The Ecology of Volcán Chiles

High-altitude Ecosystems on the Ecuador-Colombia Border

Paul M. Ramsay

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Preface

During my student days I organised three expeditions to the Ecuadorian Andes. The first of these was in 1985, to the high-altitude grasslands, or páramos, of Cajas National Park, near Cuenca in southern Ecuador. Our research programme concentrated on plant distributions in relation to altitude, burning and other forms of human disturbance. We also collected terrestrial invertebrates and investigated precocious reproductive maturity in trout as a result of local fishing practices. Two years later, I returned to Ecuador, this time collecting data for my PhD. I spent considerable time in páramos all over Ecuador, focusing on plant community ecology, dynamics and productivity. Two years further on and I returned to the páramo again, this time with a group of ecology masters students from Bangor. We looked at plant distribution and morphology with altitude, forest structure and lake diatoms in Sangay National Park in Central Ecuador. It rained the whole time—except when it snowed.

I learned a great deal from these expeditions about the Ecuadorian páramos, as well as the logistics of fieldwork in remote mountains. I found it personally rewarding too. So, when I was appointed a lecturer in ecology at the University of Plymouth, and was able to continue my páramo research, I was very keen to involve my own students. By 1996 I had formed an ambitious plan to take a group of more than 30 students to Volcán Chiles. Many of my colleagues assumed I had lost my mind. Perhaps they were right. Nevertheless, we did get there in July and August 1997 and carried out diverse ecological projects, involving plants and animals in a variety of different habitats subjected to varying degrees of disturbance. In general, the programme proved very successful and we returned to England with a wealth of information. Of course, the taxonomic problems of working with páramo animals (and to a lesser extent plants) meant that many studies were only possible at higher levels of taxonomy (family and order). In spite of this, some of these projects represented the first of their kind to be carried out in the Ecuadorian Andes.

Collecting this work together into a book, along with research from others who have worked on the same mountain over recent years, seemed the logical conclusion of the project. This book is the result. It has taken far longer to publish than I had hoped, and unfortunately there are several studies not included here because the authors were not able to do them justice in the time they had available. I have also taken a second large group of students to Volcán Chiles (the madness continues), and we now have more unpublished work in the pipeline. Perhaps an additional volume will appear in due course. If so, I would like to include some work from the Colombian side of the volcano—ecology should not respect political borders.

There are several people who deserve a special mention here. First and foremost, Pete Smithers helped me tremendously in the field and back at Plymouth in the laboratory. He endured mechanical failures, a serious car accident, a gun-point mugging, a variety of petty and not-so-petty thefts, national strikes, and the usual privations of life in the páramo, but smiled throughout. I often wonder if that smile was forced at times. I would like to thank Miguel Franco and Hector Hernandez for checking and amending the Spanish summaries. I am also grateful to the anonymous referees who improved the quality of the manuscripts. I should also express my appreciation to those authors who submitted their manuscripts early and then had to wait patiently, very patiently, for the other contributions to arrive.

I hope the work presented in this book will illustrate the incredible potential of high-altitude Andean environments for ecological studies. Clearly there is plenty of descriptive work still to be done, particularly with the animals, but it is time we moved on to more thorough testing of ideas about the underlying mechanisms that might explain the patterns we find.

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Vascular plants on Volcán Chiles and Páramo del Angel, Ecuador—a preliminary list

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SUMMARY

This list of vascular plants ocurring above 3000 m above sea level on the Ecuadorian side of Volcán Chiles and Páramo del Angel includes 569 species in 90 families. It is based on collections registered in the so-called "Ecuador-database" at the University of Aarhus and for each species habitat, elevational range and collections are given. The largest families are Asteraceae, Poaceae, and Orchidaceae with 75, 45, and 35 species respectively. Of the remaining 87 families 32 have only a single species. Of the 569 species 350 are dicotyledons, 120 are monocotyledons, and 99 are pteridophytes.

RESUMEN

Esta lista incluye las plantas vasculares que ocurren encima de los 3000 metros sobre el nivel del mar en el lado ecuatoriano del Volcán Chiles y del Páramo del Angel. Incluye 569 especies en 90 familias. La información utilizada para la lista se obtuvo de la base de datos de plantas ecuatorianas en la Universidad de Aarhus. Por cada especie se provee información sobre la planta, su hábitat, rango altitudinal en el área de estudio y los registros de sus colecciones. Las familias con más especies en la lista son Asteraceae, Poaceae y Orchidaceae con 75, 45 y 35 especies respectivamente. De las 87 familias restantes, 32 incluyen una sola especie. De las 569 especies, 350 son dicotiledóneas, 120 son monocotiledóneas y 99 son pteridofitas.

Key words: flora, tropical alpine

INTRODUCTION

This list of vascular plants from Volcán Chiles and Páramo del Angel is based on data collected over many years and in several different contexts by botanists associated with the research collaboration between Pontificia Universidad Católica del Ecuador in Quito and the University of Aarhus, Denmark. The list is *not* based on exhaustive searches for specimens from Volcán Chiles in other herbaria. It must therefore be considered preliminary. Nevertheless it is based on about 2200 specimens, and with its 568 species included I believe it covers the majority of vascular plants growing in the area. Continued collecting and a more exhaustive search in the herbaria, however, will without doubt turn up many new records for the area.

The upper reaches of Volcán Chiles (4768 m) are covered by *páramo* which is the name given to the tree-less vegetation above the timberline in northern Andes. As other *páramos* in Ecuador the one on Volcán Chiles is dominated by *Calamagrostis effusa* and other bunch grasses in the bottom layer. Presence and dominance of the giant rosettes of *Espeletia pycnophylla* however distinguishes Volcán Chiles dramatically from páramos further south. Dispersed among the bunch grasses and giant rosettes there are shrubs, often such ones with small xeromorphic leaves of the genera *Baccharis, Loricaria, Vaccinium, Pernettya, Hypericum* and others. Many slender herbs, including species of *Ranunculus, Geranium, Castilleja, Valeriana, Gentianella,* and *Lupinus* flourish between the tussocks and rosettes. Where water accumulates and create humid soils cushions plants of *Plantago rigida* and *Distichia muscoides* grow abundantly. Other cushion forming plants, such as *Azorella pedunculata,* grow well in less wet places. Being dominated by giant rosettes, bunchgrasses, cushion plants, and xeromorphic shrubs the páramo vegetation on Volcán Chiles is similar in physiognomy to the vegetation found above the treeline in other tropical areas (Mena & Balslev 1986). In erosion gulleys, and where slopes or rock outcrops provide protection against strong wind, small patches of low gnarled forest occur. These forests are formed by trees and shrubs of *Oreopanax seemannianus, Vallea stipularis, Hesperomeles obtusifolia,* various Ericaceae, and species of *Gynoxys, Miconia,* and *Polylepis*. At lower elevations the vegetation gradually changes into a cloud forest which may grow on steep ridges. The cloud forest are lush on the western slopes of Volcán Chiles where clouds constantly accumulate in warm humid winds ascending from the lowlands on the coastal plain. On the eastern slopes, towards the inter-Andean valley, the amount of rain is limited by the rain shaddow created by the cordillera and the vegetation is much less lush, and in places replaced by xeromorphic scub. The eastern slopes are also exposed to strong human impact. Hence deforestation, overgrazing, and erosion has reduced the cover of natural vegetation much more on the eastern than on the western slopes.

Páramos such as that of Volcán Chiles form an archipelago of tree-less high elevation vegetation distributed along the nort-Andean Cordillera, innundated in a sea of montane forests that in turn are surrounded by lowland forests. This páramo archipelago is like an irregular string of beads reaching from Venezuela to northern Péru. The vegetation of these páramos have been under strong human influence, and some consider them cultural landscapes (Balslev & Luteyn 1992). The Volcán Chiles páramo is contiguous with páramos in the Nariño province of southern Colombia, and also with the páramos of the eastern cordillera in Ecuador.

The flora and vegetation of these páramos developed during the past 2-4 million years, which is the time after the Andean orogeny lifted the mountains high enough to create ecological conditions for páramo

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vegetation. However environments suitable for extensive colonization of páramo plants may only have existed since the Quaternary (Van der Hammen & Cleef 1986). The páramo flora originated from immigration and evolutionary modification of the montane flora. It can be divided into several phyogeographic elements present in any páramo but with varying proportions of the species. The páramo element make up 4-9% of the species, the neotropical element 21-34%, the wide tropical element 3-28%, the the holarctic element 11-15%, the Austral-Antarctic element 5-14%, the wide temperate element 7-39%, and the Cosmopolitan element has 8-17% of the species (Cleef & Chaverri 1992, Luteyn 1999).

Due to the recent origin of the páramo flora it does not include endemic families of vascular plants though 23 genera or 5% of those occurring in the páramo are endemic (Luteyn 1999). At the species level the proportion of endemics is surely much higher but this is so far undocumented.

The entire páramo ecosystem, reaching from Venezuela to northern Peru with a few outliers in Panama and Costa Rica, has a vascular plant flora of about 3400 species, divided among 10% pteridophytes, 19% monocotyledons, and 71% dicotyledons (Table 1, Luteyn 1992, 1999). The present list from Volcán Chiles has 568 species divided among 17% pteridophytes, 21% monocotyledons, and 62% dicotyledons. The higher proporation of pteridophytes in this list may be because it uses an elevational cut-off limit of 3000 meters which means it includes some cloud forest habitats.

The most species rich families on Volcán Chiles above 3000 meters elevation and their numbers of species are Asteraceae (78), Poaceae (45), Orchidaceae (35), Rosaceae (29), Lycopodiaceae (25), and Scrophulariaceae (25). Asteraceae, Poaceae, and Orchidaceae are large families in general, and they are among the five most species rich families in the Ecuadorian flora (Jørgensen & León-Yánez 1999). Their abundance on Volcán Chiles can be seen as a mere result of their abundance and diversity in the region. Rosaceae, Lycopodiaceae, and Scrophulariaceae in contrast range between number 24 and 47 in Ecuador, and their species richness on Volcán Chiles reflect their diversification in and adaptation to high elevation ecosystems. Thirty-two of the 90 families in the list are monotypic (Table 2).

Table 1. A. Numbers of families, genera and species present on Volcán Chiles and Páramo del Angel divided by major phylogenetic groups (data from this study). B. Same for all páramos from Venezuela to Peru and including outliers in Panama and Costa Rica (data from Luteyn 1999).

	Families	Genera	Species
A. Volcán Chiles & Páramo del Angel			
Pteridophytes	17	28	99 (17%)
Monocotyledons	11	62	120 (21%)
Dicotyledons	62	177	350 (62%)
	90	267	569
B. All páramos			
Pteridophytes	22	52	352 (10%)
Monocotyledons	16	101	634 (19%)
Dicotyledons	85	346	2411 (71%)
	123	499	3397

Table 2. Numbers of genera and species of vascular plants on Volcán Chiles and Páramo del Angel, broken down by family (data from the present study).

Family	Genera	Species
Asteraceae	45	78
Poaceae	24	45
Orchidaceae	16	35
Rosaceae	4	29
Lycopodiaceae	2	25
Scrophulariaceae	9	25
Apiaceae	10	18
Ericaceae	9	17
Dryopteridaceae	4	15
Melastomataceae	4	14
Cyperaceae	6	14
Rubiaceae	6	12
Grammitidaceae	3	12
Juncaceae	4	12
Campanulaceae	5	10
Onagraceae	3	9
Solanaceae	4	9
Fabaceae	6	9
Gentianaceae	3	8
Geraniaceae	1	8
Pteridaceae	3	8
Valerianaceae	1	7
Polypodiaceae	3	7
Piperaceae	2	6
Ranunculaceae	1	6
Hymenophyllaceae	1	6
Blechnaceae	1	5
Polygonaceae	2	4
Boraginaceae	4	4
Brassicaceae	3	4
Caryophyllaceae	3	4
Clusiaceae	2	4
Cunoniaceae	1	4
Aspleniaceae	1	4
Thelypteridaceae	1	4
Bromeliaceae	4	4
Liliaceae	3	4
Urticaceae	2	3
Lamiaceae	3	3
Oxalidaceae	1	3
Passifloraceae	1	3
Plantaginaceae	1	3
Dennstaedtiaceae	2	3
Phytolaccaceae	1	2
Polygalaceae	1	2
Portulacaceae	2	2
Araliaceae	2	2
Begoniaceae	1	2
Loranthaceae	2	2
Myrsinaceae	2	2
Grossulariaceae	2	2
Nyctaginaceae	1	2
Violaceae	2	2
Viscaceae	1	2
Isoetaceae	1	2
Cyatheaceae	1	2
Gleicheniaceae	1	2
Iridaceae	1	2
Equisetaceae	1	1
Selaginellaceae	1	1
Dicksoniaceae	1	1
Lophosoriaceae	1	1
Amaranthaceae	1	1
Aquifoliaceae	1	1
Berberidaceae	1	1
Buddlejaceae	1	1
Callitrichaceae	1	1
Capparidaceae	1	1
Chloranthaceae	1	1
Clethraceae	1	1
Columelliaceae	1	1
Coriariaceae	1	1
Crassulaceae	1	1
Cuscutaceae	1	1
Elaeocarpaceae	1	1
Elatinaceae	1	1
Gesneriaceae	1	1
Gunneraceae	1	1
Haloragaceae	1	1
Lentibulariaceae	1	1
Loasaceae	1	1
Verbenaceae	1	1
Monimiaceae	1	1
Myrtaceae	1	1
Theaceae	1	1
Tropaeolaceae	1	1
Araceae	1	1
Eriocaulaceae	1	1
Juncaginaceae	1	1
Potamogetonaceae	1	1
Total	**267**	**569**

The flora and fauna of Volcán Chiles and Páramo del Angel are protected in a 15.715 hectares large ecological reserve established in 1992 (Coello 1994).

METHODS

The list of species is derived mainly from the Ecuador-database of the Herbarium AAU, at the Department for Systematic Botany, University of Aarhus. That database is specimen-based, and includes informaion about all plant collections made by AAU staff in Ecuador over the past 30 years. Since the first field trip in 1968 over 100.000 collections have been made in all provinces of Ecuador, mainly in collaboration with the Herbarium QCA at Pontificia Universidad Católica del Ecuador in Quito.

To produce the present list I extracted information about all ca. 5400 collections made in the Carchi province. I then excluded collections made below 3000 m. elevation, collections made away from Volcán Chiles and Páramo del Angel, non-vascular plants, and unidentified entries. The remaining ca. 2200 collections were arranged alphabetically by family, genus, species, and collector and number. I edited the records and checked content, spelling, and so forth. The descriptive information under each species in the list is derived from what the collectors wrote in their field notes and on the labels, and it is not based on re-examination of the specimens. I consulted the relevant literature, mainly volumes of Flora of Ecuador, but also other revisions, monographs or occasional taxonomic papers cited under each family. Two general works (Jørgensen & León-Yánez 1999, Luteyn 1999) were used for checking the entire list, and I also made extensive use of the official list of Authors of Plant Names (Brummit & Powell 1992). Information in the literature about additional species from our study area can be recognised in the list because the collector and collecting number are followed by a herbarium acronym which is not AAU. In contrast the records derived from the AAU-database are not followed by acronym since they represent specimens that should all be found in the AAU herbarium.

A list of collecting localities is arranged alphabetically by collector and is found after the species list. When combined with the list of species, it gives accurate information about localities where the individual species have been found.

The arrangement of families is alphabetical within four major natural groups: Fern Allies, Ferns, Dicotyledons, and Monocotyledons. This arrangement keeps major plant groups - which most interested biologists recognise - together. When it comes to the arrangement of families in orders and subclasses, I believe that most users of the list would be lost with a phylogenetic arrangement, so at that level I have chosen to use an alphabetic ordering. The same is true for the genera and species within the families.

FERN ALLIES

Equisetaceae

***Equisetum bogotense* KUNTH**

Disturbed soil in cloud forest and boggy areas in subpáramo, 3150-3250 m. Holm-Nielsen 5642, 23938.

Isoetaceae

Literature: Hickey 1985

***Isoetes ecuadoriensis* ASPL.**

Forming colonies in 15-30 cm deep water in lakes, 3750-3850 m. Holm-Nielsen 5469.

***Isoetes novo-granadensis* H.P. FUCHS**

Each plant ca 10 cm in diam. In wet areas near streams and in lakes, 3450-4050 m. Holm-Nielsen 5344, 5470, 5921, 5925; Øllgaard 8467.

Selaginellaceae

***Selaginella* sp.**

On humid shaded road bank, 3300 m. Balslev 831.

Lycopodiaceae

Literature: Øllgaard 1988

***Huperzia arcuata* B. ØLLG.**

In forest and humid páramo with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5341 (type); Jørgensen 92260.

***Huperzia ascendens* (HERTER EX NESSEL) HOLUB**

With long-creeping, rooting, horizontal shoots, and erect sporangium-bearing shoots. Wet soil and grass vegetation at roadsides, 3400-4050 m. Holm-Nielsen 5920; Øllgaard 98113.

***Huperzia attenuata* (SPRING) TREVIS.**

Road banks in páramo, 3650-3800 m. Øllgaard 98100, 100002.

***Huperzia brevifolia* (GREV. & HOOK.) HOLUB**

In moss-cushions between rocks and on lake shores with rocks and boulders, 3950 m. Øllgaard 8394, 8469.

***Huperzia campiana* B. ØLLG.**

Pendulous epiphyte, branches narrow, quadrangular. Upper cloud forest and elfin forest, 3450-3500 m. Holm-Nielsen 5339.

***Huperzia capellae* (HERTER) HOLUB**

Plant green. Among tussock grasses and rocks in páramo, 3500-4050 m. Holm-Nielsen 5467, 5909; Lawesson 43941; Øllgaard 8515, 98099.

***Huperzia crassa* (HUMB. & BONPL. EX WILLD.) ROTHM.**

Creeping shoots superficial; sometimes forming large clumps. Bunch grass páramo, road banks, meadows, boggy depressions, and lake areas, 3740-4050 m. Eriksen 59059; Holm-Nielsen 5464, 5466, 5907, 5927, 5928, 5929, 5930, 5933, 5958; Øllgaard 8378, 8379, 8380, 8383, 8384, 8385, 8386, 8388, 8428, 8430, 8433, 8465, 8519, 8521, 8554, 8915, 100004. (var. crassa). Holm-Nielsen 5932; Øllgaard 8427, 8431, 8434, 8511, 8516, 8518. (var. manus-diaboli B. Øllg.).

***Huperzia cumingii* (NESSEL) HOLUB**

Young plant yellowish-green with slightly reddish tinged leaf tips. Sloping lake shores with rocks and boulders, 3950 m. Øllgaard 8382.

***Huperzia eversa* (POIR.) B. ØLLG.**

Steep rocky road banks and slopes in cloud forest, 3100-3250 m. Holm-Nielsen 5640, 5644; Øllgaard 8307, 8308, 8311.

***Huperzia hohenackeri* (HERTER) HOLUB**

Shoots stiff, leaves prickly. On rocks and sloping lake shores with boulders, 3800-3950 m. Eriksen 59057; Øllgaard 8390.

***Huperzia hypogaea* B. ØLLG.**

Forming extensive colonies by means of subterranean stolons. In wet páramo with abundance of Espeletia, meadows, boggy depressions, and on open banks, 3450-4050 m. Holm-Nielsen 5343, 5466, 5926, 20946, 20950, 20987; Øllgaard 8513, 8514, 8517, 8520, 8522, 98097, 98101.

***Huperzia hystrix* (HERTER) HOLUB**

Open bank and between rocks in páramo, 3450-4050 m. Holm-Nielsen 5462, 5465, 5496, 5497, 5931, 20953; Lawesson 43940; Øllgaard 8381, 8387, 8389, 98105.

***Huperzia lindenii* (SPRING) TREVIS.**

Pendulous, epiphyte. Elfin forest in sheltered places, 3900-4050 m. Holm-Nielsen 5900; Øllgaard 8464.

***Huperzia llanganatensis* B. Øllg.**
Road banks and landslides in páramo, 3700-3850 m. Balslev 23932; Holm-Nielsen 5460; Øllgaard 98108.

***Huperzia phylicifolia* (Desv. ex Poir.) Holub**
Pendant epiphyte. Páramo with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5340.

***Huperzia polydactyla* B. Øllg.**
Small erect plants. Road banks, wet páramo, and sloping lake shores with rocks and boulders, 3700-3950 m. Holm-Nielsen 5466B; Øllgaard 8391, 8470, 98107.

***Huperzia rufescens* (Hook.) Trevis.**
Road banks and humid rocky places in páramo, 3700-4050 m. Holm-Nielsen 5463, 5914; Øllgaard 8343, 8471, 8512, 98102.

***Huperzia sellifolia* B. Øllg.**
Road banks and land slides and sometimes rocky places in páramo, 3700-4050 m. Holm-Nielsen 5914A, 23928; Øllgaard 8392, 8393, 8429, 8432, 98103, 98520.

***Huperzia tenuis* (Willd.) Trevis.**
Epiphyte in forest patches in páramo, 3450-3500 m. Holm-Nielsen 5342.

***Huperzia tetragona* (Hook. & Grev.) Trevis.**
Road banks in humid páramo, 3450-3850 m. Holm-Nielsen 5458, 5495, 20956; Øllgaard 98106, 100003.

***Huperzia urbanii* (Herter) Holub**
Slopes in cloud forest and páramo, 3150-3850 m. Holm-Nielsen 5461, 5641.

***Lycopodium clavatum* L.**
On road banks and in bunch grass and páramo with shrubs and adjacent cloud forest in ravines and in boggy areas in subpáramo, 3100-3800 m. Balslev 888; Holm-Nielsen 5498, 5499, 5505, 20947, 20988, 23940; Lawesson 43938; Madsen 36350; Øllgaard 8304, 8326.

***Lycopodium jussiaei* Desv. ex Poir.**
Steep slopes and road banks in cloud forest and bunch grass páramo with shrubs and Espeletia, 3100-3350 m. Holm-Nielsen 5643; Øllgaard 8301, 8323.

***Lycopodium magellanicum* (P. Beauv) Sw.**
Humid páramo, 3450-3850 m. Holm-Nielsen 5459, 5512.

***Lycopodium thyoides* Humb. & Bonpl. ex Willd.**
Open habitats in montane forest and páramo, 3800 m. Holm-Nielsen 20958.

FERNS

Aspleniaceae

Literature: Stolze 1986

***Asplenium cuspidatum* Lam.**
Epiphyte. Cloud forest and humid páramo with Espeletia, 3450-3500 m, Holm-Nielsen 5331, 20985.

***Asplenium monanthes* L.**
Synonym Asplenium polyphyllum Bertol

Páramo and forest with Gynoxis and Polylepis, 3850 m. Eriksen 59070.

***Asplenium sessilifolium* Desv.**
Epiphyte or on rocks. In ravines and dense scrub in páramo, 3450-3650 m. Holm-Nielsen 5332; Øllgaard 8423.

***Asplenium triphyllum* C. Presl**
In rock crevices in páramo and elfin forest on sheltered places, 3900-4050 m. Holm-Nielsen 5917.

Blechnaceae

Literature: Illum 1986, Nissen 1986

***Blechnum auratum* (Fée) R.M. Tryon & Stolze**
Tree fern, trunk 15 cm thick and 1 m high. Bunch grass páramo with shrubs and Espeletia and forest in ravines, 3200-3400 m. Madsen 36366; Øllgaard 8329.

***Blechnum fragile* (Liebm.) C.V. Morton & Lellinger**
Climbing in trees. Exposed ridge in cloud forest with large trees and dense undergrowth, 3200 m. Øllgaard 8284.

***Blechnum lineatum* (Sw.) Hieron.**
Herb. In shade in cloud forest and páramo with Espeletia, 3150-3500 m. Holm-Nielsen 5338, 5684.

***Blechnum loxense* (Kunth) Hook. ex Salomon**
Small tree fern. Páramo, 3500-3850 m. Holm-Nielsen 5484, 18233, 22870; Eriksen 59054.

***Blechnum stipitellatum* (Sodiro) C. Chr.**
Rhizome erect, fronds hanging. Cloud forest with large trees and dense undergrowth, 3200-3600 m. Holm-Nielsen 6251; Øllgaard 8263.

Cyatheaceae

Literature: Tryon 1986a

***Cyathea caracasana* (Klotzsch) Domin**
Tree-fern to 5 m high, fronds to 2.5 m long. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5659.

***Cyathea frigida* (H. Karst.) Domin**
Synonym Trichipteris frigida (H. Karst.) R. M. Tryon

Tree fern 2 m high, fronds 1.5 m long. Bunch grass páramo and cloud forest in ravines, 3200-3350 m. Øllgaard 8336.

Dennstaedtiaceae

***Histiopteris incisa* (Thunb.) J. Sm.**
Herb. Road banks in páramo, 3450-3550 m. Holm-Nielsen 5506.

***Hypolepis bogotensis* H. Karst.**
Rhizome creeping, fronds to 4 m long. Steep slopes in cloud forest and páramo with elfin forest, 3150-4050 m. Holm-Nielsen 5646, 5902, 5906.

***Hypolepis obtusata* (C. Presl) Kuhn ex Hieron.**
Rhizome creeping. In rock crevices, 3900-4050 m. Holm-Nielsen 5903; Øllgaard 8374.

Dicksoniaceae

Literature: Tryon 1986b

***Dicksonia sellowiana* Hook.**
Tree-fern to 6 m tall, fronds to 2.5 m long. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5645.

Dryopteridaceae

Literature: Stolze et al 1994

***Cystopteris fragilis* (L.) Bernh.**
Along stream in cloud forest, 3150-3250 m. Holm-Nielsen 5651.

***Dryopteris wallichiana* (Spreng.) Hyl.**
Road banks in páramo, 3450-3550 m. Holm-Nielsen 5514.

***Elaphoglossum antisanae* (Sodiro) C. Chr.**
Epiphyte. Elfin forest, 3900-4050 m. Holm-Nielsen 5911.

***Elaphoglossum cardiophyllum* (Hook.) T. Moore**
Epiphyte or saxicole. Road banks and on trees in páramo, 3750-4050 m. Holm-Nielsen 5473; Øllgaard 8342.

***Elaphoglossum dombeyanum* (Fée) T.B. Moore & Houlston**
Rock crevices in páramo with dense scrub and small trees, 3650 m. Øllgaard 8406.

***Elaphoglossum huacsaro* (Ruiz) H. Christ**
Road banks with mosses and scattered shrubs, 3100-3200 m. Øllgaard 8303.

***Elaphoglossum lindenii* (Bory ex Fée) T. Moore**
In moss cushions and on rocks in páramo ravines with shrubs and small trees, 3650 m. Øllgaard 8410.

***Elaphoglossum lloense* (Hook.) T. Moore**
Epiphyte in forest fragments in páramo, 3200-3350 m. Øllgaard 8334.

***Elaphoglossum mathewsii* (Fée) T. Moore**
Synonym Elaphoglossum hartwegii (Fée) T. Moore

To 40 cm tall. On road banks near lower border of páramo, 3400-3550 m. Holm-Nielsen 5515; Madsen 36367.

***Elaphoglossum minutum* (Pohl ex Fée) T. Moore**
Synonym Elaphoglossum leptophyllum (Fée) T. Moore

On road bank and steep slopes in cloud forest and páramo, 3250-3550 m. Balslev 885; Holm-Nielsen 5501, 6258.

***Elaphoglossum rimbachii* (Sodiro) C. Chr.**
Terreestrial or epiphytic in upper montane forest and cloud forest and páramo, 4350 m. Sklenar 658, 1205.

***Elaphoglossum rupestre* (H. Karst.) H. Christ**
On rocks in ravines in páramo with dense scrub and small trees, 3650 m. Øllgaard 8411.

Elaphoglossum squamipes (Hook.) T. Moore
Epiphyte. Cloud forest and páramo with elfin forest in sheltered places, 3150-4050 m. Holm-Nielsen 5657, 5915.

Polystichum muricatum (L.) Fée
Fronds to 3.5 m long, rhizome short erect. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5648.

Polystichum orbiculatum (Desv.) J. Remy & Fée
Synonym Polystichum polyphyllum (C. Presl) C. Presl

On road bank, rocks, in crevices in old stone bridge, and among mosses in páramo, 3300-4050 m. Balslev 836; Holm-Nielsen 5335, 5905.

Gleicheniaceae

Literature: Andersen, E Ø and Øllgaard, B submitted

Sticherus revolutus (Kunth) Ching
Synonym Gleichenia revoluta Kunth

Scrambling. Cloud forest with dense undergrowth and roadbanks in páramo, 3200-3600 m. Andersen 10890; Øllgaard 8289.

Sticherus simplex (Desv.) Ching
Synonym Gleichenia simplex (Desv.) Hook.

Roadbanks in páramo, 3350-3600 m. Andersen 10891; Balslev 860, 2618; Øllgaard 98112.

Grammitidaceae

Literature: Bishop 1988, A R Smith 1993

Ceradenia farinosa (Hook.) L.E. Bishop
Pendant epiphyte, fronds white farinose. Elfin forest in páramo, 3750-4050 m. Holm-Nielsen 5478, 5918; Øllgaard 8462.

Ceradenia intricata (C.V. Morton) L.E. Bishop ex A.R. Smith
Synonym Grammitis intricata C.V. Morton

Pendent epiphyte. Elfin forest in páramo, 3900-4050 m. Holm-Nielsen 5901.

Melpomene assurgens (Maxon) A.R. Sm. & R.C. Moran
On a steep rocky slope, 3100-3200 m. Øllgaard 8310.

Melpomene moniliformis (Lag. ex Sw.) A.R. Sm. & R.C. Moran
Synonym Grammitis moniliformis (Lag. ex Sw.) Proctor

Epiphyte or terrestrial. Humid páramo. 3750-3850 m. Holm-Nielsen 5474, 5481.

Melpomene peruviana (Desv.) A.R. Sm. & R.C. Moran
Synonym Grammitis peruviana (Desv.) C. V. Morton

Pendant epiphyte on the underside of branches. Cloud forest with large trees and dense undergrowth, 3200-3600 m. Øllgaard 8267.

Melpomene xiphopteroides (Liebm.) A.R. Sm. & R.C. Moran
Synonym Grammitis rigens (Maxon) Proctor

On road bank among mosses in cloud forest, 3150-3250 m. Holm-Nielsen 5650.

Melpomene sp.
Humid superpáramo on shallow sandy soil with rocks, 4300-4400 m. Sklenar 709 (this collection is identified by A. R. Smith (UC) in 1996 with an unpublished combination in Melpomene).

Terpsichore heteromorpha (Hook. & Grev.) A.R. Sm.
Synonym Grammitis heteromorpha (Hook. & Grev.) C.V. Morton

Pendant epiphyte. Elfin forest in páramo, 3750-4400 m. Eriksen 59081; Holm-Nielsen 5475, 5904; Sklenar 618.

Terpsichore jamesonioides (Fée) A.R. Sm.
Synonym Grammitis jamesonioides (Fée) C. V. Morton

Pendant epiphyte. Cloud forest in ravines in páramo, 3200-3650 m. Øllgaard 8331, 8403.

Terpsichore lanigera (Desv.) A.R. Sm.
Synonym Grammitis lanigera (Desv.) C. V. Morton

Epiphyte. Cloud forest with Espeletia and Puya, 3500 m. Holm-Nielsen 20974, 20989.

Terpsichore longisetosa (Hook.) A.R. Sm.
Pendant epiphyte. Very humid páramo, 3750-3850 m. Holm-Nielsen 5479.

Terpsichore pichinchensis (Hieron.) A.R. Sm.
Synonyms Grammitis pichinchensis (Hieron.) C.V. Morton, Terpsichore subscabrum (Klotzsch) A.R. Sm., Grammitis subscabrum (Klotzsch) C.V. Morton

Epiphyte. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5656.

Hymenophyllaceae

Hymenophyllum amabile C.V. Morton
Epiphyte. Elfin forest in páramo, 3900-4050 m. Holm-Nielsen 5913, 5924.

Hymenophyllum matthewsii Bosch
Pendent on shaded rock wall. Páramo, 3700 m. Øllgaard 98511.

Hymenophyllum myriocarpum Hook.
Pendant epiphyte. Elfin forest and narrow ravines with shrubs in páramo, 3200-4050 m. Holm-Nielsen 5471, 5483, 5923; Øllgaard 8285, 8364, 8422, 8463.

Hymenophyllum speciosum Bosch
Pendant epiphyte, 3950 m. Øllgaard 8463.

Hymenophyllum trichophyllum Kunth
Epiphyte on large trees in cloud forest and ravines in páramo, 3200-4050 m. Øllgaard 8268, 8296, 8339, 8405, 98527.

Hymenophyllum tunbrigense (L.) Sm.
3800-3850 m. Eriksen 59041.

Lophosoriaceae

Literature: Tryon 1986c

Lophosoria quadripinnata (J.F. Gmel.) C. Chr.
Vicinity of El Angel, 3100-3700 m, Popenoe s.n. (US).

Polypodiaceae

Literature: León 1992

Campyloneurum amphostenon (Kuntze ex Klotzch) Fée

Cloudforest with Espeletia and Puya, 3500 m. Holm-Nielsen 20986.

Campyloneurum angustifolium (Sw.) Fée
Epiphyte or terrestrial. In hedges along road, on road banks, or on trees in cloud forest or forest patches in páramo, 3150-4050 m. Holm-Nielsen 5235, 5336, 5480, 5653, 5912; Øllgaard 8330. (Numbers 5235, 5480 and 5912 are cited as C. amphostemon v. amphostemon and 5336 as C. cochense by León 1992).

Campyloneurum solutum (Klotzsch) Fée
Epiphyte. Cloud forest and páramo with Espeletia, Puya, Gynoxis, and Polylepis, 3500-3850 m. Eriksen 59071, 59080.

Pecluma divaricata (E. Fourn.) Mickel & Beitel
Synonyms Pecluma boliviana (Rosenst.) M.G. Price, Polypodium bolivianum Rosenst.

Pendant epiphyte on the underside of a large tree. Cloud forest with large trees and dense undergrowth. 3200-3600 m. Øllgaard 8269.

Pecluma eurybasis (C. Chr.) M.G. Price
Epiphyte. Steep slopes in cloud forest and páramo with forest in ravines, 3150-3350 m. Holm-Nielsen 5655; Øllgaard 8332.

Polypodium monosorum Desv.
Epiphyte. Hedges along road, shrubby páramo, road banks, and cloud forest, 3150-3850 m. Balslev 890; Eriksen 59095; Holm-Nielsen 5232, 5236, 20984.

Polypodium subandinum Sodiro
Epiphyte. Cloud forest with large trees and dense undergrowth, 3150-3250 m. Holm-Nielsen 5649; Øllgaard 8293.

Pteridaceae

Literature: Arbeláez manuscript

Eriosorus cheilanthoides (Sw.) A.F. Tryon
To 60 cm tall. Mountain forest, 3200-3300 m. Madsen 36376.

Eriosorus rufescens (Fée) A.F. Tryon
Pendent on road banks in páramo with elfin forest on sheltered places, 3700-4050 m. Holm-Nielsen 5472, 5919; Øllgaard 1206, 98104, 98519.

Jamesonia alstonii A.F. Tryon
On roadbank. Shrub páramo. 3350 m. Balslev 861.

***Jamesonia cinnamomea* Kunze**
Grass páramo to shrub and cushion páramo, 3950-4200 m. Sklenar 648; Øllgaard 8461.

***Jamesonia goudotii* (Hieron) C. Chr.**
To 60 cm tall, leaf margin covers sori, rhizome subterranean. Land slides, road banks, lake shores, and swamps in meadows and grass páramos, 3400-4050 m. Eriksen 59015; Holm-Nielsen 5456, 5457, 5910, 23906; Lægaard 54917, 54922, 54968; Madsen 36368, Øllgaard 8445, 8365.

***Jamesonia pulchra* Hook. & Grev.**
Among grass tussocks in Páramo, 3450-4050 m. Holm-Nielsen 5500, 5908, 18227, 18232, 20991; Lægaard 54919; Øllgaard 98082.

***Jamesonia scammanae* A.F. Tryon**
In deep moss in shade, on road banks, and in páramo, 3450-3850 m. Eriksen 59014; Holm-Nielsen 5337, 5477; Øllgaard 98078.

***Pteris muricata* Hook.**
Large fern, fronds pedately divided, 3 m high. Cloud forest with large trees and dense undergrowth, 3200 m. Øllgaard 8287.

Thelypteridaceae

Literature: Smith 1983

***Thelypteris caucaensis* (Hieron.) Alston**
In rock crevices and on landslides in páramo, 3700 m. Balslev 23929.

***Thelypteris corazonensis* (Baker) A.R. Sm.**
In shade in forest fragment in páramo, 3450-3500 m. Holm-Nielsen 5333.

***Thelypteris minutula* C. V. Morton**
On shaded soil banks in páramo, 3300 m. Balslev 841.

***Thelypteris supina* (Sodiro) A.R. Sm.**
Shrub páramo, 3550 m. Balslev 896.

ANGIOSPERMS — MAGNOLIOPHYTA

For the flowering plants (Division Angiosperms or Magnoliophyta) this list follows the system of Cronquist (1981). That system is widely known and hence useful in this context, even though a few families are circumscribed in a way which is odd to many botanists. In this list, for example the genus *Bomarea* is placed in Liliaceae even if most botanists place it in Alstroemeriaceae. In the same manner the genera *Phaedranassa* and *Stenomesson* are typical Amaryllidaceae to most botanists, but that family is not recognised by Cronquist who treats them as Liliaceae. Apart from Liliaceae Cronquist circumscribes the families represented in this list in a traditional way which is not different from what is common in other botanical texts. For each family its placement in order and subclass in the system of Cronquist is given in parenthesis.

DICOTYLEDONS — MAGNOLIOPSIDA

Amaranthaceae (Caryophyllales — Caryophyllidae)

Literature: Eliasson 1987

***Alternanthera porrigens* (Jacq.) Kuntze**
Crawling herb, inflorescence whitish brown, 3075 m. Jørgensen 56121 (var. piurensis (Standl.) Eliasson).

Apiaceae (Apiales — Rosidae)

Literature: Mathias & Constance 1976

***Arracacia moschata* (Kunth) DC.**
Internodes and sheats red, flowers purple, fruits green. Shrub páramo, 3250-3300 m. Jørgensen 56127.

***Azorella aretioides* (Spreng.) DC.**
Cushion-plant, flowers yellowish. Páramo, meadows and around lakes, 3800-4050 m. Eriksen 59050; Holm-Nielsen 5947.

***Azorella biloba* (Schltdl.) Wedd.**
3400m. Drew E466 (MSC, UC, US).

***Azorella corymbosa* (Ruiz & Pav.) Pers.**
Humid superpáramo on shallow sandy soil with rocks, 4300-4400 m. Sklenar 701.

***Azorella crenata* (Ruiz & Pav.) Pers.**
Cushion forming. Cliffs, bogs, road banks, and tall scrub in páramo, 3650-4050 m. Lægaard 101271, 101681; Øllgaard 8341, 98510.

***Azorella pedunculata* (Spreng.) Mathias & Constance**
Cushion plant, flowers light yellow. Páramo with abundance of Espeletia, grazed bunch grasses and bogs, 3400-3850 m. Balslev 23903; Eriksen 59043; Holm-Nielsen 5271; Madsen 36345.

***Bowlesia lobata* Ruiz & Pav.**
Páramo del Angel, 3400 m. Sparre 14222 (S).

***Eryngium humile* Cav.**
Herb, bracts white inside. Humid páramo, 3350-3500 m. Holm-Nielsen 5326; Jørgensen 56145; Madsen 36385.

***Hydrocotyle bonplandii* A. Rich.**
Tufiño, 3500 m. Asplund 17048 (S); Páramo del Angel, 3400 m. Sparre 14249 (S).

***Hydrocotyle humboldtii* A. Rich.**
Páramo del Angel, Benoist 3667 (P).

***Hydrocotyle steyermarkii* Mathias & Constance**
Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5601.

***Lilaeopsis schaffneriana* (Schltdl.) J.M. Coult. & Rose**
Submersed in the lake, 3750-3850 m. Holm-Nielsen 5409.

***Neonelsonia acuminata* (Benth.) J.M. Coult. & Rose ex Drude**
Large, scandent herb to 1.5 m, flowers light green. Cloud forest, 3150-3250 m. Holm-Nielsen 5678, 5835.

***Niphogeton dissecta* (Benth.) J.F. Macbr.**
Flowers white. Páramo, 3750-4050 m. Holm-Nielsen 5388, 5939.

***Niphogeton glaucescens* (Kunth) J.F. Macbr.**
Páramo del Angel, Benoist 4632 (P).

***Niphogeton ternata* (Willd. ex Schltr.) Mathias & Constance**
3450 m. Lægaard 101703.

***Oreomyrrhis andicola* (Kunth) Hook. f.**
Solitary plants between Festuca tufts in humid páramo, 3750-3850 m. Holm-Nielsen 5403.

***Ottoa oenanthoides* Kunth**
Páramo del Angel, 3400-3600 m. Heinrichs 668 (M).

Aquifoliaceae (Celastrales — Rosidae)

***Ilex* sp.**
Low shrub or tree to 2 m tall, flowers greenish yellow. Edge of forest and forest patches in páramo, 3200-3350 m. Øllgaard 8327, 8335.

Araliaceae (Apiales—Rosidae)

Literature: Borchsenius 1997

***Oreopanax seemannianus* Marchal**
Tree or shrub to 6 m., fruits dark green to black. Grass páramo with Espeletia and some rocks, 3600-4100 m. Balslev 4435, 4440; Jørgensen 92241.

***Schefflera* sp.**
Small tree with thick branches. Exposed ridge in cloud, 3200-3600 m. Øllgaard 8264.

Asteraceae (Asterales—Asteridae)

Literature: Anderberg 1991, Cuatrecasas 1997, Díaz-Piedrahíta & Vélez-Nauer 1993, Dillon & Ságastegui 1986, Funk 1997a,b,c, Harling 1991, Jeffrey 1992, Robinson 1978, 1997, Robinson & Funk 1997

***Achillea millefolium* L.**
Herb 0.5 m., inflorescence white. 3400 m. Jørgensen 92297.

***Achyrocline* sp.**
Hedges along the road, 3150-3300 m. Holm-Nielsen 5221.

***Aetheolaena patens* (Kunth) B. Nord.**
Synonyms Gynoxys auriculata Turcz. Lasiocephalus patens (Kunth) Cuatrec.

Scandent shrub, flowers light yellow. Ravine in páramo, 3650 m. Øllgaard 8397.

***Ageratina azangaroensis* (Sch. Bip. ex Wedd.) R.M. King & H. Rob.**
Synonym Eupatorium azangaroensis Sch. Bip. ex Wedd.

Herb to 1 m tall, flowers white. Páramo. 3400 m. Madsen 36355.

***Ageratina pseudochilca* (Benth.) R.M. King & H. Rob.**
Synonym Eupatorium pseudochilca Benth.

"chilca negra"

Shrub to 2 m tall, flowers white. Hedges along the road, 3150-3300 m. Holm-Nielsen 5230, Zarucchi 2327 (AAU).

***Ambrosia arborescens* Mill.**
Shrub to 4 m tall. Hedges along road. 3150-3300 m. Holm-Nielsen 5217.

***Aphanactis ollgaardii* H. Rob.**
Small herbs between Festuca tufts in páramo, 3750-3850 m. Holm-Nielsen 5414; Madsen 36336.

***Baccharis buxifolia* (Lam.) Pers.**
Shrub to 1.5 m, flowers light yellow to white. Cloud forest with Espeletia and Puya, secondary forest and pastures, 3280-3800 m. Holm-Nielsen 20949, 20977; Jørgensen 92253, 92290.

***Baccharis caespitosa* (Ruiz & Pav.) Pers.**
Prostrate, flowers cream colored. Espeletia páramo, 3600 m. Holm-Nielsen 24266.

***Baccharis genistelloides* (Lam.) Pers.**
Low shrub with winged stems, flowers white. Cloud forest and páramo with Espeletia and Puya, 3300-3500 m. Balslev 853; Holm-Nielsen 20971.

***Baccharis latifolia* (Ruiz & Pav.) Pers.**
Shrub, 2 m high, flowers white. Cloud forest with large trees and dense undergrowth and hedges along the road, 3150-3300 m. Holm-Nielsen 5210; Øllgaard 8300; Werling & Leth-Nissen 203 (AAU).

***Baccharis macrantha* Kunth**
Shrub or tree, 1-5 m. 3600 m. Holm-Nielsen 18257.

***Baccharis padifolia* Hieron.**
Shrub ca. 2 m high, bracts purple. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5808.

***Baccharis teindalensis* Kunth**
Shrub 2 m. Espeletia páramo, 3500 m. Holm-Nielsen 22867.

***Barnadesia spinosa* L.f.**
"espino de gato"

Shrub, 2-4 m tall. 3000-3400 m. Harling & Andersson 12184 (GB); Wiggins 10631 (NY); Werling & Leth-Nissen 200 (QCA).

***Bidens humilis* Kunth**
Synonym Bidens andicola Kunth

Herb with creeping stem, rayflowers bright yellow. Steep slopes in cloud forest and páramo, 3150-3400 m. Holm-Nielsen 5840; Madsen 36332.

***Chaptalia cordata* Hieron.**
3400-3600 m. Heinrichs (GB, MA); Fagerlind & Wibom 1505 (S).

***Chuquiraga jussieui* J.F. Gmel.**
Erect shrub 1 m, inflorescence orange. Páramo, meadows and elfin forest, 3600-4050 m. Balslev 4441; Holm-Nielsen 5952; Jørgensen 92300.

***Conyza bonariensis* (L.) Cronquist**
Flowers whitish. Hedges along the road, 3150-3300 m. Holm-Nielsen 5229.

***Conyza uliginosa* (Benth.) Cuatrec.**
Cloud forest with Espeletia and Puya, 3500 m. Holm-Nielsen 20979.

***Cotula* sp.**
Creeping herb. Humid páramo, 3900-4000 m. Holm-Nielsen 5290; Molau et al. 2569 (AAU).

***Culcitium canescens* Bonpl.**
Synonym Senecio canescens (Bonpl.) Cutrec.

Stemless rosette to 3/4 m tall, flowers yellow. Very humid páramo, 3450-3800 m. Holm-Nielsen 5508, 20962.

***Diplostephium floribundum* (Benth.) Wedd.**
Shrub 2 m tall, ray flowers white, disk flowers yellow. Steep slopes in cloud forest, 3250-3500 m. Holm-Nielsen 5636, 21001; Øllgaard 8333, 98115.

***Diplostephium glandulosum* Hieron.**
Shrub to 1.5 m tall, ray flowers lilac, disc flowers yellow. Steep slopes in cloud forest and ravines in páramo, 3150-3650 m. Holm-Nielsen 5805, 18243; Øllgaard 8395.

***Diplostephium hartwegii* Hieron.**
Shrub 2 m, ray flowers bluish-violet, disc flowers yellow. Ravines in Espeletia páramo, with dense scrub and small trees, 3300-3800 m. Balslev 856; Holm-Nielsen 20965; Øllgaard 8415.

***Diplostephium macrocephalum* S.F. Blake**
Flowers light violet. Espeletia páramo, 3500 m. Holm-Nielsen 22863.

***Diplostephium rhododendroides* Hieron.**
Shrub 1.5 m, tomentum white, flowers purplish-violet. Espeletia páramo, 3600 m. Holm-Nielsen 18250, 24270.

***Diplostephium rupestre* (Kunth) Wedd.**
Shrub 1 m, ray flowers white, disc flowers brown. Páramo, meadow and around small lakes in páramo with elfin forest on sheltered places, 3600-4050 m. Holm-Nielsen 5944, 5951; Jørgensen 92315; Øllgaard 8370, 8443.

***Diplostephium schultzii* Wedd.**
Shrub, 1 m tall, flowers light blue. Boggy depression in Espeletia páramo, dominated by cushion plants, and adjacent wet slopes, 3750-4000 m. S. León 1098 (AAU), Øllgaard 8444.

***Dorobaea pimpinellifolia* (Kunth) B. Nord.**
Synonym Senecio pimpinellifolius Kunth

Flowers yellow. Espeletia páramo and mountain forest, 3850 m. Eriksen 59066.

***Erigeron ecuadoriensis* Hieron.**
Herb to 40 cm tall, leaves red, sepals red green, petals white to darkred. Near the lower border of the páramo, 3400 m. Madsen 36360.

***Espeletia pycnophylla* Cuatrec.**
To 5 m tall, single stemmed rosette plant. Bunch grass páramo dominated by Espeletia, 3350-3850 m. Balslev 877, 23863; Eriksen 59065; Holm-Nielsen 5509, 18236, 20945, 22862; Jørgensen 92285; Madsen 36346; Øllgaard 8541.

***Gamochaeta americana* (Mill.) Wedd.**
Synonym Gnaphalium americanum Mill.

Herbs, flowers white. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5591.

***Gnaphalium antennarioides* DC.**
Synonym Pseudognaphalium antennarioides (DC) A. Anderb.

Herbs, flowers white. Very humid páramo, 3500-3850 m. Holm-Nielsen 5425; Lawesson 43942.

***Grosvenoria rimbachii* (B.L. Rob.) R.M. King & H. Rob.**
Tree to 4 m. Espeletia-páramo, 3600 m. Holm-Nielsen 18254.

***Gynoxys baccharoides* (Kunth) Cass.**
Shrub to 4 m tall, flowers yellow. Mountain forest, 3200-3300 m. Madsen 36379.

***Gynoxys buxifolia* (Kunth) Cass.**
Shrub to 3 m, flowers yellow, 3600 m. Holm-Nielsen 18252.

***Gynoxys fuliginosa* (Kunth) Cass.**
Shrub 4 m, ray florets yellow, disc florets brown. 3800 m. Holm-Nielsen 20964.

***Gynoxys sodiroi* Hieron.**
Shrub 2 m. 3600 m. Holm-Nielsen 18249.

***Gynoxys tolimensis* Cuatrec.**
Tree 3 m tall, flowers yellow. Ravine in páramo, 3650 m. Øllgaard 8418.

***Hieracium frigidum* Kunth**
Flowers yellow. Among grass tussocks in Espeletia páramo, 3750 m. León 1092 (AAU); Øllgaard 98090.

***Hypochoeris sessiliflora* Kunth**
Rosette plant, flowers yellow. Páramo, meadows and around lakes, 3400-4050 m. Eriksen 59006; Holm-Nielsen 5259, 5880; Jørgensen 92325; Madsen 36340; Øllgaard 8354, 8436, 8538.

***Hypochoeris sonchoides* Kunth**
Flowers white. On steep rocky slope, 3150-3250 m. Holm-Nielsen 5602.

***Jalcophila ecuadoriensis* M.O. Dillon & Sagásteg.**
In small tufts in páramo, 3750-3850 m. Holm-Nielsen 5362 (type).

***Jungia coarctata* Hieron.**
"matiango"

Creeping for several m, flowers white. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5844.

***Lasiocephalus gargantanus* (Cuatrec.) Cuatrec.**
Grass, shrub and cushion páramo, 4150-4200 m. Sklenar 626.

***Lasiocephalus ovatus* Schltdl.**
Synonym Culcitium reflexum Kunth

Grass páramo with Espeletia and some rocks, 3900-4100 m. Balslev 4434; Eriksen 59007.

***Lasiocephalus* sp. 1**
Cushion bog with along small stream, 4250 m. Sklenar 663.

***Lasiocephalus* sp. 2**
Wet depression in the grass páramo, 4100 m. Sklenar 1404.

***Liabum igniarium* (Kunth) Less.**
Scandent shrub with purple ray flowers. Espeletia-páramo, bogs and tall scrub, 3650-3750 m. Øllgaard 98524.

***Llerasia hypoleuca* (Turcz.) Cuatrec.**
Synonym Haplopappus hypoleucus Turcz.

Shrub to 3 m tall, flowers yellow. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5583; Øllgaard 8275.

***Loricaria thuyoides* (Lam.) Sch. Bip.**
Shrub to 1.5 m tall, inflorescence white. In cloud forest, páramo, ravines with shrubby vegetation, and boggy depressions, 3300-3850 m. Balslev 829, 23809; Holm-Nielsen 5288, 20983; Jørgensen 92323, 92328; Lawesson 43929; Madsen 36369; Øllgaard 8425, 8550.

***Lucilia* sp.**
Small tufts on path. Espeletia páramo, 3700 m. Øllgaard 98080.

***Mikania* sp.**
Shrub, flowers white to pink. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5830.

***Monticalia andicola* (Turcz) C. Jeffrey**
Synonyms Pentacalia andicola (Turcz.) Cuatrec., Senecio andicola Turcz.

Shrub to 2 m tall, densely banching, flowers yellow. Humid páramo with abundance of Espeletia, 3400-3850 m. Holm-Nielsen 5315, 5410, 18231, 18238, 20957; Jørgensen 92320; Madsen 36347; Øllgaard 8524.

***Monticalia peruviana* (Pers.) C. Jeffrey**
Synonym Senecio ericaefolius Benth.

Shrub to 4 m tall, flowers yellow. Humid páramo and boggy depressions, 3450-3740 m. Holm-Nielsen 5507; Jørgensen 92320; Øllgaard 852.

***Monticalia stuebelii* (Hieron) C. Jeffrey**
Synonyms Pentacalia stuebelii (Hieron) Cuatrec. Senecio stuebelii Hieron.

Shrub to 0.5 m tall, flowers yellow. Boggy depression in Espeletia páramo, 4000 m. Øllgaard 8450.

***Monticalia vaccinioides* (Kunth) C. Jeffrey**
Synonyms Pentacalia vaccinioides (Kunth) Cuatrec., Senecio vaccinioides (Kunth) Sch. Bip. ex Wedd.

Shrub to 2 m tall, leaves glaucuous, flowers yellow. Ravines, meadows and boggy depressions in páramo, 3300-4050 m. Balslev 832, 23859; Holm-Nielsen 5892, 18235, 22856, 24267; Jørgensen 92280, 92311; Øllgaard 8350, 8396, 8542.

***Munnozia jussieui* (Cass.) H. Rob. & Brettell**
Shrub with pendent shoots to 2 m long, ray flowers white to pale red. Steep slopes in cloud forest, 3150-3800 m. Holm-Nielsen 5829; Madsen 36380.

***Munnozia senecionidis* Benth.**
Synonym Liabum sagittatum Sch. Bip., Munnozia sagittata Wedd.

Creeping, flowers yellow. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5567; Øllgaard 8290.

***Mutisia intermedia* Hieron.**
Scandent, flowers bright red. In shrubs along old coble stone road, 3500 m. Balslev 4439. Cited as Mutisia grandiflora Humboldt & Bonpl. in Harling (1991), but Diaz-Piedrahíta & Vélez-Nauer (1993) maintain that M. grandiflora is restricted to Colombia.

***Mutisia ochroleuca* Cuatrec.**
Colombia, Nariño, Tambo, NW shoulder of Volcán Chiles, 3100 m. Ewan 16089 (F, US).

***Oligactis coriacea* (Hieron.) H. Rob. & Brettell**
Shrub to 2.5 m tall, flowers yellow, 6-10 ray flowers. Slopes and ridges in cloud forest, 3150-3250 m. Holm-Nielsen 5803; Øllgaard 8277.

***Oligactis pichinchensis* (Hieron.) H. Rob. & Brettell**
Scandent shrub to 10 m long, flowers yellow, 14-18 ray flowers. 3000-3200 m. Harling & Andersson 12412 (GB, US).

***Oritrophium peruvianum* (Lam.) Cuatrec.**
Ray flowers violet-white, rosettes filled with brownish mucilage around leaf bases. Growing in wet places in bunch grass páramo and in boggy depressions, 3740-4050 m. Eriksen 59008; Holm-Nielsen 5401, 5898; Øllgaard 8367, 8448, 8525.

***Perezia pungens* (Bonpl.) Less.**
Herb to 50 cm tall, inflorescence blue. Páramo with shrubs, 3460-3600 m. Jørgensen 92278.

***Plagiocheilus bogotensis* (Kunth) Wedd.**
Small herb, flowers white. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5571.

***Senecio formosus* Kunth**
Herb to 1 m tall, disk flowers yellow, ray flowers lilac. 3800-3850 m. Eriksen 59001; Jørgensen 92314.

***Senecio hypsobates* Wedd.**
Flowers yellow. Boggy depression and stream sides in Espeletia páramo, 3800-4100 m. Erikksen 59011; Jørgensen 92305; Sklenar 1400; Øllgaard 8453.

***Senecio tephrosioides* Turcz.**
Flowers yellow. 3600-3800 m. Eriksen 59004; Holm-Nielsen 18241, 20944.

***Sigesbeckia jorullensis* Kunth**
Synonym Sigesbeckia cordifolia Kunth

Herb, flowers yellow with an aromatic odeur. Hedges along the road, 3150-3300 m. Holm-Nielsen 5224.

***Sonchus* sp.**
Herb, 1 m tall, flowers light yellow. Espeletia páramo, 3600 m. Holm-Nielsen 24269.

***Stevia* sp.**
Shrub, flowers white to dark purple. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5851.

***Tagetes zypaquirensis* Bonpl.**
Shrub to 0.5 m tall, flowers yellow. Hedges along the road, 3150-3300 m. Holm-Nielsen 5213.

***Verbesina* sp.**
Shrub 1.5 m tall, flowers yellow. Hedges along the road, 3150-3300 m. Holm-Nielsen 5220.

***Werneria pumila* Kunth**
Cushion plant, flowers white. 3600 m. Jørgensen 92321.

***Werneria pygmaea* Gilles ex Hook & Arn.**
Synonym Werneria graminifolia Kunth

Tufted-cushion plant, flowers white. Humid páramo with abundance of Espeletia, 3450-4050 m. Balslev 23894; Holm-Nielsen 5281, 5316, 5956; Øllgaard 8523.

***Xenophyllum crassum* (S.F. Blake) V.A. Funk**
Synonym Werneria crassa S. F. Blake

Cushion forming, disk flowers yellow, ray flowers white. Boggy depression in páramo, 3800-4000 m. Eriksen 59003; Øllgaard 8451.

***Xenophyllum humile* (Kunth) V.A. Funk**
Synonym Werneria humilis Kunth

Forming hard, dome-shaped cushions, flowers white. Páramo, meadows and small lake area with boggy depressions, 3750-4050 m. Holm-Nielsen 5890, 5405; Øllgaard 8360, 8452.

Begoniaceae (Violales — Dilleniidae)

Literature: L B Smith & Wasshausen 1986

***Begonia maurandiae* A. DC.**
Flowers white to reddish, climbing in small shrubs. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5600.

***Begonia urticae* L.f.**
Scandent herb, flowers light purple. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5638, 5795.

Berberidaceae (Ranunculales — Magnoliidae)

***Berberis pichinchensis* Turcz.**
Low shrub, flowers orange. Ravine in Espeletia páramo, 3650 m. Øllgaard 8412.

Boraginaceae (Lamiales — Asteridae)

***Hackelia revoluta* (Ruiz & Pav.) I.M. Johnst.**
Synonym Cynoglossum revolutum Ruiz & Pav.

Flowers pale blue. Ravine in Espeletia páramo, 3650 m. Eriksen 59096; Øllgaard 8424.

***Moritzia lindenii* (A. DC.) Benth. ex Gürke**
Flowers blue. Margin of fog forest. 3750-3850 m. Eriksen 59018; Holm-Nielsen 5358.

***Plagiobothrys linifolius* (Willd. ex Lehm.) I.M. Johnst.**
Small mat forming herbs, flowers white to light blue-red. Humid páramo with abundance of Espeletia, 3300-3500 m. Balslev 855; Eriksen 59075; Holm-Nielsen 5293, 20993; Jørgensen 56135.

***Tournefortia fuliginosa* Kunth**
Shrub to 4 m tall, flowers greenish-white, fruits white. Hedges along the road, 3150-3300 m. Holm-Nielsen 5209.

Brassicaceae (Capparales — Dilleniidae)

***Cardamine bonariensis* Pers.**
Herb to 40 cm tall, flowers white. Cloud forest and páramo with grazed bunch grasses and bogs, 3150-3850 m. Balslev 23884; Eriksen 59005; Holm-Nielsen 5585, 5809.

***Cardamine jamesonii* Hook.**
Flowers bright lilac. Páramo, meadows and small lake area in páramo, 3750-4050 m. Holm-Nielsen 5384, 5936.

***Cremolobus peruvianus* (Lam.) DC.**
Shrub to 2 m tall, flowers white. Cloud forest and ravine in Espeletia páramo, 3150-3650 m. Holm-Nielsen 5800; Øllgaard 8413.

***Draba extensa* Wedd.**
Humid superpáramo on shallow sandy soil with rocks, 4300-4400 m. Sklenar 616.

Buddlejaceae (Scrophulariales — Asteridae)

Literature: Norman 1982

***Buddleja multiceps* Kränzl.**
Páramo del Angel, Benoist 4643 (P).

Callitrichaceae (Callitrichales — Asteridae)

***Callitriche heterophylla* Pursh**
Cushion bog with Plantago rigida and Distichia muscoides, growing in shallow water, 3850-4150 m. Eriksen 59068; Sklenar 719.

Campanulaceae (Campanulales — Asteridae)

Literature: Jeppesen 1981

***Burmeistera glabrata* (Kunth) Benth. & Hook. f.**
Scandent shrub, to 3 m, flowers green. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5590, 5854a.

***Burmeistera loejtnantii* Jeppesen**
Shrub to 1.5 m high, corolla greenish-violet outside, pure green in- side. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5838 (type), 5854.

***Centropogon chiltasonensis* Jeppesen**
Scandent shrub to 4 m long. Montane forest, 3000-3200 m. Harling & Andersson 12421 (AAU, GB).

***Centropogon dissectus* E. Wimm.**
Herb to 1.5 m tall, corolla yellow-green. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5607; Øllgaard 100005.

***Centropogon glabrifilis* (E. Wimm.) Jeppesen**
Shrub, corolla orange-red, anther tube black. Hedges along the road and steep slopes in cloud forest, 3150-3300 m. Holm-Nielsen 5237, 5608.

***Lobelia tenera* Kunth**
Rhizomatous herb to 40 cm tall, corolla pale blue, to 13 mm long. 3250 m, Asplund 17061 (K, NY, S).

***Lysipomia montioides* Kunth**
Small, branched herbs in páramo-cushions and between moss, flowers sulphur yellow. Páramo, meadows, and small lake area, 3900-4050 m. Holm-Nielsen 5943; Øllgaard 8449.

***Lysipomia muscoides* Hook. f.**
Forming small, dense cushions. Boggy depression in Espeletia páramo, dominated by cushion plants, and adjacent wet slopes, 3950-4000 m. Øllgaard 8373, 8446.

***Lysipomia sphagnophila* Griseb. ex Wedd.**
Lake shores with rocks, dominated by mosses and cushion plants in páramo, 3750-3950 m. Holm-Nielsen 5397 (type of subsp. angelensis Jeppesen); Øllgaard 8466 (subsp. variabilis McVaugh).

***Siphocampylus giganteus* (Cav.) G. Don**
Shrub to 5 m tall. Montane forest to páramo, 3200-3550 m. Holm-Nielsen 5492; Madsen 36377.

Capparidaceae (Capparidales — Dilleniidae)

***Cleome anomala* Kunth**
Shrub to 3.5 m tall, sepals bordeaux-brown, petals yellowish-green. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5589.

Caryophyllaceae (Caryophyllales — Caryophyllidae)

***Arenaria lanuginosa* (Michx.) Rohrb.**
Flowers white. Hedges along the road, 3150-3300 m. Holm-Nielsen 5225.

***Cerastium danguyi* J.F. Macbr.**
Flowers white. Páramo, bunch grasses, meadows and around small, 3000-4050 m. Balslev 844; Holm-Nielsen 5374, 5891.

***Stellaria cuspidata* Willd. ex Schltdl.**
Humid páramo with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5260.

***Stellaria recurvata* Willd. ex Schltdl.**
Boggy area in subpáramo, 3200 m. Balslev 23951.

Chloranthaceae (Piperales — Magnoliidae)

Literature: Todzia 1990

***Hedyosmum cumbalense* H. Karst.**
Tree to 8 m tall, inflorescences green. Elfin forest and páramo with shrubs, 3200-4300 m. Jørgensen 92263.

Clethraceae (Ericales — Dilleniidae)

Literature: Gustafsson 1992

***Clethra ovalifolia* Turcz.**
Shrub to 4 m tall. Montane forest, 3100-3200 m. Jaramillo 9144 (QCA).

Clusiaceae (Theales—Dilleniidae)

Literature: Robson 1987, 1990

***Clusia* sp.**
Small tree. Exposed ridge in cloud, 3200 m. Øllgaard 8292.

***Hypericum lancioides* CUATREC.**
Shrub to 60 cm. Cloud forest and boggy depressions in páramo, 3500-3800 m. Holm-Nielsen 20960, 20981; Madsen 36341; Øllgaard 8549.

***Hypericum laricifolium* JUSS.**
Shrubs to 2.5 m, flowers yellow. Páramo with abundance of Espeletia, 3400-3800 m. Balslev 23939; Holm-Nielsen 5298, 18242, 20967, 24268; Madsen 36335.

***Hypericum sprucei* N. ROBSON**
Shrub to 1 m tall, flowers yellow. Páramo with meadow and ravines, 3650-4050 m. Holm-Nielsen 5386, 5888; Øllgaard 8414, 8454.

Columelliaceae (Rosales—Rosidae)

Literature: Fagerström 1975

***Columellia oblonga* RUIZ & PAV.**
Cultivated area, 3400 m. Balslev 3662 (ssp. sericea (Kunth) Brizicky).

Coriariaceae (Ranunculales—Magnoliidae)

Literature: Skog 1987

***Coriaria ruscifolia* L.**
"shanshi"

Shrubs to 3 m tall. Cloud forest, 3150-3300 m. Holm-Nielsen 5568; Madsen 36381. All belong to C. ruscifolia ssp. microphylla (Poir.) L. E. Skog.

Crassulaceae (Rosales—Rosidae)

Literature: Bywater & Wickens 1984

***Crassula venezuelensis* (STEYERM.) M. BYWATER & WICKENS**
Creeping aquatic plant. Mossy bogs along lake, 3700-3950 m. Lægaard 101278; Øllgaard 8371.

Cunoniaceae (Rosales—Rosidae)

Literature: Harling 1999

***Weinmannia auriculifera* HIERON.**
Small tree. Bunch grass páramo and adjacent cloud forest, 3200-3350 m. Øllgaard 8325.

***Weinmannia cochensis* HIERON.**
Shrub or tree to 20 m tall. Tulcán-Maldonado rd., 3400-3500 m. Romoleroux 187 (AAU, GB).

***Weinmannia mariquitae* SZYSZYL.**
Shrub to 2 m high. Bunch grass páramo and adjacent cloud forest, 3200-3350 m. Øllgaard 8324.

***Weinmannia rollottii* KILLIP**
Shrub ca 2 m high, anthers white. Cloud forest, 3150-3250 m. Holm-Nielsen 5834.

Cuscutaceae (Solanales—Asteridae)

Literature: Austin 1982

***Cuscuta grandiflora* KUNTH**
Slender, clinging, herbaceous parasite, flowers white-brown. Hedges along the road, 3150-3300 m. Holm-Nielsen 5214.

Elaeocarpaceae (Malvales—Dilleniidae)

Literature: Jaramillo 1988

***Vallea stipularis* L.F.**
Tree 4 m tall, flowers bright pink. Bunch grass páramo and adjacent cloud forest in ravines, 3200-3500 m. Holm-Nielsen 20994; Øllgaard 8328.

Elatinaceae (Theales—Dilleniidae)

Literature: Molau 1983

***Elatine ecuadoriensis* MOLAU**
Submersed aquatic herb. Small lakes and sloping lake shores, 3750-3900 m. Holm-Nielsen 5449; Øllgaard 8468, 98084.

Ericaceae (Ericales—Dilleniidae)

Literature: Luteyn 1996

***Anthopterus wardii* BALL**
Maldonado-Tulcán road km 30, 2900-3100 m. Werling & Leth-Nissen 259 (NY).

***Cavendishia bracteata* (RUIZ & PAV. EX J. ST. HIL.) HOEROLD**
Tufiño-Maldonado rd., 3100 m, Jaramillo 9143 (AAU).

***Disterigma alaternoides* (KUNTH) NIED.**
Shrub, terrestrial or epiphytic, with hanging branches, flowers white, waxy. Steep slopes and ridges in cloud forest, 3150-3250 m. Holm-Nielsen 5584; Øllgaard 8276.

***Disterigma codonanthum* S.F. BLAKE**
Flowers brownish-green, ripe fruits white. Rocky road banks, 3200-3350 m. Øllgaard 8314.

***Disterigma empetrifolium* (KUNTH) DRUDE**
Small creeping shrubs, flowers light red, fruits red. páramo. With tussock grasses, meadows and small lakes, 3600-4050 m. Balslev 23909; Holm-Nielsen 5360, 5949; Jørgensen 92327; Øllgaard 8437.

***Gaultheria amoena* A.C. SM.**
Laguna Verde, 3910 m. Dorr & Barnett 6047 (NY, QCA).

***Gaultheria erecta* VENT.**
Southeast slope Volcán Chiles, 3292-3445 m. Jaramillo 9150 (AAU).

***Gaultheria foliolosa* BENTH.**
"takshi"

Shrubs to 50 cm tall, flowers white, fruits when ripe white. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5565.

***Gaultheria glomerata* (CAV.) SLEUMER**
Shrub to 50 cm tall, flowers red, fruits black. Cloud forest and páramo, 3150-3550 m. Balslev 891; Holm-Nielsen 5485, 5577, 20998; Madsen 36384.

***Gaultheria insipida* BENTH.**
Shrub to 1 m tall, flowers red to pink, fruits white to red. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5564; Øllgaard 8265.

***Gaultheria sclerophylla* CUATREC.**
Laguna Verde, 3910 m. Dorr & Barnett 6049 (NY, QCA, QCNE); 10 km west of Tufiño, 3850 m. Huttel 1394 (QCA); 4 km west of Tufiño, 3475 m. Luteyn 5712 (NY, QCA).

***Macleania macrantha* BENTH.**
Synonym Macleania longiflora LINDLEY

Shrub 1.5 m tall, corolla pentagonous, scarlet with pale green tip. Steep rocky road banks, 3100-3250 m. Holm-Nielsen 5569; Øllgaard 8302.

***Macleania rupestris* (KUNTH) A.C. SM.**
Shrub 3 m tall, calyx and corolla red with whitish apex. Ravines in páramo, secondary forest and pastures, 3280-3650 m. Balslev 897; Jørgensen 92250; Øllgaard 8402.

***Pernettya prostrata* (CAV.) DC.**
Shrub to 70 cm tall, berries green to red, when ripe white to bluish- blackish turgid. Cloud forest, páramo, wet meadows, 3150-4050 m. Eriksen 59090; Holm-Nielsen 5305, 5490, 5578, 5594, 5599, 5881, 20969; Jørgensen 92313; Lawesson 43932; Madsen 36357.

***Themistoclesia epiphytica* A.C. SM.**
Páramo del Angel, 3500 m. Jaramillo 10396 (AAU, NY, QCA, US).

***Thibaudia floribunda* KUNTH**
Shrub to 1.5 m high, flowers bright red with white corolla. Cloud forest with large trees and dense undergrowth, 3200 m. Øllgaard 8291.

Vaccinium *floribundum* KUNTH
Shrub to 2 m tall, flowers white to pink, fruits black. Roadside and páramo with bunch grasses and shrubs, 3270-3550 m. Balslev 869A; Holm-Nielsen 5322, 5490, 5490-a, 20997, 23946; Madsen 36354; Jørgensen 56130, 92240.

Fabaceae (Fabales—Rosidae)

Literature: Grimes 1990

***Dalea coerulea* (L.f.) Schinz & Thell.**

Shrub to 1 m tall, flowers dark blue. Hedges along the road, 3150-3300 m. Holm-Nielsen 5231.

***Lathyrus magellanicus* Lam.**

Solitary in Carex-tufts, flowers bright blue. Humid páramo with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5325.

***Lupinus pubescens* Benth.**

Shrub 1.5 m tall, flowers blue, median part of standard white. Very humid páramo, 3450-3550 m. Holm-Nielsen 5491.

***Lupinus tauris* Benth.**

Flowers lilac with a white spot on the claw. Espeletia-páramo, 3800-3850 m. Eriksen 59058.

***Otholobium brachystachium* (Spruce ex Diels) J.W. Grimes**

Flowers light blue, at the base almost white. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5814.

***Otholobium mexicanum* (L.f.) J.W. Grimes**

Synonym Psoralea mexicana (L. f.) Vail

Shrub 1 m tall, flowers dark blue. Hedges along the road, 3150-3300 m. Holm-Nielsen 5216.

***Trifolium amabile* Kunth**

Lower parts woody, flowers white, sepals at the base red-brown. Hedges along the road, 3150-3300 m. Holm-Nielsen 5222.

***Trifolium dubium* Sibth.**

Flowers yellow. Humid páramo with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5313.

***Vicia andicola* Kunth**

Scandent in grass, flowers light violet. Shrub páramo and hedges along the road, 3150-3350 m. Balslev 867; Holm-Nielsen 5218.

Gentianaceae (Gentianales—Asteridae)

Literature: Pringle 1995

***Gentiana sedifolia* Kunth**

Small herb, flowers pale blue with black scales in the throat. In páramo with bunch grasses, boggy depressions, and cushion plants, 3200-4050 m. Balslev 23956; Eriksen 59049; Holm-Nielsen 5303, 5886; Madsen 36348; Øllgaard 8442, 57203.

***Gentianella cerastioides* (Kunth) Fabris**

Herbs with blue to violet flowers. Growing in páramo with lakes and elfin forest in protcted places, 3500-4050 m. Holm-Nielsen 5955, 22864.

***Gentianella nevadensis* (Gilg) Weaver & Rüdenberg**

18 km west of Tulcán, 3300 m. Hitchcock 20933 (GH); Páramo del Angel, 37 km west of Tulcán, 3700 m. Bohlin & Bohlin 558 (GB).

***Gentianella nummulariifolia* (Griseb.) Fabris**

Herb growing in wet depressions in páramo with cushion plants, 4100 m. Sklenar 1403.

