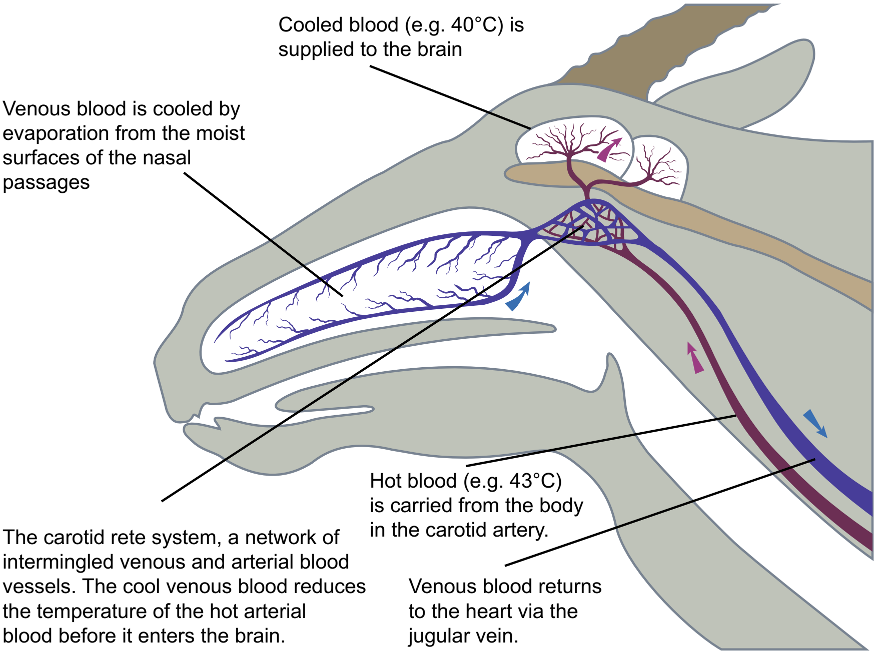

Fig. 11.8 The carotid rete system found in Gemsbok and other desert antelope. Warm arterial blood (at 43 °C) is cooled (to 40 °C) as it passes through the carotid rete before entering the brain. The animal's body temperature can rise to levels that would be lethal if the blood passing to the brain was not cooled. Redrawn from Lovegrove (1993) *The Living Deserts of Southern Africa*. Fernwood Press

11.3 Competition for Food in a Low Productivity Environment

Competition occurs when two or more individuals use a common but limited resource. The theoretical aspects of the concept are discussed in Sect. 9.5. Here a few examples from the Namib illustrate forms of competition (or avoidance of competition) relating to food, water and nutrient resources.

For an organism to survive, grow and reproduce, food is essential. In highly productive biomes, such as the tropical rain forests of Cabinda, both climatic conditions (temperature and humidity) and environmental resources (water and nutrients) are adequate for high levels of primary production. In the desert, infrequent, discrete, and unpredictable rainfall events and desiccating heat reduce primary production to very low levels. Securing a reliable food supply is an ever-present challenge. In the Namib and Kalahari, three hyaena species—Brown, Spotted and Aardwolf—coexist. Each species has defined food preferences, and interspecific competition is seldom observed. Intraspecific competion occurs along the margins of clan territories, where scents and other marking techniques are used to delimit territories. Territories are defended by borderline disputes which normally avoid fatal confrontations, while robustly protecting access to food resources. This is an example of interference competition—where some clans are winners, others are losers.

Some competitive and facilitation processes are extremely complex. An example of interactions at different scales of interspecific competition between plant species, for water and nutrients, influenced by intraspecific competition between colonies of herbivorous termites, is described in Box 11.1. Competition for water is also a driving force, influenced by fire and herbivory, in the structuring and maintenance of savannas, as described in Chaps. 7 and 8.

More frequently observed is **habitat partitioning**, where similar food resources are divided between potentially competing species occupying distinct micro-habitats. In the Namib, four species of *Onymacris* beetles share wind-blown plant detritus and dead insect food resources, but within different habitats in dune bases, slip faces, floodplains and riverbeds -all within a small area. Habitat partitioning between the *Onymacris* species is strongly defined when resources are limited, but breaks down after unusually good rains, when resources are abundant and interspecific competition relaxes.

In all resource limited environments, the **storage** of food is a common strategy. In the Namib, both termites and ants are active food harvesters, building stores to see them through the drought periods. Research by Alan Marsh on two species of harvester ants in the Namib (Marsh, 1987) suggested that ants do not practice interference competition when resources are adequate (and stores are being built up) nor when resources are low (when it is more important to collect scarce food than to expend energy on fighting neighbours). Competitive interactions are not always the most efficient use of a species' energy.

Competition is not the only strategy for acquiring and storing food. Cooperative social behaviour ensures survival under extreme conditions, as in the case of Damara Molerats, which collect vast stores of bulbs and corms, sometimes numbering thousands of propagules. These stores are essential for burrowing molerats for whom burrowing is a difficult and expensive mechanism of food harvesting. This is especially important when food must be readily available for lactating females after giving birth to and raising pups. Furthermore, the window for successful harvesting of corms is focused on wet periods, when the energy cost of burrowing through damp sand is three times less than through dry sand. As described below, social behaviour is a key to desert survival.

11.4 Defence Mechanisms: Camouflage, Deceit, Mimicry, Spines, Poisons and Social Behaviour

Adaptations that have evolved in reponse to water scarcity, temperature extremes and limited energy budgets are pointless if an organism cannot avoid being eaten by predators before transferring its genes to the next generation. An impressive arsenal of weaponry has been evolved in animals and plants to reduce the prospect of being preyed upon. Adaptations include avoidance strategies such as camouflage, deceit and mimicry; structures such as spines, thorns and horns; and chemical defences such as poisons to avoid or reduce predation.

Plants cannot run away from herbivores. They have to invest in defences, such as thorns, spines or poisons. A common evolutionary response to herbivory has been the development, in many families of plants, of **chemical** defences using **secondary compounds** such as alkaloids, glycosides and other toxic chemicals. These have no physiological role in plant growth other than as a defence mechanism. The objective (or more correctly, selective pressure) is to reduce herbivory, either because water is limiting (as in deserts and arid savannas) or because nutrients are limiting (as in mesic savannas). In general, plants in low fertility, dystrophic savannas use chemical defences, whereas plants in high fertility, eutrophic savannas use structural defences. Plants in low-nutrient soils are inherently slow-growing (from three- to five-fold slower in seedling growth rates) with low rates of photosynthesis and nutrient uptake. They cannot afford to lose leaf tissue through herbivory—thus they invest in chemical defences. In rich soils, growth is fast and rates of nutrient uptake and photosynthesis are high—they can afford to lose some photosynthetic tissue, rather than investing in chemical or other defence mechanisms. Thorns and spines slow down herbivory, but do not prevent it.

Secondary compounds include chemicals such as alkaloids, rotenoids, glycosides, tannins and phenols. Most are toxic, some such as strychnine can be fatal. The most common secondary compounds in plants are **tannins**. These interfere with digestive processes, reducing protein absorption. Glycosides cause heart failure. They occur in many species of geophytes, which are especially common in arid savannas and on the desert margins. Tannins seldom kill herbivores, but in mesic savannas, the high levels of tannins in the most abundant tree and shrub species accounts for them being avoided by browsers, and thus for the low biomass of mammalian herbivores in the biome. One mesic savanna geoxyle 'subterranean tree'—*Dichopetalum cymosum*—deserves mention. Known as 'gifblaar' (poison leaf) in South Africa, the leaves accumulate fluoroacetate, a cardiac poison. A mouthful is sufficient to kill an ox. Most indigenous herbivores avoid this and other geoxyles during their most toxic growth phase.

Unlike most mammals, insects have a high tolerance of secondary compounds. Some, such as the larvae of the African Plain Tiger butterfly *Danaus chrysippus* (Figs. 11.9 and 11.10) specialise in eating the highly poisonous milkweeds of the Asclepiadaceae family. Both caterpillars and adult butterflies accumulate the cardiac glycosides contained in the milkweeds, which makes them unattractive to birds and other predators. They are thus one of the commonest butterfly species in southern Africa. So successful in fact, that a non-poisonous butterfly—Common Diadem *Hypolimnus missipus*—has evolved an almost identical appearance, and they thus avoid predation while not having to expend resources on the production of secondary compounds. This form of mimicry (known as **Batesian mimicry**) is common in many insects. Another form of mimicry—**Mullerian mimicry**—is where two or more harmful species mimic one another's colouration and warning signals, thus spreading the odds of being preyed upon. Yet another use of colour is **aposematism**, where bold colours warn potential predators to stay away from poisonous prey species. Bright red, yellow and black patterns in some bees, wasps, snakes and toads are common examples.

Camouflage and **cryptic colouration** are also very common predation-avoidance strategies in insects and in many vertebrate species. These strategies are especially common in arid environments, where colouration patterns have evolved in insects, birds, frogs, lizards, snakes and even plants that allow them to hide in plain sight. In the Namib, Peringuey's Adder will lie in the sand, hardly visible, the tip of its tail wriggling to attract an unsuspecting lizard to within striking distance. Here both camouflage and deceit work in tandem.

A perfect form of **deceit** is that of the Pearl-spotted Owl, common in both arid and moist savannas. False eye patterns on the back of its head no doubt confuse predators

Fig. 11.9 A classic example of Batesian mimicry is that of the highly poisonous southern African Plain Tiger (Fig. 11.9) which is mimicked by the female Common Diadem (Fig. 11.10)

Fig. 11.10 The Common Diadem is non-poisonous, but persuades predators that it too, like the African Plain Tiger, is unpalatable. *Photo* Christopher Willis

into believing that they are being observed. **Colouration** also varies within species, and in harmony with the habitat. Leopards in arid environments such as Iona National Park are pale, while those in Bicuar National Park are richly coloured (Figs. 11.11 and 11.12).

A characteristic of arid savannas, evolved in tandem with the antelope fauna of Africa, is the **spinescent habit** of many trees and shrubs of these nutrient-rich ecosystems (Chap. 15).

Spines are not restricted to trees and shrubs. Protective **armour** is found in many animals such as pangolins, tortoises, porcupines and hedgehogs. Porcupines, because of the rich layer of fat below their skin, is a delicacy for some predators such as lion, leopard and hyaena. This is despite the needle-sharp cover of long spines, which inflict dangerous wounds on the predator. However, given the wide distribution and

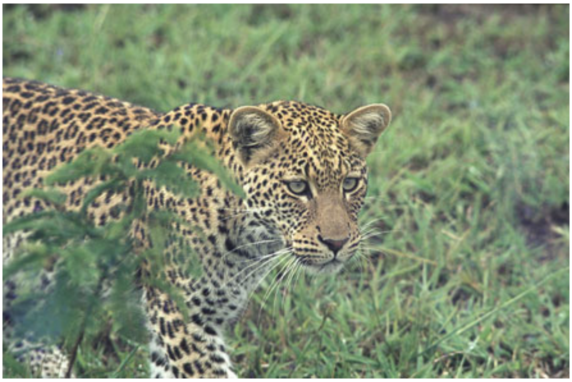

Fig. 11.11 A richly coloured leopard in the miombo of Bicuar

Fig. 11.12 A pale desert form of Iona National Park. The colouration is suited to camouflage in dark, mesic (Bicuar) and dry, light (Iona) vegetation types

resilience of porcupines across southern Africa, the defence mechanism is clearly effective in the vast majority of cases.

A major theme in ecology is the role of **social behaviour**, both as a defence mechanism and in optimising reproductive output. Here we will examine the former. In a desert, a solitary existence has serious limitations. **Cooperative behaviour** can serve many of life's demands. Teamwork allows division of labour in finding, transporting, storing and defending food resources. Some insects, including bees, termites and ants, have sophisticated social organisation systems. These are called **eusocial** species—a classic example being termites—where a queen is solely responsible for reproductive success, other females being sexually repressed. Worker termites collect food, feed offspring and build nests, while heavily armed soldiers are responsible for defence. There are very few vertebrate eusocial species. One of the rare exceptions is that of the previously mentioned Damara Molerat, where highly complex social structures have been found, with queens, workers and soldiers. A lactating solitary molerat female would soon starve in its underground midden if it did not have the support of worker females.

Brown Hyaena live in cooperative clans, with some members searching for carrion within a very large home range, walking up to 50 km a night in scavenging exercises, bringing food back to the den to be shared among the clan, even by the cubs of competing males. Here the distinction needs to be made between **home range**—the area which an animal occupies throughout the annual cycle of activities—and **territory**—the more limited area within the home range that is defended for mate selection and breeding purposes. As a clan, Brown Hyaenas can defend themselves against lion or leopard attacks. Alone, the individual hyaena would have little chance of surviving an attack by a larger predator. Such behaviour requires large clans to cooperate in searching for food in arid, resource-sparse environments. In the Kalahari, for example, Spotted Hyaenas have home ranges of 380–1770 km^2, with 4–14 members per clan. In resource-rich Serengeti, clans occupy much smaller home ranges of 30–60 km^2, and the abundance of food can sustain clans of up to 80 members.

Cooperative behaviour is no less strategic in bird populations. Doves and sandgrouse have the habit of approaching water points as a large flock, swirling in to land together, reducing the chance of raptors capturing a lone individual. Sentries within the flock can keep a lookout for raptors while the other members have more time to drink. More complex sociality has evolved in the Meerkat (Suricate), a delightfully entertaining member of the mongoose family once common on the open gravel plains of Iona (Fig. 11.13). Each colony of Meerkat occupies a home range of about 6 km radius, with three or four warrens within the area, moving from one warren to the next in search of insects and scorpions. A lookout sentry keeps watch for predators such as jackals, snakes and raptors, while other members of the clan forage in the cool of morning and late afternoon. Sentries use distinct alarm calls for different levels of threat. While adults are out foraging, young females play babysitter. Such cooperative behaviour, with multiple individual responsibilities, requires a minimum number of members to sustain the community. If group size falls to too few members, the clan will die out, as has happened to many clans in Iona.

Fig. 11.13 An alert Meerkat family at their burrow in the gravel plains of Iona. Social cohesion of individuals providing sentry, baby-sitting and hunting services ensures the survival of isolated populations

Behavioural, together with morphological and physiological adaptions, form a suite of defences against desert extremes through **tolerance** or **avoidance**. While many desert organisms can tolerate high levels of heat and aridity, they survive these extremes through various avoidance mechanisms. Some are simple—short-term **retreat** such as moving into shade, or burrowing underground. Long-term responses to stress include **escape** such as the **nomadism** of many bird species. Plants cannot move from place to place, but escape extended dry periods in the form of dormant seeds or as underground bulbs. This is particularly the case in annual species, which are very short lived, sometimes requiring only a few weeks following a rainfall event of more than 10 mm to grow, flower and set seed (Henschel et al., 2005). The mass spring flower displays in the southern Namib and especially in Namaqualand, South Africa, are world famous for their beauty.

11.5 Reproduction and Survival in Desert Environments

The success of reproduction of animals and plants is the most important, risky and expensive investment in an organism's life. In stable, predictable and productive environments such as tropical rain forests, emphasis might be given by plants to investing in complex co-evolved relationships with pollinators and other organisms to ensure successful fertilization in highly competitive, species-rich ecosystems. In deserts the challenges, as we have seen, are more physical—heat and aridity, unpredictability of rainfall timing and quantity.

Timing is key. For some groups of animals, the timing of reproduction, to ensure that births occur when resources are at their most accessible, is controlled by photoperiod (day length). **Photoperiod** is monitored by the eye, sending signals via the optic nerve to the pineal gland in the brain which triggers the release of the hormone **melatonin**. Melatonin influences the activity and growth of the sexual organs—the testes and ova. Daylength thus regulates breeding cycles.

Secondary time-givers include rainfall events and the quality of food. Rainfall at any time of the year can trigger breeding activity in the Sociable Weaver of the Kalahari, which can have as many as four broods during infrequent episodes of high rainfall. Large mammals, with long gestation periods, are less likely to be able to respond to unpredictable rainfall events and thus they rely on photoperiod. Besides triggering reproductive activity in mammals, photoperiod also signals dormancy and migration and, in plants, flowering and germination. In some habitats, breeding seasons are more limited, with large numbers of Impala or Wildebeest calves being dropped within a few weeks, thus reducing predation pressure by essentially ‘flooding the market’. Other species, such as Springbok, spread their calving over longer periods, ensuring that at least some are born during a time of sufficient forage. However, timing is but one of many factors influencing the success of the reproductive act and the patterns of reproductive optimisation for different habitats, functional suites or taxonomic groups. These various life history patterns have been classified in many ways, the most widely used being that of *r*- and *K*-selection strategies, as discussed in Sect. 9.4.

Box 11.1 The Enigmatic Fairy Circles of the Namib Desert

It is appropriate to conclude Part lll of this book on ecological concepts and processes with an account of an ecological phenomenon that has challenged scientific explanation for many decades—the ‘**fairy circles’** of the Namib Desert. The fairy circles, nowhere more abundant than in Angola, have several attributes that deserve attention:

- The circles stimulate interest because of their regular pattern over a latitudinal distance of more than 1800 km of arid, hostile environments.
- They have challenged ecologists to draw on a wide range of ecological concepts—at organismic, population, community and biome levels—to help explain the phenomenon.
- They have also demonstrated the scientific method in practice—of proposing hypotheses, collecting detailed data with which to test ideas, accepting or rejecting alternative explanations, and finally seeking a convincing understanding of complex natural phenomena.

The fairy circles are found as a narrow belt within the arid grasslands that lie along the eastern margin of the hyper-desert and below the foothills of the continental escarpment (Fig. 11.14). Isolated pockets of fairy circles are found from the Richtersveld of South Africa to Carunjamba in Angola, within a narrow zone of 80–150 mm mean annual rainfall. From the air, as shown in satellite images, the fairy circles look like polka-dot spots across the landscape, with each patch having an average of six neighbours in a regular hexagonal pattern. On the ground, the bare patches average about 5 m in diameter, but range from 2 to 55 m diameter, with from 5 to 50 patches per ha (Figs. 11.15, 11.16 and 11.17).

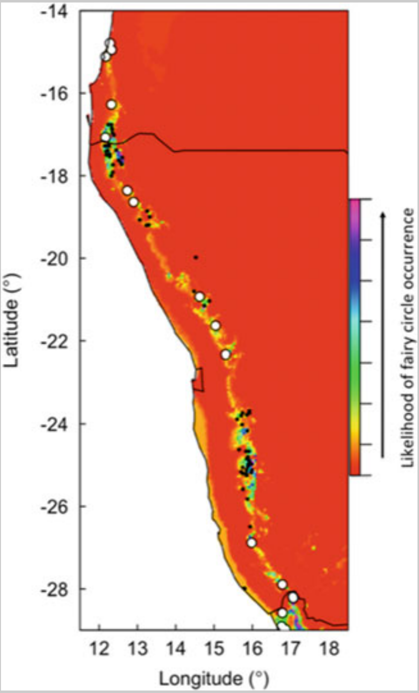

Fig. 11.14 Observed distribution of fairy circles (black and white dots) and modelled predicted locations. From Cramer and Barger (2013) *PLoS ONE*, 8, e70876

Fig. 11.15 Google Earth (Landsat/Copernicus) Satellite image of Iona National Park. The northern limits of the Cunene and Curoca Sand Seas are clearly defined, as is the sand spit of Baía dos Tigres. This image covers 60 km west to east and is centered at 16°49′20″S; 12°51′14″ E

Fig. 11.16 Stable transverse dunes in central Iona (Vale dos Rinos) pock-marked by hundreds of ‘fairy circles’. The image covers 1 km west to east. This Google Earth (Landsat/Copernicus) image is centered at 17°00′55″ S; 12°17′55 E

Fig. 11.17 Fairy Circles' on the arid grasslands of Iona National Park. Left: Two opposing dune systems, older longitudinal and younger latitudinal, on the intermontane basin of Vale dos Rinos. Serra Ongamule in background

Within a grassland **matrix** of short (20 cm) desert grasses (*Stipagrostis uniplumis* and *S. hirtigluma*) the bare **circular patches** are fringed by taller (50 cm) grasses (*Stipagrostis geissii, S. ciliata*) which form a distinct, narrow **perennial belt**. The bare patches are slightly deflated by desert winds, maintaining a shallow basin profile with a raised margin due to accumulation of sand against the perennial belt. The circles increase in diameter and decrease in density from south to north across their 1800 km latitudinal range. The circles are dynamic, appearing and disappearing over decades to centuries. A unique feature of the pattern of these regular bare patches in the arid grasslands of deep sands is that the phenomenon is known only from the Namib Desert and from an isolated area in Western Australia; nowhere else on the planet (Fig. 11.18).

Fig. 11.18 Bare patches of typical 'Fairy Circles', Iona National Park, Namibe province

Naturalists are fascinated by patterns in nature, especially non-random or **over-dispersed** (evenly spaced/ non-random) patterns. For the past half century researchers have speculated on the origin of the fairy circles. Many popular myths explaining the origin of the circles were told to visitors to Iona National Park during colonial days These anecdotal accounts related that the bare circles were sites where zebras rolled on the ground to free themselves of ticks, or that they were caused by a shower of meteorites, or that growth-inhibiting radioactive compounds killed off seedlings, or that the circles mark the sites of fossil termitaria (Huntley, 2017). Such innocent speculations have been succeeded by a surge of sophisticated research over the past two decades, leading to a heated debate conducted in leading journals of science. Several hypotheses have stimulated the discussion and deserve consideration:

- The bare patches result from the activity of **sand termites** (Juergens, 2013, Juergens et al., 2015);
- Competition between grass species for water result in patterns of **self-organisation** (Cramer & Barger, 2013; Getzin et al., 2015).
- Latex and other exudates from species of *Euphorbia* release **hydrophobic/allelopathic** chemicals which suppress or prevent grass germination and growth on the sites where dead *Euphorbia* plants decompose.
- The above hypotheses are not mutually exclusive (Pringle & Tarnita, 2017; Tarnita et al., 2017).

Sand Termite Hypothesis

Since the 1980s Norbert Juergens of the University of Hamburg has conducted studies across the full length of the fairy circle belt. He has assembled detailed and long-term data (Juergens, 2013; Juergens et al., 2020) as evidence that two species of herbivorous **sand termites** *Psammotermes allocerus* and *Microhodotermes* sp.nov. are the driving force of what he describes as fairy circle ecosystems. Juergens et al., (2020) found that the more widespread *Psammotermes* is responsible for the smaller, more densely patterned fairy circles that occur from southern Namibia to northeast Iona National Park, while *Microhodotermes* creates larger, less dense fairy circles from Iona northwards to Carunjamba. The process proposed by Juergens, specifically for *Psammotermes*, is as follows.

After an infrequent rain event, the termites remove short-lived annual grasses from an initial patch within the grassland matrix, creating a grass-free gap which allows more effective water penetration through the large pores of the sandy soil. The absence of grasses results in reduced evapotranspiration from the developing bare patch. Furthermore, the concave surface of the gap concentrates moisture from fog precipitation or during rare rainfall events. The moist sand, at a depth below 30 cm is supplemented by later rains, and builds a ’cistern’—a reservoir sufficient to maintain the termite population in their underground galleries and also the tall perennial grasses of the margin of the bare patch. The termites maintain the bare patch, removing potential competition for resources from grass invasion. This activity ensures the maintenance of the ’water trap’ created by the fairy circle. The perennial grass belt demarcating the perimeter of the fairy circle provides a food store for the termites during droughts, when the grasses of the wider matrix might be removed by herbivores, decomposition or wind erosion. In Iona National Park, the termite activity, demonstrated by the sheetings (plastering) of grass stalks of the fringing *Stipagrostis geissii* perimeter, and small dumps of sand at the termite colony entrances, are common sights, lending support to the termite hypothesis.

The result of this classic example of **ecological engineering** is a mini-oasis that persists through droughts and attracts many species of invertebrates, plus vertebrates such as sand lizards, geckos, aardvarks, gerbils, golden moles, goshawks, Bat-eared Foxes and Black-backed Jackals. Juergens (2013) documents a biodiversity two orders of magnitude greater in the patches than that of the short-grass matrix. Juergens (2013) describes a functional micro-ecosystem, with its own hydrology, microclimate, microorganisms and plant and animal diversity centred on the fairy rings. It is a perennial ecosystem in an ephemeral desert. The finding by Juergens et al. (2020), that two similar but distinctive fairy circle ecosystems in the Namib result from the activities of two termite families (Rhinotermitidae and Hodotermitidae), provides both a fascinating example of parapatric convergent evolution and strong support for the termite-driven origin of the phenomenon.

Self-organisation Hypothesis

A second hypothesis was tested by researchers from the universities of Cape Town and Colorado. Cramer and Barger (2013) proposed that fairy circles are emergent, **self-organising vegetation patterns** resulting from belowground resource competition and facilitation between grasses. While recognising the possible subsidiary roles of termites and ants, they found that local-scale availability of total nitrogen, soil moisture and rainfall resources are inversely correlated with the size and density of fairy circles. They describe the formation of bare circles as the result of initial gaps forming within individual clonal grasses, such as *Stipagrostis ciliata*, with facilitative feedback from larger, deep-rooted plants with access to deeper water resources and runoff. They cite theoretical models in support of their predictions, based on competition for water between grass clumps and neighbouring fairy circles, as the causal mechanism for the bare patches and their **over-dispersed** (evenly spaced/non-random) distribution pattern. Once a gap is established, it results in the formation of a water and nutrient reservoir, supporting the growth of larger grass species on the periphery, as described by Juergens (2013). They conclude that lower soil carbon and nitrogen and moisture field capacities of fairy circle soils compared with matrix soils are emergent properties of the circles, rather than causal factors. The maintenance of the bare circles might be facilitated by wind blowing grass propagules off the barren circles, with both termites and ants possibly contributing to grass mortality in the circles. From Cramer & Barger's field studies, they propose that competition between grasses for water and nutrients, and positive facilitation feedbacks, not termite herbivory, are the drivers of fairy circle formation and maintenance.

Further studies were undertaken by Stephan Getzin from the Helmholtz Centre in Leipzig, Germany, based remote sensing, spatial pattern analysis and vegetation modeling (Getzin et al., 2015). Using mathematical models and field observations they describe regular, large-scale self-organising vegetation patterns driven by small-scale ecological feedbacks that result from competition for scarce soil water, supporting Cramer & Barger's hypothesis.

Euphorbia Chemical Release Hypothesis

In another detailed study, combining chemical, phytochemical, historical records and GIS spatial patterning evidence, Marion Meyer and colleagues from Pretoria University (Meyer et al., 2020) propose that **hydrophobicity** (water-repellency) of latex compounds from the decomposition of *Euphorbia* species (*E. damarana, E. gummifera* and possibly *E. gregaria*) causes the sand in the circles to repel any water falling on the site of dead euphorbias. The circles are thus much drier than the surrounding matrix of grassland. Seeds that do germinate in the circles do not survive for very long. Further, the hydrophobic properties of the affected fairy circles might concentrate water at their periphery, supporting robust growth of grasses in the perennial belt. The study also reported phytotoxic, allelopathic and antibacterial activity resulting from the chemicals released by the *Euphorbia* plants. What the study did not explain was the presence of fairy circles in sites where dense populations of *Euphorbia* species are absent or rare in typical fairy circle habitats, such as the sandy plains of the Vale dos Rinos, Iona National Park. However, the absence of euphorbia communities under the present climatic conditions does not preclude the possibility that the distribution of euphorbias might have expanded and contracted with changes in the patterns of rainfall during the Pleistocene and Holocene. Today's euphorbia distribution might be the consequence of shifts in rainfall patterns, with sites previously occupied being reflected in current fairy circles, maintained by hydrophobicity 'scars' in the sands, as ecological fingerprints of the past. Not surprisingly, in the ongoing debate over the origins of fairy circles, Getzin et al. (2021) present a series of arguments contesting the hydrophobicity theory.

Integrative Systems Hypothesis

Following active debate on the termite and self-organising hypotheses, Robert Pringle and Corina Tarnita of Princeton University, USA (Pringle & Tarnita, 2017; Tarnita et al., 2017), have found that the competing proposals are valid; that intraspecific competition between territorial animals (sand termites) and scale-dependent feedbacks through facilitation and competition for resources (desert plants) can result in regular patterns in nature such as the fairy circles. Furthermore, they found multi-scale patterning in the Namib grasslands that they suggest can only be explained by integrating both mechanisms (termite foraging and plant competition), thus providing a unifying hypothesis that accounts both for pattern and for emergent properties such as ecosystem resilience to drought events.

Studies on the origin of the fairy circles provides insights into the development of ecological knowledge, beyond the scope of this book, but very instructive to the student. Detailed field biological studies, ecological modelling, and the matching of theory to observations, followed by criticisms and rebuttals, provide perspectives on what at first sight appears as a simple pattern of bare patches in homogeneous grassland. The enigmatic fairy circles of the Namib provide an elegant model of the scientific method in action and of the role of curiosity-driven, rather than what might be regarded as more socially relevant, science.

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Part IV
Ecological Features of Angolan Biomes and Ecoregions

Context: Ways of Viewing the World: Green, Brown or Black

The famous Prussian scientist, philosopher and explorer Alexander von Humboldt (1769–1859) was the first researcher with extensive field experience on which to base ideas about the patterns of vegetation distribution in relation to environmental factors across the globe. As an explorer, he traversed more than 9000 km on foot, canoe and mule across much of Venezuela, Ecuador, Peru and Brazil between 1799 and 1804. As a philosopher, he was an outspoken critic of colonialism and slavery. As a scientist, his focus on climate as the key determinant of ecosystem form and function has influenced biogeographical and ecological thinking for two centuries. His views on the convergence of vegetation physiognomy and physiology with climate (Humboldt & Bonpland 1805) were advanced by the elegantly detailed research of Schimper (1903) whose work remains a classic precursor to modern biome thinking. For inspiration, the serious student should read Humboldt's biography (Wulf 2016).

The Humboldtian climate=vegetation relationship was embedded in twentieth-century ecological theory by British (Tansley 1935) and American (Clements 1936) ecologists in concepts of plant succession. They proposed that gradual changes to the environment are facilitated by successive phases in the colonisation and development of plant communities, ultimately leading to a **climax** community, where climate determines form and function. In the tropics and most of the temperate world, the climax community would be a tree-dominated forest. In cold high latitudes, low grassy or dwarf shrub communities would be the climatically determined climax of the succession process. According to Clements's mono-climax succession theory, climate controls the process and end result by its influence on the availability of energy and moisture for plant growth. Soils are secondary determinants of vegetation structure through modifying moisture and nutrient availability.

The climate = vegetation model is still widely used, but is being energetically challenged (Bond 2005, 2019) by broader evidence and novel concepts invoking disturbance as a key determinant of vegetation form and function. This changing view of the world was triggered sixty years ago by a provocative paper by Hairston, Smith and Slobodkin (1960), often referred to as the HSS hypothesis. These authors posed

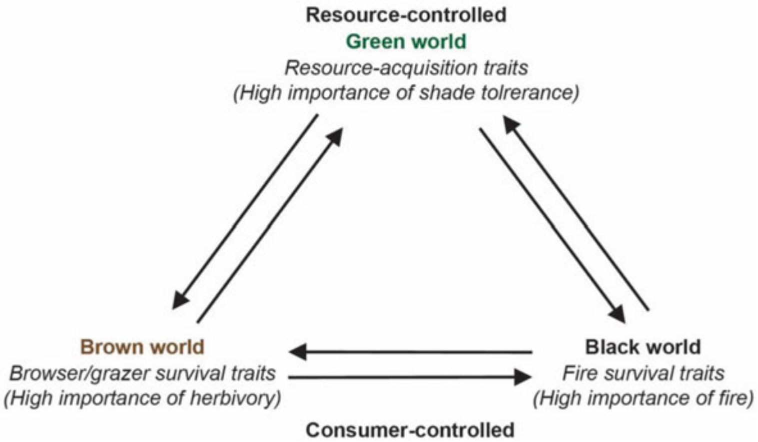

Fig. 1 Multicoloured view of the world. Angola has examples of all three hypothetical worlds—as extensive mosaics of fire-controlled mesic savannas (black world), herbivore-controlled arid savannas (brown world) and resource-controlled rain forests (green world). After Bond (2005) *Journal of Vegetation Science*, 16, 261–266.

the question: “Why is the world green, why is it not brown?” They suggested that if the abundance of herbivores was not controlled by predators, pests and pathogens, the world would be brown, not green—meaning that the climate-limited biomass and composition of plants would be considerably reduced by herbivory.

Critics of HSS argued that the hypothesis is an oversimplification: predation is not the only process controlling the levels of herbivory. Due to their high lignin and cellulose content, most plants are indigestible to herbivores. Furthermore, most plants lack the nitrogen levels essential for protein production in herbivores. Herbivores, even in the absence of predators, would never remove enough vegetation to turn the world from lush green to dusty brown. In fact, research has shown that on average, herbivores remove less than a few per cent of the net primary production of terrestrial ecosystems. The ability of herbivores to shape biomes is limited to a few special cases. The world is therefore green, not brown.

Bond (2005) expanded the debate by pointing to the fundamental role of fire over much of the globe. He recognised three worlds (Fig. 1):

- A green world in which vegetation is determined by climate.
- A brown world where vegetation is shaped by herbivores.
- A black world in which fire regulates the proportional cover of trees and grasses across landscapes.

All three ‘worlds’ can exist in a given landscape, dependent on conditions, resources and disturbance. Each has evolved distinct functional traits in response to the drivers of climate, herbivory and fire. We will examine these characteristics in the accounts of the biomes of Angola which follow. These traits include, respectively, shade tolerance in forests, grazing/browsing tolerance in arid savannas and fire tolerance in mesic savannas. In Angola, the green world is that of the rain forest biome of Cabinda and the Escarpment; the brown world includes the arid savanna and desert of the southwest and the black world the mesic savannas and woodlands of the planalto. The biota of each world have evolved adaptive traits to survive, grow and reproduce within the constraints of their environment. Against this model of diversity of resources and disturbance regimes, the biomes and ecosystems of Angola will be described.

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Chapter 12
The Guineo-Congolian Rain Forest Biome

Key Concepts and Questions: This Chapter Explains

- *What constitutes a rain forest.*
- *Why some perceptions of age, diversity, stability and intactness of rain forests have been misleading.*
- *What changes have occurred since the evolution of African rain forests that extended from the coasts of the Atlantic to the Indian Ocean.*
- *Why Africa is the 'odd man out' in terms of rain forest tree diversity.*
- *What vertebrate species characterise the Guineo-Congolian Rain Forests and how they separate their resource demands.*

Context: Global and Continental Perspectives on Tropical Rain Forests

Tropical Rain Forests (TRF) represent the global peak of biological diversity. The tropical rain forest biome has more species and ecoregions than any other on Earth. Covering only 14% of the Earth's land area, this biome supports at least 50% of the world's known plant and animal species, with many more still awaiting discovery (Dinerstein et al., 2017). The current area of African rain forests is ca. 2.3 million km^2. The largest block of forest, covering 1.8 million km^2, lies in the Congo Basin (Fig. 12.1), with a similar vast area (2.5 million km^2) of Forest/Savanna mosaics surrounding the closed forest block. The Congo Basin contains the second largest continuous expanse of tropical rain forest on the planet, after the slightly larger block of the Amazon Basin.

Definition

The classic definition of **tropical rain forest** is the brief diagnosis of Schimper (1903): "Evergreen, hygrophilous in character, at least 30 m high, but usually much taller, rich in thick-stemmed lianas and in woody as well as herbaceous epiphytes." To this, one might add: "Woody species dominate all but the sparse undergrowth, and the richness of species of trees per ha exceeds that of any other biome. Trees are tall, straight-stemmed and unbranched for the first 20–30 m, often reaching 60 m as

B. J. Huntley, *Ecology of Angola*,
https://doi.org/10.1007/978-3-031-18923-4_12

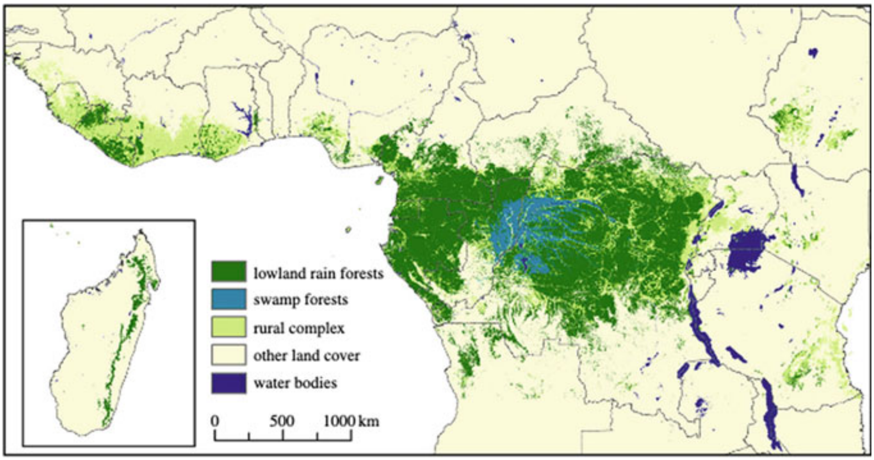

Fig. 12.1 Spatial distribution of African Rain Forests. From Mayaux et al. (2013) *Philosophical Transactions of the Royal Society B* 368: 1625. Creative Commons Attribution License 3.0

emergents from a closed canopy at 30–50 m" (Richards, 1952). Both these definitions are appropriate for the rain forests of northern Angola.

Whitmore (1998), in his authoritative and comprehensive volume on tropical rain forests, distinguishes between **evergreen ever-wet** (perhumid) forests, where over 100 mm rainfall is received during every month of the year, and **semi-evergreen seasonally dry** (monsoon) forests where regular annual periods of water stress are experienced. In addition to these two **dryland forest** (terra firme) types, extensive areas of **swamp forests** occupy one third of the Congo basin, and the narrow margins of some gallery forests of the Congo tributaries in northern Angola.

All three forest types are tall, closed canopy forests, found on all three tropical continents. Convergent evolution has produced similar responses to environmental conditions, with very similar life forms and physiognomy, despite very few floristic or faunistic links below family level. In Africa, tropical lowland evergreen ever-wet rain forest is found in Cameroon, Equatorial Guinea and Gabon. Most of Africa's rain forests belong to the seasonally dry closed forest formations, which experience at least two months with little or no rain, but high humidity levels continue through much of the dry periods.

The exceptional diversity and productivity of these forests results from the coincidence of abundant, regular and reliable rainfall and high levels of solar radiation. The biological wealth of rain forests has, for centuries, attracted romantic descriptions and perceptions of the diversity, stability and pristine condition of the biome. However, the biological richness of the Tropical Rain Forest is not shared equally across the tropics. The age and stability of rain forests vary widely, and recent paleoecological studies demonstrate that the impact of human communities on TRF dynamics has been far greater, and over a much longer period, than previously thought—especially in Africa.

Comparative Diversity

The concepts of diversity and endemism are fundamental to understanding ecosystem structure and dynamics, as discussed in detail in Sect. 9.2. In terms of botanical diversity, the global inventory of vascular plants now stands at 384,000 species (Raven et al., 2020).

- The **Afrotropical Region** (Africa south of the Sahara, including Madagascar but excluding temperate South Africa), with an area of 22.6 million km^2, is home to 30,000 plant species.
- The **Neotropical Region** (South and Central America), extending over 19.2 million km^2, has 118,000 documented species.
- Southeast Asia and Australasia (the **Indo-Pacific Region**), with an area of 5.7 million km^2, is home to approximately 50,000 indigenous species of vascular plants.

The African Tropical Rain Forest, in terms of plant species richness, is therefore almost four times poorer than the Neotropics, a region of similar area. These disparities led the pioneer of modern tropical rain forest ecology, British botanist Paul Richards (1908–1995), to describe Africa as ‘the odd man out’ because of its low tree diversity compared with the rain forests of the Neotropics and the Indo-Pacific (Richards, 1973).

Recent surveys support Richards’ description. A global count of tropical forest **tree species** has estimated a total of between 40,000 and 53,000 species, with between 19,000 and 25,000 species in both the Neotropics and Indo-Pacific, but only 4500–6000 in tropical Africa (Slik et al., 2015). Here the contrast between the tropics and the northern temperate floras is worth noting. The tree diversity of the TRF is eightfold greater than that of the combined numbers for the boreal, temperate and conifer forest biomes of the **Palearctic Region** of Eurasia, which covers an area twice that of the TRF biome. Temperate Europe has only 124 species of trees—less than the average number of tree species per hectare in most tropical rain forest ecosystems.

In terms of lizards and snakes, the low species diversity of the Afrotropics is similar to that of flowering plants, but mammals, especially primates, are more species rich in Africa than elsewhere. Despite the relative species paucity of the African TRF compared with the two other TRF regions, it is nevertheless extremely rich in species when compared with other African biomes and ecoregions, with the exception of the two extreme global botanical hotspots—the Cape Fynbos and Succulent Karoo Biomes.

Stable or Unstable?

A popular perception is that the African rain forest is an ancient biome that has remained unchanged for millions of years. However, palaeoecological studies have shown that the African TRF experienced severe aridification during the cold/dry periods of the Pleistocene. Over its long history, the African TRF has existed both as a continuous band of closed forest, extending from the west to east coasts of the continent during warm/wet periods, and as fragmented blocks during cool/dry

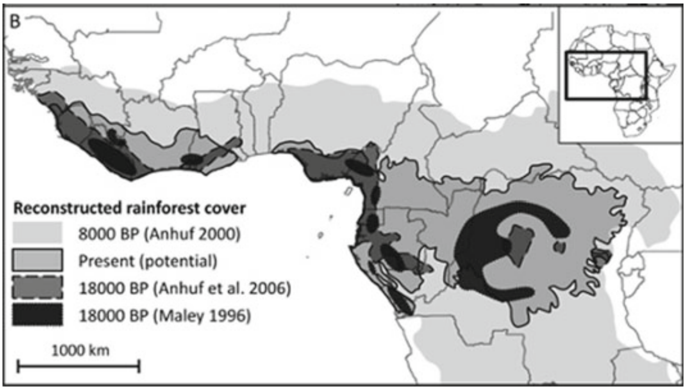

Fig. 12.2 Hypothetical range shifts in the Late Pleistocene indicating main refugia (black). From Hardy et al. (2013) *Comptes Rendus Geoscience* 345: 284–296

periods which experienced accentuated seasonality. This could account for the relative species paucity of the Guineo-Congolian forests compared with those of the Neotropics and Indo-Pacific forests, that did not suffer from such acute arid episodes. Nevertheless, centres of high species richness and endemism are found today in widely separated areas of the African rain forest. Numerous explanations have been presented to explain current patterns. These have been reviewed by Moritz et al. (2000), Weber et al. (2001), Hardy et al. (2013), Maley et al. (2018) and Couveur et al. (2020) and are summarised here.

- **Allopatric** speciation (where populations of the same species become geographically isolated) took place in isolated fragments, thus increasing species richness and endemism within the environment of surviving forests (increasing alpha diversity of each patch, and thus increasing beta diversity across the region). The forests served as important centres of diversification (evolutionary cradles) and which resemble islands in a sea of expanding savanna (**Pleistocene refugia** hypothesis, Fig. 12.2).
- An alternative explanation for the centres of richness and endemism is that they represent static sites where species accumulated due to low extinction rates and moderate speciation rates, accumulating both old (**palaeo-**) and new (**neoendemics**). These species survived as relict populations (**evolutionary museum** hypothesis) during cool/arid episodes (Fjeldså & Lovett, 1997; Huntley et al., 2019).
- In areas of high environmental diversity such as escarpments, gradient (**parapatric**) speciation dominated (even in the absence of geographic isolation) where ecological and behavioural factors facilitated speciation (Smith et al., 1997).

Today, Africa’s TRF is distributed as three main areas: the largest in Central Africa, with fragmented patches in West and East Africa. The West and Central

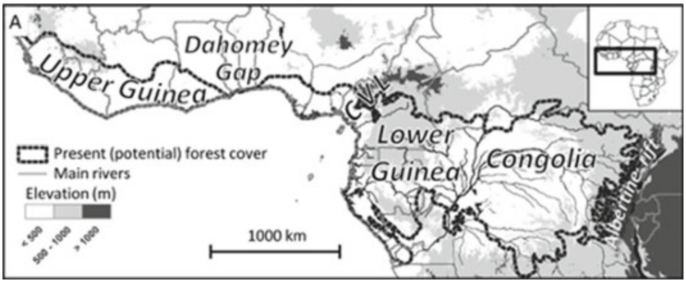

Fig. 12.3 Guineo-Congolian forest subdivisions and topography. From Hardy et al. (2013) *Comptes Rendus Geoscience* 345: 284–296

blocks, home to ca. 8000 plant species of which ca. 80% are endemic, are defined as the **Guineo-Congolian** Regional Centre of Endemism by White (1979, 1983). It includes three sub-centres: Upper Guinea, Lower Guinea, and Congolia, each with distinctive endemic floras (Fig. 12.3). Both Upper and Lower Guinea are notable for high endemism. Lower Guinea (in which the Maiombe forests of Cabinda fall), is recognised for its high species richness, with Gabon alone having over 4700 and possibly even more than 6000 plant species.

The Upper Guinea TRF of West Africa is separated from the other two Guineo-Congolian sub-centres by an arid corridor known as the **Dahomey Gap**, extending northwards from the Gulf of Guinea coast through Benin and Togo. The gap has existed intermittently as an open savanna belt for many millions of years, closing during several warm/wet periods. It is important to recognise that the entire African TRF has been subject to repeated and extensive climatic changes and tectonic events throughout its history. Pulses of forest expansion and contraction continue to the present, with the Dahomey Gap having been open during the past 3000 years. During the periods of forest contraction, centres of forest diversity and endemism survived within refugia.

Pristine Status or Transformed?

The long-held perception that much of the African TRF remains intact, in its original primal structure and floristic composition, free of human impacts, has been challenged by research in many West and Central African countries. Evidence from palaeoecological, archeological and plant phylogenetic and demographic studies, and the analysis of charcoal deposits, has demonstrated a long history of forest transformation through agricultural activities (Maley et al., 2018). It is thus not only climatic oscillations that account for the dynamics of African rain forests. The Guineo-Congolian forests have been occupied by humans for millennia, as hunter gatherers and, in the past 10,000 years (the Holocene), as agriculturists. The impact of these early farmers and iron-smelters was locally concentrated, but the sites of former villages are dispersed over a wide region. Disturbed forests eventually returned to the original physical structure, even if the species composition was dominated for many hundreds of years by pioneer species such as members of the Fabaceae and Combretaceae. Fast-growing, sun-tolerant pioneer species of genera such as *Cynometra, Erythrophleum, Gilbertiodendron* and *Julbernardia* form monospecific populations that persist for many centuries, marking the position of former human settlements (Hart, 2001). The controlled use of fire by *Homo sapiens*, dating from 150,000 years ago, has become an increasingly important factor in ecosystem dynamics, not only in savannas, but also in changing the patterns of rain forest distribution in Africa.

During modern times, particularly over the past century, the rain forests of Angola have suffered from successive waves of disturbance, first by the introduction of commercial coffee *Coffea canephora* farming during the colonial era, then by commercial timber extraction, and more recently by **deforestation** for growing bananas, manioc and other cash crops. Hunting for **bushmeat** has also resulted in a skewed faunal composition of certain mammal, bird and reptile species. As a consequence, many Angolan forests have lost their typical faunistic and physiognomic structure. The concept of **empty forests** (Redford, 1992) applies increasingly to Angolan forests, where a wide diversity of animal species are trapped or shot for local markets. Tall, multi-strata forests have been transformed into short, dense regenerating thickets, dominated by pioneer species and in many areas, by **invasive alien** species such as the fast-growing tree *Inga vera* and the dense scrambling shrub *Chromolaena odorata.*

As we will see, tropical rain forests are highly diverse, vibrantly dynamic and with much yet to be discovered.

Angola's Guineo-Congolian Rain Forests (Ecoregions 1, 2, 3)

Key Concepts and Questions: This Chapter Explains

- *What characterises the five different groups of Guineo-Congolian rain forests of Angola.*
- *How topography interacts with oceanic and atmospheric processes to produce areas of high rainfall suitable for the growth of rain forest trees.*
- *How the rich floristic composition of Angola's rain forests is influenced by access to light and position within the ground, understorey and canopy strata.*
- *What processes create the small scale patterning and dynamics of forest structure and composition.*
- *How a rich diversity of animals and plants use the multiple strata of the rain forest.*

12.1 Definitition and Distribution

In Angola, the largest block of tropical **evergreen** rain forest—the **pluviisilva** of Gossweiler and Mendonça (1939)—is found in the highest and wettest west-facing slopes of the Alto Maiombe, Cabinda. For most of Angola, the rain forests have been reduced by deforestation to small blocks of **semi-evergreen** and **semi-deciduous** forests on west-facing hills and escarpments, strongly influenced by orographic

Fig. 12.4 The canopy of Guineo-Congolian rain forest in the Alto Maiombe National Park, Cabinda. *Note* the straight trunk of a forest emergent at left, and the broken canopy in the foreground

clouds, and seldom more than 200 km from the coast. Ranging in altitude from sites at 150 m on the coastal hills of Cabinda, rain forests are found at up to 1200 m. The distribution of Ecoregions 1–3 is indicated in Figs. 2.3, 2.4 and 2.5.

The Guineo-Congolian Rain Forests of Angola fall into five groups:

- First are the Maiombe forests of Cabinda (Ecoregion 1; Figs. 2.1, 12.4). These are surrounded by the sharp transition from rain forests to the tallgrass mesic savannas of the Congo Basin (Ecoregion 2).
- Second are the forests of the mountains and escarpments between the Congo and Cuanza rivers (the Northern Escarpment forests). These include the forests of the Serras da Canda and Mucaba in Zaire, Serra Pingano in Uíge, and the Dembos and Cazengo forests in Cuanza-Norte. These forests belong floristically to Ecoregion 1, and occur within the extensive matrix of the Western Congolian Forest/Savanna Mosaic (Ecoregion 2).
- Third are the forests of the Central Escarpment between the Cuanza and Coporolo rivers and include the moderately-sized Amboim/Gabela and Seles/Cumbira forests in Cuanza-Sul. These forests, also belonging to Ecoregion 1 and fall within a matrix of grasslands, savannas and woodlands—the Angolan Escarpment Savannas, Ecoregion 6).
- Fourth, southwards from the Coporolo to the Cunene rivers, only isolated fragments of moist forest with Guineo-Congolian elements are found along the Southern Escarpment near Chongoroi and at the base of the Serra da Chela. Nearly all of these rain forests have been extensively transformed and fragmented, with

Fig. 12.5 Guineo-Congolian gallery forest penetrating Zambezian *Brachystegia* woodlands in the Southern Congolian Forest/Savanna Mosaic of Lunda-Norte. *Note* the sharp boundary between forest and savanna

few undisturbed forest communities remaining. They fall within Ecoregion 6, and await study.

- Finally, across northern Angola, hygrophilous gallery forests, dominated by Guineo-Congolian species, follow the upper reaches of tributaries of the Congo Basin in Malange and Lunda-Norte, from 600 to 1200 m (Figs. 12.5, 12.6). They lie within the Western and Southern Congolian Forest/Savanna Mosaics (Ecoregions 2 and 3).

Ecoregions 2, 3 and 6 are outlined in Chap. 2. Here we focus on the characteristics and dynamics of Ecoregion 1: the Guineo-Congolian Rain Forests of Angola.

12.2 Climate and Microclimate: The Roles of Fog (*Cacimbo*) and of Shade

The climate of Angolan rain forests is typical of the drier margins of seasonal or monsoon tropical rain forests around the globe. Local topography has a strong influence on rainfall received. In general, rainfall increases with altitude along the Angolan Escarpment, but decreases from north to south. The air temperature is hot but not excessively so (Table 12.1). It is never cold, with mean monthly temperatures typically above 18 °C. The forests of Cabinda experience two dry seasons, as illustrated in Fig. 5.9. There are short rainless periods during the hot months of December to February and an almost rainless cool period during June to August. Further south, the forests of Pingano, Gabela and Cumbira have a single but longer dry period, from June to the middle of September. The impacts of the dry periods differ between the

Fig. 12.6 *Mitragyna* swamp forest on the margin of the Luele River, Lunda-Norte

hot/dry and the cool/dry seasons and from one year to the next, and are not effectively reflected in data averaged over many years as used in climatic data and diagrams. It is important to note that in ecology, **extremes** are more important than **averages**. The number of deciduous species increases southwards in proportion to the intensity of the dry seasons.

The main factor determining the difference between the hot/dry and the cool/dry periods is the exposure to direct solar radiation and hence evapotranspiration. During mid-summer, the frequent cloudless periods between thunderstorms cause high evaporation rates off soil and plant surfaces. Air humidity decreases markedly. During the cool/dry winter, the rates of evaporation are reduced because of the almost continuous presence of the low stratiform cloud cover, the misty '***cacimbo***' which characterises the coastal belt and escarpment of Angola. Despite the absence of rain, the

Table 12.1 Climatic data for stations within the Guineo-Congolian rain forest

Station	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest month (°C)	Coldest month (°C)
Belize	Cabinda	250	1612	25.2	27.1	21.5
Buco Zau	Cabinda	350	1346	24.6	27.0	20.3
Uíge	Uíge	824	1586	22.4	23.7	19.6
Golungo Alto	Cuanza-Norte	639	1488	24.3	26.6	21.8
Gabela	Cuanza-Sul	1099	833	19.8	21.6	15.9

Mean annual precipitation (MAP), Mean annual temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

air humidity is higher in the 'dry' months of July and August than it is during mid-summer. The frequency of misty, stratus clouds, especially at more elevated areas of the escarpment, results in the term 'cloud forests' being applied to them by Barbosa (1970). These clouds do not precipitate rain, but the evergreen trees can capture the high humidity of the mists within their canopies. This process was especially important during the arid periods of the Pleistocene as it allowed forests to persist along the Escarpment, acting as refugia for lowland forest species. The oceanic and atmospheric interactions of the Benguela Current and the South Atlantic Anticyclone in the formation of the stratus clouds, especially during winter, are described in Sect. 16.3.

One of the important emergent properties of forests is the microclimate that they collectively create below their closed canopies. Above the canopy, the microclimate does not differ much from an open field or large clearing. This is quite different from the microclimate of the forest floor. Outside the canopy, wind speeds are higher, air temperatures are warmer and relative humidity is lower. Below the canopy, not only is the air still, cool and humid, but the light climate is significantly different from that of the forest canopy or that of an open forest gap. The key difference is the amount of photosynthetically active radiation (PAR) that reaches the understorey plants. Only 2% of the PAR received at the top of the forest canopy reaches the ground, and most of this is received as '**sunflecks**'—the narrow beams of sunlight that shine down through small gaps in the canopy. The larger the gap, the greater the impact of sunflecks on the understorey plants and soil. Sunflects can account for 70–80% of the solar energy reaching the forest floor. Large gaps can result in the drying and warming of the soil, promoting the germination of the seeds of pioneer species. These pioneers are light demanders—needing full sunlight and high levels of PAR for germination, seedling establishment and the rapid growth of saplings, that soon out-compete any climax species that might germinate in the gaps. Some climax species such as *Entandrophragma utile* of the Maiombe can germinate in shade, but within a year need full light, so that the faster growing pioneers most often keep them shaded, ultimately killing them. Much of the surviving rain forest of Angola is today made up of pioneer species, the result of over a century of disturbances from forestry and agricultural practices. These regenerating forests are termed **secondary forest**.

12.3 Physiognomic Structure

From a distance, the tropical rain forest offers a dark, sombre, almost monotonous appearance. But rain forest is only visually monotonous. It is exceptionally diverse, both in its multi-layered vertical structure (**stratification**) and in the rich diversity of tree species that constitute its floristic composition. The stratification of rain forests determines both community structure and microclimatic conditions such as light, temperature and humidity. The vertical layers (**strata**) commence at the ground, comprising a sparse undergrowth of shrubs, herbaceous plants, a few grasses, and sapling trees of canopy species. Litter is sparse. Mature forest is easily penetrated on foot. It is only on the margins, along rivers, or where tree-fall or human disturbance has broken the canopy and allowed light to penetrate, that the undergrowth becomes dense and impenetrable. Here **lianes** are abundant, thick, and spiralling in great loops advancing to the forest crown. **Epiphytes** include shrubby or herbaceous forms, including orchids, ferns, abundant mosses, and many **strangler** figs that send roots down to the ground. Some large epiphytes, such as the ferns *Asplenium* and *Platycerium*, create humus and rain water traps that provide habitats for frogs and mosquitoes.

Rain forests typically have three tree strata, plus the sapling and ground layers of herbaceous species. The stratification of rain forest is best described by means of profile diagrams, which provide a sample of the forest cross-section (Fig. 12.7). Each successive stratum comprises species that seldom advance above the height of the stratum, forming layered canopies at successive heights above the ground. The progression is not uniform, and is not easily identified without drawing a series of profile diagrams. Above the uppermost canopy, **emergent** trees of great height rise. The crowns of the trees are frequently narrow, although emergent trees may have crowns of up to 40 m in diameter, such as in *Entandrophragma utile* and *Piptadeniastrum africanum*. The plants of each stratum have different microclimatic requirements (light, temperature, moisture) and serve as habitats for animal communities that are adapted to such special environmental conditions, food and shelter availability, and mobility.

The largest trees often have **plank buttresses** (Fig. 12.8), bark is usually thin and smooth, unlike the thick corky fire-resistant bark of mesic savanna trees. Leaves are uniformly large (whether simple or compound), dark green, leathery, with entire margins. Most have acuminate '**drip-tips**'—the extension of the leaf tip into a narrow tongue that facilitates rapid shedding of water (Fig. 12.9). It is suggested that the drip-tips reduce the growth of **epiphylls**—minute gardens of cyanobacteria, green algae, bryophytes, lichens and filmy ferns that grow on the surfaces of the leaves of understorey trees, reducing their photosynthetic efficiency. Flowers are generally small, inconspicuous, and held in the top-most branches of the canopy or in many cases, arising directly from the bark, a feature known as **cauliflory**.

12.4 Forest Canopy Growth Cycles: Gap-Phase Dynamics

Forests are in a continuous state of flux. An understanding of forest dynamics helps explain forest history. Two terms used by forest ecologists can be confusing to students and need explanation from the outset:

- **Primary forest** refers to old, relatively undisturbed forests comprising slow-growing, shade-tolerant species. Primary forests are often referred to as **climax** or **pristine** forest.

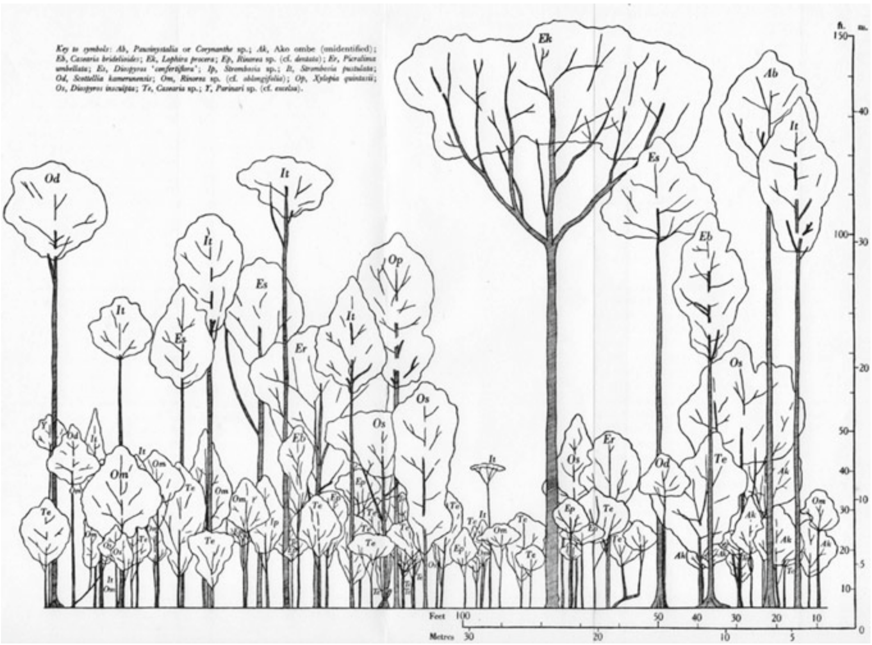

Fig. 12.7 Profile diagram of primary forest in Shasha Forest Reserve, Nigeria. From Richards (1939) *Journal of Ecology*, 27: 1–61

Fig. 12.8 Cultivation of 'robusta' coffee *Coffea canephora* below the rain forest canopy at N'Dalatando, Cuanza-Sul. Note the large buttresses on *Ceiba pentandra* trees, indicated by the person standing at the base of the buttressed tree on the right of photo. These broad buttresses support trees in the shallow soils of rain forests

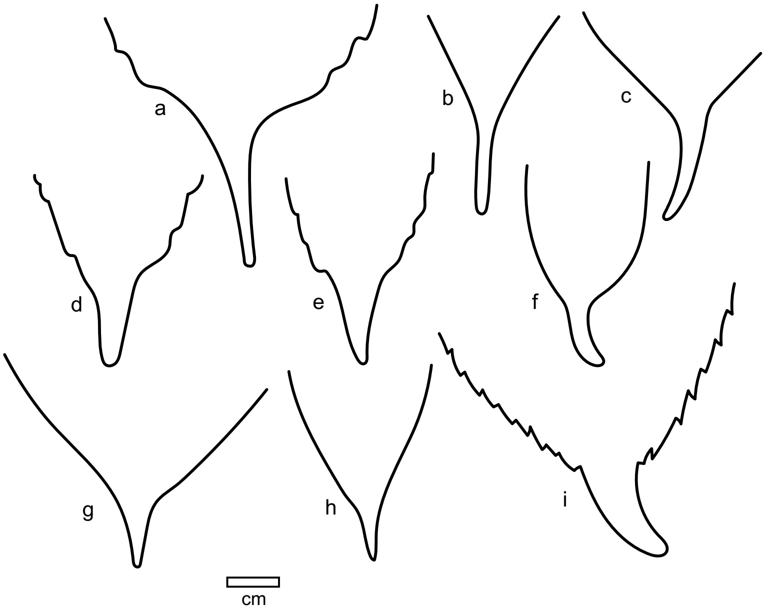

Fig. 12.9 'Drip tips' of rain forest tree leaves, Ngoye Forest Reserve, South Africa. From Huntley (1965) *Journal of South African Botany*, 31: 177–205

- **Secondary forest** refers to relatively young, regenerating forests on sites that have been transformed by storm damage or felling for timber extraction or agriculture. Secondary forest comprises fast growing, shade-intolerant species.

Disturbance of mature primary forest triggers the development of sun-tolerant pioneer species of secondary forest, which might persist for decades, gradually being replaced by shade-tolerant climax species, which might then persist for centuries before human or natural events open the canopy and allow sun-tolerant pioneers once more to enter the community.

The long-term dynamics of Africa's tropical rain forests, at continent-wide spatial scales and in geological time scales, were discussed in the introduction to this chapter. Here we will consider changes to forest structure and composition at temporal scales of a few years to centuries (the life spans of a few generations of climax tree species), and at spatial scales that range from treefall gaps to a few hectares of patch disturbance caused by cyclones, landslides or human activities. These processes constitute the forest canopy growth cycle, also known as forest **gap-phase** dynamics. The disturbance/regeneration process has three stages: the gap-phase, building-phase and the mature-phase of the growth cycle. Together, these result in the mosaic of different ages and composition that characterise rain forest.

Contrasts Between Pioneers and Climax Species' Life Histories

Following disturbance to a forest, the open patch created is colonised by **pioneer** species which typically have wide geographic ranges and ecological amplitudes. Light demanding (**heliophile**) pioneer species have a group of characteristics (traits) that distinguish them from shade-tolerant **climax** species. These features include producing small but abundant seeds with efficient seed dispersal mechanisms that reach long distances from the parent trees. The seeds of pioneers are capable of dormancy and long-term storage as seedbanks in the soil. The seeds, which germinate only in sun-lit forest gaps, produce masses of seedlings with fast growth rates and short lifespans. Pioneer tree species have wide, open crowns, rapidly filling the forest gap. They reach maturity within a few years and soon produce further abundant seeds.

Climax species have essentially the opposite characteristics, although a continuum of intermediates might be found as the process of plant succession advances, often over centuries, from disturbed forest to the composition of climax communities. But secondary forests are easily identified by a suite of **indicator** species, few in number, which form secondary forests of low species diversity. In Cabinda, and across much of the Angolan Escarpment, these include species of *Anthocleista, Ceiba, Macaranga, Maesopsis, Milicia, Musanga, Ricinodendron, Spathodea, Terminalia* and *Trema.*

Shade-demanding (**sciophile**) climax species have animal-dispersed seeds that germinate with seedlings establishing under the canopy of pioneer species. Here they persist as saplings until a small gap is created in the canopy, usually by branch fall or tree death, allowing sun flecks to enter. The saplings of climax species, led by an apical shoot, rise as spears in the shade of the lower strata, emerging into the sun and shading out competition from sun-demanding pioneer species. There is thus a continuous cyclic replacement of sun-dependent pioneer species and shade-tolerant climax species in the process of gap formation, seed germination, sapling growth and canopy occupation. The resulting pattern of the frequent opening and closing of patches, regenerating from pioneer to climax structure, is called a **shifting mosaic steady state**.

The seeds of climax species are usually fleshy and cannot be stored. They are desiccation sensitive and must germinate immediately and are called **recalcitrant** seeds. However, an exception to this general rule are the seeds of the many legume species that dominate some African rain forests. They are called **orthodox** seeds, which survive drying and can form part of the seed store of the forest floor for many years, even decades. They are poor dispersers. In the Congo basin, such as in the Ituri forest, the legume tree *Gilbertiodendron dewevrei* is monodominant over 75% of the area. It produces explosively dehiscent seed pods, most of which do not disperse very far from parent trees. The shade-tolerant juveniles persist under their parent trees, awaiting a break in the canopy that allows them to fill the gap. Extensive **monospecific** communities of *G. dewevrei* are found in the DRC, with smaller communities in Cabinda. These trees have slow growth, low dispersal capacity and low resilience to disturbance. The origin of these extensive monospecific forests of the Ituri are described by British/Gabonese ecologist Lee White (2001) as an enigma, possibly related to human activities as long ago as the Iron Age (2500–1500 BP).

12.5 Floristic Composition

Very few ecological studies have been undertaken in Angolan rain forests, but the early works of Gossweiler and Mendonça (1939), Monteiro (1962, 1965) and Barbosa (1970), as synthesised by White and Werger (1978), are important sources on their floristic composition. In the absence of quantitative information on the Angolan rain forest communities, it is not possible to provide more than indicative floristic lists of species, as recorded for the various forest blocks by Barbosa (1970).

The Guineo-Congolian rain forests of Angola occur as isolated blocks along the mountains and escarpments of western Angola (Ecoregion 1) and as rain forest fragments surrounded by a broad belt of tallgrass Zambezian mesic savannas (Ecoregions 2 & 3) that stretch across northern Angola. These forests represent the southward extension of decreasing forest area and species diversity from Cameroon, through Equatorial Guinea, Gabon and Republic of the Congo to Cabinda, and then to the last outliers of Guineo-Congolian elements such as *Piptadeniastrum africanum* and *Newtonia buchananii* in the ravines below the Chela escarpment. Guineo-Congolian mammals, birds, reptiles and amphibia follow a similar decrease of species richness from north to south.

Here we focus on the floristics of the main forest blocks found in Angolan ecoregions (1) Guineo-Congolian Rain Forests, (2) Western, and (3) Southern Congolian Forest/Savanna Mosaics that form part of the continuum of the Guineo-Congolian forest flora in Angola.

Maiombe Forests: *Cabinda* (*Ecoregion 1: Guineo-Congolian Rain Forest,* Figs. 2.1, 12.4).

In Angola, the flora of the Guineo-Congolian regional centre of endemism reaches its richest expression in the semi-evergreen and semi-deciduous Maiombe forests of Cabinda**.** The **Alto Maiombe** forests lie at between 350 and 800 m on the well-drained soils of hilly sea-facing slopes of the ridge of low mountains running from the northwest in Gabon to the southeast, along the Cabinda border with the Republic of the Congo. The forests cover about 3500 km^2 within Angolan territory. The best examples reach 60 m height, are multi-storeyed and evergreen to semi-evergreen. Rainfall ranges from 1400 to 1700 mm per year, reinforced by the influence of mist during the cooler, drier months.

- The canopy of mature forest, sometimes reaching 60 m, includes *Gilbertiodendron ogoouense, Homalium viridiflorum, Julbernardia seretii, Librevillea klainei, Mammae africana, Pentadesma leptonema, Tetraberlinia bifoliata* and *Xylopia lenombe.* Many of the canopy species are briefly deciduous during the short dry season.
- The mid-stratum, from 20 to 30 m, includes *Anopyxis klaineana, Dialium pachyphyllum, Macaranga gilletii, Monodora angolensis, Piptostigma mayumbense* and *Xylopia staudtii.* Most sub-canopy species are evergreen, but those exposed to direct sunlight by treefall, are briefly deciduous.

- Lianes include *Combretum platypterum, C. racemosum, Gigasiphon gossweileri, Letestudoxa bella, Physedra heterophylla* and *Popowia klainii.*
- In sites that have been disturbed by windfalls or logging, regeneration is led by *Alstonia boonei, Daniellia klainei, Ongokea gore, Pentaclethra macrophylla, Piptadeniastrum africanum, Ricinodendron heudelotii, Symphonia globulifera, Trichilia gilgiana* and *Xylopia hypolampra.*
- The ground strata of disturbed sites often have a dense population of *Afromomum* species.

Similar but less diverse forests (the **Baixo Maiombe**) lie below the Alto Maiombe, at 150–350 m, receiving lower rainfall (1200–1300 mm) and with fewer evergreen trees and a greater prevalence of semi-evergreen and semi-deciduous species.

- The dominants of canopies include *Balanites mayumbensis, Dacryodes buettneri, Dialium dinklageri, Gossweileriodendron balsamiferum, Guibourtia arnoldiana, Irvingia grandiflora, Ongokea gore, Oxystigma oxyphyllum, Monodora myristica* and *Pentacletra eetveldeana.*
- Here species that are not common in the Alto Maiombe appear, including *Bombax reflexum, Canarium schweinfurthii, Newtonia buchananii, Milicia excelsa, Entandrophragma utile* and *Lannea welwitschii.*
- Sun-tolerant pioneers, that grow to 45 m height, and of great economic value include *Milicia excelsa* (moreira), *Piptadeniastrum africanum* (mesinga) and *Terminalia superba* (limba).

Cazengo Forests: *Northern Escarpment* (*Ecoregion 1: Guineo-Congolian Rain Forest; Ecoregion 2: Western Congolian Forest/Savanna Mosaic,* Figs. 2.2, 12.8).

Barbosa (1970) described three sub-types of semi-deciduous forests south of the Congo—the Cazengo, Amboim and Seles forests. Typical of the **Cazengo** subtype are the 'cloud forests' of the mountains and escarpments of the Dembos in Cuanza-Norte, the Cazengo forest near Ndalatando and the Pingano forests near Uíge. These forests are surrounded by the tallgrass savannas of the Western Congolian Forest/Savanna Mosaic. The Serra do Pingano is one of several steep-sided mountains of sedimentary rocks of the West Congo System, stretching 60 km in length and 6 km breadth, from northwest to southeast. These forests are receiving increased research attention to record their biodiversity. They are currently under severe threat from deforestation (Lautenschlager & Neinhuis, 2019).

- The canopy of this subtype of forests is at 30–50 m height; taller trees include *Ceiba pentandra, Celtis gomphophylla, C. zenkeri, Entandrophragma angolense, Gilbertiodendron kisantuense, Khaya anthotheca, Macaranga angolensis, Milicia excelsa, Piptadeniastrum africanum, Pterocarpus soyauxii, P. tinctorius, Ricinodendron heudelotii, Synsepalum cerasiferum, Treculia africana* and *Zanha golungensis.*
- *Ceiba pentandra*, the kapok tree, is one of the few rain forest species found both in Africa and in the Neo-tropics. It is also one of the tallest indigenous trees in Africa, reaching 65 m, with massive buttresses (Fig. 12.8). While impressive by African forest standards, this height is, however, dwarfed by the world record

trees of 107 m and 114 m for *Eucalyptus regnans* and *Sequoia sempervirens* of temperate rain forests of Tasmania and California respectively. Even in equatorial Amazon, trees do not match the heights reached by those of temperate rain forests.

- In disturbed forests, pioneer species in areas of regeneration include *Alchornia cordifolia, Clausena anisata, Croton mubango, Harungana madagascariensis, Milletia versicola, Musanga cecropioides, Spathodea campanulata* and *Trema orientalis.*
- A shrub layer, up to 8 m tall, includes *Carapa procera, Cola welwitschii, Cyathea manniana, Fernadoa superba* and *Olax viridis.*
- Lianes include *Adenia lobata, Dalbergia altissima, Entada gigas, Hippocratea andongensis, Landolphia owarensis, Securidaca welwitschii* and *Urera thonneri.*
- Epiphytes are abundant, including many orchids, the fern *Platycerium elephantotis* and the only African species of Cactaceae *Rhipsalis baccifera.*
- In sites receiving some sunlight, herbs of genera such as *Acanthus, Aframomum, Asystasia* and *Desmodium*, and grasses represented by *Acrosceras, Isachne, Leptaspis, Olyra* and *Oplismenus* occur.

Amboim and Seles Forests: *Central Escarpment* (*Ecoregion 1: Guineo-Congolian Rain Forest; Ecoregion 6: Angolan Escarpment Woodlands;* Figs. 12.10, 12.11).

The **Amboim** subtype, identified by the former name of the town of Gabela, occurs on the Central Escarpment in Cuanza-Sul. The forests lie within the mosaic of grasslands, savannas and woodlands that constitute the Angolan Escarpment Woodlands. Most of these forests have been transformed for agricultural purposes. The species composition of the Amboim subtype is similar but less rich than the Cazengo flora. The southernmost forests, also mostly transformed into coffee plantations in colonial times, and now being cleared for cash crop farming, are the **Seles** forests. These

Fig. 12.10 Cumbira Forest, Cuanza-Sul. Regenerating forest, including species of *Albizia, Celtis* and *Ficus*. *Photo* Francisco Gonçalves

Fig. 12.11 Cumbira Forest, Cuanza-Sul. Invasion of understorey by *Inga vera*. *Photo* Francisco Gonçalves

include the Cumbira forest, lying at 680–1100 m on the western slopes of the Serra Njelo near Uku (formerly Vila Nova do Seles), Figs. 12.10, 12.11. The Cumbira forests are now very much reduced in diversity (Gonçalves & Goyder, 2016).

- Barbosa (1970) listed these forests as including *Antiaris toxicaria, Albizia glabrescens, A. glaberima, A. adianthifolia, Blighia unijugata, Bosqueia angolensis, Celtis gomphophylla, C. mildbraedii, C. zenkeri, Croton mubango, Ficus capensis, F. mucuso, Maesopsis eminii, Monodora angolensis, Piptadeniastrum africanum* and *Ricinodendron heudelotii.*

Gallery Forests: *Malange and Lunda-Norte* (*Ecoregion 3: Southern Congolian Forest/Savanna Mosaic;* Figs. 12.5, 12.6).

Across northern Angola, and including strong representation of the Guineo-Congolian flora and fauna, are the gallery forests of the Congo tributaries that extend southwards to within 100 km of the Congo-Zambezi divide that runs latitudinally through central Angola. In the lower reaches of the Congo tributaries, these dense evergreen gallery forests have closed canopies of up to 30 m height, including a mix of Guineo-Congolian, Zambezian and Afromontane elements.

- These mixed forests include *Chrysophyllum magalismontanum, Prunus africana, Syzygium guineense, Treculia africana, Uapaca guineensis* and *Xylopia aethiopica.* Palms include *Elaeis guineensis, Raphia gossweileri*, and the spiny climbing palm *Eremospatha cuspidata.*

- Swamp forests occur on poorly drained basins of the river valleys, with *Mitragyna stipulosa, Nauclea diderichii, Pandanus candelabrum, Phoenix reclinata, Syzyguim guineense, Spondianthis preussii, Treculia africana* and *Uapaca guineensis.*

12.6 Faunal Composition

The African tropical rain forest is biologically the richest biome on the African continent, exceeded only by the Cape flora in terms of plant species diversity, although it is much richer in all animal groups. Angola's Guineo-Congolian Rain Forests (within ecoregions 1, 2 and 3) belong to the Atlantic Equatorial Coastal Forests ecoregion as described by Burgess et al. (2004), which occupies 189,000 km^2 of five Central African countries. The Atlantic Equatorial Coastal Forest ecoregion has 93 amphibian, 120 reptile, 484 bird, 169 mammal and over 6000 plant species (Burgess et al., 2004). The biodiversity of Angola's rain forests has not been fully documented, but key animal species, which are restricted to or most commonly found in Angola's Rain Forest Biome, are listed in Table 12.2.

12.7 Rain Forest Mammals

Tropical rain forests are fabulously rich in animal life with twice as many species of mammals, birds, amphibians and reptiles as temperate forests. This faunistic wealth is due to the three-dimensional space provided by a tropical rain forest canopy that

Table 12.2 Vertebrate species typical of the Guineo-Congolian rain forests of Angola

- **Amphibians**: Congolese Clawed Frog, Large-spotted Reed Frog, Benito River Reed Frog, Vilhena's Reed Frog, Carqueja's Squeaker, Lameer's Squeaker, Gabon Forest Tree Frog
- **Reptiles**: Western Forest Feylinia, Owen's Chameleon, Variable Bush Viper, Gabon Adder, Forest Night Adder, Jameson's Mamba, Ringed Water Cobra, Emerald Snake, Yellow-Throated Bold-Eyed Tree Snake, Forest Twig Snake
- **Birds**: Black Guineafowl, Afep Pigeon, Grey Parrot, Red-fronted Parrot, Great Blue Turaco, Guinea Turaco, Black Bee-eater, African Pied Hornbill, Black-and-white-casqued Hornbill, Piping Hornbill, Red-rumped Tinkerbird, Yellow-crested Woodpecker, Grey-green Bushshrike, Angola White-throated Greenbul, Red-tailed Loveleaf, Banded Prinia, Forest Chestnut-winged Starling, Dusky-blue Flycatcher, Bannerman's Sunbird
- **Mammals**: African Golden Cat, Ansorge's Cusimanse, African Palm Civet, Bay Duiker, White-bellied Duiker, Black-fronted Duiker, Blue Duiker, Sitatunga, Red River Hog, Water Chevrotain, White-belled (Tree) Pangolin, Red-tailed Monkey, Moustached Monkey, Blue Monkey, Black-footed Crowned Monkey, De Brazza's Monkey, Putty-nosed Monkey, Angola Colobus, Black-crested Mangabey, Northern Talapoin, Southern Talapoin, Demidoff's Dwarf Galago, Thomas's Dwarf Galago, Western Lowland Gorilla, Central Chimpanzee, Golden Potto, Milne-Edwards's Potto, Forest Elephant, Beecroft's Scaly-tailed Squirrel

can reach up to 60 m height. The partitioning of resources provides a rich diversity of living opportunities, across different strata of the canopy, different ecological niches and feeding guilds, and through diurnal, crepuscular and nocturnal activity patterns. The forest trees themselves create microclimates and microhabitats for climbers, epiphytes, parasites, amphibians, reptiles, birds and mammals and a great diversity of invertebrates. Different feeding guilds follow the phenology of flower, pollen, fruit and leaf development, with many complex coevolved adaptations. The perennial humid and hot climate of the tropical evergreen forests provide a food source throughout the year. A seasonal succession of species come into flower and fruit through the year. Animal pollinators partition their services and resource-use across the varied phenological patterns of the different tree species. However, in seasonal semi-evergreen and semi-deciduous forests such as those in Angola, fruiting goes through a bottleneck during the dry season. This places a limit on the total biomass of frugivorous animal species that can be sustained. Some trees produce a mass of fruit during a narrow period, satiating consumers and thus ensuring that at least some seeds escape consumption, germinate and establish. The phenomenon is known as **mast fruiting**.

Forest mammals are mostly frugivores, but feeding **guilds** also include folivores, nectarivores, insectivores and carnivores. Primates, squirrels and antelope typically select different strata of the forest, from the forest floor, understorey, mid-stratum, to canopy feeders. As many as 17 sympatric species of primate and nine squirrel species occur in some of the rain forests of Gabon. The diversity of primates is also unusually high in the small enclave of Cabinda, where 14 species have been recorded, including five sympatric species of nocturnal lorises. These include the frugivorous Potto, three bush babies (the undergrowth frugivorous Thomas's Galago, the canopy insectivorous Demidov's Galago and the plant gum-eater Southern Needle-clawed Galago) and the insectivorous Golden Potto. This coexistence of similar species is possible due to partitioning of food, hunting technique and space. The diversity of life in rain forests is illustrated graphically in Fig. 12.12.

Another diverse group within the rain forests of Africa are the ungulates, of which 29 species are known, compared with 43 species found in the savannas. Whereas savanna ungulates often form large herds, forest ungulates are mostly solitary. However, like other mammal groups, many species occupy the same forest landscape, with up to 15 ungulate species being found in a single Gabon forest type (Hart, 2001). These include seven fruit and seed eaters, seven folivores and one mixed feeder. Ungulate density in mixed forests was found to be twice that found in the monodominant forests.

The largest mammals of the rain forests of Angola include Forest Elephant, Forest Buffalo Central Chimpanzee and Western Lowland Gorilla, the latter possibly surviving in isolated populations in the Maiombe forests of Cabinda ~~now extinct in Angola~~. The Forest Elephant is both genetically and behaviourally distinct from the Savanna Elephant. Given its secretive habits and isolated populations, ecological and behavioural characteristics are far less well-researched than those of the Savanna Elephant. However, studies in Gabon, Central African Republic and Republic of the Congo indicate that the species forms small groups of two to three individuals. They

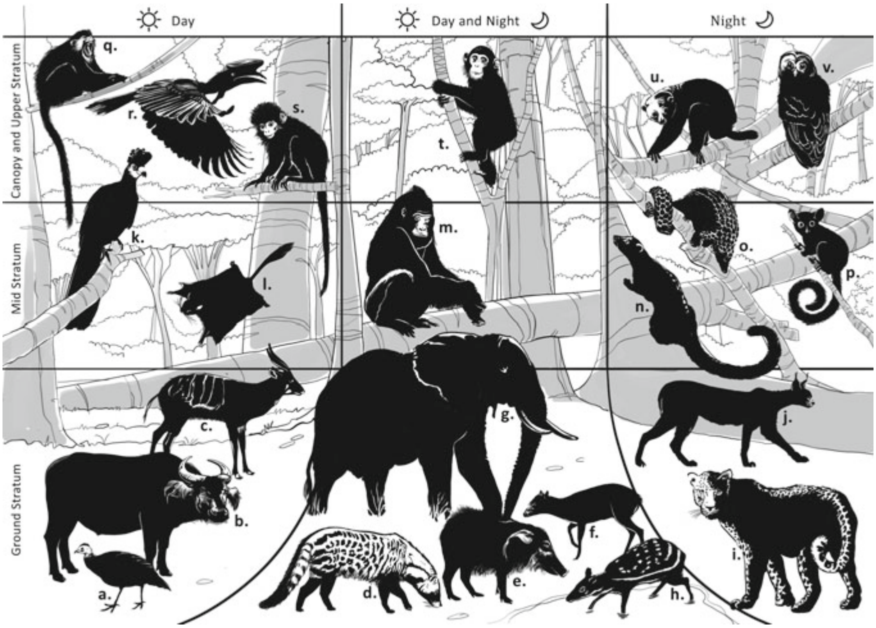

Fig. 12.12 Rain Forest animals occupy different strata of the forest, from the ground layer to the uppermost canopy, and from early morning to night. This partitioning in space and time of mammals in Maiombe Rain Forest, Cabinda has been illustrated by Angolan artists Fernando (Hugo) and Fatima Fernandes, adapted from MacKinnon (1972) The behaviour and ecology of the Orang-Utan (*Pongo pygmaeus*). PhD thesis, University of Oxford.. **Ground Stratum**: **a** Black Guineafowl, **b** Forest Buffalo, **c** Sitatunga, **d** Civet, **e** Red River Hog, **f** Blue Duiker, **g** Forest elephant, **h** Water Chevrotain, **i** Leopard, **j** Golden cat. **Mid Stratum: k** Great Blue Turaco, **l** Beecroft Scaly-scaled Squirrel, **m** Western Lowland Gorilla, **n** African Palm Civet, **o** Tree Pangolin, **p** Demidoff's Dwarf Galago. **Canopy and Upper Stratum: q** Moustached Monkey, **r** Black-casqued Hornbill, **s** Northern Talapoin, **t** Central Chimpanzee, **u** Golden potto, **v** Fishing Owl

do not form batchelor herds, single adult males instead keeping to themselves. These are features that differ markedly from the savanna species. In Gabon, the elephants prefer disturbed forest with a high biomass of tall, pithy herbs of Marantaceae and Zingiberaceae genera (Turkalo & Fay, 2001).

Of the 24 species of carnivore known from African rain forest, only two—Golden Cat and Palm Civet—are found exclusively in forests. Both occur in the rain forests of Angola. Ansorge's Cusimanse, known only from the type specimen and a recent record from Cumbira (Vaz Pinto et al., 2020), is a gregarious forest carnivore that is probably more common in Angola than published records show, as the species constituted 83% of carnivore meat surveyed in a market in the DRC (Ray, 2001).

The most iconic and charismatic of Africa's rain forest mammals are the giant apes—Gorilla and Chimpanzee. Both Western Lowland Gorilla and Central Chimpanzee were once common in the Maiombe forests of Cabinda, but are now extinct or greatly reduced in number. Gorilla still occur in strong populations, totaling over

100,000 individuals, elsewhere in Central Africa, while chimpanzee populations are estimated at between 170,000 and 300,000 across their range. The potential of re-introducing these two species into the Maiombe National Park, once effective management programmes are instituted, holds promise. The availability of long-term studies on gorilla and chimpanzee ecology and behaviour from neighbouring countries such as Gabon and Equatorial Guinea (Tutin & Vedder, 2001, White & Tutin, 2001) can be drawn on to guide the process.

Gorillas are generalist herbivores, but, more specifically, are frugivores rather than folivores. Given their large body size and high energy demands, they occur at low densities. They are nomadic within their home ranges, which in Gabon average 400 km^2—the area needed to maintain a viable population of family groups. Maiombe National Park, at 2074 km^2, would thus offer sufficient area for several populations. The Maiombe habitat has many areas of secondary regenerating forest comprising a dense understorey of Marantaceae and Zingiberaceae, including species of *Haumania* and *Aframomum*, both keystone plants for gorilla and chimpanzee in the dry season when fruits are in low supply. Chimpanzee are more ecologically adaptable than gorilla and their home range of 15–20 km^2 would allow appreciable populations to be developed and conserved in the Maiombe National Park.

The species richness of rain forest is high, but abundance is low, with many rare species occupying distinct niches and feeding guilds. Biomass too is low when compared with savanna species, which often occur in large antelope herds or bird flocks. Yet primate biomass alone may reach 2 tonne/km^2 in the rain forests of Gabon, compared with an average of 12 tonne/km^2 biomass in mammals of African savannas. Biomass of animals (or the carrying capacity of a habitat) is determined by the seasonal availability of food resources. In the seasonal (monsoon) rain forests such as those of Angola, the carrying capacity baseline for community maintenance is set by the food available during the lowest ebb of the dry season. Food resources might decline to 10% of the wet season peak, and the fauna depends on certain **keystone foods**, such as perennially fruiting *Ficus* species. Where these are removed through deforestation for agriculture, dependent frugivores will suffer. The extirpation and extinction of bird species in many Afromontane and Escarpment forest fragments of Angola is probably more the result of reduction of food, nesting sites and shelter resources than due to hunting.

12.8 Interconnections Between Plants and Animals

The close relationships between plants and animals have fascinated biologists since Darwin's pioneer studies. Not all relationships are positive. Ehrlich and Raven (1964) introduced the term coevolution, and the concept of endless 'arms races' between plants and animals. **Coevolution** is the process in which two species undergo reciprocal evolutionary change through natural selection. The '**arms race**' describes the development of increasingly efficient poisons and defensive architecture required to prevent predation. Counter-measures, to detoxify or overcome such defence mechanisms, evolved in insects and vertebrates. More recently it has been suggested that such 'arms race' arguments are less convincing than more general mutual dependencies between animals and plants, where organisms interact to their mutual benefit. A classic example of such **mutualisms** and symbiotic relationships is found in the Congo rain forest tree *Barteria fistulosa.* Stinging ants *Tetraponera aethiops* live in the tree's hollow twigs and branches, and protect the host plant against herbivory. The ant's sting is said to be able to penetrate the hide of Forest Elephant. Ants benefit from starch and sugar produced by the tree's extrafloral nectaries. Such insect-plant mutualisms are common in rain forests.

More than in any other biome, rain forest plants depend on animals as pollinators of flowers and dispersers of seeds. Most rain forest plants are pollinated by insects, while 75% of forest plants in Africa rely on animals for dispersal (White, 2001). The most complex insect-plant symbiotic relationship is that of the pollination of figs by fig wasps, that are host-specific to each of the 600 species of *Ficus.* This relationship developed multiple times over a period of 90 million years, among several unrelated wasp lineages. The wasp's eggs are laid and hatch within the specialised inverted flower inflorescence of the fig. The adult offspring mate inside the flower, where the male dies. The female exits via the mouth of the fruit, collecting pollen as she departs and flies to a young fig flower, where on laying her eggs, she pollinates the styles of the flowers of the young fig. The wasp's eggs hatch within the fig, the next generation mates and the cycle commences once again.

In the shadowy, gloomy interior of the forest, plants use nectar and pollen to attract animals. Strongly scented flowers attract bats, brightly coloured flowers attract sunbirds, and juicy fruit attracts frugivorous birds, primates and the mini-ungulates of the forest floor. Long-tubed flowers of the Rubiaceae require long-tongued moths to reach their nectar and disperse their pollen. The flowers of *Adansonia, Musa* and *Parkia* have very long peduncles, with large flowers hanging free of branches and leaves, and easily accessible to bats. Orchids have highly elaborate and coevolved pollination mechanisms, while some forest floor members of the Araceae have foul-smelling flowers that attract flies and beetles. In no other biome are animal-plant interactions more diverse and complex than in tropical rain forests.

Rain forest fruits vary in dispersal efficiency, from those that offer low qualities and quantities of reward for frugivores, to the specialist species that bear fruit that are high in fats and proteins. These are often brightly coloured, juicy drupes. In a study of fruit use by vertebrates in Gabon, Gautier-Hion and Michaloud (1989) found 39 species of frugivorous vertebrates, including seven large canopy birds, eight small and two large rodents, nine squirrels, seven ruminants and six monkeys. A similar diversity of fruit specialists might be expected in the Maiombe forests of Cabinda. An example of the close interaction between rain forest plants and animals is the ten-year study of gorilla ecology in the Lope Reserve, Gabon, conducted by Tutin & White (1998), which illustrated the role of gorilla in dispersing between 11,000 and 18,000 seeds per season of the dominant tree *Cola lizae.* Gorilla, both as seed dispersers and as disturbance agents of forest structure, create optimal conditions for *C. lizae* seed germination, growth and survival. These researchers also observed the positive influence of cool air temperature on the flowering behaviour of the tree, and postulated the potential vulnerability of this keystone species to climate warming. In a warmer world, the *C. lizae* flowers may not set seed, leading to the extinction of this narrow endemic species. The critical dependencies between threatened primate species, endemic plants, pollination systems, microclimate and global phenomena such as climate warming, illustrate the importance of ecological studies in the tropical rain forests of Africa.

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Chapter 13
The Afromontane Forest and Montane Grassland Biome

Key Concepts and Questions: This Chapter Will Explain

- *What distinguishes Afromontane forests from Guineo-Congolian rain forests.*
- *Why the forests of the Angolan highlands are of global conservation concern.*

Context: Angola's Disappearing 'Islands in the Sky'

> Angola, a neglected Afromontane Centre (due to its small size, isolation, and lack of access due to four decades of armed conflict) is not just a missing piece of the Afromontane puzzle, but a fundamental piece. (Vaz da Silva, 2015)

Globally, mountains contain half of the world's biodiversity hotspots, within less than one fifth of the planet's land area (Fjeldså et al., 2012). Angola's highlands have a special place in Africa's biogeographic history, with fragmented and fragile links to distant parts of the continent. This feature is best illustrated by the biota of the relict forests and grasslands of the country's high peaks and mountains.

These regional connections have an ancient origin. About 30 million years ago, the generally stable African continent was disturbed by a period of volcanism and mountain building, triggered by the uplift (doming) of the Earth's crust under East Africa, forming the Eastern Arc Mountains that stretch from southern Kenya and across Tanzania to northern Malawi. Today these mountain blocks, rising to 2635 m on the Uluguru Mountains, hold some of the most biodiverse ecosystems in Africa. The forests and grasslands of the mountains are host to 96 endemic vertebrates and over 800 endemic plant species (Burgess et al., 2007). They are recognised as one of the 35 global 'hotspots' of biodiversity.

These ecosystems form the Afromontane Archipelago-like Centre of Endemism (White, 1983). The term 'archipelago' refers to their similarity to oceanic islands—small patches of montane forests and grasslands that extend as a broken chain along the escarpments and highlands of Africa, surrounded by a sea of savanna and desert systems. Forests of the Afromontane centre are found in isolated sites from Sierra Leone to Somalia, and from the Sudan to Cape Town. The most distant examples are 7250 km apart, from east to west, and 6300 km from north to south. The most isolated

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of these forests are found on Angola's Mount Moco and Mount Namba and as tiny relicts in the upper ravines of the Serra da Chela. These forests lie some 3000 km distant from the Eastern Arc Mountains, 1900 km from their closest sister forests in the Cape Peninsula and 2000 km from similar forests on Mount Cameroon and the Albertine Rift.

The age and fragmentation of the Afromontane forest and grassland patches have been the focus of much discussion. The grasslands have frequently been referred to as of recent anthropogenic origin. However, paleoecological and biogeographic evidence (Meadows & Linder, 1993) indicates that while the grasslands and forests have been subjected to intense human pressures in recent times, they are nevertheless ancient ecosystems rather than human-derived artefacts. This does not deny the severe pressure currently placed on the remaining forest patches. What makes the Angolan forests of such great scientific and conservation importance is that they collectively cover less than 10 km^2. They are minute and fragile specks compared with the 3300 km^2 of the Eastern Arc forests. When measured against the 1,700,000 km^2 of the rain forests of the Congo Basin, the significance of these tiny relicts becomes even more evident. Today, after surviving 2.6 million years of climatic oscillations through the Pleistocene, the relict Afromontane forests of Angola are shrinking 'sky islands' in an ocean of fire. The biota of the forests represent fading biological fingerprints that offer clues to the past.

Despite the great scientific importance of Angola's relict Afromontane forests and the ancient grasslands that surround them, their biodiversity and ecology has only recently attracted serious interest. Although not as floristically rich as the Afromontane forests of eastern and southern Africa, the Angolan examples of this biome have distinct floristic and faunistic elements. In common with other Afromontane forests, these forests of the highlands of Angola share more tree species with other montane forest fragments across Africa than they share with the Angolan Escarpment forests or any other habitat in Angola. The Escarpment forests of Cuanza-Norte and Uíge, for example, have stronger links with the rich and extensive Guineo-Congolian flora of the Congo Basin than with the montane flora of the 'Archipelago-like Regional Centre of Endemism' as defined by White (1983).

Angola's Afromontane Forests and Grasslands (Ecoregions 4 and 5)

13.1 Afromontane Forests (Ecoregion 4)

The Afromontane archipelago-like centre of endemism is represented by two ecoregions in Angola: Afromontane Forests (Ecoregion 4) and Montane Grasslands (Ecoregion 5). Ecoregion 4, the smallest and most threatened ecoregion in Angola, has been reduced to isolated forest patches in the ravines of the highest mountains of the country's Marginal Mountain Chain (Fig. 4.10). It is probable that the combined cover of the closed Afromontane forest patches of Angola does not exceed 1000 ha (10 km^2). The forest patches at 1800–2450 m on Mount Moco total 85 ha and Mount

Namba ca. 580 ha (Mills et al., 2013). These are the only patches of Afromontane closed forest in Angola of more than a few hectares in area. They are located in deep valleys, often as narrow galleries along watercourses, and where some protection against fire is provided by steep slopes or bare rock outcrops. In earlier times, before the recent increase in human-mediated fires and increased cattle densities, a broad ecotone of fire-retarding shrubs protected the margins of forest patches.

The distribution of the high mountains and peaks of Angola and related topographic features are illustrated in Fig. 18.1. The map demarcates, in broad outline, the Angolan Escarpment Zone (see Chap. 18), plus the distribution of inselbergs that rise sharply above the surrounding landscapes. The distribution of Ecoregions 4 and 5 is indicated in Figs. 3.8 and 3.9.

The mountains include Basement Complex and West Congo granites, quartzites, schists and gneisses, with shallow regosols or deeper ferralsols, depending on gradient. Surrounding the forests and extending over a significant area, are the ancient grasslands of the high planalto of Cuanza-Sul, Benguela, Huambo, Bié and Huíla (Ecoregion 5).