***Gentianella rapunculoides* (Willd. ex Schult.) J.S. Pringle**

Herb with blue to lilac flowers. Growing cloud forest and humid depressions in the páramo, 3150-3850 m. Balslev 23943; Eriksen 59088; Holm-Nielsen 5292, 5314, 5794, 20954.

***Gentianella selaginifolia* (Griseb.) Fabris**

Erect herb, flowers white-lilac with purple rays. Growing in cushion- vegetation in very wet páramo, 3800-4250 m. Eriksen 59009; Holm-Nielsen 5884; Sklenar 683, 1410; Øllgaard 8441, 98086.

***Halenia kalbreyeri* Gilg**

Páramo del Angel, 4000 m. Bohlin & Bohlin 572 (GB); Laguna Verde, Dorr & Barnett 6064 (HAM, NY, QCA); S slopes Volcán Chiles, 4100 m. Ramsay & Meerow-Smith 892 (QCA).

***Halenia weddelliana* Gilg**

Herb, flowers yellow with 5 spurs. Wet páramos, along roads and in boggy areas, 3200-3850 m. Balslev 858, 23941; Eriksen 59052; Holm-Nielsen 5323, 22868; Jørgensen 92283; Madsen 36327, 36333.

Geraniaceae (Geraniales—Rosidae)

Literature: Halfdan-Nielsen 1995, 1996

***Geranium angelense* Halfdan-Nielsen**

Herb forming loose mats. Near Lagunas Verdes, 3960-4000 m. Halfdan-Nielsen 21 (AAU, C holotype, QCA, QCNE).

***Geranium chilloense* Willd. ex Kunth**

Scrambling herb to 2 m long. Páramo del Angel, 3320 m. Halfdan-Nielsen 10 (C, QCA).

***Geranium laxicaule* R. Knuth**

Scrambling herb to 2 m long, inflorescence 1-flowered. Páramo del Angel, 3075 m. Halfdan-Nielsen 8 (AAU, C).

***Geranium maniculatum* H.E. Moore**

Tufted herbs with white to purple flowers. Growing in páramo with bogggy depressions dominated by cushions plants and adjacent wet slopes, 3800-4050 m. Eriksen 59045A; Holm-Nielsen 5937; Øllgaard 8447.

***Geranium multipartitum* Benth.**

Perennial, matforming herb to 30 cm across. Páramo del Angel, 3400-3600 m. Heinrichs s.n. (B holotype of Geranium heinrichsae R. Knuth).

***Geranium reptans* R. Knuth**

Cushion plant, flowers white to light lilac, veins on petals dark lilac. Growing near the lower border of the páramo, 3400-3600 m. Holm-Nielsen 18240; Madsen 36337.

***Geranium sibbaldioides* Benth.**

Tufted herbs with flowers white to light red. Growing in very humid páramo with small lakes and sloping shores with rocks and boulders, 3600-3950 m. Balslev 3648; Eriksen 59045; Holm-Nielsen 5422, 18229, 18256; Øllgaard 8377, 98094.

***Geranium stramineum* Triana & Planch.**

Flowers white. Growing in moss cushions in Espeletia páramo, 3600-3700 m. Holm-Nielsen 18228; Øllgaard 98088.

Gesneriaceae (Scrophulariales—Asteridae)

Literature: Kvist & Skog 1993, Skog & Kvist 1997

***Columnea strigosa* Benth.**

Scandent shrub, peduncle red, sepals yellow-green, petals orange. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5593.

Grossulariaceae (Rosales—Rosidae)

***Escallonia myrtilloides* L.f.**

Small compact tree in the forest. Bunch grass páramo with shrubs and Espeletia and adjacent cloud forest in ravines, 3200-3350 m. Øllgaard 8321.

***Ribes hirtum* Willd. ex Roem. & Schult.**

Shrub to 2 m tall, flowers bright red. Growing in fog forest, very humid páramo, and at the roadside on rather dry places, 3750-4050 m. Eriksen 59030; Holm-Nielsen 5350, 5894.

Gunneraceae (Haloragales—Rosidae)

***Gunnera magellanica* Lam.**

Small creeping, dioecious herb, flowers reddish tinged. Growing in wet páramo with meadows and small lakes, 3740-4050 m. Holm-Nielsen 5346, 5940; Øllgaard 8526.

Haloragaceae (Haloragales—Rosidae)

***Myriophyllum quitense* Kunth**

In small páramo river with rapidly flowing water, 3300 m. Balslev 843.

Lamiaceae (Lamiales—Asteridae)

***Clinopodium nubigenum* (Kunth) Kuntze**

Synonym Satureja nubigena (Kunth) Briq.

Small, prostrate herb with white to purple flowers. In páramo, among grasses and on rocks and on road banks, 3300-4050 m. Balslev 835; Holm-Nielsen 5511, 5883, 24265; Jørgensen 92329.

***Lepechinia* sp.**

Shrub to 3 m tall, flowers white. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5804.

***Stachys* sp.**

Flowers light red-lilac with white ornaments. Growing in very humid páramo with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5294.

Lentibulariaceae (Scrophulariales—Asteridae)

Literature: Taylor 1975

Pinguicula calyptrata KUNTH
Flowers light blue. or violet with white stripes. Growing on open soil and in bogs in Espeletia páramo or on land slides in bunch grass páramo, 3700-4050 m. Balslev 23921; Holm-Nielsen 5394, 5946; Øllgaard 98098.

Loasaceae (Violales—Dilleniidae)

Literature: Weigend 1996

Nasa grandiflora (DESR.) WEIGEND
Synonym Loasa grandiflora DESR.

Herb to 2 m tall, with stinging hairs, creeping, flowers orange. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5836.

Loranthaceae (Santalales—Rosidae)

Literature: Kuijt 1986a

Gaiadendron punctatum (RUIZ & PAV.) G. DON
Synonym Gaiadendron lanceolatum (RUIZ & PAV.) BAEHNI EX J. F. MACBR.

Tree to 5 m tall, flowers bright yellow. Exposed ridge in cloud forest with large trees and dense undergrowth, 3200-3650 m. Øllgaard 8299, 8399.

Tristerix longebractatus (DESR.) BARLOW & WIENS
Green leaved hemiparasite with 4-5 cm long bright red flowers. On Gynoxis in páramo, Asplund 17002 (NY, S).

Melastomataceae (Myrtales—Rosidae)

Literature: Wurdack 1980

Brachyotum ledifolium (DESR.) TRIANA
Shrub to 2 m tall, hypanthium red, corolla yellow. 3250-3800 m. Balslev 866; Holm-Nielsen 20966; Jørgensen 56129, 92238, 92331; Madsen 36356.

Brachyotum lindenii COGN.
Synonym Brachyotum rivetii DANGUY & CHERMEZON

Shrub, 1-2 m tall, hypanthium and sepals red, petals black. 3350-3800 m. Balslev 865, 898; Holm-Nielsen 5283, 5345, 18258, 20968; Jørgensen 92284, 92317; Øllgaard 8417.

Meriania maxima MARKGR.
Western slopes of Volcán Chiles, 3000 m. Steere 8098 (F, US).

Miconia bracteolata (BONPL.) DC.
Shrub, 12-15 m. tall, flowers white. 3500 m. Holm-Nielsen 20996.

Miconia chionophila NAUDIN
Small creeping shrub, less than 10 cm tall, flowers white, berries violet. Espeletia páramo, 3600-3950 m. Eriksen 59037; Holm-Nielsen 5361, 20948; Lægaard 54932; Øllgaard 8372, 98512.

Miconia crinita NAUDIN
Tulcán-Maldonado, 3100 m. Harling & Andersson 12402 (GB, ssp. australis Wurdack).

Miconia idiogena WURDACK
Tulcán-Maldonado, 2900-3100 m. Harling & Andeersson 12403 (GB holotype, US).

Miconia latifolia (D. DON) NAUDIN
Sepals and inflorescence reddish, petals white. 3750-3850 m. Eriksen 59026; Holm-Nielsen 5377.

Miconia ligustrina (SM.) TRIANA
Small densely branched tree, to 5 m tall, flowers white, abundant. 3600-3650 m. Lægaard 54964; Øllgaard 8419.

Miconia ochracea TRIANA
Above Tufiño, 3500 m Asplund 17104 (NY, S, US).

Miconia papillosa (DESR.) NAUDIN
Shrub about 2 m tall, flowers white. 3150-3300 m. Holm-Nielsen 5228.

Miconia salicifolia (BONPL. EX NAUDIN) NAUDIN
Shrub to 4 m tall, buds white, petals pink, fruits red-green. 3400-3900 m. Balslev 3661; Holm-Nielsen 18251; Jørgensen 61544, 92282.

Miconia tinifolia NAUDIN
Volcán Chiles, 3300-3400 m. Camp E325 (NY, US); Páramo del Angel, 4100 m, Rauh E236 (NY).

Tibouchina mollis (BONPL.) COGN.
Shrub to 2.5 m tall, flowers light lilac. Fog forest, 3150-3350 m. Holm-Nielsen 5552; Øllgaard 8322.

Monimiaceae (Laurales—Magnoliidae)

Literature: Renner & Hausner 1997

Siparuna echinata (KUNTH) A. DC.
Road Tulcán-Maldonado, 3200 m. Harling & Andersson 12406 (AAU, GB).

Myrsinaceae (Primulales—Dilleniidae)

Geissanthus quindiensis MEZ
Small tree. Cloud forest, 3200 m. Øllgaard 8279.

Myrsine sp.
Tree 8 m tall, fruits green. 3460 m. Jørgensen 92272.

Myrtaceae (Myrtales—Rosidae)

Literature: Landrum 1988

Myrteola nummularia (POIR.) O. BERG
Creeping dwarf shrub, flowers pink-red, fruits red. 3600-3850 m. Balslev 3659; Eriksen 59033; Jørgensen 92326.

Nyctaginaceae (Caryophyllales—Caryophyllidae)

Literature: Bohlin 1988

Colignonia parviflora (KUNTH) CHOISY
Subshrub to 4 m tall. 2200-3100 m. Hitchcock 20943 (F, GH, NY, US).

Colignonia rufopilosa KUNTZE
Procumbent subshrubs to 12 m tall, bracts white. 3150-3250 m.; Holm-Nielsen 5559.

Onagraceae (Myrtales—Rosidae)

Literature: Berry 1982, Munz 1974

Epilobium denticulatum RUIZ & PAV.
Synonym Epilobium meridense HAUSSKN.

Small herbs, flowers white to violet-red, capsules red, brown or violet. Humid páramos with Espeletia and small streams, 3150-3500 m. Holm-Nielsen 5275, 5276, 5289, 5570, 20980; Madsen 36382.

Fuchsia cinerea P.E. BERRY
Just east of Tufiño, 3210 m. P. E. Berry 3147 (MO holotype, QCA isotype).

Fuchsia corollata BENTH.
Shrub to 1 m tall, flowers dark red. 3150-3250 m. Holm-Nielsen 5580.

Fuchsia dependens HOOK.
Shrub 3 m tall, ovary green and red, calyx tube, sepals and petals red, anthers green, stigma red. 3075 m. Jørgensen 56122.

Fuchsia loxensis KUNTH
Páramo del Angel, Benoist 3637 (P).

Fuchsia polyantha KILLIP EX MUNZ
Tulcán-Maldonado road, 2200-3300 m. Berry 3152 (MO, QCA); Gentry & Schupp 26321 (MO).

Fuchsia sessilifolia BENTH.
Tulcán-Maldonado road km 57, Boeke 828 (MO).

Fuchsia vulcanica ANDRÉ
Shrub 2-3 m tall, flowers pendulous, red. 3650-3850 m. Eriksen 59017; Øllgaard 8398 (specimens from Carchi cited as F. ayavacensis in Flora Ecuador, belong here).

Oenothera multicaulis RUIZ & PAV.
Flowers dark red at the base, orange to yellow at the apex. Páramo, 3450-3500 m. Holm-Nielsen 5256.

Oxalidaceae (Geraniales—Rosidae)

Oxalis filiformis KUNTH
Herb, 5 cm tall, sepals light green, petals yellow with short red veins. 3400 m. Madsen 36361.

Oxalis integra R. KNUTH
Twining shoots two meters long, flowers yellow, with red hairs on the outer side. 3150-3250 m. Holm-Nielsen 5845.

Oxalis mollis KUNTH
Scandent herb, several meters long, flowers yellow with red veins. 3150-3250 Holm-Nielsen 5639.

Passifloraceae (Violales—Dilleniidae)

Literature: Holm-Nielsen et al 1988

***Passiflora alnifolia* Kunth**

Vine, petals white, corona biseriate. Shrub páramo, 3150-3300 m. Jørgensen 56137, 56138.

***Passiflora cumbalensis* (H. Karst.) Harms**

Flower tube dark lilac, corona 1-seriate, white teeth less than 1 mm. Cloud forest, 3150-3300 m. Holm-Nielsen 5582, 6260.

***Passiflora mixta* L.f.**

Liana, flower tube green, sepals green to red outside, inside light red, corona teeth white, less than 1 mm in a dark violet ring. Montane forest and living fences along roads, 3075-3300 m. Jørgensen 56112; Madsen 36370; Holm-Nielsen 5238, 5239, 5240, 5241, 5242.

Phytolaccaceae (Caryophyllales—Caryophyllidae)

Literature: Eliasson 1993

***Phytolacca bogotensis* Kunth**

Herb to 75 cm tall, inflorescence reddish violet, bracts 8-12 mm. 3075 m. Jørgensen 56118.

***Phytolacca sanguinea* H. Walter**

Creeping herb with ascending shoots, flowers violet, bracts 2-3 mm. Cloud forest, 3150-3250 m. Holm-Nielsen 5637.

Piperaceae (Piperales—Magnoliidae)

***Peperomia hartwegiana* Miq.**

Epiphyte. In cloud forest in shade, 3450-3650 m. Holm-Nielsen 5274; Øllgaard 8421.

***Peperomia hispidula* (Sw.) A. Dietr.**

Tiny epiphytic herb, leaves reniform. In cloud forest, 3450-3500 m. Holm-Nielsen 5279.

***Peperomia microphylla* Kunth**

Small, succulent, terrestrial or epiphytic herb with verticillate leaves. On rocky slopes and trees in cloud forest, 3150-3250 m. Holm-Nielsen 5586, 5662, 5666.

***Peperomia parasitica* C. DC.**

Epiphyte, spike reddish tinged, leaf under-surfaces whitish. 3150-3250 m. Holm-Nielsen 5665, 5799, 5806.

***Peperomia rotundata* Kunth**

Succulent herb, terrestrial or epiphytic. On rocky slopes and trees in cloud forest, 3150-3250 m. Holm-Nielsen 5576, 5667.

***Piper rugulosum* C. DC.**

Shrub to 2 m tall, inflorescence green. Shrub páramo, 3250-3300 m. Jørgensen 56134.

Plantaginaceae (Plantaginales—Asteridae)

Literature: Rahn 1975

***Plantago australis* Lam.**

In very humid parts of *Espeletia*-páramo, on top of tufts and in bogs, 3200-3500 m. Balslev 23955; Holm-Nielsen 5285, 5296, 5304.

***Plantago linearis* Kunth**

Among bunchgrasses in very humid parts of Espeletia-páramo, 3300-3500 m. Balslev 851; Holm-Nielsen 5287.

***Plantago rigida* Kunth**

Forming cushious. Wet páramo vegetation, 3300 m. Balslev 852.

Polygalaceae (Polygalales—Rosidae)

Literature: Ferreyra 1953

***Monnina crassifolia* (Bonpl.) Kunth**

Shrubs to 1.5 m tall, flowers blue, fruit rufescent. Growing in Espeletia-páramo, 3450-3850 m. Holm-Nielsen 5286, 5297, 5379; Øllgaard 8416.

***Monnina revoluta* Kunth**

Shrub 2 m tall. 3350 m. Balslev 864.

Polygonaceae (Polygonales—Caryophyllidae)

Literature: Brandbyge 1989

***Muehlenbeckia tamnifolia* (Kunth) Meisn.**

Vine. In cloud forest, 3150-3250 m. Holm-Nielsen 5683.

***Muehlenbeckia volcanica* (Benth.) Endl.**

Matforming herb. Disturbed soil in páramo, 3300-4000 m. Balslev 23888.

***Rumex acetosella* L.**

Small weedy herb to 40 cm tall. Disturbed soil and roadsides, 3300-3400 m, Balslev 23862, Madsen 36343.

***Rumex obtusifolius* L.**

"lengua de vaca"

Weedy herb to 150 cm tall. Páramo, 3750 m, Mena 60 (GH, QCA).

Portulacaceae (Caryophyllales—Caryophyllidae)

Literature: Eliasson 1996, Lourteig 1991

***Calandrina ciliata* (Ruiz & Pav.) DC.**

19 km west of Tulcán, 3300 m. Hitchcock 20936 (US).

***Montia fontana* L.**

Covering the ground near a stream, flowers white. With Callitriche in small ponds in cloud forest and páramo, 3150-4050 m. Eriksen 59069; Holm-Nielsen 5853, 5896.

Ranunculaceae (Ranunculales—Magnoliidae)

Literature: Lourteig 1956

***Ranunculus flagelliformis* Sm.**

Herb, creeping at lake shore, 3750-3850 m. Holm-Nielsen 5392.

***Ranunculus geranioides* Kunth ex DC.**

Herb, flowers white-lilac. Growing in dense tufts in páramo meadow, 3900-4050 m. Holm-Nielsen 5889.

***Ranunculus gusmanii* Humb. ex Caldas**

Synonyms Krapfia gusmanii (Humb. ex Caldas) Standl. & J.F. Macbr., Rhopalopodium gusmanii (Humb. ex Caldas) O.E. Ulbr.

Erect herb, flowers 3-5 cm in diameter, petals orange-red. In grass páramo. 3900-4050 m. Balslev 4433; Holm-Nielsen 5954; Lægaard 101685; Øllgaard 8338.

***Ranunculus limoselloides* Turcz.**

Aquatic, leaves leaves floating, flowers yellow. 3800-3850 m. Eriksen 59053.

***Ranunculus peruvianus* Pers.**

Erect herb to 50 cm tall, flowers bright yellow. Wet Espeletia-páramo and cushion plant vegetation, 3280-4050 m. Holm-Nielsen 5378, 5935, 21000; Jørgensen 92259; Madsen 36359; Øllgaard 8532.

***Ranunculus praemorsus* Kunth ex DC.**

Growing in humid place in the páramo, 3450-3500 m. Holm-Nielsen 5270.

Rosaceae (Rosales—Rosidae)

Literature: Romoleroux 1996

***Acaena elongata* L.**

Shrub to 1 m tall. 3700 m. Balslev 23931.

***Acaena ovalifolia* Ruiz & Pav.**

Páramo del Angel, 3400 m. Sparre 14240 (S).

***Geum peruvianum* Focke**

Páramo del Angel, 3400 m. Sparre 14235 (AAU, S).

***Hesperomeles ferruginea* (Pers.) Benth.**

Tulcán-Tufiño, 3600-3900 m. Romoleroux 172 (AAU, QCA).

***Hesperomeles obtusifolia* (Pers.) Lindl.**

Shrubs to 3 m tall, with branch spines. In cloud forest, 3500-3850 m. Holm-Nielsen 5404; Lægaard 54909; Øllgaard 8401.

***Lachemilla andina* (L.M. Perry) Rothm.**

El Angel-Tulcán, 3400 m. Romoleroux 1020 (AAU, QCA).

***Lachemilla aphanoides* (Mutis ex L.f.) Rothm.**

Extended on the soil surface. Cloud forest and road sides, 3150-3250 m. Holm-Nielsen 5797; Lægaard 101705.

***Lachemilla fulvescens* (L.M. Perry) Rothm.**

On bare soil in bottom of ravines in páramo, 3650-3800 m. Lægaard 101675; Øllgaard 8408.

***Lachemilla galioides* (Benth.) Rothm.**

Espeletia páramo, 3650-3700 m. Brandbyge 60913.

***Lachemilla hispidula* (L.M. Perry) Rothm.**

In seeping water in moist páramo, 3700-3850 m. Balslev 23910; Eriksen 59056; Lægaard 101668, 101671.

***Lachemilla holosericea* (L.M. Perry) Rothm.**

Cushion forming, creeping. On disturbed ground along road, 3950-3980 m. Lægaard 101683; Øllgaard 8344.

***Lachemilla nivalis* (Kunth) Rothm.**
Herb, flowers yellow-green, inside red. In grass vegetation in páramo meadow, 3500-4050 m. Holm-Nielsen 5381, 5887, 18239, 20955, 22865; Lægaard 54918, 54931, 101263, 101267, 101670, 101682, 101684; Øllgaard 8376, 8439, 8440, 8533.

***Lachemilla orbiculata* (Ruiz & Pav.) Rydb.**
In humid Espeletia-páramo, 3450-3500 m. Holm-Nielsen 5312.

***Lachemilla paludicola* (Rothm.) Rothm.**
Mat-forming, more or less submerged. Sandy lake shore, Sphagnum swamps, and seeping water in páramos, 3475-3980 m. Eriksen 59061; Lægaard 101274A, 101320, 101669, 101696.

***Lachemilla pectinata* (Kunth) Rothm.**
Creeping herbs. Open humid soil in páramo, 3750-3850 m. Holm-Nielsen 5433A.

***Lachemilla tanacetifolia* Rothm.**
12 km west of Tufiño, 3900 m. Freire & Andersen s.n. (QCA, QCNE); south slopes Volcán Chiles, 4000 m. Ramsey & Merrow-Smith 884 (K, QCA).

***Lachemilla uniflora* Maguire**
On open places in Espeletia-páramo and cattle trails, 3600-3850 m. Balslev 3649; Holm-Nielsen 5365, 18234; Lægaard 54920B, 101268, 101269.

***Polylepis incana* Kunth**
Tree 5 m tall, leaves with three leaflets. 3050-3600 m. Lægaard 53120, 54985, 54989.

***Polylepis pauta* Hieron.**
Tree 5 m tall with pinnate leaves, dominating tree in the forest together with Gynoxys, 3850-4000 m. Eriksen 59086; Lægaard 54965, 54967A,B,C.

***Polylepis sericea* Wedd.**
Tree 6-7 m tall tree with leaves silvery white below. Forest, 3800-4000 m. Lægaard 54966, 54967D,E, 101661.

***Rubus adenotrichos* Schltdl.**
Scrambling, 2-3 m tall, stems and petioles strongly viscous from glands, leaves almost same colour on both sides. 3200-3250 m. Lægaard 54908, 101650.

***Rubus boliviensis* Focke**
Scrambling, 2-3 m tall. 3050-3250 m. Lægaard 54988, 101654.

***Rubus coriaceus* Poir.**
Shrub, scarambling, to 2 m tall, flowers red. In margin of cloud forest or in rather dry places in grass-páramo, 3500-4050 m. Eriksen 59031; Holm-Nielsen 5424, 5948; Lawesson 43928; Lægaard 54923, 101665.

***Rubus floribundus* Kunth**
Scrambling, 2-3 m tall. Hedges along road, 3200-3250 m. Lægaard 101649.

***Rubus glabratus* Kunth**
Dry shrubby slopes and Espeletia páramo, 3450-3800 m. Lægaard 54947, 101666.

***Rubus glaucus* Benth.**
Scrambling, 2-3 m tall, stem glaucous waxed or reddish pruinous, flowers white. 3200-3450 m. Lægaard 54906, 54957, 101652.

***Rubus nubigenus* Kunth**
Scandent shrub with several m long shoots hanging in the vegetation. Flowers red to purple to dark rosa, fruits black. Growing in forest, 3150-3850 m. Eriksen 59076; Holm-Nielsen 5848; Lawesson 43925; Lægaard 54952, 101651; Madsen 36378; Øllgaard 8426.

***Rubus roseus* Poir.**
Scrambling to about 1 m, 3200-3250 m. Lægaard 101653.

Rubiaceae (Rubiales—Asteridae)

Literature: Andersson 1992, 1993, Andersson & Taylor 1994, Dempster 1993, Mena 1990

***Arcytophyllum aristatum* Standl.**
Mat-forming on rocks, flowers white inside, violet tinged outside. 3950 m. Holm-Nielsen 5432; Øllgaard 8368.

***Arcytophyllum capitatum* (Benth.) K. Schum.**
Low shrub, flowers white inside. In edge of forest, 3200-3350 m. Øllgaard 8320.

***Galium aparine* L.**
Tufiño, 3200 m. Wiggins 10642 (F).

***Galium canescens* Kunth**
Tulcán, 3250 m, Asplund 17065 (S).

***Galium corymbosum* Ruiz & Pav.**
Tufiño, 3200 m, Steere 8030 (F, US).

***Galium hypocarpium* (L.) Endl. ex Griseb.**
Climbing herb, fruits orange. Ridges in cloud forest, 3200 m. Øllgaard 8282.

***Galium pseudotriflorum* Dempster & Ehrend.**
Tufiño, 3200 m. Steere 8028 (F, NY, US).

***Hedyotis* sp.**
Small herb. In hedges along the road, 3150-3300 m. Holm-Nielsen 5233.

***Manettia recurva* Sprague**
Vine, flowers white. Cloud forest, 3150-3250 m.; Holm-Nielsen 5801.

***Nertera granadensis* (Mutis ex L.f.) Druce**
Creeping herbs, fruits red. In very wet Espeletia- páramo, 3450-3850 m. Eriksen 59032; Holm-Nielsen 5284.

***Palicourea amethystina* (Ruiz & Pav.) DC.**
Shrub to 2 m, flowers bright blue to blackish-green, peduncle bordeaux. Cloud forest, 3150-3250 m. Holm-Nielsen 5606.

***Palicourea heterochroma* K. Schum. & K. Krause**
Synonym Palicourea bryophila Standl.

Shrub 1.5 m tall, peduncles bright purple, flowers bright blue. Cloud forest, 3200 m. Øllgaard 8281.

Scrophulariaceae (Scrophulariales—Asteridae)

Literature: Holmgren & Molau 1984

***Alonsoa meridionalis* (L.f.) Kuntze**
Herb 1 m tall, corolla white, inside with a violet throath. 3075 m. Jørgensen 56124.

***Bartsia inaequalis* Benth.**
Flowers dark red. Growing on steep rocky slopes, 3150-3250 m.; Holm-Nielsen 5588 (incorrectly cited as 5533 in Fl. Ecuador).

***Bartsia laticrenata* Benth.**
Erect herbs, bracts dull purple, corolla greenish-yellow. In grass-vegetation along road in the páramo, 3700-4050 m. Balslev 23922; Eriksen 59013; Holm-Nielsen 5897 Øllgaard 8366.

***Bartsia orthocarpiflora* Benth.**
Herb 20-40 cm tall, whole plant, especially in the top, reddish-tinged, flowers bluish-red to light lilac. In humid parts and stream sides in Espeletia-páramo, 3400-3850 m. Holm-Nielsen 5291, 5357, 20976; Lawesson 43935.

***Bartsia pedicularoides* Benth.**
Herb to 20 cm tall, with erect flowering stems and decumbent sterile stems. Páramo meadows, 3000-4200 m. Sparre 14150 (S).

***Bartsia stricta* (Kunth) Benth.**
Herb to 20 cm tall, Wet páramo, 3400 m. Madsen 36338 (collection mixed with B. orthocarpiflora).

***Calceolaria crenata* Lam.**
Herb, to 120 cm tall, corolla yellow. Forest, road sides, 3200-3300 m. Madsen 36374.

***Calceolaria lamiifolia* Kunth**
Herb 0.5 m, corolla yellow. Shrub páramo, 3250-3300 m. Jørgensen 56133.

***Calceolaria mexicana* Benth.**
Annual herb, flowers light yellow, leaves deeply pinnatifid. Along small stream, 3150-3250 m. Holm-Nielsen 5572.

***Calceolaria microbefaria* Kränzl.**
Small shrubs, flowers light yellow. Hanging from steep rocky slopes, 3150-3250 m.; Holm-Nielsen 5574 (ssp. fruticosa (Pennell) Molau).

***Calceolaria pedunculata* Molau**
Shrub to 0.8 m tall, flowers light yellow. Along road and on steep rocky slopes, 3100-3250 m. Holm-Nielsen 5581, 5597; Øllgaard 8309 (all are ssp. pedunculata).

***Calceolaria penlandii* Pennell**
Liana, flowers yellow, stamens light brown. On steep rocky slopes, 3750-3850 m. Eriksen 59027, 59084; Holm-Nielsen 5430.

***Calceolaria perfoliata* L.f.**
Scandent, shoots to 2.5 m long, flowers bright yellow. Hanging in the vegetation on rocky slopes, 3150-3250 m. Holm-Nielsen 5575.

Calceolaria trilobata HEMSL.
Herb 2 m tall. Espeletia-páramo, 3450-3550 m. Holm-Nielsen 5487.

Castilleja fissifolia L.F.
Herb 20-50 cm tall, lower parts somewhat ligneous, bracts bright red, corolla green Growing between Festuca-tufts and in cushions of other plants, 3150-4000 m. Balslev 23889; Holm-Nielsen 5416, 5551, 20951, 22857; Jørgensen 92296A; Madsen 36352; Øllgaard 8459, 8553, 98079.

Castilleja pumila (BENTH.) WEDD.
Prostrate herb to 9 cm long. Moist meadows, 3000-4200 m. Benoist 4638 (P).

Castilleja virgata (WEDD.) EDWIN
Boggy sub-páramo, 3200-3200 m. Balslev 23937.

Lamourouxia virgata KUNTH
Herb or subshrub to 1 m tall, flowers magenta to violet. Cloud forest road sides, 3200-3300 m. Holm-Nielsen 6259; Madsen 36371.

Limosella aquatica L.
10 cm high herb with spathulate leaves in rosette. Páramo, 3200 m. Lægaard 54907.

Mimulus glabratus KUNTH
Herb, flowers yellow, with brown spots in the throat. In oozing water in Espeletia-páramo, 3450-3500 m. Holm-Nielsen 5319.

Ourisia chamaedrifolia BENTH.
Creeping herb, flowers red, 6-12 mm. On roadbanks and in grass-páramo, 3800-4050 m. Eriksen 59039; Holm-Nielsen 5945; Øllgaard 8340.

Ourisia muscosa BENTH.
Matforming herb, flowers white with yellow throat, 2-3 mm long. Rocky super páramo, 4500 m. Sklenar 1889.

Sibthorpia repens (L.) KUNTZE
Tiny, creeping herb, flowers dark dull purple. On humid soil in Espeletia-páramo in shade, 3200-3850 m. Eriksen 59046; Holm-Nielsen 5423; Øllgaard 8316.

Veronica arvensis L.
Annual herb to 20 cm tall. Weed in open places above 3000 m. Holmgren & Holmgren (NY, QCA).

Veronica serpyllifolia L.
Herb to 50 cm tall, flowers blue-white. In very humid Espeletia-páramo, 3400-3500 m. Holm-Nielsen 5295; Madsen 36344.

Solanaceae (Solanales—Asteridae)

Literature: Knapp 1989

Brugmansia sanguinea (RUIZ & PAV.) D. DON
Shrub, 3-5 m tall. Hedges along road, 3150-3300 m. Holm-Nielsen 5215; Jaramillo 10413 (AAU).

Salpichroa diffusa MIERS
Páramo and mountain forest with Gynoxis and Polylepis, 3850 m. Eriksen 59097.

Saracha quitensis (HOOK.) MIERS
Synonym Acnistus quitensis (HOOK.) HUNZ.

Shrub, flowers brown on outside and green-yellow on inside. Woody ravine in Espeletia páramo, 3650 m. Øllgaard 8420.

Solanum aureum DUNAL
Shrub, hanging, more than 2 m long, flowers light blue, ripe berries black. Hedges along road, 3150-3300 m. Holm-Nielsen 5207.

Solanum brevifolium DUNAL
Climbing shrub, leaves below with lilac veins, flowers white with lilac veins externally, fruits red. In hedges along road and on vertical rockwalls in cloud forest, 3150-3300 m. Holm-Nielsen 5208, 5563.

Solanum macrotonum BITTER
Shrub to 1.5 m tall, flowers white, bluish tinged. Hedges along road and steep slopes in cloud forest, 3150-3300 m. Holm-Nielsen 5212, 5831.

Solanum ochranthum DUNAL
Shrub 2-3 m tall, petals yellow. 3075 m. Jørgensen 56119.

Solanum stenophyllum DUNAL
Shrub 2-3 m tall, flowers lilac. Shrub páramo with Espeletia, 3350-3850 m. Balslev 859; Eriksen 59019.

Solanum venosum DUNAL
Shrub to 2.5 m tall, flowers white. Hedges along road, 3150-3300 m. Holm-Nielsen 5219.

Theaceae (Theales—Dilleniidae)

Freziera canescens BONPL.
Large tree, flowers pale reddish-white, apparently not opening. Cloud forest, 3150-3250 m. Holm-Nielsen 5832; Øllgaard 8273.

Tropaeolaceae (Geraniales—Rosidae)

Literature: Sparre 1973, Sparre & Andersson 1991

Tropaeolum tuberosum RUIZ & PAV.
Roadbank in shrubby sub-páramo, 3200 m. Balslev 23945.

Urticaceae (Urticales—Hamamelidae)

Pilea sp.
Herb to 40 cm, stems and flowers red. Shrub páramo, 3250-3300 m. Jørgensen 56136.

Urtica dioica L.
Herb 0.5 m, inflorescence green. Secondary forest and pastures, 3280-3400 m. Jørgensen 92254.

Urtica urens L.
Herb 0.5 m tall. Weedy in Espeletia-páramo, 3850 m. Eriksen 59085.

Valerianaceae (Dipsacales—Asteridae)

Literature: Eriksen 1989

Valeriana bracteata BENTH.
Herbaceous rosette-plants with mucus between leaves, flowers white to purple. In humid depressions between cushion plants in the páramo, 3600-4050 m. Eriksen 59024; Holm-Nielsen 5953; Jørgensen 92302; Lægaard 54928; Sklenar 690; Øllgaard 8369, 8438.

Valeriana clematitis KUNTH
Scandent shrub to several m long. Montane forest 3200-3300 m. Harling & Andersson 12188 (GB).

Valeriana laurifolia KUNTH
Scandent subshrub to 3 m tall, flowers greenish. In forest, 3450-3850 m. Eriksen 59067; Lægaard 54946.

Valeriana microphylla KUNTH
Shrub to 2 m tall, flowers white, tinged with purple. In grass- and shrub-páramo, 3350-4050 m. Eriksen 59021, 59025; Holm-Nielsen 5448, 5494, 5934, 18255, 20942; Jørgensen 56147, 92296; Lægaard 53122; Madsen 36353; Øllgaard 8361, 8362.

Valeriana pilosa RUIZ & PAV.
Herb 10-50 cm tall, crowded in small groups, flowers white, tinged with purple. Espeletia-páramo between grass tussocks, 3400-3850 m. Eriksen 59023; Holm-Nielsen 5372, 22854; Lawesson 43930, 43931; Madsen 36342; Sklenar 1416; Øllgaard 8530.

Valeriana plantaginea KUNTH
Herb to 125 cm tall, flowers white, tinged with purple, leaves in basal rossette. Along rivulets and in Gynoxys forest, 3800-3850 m. Eriksen 59022.

Valeriana rumicoides WEDD.
Herb to 150 cm tall, leaves cauline. Bunch-grass and cushion plant páramo, 3850-4000 m. Molau & Eriksen 2539 (GB, QCA), 2579 (AAU, GB, QCA).

Verbenaceae (Lamiales—Asteridae)

Aegiphila ferruginea HAYEK & SPRUCE
Tree 5 m tall, fruits green. Shrub páramo, 3150-3200 m. Jørgensen 56142.

Violaceae (Violales—Dilleniidae)

Viola glandularis H. E. BALLARD & P. JØRG.
Synonym Viola glandulifera HOOK.

Small herb, flowers yellow, veins on the outside often lilac. Humid páramo and steep rocky slopes, 3450-3850 m. Holm-Nielsen 5354, 5510, 20999.

Viola scandens WILLD. EX ROEM. & SCHULT.
Synonym Viola scandens KUNTH

Flowers light purple with yellow spot in the throat, and yellow veins. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5679, 5802.

Viscaceae (Santalales—Rosidae)

Literature: Kuijt 1986b

Dendrophthora chrysostachya **(J. Presl) Urb.**
Olive-green parasite on a small tree, leaves yellowish. Exposed ridge in cloud forest with large trees and dense undergrowth, 3200 m. Øllgaard 8266.

Dendrophthora clavata **(Benth.) Urb.**
Succulent hemiparasite, curry yellow, berries wax white. Shrub páramo with many Ericaceae and melastomes, 3250-3300 m. Jørgensen 56125.

MONOCOTYLEDONS—LILIOPSIDA

Araceae (Arales—Areciadae)

Anthurium **sp.**
Herb 75 cm tall, spathe and spadix green. Exposed ridge in cloud forest with large trees and shrub páramo, 3200-3500 m. Holm-Nielsen 20990; Jørgensen 56126; Øllgaard 8288.

Bromeliaceae (Bromeliales—Zingiberidae)

Literature: Gilmartin 1972, Smith & Downs, 1974, 1977, Spencer & Smith 1993

Pitcairnia pungens **Kunth**
On a dry rock shelf, 3100-3200 m. Øllgaard 8305.

Puya hamata **L. B. Sm.**
Rosettes to 1.5 m in diameter, inflorescence to 7 m tall, flowers green to dark turquoise-blue. Espeletia páramo, 3550-3800 m. Holm-Nielsen 20963; Øllgaard 98114. 12 miles west of Tulcán, Hitchcock 20915 (US holotype).

Racinaea tetrantha **(Ruiz & Pav.) M. A. Spencer & L. B. Sm.**
Synonym Tillandsia tetrantha Ruiz & Pav.

Terrestrial or epiphytic, leaves spotted, inflorescence red, flowers yellow, reddish tinged. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5598, 5672; Øllgaard 8280.

Tillandsia complanata **Benth.**
Epiphyte, bracts bright red, flowers white-purple. Humid páramo-vegetation with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5269.

Cyperaceae (Cyperales—Commelinidae)

Literature: Seberg 1988

Carex lemanniana **Boott**
Tufted, about 1 m tall, spikes black. Steep slopes in cloud forest and boggy depression in Espeletia páramo, 3150-4000 m. Holm-Nielsen 5556, 5796, 22861; Øllgaard 8457.

Carex microglochin **Wahlenb.**
Forming mats. On muddy lakeshores and bogs in Espeletia páramo, 3700-3950 m. Øllgaard 8346, 8539, 98087.

Carex pichinchensis **Kunth**
Forming large tufts, rhizomes creeping. Boggy depression in páramo with Espeletia, 3450-3850 m. Holm-Nielsen 5310, 5359; Øllgaard 8548.

Carex pygmaea **Boeck.**
Synonym Carex tristicha Spruce ex Boott

Espeletia páramo, 3800-3850 m. Eriksen 59048.

Eleocharis acicularis **(L.) Roem. & Schult.**
Boggy páramo with Espeletia, 3740 m. Øllgaard 8536.

Eleocharis albibracteata **Nees & Meyen ex Kunth**
Forming mats at roadside. Espeletia páramo with grazed bunchgrasses and bogs, 3400 m. Balslev 23890.

Eleocharis bonariensis **Nees**
In Carex-mats on a muddy lake shore, 3950 m. Øllgaard 8346.

Isolepis inundata **R. Br.**
Small rosettes. In streaming water in outlet from lake and mossy bogs along lake, 3450-3850 m. Holm-Nielsen 5429; Lægaard 101288, 101296, 101698.

Oreobolus ecuadorensis **T. Koyama**
Cushion forming. In swamp, 3200-3800 m. Lægaard 55764.

Oreobolus goeppingeri **Suess.**
Forming small cushions to 20 cm wide between bunch-grasses. Páramo with Espeletia, tussock grasses, and shrubs, sometimes on recently burnt ground, 3200-4200 m. Balslev 23930; Grignon 84184; Lægaard 54914, 54924, 54986, 55763, 71446; Sklenar 1888; Øllgaard 8352, 8353.

Oreobolus obtusangulus **Gaudich.**
Cushion-forming with very stiff, prickly leaves. Boggy depression, burnt páramo, Polylepis forest, and swamps, 3600-4000 m. Lægaard 53130, 54915, 54927, 54963, 54973A, 54973B, 54973C, 54973D; Øllgaard 8547 (all are ssp. unispicus Seberg).

Rhynchospora ruiziana **Boeck.**
Synonym Rhynchospora macrochaeta Steud. ex Boeck.

In large tufts, inflorescence black to brown, rhizome creeping. Humid páramo-vegetation with abundance of Espeletia and steep slopes in cloud forest, 3150-3850 m. Holm-Nielsen 5308, 5442, 5493, 20970; Lægaard 54939,54940; Øllgaard 8531.

Uncinia phleoides **(Cav.) Pers.**
In large tufts. Humid páramo with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5307.

Uncinia tenuis **Poepp. ex Kunth**
Espeletia páramo with a small remain of mountain forest, 3800 m. Lægaard 101664.

Eriocaulaceae (Eriocaulales—Commelinidae)

Paepalanthus muscosus **Körn.**
Forming firm cushions, lowers pale. Boggy depression in Espeletia páramo, burnt páramo and swamps, 3400- 4000 m. Balslev 23902; Holm-Nielsen 5277, 18253; Lægaard 53131; Øllgaard 8460.

Iridaceae (Liliales—Liliidae)

Sisyrinchium trinerve **Baker**
Grass-like herb between Festuca-tufts, flowers yellow, leaves terete. Very humid Espeletia-páramo, 3750-3850 m. Eriksen 59042; Holm-Nielsen 5421, 20943.

Sisyrinchium **sp.**
Grass-like herb, flowers yellow, leaves flat with margin towards the stem. Sub-páramo, 3200-3350 m. Balslev 23953; Jørgensen 56148.

Juncaceae (Juncales—Commelinidae)

Literature: Balslev 1979, 1996

Distichia muscoides **Nees & Meyen**
Forming hard cushions in the wet places. Boggy depression in Espeletia páramo, 4000-4200 m. Lægaard 71447; Øllgaard 8435.

Juncus arcticus **Willd.**
Forming dense stands along small creek. Boggy depression in páramo, 3200-3740 m. Balslev 23950; Øllgaard 8552 (all are var. andicola (Hook.) Balslev)

Juncus bufonius **L.**
In tufts on wet rocky slopes, in seepage, and roadsides. Cloud forest, shrub páramo, Espeletia- and bunchgrass páramo, 3150-3700 m. Balslev 892, 23907; Holm-Nielsen 5555.

Juncus capillaceus **Lam.**
Páramo, 3500 m, Aslund 7110 (S).

Juncus echinocephalus **Balslev**
E slope Volcán Chiles above Tufiño, 3450 m, Drew E472 (GH, US)

Juncus ecuadoriensis **Balslev**
In lake, forming large tussocks. Espeletia-páramo, bogs and tall scrub, 3700 m. Øllgaard 98529.

Juncus liebmannii **J.F. Macbr.**
In boggy soil with red iron colour in shrub páramo, 3400-3550 m. Balslev 895, 23846; Holm-Nielsen 5257, 5317; Lægaard 54913 (all are var. quitensis (Buchenau) Balslev).

Juncus stipulatus **Nees & Meyen**
Tufted. Steep slopes in cloud forest, boggy depressions in páramo, and seepage, 3150-3740 m. Balslev 23898, 23899, 23905; Holm-Nielsen 5812; Øllgaard 8536.

Luzula gigantea **Desv.**
In cloud forest and páramo, often on distrubed soil, 3150-3850 m. Balslev 23911; Holm-Nielsen 5371, 5554; Lægaard 101663.

Luzula racemosa **Desv.**
Páramo, 3500 m, Harling & Andersson 12122 (AAU, GB).

Luzula vulcanica Liebm.
Espeletia páramo with grazed bunch grasses and bogs, 3400 m. Balslev 23896.

Rostkovia magellanica (Lam.) Hook.f.
On boggy lake shore, 3700-3900 m. Lægaard 53129; Øllgaard 98089, 98534.

Juncaginaceae (Najadales—Alismatidae)

Literature: Haynes & Holm-Nielsen 1986a

Lilaea scilloides (Poir.) Hauman
Synonym Lilaea subulata Humb. & Bonpl.

Rooted in deep mud in shallow lake, 3700 m. Lægaard 101276.

Liliaceae (incl. Alstroemeriaceae, Amaryllidaceae) (Liliales—Liliidae)

Literature: Meerow 1990

Bomarea hieronymi Pax
Vine, basal half of tepals red, apical half green, inside with blackish spots. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5798; Øllgaard 8278.

Bomarea multiflora (L.f.) Mirb.
Synonym Bomarea caldasii (Kunth) Asch. & Graebn.

Vine, petals bright red, inside with brownish spots, anthers green. Hedges along the road and steep slopes in cloud forest, 3150-3300 m. Holm-Nielsen 5211, 5573.

Phaedranassa dubia (Kunth) J.F. Macbr.
Bulbose herb, flowers red with green tips, stamens free. El Angel, 3500 m. Rau & Hirsch E-239 (MO).

Stenomesson aurantiacum (Kunth) Herb.
Bulbose herb, flowers orange, stamens fused at base. Steep shrubby slopes west of Tulcán, 3000 m. Asplund 17031 (S); northeast of El Angel, 3250 m. Mexia 7450 (UC, US).

Orchidaceae (Orchidales—Liliidae)

Literature: Garay 1978

Aa paleacea (Kunth) Rchb. f.
Synonyms Ophrys paleacea Kunth, Altensteinia paleacea (Kunth) Kunth

Terrestrial, flowers white. Steep slopes in cloud forestand wet Espeletia-páramo, 3150-4050 m. Holm-Nielsen 5452, 5630, 5811, 5882, 5957. These specimens were cited under Aa maderoi Schltr. by Garay (1978), but re-identified as Aa paleacea by C. Vargas in 1998.

Brachionidium tetrapetalum (F. Lehm. & Kränzl.) Schltr.
Terrestrial. Very humid Espeletia-páramo, 3750-3850 m. Eriksen 59073; Holm-Nielsen 5454.

Cranichis antioquiensis Schltr.
Tufiño, Wiggins 10612 (AMES, DS).

Cranichis ciliata (Kunth) Kunth
Terrestrial, labellum white with green stripes, other tepals brown with white apices. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5628, 5631, 5839.

Cranichis crumenifera Garay
Terrestrial, flowers green-white. Bunch grass páramo with shrubs and Espeletia and adjacent cloud forest in ravines, 3200-3350 m. Øllgaard 8337.

Cranichis elliptica Schltr.
Terrestrial herb to 50 cm tall. Cloud forest, 3150-3200 m. Holm-Nielsen 5688.

Cranichis lehmanniana (Kränzl.) L.O. Williams
Herb. Cloud forest, 3150-3200 m. Holm-Nielsen 5711.

Cranichis schlimii Rchb.f.
Terrestrial, flowers white, faintly greenish tinted, especially on the outside. Humid páramo and cloud forest with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5245 (type of Cranichis pachnodes Løjtnant), 20975.

Draconanthes aberrans (Schltr.) Luer
Synonym Lepanthes trachysepala Schltr.

Terrestrial, flowers dark red, tepals yellowish at base. Mountain forest and humid Espeletia-páramo, 3750-3850 m. Eriksen 59072; Holm-Nielsen 5455.

Elleanthus petrogeiton Schltr.
Terrestrial, 1.5 m tall, leaves pale green, tips yellow, petals white, sepals purple-red spotted. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5634, 5635.

Elleanthus tovarensis Ames
Terrestrial, tufted, 30-50 cm tall, leaves darkgreen, the young ones more or less purple. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5633.

Epidendrum elleanthoides Schltr.
Rather humid Espeletia páramo, 3500-3850 m. Lawesson 43939.

Epidendrum fimbriatum Kunth
Terrestrial, flowers white, labellum with purple-red spots, other tepals reddish tinted. Steep slopes in cloud forest and humid páramo, 3100-3500 m. Holm-Nielsen 5248, 5613, 6254; Øllgaard 8312, 8313.

Epidendrum frigidum Linden ex Lindl.
Terrestrial, flowers green-yellow, scentless. Steep slopes in cloud forest and humid Espeletia-páramo, 3150-3550 m. Holm-Nielsen 5486, 5626.

Epidendrum gastropodium Rchb.f.
Terrestrial, flowers dark lilac-red, labellum yellow at base. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5612, 5615.

Epidendrum rhombochilum L.O. Williams
Terrestrial, flowers brown to pale yellow-green, older flowers darker yellow. Humid Espeletia-páramo and mountain forest dominated by Gynoxis and Polylepis, 3750-3850 m. Holm-Nielsen 5451; Eriksen 59074.

Epidendrum serpens Lindl.
Epiphyte, purple tinted, flowers dark red-brown faintly green on the outside. Cloud forest and humid páramo-vegetation with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5246.

Gomphicis traceyae Rolfe
20 km S of Tulcán, El Voladero, Harling & Andersson 12044 (GB).

Gomphichis valida Rchb.f.
Terrestrial, 2 m tall. Humid Espeletia páramo dominated by grasses and with some shrubs, 3400-3850 m. Jørgensen 92295; Lawesson 43936.

Lepanthes gargantua Rchb.f.
Terrestrial, tufted, flowers yellow, petals brown along margins and in the center. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5611.

Myrosmodes cochleare Garay
Terrestrial herb to 15 cm. W of Tulcán, Hitchcock 20927 (AMES), Tufiño, Asplund 17046 (S).

Odontoglossum auropurpureum Rchb. f.
Terrestrial, labellum purple-brown, apex and callus white-yellow, other tepals darker yellow at the margins, often with brown spots. Slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5618.

Odontoglossum pardinum (Lindl.) Lindl.
Synonyms Cyrtochilum pardinum Lindl., Odontoglossum spathaceum Lindl.

Terrestrial, flowers yellow, brown spots. Hedges along the road and steep slopes in cloud forest, 3150-3300 m. Holm-Nielsen 5234, 5614.

Oncidium cultratum Lindl.
Flowers dark yellow with a brown spots at the base, callus of the lip white. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5616.

Pachyphyllum crystallinum Lindl.
Flowers green-white. Steep rocky road banks dominated by mosses and low scattered shrubs, 3200-3350 m. Øllgaard 8315.

Pachyphyllum squarrosum Lindl.
Terrestrial, tufted, flowers green, lateral petals white, labellum white-green. Steep slopes in cloud forest, 3250-3300 m. Holm-Nielsen 6252.

Pleurothallis adonis Luer
Epiphyte, flowers pale yellow and brown. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5807.

Pleurothallis bicruris Lindl.
Terrestrial. Steep slopes in cloud forest, 3250-3300 m. Holm-Nielsen 6253.

***Pleurothallis elegans* (Kunth) Lindl.** In big tufts, 50 cm tall. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5623.

***Pleurothallis ramificans* Luer**

Terrestrial in big tufts, flowers white-yellow. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5617.

***Pterichis barbifrons* (Kränzl.) Schltr.**

Terrestrial, flowers small, yellow green, petals with dark veins. Very humid Espeletia-páramo, 3750-3850 m. Holm-Nielsen 5450.

***Pterichis multiflora* (Lindl.) Schltr.**

Terrestrial, erect to 60 cm tall. Very humid Espeletia-páramo, 3750-3850 m. Holm-Nielsen 5453.

***Stelis purpurea* (Ruiz & Pav.) Willd.**

Terrestrial, tufted, exposed, flowers pale yellow with a sweet scent. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5625.

***Telipogon andicola* Rchb.f.**

Terrestrial or epiphyte, flowers pale yellow, basal part with purple-brown stripes, the central part blackish purple-red. Steep slopes in cloud forest, 3150-3250 m. Holm-Nielsen 5619.

***Trichosalpinx chamaelepanthes* (Rchb.f.) Luer**

Synonym Pleurothallis microcharis Schltr. ex Hoehne

Epiphyte. Humid páramo-vegetation with abundance of Espeletia, 3450-3500 m. Holm-Nielsen 5253.

Poaceae (Cyperales—Commelinidae)

Literature: Alexeev 1986, Hitchcock 1927, Lægaard 1987, 1997, 1998, 1998, Lægaard & Delgado 1999

***Aciachne flagellifera* Lægaard**

Páramo and super-páramo, 4100-4200 m. Lægaard 71443, 71449.

***Agrostis breviculmis* Hitchc.**

Espeletia páramo with grazed bunchgrasses and bogs, 3200-3800 m. Balslev 23901; Lægaard 54918B, 55772, 101275, 101676, 101733.

***Agrostis foliata* Hook.f.**

Synonym Agrostis nigritella Pilg.

Tufted. In wet places in páramo and super-páramo, 3200-4400 m. Holm-Nielsen 5895; Lægaard 55773B, 101272, 101677; Sklenar 1887.

***Agrostis perennans* (Walter) Tuck.**

Small tufts. In grazed Espeletia páramo with small remains of mountain forest, 3450-3800 m. Lægaard 101295, 101657, 101673, 101702.

***Agrostis tolucensis* Kunth**

Small, loose tufts. In grazed and burnt moist páramo, 3380-3800 m. Lægaard 101265, 101656, 101672, 101674, 101725.

***Anthoxanthum odoratum* L.**

Growing in loose tufts. In very humid Espeletia-páramo, on dry slope with shrubs, and in hedges along the road, 3000-3500 m. Holm-Nielsen 5328; Lægaard 54912, 54954, 101646, 101722. Introduced from Europe.

***Aphanelytrum procumbens* Hack.**

Espeletia páramo with remains of mountain forest, 3800 m. Lægaard 101662.

***Brachypodium mexicanum* (Roem. & Schult.) Link**

Roadbanks and roadsides, 3180 m. Lægaard 101713.

***Briza monandra* (Hack.) Pilg.**

Synonym Poidium monandrum (Hack.) Matthei

Dry slope with shrubs, low grassland, and small swamps, 3400-3450 m. Lægaard 54953B, 101734.

***Bromus lanatus* Kunth**

Grazed Espeletia páramo with bogs, 3000-3980 m. Balslev 23893; Lægaard 54911B, 101293, 101667, 101690, 101717, 101721.

***Bromus pitensis* Kunth**

Roadsides and hedges in páramo, 3000-3180 m. Holm-Nielsen 5280; Lægaard 53116, 101647, 101710. Renvoize (in Luteyn 1999) treats this name as a synonym of B. lanatus, but Lægaard (1999) maintains it as distinct.

***Calamagrostis bogotensis* (Pilg.) Pilg.**

Synonym Deyeuxia bogotensis Pilg.

Rhizomatous. Swamps and bogs, 3600-3700 m. Lægaard 54929, 54959, 101290.

***Calamagrostis carchiensis* Lægaard**

Low grassland and small swamps, 3200-3800 m. Lægaard 55773, 101730.

***Calamagrostis effusa* (Kunth) Steud.**

Dominating bunch grass in Espeletia páramo, spikelets dark red. Páramo and superpáramo, 3450-4200 m. Balslev 3625; Eriksen 59051; Grignon 84188; Holm-Nielsen 18237, 22858; Lægaard 53124, 54925, 54961, 71444, 71448, 101266, 101658, 101678, 101700, 101735; Øllgaard 8375, 8409, 8551.

***Calamagrostis fibrovaginata* Lægaard**

Synonym Calamagrostis coarctata (Kunth) Steud. nom. illeg.

Stiffly erect, in bog. Moist Espeletia páramo, rather disturbed by grazing and small swamps, 3500-3700 m. Lægaard 54910, 101655, 101732; Øllgaard 98085.

***Calamagrostis intermedia* (J. Presl) Steud.**

Stiffly erect tussock grass. Burnt páramo and superpáramo and swamps, 3380-4250 m. Holm-Nielsen 5383; Lægaard 53126, 71442, 101264B, 101286, 101726A; Sklenar 662; Øllgaard 98528.

***Calamagrostis jamesonii* Steud.**

Páramo-swamp, 3950- 3980 m. Lægaard 101694.

***Calamagrostis ligulata* (Kunth) Hitchc.**

Burned páramo, swamps, and mossy bogs along lake, 3600-4200 m. Lægaard 53132, 54930, 54970, 101273, 101687; Sklenar 628.

***Calamagrostis planifolia* (Kunth) Trin. ex Steud.**

Small tufts. Grass-páramo, 3380-3500 m. Lægaard 54911A, 54956, 101660, 101701, 101719.

***Calamagrostis recta* (Kunth) Trin. ex Steud.**

Tussocks, leaves rigid and brittle. Burned páramo and swamps, 3700-3980 m. Lægaard 53133, 101693.

***Chusquea lehmannii* Pilg.**

Along the road, 2000-3500 m. Lægaard 54978.

***Cortaderia bifida* Pilg.**

35 km E of Maldonado along Tulcan road, 3240 km. Young 133 (AAU, US).

***Cortaderia hapalotricha* (Pilg.) Conert**

Bunch-grass, old leaves distinctly curling. Boggy depression in Espeletia páramo, dominated by cushion plants , and adjacent wet slopes, 3700-4000 m. Lægaard 53127, 101282, 101297; Øllgaard 8345, 8347, 8455.

***Cortaderia nitida* (Kunth) Pilg.**

Tussock grass to 2 m tall with hermaphrodite and female plants. Swampy areas in páramo, 3300-3980 m. Lægaard 53121, 54945, 54960, 101283, 101688, 101689, 101699, 101714.

***Cortaderia sericantha* (Steud.) Hitchc.**

Forming small, dense tussocks. Boggy depression in páramo, with Espeletia, bunch grasses and mosses, 3700-3740 m. Lægaard 55770, 101281; Øllgaard 8546.

***Danthonia secundiflora* J. Presl**

Dense tussock. Grass-páramo with swamp, 3200-3800 m. Lægaard 54958, 55774, 101704, 101723.

***Elymus cordilleranus* Davidse & R.W. Pohl**

Synonyms Agropyron attenuatum (Kunth) Roem. & Schult., Elymus attenuatus (Kunth) Löve nom. illeg.

3300 m. Lægaard 53119.

***Festuca andicola* Kunth**

Small tufts. Páramo-swamp, 3330-3980 m. Lægaard 101692, 101718, 101731.

***Festuca asplundii* E.B. Alexeev**

Bunch-grass. Boggy depression and páramo. Mossy bogs along lake, 3700-4000 m. Lægaard 54972, 101284, 101680, 101695; Øllgaard 8545.

***Festuca sodiroana* Hack. ex E.B. Alexeev**

Roadbanks and roadsides, 3180-3300 m. Lægaard 53118, 101711.

***Festuca subulifolia* Benth.**

In large tufts, flowers bordeaux to glaucous, fire-resistent. Grass páramo with Espeletia, often burned, 3200-3900 m. Grignon 84189; Holm-Nielsen 5427; Lægaard 53125, 55771, 101264A, 101726B.

***Hierochloe redolens* (Vahl) Roem. & Schult.**

Synonym Torresia redolens (Vahl) Roem. & Schult

In loose tufts in the páramo, top often reddish tinged. Very humid Espeletia-páramo and mossy bogs along lake, 3700-3850 m. Holm-Nielsen 5431; Lægaard 101292; Øllgaard 98093.

Holcus lanatus L.
Along road in páramo, 3300 m. Balslev 848; Luteyn 10914 (AAU). Introduced from Europe.

Lolium multiflorum Lam.
3300 m. Lægaard 53114. Introduced from Europe.

Muhlenbergia ligularis (Hack.) Hitchc.
Moist páramo, 3400-3600 m. Lægaard 101737.

Nassella inconspicua (J. Presl) Barkworth
Dry slope with shrubs, roadbanks and roadsides, 3180-3450 m. Lægaard 54955, 101712.

Paspalum bonplandianum Flüggé
Mat-forming in grass-páramo, 3380- 3800 m. Grignon 84187; Lægaard 101720.

Phalaris aquatica L.
Synonym Phalaris stenoptera Hack.

In hedge along road, 3000-3600 m. Lægaard 53115, 101648, 101736. Introduced.

Poa annua L.
Roadbanks and roadsides, 3180 m. Lægaard 101707, 101708. Introduced.

Poa paramoensis Lægaard
Bog along road, 3330 m. Lægaard 101715.

Poa pauciflora Roem. & Schult.
Dense tussocks. Grass-páramo, 3500-3980 m. Lægaard 54920, 101659, 101686, 101724.

Poa subspicata (J. Presl) Kunth
Low grassland, small swamp, 3400 m. Lægaard 101729.

Polypogon interruptus Kunth
In humid Espeletia-páramo in loose tufts, 3450-3500 m. Holm-Nielsen 5318.

Trisetum irazuense (Kuntze) Hitchc.
Steep slopes in cloud forest. 3150-3300 m. Holm-Nielsen 5553; Lægaard 53117.

Vulpia bromoides (L.) Gray
Synonym Festuca bromides L.

Roadbanks and roadsides, 3180 m. Lægaard 101709.

Potamogetonaceae (Najadales – Alismatidae)

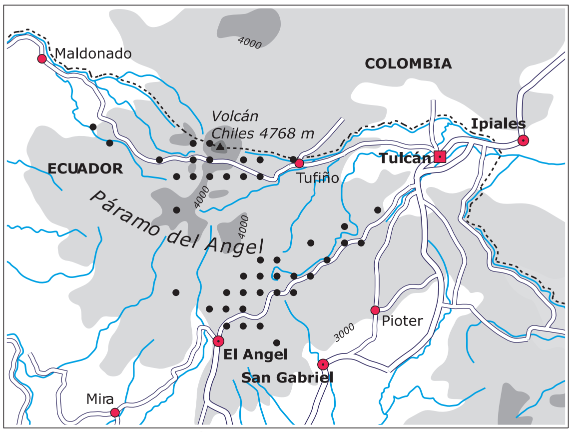
Literature: Haynes & Holm-Nielsen 1986b

Potamogeton paramoanus R.R. Haynes & Holm-Niels.
Submersed in lakes in Espeletia-páramo, 3400-3850 m. Holm-Nielsen 5390. 5513 (type); Lægaard 101277A, 101277B, 101279, 101727; Øllgaard 98531.

COLLECTORS AND LOCALITIES

This list of collectors and localities is drawn from the database at Herbarium AAU, of the Department of Systematic Botany (previously Botanical Institute), University of Aarhus. It contains the names and localities of collectors associated with that institution. The main collectors are the department´s current or previous staff members (Balslev, Borchsenius, Holm-Jeppesen, Lægaard, Nielsen, Øllgaard) and graduate students (Andersen, Eriksen, Brandbyge, Grignon, Jørgensen, Lawesson, Læsøe, Løjtnant, Madsen, Navarette) or visiting students (Sklenar). The co-collectors are colleagues (de Vries, Romoleroux) and students (Quintana, Ulloa, Gavilanes) from P. Universidad Católica in Quito, from The New York Botanical Garden (Steere), and friends and family (A. & O.Øllgaard, Kosteckova, Vive) who accompanied AAU staff on collecting trips. The localities are shown in Figure 1.

Figure 1. Collecting localities (●).



Andersen, E. Ø.
10890-10891: Road Tufiño to Maldonado, km 8. Roadbank in páramo, 3500-3600 m. 23 April 1993. 0 47 N 77 53 W.

Balslev, H. & F. Quintana
829-858: Tulcán to El Angel road, 15 km south of Las Juntas. Páramo. 3300 m. 20 November 1980. 0 41 N 77 50 W.
859-888: Tulcán to El Angel road, 21 km south of Las Juntas. Shrub páramo. 3350 m. 20 November 1980. 0 41 N 77 50 W.
889-901: Tulcán to El Angel road, 34 km south of Las Juntas. Shrub páramo. 3550 m. 20 November 1980. 0 40 N 77 51 W.

Balslev, H. & T. de Vries
3659-3661: Páramo del Angel, 13 km north of El Angel. Páramo with Espeletia. 3600 m. 29 December 1982. 0 38 N 77 53 W
3662-3662: El Angel 4 km north of the town. Agricultural areas. 3400 m. 29 December 1982. 0 38 N 77 53 W.

Balslev, H. & W.C. Steere
4429-4435: Road from Tufiño to Maldonado, eastern slope of Volcán Chiles. Grass páramo with Espeletia and some rocks. 3900-4100 m. 19 October 1983. 0 47 N 77 54 W.
4439-4439: Road from El Angel towards Tulcán, ca km 10. Live fences of shrubs along old coble stone road. 3500 m. 21 October 1983. 0 40 N 77 55 W.

Balslev, H. & F. Quintana
23884-23903: Páramo del Angel, 28 km north of El Angel. Espeletia páramo with grazed bunch grasses and bogs. 3400 m. 28 May 1980. 0 43 N 77 47 W
23905-23936: Summit on the road El Angel to Tulcán, km 17 from El Angel. Landslide in Espeletia and bunch grass páramo. 3700 m. 28 May 1980. 0 40 N 77 52 W.
23937-23956: Road El Angel to Tulcán, 10 km from El Angel. Boggy area in sub-páramo. Vegetation with shrubs. 3200 m. 28 May 1980. 0 39 N 77 54 W.

Borchsenius, F.
79-80: Road Maldonado to Tulcán, km 35. 3120 m. 04 May 1993. 0 50 N 78 3 W.

Brandbyge, J.
60910-60913: Páramo de Tufiño. Espeletia páramo. 3650-3700 m. 17 January 1987. 0 50 N 77 50 W.

Eriksen, B.
59001-59065: Road between Tulcán and Maldonado. Espeletia páramo S of Volcán Chiles. 3800-3850 m. 12-13March1985. 0 47 N 77 58 W.

59066-59097: Páramo del Angel south of Volcán Chiles. Espeletia páramo and mountain forest dominated by Gynoxis and Polylepis. 3850 m. 14March1985. 0 45 N 77 58 W.

Grignon, I.

84184-84191: Tufiño. Páramo del Angel. Espeletia páramo. 3800 m. 17 January 1987. 0 50 N 77 55 W.

Holm-Nielsen, L. B., S. Jeppesen, B. Løjtnant & B. Øllgaard

5207-5242: Ca. 2 km along the road El Angel to Tulcán. Hedges along the road. 3150-3300 m. 14 May 1973. 0 38 N 77 55 W.

5243-5344: Páramo del Angel, just before the pass on road El Angel to Tulcán. Humid páramo-vegetation with abundance of Espeletia. 3450-3500 m. 14 May 1973. 0 41 N 77 54 W.

5345-5484: Páramo del Angel, in the pass on road El Angel to Tulcán. Very humid Espeletia-páramo. 3750-3850 m. 15 May 1973. 77 54 N 0 41 W.

5485-5515: Páramo del Angel, in the pass on road El Angel to Tulcán. Very humid Espeletia-páramo. 3450-3550 m. 15 May 1973. 0 41 N 78 54 W.

5516-5855: Maldonado valley, km 53 on the road Tulcán to Maldonado. Steep slopes in cloud forest. 3150-3250 m. 17 May 1973 to 18 May 1973. 0 50 N 78 3 W.

5856-5958: Base of Volcán Chiles, km 34-36 on road Tulcán to Maldonado. Páramo, meadow and small lake area in Espeletia-páramo, elfin forest on sheltered places. 3900-4050 m. 19 May 1973. 0 47 N 77 57 W.

6251-6261: Maldonado valley, km 53 on the road Tulcán to Maldonado. Steep slopes in cloud forest. 3250-3300 m. 22 May 1973. 0 50 N 78 3 W.

Holm-Nielsen, L. B.

18227-18261: Páramo del Angel, 2 km before the pass on road El Angel to Tulcán. Espeletia páramo. 3600 m. 14 June 1979. 0 41 N 77 51 W.

20942-20970: Páramo del Angel. Espeletia páramo south of the pass. 3800 m. 12 January 1980. 0 40 N 77 52 W.

20971-21001: Páramo del Angel. Cloud forest with Espeletia and Puya. 3500 m. 12 January 1980. 0 40 S 77 52 W.

22854-22870: Páramo del Tufiño west of Tulcán. Espeletia páramo. 3500 m. 14 April 1980. 1 13 S 77 53 W.

24265-24270: Páramo del Angel, south of the pass. Espeletia páramo. 3600 m. 19 June 1980. 0 53 N 77 53 W.

Jørgensen, P. M. & S. S. Vive

56112-56124: El Angel to Las Lagunas road km 1.5. 3075 m. 07 October 1984. 0 39 N 77 56 W.

56125-56137: El Angel to Tulcán road km 3. Shrub páramo with many Ericaceae and melastomes. 3250-3300 m. 07 October 1984. 0 39 N 77 55 W.

56138-56142: El Angel to Tulcán road km 5. Shrub páramo dominated by Ericaceae and melastomes. 3150-3200 m. 08 October 1984. 0 39 N 77 54 W.

56143-56140: El Angel to Tulcán road km 11. Shrub páramo just below Espeletia páramo. 3350 m. 08 October 1984. 0 40 N 77 53 W.

Jørgensen, P. M.

61544-61549: Tulcán to Maldonado road. Polylepis and Gynoxis forest. 3850-3900 m. 13 October 1986. 0 48 N 77 56 W.

Jørgensen, P. M., C. Ulloa, K. Romoleroux & M. Gavilanes

92238-92240: El Angel to Lagunas El Voladero, km 8. Roadside. 3270 m. 07 August 1990. 0 40 N 77 54 W.

92241-92241: El Angel to Lagunas El Voladero, km 20. Roadside. 3600 m. 07 August 1990. 0 41 N 77 53 W.

92248-92279: El Angel to Tulcán main road, km 1, turn off towards east, km 4. Secondary forest and pastures. 3280-3400 m. 08 August 1990. 0 35 N 77 55 W.

92280-92297: El Angel to Tulcán, via El Voladero, km 11, turn off towards south. Páramo with shrubs. 3400 m. 08 August 1990. 0 38 N 77 53 W.

92298-92327: El Angel to Tulcán, around Lagunas El Voladero. Espeletia páramo with small islands of shrubby vegetation. 3600 m. 09 August 1990. 0 42 N 77 53 W.

92328-92336: El Angel to Tulcán, via Lagunas El Voladero, km 34. Secondery shrubby vegetation dominated by Asteraceae shrubs. 3350 m. 09 August 1990. 0 42 N 77 49 W.

Lawesson, J. E., T. Læssøe & P. M. Jørgensen

43925-43942: El Angel. The Lagunas. Rather humid Espeletia páramo dominated by Poaceae and Carex, with some shrubs. 3500-3850 m. 21 May 1983. 0 40 N 77 58 W.

Lægaard, S.

53114-53121: Hacienda La Esperanza, northeast of El Angel. 3300 m. 08 October 1984. 0 39 N 77 54 W.

53122-53137: Páramo del Angel, ca. 20 km northeast of El Angel. Burned páramo and swamps. 3700-3900 m. 09 October 1984. 0 40 N 77 53 W.

54906-54908: Km 3 on old road El Angel to Tulcán. 3200 m. 13 August 1985. 0 39 N 77 55 W.

54909-54913: Km 10 on old road El Angel to Tulcán. 3500 m. 13 August 1985. 0 40 N 77 52 W.

54914-54945: Km 18 on old road El Angel to Tulcán. Páramo near El Voladero. 3600-3700 m. 14 August 1985. 0 41 N 77 52 W.

54946-54957: Km 32 on old road El Angel to Tulcán. Dry slope with shrubs. 3450 m. 15 August 1985. 0 43 N 77 48 W.

54958-54964: West of Tufiño, near and at Los Thermales. 3600 m. 15 August 1985. 0 49 N 77 53 W.

54965-54976: Road Tulcán to Maldonado, near Volcán Chiles. Polylepis forest and páramo. 3850-4000 m. 16 August 1985. 0 48 N 77 56 W.

54977-54984: Road Volcán Chiles to Maldonado, 2000-3500 m. 16 August 1985. 0 50 N 78 0 W.

54985-54987: Road Tulcán to Maldonado, near Volcán Chiles. 3600 m. 17 August 1985. 0 49 N 77 56 W.

54988-54989: Near Tufiño. 3050-3150 m. 17 August 1985. 0 48 N 77 51 W.

55763-55774: Páramo del Angel. 3200-3800 m. 10 December 1985. 0 41 N 77 53 W.

71442-71449: Highest pass on road Tufiño to Maldonado. Páramo and super-páramo. 4100-4200 m. 09 June 1988. 0 48 N 77 56 W.

101263-101271: Páramo del Angel at Los Voladeros. Grass páramo with Espeletia, often burned. 3700-3750 m. 14 February 1992. 0 41 N 77 53 W.

101272-101297: Páramo del Angel, at the lakes at Los Voladeros. Mossy bogs along lake. 3700 m. 14 February 1992. 0 41 N 77 53 W.

101316-101330: El Angel to San Gabriel km 8 along old road. Páramo of Hacienda El Consuelo. Grass páramo with Espeletia and Blechnum. 3475-3625 m. 15 February 1992. 0 37 N 77 52 W.

101646-101648: Tufiño to Tulcán km 7. In hedge along road. 3000 m. 10March1992. 0 50 N 77 48 W.

101649-101654: 1-2 km west of Tufiño. Hedges along road. 3200-3250 m. 10 March 1992. 0 48 N 77 53 W.

101655-101660: Tufiño to Maldonado km 4. Moist Espeletia páramo, rather disturbed by grazing. 3500 m. 10 March 1992. 0 48 N 77 53 W.

101661-101679: Volcán Los Chiles, along road 9 km west of Tufiño. Espeletia páramo with a small remain of mountain forest. 3800 m. 10 March 1992. 0 49 N 77 57 W.

101680-101697: Volcán Los Chiles, along road app. 1 km east of pass. Slopes and páramo swamps. 3950-3980 m. 10 March 1992. 0 49 N 77 57 W.

101698-101704: At the Thermales de Tufiño 3450 m. 10 March 1992. 0 48 N 77 53 W.

101705-101713: Km 4 along road Las Juntas (Tulcán) to El Angel. Roadbanks and roadsides. 3180 m. 11 March 1992. 0 46 N 77 46 W.

101714-101718: Km 11 along road Las Juntas (Tulcán) to El Angel. Bog along road. 3330 m. 11 March 1992. 0 43 N 77 50 W.

101719-101726: Km 13 along road Las Juntas (Tulcán) to El Angel. Grass-páramo. 3380 m. 11 March 1992. 0 43 N 77 50 W.

101727-101734: Km 14 along road Las Juntas (Tulcán) to El Angel. Low grassland, small swamp. 3400 m. 11 March 1992. 0 43 N 77 50 W

101735-101737: Near El Angel 3400-3600 m. 11 March 1992. 0 40 N 77 54 W.

Læssøe, T.

43914-43923: El Angel. The Lagunas. Rather humid Espeletia páramo dominated by Poaceae and Carex, with some shrubs. 3500-3850 m. 21 May 1983. 0 40 N 77 58 W.

Madsen, J. E.

36332-36369: Páramo del Angel, about 20 km on the road from Tulcán to El Angel. Near lower border of the páramo. 3400 m. 26 October 1981. 0 44 N 77 48 W.

36370-36384: Along the road from Páramo del Angel to Tulcán. 15-20 km from Tulcán. Mountain forest. 3200-3300 m. 26 October 1981. 0 45 N 77 46 W.

36385-36385: Páramo del Angel, about 20 km on the road from Tulcán to El Angel. Near the lower margins of the páramo. 3400 m. 26 October 1981. 0 44 N 77 48 W.

Sklenar, P. & V. Kosteckova

616-618: Volcán Chiles, humid superpáramo on southwest slopes on shallow sandy soil with rocks. 4300-4400 m. 21 July 1995. 0 48 N 77 57 W.

626-658: Volcán Chiles, along a gully on the southwest, transition from grass páramo to shrub and cushion páramo. 4150-4200 m. 23 July 1995. 0 48 N 77 57 W.

662-690: Volcán Chiles, small cushion bog with Plantago rigida along a small stream on the southwest side. 4250-4250 m. 21 July 1995. 0 48 N 77 57 W.

701-709: Volcán Chiles, humid superpáramo on southwest slopes on shallow sandy soil with rocks. 4300-4400 m. 21 July 1995. 0 48 N 77 57 W.

719-719: Volcán Chiles, cushion bog with Plantago rigida and Distichia muscoides on southwest side. 4150 m. 23 July 1995. 0 48 N 77 57 W.

721: On the shore of Lagunas Verdes, south side of Volcán Chiles. 4000 m. 23 July 1995. 0 48 N 77 57 W.

1400-1410: Volcán Chiles, wet depression with cushions of Werneria, Plantago rigida, and Distichia in the Espeletia-grass páramo on the west side of the mountain. 4100-4100 m. 06 October 1995. 0 48 N 77 57 W.

1416: Espeletia-grass páramo along the road from Tulcán to Volcán Chiles. 3800 m. 07 October 1995. 0 47 N 77 56 W.

1885-1888: Southwest side of Volcán Chiles, super-páramo on stony slope with shallow soil. 4300 m. 20 July 1995. 0 48 N 77 57 W.

1889: Southwest side of Volcán Chiles, sparse super-páramo vegetation on rocks. 4500 m. 22 July 1995. 0 48 N 77 57 W.

Øllgaard, B.

1204-1204: Road El Angel to Laguna Voladero, beginning of Espeletia páramo. 3630 m. 22 October 1995. 0 38 N 77 54 W.

1205-1207: Road El Angel to Laguna Voladero, parking lot at lake. Espeletia páramo. 3800 m. 22 October 1995. 0 41 N 77 53 W.

Øllgaard, B. & H. Balslev

8263-8300: Road Tulcán to Maldonado, 53 km from Tulcán. Exposed ridge in cloud forest with large trees and dense undergrowth of orchids, Chusquea and Gleichenia. 3200 m. 31 July 1976. 0 50 N 78 3 W.

8301-8311: Road Tulcán to Maldonado, 53-54 km from Tulcán. Steep rocky road banks, with herbs, mosses and low scattered shrubs. 3100-3200 m. 31 July 1976. 0 50 N 78 3 W.

8312-8316: Road Tulcán to Maldonado, 50-53 km from Tulcán. Steep rocky road banks dominated by mosses and low scattered shrubs. 3200-3350 m. 01 August 1976. 0 50 N 78 3 W.

8320-8337: Road Tulcán to Maldonado, 49 km from Tulcán. Bunch grass páramo with shrubs and Espeletia and adjacent cloud forest in ravines. 3200-3350 m. 01 August 1976. 0 49 N 78 2 W.

8338-8343: Road Tulcán to Maldonado, immediately east of the pass, (base of Volcán Chiles). Road banks, bunch grass páramo with Espeletia, and rocky slopes dominated by mosses. 3950-4050 m. 02 August 1976. 0 47 N 77 57 W.

8344-8394: Road Tulcán to Maldonado, at the base of Volcán Chiles, 34-36 km from Tulcán. small lakes (Lagunas Verdes) and sloping lake shores with rocks and boulders, dominated by mosses, Lycopodium spp. and cushion plants. Few shrubs and bunch grasses. 3950 m. 02 August 1976. 0 47 N 77 57 W.

8395-8426: Road Tulcán to Maldonado, west of the pass (base of Volcán Chiles). Narrow ravine in Espeletia páramo, with dense scrub and small trees. 3650 m. 03 August 1976. 0 49 N 78 57 W.

8427-8460: Road Tulcán to Maldonado, at the pass, 38 km from Tulcán. Boggy depression in Espeletia páramo, dominated by cushion plants (Plantago rigida, Distichia, Werneria), and adjacent wet slopes. 4000 m. 04 August 1976. 0 47 N 77 57 W.

8461-8469: Road Tulcán to Maldonado, at the base of Volcán Chiles, 34-36 km from Tulcán. Small lakes (Lagunas Verdes) and sloping lake shores with rocks and boulders, dominated by mosses, Lycopodium spp. and cushion plants, few shrubs and bunch grasses. 3950 m. 05 August 1976. 0 47 N 77 57 W.

8470-8471: Road Tulcán to Maldonado, west of the pass. 3900 m. 05 August 1976. 0 47 N 77 57 W.

8511-8515: Road Tulcán to Maldonado, 29 km from Tulcán, on SE slopes of Volcán Chiles. Espeletia páramo on slopes with bunch grasses and cushion plants. 3740 m. 06 August 1976. 0 47 N 77 55 W.

8516-8554: Road Tulcán to Maldonado, on SW slopes of Volcán Chiles, approx. 43 km from Tulcán. Boggy depression in páramo, with Espeletia, Loricaria, cushion plants, bunch grasses and mosses. 3740 m. 06 August 1976. 0 48 N 77 59 W.

Øllgaard, B.

57203-57203: Road Tulcán to Maldonado, before the pass. Boggy depression in Espeletia páramo. 3650 m. 01 February 1985. 0 47 N 77 55 W.

Øllgaard, B., A. Øllgaard & O. Øllgaard

98077-98110: Páramo del Angel, km 18 along road El Angel to Tulcán. Páramo del Voladero, around large lakes near the pass. Espeletia páramo. 3750-3650 m. 09 August 1990. 0 41 N 77 53 W.

98111-98112: Old road El Angel to Tulcán, ca. km 36. Scrub at roadside. 3400 m. 09 August 1990. 0 43 N 77 48 W.

98112-981112: Old road El Angel to Tulcán, ca. km 24. Road bank. 3450 m. 09 August 1990. 0 42 N 77 52 W.
98113-98113: Old road El Angel to Tulcán, ca. km 28. Moist grass vegetation at roadside. 3400 m. 09 August 1990. 0 42 N 77 52 W.
98114-98114: Old road El Angel to Tulcán, ca. km 20. Espeletia páramo. 3550 m. 09 August 1990. 0 41 N 77 53 W.
98115-98120: Old road El Angel to Tulcán, ca. km 34. Secondary scrub. 3350 m. 09 August 1990. 0 43 N 77 48 W.

Øllgaard, B.
98510-98534: Páramo del Angel, km 18 along road El Angel to Tulcán, around laguna El Voladero, Espeletia-páramo, bogs and tall scrub. 3650-3750 m. 18 December 1990. 0 41 N 77 53 W.
100001-100001: Road Tufiño to Maldonado, before the pass, at Lagunas Verdes. Rocky bank. 4000 m. 17 April 1992. 0 48 N 77 54 W.
100002-100004: Road Tufiño to Maldonado, W of the pass. Road bank. 3800 m. 17 April 1992. 0 48 N 77 59 W.
100005-100005: Road Tufiño to Maldonado, W of the pass. Road bank. 3150 m. 17 April 1992. 0 51 N 78 2 W.

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REFERENCES

Alexeev, E. B. (1986) Festuca L. (Poaceae) in Venezuela, Colombia et Ecuador. *Novosti Sistematiki Vyschnij Rastenii,* **23:** 5–23.

Anderberg, A. A. (1991) Taxonomy and phylogeny of the tribe Gnaphalieae (Asteraceae). *Opera Botanica,* **104:** 1–195.

Andersen, E. Ø. and Øllgaard, B. (submitted) Gleicheniaceae. *Flora of Ecuador.*

Andersson, L. (1992) A provisional checklist of Neotropical Rubiaceae. *Scripta Botanica Belgica,* **1:** 1–200.

Andersson, L. (1993) Rubiaceae. Introduction; Rubiaceae-Anthospermeae. *Flora of Ecuador,* **47:** 1–17.

Andersson, L. and Taylor, C. M. (1994) Rubiaceae-Cinchoneae-Coptosapelteae. *Flora of Ecuador,* **50:** 1–112.

Arbeláez, A. L. (manuscript) La tribu Pterideae (Pteridaceae) en Ecuador.

Austin, D. F. (1982) Convolvulaceae. *Flora of Ecuador,* **15:** 1–98.

Balslev, H. (1979) Juncaceae. *Flora of Ecuador,* **11:** 1–45.

Balslev, H. (1996) Juncaceae. *Flora Neotropica Monographs,* **68:** 1–168.

Balslev, H. and Luteyn, L. (Eds. 1992) *Páramo: An Andean Ecosystemn under Human Influence.* London: Academic press.

Berry, P. E. (1982) The systematics and evolution of Fuchsia Sect. Fuchsia (Onagraceae). *Annals of the Missouri Botanical Garden,* **69:** 1–198.

Bishop, L. E. (1988) Ceradenia, a new genus of Grammitidaceae. *American Fern Journal,* **78:** 1–5.

Bohlin, J.-E. (1988) A monograph of the genus Colignonia (Nyctaginaceae). *Nordic Journal of Botany,* **8:** 231–252.

Borchsenius, F. (1997) Oreopanax (Araliaceae) in Ecuador. *Nordic Journal of Botany,* **17:** 373–396.

Brandbyge, J. (1989) Polygonaceae. *Flora of Ecuador,* **38:** 1–61.

Brummitt, R. K. and Powell, C. E. (1992) *Authors of Plant Names.* London: Royal Botanic Gardens, Kew.

Bywater, M. and Wickens G. E. (1984) New World species of the genus Crassula. *Kew Bulletin,* **39:** 699–728.

Cleef, A. M. and Chaverri, P. (1992) Phytogeography of the páramo flora of Cordillera de Talamanca, Costa Rica. In: Balslev, H. and Luteyn, J. L. (Eds.) *Páramo: An Andean Ecosystem under human influenc,* pp. 42–66. London: Academic Press.

Coello Hinojosa, F. (1994) Plan de manejo de la Reserva Ecologica "El Angel", Provincia del Carchi. Quito: Convenio MBS-INEFAN-IICA.

Cronquist, A. (1981) An Integrated System of Classification of Flowering Plants. New York: Columbia University Press.

Cuatrecasas, J. (1997) Synopsis of the neotropical genus Oritrophium (Asteraceae: Astereae) *BioLlania, Edición Especial* **6:** 287–303.

Dempster, L. T. (1993) Rubiaceae-Rubieae. *Flora of Ecuador,* **47:** 19–36.

Díaz-Piedrahíta and Vélez-Nauer, C. (1993) Revisión de las tribus Barnadesieae y Mutisieae (Asteraceae) para la Flora de Colombia. *Monografías del Jardín Botánico José Celestino Mutis* **1:** 1–160.

Dillon, M. O. and Sagástegui A., A. (1986) Jalcophila, a new genus of Andean Inuleae (Asteraceae). *Brittonia* **38:** 162–167.

Eliasson, U. (1987) Amaranthaceae. *Flora of Ecuador,* **28:** 1–137.

Eliasson, U. (1993) Phytolaccaceae. *Flora of Ecuador,* **46:** 1–43.

Eliasson, U. H. (1996) Portulacaceae. *Flora of Ecuador,* **56:** 29–53.

Eriksen, B. (1989) Valerianaceae. *Flora of Ecuador,* **34:** 1–59.

Fagerström, K. (1975) Columelliaceae. *Flora of Ecuador,* **4:** 1–5.

Ferreyra, R. (1953) A revision of the Ecuadorean species of Monnina (Polygalaceae). *Loydia* **16:** 193–226.

Funk, V. A. (1997a) Werneria s.l. (Compositae: Senecioneae) in Ecuador. In: Valencia, R. and Balslev, H. (Eds.) *Estudios Sobre Diversidad y Ecología de Plantas,* pp. 25–35. Quito: P. Universidad Católica del Ecuador.

Funk, V. A. (1997b) Compositae of Ecuador, II: Diversity and distribution. In: Valencia, R. and Balslev, H. (Eds.) *Estudios Sobre Diversidad y Ecología de Plantas,* pp. 79–95. Quito: P. Universidad Católica del Ecuador.

Funk, V. A. (1997c) Xenophyllum, a new Andean genus extracted from Werneria s.l. (Compositae: Senecioneae). *Novon,* **7:** 235–241.

Garay, L. (1978) Orchidaceae - Cypripedioideae, Orchidoideae, Neottioideae. *Flora of Ecuador,* **9:** 1–304.

Gilmartin, A. J. (1972) The Bromeliaceae of Ecuador. *Phanerog. Monogr.,* **4:** 1–255.

Grimes, J. W. (1990) A revision of the New World species of Psoraleeae (Leguminosae Papilionoideae). *Memoirs of The New York Botanical Garden* **61:** 1–113.

Gustafsson, C. (1992) Clethraceae. *Flora of Ecuador,* **45:** 1–26.

Halfdan-Nielsen, B. (1995) Flora of Ecuador. Geraniaceae. Cand. scient. thesis, University of Copenhagen.

Halfdan-Nielsen, B. (1996) Five new species of Geranium (Geraniaceae) from Ecuador. *Nordic Journal of Botany,* **16:** 267–275.

Harling, G. (1991) Compositae-Mutisieae. *Flora of Ecuador,* **42:** 1–105.

Harling, G. (1999) Cunoniaceae. *Flora of Ecuador* **61;** 1–74.

Haynes, R. R. and Holm-Nielsen L. B. (1986a) Juncaginaceae. *Flora of Ecuador,* **26:** 45–50.

Haynes, R. R. and Holm-Nielsen L. B. (1986b) Potamogetonaceae. *Flora of Ecuador,* **26:** 51–71.

Hickey, R. J. (1985) *Revisionary Studies of Neotropical Isoetes.* Ph.D. dissertation, University of Connecticut, Storrs.

Hitchcock, A. S. (1927) The grasses of Ecuador, Peru, and Bolivia. *Contributions from the United States' National Herbarium,* **24:** 291–556.

Holm-Nielsen, L. B., Jørgensen, P. M. and Lawesson, J. E. (1988) Passifloraceae. *Flora of Ecuador,* **31:** 1–129.

Holmgren, N. H. and Molau, U. (1984) Scrophulariaceae. *Flora of Ecuador,* **21:** 1–188.

Illum, S. T. (1986) A taxonomic revision of Blechnum section Lomariocycas. Cand. Scient. thesis, University of Aarhus.

Jaramillo, J. (1988) Notes on Ecuadorian Vallea (Elaeocarpaceae) with description of a new species. *Nordic Journal of Botany,* **8:** 19–23.

Jeffrey, C. (1992) The tribe Senecioneae (Compositae) in the Mascarene Islands with an annotated world check-list of the genera of the tribe. Notes on Compositae VI. *Kew Bulletin* **47:** 49–109.

Jeppesen, S. (1981) Campanulaceae, Lobeliaceae, Sphenocleaceae, Goodeniaceae. *Flora of Ecuador,* **14:** 1–183.

Jørgensen, P. M. and León-Yánez, S. (1999) *Catalogue of the Vascular Plants of Ecuador.* St. Louis: Missouri Botanical Garden Press.

Knapp, S. (1989) A revision of the Solanum nitidum group (section Holophylla proparte): Solanaceae. *Bulletin of the British Museum of Natural History (Botany),* **19:** 63–112.

Kuijt, J. (1986a) Loranthaceae. *Flora of Ecuador,* **24:** 113–197.

Kuijt, J. (1986b) Viscaceae. *Flora of Ecuador,* **24:** 11–112.

Kvist, L. P. and L. E. Skog. (1993) The genus Columnea (Gesneriaceae) in Ecuador. *Allertonia,* **6:** 327–400.

Landrum, L. R. (1988) Systematics of Myrteola (Myrtaceae). *Systematic Botany,* **13:** 120–132.

León, B. (1992) A Taxonomic Revision of the Fern Genus Campyloneurum (Polypodiaceae). Ph.D. dissertation, University of Aarhus.

Lourteig, A. (1956) Ranunculaceae de Sudamérica tropical. *Memorias de la Sociedad Cientifica La Salle (Argentina),* **16(43–44):** 19–228.

Lourteig, A. (1991) El género Montia en el Hemisferio Austral. *Revista de la Academía Colombiana de Ciencias Exactas,* **18(68):** 41–48.

Luteyn J. L. (1996) Ericaceae. *Flora of Ecuador,* **54:** 1–404.

Luteyn, J. L. (1999) Páramos - a checklist of plant diversity, geographical distribution, and botanical literature. *Memoirs of The New York Botanical Garden,* **84:** 1–278.

Lægaard, S. (1987) The genus Aciachne. *Nordic Journal of Botany,* **7:** 667–672.

Lægaard, S. (1997) Gramineae (part 1). *Flora of Ecuador,* **57:** 1–54.

Lægaard, S. (1998) New species and names in Ecuadorian grasses (Poaceae). *Novon,* **8:** 23–30.

Lægaard, S. (1999) Poaceae. In: Jørgensen, P. M. and León-Yánez, S. (Eds.) Catalogue of the Vascular Plants of Ecuador, pp. 806–838. St. Louis: Missouri Botanical Garden Press.

Lægaard, S. and Delgado, T. (1999) Keys to the tribes and genera of Ecuadorean grasses. *Herbario Loja,* **4bis:** 1–41.

Mathias, M. E. and Constance, L. (1976) Umbelliferae. *Flora of Ecuador,* **5:** 1–71.

Meerow, A. W. (1990) Amaryllidaceae. *Flora of Ecuador,* **41:** 1–52.

Mena, P. (1990) A revision of the genus Arcytophyllum (Rubiaceae: Hedyotideae). *Memoirs of The New York Botanical Garden,* **60:** 1–26.

Mena, P. and Balslev, H. (1986) Comparación entre la Vegetación de los Páramos y el Cinturón Afroalpino. *Reports from the Botanical Institute, University of Aarhus,* **12:** 1–54.

Molau, U. (1983) Elatinaceae. *Flora of Ecuador,* **20:** 17–23.

Munz, P. A. (1974) Onagraceae. *Flora of Ecuador,* **3:** 1–46.

Nissen, D. K. R. (1986) A taxonomic revision of section Lomaridium (Presl) J. Sm., genus Blechnum L. in America. Cand. Scient. thesis, University of Aarhus.

Norman, E. M. (1982) Buddlejaceae. *Flora of Ecuador,* **16:** 1–23.

Pringle, J. S. (1995) Gentiananceae. *Flora of Ecuador,* **53:** 1–131.

Rahn, K. (1975) Plantaginaceae. *Flora of Ecuador,* **4:** 23–40.

Renner, S. S. and Hausner G. (1997) Siparunaceae. *Flora of Ecuador,* **59:** 1–98.

Robinson, H. (1978) Compositae-Liabeae. *Flora of Ecuador,* **8:** 1–62.

Robinson, H. (1997) New species of Aphanactis in Ecuador and Bolivia and new combinations in Selloa (Heliantheae: Asteraceae). *Brittonia,* **49:** 71–78.

Robinson, H. and Funk, V. A. (1997) Compositae of Ecuador, I: Key to frequently collected genera. In: Valencia, R. and Balslev, H. (Eds.) *Estudios Sobre Diversidad y Ecología de Plantas,* pp. 65–75. Quito: P. Universidad Católica del Ecuador.

Robson, N. K. B. (1987) Studies in the genus Hypericum L. (Guttiferae) 7. Section 29. Brathys (part 1). *Bulletin of the British Museum of Natural History (Botany),* **16:** 1–106.

Robson, N. K. B. (1990) Studies in the genus Hypericum L. (Guttiferae) 8. Section 29. Brathys (part 2) and 30. Trigynobrathys. *Bulletin of the British Museum of Natural History (Botany),* **20:** 1–151.

Romoleroux, K. (1996) Rosaceae. *Flora of Ecuador,* **56:** 1–151.

Seberg, O. (1988) Taxonomy, phylogeny, and biogeography of the genus Oreobolus R. Br. (Cyperaceae), with comments on the biogeography of the South Pacific continents. *Botanical Journal of the Linnenan Society,* **96:** 119–195.

Skog, L. E. (1987) Coriariaceae. *Flora of Ecuador,* 30: 1–7.

Skog, L. E. and Kvist, L. P. (1997) The Gesneriaceae of Ecuador. In: Valencia, R. and Balslev, H. (Eds.) *Estudios Sobre Diversidad y Ecología de Plantas,* pp. 13–23. Quito: P. Universidad Católica del Ecuador.

Smith, A. R. (1983) Polypodiaceae-Thelypteridoideae. *Flora of Ecuador,* **18:** 1–147.

Smith, A. R. (1993) Terpsichore, a new genus of Grammitidaceae (Pteridophyta). *Novon,* **3:** 478–489.

Smith, L. B. and Downs, R. J. (1974) Pitcairnioideae, Bromeliaceae, part 1. *Flora Neotropica Monographs,* **14:** 1–660.

Smith, L. B. and Downs, R. J. (1977) Tillandsioideae, Bromeliaceae, part 2. *Flora Neotropica Monographs,* **14:** 663–1492.

Smith, L. B. and Wasshausen, D. C. (1986) Begoniaceae. *Flora of Ecuador,* **25:** 1–65.

Sparre, B. (1973) Tropaeolaceae. *Flora of Ecuador,* **2:** 1–21.

Sparre, B. and Andersson, L. (1991) A taxonomic revision of the Tropaeolaceae. *Opera Botanica,* **108:** 1–140.

Spencer, M. A. and Smith, L. B. (1993) Racinaea, a new genus of Bromeliaceae (Tillandsoideae). *Phytologia* **74:** 151–160.

Stolze, R. G. (1986) Polypodiaceae - Asplenioideae. *Flora of Ecuador,* **23:** 1–82.

Stolze, R. G., L. Pacheco and Øllgaard, B. (1994) Polypodiaceae-Dryopteridoideae-Physematieae. *Flora of Ecuador,* **49:** 1–106.

Taylor, P. (1975) Lentibulariaceae. *Flora of Ecuador,* **4:** 7–21.

Todzia, C. (1990) Chloranthaceae. *Flora of Ecuador,* **40:** 1–31.

Tryon, R. (1986a) Cyatheaceae. *Flora of Ecuador,* **27:** 17–56.

Tryon, R. (1986b) Dicksoniaceae. *Flora of Ecuador,* **27:** 1–6.

Tryon, R. (1986c) Lophosoriaceae. *Flora of Ecuador,* **27:** 7–11.

van der Hammen, T. and Cleef, A. M. (1986) Development of the high Andean páramo flora and vegetation. In: Vuilleumier, F. and Monasterio, M. (Eds.) *High Altitude Tropical Biogeography,* pp.153–201. Oxford: Oxford Universisty Press.

Weigend, M. (1996) A revision of the Loasaceae of Ecuador. *Botanische Jahrbücher,* **118(2):** 228–294.

Wurdack, J. J. (1980) Melastomataceae. *Flora of Ecuador,* **13:** 1–406.

Øllgaard, B. (1988) Lycopodiaceae. *Flora of Ecuador,* **33:** 1–155.

The zonal páramo vegetation of Volcán Chiles

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SUMMARY

A survey of the zonal páramo vegetation of Volcán Chiles was carried out in 1987. Three replicate 5 x 5 m quadrats were randomly located at each 100 m of elevation from 3600 to 4200 m on the southern, Ecuadorian side of the mountain. Quantitative measurements were made of slope, aspect and soil pH, whilst disturbance and exposure were recorded on ordinal scales. Altogether, there were 201 species in the samples (93 vascular plant species, and 108 operational cryptogam species). Species diversity, diversity at family level, and the number of growth forms were all more or less uniform across the altitudinal range, though there were more cryptogam species in the samples at higher altitudes. The survey revealed a clear distinction in composition between frailejonal at lower altitudes (dominated by *Calamagrostis* tussocks and *Espeletia* giant rosette plants) and superpáramo at higher altitudes (with more equitable community structure between tussocks, cushions and shrubs). There was also an evident transition zone at 3900-4000 m with its own particular character, which demands further investigation. Although several of the environmental variables were statistically related to the patterns of species distributions in the samples, it was impossible to determine mechanisms that might explain species distributions because many of the potentially explanatory variables were intercorrelated (*e.g.*, disturbance and climate). Controlled experiments that isolate such factors are required.

RESUMEN

Se realizó un estudio de la vegetación zonal del páramo del Volcán Chiles en 1987. Tres cuadrantes (réplicas) de 5 x 5 m se localizaron al azar en cada 100 m de elevación desde 3600 hasta 4200 m en el lado austral y ecuatoriano de la montaña. Se efectuaron medidas cuantitativas de la pendiente, la orientación y el pH del suelo, mientras que la perturbación y la exposición se registraron en escalas ordinales. En total, se encontraron 201 especies dentro de las muestras (93 especies de plantas vasculares y 108 especies operacionales de criptogamas). La diversidad de especies, la diversidad al nivel de familia y el número de formas de crecimiento fueron mas o menos uniformes a través del rango altitudinal, pero existieron mas especies de criptogamas en las muestras de mayor altitud. El estudio reveló una distinción clara en composición entre el frailejonal en las partes bajas (dominando por macollos de *Calamagrostis* y rosetas gigantes de *Espeletia*) y el superpáramo en las partes altas (con una estructura comunitaria mas equitativa entre macollos, cojines y arbustos). Hubo también una zona de transición evidente entre 3900 y 4000 m con un carácter propio que demanda mas investigación. Aunque varias variables ambientales se relacionaron estadísticamente con las patrones de distribución de las especies en las muestras, no fue posible determinar mecanismos que pudieran explicar estas distribuciones pues muchas de las variables explicativas potenciales estuvieron intercorrelacionadas (por ejemplo, la perturbación y el clima). Es necesario llevar a cabo experimentos controlados que permitan aislar tales factores.

Key words: tropical alpine, plant communities, species diversity, altitudinal zonation

INTRODUCTION

The Ecuadorian páramos, high-altitude ecosystems above the upper forest line in the Andes, are the focus of increasing ecological attention. Many remote páramos, having been subjected to very little human influence, offer the opportunity to develop theories about community structure and to study adaptation of organisms to the peculiar environmental conditions found in these mountains. The majority of páramos, though, have been altered significantly by people, especially by burning practices (Laegaard 1992, Ramsay and Oxley 1996). These areas offer the prospect of more applied ecological research (Hofstede 1995, Keating 1998, 2000, Verweij 1995, Ramsay 1999, 2001). The High Andes also provide an opportunity to examine the biogeography of páramo plants and animals, a significant proportion of which are endemic. The task of describing new species, discovering their ranges, and analysing the resulting patterns in biogeographic and phylogenetic terms is exciting but still in its early stages, even for plants (Luteyn 1999). Since the páramos provide the vital ecological service of regulating Andean hydrology (Luteyn 1999), the ecology of these systems and their management holds significance for large populations of Andean peoples.

As interest in the Ecuadorian páramos grows, so too does the importance of the vegetation as a context for a wide range of ecological investigations. One barrier to progress concerns the identification of the plants themselves. In spite of the large number of good collections from the páramos, the *Flora of Ecuador* is still in the early stages of production: Jørgensen and Ulloa (1994) estimated that it would not be complete for another 70-120 years at its current speed of publication. Therefore, it is prudent to consider alternative strategies in the meantime. Checklists and distributional studies represent one way of narrowing down the effort required to identify species, and these have been produced for the páramo domain as a whole (Luteyn 1999), as well as on national (Jørgensen and Ulloa 1994, Sklenář and Jørgensen 1999) and regional (Balslev 2001) scales.

There have been two main approaches to the description of páramo vegetation, which are incompatible with each other, focus on quite different questions, and are subject to very different forms of analysis and interpretation:

- *Phytosociological ("Plant community taxonomy")*
  This is a common approach which attempts to identify and describe types of plant assemblages ("communities") in terms of their species

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composition. It seeks out many different assemblages of plants and demonstrates the range of community composition present in an area. However, there are a number of drawbacks with this approach. Firstly, it says nothing of how representative these communities are in the vegetation as a whole, since the survey is deliberately biased to select examples of different "types". This means that the statistical treatment of the relationships between species and environmental factors is invalid. Secondly, and perhaps just as problematical, it assumes the existence of communities as entities with their own essential character. This assumption has been largely discredited in ecology, both theoretically and empirically, in favour of a more individualistic concept of community composition: species distributions are determined independently rather than in combination. The difference between these concepts can be visualised as the difference between the alphabet (communities present in various states, A, B, C, *etc.)* and a rainbow (communities continuously varying and intergrading, but with particular character at any one point). Nevertheless, the phytosociological approach can provide a valuable insight into the range of species assemblages present in an area and the diversity of habitat types.

Good examples of phytosociological treatments include Cleef's (1979, 1981) descriptions of Colombian páramos, and a recent summary of Colombian paramo vegetation by Rangel-Ch .(2000).

- *Statistical*
  A very different approach is to describe the *typical* vegetation of an area by random sampling. If done well, it can provide data appropriate to statistical analysis (no bias present), and is consistent with modern thinking on the functioning and development of communities. However, it suffers from a number of problems. One charge is that, in dealing with the typical vegetation, it usually overlooks rarer assemblages that may be of interest. Furthermore, if the number of samples is low, the representativeness of the samples is open to question and the survey may miss even quite common assemblages. One compromise is a stratified sampling design where particular vegetation types (or altitudes) are selected but then sampled in a random fashion. This approach allows an assessment of the relative contributions of different species to the vegetation, and permits statistical examination of the relationships between these species and the environment.

  This approach was first used in the páramo by Baruch (1984) in Venezuela. Two Ecuador-wide surveys of páramo vegetation have been conducted so far (Ramsay 1992, Sklenář 2000) and have already resulted in several statistical treatments of páramo vegetation (Ramsay and Oxley 1997, Sklenář and Ramsay in press). This kind of approach is well-suited to finer-scale studies, such as that reported by Coombes and Ramsay (2001) and Sklenář (2001).

Most accounts of the páramo follow Cuatrecasas (1934, 1958, 1968) in defining three broad altitudinal zones: the subpáramo, grass páramo and superpáramo *(e.g.,* Luteyn 1999). Generalised treatments of páramo zonation in Ecuador are given by Harling (1979), Jørgensen and Ulloa (1994), Ramsay (1992) and Sklenář (2000). In addition to the zonal vegetation, there are also pockets of azonal vegetation in the páramos, such as mires, woodlands and lakes, as well as along linear features like rivers and streams.

A preliminary statistical survey of the zonal vegetation of Volcán Chiles is presented here, subject to a number of criticisms outlined earlier. However, it is hoped that this study, in conjunction with those provided by Balslev (2001), Sklenář (2001), Coombes and Ramsay (2001) and Terneus (2001) will form a focus for more detailed survey work on Volcán Chiles in the future. The study defines the composition of sample plots chosen at random at seven altitudes, the patterns of species distribution and diversity in these plots, and the relationship between community structure and a small number of easily measured environmental variables.

METHODS

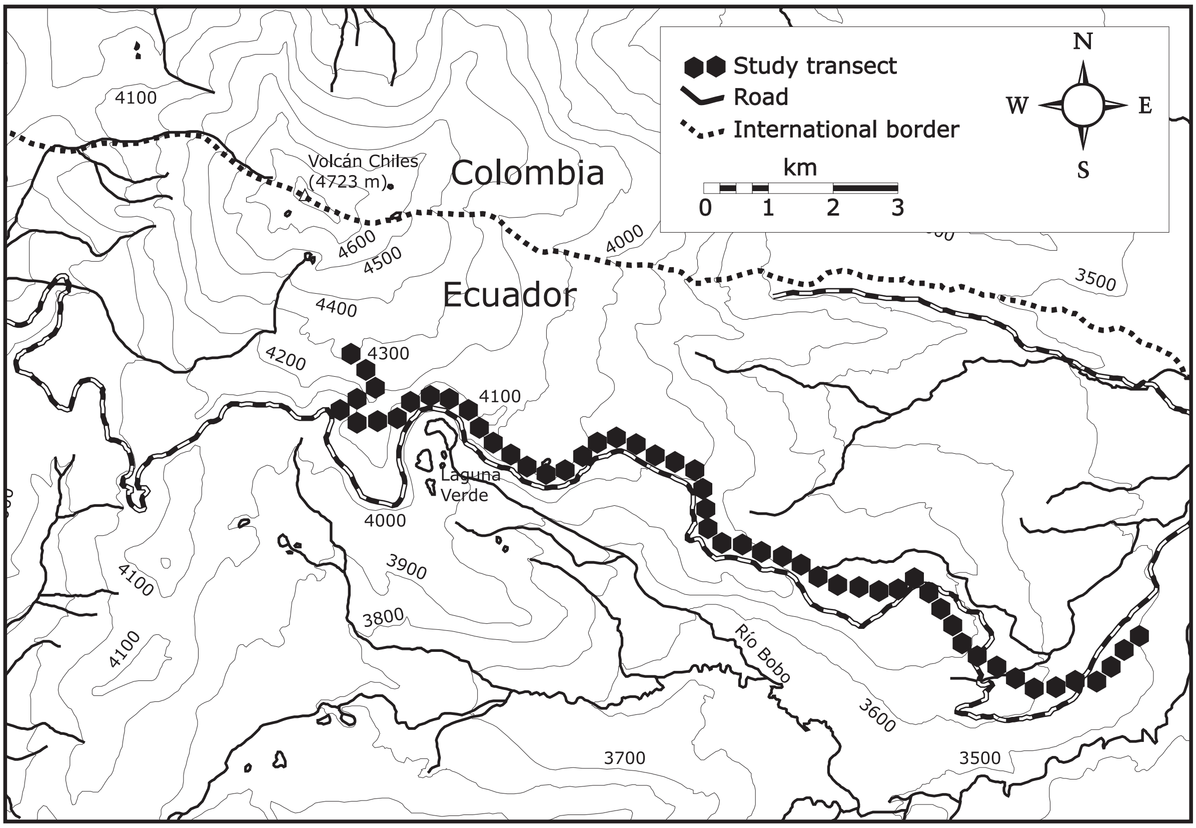
Study areas

The zonal páramo vegetation of Volcán Chiles was recorded at seven altitudes between Tufiño and the summit, along an altitudinal transect from 3600 to 4200 m, on the southern, Ecuadorian side of the mountain (Fig. 1). The survey was carried out on 20-22 October 1987.

Vegetation sampling

Three replicate 5 x 5 m quadrats were randomly located at each 100 m of elevation over the altitudinal range studied. A complete species list of both vascular plants and cryptogams (lichens, mosses and hepatics) was recorded along with corresponding Braun-Blanquet cover abundance scores for each species. Voucher specimens of vascular plants that could not be identified in the field were collected. Complete cryptogam collections were made for each quadrat and later compared to produce the species lists and voucher specimens. The cryptogams remain largely unidentified, but have been included in the analyses. Nomenclature for vascular plants follows Luteyn (1999).

Fig. 1. Location of the vegetation sampling transect on Volcán Chiles.



Environmental factors

Factors with possible influence on the vegetation were also noted. Quantitative records were made of altitude, slope and aspect. Estimates of percentage cover of bare soil and exposed rock surfaces were also made. Exposure, and overall disturbance of the vegetation (a mixture of burning, trampling and grazing intensity) were recorded on ordinal scales from 0 to 5, where 0 represents the absence of the influence and 5 the highest influence. Soil pH was measured using a Whatman pH meter (2:1 ratio of water to soil by volume).

Analyses

The Braun-Blanquet cover abundance scores were converted into their mid-point percentage cover values (1 =2.5%, 2=15%, 3=37.5%, 4=62.5%, 5=87.5%) before the analyses were performed. The vascular plant species were also placed into the growth form categories defined by Ramsay and Oxley (1997). Within a quadrat, the abundances of all species belonging to each growth form were summed. A similar approach was adopted to sum abundances of species within families.

Species diversity was examined using four different measures. The first was the number of species in each 25 m² sample (species richness, S). Shannon's index of information content, was calculated according to the formula:

$$H' = \sum_{i=1}^{S} p_i \log p_i$$

where p_i is the proportional abundance of species i in the sample. The evenness of non-zero species abundances (equitability) was calculated by:

$$E = \frac{H'}{\ln S}$$

Finally, the complement of Simpson's original index for a finite population was calculated as follows:

$$D = 1 - \sum_{i=1}^{S} p_i^2$$

It represents the likelihood that two randomly chosen individuals will be different species, reaching maximal values for a sample with all species present in equal abundance.

β-diversity, the extent of species change along the altitudinal gradient, was calculated according to the measure proposed by Wilson and Shmida (1984):

$$\beta_{\mathrm{T}} = \frac{[g(H) + l(H)]}{2\overline{\alpha}}$$

where g(H) is the number of species gained along the gradient, l(H) is the number lost and $\overline{\alpha}$ the mean number of species per sample across the entire gradient For this analysis, the composition of the three replicate quadrats at each altitude were summed, and species distributions along the gradient were simplified by assuming they were continuous within their upper and lower limits. The lowest altitude was used as the reference composition, against which all of the other altitudes were compared.

The samples and species were grouped by cluster analysis (using relative Sørensen's distance measure and Ward's method of group linkage), and indicator species for the resulting groups were determined using the method proposed by Dufrêne and Legendre (1997). The vegetation samples were ordinated (using the Bray-Curtis method, modified to use relative Sorensen's distance measure and endpoint selection by variance-regression). All of these analyses were performed with the PC-ORD) package (McCune and Mefford 1999).

Canonical Correspondence Analysis was carried out using Canoco 4 (ter Braak and Šmilauer 1998) to determine whether community structure was related to the measured environmental parameters. Before running this analysis, outlier species were identified (with PC-Ord, using the Chi-squared distance measure implicit in CCA) and eliminated to limit the bias of these species in the analysis. Without doing this, the distinctiveness of a sample may be exaggerated by the presence of rare species.

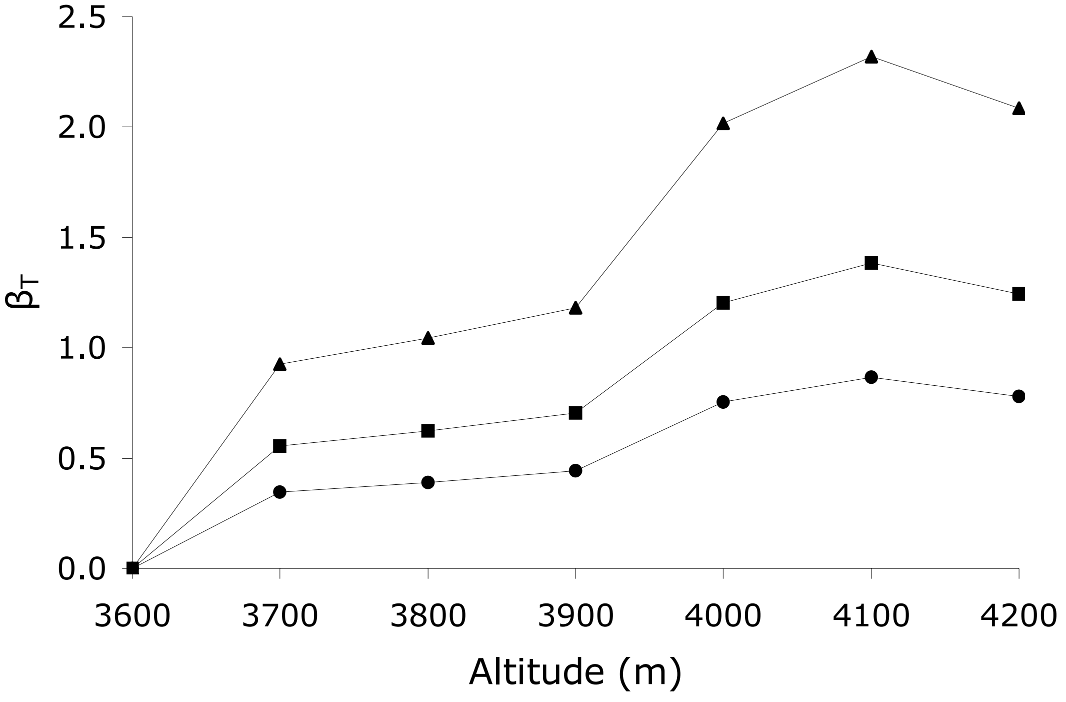
RESULTS

Altogether, there were 93 vascular plant species present in the samples. In addition, 108 operational cryptogam species were recorded, making 201 species in all. The vascular plant species present in each quadrat are shown in Appendix 1.

There was a very clear division between higher altitudes (4000 m and above), with high cryptogam species richness, and the samples at 3900 m and below which contained significantly fewer cryptogam species (Table 1). Overall, taking into account both vascular plants and cryptogams, species richness was lower at 3800 and 3900 m than at other altitudes. The number of species in 25 m² plots varied from 22 to 47, and 74 species were found in all three plots combined at 4100 m.

Family diversity and the number of growth forms were both relatively constant across the altitudinal range (Table 1). Family richness was slightly lower at the highest altitudes, and these plots lacked giant stem rosette plants (*Espeletia pycnophylla*). Species diversity was more or less uniform across the altitudinal range, with slightly higher values at altitudes 4000 m and above, particularly for species evenness of cryptogams (Table 2). β-diversity of vascular plants increased most rapidly at 4000 m

Fig. 2. Rates of species turnover in vegetation samples from 3600 m to 4200 m on Volcán Chiles. β-diversity (β_T) represents the turnover of species along the altitudinal gradient diversity for smoothed species distributions (discontinuities filled) compared with the plots at 3600 m. Symbols: ⬇, all plants; ■, vascular plants only; ⬉, cryptogams only.



(Fig. 2). The pattern is similar for vascular plants and cryptogams. This indicates a more rapid turnover of species at 4000 m than in other parts of the altitudinal gradient.

Cluster analysis (Fig. 3) and Bray-Curtis ordination (Fig. 4) of the sample composition data indicate four main types of vegetation. The vegetation from 3600-3800 m inclusive differs considerably from that at 4100–4200 m. The transition between these two zones is marked by quite distinct vegetation at 3900 m, and again at 4000 m. The most significant components of these four types of vegetation is given below:

- 4100–4200 m
  No species were dominant, with an even mix of tussock grasses (*Calamagrostis intermedia, C. guamensis, C. effusa, Agrostis foliata, Festuca asplundii*), cushion plants (*Aciacne flagellifera, Xenophyllum humile, Azorella aretioides, Plantago rigida*) and upright shrubs (*Diplostephium rupestre, Monticalia stuebelii*). Indicator species at 4200 m: *Huperzia crassa*. Indicator species at 4100 m: *Calamagrostis effusa, Plantago rigida.*
- 4000 m
  Dominated by tussocks of *Calamagrostis intermedia*, with relatively high cover of *Valeriana plantaginea.* Indicator species: *Lachemilla orbiculata, Lasiocephalus ovatus, Valeriana plantaginea, Xenophyllum crassum, Geranium* sp.
- 3900 m
  Dominated by tussocks of *Agrostis* sp. (plus *Agrostis foliata* and *Rhynchospora macrochaeta*), with giant rosettes of *Espeletia pycnophylla.* Indicator species: *Agrostis* sp., *Gynoxys fuliginosa, Poa* sp.
- 3600-3800 m
  Tussock grasses (*C. intermedia*, with *Agrostis* sp. and *Rhynchospora macrochaeta*) and giant rosette plants (*E.pycnophylla*) were co-dominant. *Lupinus prostrata* locally common at 3800 m; *Paspalum bonplandianum, Hypochaeris sessiliflora* and *Rhynchospora ruiziana* locally common at 3600 m. Indicator species at 3800 m: *Espeletia pycnophylla.* Indicator species at 3600–3700 m: *Blechnum loxense, Gamochaeta pensylvanica, Hypericum decandrum, Paspalum bonplandianum.*

Figure 3. Cluster analysis of 21 páramo vegetation samples (both vascular plants and cryptogams).

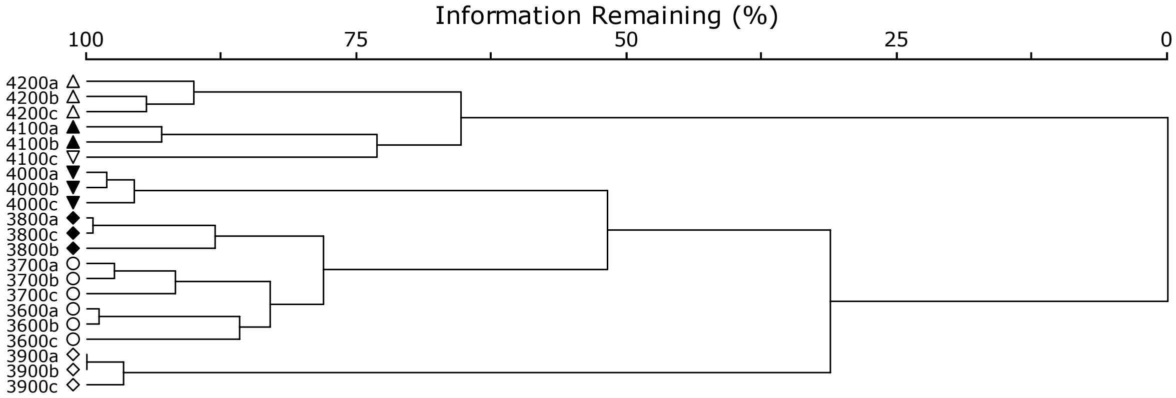


Table 1. Summary of composition of 21 samples of zonal páramo vegetation on Volcán Chiles. The mean number of taxa (± standard deviation) in three samples at each altitude ("25 m²") and the total number per altitudinal level ("Σ") are shown for vascular plants, cryptogams, and both groups combined. For vascular plants only, the number of families and growth forms ("GFs") at each altitude are also presented.

Altitude (m)	**Vascular plants**				**Cryptogams**		**Combined**	
	25 m²	**Σ**	**Families**	**GFs**	**25 m²**	**Σ**	**25 m²**	**Σ**
3600	24.0 ± 2.6	29	13.0 ± 1.0	7	8.7 ± 0.6	16	32.7 ± 2.1	45
3700	30.3 ± 3.2	44	15.0 ± 0.0	8	9.7 ± 2.5	19	40 ± 1.7	63
3800	22.7 ± 4.7	34	14.3 ± 2.3	8	4.3 ± 1.2	7	27 ± 5.6	41
3900	20.3 ± 3.5	28	13.0 ± 1.7	9	6.7 ± 1.2	13	27 ± 2.6	41
4000	19.3 ± 0.6	29	10.7 ± 0.6	8	16.0 ± 4.6	25	35.3 ± 4.5	54
4100	25.0 ± 3.5	39	12.3 ± 2.1	9	16.7 ± 4.2	35	41.7 ± 7.6	74
4200	16.0 ± 2.0	24	10.3 ± 1.5	8	20.7 ± 1.5	31	36.7 ± 2.9	55

Table 2. Mean species diversity scores (± standard deviation) for three samples of plant communities at each altitude. "H'" is the Shannon Index of Information Content, "E" is the evenness of non-zero species abundances (equitability), and "D" is Simpson's Index.

Altitude (m)	**Vascular plants**			**Cryptogams**			**Combined**		
	H'	***E***	***D***	***H'***	***E***	***D***	***H'***	***E***	***D***
3600	0.7 ± 0.1	2.4 ± 0.1	0.8 ± 0.0	1.0 ± 0.0	2.2 ± 0.1	0.9 ± 0.0	0.8 ± 0.1	2.7 ± 0.2	0.9 ± 0.0
3700	0.8 ± 0.1	2.7 ± 0.3	0.9 ± 0.1	1.0 ± 0.0	2.2 ± 0.3	0.9 ± 0.0	0.8 ± 0.1	3.1 ± 0.2	0.9 ± 0.0
3800	0.7 ± 0.1	2.2 ± 0.3	0.8 ± 0.1	1.0 ± 0.0	1.4 ± 0.3	0.8 ± 0.1	0.7 ± 0.1	2.4 ± 0.4	0.8 ± 0.1
3900	0.8 ± 0.0	2.3 ± 0.2	0.8 ± 0.1	1.0 ± 0.0	1.9 ± 0.2	0.8 ± 0.0	0.8 ± 0.0	2.7 ± 0.1	0.9 ± 0.0
4000	0.8 ± 0.0	2.3 ± 0.0	0.8 ± 0.0	1.0 ± 0.0	2.7 ± 0.3	0.9 ± 0.0	0.9 ± 0.0	3.1 ± 0.2	0.9 ± 0.0
4100	0.9 ± 0.0	3.0 ± 0.2	0.9 ± 0.0	1.0 ± 0.0	2.8 ± 0.3	0.9 ± 0.0	1.0 ± 0.0	3.6 ± 0.2	1.0 ± 0.0
4200	0.9 ± 0.0	2.6 ± 0.1	0.9 ± 0.0	1.0 ± 0.0	3.0 ± 0.1	1.0 ± 0.0	1.0 ± 0.0	3.5 ± 0.1	1.0 ± 0.0

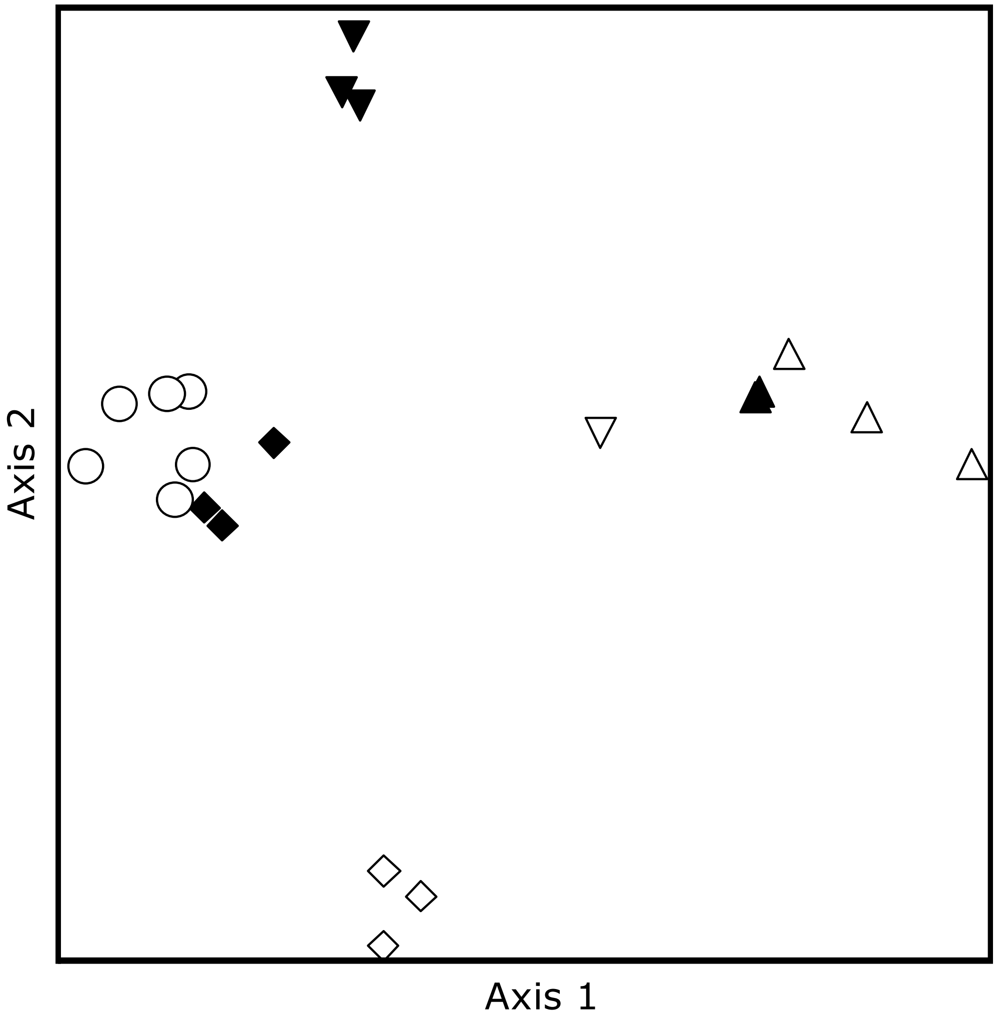
Table 3. Environmental variables associated with 21 páramo vegetation samples on Volcán Chiles. Each altitude was sampled with three replicates. The mean is shown (± standard deviation, unless the values were equal for all three replicates).

Variable	**Altitude (m)**						
	3600	**3700**	**3800**	**3900**	**4000**	**4100**	**4200**
Slope (°)	19	14 ± 7	16 ± 3	20 ± 1	15	23 ± 2	26 ± 3
Aspect (°)	180	0	180	90	180	270	90
Bare Ground (% cover)	5	1	1	1			25 ± 14
Rock (% cover)							4 ± 2
Soil pH	4	5	5	4	4	5	5
Exposure	3	3	3	4	3	4	4
Overall Disturbance	4	4	3	4	2	0	0

Although some cryptogam species were found across a wide altitudinal range, many were restricted to one particular altitude. Therefore, cryptogams may represent an important means of distinguishing and defining vegetation types in the páramo. In this study, half of the species highlighted by indicator analysis were cryptogams. Unfortunately, the current difficulties in identifying these plants limits their use in this regard.

Apart from altitude, there were other environmental differences between the samples (Table 3). Although slopes were generally similar, the aspect of the sites differed substantially. Disturbance was moderate to high up to 4000 m and was more or less absent from 4100 and 4200 m plots. The highest altitude had a high proportion of bare ground and the some rock cover. There was not much difference between the samples in terms of exposure or soil pH. Canonical correspondence analysis demonstrated that these environmental variables were significantly related to the composition of the plant communities (Monte Carlo permutation test, p=0.005). In particular, disturbance and exposure were most strongly correlated to the distribution of species within the samples. The relationship between samples in CCA ordination space was very similar to that shown in the Bray-Curtis ordination.

Fig. 4. Bray-Curtis ordination of 21 vegetation samples (both vascular plants and cryptogams included). Symbols: ○, 3600 & 3700 m; ●, 3800 m; ◇, 3900 m; ▼, 4000 m; ▽, 4100 m c; ▲, 4100 m a&b; △, 4200 m.



DISCUSSION

Although 93 vascular plant species and 108 operational cryptogam species were recorded in this survey, they represent only a small fraction of the total number of páramo species: 2.7% of the 3399 known vascular plants and 8.3% of the known non-vascular plants (Luteyn 1999). However, the total sampling area was just 525 m^2 and was restricted to zonal vegetation. More samples, and inclusion of a variety of additional habitats (*e.g.*, mires, woodlands, riparian zones) would have yielded far more species.

Tussock grasses and giant rosette plants dominate the zonal páramo vegetation at lower altitudes on Volcán Chiles (up to 3800 m). This kind of vegetation is usually referred to as frailejonal (*e.g.*, Rangel-Ch. 2000). Vascular plant species richness was relatively high, but cryptogam richness was not as great as at higher altitudes. The combination of *Calamagrostis* tussocks and *Espeletia* rosettes as dominants is consistent with reported vegetation for Colombian páramos in general (Cleef 1981, Rangel 2000). In addition, more specific comparisons show strong similarities between Chiles vegetation and that of nearby mountains across the border in Colombia. *C. effusa* tussocks and *E. pycnophylla* rosettes dominated the lower slopes of the nearest mountains, Cumbal and Azufral, while the low-altitude páramo vegetation of Galeras, further away but still in the Nariño region, was dominated by *C. effusa* tussocks and *E. hartwegiana* rosettes (Rangel-Ch. and Ariza-N. 2000). Although *C. effusa* was sometimes dominant on the Ecuadorian side of Volcán Chiles, *C. intermedia* was usually the dominant tussock-former. It may be that reported differences in the dominant tussock plants between the mountains of northern Ecuador and southern Colombia reflect discrepancies in identification: *C. effusa* is listed by Rangel-Ch. and Ariza-N. (2000) as the dominant on the Colombian side of Volcán Chiles, but *C. intermedia* is not mentioned at all. However, since Ramsay (2001) found *C. effusa* tussocks recovered faster than *C. intermedia* after a fire on Volcán Chiles, variations in land management practices either side of the border may be responsible for vegetation differences.

The frailejonal vegetation of Volcán Chiles is also similar to that found in the nearby Ecuadorian páramos of El Angel and San Francisco (pers. obs.). However, the majority of Ecuadorian páramos lack *Espeletia* giant rosette plants (Ramsay 1992, Monasterio 1980). Nevertheless, they are dominated by tussock grasses, of which *C. intermedia* is the most widespread and abundant (Ramsay 1992).

Superpáramo vegetation at higher altitudes on Volcán Chiles (4100-4200 m) was not dominated by any one species or growth form, though tussock grasses and cushion plants were common at these altitudes. Again, similar vegetation types have been reported from the nearby mountains of the Nariño region of Colombia (Rangel-Ch. and Ariza-N. 2000). Lack of dominance seems to be a characteristic feature of superpáramos in Ecuador (Ramsay 1992, Sklenar and Ramsay in press) and Colombia (Cleef 1981, Rangel-Ch. 2000). Sklenar (2001) provides a more detailed account of the superpáramo vegetation of Volcán Chiles.

The evident physiognomic difference between frailejonal (dense tussocks and giant rosette plants) and the high-altitude superpáramo (low, open vegetation on rocky ground) is likely to be important in determining the distribution patterns of other species (both plants and animals) in the páramo. There was a higher turnover of plants, especially cryptogams, at 4000 m on Volcán Chiles where this change took place. Sklenar and Ramsay (in press) have identified significant differences in species diversity between the grass páramo and superpáramo zones throughout Ecuador.

Thus, the fundamental differentiation of the vegetation of Volcán Chiles into páramo grassland and superpáramo is expected, following the pattern established for páramo vegetation elsewhere in the northern Andes (Baruch 1984, Cleef 1981, Ramsay 1992, Sklenar 2000). However, an interesting and new finding of this survey is the existence of a very distinct transition zone between grass páramo and superpáramo, located at 3900–4000 m. There appeared to be a narrow band of vegetation between grass páramo and superpáramo where tussocks of *Agrostis* spp. and *Calamagrostis* spp. formed an association with giant rosettes of *Espeletia pycnophylla*. The giant rosette plants were patchier in distribution and, in their place, *Valeriana plantaginea* was locally abundant. A number of other species appeared to be most abundant around this transition zone. It may be that throughout the páramos, there are species that take advantage of the "edge effects" at the transition from dense tussock vegetation to more open páramo vegetation. If the lower grassy páramo is a disturbance-mediated vegetation, these ecotone species may have originally inhabited the ecotone between forest and superpáramo.

Ramsay (1998) described cyclical dynamics between tussock grasses and cushion plants at the interface between grass páramo and superpáramo in central Ecuador. In that case, successional patterns in plant populations and abundance were driven by the growth and decline of tussocks and cushions. This may provide further opportunities for species in a temporal as well as spatial sense at the ecotone.

The mechanisms responsible for the transition from páramo to superpáramo are not yet understood. In this study, a few crude environmental measures were taken, and were found to relate statistically to species distribution patterns. However, these correlations are not particularly convincing because of the lack of an associated mechanism by which these factors influence plant distribution. More detailed work is required to relate environmental variables to plant distribution in the páramo. Particular emphasis should be placed on water availability, microclimates, soil types and nutrient levels. Disturbance, particularly that related to agriculture, is also a significant controlling factor.

These environmental variables, including disturbance frequencies and intensities, vary with altitude non-independently. This presents a very real problem for understanding distribution patterns in the páramo: it is impossible to assign significance to any variable if it covaries simultaneously with others. It is possible, as in this study and many others, to correlate environmental variables with the distribution patterns of organisms, but since several variables show similar trends one cannot tell which are most important in driving the patterns. Most importantly, there is a problem disentangling cause and effect with various disturbances. For example, does burning promote tussock grasses or *vice versa*? To what extent is vegetation responding to the frequencies and intensities of disturbance, or encouraging burning, grazing and trampling? Observational data cannot distinguish these potential causes of vegetation patterns because they rely entirely on correlative evidence. The matter can only be resolved with controlled experiments that isolate the factors by forcing independence. This kind of ecological work is badly needed in the páramo, but requires resources and time.

In summary, this simple survey of the zonal páramo vegetation of Volcán Chiles revealed a clear distinction between frailejonal (dominated by tussocks and giant rosette plants) and superpáramo (with more equitable community structure between tussocks, cushions and shrubs). There was also an evident transition zone with its own particular character. However, the zonal páramo is more complex than this survey suggests, composed of a mosaic of disturbance patches overlaid on a complex topography. A much more detailed survey is required to obtain a good picture of the zonal vegetation, and could include azonal habitats such as woodlands, mires and riparian zones. Explanations for the patterns that such a survey might reveal can only be achieved with controlled experiments which isolate various factors that are highly correlated in nature (*e.g.*, disturbance and climate).

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REFERENCES

Balslev, H. (2001) Vascular plants on Volcán Chiles and Páramo del Angel, Ecuador—a preliminary list. In: Ramsay, P. M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*, pp. 1–25. Plymouth: Pebble & Shell.

Baruch, Z. (1984) Ordination and classification of vegetation along an altitudinal gradient in the Venezuelan páramos. *Vegetatio,* **55**: 115-126.

Cleef, A.M. (1978) Characteristics of neotropical páramo vegetations and its subantarctic relations. In: Troll, C.L. (Ed.) *Geoecological Relations Between the Southern Temperate Zone and the Tropical Mountains*, pp. 365-390. Wiesbaden: Franz Steiner.

Cleef, A.M. (1981) *The Vegetation of the Colombian Cordillera Oriental*, University of Utrecht, Proefschrift: Utrecht.

Coombes, L. and Ramsay, P.M. (2001) Vegetation of a cushion mire at 3600 m on Volcán Chiles, Ecuador. In: Ramsay, P. M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*, pp. 47–54. Plymouth: Pebble & Shell.

Cuatrecasas, J. (1934) Observaciones geobotánicas en Colombia. *Trabajos del Museo Nacional de Ciencias Naturales Madrid, Serie Botanica*, **27***:* 1–144.

Cuatrecasas, J. (1958) Aspectos de la vegetación natural de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Fisicas y Naturales,* **10**: 221-264.

Cuatrecasas, J. (1968) Páramo vegetation and its life forms. *Colloquium Geographicum,* **9**: 163-186.

Dufrêne, M. and Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs,* **67**: 345–366.

Harling, G. (1979) The vegetation types of Ecuador—a brief survey. In: Larsen, K. and Holm-Nielsen, L.B. (Eds) *Tropical Botany*, pp. 165-174. London: Academic Press.

Hofstede, R.G.M. (1995) The effects of grazing and burning on soil and plant nutrient concentrations in Colombian páramo grasslands. *Plant and Soil,* **173**: 111-132.

Jørgensen, P.M. and Ulloa, C.U. (1994) *Seed Plants of the High Andes of Ecuador—a checklist.* AAU Reports 34. Aarhus: University of Aarhus.

Keating, P.L. (1998) Effects of anthropogenic disturbances on páramo vegetation in Podocarpus National Park, Ecuador. *Physical Geography,* **19**: 221-238.

Keating, P.L. (2000) Chronically disturbed páramo vegetation at a site in southern Ecuador. *Journal of the Torrey Botanical Society,* **127**: 162-171.

Laegaard, S. (1992) Influence of fire in the grass páramo vegetation of Ecuador. In: Balslev, H. and Luteyn, J.L. (Eds) *Páramo: An Andean Ecosystem under Human Influence*, pp. 151-170. London: Academic Press.

Luteyn, J.L. (1999) *Páramos: a checklist of plant diversity, geographical distribution, and botanical literature,* New York: New York Botanic Garden.

McCune, B. and Mefford, M.J. (1999) *PC-ORD: multivariate analysis of ecological data. Version 4,* Gleneden Beach (Oregon): MjM Software.

Monasterio, M. (1980) Los páramos andinos como región natural. Características biogeográficas generales y afinidades con otras regiones andinas. *In:* Monasterio, M. (Ed.) *Estudios Ecológicos en los Páramos Andinos,* pp. 15–27. Mérida (Venezuela): Universidad de los Andes.

Ramsay, P.M. (1992) *The Páramo Vegetation of Ecuador: the community ecology, dynamics and productivity of tropical grasslands in the Andes.* Ph.D. thesis, University of Wales.

Ramsay, P.M. (1998) Landscape mosaics in the High Andes: the role of fire in páramo communities. In: Kovář , P. (Ed.) *Present and Historical Nature-Culture Interactions in Landscapes (Experiences for the Third Millenium),* pp. 192–199. Prague: Karolinum Press.

Ramsay, P.M. and Oxley, E.R.B. (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetatio,* **124**: 129-144.

Ramsay, P.M. and Oxley, E.R.B. (1997) The growth form composition of plant communities in the Ecuadorian páramos. *Plant Ecology,* **131**: 173-192.

Ramsay, P.M. & Oxley, E.R.B. (2001) An assessment of net aboveground primary productivity in the Andean grasslands of Central Ecuador. *Mountain Research & Development*, **21**: 161-167.

Rangel-Ch., J.O. (2000) La diversidad beta: tipos de vegetación. In: Rangel-Ch., J.O. (Ed.) *Colombia Diversidad Biótica III. La región de vida paramuna,* pp. 658–719. Bogotá: Universidad Nacional de Colombia.

Rangel-Ch., J.O. and Ariza-N., C. (2000) La vegetación paramuna de los volcanes de Nariño. In: Rangel-Ch., J.O. (Ed.) *Colombia Diversidad Biótica III. La* *región de vida paramuna,* pp. 754–784. Bogotá: Universidad Nacional de Colombia.

Sklenář, P. (2000) *Vegetation Ecology and Phytogeography of Ecuadorian Superpáramos.* Ph.D. thesis, Charles University, Prague.

Sklenář, P. (2001) Superpáramo flora and vegetation of Volcán Chiles. In: Ramsay, P. M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*, pp. 39–45. Plymouth: Pebble & Shell.

Sklenář, P. and Jørgensen, P.M. (1999) Distribution patterns of páramo plants in Ecuador, *Journal of Biogeography*, **26**: 681–691.

Sklenář, P. & Ramsay, P.M. (in press) Diversity of zonal páramo plant communities in Ecuador. *Diversity and Distributions*.

ter Braak, C.J.F. and Šmilauer, P. (1998) *CANOCO Reference Manual and User's Guide to Canoco for Windows*, Wageningen: Centre of Biometry.

Terneus, E. (2001) Aquatic plant communities of the páramo lakes of Volcán Chiles, Ecuador. In: Ramsay, P. M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*, pp. 55–63. Plymouth: Pebble & Shell.

Verweij, P.A. (1995) Spatial and temporal modelling of vegetation patterns. University of Amsterdam. Ph.D.

Verweij, P.A. (1995) Spatial and temporal modelling of vegetation patterns. University of Amsterdam. Ph.D.

Wilson, M.V. and Shmida, A. (1984) Measuring beta diversity with presence-absence data. *Journal of Ecology*, **72**: 1055–1064.

Appendix 1. Vascular plant species composition of 21 vegetation samples on Volcán Chiles. Each sample is identified by its altitude (in metres) and a letter representing one of three replicates at each altitude. The percentage cover of each species is represented by the following symbols: • 1-5%, ○ 6-25%, ⭘ 26-50%, ● 51-75%. No species exceeded 75% cover. Percentage frequency represents the proportional occurrence of each species in all 21 samples.

Species	**4200a**	**4200b**	**4200c**	**4100a**	**4100b**	**4100c**	**4000a**	**4000b**	**4000c**	**3900a**	**3900b**	**3900c**	**3800a**	**3800b**	**3800c**	**3700a**	**3700b**	**3700c**	**3600a**	**3600b**	**3600c**	**%Freq**
Geranium sibbaldioides BENTH.	•			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	90
Calamagrostis intermedia (J. PRESL.) STEUD.	•	○	•	•	•	•	⭘	⭘	⭘				●	⭘	⭘	⭘	⭘	●	⭘	⭘	●	86
Carex pygmaea BOECK.		•	•				•	•	•	•				•	•		•	•	•	•	•	62
Halenia kalbreyeri GILG				•						•	•	•	•	•	•	•	•	•	•	•	•	62
Lachemilla uniflora MAGUIRE						•				•	•	•	•	•	•	•	•	•	•	•	•	62
Espeletia pycnophylla CUATREC. subsp. *angelensis* CUATREC.										○	○	•	⭘	•	⭘	○	○	•	•	○	○	57
Lachemilla nivalis (KUNTH) ROTHM.		•	•	•	•	•	•		•		•				•	•	•	•				57
Oritrophium peruvianum (LAM.) CUATR.					•	•				•	•	•	•		•		•	•	•	•	•	57
Agrostis sp.										⭘	⭘	⭘	•	•			•	•	•	•	•	48
Disterigma empetrifolium (KUNTH) DRUDE	•	•	•	•	•	•		•	•	•				•								48
Pentacalia stuebelii (HIERON.) CUATREC.				•	•			•							•	•	•	•	•	•	•	48
Oreobolus goeppingeri SUESS.										•			•	•	•	•	•	•	•	•	•	48
Pernettya prostrata (CAV.) DC.												•	•	•	•	•	•	•	•	•	•	48
Xenophyllum humile (KUNTH) V.A. FUNK	•	•	•	•	•					•	•					•	•	•				48
Azorella aretioides (SPRENG.) DC.	•	•			•					•			•	•	•	•	•					43
Jamesonia goudotii (HIERON.) C.Chr.	•	•	•	•	•	•	•	•	•													43
Lupinus prostratus AGARDH										•	•	•	•	⭘	•		•	•			•	43
Nertera granadensis (MUTIS EX L.F.) DRUCE													•	•	•	•	•	•	•	•	•	43
Agrostis foliata HOOK. f.	•	•		•	•	•				•	•	•										38
Bartsia laticrenata BENTH.	•				•	•					•	•	•	•	•							38
Sisyrinchium jamesonii BAKER										•	•	•	•	•	•	•	•					38
Calamagrostis effusa (KUNTH) STEUD.		•		•	○	•													•	•	•	33
Gentiana sedifolia KUNTH			•	•	•											•	•	•	•			33
Gynoxys fuliginosa (KUNTH) CASS.										•	•	•					•	•	•		•	33
Poa sp.						•				•	•	•		•		•	•					33
Senecio chionageton WEDD.				•	•	•			•				•	•	•							33
Blechnum loxense (KUNTH) HOOK. EX SALOMON																•	•	•	•	•	•	29
Calamagrostis guamensis ESCALONA	•	•	•	•	•	•																29
Carex pichinchensis KUNTH			○	•	•	•	•	•														29
Cerastium danguyi J.F. MACBR.					•	•			•						•	•		•				29
Gamochaeta pensylvanica (WILLD.) CABRERA															•	•	•	•		•	•	29
Hypochaeris sessiliflora KUNTH				•											•	•	•	•			●	29
Jamesonia pulchra HOOK. & GREV.										•	•	•			•				•	•		29
Pentacalia aff. *andicola* (TURCZ.) CUATREC.				•	•	•	•	•	•													29
Paspalum bonplandianum FLÜGGÉ																•	•	•	⭘	○	•	29
Rhynchospora macrochaeta STEUD. EX BOECK.										•	•	•	•	•	•							29
Sibthorpia repens (L.) KUNTZE								•						•	•			•		•	•	29
Viola sp.										•	•	•	•	•	•							29
Diplostephium rupestre (KUNTH) WEDD.	•	•	•	•	•																	24
Festuca asplundii E.B. ALEXEEV			•	•	•	○			•													24
Gentianella ? foliosa (KUNTH) FABRIS	•	•	•	•	•																	24
Hypericum decandrum TURCZ.																•		•	•	•	•	24
Lachemilla orbiculata (RUIZ & PAV.) RYDB.							•	•	•						•		•					24
Lachemilla tanacetifolia ROTHM.							•	•	•	•		•										24
Niphogeton dissecta (BENTH.) J.F. MACBR.		•		•	•		•		•													24
Stachys elliptica KUNTH		•	•	•				•	•													24
Xenophyllum crassum (S.F. BLAKE) V.A. FUNK					•	•	•	•	•													24
Aciachne flagellifera LAEGAARD	•	•	•	•																		19

Appendix 1. Species composition of 21 vegetation samples on Volcán Chiles (continued).