Mean annual rainfall is between 800 and 1600 mm (Table 13.1). The forests are subject to several desiccating months during winter (June to August). Although they are described as 'cloud forests' by Barbosa (1970), they probably receive less exposure to low cloud and fog than sites on the Escarpment, judging by the relative scarcity of epiphytes and by the sclerophyll characteristics of many tree and shrub species.

Afromontane forests have been characterised by White (1978) as those which include a suite of tree species that occur in the majority of the forests that constitute this centre of endemism. The floristic composition has few tree species in common with the lowland Guineo-Congolian rain forests, but some Afromontane species mix with Guineo-Congolian elements in the forests of the Angolan Escarpment.

The forests have continuous but irregular crowns, little stratification, and are usually less than 20 m height. Typical Afromontane species are represented in Angola by *Apodytes dimidiata, Cassipourea gummiflua, Ficalhoa laurifolia, Ilex mitis, Maesa lanceolata, Maytenus acuminata, Myrica conifera, Nuxia congesta, Podocarpus latifolius (P. milanjianus), Prunus africana, Rhamnus pruinoides* and *Strombosia scheffleri*. Other tree species found in these forest patches and in the deep ravines of high mountains and along the crest of the Angolan Escarpment include

Table 13.1 Climatic data for stations within the Afromontane forest and Grassland ecoregions

Station	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest month (°C)	Coldest month (°C)
Cassongue	Cuanza-Sul	1650	1521	19.7	21.2	16.9
Huambo	Huambo	1700	1210	21.1	22.6	17.9
Humpata	Huíla	2100	805	14.6	17.2	11.2

Mean annual precipitation (MAP), Mean annual temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

Brachylaena huillensis, Bridelia spp., Buxus benguellensis, Chrysophyllum argyrophyllum, Englerophyton magalismontanum, Erythroxylon emarginatum, Faurea speciosa, Ficus verruculosa, Hymenodictyon floribundum, Newtonia buchananii, Ochna pulchra, Parinari curatellifolia, Pittosporum viridiflorum, Polycias fulva, Pteleopsis anisoptera, P. myrtifolia, Schrebera welwitschii, Syzygium guineense and *Trema orientale.*

The broken quartzitic landscape of the Escarpment crest and incised ravines has a mix of stunted specimens of many of the above species, plus shrubs and forbs of genera such as *Berkheya, Cassia, Cyathia, Dissotis, Dolichos, Eriosema, Felicia, Geigeria, Gnaphalium, Gnidia, Helichrysum, Ipomoea, Myrsine, Polygala, Selago, Stoebe, Vernonia* and *Xerophyta.* In lightly shaded sites with ground water seepage, endemic species of *Streptocarpus* are found. Grasses include species of *Aristida, Ctenium, Eragrostis, Hyparrhenia, Loudetia*, *Monocymbium, Themeda* and *Tristachya.* On the high water-table sands of shallow valleys, members of the Cyperaceae and Orchidaceae are common.

Several genera representing Cape/Afrotemperate elements are found in the grasslands surrounding the high altitude forests, including species of *Cliffortia*, *Erica, Faurea, Kniphofia, Philippia* and *Protea.* On lower slopes of Mount Moco, short miombo woodlands occur, comprising *Brachystegia spiciformis, B. floribunda* and *Julbernardia paniculata*, often with *Protea* species.

The forest remnants are under severe pressure from regular fires around their margins, and from deforestation for firewood and cultivation. Similarly, the surrounding grasslands and shrublands have been transformed from rich mixes of shrubs and forest margin communities to short and sparse grassland. Photographs from the 1930s (Gossweiler & Mendonça, 1939) show well-developed *Protea*, *Philippia* and *Xerophyta* shrublands surrounding the forests at that time, communities that have not been recorded in recent decades. In 1960, protea authority John S. Beard photographed what he described as probably the largest protea in the world in the Moco grasslands (Beard, 1993) (Fig. 2.7). Today the grassland has been reduced to short sparse cover with abrupt margins to the forests (Fig. 13.1).

While the vegetation of these forests awaits detailed study, the avifauna has received intense interest over recent decades. The focus of attention has been on the rare and endemic species of the forests and surrounding grasslands, as discussed in Box 18.1.

13.2 Afromontane Grasslands (Ecoregion 5)

The Montane Grasslands of the Angolan Marginal Mountain Chain and Ancient Plateau (Diniz 1991) are found in the highlands of Cuanza-Sul, Benguela, Huambo, Bié and Huíla. The most extensive grasslands, known as *anharas do alto*, lie on gently undulating landscapes at from 1500 to 1800 m, the rolling hills rising to 2620 m on Mount Moco. The underlying geology mostly comprises Basement Complex crystalline rocks producing shallow leptosols, ferralsols and grading into arenosols

Fig. 13.1 Fire-cut margin of Afromontane forest on Mount Moco, with *Podocarpus milanjianus* of 25 m height. *Note* men standing at the base of the *Podocarpus*. *Photo* taken in 1972

in the east. These grasslands cover less than 1% of Angola. The sources of the Cuanza, Cubango, Cunene and upper tributaries of the Congo and Zambezi drain the high planalto, and areas of seasonally saturated soils, with impermeable lateritic horizons, result in the near absence of trees, but an abundance of grass, forb and geophyte species, including many orchids (Figs. 3.10, 13.2). Better drained areas have shrubs and low trees, often with the appearance of 'dwarf' miombo (2–5 m height) of *Brachystegia spiciformis, B. floribunda* and *Julbernardia paniculata* especially on shallow rocky soils over quartzites.

In many areas of the planalto and peneplains of the Congo and Zambezi drainage, a rich diversity of geoxyles occupy positions on the soil catena between miombo woodlands and valley grasslands, where water relations, fire and in some areas, frosts account for a rich diversity of geoxyles, with 198 species from 40 families being recorded by Meller et al. (2022). The presence of geoxyles is recognised in the local designation of these areas as the ***anharas do ongote*** (plains of the *ongote*) named for the two most abundant species of geoxyles, *Brachystegia russelliae* and *Cryptosepalum maraviense.* These geoxyles grow on sandy ferralsols, while the same

Fig. 13.2 *Aloe grata* on the slopes of Mount Moco, overlooking montane grasslands of the Huambo highlands

geoxyle habit is found in a different suite of species occupying the deep arenosols of the ***chanas da borracha*** (plains of the rubber plant—*Landolphia*) of Lunda and Moxico provinces of eastern Angola (Box 14.3).

Trees of these grasslands include species of *Faurea, Protea, Syzygium, Cussonia, Ochna* and *Parinari*. The grasses are shorter (0.5–1 m) than those of the mesic savannas, which range from 1 to 3 m height. The grass flora awaits detailed survey, with the species composition forming a continuum from short sparse grasses on shallow soils (*Aristida, Ctenium, Eragrostis, Themeda, Monocymbium*) (Fig. 3.10) to taller, more dense cover of Andropogoneae on deeper soils.

13.3 Faunal Composition of Afromontane Forests and Grasslands

The Afromontane forests and grasslands of Angola have a low diversity of mammals, with the few larger mammal species that formerly occurred in the highlands having mostly been hunted to local extinction. Other than the bird fauna, the animal fauna of the Afromontane forests and grasslands, and the flora, await detailed study. The avifauna, however, is exceptionally rich in range-restricted rare and endemic species. It has received considerable interest since the first museum expeditions to the Angolan highlands in the 1930s and increasingly over the past two decades (Dean et al., 2019).

Mills and Dean (2021) have documented the bird fauna of Mount Moco and the other Afromontane forests and grasslands of the Angolan highlands. Their checklist for Mount Moco confirms records of 299 species, including eight of Angola's 24 endemic birds: Swierstra's Francolin, Red-backed Mousebird, Pale-throated Barbet, Huambo Cisticola, Angola Slaty Flycatcher, Ludwig's Double-collared Sunbird, Landana Firefinch and Angola Swee Waxbill. In addition, Mount Moco is important for the survival of 12 subspecies endemic to the western Angolan highlands. The most important endemic at Mount Moco is Swierstra's Francolin with an estimated 75 pairs on the mountain (Mills et al., 2011).

Mills and Dean (2021) note: "Within this avifauna is found the entire continuum of the speciation process, from isolated but undifferentiated populations, such as African Olive Pigeon *Columba arquatrix*, to phenotypically divergent endemic subspecies, like the *angolensis* race of Western Green Tinkerbird *Pogoniulus coryphaea*, to species, including the endemic Swierstra's Francolin *Pternistis swierstrai*. The nearest relatives of all these birds occur in distant highland areas, and in Angola are evolving separate lineages in isolation."

The Mount Moco study area is less than 100 km^2 in extent, of which only 85 ha (0.85%) is closed Afromontane forests. Much of the forest is disturbed by human activities. Based on records from the 1930s and 1950s, several species of birds have already been driven to local extinction on Mount Moco, including Pale-throated Barbet. Orange Ground Thrush, Laura's Woodland Warbler and Bar-tailed Trogon have not been recorded this century. A larger area (ca. 580 ha) of Afromontane forests occurs at Mount Namba, which has yet to be surveyed in detail. Its importance as a final refugium for Angola's threatened Afromontane species is obvious. A shortlist for typical amphibian, bird, mammal and reptile species recorded in Angolan Afromontane forests and grasslands is given in Table 13.2.

Table 13.2 Vertebrate species typical of the Afromontane forests and grasslands of Angola

- **Amphibians**: Chela Mountain Reed Frog, Anchieta's Tree Frog, Udzungwa Ridged Frog
- **Reptiles**: Benguela Gecko, Mountain Day Gecko, Angolan Rough-scaled Lizard, Marx's Rough-scaled Lizard, Angolan Girdled Lizard, Anchieta's Chameleon, Angolan Adder, Link-Marked Sand Racer
- **Birds**: Finsch's Francolin, Swierstra's Francolin, Ruwenzori Nightjar, Fernando Po Swift, Naked-faced Barbet, Margaret's Batis, Perrin's Bushshrike, Angola Lark, Black-collared Bulbul, Brazza's Martin, Black-and-rufous Swallow, Laura's Woodland Warbler, Huambo Cisticola, Salvadori's Eremomela, Orange Ground Thrush, Angola Slaty Flycatcher, Bocage's Sunbird, Ludwig's Double-collared Sunbird, Oustalet's Sunbird, Bronzy Sunbird, Black-chinned Weaver, Dusky Twinspot, Angola Swee Waxbill, Fulleborn's Longclaw, Black-faced Canary, Thick-billed Seedeater

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Chapter 14
The Mesic Savanna Biome

Key Concepts and Questions: This Chapter Will Explain

- *What the most extensive biome in Angola is, why it is called miombo, and what its main characteristics are.*
- *Why landscape physiography and dynamics are so important in shaping the patterns of ecosystems across the Angolan planalto and peneplains, how they function and how to recognise them.*
- *What mammal species are typical of the different savanna types and why.*
- *What behavioural responses miombo trees have to climate seasonality.*
- *What accounts for the presence of 'underground forests' in miombo landscapes.*

Context: Angola's Tropical Savannas

Savannas, in their diverse forms, occupy 20% of the Earth's land surface and ca. 50% of the African continent. They cover over 80% of Angola (94% if the tallgrass savanna component of the Congolian Forest/Savanna Mosaics is included). They are represented by nine Angolan ecoregions in two biomes—the Mesic/Dystrophic savannas and Arid/Eutrophic savannas (Fig. 14.1). These two biomes equate with the '*Panda'* (*Brachystegia*) and '*Adansonia*' phytogeographic zones described by Gossweiler and Mendonça (1939). Burgess et al. (2004), in their classification of Africa's terrestrial biomes, placed 24 ecoregions in what they call the Tropical and Subtropical Grasslands, Savannas, Shrublands and Woodlands Biome. These ecoregions cover the diversity of ecosystems, from the Sahel to the Kalahari, that Huntley and Walker (1982) defined globally as tropical savannas, a concept that is now widely adopted (Archibald et al., 2013; Bond, 2019; Frost et al., 1986; Sankaran et al., 2005).

This chapter will cover the ecology of mesic/dystrophic savannas, focusing on the miombo ecosystems that characterise the Angolan planalto and eastern peneplains,

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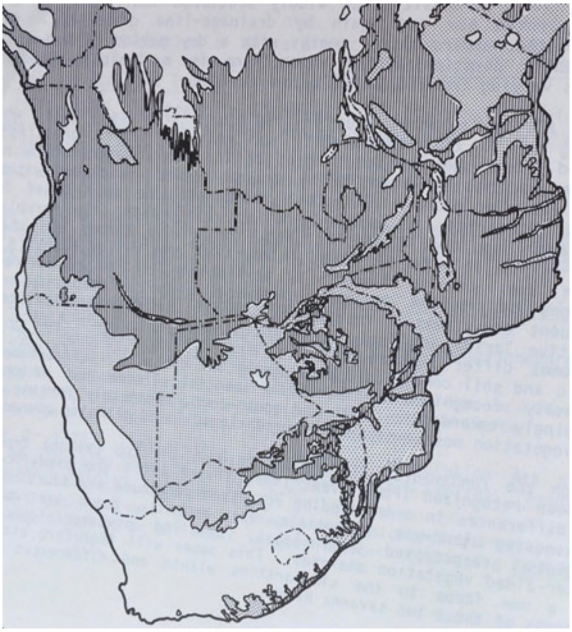

Fig. 14.1 Southern African savannas. Vertical stripes—Mesic/Dystrophic savannas; Stippled—Arid/Eutrophic savannas. From Huntley (1982) *Ecology of Tropical Savannas*. Springer. Berlin

but also including the dry *Baikiaea* open woodlands of the south. The arid/eutrophic savannas of the southwest and the coastal belt are described in Chap. 15.

Despite the importance of miombo across central Africa, relatively little research has been undertaken on the ecology and population biology of miombo ecosystems, when compared with that of fynbos, grassland, karoo and savanna ecosystems in southern Africa (Cowling et al., 1997). Barbosa (1970) and Monteiro (1970a, 1970b) provide detailed descriptions of the plant composition and structure of Angola's miombo, with the latter author giving the first systematic quantitative floristic analysis of Angolan miombo communities and the morphological characteristics of the tree species. In the past decade, studies on Giant Sable (Vaz Pinto, 2019) and aspects of the structure and dynamics of miombo communities (Finckh et al., 2021; Gomes et al., 2021; Reverman & Finckh 2019; Zigelski et al., 2019; and included references) have introduced a new wave of miombo research in the country. Beyond Angola, the extensive work in savannas by French ecologists in the Ivory Coast (Abbadie et al., 2005), Zambian ecologists Chidumayo and Frost (1996) in Zambia and Zimbabwe, Belgian ecologist François Malaisse (1983) in Shaba, DRC, and South African ecologists Scholes and Walker (1993) and the research team at Kruger National Park (Du Toit et al., 2003) provide a very sound base on savanna structure and functioning. More recently, the work of William Bond (2019), Sally Archibald (2017) and colleagues has brought a vibrant surge of new perspectives on savanna ecology, in both arid and mesic savannas. Much of what follows draws on the work of these leading scholars.

Angola's Mesic Savannas (Ecoregions 6–11)

14.1 Definition and Distribution

The key diagnostic criteria of tropical **mesic savanna** ecosystems are the **co-dominance** of trees and grasses, climatic **seasonality** of warm, wet summers, mild dry winters (between 650 and 1400 mm rainfall per year with a dry season of four to eight months), the dominance of the herbaceous stratum by **C_4 grasses**, the prevalence of infertile, **dystrophic soils,** and the role of **fire** as the main consumer of plant biomass.

The Mesic Savanna Biome occupies 68% of Angola's land area (Fig. 2.3, Table 2.3):

- Ecoregion 6—Escarpment Savannas: 5.2%
- Ecoregions 7 and 8—Miombo woodlands and grasslands: 45.1%
- Ecoregion 9—*Baikaiea* woodlands: 13.5%
- Ecoregion 10—*Cryptosepalum* dry forests: 0.05%
- Ecoregion 11—Flooded grasslands: 4.3%.

To this may be added the tall grassland components of the Congolian Forest/Savanna Mosaics of northern Angola (Ecoregions 2 and 3) which occupy 16% of Angola's land area.

Brief descriptions of these Ecoregions are given in Chap. 2, with maps pf their distribution provided in Figs. 3.11, 3.12, 3.13, 3.19, 3.20, 3.21. Here we will focus on the miombo, the typical mesic savanna ecoregion which occupies over 2.7 million km^2 of Africa, and is the dominant vegetation formation of Angola.

Miombo is a term initially adopted by English-speaking ecologists, from the Zambian name (*muombo*) for *Julbernardia paniculata* or alternatively *muuyombo* for *Brachystegia boehmii*. Gossweiler and Mendonça (1939) referred to the miombo formation as the *mata de panda*. In some parts of Angola, *J. paniculata* is known as *umpanda*, while one of the many local names for *Brachystegia spiciformis* is *mupanda* (Figueiredo & Smith, 2012). Miombo is now used internationally to describe the central, southern and eastern African woodlands, savannas and included grasslands that are dominated by the woody genera *Brachystegia, Julbernardia* and *Isoberlinia.* Figures 14.2 and 14.3 present examples of typical Angolan miombo. The interdigitation of often treeless grasslands with woodlands is a characteristic feature of miombo. Fire and soil moisture relations maintain sharp boundaries between grassland and woodland, reflected in the typical catenal sequence found in miombo landcapes (Box 14.1).

Fig. 14.2 Typical mature open miombo woodland of *Brachystegia* and *Julbernardia*, near Caconda

Fig. 14.3 Mixed miombo in a site protected from excessive fires. Barbosa Nature Reserve, Chianga Research Station, Huambo. Note continuous grass cover below the woodland canopy

14.2 Landscapes, Soils, the Catena Concept, Termitaria and Underground Forests

Miombo systems typically occur on the vast peneplains of the geologically old 'African' and 'Post-African' planation surfaces of the Central African Plateau, at 900–1400 m. In the moister western half of Angola, the underlying geology comprises crystalline Precambrian rocks (formed before 550 million years ago) which weather to produce ferralsols. In the eastern half of the country, Kalahari sands (arenosols) have been deposited by wind and water over the past five million years. Both these soil types have been strongly leached for millions of years and as a result are of low fertility (dystrophic). In the west, large granite domes are frequent, but to the east, one can travel nearly 800 km across featureless, unbroken rolling plains and shallow valleys between Huambo and Cazombo.

An important ecological feature of the miombo is the regular, repeated sequence of gently undulating rises and falls in the landscape, with associated soil and vegetation patterns—a feature known as the **catena** (Box 14.1). Catenal sequences are not limited to the mesic savannas, but also occur in many arid savanna ecosystems on granitic sands and basaltic clays, where sodic soils might develop at the base of hillslopes (Venter et al., 2003) (Box 15.1). Miombo soils are mostly highly leached, acidic, with low cation exchange capacities, and with low available nitrogen and phosphorus. The large woodland trees of the upper catena capture most of the available nutrients. As a consequence of fires and termite activity, plant litter build-up is slow and soil organic matter levels are low. The ferralsols of the west have high levels of aluminium, which place limits on crop production.

Impervious horizons in miombo soils, such as laterite layers, can cause waterlogging over poorly aerated **perched** water tables, with stunted growth of trees. Over much of Angola's moist miombo, seasonally waterlogged sites have short hygrophilous grasslands with scattered trees and shrubs and in many areas, an abundance of **termitaria**. The termitaria play a prominent role in the fine-scale patterning and nutrient relations of miombo landscapes (Box 14.2). A further remarkable feature of the miombo is the presence of **'underground forests'**—unique to the mesic/dystrophic savannas of African miombo and Brazilian cerrado (Box 14.3). These three special features of mesic savanna landscapes—the catena, the diversity of termitaria, and the extensive 'underground forests' demand detailed description and are presented in three Boxes.

Box 14.1 The Catena: a Classic Ecological Feature of African Savannas

Much of what one needs to understand about African landscapes can best be learned from the air. Neither an aircraft nor a drone is needed. With an internet connection, a remarkable aid to the ecologist is **Google Earth**. This is particularly the case for researchers exploring the many remote corners of Angola, where access can be difficult if not impossible. At the click of button, a bird's eye-view can be accessed for any point in the country or the world. What becomes immediately visible from space, over much of the Angolan planalto, is a dense pattern of dark and light shades, representing the reflectance (albedo) of different vegetation densities. The patterns are often repeated in a regular sequence, dark shades on higher ground, light shades in valleys.

A good example of pattern is found in **Bicuar National Park** in Huíla (Fig. 14.4). The border of Bicuar is clearly delineated along its northern boundary, where deforestation has left a treeless belt of pale sands, contrasting with the dark, thickly wooded landscapes protected within the park. A dendritic pattern, like lines on a fingerprint, results from alternating wooded and grassy belts. This is a sequence of distinct soils and vegetation, consistently repeated on specific facets of valleys (***mulola***) and rises (***tunda***). The drainage-line (*mulola*) grasslands occur throughout central and southern African mesic savannas where they are known as ***dambos*** in many countries. The pattern results from the slow erosion of the planalto and peneplains, and the downslope movement of water, soil particles and nutrients. The patterns reflect a chain (**catena**) of topographical/soil/vegetation sequences. In his description of the vegetation of Bicuar, Teixeira (1968) provides a map and a profile diagram of vegetation structure that illustrates the sequence of soils and vegetation (Figs. 14.5, 14.6). It is a model repeated across the Central African Plateau, from Malange in Angola, across Zambia and Malawi, to Gorongosa in Mozambique.

Fig. 14.4 Google Earth (Landsat/Copernicus) view of Bicuar National Park. Note deforested margins (pale to white) around its borders. Also, note the light lines of the grassy *mulolas*

and the dark bands of miombo and *Baikiaea/Brachystegia* woodland on the higher ground of the *tundas*. The centre of the Google Earth image, at 1242 m altitude, is located at 15° 17′ 23.02” S; 14° 44′ 15.13” E

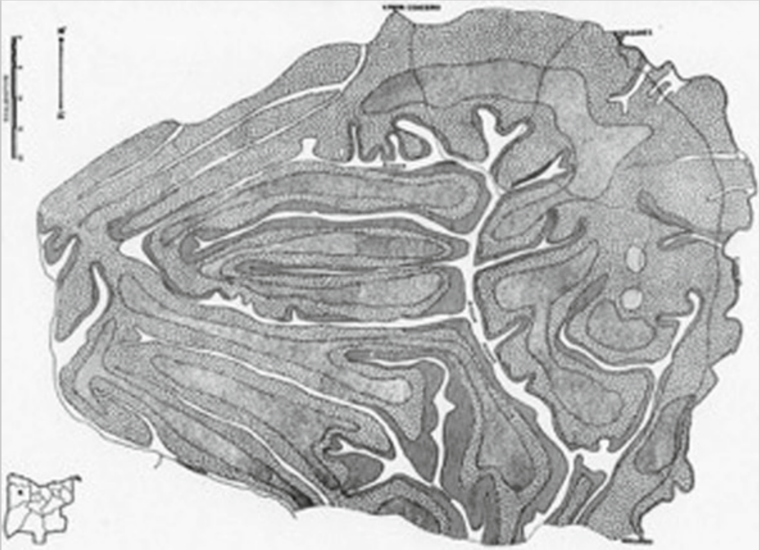

Fig. 14.5 Vegetation map of Bicuar National Park. From Teixeira (1968), which mirrors the catenal sequences seen on the 2018 satellite image

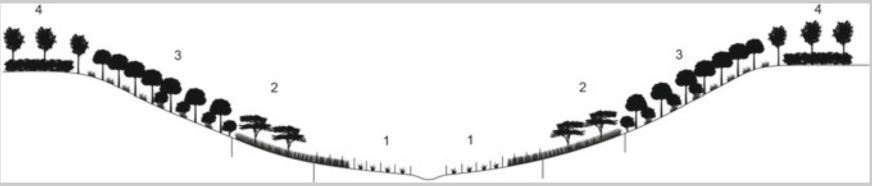

Fig. 14.6 Profile diagram of the catena across a mulola in Bicuar. **1** *Loudetia* grasslands with scattered *Parinari* and *Pygmaeothamus* geoxyles on colluvial and alluvial soil. **2** Open savanna of *Burkea, Terminalia*, *Tristachya* and *Eragrostis* on colluvial and illuvial soil. **3** Woodland of *Brachystegia*, *Julbernardia*, *Hyparrhenia* and *Andropogon* on eluvial and colluvial soil. **4** Thicket of *Hippocratia, Baphia, Croton, Combretum* and *Baikiaea* on eluvial soil. From Teixeira (1968) *Parque Nacional do Bicuar*. Instituto de Investigação Agronómica de Angola, Nova Lisboa

The catena follows a sequence of both soil moisture and nutrient conditions.

- The higher ground is well-drained, losing fine particles and basic cations (calcium, magnesium, potassium and sodium) through surface and subsurface runoff, resulting in a leaching and acidification of these coarse **elluvial** soils that have formed by weathering in-situ.
- The **colluvial** soils of the concave slope are also subject to leaching, receiving material by downslope creep. Drainage transports material further downslope and vertically to the deeper, grey **illuvial** soils at the bottom of the slope, which also receive cations from upslope with a resultant increase in their pH.
- In larger valleys, the bottomland soils might be added to by streamflow carrying loose, unconsolidated, silty **alluvial** sediments.

Catenas typically occur in mesic savannas where the seasonal climate provides enough precipitation to drive the translocation processes without flushing the cations and sediments out of the landscape.

The importance of the catena is that it is found across 60% of Angola, most typically in the miombo woodlands and savannas of the planalto and peneplains. The sequence follows a regular pattern. In Bicuar, the well-drained reddish sandy arenosols of the higher ground are occupied by *Baikiaea* woodland and *Combretum* thickets. Towards the margins of the higher ground, deep-rooted *Brachystegia* woodland transitions into a narrow fringe of *Burkea* woodland followed by a belt of shallow-rooted *Terminalia* savanna. These are found on the pale white sands at the margin of the convex slopes (Fig. 14.6). The lateral spread and shallow rooting of *Terminalia* in the oxygenated topsoil possibly accounts for its ability to grow in the seasonally waterlogged sands. During the rains, a perched water table results in a seasonal **seepline** below the *Terminalia* belt, with a fine flow of water from these white sands. This is followed by open grasslands on the seasonally high water table of the concave slope which ends in the dark poorly drained, heavier clayey fluvisols of the valley bottom. Like the grasslands, the valley soils are seasonally waterlogged, preventing tree growth. Seasonal waterlogging is revealed in the subsoil by blue and orange mottling and gleying. In some catenas, the valley bottom might include a small pool (***tala***) or a narrow line of forest trees (***muxito***), where erosion has created better-drained conditions suited to tree growth (Fig. 14.7).

Fig. 14.7 Miombo in Bicuar National Park, Huíla. The catena progresses from *Baikiaea* woodland and thicket on the top of the plateau, through *Brachystegia/Julbernardia* woodland, to a fringe of *Burkea* savanna on the margin of the bottomland, where geoxyles dot the grassland

Box 14.2 Pattern, Nutrient Hotspots and the Role of Termites in Mesic Savannas

> To understand is to perceive patterns
>
> Isaiah Berlin (1997)

The detection and understanding of spatial patterns in nature is one of the most fascinating activities for the inquisitive ecologist. Patterns appear at a wide range of scales, from continental to local. The distribution of savanna biomes is centred on the peneplains of the African Plateau (mesic/dystrophic) and the more recent erosional surfaces of the hot, arid river basins (arid/eutrophic savannas). At landscape scale, the soil/vegetation sequences of catenas are a feature of both mesic and arid savannas. At a finer scale, one of the most widespread patterns across the savannas of Africa are those created by termite colonies. Their importance as nutrient ’hotspots’ in mesic/dystrophic savannas deserves special mention, as does their role as refugia for fire-intolerant savanna species (Joseph et al., 2013). The flora of termitaria in the miombo systems is extraordinarily rich, with over 700 species of woody plants found on the termitaria of Zambia alone (Fanshawe, 1969).

Termitaria are visible both on the ground and from satellite images. Termites and their colonies come in many forms and densities (Abe et al., 2000). They are **eusocial** insects, with clearly defined roles for workers and soldiers, for dispersing winged adults, and for the king and queen, responsible for reproduction. Two main groups are of special interest: humivorous termites that ingest organic matter and soil, and ligniferous termites that consume intact plant material. Both are critical agents in the mineralization of dead plant material. Here discussion will focus on the tall mound-forming termitaria of the fungus-culturing *Macrotermes* and the small, often spheroid nests or sharp spikes of the non-fungus-culturing *Cubitermes* and *Trinervitermes*.

The great mound termitaria of woody plant- and litter-feeding *Macrotermes falciger* are particularly prominent on deep, well-drained soils in Wet Miombo. Here they average 3–5 mounds ha^{-1}, of up to 5 m in height and with a basal area of ca. 30 m^2 (Erens et al., 2015a). They cut and harvest woody material, transforming it into sawdust and feeding the masticated and regurgitated wood or grass to cellulose-decomposing fungi, with which they have a mutualistic relationship (Fig. 10.12**).** The termites do not have the enzymes needed to digest the cellulose and lignin of the plant material, but thenitrogen-rich biomass of the fungi provide the termites with most of their food. *Macrotermes* cultivate gardens of fungal mycelia in chambers within the upper section of the mounds, where the moist microclimate is ideal for fungal growth. In summer, the sporophores emerge, providing delicious mushrooms for local communities (Fig. 10.11).

The termitaria may be occupied for many centuries (Erens et al., 2015b) by successive generations of queens, which live for up to 20 years. Mound-building termites select clay particles rather than sand grains to build their nests, thus concentrating nutrients within the matrix of nutrient-poor soils. The termites forage widely. This activity concentrates nitrogen, phosphorus and exchangeable cations in the building material of the mounds, accentuated by the increased evaporation of moisture through the extensive ventilation channels in the termitarium, passing through the chimneys of these large, architecturally complex structures. As a mound grows, it develops a hard external surface, through which rain does not penetrate deep into the colony, resulting in mobile compounds (salts) concentrating in a central accumulation zone. Once exposed, it becomes a favoured **salt-lick** of many animal species. The salt licks of Cangandala National Park are the nutrient epicentres of animal life, favoured by all larger mammals, most especially by Giant Sable. Sodium levels in active termitaria were found to be 20 times higher than in the surrounding woodland soils (Baptista et al., 2012; Fig. 14.8). The nutrient richness of these hotspots is reflected in the specialised adaptations (bird dispersed fruit, spiny, browse-resistant branchlets, hard sclerophyll leaves) of the plant species that colonise the *Macrotermes* mounds. The termites thus create a **nutrient-rich hotspot**—an ecosystem of its own making which contributes to the wider range of plant species that occupy the rich soils of the mound, and to the many species of animals that are dependent on the system (Malaisse, 1978; Fig. 14.9).

Fig. 14.8 Giant Sable congregate at a termitarium salt-lick, Cangandala National Park. *Photo* Pedro Vaz Pinto

Fig. 14.9 The complex trophic web of a high termitarium in the miombo of Shaba, DRC, including 25 species representing different trophic levels. Producers include: grass *Setaria* (1); trees *Balanites* (5); succulents *Sanseviera* (11), *Commiphora* (15); shrub *Grewia* (18). Consumers include: flower-eaters *Zonabris* (3), leaf-eaters *Bunaea* (6), fruit-eaters *Treron* (7), *Cricetomys* (16). Carnivores include: *Naja* (23). Decomposers include: termites *Macrotermes* (12), mushrooms *Termitomyces* (20). Parasites include ticks *Aponomma* (24). From Malaisse (1978)

Far more abundant are the diverse structures, both above and below ground, of humus and soil-feeding *Cubitermes* and *Trinervitermes*, often built on seasonally waterlogged soils (Figs. 14.10, 14.11). These are especially abundant in Wet Miombo. In Shaba, DRC, they have a biomass twice that of the *Macrotermes* and build their nests with their faecal matter, comprising soil particles and digested humus, creating local concentrations of nutrients at a finer spatial scale than the *Macrotermes* mounds, depleting the organic matter of the zone around each nest. In the Dry Miombo-related *Burkea-Ochna* savanna in northern South Africa, the *Cubitermes* have up to 380 nests ha^{-1}, a density greatly exceeded in Wet Miombo. Goffinet (1976) found 1460 *Cubitermes* and *Trinervitermes* mounds ha^{-1} in miombo savanna of Shaba. He calculated that 10.4 million termites ha^{-1}, represented a dry weight of 22.95 kg ha^{-1}, far higher than the vertebrate biomass for miombo savannas.

Fig. 14.10 Chimney structures of humivorous termites on the soils of Wet Miombo *chanas* in Luando Strict Nature Reserve, Malange

Fig. 14.11 Chimney structures of humivorous termites on the soils of Wet Miombo *chanas* in Luando Strict Nature Reserve, Malange

As we will see later, termites also play significant roles in the patterns of ‘fairy circles’ of the Namib Desert. Across Africa, from the mesic savannas to the hyper-arid desert, termites are remarkable ecological engineers.

Box 14.3 Angola’s Underground Forests

A classic feature of the Angolan miombo is one of its most puzzling phenomena. Most miombo tree species grow into broad-crowned specimens of 10–20 m in height, forming the typical open woodlands of the planalto. But some of their close relatives live separate lives as ‘underground trees’, often just a few metres away. The ***anharas do ongote*** of Huambo and Bié (on ferralitic soils) and the ***chanas da borracha*** of the Lundas (on arenosols) form part of specialised plant communities described by White (1976) as ‘underground forests’, dominated by **geoxylic suffrutices**—now better known as geoxyles.

Geoxyles are woody plants that have reduced their aboveground stems and branches to short shoots which produce leaves, flowers and fruits immediately after the passage of the frequent fires that sweep across miombo ecosystems (Fig. 14.12). Geoxyles invest their woody growth in underground rootstocks (lignotubers or xylopodia), often with a dense network of rhizomes and roots that can cover over 50 m^2 (Fig. 14.13). They thus place their regenerative organs underground for most of the year to protect them from damage by fire, frost or herbivory (Figs. 14.14, 14.15 and 14.16).

Fig. 14.12 A brightly coloured orange and yellow 'lawn' of the geoxyle *Cryptosepalum maraviense* on the margins of a mulola near Chitembo, Bié. The white sands exposed on the margin of the *Cryptosepalum* community probably indicates the position of the seepline on the soil catena. *Photo* John Mendelsohn

Fig. 14.13 Exposed underground rhizomes of a geoxyle, *Ochna arenaria. Photo* Amândio Gomes

Fig. 14.14 Above-ground leaves of *Ochna arenaria. Photo* Amândio Gomes

Fig. 14.15 Flowering *Cryptosepalum maraviense*—the dominant geoxyle of the *anharas do ongote. Photo* John Mendelsohn

Fig. 14.16 Fruiting *Ficus* sp. geoxyles on the Bulozi Floodplain. *Photo* John Mendelsohn

The first scientist to describe the geoxyle habit was pioneer Danish ecologist Eugen Warming. Working in the **cerrado** of Brazil (the South American equivalent of miombo) in 1865, Warming illustrated the underground root systems of the Brazilian geoxyle *Andira laurifolia* (Warming, 1908). He described its "curious mode of growth, for this is a clear example of a tree which due to fires was forced to live a life under the ground." The pioneer of Angolan plant ecology, Swiss-born John Gossweiler, provided a detailed description of the geoxyles of anharas and chanas, and noted that: "With the appearance of grasses, the community turns **pyrophilic** and it is precisely the fire that stimulates the dominants to develop flowers eight days later. The maturation of fruits occurs in less than three months, before the first rains of September, with the result that the seeds are ready to germinate in exactly this season" (Gossweiler & Mendonça, 1939). *["Com o aparecimento das gramineas a comunidade torna-se pirofitica, e e precisamente a queimada que estimulando o desenvolvimento os dominantes provoca a sua floracao oito dieas depois. A maturacao do fruto realiza-se em menos de tres meses, antes das primeiras chuvas de Setembro, de tal sorte que as sementes estao aptas a germinar precisamente nesta epoca."]*

The growth cycle of grasses follows that of geoxyles, growing and flowering in mid-summer, by which time they cover the geoxyle aerial organs. The geoxyles effectively disappear from sight. However, Gossweiler was ambivalent about fire being the key driver of geoxyle evolution, mostly because of the low fuel load of the sparse chana grasslands. He also pointed to the very sandy and nutrient-poor soils as a constraint to woody plant growth. This opinion was supported by forest botanist Romero Monteiro (1970a, 1970b), in his detailed study of the miombo of the Bié Plateau. He considered edaphic factors more important than fire. White (1976) also placed emphasis on the highly leached and very poor nutrient status of miombo soils, and on the summer season waterlogging of the sites on which they abound, with dry winters, as key constraints on their growth into trees. White, like Gossweiler and Monteiro, did not mention frost as a factor.

Until recent decades, the study of miombo and cerrado ecosystems had been rather neglected by ecologists. But the evolution of geoxyles is now a hotly debated topic. Researchers in Angola (Finckh et al., 2016) have supported an early proposal from South Africa (Burtt Davy, 1922) that frost is the prime causal factor. However, frost is rare or absent over most of the geographic range of geoxyles in southern Africa and Brazil. While direct field observation of geoxyles has proved inconclusive, phylogenetic research on the evolutionary history of geoxyles has provided new insights.

South African savanna ecologist William Bond and colleagues have used modern phylogenetic analyses of over 1400 woody species to test whether the geoxyle habit evolved simultaneously in Africa and South America. They also sought to date the first appearance of tropical humid savannas (miombo and cerrado). They found that the geoxyle life-form evolved independently multiple times during the Pliocene (from ca. 5.3 Ma), in both miombo and cerrado, always associated with the mesic savanna biome in which fires are a regular and ecologically significant feature (Maurin et al., 2014). In nutrient-poor, seasonally waterlogged soils, the slow growth rates of juvenile trees reduces their probability of rising above the kill-zone (‘fire-trap’) of fires. Selection for plants with adaptations to protect regenerative organs from fire by hiding them below the ground would be a selective advantage (Bond, 2019). A further selective driver is against herbivory of these slow-growing plants. Many geoxyles are defended against herbivory by accumulating secondary compounds, including poisons, that retard digestion or in some cases, can be lethal (Sect. 11.4).

German ecologist Paulina Zigelski (2019) and Angolan colleague Amandio Gomes found the geoxyle life-form in 198 species in 40 families within the miombo—a perfect example of convergent evolution of an adaptive strategy. Amandio Gomes et al. (2019) found that related pairs of tree and geoxyle life-forms are found within sub-species, between species of the same genus, and between species of different genera. They concluded that although trees and geoxyles differ considerably in their growth form, they are remarkably similar in other morphological traits. Studies of the eco-physiology and plant functional traits are beginning to explain some features of the life of underground trees, but as Gossweiler and Mendonça (1939) observed nearly a century ago: “Not only the ecology but also the genetic dynamics of the ‘Chana da Borracha’ offers a wide field for future work.”

14.3 Climate and Seasonality

Climate is the primary determinant of the potential distribution of tropical savannas, regionally moderated by soils, fire and herbivory. The mesic savannas of Angola, lying mostly between 900 and 1400 m above sea level, but ranging from sites at 800–2400 m, have warm to hot summers and mild winters, with rainfall from 650 to 1400 mm per year (Table 14.1). To the north, the Congolian Forest/Savanna Mosaic occupies higher rainfall areas with precipitation of 1400–1700 mm per year.

Seasonality of temperature and rainfall is one of the key characteristics of tropical savannas, and accounts for the limited availability of soil moisture for plant growth during the dry season. In the Angolan mesic savannas, moisture availability in the upper 30 cm of the soil drops below permanent wilting point for up to eight months of the year. Soil water availability increases with depth, and below 90 cm water is available to deeply rooted plants throughout the year.

Rainfall seasonality results in marked deciduous properties in most tree and shrub species, and the regular drying out of the grass cover, with consequent frequent natural fires. Deciduous trees translocate about half their leaf potassium and phosphorus back into their branches before leaf fall. This pattern of translocation does not take place in the trees of arid/eutrophic savannas. Mesic savanna grasses translocate nutrients from foliage to roots at the end of the growing season, further reducing their nutritional value to herbivores. Fire and herbivory have resulted in adaptations to repeated defoliation. Some highland valleys have frequent frosts in winter, but over most of the mesic savannas, frosts are of rare occurence.

Table 14.1 Climatic data for stations within the Mesic Savannas

Station	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest month (°C)	Coldest month (°C)
Malange	Malange	1139	1195	21.8	22.9	19.5
Huambo	Huambo	1700	1210	18.8	20.6	15.7
Cazombo	Moxico	1180	1441	22.2	24.3	18.8
Caconda	Huíla	1650	1055	20.0	21.6	17.5
Mavinga	Cuando Cubango	1188	877	20.7	24.1	14.8
Mucusso	Cuando Cubango	890	774	23.9	26.6	16.0

Mean annual precipitation (MAP), Mean annual temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

14.4 Floristic Composition, Physiognomic Structure and Phenology

The key feature of miombo woodlands, which distinguishes them from all other African ecosystems, is the dominance, or at least strong prominence, of species of two genera—***Brachystegia*** and ***Julbernardia***. These and several other miombo trees belong to the legume family **Fabaceae**, sub-family **Detarioideae**. The miombo flora is rich, and is at the heart of the Zambezian regional centre of endemism, which has an estimated 8 400 species within its range across southern, central and eastern Africa (White, 1983). Barbosa (1970) describes in some detail seven types of miombo in Angola. These fall into two ecoregions: Angolan Wet Miombo—(Ecoregion 7) and Angolan Dry Miombo (Ecoregion 8). To the south, these transistion into Zambezian Baikiaea Woodlands—(Ecoregion 9). To the north of the main miombo woodlands, two further ecoregions, the Western and Southern Congolian Forest/Savanna mosaics (Ecoregions 2 and 3), form a transition from the Zambezian centre of endemism to the Guineo-Congolian centre of endemism as defined by White (1983). A narrow belt of mixed mesic savanna follows the Central Escarpment (Ecoregion 6). Furthermore, two ecoregions, Flooded Grasslands (Ecoregion 11) and Cryptosepalum Dry Forests (Ecoregion 10), fall fully within the mesic savanna biome. All of these ecoregions are outlined in Chap. 2. The present chapter focuses on the characteristics of miombo ecosystems of Ecoregions 7 and 8.

Across the vast expanse of the miombo, a remarkable uniformity of structure prevails, varying in detail but not in the repeated catena structure of woodlands interspersed with open savannas and grasslands. Smaller pockets of dry evergreen/semi-deciduous closed forest might occur on deeper soils and as gallery or riverine forest along watercourses.

The broad crowns of the dominant trees reach up to 25 m in height in mature Wet Miombo on deep soils, but the canopy is usually lower, down to 8 m in height, in Dry Miombo. The understorey comprises shrubs and saplings, and the woodland floor carries a sparse cover of grasses and forbs. Climbers and epiphytes are rare, except in the *Cryptosepalum/Marquesia* dry forests, where lichens and mosses might cover tree trunks and soil.

Over 90% of the dominant species of miombo woodland trees are deciduous, but do not normally drop all their leaves every year. Annual leaf loss is about 60% in miombo trees, compared with 90% in trees of arid savannas. Shrubs of the miombo woodland understorey are less deciduous than trees. Shallow-rooted miombo shrubs such as *Vangueria infausta* and *Lannea discolor* shed leaves early in the dry season and do not flush new foliage until after the rains.

A phenomenon peculiar to miombo trees is the flush of brightly coloured new leaves immediately after leaf fall in August/September, weeks before the first rains. The colouration is due to the presence of **anthocyanin** pigments initially predominating over chlorophyll, which might protect the soft young leaves from herbivores (Figs. 14.17, 14.18). The early flush is made possible by the internal recycling of nutrients, especially nitrogen, before the previous season’s leaves fall in late winter; a unique feature of miombo trees. Furthermore, water, carbohydrate and nutrient reserves held in the trunk, branches and roots stored from the previous growing season, and access to soil water from deep root systems of the miombo trees, contribute to this eco-physiological characteristic. Heating of the soil surface might be a trigger for the early flush of miombo leaves (Malaisse et al., 1975). Or perhaps the early leaf emergence might be triggered by the lengthening photoperiod following the spring equinox (Frost, 1996; Ryan et al., 2017). While some arid savanna trees flush before the first rains, few display the richly coloured pigmentation of miombo species.

Fig. 14.17 Spring colours in the pre-rain flush of foliage of miombo trees, typical of mesic savanna

Fig. 14.18 Spring colours in the pre-rain flush of foliage of miombo trees, typical of mesic savanna

For most canopy trees, flowering occurs immediately following leaf flush, except for *Julbernardia paniculata* which flowers in mid-summer. Fruits take at least six months to mature, with the dry pods of the dominant genera *Brachystegia, Julbernardia* and *Isoberlinia* dispersing seeds by explosive dehiscence. This dispersal mechanism is effective for only a short distance from the tree (within 5–20 m), placing limitations on re-population of miombo in sites clear-felled and converted to crops.

There is no dormancy in miombo seeds, which germinate soon after they fall. Seed establishment is low, mortality is high (due to low soil moisture availability and heat stress), and growth is slow. Most seedlings die before reaching the sapling stage, which can take eight years, during which period they are vulnerable to damage by fires. The main strategy for regeneration after disturbance (such as fire or felling) is through regrowth by **coppicing** from stems or branches, or from root suckers. In this respect, miombo is very resilient to disturbance if the tree stumps are not killed, and recovery back to woodland physiognomy and floristic composition can be achieved in 30–50 years. However, the rate of total transformation of woodlands for charcoal or agricultural production, currently accelerating over most of the Angolan miombo, is resulting in the long-term degradation of these ecosystems.

14.5 Faunal Composition of Mesic Savannas

The mesic savannas of Angola are rich in most vertebrate groups, while lower in overall vertebrate biomass when compared with untransformed arid savannas (Sect. 10.5). Table 14.2 provides a shortlist of vertebrate species of miombo woodlands and grasslands, which are the most extensive mesic savanna ecoregions of Angola.

Table 14.2 Vertebrate species typical of Angolan Miombo Woodlands, Savannas and Grasslands

- **Amphibians**: Peter’s Clawed Frog, Merten’s Striped Toad, Banded Rubber Frog, Guinea Snouted Burrower, Angolan Reed Frog, Benguela Long Reed Frog, Senegal Kassina, Bocage’s Burrowing Tree Frog, Angola Ornate Frog, Sharp-nosed Grass Frog
- **Reptiles**: African Dwarf Mud Turtle, Queen Nzinga’s Gecko, Iven’s Skink, Bayão’s Skink, Angola Tree Agama, Anchieta’s Cobra, Spotted Boomslang
- **Birds**: Pale-billed Hornbill, Miombo Barbet, Western Black-headed Batis, Souza’s Shrike, Miombo Tit, Red-capped Crombec, Short-winged Cisticola, Miombo Wren Warbler, Black-necked Eremomela, Yellow-bellied Hyliota, Sharp-tailed Starling, White-winged Babbling Starling, Miombo Scrub Robin, Congo Moor Chat, Anchieta’s Sunbird, Chestnut-backed Sparrow-weaver, Bocage’s Weaver, Bar-winged Weaver
- **Mammals**: Side-striped Jackal, African Hunting Dog, Caracal, Lion, Leopard, Spotted Hyaena, Miombo Genet, Lichtenstein’s Hartebeest, Yellow-backed Duiker, Common Wildebeest, Tsessebe, Roan Antelope, Sable, Antelope Giant Sable Antelope, Common Waterbuck, Defassa Waterbuck, Southern Lechwe, Puku, Oribi, Southern Reedbuck, Common Duiker, Common Eland, Sitatunga, Bushpig, Greater Galago

14.6 Mammals of the Angolan Mesic Savannas

The reliable summer rainfall and abundance of perennial rivers and streams that characterise Angola's mesic savannas account for most herbivores found in these woodlands, savannas and grasslands being water-dependent grazers. These include Giant Sable Antelope, Roan Antelope, Lichtenstein's Hartebeest, Defassa Waterbuck, Red Lechwe, Puku, Oribi, Southern Reedbuck and Common Eland. All of these are low-density species, which are either roughage feeders or are very selective of higher nutrition herbage in a generally poor-nutrient environment. Red Lechwe form large herds on the open grasslands of river floodplains, once numbering over 1500 along the Luando River. Oribi also prefer open shortgrass habitats. Nomadic Eland, once numbering over 1000 in Quiçama, and 500 in Bicuar, made seasonal movements over home-ranges of several hundred km^2. All the other species mentioned are rather sedentary, with home-ranges in tens of km^2. While Africa's largest roughage feeder, the Savanna Elephant, is widespread across most African savannas, the species is absent or very rare in Angola's mesic savannas, even according to historic records. Similarly, neither Cape nor Forest Buffalo has been known to occur in more than small populations in Angola's mesic savannas. Forest Buffalo were known from records across Northern Angola, from Quiçama to Luando and to Lunda Norte. Few if any viable populations remain.