Species	**4200a**	**4200b**	**4200c**	**4100a**	**4100b**	**4100c**	**4000a**	**4000b**	**4000c**	**3900a**	**3900b**	**3900c**	**3800a**	**3800b**	**3800c**	**3700a**	**3700b**	**3700c**	**3600a**	**3600b**	**3600c**	**%Freq**
Arcytophyllum aristatum Standley										•	•				•		•					19
Huperzia crassa (Humb. & Bonpl. ex Willd.) Rothm.	•	•	•	•																		19
Plantago rigida Kunth		•	•	○	•																	19
Valeriana plantaginea Kunth						•	○	○	•													19
Bartsia crisafullii N. Holmgren																•	•	•				14
Diplostephium sp.										•	•			•								14
Eryngium humile Cav.																•	•	•				14
Geranium ? maniculatum H.E. Moore							•	•	•													14
Hypericum thuyoides Kunth																•			•		•	14
Lasiocephalus ovatus Schltdl.							•	•	•													14
Lycopodium clavatum L. subsp. *contiguum* (Klotzsch) B.Øllg.																			•	•	•	14
Oritrophium hieracioides (Wedd.) Cuatrec.																	•			•	•	14
Rhynchospora ruiziana Boeck.																			•	•	○	14
Agrostis breviculmis Hitchc.																•		•				10
Aphanactis jamesoniana Wedd.													•			•						10
Castilleja fissifolia L.f.													•				•					10
Melpomene cf. *moniliformis* (Lag. ex Sw.) Proctor		•			•																	10
Lycopodium magellanicum (P. Beauv.) Sw.																				•	•	10
Ourisia chamaedrifolia Benth.	•				•																	10
Perezia pungens (Humb. & Bonpl.) Less.							•	•														10
Poa sp.							•	•														10
Satureja nubigena (Kunth.) Briq.							•		•													10
Valeriana sp.				•		•																10
Altensteinia ? fimbriata Kunth															•							5
Asteraceae					•																	5
Azorella crenata (Ruiz & Pav.) Pers.									•													5
Bromus lanatus Kunth								•														5
Cotula australis (Sieber ex Spreng.) Hook f.																•						5
Gnaphalium antennarioides DC.											•											5
Huperzia cf. *capellae* (Herter) Holub																	•					5
Luzula gigantea Desv.				•																		5
Lycopodium sp.																	•					5
Melastomataceae							•															5
Monnina crassifolia (Bonpl.) Kunth																					•	5
Ophioglossum crotalophoroides Walt.																	•					5
Orchidaceae										•												5
Pinguicula calyptrata Kunth															•							5
Puya clava-herculis Mez & Sodiro										•												5
Ranunculus peruvianus Pers.																		○				5
Ribes ? hirtum Willd. ex Roem. & Schult.							•															5
Rumex acetosella L.																•						5
Senecio canescens (Humb. & Bonpl.) Cuatrec.																•						5
Valeriana ? niphobia Briq.						•																5
Valeriana microphylla Kunth				•																		5

Superpáramo flora and vegetation of Volcán Chiles

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SUMMARY

A floristic and vegetation survey of the northernmost Ecuadorian superpáramo, on Volcán Chiles, resulted in 105 species of vascular plants. Ordination analysis of twelve vegetation samples, recorded using the Braun-Blanquet approach, distinguished three groups. The major change in the vegetation composition is between the lower and upper superpáramo at 4200-4300 m. This is documented also by the patterns of changes in community diversity and soil data. The floristic composition is discussed in the context of other superpáramo areas.

RESUMEN

Un estudio de la flora y vegetación del superpáramo en el Volcán Chiles resultó en 105 especies de plantas vasculares. Análisis de ordenamiento de las doce muestras de vegetación, mostrado utilizando el enfoque de Braun-Blanquet, distinguió tres grupos. Entre 4200-4300 m la vegetación cambia del superpáramo bajo al superpáramo alto. La transición es también documentada por los resultados de los análisis del suelo y por los índices de diversidad. Se discute la composición florística en el contexto de otras áreas de superpáramo.

Key words: Ecuadorian Andes, ordination analysis, tropical alpine vegetation, páramo, high altitude flora.

INTRODUCTION

Owing to the presence of giant-rosette plants, the páramos of northern Ecuador are unique in the country. Large populations of *Espeletia pycnophylla* CUATREC. cover vast areas of grass páramos in El Angel and Volcán Chiles. Unlike the grass páramo, the superpáramo of northernmost Ecuador is present only on the slopes of Volcán Chiles. Compared with most superpáramos in the rest of Ecuador, its area is rather small, and is developed from about 4200 m to the summit at 4723 m. The closest superpáramo areas are on Volcán Cumbal (4768 m), about 15 km to the north across the border with Colombia, and the mountain Yanaurcu de Piñán (4535 m) located in the same (western) cordillera about 60 km to the south-west.

Superpáramo is a relatively narrow zone in the tropical high Andes found from 4100 m to the snow line at 4800 m (Luteyn 1992). The vegetation of this zone has been described elsewhere (*e.g.,* Monasterio 1980, Cleef 1981, Acosta-Solís 1984, Berg 1998). Superpáramos are isolated areas restricted to the highest mountains, such as Volcán Chiles in Ecuador. Jørgensen (1992) counted 91 and 500+ species of seed plants occurring in the páramos of Ecuador above 4500 m and 4000 m, respectively. The endemism in the Ecuadorian superpáramo flora has been estimated at 16-18% (Sklenář & Jørgensen 1999).

In this study, the superpáramo has been defined as the natural vegetation above the original tree line (*sensu* Lægaard 1992) without human influence, *i.e.,* burning and grazing. In Ecuador, the lower limit of the superpáramo occurs between 4100-4300 m where the tussock grasses give way to dwarfshrubs and cushion plants (Ramsay 1992). The altitudinal position of this transition varies with the geographical location, depending presumably on the precipitation in the area.

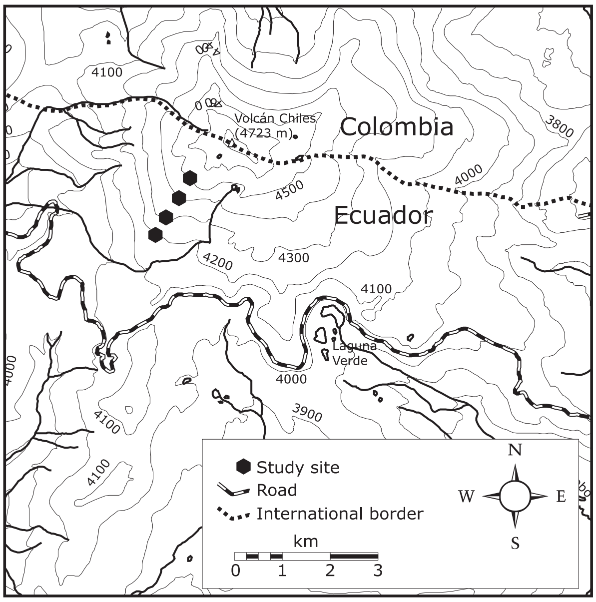
The grass páramo of Ecuador has been described by Ramsay (1992) who also surveyed the area of Volcán Chiles between 3600-4200 m (Ramsay 2001). This paper gives a brief description of the superpáramo of this mountain. The contribution presents a small subset of data of a floristic and vegetation survey of the high Ecuadorian Andes.

METHODS

The south-western side of Volcán Chiles was explored in June and October 1995. The zonal superpáramo vegetation was examined employing the method of stratified random sampling which was also used by Ramsay (1992, 2001). Between 4200 m and 4500 m, twelve sample plots (three randomly set replicate plots at 100 m altitudinal intervals) were established (Fig. 1) and vegetation sampled according to Braun-Blanquet methods (Mueller-Dombois & Ellenberg 1974). The size of most of the plots was 5 x 5 m, but at 4500 m the size was increased to 10 x 10 m. For each plot the following characteristics were estimated in percentage cover: total vegetation cover, bare ground, rocks, shrub layer (E_2, woody species higher then 1 m), herb layer (E_1), bryophytes and lichens layer (E_0, excluding epiphytes). A species list was recorded and their respective covers were estimated using an 8-point scale (r < 0.1%, + < 1%, 1 < 5%, 2a < 15%, 2b < 25%, 3 < 50%, 4 < 75%, 5 < 100%); in the further data treatment, the cover estimates were converted to scores using their midpoint values. Soil samples were taken from the upper 5-10 cm soil layer (bulked from five different spots within the plot) and an average soil depth was estimated by a 50 cm long iron bar. Species growing outside the vegetation plots and in azonal communities (*e.g.,* in boggy depressions, rocky outcrops) were also recorded. Collections of voucher specimens have been deposited at the herbaria AAU, PRC, QCA and QCNE, with a few duplicates located elsewhere.

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 39-45.

Figure 1. Map of study area with the locations of the vegetation samples.



Diversity of the superpáramo vegetation was estimated using the following measures. Within community diversity was estimated with two indices, Simpson's dominance index for the finite sample size:

$$D = \frac{1}{\sum \left(\frac{n_i(n_i - 1)}{N(N-1)} \right)}$$

where n_i is the cover value of the species i, and N is the total sample cover (Peet, 1974), and equitability:

$$E = \frac{D}{S}$$

where S is the species richness of the sample. Between community diversity was estimated acording to Wilson and Shmida (1984):

$$\beta_{\mathrm{T}} = \frac{[g(H) + l(H)]}{2\overline{\alpha}}$$

where the $g(H)$ and $l(H)$ are numbers of species gained and lost, respectively, in the samples along the altitudinal gradient, and $\overline{\alpha}$ is the average species richness. Additionally, turnover of species along the altitudinal gradient was estimated calculating the above index for pairs of adjacent altitudinal levels. The index was calculated with the three sample plots from each altitude pooled to one, and with the vertical distribution of species considered continuous between their maximum and minimum occurrence (Wilson & Shmida 1984).

Soil analyses were carried out in laboratories of the Department of Botany and of the Botanical Institute (Czech Academy of Sciences) in Prague. The following measures were estimated:

- pH–H_2O (1:2 water solution), with an HI 9321 pH-meter
- pH–KCl (1:2 KCl 1.0 normal solution), with an HI 9321 pH-meter
- conductivity (1:2 water solution), with a GRYF 106 LIII meter
- carbon content with a Heraeus Elementary CHN-Rapid Analyzer
- nitrogen content with a Heraeus Elementary CHN-Rapid Analyzer

Correspondence analysis (CA) was performed using the Canoco statistical package (ter Braak & Šmilauer 1998). Indirect rather than direct ordinations were employed since only a small number of samples were available with regards to the number of environmental variables. These were post-hoc fitted as passive variables to the ordination diagram. Nomenclature used in the text follows Luteyn (1999).

RESULTS

In the superpáramo of Volcán Chiles 88 species of vascular plants were recorded above an altitude of 4200 m. Of the 88 species, 62 occurred in the twelve vegetation plots and 26 outside the samples. Additional 17 species, often found in the superpáramo belt elsewhere, were recorded in the grass páramo belt with patches of boggy depressions and rocky outcrops between 4100 and 4200 m. Therefore, a total of 105 species was found (Appendices 1 and 2 provide a full listing). The most important family was Asteraceae with twelve genera and 28 species. Other well represened families were Poaceae (5/8), Cyperaceae and Scrophulariaceae (3/7). The genus *Senecio* L. (including *Culcitium* Bonpl.) had six species. Two other genera, *Lachemilla* (Focke) Rydb. and *Lasiocephalus* Willd. ex Schltdl., were represented by five species each, while 29 genera have only one species each.

The majority of bryophyte and lichen collections are still undergoing determination work. So far the following genera of hepatics have been recognized: *Anastrophyllum* (Spruce) Steph., *Calypogeia* Raddi, *Lepidozia* (Dumort.) Dumort., *Leptoscyphus* Mitt., *Odontoschisma* (Dumort.) Dumort., *Plagiochila* (Dumort.) Dumort., *Riccardia* Gray. The moss genera are *Ångstroemia* Bruch & Schimp., *Breutelia* (Bruch & Schimp.) Schimp., *Bryum* Hedw., *Dicranum* Hedw., and *Racomitrium* Brid. Finally, the following genera of lichens have been determined: *Alectoria* Ach., *Cladia* Nyl., *Cladonia* Hill ex P.Browne, *Dictyonema* Agardh ex Kunth, *Hypotrachyna* (Vain.) Hale, *Oropogon* Th.Fr., *Stereocaulon* Hoffm., and *Thamnolia* Ach. ex Schaerer.

Table 1 shows the pattern of the within community diversity. Number of species per plot decreases with altitude from 22 species at 4200 m to less than 7 species at 4500 m. Both, Simpson's and equitability indices increase from 4200 m and peak at 4300 m. Simpson's index continuously decreases above 4300 m and reaches its minimum at 4500 m, while equitability tends to be constant between 4400 m and 4500 m, and higher than at 4200 m. The between community diversity index calculated for the whole altitudinal gradient is $\beta_t = 1.66$ (species gained $g = 23$, species lost $l = 54$, average species richness $\overline{\alpha} = 23.25$). The turnover of species along the altitude is shown in Fig. 2. Highest change is found between 4200-4300 m. The species turnover notably decreases 100 m higher, and tends to increase again at the highest altitude.

Results of the ordination analysis distinguish three groups of sample plots (Fig. 3a). The three plots at 4200 m form a group representing the lower superpáramo (*sensu* Cleef 1981). This is a narrow belt of shrubby vegetation, on Volcán Chiles comprising *Loricaria ilinissae*, *L. complanata*, *Pentacalia stuebelii*, *P. andicola*, and *Diplostephium rupestre*. Along with the dwarfshrubs, tussock grasses of *Calamagrostis effusa* and *C. intermedia*, small, prostrate shrubs of *Disterigma empetrifolium* and *Arcytophyllum aristatum*, and various herbs (*e.g.*, *Geranium sibbaldioides*, *Jamesonia cinnamomea*, *Lachemilla nivalis*) characterize the lower superpáramo. The position of species in the ordination diagram is shown in Fig. 3b. In the three lower superpáramo plots a total of 37 species were recorded. Lower superpáramo is associated with deep soils and high shrub and herb (E_1, E_2 layers) cover (Fig. 3a, Table 2).

Above 4200 m the shrubs disappear and the vegetation changes into the upper superpáramo (*sensu* Cleef 1981). Its nine vegetation plots located between 4300 m and 4500 m contained 32 species. Some species occurred through the whole gradient (*e.g.*, *Azorella corymbosa*, *Calamagrostis ligulata*, *Huperzia crassa* and *Senecio nivalis*), while other species were recorded from just one altitude (*e.g.*, *Bartsia laticrenata*, *Luzula racemosa*, *Xenophyllum humile*). The three plots at 4300 m form a separate group in the ordination diagram. There are several species occurring only at this altitude (*e.g.*, *Bartsia laticrenata*, *Carex* sect. Aciculares, *Draba extensa*, *Elaphoglossum mathewsii*). In addition, the rather rich bryophyte cover distinguishes the vegetation at this altitude from other upper superpáramo plots (Fig. 3a, Appendix 1). The remaining six plots from 4400 m and 4500 m tend to overlap in the biplot and the altitudinal distinction in vegetation composition is not as evident as in the lower altitude plots.

Table 1. Within community diversity values (mean ± 1 sd, n = 3); D, Simpson's diversity index; E, equitability; S, species richness.

Altitude (m)	D	E	S
4200	8.82 ± 1.28	0.40 ± 0.03	22.3 ± 4.64
4300	18.71 ± 6.34	1.04 ± 0.41	18.3 ± 0.94
4400	8.97 ± 2.86	0.76 ± 0.03	11.7 ± 3.30
4500	5.07 ± 1.10	0.76 ± 0.03	6.7 ± 1.25

Figure 2. Turnover of species along the altitudinal gradient.

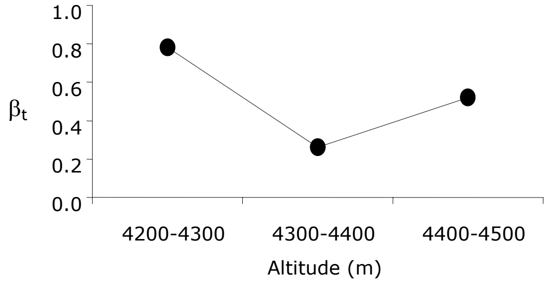
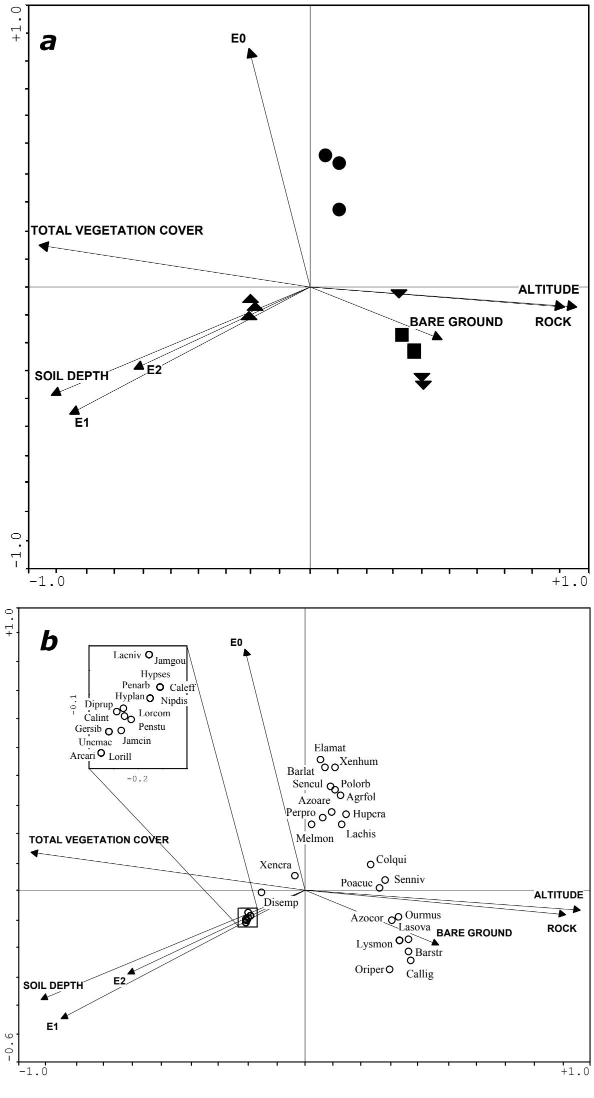


*Figure 3. Results of the correspondence analysis as biplot diagrams. **a.** Vegetation samples (▲, 4200 m; ●, 4300 m; ■, 4400 m (two plots are overlapping); ▼, 4500 m. **b.** Species: each code is constructed with the first three letters of the genus name followed by the first three letters of the species name (refer to Appendix 1 for full names). Due to overlaps not all species are shown. Passive variable are superimposed as dashed arrows, eigenvalues of the ordination axes λ_1=0.876, λ_2=0.625.*



The results of soil analysis are summarized in Table 2. The soils at 4200 m are rather deep without stones and with a small proportion of coarse material (> 2 mm), and a relatively high content of carbon and nitrogen. Above this altitude the soils become poorly developed and at the highest elevation, the soil occurs in small patches scattered amongst the rocks. The sandy substratum is very shallow, with stones and much of coarse material, and the content of carbon and nitrogen is low. The pH tends to increase, and conductivity, C and N decrease with altitude; only at the highest elevation is this reversed.

DISCUSSION

The survey of the superpáramo of Volcán Chiles resulted in 105 species of vascular plants in 56 genera and 28 families. However, as only one side of the volcano was visited (the Ecuadorian side), it can be expected that with further exploration of the whole area additional species will be found. The superpáramo flora of Volcán Chiles is rather rich in species considering its small area. For a comparison, Ecuadorian superpáramos as a whole contain over 300 species (Petr Sklenář, unpublished data). Van der Hammen and Cleef (1986) recorded 107 and 75 species for the superpáramos of Cocuy and Sumapaz, respectively, both in the Colombian Cordillera Oriental. In the superpáramo of Mérida in Venezuela, Berg (1998) found 168 species in 146 phytosociological relevés recorded from both zonal and azonal plant communities.

The flora of Volcán Chiles is representative of most superpáramos of northern and central Ecuador. The majority of its species are widespread and common in Ecuador, and usually also outside the country (*e.g., Bartsia stricta, Diplostephium rupestre, Hypochaeris sessiliflora, Luzula racemosa, Valeriana microphylla, Xenophyllum humile*). However, there are few exceptions which make the flora of a particular phytogeographical interest. Volcán Chiles is the only Ecuadorian locality, and the southern limit of a gentian species *Gentianella selaginifolia*, which can be found growing in open, wet places between 4100-4250 m. Other species (*e.g., Calamagrostis guamanensis, Draba aretioides, D. extensa, Lasiocephalus sodiroi, Senecio culcitioides* and *Senecio nivalis*) may have their northern limit here (Luteyn 1999). The high Andean genus *Nototriche* TURCZ. is absent from Volcán Chiles—suggesting this mountain lies just north of the genus' geographical limit. The closest records of this genus are from the similar superpáramos of Cerro Imbabura and Nevado Cayambe to the south (Petr Sklenář, unpublished data). Some species, such as *Lachemilla tanacetifolia*, *Lasiocephalus gargantanus* and *Pentacalia stuebelii*, have few records in other superpáramos of Ecuador; nevertheless they can be considered rare in the country, and their occurrence on Volcán Chiles is important from the conservation point of view. A few very typical Ecuadorian superpáramo species (*e.g., Baccharis caespitosa* (RUIZ & PAV.) PERS., *Bromus lanatus* KUNTH, and *Cerastium floccosum* BENTH.) were not recorded on Volcán Chiles. However, as they are known to exist in Colombian páramos (Luteyn 1999), their occurrence on the mountain cannot be ruled out.

The presence of certain elements indicate that climate of Volcán Chiles is rather humid, perhaps even comparable with very wet páramos of the Ecuadorian Eastern Cordillera. These indicator taxa include the fern genus *Jamesonia* HOOK & GREV., and species such as *Calamagrostis guamanensis*, *Carex collumanthus*, *Carex* sect. Aciculares, *Ranunculus gusmannii*, *Senecio hypsobates* and *Valeriana bracteata*. The abundance of bryophytes, and especially hepatics, also indicates rather humid environment of the area (Gradstein 1994, Luteyn 1999).

The ordination analysis clearly separated the lower from the upper superpáramo vegetation. The *Loricaria*-dominated shrubby vegetation is very distinct and is characteristic of most high páramos of Ecuador (Ramsay 1992) and Colombia (Cleef 1981). The lower superpáramo at 4200 m on Volcán Chiles is close to the community *Loricarietum complanatae* described from the Colombian Cordillera Oriental (Cleef 1981). The vegetation cover is closed, and some shrubs reach the E_2 level. Bryophytes are abundant, and on the twigs of *Loricaria* WEDD. and *Pentacalia* CASS. epiphytic lichens, mosses, and liverworts may be present. The soil is deep with a well developed A horizon.

The vegetation of the upper superpáramo lacks the dwarfshrubs and tussock grasess, and only a few species are shared with the lower superpáramo (*e.g., Disterigma empetrifolium, Xenophyllum crassum*). Other growth forms are important there, such as short-stem grasses (*e.g., Agrostis foliata, Poa cucullata*), erect herbs (*e.g., Bartsia stricta, Elaphoglossum* spp., *Huperzia crassa*), basal rosettes (*e.g., Senecio nivalis*) and cushion plants (*e.g., Azorella corymbosa, Xenophyllum humile).*

Table 2. Soil characteristics of the superpáramo vegetation samples (mean ± 1 sd, n = 3). Coarse material (soil particles >2 mm), carbon and nitrogen in percentage of dry weight. Some readings of soil depth were beyond the 50 cm scale of the measuring tool.

Altitude (m)	Soil depth (cm)	Coarse	Conductivity (mS)	pH–H_2O	pH–KCl	C	N
4200	>50.0	1±2.2	0.08±0.03	4.5±0.37	3.7±0.22	11.6±1.86	0.68±0.18
4300	7.7±3.67	39±2.2	0.04±0.02	5.1±0.09	4.0±0.06	1.9±0.86	0.13±0.07
4400	5.9±1.53	38±4.5	0.02±0.00	5.5±0.27	4.2±0.16	0.7±0.15	0.05±0.01
4500	1.3±0.58	33±4.5	0.03±0.00	4.7±0.04	3.9±0.04	2.01±0.33	0.16±0.02

The cushions, however, seem to be less abundant when compared with other Ecuadorian superpáramos. Bryophytes, especially the moss genus *Racomitrium*, ferns, and the clubmoss *Huperzia crassa* were conspicuous at 4300 m, where the vegetation developed on a scree slope. At 4500 m, smooth solid rocks predominated, and only a limited number of species occurred in cracks or in shallow pockets of sandy soil. Single individuals of *Agrostis foliata*, *Poa cucullata*, *Senecio culcitioides*, and *Senecio nivalis* were found on favourable places almost as high as the mountain summit. However, the upper limit of vegetation on Volcán Chiles can be considered below 4600 m.

The diversity indices show a rather clear pattern and support the above statements. Species richness decreases steadily with altitude, but Simpson's and equitability indices reach the maximum at 4300 m and tend to be higher in the upper than in the lower superpáramo. In the lower superpáramo at 4200 m, a few species tend to dominate the vegetation (*e.g., Pentacalia stuebelii, Jamesonia cinnamomea, Calamagrostis effusa*; Appendix 1). As a result, the Simpson's diversity index and the equitability (evenness) are low despite the highest species richness. In contrast, no species is dominant at 4300 m, and consequently the diversity rises despite the loss of species.

The small superpáramo of Volcán Chiles surrounded by *Espeletia*-dominated grass páramo is interesting in several aspects, which were briefly discussed here. From its species composition it is close to the humid superpáramos of the Eastern Cordillera of Ecuador. Nevertheless, clear links to the Colombian páramos can also be seen (*Espeletia* MUTIS EX HUMB. & BONPL., *Calamagrostis effusa*, *Gentianella selaginifolia*). As only one part of the mountain was explored, the presented list of species should not be considered complete and further botanical research from both Ecuadorian and Colombian sides is recommended.

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REFERENCES

Acosta-Solís, M. (1984) *Los Páramos Andinos del Ecuador,* Quito: Publicaciones M.A.S.

Berg, A.L. (1998) Pflanzengesellschaften und Lebensformen des Superpáramo des Parque Nacional Sierra Nevada de Mérida in Venezuela. *Phytocoenologia*, **28**: 157–203.

Cleef, A.M. (1981) *The Vegetation of the Páramos of the Colombian Cordillera Oriental*, Dissertationes Botanicæ 61, Vaduz: J. Cramer.

Gradstein, S.R. (1994) Hepatic diversity in the neotropical páramos. In: Fortunato, R. and Bacigalupo, N. (Eds.) *Proceedings of the VI Congreso Latinoamericano de Botánica*, pp. 69–85. St. Louis: Missouri Botanical Garden Press.

Jørgensen, P.M. (1992) *Vegetation of the High Andes of Ecuador*, Ph.D. thesis, Aarhus University, Aarhus.

Lægaard, S. (1992) Influence of fire in the grass páramo vegetation of Ecuador. In: Balslev, H. and Luteyn, J.L. (Eds.) *Paramo: An Andean Ecosystem under Human Influence,* pp 151–170. London: Academic Press.

Luteyn, J.L. (1992) Páramos: Why study them? In: Balslev, H. and Luteyn, J.L. (Eds.) *Paramo: An Andean Ecosystem under Human Influence*, pp 1–14. London: Academic Press.

Luteyn, J.L. (1999) *Páramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature.* Memoirs of the New York Botanical Garden, 84. New York: New York Botanic Garden.

Monasterio, M. (1980) Las formaciones vegetales de los páramos de Venezuela. In: Monasterio, M. (Ed.) *Estudios Ecológicos en los Páramos Andinos*, pp. 93–158. Mérida (Venezuela): Ediciones de la Universidad de Los Andes.

Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and Methods of Vegetation Ecology*, New York: John Wiley & Sons.

Peet, R.K. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics*, **5**: 285–307.

Ramsay, P.M. (1992) *The Páramo Vegetation of Ecuador: the Community Ecology, Dynamics and Productivity of Tropical Grasslands in the Andes,* Ph.D. thesis, University of Wales, Bangor.

Ramsay, P.M. (2001) The zonal páramo vegetation of Volcán Chiles. In: Ramsay, P. M. (Ed.), *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*, pp. 27-38. Plymouth: Pebble & Shell.

Sklenář, P. and Jørgensen, P.M. (1999) Distribution patterns of páramo plants in Ecuador, *Journal of Biogeography*, **26**: 681–691.

ter Braak, C.J.F. and Šmilauer, P. (1998) *CANOCO Reference Manual and User's Guide to Canoco for Windows*, Wageningen: Centre of Biometry.

Van der Hammen, T. and Cleef, A.M. (1986) Development of the high Andean páramo flora and vegetation. In: Vuilleumier, F. and Monasterio, M. (Eds.) *High Altitude Tropical Biogeography*, pp. 153–201. Oxford: Oxford University Press.

Wilson, M.V. and Shmida, A. (1984) Measuring beta diversity with presence-absence data. *Journal of Ecology*, **72**: 1055–1064.

Appendix 1. Table of the twelve vegetation relevés from the superpáramo of Volcán Chiles. The species′ scores represent the midpoint of their cover estimates (see Methods).

Environmental variables	**Relevé number**											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Altitude (m)	4200	4200	4200	4300	4300	4300	4400	4400	4400	4500	4500	4500
Total vegetation cover (%)	95	100	85	70	70	75	30	40	20	25	15	20
Bare ground (% cover)	5	0	10	5	5	5	45	15	10	5	5	5
Rock (% cover)	0	0	5	25	25	20	25	45	70	70	80	75
Soil depth (cm)	>44	>48	>45	12	5	6	7	4	5	2	1	1
E_2 (% cover)	0	<5	<5	0	0	0	0	0	0	0	0	0
E_1 (% cover)	70	95	60	10	10	10	20	20	10	10	<10	10
E_0 (% cover)	25	40	25	60	60	65	10	20	10	15	<10	10
Species												
Pentacalia stuebelii (Hieron.) Cuatrec.	10	10	10									
Diplostephium rupestre (Kunth) Wedd.	2.5	10	2.5									
Loricaria complanata (Sch.Bip.) Wedd.	10	20	2.5									
Loricaria ilinissae (Benth.) Cuatrec.		2.5	20									
Jamesonia cinnamomea Kunze	10	20	10									
Lachemilla nivalis (Kunth) Rothm.	2.5	0.5	0.5									
Calamagrostis effusa (Kunth) Steud.	38		20									
Calamagrostis intermedia (J.Presl) Steud.		10	2.5									
Pentacalia andicola (Turcz.) Cuatrec.		0.1	10									
Jamesonia goudotii (Hieron.) C.Chr.	2.5	0.5	2.5									
Aciachne flagellifera Laegaard	0.5	0.5										
Arcytophyllum aristatum Standl.		2.5										
Calamagrostis guamanensis Escalona		0.5										
Carex sp.	0.5	0.5										
Senecio canescens (Humb. & Bonpl.) Cuatrec.		0.1										
Gentiana sedifolia Kunth	0.1											
Geranium angelense Halfdan-Niels.		0.5										
Geranium sibbaldioides Benth.		2.5	0.5									
Gunnera magellanica Lam.		0.5										
Hypericum lancioides Cuatrec.	0.5	0.1										
Hypochaeris sessiliflora Kunth	0.5											
Miconia chionophila Naudin	0.5											
Niphogeton dissecta (Benth.) J.F.Macbr.	2.5	0.5										
Oreobolus goeppingerii Suess.		0.5										
Pentacalia arbutifolia (Kunth) Cuatrec.	0.5											
Plantago rigida Kunth		0.5										
Senecio chionogeton Wedd.	0.5											
Uncinia macrolepis Decne.		0.5	0.1									
Lasiocephalus involucratus (Kunth) Cuatrec.		0.1										
Luzula gigantea Desv.			0.5									
Calamagrostis ligulata (Kunth) Hitchc.					0.5		10	10	10	10	10	10
Azorella corymbosa (Schltdl.) Wedd.						10	10	10	10	2.5	0.5	2.5
Huperzia crassa (Humb. & Bonpl. ex Willd.) Rothm.				2.5	10	10	0.5			0.5	0.5	0.5
Ourisia muscosa Benth.				0.5	0.5		2.5	2.5	0.5	0.5	0.5	0.5
Senecio nivalis (Kunth) Cuatrec.				0.5	0.5	0.5	0.5		0.5	0.1		0.5
Disterigma empetrifolium (Kunth) Drude	20	38	38		10	10						
Xenophyllum crassum (S.F.Blake) V.A.Funk	10	0.5		2.5	2.5	0.5	2.5					
Melpomene moniliformis (Lag. ex Sw.) A.R.Sm. & R.C.Moran	0.5	0.5	0.5	0.5	2.5	0.5		0.5				
Pernettya prostrata (Cav.) DC.	2.5			2.5	2.5	10	0.5					

Species	**Relevé number**											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Azorella aretioides (Spreng.) DC.	0.5			0.5	2.5	10			0.5			
Poa cucullata Hack.				0.5		0.5	0.5	0.5	0.5			
Polystichum orbiculatum (Desv.) J.Remy & Fée				0.5	0.5	0.5			0.1			
Senecio culcitioides Sch.Bip.				0.5	2.5	2.5		0.1				
Myrosmodes sp.				0.5	0.5	0.1						
Bartsia stricta (Kunth) Benth.							0.5	0.5	0.5			
Agrostis foliata Hook.f.				2.5	2.5	0.5	0.5		0.5			
Colobanthus quitensis (Kunth) Bartl.				0.5			0.5		0.1			
Lachemilla hispidula (L.M.Perry) Rothm.					0.5	2.5	0.5					
Azorella sp.				2.5	10							
Bartsia laticrenata Benth.				0.5	2.5	0.5						
Luzula racemosa Desv.					2.5	0.5						
Draba extensa Wedd.				0.5	0.5							
Elaphoglossum mathewsii (Fée) T.Moore					10	0.5						
Carex sect. Aciculares					0.5	2.5						
Castilleja fissifolia L.f.						0.5						
Castilleja nubigena Kunth				0.1								
Xenophyllum humile (Kunth) V.A.Funk										2.5	2.5	0.5
Melpomene sp.							0.5					
Lachemilla holosericea (L.M.Perry) Rothm.							0.5					
Lysipomia montioides Kunth							0.5					
Lasiocephalus ovatus Schltdl.		0.1								0.5		
Oritrophium peruvianum (Lam.) Cuatrec.	0.1											0.1

Appendix 2. Additional 43 superpáramo species of Volcán Chiles found outside sample plots of Appendix 1 and between 4100-4200 m.

Apiaceae: *Azorella pedunculata* (Spreng.) Mathias & Constance, *Oreomyrrhis andicola* (Kunth) Hook.f.

Asteraceae: *Chrysactinium* sp., *Chuquiraga jussieui* J.F.Gmel., *Diplostephium rhomboidale* Cuatrec., *Erigeron ecuadoriensis* Hieron., *Hypochaeris sonchoides* Kunth, *Lasiocephalus* cf. *pichinchensis* (Cuatrec.) Cuatrec., *L. gargantanus* (Cuatrec.) Cuatrec., *L. sodiroi* (Hieron.) Cuatrec., *Oritrophium limnophilum* (Sch.Bip.) Cuatrec., *Senecio formosus* Kunth, *S. hypsobates* Wedd., *Werneria pygmaea* Gillies ex Hook. & Arn.

Brassicaceae: *Draba aretioides* Kunth

Caryophyllaceae: *Cerastium danguyi* J.F.Macbr.

Cyperaceae: *Carex collumanthus* (Steyerm.) G.A.Wheeler, *C. pichinchensis* Kunth, *Uncinia subsacculata* G.A.Wheeler & Goetgh.

Dryopteridaceae: *Elaphoglossum* aff. *yatesii* (Sodiro) H.Christ, *E. rimbachii* (Sodiro) H.Christ

Fabaceae: *Lupinus tauris* Benth.

Gentianaceae: *Gentianella nummularifolia* (Griseb.) Fabris, *G. selaginifolia* (Gilg) Fabris, *Halenia weddelliana* Gilg

Geraniaceae: *Geranium maniculatum* H.E.Moore

Grammitidaceae: *Terpsichore heteromorpha* (Hook. & Grev.) A.R.Sm.

Grossulariaceae: *Ribes hirtum* Willd. ex Roem. & Schult.

Juncaceae: *Distichia muscoides* Nees & Meyen

Lamiaceae: *Satureja nubigena* (Kunth) Briq.

Lycopodiaceae: *Huperzia sellifolia* B.Øllg.

Plantaginaceae: *Plantago linearis* Kunth

Poaceae: *Cortaderia sericantha* (Steud.) Hitchc.

Ranunculaceae: *Ranunculus gusmannii* Humb. ex Caldas, *R. peruvianus* Pers.

Rosaceae: *Lachemilla mandoniana* (Wedd.) Rothm., *L. tanacetifolia* Rothm.

Scrophulariaceae: *Bartsia pedicularoides* Benth., , *Ourisia chamaedryfolia* Benth.

Valerianaceae: *Valeriana bracteata* Benth., *V. microphylla* Kunth, *V. plantaginea* Kunth, *V. rumicoides* Wedd.

Vegetation of a cushion mire at 3600 m on Volcán Chiles, Ecuador

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SUMMARY

Cushion mires are found in tropical alpine regions of the world, throughout the Andes, and in Australasia. A survey of a páramo cushion mire at 3600 m on Volcán Chiles (Ecuador-Colombia border) is presented here. Eight vegetation types were distinguished by TWINSPAN analysis, representing variants of the central mire area, dominated by cushions of *Oreobolus obtusangulus with* pools between them, and the edge communities that were drier and had fewer cushions. The vegetation patterns were related to three principal factors. First, large-scale environmental heterogeneity separated the depressed central part of the mire from the slightly raised, and therefore drier, edges. Rhizosphere acidity was pH 4.8 in every sample. Other environmental measures, such as water conductivity and nutrient concentrations, varied considerably and were related to vegetation patterns. Second, topographic differences within the cushion-hollow mosaic were reflected in small-scale variation in the distribution of species. Third, characteristic species composition was associated with various stages in the development of *Oreobolus* plants, from young to senescent cushions.

RESUMEN

Las turberas acojinadas se localizan en las regiones altas y tropicales del mundo, a lo largo de los Andes y en Australasia. Aquí se presenta un estudio de un turbera paramuna a 3600 m de altitud en el Volcán Chiles (en la frontera Ecuador-Colombia). Utilizando un análisis de TWINSPAN, se distinguieron ocho tipos de vegetación. Estos tipos representan variantes del área central de la turbera, dominada por almohadillas de *Oreobolus obtusangulus*, con charcas entre ellas, y las comunidades de la orilla de la turbera, las cuales fueron mas secas y tuvieron menos almohadillas. Los patrones de la vegetación se relacionaron con tres factores principales. Primero, la heterogeneidad ambiental separó la depresión central de la turbera de las orillas, las cuales ocupaban una posición más elevada y, por lo tanto, más seca. La acidez de la rizosfera fue de pH=4.8 en cada muestra. Otras variables ambientales, tales como la conductividad de agua y la concentración de nutrientes, variaron considerablemente y estuvieron relacionadas con los patrones de la vegetación. Segundo, las diferencias topográficas dentro del mosaico almohadilla-charca se reflejaron en la variación en la distribución de las especies a escalas pequeñas. Tercero, la composición de especies estuvo asociada con las varias etapas en el desarrollo de las plantas de *Oreobolus*, desde almohadillas jóvenes hasta senescentes.

Key words: páramo, cushion bog, tropical alpine, Andes

INTRODUCTION

Mires are peat-forming areas, with complex and varied terminology; the various types determined largely by water and ionic supply (Heathwaite *et al.* 1993). However, as Pfadenhauer *et al.* (1993) point out, the convential mire and peat classifications—based on temperate conditions—do not apply well to tropical mires. In the tropics, variation in the physical, chemical and biological traits of mires are strongly linked to altitude: tropical lowland mires support vigorous plant cover, even where soils are poor, and only in the tropical mountains does the vegetation reduce to a low cover of herbaceous plants and mosses (Pfadenhauer *et al.* 1993).

Mires are frequent in some parts of the Andes, reaching their altitudinal extremes in the páramos and punas but, in common with Latin American mires in general, have received very limited attention (Pfadenhauer *et al.* 1993). Mires often form azonal habitats within the more typical zonal páramo grasslands of the Northern Andes (Ramsay 1992, Bosman *et al.* 1993). According to Pfadenhauer *et al.* (1993) three types of mire can be found in the Andean páramo:

- **fens**
  These mires are mainly formed from Cyperaceae and Poaceae, often in tussock form, and containing a high proportion of Eriocaulaceae and Xyridaceae. Mosses are sometimes present, along with dwarf shrubs, and hummock-hollow formations may develop. Peat depth usually reaches no more than 2 m. These kinds of mire are represented by the grass and sedge riparian mires (sometimes also found in depressions fed by springwater) in the páramos of Venezuela and Colombia (Cleef 1981). These formations also occur in the Ecuadorian páramos (P.M. Ramsay, pers. obs.).
- ***Sphagnum* mires**
  From Costa Rica to Colombia some mires are dominated by peat-forming mosses belonging to the genus *Sphagnum* (Cleef 1981)—but these mires are not comparable to the European raised mires characterised by vertical peat growth (Pfadenhauer *et al.* 1993). They can form by infilling of lakes (terrestrialisation) or by replacing grassland or forest (paludification). Again, these mires are present further south in the Ecuadorian páramos (P.M. Ramsay, pers. obs.).
- **cushion mires**
  According to Pfadenhauer *et al.* (1993), cushion mires are sometimes fed directly by springwater, but most are paludified. However, in Ecuador at least, cushion mires can also form by a process of terrestrialisation and are commonly found at lake margins (P.M. Ramsay, pers. obs.). Cushion mires are characterised by low-growing cushion plants, which sometimes form peat deposits which are acidic and low in nutrients (Troll 1968, Godley 1978). They occur throughout the Andes, from Colombia and Venezuela to Argentina. They are most abundant in the Southern Hemisphere and

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 47-54.

tropical alpine regions (Gibson & Kirkpatrick 1985, Gibson & Hope 1986, Lough *et al*. 1987, Smith & Young 1987, Bosman *et al*. 1993, Archibold 1995), though they have occasionally been reported in the Northern Hemisphere (Mani 1978, Gibson & Hope 1986).

Despite being common in the páramos, and elsewhere in the Andes, there have been few published descriptions of high-altitude cushion bogs. Those studies which are available focus on the Colombian Andes (Cleef 1981, Sánchez *et al*. 1989, 1990, Bosman *et al*. 1993, Rangel-Ch. 2000). It is not yet clear to what extent these descriptions represent páramo cushion bog communities elsewhere, and how the composition of páramo bogs varies with altitude. Furthermore, páramo cushion bogs tend to show internal variability (Bosman *et al*. 1993), but the processes responsible for this patterning have yet to be determined.

This study describes a cushion bog community at 3600 m on Volcán Chiles, Ecuador, and examines the relationship between vegetation and a range of environmental factors.

METHODS

Site Description

The mire was situated at an elevation of 3600 m on the south-eastern slopes of Volcán Chiles, a few kilometres from the Ecuador-Colombia border (00° 48′ N 77° 54′ W; Fig. 1). The mire was approximately 100 x 200 m in area and lay in a shallow basin, surrounded by small hills. It was fed by direct precipitation and run-off from the surrounding slopes. The mire was in a relatively exposed position, though protected a little from strong winds by the surrounding hills. There were no climatic data available for Volcán Chiles, but the temperature of the ground water in the mire during the study period ranged between 4–8°C. There was no evidence of grazing by livestock—cropped vegetation, faeces, hoofprints—though cattle and horses were observed foraging in the surrounding grassland at the time of survey.

The vegetation of the surrounding area was typical for this altitude on Volcán Chiles: dominated by tussock grasses (especially of *Calamagrostis intermedia*) and giant rosette plants of *Espeletia pycnophylla* subsp. *angelensis*. Several other, smaller mires were present in the vicinity.

Field Survey, herbarium and laboratory work

The survey was carried out in July 1997. In all, forty-two 1 x 1 m randomised quadrats were used to sample the vegetation of the mire. For each quadrat the percentage cover of all vascular plants, bryophytes, liverworts and lichens were noted, and voucher specimens collected and deposited in herbaria in Quito (QCA) and the University of Plymouth (Muirhead Herbarium, PLYP). The vascular plants were identified to species at QCA. Determinations of the bryophytes, liverworts and lichens is still in progress, and the names presented here must be considered provisional at this stage.

A small dip well was created in the centre of each sample, using a 10 cm diameter plastic cylinder, and the water table allowed to recover to its normal level. The acidity and conductivity of the ground water was measured with indicator paper and a Hanna HI8424 meter, respectively. The depth of the water table, relative to the highest and lowest points in the samples were also noted (up to a depth of 40 cm, beyond which it was not possible to measure or collect water). For quadrats where pools were present the minimum depth was recorded as zero. The thickness of the peat layer was investigated with a 1 m long metal rod; however, in every case the peat layer was deeper than 1 m and no gravel or bedrock layer was reached. Peat samples were taken from 5 cm depth for subsequent chemical analysis in the laboratory.

Laboratory work was conducted at the University of Plymouth. Organic matter content of the peat was determined using a simple loss-on-ignition method: dry burning 1 g of air dried peat at 420°C. A range of available cation concentrations (calcium, magnesium, sodium, potassium, zinc, iron, manganese, aluminium) were measured using a Varian Spectra AA-600 flame atomic absorption spectrophotometer, after extraction with ammonium acetate (Hesse 1971, Smith & Atkinson 1975, Avery & Bascomb 1982, Rowell 1994). Available phosphorus was determined using Olsen's Bicarbonate method (Olsen *et al*. 1954) with a Specord M500 spectrophotometer. Total nitrogen was determined with the Kjeldahl method (Smith & Atkinson 1975, Avery & Bascomb 1982) and a Technican II Autoanalyser.

Data analysis

TWINSPAN (Hill 1979) was used to identify vegetation types from the quadrat data. Canonical correspondence analysis was performed with CANOCO (ter Braak 1987), and used to investigate the relationshps between vegetation composition and measured environmental variables. Two environmental variables—minimum depth to water table and conductivity—were omitted from the initial CANOCO analysis because multicollinearity was detected. These variables were later incorporated as passive variables.

RESULTS

Vegetation types

In total, 63 species of vascular plants, bryophytes, liverworts and lichens were present in the 42 samples. From these samples, eight vegetation types were identified by TWINSPAN (Fig. 2, Table 1).

A summary of the environmental data associated with each group is shown in Table 2. A Monte Carlo test (carried out with CANOCO) demonstrated that there was a significant relationship between the composition of the samples and the environmental variables recorded (p=0.05).

In essence, there were two principal types of vegetation in the bog:

- Central mire communities consisting of cushions and pools. Here developing, mature and senescent cushions of *Oreobolus obtusangulus* formed the dominant cover. Represented by vegetation types I, II, III, IV and V.
- Edge communities where *Oreobolus* was present but without pools, and the cover of associated plants was always greater. Represented by vegetation types VI, VII and VIII.

These two vegetation types will now be considered in more detail.

Central mire communities

Twinspan analysis identified five clear composition categories within the central part of the mire.

The two samples belonging to vegetation type I were situated relatively high above the water table, and consisted of senescent *Oreobolus* cushions mostly covered by mosses (especially *Grimmia* sp. [2047], *Marsupella* sp. [2079] and *Racomitrium* [2048]), but also with *Myrteola nummalaria*. A number of dry hollows were also present, with some moss cover. The peat samples demonstrated low cation concentrations, moderate amounts nitrogen and high phosphorus.

Fig. 1. The location of the páramo mire described in this study.

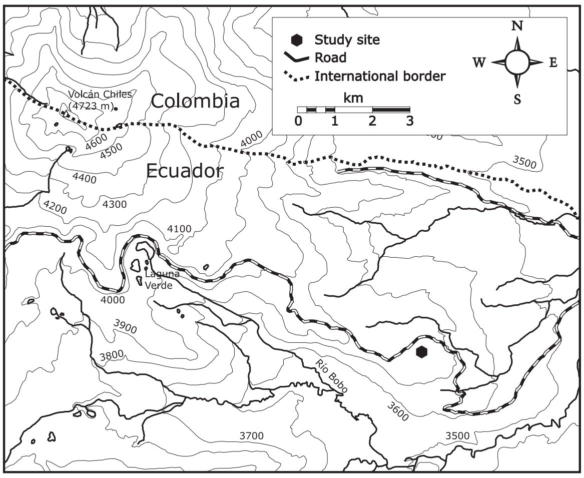
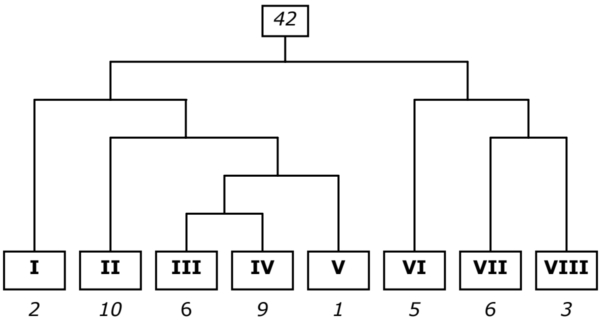


Fig. 2. Twinspan analysis, resulting in the simplification of 42 samples into eight vegetation types. The number of samples in each group is shown beneath each group code.



Samples in vegetation type II consisted of small cushions of *Oreobolus*, 10–30 cm in diameter, with *Paepalanthus* sp. [2121], *Disterigma empetrifolium* and various bryophytes growing on them. The tops of the cushions were, on average, more than 25 cm from the water table. Between the cushions were dry or muddy hollows, with *Sphagnum recurvum* growing around their edges and *Juncus stipulatus* in the centres. This was the most diverse community type in the centre of the mire. The peat samples taken from these samples were characterised by low cation, moderate nitrogen and high phosphorus concentrations.

Vegetation type III was characterised by large, flat *Oreobolus* cushions colonised by *Marsupella* sp. [2079], *Paepalanthus* sp. [2121], *Disterigma empetrifolium,* and a *Cladonia* sp. [2053]. Large water- and mud-filled hollows were present between the cushions and contained *Sphagnum compactum*, with a liverwort [2050] around the edges. These samples were very close to the water table, and peat samples contained high concentrations of cations with moderate nutrient levels.

Vegetation type IV also consisted of large, flat *Oreobolus* cushions. This time, they were associated with *Disterigma empetrifolium, Marsupella* sp. [2079], and Dicranaceae [2128]. Between the cushions, *Sphagnum recurvum* lined the hollows, which were smaller and drier than in vegetation type III. The peat from these samples contained high concentrations of cations, moderately high nitrogen, but low phosphorus.

Only one sample represented the association between *Oreobolus* cushions, *Sphagnum compactum*, *Paepalanthus* sp. [2121], *Puya hamata*, and the grasses *Calamagrostis nuda*, *Festuca dolichopylla* and *Agrostis tolucensis* (vegetation type V). Hollows between the cushions were colonised by *Sphagnum compactum*. This sample was relatively dry, being further away from the water table than almost all other samples from the centre of the mire. The peat sample was found to have high cation concentrations, a high nitrogen level, but low phosphorus concentration.

Edge communities

There were three edge community types distinguished by TWINSPAN. Samples from these areas tended to be more species rich and more variable than those from the centre of the mire.

Samples grouped together by TWINSPAN as vegetation type VI were found in flat areas around the edge of the mire. Although there were no pools present, the ground was quite soft and wet, though sometimes the water table was more than 40 cm below the surface.

Table 1. Vegetation composition of the eight vegetation types identified by Twinspan analysis. Values are mean percentage cover in each vegetation type ("+" indicates ≤0.5% cover). Species are arranged in descending order of overall abundance in all samples. For each species, voucher specimens were collected and the relevant collection numbers are given in parentheses after each name. Vascular plants nomenclature follows Luteyn (1999).

Species name	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**
n	2	10	6	9	1	5	6	3
Number of species in vegetation type	15	28	18	19	17	40	36	27
Mean overall % vegetation cover	110	92	98	77	112	105	103	103
Oreobolus obtusanglus Gaudich. [2119]	20.0	55.0	57.0	53.0	60.0	11.0	19.0	10.0
Disterigma empetrifolium (Kunth) Drude [2122]	1.0	3.0	3.0	6.0		11.0	14.0	17.0
Paepalanthus sp. [2121]	13.0	9.0	7.0		10.0	9.0	5.0	1.0
Marsupella sp. [2079]	13.0	2.0	16.0	4.0	+	+	+	
Sphagnum compactum [2051 & 2059]	+	1.0	+	+	20.0	3.0	11.0	34.0
Sphagnum recurvum [2069 & 2081]		10.0	1.0	6.0	1.0	6.0		
Calamagrostis nuda (Pilg.) Pilg. [2090]	+		1.0	+	+	20.0	3.0	7.0
Grimmia sp. [2047]	50.0	+	1.0	1.0	+	2.0	+	
Cortaderia sericantha (Steud.) Hitchc. [2120]							19.0	
Myrteola nummalaria (Poir) O.Berg [2100]	3.0	+		+	+	8.0	7.0	3.0
Cladonia sp. [2053 & 2057]	1.0	1.0	7.0	2.0	+	+	+	
Amblystegiaceae (?*Caliergon*) [2054]		2.0	4.0	1.0	2.0			
Campylopus sp. [2042, 2063, 2075]	1.0	+	+	+		1.0	8.0	4.0
Distichium capillaceum (Hedw.) Bruch & Schimp. [2077, 2049]		1.0				+	7.0	5.0
Cladonia sp. [2058]						8.0		
Pohlia sp. (Bryaceae) [2056]						7.0	+	
Carex pichinchensis Kunth [2094]								12.0
Agrostis tolucensis Kunth [2093]	+	+			+	5.0	1.0	
Puya hamata L.B.Sm. [2124]					10.0	3.0	+	
Loricaria thuyoides (Lam.) Sch.Bip. [2131]							4.0	+
Carex cf. *crinalis* Boott [2095]		2.0				1.0	+	
Festuca dolichophylla J. Presl. [2089]				1.0	+	2.0	1.0	1.0
Dicranaceae [2128]		1.0		2.0				
Cladia sp. 1 [2052]	+	1.0	1.0	1.0	+	+	+	
Jungermannia sp. [2060]		1.0	1.0	1.0	+		+	+
Sphagnum cuspidatum [2041]							+	5.0
Racomitrium [2048]	8.0							
Liverwort [2050]		1.0	+	+	3.0			
Carex sp. [2133]						2.0		
Riccardia sp. [2044 & 2071]						1.0	1.0	1.0
Peltigera sp. [2025]		1.0						
Juncus stipulatus Nees & Meyen [2098]		1.0						
Moss [2062]		+	+					+
Usnea sp. 1 [2043]						+	+	1.0
Carex microglochin Wahlenb. [2099]	1.0	+	+					
Moss [2045]		+	+					
Hypericum lancifolium Gleason [2130]						+		1.0
Lichen [2046]		+		+		+		
Plagiochila sp. [2064]						+	+	+
Sphagnum sp. [2080]	+				+	+	+	
Lichen [2061]						+	+	
Cladina ? arctuata (Ahti) Ahti & Follmann [2076]		+		+				
Gentianella selaginifolia (Gilg) Fabris [2088]						+	+	+
Moss [2070]						+	+	
Everniastrum sp. [2073]						+	+	+
Baccharis cf. *macrantha* Kunth [2091]						+	+	
Jungermannia sp. [2078]		+	+	+				
Diplostephium rupestre (Kunth) Wedd. [2132]						+	+	+
Pentacalia andicola (Turcz.) Cuatrec. [2092]						+		+
Pernettya prostrata (Cav.) DC. [2126]		+					+	+
Dicranaceae [2068]						+	+	
Senecio chionageton Wedd. [2123]							+	+
Racomitrium sp. [2086]						+		
Asplenium sp. [2097]							+	
Agrostis haenkeana Hitchc. [2102]		+						
Azorella aretioides (Spreng.) DC. [2127]								+
Usnea sp. 2 [2072 & 2055]							+	+
Crustose Lichen [2066]						+		
Ceratodon [2040]						+		
Cladonia ? chlorophaea (Flörke ex Sommerf.) Spreng. [2087]						+		
Nertera granadensis (Mutis ex L.f.) Druce [2129]								+
Cladia sp. 2 [2065]						+		
Moss [2067]						+		

Table 2. Environmental characteristics associated with each vegetation type. The values shown are means (± standard deviations). The number of samples, n, *used to calculate these statistics is shown in each case (paretheses show the number of samples where a water table was found in the dip well—used for variables associated with the water table: conductivity and depths to water table). "—" indicates vegetation types where no water was present in any of the dip wells and no measurements could be made. The topographic index was the difference between the maximum and minimum depths to water table in each sample.*

Type:	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**
N	2	10	6	9	1	5 (3)	6 (4)	3
OM (% loss on ignition)	93.5 ± 2.2	94.5 ± 2.3	93.5 ± 1.7	95.5 ± 1.9	91.0	92.8 ± 1.1	95.2 ± 1.0	94.7 ± 2.1
P (µg g^{-1})	3.2 ± 1.1	2.7 ± 1.6	2.5 ± 1.5	2.0 ± 0.9	1.7	3.2 ± 0.7	3.1 ± 1.7	0.8 ± 0.4
N (µg g^{-1})	77.4 ± 7.6	71.0 ± 38.5	55.8 ± 44.4	68.2 ± 40.9	149.5	84.6 ± 49.7	62.6 ± 42.9	20.3 ± 16.4
Ca (µg g^{-1})	124 ± 57	1029 ± 735	1228 ± 846	1197 ± 1270	1390	242 ± 119	252 ± 134	966 ± 605
Mg (µg g^{-1})	35.4 ± 19.6	129.4 ± 54.3	154.0 ± 62.2	122.8 ± 58.9	135.6	119.3 ± 95.5	68.1 ± 17.6	393.3 ± 170.9
Al (µg g^{-1})	1.5 ± 0.8	10.4 ± 7.3	9.8 ± 11.5	8.5 ± 7.0	11.0	2.7 ± 1.7	2.0 ± 1.3	11.5 ± 7.4
K (µg g^{-1})	59.5 ± 15.8	230.0 ± 97.3	286.9 ± 115.7	219.5 ± 90.7	258.8	87.1 ± 38.5	130.3 ± 51.1	422.7 ± 126.4
Na (µg g^{-1})	8.8 ± 4.5	70.1 ± 42.4	93.8 ± 64.1	62.7 ± 35.3	49.1	19.9 ± 13.4	12.5 ± 4.1	85.3 ± 43.4
Fe (µg g^{-1})	0.3 ± 0.1	1.2 ± 1.0	1.4 ± 0.9	1.1 ± 0.8	1.5	0.8 ± 0.1	0.6 ± 0.7	1.4 ± 1.1
Mn (µg g^{-1})	2.9 ± 0.8	21.6 ± 10.9	15.1 ± 10.1	17.6 ± 12.2	19.5	12.2 ± 14.3	13.0 ± 8.0	195.5 ± 54.0
Zn (µg g^{-1})	0.1 ± 0.1	0.6 ± 0.3	0.5 ± 0.6	0.4 ± 0.4	0.4	0.3 ± 0.2	0.4 ± 0.1	4.3 ± 2.3
pH	4.8 ± 0.0	4.8 ± 0.0	4.8 ± 0.0	4.8 ± 0.0	4.8	4.8 ± 0.0	4.8 ± 0.0	4.8 ± 0.0
Conductivity (mS s^{-1})	—	36.6 ± 5.9	42.6 ± 12.2	38.6 ± 5.9	42.0	26.1 ± 5.4	29.2 ± 4.6	—
Min. depth to water table (cm)	—	8.0 ± 6.2	3.8 ± 5.5	8.3 ± 7.8	11.0	9.0 ± 3.0	13.0 ± 1.4	—
Max. depth to water table (cm)	—	26.0 ± 3.7	19.2 ± 4.0	19.2 ± 3.3	23.0	29.7 ± 5.1	26.8 ± 5.9	—
Topographic index	—	18.0 ± 6.3	15.3 ± 3.8	10.9 ± 6.4	12.0	20.7 ± 2.3	13.8 ± 7.1	—

The vegetation consisted of a diverse mixture of species, including *Oreobolus*, *Disterigma*, two species of *Sphagnum* (*S.compactum* and *S.recurvum*), *Paepalanthus* sp. [2121], *Calamagrostis nuda*, *Agrostis tolucensis*, *Myrteola nummalaria*, *Puya hamata*, *Pohlia* sp. [2056], two species of *Carex*, and *Cladonia* sp. [2058]. In all, 40 species were associated with this kind of community. The peat samples were moderately low in cations and nitrogen, but high in phosphorus.

Cortaderia sericantha tussocks dominated the samples of vegetation type VII, again located on flat areas around the edge of the mire. The tussocks were associated with species such as *Oreobolus*, *Disterigma*, *Paepalanthus* sp. [2121], *Marsupella* sp. [2079], *Calamagrostis nuda*, *Agrostis tolucensis*, *Myrteola nummalaria*, *Loricaria thuyoides*, *Puya hamata*, and various bryophyte species (*e.g.*, Dicranaceae [2063], *Distichium capillaceum* [2049], Dicranaceae [2075]). The depressions between the hummocks formed by the tussocks and cushions were occupied by *Sphagnum compactum* and a liverwort [2044]. The peat samples contained moderate cation and nitrogen concentrations, but were high in phosphorus.

Three samples from the edge of the mire (type VIII) showed very high coverage by *Sphagnum* mosses. Mounds originally formed by *Oreobolus*, had developed very high cover of *Sphagnum compactum*, with *Disterigma*, *Calamagrostis nuda*, *Myrteola nummalaria*, Dicranaceae [2063], and *Sphagnum cuspidatum*. Between the mounds, *Sphagnum compactum* and *Carex pichinchensis* were abundant. These samples were relatively dry, located at least 40 cm above the water table, and peat samples contained high cations concentrations, but had low nutrient levels.

DISCUSSION

Similarities with other mires

The mire studied here was dominated by cushion plants, which contrasts sharply with temperate mires (*e.g.*, the tundra and taiga of northern latitudes, and the blanket and raised mires of western Europe) and the lush fens and forested wetlands of the lowland tropics. However, cushion mires are relatively common in some parts of the world.

Pisano (1983) provides a detailed review of the main mire vegetation characteristics of the tundra region of southern Chile and Argentina, which contains significant coverage of cushion-dominated vegetation. Cushion mires (along with other kinds of cushion communities) are also found in Australasia: in Tasmania (Gibson and Kirkpatrick 1985, Campbell 1983); South Island of New Zealand and Stewart Island (Dobson 1979, Gibson and Kirkpatrick 1985); Macquarie Island (Gibson and Hope 1986); and New Guinea (Hope 1976, Hope 1980, Gibson and Hope 1986). They are also present on Antarctic islands (Dobson 1979). Common cushion mire genera in Australasia include *Abrotanella, Donatia, Colobanthus, Oreobolus, Centrolepis, Plantago, Astelia,* and *Danthonia*.

Cushion mires are also present in many of the world's tropical alpine regions:

- Hawaiian volcanoes with *Oreoblus furcatus* (Skottsberg 1939)
- Sumatra between 3200-3400 m with the cushion-forming grass *Monostachya oreoboloides* (Van Steenis 1938, 1962)
- the puna of Peru, Bolivia and northern Argentina (Ruthsatz 1978; Gutte 1980) where they have developed from *Werneria pygmaea, Distichia muscoides* and *Scirpus deserticola* (Pfadenhauer *et al*. 1993)
- Northern Andes of Ecuador, Colombia and Venezuela (Cleef 1978, 1981; Ramsay 1992)
- Cerro Neblina in Brazil (Cleef 1978).

Oreobolus obtusangulus, the dominant species in the mire studied here, has a widespread distribution from Colombia, Venezuela and Brazil (on Cerro Neblina) to Tierra del Fuego (Cleef 1978). Other cushion-forming plants belonging to the same genus have been recorded in Sumatra and Borneo (Kern 1974), and in New Guinea, New Zealand, Hawaii, and the Falkland Islands (Skottsberg 1960). Cleef (1981) describes a cyperaceous páramo cushion bog dominated by *Oreobolus obtusangulus*, which was recorded only from the Colombian Cordillera Oriental but suspected to extend in distribution southwards into Ecuador. More commonly, cushion bogs in this part of the Andes composed of *Distichia muscoides*, *Plantago rigida* and *Oreobolus cleefii* cushions (Bosman *et al* 1993). No other *Oreobolus*-dominated cushion mires were reported in a recent review of Colombian páramo vegetation types (Rangel-Ch. 2000).

In the Ecuadorian Andes, *Oreobolus* cushion mires are relatively common, from the Colombian border as far south as Loja province. Nevertheless, many mires are dominated by other cushion-forming species such as *Plantago rigida* and *Distichia muscoides* (Ramsay, pers. obs.). Øllgaard and Balslev (1979) provide brief descriptions and selected plant listings of cushion plant vegetation in boggy areas throughout the Ecuadorian páramos and including two from Volcán Chiles (locations 6, 10, 15, 23, 28, 36, 66, 72).

Just a few kilometres from the mire studied here, at 4100 m on Volcán Chiles, a mixed *Plantago rigida-Distichia muscoides* cushion mire has been studied, though it does contain occasional *Oreobolus obtusangulus* plants (Ramsay & Hill, unpublished). A photograph of this mire was reproduced by Luteyn (1999: Colour Plate II). It was more similar to the mire described by Bosman *et al* (1993) in the Colombian Cordillera Oriental, than to the one described here from a lower altitude. The higher altitude mire was also similar to the "Distichio muscoidis-Plantaginetum rigidae" association (3800-4200 m) described by Rangel-Ch. and Ariza-N. (2000) for the Colombian side of Volcán Chiles.

Within-mire heterogeneity

The mire was internally variable, sometimes with distinct areas of particular vegetation types, consistent with Bosman *et al.*'s (1993) treatment of a Colombian mire, which they classified into six vegetation types. Although the dominant species and vegetation types were different in the mire described in the present study, the internal heterogeneity is evident and is undoubtedly a feature of páramo cushion mires in general.

There are three principal causes for the observed heterogeneity within the mire:

1. *large-scale environmental heretogeneity*
   The mire could be divided into two distinct zones based on topography: the central mire, and the raised edge communities. The central area was dominated by cushions of *Oreobolus* and associated pools (being closer to the water table). The edge communities, with lower cover of *Oreobolus*, were more variable in composition and, because they were further away from the water table, lacked pools. There was little evidence to support the notion that the edge communities received additional nutrient inputs as a result of run-off from surrounding slopes, and given the peaty nature of the páramo soils around these areas, this is not surprising. In fact, water conductivity (where water was reached) was highest in the centre of the mire. Nevertheless, there was variability in cation, nitrogen and phosphorus concentrations within both areas, but this must be driven by factors other than runoff.

   Incidentally, the pH of the rhizosphere in every samples was 4.8, which matches exactly Cleef's (1978) optimum reported for Colombian *Oreobolus* mires.

2. *small-scale topography of cushion-hollow mosaic*
   The topographic variability of the cushion mire permits niche differentiation between species, relating to different levels of waterlogging, nutrient levels and shelter. Many species were associated with particular topographic positions within the cushion-pool matrix. Species such as *Sphagnum recurvum* and the bryophyte 2050 were found exclusively on the sides of *Oreobolus* cushions, hanging or submerged in the pools and wet muddy hollows. Similarly, *Sphagnum compactum* and *Sphagnum* sp. [2080] were usually found together in the small dips and depressions between the cushions. The cladoform lichens (*e.g.*, *Cladia* sp. 1 [2052], *Cladonia* sp. [2053], and lichen [2046],) were only to be found in the drier places

such as the top of the raised domes of aging *Oreobolus*. *Disterigma empetrifolium* also preferred the drier areas above the water table, and was often dominant in the centres of raised, older cushions.

Several species were associated with each other and may demonstrate highly specialized habitat preferences. For example, *Plagiochila* sp. [2064] was always found between the fronds of *Sphagnum* spp. (such as *S.compactum* and *Sphagnum* sp. [2080]); moss sp. [2070] was associated with *Paepalanthus* sp.; and two foliose lichens, *Usnea* sp. 1 [2043] and *Usnea* sp. 2 [2072], were found on the branches of dead shrubs in the edge zone.

3. *small-scale heterogeneity associated with cushion development*
   Many of the differences within the central mire, and to some extent the edge communities, appeared to be related to the development of *Oreobolus* cushions. Young cushions were associated with rather wet conditions, and the presence of many hollows and pools. As the cushions grow larger, they rise higher in the centre and the edges of neighbouring cushions meet. Sometimes, a continuous flat expanse of cushion over a relatively large area can be observed. Eventually, the cushions begin to senesce in their higher, central parts and the organic matter may disappear. At this stage, a new cushion may form in the depression. The vegetation types of the central mire were related to this cycle in the sequence II—III—IV—I, from small, through mature, to senescent cushions.

   Bosman *et al.* (1993) suggest that cushions of *Oreobolus cleefii* become dominant during certain phases in the development of *Plantago rigida* and *Distichia muscoides* mires. There was no evidence that this was true of the mire described in the current study—in fact, neither *Plantago rigida* nor *Distichia muscoides* were recorded in the mire. However, in a nearby, higher-altitude mire it was observed that *Oreobolus obtusangulus* sometimes established at the edge of senescent *Plantago* and *Distichia* cushions (Ramsay and Hill, unpublished).

The páramos of Ecuador, as elsewhere in the Northern Andes, contain numerous cushion mires. Here, one example is described. However, they vary considerably in altitude and in species composition, including the plants that form the cushions. More descriptions are necessary. The relationship between general environmental factors and the relative dominance of cushion-forming species in this region would be an interesting project. There is also more detailed patterning in the distribution of species within the habitat complexity of the cushion-hollow topography, and studies of these patterns would make a useful contribution to our understanding of these remarkable systems. Finally, there are clear similarities between the vegetation of cushion mires and that of high-altitude cushion páramos (of which *Oreobolus obtusangulus* and *Plantago rigida* are common components (Ramsay 1992). What environmental and evolutionary factors account for these similarities?

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REFERENCES

Archibold, O.W. (1995) *Ecology of World Vegetation*, London: Chapman & Hall.

Avery, B.W. and Bascomb, C.P. (1982) *Soil Survey Laboratory Methods*, Dorking: Bartholemew.

Bosman, A.F., van der Molen, P.C., Young, R. and Cleef A.M. (1993*)* Ecology of a paramo cushion mire. *Journal of Vegetation Science,* **4**: 633–640.

Campbell, E.O. (1983) Mires of Australasia. In: Gore, A.J.P. (Ed.) *Ecosystems of the World 4B. Mires: Swamp, Bog, Fen and Moor. Regional Studies,* pp. 153–180. Amsterdam: Elsevier.

Cleef, A.M. (1978) Characteristics of neotropical páramo vegetations and its subantarctic relations. In: Troll, C.L. (Ed.) *Geoecological Relations Between the Southern Temperate Zone and the Tropical Mountains*, pp. 365–390. Wiesbaden: Franz Steiner.

Cleef, A.M. (1981) *The vegetation of the páramos of the Colombian Cordillera Oriental*, Dissertationes Botanicae, 61. Vaduz: J. Cramer.

Dobson, A.T. (1979) Mire types in New Zealand. *Proceedings of the International Symposium for the Classification of Peat and Peatlands, Hyytiälä 1979,* pp. 82–94. Helsinki: International Peat Society.

Gibson, N. and Hope G. (1986) On the origin and evolution of Australasian alpine cushion plants. In: Barlow, B.A. (Ed.) *Flora and Fauna of Alpine Australasia: Ages and Origins,* pp. 63–81. Melbourne: CSIRO.

Gibson, N. and Kirkpatrick, J.B. (1985) A comparison of the cushion plant communities of New Zealand and Tasmania, Australia. *New Zealand Journal of Botany,* **23**: 549–566.

Godley, E.J. (1978) Cushion Bogs. In*:* Troll, C. and Lauer, W. (Eds.), *Geoecological Relations Between the Southern Temperate Zone and the Tropical Mountains,* pp. 139–158. Wiesbaden: Franz Steiner.

Gutte, P. (1980) Beitrag zur Kenntnis zentralperuanischer Pflanzengesellschaften. II. Die hochandinen Moore und irhe Kontaktgesellschaften. *Feddes Repertorium*, **91**: 327–336.

Heathwaite, A.L., Göttlich, Kh., Burmeister, E.G., Kaule, G. and Gospietsch, Th. (1993) Mires: definitions and form. In: Heathwaite, A.L. and Göttlich, Kh. (Eds) *Mires: Process, Exploitation and Conservation,* pp. 1–75. Chichester: Wiley.

Hesse, P.R. (1971) *A Text Book of Soil Chemical Analysis*, London: Clowes.

Hill, M.O. (1979) *TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes*, Ithaca (NY): Cornell University.

Hope, G.S. (1976) Vegetation. In: Hope, G.S., Peterson, J.A., Radok, U. and Allison, I. (Eds) *The Equatorial Glaciers of New Guinea,* pp. 113-172. Rotterdam: Balkema.

Hope, G.S. (1980) New Guinea mountain communities. In Van Royen, P. (Ed.) *Alpine Flora of New Guinea,* pp. 153-222. Vaduz: Cramer.

Kern, J.H. (1974) *Oreobolus*. *Flora Malesiana*, **1**: 681–688.

Lough, T.J., Wilson, J.B., Mark, A.M. and Evans, A.C. (1987) Succession in a New Zealand alpine cushion community: a markovian model. *Vegetatio*, **71**: 129–138.

Luteyn, J.L. (1999) *Páramos: a checklist of plant diversity, geographical distribution, and botanical literature,* New York: New York Botanic Garden.

Mani, M.S. (1978) *Ecology and Phytogeography of High Altitude Plants of the Northwest Himalaya,* London: Chapman & Hall.

Øllgaard, B. and Balslev, H. (1979) *Report on the 3rd Danish Botanical Expedition to Ecuador.* Reports from the Botanical Institute, University of Aarhus, No. 4. Aarhus: University of Aarhus.

Olson, G.W. *et al.* (1954) *The Analysis of Agricultural Materials,* London: HMSO.

Pfadenhauer, J., Schneekloth, H., Schneider, R. and Schneider, S. (1993) Mire distribution. In: Heathwaite, A.L. and Göttlich, Kh. (Eds) *Mires: Process, Exploitation and Conservation,* pp. 77–121. Chichester: Wiley.

Pisano, E. (1983) The Megallanic tundra complex. In: Gore, A.J.P. (Ed.) *Ecosystems of the World 4B. Mires: Swamp, Bog, Fen and Moor. Regional Studies,* pp. 295–329. Amsterdam: Elsevier.

Ramsay, P.M. (1992) *The Páramo Vegetation of Ecuador: the community ecology, dynamics and productivity of tropical grasslands in the Andes.* Ph.D. thesis, University of Wales.

Rangel-Ch., J.O. (2000) La diversidad beta: tipos de vegetación. In: Rangel-Ch., J.O. (Ed.) *Colombia Diversidad Biótica III. La región de vida paramuna,* pp. 658–719. Bogotá: Universidad Nacional de Colombia.

Rangel-Ch., J.O. and Ariza-N., C. (2000) La vegetación paramuna de los volcanes de Nariño. In: Rangel-Ch., J.O. (Ed.) *Colombia Diversidad Biótica III. La región de vida paramuna,* pp. 754–784. Bogotá: Universidad Nacional de Colombia.

Rowell, D.L. (1994) *Soil Science*, Harlow: Longman Scientific and Technical.

Ruthsatz, B. (1978) Las plantas en cojín de los semi-desiertos andinos del Noroeste Argentino. *Darwiniana*, **21**: 491–539.

Sánchez, R., Rangel, O., and Aguirre, J. (1989) Estudios ecológicos en la Cordillera Oriental Colombiana. IV. Aspectos sinecológicos de la brioflora de los depósitos turbosos paramunos de los alrededores de Bogotá. *Caldasia,* **16**: 41–57.

Sánchez, R. and Rangel, O. (1990) Estudios ecológicos en la Cordillera Oriental Colombiana. V. Análisis fitosociológico de la vegetación de los depósitos turbosos paramunos de los alrededores de Bogotá. *Caldasia,* **16**: 155–192.

Skottsberg, K. (1939) Report on Hawaiian bogs. *Proceedings of the 6th Pacific Congress, IV*. Stanford (SF): Berkeley.

Smith, A.P. and Young, T.P. (1987) Tropical alpine plant ecology. *Annual Review of Ecology and Systematics,* **18**: 137–158.

Smith, R.T. and Atkinson, K. (1975) *Techniques in Pedology: a handbook for environmental and resource studies.* London: Elek.

ter Braak, C.J.F. (1988) *CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (Version 2.1).* Report LWA-88-02, Wageningen: Agricultural Mathematics.

Troll, C. (1968) The Cordilleras of the tropical Americas: aspects of climatic, phytogeographical and agrarian ecology. In: Troll, C. (Ed.) *Geo-ecology of the Mountainous Regions of the Tropical Americas*, pp. 15–56. Bonn: Ferd. Dümmlers Verlag.

Van Steenis, C.G.G.J. (1938) Exploraties in de Gajolanden. *Tijdschrift der Koninklijke Nederlandsche Aardrijkskund Genootsch. Leiden*, **5**.

Van Steenis, C.G.G.J. (1962) The mountain floras of the Malaysian tropics. *Endeavour*, **21**: 183–194.

Aquatic plant communities of the páramo lakes of Volcán Chiles, Ecuador

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SUMMARY

A study was carried out of seven high-altitude lakes, all located above 3,800 m on the slopes of Volcán Chiles in northern Ecuador, to determine the aquatic plant species found in each lake and the environmental factors associated with their distributions. Floristic data were correlated with environmental variables to identify potential controlling factors associated with the species' preferences for particular habitats within this aquatic ecosystem. This was performed using canonical correspondence analysis and TWINSPAN analysis classifying the lakes according to vegetation, linked with environmental factors. Profiles of the vegetation were constructed to illustrate the distribution of the species in relation to the depth gradient. The results demonstrated that species richness decreased as depth increased, and each species showed a preference for part of the gradient. Aspects of water chemistry (such as conductivity, pH and mineral content) as well as the nature of the substrate were associated with species' distributions. Only two species were present in all of the lakes: *Isolepis inundata* (POIR) R.BR. and *Ranunculus limoselloides* TUREZ.

RESUMEN

Se realizó un estudio en siete lagunas altoandinas ubicadas sobre los 3.800 m de altura, en las faldas del Volcán Chiles, al norte del Ecuador, con el propósito de estudiar su flora y los factores medioambientales que inciden en la distribución de las especies. Se correlacionó la composición florística con variables ambientales para examinar las preferencias de las especies por ocupar estratos diferentes dentro del ecosistema. Se aplicó un análisis canónico de correspondencias y un análisis TWINSPAN, los cuales permitieron clasificar las lagunas de acuerdo a la vegetación y a la incidencia de factores ambientales. Se diseñaron perfiles de vegetación para ilustrar la estratificación y distribución de las especies con relación a una gradiente de profundidad. Los resultados muestran que la riqueza de especies disminuye con el aumento de profundidad y cada especie tiene preferencia por ocupar un estrato. Los factores químicos del agua como la conductividad, pH y minerales, así como el tipo de sustrato, son elementos de alta incidencia en la distribución de las especies. Sólo dos especies están compartidas entre las lagunas estudiadas: *Isolepis inundata* (POIR) R.BR. y *Ranunculus limoselloides* TUREZ.

Key words: freshwater vegetation, high-altitude lakes, water chemistry, zonation

INTRODUCTION

In Ecuador there are hundreds of lakes situated above 3000 m altitude. Some regions have several hundred such lakes concentrated in relatively small areas (*e.g.*, Cajas, Papallacta, Llanganates), while other lakes are much more isolated, sometimes in small groups (*e.g.*, El Compadre in Parque Nacional Podocarpus) or singly (*e.g.*, Laguna Quilotoa). The majority of these lakes are of glacial origin, but a large proportion of the remainder occupy volcanic craters. The topography and geology of the Andean cordilleras restrict almost all the lakes to these high altitude areas or to the lowlands—very few lakes exist at intermediate elevation between 400 m and 2500 m.

Aquatic plants are fundamental to the functioning of high altitude lake ecosystems in the Andes. They form the basis of the food chain and shelter for many animal species (both vertebrates and invertebrates). The páramo zone supplies many Andean towns and cities with water (Luteyn 1992) and lake plants in this zone perform a valuable role in cleansing and oxygenating this water (Moss 1980; Goldman & Horne 1983; Archibold 1990).

Productivity and biomass in the illuminated surface waters are greatly affected by the relative abundance of the different plant types (Toivonen & Lappalainen 1980; Duarte & Kalff 1990). In the Highlands, submerged rooted plants are the dominant life form and their root systems account for as much us 80% of the plant biomass (Wetzel 1975).

The aquatic plants of the páramo have been poorly collected and their ecology is even less well-known. However, an understanding of the ecology of these plants might enable their use as bioindicators of water chemistry and quality, without the need to carry out expensive chemical tests.

The aquatic plants of the highlands may also be interesting in terms of their ecophysiology. They might demonstrate adaptations to low nutrient concentrations, low and variable temperatures (Sand-Jensen & Sondergaard 1997), and the highly variable water chemistry in a region with active volcanism and relatively young geology (Colinvaux et al. 1985). Their biogeography is also interesting. They form island habitats in the high altitude páramos, which are themselves cool-climate islands in a tropical lowland "sea". These biogeographical patterns may be investigated at both local and regional scales. Within one particular area, sharing similar geology and climate, one might think that neighbouring lakes would be similar in their floristic composition, but other factors also affect the distribution of plant species and the composition of aquatic plant communities. For example, water chemistry may vary considerably from lake to lake (variables like pH, temperature, electrical conductivity, mineral salts, etc.) and ultimately these differences might influence the distribution patterns of aquatic plant species (Barko 1986). In the same way, the nature of the substrate, and the type and quantity of nutrients can vary within and between lakes (McFarland & Barko 1986). These differences are related to geology and climate, but are

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 55-63.

also influenced by anthropogenic activities (grazing, burning, etc.) and processes of leaching and sediment transport.

Furthermore, within an individual lake, there are several factors which determine plant distributions, such as depth, substrate type and water chemistry (Kunii 1991). In lakes, habitat conditions change as water depth increases away from the shore, and markedly concentric patterns of vegetation zones may sometimes develop (Keddy 1984). The distance this zone extends from the shoreline depends on the morphometry of the lake basin and the transparency of the water (Toivonen & Huttunen 1995). The nutrient concentration is higher closer to the shoreline than in deeper waters because of the better substrate development there, promoting plant growth (Tracy et al. 1998).

A few studies have been carried out in Latin America: Novelo & Bonilla (1995) for Mexico, Velázquez (1994) for Venezuela, Kahn & Leon (1993) for Peru and Rangel *et al.* (1983, 1997) for Colombia. Freshwater aquatic ecosystems have been poorly studied in Ecuador. Only two studies of lake macrophytes have been carried out in Ecuador, both on the coastal plain (Bravo & Balslev 1983; Briones et al. 1997). The only Andean lake studies concern diatoms (*e.g.*, Steinitz-Kannan *et al*. 1983).

As part of a larger study of the high altitude lakes of Ecuador, the macrophytes of the lakes of Volcán Chiles were surveyed to determine species composition and its relationship with environmental and geographical factors.

METHODS

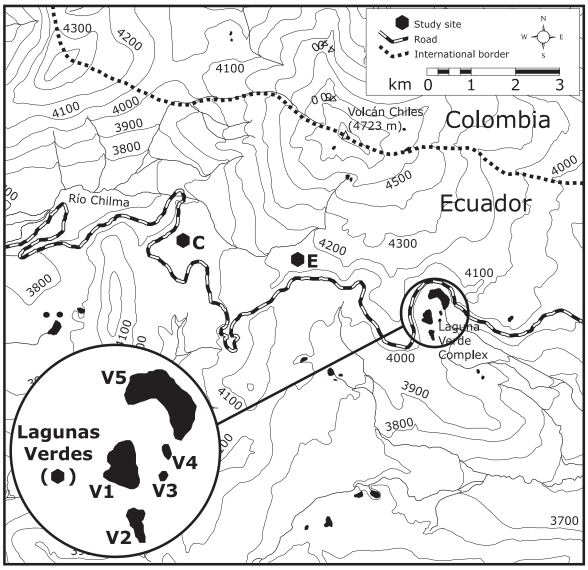
Study Area

The study was carried out on Volcán Chiles, on the Ecuador-Colombia border, in the Lagunas Verdes (00º47'50 " N 77º55'46 " W), and two smaller waterbodies nearby which were named for the purpose of this study Esteban and Corazón (00°48'23 " N 77°57'15 " W and 00°47'37 " N 77°56'21 " W, respectively). All of these lakes are situated between 3,800–3,900 m in altitude, close to the Tulcán–Maldonado road (Fig. 1).

The climate in the páramo of the Volcán Chiles is cold, with mean temperatures of between 9 and 11ºC, but with a daily range from up to 22ºC by day and several degrees below zero at night. Precipitation is variable from day to day, but reaches about 1,500 mm per year (INAMHI 1994).

This páramo is characterized by large extensions of the typical vegetation of this sector, dominated by giant rosette plants (*Espeletia pycnophylla* ssp *angelensis* CUATR., known locally as frailejón). It grows from about 3,200 to 4,200 m in altitude. This giant rosette plant is only found in two páramo regions in Ecuador: the páramo of the far north (including this study area) and that of the Llanganates in central Ecuador (Josse 1996).

Fig. 1. The location of the studied lakes. The lakes belonging to the Laguna Verde complex (V1–V5) are shown in detail in the inset. Lagunas Corazón and Esteban are denoted on the main map by "C" and "E", respectively.



The soil of the study area is developed from deep volcanic ashes loose sand, with high water retention, an acid pH and a high content of organic matter (Coello 1994).

Sampling

Line transects were used to evaluate changes in the vegetation corresponding to a depth gradient (Matteucci 1982). The lake margins were sampled using 1 m^2 quadrats spaced at regular intervals along transects. The number of transects in each lake was determined by the variability of the vegetation within it (Pedralli 1990). The transects ran from the edge towards the centre of the lake and stopped only when the vegetation disappeared or the water became too deep to work safely (1.6 m). Within each quadrat estimates of plant cover and bare ground were recorded. Furthermore, the frequency of each species (the number of quadrats occupied in each transect) was calculated.

Voucher specimens of all plant species were collected from the transects for later identification, with the help of taxonomic keys and preserved plant material deposited in herbaria in Quito (QCA) and Aarhus, Denmark (AAU). Moss species were aggregated for this study.

Environmental data were also measured:

- pH—using Machery-Nagel 92110 indicator paper
- water temperature— using a mercury thermometer
- electrical conductivity (Hanna Hi 8633 meter)
- geographic position using a Trimble navigation GPS
- altitude with a Thommen altimeter
- quantitative concentrations of macronutrients were analysed at the University of Plymouth using a

Varian SpectrAA-600 Flame atomic absorption spectrophotometer and a Technicon AutoAnalyzer II.

- texture of the substrate was assigned to basic categories in the field using finger texturing.

Data analysis

Multivariate statistical analysis was used to compare the lake communities in terms of their species composition and environmental characteristics. TWINSPAN (Hill 1979, modified by P.R. Minchin according to the criteria specified by Oksanen & Minchin 1997) was used to classify the samples and species using compositional data (Jongman & ter Braak 1987). These same data were ordinated in relation with environmental variables (Kent & Coker 1992) using canonocal correspondence analysis (CCA, performed using CANOCO v. 4.02—ter Braak & Smilauer 1998).

Depth profile diagrams of each transect were drawn to illustrate the stratification of species, their associations and life forms (Novelo 1995). Correlations were carried out between the number of species and depth.

RESULTS

Table 1 outlines the sampling carried out in each lake and several general characteristics relating to depth and vegetation. Three of the lakes were sufficiently variable to merit two transects. Altogether, 10 transects were used, with 70 quadrats. Each transect was between 7 and 16 m in length, and therefore, the number of quadrats recorded in each varied accordingly. All of the lake margins were relatively shallow for many metres from land and this is reflected in the transects (e.g., Laguna Esteban was just 12 cm deep 10 m from the shore). Each transect contained 2–7 species, and the vegetation covered 8–100% of the lake bottom.

Ten species were present in the transects, corresponding to nine families within the bryophytes, pteridophytes and angiosperms (Table 2). The greatest diversity was found in the dicotyledons, followed by the monocotyledons, bryophytes and pteridophytes. These plants belonged to three life forms: submerged rooted hydrophytes, emergent rooted hydrophytes, and floating rooted hydrophytes. *Crassula* and *Elatine* were often associated, while *Isolepis inundata* and the moss sp. registered the greatest abundances.

The depth profiles show the changing species composition of each transect with depth (Fig. 2). The preference of each species for a particular depth range is evident. *Isoetes* and the moss spp. occupy the deepest zones. Fig. 3 shows the relationship between depth and species richness: shallower substrates were more variable in species richness than deeper ones, but otherwise no trend is evident.

Table 1. Summary of transect sampling. The abundance of vegetation is represented in two ways: "cover" shows the mean proportion of quadrat covered by plants, and "frequency" is the proportion of quadrats within a transect in which plants are present. Laguna Verde 4, Laguna Verde 5 and Laguna Corazón were sampled with two transects each—details are shown separately for each transect ("T1" and "T2").

Lake		No of transects	No of quadrats	Transect length (m)	Max depth (m)	No of species	Mean Cover (%)	Frequency (%)
Verde 1		1	9	9	1.05	6	86.5	56.6
Verde 2		1	9	9	0.68	5	79.4	72.0
Verde 3		1	7	7	0.36	2	49.4	57.0
Verde 4	T1	2	6	6	0.30	2	30.8	50.0
	T2		1	1	0.12	3	75.0	100.0
Verde 5	T1	2	10	10	0.61	3	73.6	75.0
	T2		6	6	0.80	3	100.0	58.5
Esteban		1	10	10	0.12	4	95.0	55.0
Corazón	T1	2	8	8	0.40	7	8.1	55.7
	T2		4	4	0.35	3	96.2	91.6

Table 2. Summary of the species composition within the transects. Life forms: "S", submerged rooted hydrophyte; "F", floating rooted hydrophyte; "E", emergent rooted hydrophyte. Frequency (proportion in which the species is present) is given for lakes (n=7), transects (n=10) and quadrats (n=68; two of the original 70 quadrats had no species of macrophyte). The mean cover of each species for all quadrats is also shown.

Species	**Life form**	**Taxonomic group**	**Mean Frequency (%)**			**Mean Cover (%)**	**Max depth (cm)**	**Depth range (cm)**
			Lakes	**Transects**	**Quadrats**			
Lilaeopsis schaffneriana	E	monocot	14.2	10	1	0.3	40	0–50
Ranunculus limoselloides	F	dicot	57.1	40	15	7.7	30	0–50
Sphagnum sp.	F	bryophyte	28.5	20	10	6.9	50	0–50
Werneria pygmaea	E	dicot	14.2	20	14	5.2	20	0–50
Isolepis inundata	S	monocot	85.7	70	20	6.7	70	51–100
Elatine ecuadoriensis	S	dicot	42.8	30	20	8.2	70	51–100
Crassula venezuelensis	S	dicot	42.8	30	22	8.4	80	51–100
Juncus stipulatus	S	monocot	14.2	20	10	1.9	80	51–100
Moss spp.	S	bryophyte	71.4	70	37	26.7	>100	>100
Isoetes sp.	S	pteridophyte	42.8	40	17	1.6	>100	>100

Fig. 2. Profile diagrams of nine transects, continued on next page with key to species. Water depth is shown by the lines (the top of each graph represents the water surface), and vegetation cover is shown by the bars (subdivided to indicate each species' contribution). One sample was recorded from a second transect in Laguna Verde 4 (not shown here: depth 12 cm; Isolepis inundata *10%, Moss sp. 50%,* Sphagnum *sp. 15%).*

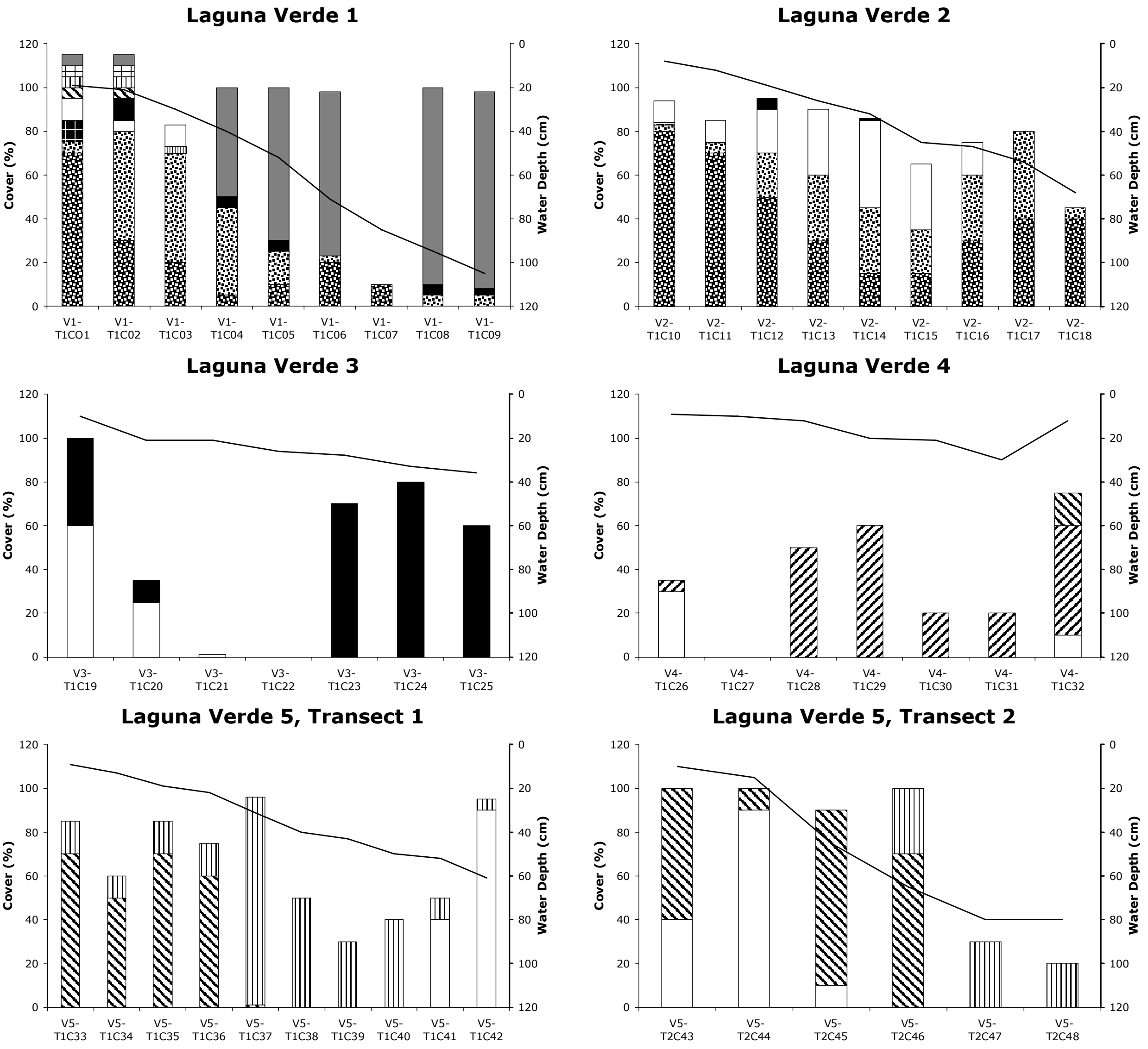
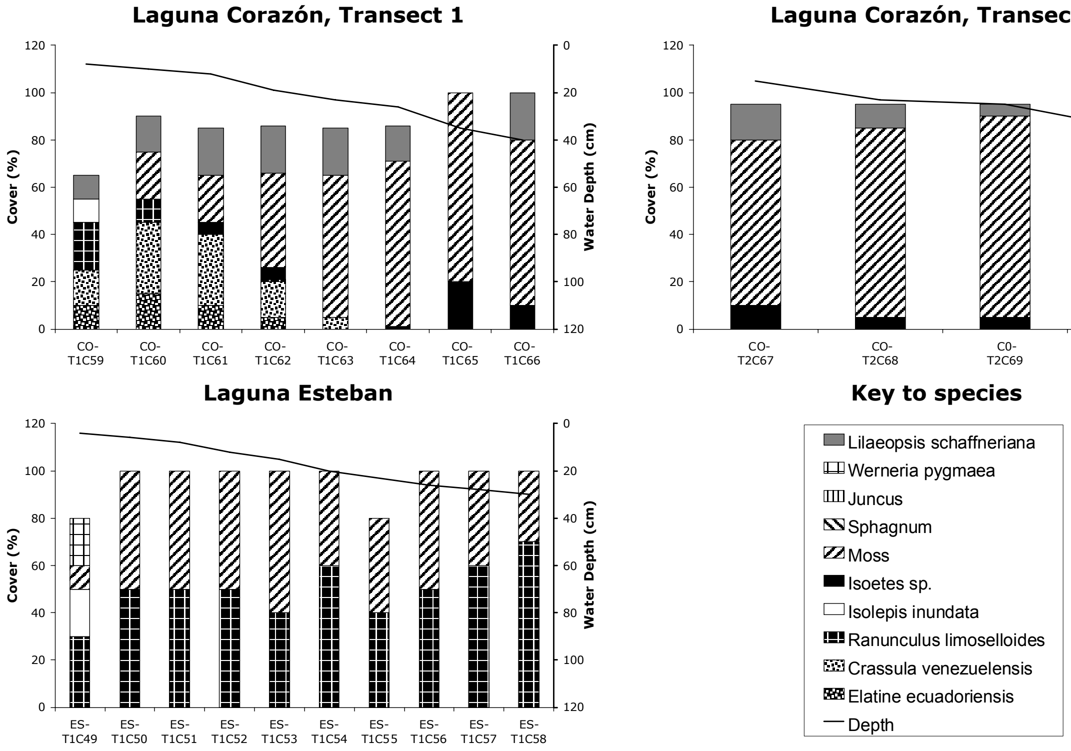


Fig. 2 (continued from previous page). Profile diagrams of the ten transects.

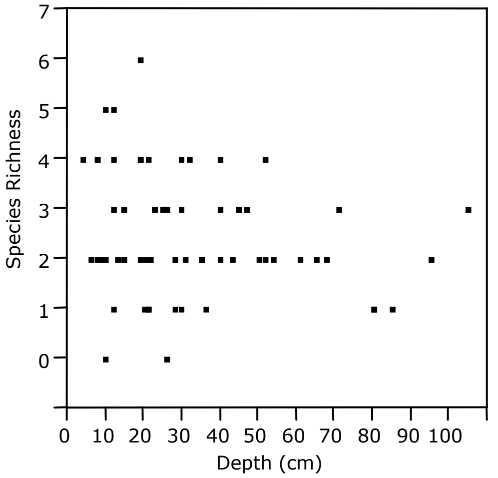


All of the lakes were situated between 3800 and 3900 m (Table 3). The environmental variables show clearly the higher conductivity readings present in Lagunas Verde 2 and 5, and higher SO_4 readings from Lagunas Verde 3 and 5, and Laguna Corazón. The pH values were all very similar, between 5.0 and 6.0, and most substrates were at least partly composed of organic material, though a few lakes had substrates of mud, silt and sand. There were strong correlations in water chemistry in the concentrations of calcium, magnesium, sodium, iron and sulphate.

TWINSPAN highlighted two basic groups of lakes based on the vegetation composition (Fig. 4): Laguna Verde 5 formed a separate group, with the remaining lakes of the Laguna Verde complex plus Esteban and Corazón forming the second group. This indicates that Laguna Verde 5 possesses very different vegetation characteristics from the rest of the lakes.

The canonical correspondence analysis confirmed the difference between Laguna Verde 5 and the other lakes (Fig. 5), though every lake was distinct from the others to some extent. There was a statistically significant relationship between the measured environmental variables and the composition of the vegetation (Monte Carlo test, *p*=0.005). The relationship is presented graphically in Fig. 5. The concentration of calcium (highly correlated with the concentrations of other measured cations in solution, and, therefore, with conductivity) was the most significant factor, with sulphate concentration and pH. Furthermore, the spread of plant species lies mostly between the centroids for sandy and organic substrate types, suggesting this may also be an important factor in plant distribution. Water depth was not useful in explaining the pattern of species' distributions in these lakes.

Fig. 3. Species richness and depth.



The CCA infers some key characteristics of the environmental preferences of particular species (Fig. 5). *Juncus stipulatus* and *Sphagnum* were only present in Laguna Verde 5, and were therefore associated with the environmental conditions of this lake, namely relatively high conductivity (compared to the other lakes in this study). *Elatine ecuadoriensis* and *Crassula venezuelensis* were both characterized by sandy substrates and relatively high pH. *Lilaeopsis schaffneriana, Isoetes* sp. were present in lakes with low calcium content. Predominantly organic substrates were often occupied by *Ranunculus limoselloides* and *Werneria pygmaea* (found only once in Laguna Verde 4). The moss was associated with soft substrates, particularly of mud and soft organic material. *Isolepis inundata* was not associated with extremes of any variables.

Table 3. Environmental characteristics of each lake. The presence of substrate characteristics indicated by "●".

	Verde 1	**Verde 2**	**Verde 3**	**Verde 4**	**Verde 5**	**Esteban**	**Corazón**
Altitude (m)	3800	3800	3800	3800	3900	3900	3900
pH	6.0	5.5	5.5	5.5	5.5	5.5	5.0
Temperature (ºC)	16.7	13.4	18.6	19.3	17.8	16.3	17.4
Conductivity (µS)	5.4	30.5	6.3	8.8	56.5	9.1	5.3
Ca mg l^{-1}	0.293	3.130	0.446	0.191	2.951	0.185	0.679
Mg mg l^{-1}	0.064	0.252	0.084	0.049	1.362	0.077	0.306
Na mg l^{-1}	0.298	0.874	0.196	0.153	1.183	0.314	0.781
K mg l^{-1}	0.495	0.579	0.165	0.211	0.662	0.830	0.494
Al mg l^{-1}	0.847	0.426	1.173	1.082	1.556	0.837	0.785
Fe mg l^{-1}	2.71	2.99	2.64	2.43	3.62	2.62	3.66
Pb mg l^{-1}	0.035	0.024	0.047	0.041	0.045	0.047	0.062
$S0_4$ mg l^{-1}	4.5	2.5	15.5	2.0	21.0	3.0	33.5
Substrate characteristics:							
Organic	●	●	●	●		●	
Mud							●
Silt				●	●		
Sand		●					

Fig. 4. Two-way indicator analysis (Twinspan) of 68 vegetated quadrats of the aquatic lake margins. For each group, the number of quadrats (shown after the dash) is presented for each lake.The five lakes making up the Laguna Verde complex are coded by V plus the corresponding number, while the lakes of Esteban and Corazón are represented by "ES" and "CO", respectively.

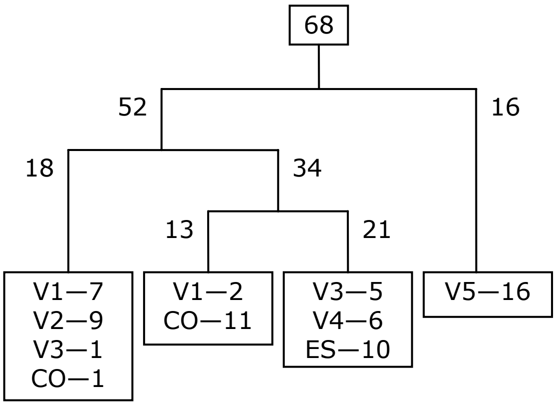
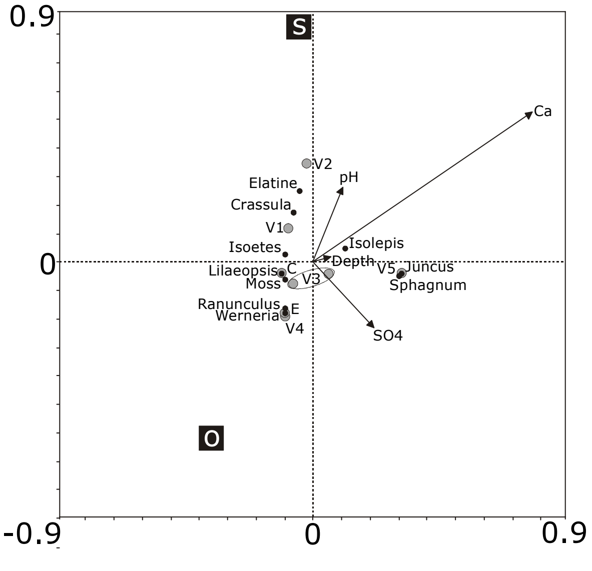


Fig. 5. Canonical correspondence analysis biplot of 68 aquatic vegetation samples (larger grey circles) and 10 plant species (black circles). The centroids for sandy ("s") and organic ("o") substrates are highlighted in boxes. Axes are scaled by 0.164 for both species and samples. The lakes are indicated by the same letter codes as in Fig. 1.



DISCUSSION

Aquatic plants tend to occupy the lake margins. Thus, the greatest diversity of species in this study was found in the shallows, owing to the concentration of nutrients associated with the largely organic substrate in the littoral zone. This is typical of aquatic lake vegetation, often exhibiting zonation intimately associated with the water level, substrate and topography (Lot & Novelo 1978). The distribution and permanence of each plant association depends on the substrate type, as shown by the frequent co-occurrence of *Crassula* and *Elatine* in the samples on Volcán Chiles (though it could be a mutualistic association). However, physical factors such as wave action and changes in water level also directly affect the spatial distribution of the species (Szmeja 1994), and these would have to be studied in the future.

Various environmental factors (such as temperature, conductivity, pH, the chemical composition of the water, and substrate characteristics) have a direct influence on the productivity, distribution and composition of aquatic vegetation (Barko *et al.* 1986). In general terms, the higher the water temperature, the greater the productivity of aquatic plants (McFarland & Barko 1986). Water temperature varies rapidly on Volcán Chiles according to the amount of solar insolation, and with wide diurnal oscillations, but all of the lakes in this study are subject to broadly similar climatic conditions. Shallow, crystal-clear waters warm up quickly in sunlight and plant productivity is increased. It is this which partly explains the high plant abundance around the margins of lakes and throughout shallow water bodies like Corazón.

Water chemistry is also closely related to the distribution of aquatic plant species (Barko 1986). Electrical conductivity measures the total amount of ions dissolved in the water, based on the capacity that a solution has to carry an electrical current. Therefore, water bodies with higher concentrations of ions record greater conductivity, and oligotrophic lakes, like Corazón, have low water conductivity. Typical dissolved ions are the macronutrients calcium, magnesium, sodium, potassium, aluminium, iron, lead and sulphate and their concentration varies according to the nature of the surrounding land (Roldán 1995). Although generally low compared with lowland lake systems, the concentrations of macronutrients in the studied lakes were highly inter-correlated, and helped to explain patterns of floristic composition. The highest macronutrient levels were associated with *Juncus stipulatus* and *Sphagnum*.

Water pH is related to conductivity, since it refers to the concentration of dissolved hydrogen ions in the water. It is a useful aid in determining the status of water bodies as oligotropic or eutrophic. Low pH is associated with lower productivity, demonstrated by low chlorophyll a levels, and increases the transparency of the water (Roldán 1995). High-altitude lakes in Ecuador have low pH and this is reflected in the plant communities— the presence of *Sphagnum* mosses and *Isoetes* is a strong indication of oligotrophic conditions. These plants bind cations and phosphates, inhibiting their recycling and adds to the oligotrophication (Roldán 1995). That these species were found in the lake with the highest concentrations of nutrients emphasizes the overall low productivity of these water bodies.

The dominance of certain species (such as *Isolepis inundata*, *Juncus stipulatus* and other species of *Sphagnum*) may be linked with high sulphate concentrations. The high sulphate concentrations found in some lakes (*e.g.*, Verde 3, Verde 5 and Corazón) seems to be fed by springs beneath the water surface, which are connected to the volcanic activity of the mountain. Sulphurous thermal springs do occur in a number of locations on this mountain, though there is no evidence of a thermal input into the lakes studied here. The other lakes, with normal sulphate concentrations, receive their water directly from rainfall, and from runoff from surrounding slopes.

The data suggest that there is an important relationship between the nature of the substrate and the presence of plant species. Some species, such as *Elatine ecuadoriensis* and *Crassula venezuelensis* were associated with sandy substrates, while mosses (other than Sphagnum) were found in mud and soft organic material. The nature of the substrate was only recorded in qualitative terms in this study, but a more detailed examination would be worthwhile in future.

The vegetation of these lakes supports a range of aquatic invertebrates (*e.g.*, amphipods, copepods, rotifers), many of which feed directly on benthic mosses and vascular plants, or on plant detritus (Gregory 1983). The vegetation also provides shelter for these invertebrates. Some initial studies of the invertebrate communities are also being carried out at the moment, and this should provide a clear indication of the role of plants in their distributions. However, taxonomic studies are also required to describe the new species found in these habitats.

Further studies of the kind reported here are already underway in different lakes above 3000 m across the Andean Cordilleras in Ecuador. Nevertheless, a number of interesting questions have yet to be addressed. For example, the effects of UV radiation on benthic plant communities in high-altitude lakes has not been properly investigated. The relationship between the benthic plants of lakes and the streams and rivers connecting them is also an interesting avenue of research.

In conclusion, the distribution of aquatic plant species in the lakes of Volcán Chiles depends to a large extent on the characteristics of the substrate in which they grow and the chemistry of the water in which they are immersed. These characteristics vary considerably even within some lakes, a consequence of the interesting geology of this mountain.

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REFERENCES

Archibold, O.W. (1990) *Ecology of World Vegetation,* London: Chapman & Hall.

Barko, J.W. (1986) *Ecology of Submersed Macrophytes: an Overview,* Vicksburg, Mississippi: U.S. Army Engineer Waterways Experiment Station.

Barko, J.W., Adams, M.S. and Clesceri, N.L. (1986) Environmental factors and their consideration in the management of submersed aquatic vegetation—a review. *Journal of Aquatic Plant Management,* **24**: 1–10.

Bravo, V.E. and Balslev, H. (1983) *Ecología y Adaptación de Algunas Plantas Acuáticas del Ecuador,* Quito: Pontificia Universidad Católica del Ecuador.

Briones, E. and Flachier, J. (1997) *Inventario de Humedales del Ecuador. 1. Humedales Lénticos de las Provincias de Esmeraldas y Manabí,* Quito: EcoCiencia/INEFAN/Convención RAMSAR.

Coello, F. (1994) *Plan de Manejo de la Reserva Ecológica "El Angel" Provincia del Carchi,* Quito: Convenio MBS - INEFAN - IICA.

Colinvaux, P.A., Miller, M.C., Liu, K.B., Steinitz-Kannan, M., Frost, I. (1985) Discovery of permanent Amazon lakes and hydraulic disturbance in the upper Amazon basin. *Nature,* **313**: 42–45.

Duarte, C.M. and Kalff, J. (1990) Patterns in the submerged macrophyte biomass of lakes and the importance of the scale of analysis in the interpretation. *Canadian Journal of Fisheries and Aquatic Sciences,* **47**: 357–362.

Goldman, C. R. and Horne, A.J. (1983) *Limnology,* New York: McGraw-Hill.

Gregory, S.V. (1983) Plant-herbivore interactions in stream systems. In: Barnes, J.R. and Minshall, G.W. (Eds) *Stream Ecology*, pp.157–89. New York: Plenum Press.

Hejny, S., Raspopov, I. and Kvet, J. (1986) *Studies on Shallow Lakes and Ponds,* Prague: Czechhoslovak Academy of Sciences.

Hill, M.O. (1979) *TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes,* New York: Cornell University.

INAMHI (1994) *Anuario Meteorológico 1994,* Quito: Ecuador.

Jongman, H.G. and ter Braak C.J.F. (1987) *Data Analysis in Community and Landscape Ecology,* Wageningen: Pudoc.

Josse, C. (1996) *Guía para los Páramos del Sistema Nacional de Areas Protegidas del Ecuador,* Quito: Proyecto Inefan-Gef.

Kahn, F., León, B. and Young, K. (1993) *Las Plantas Vasculares en las Aguas Continentales del Perú,* Lima: IFEA.

Keddy, P. (1984) Plant zonation on lakeshores in Nova Scotia: a test of the resource specialization hypothesis. *Journal of Ecology,* **72**: 797–808.

Kent, M. and Coker, P. (1992) *Vegetation Description and Analysis,* London: Belhaven Press.

Kunii, H. (1991) Aquatic macrophyte composition in relation to environmental factors of irrigation ponds around lake Shinji, Shimane, Japan. *Vegetatio,* **97**: 137–148.

Lot, A. and Novelo, A. (1978) *Laguna de Tocomulco, Hidalgo,* Guías Botánicas de Excursiones en México. Mexico City: Sociedad Botánica de México.

Luteyn, J.L. (1999) *Páramos: a checklist of plant diversity, geographical distribution, and botanical literature,* New York: New York Botanic Garden.

Matteucci (1982) *Metodología para el estudio de la vegetación,* Monografía 22. Washington: OEA, Programa Regional de Desarrollo Científico y Tecnológico.

McFarland, D.G. and Barko, J. W. (1986) *Effects of temperature and sediment type on growth and morphology of monoecius and dioecius* Hydrilla, Vicksburg, Mississippi: US. Army Engineer Waterways Experiment Station.

Moss, B. (1980) *Ecology of Freshwaters: aquatic plant habitats,* Oxford: Blackwell Scientific.

Novelo, A. and Bonilla, J. (1995) *Manual de Identificación de Plantas Acuáticas del Parque Nacional Lagunas de Zampoala, México,* Mexico City: Universidad Nacional Autónoma de México.

Oksanen, J.and Minchin, P.R. (1997) Instability of ordination results under changes in imput data order: explanations and remedies. *Journal of Vegetation Science,* **8**: 447–454.

Pedralli, G. (1990) Macrófitas acuáticas: técnicas y métodos de estudio. *Curitiba*, **26**: 5–24.

Rangel, O., Lowly, P. and Aguillar, M. (1997) *Tipos de vegetación en Colombia. Diversidad Biótica II,* Bogotá: Universidad Nacional de Colombia.

Rangel, O. and Aguirre, J. (1983) Comunidades acuáticas altoandinas. I. Vegetación sumergida y de ribera en el lago de Tota, Boyacá, Colombia. *Caldasia*, **13**: 725–742.

Roldán, G. (1995) *Fundamentos de Limnología Neotropical,* Universidad de Atioquia.

Sand-Jenssen, K. and Sondergaard, M. (1997) Plants and environmental conditions in Danish *Lobelia*-lakes. In: *Freshwater Biology, Priorities and Development in Danish Research,* pp. 54–73. Copenhagen.

Steinitz-Kannan, M., Colinvaux, P.A. and Kanna, R. (1983) Limnological studies in Ecuador: I A survey of chemical and physical properties of Ecuadorian lakes. *Archiv fur Hydrobiologie*, **1**: 61–103.

Szmeja, J. (1994) Dynamics of the abundance and spatial organization of isoetid populations in an oligotrophic lake. *Aquatic Botany*, **49**: 19–32.

ter Braak, C.J.F. and Šmilauer, P. (1998) *CANOCO Reference Manual and User's Guide to Canoco for Windows*, Wageningen: Centre of Biometry.

Toivonen, H. and Huttunen, P. (1995) Aquatic macrophytes and ecological gradients in 57 small lakes in southern Finland. *Aquatic Botany*, **51**: 197–221.

Toivonen, H. and Lappalainen, T. (1980) Ecology and production of aquatic macrophytes in the oligotrophic, mesohumic lake Suomunjarvi, eastern Finland, *Annales Botanici Fennici*, **17**: 69–85.

Tracy, E., Karapatakis, K., Guy, J. and Mackey, H. (1998) The relative effects of water depth, fetch and other physical factors on the development of macrophytes in a small southeastern US pond. *Aquatic Botany*, **61**: 289–299.

Velásquez, J. (1994) *Plantas Acuáticas Vasculares de Venezuela,* Caracas: Universidad Central de Venezuela.

Vestergard, O. (1997) *Artsrigdom og vobredelse of vanoplanter i deanske soer.* Thesis, Freshwater Laboratorium, University of Copenhagen.

Wetzel, R. G. (1975) *Limnology*, Fort Worth: Saunders College Publishing.

Páramo vegetation recovery in the first two years after a fire on Volcán Chiles, Ecuador

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SUMMARY

A large area of páramo to the south of the summit of Volcán Chiles was burned in December 1996. To monitor mortality rates, changes in occupancy and the colonization of gaps, both sides of a ridge at 4000 m within this area was monitored for two years after the fire using 1 cm^2 microquadrats. During the first two years after the fire, 29 species were recorded in the microquadrats. The leeward and windward slopes of the ridge showed different mortality rates, patterns of recovery, species diversity values and community composition. Fewer species and individuals of plants survived the fire on the leeward side of the ridge compared with the windward side, but post-fire mortality was higher on the more exposed windward slope. However, those tussock grasses, mosses, cushion-formers and reptant species which survived the fire were able to spread into gaps. At each monitoring visit, the communities within the transects were different on each side of the ridge, and the two sides of the ridge followed a different pattern of recovery. These patterns may be related to the fire regimes experienced on the two slopes, the environmental conditions which characterize the two areas, and the dispersal strategies of plant species.

RESUMEN

En diciembre de 1996 un área grande de páramo al sur de la cima del Volcán Chiles fue quemada. Con objeto de registrar las tasas de mortalidad, los cambios en la ocupación de espacio y la colonización de claros, se monitorearon ambos lados de una cresta a 4000m durante los siguientes dos años después del fuego, usando microcuadrantes de 1 cm^2. Durante el curso del estudio se observaron 29 especies de plantas. Ambas laderas (barlovento y sotavento) mostraron diferentes tasas de mortalidad, patrones de recuperación, diversidad de especies y composición de sus comunidades. Un menor número de especies e individuos sobrevivieron el fuego en la vertiente de barlovento, en comparación con la vertiente de sotavento, pero la mortalidad pos-fuego fue más alta en esta última. No obstante, los pastos amacollados, los musgos, las plantas en cojín, y las plantas rastreras que sobrevivieron el fuego fueron capaces de extenderse hacia los claros. En cada visita, las comunidades dentro de los transectos permanecieron diferentes en cada lado de la cuesta y las dos vertientes siguieron un patrón de recuperación diferente. Estos patrones podrían estar relacionados a los regímenes de fuego sufrido en los dos vertientes, las condiciones ambientales que caracterizan las dos áreas y las estrategias de dispersión de las diferentes especies.

Key words: fire, regeneration, tropical alpine, patchiness, species diversity

INTRODUCTION

Fires are the most significant human impact in páramos from Ecuador to Costa Rica (Horn 1989; Laegaard 1992; Luteyn 1992; Ramsay & Oxley 1996), resulting in a landscape mosaic of burned patches in various stages of recovery (Ramsay 1999). Their effect on vegetation has been the subject of debate for many years, since Ellenberg (1958) proposed that the páramos were artificial, created and maintained by burning. Fires do have a long history in the páramos—of up to 10000 years before present in Costa Rica (Horn 1993)—but the role of humans in starting fires is unclear set against potential natural causes (*e.g.*, lightning, volcanism, sparks from rockfalls).

Whatever the balance in the past, fires appear to be increasing in frequency nowadays, and might be started for several reasons, including:

- *Agriculture*
  to improve livestock grazing by encouraging the growth of new, green shoots and removing dead leaf material.
- *Hunting*
  to flush out game, especially rabbits and deer.
- *Trail maintenance*
  to burn away dense vegetation from trails which have become difficult to follow.
- *Accidents*
  small fires—lit for cooking or to drive away biting flies—sometimes spread; these kinds of fires are particularly common near lakes and streams seeded with trout which are often visit ed by fishermen.
- *Arson*
  visitors sometimes take pleasure in burning hillsides for fun.

Managing this rise in fire frequency in a sustainable way requires information about the inherent ability of páramo vegetation to recover from burning. Various attempts have been made to compare burned areas of páramo with "unburned" ones. Studies of this kind have been carried out in Colombia (Verweij and Budde 1992; Verweij and Kok 1992; Hofstede 1995a,b; Hofstede and Rossenaar 1995; Hofstede, Chilito and Sandovál 1995; Hofstede, Mondragón and Rocha 1995), Ecuador (Keating 1995), and Costa Rica (Horn 1988, 1989). A more direct method is to monitor vegetation recovery through time after fires, an approach which has been applied in Ecuador (Ramsay and Oxley 1996; Keating 1998).

This study takes the latter approach, and examines the development of páramo vegetation in the first two years after an intense fire on Volcán Chiles, in the north of Ecuador, which burned in December 1996. It considers small-scale changes in the vegetation at the level of the individual plant to determine rates of mortality, replacement and colonization. It also

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 65-73.

compares leeward and windward sides of the same ridge system.

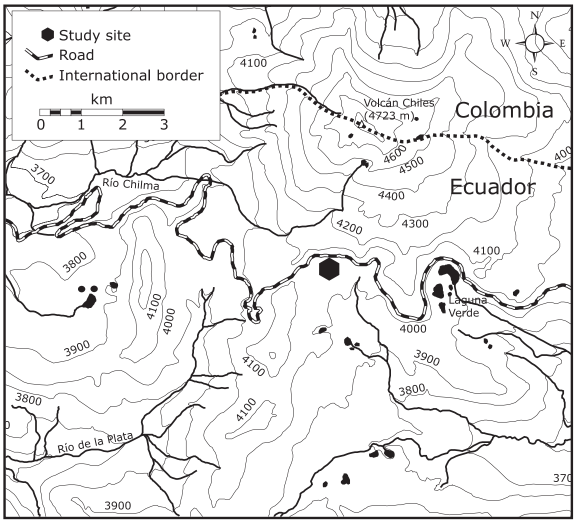
METHODS

Study area

Volcán Chiles is located approximately 40 km west of Tulcán, on the border between Ecuador and Colombia. Farmers burned a large area to the south of the summit of the volcano on 9 December 1996, following an extended period of dry weather. A small ridge within this area, running north-to-south at 4000 m, was chosen for long-term monitoring because of its easy access from the Tulcán–Maldonado road (Fig. 1).

The vegetation near this area was described by Ramsay (2001) based on survey work carried out in 1987. It was dominated by tussocks of *Calamagrostis* species and giant stem rosettes of *Espeletia pycnophylla* subsp. *angelensis*. Between the tussocks and giant rosette plants, were a variety of acaulescent rosette plants, herbs and prostrate shrubs with occasional cushion plants.

Fig. 1. The location of the study area on Volcán Chiles.



Vegetation monitoring

The basic unit of a plant community is the individual plant, and to study dynamics at this level requires a sampling technique with sufficient resolution to differentiate between individuals. It must also be capable of recognizing gaps which might be important in the regeneration process (Grubb 1977). In a study of post-fire dynamics in another Ecuadorian páramo, Ramsay & Oxley (1996) found 1 cm^2 to be adequate for this purpose, containing one plant only with reasonable consistency. Therefore, this sampling unit was used as the basis for this investigation.

To record changes in occupancy, 1 m x 1 cm belt transects were used, each containing one hundred 1 cm^2 areas (microquadrats) in which the presence of individuals was noted, similar to the approach adopted by Thórhallsdóttir (1990). Twenty 1 m transects were established at random among the burned vegetation. Both ends were marked with lengths of plastic water pipe (buried 35 cm deep with 5 cm remaining above ground), allowing 20-30 cm either side to avoid interference of the marker posts with the vegetation of the transect. Ten transects were located within the west-facing, leeward side of the ridge and the remaining ten on the east-facing windward ridge. These two areas were only 5-10 m apart.

At each monitoring visit, the plants occupying the microquadrats were recorded along the length of each transect. Occupancy was defined as any plant rooted within the microquadrat. It did not include plant shoots which lay across the transect but which were not rooted there. Sampling units in which nothing was rooted were defined as gaps.

Single rooted plant modules were generally treated as individuals for vascular plants, but grouped together for grass tillers and mosses (for these plants the presence of a species in a microquadrat was counted as one individual, regardless of the actual number of individuals there). If one of the larger plant species was rooted across several microquadrats, it was recorded for each of those micorquadrats (for example, the large tap root of *Hypochaeris sessiliflora* can span 3-4 cm). Furthermore, no special treatment was made for clonal individuals: if rooted in the sampling units they were recorded as individuals. This is an important point since many páramo plants reproduce vegetatively.

Where more than one species occurred within a unit, the frequency was recorded as a fraction of 1. Thus, two individuals in the same microquadrat each received a score of ½. Using this method, the total frequency for each transect always added up to 100.

Observations were made one month after the fire (7 January 1997), and approximately one and two years later (19 December 1997 and 7 January 1999). In total 1000 microquadrats were recorded on each side of the ridge at each visit.

Data analysis

Community composition in each transect was estimated by the number of occurrences of each species in the microquadrats. Similarity between transects at different times was investigated using detrended correspondence analysis (Hill 1979). Simpson's index was calculted for each transect on each occasion according to the formula:

$$D = 1 - \sum_{i=1}^{S} p_i^2$$

where S is the number of species in each 25 m^2 sample (species richness) and p_i is the proportional abundance of species i in the sample. It represents the likelihood that two randomly chosen individuals will be different species, reaching maximal values for a sample with all species present in equal abundance.

The pattern of replacement of species within the sampling plots over a particular time interval was analysed by constructing a matrix such that the rows represented the species recorded at time 1, the columns the species present at time 2. The j^{th} column of the i^{th} row represents the number of microquadrats where species *i* has been replaced by species *j*. It is then possible to test the individual cells in the matrix, using Chi-Square (X^2) analysis, to determine whether the pattern of replacement was random or not.

The analysis is complicated by an assumption inherent in the X^2 test. Consider the case where a microquadrat is occupied by a certain species both at the start and the end of the experiment. The X^2 test assumes that the last individual has replaced a member of the same species over the course of the experiment. Since the experiment was conducted within the lifetime of many plants, this is probably not the case: the same individual has probably persisted during the time interval. This would result in an over-estimation of the frequency with which a species replaces one of its own kind, and may disguise the actual changes taking place elsewhere. This situation is undesirable and therefore the principal diagonals of the matrix (representing "no change") were eliminated from the X^2 test. Of course, this hides any replacement of a species by another individual of the same species and no probabilities are available for such transitions.

Another assumption of the X^2 test is that every change of occupancy is a single transition. Bearing in mind the brevity of the experiment this is a reasonable assumption in most cases. Nevertheless, the possibility exists of an individual replacing another then being itself replaced between monitoring visits.

Simply stated, the X^2 test will determine the probability that the pattern of replacement observed is completely random. If for each species pair, the species present at time 1 is called the i^{th} species and the species present at time 2 the j^{th} species, then the null hypothesis states that "species *i* will be replaced by species *j* in that proportion which the total replacements made by species *j* contribute to the overall number of changes" or:

$$E_{ij} = \frac{\Sigma(n_{ir} - n_{ii}).(n_{rj} - n_{jj})}{\Sigma(n_{rj} - n_{jj})}$$

where *r* represents all species other than *i* or *j*, n_{ir} the total number of times species *i* is followed by all other species, n_{ii} the total number of quadrats occupied by species *i* at time 1 and time 2, n_{rj} the total number of times species *j* follows all other species, and n_{jj} the total number of quadrats occupied by species *j* at time 1 and time 2 (Thórhallsdóttir, 1990). Put another way, the expected value is:

$$E_{ij} = \frac{\text{Total number of quadrats vacated by } i^{th} \text{ species} \times \text{Total number of quadrats invaded by } j^{th} \text{ species}}{\text{Grand total of all changes}}$$

provided the diagonal terms (the species replacing themselves) in the matrix are subtracted before making the calculation.

Most of the species involved in the data were rare and to avoid bias in the X^2 values those species with an expected value less than 5 were not subjected to a X^2 test. The rarer species were treated as a group to overcome this problem. Yates' correction for continuity was applied (Zar, 1984).

RESULTS

During the first two years after the fire, 29 species of plants were encountered within the study plots, and the vegetation composition changed over time (Table 1). On the leeward side of the ridge, only two species were evidently alive one month after the fire, the tussock grass, *Calamagrostis intermedia,* and the sedge *Rhynchospora hieronymi*. Both species increased their abundance during the first two years of recovery. However, the sharp fall in bare ground during this time was mostly due to the arrival of two moss species (together responsible for almost 50% cover two years after the fire). On the windward side of the ridge, plant cover was initially higher but did not increase as quickly. Moss cover was not as significant on this side of the ridge, though one of the species did increase significantly in abundance during the second year. *Calamagrostis intermedia* tussock cover declined during the second year, while *Calamagrostis effusa,* another tussock grass, colonized. An ericaeous species, *Disterigma empetrifolium*, also increased significantly in abundance during the second year.

After two years of recovery, the tussocks on the leeward side of the ridge were commonly 35-40 cm tall, but just 15-25 cm tall on the windward side. The size of gaps decreased during the two year period, and the vegetative spread of some species was evident (Table 2). In particular, *Calamagrostis intermedia* tussocks and patches of mosses (Moss A and Moss B) increased in diameter.

Changes in community composition during the first two years after the fire are represented graphically by detrended correspondence analysis (Fig. 2). Transects with similar composition are close together on the graph, those with dissimilar composition further apart. On the leeward slope, transects had a more or less distinct composition in each of the three years. The composition immediately after the fire was very consistent. The windward slope exhibited more variability, with the species composition of the transects similar immediately after the fire and a year

Table 1. Changes in percentage rooted frequency of plants within 1000 microquadrats on the leeward and windward sides of the ridge (n = 1000 for each side) during the first two years after the fire. The total number of species recorded in the transects each time is also given. A gap is defined as an unoccupied microquadrat. Lupinus tauris *was responsible for much higher cover on the leeward side of the ridge than these measures of rooted frequency suggest. Several species were not recorded in the transects but were observed nearby:* Lasiocephalus ovatum *(leeward),* Orebolus obtusangulus *(windward) and* Xenophyllum humilis *(windward).*

Plant species	**Leeward side of ridge**			**Windward side of ridge**		
	1 month	**1 year**	**2 years**	**1 month**	**1 year**	**2 years**
Gaps	95.1	77.4	35.3	88.7	85.2	62.2
Calamagrostis intermedia (Presl.) Steud.	4.8	7.6	7.5	5.6	6.1	0.4
Rhynchospora hieronymi Böckeler.	0.1	0.3	0.8	1.3	1.1	1.8
Vascular plant seedlings		0.1				0.3
Ranunculus praemorsus Kunth		0.7				
Gentiana sedifolia Kunth		0.1				
Lupinus tauris Benth.		0.1				
Disterigma empetrifolium (H.B.K.) Drude		0.2	2.1	1.8	5.3	10.3
Moss A		7.2	21.0		0.1	0.1
Moss B		5.3	26.6		0.1	8.9
Pernettya prostrata (Cav.) DC.		0.5	1.7		0.7	1.9
Halenia weddelliana Gilg.		0.2	0.3			0.2
Gramineae		0.2	0.1			0.1
Calamagrostis effusa (Kunth) Steud.			3.0			8.8
Agrostis nigritella Pilger			0.4			0.4
Azorella crenata (R. & P.) Pers.			0.1			
Sibthorpia repens (Mutis ex L.) Kuntze			1.2			
Lachemilla orbiculata (R. & P.) Rydb.			0.1			
Lachemilla uniflora Maguire				0.1		
Jamesonia goudotii (Hieron.) C.Chr.				0.1	0.1	0.1
Azorella aretoides (Spreng.) DC.				0.5	0.7	2.2
Oreobolus goeppingeri Svess.				1.3		0.3
Moss C				0.5		0.6
Carex (small sp.)					0.2	
Oritrophium peruvianum (Lam.) Cuatr.					0.3	0.3
Arcytophyllum aristatum Standley					0.2	0.5
Usnea sp.						0.6
Bartsia laticrenata Benth.						0.1
Number of species	2	12	13	8	11	19

Table 2. Number and diameter of vegetative patches (means ± standard deviation) during the first two years after a fire for selected species. Patch diameter was defined as the number of consecutive 1 cm^2 microquadrats occupied by a colony. Bare patches do not include areas with standing dead plants of Calamagrostis inetrmedia, Disterigma empetrifolium, Azorella aretoides *and* Rhynchospora hieronymi *(which were particularly important immediately after the fire). Microquadrats which were shared by two plants were omitted from this analysis (three microquadrats one year after the fire, six microquadrats two years after the fire).*

	one month after fire		**one year after fire**		**two years after fire**	
	n	**diameter (cm)**	***n***	**diameter (cm)**	***n***	**diameter (cm)**
Gaps (bare)	111	13.1 ± 18.0	186	8.7 ± 10.0	241	4.0 ± 3.7
Calamagrostis intermedia	69	1.5 ± 0.9	69	2.0 ± 1.3	29	2.7 ± 2.1
Arcytophyllum aristatum			2	1.0 ± 0.0	3	1.7 ± 1.2
Disterigma empetrifolium	14	1.3 ± 0.6	45	1.2 ± 0.5	74	1.7 ± 1.7
Rhynchospora hieronymi	13	1.1 ± 0.3	14	1.0 ± 0.0	25	1.0 ± 0.2
Azorella aretoides	1	5.0	4	1.8 ± 1.5	12	1.8 ± 2.3
Pernettya prostrata			11	1.1 ± 0.3	33	1.1 ± 0.3
Halenia weddelliana			2	1.0 ± 0.0	5	1.0 ± 0.0
Agrostis nigritella			1	2.0	6	1.3 ± 0.5
Moss A			36	2.0 ± 2.2	61	3.4 ± 3.8
Moss B			14	3.9 ± 3.8	58	6.1 ± 7.6
Calamagrostis effusa					58	2.0 ± 1.4
Sibthorpia repens					7	1.6 ± 1.0

later. Two years after the fire, however, the plant community composition was distinct from that of the previous two years. The ordination also highlights differences in species composition between the two slopes—the transects of the two slopes occupy different areas of the ordination space each year.

Fig. 2. Detrended correspondence analysis of 20 vegetation transects recorded on three occasions: one month (black symbols), one year (grey symbols), and two years (white symbols) after burning. The analysis was carried out for all transects together, but the ten leeward (upper figure) and ten windward (lower figure) transects are shown separately for clarity.

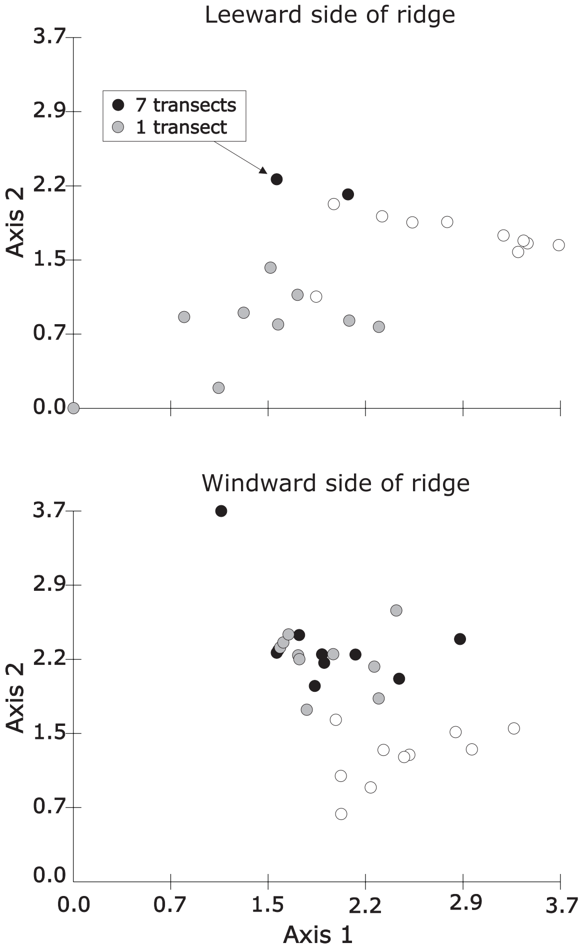


Table 3. Changes in diversity (means ± standard deviation) within ten replicate transects at each site during the first two years after fire.

	Leeward slope	Windward slope
Number of species		
1 month	0.90 ± 0.57	2.90 ± 1.10
1 year	4.22 ± 2.08	3.40 ± 1.58
2 years	4.75 ± 1.55	6.40 ± 1.51
Simpson's Index		
1 month	0.05 ± 0.13	0.44 ± 0.22
1 year	0.60 ± 0.21	0.55 ± 0.18
2 years	0.47 ± 0.16	0.67 ± 0.10

A similar picture emerges from examination of changes in species diversity (Table 3). Diversity was much lower on the leeward slope immediately after the fire but recovered relatively rapidly during the first year. The diversity of the windward slope was initially higher, but did not change much until the second year. After two years, the windward slope had higher species diversity than the leeward slope of the ridge.

Most replacements, where one species replaced another, were random. Colonization of bare ground was also (mostly) random. However, several replacements deviated significantly from that expected by chance, and these are shown in Fig. 3. During the first year on the leeward slope, all replacements followed a random pattern. During the second year, Moss B colonized gaps more often than expected by chance but was inhibited by *Calamagrostis intermedia*, Moss A and rarer species. *Disterigma empetrifolium* colonized gaps less often than expected.

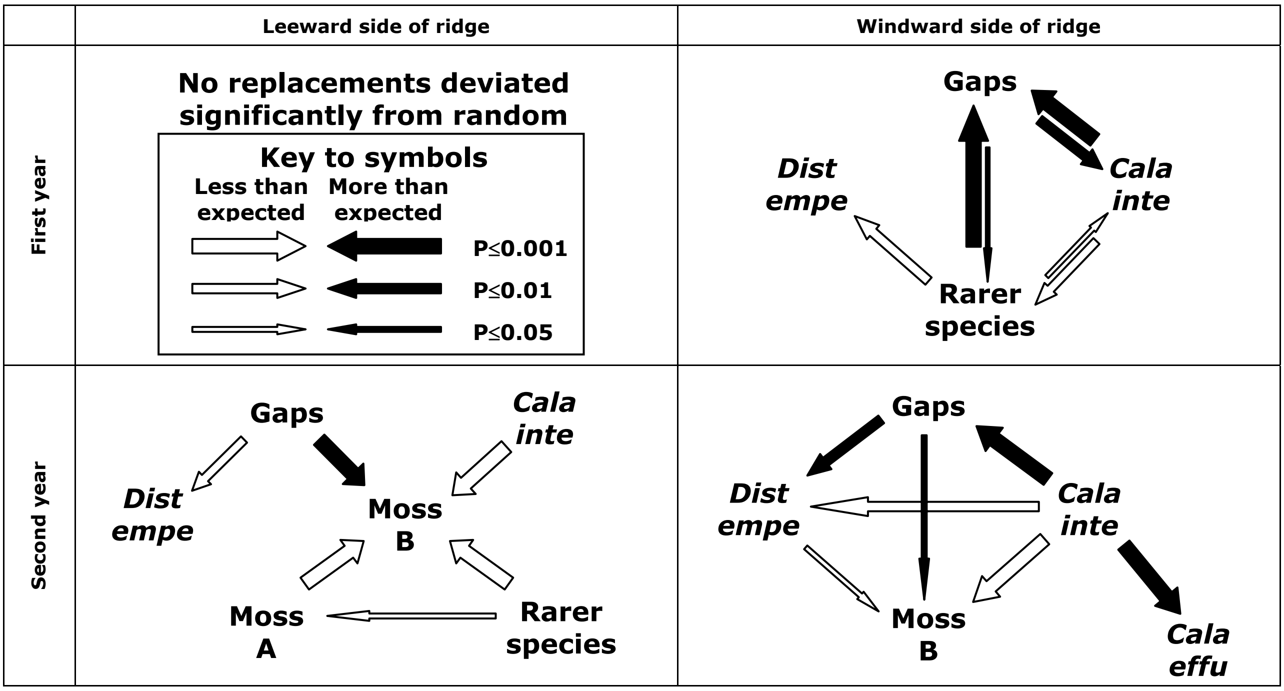
On the windward slope, post-fire mortality of *Calamagrostis intermedia* and the rarer species was evidenced by higher than expected replacement of these species by gaps during the first year. However, both colonized gaps during the same period but inhibited each other's colonization. *Disterigma empetrifolium* was also inhibited by the presence of the rarer species. During the second year, *Calamagrostis intermedia* exhibited high mortality (replacement by gaps) and was frequently replaced by another tussock-forming grass of the same species, *Calamagrostis effusa*. However, it resisted invasion by *Disterigma empetrifolium* and Moss B. These latter species both colonized gaps more than expected by chance, though the presence of Moss B inhibited the arrival of *Disterigma empetrifolium*.

DISCUSSION

The leeward and windward slopes of the same ridge showed different mortality rates, patterns of recovery, species diversity values, and community composition following the fire. The assumption that páramo vegetation recovery follows one particular successional pattern is very clearly invalidated. The effects of a fire and the subsequent recovery of plants depend on a number of interrelated factors:

- *pre-fire community structure*
  This may be related to environmental conditions and determines the nature of vegetation structure and fuel (mostly dead tussock grass leaves).
- *fire event conditions*
  Weather conditions prior to and during the fire may modify the intensity of the fire beyond that determined by the inherent patchiness in vegetation structure and fuel.
- *susceptibility to fire mortality*
  Some species are more susceptible to fire-induced mortality than others. Species also differ in their ability to resprout from surviving parts.

Fig. 3. Deviations from random species replacement in the transects. "Rarer species" were grouped together for the analysis: Azorella aretioides, Oreobolus goeppingeri, Rhynchospora hieronymi, Disterigma empetrifolium, *Moss C,* Jamesonia goudotii *and* Lachemilla uniflora *on the windward slope in the first year;* Ranunculus praemorsus, Pernettya prostrata, Rhynchospora hieronymi, Disterigma empetrifolium, Halenia weddelliana, *Gramineae seedlings, other vascular plant seedlings,* Lupinus tauris, Agrostis nigritella *and* Gentiana sedifolia *on the leeward slope in the second year.*



- *post-fire environmental conditions*
  Some plants may survive the fire, but not the modified environmental conditions which prevail after burning—both thermal and light regimes may be very different compared with pre-fire conditions. These conditions may also favour colonisation, establishment or growth of some species more than others.
- *seed rain from outside the burned area*
  New individuals may enter the community as seed; the range of species arriving in this way, and their abundances, are partly determined by the species composition of the surrounding areas.

Since all of these factors vary temporally and spatially, in an interdependent way, it is no surprise that vegetation recovery shows fine-scale patterning. The recovery patterns observed in this study will now be set in this context and discussed in more detail.

Fewer species and individuals of plants survived the fire on the leeward side of the ridge compared with the windward side. There are two possible explanations for this, and they are not mutually exclusive. First, environmental conditions may have favoured a different community on the two sides of the ridge, and the species favoured on the leeward slope were more susceptible to fire damage. Second, the two slopes suffered different fire intensities leading to differential mortality rates.

This study did not allow comparison of post-fire vegetation with the communities present before burning, and it is not possible to refute the first explanation, above. This difficulty highlights one of the major drawbacks of this kind of study: defining an appropriate baseline—the expected make-up of the community in the absence of fire. There were evidently some differences in composition. After the fire, the windward side of the ridge had a more open structure and a greater abundance of (mostly dead) cushion plants. Therefore, it is possible that differences in species composition could result in higher mortality rates on one slope if the species there were more susceptible to fire damage. Nevertheless, the presence on the leeward slope of dead *Calamagrostis intermedia, Disterigma empetrifolium, Azorella aretoides* and *Rhynchospora hieronymi* suggested some similarities in composition—all of these species were present (dead and alive) on the windward side.

It is likely that the slopes did experience different intensities of fire, though fire temperatures and duration were not measured. Headfires (moving with the wind or upslope) progress more quickly and tend to burn less intensely than backfires (moving against the wind or downslope), and so backfire mortality is often higher than headfire mortality (Bidwell *et al.* 1990). The fire which burned the study plots was carried by the wind westwards and upslope. Thus, the fire would have passed quickly over the eastward-facing slope, carried uphill by the wind, and then burned more intensely as it made its way downhill on the other side of the ridge. This may explain the higher mortality on the leeward relative to the windward slope.

However, on both sides of the ridge, some plants did survive. Most of these species were able to resprout from below-ground parts which were protected from lethal fire temperatures. Occasionally, aboveground parts survived; perhaps they were not exposed to lethal temperatures because of patchiness in fire intensity. Resprouting from these survivors was mostly responsible for the colonization of gaps during the recovery phase. Vegetative growth into gaps was observed in tussock grasses, mosses, cushion-formers and reptant species. In the latter case, this process was only registered if the new ramets (Harper 1977) rooted into the new ground. Otherwise, they were not counted and this underestimated the abundance of several reptant species, especially *Lupinus tauris* which tended to cover soil without rooting into it. It should be noted that there did not appear to be a post-fire burst of growth based on nutrients released after burning, as described for woody perennials in Costa Rican páramos (Horn 1989). Hofstede (1995b) noted that mineral nutrients are quickly mopped up by páramo soils and micoorganisms—probably beyond the response time of páramo vegetation to take advantage.

Other survivors did less well. There was relatively high mortality in several species after the fire, often higher on the more exposed windward slope. Even the tussock grass, *Calamagrostis intermedia*, exhibited significant rates of mortality during the first year, continuing into the second year. Some species seemed particularly vulnerable to latent fire damage, *e.g.*, the cushions of *Oreobolus goeppingeri*—92% of individuals which still showed signs of life a fortnight after the fire were dead within a year. This is similar to the situation reported by Ramsay & Oxley (1996) for another Ecuadorian páramo: more than 70% of *C. intermedia* tillers had died just 15 weeks after the fire, and recovery was generally a slow process. Hofstede, Chilito and Sandovál (1995) reported lower rates of *C. effusa* leaf elongation in burned and grazed areas compared with undisturbed ones, though this was compensated by increased tillering in moderately disturbed paramo. The poor performance of tussocks in their heavily burned and grazed site was linked to temperature regime and, particularly, UV-B exposure.

It seems that two contradictory processes operated at the same time, even within a particular species. Some individuals thrived and expanded into gaps whilst others died. The balance between these processes results in the overall pattern of expansion or contraction. It is important to emphasise that even if a species increases in abundance during the post-fire recovery phase there may be considerable mortality taking place. It is only by monitoring the fate of individual plants that both growth and mortality can be considered together.

Gaps were also colonised by seeds or spores, clearly demonstrated by *Disterigma empetrifolium, Rhynchospora hieronymi, Azorella aretoides, Pernettya prostrata, Halenia weddelliana, Agrostis nigritella,* Moss B, Moss A, *Calamagrostis effusa* and *Sibthorpia repens*. Some of these species, and a number of relatively rare species within the transects, showed a preference for one side of the slope or other. This may be related to differences in environmental conditions. The leeward slope was more humid, receiving less direct sun and was more sheltered from the wind. However, the absence of information about the ecological preferences of these species makes it difficult to determine the relative importance of these factors in páramo recovery.

Another mechanism that may lead to differences in the abundance of certain species on the ridge is wind dispersal of seeds. Seeds are deposited when they drop out of the air stream at low wind speeds, and topography creates patchiness in wind speed and direction. The windward slope experienced greater wind speeds and so seed deposition rates would be expected to be lower, especially for the lightest seeds. In contrast, the sheltered leeward slope would be expected to receive considerable seed rain. Again, the lack of information about seed dispersal strategies for the species observed in this study permits only speculation about this mechanism. The colonization and subsequent disappearance of several species on both sides of the ridge suggest seed dispersal may not be sufficient explanation in itself.

The combination of differential species mortality, colonization and growth rates resulted in differences at the community level between the two slopes, evident in the ordinations at every visit. The leeward community showed clear changes year on year, whereas the windward vegetation exhibited little difference in the first two visits, but changed during the second year. This suggests that recovery followed a different pattern on the two sides of the ridge. On the leeward slope, high mortality was followed by an accumulation of colonists during the first year, some of which did not survive to the end of the second year, by which time other colonists had arrived. Particularly during the second year, moss cover increased dramatically. Meanwhile, the windward side of the same ridge experienced lower rates of mortality during the fire and, despite the arrival of a few colonists, the vegetation had changed little during the first year. However, recovery proceeded more rapidly in the second year, with colonization by new species and increased abundance of plants already present. At the end of the study period, the leeward plots were dominated by mosses and the tussock grass, *Calamagrostis intermedia*. Dominance of the windward transects was shared by *Disterigma empetrifolium*, a moss and a different species of tussock grass, *Calamagrostis effusa*. Overall vegetative cover was 65% and 38% for the leeward and windward plots, respectively.

Thus two sides of the same ridge, burned in the same fire showed very different patterns of recovery, and these may be related to the fire regimes experienced on the two slopes, the environmental conditions which characterize the two areas, and the life history strategies of páramo plant species. It is not clear what the driving forces in the observed patterns of succession are, but candidates include differential susceptibility to fire mortality, different seed dispersal strategies, competitive interactions between species, and changes in environmental conditions as vegetation and soil structure develop. Perhaps the pattern will become clearer as monitoring of these plots continues into the future. Additional information about the ecological requirements of species and their dispersal strategies would aid interpretation of this kind of study. Vargas-Ríos (1997) associated plant species of the Colombian páramo with particular life history traits (following the vital attributes philosophy of Nobel and Slatyer 1981), and used this approach to explain successional patterns in post-fire vegetation regeneration. However, life history strategies operate within the context of fire regime and cannot be considered in isolation. For example, Janzen's (1973) description of a vigorously resprouting population of *Hypericum irazuense* in a Costa Rican páramo after a fire has been contradicted by observations of high mortality and low resprouting rates in the same species after other fires (Williamson *et al*. 1986, Horn 1989). Following another fire at Janzen's site, Horn (1997) determined that this population also showed poor resprouting success and mostly recolonised by seed—she suggested the differential response in the two fires may relate to variations in environmental and burning conditions.