As may be expected in ecosystems with low biomasses of prey species, predatory carnivores are also scarce in the mesic savannas. While African Lion and Southern African Cheetah occurred across the savannas from the Cunene to the Cassai in the mid-twentieth century, they are extinct or nearly so over the mesic savannas today. Rare sightings of lion have been made in Luando, while cheetah remain in low numbers in the arid savanna of Iona. African Leopard were once ubiquitous across all biomes in Angola. Medium-sized carnivores that occur in small populations throughout Angola's mesic savannas include Side-striped Jackal, Caracal, Serval and African Wild Dog.

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Chapter 15
The Arid Savanna Biome

Key Concepts and Questions: This Chapter Will Explain

- *Why soil nutrient status, moisture relations and herbivory are the key drivers of arid savanna structure and function.*
- *How to define, recognise and understand the concept of 'arid/eutrophic' savannas.*
- *What the main types of arid savannas are, where they are to be found and what characterises them.*
- *Why a single tree species (*Colophospermum mopane—mutiati*) dominates such a large area of southern Africa, and what determines its distribution.*
- *How soil nutrients, drainage and chemico-physical reactions result in specialised plant/animal communities.*
- *Why a series of arid savanna ecoregions extend from the Cunene to the Congo—over the 1650 km of Angola's coastline.*

Context: The Arid/Eutrophic Savannas

Two features characterise arid/eutrophic savannas:

- Low and unpredictable rainfall which accounts for variable and usually low levels of primary production and thus low fuel loads for combustion by fire;
- Moderate to high soil nutrient status which supports nutritious grass and tree foliage that sustains high densities of mammalian herbivores.

Within the concept of arid/eutrophic savannas, a wide diversity of habitat physiognomies is found, including short grasslands, shrublands, open tree savannas, woodlands, thickets and dry forests. The general physiognomy of arid savannas (a variable mix of grasses, forbs, shrubs and trees) is not strikingly different to that of mesic savannas. However, the two savanna biomes differ significantly in the physical environments they occupy, and the evolved adaptations that account for their success. Arid/eutrophic savannas are typically found where mean annual precipitation ranges from ca. 250–650 mm, with more than eight dry months. Summers can be very hot; winters can have occasional to frequent frosts. Soils are mostly fine-textured,

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eutrophic, with an exchangeable base status of above 15 milli-equivalents per 100 g of clay. Mammalian herbivores are notable for their diversity, high biomass and their impacts on vegetation structure. Fires are infrequent, and usually follow seasons of exceptional rainfall and herbage growth. Other characteristics are summarised in Box 1.2.

Unlike the mesic savannas which typically occur on the old planation surfaces of the Central African Plateau, arid savannas occupy lower elevations, often on younger, eroded landscapes, or down-warped basins and rift valleys. Here the vegetation is mixed both structurally and floristically, especially at the interface between arid and mesic savannas. The baobab *Adansonia digitata* is found throughout the arid savannas of Angola and is emblematic of the country's hot dry lowlands.

In Angola, arid savannas include three ecoregions of the southwestern and coastal lowlands, from the lower slopes of the Angolan Escarpment to the sea. Maps of the distribution of these ecoregions are given in Figs. 3.30–3.32 to which reference should be made to orientate the following outlines.

- The Angolan Mopane Woodlands (Ecoregion 12, Fig. 3.30) of Cunene, Namibe and Benguela provinces merge gradually westwards into the
- Namib Savanna Woodlands (Ecoregion 13, Fig. 3.31) of Namibe and Benguela provinces, which in turn transition as rainfall drops below 150 mm per year to the
- Continuing northwards from the Namib Savanna Woodlands, from Sumbe, across Cuanza-Sul and Bengo provinces, as a narrow tongue to the coastal belt of Cabinda, is the Coastal Arid Savanna (Ecoregion 14, Fig. 3.32).

The Coastal Arid Savanna includes some of what Burgess et al. (2004) included in their definition of Angolan Scarp Savannas and Woodlands, here re-defined to separate the coastal lowlands from the escarpment. Some areas of the Baixa de Cassange might well fall into the category of arid/eutrophic savanna, but the lack of field information accounts for its inclusion in this study as part of the Western Congo Forest/Savanna mosaic (Ecoregion 2).

Angola's Arid/Eutrophic Savannas (Ecoregions 12–14)

15.1 Angolan Mopane Woodlands (Ecoregion 12)

Distribution and Climate

This ecoregion (WWF 34, Barbosa 20, 21) is unique in Angola, and indeed in Africa, for being dominated and characterised by a single tree species—*Colophospermum mopane*. Known as *mutiati* in Angola or *mopane* over most of its range, it is a leguminous tree or multi-stemmed shrub of the Fabaceae family. Mopane-dominated ecosystems occupy 607,000 km^2 of southern Africa (Burgess et al., 2004), lying between 9 and 25 degrees of latitude, across Angola, Botswana, Malawi, Mozambique, South Africa, Zambia and Zimbabwe (Fig. 15.1). It is not found on the Central

African Plateau, being confined to the hot dry valley bottoms and adjacent plains of the Cunene, Zambezi, Luangwa, Save, Shire and Limpopo rivers. Throughout its range, mopane is found on rich alluvial and basaltic plains, on calcisols over calcrete pavements and on well-drained slopes of rocky hills. *Colophospermum mopane* is usually found on fine-textured (clayey) soils, but will penetrate sandy soils where they overlie clay or calcrete. At its boundaries with other ecoregions, the transition of soils and vegetation type often happens abruptly—over a few metres - for example, where clay soils meet the sands of the Kalahari, and where *Colophospermum* woodland is replaced by *Baikiaea* woodland.

In Angola, *Colophospermum mopane* occurs in the far southwest, from Mupa National Park, down the Cunene, across the foothills of the Chela Escarpment to within 40 km of the sea near the mouth of the Coporolo river (Fig. 3.30). Ranging in altitude from ca. 1000 m on the slopes of the Serra da Chela, to 100 m near the coast, it occupies arid regions with less than 650 mm annual rainfall, hot summers and dry mild winters during which frost is infrequent. However, in the lower Cunene valley, occasional heavy frosts do occur. (Figs. 3.33, 15.2 and 15.3). Mopane is an extremely resilient species, and extends deep into the Namib Woodlands and the

Fig. 15.1 The distribution of *Colophospermum mopane* in Africa. From Stevens (2021) *Ecology and Evolution,* https://doi.org/10.1002/ece3.7377

Angolan Namib ecoregions as scattered trees and shrubs, within rainfall zones of less than 150 mm per annum (Table 15.1).

Floristic Composition and Physiognomy

Over much of its range, *Colophospermum* is the dominant tree species, varying in density from short, stunted and dense shrublands of 1–4 m in height, through open tree savannas of 5–10 m in height with several companion species, to tall mono-specific woodlands of 10–20 m in height on deep alluvial soils. Soil depth and water relations appear to be responsible for the great diversity of *Colophospermum* growth form. Shallow calcisols derived from calcrete, with limited root access to permanent water

Fig. 15.2 Mixed mopane woodlands and thicket below granite domes and inselbergs below the Angolan Escarpment, between Lubango and Caraculo

Fig. 15.3 Mixed mopane woodlands and thicket below granite domes and inselbergs below the Angolan Escarpment, between Lubango and Caraculo. Morro Maluco (*Dente do Dragão*) in background

Table 15.1 Climatic data for stations in Angolan Mopane Woodlands

	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest month (°C)	Coldest month(°C)
Chitado	Cunene	1000	405	24.0	27.4	19.2
Bruco	Namibe	699	466	23.8	25.7	19.5

Mean Annual Precipitation (MAP), Mean Annual Temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

supplies, result in dense shrub communities. Where breaks in the calcrete substrate allow deep penetration of roots to more reliable water supplies, tall trees establish, often forming single- or multi-stemmed groves of trees to 20 m height. In Angola, most of the tall woodlands that used to occupy the richer, deeper soils at the base of the Chela escarpment have been felled for charcoal production. Mature stands of tall mopane woodland survive in parts of Mupa National Park and the western Cuvelai.

The Angolan Mopane Woodlands ecoregion has a very low diversity of plant species, both within communities (alpha diversity), between communities (beta diversity) and across landscapes (gamma diversity). This characteristic has not been explained, and is remarkable given the wide geographic range of mopane and the diversity of landscapes, soils and regional climates that it occupies. *Colophospermum mopane* has a number of companion species across its extensive range, including *Acacia nigrescens, A. nilotica, A. tortilis, Adansonia digitata, Albizia harveyi, Balanites angolensis, Boscia foetida, B. albitrunca, Combretum apiculatum, Commiphora spp., Dalbergia melanoxylon, Kirkia acuminata, Sclerocarya birrea, Spirostachys africanus, Terminalia prunioides* and *Zizyphus mucronata*. Grasses of the genera *Anthephora, Aristida, Cenchrus, Eragrostis, Enneapogon, Schmidtia, Stipagrostis* and *Themeda* dominate the short, herbaceous layer.

Grass cover can vary from very sparse during dry periods to dense after rains. Mopane herbaceous communities are climate-driven, being dependent on infrequent but occasionally high intensity rainfall, differing fundamentally from the herbaceous strata of mesic miombo systems, which are fire-driven. Drought conditions are frequent, broken by rare but powerful floods. Fires are infrequent, especially if herbivore biomass is high relative to the available forage. While the woody component is resilient to rainfall variations from year to year, the herbaceous layer is very sensitive. In droughts, perennial grasses and herbs might be completely removed by the grazing and trampling of herbivores, with rapid replacement by annual grasses and herbs following the first rains. Perennial grasses usually have a good seed store in the otherwise barren soil, and within one or two good rainy seasons these grasses can recover to pre-drought cover and biomass.

Soils play an important role in the species composition of *Colophospermum mopane* communities. Where clays transition to sands, *Terminalia sericea* replaces *T. prunioides*. On the vertic swelling/shrinking clays of basalts, such as those along the Caculovar, *Acacia kirkii* is abundant together with stunted *Colophospermum*, replacing *A. tortilis* and *A. nigrescens* as companion species. On the rocky, shallow soils of well-drained hills, *Combretum apiculatum* is in mixed communities with *Colophospermum mopane, Boscia foetida, Terminalia prunioides, Commiphora angolensis* and the shrubs *Catophractes alexandri, Grewia flava, Rhigozum brevispinosum* and *Sesamothamnus lugardii*. The range occupied by *Colophospermum* extends deep into the Namib, where it is found together with *Welwitschia mirabilis* in deep coarse sands of dry river beds.

Determinants of Distribution and Population Dynamics

Perhaps because of the singular physical characteristics of mopane and its sharply delimited geographic range, the factors that determine its distribution have attracted much interest from ecologists. Recently, researchers have provided mechanistic models of key constraints to *Colophospermum mopane* distribution and growth form, at local scales in terms of physiological performance (February et al., 2020), and at regional scales in terms of environmental determinants (Makhado et al., 2014) and demographic dynamics (Stevens, 2021).

Early studies suggested that the southern limit of mopane occurs where the average July minimum temperatures fall below 5 °C, and where frequent frosts and cold snaps in valleys caused by cold-air drainage result in tree mortalities. The northern limit was explained by higher rainfall, with higher fuel loads and higher fire impacts on seedling and sapling recruitment. Rainfall timing and amount was also considered to influence competition from faster growing grasses for resources such as moisture, nutrients and sunlight. Day length, and hence latitude, too, were considered, as were excessive herbivory and damage by elephants. Locally, soil conditions, through physiological drought in clay soils, or waterlogging on sites with impeded drainage, were also proposed as constraints to the distribution of mopane. These explanations of the sharp limits to mopane distribution have recently been addressed systematically by Stevens (2013, 2021).

Stevens has reviewed available literature and has undertaken field and laboratory studies on the demographic factors that influence mopane seed production and germination, and seedling, sapling and adult growth and survival to reproduction. She concluded that a series of demographic processes and environmental pressures interact to shape the species' current range. Individual plants have to pass through several **growth thresholds**, most importantly, to escape top-kill. **Top-kill** is the process whereby fire or herbivory suppresses saplings from developing into mature trees. Once saplings reach over 2 m height, they can escape such damage. Stevens found that these pressures often maintain mopane at a coppicing multi-stemmed shrub form, which is functionally sterile (Fig. 15.4). The growth thressholds include:

- First, specific rainfall events and adequate seed resources must be sufficient to drive a pulsed episodic recruitment of seedlings;
- Second, seedling root growth must be sufficiently rapid to reach moisture below the evaporation layer of the topsoil;
- Third, sapling growth must be sufficiently fast to reach over 2 m height in order to escape top-kill from fires and herbivory; and,

Fig. 15.4 Shrub growth form of *Colophospermum mopane* in central Kruger National Park, with isolated tall trees where access to water or protection from fire resulted in rapid growth above the fire and herbivore 'top-kill'. *Photo* Izak Smit

- Fourth, adults must pass a height threshold of 4 m at which flowering, wind and insect pollination, and the production of seeds is more successful.

Once established, mopane communities of either shrub or tree forms are resilient to drought, heat, frost, fire and herbivory. While top-kill can result in coppicing, mortality resulting from this process is seldom recorded, except in local patches during extended droughts, or recurrent fires, or where elephants exert high levels of damage, transforming tall woodlands into isolated trees within a coppicing shrubland. Once the structure of a tall woodland has been reduced by damage into a shrubland, return to a woodland is prevented by a strong coppicing habit in response to disturbance. Stevens (2021) noted that mopane trees do not self-prune, and that the coppicing shoots do not thin out to develop a single leading shoot that becomes a tree. Instead, the multi-stemmed shrub form persists. In the absence of tall trees, the seed source for seedling recruitment is severely reduced.

In the Luangwa National Park of Zambia, Caughley (1976) reported that large areas of mopane woodland had been transformed by elephant damage into a functionally sterile shrubland. During the drought of 2015/2017, a similar impact from elephant damage was experienced in Kruger National Park.

In summary, Stevens (2021) proposed that the range limits of *Colophospermum mopane* and the development of short mopane shrublands are determined by the interactions of disturbance events (fire, frost and herbivory). These factors lead to a high proportion of effectively sterile shrubs, and the lack of recruitment of mature, fertile trees sufficient to maintain a viable population. Stevens planted mopane experimentally at sites outside its natural range—at higher, cooler elevations and higher latitudes (more than 500 km south of its southern limit). She found that the seedlings survived and grew especially in the absence of grass competition, so that climate and soil did not directly limit distribution. She therefore argued that climate-based range predictions for mopane do not reflect the demographically-driven constraints on the species' distribution, determined by top-kill, by fire or by herbivory, and therefore not by climate. This hypothesis merits testing in Angola, especially in the lower Cunene Basin, where frost can be a limiting factor.

Box 15.1 Sodic Soils and Salt Licks in Mopane Woodlands

A common feature of mopane woodlands and other arid savannas are **sodic soils**, often found at the base of catenas in the granite hills of undulating landscapes. In these sites, *Colophospermum mopane* forms a pattern of wooded patches scattered within a matrix of bare, salt-rich soils. The shrub *Euclea divinorum* and succulents such as *Sanseviera pearsonii* and *Aloe zebrina*, and even the epiphytic orchid *Ansellia gigantea* on large mopane trees, are typical of such communities along the Cunene River near Humbe.

Such bare patches of pale-coloured clay soils are often considered to be due to local overgrazing by herbivores, but they are a world-wide phenomenon in arid savannas. They are typically formed by natural, evapotranspiration-driven hydrologic processes in sodium-rich granitic landscapes (Khomo & Rogers, 2005). The colluvial runoff of salts down the catena accumulates at the base of slopes. Salts are further concentrated by the high evapotranspiration rates of the hot dry climate. On filtering into the soil, the sodium causes clays in the A-horizon to **deflocculate** (disperse) and form an impermeable B-horizon, cutting off the movement of water that would normally move upwards by hydrological processes. This sodic water seal causes the death of plants not adapted to such conditions. Bare patches are typically associated with such sodic soils (Fig. 15.5).

Fig. 15.5 An example of a sodic patch in Kruger National Park. These open sites in wooded landscapes are often at the foot of granite hills, or next to rivers. Their whitish appearance is due partly to their high sodium content. They play a critical role in the life of herbivores in arid savannas. *Photo* Izak Smit

While sodium is not an essential plant nutrient, it is essential for mammals. The bare patches are thus attractive to herbivores, not only because of the salt content of the soil, but also because these soils are favoured by nutritious grasses, which have higher levels of sodium in their leaves than even the same species growing on adjacent low sodium soils. The herbivores concentrate on these bare patches, reducing plant cover, increasing soil nutrition via their faeces, compacting the surface through trampling, and gradually reinforcing the denudation of the habitat. Pools formed during rainy periods are rich in clays and are used as mud baths by warthogs. Sodic patches provide fascinating venues to study soil/plant/animal interactions within the broader matrix of arid savannas.

15.2 Namib Savanna Woodlands (Ecoregion 13)

Distribution

The Namib Savanna Woodlands Ecoregion (WWF 104; Barbosa 27) is a narrow belt of arid shrublands, savannas and woodlands extending northwards from the Cunene

River to Sumbe in Cuanza-Sul (Fig. 3.31). It lies between the Angolan Namib Desert and the Angolan Mopane Woodlands ecoregions. In the south, it occurs on the hilly and mountainous hinterland of Iona National Park and up the rugged Cunene valley to Chitado. Barbosa (1970) used the term 'steppe' for this vegetation formation, but this term is inappropriate for use in Africa. The vegetation comprises short trees, shrubs and grasses—a typical tropical arid savanna. Rainfall increases from south to north, and from west to east, and ranges from 150 to 400 mm per annum. The high peaks of the Cafema and Tchamalinde mountains in Iona National Park possibly receive somewhat more rain than the plains, but the vegetation throughout is arid to sub-desertic.

The topography varies from broad, almost flat coastal peneplains, often with extensive calcrete pavements, to scattered hilly outcrops of limestone, sandstone, gneiss, granite and schist. Soils are shallow and comprise calcisols, lixisols, leptosols and arenosols. Ephemeral rivers and streams cut across the landscape. The valleys are usually shallow, but in some cases, rivers such as the Curoca, Bero, Giraul and Bentiaba, have cut deep ravines, with sandy bottoms, subject to rare but intense flooding events. The perennial Cunene follows a deep gorge between the Tchamalinde Mountains of Angola and the Baynes Mountains of Namibia, both of which reach over 2000 m.

Serra da Neve, an isolated inselberg of igneous alkaline carbonatite (Fig. 15.6), which rises above the plains covered in Namib Savanna Woodlands, is of particular biogeographic interest. Reaching 2489 m above sea level, it carries a succession of vegetation types similar to those on the Leba Pass described in Chap. 5.7, but awaits detailed exploration. The high peaks of Serra da Neve, Cafema and the Tchamalinde possibly also benefit from orographic cloud brought in off the Benguela Current, but this has yet to be documented (Fig. 15.7 and Table 15.2).

Floristic Composition and Physiognomy

This ecoregion, perhaps more than any other in Angola, has fine-scale vegetation patterns where topography, geology, soil depth and texture offer different moisture and nutrient conditions. Between Sumbe and Iona, over a distance of 550 km, plant communities display a rapid turnover in floristic and structural composition. Although species diversity is low, the floristic composition and height, density and architecture of both woody and herbaceous components, is ever changing.

The general pattern is a mix of a limited set of woody and herbaceous species, forming short open savannas and woodlands on hills and open grassland on the deeper sands of intermontane plains. Communities of *Acacia mellifera* can cover large areas, to be followed by savannas of *Acacia nilotica, A. tortilis* or *A. reficiens*, or mixed communities including *Acacia tortilis, Balanites angolensis, Boscia albitrunca, B. foetida, Catophractes alexandri, Colophospermum mopane, Combretum apiculatum, Dichrostachys cinerea, Maerua angolensis, Rhigozum brevispinosum, Salvadora persica, Spirostachys africana, Sterculia setigera*, *Terminalia prunioides* or various species of *Commiphora* on shallow, rocky soils and on schist or granite outcrops. Short nutritious grasses include species of *Cenchrus, Enneapogon, Schmidtia, Stipagrostis, Themeda, Tricholaena* and *Urochloa.* Succulents are common, such as

Fig. 15.6 Mixed Namib Savanna Woodlands south of Serra da Neve, which rises to 2489 m. The dark green line of tall trees in the middle-distance marks the Bentiaba river

Fig. 15.7 Namib Savanna Woodlands dominated by *Acacia* species on the Talamajamba plateau, 40 km inland of Benguela. Rich grasslands following summer rain. *Photo* Antonio Martins

Table 15.2 Climatic data for stations within the Namib Savanna Woodland ecoregion

Station	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest Month (°C)	Coldest Month (°C)
Sumbe	Cuanza-Sul	10	389	24.0	27.0	20.1
Baía Farta	Benguela	3	389	22.4	26.3	18.0
Caraculo	Namibe	440	123	22.9	26.4	17.2

Mean Annual Precipitation (MAP), Mean Annual Temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

Aloe littoralis, A. catengiana, Cyphostemma currorii and *Sansevieria pearsonii*, with many succulent arborescent species, including *Adansonia digitata*, *Euphorbia eduardoi, Moringa ovalifolia* and *Pachypodium lealii.*

The deep sands of ephemeral rivers, such as the Curoca, Bero, Giraul and Bentiaba are intermittently lined by tall woodlands of **phreatophytes** (plants using deep water sources) such as *Acacia erioloba*, *Combretum imberbe, Faidherbia albida, Ficus sycomorus, Sclerocarya birrea* and thickets of *Cadaba benguellensis, Cordia ovalis, Euclea pseudebenus, Salvadora persica* and *Tamarix usneoides.*

Typical of arid/eutrophic savannas, this ecoregion has many spinescent trees and shrubs (including species of *Acacia*, *Balanites, Euphorbia, Gymnosporia, Pachypodium* and *Zizyphus*) and even herbs and grasses can be armed with spines. Grasses are generally of high nutritional value through the year, historically supporting large herds of grazers such as Gemsbok and both Plains and Mountain Zebra, and mixed feeders such as Springbok. Most large mammals have been eradicated by humans over the past century and replaced by cattle and goats as the main herbivores.

15.3 Coastal Arid Savannas (Ecoregion 14)

Distribution, Landscapes and Climate

The Coastal Arid Savanna ecoregion includes the coastal lowlands (from sea level to 500 m) where annual precipitation ranges from 350 to 650 mm, from Sumbe in the south to the coast of Cabinda in the north (Fig. 3.32). The ecoregion follows the mostly narrow lowlands of the sedimentary basins of Angola's coastline, a mix of Quaternary and Tertiary marine sediments. Pleistocene sands of former beaches form flat plateaus of red, yellow and grey sands (musseques) which cover earlier Lower Cretaceous to Miocene sediments of clays, limestones, marls, sandstones and conglomerates. The ecoregion extends up the Cuanza valley for 180 km, but is mostly less than 50 km in width.

The cooling and drying impact of the Benguela Current has a profound influence as it moves northwards along the Angolan coast. A narrow belt of low mean annual precipitation, but high relative humidity, creates a climate in which arid savanna elements extend to the mouth of the Congo River where mean annual precipitation is 590 mm. The unusual and dense coverings of the lichenised fungus *Roccella tinctoria* on the trunks of *Adansonia digitata* trees, and tresses of fruticose lichens (*Usnea* spp) hanging from the branches of thicket trees, is at first sight somewhat surprising in this arid environment. High relative humidity, accompanied by coastal fogs and persistent low stratus clouds (*cacimbo*), are accounted for by the presence of a persistent temperature inversion over the cool Benguela Current (Fig. 16.6).

Floristic Composition and Physiognomy

Due to the erosion and planation of successive marine and terrestrial sedimentary strata, the vegetation cover of Coastal Arid Savanna presents a repeated and predictable sequence of floristic composition and physiognomic structure. Barbosa (1970) recognised nine sub-types within his vegetation type 23. From south to north, one tree species characterises the diverse grasslands, savannas, woodlands, thickets and dry forests of this ecoregion: *Adansonia digitata.* The baobab (*imbondeiro*) has several companion species—*Acacia welwitschii, Euphorbia conspicua* and *Sterculia setigera.*

The fine-scale pattern of communities is reflected in detail in the vegetation map of Quiçama National Park (Huntley, 1972; Fig. 15.8), which includes 28 mapped units over the Park's 9960 km^2. Quiçama plant communities represent the vegetation of the ecoregion, and a few examples will illustrate the diversity of habitats. Grasslands, savannas and woodlands, thickets and dry forests are the main physiognomic types, but closed-canopy gallery forests, floodplain wetlands, mangroves and coastal strand communities, add to ecosystem diversity.

The wide floodplains of the perennial rivers (Cuanza and Longa) that form the northern and southern limits of Quiçama National Park have extensive wetlands dominated by *Cyperus papyrus, Typha capensis* and *Phragmites mauritianus,* with marginal grasslands of *Echinochloa stagnina, E. pyramidalis, Oryza stapfii* and *Vetiveria nigritana* (Fig. 15.9). The escarpment above the floodplain carries deciduous dry thicket (Fig. 15.10).

A rather unique grassland community of this ecoregion is treeless—the monospecific tall grasslands of *Setaria welwitschii* (Fig. 15.11) which occupy the deep swelling and shrinking vertic clays (*terras de Catete*) of Cretaceous marine sediments. On the plateau sands, grasslands are dominated by *Eragrostis superba* and *Digitaria milanjiana*, with tree and shrub clumps associated with termitaria. These grasslands were the richest grazing lands for Quiçama's formerly large herds of Roan Antelope, Eland, Forest Buffalo and Savanna Elephant. Less nutrient-rich grasslands of *Schizachyrium sanguineum, Heteropogon contortus, Andropogon gayanus* and *Pogonarthria squarrosa* form the herbaceous stratum of tree and clump savannas, with the typical mix of tree species already mentioned, plus *Balanites angolensis, Combretum camporum, C. molle, C. zeyheri, Hyphaene guineensis, Maerua angolensis, Strychnos spinosa* and *Terminalia sericea* (Fig. 3.22).

Dense thickets of 5–10 m height are found on plateau red sands with a high clay content (*terras de musseque*) (Figs. 15.12, 15.13, 15.14 and 15.15). These have a mix of deciduous (*Clerodendrum myricoides, Combretum camporum, Grewia*

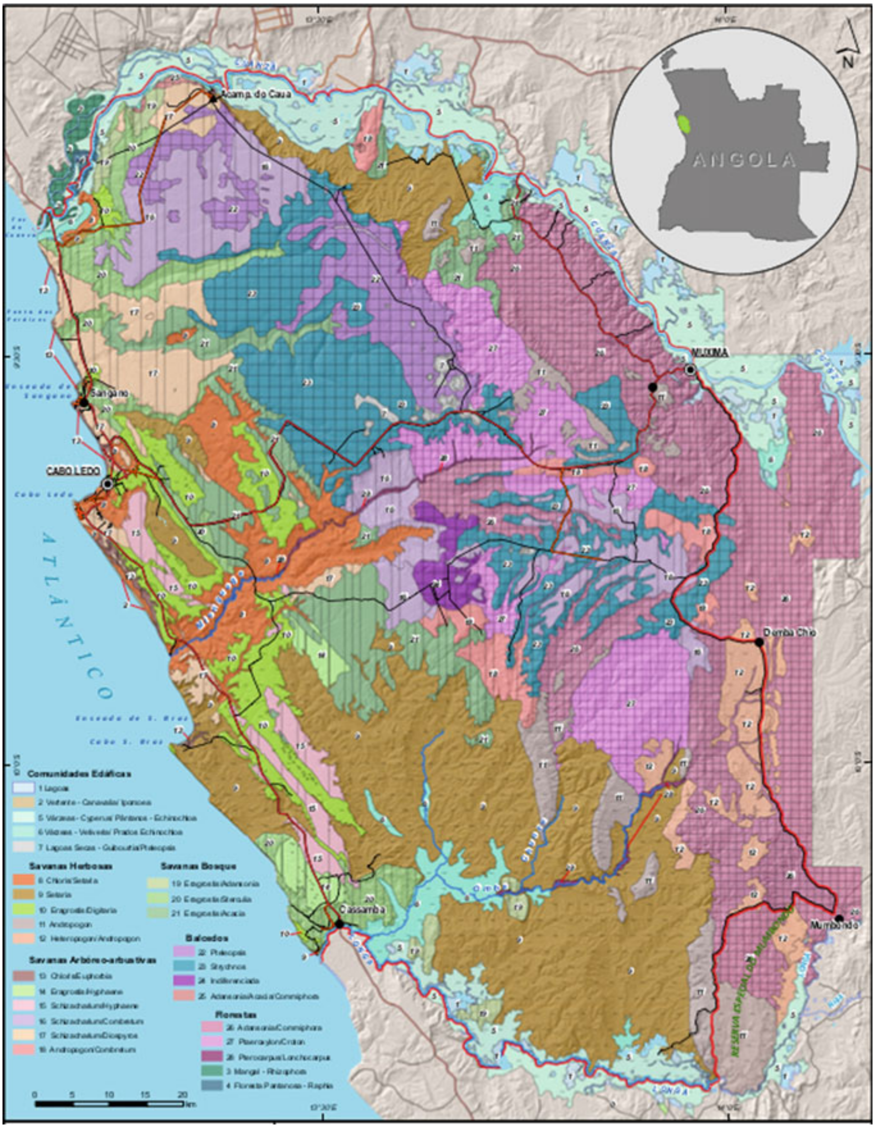

Fig. 15.8 Vegetation map of Quiçama National Park. This 9960 km^2 conservation area has 28 mapped vegetation types, reflecting the diversity of marine and terrestrial sediments on gently undulating landscapes. From Huntley (1972) Parque Nacional da Quiçama. Vegetation Map. Serviços de Veterinária, Luanda

Fig. 15.9 The Cuanza River floodplain below Acampamento da Caua, Quiçama National Park. Dry season deciduous thicket in foreground with grasslands and wetlands on the floodplain. *Photo* Kostadin Luchansky

Fig. 15.10 The Cuanza floodplain, viewed from Acampamento da Caua, Quiçama National Park. Dense dry forest and thicket below the escarpment of the sand plateau, with gallery forest on the margin of the floodplain, lush green during the summer rain season

Fig. 15.11 Tall mono-specific *Setaria welwitschii* grasslands on the deep vertic clays of Quiçama

welwitschii, *Pteleopsis myrtifolia, Strychnos henningsii* and *S. spinosa*) and evergreen (*Garcinia livingstonii*, *Guibourtia carrissoana, Tessmannia camoneana*) shrubs, short trees and emergent succulents (*Euphorbia conspicua*). Grasses (and fires) are rare in the thickets, which are a preferred habitat of Blue Duiker and Bushbuck.

Fig. 15.12 The epiphytic lichen *Usnea* sp. on the branches of *Copaifera coleosperma* in dry thicket

Fig. 15.13 Dry thicket of *Acacia welwitschii, Euphorbia conspicua, Grewia welwitschii* and *Sansevieria cylindrica* on the escarpment slopes above the Cuanza floodplain

Fig. 15.14 Evergreen thicket on deep pale sands of the Quiçama plateau

Dry deciduous forests of up to 15 m height are found on the broken relief of the slightly less arid inland margin of this ecoregion, where it abuts the Angolan Escarpment ecoregion and includes part of Barbosa's (1970) vegetation type 11. Here, on alkaline calcareous soils, the trees, mostly deciduous, include *Adansonia digitata, Acacia welwitschii, Commiphora africana, Croton angolensis, Ptaeroxylon obliquum* and *Pteleopsis myrtifolia.* Where seasonal watercourses cut through the landscape, closed canopy gallery forests of up to 25 m height (*Adina microcephala, Albizia glaberrima, Lonchocarpus sericeus, Millettia thonningii* and *Pterocarpus tinctorius*) are found (Fig. 15.16).

Fig. 15.15 Deciduous thicket on the plateau 'musseque' red sands of Quiçama

Fig. 15.16 Open woodland of *Adansonia digitata* on the margins of the Cuanza floodplain, Quiçama National Park

15.4 Faunal Composition of Arid Savannas

The Arid Savannas of Angola (Ecoregions 12–14) have a distinctive mammalian fauna compared with that of the Mesic Savannas. Typical of arid/eutrophic savannas, many of the herbivores form large herding populations that can number several hundred individuals where they occur in untransformed landscapes. The largest, nomadic herds are formed by Springbok, Gemsbok and Blue Wildebeest. While the first two species are limited to the arid savanna of the southwest, Blue Wildebeest were once numerous in Bicuar, Cuando Cubango and the grasslands of Cameia. Other herding species that occur in the arid savannas and drier limits of mesic savanna include Plains Zebra, Hartmann's Zebra, Cape Buffalo, Red Hartebeest, Common Impala, Topi, Greater Kudu and Giraffe. Black-faced Impala, Black Rhino and African Elephant, once common in the southwest, are now extinct in the area.

Three mini-ungulates, Kirk's Dik-dik, Klipspringer and Steenbok, well-adapted to survival in the absence of free water, were once common in the southwest. Forest Buffalo, Savanna Elephant, Eland and Roan Antelope were once abundant along the northern Coastal Arid Savanna of Quiçama, but were decimated during the civil war.

Many carnivore species, from African Lion to Cape Fox, occur in the arid savannas of southwest Angola. These include African Lion, Leopard, Cheetah, Brown Hyaena, Spotted Hyaena, Aardwolf, Black-backed Jackal, Bat-eared Fox, Meerkat and Honey Badger. Table 15.3 provides a shortlist of typical vertebrate species of the Arid Savanna Biome (Fig. 15.17 and Table 15.4).

Table 15.3 Climatic data for stations in Coastal Arid Savanna

Station	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest month (°C)	Coldest month (°C)
Luanda	Luanda	44	405	24.3	27.0	20.1
Nzete	Zaire	15	381	24.2	26.8	20.1
Dondo	Cuanza-Norte	38	614	26.2	28.5	21.4
Soyo	Zaire	10	590	25.9	28.2	21.2

Mean Annual Precipitation (MAP), Mean Annual Temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

Fig. 15.17 Forest Buffalo (*pacassa*) in dry thicket on the margin of the Cuanza River, Quiçama National Park. This once abundant emblem of Quiçama is now extinct in the Park. *Photo* Merle Huntley

Table 15.4 Vertebrate Species Typical of the Arid Savannas of Angola

- **Amphibians**: Dombe Toad, Grandison's Pygmy Toad, Marbled Rubber Frog, African Bullfrog
- **Reptiles**: Leopard Tortoise, Ansorge's Leaf-toed Gecko, Angola Banded Thick-Toed Gecko, Huntley's Sand Lizard, Sundevall's Writhing Skink, Horned Adder, Western Banded Spitting-Cobra
- **Birds**: Ostrich, Secretary Bird, Monteiro's Hornbill, White-tailed Shrike, Benguela Long-billed Lark, Rockrunner, Benguela Long-tailed Starling, Rufous-tailed Palm Thrush, Cinderella Waxbill
- **Mammals**: Black-backed Jackal, African Hunting Dog, Bat-eared Fox, Cape Fox, Cheetah, Caracal, Lion, Leopard, Spotted Hyaena, Brown Hyaena, Aardwolf, Common Impala, Black-faced Impala, Red Hartebeest, Springbok, Common Wildebeest, Tsessebe, Roan Antelope, Common Waterbuck, Kirk's Dik-dik, Klipspringer, Gemsbok, Steenbok, Cape Buffalo, Common Eland, Greater Kudu, Giraffe, Common Warthog, Plains Zebra, Hartmann's Mountain Zebra, Black Rhino

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Chapter 16
The Namib Desert Biome

Key Concepts and Questions: This Chapter Will Explain

- *What defines a desert.*
- *When and how the Namib Desert landscape was formed.*
- *How the South Atlantic Anticyclone, the Benguela Current, and associated wind systems determine the nature of the climate and ecological processes along the Angolan coast.*

Context: What defines a desert?

Geographers apply the term **desert** to areas where the mean annual precipitation is below 250 mm. In this volume the term is used in a narrower sense, for the extremely arid Namib Desert of Angola and Namibia, where annual rainfall averages less than 150 mm per annum and where animals and plants exhibit remarkable adaptations to survive, grow and reproduce under unusually harsh environmental conditions. A **harsh environment**, such as a desert or an arctic tundra, is defined as one in which specialised morphological, physiological or behavioural adaptations, that are not found in related species, have evolved to survive such conditions.

The Namib Desert extends as a narrow belt, less than 200 km wide, across 2100 km of the southwest African coastline, from the Carunjamba River in Namibe province of Angola to just south of the Orange River near Namibia's border with South Africa. The environmental conditions across this long narrow belt of hyper-arid climate are not uniform, and range from summer rainfall in the north to winter rainfall in the south. The rainfall within the belt decreases 6- to tenfold from the Escarpment to the Atlantic Ocean. Linear oases follow some of the ephemeral rivers that cross the desert, with associated large mammals such as Savanna Elephant, Black Rhinoceros and Giraffe penetrating deep into the desertic landscapes.

In Angola, the Namib Desert occupies a narrow belt 20–80 km wide along the coastal plain, as a wedge between the Atlantic Ocean and the first foothills of the Angolan Escarpment, where it transitions into the Namib Savanna Woodlands ecoregion. The Angolan Namib Desert ecoregion includes vegetation types 28 and 29 of

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https://doi.org/10.1007/978-3-031-18923-4_16

Barbosa (1970) merging with the western half of Type 27. This defines the ecoregion as a narrow tongue, northwards from the Cunene, past Moçâmedes to the Carunjamba River near Lucira (Fig. 2.37).

Angola's Namib Desert (Ecoregion 15)

16.1 The Age and Evolution of the Namib Desert

The Namib Desert of Angola and Namibia, and the Atacama Desert of Chile, are reputed to be the oldest deserts in the world. Exactly how old they are is still uncertain, and the history of the Namib is still the subject of much debate. John Ward, a South African geologist with extended experience in Angola and Namibia, reviewed hypotheses on the age of the Namib in two important papers (Ward et al., 1983, Ward and Corbett, 1990). Based on an understanding of the stratigraphy (layering of geological sediments) of southwestern Africa, Ward described five phases to illustrate the long history of Namib aridification.

Post-Gondwana Erosion Phase (*Cretaceous*: 130–80 Ma)

Following the breakup of Gondwana (130 Ma), much of the Great Escarpment was formed between 120 and 100 Ma by the uplift of the Earth's crust, with some features of the escarpment dating back to much earlier times, relicts from 300 million years ago. The evolving Namib landscape was eroded by both marine and terrestrial forces. As much as 2 km depth of soil and rock was stripped off the landscape. In Angola, some of the products of this erosion are known as the Giraul conglomerates, exposed along the Giraul River in Namibe. Offshore deposits are several km thick, the result of many millions of years of erosion of the terrestrial landscape. Marine erosion resulted in a beveled platform named the **Namib Unconformity Surface**. This landscape feature, which cuts across schists, gneisses and granites, dates from 85 Ma. Numerous inselbergs rise above the coastal plains. By 80 Ma, the separation of Africa from South America and the establishment of the South Atlantic Ocean was concluded. At the end of the Cretaceous (66 Ma), the physical boundaries of the Namib (Great Escarpment, Atlantic Ocean, and the Namib Unconformity Surface) were in place.

Proto-Namib Desert Phase (*Paleogene*: 55–23 Ma)

The earliest unequivocal evidence of desert conditions in the Namib (from 55 Ma—the Eocene Epoch) is provided by extensive fossil dunes known as the **Tsondab Sandstone Formation**. Southerly winds, driven by **the South Atlantic Anticyclone** which had established by this time, and the position of the Namib in the southwestern rain-shadow of the southern African subcontinent, were the key drivers of aridity and the formation of the extensive sand dunes of the Proto-Namib (also known as the Palaeo-Namib).

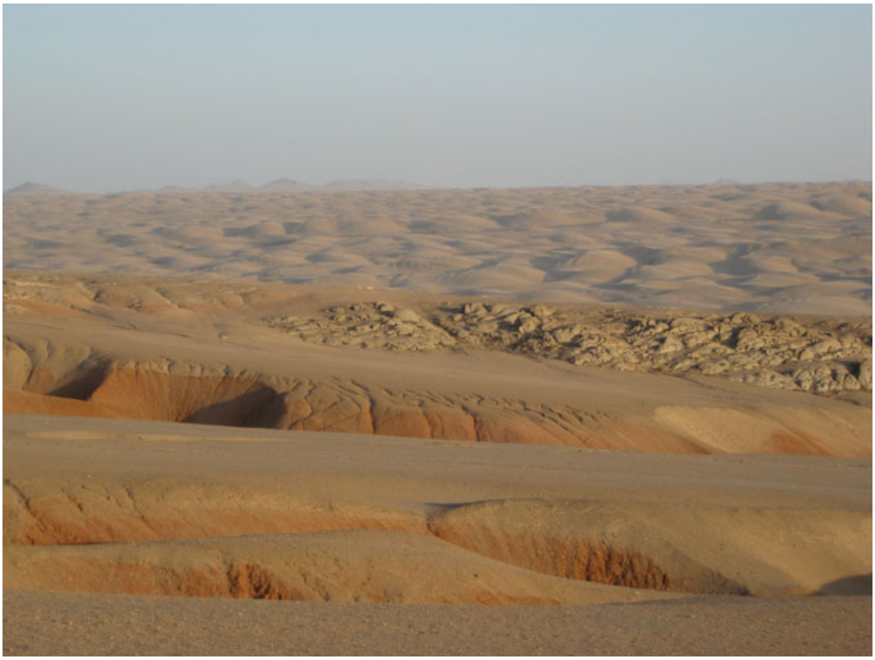

Fig. 16.1 Ancient and modern dune systems of the Namib Desert. In the foreground, the eroding face of a deep red fossil dune of Tsondab Sandstone underlies the paler sands of the modern Namib. In the background, behind the granite exposure, and south of the Cunene (hidden from view), lie the dunes of the Cunene Sand Sea

The reddish-brown Tsondab sandstones, of up to 220 m depth, were deposited over a period of 20–30 million years. They extend from central Namibia to the Curoca River in Angola. Remnants of these ancient dunes are mostly preserved under later gravel, calcrete and sand deposits, but an example can be seen in Iona National Park, at the southern end of the Vale dos Rinos (Fig. 16.1).

The environmental conditions through this long period were not uniformly stable. Fossil evidence from 47 to 42 Ma, for example, reveals humid summer-rainfall conditions with wooded vegetation in the area that is now Namib Desert. But by 34 Ma the Antarctic Ice Sheet had formed, with consequent aridification in the period known a ‘Ice-house Earth’. Semi-arid climates with woodlands and early African mammals (Afrotheria) such as elephant shrews, golden moles and hyraxes are revealed in the fossil record. Even primate fossils were found in these fossil beds. But as Ward et al. (1983) caution, the presence of primates (and other mammals associated with wooded vegetation, such as elephant, giraffe and rhino) does not imply widespread mesic conditions. These mammals today penetrate deep into the Namib Desert along the linear oases of wooded river beds, which provide narrow fingers of suitable habitat within an otherwise hostile environment.

Pluvial (Humid) Phase (*Early-Middle Miocene*: 23–14 Ma)

A period of more humid conditions during the Early to Mid-Miocene is indicated by widespread deposits of gravels that overlie the Tsondab Sandstone Formation. The erosion and deposition of these gravels would have required a wet period reflecting higher rainfall on the interior plateau, escarpment and desert tract. This period was not necessarily uniformly moist. Eggshells of three genera and eight species of ostrich, including Giant Ostrich—*Diamantornis wardi*—associated with arid environments—have been found in the Tsondab sandstones of ca. 19 Ma.

Pedogenic (Calcrete) Phase (End Miocene: 14–11 Ma*)*

Following the more humid phase, a semi-arid period of summer rainfall with 350–450 mm per annum, supported the development of calcareous soils, signaling the onset of aridity with the full establishment of the Benguela **up-welling** system from 10 to 7 Ma. These calcretes, of up to 5 m thick, cover the older gravels and sandstones, and predate their erosion by westward flowing rivers (Cunene, Ugab, Kuiseb) that cut across the Namib in response to uplift during the Pliocene (5.3–2.6 Ma).

Namib Desert Phase (Late Miocene—Holocene: 10 Ma*—present)*

The Namib reached its extreme aridity in the Late Miocene (about 10–7 Ma) when the Antarctic Ice Sheet reached full development. The establishment of the cold, upwelling Benguela Current occurred during this period and accentuated desertic conditions. While it is not considered a primary contributor to the formation of the Namib Desert, the Benguela Current has played a key ecological role through the coastal fog that it triggers (Sect. 16.3). Behavioural adaptations such as 'fog-basking' in Tenebrionid beetles would have followed the establishment of the Benguela Current and the high frequency of coastal fogs. The combined forces of the northward-moving Benguela Current, and the easterly trade winds that blow across its surface waters, cause the upwelling of cold water from 300 m depth, which brings rich nutrients to the surface. These waters, when exposed to sunlight, create ideal conditions for marine productivity, based on abundant phytoplankton, and supporting vast populations of fish, seals and seabirds.

The dunes of the Central Namib Sand Sea are considered of Plio-Pleistocene age, (from 5 Ma) with those of the Curoca being more recent, and their development continues to the present day.

Source of the Dune Sands

Besides the age of the Namib, a second question relating to the evolution of the Namib has enjoyed much interest: the source of the sands that characterise the desert dunes. The answer lies in the patterns of landscape evolution over many millions of years. The courses of most rivers draining southern Africa have changed dramatically since the continent's formation. At about 42 Ma, the Orange River (on the border between South Africa and Namibia) cut a deep course through the landscape, eroding the Jurassic sandstones of the South African Drakensberg. About this time, the Orange River breached the Great Escarpment, thereafter depositing vast amounts of sediment sourced from the eroded sandstone into the sea. The geological, oceanographic and climatic history following these events resulted in dune systems being formed on the coasts of Namibia and Angola. These dunes accumulate sand through the combination of river, marine and wind transport of the sediments.

Today, as in the past, the sediments from the interior of southern Africa are carried to the sea by the Orange River and are transported northwards by strong and persistent **longshore swell-driven waves**, which create what is described as a **marine conveyor belt**. Some of these sediments are washed ashore and blown inland by the southerly and southwesterly winds generated by the South Atlantic Anticyclone, as described in Sect. 16.3. The marine conveyor belt system, starting at the mouth of the Orange River, ends 1750 km farther north in the marine canyons at the mouths of the Bero and Giraul rivers. These deep canyons direct the remaining Orange River sediments out to the deep ocean, preventing their further migration up the coast. The submarine sand conveyor provided by the coastal waters off Namibia and southern Angola is the longest 'sand highway' on Earth (Garzanti et al. 2014, 2017). Most of the sand from the Orange River ends up in the Central Namib Sand Sea of Namibia but sufficient quantities reach Angola to provide 74% of the sand of the dunefields of Iona National Park. The balance of sand of the Iona dunes comes from the Cunene River (18%) and the Hoarusib River (8%) in Namibia.

Synopsis

While geologists continue to debate the age of the Namib Desert, they agree on the three key drivers of its origin and ecology. These are the combined influences of the South Atlantic Anticyclone, the subcontinental rain shadow, and the upwelling of the Benguela Current. Collectively, these factors have resulted in hyper-aridity, off-shore and onshore winds, and fog—the forces driving the formation of the Namib Desert over many millions of years, and of the unique adaptations evolved in animal and plant life.

16.2 Landscapes and Soils

Today the Namib Desert comprises a wide diversity of landscapes, the most iconic of which are the Sand Seas of the Central Namib and the Cunene-Curoca dunes south of Moçâmedes. Most of the Namib Desert lies on an extensive peneplain, a gentle seawards-tilted erosional surface. The erosion reveals a complex pattern of geological evolution through 1800 million years, from the oldest intrusive igneous anorthosite rocks of the Kunene Complex to the modern mobile sands of the Namib Sand Sea.

The Namib presents a living text book on Angolan geology. Along the coast, in addition to the Pleistocene sands, the deep marine deposits of the Benguela and Namibe Sedimentary Basins include Lower Cretaceous to Miocene clays, limestones, sandstones and conglomerates. Many of these are rich in fossils of marine vertebrates and invertebrates (Mateus et al., 2019). Further inland, extensive plains stretch to the horizon. The landscape is traversed by geological features such as jointing, onion-skin weathering, dolerite dykes, and quartzitic and marble exposures. Outcrops of metamorphic and igneous intrusions, including granite, limestone, dolorite, schist and amphibolite, interrupt the plains. The surface is a mix of gravel and broken rocks, formed from the breakdown of duricrusts. These planation surfaces have been incised by small gullies, but are also bisected by major rivers, some perennial (Cunene), but mostly ephemeral (Curoca, Bero, Giraul, Bentiaba, Carunjamba). Figures 16.2, 16.3, 16.4 and 16.5 illustrate some Namib Desert landscapes.