A glance at any undergraduate ecology text will testify to the relationship between patchiness and high levels of species diversity. Patchiness resulting from fires is evident in fire mosaics at the landscape scale in páramos (Ramsay 1999). At the same time, much finer-scale patchiness is also demonstrated in this study and that of Ramsay and Oxley (1996). Fine-scale heterogeneity in vegetation structure (particularly with regard to tussock grasses) results in a patchy distribution of fuel and variable fire temperatures. After the fire has passed, patchy survival is the norm and in the months and years that follow there is differential mortality, colonisation and growth—even within particular plant species—from which is derived the recovered vegetation. It should be clear that fire may represent a powerful mechanism of promoting and maintaining species diversity in páramo grasslands by providing fine-scale heterogeneity.

Given the long history of burning in the páramos (Horn 1993), whether anthropogenic or not, it seems likely that most páramos are the result of intermittent burning cycles, and can sustain some level of fire disturbance by people. However, it is also clear from recent studies (Hofstede 1995a, 1995b; Ramsay & Oxley in press) that repeated, high-frequency burning of the páramos is not sustainable. Investigations concerning the impact of burning, at various frequencies and intensities, need to be given a higher profile. Whilst priority should be given to vegetation, efforts should also be directed towards animal responses to fire in the páramo.

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REFERENCES

Bidwell, T.G., Engle, D.M. and Claypool, P.L. (1990) Effects of spring headfires and backfires on tallgrass prairie. *Journal of Range Management*, **43**: 209–212.

Ellenberg, H. (1958) Wald oder Steppe? Die natürliche Pflanzendecke der Anden Perus. I. *Umschau Heft*, **21**: 645–648.

Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**: 107–145.

Harper, J.L. (1977) *Population Biology of Plants*, London: Academic Press.

Hill, M.O. (1979). *DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging.* Cornell University, Ithaca (NY): Cornell Ecology Programs Series.

Hofstede, R.G.M. (1995a) Effects of livestock farming and recommendations for management and conservation of páramo grasslands (Colombia). *Land Degredation and Rehabilitation*, **6**: 133–147.

Hofstede, R.G.M. (1995b) The effects of grazing and burning on soil and plant nutrient concentrations in Colombian páramo grasslands. *Plant and Soil*, **173**: 111–132.

Hofstede, R.G.M. and Rossenaar, A.J.G.A. (1995) Biomass of grazed, burned, and undisturbed páramo grasslands, Colombia. II. Root mass and aboveground:belowground ratio. *Arctic and Alpine Research*, **27**: 13–18.

Hofstede, R.G.M., Chilito, E.J. and Sandovál, E.M. (1995) Vegetative structure, microclimate, and leaf growth of a páramo tussock grass species, in undisturbed, burned and grazed conditions. *Vegetatio*, **119**: 53–65.

Hofstede, R.G.M., Mondragón, M.X. and Rocha, C.M. (1995) Biomass of grazed, burned, and undisturbed páramo grasslands, Colombia. I. Aboveground vegetation. *Arctic and Alpine Research,* **27**: 1–12.

Horn, S.P. (1988) Effect of burning on a montane mire in the Cordillera de Talamanca, Costa Rica. *Brenesia,* **30**: 81–92.

Horn, S.P. (1989) Postfire vegetation development in the Costa Rican páramos. *Madroño,* **36** : 93–114.

Horn, S.P. (1993) Postglacial vegetation and fire history in the Chirripó paramo of Costa Rica. *Quaternary Research,* **40**: 107–116.

Horn, S.P. (1997) Postfire resprouting of *Hypericum irazuense* in the Costa Rican páramos: Cerro Asunción revisited. *Biotropica,* **29***:* 529–531.

Janzen, D.H. (1973) Rate of regeneration after a tropical high elevation fire. *Biotropica,* **5**: 117–122.

Keating, P.L. (1995) Disturbance regimes and regeneration dynamics of upper montane forest and páramos in the southern Ecuadorian Andes. PhD thesis, University of Colorado.

Keating, P.L. (1998) Effects of anthropogenic disturbances on Paramo vegetation in Podocarpus National Park, Ecuador. *Physical Geography,* **19**: 221–238.

Laegaard, S. (1992) Influence of fire in the grass páramo vegetation of Ecuador. In: Balslev, H. & Luteyn, J.L. (Eds) *Páramo: An Andean Ecosystem under Human Influence,* pp. 151–170. London: Academic Press.

Luteyn, J.L. (1992) Páramos: why study them? In: H. Balslev & J.L. Luteyn (Eds) *Páramo: An Andean Ecosystem under Human Influence,* pp. 1–14. London: Academic Press.

Noble, I.R. and Slatyer, R.O. (1981) Concepts and models of succession in vascular plant communities subject to recurrent fires. *In:* Gill, A.M., Groves, R.H. and Noble, I.R. (Eds) *Fire and the Australian Biota,* pp. 311–335. Canberra: Australian Academy of Science.

Ramsay, P.M. (1999) Landscape mosaics in the High Andes: the role of fire in páramo communities. In: Kovář, P. (Ed.), *Present and Historical Nature-Culture Interactions in Landscapes: Experiences for the Third Millenium*. pp. 192–199. Prague: The Karolinum Press.

Ramsay, P.M. (2001) The zonal páramo vegetation of Volcán Chiles. In: Ramsay, P.M. (ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 27–38. Plymouth: Pebble & Shell.

Ramsay, P.M. & Oxley, E.R.B. (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetatio,* **124**: 129–144.

Ramsay, P.M. & Oxley, E.R.B. (2001) An assessment of net aboveground primary productivity in the Andean grasslands of Central Ecuador. *Mountain Research and Development,* **21**: 161–167.

Thórhallsdóttir, T.E. (1990). The dynamics of a grassland community: a simultaneous investigation of spatial and temporal heterogeneity at various scales. *Journal of Ecology,* **78**: 884–908.

Vargas-Ríos, O. (1997) Un modelo de sucesión-regenración de los páramos después de quemas. *Caldasia,* **19**: 331–345.

Verweij, P.A. and Budde, P.E. (1992) Burning and grazing gradients in páramo vegetation: initial ordination analyses. In: Balslev, H. and Luteyn, J.L. (Eds) *Páramo: An Andean Ecosystem under Human Influence*, pp. 177–195. London: Academic Press.

Verweij, P.A. and Kok, K. (1992) Effects of fire and grazing on *Espeletia hartwegiana* populations. In: Balslev, H. and Luteyn, J.L. (Eds) *Páramo: An Andean Ecosystem under Human Influence*, pp. 215–229. Academic Press: London.

Williamson, G.B., Schatz, G.E., Avlarado, A., Redhead, C.S., Stam, A.C. and Sterner, R.W. (1986) Effects of repeated fires on tropical páramo vegetation. *Tropical Ecology,* **27***:* 62–69.

Zar, H. (1984). *Biostatistical Analysis,* London: Prentice-Hall.

Surface leaf structures of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis*

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SUMMARY

The microscopic leaf surface morphology of *Espeletia pycnophylla* subsp. *angelensis* is described with the aid of optical and scanning electron micrographs. Leaf material was collected from giant rosette plants at 3900 m on Volcán Chiles, on the Ecuador-Colombia border. Elliptical stomata were situated in crypts on the abaxial leaf surfaces. Three kinds of trichome (leaf hair) were identified on both abaxial and adaxial leaf surfaces. Long trichomes formed dense pubescence over the leaf, short trichomes were situated around and within the stomatal crypts, and bulbous trichomes were generally dispersed over all surfaces. The adaptive significance of both stomatal crypts and trichomes is discussed.

RESUMEN

La morfología microscopica de la superficie de las hojas de *Espeletia pycnophylla* subsp. *angelensis* se describió con la ayuda de micrografías ópticas y electrónicas de barrido. El material foliar se colectó de rosetas gigantes a 3900 m en el Volcán Chiles, en la frontera Ecuador-Colombia. Los estomas elípticos se situaron en criptas en la superficie abaxial de la hoja. Tres tipos de tricomas (pelo foliar) se identificaron tanto en la superficie abaxial como en la superficie adaxial de la hoja. Los tricomas largos formaron una pubescencia densa sobre la hoja, los tricomas cortos se situaron alrededor y dentro de las criptas estomáticas, y los tricomas bulbosos se dispersaron generalmente por todas las superficies. Se discute la importancia adaptativa de las criptas estomáticas y los tricomas.

Key words: tropical alpine, trichomes, stomata, electron microscopy

INTRODUCTION

Caulescent giant rosette plants occur solely in the high mountains of the equatorial zones of South America and East Africa, mainly at altitudes between 3000m and 4500m (Sakai and Larcher 1987). In these tropical mountains, daily oscillations of temperature are much more pronounced than seasonal ones (Lüttge 1997). Low temperature slows down metabolic reactions which influence growth, uptake of water and the translocation of assimilates. Brief periods of nocturnal freezing, usually of 3-4 hours, and desiccating winds expose plants to injury and possibly death.

Espeletia pycnophylla CUATREC. subsp. *angelensis* CUATREC. is found in Northern Ecuador in the páramos of El Angel and Volcán Chiles, and this species has the most southerly distribution of its genus. It is a perennial plant, distinguished by one erect stem of up to 3m tall, with an evergreen rosette of large densely pubescent leaves. It has a number of gross morphological features which are considered adaptive:

- *Leaf rosette*
  The apical bud is insulated by the surrounding layers of more mature leaves. The heat storage capacity within the rosette ensures high growth rates considering the low mean air temperature (Estrada 1984). Goldstein & Meinzer (1983) never recorded temperatures below 0°C within the bud of other *Espeletia* species. Some *Espeletia* species exhibit nyctinasty, the inward bending of the rosette leaves during the night, which buffers bud temperature even more (Smith 1974).
- *Insulated, water reservoir in stem*
  Soil temperature in the root zone can be near freezing in the early hours of the morning, when transpiration are high because of intense solar radiation. If transpiration begins without a supply of water, cavitation in the xylem elements can occur, resulting in serious problems if it is associated with embolism (Lüttge 1997). In *Espeletia* species the daily minimum water potential generally coincides with the period of maximum transpiration (Meinzer *et al.* 1994), but the central core of spongy pith in the stem acts as a water reservoir (Goldstein *et al.* 1985). Thus, the water status of the plant does not undergo significant change, owing to the buffering effect of the stem. Water storage in the stem pith has been shown to support several hours of transpiration in some species (Meinzer *et al.* 1994). *Coespeletia timotensis* (CUATREC.) CUATREC. (a Venezuelan species sometimes referred to by its synonym, *E.lutescens),* also stores significant amounts of physiologically available water within other leaf tissues, the secondary xylem, midribs and probably the periderm (Meinzer *et al.* 1994).

Freezing avoidance through supercooling has also evolved in *Espeletia* plants— leaf tissue of *Espeletia* species supercool to relatively low temperatures avoiding extracellular freezing of leaf tissues (Rada *et al.* 1987). Hedberg & Hedberg (1979) recorded evidence of photosynthesis in leaves of *Espeletia semiglobulata* at temperatures of -8°C.

Adaptive traits in leaf morphology at the microscopic level may be equally significant in the survival of this species at high altitude. The loss of water during photosynthesis can be reduced if the stomata are arranged in pits, known as crypts. Crypts increase the boundary layer and are sometimes surrounded by a system of hairs. Such pockets have been reported for the abaxial surfaces of *Espeletia* leaves (Carlquist 1994).

Leaf hairs (trichomes) are generally thought to keep the leaf cool and to protect the surface of the leaf from rapid wind currents that would remove water vapour from transpiring areas (Baron 1979). Hydrophobic trichome layers can also act as a barrier, preventing wetting of the leaf surface, and thus external ice formation (Goldstein *et al.* 1985, Rada *et al.* 1985). In addition, leaf trichomes can represent an effective barrier mitigating against high light stress (including UV radiation) and overheating. Thus, at high altitudes,

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 75-80.

trichomes may be important in preventing photoinhibition and damage to the photosynthetic structures (Lüttge 1997). Pubescence can also aid to protect the leaf against herbivorous attack and prevent stomatal obstruction by water or particulate matter.

The aim of this study was to examine and describe the surface morphological leaf structures of the equatorial alpine plant *E.pycnophylla* subsp. *angelensis* and to hypothesise on their function.

METHODS

Leaf material

Leaf material was harvested from *E. pycnophylla* subsp. *angelensis* at 3900 m on the south-western side of Volcán Chiles, Ecuador (0° 50′ 91″ N 78° 01′ 72″ W). Cross (2001) reports data from an *Espeletia* population *in situ* at this site. The area was dominated by tussock grasses and *Espeletia* giant rosettes. Ramsay (2001) provides a more detailed account of the páramo vegetation of the mountain, though his transect was located on the south-eastern side of the volcano. Collected leaf material was stored in polythene bags and, with the exception of the air transit, kept in refrigerated conditions until sectioned.

Light microscopy

Pieces of tissue from the base, middle and apex of the leaves were shaved, to remove most of the dense surface pubescence, and dehydrated with alcohol. The leaf pieces were then set in resin moulds and sectioned using an Autocut 1140. Longitudinal sections were taken of thicknesses from 3 to 10 μm. The structure of crypts was shown to best effect at 5 μm thickness. Transverse sections were made at 3 μm thickness.

The sections were examined using an Olympus BH light microscope. Photographs were taken to illustrate particular features using an Olympus Vanox AH-2.

Scanning Electron Microscopy

Leaf material of approximately 1cm^2 surface area was taken from the base, middle and apex of the leaves. Parts of these leaf pieces were shaved, to remove dense surface pubescence, while other parts were left unshaved. The material was then cut to appropriate sizes for mounting onto SEM stubs and subjected to critical point drying, freeze drying and freeze fracturing.

The prepared tissues were mounted onto aluminium stubs with colloidial silver adhesive, fractured surfaces uppermost, and coated in gold using an EMITECH K550 Sputter Coater. They were then examined with a JEOL 5300 Scanning Electron Microscope.

Leaf imprints

As a separate study, leaf imprints were taken from living leaves in the field using dental impression material of low viscosity ("Xantopren"), following the method of Weyers & Meidner (1990). Imprints were taken from the abaxial surface of shaved leaves. Slides were compiled and inspected using an Olympus Vanox AH-2 microscope and a Quantimet 570 Image Analyser. Unfortunately, the presence of deep leaf crypts and residual trichomes hindered the use of this technique—microscopic measurements of stomatal aperture can only be made readily if the stomatal pores are relatively large and not sunken into crypts or obscured by hairs (Weyers & Meidner 1990). Therefore, these leaf imprints were not used in any of the work described here.

RESULTS

Light Microscopy

E.pycnophylla spp angelensis posseses hypostomatous leaves with elliptical stomata. Stomatal crypts were randomly scattered over the abaxial epidermal surface of the leaf. They were variable in size—the mean stomatal crypt area was 4881 μm^2 (Table 1), ranging from 704 to 23,321 μm^2. The stomata were located within these crypts (Figs. 1 and 2), measuring 23 μm on average in length (Table 1). In some cases the crypts branched into sub-crypts (Fig. 3).

Table 1. Measurements of surface leaf structures

Morphological features	**Light Microscopy**		**Scanning Electron Microscopy**	
	n	***Mean ± sd***	**n**	***Mean ± sd***
Length of stomata (μm)	20	23.73 ± 2.54	20	22.30 ± 2.08
Area of Stomatal Crypts (μm2)	19	4882 ± 6307		
Depth of Crypts (μm)			5	185.20 ± 77.87
Length of Small Trichome (μm)			11	74.00 ± 13.81
Length of Bulbous Trichomes (μm)			6	43.92 ± 11.76

Fig. 1. Transverse 3 µm section of the abaxial epidermal surface of Espeletia pycnophylla *subsp.* angelensis *(optical microscope). Scale bar represents 50 µm. M, mesophyll; S, stomata; X, xylem.*

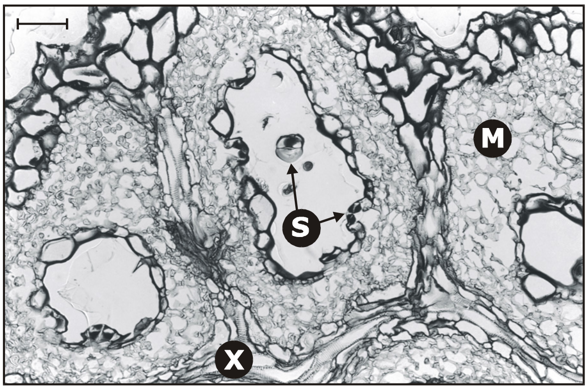


Fig. 2. Transverse 3 µm section of the abaxial epidermal surface of Espeletia pycnophylla *subsp.* angelensis *(optical microscope). This plate clearly displays stomata within the crypts. Scale bar represents 50 µm. L, cuticular lips; E, epidermal cells; G, guard cells; M, mesophyll; S, stomata.*

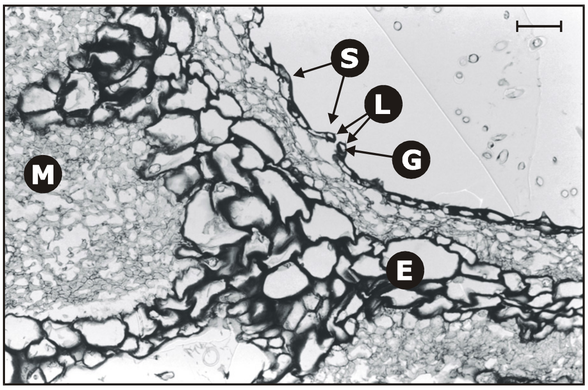
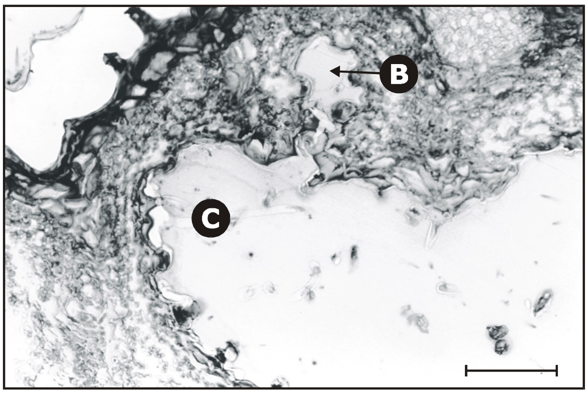


Fig. 3. Longitudinal 10 µm section of the abaxial epidermal surface of Espeletia pycnophylla *subsp.* angelensis *(optical microscope). Branching of the stomatal crypt is evident. Scale bar represents 50 µm. B, branching into sub-crypt; C, crypt.*



Scanning Electron Microscopy

Stomatal crypts are clearly visible in Figs. 4 and 5, while Fig. 6 shows branching of a crypt. In addition to stomatal crypt area, measurements were made of crypt depth (Table 1). Mean crypt depth was 185.2 µm, but varied considerably. The stomata protrude slightly from the walls of the crypt and they do not appear to have any subsidiary cells surrounding the guard cells (Figs. 7 and 8). The stomata are evidently eliptical (Fig. 7), their longest diameter ranged from 18 to 26 µm (mean 22 µm).

Three different types of epidermal trichomes were observed on both adaxial and abaxial surfaces:

1. long trichomes
   This type of trichome rises perpendicular to the epidermal surface of the leaf and along the main veins. They twist repeatedly to form a mat of trichomes overlying the leaf (Fig. 4). These trichomes often exceed 600 µm.
2. short trichomes
   These hairs are unicellular and situated around and within the stomatal crypts (Fig. 9), measuring between 68 and 96 µm (mean 74 µm—Table 1).
3. bulbous trichomes
   These trichomes are mushroom-shaped (Fig. 10), with hollow chambers within. They range in height from 28 to 62 µm (mean 43 µm—Table 1). They are scattered amongst the other two trichomes (Fig. 9), and are also present at the entrance and inside the crypts. Figs. 5 and 9 have signs of surface material which may be secreted by these bulbous trichomes.

DISCUSSION

Espeletia pycnophylla subsp. *angelensis* presents an array of microscopic features which may enable this giant rosette plant to survive at high altitudes in the Andes. One of the main challenges to plant life in the páramo is the water stress caused by early morning physiological drought (Meinzer *et al*. 1994)—when transpirational demand for water outstrips the plant's ability to provide it at low temperatures. It might be expected that at least some of the microscopic features of *Espeletia* leaves, dominated by stomatal crypts and trichomes might be related to water stress.

The presence of stomata in crypts usually represents an adaptation to reduce transpirational water losses. The crypts provide a small pocket of air, which may become saturated with water vapour, reducing the passage of water molecules from the saturated air spaces of mesophyll out into the atmosphere (Baron 1979). Many water molecules which do diffuse out of open stomatal pores, bounce around the crypt and re-enter stomata rather than being blown away (Mauseth 1995).

Transpirational water losses are reduced yet further by the dense surface pubescence—promoting a thick boundary layer of still air around the leaf—and the short trichomes lining the crypts. Nevertheless, as Hartshorne (1980) points out, there is no reason to

Fig. 4. SEM of a freeze-fractured longitudinal section through an Espeletia pycnophylla *subsp.* angelensis *leaf. Stomatal crypts are limited to the abaxial surface of the leaf. Dense pubescence covers the abaxial and adaxial leaf surface. C, crypt.*

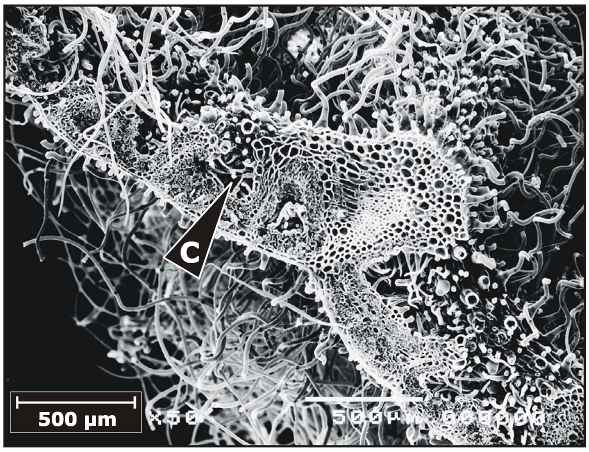


Fig. 5. SEM of the abaxial epidermal surface of an Espeletia pycnophylla *subsp.* angelensis *leaf. The main vein runs along the top of the plate and the stomatal crypts lie either side of this vein. C, crypt; V, main vein.*

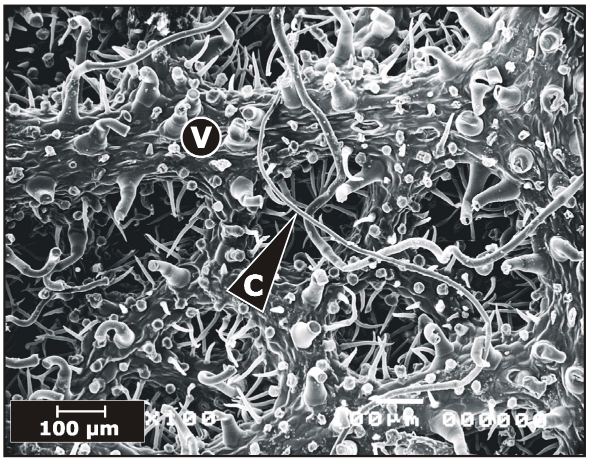


Fig. 6. SEM of a freeze-fractured longitudinal section through an Espeletia pycnophylla *subsp.* angelensis *leaf. A stomatal crypt branches into two sub-crypts. The crypts are relatively deep and in this case reach almost to the epidermal cells. The three types of trichomes are visible. B, bulbous trichome; L, long trichome; S, sub-crypt; T, small tichome; U, upper epidermis.*

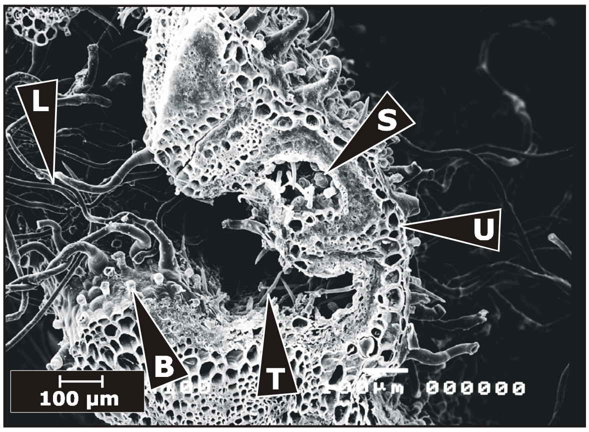


Fig. 7. SEM of an elliptical stoma from an Espeletia pycnophylla *subsp.* angelensis *leaf. L, cuticular lips; G, guard cells; O, stomatal opening.*

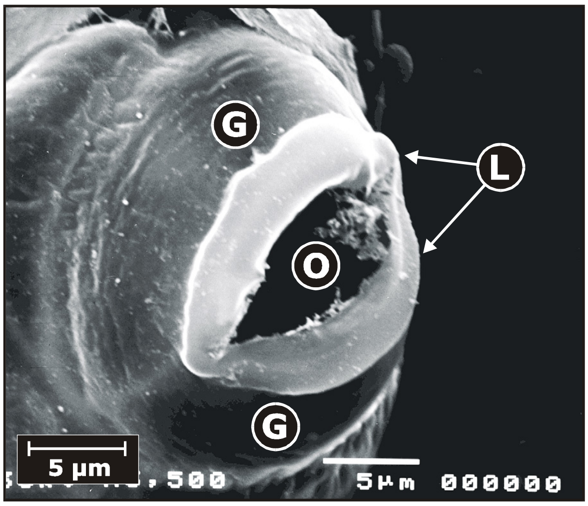


Fig. 8. SEM of the inside of a crypt of an Espeletia pycnophylla *subsp.* angelensis *leaf. The location of the stomata are not regular and they are protruding slightly from the walls of the crypt. L, cuticular lips; G, guard cells; S, stomata.*

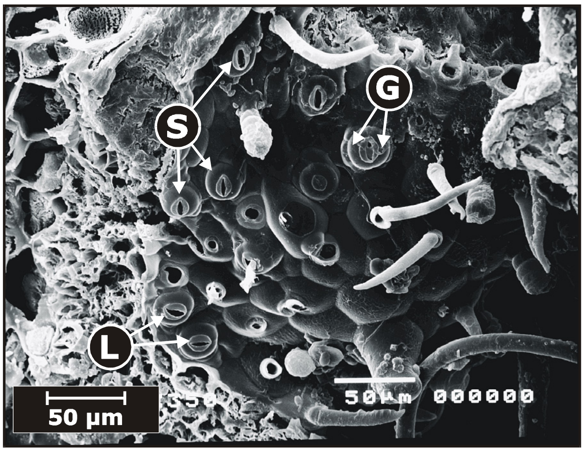


Fig. 9. SEM of a stomatal crypt surrounded by epidermal trichomes on the abaxial surface. C, crypt; T, small trichome.

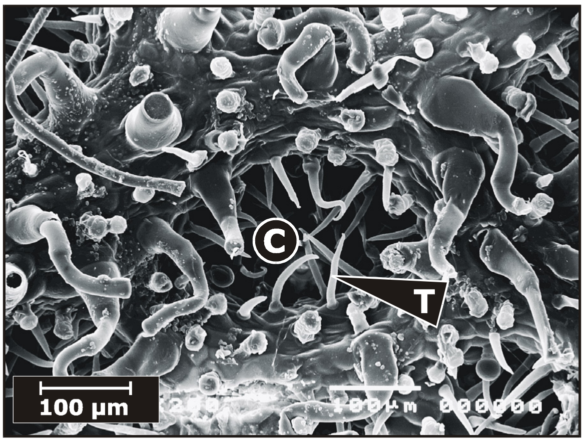
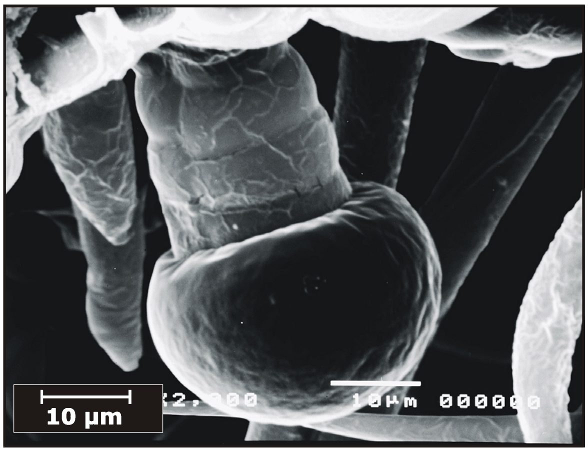


Fig. 10. SEM of a bulbous trichome.



expect that every feature of a plant subjected to water stress should show indications of xerophytic adaptation. In fact, stomatal crypts might, by themselves, mitigate water loss to the point where the plants could survive. For example, protruding stomata were observed in *Espeletia,* which tends to increase transpiration, and consequently water loss. Therefore, although epidermal trichomes might be principally involved in reducing water loss, they might instead be serving other functions.

Rada *et al*. (1985) showed that leaves of *Eucalyptus unigera* survived frosts better when dry. The twisted mat of long trichomes on *Espeletia* leaves might provide an effective barrier against water penetration, thereby increasing the ability of the leaf to avoid freezing damage. The short trichomes might perform this function on a smaller scale, preventing water entering the crypts and freezing on cold nights (many of the leaves in the rosette are held vertically with the undersides of the leaves exposed to the wind, rain and cold).

The dense pubescence might also serve to reduce excessive amounts of UV radiation reaching the leaf surface, in an environment subjected to high level of UV light (Cross 2001). The large vacuoles and the presence of flavanoids in the double layer of adaxial epidermal cells in the *Espeletia* leaves may also contribute to protection from UV radiation.

Leaf hairs often reduce the efficiency of insect herbivores, making it difficult for these animals to chew or walk. The dense pubescence in *Espeletia* may perform a secondary role as an anti-herbivore defence. Furthermore, the bulbous trichomes might be responsible for secreting resin (terpenes), to protect the leaf from herbivore attack. A rich fauna of insects including species of *Coleoptera* and *Bibionidae* were found on the flower heads of *Espeletia grandiflora* in the páramo region of Colombia (Sturm 1989), and in Venezuela *Espeletia* rosettes were each found to have an arthropod population of 2000-4000 individuals despite producing terpenic resin in the leaves (Garay and Lamotte 1989). The glandular hairs of *Helianthus maximiliani* appear very similar in superficial morphology to the ones found in *Espeletia* : terpenes are thought to be synthesised in the cells of the *Helianthus* trichome and stored in the rounded cap at the top (Taiz & Zeiger 1991). Further investigation would be required to confirm this function in the bulbous trichomes of *Espeletia*.

The bulbous trichomes might also enhance the boundary layer effect described earlier, in a similar way to that of the balloon-shaped trichomes of *Chenopodium amaranticolor* leaves (Juniper and Jeffree 1983).

Intercellular spaces inside the leaves of *Espeletia pycnophylla* were relatively small, which may aid supercooling (Levitt 1980; Goldstein *et al*. 1985). The only large spaces were the substomatal chambers, located immediately behind the stomata.

The morphological structures of crypts, stomata and epidermal trichomes on leaves of *E.pycnophylla* subsp. *angelensis* may represent adaptive features to reduce transpiration, assist in freezing avoidance, absorb excessive UV radiation, and reduce herbivore attack. More detailed physiological work is required to determine the contribution of each of these features to each strategy.

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REFERENCES

Baron, W. (1979) *Organization in Plants*, London: Edward Arnold Limited.

Carlquist, S. (1994) Anatomy of tropical alpine plants. In: Rundel, P.W., Smith, A.P. and Meinzer, F.C. (Eds.) *Tropical Alpine Environments: Plant Form and Function*, pp. 111–128. Cambridge: Cambridge University Press.

Cross, S.K. (2001). Adaptation of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis*, to ultraviolet radiation over an elevation gradient on Volcán Chiles. In: Ramsay, P.M. (ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 81–90. Plymouth: Pebble & Shell.

Estrada, C. (1984) Dinámica del crecimiento y reproducción de *Espeletia* en el páramo desértico. M.Sc. Thesis, Universidad de los Andes, Mérida, Venezuela.

Garay, I. and Lamotte, M. (1989) Le peuplement animal des rosettes d'*Espeletia* dan le páramo désertique des Andes du Venezuela. *Societa Italiana di Ecologia Atti (Sienne),* **7**: 55–59.

Goldstein, G. and Meinzer, F. (1983) Influence of insulating dead leaves and low temperatures on water balance in an Andean giant rosette plant. *Plant Cell and Environment,* **6**: 649–656.

Goldstein, G., Rada, F. and Azócar, A. (1985) Cold hardiness and supercooling along an altitudinal gradient in an andean giant rosette species. *Oecologia,* **68**: 147–152.

Hartshorne, S. (1980) *Lowson's Textbook of Botany*, Norfolk: Fakeham.

Hedberg, I. and Hedberg, O. (1979) Tropical-alpine life-forms of vascular plants. *Oikos,* **33**: 297–307.

Juniper, B. and Jeffree, C. (1983) *Plant Surfaces*, London: Edward Arnold.

Levitt, J. (1980) *Response of Plants to Environmental Stresses,* Vol. 1, New York: Academic Press.

Lüttge, U. (1997) *Physiological Ecology of Tropical Plants,* Berlin: Springer.

Mauseth, J. (1995) *Botany,* Fort Worth: Saunders.

Meinzer, F.C., Goldstein, G., and Rundel, P.W. (1994) Comparative water relations of tropical alpine plants. In: Rundel, P.W., Smith, A.P. and Meinzer, F.C. (Eds.) *Tropical Alpine Environments: Plant Form and Function*, pp. 61–76. Cambridge: Cambridge University Press.

Rada, F., Goldstein, G., Azócar, A. and Meinzer, F. (1985) Freezing avoidance in Andean giant rosette plants. *Plant Cell and Environment,* **8**: 501–507.

Rada, F., Goldstein, G., Azocar, A. and Torres, F. (1987) Supercooling along an altitudinal gradient in *Espeletia schultzii*, a caulescent giant rosette species. *Journal Of Experimental Botany,* **38**: 491–497.

Ramsay, P.M. (2001) The zonal páramo vegetation of Volcan Chiles. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 27–38. Plymouth: Pebble & Shell.

Sakai, A. and Larcher, W. (1987) Frost survival of plants: responses and adaptations to to freezing stress, Berlin: Springer.

Smith, A.P. (1974) Bud temperature in relation to nyctinastic leaf movement in an Andean giant rosette plant. *Biotropica,* **6**: 263–266.

Sturm, H. (1989) Beziehungun zwischen den Blüten einiger hochandiner Wollschopfpflanzen (Espeletiinae, Asteraceae) und Insekten. *Studies on Neotropical Fauna and Environment,* **24**: 137–155.

Taiz, L. and Zeiger, E. (1998) *Plant Physiology*, Sunderland (MA): Sinauer Associates.

Weyers, J. and Meidner, H. (1990) *Methods in Stomatal Research*, Harlow: Longman Scientific.

Adaptation of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis*, to ultraviolet radiation over an elevation gradient on Volcán Chiles

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SUMMARY

Tropical alpine ecosystems receive some of the highest natural radiation levels in the world. Species that exist in this stressful environment may be highly adapted to these radiation levels. Understanding the mechanisms that allow these organisms to survive is important in order to address the potential acclimation of other species to increased levels of UV-B, which might result from depletion of the ozone layer. To identify whether the giant rosette plant *Espeletia pycnophylla* subsp. *angelensis*, endemic to the northern Andean páramos, has adapted to the high levels of radiation leaf thickness, pubescence weight and pubescence ultraviolet absorbance were measured over an elevational gradient on Volcán Chiles, Ecuador. Results showed definite trends of increasing leaf thickness and pubescence with elevation. Leaf thickness may be important as an attenuator of radiation, due to increased epidermal thickness reducing transmittance. Although pubescence may be more important as an adaptation to temperature and water stress, UV absorbance by pubescence was demonstrated in *Espeletia*. The concentration of UV-absorbing compounds increased with altitude, particularly in leaves at the top of the rosette. The pubescence of leaves from higher altitudes also showed a greater ability to absorb radiation of the shorter UV-B wavelengths.

RESUMEN

Los ecosistemas alpinos tropicales reciben algunos de los niveles más altos de radiación natural en el mundo. Especies en este ambiente podrían estar finamente adaptadas a estos niveles de radiación. Con el propósito de indagar acerca de la aclimatación potencial de otras especies a elevados niveles de luz ultravioleta (UV-B), como resultado del adelgazamiento de la capa de ozono, es necesario entender los mecanismos que permiten la sobrevivencia de estos organismos en estos ambientes. Así, con el propósito de verificar si la roseta gigante *Espeletia pycnophylla* subsp. *angelensis*, endémica a los páramos andinos norteños, se ha adaptado a los altos niveles de radiación, el espesor de la hoja, el peso de la pubescencia y la absorción de rayos ultravioleta por la pubescencia se midieron a lo largo de un gradiente altitudinal en el Volcán Chiles, Ecuador. Los resultados mostraron tendencias claras de incremento en el espesor de la hoja y la pubescencia con la altitud. El espesor de hoja puede ser importante como un atenuador de la radiación debido a que a mayor grosor de la epidermis hay una menor transmitancia de la radiación. Aunque la pubescencia en *Espeletia* puede ser más importante como una adaptación a cambios en la temperatura y la disponibilidad de agua, se demostró la absorción de UV por la pubescencia. Además, la concentración de compuestos que absorben la radiación ultravioleta aumentó con la altitud, particularmente en las hojas superiores de la roseta. Por último, las hojas provenientes de sitios más elevados mostraron una mayor capacidad para absorber radiación en las menores longitudes de onda de UV-B.

Key words: UV radiation, UV-B, leaf pubescence, leaf thickness

INTRODUCTION

Low latitude, high elevation sites, such as the páramo grasslands of the Northern Andes, can receive UV-B irradiance nearly six times greater than the maximum dose received at the poles (Caldwell *et al.* 1980). For this reason, plants have evolved specific adaptations in order to survive in this high UV-B environment. Knowledge of these adaptive mechanisms might allow greater understanding of the potential acclimation of other species under circumstances of potentially increased UV-B radiation due to ozone depletion.

Knowledge of plant adaptation to UV-B is to a large extent based on laboratory experiments (Robberecht and Caldwell 1978; Caldwell and Flint 1994; Ziska *et al.* 1992) and crop plants (Rozema *et al.* 1992), with few relating to natural ecosystems. Studying species that exist naturally over large elevational gradients offers the opportunity to test plant responses to increased levels of solar radiation outside laboratory conditions.

Tolerance and avoidance of UV-B stress is manifested in a variety of strategies. Studies often indicate increased leaf thickness (Rozema *et al.* 1997: Barnes *et al.* 1990) and UV absorbing compounds with elevation (Ziska *et al.* 1992: Rozema *et al.* 1997: Caldwell and Flint 1994). These responses can be viewed as functional adaptations to the increased levels of UV-B. A longer optical path through thicker leaves and absorption of UV-B radiation by specific compounds, such as flavonoids, will help to reduce the amount of radiation penetrating the leaf, consequently limiting metabolic damage (Rozema *et al.* 1997). However, increased levels of UV-B absorbing compounds do not necessarily indicate increased resistance to UV-B radiation, for example, Rozema *et al.* (1997) found that in Jamaican Tropical Montane Cloud Forests, increased levels of phenolic compounds may be due to soil nutrient deficiencies.

Quantitative and qualitative changes in the accumulation of secondary compounds in leaf epidermis's on exposure to UV-B may play an important role in determining UV sensitivity (Sullivan *et al.* 1992). When combined with other cell wall components, secondary compounds can reduce the incident solar radiation by one or two orders of magnitude (Robberecht and Caldwell 1978). It has

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 81-90.

been noted that epidermal flavonoids are inducible in the presence of elevated radiation levels, showing a two-fold increase compared to plants not exposed (Lumsden 1997). It has also been demonstrated that in parsley, flavonol accumulation is linearly correlated with exposure to UV-B radiation (Lumsden 1997).

In order to maintain effective protection against UV radiation there are variations in the distribution of compounds within individual leaves. For example, different sets of secondary phenolic substances have been localised in epidermal and mesophyll tissues (Anhalt and Wisenbock 1992). Flavonoid compounds have been termed 'epidermis-specific' (Lumsden 1997), yet certain *Verbascum* and *Olea* species have been reported to have UV absorbing trichomes (Karabourniotis *et al.* 1992). Skaltsa *et al.* (1994) reported that non-glandular leaf hairs of *Quercus ilex*, which were denser on the abaxial surface, contained UV-B absorbing flavonoids that functioned as filters.

Flavonol and phenolic compounds, as well as offering UV protection, also have other ecological implications by providing resistance to pathogens and a deterrent against herbivores. Flavonoids, glucosinolates and terpenoids can attract and deter insects and herbivores. Attractiveness of plants may be altered not only by changes in chemistry but also by altered tissue morphology such as foliage toughness (Caldwell and Flint 1994); a common response to UV radiation being increased leaf thickness (Barnes *et al.* 1990).

Other adaptations to high UV radiation environments include the significance of leaf pubescence, which despite a lack of extensive study indicates increased thickness with elevation (Meinzer and Goldstein 1985: Meinzer *et al.* 1985). The presence of (individual) hairs or trichomes, or (collective) pubescence on leaf surfaces is widespread. The evolutionary significance of pubescence has been the subject of much debate, but it is generally accepted that its ubiquitous nature can be related to the presence of particular environmental conditions (Johnson 1975), for example water stress and increased UV radiation.

Trichomes originate from epidermal tissue and then develop through growth, differentiation or cell division to become hair like projections extending from the epidermal surface. Morphologically, trichomes have a broad spectrum of variation, with different types of trichome being produced at different stages in development (Johnson 1975). Thus, Hammond and Mahlberg (1973) identified three successive morphological types of glandular trichome on the floral bracts of *Cannabis sativa.*

Pubescence cover varies between species, within species and even from organ to organ on an individual plant. Younger organs often have a dense covering, which as the organ develops become more dispersed. Meinzer and Goldstein (1985) noted that the younger, vertically orientated expanding leaves on *Espeletia timotensis,* have thicker pubescence than the older, more horizontal leaves. However, trichome production may keep pace with age and expansion to maintain a dense covering for the lifetime of the plant (Johnson 1975).

In relation to *Espeletia* species Baruch and Smith (1979) hypothesised that the adaptive value of leaf pubescence lay in its ability to reduce leaf temperature, radiation absorption and transpiration. More recently Meinzer and Goldstein (1985) concluded that increased pubescence modifies energy balance by increasing boundary layer thickness and resistance to latent and convective heat transfer, resulting in potentially higher leaf temperatures in relation to air temperature and more efficient use of solar radiation. It was found that pubescence induced increases in leaf temperature of 5°C or more could be attained without significant increases in transpiration if stomatal resistance could be maintained.

It has also been proved that pubescence, in certain species, plays a significant role in the reflection of incoming solar radiation, due to its structure and orientation and may absorb light through its possible colour constituents (Karabourniotis *et al.* 1992). However, Meinzer *et al.* (1985) reported that despite an increase in mean leaf pubescence from 1.1 mm at 2600 m to 2.6 mm at 4200 m elevation in the Venezuelan species *Espeletia schultzii*, the leaf hairs of this species are not very efficient reflectors of solar radiation.

Nevertheless, the presence of leaf hairs in some species will not only increase the reflectance of that surface, but according to evidence from Eller (1977), pubescence on the lower leaf surface can increase reflection from the upper surface. In the presence of hairs, the transmitted radiation emerging from the lower epidermis is partially reflected back into the leaf. The radiation passes once again through the different leaf tissues. The level of absorbance of specific wavelengths will determine how much of the reflected radiation is absorbed by the leaf and how much is emitted from the upper epidermis.

Many investigations have been carried out into adaptations that may protect against ultraviolet radiation, yet there is still much contradictory evidence. Interspecific variations such as increasing leaf thickness and pubescence, despite being well documented, still require much investigation. Many interactions are closely linked indicating that there are a variety of inter-relating adaptations that may all need to be present to be affective.

The purpose of this study, therefore, is to investigate the adaptive value of leaf pubescence, levels of UV-B absorbing flavonoid compounds within the leaf pubescence and leaf thickness. This will be carried out over an elevational gradient in the species *Espeletia pycnophylla* subsp. *angelensis* CUATR. by examining:

- Correlation between leaf thickness and elevation. Leaf thickness will be measured on younger and senescing leaves to identify any differences with age.
- Alteration in pubescence weight with altitude. Pubescence will be measured on abaxial and

adaxial surfaces and on leaves of different ages, and hence, orientation.

- The ability of the pubescence to absorb radiation. Flavonoid extracts will be tested for their ability to attenuate different UV wavelengths. This will demonstrate whether the presence of higher concentrations of flavonoids within the leaf pubescence is correlated to increased protection from certain wavelengths, and any amplification of this protection with elevation.
- Leaf structure and pubescent morphology using Scanning Electron Microscopy.

METHODS

Site description

The Northern Andes contains several ecological zones, which vary in relation to elevation. The zone with which this investigation is concerned is the tropical alpine zone, occurring between the upper limit of continuous closed canopy growth (3100–3500 m) and the upper limit of plant life (4600–4900 m) (Hedberg 1964). Northern tropical alpine grasslands are known as páramos and are found from Costa Rica to northern Bolivia and Peru, with Ecuador containing extensive areas estimated to cover 20000 km^2 (Ramsay and Oxley 1996).

Tropical alpine areas are characterised by high inputs of solar radiation in the presence of low inputs of thermal energy (Meinzer *et al.* 1994: Baruch 1979). Tropical latitudes have relatively constant levels of high solar irradiance over annual cycles. For example, over a twelve-month cycle at the Equator, the daily maximum irradiance is only 13% higher than the minimum level (Rundel 1994). They are also described as having "summer every day and winter every night" (Hedberg 1964), with extreme daily temperature fluctuations, and almost complete lack of seasonal variation, creating a highly stressful environment for any organism living there. Much of the difference between daily and seasonal temperature results from the latitudinal effect on annual change in solar radiation at the outer surface of the atmosphere.

The extreme temperatures, and the intense sunlight that occur at the Equator, are key selective forces in adapting to high tropical environments and for this reason only highly adapted organisms can survive. Species such as the giant rosette plants of the genus *Espeletia* are endemic to the Northern Andean páramos. They thrive in this environment, constituting a distinctive part of the landscape with different species occupying a wide variety of habitats. The Ecuadorian páramos in particular are dominated by giant stem rosettes of the species *Espeletia pycnophylla* subsp. *angelensis* and basal rosettes of *Puya* (Bromeliaceae) spp.

Study sites

Data was collected from the páramo of Volcán Chiles, on the border between Ecuador and Colombia (0° 49′ 00″ N 77° 56′ 15″ W). This particular páramo ranges from 3300 m to the summit at 4723 m. Adaptation of *Espeletia pycnophylla* subsp. *angelensis* to the high levels of radiation found in this environment was studied at nine sites over an elevational gradient within the páramo area. Sampling took place at 100 m intervals of altitude, from 3300 m to 4100 m inclusive (Fig. 1). Table 1 gives a brief description of each site. At each altitude ten plants were sampled, with one leaf taken from the base and one from the crown of each plant.

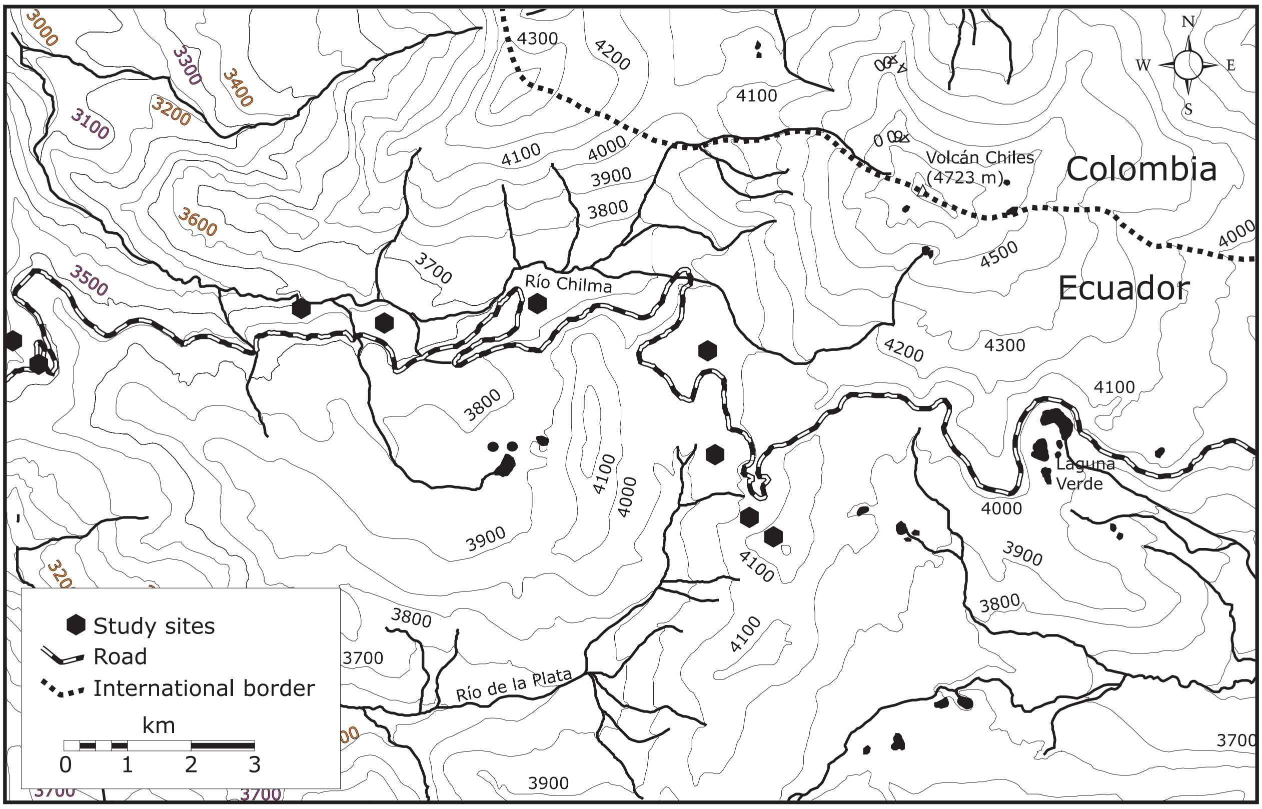
Table 1. Description of Sampling Sites

Altitude	Site Description
3300 m	Diverse area near road with trees and shrubs.
3400 m	West-facing 45° slope at the road side, small trees and shrubs present.
3500 m	Shallow slope at the bottom of a valley. Dominated by tussock grass.
3600 m	30° slope in the base of a valley, large numbers of *Puya* spp.
3700 m	15° northwest-facing slope adjacent to the road. Abundant tussock grass.
3800 m	Relatively flat area in the base of a valley, waterlogged ground.
3900 m	Northwest-facing, exposed, almost flat area.
4000 m	West-facing with 30° slope, tussock grass.
4100 m	Northwest-facing, steeply sloped, with tussock grass, signs of burning.

Table 2. Estimated daily doses of UV-B in the study area compared with theoretical sea level values. Calculations were performed following Björn and Murphy (1985) and Green (1983), but refined by Fiscus and Booker (unpublished). Unweighted doses refer to direct irradiance values. Weighted doses are the unweighted values multiplied by Caldwell's (1971) generalised plant response action spectrum, summarising the UV-B effect on plants in a comparable way.

Altitude (m)	Pressure (mb)	Daily Dose of UV-B (KJ m^{-2})	
		Unweighted	Weighted
0	1000	45.1	9.6
3300	700	51.7	10.6
4100	635	53.3	10.9

Fig. 1. Location of the study sites.



Fieldwork was carried out at Volcán Chiles from 25 July to 1 August 1997. All samples were collected during daylight hours. The nine altitudes were not situated along one incline with uniform exposure, but followed the path of the road in most cases, leading to some variation in aspect and slope conditions at the individual sites. The UV-B dose at 4100 m (the highest sampling site) is estimated to be about 13.5% higher than at sea level in this part of the world (Table 2). The highest sampling site receives approximately 3% more UV-B than the lowest sampling site at 3300 m.

Pubescence

Measurements were made by determining the weight of pubescence per unit area of leaf surface. The leaf area was measured using a size 12 cork borer of 17 mm diameter. The pubescence was plucked and shaved from the both the abaxial and adaxial leaf surfaces and weighed. It must be noted however, that the method was unable to completely remove all the hair on the surface.

Leaf Thickness

Measurements were taken from the mid point along the leaf using digital callipers.

Pubescence Ultraviolet Absorbance

In order to assess the ability of the leaf pubescence to absorb UV radiation, flavonoid compounds were extracted from five samples of leaf pubescence from each of nine altitudes from 3300–4100 m. The abaxial and adaxial surfaces of both the base and crown leaf were tested. The samples were immersed in a methanol-water-HCL solution (5ml: 70:20:1v/v) for 15 minutes (Robberecht and Caldwell 1978) and filtered to remove the hairs. The samples were then analysed using UV/VIS spectroscopy over the wavelengths 570–230 nm. The pubescence samples were those used for the weight per unit area and were taken from an area of known size. Therefore, the amount of pubescence on which the extractions were performed could have increased with altitude. Thus, the quantity of compounds extracted may have increased, rather than their concentration within the pubescence.

To obtain quantitative data the graphs produced by the extractions were measured at specific points. The measurements coincided with peaks that were observed on the graphs in the areas of UV-C (<280 nm), UV-B (280–320 nm) and UV-A (320–400 nm). The exact measuring points were 260 nm, 295 nm and 350 nm.

Scanning Electron Microscopy (SEM)

This technique was used to observe the structure of *E. pycnophylla* subsp. *angelensis* leaves in detail. Material for examination under the SEM was fixed either mechanically (freeze drying) or chemically. Initially only the surface of the leaf was viewed, but in order to see the structure of the leaf more clearly fracturing was employed to provide a cross section.

RESULTS

Pubescence Weight

Fig. 2 shows the mean pubescent weight for each leaf surface. It should be noted that adaxial surfaces are higher than abaxial surfaces and that each crown surface is higher than the equivalent base surface. It should also be noted that there is a greater difference between the results for the two surfaces on the crown leaf (3.32 mg), than the base leaf (2.21 mg).

Fig. 3 shows elevational changes in the pubescence weight. It is noticeable that the increase is not linear, and that peaks and troughs are present. However, it is possible to identify that pubescence weight on all surfaces peak at mid elevations, from 3800 m to 4000 m.

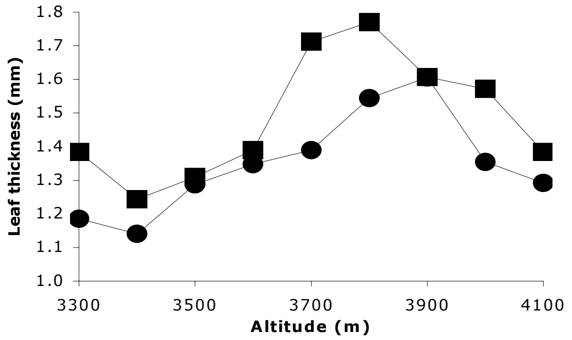
In order to identify if a significant relationship exists between pubescence weight and altitude an analysis of variance (ANOVA) was applied to both surfaces of the base and crown leaves. This test aims to find any variations of the means in the data. The analysis showed there is a highly significant relationship between altitude and pubescence weight ($p \leq 0.0001$) and a highly significant relationship between pubescence weight and leaf surface ($p = 0.000$). There was, however, no interaction between leaf surface and altitude with all leaf surfaces responding in the same way to altitude ($p = 0.05$).

Leaf Thickness

Changes in base and crown leaf thickness with elevation are shown in Fig. 4. It is apparent that there is not a consistent increase in thickness with elevation. Both leaves have a pronounced decrease in thickness at 3400 m to a mean of 1.09 mm and 1.24 mm for the base and crown leaves respectively. Again, highest values are recorded at mid elevations of 3800 m for the crown and 3900 m for the base.

The ANOVA for leaf thickness showed there is an extremely significant relationship between altitude and thickness (p=0.0001). The results also identified a significant difference ($p = 0.0132$) between base and crown leaf thickness over altitude. The analysis also indicated ($p = 0.8301$) that the base and crown leaves respond in the same way to increasing altitude.

Fig. 4. Elevational changes in leaf thickness of base (●) and crown (■) leaves.



Pubescent Ultraviolet Absorbance

Altitudinal changes in pubescent UV absorbance (Fig. 5) demonstrate a significant correlation ($p \leq 0.0001$) and exhibit a highly similar pattern for each leaf surface ($p \leq 0.0001$). Each surface shows the same pattern of peaks at 3400 (excluding crown adaxial surface) 3900 and 4100 and troughs at 3600 m and 4000 m. The base adaxial surface produces particularly pronounced peaks at 3400, 3900 and 4100 m, indicating a highly significant interaction between altitude and leaf surface ($p \leq 0.0001$).

Fig. 2. Pubescence weight from the abaxial and adaxial surfaces of base and crown leaves (± 1 sd).

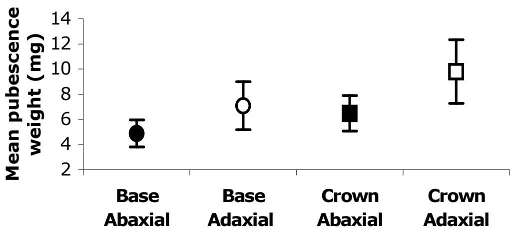


Fig. 3. Elevational changes in pubescence weight belonging to base abaxial (●), base adaxial (○), crown abaxial (■), and crown adaxial (□) leaf surfaces.

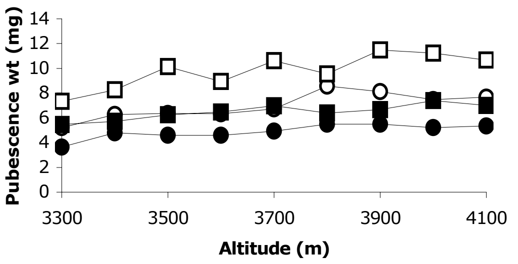


Fig. 5. Altitudinal variation in UV absorbance (inclusive of all wavelengths) of pubescence belonging to base abaxial (●), base adaxial (○), crown abaxial (■), and crown adaxial (□) leaf surfaces.

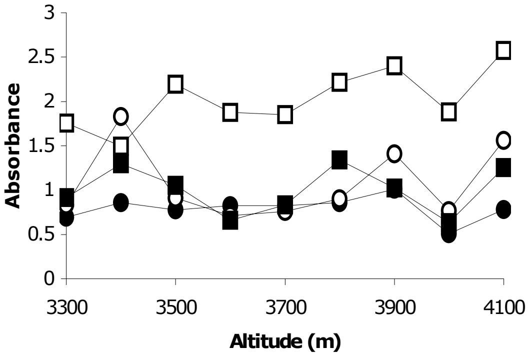


Fig. 6. UV absorbance of pubescence (averaged across all altitudes) by base abaxial (●), base adaxial (○), crown abaxial (■), and crown adaxial (□) leaf surfaces.

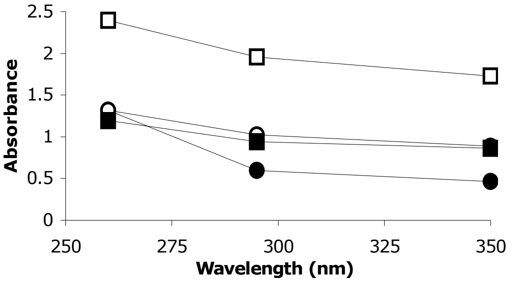


Fig. 7. UV absorbance (averaged for all leaf surfaces) across the altitudinal range at 260 nm (●), 295 nm (■), and 350 nm (▲).

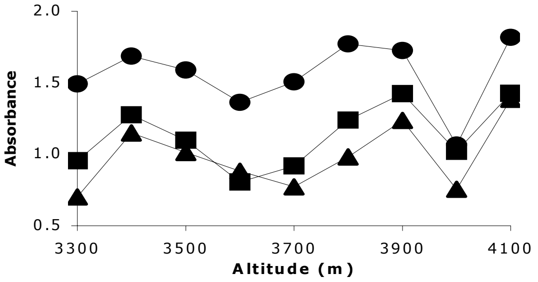


Fig. 8. SEM of a cross section through an Espeletia pycnophylla *subsp.* angelensis *leaf.*

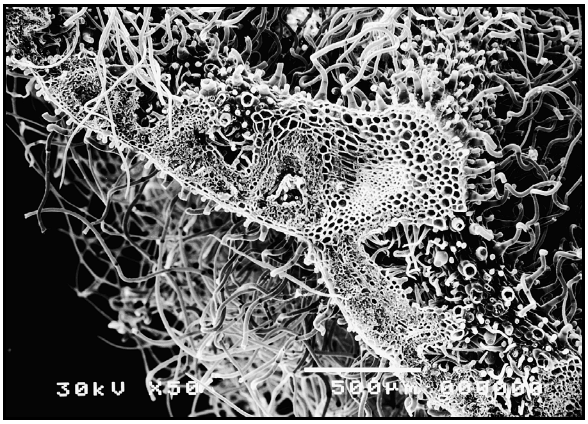


Fig. 9. SEM of multiple trichome layers on the surface of Espeletia pycnophylla *subsp.* angelensis.

Fig. 10. SEM of a bulbous trichome in a crypt of Espeletia pycnophylla *subsp.* angelensis.

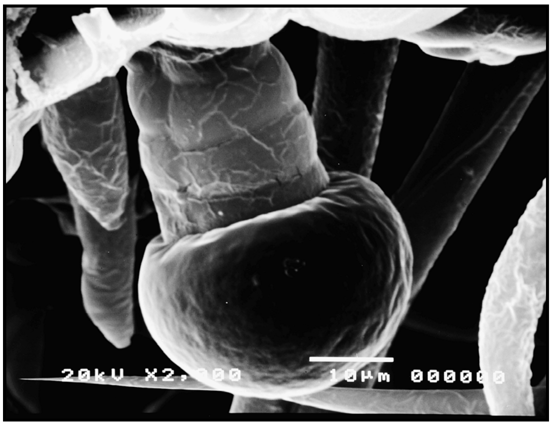


Fig 11. SEM of a crypt on the abaxial surface of Espeletia pycnophylla *subsp.* angelensis.

Leaf surface would also appear to influence the level of absorbance of different wavelengths. Statistical analysis showed a significant interaction between leaf surface and wavelength (p=0.096). Fig. 6 highlights this relationship showing the greater capacity of the crown adaxial surface to absorb all wavelengths and the ability of all surfaces to attenuate higher levels of short-wave UV-C.

Elevational changes in UV absorbance in the UV-C, UV-B and UV-A regions are shown in Fig. 7. Highest absorbance is in the 260 nm (UV-C) region, followed by 295 nm (UV-B), with the lowest amounts being absorbed in the UV-A region. A similar pattern is exhibited by each wavelength and again there is a pronounced dip in absorbance at 4000 m.

Scanning Electron Microscopy

Scanning Electron Microscopy allowed clear examination of the leaf structure, to identify the precise nature of the pubescence and leaf surface. As Fig. 8, a cross section through the leaf, demonstrates, despite considerable attempts to denude the abaxial surface, a vast amount of pubescence still remains. The unshaved adaxial surface highlights how long the trichomes are in relation to leaf thickness. The thickness of the leaves, especially at the point of the veins is noteworthy.

A closer examination of the surface is provided by Fig. 9 from which it is possible to identify two morphologically distinct trichomes. Here, larger trichomes, which have been damaged during shaving of the surface, are interspersed with bulbous trichomes. Fig. 10, a high magnification picture of the bulbous trichome structure, shows the presence of veins upon the stem and formation of a distinct "mushroom" shape. Fig. 11 provides an examination of the surface, from which it is possible to identify a third trichome exhibiting a different morphology. These hairs are situated around the edges of the crypts, or submerged within them pointing into the centre.

DISCUSSION

Without doubt pubescence is a very important characteristic in *Espeletia* species. As an adaptation dense pubescence cannot be seen simply as protecting from UV; it also provides an evolutionary answer to other environmental factors.

Leaf pubescence in several *Espeletia* species has been demonstrated to increase with elevation (Meinzer and Goldstein 1985: Meinzer *et al.* 1985), this has also proven to be the case with *Espeletia pycnophylla* subsp. *angelensis*. The method employed here does not determine whether it is the dimensions of the trichomes that increase, or their density on the surface of the leaf. A thick pubescent covering may create a hydrophobic layer on the leaf surface that could create a barrier against external ice nucleation, delaying or impeding ice crystal formation. Thomas and Barber (1979) confirm this by stating that supercooling of *Eucalyptus urnigera* was possible down to -10°C if the leaf was dry, but only -2°C if the leaf was wet.

The delay of ice crystal formation is an adaptation to the freezing nocturnal temperatures of tropical alpine environments. Over-wintering plants of temperate regions need only exhibit seasonal fluctuations in frost hardiness, but in high tropical environments such as the Andes, freezing is possible on any night of the year. Under these conditions organisms have been observed to adopt freezing avoidance as opposed to tolerance as a means of adapting to this selection pressure. It is highly possible that in certain species a combination of these two strategies may prove to be the most successful solution as Lipp *et al.* (1994) noted in species growing at high elevations in Hawaii.

Due to the different extremes placed on species during daylight and nocturnal hours, morphological features may perform distinct roles at different times of the day and on structures of different ages. Species with the greatest chance of survival are those that are equally well adapted to each of the environmental conditions to which they are subjected rather than being exceptionally well conditioned to just one.

In *Espeletia* species it has been suggested that pubescence, as well as preventing external ice nucleation, plays a role in separating leaf temperature from atmospheric temperature, the hypothesis being that pubescence raises nocturnal leaf temperatures above freezing air temperatures due to reduced radiative heat loss, preventing the formation of potentially fatal ice crystals. Ramsay (2001) showed this to be true for *Espeletia pycnophylla* subsp. *angelensis* with the leaf surface, stem beneath marcescent leaves and even the bare stem remaining above freezing at night. The effect of pubescence, although only minor, is of most value in the apical bud. Here the pubescence of successive layers of leaves has an insulating effect, reducing heat conduction and convection from one leaf layer to the next, preventing freezing of the apical meristem during nyctinastic inward bending of the leaves at night (Goldstein *et al.* 1985).

Espeletia pycnophylla subsp. *angelensi*s does not exhibit nyctinasty (Ramsay 1999), but pubescence is thickest on the crown leaves, which also have the highest stomatal resistances (Goldstein *et al.* 1985); both these features enhance temperatures created by high radiation loads. Experiments by Krog (1955) also suggest that pubescence may be of general adaptive value whenever relatively rapid growth is to occur in the presence of low air temperatures, providing more evidence of its increased value on the younger vertical leaves. Conversely, pubescence has also been reported to play a negative role in photosynthesis by decreasing the amount of light reaching chloroplasts and by increasing boundary layer resistance to CO_2 (Baruch and Smith 1979). However, in an environment such as tropical mountains where there is not a pronounced growing season, this poses less of a problem.

The potential for pubescence to produce higher nocturnal leaf temperatures has always been considered to be its primary feature in relation to temperature. This theory has recently been challenged by Ramsay (2001), who suggests that raised nocturnal leaf temperature in relation to air temperature increases water loss through the cuticle. Consequently, this may affect the role of pubescence, causing it to be most significant in terms of reducing transpirational water loss during the day and less important for thermal control at night.

In support of the theory that strategies may be used in combination, although apical leaves remain warm mature leaves often experience freezing as temperatures drop below 0°C during pre-dawn hours, indicating that pubescence offers no protection. It is likely that as the leaves senesce pubescent production decreases in favour of directing resources towards the younger developing leaves. It is reasonable to suggest that pubescent production in *Espeletia* spp. constitutes a considerable resource allocation, and that energy must be directed to where it is needed the most.

In order to aid supercooling or to limit the stress of limited water availability certain additional morphological features may have evolved. Bulbous trichomes identified on the leaf surface may produce a waxy substance that aids cooling of the leaf, or may aid water relations by absorbing water directly from the atmosphere and its precipitation's (Rundel 1982) and possibly storing it. The presence of these bulbous trichomes on both surfaces of the leaf however, would rule out a possible role in guard cell protection. Nonetheless, the smaller hairs identified around and submerged within the crypt may increase boundary layer resistance within the crypts by trapping a layer of still air through which water vapour must diffuse.

The retention of the thick layer of dead leaves below the crown helps sustain higher temperatures within the stem and allows the maintenance of water flow, which is limited due to sub zero soil temperatures. Increased pubescence is linked to high water stress environments, where according to Baruch (1979), pubescence may increase the surface for water condensation during the night, providing additional water to the soil below the plant.

Pubescence has also been linked with the reflectance and absorbance of radiation. Eller (1977) proved that pubescence on the lower leaf surface of *Tussilago fargara* can act as a reflecting layer. Meinzer *et al.* (1985) however, concluded that the leaf hairs of *E. schultzii* were not very efficient reflectors of radiation, while Foley (2001) noted that epidermal reflectance increases with altitude, so reducing the need for pubescent reflectance.

Although the pubescence may only have a limited ability to reflect radiation, absorbance could be achieved through the presence of UV absorbing compounds. The spatial distribution of compounds within the leaf will determine the level of protection, most notably epidermal flavonoids reducing transmittance. For *E. pycnophylla* it has been demonstrated that these compounds are present in the pubescence, possibly providing another line of defence against the high radiation levels found in tropical mountain areas.

Results at the three wavelengths for *E. pycnophylla* indicate lowest absorbance in the UV-A region. This could be due its potential ability to drive repair mechanisms (Caldwell *et al.* 1995) and its capacity to elicit not necessarily negative plant responses, such as base curvature of *Avena coleoptiles* (Curry *et al.* 1956). Highest absorbance was recorded in the UV-C region, however, these results do not increase with elevation because UV-C does not penetrate the atmosphere and therefore poses little threat to plant health. UV-B and UV-A results however, do increase indicating an adaptive change to these wavelengths.

Altitudinal changes in absorbance followed a similar pattern in all leaf surfaces and exhibited an extremely strong correlation. Adaxial surfaces, particularly the crown, attenuated radiation more effectively than the abaxial surfaces. However, according to Sullivan *et al.* (1992) a simple correlation between UV-B sensitivity and the concentrations of methanol-extractable UV-B absorbing compounds does not exist as other mechanisms may play a role.

It is at this point that we again need to remember that environmental factors do not work in isolation. Caldwell *et al.* (1995) comment upon the ability of plants in water stressed environments to produce increased concentrations of leaf flavonoids, while the quality as well as the quantity of the compounds produced will affect their ability to reduce UV damage. The pronounced decrease in absorbance for all three wavelengths at 4000 m suggests the significant effect micro-climatic conditions can have on flavonoid production.

The role of compounds within the leaf may not just be related to protection from UV radiation. They may also play a role in deterring insects and herbivores from consuming plant tissue and may contribute a resistance to pathogens. Structural compounds such as lignin, which may also be an important attenuator of radiation (Day 1993), are related to flavonoids and phenolic compounds and may have some bearing on the decomposition of leaf material. Pubescence on the senescing basal leaves acting as a hydrophobic layer may reduce wetting, and therefore rotting of leaves, while flavonoids within the pubescence may prevent decomposition, allowing the leaves to remain as vital insulation. The presence of flavonoids within the leaf epidermis and mesophyll may be a deterrent to herbivores and insects such as leafhoppers and beetle larvae (Baruch 1979).

Increasing leaf thickness with elevation is a common phenomenon within *Espeletia* species as has been repeatedly demonstrated. (Meinzer and Goldstein 1985: Meinzer *et al.* 1985). The measurements for *Espeletia pycnophylla* subsp. *angelensis* leaf thickness presented here do not disprove this hypothesis, showing a strong relationship between increasing leaf thickness and elevation. Maximum leaf thickness at mid elevations, rather than at the peak, could be due to precipitation levels. Increased cloud cover at the summit may decrease UV levels making thick leaves less significant.

It would also appear that base and crown leaves, while showing considerable variances in thickness, have the same response to changes in elevation. Increased leaf thickness has been related to withstanding desiccation and abrasion as well as being a factor in UV screening. The peak at 3800 m in crown leaf thickness for *E. pycnophylla* could be related to a particularly cold micro-environment, due to the site being situated in depression. Areas such as these are often affected by temperature inversions and become particularly cold, a hypothesis backed by Goldstein *et al.* (1985).

Changes in leaf thickness would also allow for alteration in leaf structure such as increased epidermal thickness which reduces transmittance (Day 1993). However, Rada *et al.* (1987) demonstrated that epidermal and mesophyll cell size, along with intercellular air spaces, decrease with elevation as an avoidance mechanism at higher altitudes. Thicker leaves do, however, offer a longer optical path, which along with the multiple epidermis containing UV absorbing compounds will help to reduce the amount of light penetrating the leaf. According to Foley (2001) the epidermis plays an important role in reducing transmittance. It could also be possible that increasing thickness is related to the increased levels of pubescence on the surface adding to their bulk.

Work already published has demonstrated the existence of certain adaptations, for example increasing pubescence, resulting in the need for verification in this particular species. In other areas, such as pubescent absorbance, less is known about this species and is an area in which more work needs to be carried out, such as, specifically identifying the compounds within the pubescence and their concentration. Indeed, identifying spatial compound concentrations such as their levels within the mesophyll, or temporally, whether they illicit a response to increased UV levels within the leaf, would allow analysis of the their potential contribution to protection from UV and prevention of decomposition.

Overall, it is reasonable to suggest that the primary role of leaf pubescence in *Espeletia pycnophylla* subsp. *angelensis* is as an adaptation to temperature and water stress, rather than as a reflector or absorber of radiation. Pubescence may well play a role in reflecting radiation and absorbing it, due to its flavonoid content, but it is highly probable that the epidermis attenuates radiation more effectively.