Soils are seldom formed in this dry, hot, windswept landscape. What one finds in most areas is a hard crust formed by the cementation of quartz gravel or through evaporation of the little water received from rain and fog. Evaporation concentrates gypsum or calcium to form gypcretes or calcretes respectively. But some raw soils accumulate in breaks in the hard surface, providing enough reserves of nutrients and water to sustain the sparse vegetation that can survive this harsh environment.

Gypsum (calcium sulphate) is formed by the reaction of sulphuric acid with calcium carbonate, with the moisture provided by fog, and the sulphate produced by marine phytoplankton, and carried inland by the southwesterly winds. Over millions of years, the influence of the Benguela Current has produced gypcrete pavements of over four metres in depth. Gypcretes are usually found within 50 km of the sea. These

Fig. 16.2 Landscapes of the Angolan Namib. Contrast between a white marble and black dolerite

Fig. 16.3 A quartz gravel pavement with scattered *Commiphora* and *Acacia trees*

Fig. 16.4 Landscapes of the Angolan Namib. Calcrete pavements broken by a dry stream bed

Fig. 16.5 Sand dune and marble outcrop, central Iona

pavements are the habitat of profuse lichen fields in the Central Namib of Namibia, but lichen communities are less well developed on the Angolan coast.

Calcrete crusts are formed in situ by atmospheric precipitation of calcium carbonate in an arid environment. Calcretes cover much of the Angolan Namib, as extensive plains, bare of anything but sparse dwarf shrubs and hardy grasses for most of the time. However, following episodic rain showers, the gravel plains turn verdant green with annual species of *Aristida, Schmidtia* and *Stipagrostis* grasses. Rain events, in which from 10 to 50 mm may fall over only a few days, are sufficient to trigger the rapid growth of the annual grasses.

Most symbolic of deserts are the mobile sand dunes that have formed the dune system between the Foz do Cunene and the Curoca River. The Angolan Namib dunes take on a variety of forms—linear, star, barchan or longitudinal—depending on wind direction and age of formation. Many dunes preserve evidence of changed wind patterns through drier and wetter phases of the Pleistocene, processes that continue to the present day.

The sand dunes do not develop organic soil as it is normally understood, with recognizable horizons and general stability. But even these moving sands have been colonised by sand-stabilizing grasses such as *Stipagrostis sabulicola* and succulent shrubs such as *Trianthema hereroensis* (in Namibia), and the spiny *Acanthosicyos horridus* (in Angola). Despite their inhospitable appearances, the Namib dunes support a diverse spectrum of vertebrate and endemic invertebrate animals (including the iconic bicolour fog-basker *Onymacris bicolor* (Fig. 11.7).

16.3 Climate: The South Atlantic Anticyclone, the Benguela Current and Wind

Whereas factors such as soils, fire and herbivory shape the mesic and arid savannas of Angola, it is the extreme aridity of the Namib, and subtle aspects of rare moisture sources, that dominate its ecosystem structure and functioning. Here the climatic processes, developed over many millions of years, will be discussed, addressing a central question: why is the Namib so dry? It will also show why wind (the movement of air from areas of high atmospheric pressure to areas of low pressure) is such an important factor in the evolution and dynamics of the Namib.

Three major oceanic/atmospheric processes interacting in diverse ways account for the maintenance of the hyper-aridity of the Namib and its extraordinary biota. These are the quasi-stationary offshore South Atlantic Anticyclone, the Benguela Upwelling Current, and the winds associated with these oceanic and atmospheric phenomena.

As described in Chap. 5.3, the atmosphere over southern Africa is dominated by two pressure systems. These are the low-pressure Intertropical Convergence Zone (ITCZ), which lies over the Equator, and a sub-tropical belt of high pressure (which includes the South Atlantic Anticyclone) which lies over the Tropic of Capricorn. In summer, moist air produced along the ITCZ moves south, sheds its moisture, and sinks, as dry air, in the high-pressure belt. Moisture from the ITCZ, which accounts for the high rainfall of northern Angola, does not reach the Namib.

Paradoxically, despite its position bordering the Atlantic Ocean, the Namib receives its sparse rain not from the Atlantic, but from the Indian Ocean. In summer, the southeast trade winds bring moisture across the continent from the Indian Ocean. With rare exceptions, most of this moisture is lost before it reaches the west coast. But a little moisture reaches the Namib in unpredictable showers that can bring an abundance of life to the desert. These episodic rainfall occurences are especially evident during **La Niña** events, when the easterly trade winds strengthen and carry Indian Ocean moisture further west than normal. In 1976, during such an event, over 100 mm rain fell over the Central Namib, with the grasslands producing 56 times the normal standing crop, attracting Gemsbok and Springbok populations of 50 times the density of surrounding areas (Seely & Louw, 1980). A similar event occurred in January 2021 during the passage of cyclone Eloise across southern Africa.

The South Atlantic Anticyclone, positioned over the ocean, creates a pressure gradient from west to east, between cold sea and warm land, which in turn produces strong **onshore** winds through most of the year. These winds become **southwesterlies** due to the effect of the Coriolis force, and are strongest in early to mid-summer. They are responsible for maintaining the northward movement of sands from the Foz do Cunene—probably the windiest place in Angola—to the Curoca, where the dune head is periodically washed out to sea by once-in-a-century floods.

To residents in Moçâmedes, an all too familiar weather feature is that of the dust-laden but warm **easterly winds** that occur during autumn and winter. These winds are due to the periodic weakening of the South Atlantic Anticyclone. At these times the air pressure over the subcontinent is higher than that over the Atlantic. A pressure gradient from east to west brings the east winds across the warm land surface, with the air being heated further by **adiabatic** heating due to the increased pressure on the air mass as it descends down the escarpment. These winter **katabatic 'berg'** winds pick up dust and plant debris as they move across the landscape and down the escarpment, bringing nutrients to the animals of the dune sea, and depositing the fine organic matter that they carry from the interior.

The prevalence of **fog** (***cacimbo*****),** for up to 120 days per year, is a unique and critically important feature of the Namib. The narrow coastal belt from Tômbua to Lucira, in particular, experiences drenching over-night fog as a result of a **temperature inversion** created by the cold Benguela Upwelling Current. Normally, air temperatures decrease with altitude by between 0.6 and 0.9 °C per 100 m rise in elevation (Chap. 5.4). However, over the cold Benguela Current, the air temperature increases with height. The warm air above acts as a 'cap' to normal convection, inhibiting the rise of the cool, moist air which would normally form rain clouds. Instead, this humid air moves inland as a shallow layer of fog, bringing very limited, but important moisture to a narrow belt along the Namib coast. Figure 16.6 illustrates the atmospheric processes along a latitudinal cross-section above the Angolan coast, from the Congo to the Cunene.

Two types of fog occur over the Namib. First, a shallow bank of very moist air, usually up to 200 m high, is borne on southwesterly winds and carried up to 15 km into the desert. The fog is deposited as a fine drizzle or film of moisture on soil, plants or animals, such as *Onymacris* beetles, behaviourally adapted to intercept fog on the crests of desert dunes. Second, a high fog (more correctly a low **stratus or strato-cumulus** cloud) forms at 100–600 m height in the atmosphere as a wedge of

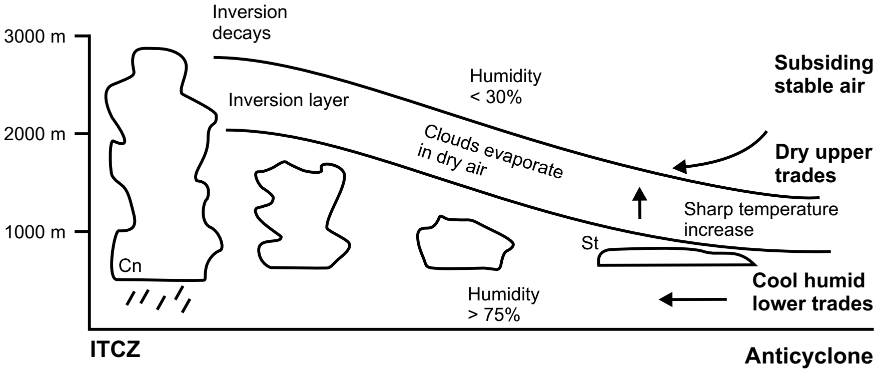

Fig. 16.6 A simplified cross-section of the atmosphere above the Angolan coast from the Congo River (left), to the Cunene River (right). Note the influence of the inversion layer over the cool southern coast, rising and breaking down before the Inter-tropical Convergence Zone in the north. St = fog-bearing stratus clouds; Cn = rain-bearing cumulo-nimbus clouds. Redrawn with permission after Leal (2004) *The African rain forest during the Last Glacial Maximum.* Ph.D. thesis, Wageningen University, Wageningen

Table 16.1 Climatic data for Stations in the Angolan Namib Desert Ecoregion

Station	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest month(°)	Coldest month (°C)
Lucira	Namibe	5	104	21.2	26.2	18.0
Moçâmedes	Namibe	44	37	20.0	24.2	15.5
Tômbua	Namibe	4	12	20.1	24.2	14.5

Mean Annual Precipitation (MAP), Mean Annual Temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

moist air trapped below an inversion layer of warmer air. This fog penetrates up to 100 km inland from the coast, especially up valleys and into depressions. Beyond the Namib, it is particularly important along the Angolan Escarpment, where it supports a rich diversity of vegetation, including the ‘coffee forests’ of Uíge and Cuanza-Sul.

Research in the Namib has shown that fog deposits up to five times more moisture than rain in the narrow belt of the ‘hyper-arid’ coast. Fog supports a rich lichen flora on the coast northwards of Moçâmedes, where crustose lichens cover the rocky desert surface, and foliose lichens hang as tassels from the shrubs and short trees of an otherwise desolate landscape.

In the creation and maintenance of the Namib Desert, **wind** has been a key contributor to processes at macro to micro levels. From the earliest events that triggered the aridification of the Namib, through the development of the marine conveyor belt of sand transportation and deposition, the processes of dune formation and dynamics, the transfer of infrequent and sparse rainfall from the Indian Ocean to the Namib, and of fog from the Atlantic to the Namib coast, wind driven by atmospheric forces has shaped the desert. At the micro-scale, organic detritus carried into the dune fields by ‘berg’ winds supports the abundant life of a harsh environment, sustained by the fog carried by cool breezes from the ocean. Few ecological systems demonstrate the interactions between ocean, atmosphere and land more clearly than the Namib.

There are very few weather stations in the Angolan Namib Desert, but the few that exist give an indication of the extreme aridity of the ecoregion (Table 16.1). The importance of fog as a source of moisture is not captured in the rainfall statistics, nor is the cooling influence of the ‘wind chill’ factor of cold northerly winds that are a characteristic of the coastal margin.

16.4 Floristic Composition and Physiognomy of the Angolan Namib Desert Ecoregion

The phytogeography of Angola was briefly described in Chap. 1. Most of Angola is covered by the mesic and arid savannas of the Zambezian regional centre of endemism. The far north of Angola falls within the Guineo-Congolian regional centre of endemism. Small outliers of the Afromontane centre of endemism occur as relict forests along the high mountains of Huíla and Huambo. The southwest of Angola has representatives of the Karoo-Namib regional centre of endemism, a floristic division that includes much of Namibia and South Africa, characterised by an arid climate with less than 500 mm rainfall per annum.

Within the Karoo-Namib regional centre of endemism, several local Centres of Endemism have been recognised by botanists. The Angolan Namib Desert ecoregion, as defined here, forms the extremely arid western component of the floristic 'Kaokoveld Centre of Endemism' (KCE) as described by Craven (2009). The KCE, defined on purely floristic composition, includes two further ecoregions in Angola, the Namib Savanna Woodlands and the Angolan Mopane Woodlands, both of which are defined according to their ecological characteristics. As Craven (2009) suggests, the flora of the Angolan Namib is much more closely related to that of Namibia than it is to the rest of Angola.

The KCE embraces the full geographic range of *Welwitschia mirabilis*, which is the floral icon of the Namib. In addition to this charismatic species, over 1600 plant species are found in the KCE, with 20% being endemic. The history of the flora and fauna of the KCE is complex. The KCE has many species, of both animals and plants, that have close relatives in the **Horn of Africa**, some 5000 km distant. These include species of mammals (Dik-dik, Gemsbok, Bat-eared Fox); amphibians, scorpions of the genus *Parabuthus* and plant genera such as *Kissenia, Pterodiscus, Thamnosma, Tribulocarpus,* and *Turnera.* These **disjunct distributions** are explained through the existence of an **arid corridor** running across Africa during dry phases of the Pleistocene, along the hot dry valleys and lowlands of the Rift Valley and of the Luangwa, Zambezi and Limpopo rivers (Juergens et al. 1991). The arid corridor would have expanded and closed during successive cold/dry and warm/moist periods of the Pleistocene Ice Ages, affecting not only arid ecosystems but also rain forests, as decribed in Chap. 12.1. The link between *Welwitschia* and its relatives in South America go back much further, perhaps to the Cretaceous.

In her detailed study of the flora of the KCE, Namibian botanist Patricia Craven (2009) defined three groups that form clear patterns in Angola.

The Welwitschia Group

The *Welwitschia* Group is characterised by *Arthraerua leubnitziae, Adenia pechuelii Welwitschia mirabilis*, *Zygophyllum stapffii, Z. orbiculatum* and *Z. simplex.* It is confined to the coastal strip, on coastal sands, gravel plains, hills and rocky outcrops. The climate is characterised by frequent fog reaching up to 60 km inland from the ocean. Mean annual precipitation is less than 200 mm, usually received in summer. The area occupied by this Group is subjected to strong, hot, dry east winds alternating with cold, moist southwesterly winds. It has a recorded flora of more than 200 species, of which 55 are endemic to Angola. Genera with endemic species include *Aloe, Commiphora, Euphorbia, Indigofera, Lotononis, Merremia* and *Petalidium.* Of particular interest is the very high diversity of succulent tree genera. These includes 12 species of *Euphorbia*, of which five occur only in Angola, and 11 species of

Commiphora. Life forms include short-lived non-woody dwarf shrubs with deciduous, succulent leaves (*Zygophyllum orbiculatum*) or rod-like stems (*Euphorbia damarana*).

The Kaoko Group

The Kaoko Group of the KCE is characterised by *Sesamothamnus guerichii.* It lies inland of the *Welwitschia* Group, reaching the Escarpment, up to the 1500 m contour, across rocky slopes, water courses, rugged mountains and hills. Annual rainfall is received mostly in summer, of up to 200 mm in the west and up to 350 mm in the east. It experiences no frost nor does it receive any moisture from fog. The flora has been poorly studied in Angola, but a high level of endemicity has been recorded with about 60 species known to be endemic to the Group. Endemic species include those in the genera *Bayensia, Hibiscus, Petalidium*, *Salsola, Sesamothamnus* and *Stipagrostis.* This group includes five species of *Commiphora*, and seven species of *Euphorbia.*

The Northern Succulent Group

In addition to these two groups, Craven (2009) describes a Northern Succulent Namib Desert Group, found in the coastal rocky hills and sandy valleys from Moçâmedes to Carunjamba River near Lucira. This includes a remarkable diversity of succulents, many of which are **pachycauls** (thick stemmed succulent trees, stout with few branches) such as species of *Adenium*, *Cyphostemma, Moringa, Sesamothamnus* and *Sterculia.* Other succulents here include species of *Euphorbia, Hoodia, Huernia, Kalanchoe, Kleinia, Talinum* and *Tavaresia.*

Physiognomy of the Vegetation

The physiognomy of the sparse vegetation of these three groups is dominated by dwarf shrubs and short trees, with short grasses, both annuals and perennials. These may be lush green and dense immediately after rain but are soon grazed by antelope or become moribund and gradually decompose as termites, ants and winds reduce them to a grey stubble. Trees and shrubs are often spinescent or succulent. The shrublands often have *Welwitschia mirabilis* as a conspicuous feature, but this amazing plant (Box 16.1) is most robust in the deep coarse sands of dry riverbeds (***chanas***). It is also found on rocky outcrops, together with succulent species of *Cissus, Commiphora, Euphorbia, Hoodia, Sterculia*, and hardy forbs and shrubs such as *Blepharis, Dicoma, Galenia, Helichrysum* and *Pterodiscus.* Close to the coast, succulent-leaved dwarf shrubs of *Mesembryanthemum, Salsola* and *Zygophyllum* become conspicuous.

As one progresses inland, the vegetation physiognomy and floristic composition gradually transition to that of the Namib Savanna Woodlands. Trees of such genera as *Acacia, Boscia, Colophospermum, Combretum, Commiphora, Sterculia* and *Terminalia* become more abundant, forming small savanna woodland communities on rocky outcrops, with grasses and shrubs on the deeper sands. A striking feature in Iona National Park are the broad inter-montane plains. These are covered with a rich carpet of *Stipagrostis* and *Schmidtia* annual grasses after infrequent rains (Fig. 16.7).

Fig. 16.7 Annual and perennial grasslands (*Stipagrostis, Schmidtia*) on the intermontane plains of Iona National Park

Conspicuous on these plains are the ’fairy circles’ (Fig. 11.16; Box 11.1), the origin and dynamics of which continue to puzzle scientists (Fig. 16.8).

16.5 Faunal Composition of the Namib Desert

The extreme aridity of the Namib Desert places severe limits on the survival of most vertebrates, especially amphibians. However, many reptiles and birds have developed successful adaptations to life in the desert (Chap. 11). The largest bird on Earth, the African Ostrich, was once common on the margins of the Namib, while two large bustards (Ruppell’s Korhaan and Ludwig’s Korhaan) are still to be found on the gravel plains and intermontane grasslands of Iona. Mammal species include nomadic herds of Springbok, Gemsbok, Plains and Hartmann’s Zebras, and sedentary carnivora such as Meerkat and Aardwolf. Brown Hyaena and Cheetah range widely over the desert margins. Table 16.2 lists vertebrate species typical of the Namib Desert Biome.

Box 16.1 Welwitschia Mirabilis: The Miracle Plant of the Namib

The botanical icon of the Namib, *Welwitschia mirabilis* has a long and illustrious history and a remarkable biology which should be studied by every

Fig. 16.8 The inland margin of the Angolan Namib Desert interfaces with Namib Savanna Woodlands

Table 16.2 Vertebrate Species Typical of the Namib Desert of Angola

- **Reptiles**: Feathered-Tailed Gecko, Namib Web-Footed Gecko, Common Namib Day Gecko, Anchieta's Dune Lizard, Kaokoveld Girdled Lizard, Desert Plated Lizard, Speckled Sand Skink, Dotted Blind Dart Skink, Namaqua Chameleon, Namib Rock Agama, Anchieta's Dwarf Python, Peringuey's Adder, Western Sand Snake
- **Birds**: Lappet-faced Vulture, Ludwig's Bustard, Ruppell's Korhaan, Burchell's Courser, Gray's Lark, Herero Chat, Tractrac Chat
- **Mammals**: Bat-eared Fox, Meercat, Brown Hyaena, Aardwolf, Springbok, Kirk's Dik-dik, Gemsbok, Hartmann's Mountain Zebra

Angolan ecologist. This unique, monotypic genus and family represents an early Gymnosperm order (Gnetales) that was present in Brazil and Angola long before South America and Africa split apart in the late Cretaceous (100 Ma). Its only known relatives are preserved as fossils from the early Cretaceous (112 Ma), including *Priscowelwitschia austroamericana* from Crato, northeast Brazil.

This extraordinary plant was discovered for science by the Austrian botanist and physician Friedrich Martin Joséph Welwitsch on 3 September 1859, while collecting botanical specimens just south of Moçâmedes. Welwitsch was truly the father of Angolan botany. In his relatively short time in the country from

1853 to 1861, he collected over 8000 herbarium specimens, representing 5000 species (over 80% of the country’s flora), of which 1000 were new to science. He is honoured not only in order (Welwitschiales), family (Welwitschiaceae) and genus names of *Welwitschia*, but also in the names of over 300 other species of plants. He collected from the Congo basin to the Namib, and from the coast to the central highlands. His correspondence with the leading botanists of the day placed the then scientifically unknown Portuguese colony of Angola on the global botanical map.

Fig. 16.9 Probably the largest and oldest specimen of *Welwitschia mirabilis*

Welwitsch was immediately aware of the scientific importance of the peculiar plant he found scattered about on the desert landscape, possessing features of widely different plant families: proteas, casuarinas and conifers. He recorded the sensations he felt: “I could do nothing but kneel down on the burning soil and gaze at it, half in fear lest a touch should prove it a figment of the imagination.” He sent material to Sir Joseph Hooker, Director at the famous Royal Botanic Gardens, Kew, London. Hooker’s response was equally enthusiastic: “A discovery that I do not hesitate to consider the most wonderful, in a botanical point of view, that has been brought to light in the present century.” Hooker named the plant as a new genus *Welwitschia*, in the Class Gnetales in honour of Welwitsch.

Interestingly, it was Joachim John Monteiro, the British-trained mining engineer and naturalist who sent additional material to Hooker, on which his monograph on *Welwitschia* was based (Hooker, 1863). Monteiro collected plants, birds and butterflies while on his extensive geological explorations of the country from 1858 to 1876. A final historical fact worthy of mention was that the founder of the famous Kirstenbosch Botanical Garden in Cape Town, Harold Pearson, who visited Angola in 1909 to study the species, was the first botanist to observe that *Welwitschia* is pollinated by insects, and to observe that *Welwitschia* has the ability, when two or more plants grow closely together, to form natural grafts. This early observation explains the enormous specimens one finds in Angola, that are possibly several plants growing back-to-back, pushing up vertically rather than spreading laterally (Figs. 16.9 and 16.10).

Fig. 16.10 Female cones of *Welwitschia*, with two permanent leaves emerging from the meristematic apical rim of the corky tree trunk

Welwitschia mirabilis occurs in numerous, often disjunct populations from just north of Bentiaba in Angola to the Kuiseb River in Namibia, over a distance of 1096 km. It has been found within 5 km of the coast to nearly 150 km inland. Its main distribution falls in the summer rainfall, northern Namib, mostly to the west of the 100 mm isohyet, although extending across an annual rainfall gradient from 20 mm to over 200 mm. At the moister, eastern limit, competition for resources with angiosperm trees, shrubs and grasses may limit the successful establishment of *Welwitschia*. In Angola, two main populations are found. One lies from 10 km inland of the coast near the species's type locality at Cabo Negro and stretches inland towards Virei. The other major population, also from about 10 km from the coast, is centred on Espinheira and extends inland towards Iona Posto. The species occurs across an extremely wide range of rocky substrates—granite, limestone, basalt, sandstone, mica schist, calcrete, gypcrete and gravel—but is most robust on the sandy alluvial soils of dry riverbeds. In a detailed study of the phylogeography of *Welwitschia*, Juergens et al. (2021) confirmed the existence of two distinct gene pools, representing two subspecies. The two subspecies (*Welwitschia mirabilis ssp. mirabilis* and *W. mirabilis ssp. namibiana*) are separated not by a clear physical barrier such as the Cunene River, but by a more subtle change in environmental factors some 200 km south of the river.

So what makes *Welwitschia* deserve the name *mirabilis* (the miracle plant)? What is it that so fascinates scientists? There are two lines of interest.

The gymnosperms reached their peak during the Triassic and Jurassic geological periods—250–145 million years ago—during the age of the dinosaurs. This makes *Welwitschia mirabilis* a ‘living fossil’—a faint shadow from the distant past. But while having the typical gymnosperm characteristics of ‘naked seeds’ and nutrient conducting sieve cells, it has angiosperm-like water conducting vessels (xylem) and angiosperm-like male flower characters. It also has parallel-veined leaves like the monocotyledons (grasses) and many more intriguing and contradictory anatomical features. *Welwitschia* therefore follows none of the carefully designed rules of evolutionary biologists. It also provides some surprises for the ecologist, as described below. It ignores all the rules for survival in the oldest desert in the world. *Welwitschia* grows very slowly and lives to a very great age, unlike the fast-growing and short-lived desert annuals that pop up in their millions after rare rain events to flower, set seed, and go dormant for many years before reappearing after the next shower of rain.

On germinating, *Welwitschia* seeds produce two short-lived seed leaves (cotyledons) and immediately thereafter, another two, opposite, foliage leaves—which it keeps for life. No other plant shares this unique character. Nothing more—no flushes of bright new leaves every spring, no spreading branches to carry flowers and fruit—just a stumpy, short, headless trunk. Basically, the plant has a modest taproot, a stunted stem, and two long strap-like leaves. The two leaves are extruded, conveyor-belt fashion, at a rate of about 13 cm per annum from the meristematic tissue that forms the margins of the truncated head of the plant. The leaves are finely grooved and sinuous. Continuous growth means that the ends of the leaves are repeatedly beaten by the desert winds, drying out into tattered, grey or brown tassels. Some leaves have been recorded as long as 11 m, and the breadth of leaf bases can be as much as a metre.

Welwitschia, in common with many gymnosperms, is dioecious, with separate male and female plants carrying their reproductive organs on short branches. These produce secretions that are visited by a diversity of insect pollinators. The leathery leaves have none of the characteristics expected in desert plants—such as small size, deciduousness and succulence. However, recent research by Gert Kruger and colleagues from North-West University in South Africa found novel anatomical and physiological features in *Welwitschia* that can account for its success. The broad leaves have abundant, deeply sunken stomata (Fig. 16.11) on both upper and lower surfaces, which are further protected from dehydration by a thick cuticle. Despite the exposure of the broad, lengthy leaves to solar radiation throughout the day, strong structural features prevent wilting and the collapse of the mesophyll cells which contain the photosynthetically active chloroplasts. The leaves have vertically aligned 'walls' of stiff hypodermal fibres, which act like reinforcing structures, supporting the mesophyll cells against collapse should turgor pressure be lost during prolonged drought. (Fig. 16.12). Kruger et al. (2017) found that the combination of anatomical structure and photosynthetic response to moisture availability has enabled an opportunistic survival strategy through rapid and reversible switch-over from water conservation to CO_2 assimilation as required. It is these specialised features that have ensured the survival of *Welwitschia* in the Namib Desert for perhaps 100 million years.

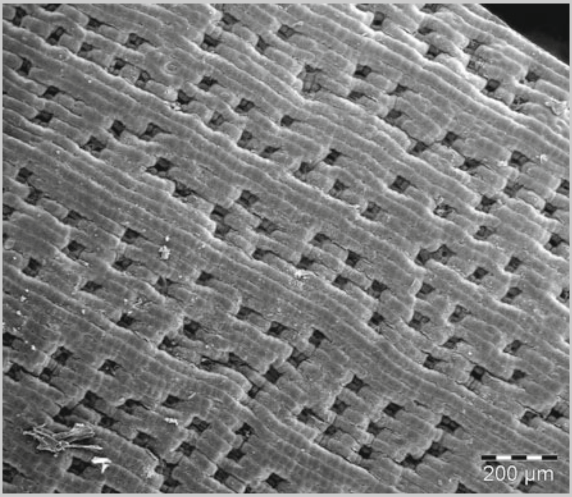

Fig. 16.11 Anatomical adaptations to aridity in *Welwitschia mirabilis* leaf. Leaf epidermis with stomata and deeply sunken subsidiary and guard cells. *Photo* Gert Kruger

Fig. 16.12 Light micrograph of the supportive 'beams' of hypodermal fibers (pink) which prevent the collapse of substomatal space and mesophyll during high levels of drought stress. *Photo* Gert Kruger

Much has been speculated about the adaptation of *Welwitschia*'*s* leaves to harvest water from the fog that prevails over part of its range. This suggested dependency on fog cannot explain for the many *Welwitschia* that grow on the hot rocky outcrops and valleys in the eastern hills of Iona, seldom reached by the cool winds and fog off the Benguela Current. Long-term studies in Namibia (Henschel & Seely, 2000) found no direct correlation between fog deposition on leaves and their growth, nor was it recorded in the study by Kruger et al. (2017).

The stem of *Welwitschia* is woody, covered in a corky bark, and is hollowed into a basin-shaped crown. Most of the stem lies below ground, seldom rising more than half a metre above the surface. The carrot-like taproot does not, contrary to early speculation, appear to penetrate deep into the desert sands. Henschel et al. (2019) excavated seven mature plants and found them to lack taproots greater than 2 m depth. Henschel measured lateral roots extending up to 9 m, while lateral roots of up to 15 m have been mentioned in earlier studies. The rooting strategy is opportunistic, with a dense network foraging for water from the shallow surface layers of the soil. A remarkable finding by Henschel et al. (2019) was that the study plants sourced moisture from perched water within the gypsum substrate. **Perched water** is that which is held in upper soil layers by an impenetrable substrate (gypcrete or calcrete) below them. They concluded that the surface soil water would be supplemented overnight from fog, or by upwards diffusion from within the gypsum horizon. What is clear is that successful germination and seedling establishment requires a good rain event to provide the water needed to sustain root growth within the surface soil. Recruitment is episodic, reflected in the age distribution profiles of *Welwitschia* populations in different areas of Iona. In January 2009, following good rains in 2008, there was an abundance of small, 20-cm-tall seedlings around Espinheira. Most of these had died by December 2011. For establishment success, *Welwitschia* seedlings need successive episodes of above average rainfall.

As might be expected with slow growth, *Welwitschia* plants, once established, live to a great age. Accurate measurements have not been achieved, but a combination of evidence from growth rates of known-age plants, counts of growth rings, and carbon dating, suggests that large plants might be 500 years old, and the rare, exceptionally large plants, as much as 1800 years old. A peculiarity of *Welwitschia* is that in contrast to most trees, which have their growth rings in the inside of the stem, *Welwitschia* has its growth lines on the outside—along the growing tissue on the rim of its basin-shaped head.

The apparent poor fit of *Welwitschia*'*s* growth form, morphology and natural history to its harsh environment is difficult to explain. Yet it has succeeded, indeed prospered for many millions of years, in the world's oldest desert. It has also puzzled, perplexed, intrigued and entertained the intellect of scientists for 150 years, and will surely continue to do so for many more.

As a recent review of the evolution of seed plants suggests: "The placement of the Gnetales and ramifications for angiosperm evolution remains one of the most controversial issues in seed plant phylogeny" (Ran et al. 2018).

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Chapter 17
The Mangrove Biome

Key Concepts and Questions: This Chapter Will Explain

- *How a few species of flowering plants have returned to life in the sea.*
- *Plant adaptations to fluctuating salinity, oxygen and light conditions.*
- *What specialised animals live in the mangroves and seagrass meadows of Angola.*

Context: A Return to the Sea: Mangroves and Seagrasses

The early ancestors of vascular plants migrated from the sea to the land in the Silurian (444–419 Ma). By the Triassic (252–201 Ma), advanced land plants (the seed-bearing Spermatophytes) had evolved, which in turn were succeeded by the first flowering plants (Angiosperms) by the beginning of the Cretaceous (145 Ma). Flowering plants radiated across terrestrial biomes which they soon came to dominate. However, during the late Cretaceous (100–66 Ma), a small group of angiosperm members recolonised the coastal and marine environments from which their vascular plant ancestors had migrated. These plants now occupy very specialised habitats known as **mangroves** and **seagrass meadows**.

The challenges faced by flowering plants in colonizing marine environments are reflected in the fact that out of the over 350,000 species of living flowering plants known to science, only 55 species have succeeded as mangroves, and 70 species as seagrasses. Representatives of these extraordinary plants, and the ecosystems that they have created, are found in Angola.

Angola's Mangroves and Seagrass Meadows (Ecoregion 16)

17.1 Definition and Distribution

Mangroves have acquired the unfortunate image of mud, methane and mosquitoes (Hogarth, 2007). Floristically, they are the most species-poor biome in Africa and they

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are among the least-well documented ecosystems of Angola. Yet despite their limited biodiversity and uncomfortable milieu for humans, mangroves provide outstanding examples of adaptations by angiosperm plants to inhospitable physical environments. They are currently enjoying increased study by Angolan ecologists.

Mangroves are recognised as a distinctive biome because of the remarkable habitat which they occupy—at the interface between terrestrial and marine environments. They are exposed to inundation by sea and river water of widely varying salt concentrations (**salinity**), low oxygen concentrations and often anoxic conditions. They are subjected to repeated wave erosion and occasional storm surges, daily fluctuations in water levels due to tides, and seasonal fluctuations in water levels and salinity according to rainfall and riverflow patterns. They have remarkable adaptations to life in tidal zones, with specialised **stilt roots** for physical support (Fig. 17.1) and breathing roots (**pneumatophores**) for gas exchange.

Globally, mangroves occupy 180,000 km^2 of tropical river mouths, deltas and tidal mudflats. They occur as isolated ‘ecological islands’ along tropical coasts, at river mouths and in coastal lagoons, often separated by hundreds of kilometres from one another. The stabilizing effect of dense mangrove forests are important to many other organisms, and play a key role as natural buffers in reducing impacts of human-mitigated disturbances such as floods, and of natural disasters such as tsunamis.

The global distribution of mangroves corresponds to tropical coastlines where the mean monthly air temperature of the coldest month exceeds 20 °C. In Africa, mangroves are found along the East African coast from Somalia to South Africa, and

Fig. 17.1 A dense web of stilt roots support mangroves at Foz da Longa lagoon, Cuanza-Sul

on the West African coast, from Mauritania to Angola. The Indian Ocean distribution stretches as far south as East London in South Africa at 32° S, and the Atlantic Ocean distribution extends as far south as Lobito at 12° S. The considerable difference in southern limits on east and west coasts results from the influence on local climates of the warm Mozambique Current of the Indian Ocean, and the cold Benguela Current of the Atlantic Ocean. The most extensive mangrove communities in Angola are in Cabinda and Zaire provinces, at the mouths of the Massabe and Congo rivers (Figs. 3.40, 3.41 and 3.42), and in Bengo province at the mouth of the Cuanza. The Congo mangroves cover some 500 km^2, those at the Cuanza approximately 40 km^2. The salinity of the water in which mangroves grow at the river mouths range from 0.5 to 35 parts per thousand, with a tidal range from 0.5 to 1.8 m.

Associated with mangroves is another specialised ecosystem—seagrass meadows. In Angola, these are restricted to the Baía do Mussulo, just south of Luanda, and deserve special mention because of their ecological adaptations and conservation importance.

17.2 Floristic Composition and Physiognomy

The global mangrove flora of 55 mangrove species (including 35 tree species and 20 associated species comprising shrubs, climbers, ferns and epiphytes) represent 16 families and 20 genera. The taxonomic diversity of the mangrove flora reflects independent but convergent evolution of their specialised physiological adaptations for survival, growth and reproduction in 16 distinct families. Two families, Avicenniaceae and Rhizophoraceae, contribute 30 species to the flora. In Angola, three species of red mangroves—*Rhizophora racemosa, R. mangle* and *R. harrisonii*, and two species of white mangroves—*Avicennia germinans* and *Laguncularia racemosa* have been recorded out of a total of six mangrove species known from West Africa.

The low species diversity in mangrove ecosystems and the limited topographic diversity of their coastal riverine and estuarine habitats result in relatively simple patterns of community structure. Most mangroves have monospecific stands of species distributed in zones according to multiple interacting factors. These include the ability of their propagules to disperse and survive in a site determined by shore morphology, the influence of tides and river flow, and the variations in salinity and sedimentation (Hogarth, 2007).

Due to the steep gradient of the Angolan coastal margin, large deltas dominated by mangrove forests, such as are found at the mouths of the Amazon, Niger, Zambesi, Brahmaputra and Mekong rivers, are not found in Angola. At the mouths of the Cuanza and Congo, strong river currents flow directly into the sea, with a narrow belt of mangroves on their banks. The mangroves extend from the margins of the rivers into adjacent floodplains and swamp forests, wetlands and mudflats. The physiognomic and floristic structure of the communities varies with edaphic conditions. The mangroves of the Congo extend 40 km, and of the Cuanza 15 km, up river, succeeded by thickets of *Raphia matombe* palms in marginal swamps (Fig. 17.2).

Fig. 17.2 Raphia palms on the river margin upstream of mangrove forest, Cuanza River

Mixed riverine forests occur on higher ground where palms such as *Elaeis guineensis* and *Phoenix reclinata* and deciduous trees such as *Albizia glaberrima, Pterocarpus tinctorius, Lonchocarpus sericeus* and *Hibiscus tiliaceus* are common.

The mangrove forests differ from other forests in Angola in their extreme paucity of species and a virtual absence of understorey vegetation. Exceptions occur through disturbance factors. Gaps in the forest canopy are occasionally caused by tree fall, while the forests at Barra da Cuanza were exploited for construction timber during the colonial era, and the raphia thickets continue to be harvested for poles. Disturbed areas of the Cuanza mangroves have a dense undergrowth of shrubs and climbers, including *Dalbergia ecastaphyllum, Machaerium lunatum* and *Sarcocephalus pobeguini* and the mangrove fern *Acrostychyum aureum.*

Rhizophora mangle dominates the mangroves of Cabinda and with *R. racemosa* reaches 25 m in height. The diversity and height of mangroves decreases southwards to the Longa and Queve estuaries. *Avicennia germinans* seldom exceeds 5 m height, with stunted *R. mangle* and *Laguncularia racemosa* at their southern limit of Angolan mangroves in Lobito, where most mangroves have been destroyed by urban development.

17.2.1 Mangrove Adaptations to Waterlogged Soil

The roots of most terrestrial plants access oxygen for respiration through gas diffused through pores in the soil. The soil of mangrove communities has the pores filled with water, and the little oxygen present is depleted by anaerobic respiration of soil bacteria, creating **anoxic** conditions. The complex biochemical reactions involved in these stagnant waterlogged soils results in the production of methane, which accounts for the unpleasant smell of mangrove ecosystems.

A key adaptation to these soil conditions is illustrated by various forms of aerial roots. Unlike dryland plants, which have their roots branching below ground from the base of their trunks, mangrove trees have roots descending from up to two metres above the ground, radiating out around the tree as buttresses. Known as **stilt roots**, these provide physical support to the trees, which lack tap roots. In *Rhizophora racemosa* the primary roots give off looping horizontal roots that radiate outwards, crossing those of adjoining trees and forming an impenetrable network (Figs. 17.1 and 17.3).

The aerial roots have specialised absorptive pores—**lenticels**—which absorb air while exposed above the water surface, but which close as soon as the incoming tide reaches them. The roots contain very porous **aerenchyma** tissue, providing channels for the transfer of oxygen to the deeper roots which lie in the anoxic, waterlogged soil. Aerenchyma comprises up to 70% of the root volume. In *Avicennia germinans*, which covers the mudflats around Ilha dos Pássaros at Mussulo, the main roots radiate

Fig. 17.3 Mangrove forest on margins of Cuanza River. Note stilt roots exposed at base of trees by an out-going tide

outwards from the tree base, just below the mud surface, and give rise to hundreds of short vertical roots that are called **pneumatophores** which serve as conduits of atmospheric oxygen to the root tissues. A single *Avicennia* may have more than 10,000 pneumatophores (Hogarth, 2007).

17.2.2 Adaptations to Changes in Salinity

Mangroves are found at the mouths of large tropical rivers, on the mudflats adjoining river estuaries, or in sheltered lagoons. These sites experience salinities ranging from that of fresh water (zero parts per thousand salt), to that of sea water (35 parts per thousand salt), to far higher salt concentrations where evaporation has taken place on the surfaces of mudfats exposed to the sun during low tide. The high negative osmotic potential of the soil water is addressed by several mechanisms. These include the exclusion of salt by the roots, tolerance of high tissue salt concentrations, and elimination of excess salt by excretion. Some species of *Avicennia* have salt glands on their leaves, excreting salt crystals which are visible to the naked eye. The mechanisms must deal not only with high levels of salinity, but also with large fluctuations in salinity, due to the variable impacts of tidal fluxes, river flows and evaporation. In addition to the challenges of waterlogging and salinity, soils in which mangroves grow are low in nutrients. Like the trees of the mesic/dystrophic savannas, they withdraw a high proportion of nitrogen and phosphorus before dropping their leaves. They also retrieve nutrients from the soil, from decaying roots of other trees or from the leaves decomposed by crabs.

17.2.3 Reproductive Adaptations

Pollination is the first step needed for successful reproduction in plants. Mangrove trees have not developed many elaborate floral morphologies to attract pollinators, other than rather simple mechanisms of scent and large flowers that attract bats, with smaller flowers attracting butterflies, bees, flies and other small insects. Fertilization success is low, from 3 to 7% in flowers studied.

While their flowers are unsophisticated, mangrove **propagules** are not. All mangroves disperse their unusually large fruit by water. Unlike most land plants, mangroves do not produce dry, dormant seeds; instead, they produce large actively growing seedlings, where the embryo remains on the tree until the seedling is well developed. This reproductive trait is known as **vivipary**, evolved independently in 16 mangrove families. The propagule inherits the physiological adaptations to salinity and water, begins photosynthesis while still attached to the adult tree, and develops an extended embryonic axis or **hypocotyl**, which in *Rhizophora mangle* might be

25 cm length. Such fruiting behaviour comes at a cost to the adult, and reproductive effort in typical mangrove species might be as much as 10–40% of the tree's investment in growth (Hogarth, 2007).

The purpose of this great investment in large, actively growing propagules seems related to dispersal by floating on the water currents of streamflow, sea tides, and storm surges. The propagules of *Rhizophora harrisonii* can remain viable for a year or more. Once stranded on a mudbank, the propagule will send out roots to anchor in the mud and shoots and leaves to establish themselves as seedlings. The advantages of vivipary are poorly understood, but it provides a diversity of dispersal and colonization mechanisms that vary in space and time—ideal for patchy and challenging environments.

17.2.4 Seagrass Meadows

Along the Angolan coast, sediments carried from the mouths of the Catumbela, Queve, Longa and Cuanza rivers are transported northwards by the coastal current driven by southwesterly winds. Some of these sediments are deposited on the coast, and form long sandspits (***restingas***) to the north of the river mouths. The sandspits often have lagoons on their landward margin. In the case of the 30 km-long Restinga das Palmeirinhas, both mangroves and **seagrass meadows** have developed on the sandy and muddy sediments within the **Baía do Mussulo**. These ecosystems have been studied by Portuguese and Angolan biologists for several decades (Costa et al., 1994; Santos, 2007).

Seagrasses belong to a small group of monocotyledons which, like mangroves, are adapted to challenging environments at the terrestrial/marine interface. Although they might have the general appearance of grasses, they are not members of the Poaceae. Globally, about 70 species of seagrass have been described from tropical to temperate regions, of which six species occur along the west coast of Africa. Only two species, *Halodule wrightii* and *Cymodocea nodosa* (both of the family Cymodoceaceae), are known from Angola.

In the Mussulo lagoon, seagrass meadows are found in basins of shallow water, adjacent to mudflats. The challenges to establishment, growth and reproduction are great. The sandy and muddy sediments in which the seagrasses grow are not only unstable, but like mangroves, seagrasses have to transfer gases from submerged organs—leaves and stems—to belowground roots, requiring complex physiological adaptations. Their photosynthetic leaves have no stomata, instead, they have a thin cuticle layer which allows gases and nutrients to be exchanged directly with the surrounding water. For effective photosynthesis, the permanently submerged leaves of seagrasses must absorb adequate light. Most seagrasses are found in shallow waters of 1–3 m depth with high levels of light. Like mangroves, they also have to tolerate high and variable levels of salinity at or above that of seawater. Finally, for reproduction, they have to overcome the challenges of successful pollination and seed dispersal while their flowers are permanently submerged. Given the complexity of these adaptations, it is not surprising that only 70 species of seagrasses have evolved in the 100 million years of the group's evolution.

Seagrass meadows and mudflats are exposed to inflowing and receding tides, with widely fluctuating salinity levels. The mudflats are in constant flux, due to tidal and wave action. As alluvium is gradually deposited, developing new areas of mudflats, they are colonised by mangrove pioneers, and on the drier salt flats such as the Saco dos Flamingos at the head of Baía do Mussulo, salt tolerant plants (**halophytes**) such as *Sesuvium crithmoides, S. portulacastrum, Salicornia* sp. and *Arthrocnemum* sp.*,* form a short carpet of succulents, with grasses such as *Sporobolus virginicus* on higher ground above tidal waters.

17.3 Faunal Composition of Mangrove and Seagrass Meadow Ecosystems

The mosaic of habitats created by rivers, estuaries, sandspits, mangroves, mudflats, seagrass meadows and salt marshes support a great diversity of animal life, even though the diversity of flowering plants living in these physical environments is very limited when compared with terrestrial communities. Vertebrate species breeding in the mangrove forests, seagrass meadows, rivers and coastal shores are noted in Table 17.1.

The Massabe and Congo river mouths have populations of West African Slender-snouted Crocodile, African Dwarf Crocodile and Nile Crocodile. The Cuanza has only the latter species. The West African Manatee occurs in the Cuanza, Congo and Massabe rivers, the African Softshell Turtle occurs in most rivers from Cabinda to the Cunene, while five species of marine turtle (Loggerhead, Green, Olive Ridley, Hawksbill and Leatherback) are known to breed on the sandy beaches and sandspits of Angola, especially northwards from the Restinga dos Palmeirinhas. Green and Olive Ridley turtles have also been reported from the Mussulo lagoon, possibly grazing on the seagrass meadows.

The dense matrices of mangrove roots, especially the pneumatophores of *Avicennia germinans*, create traps for sand and mud, thus stabilizing the sediments as they are transported across the root mats with the ebb and flow of tides. These repeated inundations of the mudflats and interactions with the seagrass *Halodule wrightii* and the epiphytic brown alga *Acanthophora spicifera*, and nutrient, water and oxygen cycles create diverse habitats for many specialised animals, especially

Table 17.1 Vertebrate Species Breeding in Mangrove Forests, Rivers and Coastal Shores

Reptiles: Loggerhead Turtle, Green Turtle, Olive Ridley Turtle, Hawksbill Turtle, Leatherback Turtle, West African Slender-snouted Crocodile, African Dwarf Crocodile, Nile Crocodile
Avifauna: Palm-nut Vulture, African Pygmy-kingfisher, Grey Parrot, Swamp Boubou, Mangrove Sunbird, Loango Weaver
Mammals: Blue Monkey, Malbrouch Monkey, Northern Talapoin, West African Manatee

crabs, barnacles, oysters, mussels, and mudskipper fishes. Angolan marine biologist Carmen Santos made a detailed study of the macroinvertebrates and fishes associated with the seagrass meadows of the Mussulo lagoon and recorded 163 taxa belonging to 10 phyla from this habitat (Santos, 2007). The fish fauna of the seagrass meadows included 17 species, while a survey of the more diverse mangrove habitat (Costa et al., 1994) recorded 36 species. The mudflats are also important feeding grounds for migratory shorebirds, which motivated proposals for the declaration of Ilha dos Pássaros as a Ramsar site (Morais, 2004).

The fauna of Angola's mangrove forests at the mouths of the Cuanza and Congo includes populations of three monkeys (Malbrouch, Northern Talapoin and Blue Monkey) while birds characteristic of the habitat include: Palm-nut Vulture, African Pygmy-kingfisher, Grey Parrot, Swamp Boubou, Mangrove Sunbird and Loango Weaver. The fauna of these forests awaits detailed study.

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Chapter 18
The Angolan Escarpment Zone

Key Concepts and Questions: This Chapter Will Explain

- *Why the Escarpment Zone is considered a physiographic concept rather than a single ecoregion.*
- *How diverse environments are reflected in the habitats and biota of the Escarpment.*
- *How the forests of the Escarpment Zone and the Angolan Highlands relate to the Guineo-Congolian and Afromontane biomes.*
- *Why the avifauna of the Escarpment Zone and adjoining highlands provides such important insights into the evolution of African forests.*

Context: An Escarpment Zone Extending from Rain Forest to Desert

In the preceeding chapters of Part 4, the ecological characteristics of the six Angolan biomes have been described. Each of these biomes have specific structural and functional attributes that distinguish them from one another, and justify their recognition as representatives of global biomes. Cutting across these biomes, from north to south, is the Angolan Escarpment, a geographical spine that separates the coastal lowlands from the interior plateaus. The vegetation that covers the Escarpment landscapes range from tropical rain forest to desert, and includes five ecoregions. For this reason, the description of the Angolan Escarpment Zone is presented as the concluding chapter of Part 4, given its complexity and need for a specific format.

The Angolan Escarpment Zone forms part of the 5000 km-long **Great Escarpment of Southern Africa,** which lies between 50 and 200 km inland of the coasts of Mozambique, South Africa, Namibia and Angola. The Great Escarpment rises from 500 to 2000 m over most of its range, with the highest peaks of mountains above the Escarpment attaining 2620 m in Angola, and 3450 m in Lesotho. Across its 5000 km length, climates range from tropical summer rainfall to warm temperate winter rainfall, and from 250 to 1600 mm per year. The extensive Great Escarpment of Southern African and associated highlands are estimated to host over 8500 plant

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species, of which 1460 species are endemics. It has at least 126 endemic vertebrate species (Clark et al., 2011).

The Angolan Escarpment Zone (Figs. 4.10 and 18.1) extends across 1400 km from northern Cabinda to the Cunene River. The strong latitudinal gradient in rainfall, and longitudinal gradient in altitude, with accompanied diversity of habitats, flora and fauna, accounts for the inclusion of part or all of eight ecoregions within the Zone. The Angolan Escarpment Zone is bounded on the west (below ca. 500 m) by the coastal lowlands, and to the east by the upper reaches of the Marginal Mountain Chain and the Ancient Plateau (senso Diniz, 1991). The central Angolan **highlands** rise above the Escarpment, from 1700 to 2620 m, and drop eastwards across the interior plateau (planalto). The Escarpment Zone includes several prominent **scarps**, where the landscape is broken by abrupt increases in altitude over a few km (Fig. 4.3). It is also characterised by the presence of many **inselbergs** – isolated geomorphological features that rise as steep-sided hills or mountains formed of resistant bedrock, surrounded by lower-elevation lowlands, such as Serra da Neve. Rising to 2489 m, Serra da Neve is isolated both physically and geologically from the main escarpment but with similarly interesting endemic species and habitat diversity (Fig. 15.6). A variant of an inselberg that is particularly common in the Escarpment Zone is known as a **bornhardt**, a domed-shaped hill, often of Basement Complex granite (Fig. 4.2).

The climate of the Angolan Escarpment Zone varies widely, from humid in the north, with up to 1600 mm precipitation per annum, to arid in the south where it forms the interior margin of the Namib Desert, receiving less than 250 mm. Rainfall is confined to the summer months, with low clouds and fog supplementing rainfall in the forests of the steep, seaward-facing slopes of the Escarpment.

The geology is very mixed, but mostly comprises crystalline Precambrian rocks—gneisses, quartzites, schists, granites, gabbros, amphibolites and migmatites. Soils include ferallitic and paraferralitic ferralsols and well-drained ferralitic nitisols, and in some areas, more fertile lixisols and cambisols.

The Angolan Escarpment cannot be regarded as a single ecoregion (as in Burgess et al., 2004), but rather as a series of ecoregions within an Escarpment Zone. Chapter 2 maps and outlines the ecoregions that occur along the escarpment: (1. Guineo-Congolian Rain Forests, 2. Western Congolian Forest/Savanna Mosaics, 6. Angolan Escarpment Savannas, 12. Angolan Mopane Woodlands, and 13. Namib Savanna Woodlands), and the complex of Arid Savanna, Mesic Savanna and Afromontane ecoregions that lie to their west and east.

18.1 Sectors of the Angolan Escarpment Zone

The paucity of geo-referenced data on Angolan plant and animal species precludes an objective and statistically-based classification of biogeographic sectors of the Angolan Escarpment Zone. However, the Zone can be divided into four sectors, based on general physiographic and climatic characteristics. The abbreviated outlines

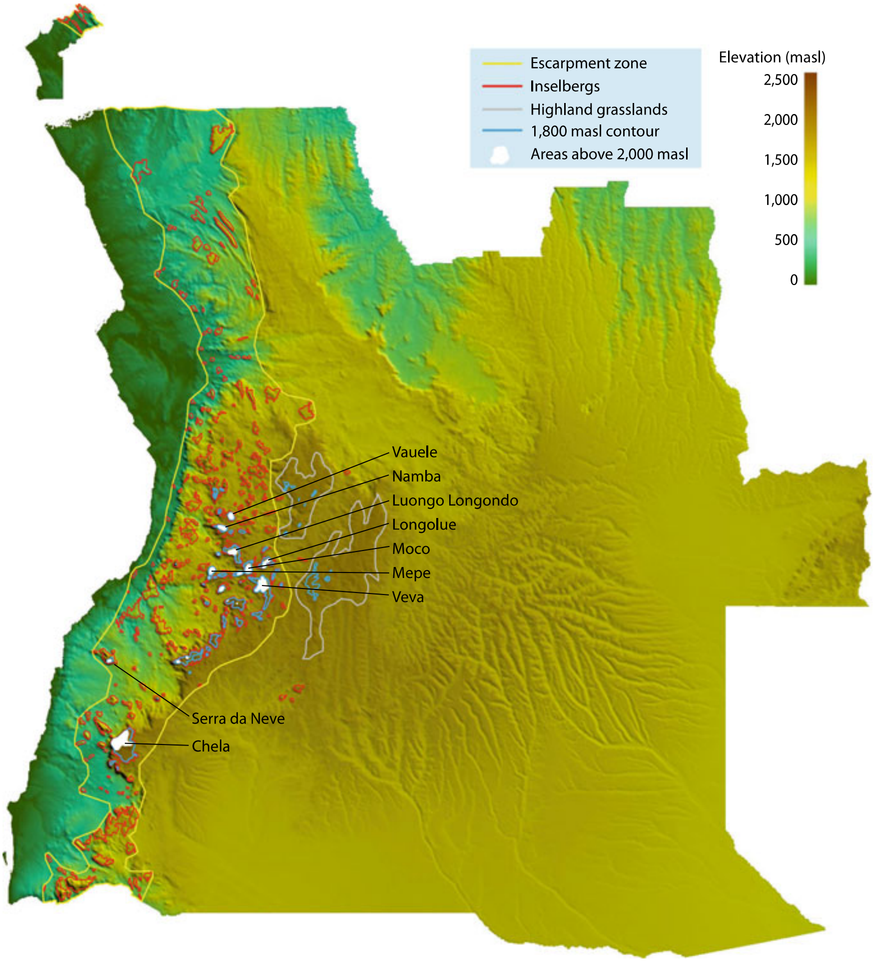

Fig. 18.1 The Highlands and Escarpment Zone of Angola. The Angolan Escarpment Zone is broadly outlined by the yellow line, and includes the highlands and inselbergs (red dots) that characterise the rugged topography of the Escarpment Zone. Also indicated are the areas of land rising above 1800 (blue) and above 2000 m (white), where isolated remnants of Afromontane Forest might be found. The names of key peaks are given. To the east of the Escarpment Zone, the montane grasslands of the high plateaus are indicated by the green line. Cartography John Mendelsohn

which follow need refinement through active data collection in the field, especially to test the faunistic and floristic patterns relating to the physiographic sectors.

Escarpment of Cabinda

- From Gabon southwards, and inland of the coast, low hills give way to steep ridges of a narrow escarpment belt which ends just north of the Congo River.

- In Cabinda, these hills form the southern extension of the Mayombe Massif, which is known as the Alto Maiombe in Cabinda, reaching 780 m at its highest point (Ecoregion 1).
- The closed forests comprise Guineo-Congolian species, and are surrounded by tallgrass savannas of Western Congolian Forest/Savanna Mosaic communities (Ecoregion 2).

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Northern Escarpment, from the Congo River to the Cuanza River

- South of the Congo River, the landscape comprises a highly dissected relief with hills and low mountains rising eastwards to 1300 m.
- The width of this sector decreases from 200 km in the north to 100 km in the south.
- Mean annual precipitation increases from 500 to 1600 mm, from the coast to the interior.
- Several large forest blocks and numerous smaller fragments of semi-deciduous Guineo-Congolian forest occur below and along the escarpments and in riverine galleries (Ecoregion 1).
- The forests are dispersed within a matrix of Western Congolian Forest/Savanna Mosaics of tall grasslands with fire-tolerant woody species and with moist forest patches in valleys and on hills (Ecoregion 2).
- The flora is predominantly Guineo-Congolian and Zambezian, with an absence or low frequency of Afromontane elements.
- Both flora and fauna has a species richness of all taxa, with dominance of Guineo-Congolian species in forests and Zambezian species in savannas (Ecoregion 6).

Central Escarpment, from the Cuanza River to the Coporolo River

- The Central Escarpment forms a low, narrow but stepped landscape from about 200 to 400 m along the base, rising within 50 km from the coast to 1000 m (and to 1690 m at highest points on Serra Njelo).
- A second, broken, escarpment lies between 100 and 150 km from the coast, rising above 1600 m along the Marginal Mountain Chain, and to 2620 m at Mount Moco, descending eastwards across the Planalto.
- Mean annual precipitation increase from 500 to 1000 mm from the coast to the highlands.
- Arid savannas, woodlands, thickets and dry forests occur as a mosaic along its base, transitioning into mixed Mesic savannas above 500–800 m; with *Acacia, Annona, Cochlospermum, Erythrina, Piliostigma* savannas up to 800 m and *Brachystegia, Julbernardia, Combretum, Terminalia* woodlands along the upper escarpment (Ecoregion 6).
- Guineo-Congolian elements are mixed with Zambezian elements in the fragmetas of rain forest at Amboim-Gabela and Seles-Cumbira, at altitudes from 500 to 800 m. These represent species-poor outliers of Ecoregion 1).
- Above 800 m a transition to medium-height grassland and in some places, ravine forests with Afromontane elements.
- The rain forests and adjoining dry thickets are of biological and conservation important for their high richness of endemic and narrow-range bird species, and seven primate species.

Southern Escarpment, from the Coporolo River to the Cunene River

- The Escarpment becomes increasingly narrow, very steep and very high 100 km inland of the coast at Moçâmedes. The scarp face rises from 500 to 2000 m over a distance of 10–40 km, due west of Humpata, where it is well defined by the Chela quartzites (Fig. 6.1).
- Southwards from the Serra da Chela the escarpment becomes more diffuse and broken as it follows arid mountains east of Virei and as it approaches the Cunene River.
- Mean Annual Precipitation decrease from 150 to 850 mm, from the base of the Escarpment to the Humpata Plateau.
- The Southern Escarpment includes an exceptional altitudinal diversity of habitats, as described in Sect. 5.7.
- Arid woodlands and thickets, including *Acacia, Adansonia, Colophospermum* occur along the foothills, with *Albizia, Brachylaena, Combretum, Commiphora, Tarchonanthus* woodlands and thickets on the higher levels. With increasing aridity, species composition and structure changes southwards to semi-desert towards the Cunene River (components of Ecoregions 6, 12, 13).
- Very restricted deciduous forest patches/galleries in lower areas with a few Guineo-Congolian floristic elements including *Piptadeniastrum* and *Newtonia.*

- The upper crest, at 1800–2000 m, leads to plateau grasslands and ravine forests of Afromontane elements including *Protea, Faurea, Nuxia* and *Podocarpus* on the Humpata and Huíla plateaus (Ecoregion 4).
- The Humpata and Huíla plateaus, comprising Wet Miombo (Ecoregion 7) has many endemic 'highland' elements in the short grasslands (Ecoregion 5).
- Endemic birds include species of rocky outcrop, grassland and thicket habitats.

The combination of high rainfall and good soils on the Cabinda, Northern and Central Escarpments have enabled high agricultural productivity, most specifically for the production of 'robusta' coffee *Coffea canephora* during the colonial period, and for bananas and other cash crops thereafter. As a consequence, deforestation has severely reduced the cover of the moist forests of the Escarpment Zone, while invasive plant species (*Inga vera* and *Chromolaena odorata*) have infested disturbed sites. Along the Southern Escarpment, in more arid areas, the cactus *Opuntia stricta* has invaded large areas (Rejmánek et al., 2016). Across the length of the Angolan Escarpment, hunting for bushmeat and the felling of trees for the production of timber, firewood or charcoal have had serious impacts on biodiversity.

In the absence of formally designated and effectively managed conservation areas, the extremely rich biota and ecosystems of the Angolan Escarpment Zone are currently vulnerable to irreversible degradation.

18.3 Vertebrate Fauna of the Escarpment Zone

As already noted, the Angolan Escarpment Zone and adjoining montane highlands need intensive surveys to provide a detailed characterisation of their fauna and flora. It is nevertheless possible to provide an indicative listing of vertebrate species with distributions centred on the Northern and Central Escarpments (Table 18.1). In common with the Great Escarpment of southern Africa, the Angolan Escarpment

Table 18.1 Vertebrate species typical of the Angolan Northern and Central Escarpments (excluding Cabinda)

Amphibians: Parker's White-lipped Frog, Congulo Forest Tree Frog
Reptiles: Long-Headed Tropical Gecko, Gabon Adder
Birds: Grey-striped Francolin, Red-crested Turaco, Gabon Coucal, Red-backed Mousebird, Naked-faced Barbet, Anchieta's Barbet, White-headed Barbet, Angola Batis, White-fronted Wattle-eye, Gabela Helmet-shrike, Monteiro's Bushshrike, Braun's Bushshrike, Gabela Bushshrike, Yellow-throated Nicator, Yellow-necked Greenbul, Yellow-necked Greenbul, Pale-olive Greenbul, Pulitzer's Longbill, Bubbling Cisticola, Hartert's Camaroptera, Bocage's Akalat, Gabela Akalat, White-capped Robin-chat, Angola Cave Chat, Forest Scrub Robin, Golden-backed Bishop, Red-faced Crimsonwing, Landana Firefinch
Mammals: Ansorge's Cusimanse, African Palm Civet, Blue Monkey, Southern Talapoin, Angolan Dwarf Galago

Zone and its adjoining highlands are of considerable biogeographic and evolutionary interest, as outlined in Box 18.1.

Box 18.1: The Evolutionary Importance of the Angolan Escarpment and Highlands

Understanding patterns in the distribution and abundance of species is a recurrent theme of ecological enquiry. Biomes and ecoregions provide a coarse-grained outline of Angola's biodiversity structure. At a finer geographic scale, the birds of Angola are better documented than are plants or even vegetation, and provide valuable insights into evolutionary relationships of the highland biota. Birds are often the trigger of natural history interest among students, and an accessible entry point to the wider spectrum of biodiversity knowledge. Michael Mills, a South African ornithologist, has done much to document and popularise the avifauna—both common and rare species—of Angola. In his guidebook to the 'special' birds of the country, Mills (2018) lists 70 species that are notable for their rarity or endemicity. The list indicates that most restricted-range species are from forests, or from the thickets, shrublands and grasslands associated with forests of the Angolan Escarpment and Afromontane ecoregions. Of the country's 29 endemic bird species, 12 are confined to the Escarpment and 8 more are narrow endemics that occur along the Escarpment but are not restricted to it. Similar narrow distributions, limited to the Escarpment Zone, are found among reptiles, amphibia, butterflies and dragonfly groups (Huntley et al., 2019 and references therein).

These patterns of endemism and rarity have long attracted the attention of biologists, first to collect, describe and document diversity, and more recently, to explain evolutionary relationships. In 1957, Patricia Hall of the British Museum, London, collected 250 species of passerine birds along the Angolan Escarpment and adjoining landscapes. Based on her field knowledge and on museum specimens, she published a paper titled *The Faunistic Importance of the Scarp of Angola* (Hall, 1960) in which she proposed a series of hypotheses regarding the evolution of the patterns of bird distribution that she had studied. She defined the 'Escarpment Zone' as:

- "A wedge of richer vegetation lying between the drier areas of thornveld or grassland and brachystegia woodland. In the north it is wide with considerable patches of forest; in the south it tapers to a very narrow belt along the escarpment with forest patches rarer and less extensive."

This characterisation agrees with the definitions of the Angolan Escarpment Zone, Coastal Arid Savanna and Wet Miombo ecoregions used in this volume. Hall excluded the Afromontane Forests and Grassland ecoregions from her 'Escarpment Zone'. This distinction is upheld by the composition of plant and animal communities (despite the general physiognomic similarity) of Escarpment and Afromontane forests.

Hall (1960) proposed that the faunistic importance of the escarpment relates to three speciation processes:

- Firstly, the role of the escarpment as a centre of speciation. This she illustrated by a number of examples in which birds found in the Escarpment Zone differ in some striking character from all others of the same species throughout Africa, and which do not apparently interbreed with their relatives in other zones.
- Secondly, the Escarpment Zone is of importance in providing a barrier of some distance between members of a species present in the two drier zones (*Acacia* thornveld and *Brachystegia* woodland), but with the species absent from the Escarpment Zone, allowing subspecies to develop in each of the two geographically separate and drier zones.
- Thirdly, the Escarpment Zone is important in containing a number of 'old' endemic and near endemic species.

Hall was able to demonstrate numerous cases that supported her three hypotheses. The vast majority of the 250 species she examined were found in only one of the three habitats—arid coast, moist escarpment forests, or mesic miombo. Only five species were found in all three zones. Her explanation of speciation processes proposed successive wetter and drier climatic episodes, with forests retracting and expanding, and with allopatric speciation taking place in the three distinct zones where the escarpment zone provided both a barrier and a refuge. The persistence of moist conditions and stable habitats and corridors along the escarpment was possible due to the orographic fog and higher rainfall sustained under the influence of the Benguela Current, even during arid episodes.

More than 60 years after the publication of Hall's paper, the Angolan Escarpment and Afromontane forests continue to attract both professional and amateur biologists. Hall's (1960) hypotheses, based purely on the morphological and plumage characters of her study specimens, and on speculations about climate change, preceded the extensive literature on the evolution of African rain forests and the biogeography of Afromontane species. Hall focused on the relationship between Escarpment species with those of the adjoining coastal lowlands and plateau highlands, with limited reference to the disjunct bird faunas of the 'sky islands' of the Afromontane Archipelago.

Since Hall's paper, the Escarpment and Afromontane forests have been identified as critical areas for conservation—the Western Angola Endemic Bird Area. This Endemic Bird Area includes 14 restricted range birds which are considered 'endemic birds of global conservation concern' (Stattersfield et al., 1998). Nine of these are found at just one of the escarpment forests—Cumbira. Cumbira also holds the highest number of Angolan endemic species (11 of 17). These findings (Mills, 2019) demonstrate the scientific and conservation importance of this seriously threatened forest. The endemic bird species include:

Gabela Akalat, Pulitzer's Longbill, Gabela Bushshrike, Gabela Helmetshrike, Monteiro's Bushshrike, Grey-striped Francolin and White-fronted Wattle-eye.

A detailed study of the distribution of forest bird species of the Angolan Escarpment (Mills, 2010) revealed three distinct bird communities occupying different forest habitats. Of the 91 forest species surveyed, 47 were identified as being limited to or having isolated populations on the escarpment. The moist forest types of the northern escarpment (Cazengo, Dembos, Uíge) are richest in Congolian species, but have only one endemic—Braun's Bushshrike. The central (Amboim/Cumbira) escarpment forests at between 500 and 1000 m are drier, more fragmented, and are surrounded by thickets and arid savanna, especially at altitudes below 300 m. Interestingly, the low-altitude dry forests have more threatened endemic species than the moister mid-scarp forests, which are richer in Congolian species. Mills (2010) suggests that the endemic and range-restricted species of the escarpment evolved during phases of aridity during glacial maxima when the moist forests contracted and were isolated from the Congo Basin, at which time the forests would have been similar to the present drier fringing habitats. He infers that the endemic taxa might have moved to the periphery of the escarpment when the main forests became moister, with better connections to the Congo Basin. He proposed that molecular phylogenetic studies would provide greater clarity to the processes of speciation along the escarpment.

Rapid advances in research approaches to studying the evolution of the rare birds of Angola, such as electronic and georeferenced databases, molecular phylogenetics, climate change modelling and ecological niche models are now available. These tools were used by Portuguese student Bruno Vaz da Silva to study the evolutionary history of the birds of the Angolan highlands, focusing on the forests of Mount Moco and Mount Namba. Vaz da Silva (2015) used five species as study subjects: Evergreen Forest Warbler, Thick-billed Seedeater, Bocage's Akalat, Red-faced Crimsonwing and African Hill-babbler. All five have relatives in the Afromontane ecosystems of Cameroon, Ruwenzori and the Eastern Arc mountains of Tanzania. These sites are all more than 2000 km distant from Angola's montane forests (Fig. 18.2).

Fig. 18.2 The present distribution of five Afromontane bird species. From Vaz da Silva (2015). Bird figures from Lynx Edicions and maps from BirdLife International and Handbook of the Birds of the World (2021), with permission

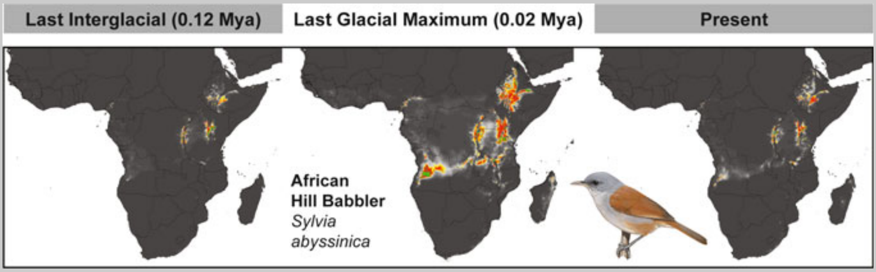

Fig. 18.3 Species distribution modelling results for African Hill-babbler: Left—the beginning of the last glacial period (120 thousand years ago), Centre—the Last Glacial Maximum (21 thousand years ago), compared with Right—the projection for the present. The existence of a corridor across Angola via Zambia during the Last Glacial Maximum was suggested for all five species studied. From Vaz da Silva (2015). Bird figures from Lynx Edicions and maps from BirdLife International and Handbook of the Birds of the World (2021), with permission

Vaz Silva's study aimed at establishing a comparative phylogeography of the species and to describe the niches currently occupied. This would help understand the dynamics of disjunction and reconnection—where fragmentation occurred and where corridors between isolated habitats existed. The results of the study provided strong evidence of ecologically suitable habitats existing as corridors between Angola and East Africa via Zambia during the last 120,000 years of the Pleistocene, with weaker ecological connections to Cameroon (Fig. 18.3). Stepping stones for such forest species still exist across Angola in the gallery forests of the upper reaches of the Congo and Zambezi basins, and the escarpment forests above the Baixa de Cassange at Quela and Tala Mungungo, at the waterfalls at Dala in Lunda-Sul and across the Zambian highlands.

The phylogenies indicate that speciation was driven by arid periods with habitat fragmentation, followed by reconnection, going back to the Pliocene (3.1 Ma), with recurrent events through the Pleistocene. The timing and frequency of genetic divergence in the study species, at 3.1, 2.7 and 1.7 Ma coincide with episodes of aridity. The evidence suggests that both dispersal and **vicariance** (geographical separation preventing gene exchange) processes might have played important roles in shaping montane bird communities (Fjeldså & Bowie, 2008). Most interestingly, the results indicate that Angola may be an old and stable Afromontane centre, from which other centres may have been recolonised following extinctions (Vaz da Silva, 2015). The study confirms the critical importance of conserving Angola's Escarpment and Afromontane forests, as reported nearly 50 years ago (Huntley, 1974).

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Part V
Synopsis and Conclusions

Chapter 19
Key Elements of Angolan Terrestrial Ecology

Key Concepts and Questions: This Chapter Will Explain

- *How Angola's landscapes were developed over the 550 million years since the formation of Gondwana.*
- *What dramatic climatic changes and evolutionary innovations led to the development of the African savannas and their abundant wildlife.*
- *How climate, soils, fire and herbivory shape Angola's biomes and ecoregions.*
- *What unifying ecological concepts explain how ecosystems are structured and how they function.*
- *Why ecology is an important and exciting career.*

Context: Angola as a Microcosm of Africa's Ecological Diversity

The aim of this volume is to provide Angolan students with an introduction to terrestrial ecology, presenting strongly African, and specifically Angolan, perspectives. In reading the chapters, it soon becomes apparent is that Angola is a microcosm of Africa, with an unparalleled diversity of biomes and ecoregions, from rain forest to desert in one country. This richness obliges the Angolan student to become familiar with a much broader and more complex suite of concepts, phenomena and technical terms than is the case for students of less biodiverse countries.

This concluding chapter provides a synopsis of key elements of Angola's ecological structure and functioning, highlighting features and concepts that emerge in individual chapters. These elements provide the student with a toolkit of fundamental concepts and processes that will guide an understanding of Angola's terrestrial ecosystems.

Four themes or 'leitmotifs' recur throughout this book and underpin its didactic objectives:

- **Ecology is about recognizing patterns and processes that** operate at widely differing scales of time and space.
- **Ecology is about the unique mechanisms of survival, growth and reproductive output** of organisms in relation to their environment.

B. J. Huntley, *Ecology of Angola*,
https://doi.org/10.1007/978-3-031-18923-4_19

- **Ecology does not make sense except in the light of evolution**. But equally, very little in evolution makes sense except in the light of ecology.
- **The whole is greater than the sum of its parts**. Interactions and webs of interdependencies between individuals, species and populations and their environments create collective, **emergent properties** that shape ecosystem structure and function.

19.1 The Big Picture: Global Tectonic and Climatic Forces that Have Shaped Angola's Biomes and Biota

A long-term perspective of global geological and climatic dynamics provides an essential backdrop against which to understand African and Angolan landscapes and biota. These developed across hundreds of millions, indeed billions of years, through processes of change that continue to this day. Presenting the 'big picture' of Angola's history must therefore refer to the dramatic forces (tectonic, oceanic, atmospheric) that have shaped life on Earth.

The Gondwanan Origins of Angola

Since Earth's origin 4.5 billion years ago, tectonic events across the Earth's crust resulted in the creation of supercontinents, such as Laurasia and Gondwana. Gondwana formed 550 Ma and started to break up from 180 Ma, finally splitting off the southern continents (South America, Antarctica, Africa, Australia) by 130 Ma. With the separation of the southern continents, the vast oceans of the southern hemisphere were formed. Over land and sea, major atmospheric air masses circulated between zones of low pressure (such as the Intertropical Convergence Zone) and high pressure (the South Atlantic Anticyclone). The circulation of the air masses produced the winds that created ocean currents (such as the Circum-Antarctic, the Benguela and the Mozambique currents). These atmospheric and oceanic dynamics have been the drivers of climate patterns over Africa throughout the Cenozoic Era (the past 66 million years). Through the Cenozoic, the climate has included warmer, wetter periods (known as 'Hothouse Earth') and cooler, drier periods ('Icehouse Earth') due to changes in the Earth's planetary orbit around the Sun and the position of continents relative to the Poles and the Equator. The most recent major oscillations in climate, known as the Pleistocene Ice Ages, commenced 2.6 Ma and continue to this day.

The Shaping of Angola's Landscapes

During the creation of Gondwana, and following the separation of the continents, further tectonic events caused uplift and erosion, and depression and sedimentation, of vast areas of the continental surface. In Angola, these uplift areas are today represented by the Mayombe and Bie Swells, and the Angolan Escarpment and Marginal Mountain Chain. The depressions include the Congo and Kalahari Basins. But for most of the Cenozoic, Africa has been relatively stable, with a slow downward erosion of the land surface to form the vast Central African Plateau, including

Angola's planalto and the extensive peneplains of the Congo and Zambezi upper catchments. The soils of these landscapes have been leached by the abundant rainfall and relatively cool and humid climate of the interior. The margins of these 'old' landscapes have been re-shaped by later erosional cycles, cutting the deep valleys of the Cuanza, Cunene and other westward-flowing river systems that drain the highlands. The 'younger' landscapes formed by the new erosional processes, themselves triggered by periods of coastal uplift, are characterised by soils that have not been heavily leached, and are therefore generally richer in nutrients. Their lowland situation results in them having climates that are warmer and drier than the highlands and peneplains.

Game-changing Evolutionary Innovations

The major climatic and landscape changes described above provided the stage for the evolution of Africa's modern fauna and flora. Genetic differentiation, isolation, speciation and extinction accounts for continuous waves of terrestrial plant and animal families and species. However, several game-changing evolutionary innovations stand out and deserve mention. These innovations—C_4 photosynthesis, hypsodont teeth, ruminant digestion—had dramatic consequences for the structure and functioning of African ecosystems.

The cooling and aridification of Africa during the mid- to late-Cenozoic led to an increase in the frequency of fire, the fragmentation of the forests, and, with enhanced rainfall seasonality, the formation of open savanna ecosystems. The stage was set by the new fire-driven ecosystems for physiological and morphological adaptations in plants and animals on a grand scale. These new ecological pressures and opportunities resulted in the evolution of the C_4 photosynthetic pathway in sun-dependent and fire-tolerant savanna grasses. These physiological adaptations in turn resulted in high water-use efficiency, a key advantage in seasonally dry environments. These aridity-adapted grasses gradually out-competed the C_3 grasses that had evolved in shady, humid forest communities. Because the plant tissues of the C_4 grasses had a high silica content, and their leaves were often covered in gritty dust blown across the open savannas, they posed a challenge for grazing mammals. In addition, the leaves of these robust C_4 grasses have high levels of cellulose and other structural carbohydrates, which are difficult to digest. Two further functional adaptations, during the Miocene (23–5 Ma), solved these challenges of gritty, indigestible grass, and led to the rapid radiation of mammalian herbivores, adapted to the open landscapes of Africa's tropical savannas. By the development of high-crowned (hypsodont) dentition, the ungulates were able to make effective use of the gritty grasses, without the wearing down of their teeth. Secondly, equally important for herbivores in tropical savannas, was the development of the ruminant gut. Here a symbiotic relationship with microorganisms resulted in efficient use of savanna grasses. The microorganisms of the ruminant stomach possess a special enzyme, cellulase, that can break down the indigestible cellulose, thus leading to the success of African ruminants. By the end of the Miocene epoch, Africa as we know it, with its tropical savannas, and modern plant, bird and mammal families and genera, had been established.

Many further adaptations through natural selection provided the capacity to occupy the new landscapes created by large-scale geological and climatic changes. The outcomes are reflected in the functional traits that species exhibit—such as thick bark in mesic savanna trees, spines in arid savannas trees and shrubs, and complex physiological processes such as the temperature regulating carotid rete in desert antelope. At finer time and spatial scales, research on speciation in forest birds provides insights on the expansion and contraction of forests through wet and dry periods of the Pleistocene. Such knowledge, on forest dynamics and faunal speciation, is of increasing importance to strategic and systematic conservation planning to save Angola's critically endangered Escarpment and Afromontane forests and their endemic fauna and flora.

At all scales, the processes of speciation through natural selection in response to climatic and geophysical dynamics, and competition for resources by plants and animals, underpins an understanding of ecological phenomena. Studies on the evolution of Angola's rich biodiversity is not only of academic interest, but also directly applicable in conservation planning and management.

19.2 Contemporary Drivers of Ecosystem Structure and Function in Angola

The determinants of the distribution of species and ecosystems in Angola include:

- Conditions (temperature and humidity) which influence the life of organisms but which cannot be consumed;
- Resources (light, water and nutrients) which can be consumed and for which organisms compete; and
- Disturbances (fire, floods, droughts, herbivory) which operate at the ecosystem rather than the individual level.

Here examples of key resources and disturbance pressures will be illustrated.

Resources: Solar Radiation and Energy

Life on Earth is possible because of the energy it receives from the Sun. The tilt of the Earth's axis as it moves around the Sun creates the annual seasonality of climate, of day length, temperature and rainfall patterns. More directly, solar energy received at the Earth's surface is harnessed through photosynthesis—the biochemical reactions that transform atmospheric carbon dioxide and water into carbohydrates, and release oxygen. The process of energy capture and transformation into simple sugars and cellulose in the chloroplasts of plant cells (primary production) is at the base of all food chains and the transfer of energy from one trophic level to the next. Plant tissues are consumed by herbivores, which in turn are consumed by predators, ultimately to be decomposed and mineralised by microorganisms or fire. The whole energy cycle is governed by the laws of thermodynamics.

The first law of thermodynamics states that energy cannot be created or destroyed, but can be transformed from one state to another. When wood burns, stored chemical energy is transformed into heat and light. In food chains, energy is used to do work—such as in growth, movement, reproduction and the production of complex molecules. Some of the energy is transformed into heat and is no longer available to do work. The total amount of energy in the system does not change, but the energy available to do work decreases from one trophic level (primary producer, consumer, predator, decomposer) to the next.

The second law of thermodynamics states that this transfer of energy through transformation reaches a point where there is no remaining usable energy for work. The deficit is continuously filled by energy derived from the Sun, through photosynthesis. At each step of the process—of energy transfer from primary producers to consumers, to predators and to decomposers—about 90% of the energy is used up as heat. Food chains are therefore short, usually of only three or four levels, due to the energy required for work being dissipated as heat in each transfer.

Resources: Atmospheric Systems and Rainfall

The macroclimates of Angola are driven by global atmospheric and oceanic dynamics, in particular the movements of air masses in relation to regions of low and high pressure. The Earth's atmosphere exerts pressure on the surface. Areas of high and low pressure are caused by ascending and descending air. As air warms it ascends, leading to low pressure at the Earth's surface. As air cools it descends, leading to high pressure at the surface. Air masses move from areas of high pressure to areas of low pressure, resulting in winds and ocean currents.

A low pressure belt over the Equator (the Intertropical Convergence Zone) draws in warm, moist, converging air masses which rise above the Equator, condense and result in the high rainfall received across northern Angola. A region of high pressure over the Tropic of Capricorn (the South Atlantic and Botswana Anticyclones) creates descending, dry air over southwestern Africa, and accounts for the aridity of the Namib Desert. The little rain which reaches the Namib comes not from the adjoining Atlantic Ocean, but from the Indian Ocean. Most of the rainfall from the Indian Ocean, carried across central Africa by easterly winds, is precipitated before reaching the Namib, which lies in the rain shadow of the highlands of eastern and central Africa. For the extreme hyper-arid coastal areas of the Namib, more moisture is received in the form of fog and low stratus clouds, than from rainfall. Fog and stratus clouds are driven over the coast by south-westerly winds. The moisture is trapped below a temperature inversion created by the cold, upwelling Antarctic waters of the Benguela Current. The south-westerly winds, and the Benguela Current, are driven by the air masses of the South Atlantic Anticyclone.

Resources: Soils and Nutrients

Soil is a primary resource essential for plant growth, survival and reproduction. The availability to plants of moisture and nutrients held in soils, determines the composition, structure and distribution of vegetation. Soil types, like vegetation types, vary widely in their structure and composition, and the distribution of soil and vegetation types is often highly correlated. In simple terms, soils consist of clays, loams and sands. Clays are usually darker, less permeable to water, and usually have higher nutrient content than sands. Sands are generally pale, quick draining and of low nutrient value. Loams are a mix of both clay and sand components. Two terms—eutrophic (neutral to basic pH, moderate to high nutrient value) and dystrophic (acidic, low nutrient value) are used frequently when referring to Angolan soil types. Based on these criteria, Angolan soils can be conveniently, if somewhat simplistically, divided into four soil groups, reflecting their broad distribution patterns and ecological characteristics.

- Over half of Angola is covered by the nutrient-poor arenosols of the Kalahari sands of the interior peneplains, lying east of approximately 18° longitude. The sands were deposited by wind and water over the last five million years. These old peneplains receive from 800 to 1400 mm rainfall per year, and are highly leached. Despite being acidic and nutrient-poor, they support a robust cover of grasslands and woodlands.
- Cutting longitudinally across the western highlands and planalto of Angola is a spine of crystalline rocks, including granites, gabbros, quartzites and schists. These rocks have produced highly leached ferralsols, low in nutrients and high in aluminium. They receive from 650 to 1200 mm rainfall per year. Ferralsols cover 23% of the country.
- Further west, along the Angolan Escarpment, a mix of moderately fertile soils occur, on young, rapidly eroding landscapes, receiving 500–1600 mm per year. These landscapes have high agricultural potential, and once carried extensive rain forests.
- The arid coastal lowlands, from the base of the escarpment to the Atlantic Ocean, comprise marine and terrestrial sediments, with moderate to high soil nutrient status. Rainfall ranges from 500 mm at the base of the escarpment to as low as 20 mm per year on the coast, where the sand seas of the Namib Desert dominate the landscape.

Disturbance: Fire and Herbivory, Equilibrium and Feedbacks

The importance of disturbance factors, such as fire and herbivory, has lacked emphasis in classical ecology textbooks. Yet fire, the great consumer of Africa, is the key determinant of structure in mesic savannas and is the environmental pressure that maintains a dynamic equilibrium between forests and savannas across northern Angola. Fire has an ancient history in global ecosystems, operating over hundreds of millions of years, most importantly as the environmental force that triggered the evolution of C_4 grasses during the mid-Cenozoic (ca. 35 Ma) and the rapid expansion of tropical savannas during the past 10 million years. Multiple adaptive traits have evolved in mesic savanna trees and shrubs, in response to frequent fires. These include thick bark, epicormic buds, self-thinning, and geoxyles. These adaptive traits have evolved independently in multiple families both in African miombo and in South American cerrado ecosystems.

In arid savannas, fire is of less importance than in mesic savannas, although rare, intense, hot fires following unusually wet periods can have significant impacts. Grazing and browsing mammals are richer in species and of higher biomass in the nutrient-rich arid savannas than in mesic savannas. Herbivory is therefore of greater importance in shaping arid savanna structure than that of mesic savanna, and accounts for the evolution of defensive mechanisms against browsing, such as spines, thorns and prickles found on many tree and shrub species.

Linked to the processes of ecological disturbance are the concepts of equilibrium, resilience and feedback mechanisms. Ecological equilibrium is a state where an ecosystem may be subject to slight fluctuations in structure and composition, but returns to the original state when the disturbance (or perturbation) process ceases. The ability to return to the original state, and not change to a new state, is called resilience. Feedback loops play a key role in maintaining equilibrium. Frequent fires maintain an open landscape in tallgrass mesic savannas, even where there is sufficient rainfall to support closed rain forests. Negative feedbacks (such as fires in savannas that kill forest tree saplings) counteract change and maintain the status quo. Positive feedbacks (such as fire exclusion) amplify change from one stable state (open savanna) to a new alternative stable state (closed canopy forest).

Determinants, Pattern, Structure and Ecological Terminology

The interactions between resources and disturbance factors result in the diverse ecosystems, ecoregions and biomes found across Angolan landscapes. While the Guineo-Congolian forests and the Namib Desert are clearly distinctive in physiognomic structure and floristic and faunistic composition, the most extensive biomes, the Mesic/Dystrophic and Arid/Eutrophic savanna biomes are functionally distinctive but structurally rather similar. Both biomes comprise a mix of grasslands, savannas, woodlands and thickets. It is therefore important to address a significant challenge for Angolan students—the inconsistent use by ecologists of terms for ecological patterns, structure, processes and phenomena.

The early literature on Angolan vegetation adopted terms directly from Europe. However, Barbosa (1970) followed many of the terms used more broadly in Africa, and much of his terminology is followed in this volume. More recently, visiting scientists, predominantly from Europe, have applied the term forest to fire-tolerant miombo woodlands (the dominant ecoregion of Mesic/Dystrophic Savanna Biome), which are structurally and functionally distinct from the forests of the Guinea-Congolian Rain Forest Biome. In this volume, the term forest is reserved for the closed-canopy, stratified and fire-intolerant communities that lack a grassy ground layer—rain forests, gallery forests and swamp forests.

The modern definition of tropical savannas includes the co-dominance of fire-tolerant trees and C_4 grasses in a continuum of grasslands, savannas, and woodlands. This definition is followed in this volume for the Mesic/Dystrophic and the Arid/Eutrophic Savanna biomes. The use of some collective terms for different levels of vegetation structure can, however, be confusing. This volume also uses the term savanna to describe grasslands with scattered trees. Until recently, the ecological and evolutionary distinctions between arid/eutrophic and mesic/dystrophic savannas were ignored by many ecologists, who placed all savanna ecosystems into a single savanna biome. For these reasons, an extensive Glossary of Ecological Terms is provided.

19.3 Ecological Patterns at African and Angolan Scales

Development of Angola's Biomes

The end of the Mesozoic Era (the Age of Dinosaurs), some 66 million years ago, saw the extinction of the dinosaurs and the dawn of the Cenozoic Era (the Age of Mammals). Gymnosperms were being replaced by Angiosperms (flowering plants) as the dominant flora of the world. In tropical Africa, the vegetation cover changed from closed dark forests, to more open sunny savanna landscapes. The broad-leaved lowland forests are today represented by extensive rain forests, while the highlands carry remnant fragments of montane forests. As the African climate cooled, an arid savanna and semidesert flora evolved and occupied the hot, drier lowlands, while on the cooler and more humid plateaus, mesic savanna woodlands were established.

Today, Angola includes representatives of six of Africa's nine biomes: Guineo-Congolian Rain Forest, Afromontane Forest and Grassland, Mesic/Dystrophic Savanna, Arid/Eutrophic Savanna, Namib Desert and Mangrove biomes. The biomes can be characterised by structural and functional features, which can be observed through the medium of satellite imagery. The main structural types include forest, thicket, woodland, savanna, shrubland, grassland, mangrove and desert. Closer study reveals regional centres of floristic endemism. These include the Guineo-Congolian, Afromontane, Zambezian and Karoo-Namib regional centres of endemism. While centres of endemism are defined by their floristic composition, and are explained by evolutionary relationships, biomes are defined by ecological structure and function, determined by the conditions under which they grow, the resource*s* available to them, and the impacts of disturbance factors.

While this coarse-grained classification of African and Angolan biomes and regional centres of endemism provides a useful introduction to the continent's ecological and biological diversity, it must be recognised that at the interfaces of biomes and centres of endemism, broad transition zones and mosaics occur. This is especially the case where the closed-canopy Guineo-Congolian Rain Forest Biome forms a mosaic with the open woodlands and tallgrass savannas of the Mesic Savanna Biome. Throughout this volume, emphasis is placed on predominant patterns and processes, rather than the frequent exceptions to these.

Recognising Biomes and Ecoregions in the Field

A helpful starting point in learning to recognise patterns in nature, and the division of biomes into ecoregions, is observation at the landscape scale. This can be facilitated by the use of satellite imagery and aerial photography, scoping down to low altitude, where topographic features and vegetation structure can reveal patterns from continental to local scales. However, ground-based fieldwork should always be the primary source of ecological information. A working knowledge of the key landscapes, geological formations and soil types, and plant and vertebrate species of one's study area, is essential. For this reason, in the description of biomes and ecoregions, reference is made to the key abiotic and biotic features that characterise the units. The challenge to learn to identify plant and animal species is not insurmountable. For all biomes and ecoregions, a shortlist of indicator plants, birds and mammals can be focused on.

By way of example, the main biomes of Angola can be identified by the presence or absence of a few tree species. The vast miombo (typical of the country's Mesic/Dystrophic Savanna Biome) is identifiable by the presence of *mupanda* (*Brachystegia spiciformis*). The Arid/Eutrophic Savanna Biome is recognised by the presence of *imbondeira* (*Adansonia digitata*); the Guineo-Congolian Rain Forest Biome by *moreira* (*Milicia excelsa*); and Afromontane Forest Biome by *pinho-de-muxito* (*Podocarpus milanjiana*). With the addition of a few more tree species, the ecoregion can be identified, and confirmed by reference to a few bird, mammal or reptile species. Some ecoregions are characterised by single tree species, such as the Zambezian Dry Evergreen Forests (*Cryptosepalum exfoliatum*), the Angolan Mopane Woodlands (*Colophospermum mopane*), and the Zambezian *Baikiaea* Woodlands (*Baikiaea plurijuga*). Ecological studies that ignore the identity of the subject species, especially the indicators, have limited utility.

19.4 Patterns at Landscape Scale in Angola

Recognising patterns at both spatial and temporal scales is fundamental to understanding ecological phenomena. The interactions between termites and grasses within a 5 m diameter 'fairy circle' of the Namib Desert are as intriguing as those between the precipitation, soil nutrient, herbivory and fire regimes of the arid/eutrophic and mesic/dystrophic savannas that cover over 90% of Angola's land area. Temporal scales range from hundreds of millions of years, such as in the development of Angola's geological foundations, to the milliseconds of molecular activity in photosynthesis. The following concepts, phenomena and interconnections are mentioned to illustrate that scale is a fundamental concept in ecology, and a reason for students to gaze across landscapes as well as to peer down microscopes.

The Catena Concept

The landscapes of the Angolan planalto and peneplains are characterised by a dense pattern of soil and vegetation sequences. A catena (chain) is a repeated series of soil forms across gently rolling landscapes, with woody communities on the rises and treeless grasslands in the valleys. The pattern reflects the soil formation processes of leaching, transport and deposition of water and nutrients across the soil profiles of upland, slope and bottomland. Fire, and in some locations frost, are also factors maintaining the vegetation pattern.

Duricrusts: Laterites and Silcretes

An important edaphic feature of many ferralsols and arenosols is the presence of impervious duricrusts (laterites or silcretes) at a metre or more below the surface. These cemented bands result in a barrier to tree growth, because of impeded drainage (causing seasonally anaerobic, waterlogged soils), but also because the duricrusts prevent root penetration and limit root access to moisture during the extended dry season.

Termitaria as Nutrient Hotspots

The low nutrient availability (dystrophic) status of mesic savannas accounts for the importance of nutrient hotspots in an otherwise uniform cover of miombo trees and grasses. The concentration of nutrients is due to the activity of termites that gather the limited clay particles of the sandy soils, plus organic material, in building their colonial nests (termitaria), that total between 100 and 1000 nests per hectare. The nutrient concentration of salts in the termitaria has been recorded as 20 times higher than the surrounding soils of the miombo. As a result, many mammal species use the old termitaria as salt-licks, while a great diversity of plants, vertebrates and invertebrates form distinctive habitats around the larger termitaria—biodiverse islands in a sea of low-diversity woodlands. In the miombo woodlands of Zambia, for example, over 700 tree species are associated with termitaria.

Mycorrhizae, Termites and Miombo Trees

Mutualistic associations exist between tree roots and fungi (mycorrhizae) in nutrient-poor mesic savannas, most typically in the dominant miombo trees—*Brachystegia* and *Julbernardia*. These mycorrhizal interactions are complex. Mycelia (networks of fine root-like hyphae of fungi) encircle or penetrate the root hairs of trees and transfer to the trees nutrients sourced from organic matter. Some species of termites create fungal gardens within their nests, feeding the fungi with organic material that the termites collect from the plant litter of the surroundings. These termite/fungal/tree associations maintain a robust woodland in an otherwise dystrophic savanna. The reproductive organs of the fungi (better known as mushrooms) provide a seasonal source of food for local human populations.

Geoxyles: Underground Forests

A further phenomenon unique to the mesic/dystrophic savannas of Africa and Brazil is that of ‘underground forests’. These are communities of geoxyles—dwarf shrubs that form extensive carpets of brightly coloured leaves and flowers which appear after fires and before the rain season. Geoxyles occur from the highlands of Benguela to the floodplains of Moxico—and across Africa to Mozambique and northwards to the Sudan—wherever mesic/dystrophic savannas are found. The dwarf shrubs are often closely related to the trees of the adjoining woodland. Geoxyles protect their growing points by keeping them, plus their branches and woody storage organs, below the soil surface. The Angolan miombo has possibly over 200 species of geoxyles, belonging to more than 40 plant families. They, like their Brazilian counterparts, evolved over the past five million years. Their unusual morphology has puzzled ecologists for 150 years and, despite strong arguments that the geoxyle habit is an adaptation to fire, nutrient poverty, high water table, herbivory, or frost, or combinations of these factors, the explanations proposed thus far remain contested.

Age and Diversity of Guineo-Congolian Rain Forests

With regard to the Guineo-Congolian rain forests, perceptions of the age, stability and floristic diversity of the extensive forest blocks of the Congo have been clarified during the past two decades through palaeoecological, archeological and phylogenetic studies. The belief that these forests represent ancient, exceptionally species-rich and stable ecosystems has been countered by evidence that the forests underwent major contractions and expansions through the Pleistocene. Furthermore, during the Holocene, human activities of agriculture, hunting and iron smelting brought significant changes to forest composition and structure. Large areas of monospecific tree communities point to deforestation followed by secondary succession with single tree species dominating the community for hundreds of years. The perception that much of the forest represents a stable climatic climax of the vegetation has been shown to be incorrect. Further, the richness of the African rain forest tree flora is less than a quarter of that of the Neotropics, within a similar land area. The relative paucity of tree species of African rain forests remains a topic of debate. These forests are nevertheless richer in bird, mammal and amphibian species diversity than those of any other African biome.

Mesic/Dystrophic and Arid/Eutrophic Savannas Compared

Emphasis has purposely been given in this volume to the mesic/dystrophic savannas, which cover over 80% of Angola, compared with arid/eutrophic savannas, which cover 13% of the country. However, the ecology of Africa's arid/eutrophic savannas is better known to scientists that the miombo and similar ecosystems, perhaps because of the concentration of ecological research over past decades in large conservation areas such as the Serengeti and Kruger National Parks, where arid/eutrophic savannas dominate the landscapes.