As an adaptation to temperature, pubescence has an nocturnal insulating effect in the apical bud that will enhance any temperature increases attained by the reflected shortwave and emitted longwave radiation during the daytime. In other leaves pubescence probably plays less of a role in heating and may play more of a role in water relations.

In an environment where water, although present in the soil may not be available for uptake, the stratified pubescent layer may act to condense water during the night and may also prevent water reaching the leaf surface, which will reduce its supercooling ability and prevent rotting.

Leaf thickness is most probably increased as an adaptation to attenuating radiation rather than as a supercooling mechanism, which has been proven to reduce the size of epidermal and mesophyll cells, with elevated pubescence on leaf surfaces increasing their thickness.

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REFERENCES

Anhalt, S. and Weisenbock, G. (1992) Subcellular localisation of luteolin glucuronides and related enzymes in rye mesophyll. *Planta,* **187**: 83–88.

Barnes, P., Flint, S. and Caldwell, M. (1990) Morphological response of crop and weed species of different growth forms to ultraviolet-B radiation. *American Journal of Botany,* **77**: 1354–1360.

Baruch, Z. (1979) Elevational differentiation in *Espeletia schultzii* (Compositae), a giant rosette plant of the Venezuelan Páramos. *Ecology,* **60**: 85–98.

Baruch, Z. and Smith, A. P. (1979) Morphological and physiological correlates of niche breadth in two species of *Espeletia* (Compositae) in the Venezuelan Andes. *Oecologia,* **38**: 71–82.

Björn, L.O. and Murphy, T.M. (1985) Computer calculation of solar ultraviolet radiation at ground level. *Physiologie Vegetale,* **23**: 555–561.

Caldwell, M.M. (1971) Solar UV irradiation and the growth and development of higher plants. In: Giese, A.C. (ed.) *Phytophysiology*, pp. 131–177. New York: Academic Press.

Caldwell, M. and Flint, S. (1994) Stratospheric ozone reduction, solar UV-B radiation and terrestrial ecosystems. *Climatic Change,* **28**: 375–394.

Caldwell, M., Robberecht, R. and Billings, W. D. (1980) A steep latitudinal gradient of solar ultraviolet-B radiation in the arctic alpine life zone. *Ecology*, **61**: 600–611.

Caldwell, M. M., Teramura, A. H., Tevini, M., Bornman, J., Björn, L. and Kulandiavelu G. (1995) Effect of solar ultraviolet radiation on terrestrial plants. *Ambio,* **24**: 166–173.

Curry, G., Thimann, K. and Ray, P. (1956) The base curvature response of *Avena* seedlings to the ultraviolet. *Physiologia Planatarum*, **9**: 429–440.

Day, T. A. (1993) Relating UV-B radiation screening effectiveness of foliage to absorbing-compound concentration and anatomical characteristics in a diverse group of plants. *Oecologia,* **95**: 542–550.

Eller, B. M. (1977) Leaf pubescence: the significance of lower surface hairs for the spectral properties of the upper surface. *Journal of Experimental Botany*, **28**: 1054–1059.

Foley, P. (2001) Morphological and biochemical adaptations of the giant rosette plant *Espeletia pycnophylla* subsp. *angelensis* to ultraviolet radiation over an elevation gradient on Volcán Chiles. In: Ramsay, P.M. (Ed.), *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 91–99. Plymouth: Pebble and Shell.

Goldstein, G., Rada, F. and Azocar, A. (1985) Cold hardiness and supercooling along an altitudinal gradient in Andean giant rosette species. *Oecologia,* **68**: 147–152.

Green, A.E.S. (1983) The penetration of ultraviolet radiation to the ground. *Physiologia Plantarum,* **58**: 351–359.

Hammond, C. T. and Mahlberg, P.G. (1973) Morphology of glandular hairs of *Canabis sativa* from Scanning Electron Microscopy. *American Journal of Botany*, **60**: 524–528.

Hedberg, O. (1964) Features of afroalpine plant ecology. *Acta Phytogeographica Suecica,* **49**: 1–144.

Johnson, H. B. (1975) Plant pubescence: an ecological perspective. *The Botanical Review,* **41**: 233–256.

Karabourniotis, G., Papadopoulos, K. Papamarkou, M. and Manetas, Y. (1992) Ultraviolet-B radiation absorbing capacity of leaf hairs. *Physiologia Plantarum,* **86**: 414–418.

Krog, J. (1955) Notes on temperature measurements indicative of special organisation in arctic and sub-arctic plants for utilisation of radiated heat from the sun. *Physiologia Planatarum*, **8**: 836–839.

Lipp, C., Goldstein,G., Meinzer, F. and Niemczura, W. (1994) Freezing tolerance and avoidance in high elevation Hawaiian plants. *Plant, Cell and Environment,* **17**: 1035–1044.

Lumsden, P. (1997), *Plants and UV-B: Responses to Environmental Change*, Cambridge: Cambridge University Press.

Meinzer, F. and Goldstein, G. (1985) Some consequences of leaf pubescence in the Andean giant rosette plant *Espeletia timotensis. Ecology*, **66**: 512–520.

Meinzer, F., Goldstein, G. and Rundel, P. (1985) Morphological changes along an altitude gradient and their consequence for an Andean giant rosette plant. *Oecologia,* **65**: 278–283.

Meinzer, F., Goldstein, G. and Rada, A. (1994) Páramo microclimate and leaf thermal balance of Andean giant rosette plants. In: Rundel, P.W., Smith, A.P. and Meinzer, F.C. (Eds.) *Tropical Alpine Environments: Plant Form and Function,* pp. 44–74. Cambridge: Cambridge University Press.

Rada, F., Goldstein, G., Azocar, A. and Torres, F. (1987) Supercooling along an altitudinal gradient in *Espeletia schultzii*, a caulescent giant rosette species. *Journal of Experimental Botany,* **38**: 491–497.

Ramsay, P. M. and Oxley, E. R. B. (1996) Fire temperature and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetatio,* **124**: 129–144.

Ramsay, P. M. (2001) Diurnal temperature variation in the major growth forms of an Ecuadorian páramo plant community. In: Ramsay, P.M. (Ed.), *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 101–112. Plymouth: Pebble & Shell.

Robberecht, R. and Caldwell, M. (1978) Leaf epidermal transmittance of ultraviolet radiation and its implications for plants sensitivity to ultraviolet-induced injury. *Oecologia,* **32**: 277–287.

Rozema, J., van de Staaj, J.W., Costa, V., Torres Pereira, J., Broekman, R. A., Lenssen, G. M. and Stroetenga M. (1992) A comparison of growth, photosynthesis and transpiration of wheat and maize in response to enhanced UV-B radiation. In: Abrol, Y. *et al.* (Eds) *Impact of Global climatic changes on photosynthesis and plant productivity,* pp. 163–174. Sittingbourne: A.P.H.

Rozema, J., Chardonnens, A., Tosserams, M., Hafkenscheid, and Bruijnzeel, S. (1997) Leaf thickness and UV-B absorbing pigments of plants in relation to an elevational gradient along the Blue mountains, Jamaica. *Plant Ecology*, **128**: 150–159.

Rundel, P. (1982) Water uptake by organs other than roots. In: Lange, O.L., Nobel, P.S., Osmond, C.B. and Zeigler, H. (Eds.). *Encyclopaedia of Plant Physiology New Series*, Vol 12B, pp. 111– 134. Berlin: Springer-Verlag.

Rundel, P. (1994) Tropical alpine climates. In: Rundel, P., Smith, A and Meinzer, F. (Eds.) *Tropical Alpine Environments: Plant Form and Function*, pp. 21–43. Cambridge: Cambridge University Press.

Skaltsa, H., Verykoidou, E., Harvala, C., Karabourniotis, G. and Manetas, Y. (1994) UV-B protective potential and flavonoid content of leaf hairs of *Quercus ilex. Phytochemistry,* **37**: 987–990.

Sullivan, J., Teramura, A. and Ziska, L. (1992) Variation in UV-B sensitivity in plants from a 3,000 m elevational gradient in Hawaii. *American Journal of Botany,* **79**: 737–743.

Thomas,D.A. and Barber, H.N. (1974) Studies on characteristics of a cline of *Eucalyptus urnigera* from Mount Wellington, Tasmania. I. Water repellancy and the freezing of leaves. *Australian Journal of Botany*, **22:** 501–512.

Ziska, L., Teremura, A. and Sullivan, J. (1992) Physiological sensitivity of plants along an elevational gradient to UV-B radiation. *American Journal of Botany*, **79**: 863–871.

Morphological and biochemical adaptations to UV-B exposure in the Andean giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis*

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SUMMARY

Selected morphological and biochemical aspects of *Espeletia pycnophylla* subsp. *angelensis*, a giant rosette plant of the Ecuadorian high Andes, were measured over an elevation gradient from 3300m to 4300m. *E. pycnophylla* appears to utilise several adaptive strategies in response to exposure to UV-B at high altitudes. The combination of strategies used appeared to vary with leaf age and position in the rosette. Leaves were thicker at higher altitudes allowing greater accumulation of UV-B absorbing compounds and/or offering greater protection to vulnerable inner cells through reduced penetration of UV-B. Leaf extracts of UV-B absorbing compounds showed greater absorbance capacity in samples from higher altitudes, and reflectance of *in* vivo leaf discs was also greater in leaves from higher altitudes. A decrease in leaf sap pH was observed with increasing altitude and may be linked with an accumulation of the anti-oxidant, ascorbic acid. Acidification of sap pH during the hours of darkness may imply that this plant employs a form of CAM photosynthetic pathway. However, there may be other explanations for the observed acidity patterns, which do not require the involvement of CAM.

RESUMEN

Algunos aspectos morfológicos y bioquímicos seleccionados fueron medidos en *Espeletia pycnophylla* subsp. *angelensis*, una planta arosetada gigante de los altos Andes ecuatorianos, en un gradiente altitudinal de 3300m a 4300m. *E. pycnophylla* parece utilizar varias estrategias adaptativas como respuesta a la exposición a la luz UV-B a grandes altitudes. La combinación de estrategias utilizadas pareció variar con la edad de la hoja y la posición dentro de la roseta. Las hojas fueron más gruesas en los sitios más altos, permitiendo una mayor acumulación de compuestos que absorben la UV-B y/o ofreciendo mayor protección a las células internas más vulnerables a través de la reducción de la penetración de UV-B. Los compuestos que absorben la UV-B extraídos de las hojas mostraron una mayor capacidad de absorción en muestras de mayor altitud, y la reflectancia de cortes circulares de hojas *in vivo* fue también mayor en las muestras provenientes de mayores altitudes. Fue observada una disminución en el pH de la savia de la hoja con la altitud y ésta pueda estar vinculada con una acumulación del anti-oxidante ácido ascórbico. La acidificación de la savia de la hoja durante las horas de oscuridad puede implicar que esta planta emplea una ruta fotosintética de tipo MAC (metabolismo ácido de las crassulaceas). Sin embargo, es posible que haya otras explicaciones para los patrones de acidez observados que no requieran la implicación del MAC.

Key words: UV absorbance, UV reflectance, sap acidity, páramo, tropical alpine,

INTRODUCTION

The ozone layer limits the amount of ultra-violet (UV) radiation that reaches the earth's surface, but there are concerns about its future integrity. Any reduction in ozone results in a very specific increase in short-wave (280–315 nm) UV-B radiation, the bioactive portion of the spectrum. A decrease of 10% of the total ozone would result in an increase of about 20% in the weighted sum of UV-B (Biswas 1977).

Exposure to UV-B can have both direct and indirect effects on plants. DNA can become damaged by the absorption of the high energy UV-B photons, and photo-oxidation by free radicals (Rozema *et al.* 1997a). Membrane damage can occur via photo-absorption, peroxidation of unsaturated fatty acids and changes in membrane lipid composition. Damage to the molecular photochemical systems can occur, *e.g.*, the partial inhibition of photosynthesis brought about by the absorption of UV-B by the photosystem II reaction centre (PS II α and PS II β) (Terimura and Sullivan 1988). Plant growth has been shown to be adversely affected beyond that expected by reduced photosynthesis alone. The photo-oxidation of indoleacetic acid (IAA) a phytohormone to 3-methyl oxidol, and/or direct DNA damage may be responsible for the observed reduction in growth (Caldwell *et al.* 1989). UV-B can have secondary consequences in plant morphogenesis and metabolism. Radiation-induced effects on plant form (photomorphogenesis) include changes in plant height, leaf area, leaf thickness, branching and plant phenology (Rozema *et al.* 1997a). Plants may compensate for high UV-B by increasing leaf thickness thereby reducing UV transmission to the sensitive cells in the centre of the leaf, but they may also control the internal light gradient through simultaneously altering pigment content and light scattering properties (Bornman and Vogelmann 1991). Changes in plant morphogenesis may lead to changes in ecosystem structure and processes; such as decreased primary production, altered plant species composition and altered secondary chemistry, with implications for herbivory, litter decomposition and biogeochemical cycles (Caldwell and Flint 1994).

Plants have evolved three principal protective mechanisms to withstand UV damage: avoidance, shielding and repair. Avoidance mechanisms include altering the angle of inclination of the leaf towards direct insolation, and the growth of young vegetative buds at night or in periods when UV is low (Caldwell and Wellmann 1979).

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble and Shell. Pp. 91-99.

Mechanical protective measures include waxy leaf coverings, which act to reduce penetration by increasing reflectance of UV, although for most leaves reflection is not more than 10% (Caldwell *et al.* 1995). Trichomes may form a epidermal covering (indumentum) which is highly responsive to UV levels (Johnson 1975).

UV-filtering pigments (*e.g.*, phenolics, flavonoids and anthocyanins) are commonly found in epidermal cells (Robberecht and Caldwell 1978). Phenolics and flavonoids are ideal as UV-B screens since they show high transmittance for photosynthetically active radiation (PAR) but absorb strongly in the UV-B range, re-radiating the excitation energy produced as heat, fluorescence or at longer wavelengths (Manetas 1995). Flavonoids have also been shown to increase in response to UV-B exposure (Caldwell *et al.* 1995), and may be concentrated in leaf indumentum (Karaborniotis *et al.* 1992).

Whatever the defence mechanism employed by the plant there is inevitably a degree of UV-B that reaches the vulnerable tissues (Bornman and Vogelmann 1991). DNA repair (photoreactivation) is driven by visible and UV-A illumination: the enzyme DNA photolyase repairs the damage caused by the formation of pyrimidine dimers (Caldwell *et al.* 1995).

Most of the work on UV-B has occurred over the last two decades in response to concerns over stratospheric ozone (Caldwell and Flint 1994). The majority of this work has been carried out with herbaceous, agricultural plants under laboratory or glasshouse conditions (Caldwell *et al.* 1995). Recent studies include crop plant and alpine plant growth experiments under controlled conditions (Ziska *et al.* 1992; Sullivan *et al.* 1992). However, there exists only limited research on indigenous plants of naturally high UV-B irradiated environments.

Solar UV-B increases by 14–18% per 1000 m elevation (Manetas 1995) but much larger changes are observed with latitude due to differences in prevailing solar angles. Furthermore, there is a natural latitudinal gradient in the ozone layer—thinnest at the equator and thickest at the poles (Caldwell *et al.* 1989). High-altitude tropical alpine areas the highest naturally exposed areas on Earth (Manetas 1995). Caldwell *et al.* (1980) showed that on a global basis, daily UV-B irradiance at low latitude, high elevation sites can be nearly six times greater than the maximum dose received at arctic latitudes. Where UV levels are naturally high, evolution has selected for species with the capability to repair and/or protect against UV induced damage. Both physical and chemical defences are common among plants found in such extreme conditions and they provide an invaluable resource in examining how nature has adapted to this increasingly relevant form of stress.

This study assesses various morphological and biochemical responses to UV-B exposure in the the giant rosette plant, *Espeletia pycnophylla* CUATREC. subsp. *angelensis* CUATREC. (Asteraceae). This genus contains about 130 species endemic to the northern Andes (Monasterio and Sarmiento 1991), some of which have been the focus for previous ecophysiological research (*e.g.*, Goldstein *et al*. 1985, Meinzer *et al.* 1985, Rozema *et al.* 1997b).

METHODS

Study areas

The work was carried out over an altitudinal range of 3300–4300 m in the páramo grassland of Volcán Chiles, situated on the border between Colombia and Ecuador. The area extends above the upper limit of contiguous, closed canopy forest and, like other páramo regions, is characterised by high inputs of solar radiation in the presence of low inputs of thermal energy (Meinzer *et al.* 1985). Observations and plant samples were collected from 11 sites on the southern and western slopes of the mountain (Fig. 1). The zonal vegetation of Volcán Chiles has been described by Ramsay (2001).

Field measurements

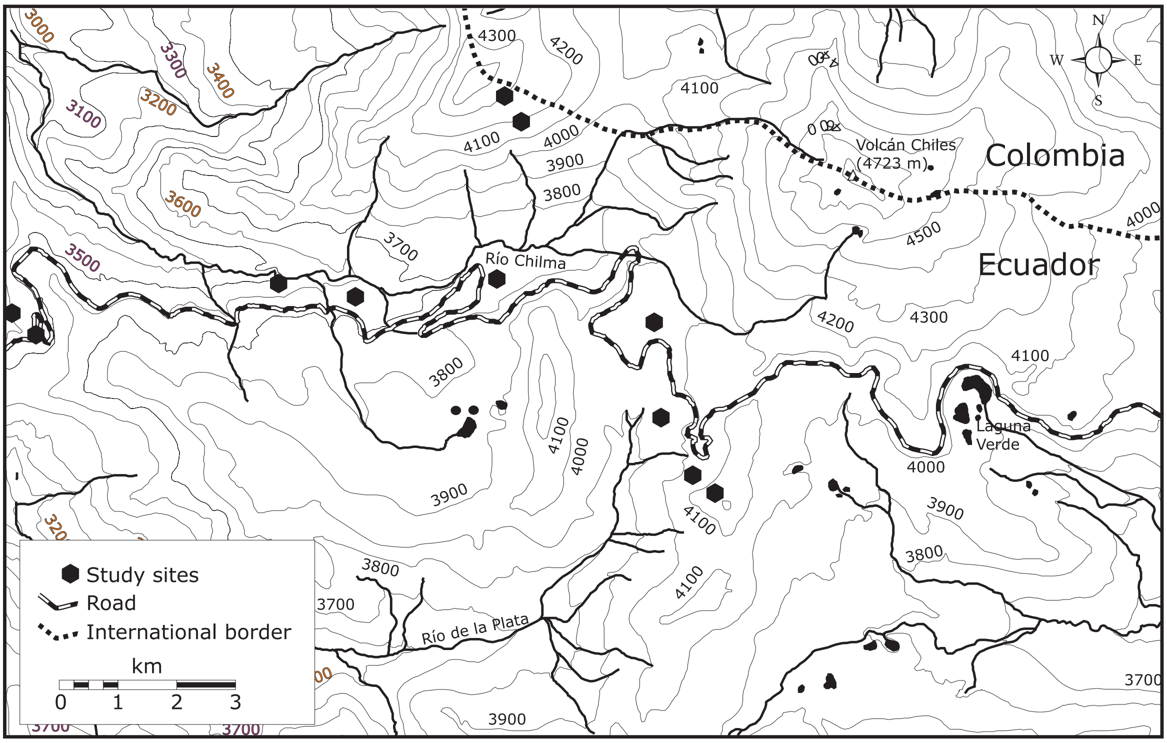
Measurements were taken of *Espeletia pycnophylla* subsp. *angelensis* at each of the eleven altitudes, which covered this species' distributional range on Volcán Chiles. At each altitude, ten plants were selected at random within a 10 x 10 m area.

The height of each plant was recorded from its base to the highest leaf on the rosette, taken from the up-slope side of the plant. Furthermore, the length of one leaf from the top of the rosette ("crown") and another at the base of the rosette ("basal") was measured for each plant. The thickness of the same leaves was also measured with electronic callipers (Mitutoyo Digimatic Calliper 0–150mm, accurate to the nearest 0.01 mm). The measurement was taken each time in the middle of the leaf avoiding the middle vein. The leaves were always sampled from the western side of each plant, since this side generally receives more insolation (Smith and Young 1987) and so is more relevant to the study of effects of UV-B.

The same leaves that were measured were split along the central vein and the sap pH determined with narrow range (pH 4–6) BDH litmus paper.

A crown and basal leaf was collected from each of two *Espeletia* plants at every altitude for later work in the laboratory.

Fig. 1. Location of the study areas.



At 3900 m only, the diurnal rhythm of pH change within the sap was recorded. Three plants were of similar size selected at random. One plant was left exposed to natural sunlight ("insolated"). The second was covered with black plastic ("black"), preventing light from reaching the leaves but still allowing temperature changes. The third plant was covered with reflective silver sheeting ("silver"), blocking light and minimising temperature changes caused by solar radiation. The "black" and "silver" plants were covered two hours before the start of the experiment at 06:00. Thereafter at two-hour intervals, the pH of the plants was measured three times for crown and three times for basal leaves for 24 hours. During the experimental period the protection was not removed.

Laboratory studies

The amounts of UV absorbing compounds within the leaf samples collected from each of the 11 sites were determined by means of an ethanolic extraction. The thickness of each leaf was measured accurately using electronic callipers prior to removing the leaf disks with a 0.5mm stainless steel punch. Five leaf disks were removed from each of the leaves and quickly put into tubes containing the extraction medium (5cm^3 for each leaf disc) and sealed. The extraction medium consisted of a solution of acidified ethanol (ethanol: conc. hydrochloric acid: water in the ratio of 79: 20: 1, after Rozema *et al.* 1997b). The sealed tubes were then heated in a water bath at 70°C for two hours or until the discs were completely bleached. Some of the extract was then removed and placed in a quartz cuvette. Absorbance of the extract was then analysed at 280, 300 and 320nm wavelengths using a PU8700 series UV/Vis spectrophotometer.

Three samples were analysed for each altitude, taking cuttings from three portions of the leaf tip, middle and base.

Transmittance and reflectance (from 200–750 nm) were measured for three samples of leaves (leaf tip, middle and base) from each altitude, using a Pye Unicam SP8-100 UV/Vis spectrophotometer with a diffuse reflectance accessory. Absorbance was subsequently calculated from the equation:

absorbance = 100 – transmittance + reflectance

First, measurements were made of intact leaves, and then repeated for leaves with the pubescent hairs shaved off.

RESULTS

The allometric measurements made across the altitudinal range are shown in Table 1. There were no statistical correlations between altitude and any of the measurements, with the exception of a weak positive relationship with basal leaf thickness.

An inverse relationship between sap pH and altitude was recorded for both crown and basal leaves of the rosette (p<0.01; Fig. 2). The pH of leaf sap also varied over the 24-hour cycle (Fig. 3). Leaves of all three treatments showed periods of higher sap pH during the afternoon and early morning before dawn. Intervening periods of more acidic sap pH occurred after sunset and in the early morning around dawn on the second day of the experiment. There was no significant difference between the "black" and "silver" treatments, nor between crown and basal leaves of the rosette. Insolated leaves showed much higher sap pH than the other treatments during the first morning, and remained acidic until dawn on the second morning.

Table 1. Allometric measurements of Espeletia pycnophylla *plants over an altitudinal gradient on Volcán Chiles. The values shown are means from ten measurements made on different plants.*

altitude (m)	plant height (cm)	basal leaf length (cm)	crown leaf length (cm)	basal leaf thickness (mm)	crown leaf thickness (mm)
3300	74.0	22.95	22.60	1.186	1.389
3400	95.6	24.95	23.70	1.054	1.315
3500	111.5	23.55	22.10	1.267	1.326
3600	74.8	22.90	21.25	1.128	1.607
3700	84.1	23.80	23.30	1.396	1.572
3800	163.3	30.30	30.25	1.549	1.763
3900	109.1	26.65	26.60	1.606	1.607
4000	92.4	23.43	22.75	1.386	1.572
4100	117.7	24.30	22.70	1.275	1.388
4200	102.9	21.35	22.40	1.374	1.428
4300	103.1	22.85	21.15	1.480	1.422

Fig. 2. Inverse relationship of crown (▲) and basal (■) leaf pH with altitude. The fitted relationships are also shown (- - -, crown leaves;— — basal leaves).

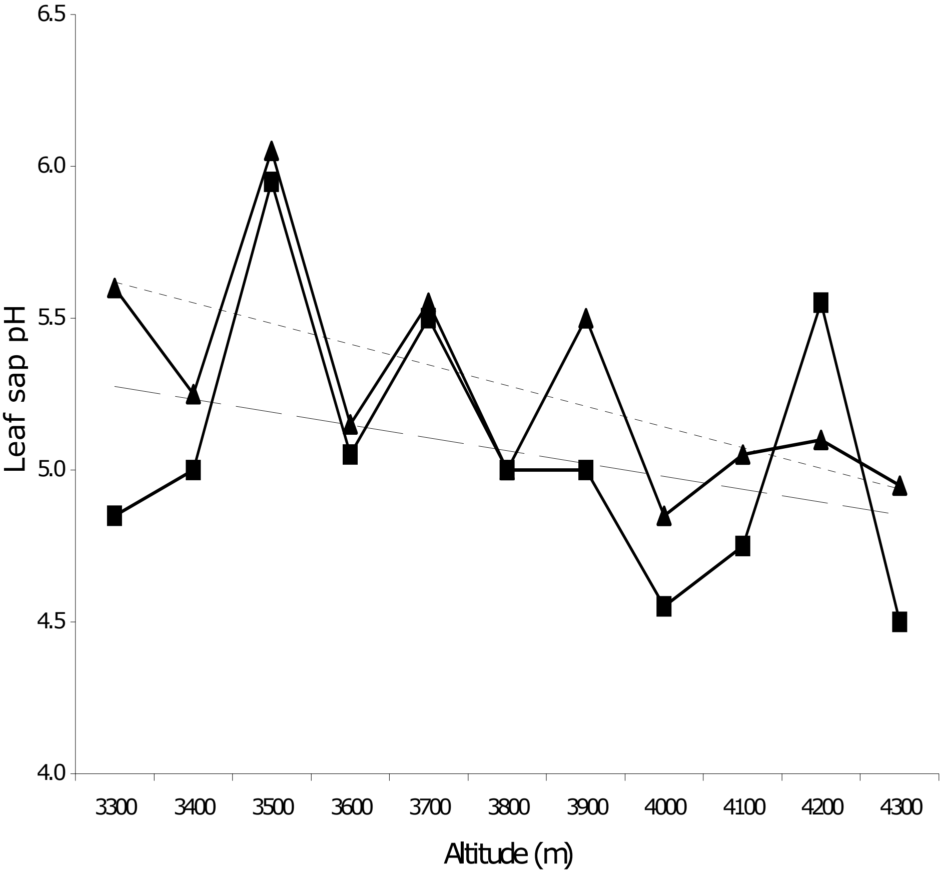
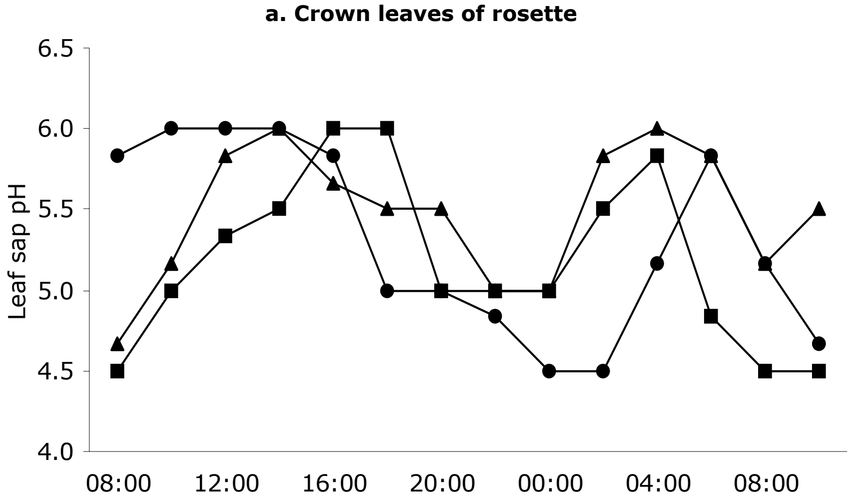


Fig. 3. Diurnal variations of sap pH in Espeletia pycnophylla *leaves. Symbols: ●, exposed to sunlight; ■, covered in black plastic; ▲, covered in silver plastic.*
a. Crown leaves of rosette. b. Basal leaves of rosette.



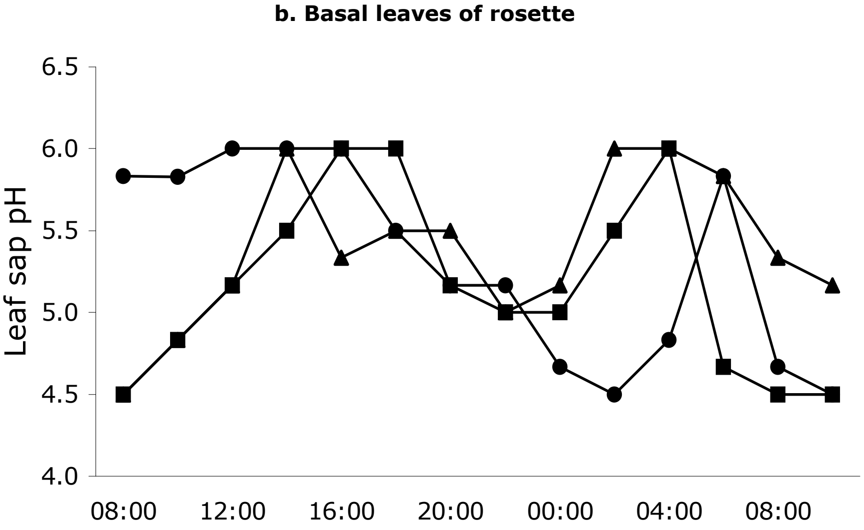
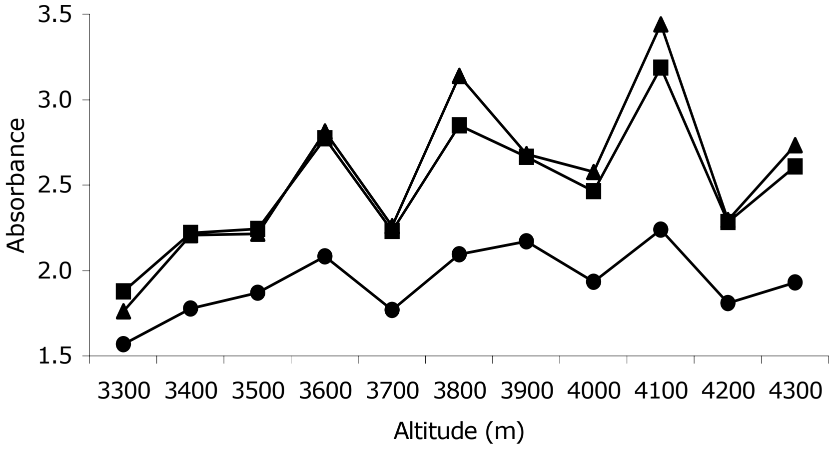


Fig. 4. Absorbance of leaf extracts over the altitudinal gradient. Symbols: ●, 280 nm; ■, 300 nm; ▲, 320 nm.



There was no statistically significant trend in leaf extract absorbance over the altitudinal gradient, though there was a tendency for absorbance to increase with altitude (Fig. 4).

From spectral analysis of leaf discs, absorbance decreased with altitude (Table 2), particularly for discs with the pubescence removed (Fig. 5). Reflectance increased with altitude. The presence of leaf pubescence was associated with higher levels of reflectance, especially at the highest altitudes. Transmittance was less than 1% in all samples, and showed little relationship with altitude.

A leaf from 3300 m was exposed to a wider spectral analysis (200–750 nm). The intact leaf absorbed almost all light until 390 nm, then reflectance increased steadily as the wavelength increased until more light was reflected than absorbed at 730 nm and above (Fig. 6). The same leaf, with its pubescent layer removed, absorbed a much higher proportion of light at longer wavelengths due to decreased reflectance.

DISCUSSION

The only morphological trend with altitude was that basal leaf thickness showed a positive correlation with altitude. Similarly, Cross (2001) reported elevational changes in leaf thickness of the same species on Volcán Chiles. The observed increase in thickness in basal leaves may be a response to intensified UV-B exposure at higher altitudes. The benefits of increased leaf thickness include the capacity to contain more UV-B screening pigments and reduced penetration. Bornman and Voglemann (1991), using fibre optics to study the response of certain plants to UV exposure, concluded that leaves may compensate for UV stress by increasing leaf thickness but they may control simultaneously the internal light gradient through modifications of pigment content and light scattering properties.

Crown leaf thickness did not show this pattern. There are three potential explanations for this. Firstly, the leaves at the top of the *Espeletia* rosette are held vertically. This may be considered an avoidance mechanism, which reduces the interception of UV radiation (Caldwell and Wellmann 1979). Secondly, the pubescence of crown leaves is thicker than in older basal leaves (becoming thinned and flattened as the leaf ages). As a consequence, reflectance is higher in crown leaves than in basal leaves. Thirdly, *Espeletia* retains dead leaves on the stem as insulation for the water-storing pith in the stem, and as a reservoir of nutrients (Monasterio and Sarmiento 1991). Older leaves at the base of the rosette are often undergoing senescence and may no longer require UV-B protection. Therefore, both leaf inclination and the condition of the pubescence layer in crown leaves reduce the amount of UV radiation reaching the leaf tissues, and reducing the requirement for thicker leaves to filter out UV wavelengths. UV-B protection for older, senescing leaves may not be so important and the defensive strategies may be reduced. It seems likely, then, that the array of UV-B related strategies employed in *Espeletia* leaves changes as the leaves age and alter their position in the rosette.

*Table 2. Summary of simple regression analyses of spectral analysis data at each of the five UV-B wavelengths. CC, correlation coefficient. Significance symbols: NS, not significant; *, p≤0.05; **, p≤0.01; ***, p≤0.001.*

Wavelength	R^2	CC	*P*	Signif
Absorbance				
320	58.1	-0.762	0.0064	**
310	60.6	-0.779	0.0047	**
300	50.9	-0.714	0.0137	*
290	55.5	-0.745	0.0085	**
280	35.0	-0.591	0.0554	NS
Reflectance				
320	55.5	0.745	0.0085	**
310	56.1	0.749	0.0080	**
300	50.2	0.709	0.0146	*
290	51.2	0.716	0.0133	*
280	39.7	0.630	0.0376	*
Transmittance				
320	0.7	0.083	0.8090	NS
310	34.4	0.586	0.0579	NS
300	7.9	0.281	0.4020	NS
290	46.1	0.679	0.0216	*
280	11.9	0.345	0.2990	NS

An inverse relationship between leaf sap pH and altitude was detected for both crown and basal leaves of the rosette. This relationship may be attributable to an increase in production of ascorbic acid as a defence against the elevated UV-B levels. Wildi and Lutz (1996) reported a 48% increase in the ascorbic acid content of *Homogyne* plants over a 1000 m gradient. Such an increase, if mirrored in *Espeletia,* may explain the fall in sap pH with altitude. The crown leaves were almost always more acidic than the basal leaves, which again suggests that the array of UV defences in *Espeletia* leaves varies with age and position in the rosette.

Leaf sap pH fell at night and during the sunshine of the early morning. There were no differences between basal and crown rosette leaves. Interpreting this pattern is difficult, but two ideas are worth considering. One obvious link would be to the production of ascorbic acid in response to UV-B radiation. Leaves would become more acidic during high insolation in the daytime and the pH would rise during the hours of darkness. This is not the observed pattern, with the most pronounced period of low pH occurring at night. Wildi and Lutz (1996) report similar observations, with diurnal changes in the acidity of *Taraxacum alpinum* contrary to expectation if the pH variation were an indicator

Fig. 5. Mean absorbance (■□) and reflectance (●○) of Espeletia pycnophylla *leaves over an altitudinal gradient (from readings at 280, 290, 300, 310 and 320 nm) for pubescent (●■) and shaved, hairless (○□) leaves.*

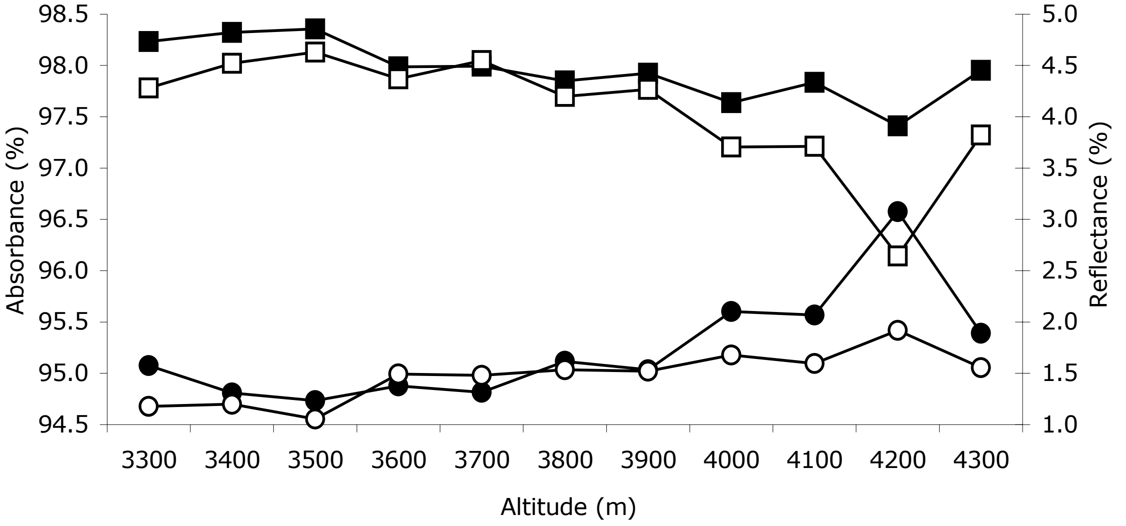
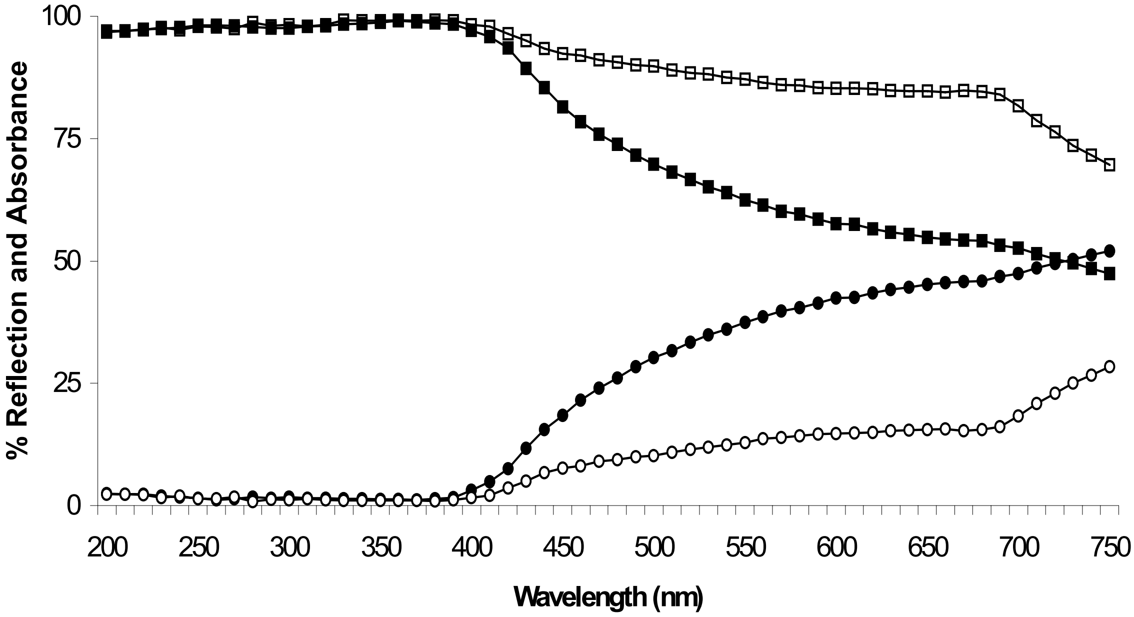


Fig. 6. Spectral behaviour of E. pycnophylla *leaf from 3300m, showing absorbance (■□) and reflectance (●○) for pubescent (●■) and shaved, hairless (○□) leaves.*



of ascorbic acid production. However, the morning fall in *Espeletia* leaf sap pH might relate to ascorbic acid production. The early morning is the sunniest time of the day in the páramo because the skies tend to be clear. Later in the day, clouds form and solar radiation tends to be lower. However, since the same pattern was observed in plants that were shielded from incoming radiation, the likelihood of the phenomenon being an induced response to UV-B seems low.

Another possibility is that *Espeletia* uses a form of Crassulacean Acid Metabolism (CAM), instead of the typical C_3 photosynthetic pathway employed by most tropical alpine plants. Plants that utilise CAM open their stomata at night to reduce water loss and fix the CO_2 into malic acid. The malic acid produced in the night is stored in the vacuole, accumulating at concentrations of 0.3 M or more, creating pH as low as 4 during the night (Salisbury and Ross 1992). When the sun rises and the plant is illuminated the stomata close and the leaf de-acidifies as the malic acid is recovered from the vacuole and undergoes decarboxylation. The CO_2 that is released is prevented from escaping by stomatal closure and is fixed by the C_3 PCR cycle (Taiz and Zeiger 1991). The night-time drop in pH would be consistent with CAM, but the pattern is not conclusive. There has been little work carried out on the photosynthetic pathways of tropical alpine plants (Smith and Young 1987), and further research is needed to substantiate or refute this hypothesis.

There was no statistically significant trend in leaf extract absorbance over the altitudinal gradient, though there was a tendency for absorbance to increase with altitude. This increase in absorbance with altitude suggests that plants from higher elevations contain a greater concentration of absorptive compounds, which is to be expected with the 25% increase in UV-B for every 1500 m ascended (Manetas 1995). The findings are in general agreement with those of Wildi and Lutz (1996), who found an "altitude-dependant accumulation of antioxidants in all the high alpine plants examined, with plants at higher altitude having higher concentrations of antioxidants". This is an obvious adaptation to increased UV exposure. The weaker trend at 280 nm is not surprising since UV of this wavelength very rarely reaches the Earth's surface and so plants are not usually responsive to this part of the spectrum. The results of this study are therefore consistent with the findings of Rozema *et al.* (1997b) and Wand (1995).

By contrast, spectral analysis of *in vivo Espeletia* leaf discs showed a decrease in absorbance with altitude. The absorbance readings from 280–320nm all show a negative correlation. At first sight, this appears to contradict the findings from the leaf extracts. However, this pattern is more a consequence of enhanced reflectance by leaves from higher altitudes, letting less radiation through to be absorbed by the tissues of the leaves. Over the altitudinal range studied, reflectance almost doubles. Thus, a double defence strategy seems to be employed as higher altitudes: both an enhanced ability to reflect incoming UV-B light and the mopping up of UV-B that enters the leaves by UV-B absorbing compounds. At the higher altitudes with elevated UV-B radiation, *Espeletia* leaves are more efficient at reflecting the light away, reducing the amount of UV-B absorbed. This reflectance ability appears to be partially linked to the dense pubescence covering all surfaces of the leaves. Removing these hairs results in significantly lower reflectance, especially at the highest altitudes. Cross (2001) found that pubescence thickness increased in leaves of *Espeletia pycnophylla* with altitude on Volcán Chiles, and that the leaf hairs were able to absorb UV-B radiation. Nevertheless, most UV-B is not reflected, but enters the leaf where it is effectively neutralised by the absorptive compounds contained inside the leaves.

Transmittance of UV-B through the leaf was negligible in all cases, but one significant relationship did occur, suggesting that more UV-B passes through leaves from higher altitudes.

The full spectral analysis of the leaf provides valuable information on the response to the longer wavelengths as well as the higher energy shorter wavelengths. Longer wavelengths (750–450 nm) were reflected much more readily than the shorter wavelengths, which were almost all absorbed. When the layer of pubescence was removed, the UV-B portion of the spectrum was more or less unaffected, whereas the reflectance of the longer wavelengths decreased by about 30%. This suggests that the main function of these hairs may be linked, not to UV-B protection, but to temperature control through attenuation of the longer wavelength red and infra-red. Meinzer and Goldstien (1985) suggest that leaf pubescence in *Espeletia timotensis* serves primarily to modify the thermal balance by increasing boundary layer resistance to convective and latent heat transfer and that change in solar radiation absorbance are minor in comparison. Meinzer *et al.* (1985) refer to other species of the genus *Espeletia* in this context.

The results obtained from this study on *Espeletia pycnophylla* provide an interesting insight into the adaptations of this species whist outlining general strategies in UV-B protection. This study has identified several adaptive strategies utilised by *E. pycnophylla* in response to the increasing exposure to UV-B provided by the altitudinal gradient of Volcán Chiles. The production of absorbing compounds within the leaf was shown to be related to altitude, and reflectance of *in* vivo leaf discs was also greater in leaves from higher altitudes. In addition, as altitude increases, leaves tend to become thicker (increasing their ability to absorb UV-B). The combination of strategies used appears to vary with leaf age and position in the rosette. The decrease in leaf sap pH observed with increasing altitude may be linked with an accumulation of the anti-oxidant, ascorbic acid, but further study is needed. Inadvertently, this study has also raised a question as to the photosynthetic pathway used by *E. pycnophylla*: there are some indications from diurnal pH variations that it may employ a form of CAM. However, there may be other explanations for the observed acidity patterns, which do not require the involvement of CAM.

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REFERENCES

Biswas, A.K. (1977) *The Ozone Layer*. Oxford: Pergamon Press.

Bornman, J.F. and Vogelmann, T.C. (1991) Effect of UV-B radiation on leaf optical properties measured with fibre optics. *Journal of Experimental Botany*, **42:** 547–554.

Caldwell, M.M. and Flint, S.D. (1994) Stratospheric ozone reduction, solar UV-B radiation and terrestrial ecosystems. *Climate Change*, **28:** 375–394.

Caldwell, M., Robberecht, R., & Billings, W. D. (1980) A steep latitudinal gradient of solar ultraviolet-B radiation in the arctic alpine life zone. *Ecology*, **61**: 600–611.

Caldwell, M.M., Teramura, A.H. and Tevini, M. (1989) The changing solar climate and the ecological consequences for higher plants. *Trends in Ecology and Evolution*, **4:** 363–366.

Caldwell, M. M., Teramura, A. H., Tevini, M., Bornman, J., Björn, L. & Kulandiavelu G. (1995) Effect of solar ultraviolet radiation on terrestrial plants. *Ambio*, **24**: 166–173.

Cross, S.K. (2001) Adaptation of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis*, to ultraviolet radiation over an elevation gradient on Volcán Chiles. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: High-altitude Ecosystems on the Ecuador-Colombia Border*, pp. 81–90. Plymouth: Pebble & Shell.

Goldstein, G., Rada, F. and Azocar, A. (1985) Cold hardiness and super-cooling along an altitudinal gradient in Andean giant rosette species. *Oecologia*, **68:** 147–152.

Johnson, H.B. (1975) Plant pubescence: an ecological perspective. *Botanical Review*, **41:** 233–258.

Karabourniotis, G., Papadopoulos, K. Papamarkou, M. & Manetas, Y. (1992) Ultraviolet-B radiation absorbing capacity of leaf hairs. *Physiologia Plantarum*, **86**: 414–418.

Manetas, Y. (1995) Effects of UV-B radiation on terrestrial pants. In: C.S. Zerefos and A.F. Bais (Eds.) *Solar Ultraviolet Radiation: Modelling, Measurements and Effects*, Berlin: Springer.

Meinzer, F. and Goldstein, G. (1985) Some consequences of leaf pubescence in the Andean giant rosette plant *Espeletia timotensis. Ecology*, **66:** 512–520.

Meinzer, F.C, Goldstein, G.H, and Rundel, P.W. (1985) Morphological change along an altitude gradient and their consequences for an Andean giant rosette plant. *Oecologia*, **65**: 278–283.

Monasterio, M. and Saramiento, L. (1991) Adaptive radiation of *Espeletia* in the cold Andean tropics. *Trends in Ecology and Evolution*, **6:** 387–391.

Ramsay, P.M. (2001b) The zonal páramo vegetation of Volcán Chiles. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: High-altitude Ecosystems on the Ecuador-Colombia Border*, pp. 27–38. Plymouth: Pebble & Shell.

Robberecht, R. and Caldwell, M.M. (1978) Leaf epidermal transmittance of ultraviolet radiation and its implications for plant sensitivity to ultraviolet radiation induced injury. *Oecologia (Berlin)*, **32:** 277–287.

Rozema, J. van de Staaij, J. Bjorn, L.O. and Caldwell, M. (1997a) UV-B as an environmental factor in plant life: stress and regulation. *Trends in Ecology and Evolution*, **12:** 22–28.

Rozema, J., Chardonnens, A., Tosserams, M., Hafkenscheid, R. and Bruijnzeel, S. (1997b) Leaf thickness and UV-B absorbing pigments of plants in relation to an elevational gradient along the Blue Mountains, Jamaica. *Plant Ecology*, **128**: 150–159.

Salisbury, F.B. and Ross, C.W. (1992) *Plant Physiology*, 4th Edition, Belmont (CA): Wadsworth.

Smith, A.P. and Young, T.P. (1987) Tropical alpine plant ecology. *Annual Review of Ecology and Systematics*, **18:** 137–158.

Sullivan, J.H., Teramura, A.H. & Ziska, L.H. (1992) Variation in UV-B sensitivity in plants from a 3,000 m elevational gradient in Hawaii. *American Journal of Botany*, **79**: 737–743.

Taiz, L. and Zeiger, E. (1991) *Plant Physiology*. Addison Wesley.

Teramura, A.H. and Sullivan, J.H. (1988) Effects of ultraviolet-B radiation on soybean yield and seed quality: a six-year study. *Environmental Pollution*, **53:** 466–468.

Wand, S.J.E. (1995) Concentration of Ultraviolet-B radiation absorbing compounds in leaves of a range of fynbos species. *Vegetatio*, **116**: 51–61.

Wildi, B. and Lutz, C. (1996) Antioxidant composition of selected high alpine plant species from different altitudes. *Plant, Cell and Environment*, **19:** 138–146.

Ziska, L.H, Teramura, A.H, and Sullivan, J.H. (1992) Physiological sensitivity of plants along an elevational gradient to UV-B radiation. *American Journal of Botany*, **79:** 863–871.

Diurnal temperature variation in the major growth forms of an Ecuadorian páramo plant community

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SUMMARY

Tropical alpine areas are characterised by a climate of warm days and cold nights, and frosts can occur on any night of the year. The extent to which six typical growth forms were decoupled from ambient air and soil temperatures was investigated in the páramo of Volcán Chiles, on the Ecuador-Colombia border. A giant stem rosette species (*Espeletia pycnophylla* subsp. *angelensis*) maintained higher than expected leaf and stem temperatures at night by means of pubescence and an insulating jacket of dead leaves. Plant height affected the temperatures experienced by the leaf rosette. Tussock plants (*Calamagrostis intermedia* and *Cortaderia sericantha*) benefited from trapped air between the leaves, which cooled slowly after dark. Sessile rosettes (*Valeriana bracteata, Senecio hypsobates*, and *Oritrophium peruvianum*), at the soil-air interface, remained warmer than air at night, perhaps as a result of heat output from the ground. The surface rosettes of cushion plants (*Xenophyllum humile, Oreobolus obtusangulus*, and *Plantago rigida*) followed a similar pattern, but the internal temperature of the cushion was remarkably stable. Erect shrubs (*Loricaria ilinissae, Pentacalia stuebelii, Pentacalia andicola*, and *Hypericum sprucei*) and herbs (*Jamesonia goudotii, Huperzia crassa, Perezia pungens, Castilleja fissifolia*, and *Lasiocephalus ovatus*) mirrored ambient air temperatures by night and were warmed by direct sunlight by day. In some cases, physiological and morphological tolerance mechanisms mitigate the need for avoidance strategies. Nevertheless, avoidance of low night-time temperatures has evolved in a number of plants: shielding sensitive plant parts with dead, hardy or expendable parts; using pubescence to increase the boundary layer of still air and reduce convective heat transfer from leaf to air; and occupying the soil-air interface where low temperatures are moderated by the warmer soil.

RESUMEN

Las zonas alpinas tropicales se caracterizan por tener un clima de días calurosos y noches frías, y las heladas pueden suceder en cualquier noche del año. Por este motivo, se investigó hasta que punto la temperatura de seis formas de vida típicas de estas comunidades en páramos del Volcán Chiles, en la frontera entre Ecuador y Colombia, son independientes de las temperaturas del aire y el suelo. Una especie de roseta caulirosula gigante (*Espeletia pycnophylla* subsp. *angelensis*) mantuvo temperaturas de hoja y tallo más elevadas que las esperadas por medio de pubescencia y una cubierta aislante de hojas muertas. La altura de la planta influyó sobre las temperaturas experimentadas por las hojas de la roseta. Las plantas que forman macollos (*Calamagrostis intermedia* y *Cortaderia sericantha*) se beneficiaron del aire atrapado entre las hojas, el cual se enfría lentamente después de anochecer. Las rosetas sésiles (*Valeriana bracteata, Senecio hypsobates* y *Oritrophium peruvianum*) se mantuvieron más calientes en la interfase suelo-aire que el aire de la noche, quizás como consecuencia de la liberación de calor por parte del suelo. Las rosetas de superficie de las plantas en cojín (*Xenophyllum humile, Oreobolus obtusangulus* y *Plantago rigida*) siguieron un patrón parecido al grupo anterior, pero la temperatura interna de la almohadilla fue extraordinariamente estable. Los arbustos erectos (*Loricaria ilinissae, Pentacalia stuebelii, Pentacalia andicola* y *Hypericum sprucei*) y las hierbas erectas (*Jamesonia goudotii, Huperzia crassa, Perezia pungens, Castilleja fissifolia* y *Lasiocephalus ovatus*) reflejaron las temperaturas ambientales del aire durante la noche y fueron calentados por la luz directa del sol durante el día. En algunos casos, los mecanismos de tolerancia morfológicos y fisiológicos mitigan la necesidad de estrategias de evasión. No obstante, la evasión de temperaturas nocturnas bajas ha evolucionado en un buen número de plantas: protejiendo las partes sensibles con partes muertas, resistentes o desechables; utilizando pubescencias que incrementan el grosor de la capa de aire inmóvil alrededor de la planta y reducen la transferencia de calor convectivo de la hoja al aire circundante; y ocupando la interfase suelo-aire donde las bajas temperaturas son moderadas por el relativamente mas caliente suelo.

Key words: plant morphology, cold resistance, cold tolerance, cold avoidance, Andes

INTRODUCTION

High elevation tropical grasslands have often been used as an example of convergent evolution (*e.g.*, Monasterio 1986). Accepting Fisher's (1930) view that "no character is likely to remain immune from selection for very long", the structure and form of tropical alpine plants can be considered to be adapted to the prevailing environment. Similar selective agents in East Africa and the Andes, for example, will give rise to plants that are ecologically equivalent and therefore alike in form and function. In fact, Hedberg (1964) proposed five growth forms, which typify this kind of environment: giant rosettes, tussocks, cushions, sessile rosettes, and sclerophyllous shrubs. Later, Ramsay & Oxley (1997) expanded the system to ten growth forms, including various additional ones, which Hedberg (1964) considered showed "less conspicuous adaptations to this environment".

One striking aspect of the tropical alpine environment, which differentiates it from other alpine and arctic regions, is the diurnal temperature climate. Having "summer every day and winter every night" (Hedberg 1964) presents unique problems to tropical alpine plants. Daily temperature fluctuations can greatly exceed seasonal variations, often 3–10 times greater (Rundel 1994). Daytime temperatures can reach 20ºC or more, but frosts can occur on any night of the year, and the frequency of these frosts may be a key selective force (Rundel 1994).

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 101-112.

Temperature, and its effects on water balance, have been repeatedly used to explain convergent evolution in páramo plant growth forms (Walter 1973; Carlquist 1974; Hedberg 1964; Hedberg & Hedberg 1979; Monasterio 1986). Temperature regulation, along with water relations and other physiological functions, help to explain the adaptive significance of the giant rosette form (Meinzer *et al.* 1994, Monasterio 1991 for the Andean páramo; Beck 1994 for the East African mountains). However, other tropical alpine growth forms have received rather less attention (Azócar *et al.* 1992, Beck 1994, Hedberg & Hedberg 1979, Ramsay & Oxley 1997), and their adaptive significance is poorly understood. Maintaining higher temperatures during the day has been shown to speed up flower production (Smith 1972) and increase seed set (Miller 1986) in some species.

Hedberg & Hedberg (1979) presented temperature records for five species, each representing one of Hedberg's (1964) growth forms, from the Venezuelan páramo in Mucubají, Mérida. The evidence supported the hypothesis that the various growth forms represent different strategies to maintain the water balance in the tropical alpine environment. Pfitsch (1988) stated that of Hedberg's five growth forms that characterise the páramos, only sclerophyllous shrubs have no morphological means of moderating the temperature extremes experienced by growing plant tissues.

This study, applying a similar approach to that taken by Hedberg & Hedberg (1979), investigates the extent to which representative species of plant growth forms in an Ecuadorian páramo are decoupled from ambient temperatures.

METHODS

Study Site

This study was carried out in the páramo of Volcán Chiles, between Laguna Verde and the pass on the Tulcán-Maldonado road (0°48′16″ N 78°56′10″ W). The majority of the measurements were made in or near a boggy depression at around 4,000m.

The central part of the boggy area was permanently waterlogged and consisted of cushions of *Plantago rigida* KUNTH, *Oreobolus obtusangulus* GAUDICH, and *Distichia muscoides* NEES & MEYEN with water between them. A number of other species were common growing on these cushions including *Hypochaeris sessiliflora* KUNTH, *Disterigma empetrifolium* (KUNTH) DRUDE, *Valeriana bracteata* BENTH., *Paepalanthus muscosus* KÖRN., and a diverse assemblage of mosses and lichens. *Senecio hypsobates* WEDD. was often found at the very edges of these cushions or in the substrate of the shallow pools themselves.

Plantago cushions were also common growing on the drier soil around the edge of the boggy depression, alongside tussocks of *Calamagrostis effusa* (KUNTH) STEUD., and upright shrubs such as *Diplostephium rupestre* (KUNTH) WEDD., *Chuquiraga jussieui* J.F. GMEL., *Loricaria ilinissae* (BENTH.) CUATREC., *Pentacalia stuebelii* (HIERON.) CUATREC., *Pentacalia andicola* (TURCZ.) CUATREC., and *Hypericum sprucei* N.ROBSON. Large rosettes of *Puya hamata* L.B. SM. were also abundant in this zone, as were tussocks of *Cortaderia sericantha* (STEUD.) HITCHC., cushions of *Xenophyllum humile* (KUNTH) V.A. FUNK, and the sessile rosettes of *Oritrophium peruvianum* (LAM.) CUATREC. Occasional clumps of *Carex lemanniana* BOOTT were also present.

The drier slopes above the boggy depression were dominated by tussocks of *Calamagrostis intermedia* (J. PRESL) STEUD. and giant rosettes of *Espeletia pycnophylla* CUATREC. subsp. *angelensis* CUATREC. Between these plants grew smaller plants such as *Jamesonia goudotii* (HIERON.) C.CHR., *Huperzia crassa (*HUMB. & BONPL. EX WILLD.) ROTHM., *Perezia pungens* (HUMB. & BONPL.) Less., *Castilleja fissifolia* L.f., *Lasiocephalus ovatus* SCHLTDL., and *Lachemilla nivalis* (KUNTH) ROTHM.

Øllgaard & Balslev (1979) visited the site during the third Danish botanical expedition to Ecuador in 1976 (Location 23) and described it floristically in more detail. Ramsay (2001) provides a phytosociological description of the grassy páramo nearby, as part of a study of the zonal vegetation of the mountain.

Temperature Measurements

Measurements were collected during two visits to Volcán Chiles. Observations of a range of growth forms were made on the 20th and 21st of October 1987, then further data were collected on tussock and stem rosette temperatures during December 1996 and January 1997.

The 1987 data consist of five records over a 24 hour period: on the first day at 14:30 and just after sunset at 18:30, then on the second day at 01:30, 05:30 (just before sunrise) and finally at 13:30. It was not possible to measure all plants simultaneously and so these times mark the start of the temperature recording sessions each of which lasted approximately 15 minutes. During the study, the sky was overcast during the day and for most of the night, with intermittent drizzle, though occasional patches of clear sky appeared during darkness hours.

A Comark 2007 digital thermometer, equipped with thermocouples (wire and probe attachments), was used to record temperatures of plants at various positions within their structure. Measurements were also carried out to provide contemporaneous records of air (1.5 m above ground surface, shielded from the sun) and soil temperature (10 cm below ground surface) near the plants involved in the study.

In all, 18 species were studied, belonging to six growth forms:

- Giant stem rosettes—*Espeletia pycnophylla* subsp. *angelensis*
- Tussock plants—*Calamagrostis intermedia*, *Cortaderia sericantha*
- Sessile rosettes—*Valeriana bracteata, Senecio hypsobates*, *Oritrophium peruvianum*.

- Cushion plants—*Xenophyllum humile, Oreobolus obtusangulus, Plantago rigida*
- Upright shrubs—*Loricaria ilinissae., Pentacalia stuebelii, Pentacalia andicola, Hypericum sprucei*
- Erect herbs—*Jamesonia goudotii, Huperzia crassa, Perezia pungens, Castilleja fissifolia, Lasiocephalus ovatus*

Three simultaneous recordings of temperatures were obtained in December 1996 and January 1997 using Tinytalk II -40/75(125)°C dataloggers attached to wire thermocouples. The first set of data was collected from 13 to 17 December 1996 (4 days), with one datalogger suspended from a wire 1 m above ground, another placed on the ground between *Calamagrostis intermedia* tussocks, and a third located within the basal leaves of a tussock. Another set of observations was obtained from 17 December 1996 to 9 January 1997 (23 days) from the centre of *Espeletia* rosettes (next to the leaf buds): dataloggers were placed in rosettes 0.2 m, 1.4 m and 2.2 m above ground.

RESULTS

Over the period of study in 1987, the air temperature fluctuated between 3.7 and 8.9°C (Fig. 1), a relatively narrow range as a consequence of the low cloud cover. The ground surface had a similar range of temperatures as the air, but was up to 5°K warmer during the day and at least 0.5°K warmer at night. The temperature of well-drained soil was more or less constant (6.4 to 6.9°C) throughout the study period, whereas the waterlogged soil was generally higher but varied more (5.8 to 9.6°C).

Espeletia pycnophylla subsp. *angelensis* was the only species of giant rosette plant examined (Fig. 2). In general, all plant parts remained within 0.3–0.6°K of air temperatures during the night. The stem covered with dead, marcescent leaves took longer to warm up in the morning and the charred bare stem temperature rose to more than 10°K above the air temperature on one occasion during the day. Leaf and flower temperatures were approximately 5–6°K warmer than the air temperature during the early afternoon.

Fig. 3 summarises the differences in temperature within the leaf rosette of *Espeletia* plants of different heights. During the daytime, the 0.2 m tall plant was coolest, and the rosette 1.4 m above ground was the warmest—the 2.2 m rosette was intermediate between the other two plants. At night, the 1.4 m and 2.2 m plants were, on average, the same temperature (3.4°C), but the 0.2 m rosette was 0.5°K colder. The 0.2 m rosette was exposed to the coldest minimum night-time temperatures (0.12°C, averaged over the darkness hours), the 2.2 m rosette warmest (0.72°C) and the 1.4 m plant intermediate (0.36°C).

Two species of tussock grasses were represented in this study, *Calamagrostis intermedia* and *Cortaderia sericantha* (Figure 4). The former species is co-dominant over most of the area, the latter is a common element of the flora on boggy ground.

Figure 1. Temperatures at 4,000 m on Volcán Chiles of air at 1.5 m above ground (×), the ground surface (●), and 10 cm deep in well-drained soil (□) and waterlogged soil (■). The black line at the bottom of the figure represents night-time.

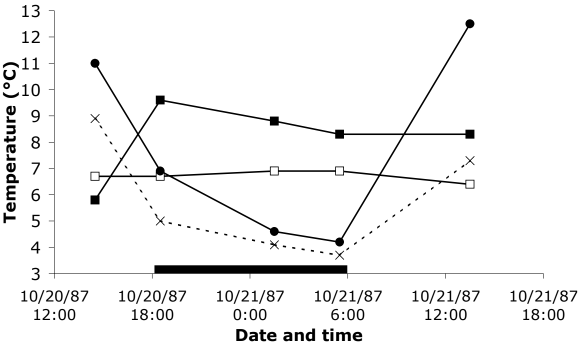


Figure 2. Temperatures of Espeletia pycnophylla *subsp.* angelensis *leaf (○), flower (●), stem covered with marcescent leaves (□) and bare stem (■) relative to ambient air temperatures.*

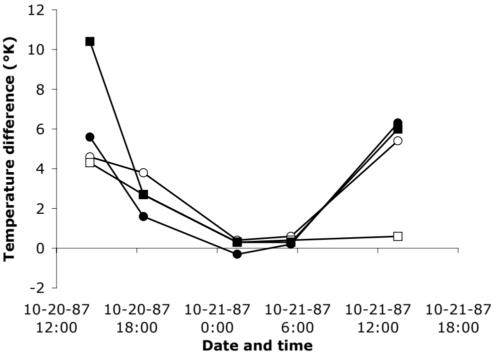
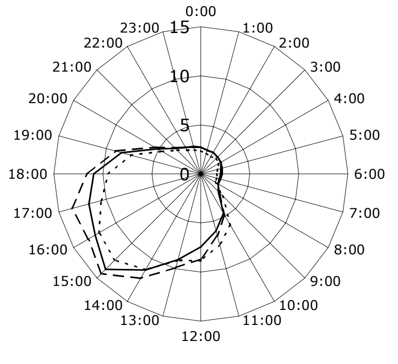


Figure 3. Mean temperatures over the diurnal cycle within the rosette of three Espeletia plants: 0.2 m tall (- - -), 1.4 m tall (– – –), and 2.2 m tall (——). Means represent 23 days' measurements. Hour of the day is shown around the circumference and the radial axis is the temperature (°C).



A second set of tussock temperature measurements was taken in December 1996 (Fig. 5). These show that, usually, both the tussock base and the ground between tussocks are warmer than the ambient air temperature at 1 m. During the day, the tussock base is on average approximately 0.5ºK warmer than the air, the intertussock ground surface about 1.3ºK warmer. At night, temperatures within the tussock are again about 0.5ºK warmer than the air, on average, while the ground surface is just 0.3ºK warmer. However, even though the air temperature never fell below 0ºC during the four day period, at temperatures below 2ºC, both the interior of the tussock and the ground surface were colder than the air above the tussocks—even dropping below freezing on the last night of the study.

Temperatures of sessile rosette species are shown in Fig. 6. In general, daytime temperatures of rosettes and flowers exceeded air temperatures by between 3–13ºK. At night rosettes were 1.0–1.8ºK warmer, and the flowers 0.1–1.0ºK warmer than ambient air temperatures.

The surfaces of cushion plants were often more than 10ºK higher than the ambient air temperature during the day (Fig. 7). The interior of the cushions, at 10 cm depth, was about the same as air temperatures during the day, but was maintained approximately 3–4ºK warmer than the air at night.

At night, the branch tips and flowers of upright shrubs were within 1ºK of ambient air temperatures (usually slightly higher), but during the daytime they were much more variable—between 1–9ºK higher than the air temperature (Fig. 8). The interior of *Pentacalia andicola* remained just above ambient air temperature throughout the night and was little affected by insolation during the day.

A similar pattern was observed for the erect herb growth form category (Fig. 9). All of the monitored plants followed the ambient air temperature closely at night, except for *Jamesonia goudotii*, which maintained a temperature, some 0.5–1.2ºK higher. During the daytime, temperatures were 3–5ºK higher than that of the air, though *Huperzia crassa* was much warmer than the other plants in this category on the first afternoon, over 10ºK above ambient air temperature.

Figure 4. Temperatures within grass tussocks relative to ambient air temperatures: upper tussock leaves (◇) and tussock base (□) of Calamagrostis intermedia*; flower (●) and tussock base (■) of* Cortaderia sericantha*.*

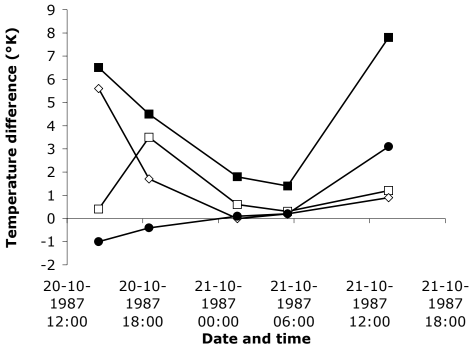


Figure 5. Temperatures measured within dense tussock base of Calamagrostis intermedia *(——), on the ground between tussocks (- - -), and air at 1 m above ground (o o o).*

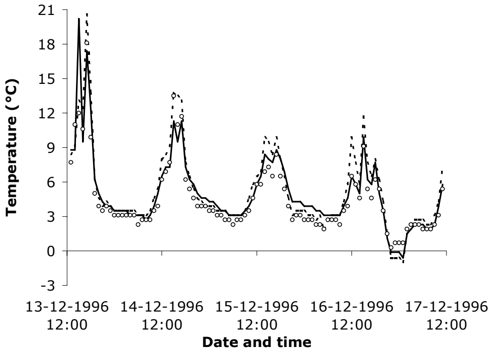


Figure 6. Temperatures of sessile rosettes relative to ambient air temperatures: rosette (○) and flower (●) of Valeriana bracteata*; rosette (□) and flower (■) of* Senecio hypsobates*; rosette (◇) and flower (◆) of* Oritrophium peruvianum*.*

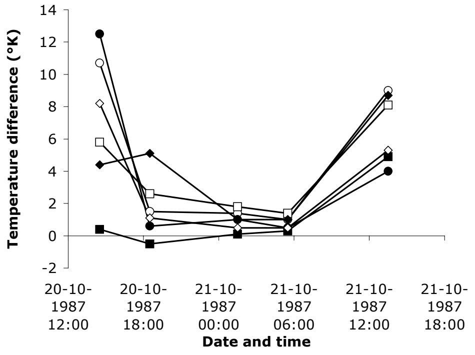


Figure 7. Temperatures of cushion plants relative to ambient air temperatures: surface (○) and 10 cm depth (●) of Xenophyllum humile*; surface (□) and 10 cm depth (■) of* Plantago rigida*; surface (◇) of* Oreobolus obtusangulus*.*

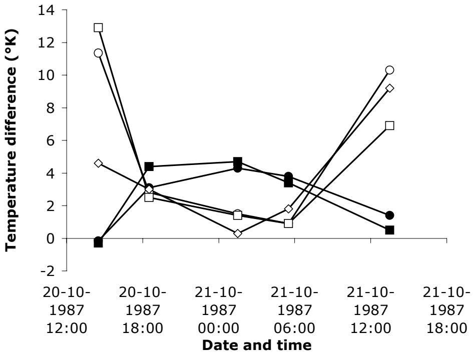


Figure 8. Temperatures of upright shrubs relative to ambient air temperatures: branch tips of Loricaria ilinissae *(○),* Hypericum sprucei *(□),* Pentacalia stuebelii *(△) and* Pentacalia andicola *(◇); flower of* Hypericum *(■); interior of* Pentacalia andicola *shrub (◆).*

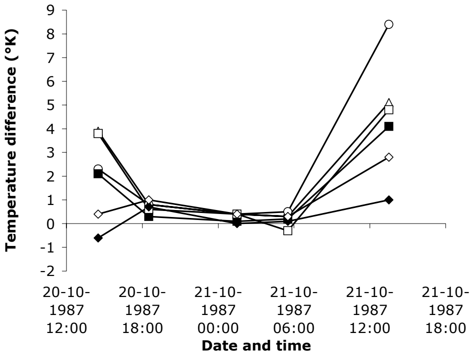
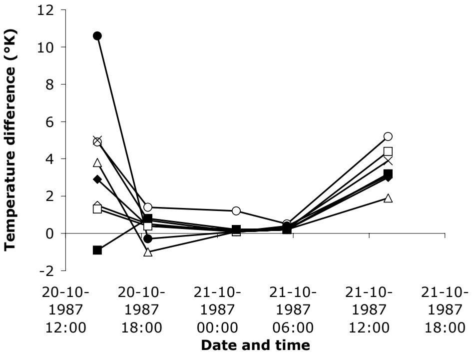


Figure 9. Temperatures of plants with the erect herb growth form, relative to ambient air temperatures: stalk tips of Jamesonia goudotii (○) and Huperzia crassa (●); bud (×), flower (◇) and stem (◆) of Perezia pungens; flower of Castilleja fissifolia (△); and flower (□) and stem (■) of Lasiocephalus ovatus.



DISCUSSION

The seasonal climates of the temperate zone permit plants there to operate different metabolisms at different times of the year. This maximises growth rates during the favourable season(s) and reduces the risk of death during the unfavourable season(s). The tropical alpine climate presents a very different challenge, with summer every day and winter every night (Hedberg 1964). At the highest altitudes, plants must be able to survive freezing night-time air temperatures throughout the year, but continue photosynthesising and growing the next day. In order to grow efficiently during cool days, plants might be expected to harness solar radiation to heat their leaves. Both of these pressures might select for plants which are decoupled from ambient air temperatures: warmer than air by night and by day.

Cold nights are better for examining the adaptive significance of growth forms in relation to cold temperatures. Hedberg & Hedberg (1979) derived their evidence from just one of the three nights for which they had recorded data. On this night, temperatures dropped to around +1°C, but reached only about 7–9°C on the remaining two nights (when the thermoregulatory properties of their study plants were not so pronounced, if apparent at all). In this study, night-time temperatures were not particularly low. The minimum temperature recorded during the one night in October 1987 was 3.7°C, though Øllgaard & Balslev (1979) had measured a night-time minimum of about +1°C nearby in 1976. Air temperatures did not drop to freezing during the 4-day study of tussock temperatures in December 1996, but a ground frost did occur on one night. In the measurements obtained from inside *Espeletia* rosettes, temperatures below zero were recorded in 8 nights out of a possible 23.