What is evident is that studies comparing the patterns and ecological processes in the two savanna biomes highlight the importance of rainfall, soil texture, nutrient status, fires and herbivory on their structure and functioning. Fire is a key determinant of habitat structure in mesic savannas, but less important in arid savannas. Herbivory by grazers and browsers, in contrast, is a driver of vegetation structure in arid savannas, but has comparatively little influence in mesic savannas. Nutrient cycling in arid savannas is via decomposer organisms, mostly invertebrates, but in mesic savannas, is largely driven by fires and mycorrhizae. It is these dichotomies in ecological processes and responses that make the tropical savanna biomes of Angola such attractive fields for research.

19.5 Ecological Concepts and Theories Relevant to Conserving Angolan Species

Two centuries have passed since Alexander von Humboldt first published ideas on the relationships between global vegetation patterns and climate, and since the schoolboy Charles Darwin started collecting plants and animals and asking questions about the origins of species. Over this time a substantial body of ecological concepts, theories and laws have been proposed and tested, accepted or rejected. Dozens of excellent textbooks are now available on the history, scope and application of the fundamentals of ecology. In this volume only a selection of the key elements of ecology are described. Even fewer of these can be mentioned in this synopsis, where emphasis is given to those with immediate relevance to the study, documentation and conservation of Angolan species and ecosystems.

Species Richness and Endemism

The measurement of species richness, and the explanation of why some communities have more species than others, are basic activities in ecological study. Related to measurements of species richness are measures of their abundance, density, evenness and distribution. Species with very limited areas of distribution, and which are restricted to a single country or biome—endemics—have long held the interest of conservation biologists. Very few analyses of species richness and endemism have been undertaken in Angola. The knowledge base is notoriously fragmented, and vast areas of Moxico and Cuando Cubango provinces lack anything more than preliminary surveys. Even for the country's iconic plant, *Welwitschia mirabilis*, extensions to its area of occurrence continue to be made, as previously unrecorded populations are found. The richest biome of Angola, the Maiombe rain forest of Cabinda, has not been surveyed since the 1970s. Comprehensive species inventories are not available for any national park, beyond preliminary checklists of a few vertebrate groups. Recent efforts to synthesise knowledge on Angola's biological diversity (Huntley et al., 2019) provide testimony of the country's natural wealth, and to the urgent need to survey, document and effectively protect it.

Threatened Species and Hotspots

Emphasis had been given by conservation scientists to identifying species whose survival is threatened by overexploitation, land transformation, invasive species or other causes. Preliminary Red Lists of Angolan plant and vertebrate species have been prepared, but lack data with which the degree and pace of threat can be determined for the majority of species. What is evident is that many Angolan mammals are in peril of extinction, if they are not already extinct. No sightings have been made, in the past several decades, of Lowland Gorilla, Lichtenstein's Hartebeest, Puku, Angolan Giraffe and Black Rhino. Other species (Forest Buffalo, Forest Elephant) are known only from very small and isolated populations. However, remarkable recoveries have been achieved. The country's most threatened mammal—Giant Sable—has been rescued from imminent extinction by meticulously planned, dedicated and long-term programmes (Vaz Pinto, 2019).

Local concentrations of endemic and threatened species are designated as global (or national) biodiversity hotspots. Efforts have been made since the early 1970s to identify Angolan hotspots, and to motivate for their detailed survey and proclamation as conservation areas. Several of these (Lagoa Carumbo, Serra do Pingano, Morro Moco, Namba, Cumbira) have attracted government attention, but still lack effective conservation measures. Actions to implement proposed management plans for these hotspots are urgently needed.

Theories of Island Biogeography and of Metapopulations

Two ecological theories—of island biogeography and of metapopulations—deserve more intensive application in conservation research in Angola. The theory of island biogeography is relevant to planning and management of conservation areas for the relict 'islands' of Afromontane forests of the Angolan highlands. The theory is based on the balance between immigration to, and extinction on, islands, whether they are oceanic islands or isolated forests in fire-prone savannas. As the remaining fragments of these forests decline in area and structure, so too do the chances of maintaining viable breeding populations of endangered species. Isolation further limits immigration of recruits to the forest patches, and together with habitat transformation, has resulted in local extinctions, as recorded for bird and mammal species on Mount Soqui and Morro Moco.

The concept of metapopulations is closely related to that of island biogeography. It is applied to all the local populations of a species that are separated from other populations of the same species by some form of disturbance or barrier. For each population, there is a minimum viable population size needed to maintain genetic diversity. Connectivity between populations is essential to maintaining the species' gene pool. Angola has many species that are fragmented, even though they survive in very small, declining populations across extensive ranges in Angola. These include Lion, Cheetah, Forest and Cape Buffalo, and Forest and Savanna Elephant. The populations of all these species are threatened by local events, whether within the population structure (demographic) or due to random (stochastic) environmental dynamics. The conservation of these species within their natural range in Angola will require initiatives such as those implemented to rescue the Giant Sable population of Cangandala National Park.

19.6 Conclusions: Why Ecology? An Opportunity for Young Angolan Students

Two of the key questions raised in the introduction to this book should challenge and motivate the student: Why is an understanding of ecology critical to Angola's sustainable development? Why ecology? Here a concluding, personal remark is offered.

Having been involved in ecological research and biodiversity conservation projects for the past 55 years, I have often paused to consider whether an ecological understanding of Africa's fauna and flora, and of its landscapes and biomes, is of any importance to ecosystems, economics or society. Like many ecologists across the globe, I have witnessed the rise and fall of wildlife populations and habitats, which, in all cases, were the result of political and not science-based decisions. I have suffered from occasional moments of frustration, even despair. But repeated examples of success rise above the continent's dismal record of failure. The rescue and conservation of Angola's Giant Sable population, and the restoration of Gorongosa National Park in Mozambique, are but two examples of good science, visionary leadership and indefatigable perseverance paying rich dividends (Huntley 2023).

Success is possible. But sound and innovative research, and above all, good governance, is needed to underpin any conservation effort, and to reverse the negative impacts of the processes eroding the biodiversity of Africa. The continental trends—of deforestation of forests and woodlands for agriculture, timber, fuelwood, charcoal and curios; of the overpopulation of domestic livestock and degradation of the productive capacity of rangelands; of the bushmeat trade that is creating 'empty forests'; of invasive plants infesting forests and agricultural lands; and of the global problem of climate change—demand a convincing response from conservation professionals based on science rather than on passion.

The diversity and richness of Angola's natural living resources and biomes have few parallels in Africa. What the country lacks is a strong body of active ecologists—young professionals dedicated to working in the field rather than in an office—using the vast literature on African ecosystems to stimulate and guide their curiosity and energy. This volume is therefore a humble attempt to support the process of ecological training and the implementation of effective conservation efforts in Angola.

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Appendix
Names of Vertebrate Species Mentioned in This Volume

The taxonomic arrangements of orders, families and genera follow Marques et al. (2018) for amphibians and reptiles, Mills and Melo (2013) for birds and Beja et al. (2019) for mammals. English names follow these authorities, and Portuguese or vernacular names follow Beja et al. (2019) for mammals, Baptista et al. (2019) for amphibians, Branch et al. (2019) for reptiles and Mills and Melo (2013) for birds. The biome in which a species is most typically (or historically) recorded, but not necessarily exclusively found, is indicated by abbreviations: AM (Afromontane Forests and Grasslands), AS (Arid Savannas), EZ (Escarpment Zone), GC (Guineo-Congolian Forests), MM (Mangrove or Marine), MS (Mesic Savannas), ND (Namib Desert). Species occurring in more than one biome are indicated by NS (non-specific distribution). Where a mammal species occurs in two biomes, both are indicated. Details of the distribution and ecology of most Angolan amphibian and reptile species are still poorly documented, thus the allocation of species to specific biomes are tentative.

Biome	Scientific name	English name	Portuguese or Vernacular name
AMPHIBIA			
GC	*Xenopus epitropicalis*	Congolese Clawed Frog	Rã-de-unhas-congolesa
MS	*Xenopus petersii*	Peter's Clawed Frog	Rã-de-unhas-de-peter
AS	*Poyntonophrynus dombensis*	Dombe Toad	Sapo-pigmeu-do-dombe
AS	*Poyntonophrynus grandisonae*	Grandison's Pygmy Toad	Sapo-pigmeu-de-grandison
MS	*Sclerophrys pusilla*	Merten's Striped Toad	Sapo-de-costas-planas-do-sul
AS	*Phrynomantis annectens*	Marbled Rubber Frog	Rã-de-borracha-marmoreada
MS	*Phrynomantis bifasciatus*	Banded Rubber Frog	Rã-de-borracha-de-duas-riscas
MS	*Hemisus guineensis*	Guinea Snouted Burrower	Rã-escavadora-de-guiné
EZ	*Afrixalus osorioi*	Osorio's Spiny Reed Frog	Rela-espinhosa-de-osório
MS	*Hyperolius angolensis*	Angolan Reed Frog	Rela-de-angola

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Biome	Scientific name	English name	Portuguese or Vernacular name
MS	*Hyperolius benguellensis*	Benguela Long Reed Frog	Rela-comprida-de-benguela
AM	*Hyperolius chelaensis*	Chela Mountain Reed Frog	Rela-da-chela
GC	*Hyperolius ocellatus*	Large-spotted Reed Frog	Rela-pintalgada
GC	*Hyperolius platyceps*	Benito River Reed Frog	Rela-do-rio-luinha
GC	*Hyperolius vilhenai*	Vilhena's Reed Frog	Rela-de-luita
MS	*Kassina senegalensis*	Senegal Kassina	Kassina-do-senegal
GC	*Arthroleptis carquejai*	Carqueja's Squeaker	Rã-guinchadora-de-carqueja
GC	*Arthroleptis lameerei*	Lameer's Squeaker	Rã-guinchadora-de-lameer
AM	*Leptopelis anchietae*	Anchieta's Tree Frog	Rã-arborícola-de-anchieta
GC	*Leptopelis aubryi*	Gabon Forest Tree Frog	Rã-arborícola-da- floresta-do-gabão
MS	*Leptopelis bocagii*	Bocage's Burrowing Tree Frog	Rã-arborícola- escavadora-de-bocage
EZ	*Amnirana parkeriana*	Parker's White-lipped Frog	Rã-de-labios-brancos-de-parker
EZ	*Leptopelis jordani*	Congulo Forest Tree Frog	Rã-arborícola-da-floresta-do-congulo
MS	*Hildebrandtia ornatissima*	Angola Ornate Frog	Rã-enfeitada-da-angola
MS	*Ptychadena oxyrhynchus*	Sharp-nosed Grass Frog	Rã-foguete-de-focinho-bicudo
AM	*Ptychadena uzungwensis*	Udzungwa Ridged Frog	Rã-foguete-de-udzungwa
AS	*Pyxicephalus adspersus*	African Bullfrog	Mafuma
AS	*Tomopterna tuberculosa*	Rough Sand Frog	Rã-da-areia-de-pele-rugosa
REPTILIA			
MM	*Caretta caretta*	Loggerhead Sea Turtle	Tartaruga-cabeçuda
MM	*Chelonia mydas*	Green Sea Turtle	Tartaruga-verde
MM	*Lepidochelys olivacea*	Olive Ridley Sea Turtle	Tartaruga-oliva
MM	*Eretmochelys imbricata*	Hawksbill Sea Turtle	Tartaruga-de-pente
MM	*Dermochelys coriacea*	Leatherback Sea Turtle	Tartaruga-de-couro
MS	*Pelusios nanus*	African Dwarf Mud Turtle	Tartaruga-de-plastrão-articulado-anã
GC	*Kinixys erosa*	Forest Hinged-Back Tortoise	Cágado-de-carapaça-articulada-da-floresta
AS	*Stigmochelys pardalis*	Leopard Tortoise	Cágado-leopardo
NS	*Crocodylus niloticus*	Nile Crocodile	Crocodilo-do-nilo
GC/MM	*Mecistops cataphractus*	West African Slender-Snouted Crocodile	Crocodilo-de-focinho-fino

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Biome	Scientific name	English name	Portuguese or Vernacular name
GC/MM	*Osteolaemus tetraspis*	African Dwarf Crocodile	Crocodilo-anão-africano
AS	*Afrogecko ansorgii*	Ansorge's Leaf-toed Gecko	Osga-de-dedos-de-folha-de- ansorge
AM	*Hemidactylus benguellensis*	Benguela Gecko	Osga-das-casas-de-benguela
EZ	*Hemidactylus longicephalus*	Long-Headed Tropical Gecko	Osga-das-casas-de-cabeça- comprida
MS	*Hemidactylus nzingae*	Queen Nzinga's Gecko	Osga-da-rainha-nzinga
ND	*Kolekanos plumicaudus*	Feathered-Tailed Gecko	Osga-de-cauda-de-pluma
AS	*Pachydactylus angolensis*	Angola Banded Thick-Toed Gecko	Osga-de-dedos-grossos-de-angola
ND	*Pachydactylus rangei*	Namib Web-Footed Gecko	Osga-de-dedos-grossos-com-membranas-nos-dedos
ND	*Rhoptropus afer*	Common Namib Day Gecko	Osga-diurna-do-namibe-comum
ND	*Rhoptropus boultoni*	Boulton's Namib Day Gecko	Osga-diurna-do-namibe-de- boulton
AM	*Rhoptropus montanus*	Namib Mountain Day Gecko	Osga-diurna-do-namibe-montana
AM	*Ichnotropis bivittata*	Angolan Rough-scaled Lizard	Lagarto-de-escamas-aspersas-de-angola
AM	*Ichnotropis microlepidota*	Marx's Rough-scaled Lizard	Lagarto-de-escamas-ásperas-pequeno
ND	*Meroles anchietae*	Anchieta's Dune Lizard	Lagarto-do-deserto-de-focinho-de-pá
ND	*Pedioplanis huntleyi*	Huntley's Sand Lizard	Lagartixa-da-areia-de-huntley
AM	*Cordylus angolensis*	Angolan Girdled Lizard	Lagarto-espinhoso-de-angola
ND	*Cordylus namakuiyus*	Kaokoveld Girdled Lizard	Lagarto-espinhoso-do-kaokoveld
ND	*Gerrhosaurus skoogi*	Desert Plated Lizard	Lagarto-de-placas-do-deserto
GC	*Feylinia currori*	Western Forest Feylinia	Lagartixa-do-subsolo-gigante-de-curror
MS	*Lubuya ivensii*	Iven's Skink	Lagartixa-de-água-de-iven
AS	*Mochlus sundavalii*	Sundeval's Writhing Skink	Lagartixa-contorcionista-de-sundeval
MS	*Trachylepis bayoni*	Bayão's Skink	Lagartixa-de-bayão
ND	*Trachylepis punctulata*	Speckled Sand Skink	Lagartixa-pintalgada
ND	*Typhlacontias punctatissimus*	Dotted Blind Dart Skink	Lagartixa-fossorial-ocidental- sarapintada
AM	*Chamaeleo anchietae*	Anchieta's Chameleon	Camaleão-de-angola
ND	*Chamaeleo namaquensis*	Namaqua Chameleon	Camaleão-de-namaqua
GC	*Trioceros oweni*	Owen's Chameleon	Camaleão-de-três-cornos-de-owen
MS	*Acanthocercus cyanocephalus*	Angola Tree Agama	Agama-das-árvores-de-angola
ND	*Agama planiceps*	Namib Rock Agama	Agama-das-pedras-do-namibe
ND	*Python anchietae*	Anchieta's Dwarf Python	Pitão-anã-do-namibe

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Biome	Scientific name	English name	Portuguese or Vernacular name
GC	*Atheris squamigera*	Variable Bush Viper	Víbora-das-árvores-variável
AS	*Bitis caudalis*	Horned Adder	Víbora-cornuda
GC/EZ	*Bitis gabonica*	Gabon Adder	Víbora-do-gabão
AM	*Bitis heraldica*	Angolan Adder	Víbora-de-angola
ND	*Bitis peringueyi*	Peringuey's Adder	Vibora-de-peringuey
GC	*Causus lichtensteinii*	Forest Night Adder	Víbora-nocturna-de-lichtenstein
AM	*Psammophis ansorgii*	Link-Marked Sand Racer	Cobra-da-areia-de-ansorge
ND	*Psammophis trigrammus*	Western Sand Snake	Cobra-da-areia-ocidental
GC	*Dendroaspis jamesoni*	Jameson's Mamba	Mamba-de-jameson
MS	*Naja anchietae*	Anchieta's Cobra	Cobra-de-anchieta
GC	*Naja annulata*	Ringed Water Cobra	Cobra-de-água-de-bandas
AS	*Naja nigricincta*	Western Banded Spitting-Cobra	Cobra-cuspideira-de-bandas
MS	*Dispholidus typus punctatus*	Spotted Boomslang	Cobra-de-papo-às-pintas
GC	*Hapsidophrys smaragdinus*	Emerald Snake	Cobra-esmeralda
GC	*Thrasops flavigularis*	Yellow-Throated Bold-Eyed Tree Snake	Cobra-arborícola-de-garganta-amarela
GC	*Thelotornis kirtlandii*	Forest Twig Snake	Cobra-dos-ramos-da-floresta
AVES			
AS	*Struthio camelus*	Ostrich	Avestruz
GC	*Agelastes niger*	Black Guineafowl	Pintada-preta
AM	*Scleroptila finschi*	Finsch's Francolin	Francolim-de-finsch
EZ	*Pternistis griseostriatus*	Grey-striped Francolin	Francolim-de-estrias-cinzentas
AM	*Pternistis swierstrai*	Swierstra's Francolin	Francolim-da-montanha
AS	*Sagittarius serpentarius*	Secretary Bird	Secretário
MM	*Gypohierax angolensis*	Palm-nut Vulture	Abutres-das-palmeiras
ND	*Torgos tracheliotus*	Lappet-faced Vulture	Abutre-real
ND	*Neotis ludwigii*	Ludwig's Bustard	Abetarda-de-ludwig
ND	*Eupodotis rueppelii*	Ruppell's Korhaan	Abetarda-de-ruppell
ND	*Cursorius rufus*	Burchell's Courser	Corredor-de-burchell
GC	*Columba unicincta*	Afep Pigeon	Pombo-pálido
GC	*Psittacus erithacus*	Grey Parrot	Papagaio-cinzento
GC	*Poicephalus gulielmi*	Red-fronted Parrot	Papagaio-de-coroa-vermelha
GC	*Corythaeola cristata*	Great Blue Turaco	Turaco-gigante
GC	*Turaco persa*	Guinea Turaco	Turaco-da-guiné

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Biome	Scientific name	English name	Portuguese or Vernacular name
EZ	*Tauraco erythrolophus*	Red-crested Turaco	Turaco-de-angola
EZ	*Centropus anselli*	Gabon Coucal	Cucal-do-gabão
AM	*Caprimulgus ruwenzorii*	Ruwenzori Nightjar	Noitibó-da-montanha
AM	*Apus sladeniae*	Fernando Po Swift	Andorinhão-de-bioko
MM	*Ispidina picta*	African Pygmy Kingfisher	Pica-peixe-pigmeu
GC	*Merops gularis*	Black Bee-eater	Abelharuco-preto
EZ	*Colius castanotus*	Red-backed Mousebird	Rabo-de-junco-de-angola
GC	*Tockus fasciatus*	African Pied Hornbill	Calau-pretibranco
MS	*Tockus pallidirostris*	Pale-billed Hornbill	Calau-de-bico-marfim
AS	*Tockus monteiri*	Monteiro's Hornbill	Calau-de-monteiro
GC	*Bycanistes subcylindricus*	Black-and-white-casqued Hornbill	Calau-de-casquete-preto-e-branco
GC	*Bycanistes fistulator*	Piping Hornbill	Calau-galhofeiro
EZ/AM	*Gymnobucco calvus*	Naked-faced Barbet	Barbaças-careca
EZ	*Stactolaema anchietae*	Anchieta's Barbet	Barbaças-de-anchieta
GC	*Pogoniulus atroflavus*	Red-rumped Tinkerbird	Barbabadinho-d'uropígio-vermelho
MS	*Tricholaema frontata*	Miombo Barbet	Barbaças-do-miombo
EZ	*Lybius leucocephalus*	White-headed Barbet	Barbaças-de-cabeça-branca
GC	*Dendropicos xantholophus*	Yellow-crested Woodpecker	Pica-pau-de-testa-dourada
AM	*Batis margaritae*	Margaret's Batis	Batis-da-margarida
MS	*Batis erlangeri*	Western Black-headed Batis	Batis-de-erlanger
AS	*Lanioturdus torquatus*	White-tailed Shrike	Picanço-palrador
EZ	*Batis minulla*	Angola Batis	Batis-de-angola
EZ	*Platysteira albifrons*	White-fronted Wattle-eye	Olho-de-carúncula-de-angola
EZ	*Prionops gabela*	Gabela Helmet-shrike	Atacador-preto-da-gabela
MM	*Lanarius bicolor*	Swamp Boubou	Picanço-dos-pântanos
EZ	*Malaconotus monteiri*	Monteiro's Bushshrike	Picanço-de-monteiro
GC	*Chlorophoneus bocagei (647)*	Grey-green Bushshrike	Picanço-de-bocage
AM	*Telophorus viridis*	Perrin's Bushshrike	Picanço-de-perrin
EZ	*Laniarius brauni*	Braun's Bushshrike	Picanço-de-braun
EZ	*Laniarius amboimensis*	Gabela Bushshrike	Picanço-do-amboim
MS	*Lanius souzae*	Souza's Shrike	Picanço-de-souza
MS	*Parus griseiventris*	Miombo Tit	Chapim-do-miombo
EZ	*Nicator vireo*	Yellow-throated Nicator	Tuta-picanço-de-garganta-amarela

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Biome	Scientific name	English name	Portuguese or Vernacular name
AM	*Mirafra angolensis*	Angola Lark	Cotovia-de-angola
AS	*Certhilauda benguelensis*	Benguela Long-billed Lark	Cotovia-de-bico-comprido-do-namibe
ND	*Ammomanopsis grayi*	Gray's Lark	Cotovia-da-namíbia
GC	*Phyllastrephus albigularis*	Angola White-throated Greenbul	Tuta-de-garganta-branca
AM	*Neolestes torquatus*	Black-collared Bulbul	Bulbul-picanço
EZ	*Chlorocichla falkenstein*	Yellow-necked Greenbul	Tuta-de-falkenstein
GC	*Phyllastrephus scandens*	Red-tailed Loveleaf	Tuta-das-folhas
EZ	*Phyllastrephus fulviventris*	Pale-olive Greenbul	Tuta-de-angola
AM	*Phedina brazzae*	Brazza's Martin	Andorinha-das-barreiras-de-brazza
AM	*Hirundo nigrorufa*	Black-and-rufous Swallow	Andorinha-preta-e-ruiva
AS	*Achaetops pycnopygius*	Rockrunner	Salta-pedras
EZ	*Macrosphenus pulitzeri*	Pulitzer's Longbill	Bico-longo-de-angola
MS	*Sylvietta ruficapilla*	Red-capped Crombec	Rabicurta-de-barrete-vermelho
AM	*Phylloscopus laurae*	Laura's Woodland Warbler	Felosa-de-laura
EZ	*Cisticola bulliens*	Bubbling Cisticola	Fuinha-fervilhante
MS	*Cisticola brachypterus*	Short-winged Cisticola	Fuinha-d'asa-curta
GC	*Prinia bairdii*	Banded Prinia	Prínia-riscada
AM	*Cisticola lepe*	Huambo Cisticola	Fuinha-de-angola
EZ	*Camaroptera harterti*	Hartert's Camaroptera	Camaroptera-de-angola
MS	*Calamonastes undosus*	Miombo Wren Warbler	Felosa-carriça-do-miombo
AM	*Eremomela salvadorii*	Salvadori's Eremomela	Eremomela-de-salvadori
MS	*Eremomela atricollis*	Black-necked Eremomela	Eremomela-de-colar
MS	*Hyliota flavigaster*	Yellow-bellied Hyliota	Hiliota-de-papo-amarelo
MS	*Lamprotornis acuticaudus*	Sharp-tailed Starling	Estorninho-de-cauda-acuminada
GC	*Onychognathus fulgidus*	Forest Chestnut-winged Starling	Estorninho-de-asa canela
MS	*Neocichla gutturalis*	White-winged Babbling Starling	Estorninho-de-asa-branca
AS	*Lamprotornis benguelensis*	Benguela Long-tailed Starling	Estorninho-rabilongo
AM	*Geokichla gurneyi*	Orange Ground Thrush	Tordo-da-terra laranja
EZ	*Sheppardia bocagei*	Bocage's Akalat	Pisco-de-bocage
EZ	*Sheppardia gabela*	Gabela Akalat	Pisco-da-gabela
EZ	*Cossypha heinrichi*	White-capped Robin-chat	Cossifa-de-cabeça-branca

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Biome	Scientific name	English name	Portuguese or Vernacular name
EZ	*Xenocopsychus ansorgei*	Angola Cave Chat	Chasco-das-furnas
ND	*Namibornis herero*	Herero Chat	Chasco-de-herero
AS	*Cichladusa ruficauda*	Rufous-tailed Palm Thrush	Tordo-das-palmeiras-de-cauda-vermelha
EZ	*Erythropygia leucosticta*	Forest Scrub Robin	Rouxinol-do-mato-de-sobrancelha
MS	*Erythropygia barbata*	Miombo Scrub Robin	Rouxinol-do-mato-do-miombo
ND	*Emarginata tractrac*	Tractrac Chat	Chasco-pálido
MS	*Myrmecocichla tholloni*	Congo Moor Chat	Chasco-formigueiro-do-congo
AM	*Dioptrornis brunneus*	Angola Slaty Flycatcher	Papa-moscas-de-angola
GC	*Muscicapa comitata*	Dusky -blue Flycatcher	Papa-moscas-ardósia
MS	*Anthreptes anchietae*	Anchieta’s Sunbird	Beija-flor-de-anchieta
MM	*Anthreptes gabonicus*	Mangrove Sunbird	Beija-flor-dos-mangais
AM	*Nectarinia bocagii*	Bocage’s Sunbird	Beija-flor-de-bocage
GC	*Cyanomitra bannermani*	Bannerman’s Sunbird	Beija-flor-de-bannerman
AM	*Cinnyris ludovicensis*	Ludwig’s Double-collared Sunbird	Beija-flor-das-montanhas
AM	*Cinnyris oustaleti*	Oustalet’s Sunbird	Beija-flor-de-oustalet
AM	*Nectarinia kilimensis*	Bronzy Sunbird	Beija-flor-bronzeado
MS	*Plocepasser rufoscapulatus*	Chestnut-backed Sparrow-weaver	Tecelão-pardal-de-dorso-arruivado
AM	*Ploceus nigrimentus*	Black-chinned Weaver	Tecelão-de-mento-preto
MM	*Ploceus superpersonatus*	Loango Weaver	Tecelão-do-loango
MS	*Ploceus temporalis*	Bocage’s Weaver	Tecelão-de-bocage
MS	*Ploceus angolensis*	Bar-winged Weaver	Tecelão-de-asas-riscadas
EZ	*Euplectes aureus*	Golden-backed Bishop	Cardeal- tecelão-de-angola
EZ	*Cryptospiza reichenovii*	Red-faced Crimsonwing	Asa-vermelha-de-mascarilha
AM	*Euschistospiza cinereovinacea*	Dusky Twinspot	Pintadinho-cinza
EZ	*Lagonosticta landanae*	Landana Firefinch	Peito-de-fogo-de-landana
AM	*Coccopygia bocagei*	Angola Swee Waxbill	Bico-de-lacre-de-angola
AS	*Estrilda thomensis*	Cinderella Waxbill	Cinzentinh- de-angola
AM	*Macronyx fuelleborni*	Fulleborn’s Longclaw	Sentinela-de-fülleborn

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Biome	Scientific name	English name	Portuguese or Vernacular name
AM	*Crithagra capistrata*	Black-faced Canary	Canário-de-faces-pretas
AM	*Crithagra burtoni*	Thick-billed Seedeater	Canário-cinzento-das-montanhas
MAMMALIA			
MS	*Canis adustus*	Side-striped Jackal	Chacal-de-flancos-raiados
AS	*Canis mesomelas*	Black-backed Jackal	Chacal-de-manto-negro
MS/AS	*Lycaon pictus*	African Hunting Dog	Mabeco
AS/ND	*Otocyon megalotis*	Bat-eared Fox	Raposa-orelhuda
AS	*Vulpes chama*	Cape Fox	Raposa-das-areias
AS	*Acinonyx jubatus*	Cheetah	Chita
GC	*Caracal aurata*	African Golden Cat	Gato-dourado
MS/AS	*Caracal caracal*	Caracal	Caracal
AS/MS	*Panthera leo*	Lion	Leão
AS/MS	*Panthera pardus*	Leopard	Leopardo
GC/EZ	*Crossarchus ansorgei*	Ansorge’s Cusimanse	Manguço-de-ansorge
ND	*Suricata suricatta*	Meercat	Suricata
AS/MS	*Crocuta crocuta*	Spotted Hyaena	Hiena-malhada
ND/AS	*Parahyaena brunnea*	Brown Hyaena	Hiena-castanha
AS/ND	*Proteles cristata*	Aardwolf	Protelo
GC/EZ	*Nandinia binotata*	African Palm Civet	Civeta-das-palmeiras
NS	*Civettictis civetta*	African Civet	Civeta-africana
MS	*Genetta angolensis*	Miombo Genet	Geneta-de-angola
AS	*Aepyceros m. melampus*	Common Impala	Impala-comum
AS	*Aepyceros m. petersi*	Black-faced Impala	Impala-de-face-negra
AS	*Alcelaphus buselaphus*	Red Hartebeest	Vaca-do-mato
MS	*Alcelaphus b. lichtensteini*	Lichtenstein’s Hartebeest	Tchicolocossi
AS/ND	*Antidorcas marsupialis*	Springbok	Cabra-de-leque
GC	*Cephalophus dorsalsi*	Bay Duiker	Cabra-do-mato-de-banda-dorsal-negra
GC	*Cephalophus leucogaster*	White-bellied Duiker	Cabra-do-mato-de-barriga-branca
GC	*Cephalophus nigrifrons*	Black-fronted Duiker	Cabra-do-mato-de-fronte-negra
MS	*Cephalophus silvicultor*	Yellow-backed Duiker	Cabra-do-mato-de-garupa-amarela
MS/AS	*Connochaetes taurinus*	Common Wildebeest	Boi-cavalo
MS/AS	*Damaliscus lunatus*	Tsessebe	Cacu
MS/AS	*Hippotragus equinus*	Roan Antelope	Palanca-ruana
MS	*Hippotragus niger*	Sable Antelope	Palanca-negra

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Biome	Scientific name	English name	Portuguese or Vernacular name
MS	*Hippotragus n. variani*	Giant Sable Antelope	Palanca-negra-gigante
MS/AS	*Kobus e. ellipsiprymnus*	Common Waterbuck	Cobo-de-crescente
MS	*Kobus e. defassa*	Defassa Waterbuck	Quissema
MS	*Kobus leche*	Southern Lechwe	Songue
MS	*Kobus vardonii*	Puku	Puco
AS/ND	*Madoqua kirkii*	Kirk's Dik-dik	Cachine
AS	*Oreotragus oreotragus*	Klipspringer	Cabra-das-pedras
AS/ND	*Oryx gazella*	Gemsbok	Órix
MS	*Ourebia ouribi*	Oribi	Oribi
AS/GC	*Philantomba monticola*	Blue Duiker	Seixa
AS	*Raphicerus campestris*	Steenbok	Punja
MS	*Redunca arundinum*	Southern Reedbuck	Nunce
MS	*Sylvicapra grimmia*	Common Duiker	Bambi
AS	*Syncerus c. caffer*	Cape Buffalo	Búfalo-cafre
NS	*Syncerus c. nanus*	Forest Buffalo	Pacaça
AS/MS	*Tragelaphus oryx*	Common Eland	Gunga
NS	*Tragelaphus scriptus*	Bushbuck	Golungo
GC/MS	*Tragelphus spekii*	Sitatunga	Sitatunga
AS	*Tragelaphus strepsicerus*	Greater Kudu	Olongo
AS	*Giraffa camelopardalis*	Giraffe	Girafa
NS	*Hippopotamus amphibius*	Hippopotamus	Hipopótamo
AS	*Phacochoerus africanus*	Common Warthog	Facochero
MS	*Phacochoerus larvatus*	Bushpig	Porco-do-mato
GC	*Phacochoerus porcus*	Red River Hog	Porco-vermelho
GC	*Hyemoschus aquaticus*	Water Chevrotain	Cabrito-do-rio
AS	*Equus q. quagga*	Plains Zebra	Zebra-de-planície
AS/ND	*Equus zebra hartmannae*	Hartmann's Mountain Zebra	Zebra-de-montanha-de-hartmann
AS	*Diceros bicornis*	Black Rhino	Rinoceronte-preto
GC	*Phataginus tricuspis*	White-belled (Tree) Pangolin	Pangolim-de-barriga-branca
GC	*Cercopithecus ascanius*	Red-tailed Monkey	Cercopiteco-de-cauda-vermelha
GC	*Cercopitecus cephus*	Moustached Monkey	Cercopiteco-de-bigode

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Biome	Scientific name	English name	Portuguese or Vernacular name
GC/EZ	*Cercopithecus mitis*	Blue Monkey	Cercopiteco-azul
GC	*Cercopithecus pogonias nigripes*	Black-footed Crowned Monkey	Cercopiteco-coroado-de-pés-pretos
GC	*Cercopithecus neglectus*	De Brazza's Monkey	Cercopiteco-de-brazza
GC	*Cercopithecus nictitans*	Putty-nosed Monkey	Cercopiteco-de-nariz-branco
NS	*Chlorocebus cynosuros*	Malbrouck Monkey	Macaco-de-cara-preta
GC	*Colobus angolensis*	Angola Colobus	Colobo-de-angola
GC	*Lophocebus aterrimus*	Black-crested Mangabey	Cercocebo-negro
GC	*Miopithecus ogouensis*	Northern Talapoin	Talapoim-do-norte
GC/EZ	*Miopithecus talapoin*	Southern Talapoin	Talapoim-de-angola
GC	*Galagoides demidoff*	Demidoff's Dwarf Galago	Gálago-de-demidoff
EZ	*Galagoides kumbirensis*	Angolan Dwarf Galago	Gálago-da-kumbira
GC	*Galagoides thomasi*	Thomas's Dwarf Galago	Gálago-de-thomas
MS	*Otolemur crassicaudatus*	Greater Galago	Gálago-de-monteiro
GC	*Gorilla g. gorilla*	Western Lowland Gorilla	Gorila-ocidental
GC	*Pan t. troglodytes*	Central Chimpanzee	Chimpanzé-central
GC	*Arctocebus aureus*	Golden Potto	Poto-dourado
GC	*Perodictus edwardsi*	Milne-Edwards's Potto	Poto-de-edwards
NS	*Loxodonta africana*	Savanna Elephant	Elefante-de-savana
GC	*Loxodonta cyclotis*	Forest Elephant	Elefante-de-floresta
GC	*Anomalurus beecrofti*	Beecroft's Scaly-tailed Squirrel	Rato-voador-de-beecroft
NS	*Hystrix africaeaustralis*	Cape Porcupine	Porco-espinho-austral
MM	*Trichechus senegalensis*	Manatee	Manatim

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Glossary of Ecological Terms

Abiotic the non-living part of an ecosystem that shapes its environment. In a terrestrial ecosystem, examples might include temperature, light, and water. (Cf. biotic).

Abundance the number of individuals in a population. (Cf. population density).

Acacia a collective term for members of trees and shrubs of the genus *Acacia*, now succeeded by *Senegalia* and *Vachellia* in African species. However, in this volume, the original use of *Acacia* is followed.

Acid soil soils with a pH value of less than 5.5 for most of the year. Typical of Mesic/Dystrophic savannas.

Adenosine triphosphate (ATP) the energy received from the Sun and captured in plants by photosynthesis is stored as carbohydrates and as a high-energy molecule **(adenosine triphosphate ATP)** which carries energy within and across cells. (Cf. photosynthesis).

Adiabatic lapse rate ~~is~~ the rate at which the temperature of air masses change through compression or expansion associated with descending or rising in elevation. (Cf. lapse rate, Berg winds).

Aeolian the wind-blown transport and deposition of sands, such as the Kalahari sands of the Kalahari Basin.

Aerenchyma specialized tissue in the roots of mangroves which provide channels for the transfer of oxygen to the deeper roots which lie in the anoxic, waterlogged soil. (Cf. mangroves, pneumatophores, lenticels).

African Surface the extensive interior plains of central and southern Africa, resulting from many millions of years of downward and backward erosion. (Cf. Post-African Surface, Planalto).

Afromontane the highland ecosystems of Africa, usually at altitudes above 1600 m above sea level, comprising closed forests and open grasslands; also refers to the 'archipelago-like' regional centre of floristic endemism.

Albedo the proportion of sunlight that is reflected back into the atmosphere by different land surfaces.

Allelopathy a common biological phenomenon by which one organism produces biochemicals that influence the growth, survival, development, and reproduction

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of other organisms. These biochemicals are known as allelochemicals and have beneficial or detrimental effects on target organisms.

Allopatric sub-populations occurring in geographically separate locations. (Cf. sympatric).

Alluvial soils deposited by water, such as along river floodplains. (Cf. illuvial, colluvial).

Alpha diversity a count of species (or a taxonomic group) at the scale of communities. (Cf. beta diversity, gamma diversity).

Alternative stable state the state of an ecosystem, maintained at equilibrium by negative feedbacks. (Cf. feedbacks, tipping point, stable state).

Altricial species with a developmental strategy where the young are born or hatched helpless. (Cf. precocial).

Andropogoneae a large tribe of grasses, typical of mesic savannas. All species in the tribe use C_4 carbon fixation, which makes them competitive under warm, high-light conditions. (Cf. Chloridoideae).

Anharas do ongote open grassy plains of the Angolan highlands, often with numerous geoxyle species (Cf. geoxyle).

Anions negatively charged ions that include chloride Cl^-, nitrate $NO_3{}^-$, phosphate $PO_3{}^-$, carbonate $CO_3{}^-$ and sulphate $SO_4{}^-$. (Cf. ions).

Anthocyanin blue, red and purple pigments in the young leaves of many miombo trees and shrubs, initially predominating over chlorophyll, and which might protect the soft young leaves from herbivores.

Anticyclone a large wind system that rotates clockwise about a centre of high atmospheric pressure in the Northern Hemisphere and counter-clockwise in the Southern Hemisphere. Its flow is the opposite of that of a cyclone. (Cf. Southern Hemisphere Anticyclone).

Arenosol a sandy-textured soil that lacks any significant soil profile development, typical of the Kalahari sands of Mesic Savannas.

Arid referring to climates with low rainfall, here used in reference to the arid savanna biome of Africa, where seasonal, summer rainfall is 650 or less, but above 250 mm per year. (cf. mesic).

Arid Savanna Biome the arid/eutrophic grasslands, savannas and woodlands of Angola—typically found where mean annual precipitation ranges from ca. 250–650 mm, with more than eight dry months. Summers can be very hot; winters can have occasional to frequent frosts. Vegetation comprises many spinescent trees and shrubs, with grasses frequently of high nutrition value. Herbivores are important drivers of structure; fire is an infrequent but important disturbance factor. (Cf. Mesic/Dystrophic Savanna Biome).

Artiodactyles even-toed ungulates pigs, hippopotamus, antelope.

Assimilation efficiency the ratio of assimilation to ingestion. (Cf. production efficiency).

Autecology is the study of how a single species interacts with the environment. (Cf. synecology).

Autotrophs primary producers, which receive their energy directly from the Sun via photosynthesis. (Cf. heterotrophs).

Basement Complex refers to rocks, mostly igneous or highly metamorphosed, that underlie later sedimentary deposits. Often comprising crystalline rocks such as granites and gneisses.

Base status the base status of soils (also referred to as the S-status) refers to the ratio of major nutrient cations (Ca, Mg, K, and Na) to the clay percentage of soil.

Basic soil soil with a neutral or slightly alkaline pH value, typical of Arid/Eutrophic savannas.

Batesian mimicry a form of mimicry that occurs when a palatable or undefended species (the 'mimic') resembles an unpalatable or otherwise defended species.

Benguela Current the broad, northward flowing ocean current that forms the eastern portion of the South Atlantic Ocean gyre, which lies to the west of Namibia and Angola. The cool, nutrient-rich upwelling waters of the Benguela current account for the rich marine life of the coastal waters of Namibia and Angola. The cool south-westerly winds associated with the current contribute to the maintenance of the Namib desert, while also bringing fog conditions to the immediate coastal zone. (cf. South Atlantic Anticyclone).

Berg wind a Namibian term for a hot dry (katabatic) wind blowing down the Great Escarpment from the interior plateau to the coast, with air warming through compression as it descends according to the adiabatic lapse rate. (Cf. adiabatic lapse rate).

Beta diversity describes the rate at which species composition changes (the species turnover) across a region, or along a gradient or transect. (Cf. alpha diversity, gamma diversity).

Biodiversity defined by the United Nations Convention on Biological Diversity as: 'the variability among living organisms and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems'. The term has been broadened to include the evolutionary, ecological and cultural processes that sustain life.

Biogeographic realms reflect global scales of shared evolutionary relationships (lineages) of floras and faunas. Eight biogeographic realms are recognised across the globe, of which two—the Palearctic and the Afrotropical are found in Africa. (Cf. lineages).

Biogeography the study of the patterns of distribution of plant and animals species.

Biome the largest category of structurally and functionally similar habitats which share climates, soils and disturbance factors. Biomes, such as equatorial rain forests, tropical savannas, temperate grasslands and deserts, occur on many continents, but often with very different floristic and faunistic compositions.

Biota a collective terms for animals, plants and microorganisms.

Biotic the living components of an ecosystem. (Cf. abiotic, biota).

Bornhardt a dome-shaped hill, which rises prominantly above the surrounding landscape, often of granite. (Cf. inselberg).

Boundary layer a thin zone of calm air that influences how quickly energy (or gas) is exchanged between soil or leaf surfaces and the surrounding air.

Browser a herbivore (or, more narrowly defined, a folivore) which feeds on leaves, soft shoots, or fruits of woody plants such as shrubs.

Bush-encroachment the formation of dense thickets of (typically) spiny trees and shrubs, often associated with intensive grazing and the absence of regular fires.

Bushmeat a general term for meat from wildlife species that are hunted for human consumption.

C_3 grasses grasses physiologically adapted to growing in shaded and/or cool, moist conditions, such as forest floors or cool, montane or temperate climates. (Cf. C_4 grasses).

C_4 grasses grasses physiologically adapted to warm dry conditions. By supressing photorespiration In high light and temperature environments, C_4 plants tend to be more competitive and productive than C_3 plants, while also using less water. (Cf. C_3 grasses, photorespiration, photosynthesis).

CAM (Crassulacean Acid Metabolism) a photosynthetic pathway that increases water use efficiency, by closing the leaf stomata during the day, and opening them at night. (Cf. photosynthesis).

Cacimbo an Angolan term for the coastal fog and low stratus clouds that result from the inflow of cool oceanic air off the Benguela Current during the winter season (the winter season is also termed the *cacimbo*).

Caduciform short, usually succulent, growth form of trees, usually found in arid areas.

Calcrete cemented calcium carbonate deposited as a hardpan in the subsoil horizon of soils in many semi-arid and arid regions. (Cf. duricrust, hardpan).

Capillary force the process of a liquid flowing in a narrow space (such as between soil grains, or within plant tissues) without the assistance of, or in opposition to, external forces like gravity. (Cf. capillary water, field capacity).

Capillary water the water held in the soil profile by capillary forces after excess water has drained off, at which point the soil is said to be at field capacity. (Cf. capillary force).

Carnivores meat eaters, consumers of other animals, also referred to as secondary consumers. (Cf. predator).

Carrying capacity refers to the capacity of a habitat's resources (water, food, light, shelter) to sustain a given population of species.

Catena a series (chain) of distinct but co-evolving soils arrayed down a slope. Each soil type differs somewhat from its neighbours, but all occur in the same climate and on the same underlying parent material. Typical of miombo ecosystems of the Mesic Savanna Biome.

Cations positively charged ions such as calcium (Ca), magnesium (Mg), potassium (K), sodium (Na) and ammonium (NH_4). (Cf. anions).

Cation exchange capacity (CEC) the total number of cations a soil can hold—or its total negative charge. The higher the CEC, the higher the negative charge and the more cations that can be held. CEC is measured in milli-equivalents per 100 g of clay (meq/100 g). (Cf. dystrophic, eutrophic, mesotrophic).

Cauliflory flowers arising directly from the bark of stems and trunks of rain forest trees.

Cavitation the blocking (by air bubbles) of xylem vessels (the water conducting tissue) of trees and shrubs when the plant is subjected to high temperatures by hot fires.

Cellulase any of several enzymes produced chiefly by fungi, bacteria, and protozoans that facilitate the decomposition or breaking down (hydrolysis) of cellulose, a major constituent of grasses that are difficult to digest.

Cenozoic Era the most recent of the major Eras of Earth's history, beginning about 66 million years ago and extending to the present. It was the interval of time during which the continents assumed their modern configuration and geographic positions, and during which Earth's flowering plant flora and bird and mammal fauna evolved toward those of the present. The Cenozoic comprises three periods—Paleogene, Neogene and Quaternary. (Cf. Paleogene, Neogene, Quaternary).

Cerrado collective name for the mesic savannas of South America, structurally and ecologically very similar to the mesic savannas of Africa. (Cf. miombo).

Chana variously used to describe extensive grassy plains (in Angola's highlands and eastern interior) or dry river valleys (in the Namib). (Cf. *mulola*).

Chanas da borracha open plains on deep Kalahari sands, typically those of Lunda-Norte, with tall grasses and abundant geoxyles, especially the rubber plant *Landolphia* sp. (Cf. geoxyle).

Chloridoideae one of the largest subfamilies of grasses—typically found in arid regions. (Cf. Andropogoneae).

Climate refers to the long-term average pattern of weather at local, regional and global scales, such as the cool desert climate of Tômbua or the wet tropical climate of Buco Zau. (Cf. weather).

Climax community a climax community is a community of plants, animals and fungi which has, through the process of ecological succession in the development of vegetation in an area over time, reached a steady state. (Cf. seral, succession).

Climax forest mature, old-growth forest that is considered free of any previous disturbance by human activities or impacts of hurricanes or landslides. (Cf. primary forest, secondary forest).

Cline the changes in the phenotype and genotype of a species across environmental gradients.

Coevolution the process of reciprocal evolutionary change that occurs between pairs of species or among groups of species as they interact with one another. The activity of each species that participates in the interaction applies selection pressure on the others.

Colloids negatively charged mineral or organic soil aggregates which are invisible to the human eye (microscopic). They are dispersed as insoluble particles suspended throughout another substance—such as clay in muddy water.

Community a biological community is an interacting group of all the organisms living in a given location. (Cf. ecosystem).

Competition occurs when two or more individuals use a common but limited resource.

Conditions the physicochemical characteristics of the environment such as temperature and humidity that influence the life of organisms, but which cannot be consumed.

Congolian refers to the flora, fauna and ecosystems that characterise the Congo Basin, with outliers following the river valleys and coastal escarpment southwards across Angola.

Conservation biology the study of the world's biodiversity, the threats to its sustainability, and the prevention of extinction of species, ecosystems and their services to society.

Consumers organisms that eat the producers (plants) are primary consumers (herbivores). Secondary consumers (carnivores) eat primary consumers. Fire is also considered a consumer, as it behaves like an indiscriminant herbivore, removing plant material from the landscape. (Cf. producer, carnivores, predator, food chain).

Convection is the process whereby fluids (water or air) move from a cooler to a warmer place or region.

Convergent evolution Convergent evolution is the independent evolution of similar features in species of different continents or during different periods or epochs in time. Convergent evolution creates analogous structures that have similar form or function but which were not present in the last common ancestor of those groups. It is the process whereby organisms evolve similar traits to adapt to similar necessities, e.g. geoxyles, wings of insects, birds, bats. (Cf. evolution, geoxyles).

Cold air drainage the phenomenon of cold, dense and heavy air moving down a sloping site, often accumulating in a valley, where frost might occur in winter. Cold air drainage typically occurs on still, cloudless nights when heat loss from the land surface is rapid and an inversion occurs over valley bottoms, often accompanied by the appearance of mists over low ground or frost on the ground. (Cf. temperature inversion).

Colluvial soils soils consisting of locally transported materials from the upper sections of slopes through water erosion or landslides. (Cf. alluvium, catena, elluvium, illuvium).

Coppicing the behaviour of many woody plants (trees and shrubs) to produce new branches from the base of the stem if the main growing point is damaged by browsing or fire. (Cf. top-kill).

Coriolis Effect the pattern of deflection taken by objects not firmly connected to the ground (such as circulating air or ocean currents) as they travel long distances around the Earth. As the Earth spins on its axis, the relative ground speed at the Earth's surface increases from the poles to the Equator (because of the great differences in the Earth's circumference between low and high latitudes). This phenomenon is known as the Coriolis Effect. As a result, circulating air and water currents are deflected to the right (clockwise) in the Northern Hemisphere and to the left (anticlockwise) in the Southern Hemisphere).

Craton the extensive and stable foundation of the continental lithosphere, such as the Congo Craton which underpins most of Angola, also known as the Angolan Shield. (Cf. lithosphere).

Crystalline rocks rocks composed entirely of crystallised minerals—including many igneous (granite, gabbro) and metamorphic (gneiss, schist) rocks. (Cf. igneous, metamorphic).

Dambo a shallow depression or drainage-line, dominated by grasses, typical of miombo landscapes of central Africa. (Cf. catena, miombo, *mulola*).

Deciduous refers to trees, often in seasonal climates such as tropical savannas, where leaves drop and are replaced every year. (Cf. evergreen).

Decomposers the organisms (invertebrates and microorganisms, such as bacteria, protozoa, fungi) that breakdown dead organic matter produced by higher trophic levels. (Cf. primary producers, primary consumers, secondary consumers, trophic levels).

Decomposition the breaking down of plant and animal tissues by physical, chemical and biological processes, leading to the release of nutrients through mineralization. (Cf. mineralization, immobilization).

Deflocculate the chemical process whereby fine clay particles (floccules) break up and disperse into suspension in a liquid.

Desert regions typically receiving less than 250 mm rainfall per year, where plants and animals usually display special adaptations to water and heat stresses.

Detarioideae a subfamily of the Fabaceae, represented in Angola by many of the dominant trees of the miombo (mesic/dystrophic savannas).

Determinant a factor or a combination of factors that have a decisive affect on the outcome of an interaction or process. (Cf. driving force).

Deterministic refers to a process (usually in mathematics, physics or chemistry, and in ecological modelling) where the results are exactly predictable (non-random). (Cf. stochastic).

Disjunction the separation or fragmentation of populations of animals and plants, sometimes leading to speciation within the isolated populations.

Disturbance changes in the structure and functioning of ecosystems can result from both natural and human-induced disturbances. At ecosystem level, disturbances might result from episodic events such as floods, droughts or frosts. Other disturbances include those of intense fires, herbivory or land transformation through agriculture or deforestation. (Cf. stress).

Drip-tips the extension of the tip of the leaves of rain forest trees into a tapering tongue that facilitates the rapid shedding of water.

Driving forces the forces or factors that determine where a species will occur, based on its survival, growth and reproductive success. Ecosystems are shaped by the driving forces of climate, geology, hydrology, soils, fire and herbivory. (Cf. determinant).

Dry forest a dense community of closed-canopy trees, often with a shrub or sapling understorey, usually deciduous, but occasionally evergreen as in *Cryptosepalum* Dry Forest.

Duricrust a resistant layer in soils formed by chemical precipitation, such as in laterites, silcretes and calcretes. (Cf. calcrete, laterite).

Dystrophic soils have a low base status with the sum of exchangeable (as opposed to soluble) Ca, Mg, Na and K of below 5 milli-equivalents/100 g clay. Typical of soils of low nutrient status of mesic/dystrophic savannas. (Cf. eutrophic, mesotrophic).

Earth system science refers to research at the scale of the whole planet, where the web of oceanic, terrestrial and atmospheric interdependencies, and socio-economic consequences, is the focus.

Ecological services the benefits provided to human societies by healthy ecosystems. These include provisioning services such as food and water; regulating services such as flood, pest, and disease control; cultural services such as spiritual and recreational benefits; and supporting services, such as nutrient cycling.

Ecology the scientific study of the distribution and abundance of organisms and the interactions that determine their distribution and abundance.

Ecoregion a large unit of land or water that contains a distinct assemblage of species, habitats and processes, and whose boundaries attempt to depict the original extent of natural communities before major land use change.

Ecosystem all the living organisms in a community, together with their non-living (abiotic) environment, interacting together, constitute flow an ecosystem. (Cf. abiotic, biotic, community).

Ecosystem services see ecological services.

Ecotone the transition area between two distinct communities, such as between forest and grassland, where a narrow belt of distinctive species (edge species) is found.

Ectotherm an organism in which internal physiological sources of heat are of relatively small or of quite negligible importance in controlling body temperature, e.g. insects, amphibians, reptiles. They are tolerant of relatively wide temperature fluctuations. Such organisms rely on environmental heat sources, such as sunlight or hot rock surfaces, which permit them to operate at very economical metabolic rates. (Cf. endotherm).

Edaphic soil physical or chemical properties such as drainage, texture and nutrient status.

El Niño or El Niño-Southern Oscillation (ENSO) is a climatic pattern with a two- to seven-year cycle, which often results in extreme weather events such as droughts or floods. (Cf. La Nina).

Eluviation the removal of mineral or organic soil material in solution or suspension from part of, or the whole of, a soil profile. (Cf. illuviation, soil profile).

Eluvium or eluvial deposits, are those geological deposits and soils that are derived by in-situ weathering or weathering plus gravitational transfer. (Cf. alluvium, illuvium).

Emergent properties properties that emerge from the collective interactions of many different individuals within the system. Emergent properties can simply be stated a properties which a collection or complex system has, but which the individual members do not have—such as the microclimate below the canopy of trees.

Emergent trees the tallest trees of rain forests that rise high above the general profile of the canopy.

Endemic a species or subspecies ~~occupying~~ only occurring within a defined and limited area, usually referring to a single country or biome.

Endorheic basin a subsiding internal drainage basin, such as those of Cuvelai, Etosha and Okavango.

Endotherm Endotherms use internally generated heat to maintain body temperature. Their body temperature tends to remain steady regardless of environment, e.g. birds, mammals. (Cf. ectotherms).

Ephemeral streams and rivers that only flow for short periods after rain events typical of the rivers (linear oases) of the Namib Desert.

Epicormic buds buds that lie beneath the bark of a tree stem or branch, and are thus protected from fire damage.

Epiphylls minute gardens of cyanobacteria, green algae, bryophytes, lichens and filmy ferns that grow on the surfaces of the leaves of understorey trees in rain forests, reducing the leaves photosynthetic efficiency.

Equinox the equinox is the moment when the centre of the Sun is directly above the Equator this happens on 21 March and 22 September. (Cf. solstice).

Escarpment a sharp change in the landscape where the elevation changes rapidly along a scarp or cliff-face. Escarpments are formed by backward erosion of the landscape, or by tectonic movements along fault-lines.

Eruption the rapid population growth and subsequent crash in certain bird or rodent species correlated with climatic or predator cycles.

Eusocial organisms the highest level of organization of sociality in animals, defined by the following characteristics: cooperative brood care, overlapping generations within a colony of adults, and a clear division of labour into reproductive and non-reproductive groups, e.g. bees, termites.

Eutrophic soils soils which have a high base status with exchangeable cations of more than 15 milli-equivalents/100 g clay. These are soils with a high nutrition status for plant growth, are typically found in arid/eutrophic savannas. (Cf. dystrophic, mesotrophic).

Evapotranspiration the sum of water loss both from plant stomata (transpiration) and from the soil surface (evaporation).

Evergreen refers to plant species, most especially perennial trees, that retain their leaves for several years. (Cf. deciduous).

Evolution the process of change in heritable characteristics carried from one generation to the next. These heritable characteristics are the expressions of genes that are passed on from parent to offspring during reproduction. (Cf. genes, natural selection).

Extinct known only from non-living specimens in museum, herbarium or other historical records.

Fabaceae the legume family of plants (previously Leguminosae), including many genera typical of the mesic/dystrophic savannas. (Cf. Detarioideae).

Fairy circles bare, circular sandy patches within a matrix of short grasslands of the Namib desert margins.

Fauna the zoological composition of a region, country or habitat. Usually measured in terms of the animal species found within a defined area, or the animal species with similar evolutionary relationships.

Feedbacks There are two types of feedback—negative feedbacks and positive feedbacks. A negative feedback counteracts the change in input or impact, tending to maintain the system in its current state. A positive feedback amplifies the change in input or impact, pushing the system toward a more pronounced change and sometimes leading to another state. (Cf. tipping point).

Ferralitic soils highly weathered and leached soils of the humid tropics, typically enriched in iron and aluminium. (Cf. ferralsol, sesquioxides, leaching).

Ferralsols old, highly leached soils of humid tropics. (Cf. ferralitic soils).

Fire regime a collective term that incorporates features of individual fires, including fire frequency, fire intensity, fire season and fire size.

Fire storm an exceptional phenomenon of forest and bush fires associated with the simultaneous combination of three weather factors that increase fire intensity: air temperature above 30 °C, relative humidity below 30%, and a wind speed of over 30 km/hr.

Flammability the property of an ecosystem (e.g., high load of dry organic material) to ignite and propagate a fire.

Flora the botanical composition of a region, country or habitat—usually measured in terms of the plant species found within a defined area, or plant species with similar evolutionary relationships.

Fog-basking a behaviour of some desert insects where they position themselves on dune crests in order to capture moisture from fog.

Food chain a series of links in food consumption, starting from the producer organisms and ending with apex predators. (Cf. consumers, decomposer, food web, primary producers,).

Food web a web of interacting food chains, representing the multiple linkages of which organisms eat what within a complex network of interactions.

Forb a non-graminoid, herbaceous flowering plant, typically of grasslands.

Forest a plant community with a closed tree canopy of touching or interlocking crowns, with 50% or more, typically 75%, projected crown cover. Forests usually have two or more layers (strata) with a shrub and sapling layer and a discontinuous herb layer. Forests are characterised by poor light penetration to the ground layer, the lack of a grassy understorey and the consequent absence of fires penetrating their perimeters.

Functional traits morphological, biochemical, physiological, structural, phenological, or behavioural characteristics that are expressed in phenotypes of individual organisms in response to their environment.

Fynbos shrubland and heathland vegetation, typically of the winter rainfall region of the Cape provinces of South Africa. A biome of extreme floristic diversity and endemism. (Cf. garrigue, maquis).

Gallery forest the narrow bands of forest that follow permanent water courses draining the savannas and woodlands of open landscapes.

Gamma diversity the total number of species across all communities in a defined geographic area. (Cf. alpha diversity, beta diversity).

Garrigue the open shrubby vegetation of dry Mediterranean regions, consisting of spiny or aromatic dwarf shrubs interspersed with colourful ephemeral species. (Cf. fynbos, maquis).

Gene the basic physical and functional unit of heredity that occupies a specific location on a chromosome. (Cf. genotype, genetics).

Genetics the branch of biology concerned with the study of genes, genetic variation, and heredity in organisms.

Genotype the complete set of an organism's genetic material. (Cf. phenotype).

Geophytes plants typically with underground storage organs, where the plants hold energy and water. Geophytes ~~also~~ include plants with bulbs, tubers, corms or rhizomes. (Cf. geoxyle).

Geoxyles plants with woody structures (lignotubers, stems, branches, roots) that escape fire damage by remaining below the soil surface. Flowers and fruits are carried on short branches, seldom rising more than 50 cm above the soil surface. The geoxyle habit has developed independently in many plant lineages in Africa and South America. Typical of the mesic savannas of Africa and South America. (Cf. geophyte, lignotuber).

Gley soil a nutrient poor, acidic, organic soil of wetlands, often with bluish/black coloration.

Gondwana the supercontinent formed about 550 million years ago (Ma), and which began to break up from 180 Ma, into the future continents of South America, Antarctica, Africa, Australia and India, by a process known as Continental Drift. (Cf. tectonic movements).

Grassland a plant community dominated by grasses (tufted, stoloniferous or wiry) and forbs (broad-leaved herbaceous, non-graminoid flowering plants), with few if any woody species. (Cf. forbs, savanna, woodland, forest).

Grazer a herbivore which feeds predominantly on grass leaves, in contrast to a browser, that feeds mostly on tree and shrub leaves.

Grazing lawn a short-grass lawn resulting from repeated grazing by herbivores such as White Rhinoceros, Hippo, Wildebeest, etc.

Greenhouse effect (Cf. greenhouse gases).

Greenhouse gases water vapour, carbon dioxide, methane and other gases which provide a thin envelop around the Earth, absorbing some of the infrared radiation emitted by the Earth and retaining some of the heat that would be lost in the absence of greenhouse gases. The natural composition of greenhouse gases maintains the average global temperature at about 15 °C. In recent centuries, human activities have resulted in increased concentration levels of carbon dioxide, methane and other greenhouse gases in the lower atmosphere, resulting in the greenhouse effect—the warming of the Earth's climate.

Guild a group of species that use similar resources, or which use different resources in a similar fashion. The term is often applied to bird communities such as fruit-eaters or seed-eaters. (Cf. niche).

Guineo-Congolian the floristic regional centre of endemism which includes the rain forests of west and central Africa.

Gular fluttering a cooling process where a bird will open its mouth and "flutter" its neck muscles, promoting heat loss (the avian version of panting in dogs).

Gyre large systems of circulating currents—oceanic whirlpools -created by the clockwise (Northern Hemisphere) and anti-clockwise (Southern Hemisphere) circulation of ocean currents. (Cf. Coriolis effect).

Habitat the place or environment where an organism makes its home—where food, shelter, water and safety permit successful survival, growth and reproduction of the species.

Halophyte salt-tolerant plant.

Heliophile sun-loving (shade intolerant) plant species, such as savanna grasses. (Cf. sciophile).

Herbivome a collective term for the classification and mapping of herbivory regimes, analogous to the terms biome and pyrome.

Heterotrophs consumers of animal and plant tissue. (Cf. autotrophs).

Hibernation a state of minimal activity in some animals exposed to cold or dry conditions. In cold climates this might include seasonal heterothermy, characterised in winter by low body temperature, slow breathing and heart-rate. (Cf. torpor).

Holocene the current geological epoch—beginning from about 11,650 years before present, following the last glacial period. The Holocene and the preceding Pleistocene form the Quaternary period. The Holocene saw the extinction of many megafaunal species such as mammoths, probably due to hunting by humans. (Cf. Pleistocene, Quaternary).

Homeostasis the mechanism by which body temperature is regulated to the desired state (the set point) during changes in the external temperature. (Cf. hypothermia, hyperthermia, feedbacks).

Home range the area occupied both seasonally and permanently by a population of animals. (Cf. territory).

Hotspot an area of very high biological diversity, endemism and threat.

Hydrophobic the physical property of a molecule that is seemingly repelled from a mass of water (known as a hydrophobe) hydrophobic soils have the property of repelling water from the soil surface.

Hyperthermia abnormally high body temperature caused by the failure of the heat-regulating mechanisms of the body to deal with the heat coming from the environment. (Cf. hypothermia).

Hypothermia abnormally low body temperature, resulting from prolonged and possibly fatal exposure to very cold temperatures. (Cf. hyperthermia).

Hypothesis an hypothesis results from a process of the careful and repeated observation and measurement of a phenomenon, the definition of questions arising from the observations, gathering explanatory evidence, and finally formulating an hypothesis to propose answers to the questions and that predict outcomes of the phenomenon.

Hypsodont teeth high-crowned teeth with enamel extending beyond the gum line, providing protection against wear and tear.

Igneous rocks formed deep within the Earth's crust, include granites and gabbros.

Illuviation the deposition of soil material removed by percolating water from one part of the soil profile to another. (Cf. alluvial, catena, eluviation, soil profile).

Illuvium material displaced across a soil profile, from one layer to another one, by the action of rainwater. (Cf. alluvium, elluviation, illuviation).

Immobilisation in soil science it is the conversion of inorganic compounds to organic compounds by microorganisms, thus into a form inaccessible to plants. (Cf. mineralisation).

Inselberg an isolated mountain that rises several hundred metres above the surrounding landscape.

Intercalary meristems the growing points in grass stems and at the base of grass leaves that allow rapid growth after damage, such as that caused by frequent grazing.

Interspecific interactions between members of different species.

Interspecific competition refers to the interaction between two or more species for the same resource.

Intertropical Convergence Zone (ITCZ) the atmospheric system where the converging air masses that are warmed over the equatorial regions rise into the lower atmosphere, thereby establishing an area of low pressure at the Earth's surface—the equatorial low. The rising air condenses, producing the heavy rainfall experienced along the Equator. (Cf. Anticyclone, South Atlantic Anticyclone).

Intraspecific interactions between members of a single species.

Invasive species a non-native (alien) species that out-competes native species and can negatively dominate the environment, often preventing the re-establishment of native (indigenous) species, especially in sites disturbed by human activities such as agriculture or deforestation.

Inversion a temperature inversion occurs when the normal heat gradient of the atmosphere is reversed. The normal pattern is a deceasing air temperature with increasing height above the Earth's surface. This is illustrated where the cool moist air over the Benguela Current is trapped below a layer of warmer air, resulting in the formation of a band of fog or stratus cloud. Temperature inversions, creating fog or mist, are also experienced in the valleys of the interior highlands. (Cf. Benguela Current).

Ions particles, atoms or molecules with an electrical charge—positively charged particles in soils are cations, negatively charged particles are anions. (Cf. anions, cations).

Ion exchange capacity the availability of charged sites on soil particles (Cf. cation exchange capacity).

Island biogeography the study of the factors that affect the species richness and diversification of isolated natural communities.

Kalahari Basin also referred to as the Kalahari depression—is a large endorheic (internal drainage) basin of over 2.5 million km^2, centred on Angola and Botswana, and including the Okavango Basin.

Kalahari sands the extensive sand deposits of the Kalahari Basin—considered the largest continuous body of sand in the world. (Cf. Kalahari Basin).

Kaolin a type of non-shrinking clay, produced by the chemical weathering of aluminium silicate minerals in moist tropical climates, typical of ferralsols. (Cf. montmorillonite/smectite).

Karoo-Namib a floristic regional centre of endemism, that includes the extreme southwest of Angola, much of Namibia and the Karoo of South Africa.

Keystone species species that influence community structure and function disproportionally to their size or numbers.

***K*-selected species** organisms (e.g., elephants, rhinos) with life history patterns that include large size, slow development, long life, reproduction at an older age and the production of fewer progeny when compared with r-selected species. They live in seasonal or predictable habitats. (Cf. *r*-selected species.)

Landscape ecology the study of the composition, structure, function and use of landscapes.

Laterite a soil or rock type rich in iron and aluminium, typical of hot wet tropical countries. (Cf. sesquioxides, ferralitic, ferralsols, latosols, duricrusts, indurated, calcretes, silcretes).

Latosols ‘tropical red earth’ soils with high iron and aluminium content, also known as ferralsols or oxisols. (Cf. ferralsols).

Law in science, a law results from the failure of successive attempts to disprove a set of hypotheses that underpin a theory.

Lapse rate is the rate at which atmospheric air temperature decreases with altitude.

Leaching the loss of water-soluble plant nutrients from the soil, typical of the soils of higher rainfall areas such as Mesic/Dystrophic savanna and tropical rain forests.

Lenticels specialised pores in the aerial roots of mangroves which absorb air while they are above the water surface, and close as the incoming tide reaches them. (Cf. mangroves, pneumatophores).

Lichen a composite symbiotic organism that arises from algae or cyanobacteria living among filaments of multiple fungi species. This is an intimate mutualistic and beneficial relationship. Lichens have properties different from those of their component organisms. (Cf. mutualism).

Life form various classification systems have been developed to classify plants in terms of their life forms—such as herbs, shrubs, trees, or in relation to the protection afforded their growth points, such as the Raunkaier system.

Lignotuber a woody swelling of the root crown in some plant species as a protection against destruction of the plant stem, such as by fire. (Cf. geoxyle).

Lineages a sequence of genetically related species, each of which is considered to have evolved from its predecessor. (Cf. evolution).

Linear oases the narrow bands of wooded communities of deep-rooted trees and shrubs (phreatophytes) that grow in the deep sands of seasonally dry riverbeds that cross the Namib Desert. (Cf. phreatophytes).

Lithosphere the two uppermost layers of the Earth—the crust and the mantle.

Loam a soil composed of sand, silt and clay, in the proportion by weight of approximately 40:40:20.

Long wave radiation electromagnetic radiation of wavelengths from 3 to 100 μm emitted from Earth and its atmosphere out to space in the form of thermal radiation. (Cf. short wave radiation).

Ma Million Years Ago—the abbreviation of the geological age of Eras, Periods and Epochs.

Macronutrients nutrients needed in large amounts for plant growth—including carbon (C), hydrogen (H), oxygen (O) (the basic constituents of all organic matter), nitrogen (N), calcium (Ca), phosphorus (P), magnesium (Mg), sulphur (S) and potassium (K).

Mangrove trees or shrubs adapted to growing in coastal saline or brackish water, usually at the mouths of tropical rivers, where they form distinctive ecosystems known as mangroves. (Cf. lenticels, pneumatophores).

Maquis a scrubland vegetation of the Mediterranean region, composed primarily of leathery, broad-leaved evergreen shrubs or small trees. (Cf. fynbos, garrigue).

Megaherbivores herbivores such as rhinos, elephants and hippos with a body mass greater than 1000 kg.

Mesic referring to habitats receiving a medium rainfall, usually of between 650 and 1400 mm per year, in seasonal climates of the tropics, typically of the mesic savanna biomes of Africa and South America. (cf. miombo, cerrado).

Mesic Savanna Biome the spatially dominant biome of Angola—characterised by the co-dominance of trees and grasses, climatic seasonality of warm, wet summers, mild dry winters (between 650 and 1400 mm rainfall per year with a dry season of four to eight months), the dominance of the herbaceous stratum by C_4 grasses, the prevalence of infertile, dystrophic soils, and the role of fire as the main consumer of plant biomass.

Mesotrophic soils of intermediate base status (5–15 milli-equivalents/100 g clay). (Cf. base status, eutrophic, dystrophic).

Metabolic constituents proteins and soluble carbohydrates, the constituents of plant tissue that herbivores require for growth. (Cf. structural carbohydrates).

Metamorphic rocks the product of the transformation by heat and pressure of igneous or sedimentary rocks. Under such conditions limestone transforms into marble, shale into schist, granite into gneiss and sandstone into quartzite. (Cf. igneous, sedimentary).

Metapopulation individual, isolated populations within the geographic range of a species form part of a metapopulation of that species.

Microclimate the climate near the ground, usually within a few metres of the ground surface, and in a small area, where the temperature, moisture and air movement is modified due to micro-relief, by the structure of the landscape, or by vegetation cover. The microclimate of a site differs from the climate of the general area—for example, the microclimate of a cool shady patch under a large evergreen tree growing differs from that of the surrounding open grassland.

Micronutrients trace elements that are needed in very small quantities for plant growth, and include chlorine (Cl), iron (Fe), manganese (Mn), boron (B), copper (Cu), molybdenum (Mo), zinc (Zn) and nickel (Ni).

Mimicry an evolved resemblance between an organism and another object, e.g. stick insects, or another species as in the Batesian mimicry in butterflies. (Cf. Batesian mimicry).

Migration the regular, usually seasonal, long-distance movement of all or part of an animal population, such as swallows, wildebeest in the Serengeti, Monarch butterflies.

Mimosoideae a large subfamily of the Fabaceae, typical of the Arid/Eutrophic savannas of Angola, including the many species of *Acacia* (now classified within the genera *Senegalia* and *Vachellia*). The former genus name *Acacia* is used in this volume.

Mineralisation the main process by which soil organic matter is decomposed and converted by microorganisms into plant-available forms of inorganic compounds, most importantly, the nutrients essential for plant growth.

Miocene an ecologically important epoch between 23 and 5.3 Ma (Million Years Ago). During the Miocene, several key environmental changes, and physiological innovations evolved. (Cf. Benguela Current, C_4 grasses, hypsodont teeth, ruminant gut, spinescent woody plants).

Miombo the most extensive vegetation type of Angola (and of central Africa), a Mesic/Dystrophic savanna dominated by tree species of the genera *Brachystegia, Julbernardia, Isoberlinia, Burkea*, etc.

Model ecological models are simplified representations of real systems. Models might be simple descriptive statements, charts, webs or data-based mathematical models that help simulate interactions and predict outcomes.

Monospecific refers to plant communities dominated by a single species—such as *Colophospermum mopane* woodlands and *Setaria welwitschia* grasslands.

Montmorillonite an expanding/shrinking clay (also known as smectite), with high sodium content, usually found in arid and semi-arid regions. (Cf. kaolin)

Mopane a leguminous tree *Colophospermum mopane* (*mutiati*) that dominates an extensive area of southern Africa. (Cf. monospecific, *mutiati*)

Mosaics where fragments of different vegetation types, habitats or biomes form a complex patchwork or mosaic—such as in the transition from closed forest to open woodlands or savannas.

Mulola a shallow depression or drainage-line, dominated by grasses, typically of miombo landscapes of the Angolan planalto and peneplains. (Cf. catena, dambo, tunda).

Mutations heritable changes in a gene or chromosome.

Mutiati a leguminous tree *Colophospermum mopane* (known as mopane in most countries) that dominates an extensive area of southern Africa.

Muxito a typically narrow gallery forest found along the drainage-line depressions in rolling landscapes.

Mycorrhizae a group of fungi which mobilise nutrients and water in exchange for carbohydrates provided by their host plants. (Cf. nitrogen-fixing bacteria).

Namib refers to the desert of coastal Angola and Namibia.

Natural selection the differential survival and reproduction of individuals due to differences in phenotype and adaptation to environmental conditions. It is a key mechanism of evolution—the change in the heritable traits characteristic of a population over generations. (Cf. evolution, genetics, genotype, phenotype).

Niche an ecological concept that describes how and where an organism can live, grow and reproduce, influenced by multiple environmental conditions, resource needs and tolerances. Conditions such as temperature, humidity, pH and wind velocity, together with resources such as space, nutrients, water and shelter determine an organism's habitat and its way of life—and are used to define its niche.

Nitrogen-fixing bacteria—bacteria that form nodules on the root hair cells of their host plant. They receive carbon from the plant in exchange for the nitrogen that they fix and make available to the host. (Cf. mycorrhizae).

Ongote an Angolan vernacular name for various species of *Cryptosepalum* geoxyles, common on the highland plateau of central Angola (Cf. *anharas do ongote*, geoxyles).

Orographic a geomorphological term referring to escarpments and mountains, and more specifically to the rainfall produced when moist air, especially that from the ocean, is forced to rise, condense and then precipitate. Inland of the mountain, the air, having lost its moisture content, is dry, resulting in a 'rain-shadow' where much drier conditions are experienced than along the 'orographic' mountain barrier.

Orthodox seeds seeds that can be stored for long periods in very dry, cool conditions. (Cf. recalcitrant seeds).

Over-dispersed a statistical measure of pattern, relating to evenly spaced/non-random distribution.

Pachycaul the growth form of some short, stout, succulent trees of arid and desert environments. (Cf. caduciform).

Palaeoecology the study of past ecosystems using palaeontological methods—including geological and biological (fossil plant and animal) evidence.

Partitioning the separation of resource availability in space and time, e.g. trees and grasses in savannas.

Peat the surface organic layer of a soil that consists of partially decomposed organic matter, derived mostly from plant material. Peat accumulates under conditions of waterlogging, high acidity and nutrient and oxygen deficiency. (Cf. wetland).

Pediplains extensive plains caused by backward erosion of the continental surface over many millions of years. (Cf. peneplain).

Pedology the study of soils.

Peneplains extensive plains formed by the erosion of the continents, a process known as peneplanation where the erosion is downward, or pediplanation where the erosion is backward. (Cf. pediplain, planalto, African Surface, Post-African Surface).

Perched water table is an aquifer that occurs above the regional water table. This typically occurs when there is a relatively impermeable layer above the main water table/aquifer, but below the land surface. (Cf. duricrust).

Perissodactyles even-toed ungulates—zebra, rhinos.

pH a scale used to indicate the acidity or basicity of an aqueous solution. The abbreviation 'pH' refers to the 'potential of hydrogen', in a logarithmic scale which inversely indicates the concentration of hydrogen ions in a solution. Solutions with a pH of above 7 indicates alkaline (basic), below 7 indicates acidic.

Phenology refers to the seasonal growth, flowering and fruiting pattern of a plant species.

Phenotype the observable characteristics or traits of an organism. (Cf. genotype).

Photoperiod photoperiodism is the physiological reaction of organisms to the length of night or a dark period. It occurs in plants as well as animals. Photoperiodism can also be defined as the developmental responses of plants to the relative lengths of light and dark periods.

Photorespiration the process of light-dependent uptake of molecular oxygen (O_2) concomitant with release of carbon dioxide (CO_2) from organic compounds. The gas exchange resembles respiration and is the reverse of photosynthesis where CO_2 is fixed and O_2 released. (Cf. photosynthesis, rubisco).

Photosynthesis the series of biochemical reactions by which atmospheric carbon dioxide and water are transformed by light energy into carbohydrates (simple sugars), with oxygen released as a by-product. (Cf. photorespiration, stomata).

Phreatophytes deep-rooted plants which obtain water from deep below the ground surface, typical of the large trees of the sandy, dry river linear oases of the Namib desert. (Cf. linear oases).

Phylogenetics the study of the evolutionary relationships among organisms—species, individuals or genes—using molecular analytical methods. The results of such studies are often presented as hypothetical 'phylogenetic trees' showing the relationships and ages of branching—i.e., where younger members have common ancestors.

Physiognomy the structure of vegetation, based on the life forms (trees, shrubs, grasses, herbs) that dominate the community and provide a distinctive vertical layering and horizontal spacing that characterise the vegetation.

Phytogeography the study of the patterns of distribution of plant species.

Pioneer species plant species that are the first to colonise areas that have been denuded of vegetation by land clearing, erosion, landslides, melting of glaciers or flood events. (Cf. plant succession).

Pisolith small concretions of calcium carbonate or red ferruginous material, often as pea-sized nodules in a soil profile.

Planalto the extensive high plateau of the Angolan interior. (Cf. African Surface, Post-African Surface, peneplain, pediplain).

Plant succession where plants of pioneer species colonise open sites (coastal sand dunes, landslides, volcanic lava flows) and gradually build soils and initiate a primary succession of simple plant communities. Pioneer communities are succeeded by a series of floristically and structurally more diverse communities, and ultimately the climax community, which in tropical and temperate climates might be forest. (Cf. pioneer species).

Pleistocene the geological epoch that lasted from about 2.6 million years ago (Ma) to the Holocene, which began ca. 11,600 years before present. The Pleistocene is known as the 'Ice Age' which was characterised by successive periods (glacials) of extensive ice sheets over the northern continents, followed by warmer, wetter periods (interglacials).The Pleistocene was the Earth's most recent period of repeated glaciations. (Cf. Holocene, Miocene, Pliocene).

Pleistocene refugia isolated centres of speciation or survival from extinction for plant and animal species during the shrinking of forest communities through the cold dry episodes of the Pleistocene Ice Ages.

Pliocene the geological epoch extending from 5.3 to 2.6 Ma, a time of global cooling after the warmer Miocene. The Pliocene immediately preceeded the Pleistocene Ice Age. (Cf. Pleistocene).

Pneumatophores lateral roots of mangroves that rise above the water surface and facilitate the exchange of oxygen and carbon dioxide to the roots that are submerged in water. (Cf. mangroves).

Podsol acidic, strongly leached soils of cool, moist regions, where there is an accumulation of pale, bleached organic material over dark sandy soils of low nutrient levels.

Population a group of individuals of the same species that inhabit a given area.

Population density the number of individuals per unit area. (Cf. abundance).

Post-African Surface the extensive peneplains of southern Africa, formed after the earlier African Surface. (Cf. African Surface, peneplains).

Precambrian Era the earliest geological era, dating from the birth of the planet approximately 4600 Ma ago to 541 Ma.

Precocial species in which the young are relatively mature and mobile from the moment of birth or hatching, e.g. sandgrouse. (Cf. altricial).

Predator animal species that hunt and kill their prey, usually eating all or part of their prey (Cf. carnivore).

Primary consumers herbivores (heterotrophs) that consumer plant tissue. (Cf. primary producers, primary consumers, secondary consumers).

Primary forest pristine forest that does not show signs of previous disturbance by human activity, or natural causes such as hurricanes or landslides. (Cf. climax forest, secondary forest).

Primary producers the autotrophic component of an ecosystem, which is dependent on solar energy, water and nutrients typically the plants. (Cf. primary consumers).

Production efficiency the ratio of consumption to assimilation. (Cf. assimilation efficiency).

Pyromes collective term for large scale units of distinctive fire regimes, classified and mapped at continental or global scale. (Cf. biomes, herbivomes).

Pyrophobic fire-intolerant plants that do not survive regular fires. (Cf pyrophilic).

Pyrophilic fire-tolerant plants that are adapted to and survive frequent fires. (Cf. pyrophobic).

Quadrat a sample area, usually a square, used in surveys of vegetation, often used in comparing the floristic composition of plant communities. (Cf. transect).

Quaternary Period the geological period—known as the 'Age of Humans' from 2.6 Ma to the present. The Quaternary comprises two Epochs—the Pleistocene and the Holocene. (Cf. Holocene, Pleistocene).

Queimada a term used in Angola with reference to bush fires.

Recalcitrant seeds seeds that cannot survive drying or cold temperatures, typical of the tropical rain forest. (Cf. orthodox seeds).

Regime shift the process where an ecosystem is changed by positive feedbacks from one stable state to another. (Cf. feedbacks, alternative stable states, tipping point).

Regional centre of endemism a biogeographical unit or area having more than 50% of its species confined to it, and a total of more than 1000 endemic species. (Cf. endemic).

Regolith the loose, unconsolidated layer of rocky material formed by the weathering of the bedrock. (Cf. saprolite).

Resilience the ability of a system to absorb disturbance and thereafter return to its original state following a perturbation. A resilient ecosystem maintains its self-organised structure, function and feedback processes (its alternative stable state). Elasticity is the speed of the return to the original state. (Cf. disturbance, perturbation, stability, stress).

Resources the energy and materials that are consumed by organisms and for which they compete with other organisms. (Cf. conditions).

Rhizosphere the rooting zone of plants.

River capture the geomorphological process whereby a fast-eroding tributary of one river cuts backwards into another river, thereby diverting this river from its own bed and 'capturing' the river.

Restinga long sandspit formed along the coast up-current from the mouths of large rivers, e.g. *Restinga das Palmeirinhas.*

Rubisco the enzyme Rubisco, an abbreviation for ribulose-1,5-bisphosphate carboxylase/oxygenase, is the enzyme that incorporates CO_2 into plants during photosynthesis. (Cf. photosynthesis).

Ruminants large hoofed herbivorous grazing or browsing mammals that are able to acquire nutrients from plant-based food by fermenting it in a specialised stomach (the rumen) prior to digestion, principally through microbial actions. The process, which takes place in the front part of the digestive system, typically requires the fermented ingesta (known as cud) to be regurgitated and chewed again.

***r*-selected species** a classification of life-history patterns in species, where r-selected species are typically small, have relatively fast growth rates, reproduce at an early age, produce large progeny, and are short-lived. They typically occur in unpredictable habitats. (Cf. *K*-selected species).

Salinised soil a soil with a salt deposit in the subsoil or on the surface, due to evaporation exceeding precipitation in arid regions.

Salinity the concentration of salts in water or soils. Sea water is typically about 35 parts salt per thousand (or 3.5% of sea water comprises dissolved salts).

Salt-lick a salt-rich deposit, usually concentrated in old termitaria, used by many mammals as a source of salts to supplement their diet in nutrient-poor ecosystems, such as mesic savannas. (Cf. termitarium).

Saprolite the product of the chemical weathering of the bedrock surface at the base of a soil profile. (Cf. regolith).

Savanna a plant community with a discontinuous layer of woody species (trees or shrubs) whose individuals are spaced more than one crown diameter apart and usually with a dense ground layer of non-woody species of grasses and forbs. Savannas might be dominated by trees (tree savanna) shrubs (shrub savanna) or clumps of woody species usually associated with termitaria (clump savanna). (Cf. forest, thicket, woodland, grassland).

Savanna Biomes (Arid and Mesic) the collective term for the tropical ecosystems that comprise a mix of structural/physiognomic components, including open grasslands, wooded grasslands, savannas, woodlands and thickets. All tropical savannas are characterised by the dominance, in the herbaceous stratum, of grasses that are physiologically adapted to warm, sunny and dry conditions (C_4 grasses). Two distinct savanna biomes (Arid/Eutrophic and Mesic/Dystrophic) dominate most of tropical Africa, with transitional mosaics at the interface with rain forest and desert biomes. Mixed savannas occur at the interface between arid and mesic savannas.

Scale spatial scale refers to the area or physical extent of a phenomenon; temporal scale refers to the duration of a phenomenon—from seconds to millions of years.

Sciophile shade loving (sun-intolerant) plant species, such as those of the forest floor. (Cf. heliophile).

Seagrass the only flowering plants which grow below the water surface in marine environments. They are not grasses, but are so named because of their long green grass-like leaves. There are about 60 species of fully marine seagrasses which evolved from terrestrial plants which recolonised the ocean 70–100 million years ago. (Cf. mangroves).

Secondary compounds compounds that serve as effective defences against herbivory of plants. Secondary compounds include alkaloids, glycosides, phenolics, uncommon proteins and unusual free amino acids.

Secondary consumers consumers of primary consumers—comprising carnivores and omnivores. (Cf. primary consumers, primary producers).

Secondary forest a term used to categorise young, regenerating forest communities that replace the original ‘primary’ forest, usually following deforestation of old ‘pristine’ forest. (Cf. climax forest, primary forest).

Sedimentary basins large accumulations of sediments deposited in oceans, lakes and interior depressions. These include the marine basins along the Angolan coast, and the Kalahari Basin of the interior.

Sedimentary rocks rocks formed where eroded materials—gravel, sand and mud—accumulate on the floor of basins (depressions, lakes, oceans) and become cemented over time into conglomerates, sandstones and shales. (Cf. igneous rocks, metamorphic rocks).

Self-organization the emergence of pattern and order in a system by internal processes, rather than through external constraints or forces. Ecological examples range from the structure of animal social groups to spatial patterns associated with plant distributions.

Self-pruning the shedding by trees of branches that are shaded or diseased, and which are potentially a drain on the resources of the tree. Common in the trees of mesic savannas, where the dropping of dead branches prevents fire advancing into the tree crown.

Seral A seral community is one of the series of communities representing stages in the ecological succession as it advances towards its climax community. (Cf. climax community, succession)

Serotiny the storage of seeds in the inflorescences of plants (e.g. species of *Protea*, *Pinus*) as an adaptation to fire, where the seeds are released only after the passage of a fire, dispersing large numbers of seeds onto bare soil, when competition for resources for seedling growth is limited.

Sesquioxides oxides of iron and aluminium that accumulate in certain tropical soils. Sesquioxides are not leached from ferrallitic soils (ferralsols), and display a red colour through the oxidation of iron. (Cf. ferralsols, ferrallitic soils).

Shortgrass savanna savannas or grasslands that are dominated by grass species that are typically below 1.0 m height.

Shortwave radiation radiant energy produced by the sun with wavelengths ranging from infrared through visible to ultraviolet—received by the Earth as solar energy—the source of all life. (Cf. longwave radiation).

Soil profile the vertical succession of layers (horizons) in soils, which can be used to classify soil types according to their texture, colour and chemistry.

Solstice the moment when the Sun is furthest north or south of the Equator—which occurs on 22 June and 22 December respectively. (Cf. equinox).

South Atlantic Anticyclone a semi-permanent subtropical cell of high atmospheric pressure that lies over the South Atlantic (off-shore of Angola and Namibia). The South Atlantic Anticyclone creates south-westerly winds, which bring cold Antarctic waters to the southwest African coast and cause upwelling of deep, cold, nutrient-rich Antarctic water. (Cf. Benguela Current).

Spinescence the plant trait that includes spines, prickles, thorns and other sharply pointed defensive adaptations.

Speciation the evolutionary process where populations evolve to become distinct species that are reproductively isolated from one another.

Species most simply defined as populations that can potentially breed together and produce fertile offspring.

Species diversity a measure of the number of species in a community, and of the abundance of each species. (Cf. species evenness, species richness).

Species evenness the distribution of abundance of species in a community. (Cf. species diversity, species richness).

Species richness the number of different species that occur within a given community or area.

Stability a system in which the variables that define the state of the system (known as state variables: species composition, relative abundances, biomass, productivity) change little in response to outside pressures (e.g., stress or disturbance) such as drought, fire, herbivory. If disturbed, state variables return rapidly to their original values. A stable system therefore shows little variability through time in its state variables. Compositional stability (species composition and abundance) and functional stability (constancy of primary production and primary consumption) can vary independently as stress and disturbance factors fluctuate. (Cf. disturbance, resilience, stress).

Standing crop biomass the amount of accumulated organic matter at a given time per unit area.

State variables characterise the state of an ecosystem, and include species composition, relative abundance, biomass and productivity. (Cf. state variables).

Stochastic environmental events or biological phenomena, where the outcome has a random probability distribution and is not predictable. (Cf. deterministic).

Stomata the minute openings in the epidermis of plant leaves, through which the transfer of gases such as carbon dioxide, oxygen and water vapour into and out of plant tissues is controlled. (Cf. photosynthesis).

Strata the layering of tree species in forests, usually into ground-, mid-, canopy- and emergent-strata species.

Stromatolites representing the earliest forms of life on Earth, stromatolites are formed by the growth of blue-green algae, preserved as layered deposits of limestone. First formed 3.5 billion years ago, they continue to form in certain coastal areas.

Stratigraphy the study of the succession of rock formations and their evolutionary history.

Stratus cloud low-level clouds characterized by horizontal layering with a uniform base, often as a result of a temperature inversion, as opposed to convective or cumuliform clouds that are formed by rising thermals. (Cf. inversion).

Stress the term is used in a physiological sense to describe a constraining environmental influence that affects the productivity and efficiency of an individual and, by extension, an ecosystem. Such stresses usually operate when an environmental variable, such as temperature, light, water, nutrients or defoliation, deviates from its normal range of values in the system. Stress seldom results in mortality. (Cf. disturbance, resilience, stability).

Striations scratches left on rocks by the abrasive action of harder rocks carried in the base and margins of glaciers.

Structural carbohydrate constituents cellulose, hemicellulose and lignin—the constituents of living plant tissue that are required by grasses for growth and structural support. (Cf. metabolic constituents).

Succession refers to ecological or plant succession—the process of change in the species structure of an ecological community over time scales of decades, or even millions of years. (Cf. climax community).

Successive approximation the repeated, iterative process of observation, testing and eliminating incorrect interpretations of natural patterns and phenomena, leading to conclusions of which one can be confident.

Succulent plants with parts that are thickened, fleshy, and engorged, usually to retain water in arid climates. (Cf. cauduciform, pachycaul).

Sunflecks the narrow beams of sunlight that shine down through small gaps in the canopy of forests.

Swamps permanently waterlogged wetlands, typically along the margins of floodplains of large rivers such as the Cuanza, Cuando and Cuito.

Sympatric subpopulations occurring in the same geographic location. (Cf. allopatric).

Synecology the study of how species interact with each other at the ecosystem level and at higher levels of integration, such as populations or communities. (Cf. autecology).

Taiga the world's largest terrestrial biome, covering much of extreme northern America, Asia and Europe, and characterised by coniferous forests, in a climate of long cold winters and short wet summers.

Tallgrass savanna savannas which are dominated by grass species that exceed 3 m height, typically members of the Andropogoneae. (Cf. shortgrass savanna).

Tectonic movements large-scale vertical or horizontal movement of the Earth's crust due to processes of upwelling or subsidence of the Earth's mantle.

Tectonic plates vast pieces of the Earth's crust and mantle, together referred to as the lithosphere. Movement of the plates over the molten upper crust of the mantle is known as Continental Drift. (Cf. craton, Gondwana, lithosphere).

Temperature inversion a situation in which the temperature over land or water increases rather than decreases with increasing altitude. Cold air is trapped under a layer of warm air. The warmer air forms a cap over the cooler air body, as occurs over the cool Benguela Current, which has a stabilizing effect on the lower atmosphere and inhibits the evaporation and upward movement of moist, rain-forming air off the ocean. Fog is formed in the trapped, cool, moist air—known in Angola as *cacimbo*. (Cf. inversion, stratus cloud, Benguela Current).

Termitarium the nest built of soil and organic particles by a colony of termites, often forming a tall mound or tower, typical in tropical savannas. (Cf. eusocial organisms, salt-lick).

Terras de Catete deep swelling and shrinking vertic clays of Cretaceous marine sediments, typical of those of the monospecific *Setaria welwitschii* grasslands of Quiçama National Park.

Territory the area within an animal's home range that is defended against competitors of the same species, usually related to mate selection and breeding purposes. (Cf. home range).

Theory an integrated set of hypotheses that together explain a broader set of observations rather than any single hypothesis.

Thicket a very dense, often impenetrable plant community of large multi-stemmed shrubs and trees. Climbers can be abundant, but grasses are sparse. Thickets can be evergreen or deciduous, thorny or non-thorny. (cf. forest, savanna, woodland).

Tipping-point where change in a system accelerates beyond its state of equilibrium, pushing it into a new (alternative) stable state. (Cf. feedbacks, alternative stable state).

Top-kill injury caused to the growing point of tree saplings by fire, not resulting in the death of the plant, but causing die-back of the growing point and inducing coppicing from the stem base.

Torpor a state of decreased physiological activity in an animal, usually by a reduced body temperature and metabolic rate. Torpor enables animals to survive periods of reduced food availability.

Trade winds or ‘easterlies’ are the permanent east-to-west prevailing winds of the Earth’s equatorial regions. The winds blow from the sub-tropical high-pressure belts towards the low-pressure belt of the Intertropical Convergence Zone (ITCZ). (Cf. Intertropical Convergence Zone).

Transect a linear profile or series of samples across a habitat or landscape, used in measuring and comparing changes along a gradient of change. (Cf. quadrat).

Transpiration the process whereby water is lost to the atmosphere during the opening of leaf stomata for the purpose of gas transfer during photosynthesis. (Cf. photosynthesis, stomata).

Triage the sorting of priorities for conservation action in terms of the chances of sustained success.

Trophic relating to, or pertaining to nutrition, as in the feeding relationships between organisms in a food chain. (Cf. food chain, trophic structure).

Trophic structure the composition of a community in terms of the trophic levels and components of its food web. (Cf. primary producers, primary consumers, secondary consumers, decomposers).

Tunda the plateau within rolling landscapes of typical miombo woodlands—dominated by trees and shrubs, with light grass cover. Part of the series of a catena, where the drainage-line is known as a *mulola*, and the raised plateau is known as the *tunda*. (Cf. catena, miombo, *mulola*).

Ubiquitous species species which occur over a wide geographic area, often across many countries and habitats. (Cf. endemic species).

Underground forests communities of geoxyles which have been somewhat inaccurately referred to as ‘underground forests’. Typical of many mesic savanna ecosystems. (Cf. geoxyles).

Upwelling process in which ocean currents bring deep, cold water to the surface. Upwelling is a result of winds and the rotation of the Earth. (Cf. Benguela Current).

Vegetation an assemblage of plant species forming a community, usually with distinctive structural characteristics. (Cf. grassland, forest, savanna).

Vertisols clay-rich soils that shrink and swell with changes in moisture content. These soils contain a high content of expansive montmorillonite clay minerals. (Cf. montmorillonite, kaolin).

Vicariance the fragmentation of populations of a species into isolated sub-populations through major environmental events such as continental drift or climate change, often leading to speciation.

Vivipary the production of large, actively growing seedlings, where the embryo remains on the tree until the seedling is well developed, common in mangrove species. (Cf. mangroves).

Volatilization the loss of nitrogen and sulphur through vaporization during fires with temperatures exceeding 700 °C.

Water table also known as the groundwater table—the upper level of an underground surface in which the soil and rocks are permanently saturated with water. (Cf. perched watertable).

Water-towers the vast catchment areas of the main river systems of the Angolan planalto, that capture rainfall in their wetland sponges and provide a permanent flow of water to much of central and southern Africa.

Weather the temperature, humidity, rainfall and wind experienced at a particular place and at a specific time such as a hot, humid summer afternoon in Luanda. (Cf. climate).

Wetland a seasonally or permanently waterlogged area, usually dominated by grasses and sedges and often forming a deep organic layer known as peat. (Cf. peat).

Woodland a stratified plant community with an open tree layer (less than 50% projected canopy cover) with crowns less than one diameter apart or touching, but usually not overlapping. Woody species might be trees or shrubs, usually single-stemmed but occasionally multi-stemmed. (cf. forest, thicket, savanna, grassland).

Zambezian the floristic regional centre of endemism that includes most of southern Africa and over 90% of Angola.

Zoogeography the study of the patterns of distribution of animal species.