In general, temperatures fell rapidly as the sun set (loss of solar energy input), and then continued to fall more slowly throughout the night (radiation emission), reaching minima just before dawn. After sunrise, temperatures increased more rapidly due to the effects of insolation. Surface temperatures may rise and fall much more rapidly than air in response to insolation changes. This is not apparent from some of the figures, because the interval of measurement was too long.

Radiation frost—the loss of radiated heat from surfaces—is an important consideration in interpreting the results of this study for night-time temperatures. Surfaces of vegetation or ground would be expected to cool down several degrees more than air at 2m. Usually, minimum plant temperatures on clear nights are 1–3°C below the minimum air temperature (Larcher & Bauer 1981). Therefore, plant parts at similar temperatures to ambient air values at night still suggest temperature regulation because radiation frost is avoided. According to Grace (1988), short vegetation would be expected to be cooler than tall vegetation because mixing of air is reduced closer to the ground and therefore radiated losses are more important.

Before discussing certain generalities which emerge from this study, it is useful to consider each growth form in turn.

Stem rosette

Espeletia pycnophylla subsp. *angelensis* demonstrates an ability to avoid radiation frost. Only the flower fell below air temperature at night, while the temperatures of the leaf surface, the stem beneath marcescent leaves, and even the bare stem remained slightly above that of the air.

Studies on *Espeletia* species elsewhere in the Northern Andes, and of *Dendrosenecio* in East Africa, have demonstrated a number of adaptations of the stem rosette growth form, which have been linked with its success at high altitudes. Their stems contain voluminous, parenchymatous pith that acts as a water source during periods of low water availability when the ground is cold in the early morning (Hedberg 1964; Goldstein *et al.* 1984).

Some species of *Espeletia* show nyctinasty—the leaves close around the single apical bud at night and open during the day (Smith 1974)—but this was not true of

E. pycnophylla. However, the living leaves making up the apical rosette were densely pubescent—Acosta-Solís (1984) referred to them as "donkey's ears". This fur-like covering may reduce the extremes of temperature experienced by the leaf, maintaining higher temperatures at night (Meinzer & Goldstein 1985) and reducing radiation absorption during the day (Hedberg 1964, Baruch & Smith 1979). This is supported by the data in this study, which shows that the leaf surface experienced similar temperatures to that of the stem beneath the mantle of dead leaves. However, at the temperatures recorded, Meinzer & Goldstein's (1985) prediction that leaf pubescence could result in up to 5°C higher leaf temperature at night could not be tested.

Flower temperatures were close to ambient air temperatures for most of the 24-hour period, and indicates that the inflorescences may rely on avoidance of low temperature damage by supercooling. Nevertheless, flower temperature may well affect reproductive potential. Smith (1974) found fewer flowers on the windward sides of *Espeletia* plants in Venezuela, and Miller (1986) showed that pubescence on the inflorescence of another Ecuadorian giant rosette plant, *Puya hamata,* increased tissue temperature, and thus seed production, significantly.

A clear effect of the dead, marcescent leaves on the surface temperature of the stem was observed. The diurnal range of temperature was reduced from 18.8°C to 9.9°C by this covering of dead leaves, though minimum surface temperatures on the stem were approximately the same regardless of the presence of marcescent leaves. The buffering effect of the marcescent layer was, therefore, largely in the prevention of extreme high temperatures. Hedberg & Hedberg (1979) demonstrated the good insulating capacity of the mantle of marcescent leaves in *Espeletia schultzii*, which remained remarkably constant at around 7.5°C, regardless of the temperature outside the mantle. Over the course of the present study, the mean temperature of the stem beneath the dead leaves of *E. pycnophylla* subsp. *angelensis* was also 7.5°C.

The marcescent leaf mantle was incomplete—the lower portion having been destroyed by fire—and this may have resulted in some loss of insulatory protection. Goldstein & Meinzer (1983) removed the dead leaf layer of *Espeletia timotensis* and showed that stem temperature was altered, resulting in transient and permanent effects on water balance. Smith (1979) and Goldstein *et al.* (1984) report similar conclusions. The mechanism attributed to this effect by Goldstein & Meinzer (1983) was considered to be one or more of the following: the inhibition of pith recharge by subfreezing stem temperatures, the formation of embolisms in the stem xylem and freezing injury to pith tissue.

Mabberley (1986) attributed damped heating and cooling of stem rosettes to their massive construction. Although this view may be supported by the findings of Smith (1980) that *Espeletia schultzii* plants were larger at higher altitudes, the effects of radiation frost may be an alternative explanation. In the current study, leaf rosettes near to the ground were subjected to colder temperatures at night than taller rosettes.

During the day, leaf temperatures were elevated above the ambient air temperatures by more than 4ºK. However, the temperatures recorded in rosettes just 0.2 m tall were lower than that in taller rosettes. The leaves of 2 m tall plants were on average about 1ºK cooler than those of 1.5 m plants. Thus, despite the advantage of warmer air temperatures at night, there may be a cost in lower daytime temperatures and growth rates to plants over 2 m tall.

The microclimate around stem rosette plants may be ameliorated by their presence. Smith (1981) observed that adult giant rosette plants (*E. schultzii* and *E. floccosa)* acted as "nurse" plants, reducing the mortality of juvenile plants by providing shelter. No data was collected during the present study to test for such an effect with *Espeletia pycnophylla*.

Tussock

Tussocks provide a well-defined boundary layer of still air (Geiger 1966; Jones 1983), and provide stable growth conditions against fluctuations in water level, air temperature and other factors (Nishikawa 1990). The retention of dead leaves by páramo tussock plants should further enhance this effect by trapping yet more air. Therefore, the temperatures within tussocks should be warmer than air at night and day (reduced mixing of air), though the range of temperature should be lower in the dense base of the tussocks compared with the outer regions where air movement is greater and shading is lower.

These expectations are borne out by the results of this study. The dense tussock bases of *Calamagrostis,* where leaf buds are found and leaf elongation occurs, are well insulated against extremes of temperature, cooling slowly after dark and rarely exceeding 10°C during the day. The outer portion of the *Calamagrostis* tussock, the leaf tips, were subject to greater temperature variability than the basal leaves, but nevertheless, the trapping of air within the upper part of the tussock allowed the temperature to rise more than 5°C above that of the ambient air during daylight hours. At night the temperature did not deviate greatly from the ambient air temperature, but since the leaf meristems are located at the base of the leaves, low temperatures in the upper region may not be damaging.

Hedberg (1964) observed that the dense base of a tussock of *Festuca pilgeri* subsp. *pilgeri* on Mount Kenya, East Africa, was 7.5°C warmer than the -5°C temperature in the outermost zone of the tussock. Coe (1967) presented similar findings for the same species. In the Venezuelan Andes, Hedberg & Hedberg (1979) showed a similar phenomenon in *Stipa* sp. Beck (1994) presented detailed data for *Festuca pilgeri* which showed a less pronounced difference, and suggested that trapped air acts more as a buffer which delays cooling in the centre of the tussock as air temperature falls.

On this evidence, it would appear likely that during severe frosts the surrounding leaves protect the developing tillers of *Calamagrostis*. However, there is some evidence that this may not always be true. On one night In December 1996, the temperature in the tussock and on the ground surface nearby fell below zero even though the air temperature was 0.3–0.7ºC.

The hairs on the basal leaves of *Cortaderia* serve a similar function to the pubescence on the marcescent *Espeletia* leaves, with the same result—leaf surfaces were warmer than air temperatures at night, and were higher than for the tussocks of *Calamagrostis*.

The flowers of *Cortaderia* project beyond the vegetative leaves of the plant, and therefore cannot benefit from the buffered temperature regime within the tussock. Although this results in lower night-time temperatures and perhaps lower seed production, it presumably enhances wind pollination and seed dispersal which requires good air circulation to be effective.

The insulatory properties of tussocks help these plants to survive fires too. During a fire, the developing leaves of the tussock are shielded against radiated heat in much the same way as they are from intense cold at night (Ramsay & Oxley 1996).

Sessile Rosette

Hedberg & Hedberg (1979) proposed that sessile rosette plants are able to buffer temperature variation because of their position at the air/soil interface. They do not offer a mechanism for this, nor explain their results for *Hypochaeris sessiliflora* in Venezuela, which show the rosette temperature above both air and soil surface temperature over the three day period. The present study confirms the same pattern: higher rosette temperatures at night compared with the air temperature. In particular, *Senecio hypsobates* showed the same degree of difference between these temperatures as *Hypochaeris sessiliflora* in Venezuela.

Carlquist (1974) suggested that these plants take advantage of the beneficial heat output of groundwater during cold nights. The three species measured in the present study are found on soil that is heavily waterlogged, and several degrees warmer than well-drained soil nearby. These higher soil temperatures may help plants considerably in buffering extreme cold. Even the well-drained soil remains warmer than the air temperature, and thus sessile rosettes may exploit the thermal benefits of the soil-air interface here too.

There are alternative explanations for the success of this growth form at high altitudes, which do not require these plants to maintain warmer than air temperatures at night. Hedberg (1964) noted that water is more viscous at low temperatures and that the short internodes of sessile rosettes mitigate the problem of transporting water to the leaves during such times. Another possibility might be that the outermost leaves of the rosette plants shield the developing, more sensitive leaves from the coldest temperatures. A similar theory has been proposed to explain how sessile rosette plants survive high-temperature fires (Laegaard 1992; Ramsay & Oxley 1996).

The flower temperatures of *Valeriana bracteata* and *Oritrophium peruvianum* were observed to be 0.5–1.0°C higher than the air temperature at night. This is a surprising result and it is difficult to establish an explanation. One possible answer may be that these structures are able to exploit the heat release associated with condensation of water vapour on the flower surface. By encouraging condensation, the flowers may sustain a higher temperature than the surrounding air through the night.

During the day, sessile rosette plant parts were often more than 10ºK higher than ambient air temperatures, offering the possibility of much higher growth rates than otherwise.

Cushion

Cushion plants are efficient heat traps on sunny days (Körner and DeMoraes 1979), but the data presented here were taken with overcast skies, more typical of the Ecuadorian páramo. The surface temperatures of the cushions followed a similar diurnal pattern to that found by Hedberg & Hedberg (1979) for *Plantago rigida* in Venezuela. By day, temperatures reached in excess of 20°C, while at night these surfaces fell to within a few degrees of the air temperature. Ruthsatz (1978) observed the diurnal temperature regimes of five cushion species in the puna of North-west Argentina and reported similarly wide thermal fluctuations just beneath the cushion surface. Hedberg & Hedberg (1979) point out that cushions merely represent an aggregate of sessile rosettes and they may be viewed as adopting a similar approach to thermoregulation, that is, taking advantage of the soil-air interface (Rauh 1939; Hedberg 1964; Billings & Mooney 1968; Billings 1973; Armesto *et al.* 1980).

However, the inside of the cushions (10 cm below the surface) remained markedly constant—more so than the soil at the same depth—at around 9°C in both *Plantago rigida* and *Xenophyllum humile*. In support of these observations, Ruthsatz (1978) found that temperature measurements 10 cm deep within five cushion species in Argentina had much smaller oscillations than the ambient conditions.

Therefore, it seems that these cushion plants can effectively raise to their rosettes the temperatures found at the soil-air interface. The increased height of cushions might give these plants a competitive edge over sessile rosettes in light capture, reduce waterlogging, and provide mutual protection of rosettes against strong winds and desiccation. Perhaps equally importantly, cushions provide a self-contained, recycling supply of nutrients within the dome shape. Some cushions may capture nutrients by growing over tussock grasses—observed in the Ecuadorian páramos (Ramsay 1999) and in the mountains of New Zealand (Lough *et al.* 1987).

Alliende & Hoffmann (1985) demonstrated that cushions provide an ideal germination substrate for some puna plant species; indeed, some species were found almost exclusively on cushion plants—another indication of the ameliorated physical characteristics associated with cushions.

Upright shrub

These plants showed little adaptation towards temperature regulation, presumably relying on other low temperature resistance mechanisms. By day they were warmed by insolation and by night they cooled with the air temperature. Hedberg & Hedberg (1979) proposed that these plants do not possess morphological features to avoid low temperatures; instead, their morphology enables these plants to withstand them. Thus the scale-like leaves of *Loricaria ilinissae*, the needle-like leaves of *Hypericum* sp., the waxy leaves of *Pentacalia stuebelii*, and the leathery leaves of *Pentacalia andicola* all serve to reduce transpiration during low temperatures, and by these means prevent water stress. If this were so, then one would expect to see increasing xeromorphy as conditions become more severe. Hedberg (1957) found this to be the case in East Africa, but Andean studies are lacking.

Carlquist (1974) affirmed the frost resistant function of the "cupressoid" habit of *Loricaria* and added the functions of minimising transpiration and withstanding the effects of alpine light conditions. *Loricaria thuyoides* has ultraspecialized wood with an abundance of vasicentric tracheids providing overcapacity of conducting cells, rather like conifer wood (Carlquist 1994).

Erect Herb

Like the shrubs, it would appear that four of the five erect herbs in this study do not possess morphological features to ameliorate their temperatures. *Huperzia crassa* appears to rely on low temperature tolerance and was found to show significant altitudinal trends in leaf and plant size on Volcán Chiles (Ramsay, unpublished data) and in a Central Ecuadorian páramo (Buckland & Ramsay, unpublished), which may be a response to temperature and water stress.

Lasiocephalus ovatus has leaves covered with downy hairs, but does not appear to gain thermal benefit from this pubescence at the temperatures encountered in this study. These hairs may instead serve to reduce transpiration during periods of water stress, or prevent UV damage.

Unlike *Lasiocephalus*, *Jamesonia goudotii* was found to stay approximately 0.5–1.0°C above the air temperature overnight. Dense pubescence around the developing frond tip and along the midrib characterises this species, and may explain the slightly higher temperatures.

In a cold environment, there is strong selective pressure for the evolution of freezing avoidance and/or tolerance mechanisms (Azocár *et al.* 1988). In habitats where temperatures at night do not fall far below zero and remain there only for short periods of time, the main resistance mechanism should be freezing avoidance (Larcher 1981; Sakai & Larcher 1987). On the other hand, if temperatures drop well below freezing at night and stay there for several hours, tolerance should be the selected resistance mechanism (Larcher 1981; Rada *et al.* 1985; Sakai & Larcher 1987).

In the study area, temperatures rarely fell below zero and stayed there only for brief times. Therefore, avoidance mechanisms would be expected. However, several species used in this study are found at higher altitudes on Volcán Chiles where temperatures fall below freezing more often and for longer periods of time. These species may well demonstrate a combination of both avoidance and tolerance strategies.

In the case of tolerance, physiological adaptations are most important permitting tropical alpine plants to recover their full photosynthetic capacity after a night frost (Schulze *et al.* 1985). Azócar *et al.* (1988) studied *Draba chionophila* in the Venezuelan páramo. This rosette plant was not insulated from low night-time temperatures and leaves, pith and roots were observed to freeze without causing injury to the plant.

Freezing avoidance can be achieved by supercooling, the prevention of ice formation at subfreezing temperatures. This study was concerned with other forms of freezing avoidance, and several strategies have been adopted by páramo plant species.

One approach is the shielding of delicate parts with dead, hardy or expendable parts: as in the case of the marcescent leaf mantle clothing the *Espeletia* stem, or the protection of developing tillers and leaf growing points by the less sensitive leaf blades and tips in tussock grasses. Many rosette plants protect their inner developing leaves with outer ones (for example, *Puya hamata, Werneria nubigena*). Trees of the genus *Polylepis* buffer temperatures by means of many thin layers of exfoliating bark (Simpson 1979)—a significant reduction in the extremes of high and low temperatures beneath the bark was measured by Liley (1986). As mentioned earlier, insulatory functions of a plant can increase its survival rate after a fire by shielding part of the plant from intense radiated heat.

Pubescence is another common strategy for low temperature avoidance. Meinzer & Goldstein (1985) demonstrated by model simulation that leaf pubescence works by increasing the thickness of the boundary layer of still air and reducing convective heat transfer from leaf to air. This is particularly pronounced when many pubescent layers lie together (as in a developing bud). In this study, *Cortaderia sericantha* and *Jamesonia goudotii* maintained higher temperatures than that of the air by means of hairiness. Although more densely pubescent than the above species, *Espeletia pycnophylla* did not show such a marked effect, and was less than 1^{o}K above ambient air temperature throughout the night. Meinzer &

Goldstein (1985) found that in *Espeletia timotensis*, a Venezuelan páramo plant, the pubescence increased daytime temperatures but not night-time ones. Beck *et al*. (1982) reported no difference between the temperature of the epidermis beneath the dense indumentum of *Senecio keniensis* and its outer surface during course of an entire night. Therefore, it seems likely that leaf pubescence in several giant rosette plants cannot be explained solely as a freezing avoidance mechanism.

Nevertheless, Cross (2001) found that the thickness of leaf pubescence in *E. pycnophylla* varied with altitude, suggesting it is linked to a factor which does vary with elevation. Miller (1986) reported an increase in inflorescence pubescence with altitude for various species of *Puya,* and using a combination of temperature measurements and pubescence removal demonstrated that the layer of hairs was responsible for up to 80% of the difference between flower and air temperature. He then linked this higher thermal regime with increased success in seed production.

Another mechanism for freezing avoidance is found in small rosette plants. By inhabiting the boundary between soil and air, some smaller plants are able to benefit from the warmer soil temperatures at night just below the surface. The sessile rosette growth form adopts this strategy, as do mat-forming species. Taken one stage further, cushion plants are able to raise the soil surface, perhaps increasing their competitive abilities or reducing the effects of waterlogging. In addition, by retaining a smooth surface, the individuals of a cushion or mat are able to offer mutual protection from desiccation and wind action.

In some cases, both avoidance and tolerance strategies occur in combination. For instance, nyctinasty was found to enhance the avoidance of low temperatures in young leaves at night in *Espeletia semiglobulata*, whilst the outer leaves undergo regular freezing and appear to be undamaged (Larcher 1975). The sessile rosette, *Senecio hypsobates*, and the tussock, *Cortaderia sericantha*, both employ avoidance in their vegetative parts (by means of the soil-air interface and pubescence/mutual shelter, respectively) and perhaps tolerance to freezing in the floral parts.

A basic division of low temperature strategies depending on growth form has been suggested (Cabrera 1996, Squeo *et al*. 1991): plants which grow at soil level show tolerance, taller plants (trees and giant rosettes) show avoidance, and those of intermediate height exhibit both mechanisms. These suggestions were based on work carried out on high-altitude plants in Venezuela and Chile (Beck 1994, Lipp *et al*. 1994, Squeo *et al*. 1991, Squeo *et al*. 1996). This pattern may not be the same in some Ecuadorian páramos, particularly with regard to plants near to ground level, because soil conditions are more humid. The water in the soil would be expected to buffer particularly cold temperatures at night, changing the relative merits of the strategies. Nevertheless, in the absence of direct investigations into freezing temperatures in Ecuador, like those conducted in Venezuela and Chile, such a conclusion remains speculative.

Direct damage to tissues by low temperatures is not the only stress caused by freezing temperatures. Indirect water stress is particularly significant, especially in the early morning as water transport to photosynthesising leaves may be inhibited by cold temperatures (Goldstein & Meinzer 1983). Minor thermal differences can have a significant effect on plant water balance (Goldstein & Meinzer 1983) and survival (Smith 1979). A typical Q_{10} for translocation and leaf expansion may be about 2, so temperature increases of just a few degrees could be highly significant, especially in an environment lacking in temperature seasonality (Meinzer *et al.* 1994).

Many of the plants in this study have leaves which fall close to air temperature at night, but this may not represent the absence of a strategy. The intuitive view that warmer leaves at night represent an advantage to páramo plants deserves to be challenged. The absolute water vapour content of air at high altitudes is very low, and may represent a more significant limitation to plant survival at high altitudes than frost (Beck 1994). Water balance is more than just a problem in the early morning.

Water loss is determined by two main factors: the water vapour concentration gradient from leaf to air, and resistance to the diffusion of water vapour. During the day, when the stomata are open, diffusion is the most significant route for water loss. At night, with the stomata closed, diffusion is largely unimportant and water loss occurs primarily through the cuticle, driven by the vapour concentration gradient, which is dependent upon the leaf being warmer than the air around it (Marchand 1996). This form of water loss does not take place in leaves which are the same temperature as the surrounding air. Therefore, páramo plant leaves at ambient air temperature by night may lose less water than warmer leaves.

It follows from the same argument that páramo plants should demonstrate mechanisms to reduce water loss during the day by diffusion. One way this can be achieved is by maintaining a boundary layer of air around the leaves (*e.g.*, with pubescence). Thus, the role of leaf pubescence may be most useful in reducing transpirational water loss by day, and its insulating properties are secondary in some plants. Furthermore, the pubescence of *Espeletia* leaves contain UV-absorbing compounds and may serve an additional function in reducing UV-damage to leaves (Cross 2001).

According to Dobzhansky (1950), any organism that is exposed to sharply different climates must be at least tolerably well adapted to every one of the environments which it regularly meets if it is to survive and reproduce. Changeable environments put the highest premium on versatility rather than perfection in adaptation. This view is supported by Tomlinson (1987) who suggests that plasticity is more significant in adaptive terms than initial architecture.

The thermal regime is just one of the elements of the environment addressed by growth form. It has already been mentioned that resistance to fire, protection from solar radiation, transpiration, reproduction and light competition are rival considerations for inclusion in the overall form of a páramo plant. Therefore, the form of a plant represents the outcome of many selection pressures, some more important than others. The form is a structural and functional compromise which allows for the optimisation of cost-benefit relationships (Baruch 1982). As long as a plant gains more carbon than it pays for its architecture and physiology it may survive (Küppers 1989).

So, the inflorescence may suffer reduced seed production in an exposed position, but the fewer seeds that are produced may be dispersed more efficiently. Such forces are not necessarily antagonistic: it has already been cited that morphological features which insulate sensitive tissues from extremes of climatic temperature can also serve to protect against the high temperatures experienced during a páramo fire. Givnish *et al.* (1986) suggest that fire rather than low temperatures has driven the evolution of a stem rosette species in a Venezuelan tepui, and were able to demonstrate that fire survival was correlated with rosette height. Beck *et al.* (1986) found that tussock grasses were increased after an East African alpine fire, suggesting that fire favours the tussock form.

Despite competition from other selection forces, it is clear from the results of this study that avoidance of low night-time temperatures has evolved in a number of plants and the growth form plays a major role in this. A study of this kind, performed on a very cold night, would provide further and possibly more conclusive evidence for thermoregulation by growth form and other morphological features. However, the unpredictable occurrence of such cold nights makes this difficult, and more a matter of luck than judgement.

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REFERENCES

Acosta-Solís, M. (1984) *Los Páramos Andinos del Ecuador,* Quito: Publicaciones Científicas M.A.S.

Alliende, M.C. and Hoffmann, A.J. (1985) Plants intruding *Laretia acaulis* (Umbelliferae), a high Andean cushion plant. *Vegetatio*, **60**: 151–156.

Armesto, J.J., Arroyo, M.T.K. and Villagran, C. (1980) Altitudinal distribution, cover and size structure of umbelliferous cushion plants in the high Andes of Central Chile. *Oecologia Generum*, **1**: 327–332.

Azócar, A., Rada, F. and Goldstein, G. (1988) Freezing tolerance in *Draba chionophila*, a 'miniature' caulescent rosette species. *Oecologia*, **75**: 156–160.

Baruch, Z. (1982) Patterns of energy content in plants from the Venezuelan páramos. *Oecologia*, **55**: 47–52.

Baruch, Z. and Smith, A.P. (1979) Morphological and physiological correlates of niche breadth in two species of *Espeletia* (Compositae) in the Venezuelan Andes. *Oecologia*, **38**: 71–82.

Beck, E. (1994) Cold tolerance in tropical alpine plants. In: Rundel, P.W., Smith, A.P. and Meinzer, F.C. (Eds.) *Tropical Alpine Environments: Plant Form and Function*, pp. 77–110. Cambridge: Cambridge University Press.

Beck, E., Senser, M., Scheibe, R., Steiger, H.-M. & Pongratz, P. (1982) Frost avoidance and freezing tolerance in Afroalpine 'giant rosette' plants. *Plant Cell and Environment,* **5**: 215–222.

Beck, E., Scheibe, R. and Schulze, E.D. (1986) Recovery from fire: observations in the alpine vegetation of western Mt. Kilimanjaro (Tanzania). *Phytocoenologia*, **14**: 55–77.

Billings, W.D. (1973) Arctic and alpine vegetations: similarities, differences and susceptibility to disturbance. *Bioscience*, **23**: 697–704.

Billings, W.D. and Mooney, H.A. (1968) The ecology of arctic and alpine plants. *Biological Reviews*, **43**: 481–529.

Cabrera, H.M. (1996) Temperaturas bajas y límites altitudinales en ecosistemas de plantas superiores: respuestas de las especies al frío en montañas tropicales y subtropicales. *Revista Chilena de Historia Natural,* **69**: 309–320.

Carlquist, S. (1974) *Island Biology*, New York: Columbia University Press.

Carlquist, S. (1994) Anatomy of tropical alpine plants. In: Rundel, P.W., Smith, A.P. and Meinzer, F.C. (Eds.) *Tropical Alpine Environments: Plant Form and Function*, pp. 111–128. Cambridge: Cambridge University Press.

Coe, M.J. (1967) *The Ecology of the Alpine Zone of Mount Kenya*, The Hague: Dr. W. Junk.

Cross, S.K. (2001). Adaptation of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis*, to ultraviolet radiation over an elevation gradient on Volcán Chiles. In: Ramsay, P.M. (ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 81–90. Plymouth: Pebble & Shell.

Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*, **38**: 209–221.

Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Oxford: Clarendon Press.

Geiger, R. (1966) *The Climate Near the Ground*, Cambridge (MA): Harvard University Press.

Givnish, T.J., McDiarmid, R.W. and Buck, W.R. (1986) Fire adaptation in *Neblinaria celiae* (Theaceae), a high elevation rosette shrub endemic to a wet equatorial tepui. *Oecologia*, **70**: 481–483.

Goldstein, G. and Meinzer, F. (1983) Influence of insulating dead leaves and low temperatures on water balance in an Andean giant rosette plant. *Plant Cell and Environment*, **6**: 649–656.

Goldstein, G., Meinzer, F. and Monasterio, M. (1984) The role of capacitance in the water balance of Andean giant rosette species. *Plant Cell and Environment*, **7**: 179–186.

Grace, J. (1988) The functional significance of short stature in montane vegetation. In: Werger, M.J.A., van der Aart, P.J.M., During, H.J. and Verhoeven, J.T.A. (Eds.) *Plant Form and Vegetation Structure*, pp. 201–209. The Hague: SPB Academic.

Hedberg, I. and Hedberg, O. (1979) Tropical-alpine life-forms of vascular plants. *Oikos*, **33**: 297–307.

Hedberg, O. (1957) Afroalpine Vascular Plants: a Taxonomic Revision. *Symbolae Botanicae Upsaliensis,* **15**: 1–411.

Hedberg, O. (1964) Features of Afroalpine Plant Ecology. *Acta Phytogeographic Suecica*, **49**: 1–144.

Jones, H.G. (1983) *Plants and Microclimate*, Cambridge: Cambridge University Press.

Körner, C. and DeMoraes, J.A.P.V. (1979) Water potential and diffusion resistance in alpine cushion plants on clear summer days. *Oecologia Plantarum*, **14**: 109–120.

Küppers, M. (1989) Ecological significance of above-ground architectural patterns in woody plants: a question of cost-benefit relationships. *Trends in Ecology & Evolution*, **4**: 375–379.

Laegaard, S. (1992) Influence of fire in the grass páramo vegetation of Ecuador. In: Balslev, H. and Luteyn, J.L. (Eds.) *Páramo: An Andean Ecosystem under Human Influence*, pp. 151–170. London: Academic Press.

Larcher, E. (1975) Pflanzenokologische Beobachtungen in die Paramostufe der Venezolanische Anden. *Anzeiger der Österreichischen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse*, **11**: 194–213.

Larcher, W. (1981) Physiological basis of evolutionary trends in low temperature resistance in vascular plants. *Plant Systematics and Evolution*, **137**: 145–180.

Larcher, W. and Bauer, H. (1981) Ecological significance of resistance to low temperature. In: Lange, O.L., Nobel, P.S., Osmond, C.B. and Ziegler, H. (Eds.) *Physiological Plant Ecology. I. Responses to the Physical Environment*, pp. 403–437. Berlin: Springer.

Liley, M. (1986) Study of *Polylepis incana*. In: *Report of the Cambridge Ecuadorian Andes Expedition 1985*, pp. 17–23.

Lough, T.J., Wilson, J.B., Mark, A.F. and Evans, A.C. (1987) Succession in a New Zealand alpine cushion community: a markovian model. *Vegetatio*, **71**: 129–138.

Mabberley, D.J. (1986) Adaptive syndromes of Afroalpine species of *Dendrosenecio*. In: Vuilleumier, F. and Monasterio, M. (Eds.) *High Altitude Tropical Biogeography*, pp. 81–102. Oxford: Oxford University Press.

Marchand, P.J. (1996) *Life in the Cold: an Introduction to Winter Ecology*, Hanover: University Press of New England.

Meinzer, F. and Goldstein, G. (1985) Some consequences of leaf pubescence in the Andean giant rosette plant *Espeletia timotensis*. *Ecology*, **66**: 512–520.

Meinzer, F.C., Goldstein, G. and Rada, F. (1994) Páramo microclimate and leaf thermal balance of Andean giant rosette plants. In: Rundel, P.W., Smith, A.P. and Meinzer, F.C. (Eds.) *Tropical Alpine Environments: Plant Form and Function*, pp. 45–59. Cambridge: Cambridge University Press.

Miller, G.A. (1986) Pubescence, floral temperature and fecundity in species of *Puya* (Bromeliaceae) in the Ecuadorian Andes. *Oecologia*, **70**: 155–160.

Monasterio, M. (1986) Adaptive strategies of *Espeletia* in the Andean desert paramo. In: Vuilleumier, F. and Monasterio, M. (Eds.) *High Altitude Tropical Biogeography*, pp. 49–80. Oxford: Oxford University Press.

Monasterio, M. and Sarmiento, L. (1991) Adaptive radiation of *Espeletia* in the cold Andean tropics. *Trends in Ecology & Evolution*, **6**: 387–391.

Nishikawa, Y. (1990) Role of rhizomes in tussock formation by *Carex thunbergii* var. *appendiculata*. *Ecological Research*, **5**: 261–269.

Øllgaard, B. and Balslev, H. (1979) Report on the 3rd Danish Botanical Expedition to Ecuador. Reports from the Botanical Institute, University of Aarhus, No. 4, University of Aarhus: Aarhus:

Pfitsch, W.A. (1988) Microenvironment and the distribution of two species of *Draba* (Brassicaceae) in a Venezuelan páramo. *Arctic and Alpine Research*, **20**: 333–341.

Rada, F., Goldstein, G., Azócar, A. and Meinzer, F. (1985) Freezing avoidance in Andean giant rosette plants. *Plant Cell and Environment*, **8**: 501–507.

Ramsay, P.M. (1999) Landscape mosaics in the High Andes: the role of fire in páramo communities. In: Kovář, P. (Ed.), *Present and Historical Nature-Culture Interactions in Landscapes: Experiences for the Third Millenium*. pp. 192–199. Prague: The Karolinum Press.

Ramsay, P.M. (2001) The zonal páramo vegetation of Volcán Chiles. In: Ramsay, P. M. (Ed.), *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*, pp. 27–38. Plymouth: Pebble & Shell.

Ramsay, P.M. and Oxley, E.R.B. (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetatio*, **124**: 129–144.

Ramsay, P.M. and Oxley, E.R.B. (1997) The growth form composition of plant communities in the Ecuadorian páramos. *Plant Ecology*, **131**: 173–192.

Rauh, W. (1939) Über polsterförmingen Wuchs. *Nova Acta Leopoldina N. F. 7*, **49**: 267–508.

Rundel, P.W. (1994) Tropical alpine climates. In: Rundel, P.W., Smith, A.P. and Meinzer, F.C. (Eds.) *Tropical Alpine Environments: Plant Form and Function*, pp. 21–44. Cambridge: Cambridge University Press.

Ruthsatz, B. (1978) Las plantas en cojín de los semi-desiertos andinos del Noroeste Argentino. *Darwiniana*, **21**: 491–539.

Sakai, A. and Larcher, W. (1987) *Frost Survival of Plants: responses and adaptations to freezing stress*, Berlin: Springer.

Sarmiento, G. (1986) Ecological features of climate in high tropical mountains. In: Vuilleumier, F. and Monasterio, M. (Eds.) *High Altitude Tropical Biogeography*, pp. 11–45. Oxford: Oxford University Press.

Schulze, E.-D., Beck, E., Scheibe, R. and Ziegler, P. (1985) Carbon dioxide assimilation and stomatal response of afroalpine giant rosette plants. *Oecologia*, **65**: 207–213.

Simpson, B.B. (1979) A revision of the genus Polylepis (Rosaceae: Sanguisorbeae). Smithsonian Contributions to Botany, **43**: 1–62.

Smith, A.P. (1972) Notes on wind-related growth patterns of páramo plants in Venezuela. *Biotropica*, **4**: 10–16.

Smith, A.P. (1974) Bud temperature in relation to nyctinastic leaf movement in an Andean giant rosette plant. *Biotropica*, **6**: 263–266.

Smith, A.P. (1979) Function of dead leaves in *Espeletia schultzii* (Compositae), an Andean caulescent rosette species. *Biotropica*, **11**: 43–47.

Smith, A.P. (1980) The paradox of plant height in an Andean giant rosette species. *Journal of Ecology*, **68**: 63–73.

Smith, A.P. (1981) Growth and population dynamics of Espeletia (Compositae) in the Venezuelan Andes. *Smithsonian Contributions to Botany*, **48**: 1–45.

Squeo, F.A., Rada, F., Azócar, A., and Goldstein, G. (1991) Freezing tolerance and avoidance in high tropical Andean plants: is it equally represented in species with different plant height? *Oecologia*, **86***:* 378–382.

Squeo, F.A., Rada, F., Garcia, C., Ponce, M., Rojas, A., & Azocar, A. (1996) Cold resistance mechanisms in high desert Andean plants. *Oecologia,* **105***:* 552–555.

Tomlinson, P.B. (1987) Architecture of tropical plants. *Annual Review of Ecology and Systematics*, **18**: 1–21.

Walter, H. (1973) *Vegetation of the Earth in Relation to Climate and the Eco-physiological Conditions*, London: English Universities Press.

Effects of burning on *Espeletia pycnophylla* stands in the páramo of Volcán Chiles, Ecuador—a short-term case study

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SUMMARY

Fire is one of the most important anthropogenic factors influencing the vegetation structure of the Andean páramos. A study was carried out to investigate the effects of fire on populations of *Espeletia pycnophylla* subsp *angelensis* on the slopes of Volcán Chiles, Ecuador, with the following findings. At 4100 m, unburned plots had a greater density of *Espeletia* plants, both adults and juveniles. For burned populations, the number of juveniles decreased with increasing altitude (from 3600 to 4100 m). There was no clear relationship between adult plant height and altitude. The length of bare stem increased with increasing altitude. The number of inflorescences of *Espeletia* per unit area was comparable in both burned and unburned stands, but unburned plots yielded higher numbers of individual flower heads per inflorescence.

RESUMEN

El fuego es uno de las mas importantes factores antropogénicos que influyen sobre la estructura de la vegetación en los páramos de los Andes. Por ello, se realizó un estudio para investigar los efectos del fuego sobre las poblaciones de *Espeletia pycnophylla* subsp *angelensis* en las faldas del Volcán Chiles, Ecuador, con los siguientes resultados. A una altitud de 4100 m, la densidad mas elevada de adultos y juveniles de *Espeletia* fue registrada en áreas no sometidas a quema. En áreas quemadas, el número de individuos juveniles decreció con la altitud (de 3600 a 4100 m). No hubo una relación clara entre la altura de los individuos adultos y la altitud. La longitud de la parte deshojada del tallo de las plantas adultas aumentó con la altitud. El número de inflorescencias por unidad de superficie fue comparable en ambas áreas, quemadas y no quemadas, pero el número de capítulos por inflorescencia fue mayor en las áreas no sometidas a quema.

Key words: fire, disturbance, giant rosette plants, population parameters

INTRODUCTION

The genus *Espeletia* s.l. (Compositae, Heliantheae), with about 130 species, is endemic to the Andes of Venezuela, Colombia and Northern Ecuador (Smith 1981). These perennial caulescent plants are characterized by rosettes of large leaves supported by unbranched or little-branched stems. Young leaves form a dense bud around the apical meristem. Dead leaves are often persistent, forming a thick cylinder around the stem. This life form is assumed to be an adaptive response to the tropical alpine environment (Hedberg 1964) and its study may help us understand plant forms typical of high tropical mountains. Caulescent and acaulescent rosette species occur at elevations from about 2700 to 4600 m.

Espeletia is considered to be one of the best examples of diversification and adaptive radiation in a novel environment (Monasterio & Sarmiento 1991). After the retreat of Andean glaciers in the Pleistocene, an open habitat of páramo vegetation created islands at high elevation, spatially heterogeneous owing to the effects of altitude and the fragmentation of the original forests during climatic changes. It is hypothesized that the genus has diversified from ancestral rainforest species with tree-like forms and developed adaptations to the particular combinations of environmental factors at high altitude. Three morphological features seem to be the most significant in the evolution of the Espeletiinae: leaves, inflorescences and biotypes (Cuatrecasas 1986).

Espeletia pycnophylla is the only representative of this genus in Ecuador and it is considered to be probably the most recent species of *Espeletia* (Cuatrecasas 1986). It shows regional variability within the species: *E. pycnophylla* subsp *angelensis*, bordering Colombia, and *E. pycnophylla* subsp *llanganatensis*, occurring in the Cordillera de los Llanganatis. The subject of my study belongs to the Ecuadorian population of *Espeletia pycnophylla* subsp *angelensis* on Volcán Chiles.

The rarity of *Espeletia* species in Ecuador highlights the need to study the ecological factors affecting this plant which is vulnerable to human impacts such as disturbances by fire or cattle grazing. According to Ramsay & Oxley (1996), the frequency of burning depends on the rate of vegetation recovery after fire, typically every 2-4 years. The increasing intensity of agriculture and recreation in páramos is likely to bring about higher frequency of grassland fires, which would result in species disappearance from this ecosystem with high biodiversity (Luteyn 1992).

Several relationships between environmental factors and *Espeletia* species have been identified in the literature. This study sets out to test a number of hypotheses relating to the effects of anthropogenic burning on *Espeletia* populations on Volcán Chiles:

1. Density of individual plants should be higher in burned páramo owing to:
    a. enhanced germination and seedling establishment in *Espeletia* following fire (Laegaard 1992 for *E. pycnophylla*).
    b. lower mortality of plants as a result of interspecific competition with grass tussocks which are removed by fire (Ramsay & Oxley 1996 for *E. pycnophylla*).

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 113-118.

2. Density of *Espeletia* should be greater at higher altitudes because tussock grass cover declines with increasing altitude and this reduces interspecific competition and, therefore, mortality (Smith 1980 for *E. schultzii*).
3. Burning should increase mortality, particularly for adult individuals (Verweij & Kok 1992 for *E. hartwegiana*, Laegaard 1992 for *E. pycnophylla*).
4. The height of adult plants should increase with increasing altitude (Smith 1980 for *E. schultzii*).

METHODS

Study sites

Observations were made in the humid páramo of Volcán Chiles, in northern Ecuador on the border with Colombia. Sampling occurred at three altitudes: 3600, 3850 and 4100 m (Fig. 1). Ramsay (2001b) and Sklenář (2001) provide more details of the vegetation composition on this mountain.

Data collection

Data were collected in October 1995. In each sampling area, four 5 x 5 m quadrats were randomly located in both burned and unburned páramos. Burned páramo was recognized by fire damage to *Espeletia* plants: their trunks were mostly lacking old leaves as a result of previous fire damage. The only unburned páramo was found at 4100 m; all the vegetation with *Espeletia pycnophylla* in the other altitudes bore obvious features of the fire disturbance. Therefore, our data enable us to compare the burned and unburned páramos at one elevation (4100 m) and the burned páramos at three different elevations (3600, 3850 and 4100 m).

For each 25 m^2 sampling unit, the relative abundances (as percentage cover) were recorded for *Espeletia*, shrubs, grasses and other herbs, mainly cushion plants. The number of *Espeletia* individuals was counted in three age-size categories:

- juveniles (<0.3 m tall)
- intermediates (0.3-1.1 m tall)
- adults (>1.1 m tall).

The exact relationship between the size of *Espeletia* plants and their age is not known. Ramsay (unpublished data) measured the production of *Espeletia* leaves at 4000 m on Volcán Chiles over an 8-month period and related this to the height growth of the plants. These data showed that the mean growth rate was 16 mm per year, but there was a relationship between plant height and growth rate (taller plants grew faster). There was no difference in leaf production between burned and unburned plants. Based on these data, juveniles, intermediates and adults (as defined here, and at their upper height limit) would be on average 18, 68 and 112 years old, respectively. However, the local circumstances might make this estimation even more complicated.

The number of flowering plants and dead individuals were also registered in each quadrat. The following parameters of *Espeletia* individuals were measured: the height of the plant (trunk plus leaf rosette), the height of the bare stem (lacking dead leaf blades), the height of the dead leaf column, the height of the leaf rosette, the number of inflorescences per individual, and the number of capitula per inflorescence.

RESULTS AND DISCUSSION

Density and mortality

It was hypothesized that the density of *Espeletia* plants should be higher in burned páramo because of supposed enhanced germination and establishment compared with unburned páramo. However, comparing burned and unburned plots at 4100 m, the mean density of *Espeletia* plants of all categories was higher in the unburned plots, even for juveniles (Table 1). It may be that at this altitude, with relatively high environmental stress, fire has a minor effect on *Espeletia* density.

Plots with lower tussock grass cover supported a greater number of juvenile *Espeletia* plants (Tables 1 and 2). A similar tendency, associated with removal of interspecific competition by fire, was mentioned by Hofstede (1995) for a Colombian páramo.

The density of older (taller) plants is lower than younger (shorter) individuals (Fig. 2). This relationship is consistent with a scenario of mortality resulting from competition between *Espeletia* and tussock grasses. The regression analysis suggests a mortality rate of one plant every 2.8 years in a 25 m^2 area, though most of the mortality appears to take place during the transition from juvenile to intermediate size (Table 1).

Laegaard (1992) suggested that adult *Espeletia* plants would die if subjected to excessive burning which removed the protective, moist leaf sheath. There were fewer living adult plants and more dead plants in burned plots (Table 1), supporting Laegaard's (1992) hypothesis.

Verweij & Kok (1992) noted that burning increased mortality of *E. hartwegiana* in Colombian páramo, particularly for adult individuals. Nevertheless, it seems likely that mortality depends partly on fire intensity, and *E. pycnophylla* is likely to profit from low intensity fires because it is light-demanding and tolerates them relatively well compared with competitors (Laegaard 1992).

Table 1. Mean density (number per 25 m^2) of Espeletia *plants at each site (*n=4, *± standard deviation).*

Category	**3600 m burned**	**3850 m burned**	**4100 m burned**	**4100 m unburned**
adult	2.5 ± 0.1	5.3 ± 0.2	3.8 ± 0.1	13.3 ± 0.4
intermediate	15.1 ± 0.1	4.4 ± 0.2	5.3 ± 0.4	13.7 ± 0.4
juvenile	137.6 ± 3.9	38.9 ± 1.7	10.3 ± 0.5	35.1 ± 0.7
total	155.1 ± 3.9	48.6 ± 1.5	19.3 ± 0.5	62.1 ± 1.2
dead	6.0 ± 0.0	3.6 ± 0.2	6.0 ± 0.5	2.4 ± 0.0

*Table 2. Mean percentage cover of the stand components in four 25m^2 quadrats categories (*n=4, *± standard deviation).*

Stand component	**3600 m burned**	**3850 m burned**	**4100 m burned**	**4100 m unburned**
Espeletia	31.8 ± 0.2	15.1 ± 0.3	19.9 ± 0.6	30.0 ± 0.0
Cushion plants	16.2 ± 0.2	45.6 ± 0.6	2.5 ± 0.4	3.7 ± 0.4
Grasses	53.6 ± 0.9	57.6 ± 1	68.6 ± 0.4	79.1 ± 0.4
Shrubs	6.6 ± 0.5	5.3 ± 0.2	6.1 ± 0.4	10.1 ± 0.7

Fig. 1. Location of the three sampling sites on Volcán Chiles. Four burned plots were recorded at each altitude, and four unburned plots at 4100 m.

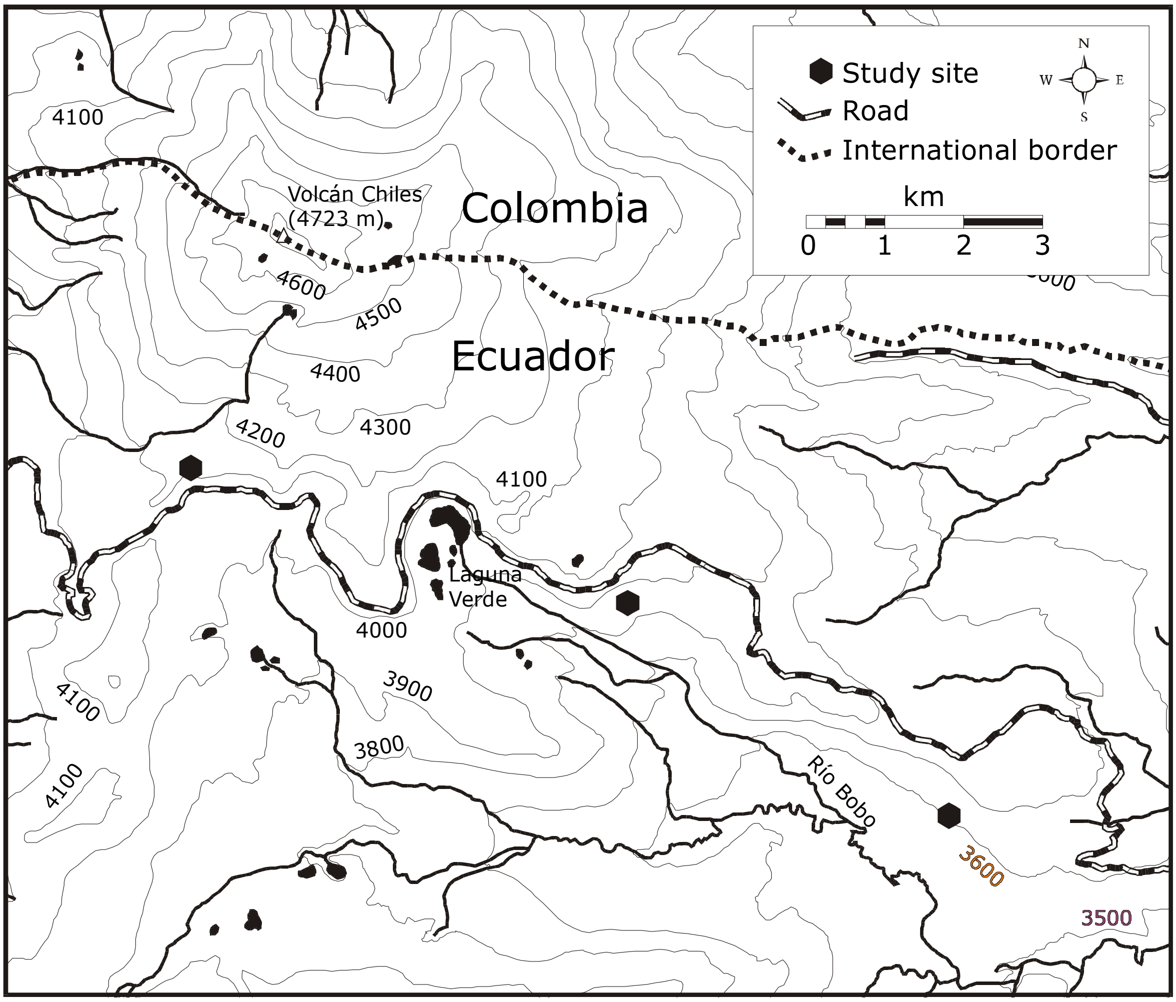
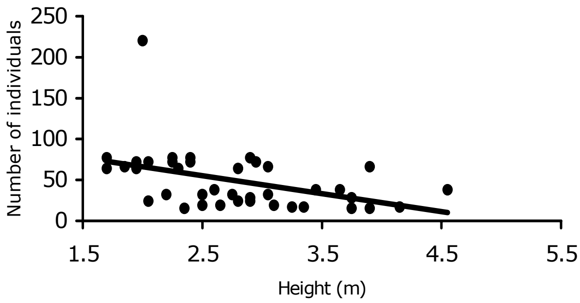


Fig. 2. The number of Espeletia *plants in each 25* m^2 *burned stand belonging to each of the three age-size categories plotted against the mean height for that category (*$r=-0.43$*; fitted line equation is* $y=110 - 22x$*).*



Ramsay & Oxley (1996) measured the temperatures in páramo fires and found they differed considerably within the vegetation structure. The highest temperatures were found at 1 m above ground, the upper limit of the grass tussocks which were the main source of fuel and responsible for spreading the fire. Thus the height of a plant at the time of a fire may be important in determining the likelihood of mortality: juveniles and intermediates may suffer higher mortality than taller adults. However, Ramsay (2001a) noted that different-sized *Espeletia* plants were also subjected to different microclimatic regimes and this may also have an impact on mortality.

Plant height

Based on Smith's (1980) work on *E. schultzii,* it was proposed that the height of adult plants should increase with increasing altitude. Although the shortest adult populations were found at the lowest altitude, the pattern was not so clear in the two other plots (Table 3). However, the impact of fire on these stands may have confounded the results for adult height. Certainly, there were differences between the burned and unburned plots at 4100 m in terms of the relative amount of marcescent leaf cover to overall plant height (Fig. 3).

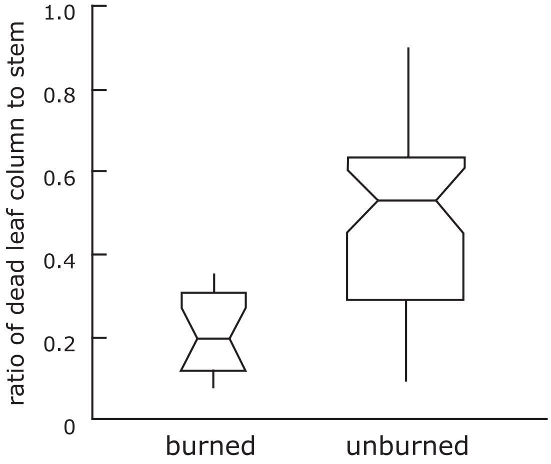
Phenology

Useful comparisons can often be made between disturbed and natural habitats in terms of plant life histories and flowering. The numbers of inflorescences per plot were comparable in both burned and unburned *Espeletia* stands at 4100 m (Table 3), but burned plants had more inflorescences and more capitula per inflorescence than unburned individuals. It seems that fire stimulates flowering in *E. pycnophylla*.

Table 3. Mean growth parameters of Espeletia *plants at each site, according to age-size categories (*$n=4$*, ± standard deviation).*

	3600 m burned	**3850 m burned**	**4100 m burned**	**4100 m unburned**
Height of individual (m)				
adults	1.33 ± 0.09	2.08 ± 0.15	1.89 ± 0.11	1.61 ± 0.07
intermediates	0.54 ± 0.03	0.70 ± 0.05	0.76 ± 0.05	0.67 ± 0.03
juveniles	0.10 ± 0.00	0.11 ± 0.01	0.24 ± 0.02	0.15 ± 0.01
Height of bare stem (m)				
adults	0.76 ± 0.12	0.86 ± 0.12	1.29 ± 0.11	0.59 ± 0.06
intermediates	0.12 ± 0.02	0.10 ± 0.04	0.27 ± 0.04	0.11 ± 0.02
Dead leaf column (m)				
adults	0.38 ± 0.10	0.95 ± 0.08	0.37 ± 0.04	0.80 ± 0.06
intermediates	0.19 ± 0.01	0.38 ± 0.05	0.32 ± 0.02	0.36 ± 0.02
Height of leaf rosette (m)				
adults	0.27 ± 0.01	0.27 ± 0.01	0.21 ± 0.02	0.21 ± 0.01
intermediates	0.23 ± 0.01	0.26 ± 0.02	0.22 ± 0.01	0.20 ± 0.01
Inflorescences				
adults (no per individual)	4.64 ± 1.02	1.76 ± 0.92	3.13 ± 1.24	1.57 ± 0.47
intermediates (no per individual)	0.97 ± 0.31	0.38 ± 0.27	2.55 ± 0.88	0.28 ± 0.17
total (no per 25 m^2)	19.39 ± 0.76	10.18 ± 1.01	25.95 ± 3.62	27.07 ± 1.38
Capitula per inflorescence				
adults	22.92 ± 5.31	8.94 ± 5.07	9.40 ± 3.68	4.81 ± 1.51
intermediates	5.22 ± 1.71	2.11 ± 1.49	7.10 ± 2.59	0.97 ± 0.62
total (no per 25 m^2)	96.06 ± 4.39	54.1 ± 5.83	74.6 ± 10.1	84.49 ± 4.24

Fig. 3. Ratio of dead leaf column to stem height in adult individuals of Espeletia *in burned and unburned sites at 4100 m. The box encloses the middle 50% of data, with the median in the middle. The length of the notch represents an approximate 95% confidence interval for the median. Whiskers extend to 1.5 interquartile ranges from the quartile.*



Conclusions

The effect of fire on *Espeletia pycnophylla* stands differs with altitude within the 800-1000 m wide belt of its occurrence. Burning does not necessarily increase population density at the upper altitudinal limit because the stress created by both substrate and climatic conditions limits the growth of populations. At lower altitudes, however, fire might have a positive effect by promoting a higher density of young *Espeletia pycnophylla* plants by suppressing competition from other species. Fire might also promote sexual reproduction by stimulating more abundant flowering. There was no apparent relationship between the height of mature plants and altitude.

At high altitudes in the Andes, the effects of natural stress and fire-induced disturbance must be carefully separated to understand how *Espeletia* populations are affected by burning and to predict responses by these plants to fires in the future. Studies of the other population of *Espeletia—E. pycnophylla* subsp. *llanganatensis*—in the undisturbed Llanganatis area of Ecuador might reveal more general patterns in the population dynamics and demography of the giant rosette plant.

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REFERENCES

Cuatrecasas, J. (1986) Speciation and radiation of the Espeletiinae in the Andes. In: Vuilleumier, F. and Monasterio, M. (Eds) *High Altitude Tropical Biogeography,* pp. 267-303. Oxford: Oxford University Press.

Ellenberg, H. (1979) The Tansley Lecture: Man's influence on tropical mountain ecosystems in South America. *Journal of Ecology,* **67***:* 401-416.

Hedberg, O. (1964) Features of Afroalpine plant ecology. *Acta Phytogeographica Suecica*, **49**: 1-144.

Hofstede R.G.M. (1995) *Effects of Burning and Grazing on a Colombian Páramo Ecosystem.* PhD Thesis, University of Amsterdam.

Laegaard, S. (1992) Influence of fire in the grass páramo vegetation of Ecuador. In: Balslev, H. and Luteyn, J.L. (Eds) *Páramo: an Andean ecosystem under human influence*, pp. 151-170. London: Academic Press.

Luteyn, J.L. (1992) Páramos: why study them? *In:* Balslev, H. and Luteyn, J. L. (Eds) *Páramo: An Andean Ecosystem under Human Influence.* pp. 1-14. London: Academic Press.

Monasterio, M, & Sarmiento, L. (1991) Adaptive radiation of *Espeletia* in the cold Andean tropics. *Trends in Ecology and Evolution,* **6***:* 387-391.

Ramsay, P.M. (2001a) Diurnal temperature variation in the major growth forms of an Ecuadorian páramo plant community. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 101–112. Plymouth: Pebble & Shell.

Ramsay, P.M. (2001b) The zonal páramo vegetation of Volcán Chiles. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 27–38. Plymouth: Pebble & Shell.

Ramsay, P.M. and Oxley, E.R.B. (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass paramo. *Vegetatio,* **124**: 129-144.

Sklenář, P. (2001) Superpáramo flora and vegetation of Volcán Chiles. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 39–45. Plymouth: Pebble & Shell.

Smith, A.P. (1980) The paradox of plant height in an Andean giant rosette species. *Journal of Ecology,* **68***:* 63-73.

Smith, A.P. (1981) Growth and population dynamics of *Espeletia* (Compositae) in the Venezuelan

Andes. *Smithsonian Contributions to Botany,* **48***:* 1-45.

Verweij, P.A. and Kok, K. (1992) Effects of fire and grazing on *Espeletia hartwegiana* populations. *In:* Balslev, H. and Luteyn, J. L. (Eds), *Páramo: an Andean ecosystem under human influence,* pp. 215-229. Academic Press: London.

The causes of leaning in *Espeletia pycnophylla* subsp. *angelensis*

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SUMMARY

The causes of leaning in *Espeletia pycnophylla* subsp. *angelensis* were investigated at four altitudes on Volcán Chiles, Ecuador: 3600, 3800, 4000 and 4200 m. Between 18 and 41% of plants were leaning in sample plots. Paired leaning and upright plants, matched for height, were used to examine differences in morphology, exposure and soil compaction around each plant. Leaning plants were significantly more exposed than their upright neighbours, though the angle of lean did not correlate with either exposure or height of plants. There was also a match between the direction of lean and the prevailing wind direction at each site. The soil into which plants leaned was less compacted than the rest of the soil around these plants, and when compared with the soil around upright plants. It is suggested, tentatively, that *Espeletia* plants tilt as a result of repeated exposure to strong winds and this may occur more readily in taller plants. Leaning tends to loosen the soil on one side of the plant. Several consequences of leaning are discussed, including increased light competition, changes in the temperature regime of leaf rosettes, and damage by fire.

RESUMEN

Se investigaron las causas y las consecuencias de la inclinación en individuos de *Espeletia pycnophylla* subsp. *angelensis* en cuatro altitudes del Volcán Chiles, Ecuador: 3600, 3800, 4000 y 4200 m. Entre 18 y 41% de las plantas presentaban inclinación. Utilizando pares de plantas, inclinadas y rectas, de la misma altura, se examinaron sus diferencias en morfología, exposición y compactación del suelo alrededor de ellas. Las plantas inclinadas estuvieron significativamente más expuestas que sus vecinos erectos, aunque el ángulo de inclinación no se correlacionó con la exposición o la altura de las plantas. Además, hubo una correspondencia entre la dirección de inclinación y la dirección predominante del viento en cada sitio. El suelo debajo de las plantas inclinadas fue menos compacto que el resto del suelo alrededor de estas mismas y que el suelo alrededor de las plantas rectas. Se sugiere, tentativamente, que las plantas de *Espeletia* se inclinan a consecuencia de la exposición frecuente a vientos fuertes y que ello ocurre más fácilmente en plantas de mayor altura. La inclinación tiende a aflojar el suelo en un costado de una planta. Se discuten algunas consecuencias de la inclinación tales como la competencia por luz, los cambios en el régimen de temperatura de las rosetas de hojas y el daño por fuego.

Key words: giant rosette, tropical alpine, Ecuador, wind exposure, soil compaction

INTRODUCTION

Espeletia is a characteristic giant stem rosette plant genus of the high-altitude páramos of northern Ecuador, Colombia and Venezuela. These páramos have an unusual climate of low seasonal temperature variation but high daily fluctuations (Rundel 1994). Other areas with similar climatic conditions are found in East Africa and South-east Asia, and these too are characterized by giant rosette plants belonging to different plant taxa (*e.g.*, *Dendrosenecio* in East Africa and *Cyathea* in Malaysia—Smith 1994). That this giant rosette plant has evolved independently in various parts of the world suggests that it possesses a set of traits suited to these high-altitude environments.

High-altitude species of *Espeletia* consist of an unbranched stem, which contains a voluminous central pith made up of parenchmatous tissue surrounded by a thick layer of marcescent dead leaves (Smith 1981). The living leaves form a rosette at the apex of the stem. Goldstein *et al.* (1985) discovered that mortality rates in *Espeletia timotensis*, a Venezuelan páramo species, were high for very small and very large plants. Juvenile plant mortality was linked to water stress, which is particularly acute in small plants with low-volume pith reservoirs of water. In very large plants, the main cause of death was leaning, started by solifluction processes of soil freeze-thaw cycles (Goldstein *et al* 1985).

Espeletia timotensis does not extend beyond the Venezuelas Andes, but related speces of the same genus are found further south. The most recently evolved, and the one with the most southerly distribution, is *Espeletia pycnophylla*, found in Southern Colombia and Ecuador (Cuatrecasas 1986). Two subspecies are known to exist: *E. pycnophylla* subsp. *angelensis* (in northern páramos of Ecuador such as El Angel and Volcán Chiles) and subsp. *llanganatensis* (restricted to one small population in Central Ecuador).

Only one study of the population structure of *Espeletia pycnophylla* has been published so far (Kovář 2001), though additional work has been carried out (Ramsay, unpublished manuscript). Neither of these studies considered the significance of leaning in these plants. This study attempts to establish the causes and consequences of leaning in *Espeletia pycnophylla* in the páramo of Volcán Chiles.

METHODS

Study areas

Data were collected from four localities in the páramo of Volcán Chiles, on the border of Ecuador and Colombia, at 200 m intervals of altitude. The four sites were situated at 3600, 3800, 4000 and 4200 m (Fig. 1).

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 119-124.

The vegetation at these sites was dominated by tussocks of *Calamagrostis* and the giant rosettes of *Espeletia pycnophylla*. Ramsay (2001b) provides an account of the vegetation on Volcán Chiles which is generally consistent with these study sites.

No meteorological data are available for the sites. Personal observations of wind directions and velocities provide anecdotal evidence of prevailing wind patterns, which are consistent with local topography. The site at 3600 m was sited in the main valley of the Río Chilma and the movement of winds up and down the valley followed a roughly east-west pattern. However, very strong winds occasionally blew across the valley to and from the flatter area to the south of this study site. The 3800 m most often experiences winds from the south and south-east. Wind patterns in both the 4000 and 4200 m plots were principally north-south.

Proportion of leaning plants

Three 10 x 30 m plots were established at random at each of the four study areas. The number of *Espeletia* plants which were upright and the number of those which were leaning were counted.

Causes of leaning

At each altitude, 30 leaning plants were selected at random, and upright plants of matching heights (± 5 cm) were also selected for direct comparison.

For each plant a set of allometric measurements was made: plant height, rosette height, length of stem insulated by marcescent leaves, length of stem clothed only in clasping leaf bases, and length of stem with no dead leaf cover at all (Fig. 2). For leaning plants, the angle and bearing of lean were measured with a clinometer and compass.

Soil compaction was measured at the base of each plant using a penetrometer (ELE). For leaning plants, one measurement was taken on the side of the direction of lean, another on the opposite side, and two more at 90° to the others. For upright plants, measurements were recorded at the four primary compass bearings (0°, 90°, 180° and 270°). The relative compactness of the soil around a particular plant may be more important than the absolute compactness. For this reason a soil compaction index relative to one particular side of a plant was calculated thus:

$$I = \frac{X_i - \min}{\max - \min}$$

where X_i is the reading for the particular side in question, and "min" and "max" represent the minimum and maximum values recorded around that plant. It ranges in value from 0 to 1 (where that side of a plant was the least and most compacted, respectively).

Finally, for each plant a topographical exposure index was calculated. This was based on four exposure scores for each plant, one in the direction of each of the primary compass points. Each score consisted of the difference in relative height of the ground surface at the base of the plant and 10 m away from it, calculated from clinometer readings (Fig. 3). In this way, a score would be negative if the ground sloped downwards from the plant, or positive if it sloped upwards. The exposure index was simply the sum of the four individual exposure scores for each plant.

Fig. 1. Location of the four study areas on Volcán Chiles.

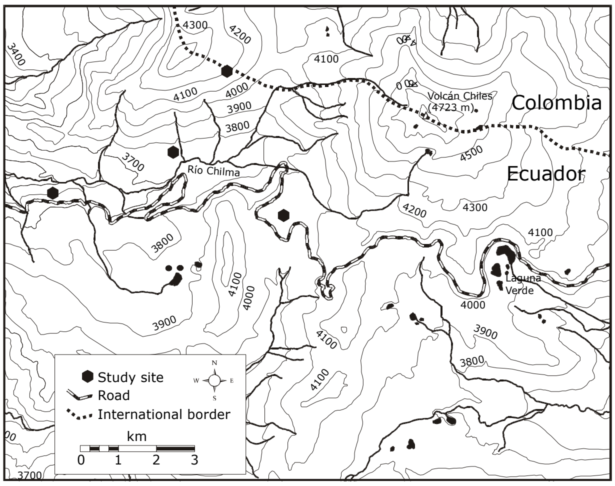


Fig. 2. Diagrammatic representation of an Espeletia *plant, indicating the parameters measured.*

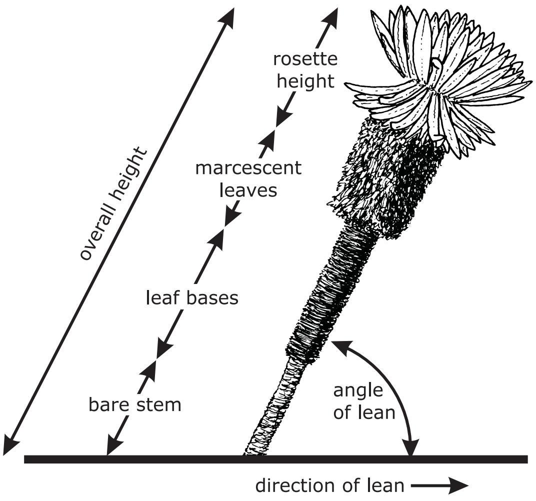
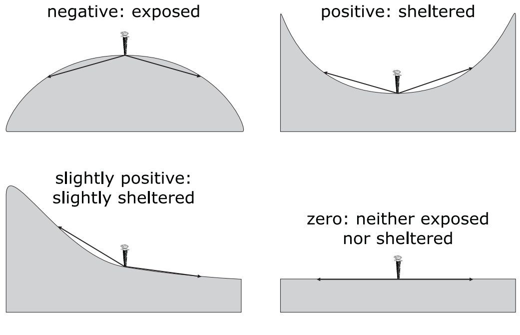


Fig. 3. Diagrammatic representation of the basis for the topographic exposure index. Further explanation is given in the text.



RESULTS

Proportion of leaning plants

There were no significant differences between the four sites in terms of the proportion of leaning plants (Table 1). Between 18 and 41% of plants were leaning in any one sample area. The mean proportion of leaning plants was relatively high, up to around 40% in one site.

Table 1. The mean percentage of leaning plants at three replicate 10 x 30 m plots at four altitudes.

Altitude (m)	Mean percentage of leaning plants (± sd)
3600	26 ± 6
3800	39 ± 3
4000	37 ± 7
4200	28 ± 8

Causes of leaning

There were differences in the size and shape of *Espeletia* plants between the four sites (Table 2). Plants were significantly shorter at 3600 m (p<0.001). Rosette height was also smaller at 3600 m, reaching a maximum at 4200 m (p<0.001). The proportion of stem clothed in marcescent leaves was greatest at 3600 and 4200 m (p=0.050 and p<0.001 for leaning and upright plants, respectively), with the pattern reversed for leaf base only cover (p<0.001 for both groups of plants). Bare stems with no leaf cover at all were rare, occurring only at the highest two sites.

Plants at 3800 and 4200 m leaned at a greater angle than those at the other two sites (p=0.012). The direction of lean varied from site to site (Fig. 4). Plants leaned most often to the south and west at 3600 m, to the west and north-west at 3800 m, and to the north and south at both 4000 and 4200 m. There was no relationship between the height of plants and the angles at which they leaned.

There were no differences between leaning and upright plants for rosette height (p=0.091), marcescent leaf cover (p=0.370) or basal leaf cover (p=0.284). Although the proportion of plants with completely bare sections of stem was low, this condition was significantly more common in leaning rather than upright plants (p=0.046).

In general, soil compaction was greater in the plots at 3600 m and 4000 m than in the other two sites (p<0.001, Table 3). Compaction was significantly lower on the leaning side of plants (p<0.001), but there were no significant differences between sides of upright plants (p=0.124)—this pattern was even clearer with the relative compaction data (p<0.001 and p=0.282, respectively). Table 4 demonstrates the significantly lower relative compaction on the leaning sides of plants compared with each of the compass points for upright plants (p<0.001). There were no differences between altitudes using relative compaction data.

Table 2. Allometric measurements for 30 pairs of leaning (L) and upright (U) plants at each altitude (means ± standard deviation).

Altitude (m)	Plant height (cm)		Rosette height (cm)		Length (cm) of stem covered with:						Lean angle (°)
					Marcescent leaves		Leaf bases only		No leaves		
	L	U	L	U	L	U	L	U	L	U	
3600	79.6 ± 15.3	79.7 ± 14.3	23.4 ± 5.2	24.2 ± 4.3	23.2 ± 7.1	24.1 ± 4.4	32.9 ± 15.2	31.5 ± 12.9	0	0	23.9 ± 13.4
3800	118.8 ± 26.3	119.9 ± 26.2	27.9 ± 4.5	29.9 ± 4.4	30.5 ± 9.4	31.3 ± 10.7	59.4 ± 24.1	59.2 ± 25.9	0	0	30.7 ± 13.2
4000	100.7 ± 26.9	100.4 ± 27.4	26.8 ± 5.6	29.2 ± 6.0	26.6 ± 13.0	23.9 ± 8.7	48.1 ± 18.3	47.2 ± 18.6	0.9 ± 3.1	0	24.3 ± 14.1
4200	117.9 ± 27.6	122.7 ± 27.4	33.9 ± 8.5	33.1 ± 6.0	37.1 ± 21.4	43.3 ± 17.0	46.9 ± 24.7	42.2 ± 24.1	3.0 ± 8.9	0.3 ± 1.6	34.9 ± 18.6

Table 3. Mean soil compaction around Espeletia *plants in the four plots. The absolute soil compaction readings at each site for leaning plants, upright plants and both combined are shown (means ± standard deviation). Four measurements were made around each plant. Four relative soil compaction score were calculated for each plant (each side relative to the others as described in the text) and the overall averages of these scores are shown for leaning and upright plants at each site.*

Altitude (m)	Absolute soil compaction (g cm^{-2})			Relative soil compaction	
	Leaning	Upright	Overall	Leaning	Upright
3600	2100 ± 296	2046 ± 301	2073 ± 299	0.53	0.45
3800	1495 ± 349	1596 ± 302	1545 ± 330	0.49	0.49
4000	2065 ± 380	1963 ± 355	2014 ± 371	0.47	0.51
4200	1527 ± 480	1795 ± 463	1661 ± 489	0.46	0.49

Leaning plants were significantly more exposed than upright ones in the three highest plots (Table 5). The plot at 3800 m was more exposed than the others (p=0.001). However, there was no relationship between the exposure score and lean angle (p=0.563).

DISCUSSION

A high proportion of *Espeletia pycnophylla* plants lean, and this may represent a significant force in shaping the population structure of this species. Therefore, understanding the reasons for leaning in this plant may help to explain its demographic patterns.

Given that many *Espeletia* plants do lean, what might be responsible for this? Potential causes include top heaviness, wind and soil factors.

Top heaviness

As plants grow, bearing a large rosette at the apex of a relatively thin stem, they may become top heavy and begin to lean. The experimental design used in this study involved the selection of pairs of plants (one leaning, the other upright), matched for height. Therefore, these data do not permit consideration of whether taller plants tend to lean more often than shorter ones. However, it would be relatively easy to collect data which would allow this idea to be tested. The current study does demonstrate, though, that the rosettes of leaning plants are no different in size to those of upright plants of similar sizes. Furthermore, the angle at which a plant leans does not correlate with that plant's height.

Wind

Smith & Young (1987) contend that winds are not strong in the páramo, but this is not entirely true. In some areas winds do occur and can be very violent. Windspeeds in excess of 100 kmph are frequent on Volcán Chiles, capable of breaking tent poles and ripping tent fabric (P .Ramsay , personal observation at the 3600 m plot). *Espeletia* plants must withstand these conditions. Unfortunately, there are no detailed records of windspeeds available for this mountain or any others in the Ecuadorian Andes.

The strength of the wind varies from place to place according to topography (for example, passes and ridges are particularly windy), and subtle differences in exposure can occur between individual plants as a result of fine-scale topographic differences. Therefore, it might be expected that leaning plants would be located in slightly more exposed situations than non-leaning neighbours. Indeed, this pattern was found in this study, though the angle of lean did not increase with exposure. Moreover, there was a clear match between the direction of lean and the prevailing wind patterns.

This factor may be linked to plant height in that a boundary layer exists near to the ground. Plants which grow out of this layer may become subjected to greater wind speeds and may be more likely to tilt.

Fig 4. Radar chart showing the frequency of leaning plants associated with each major compass bearing at each altitude.

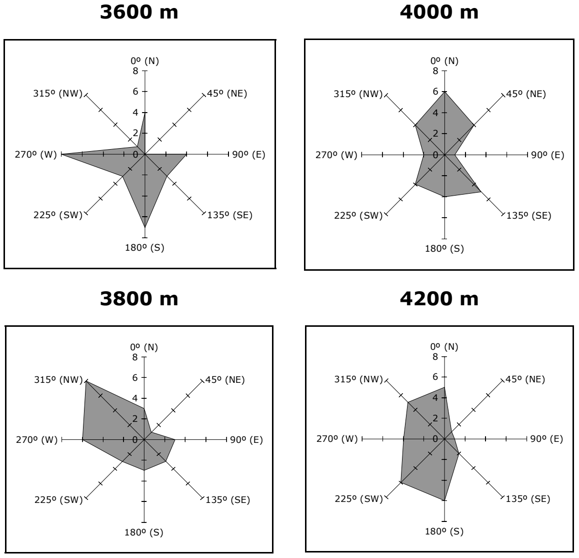


Table 4. Absolute and relative soil compaction values (means ± standard deviation). For leaning plants mean absolute and relative values are given for the direction towards which the plant leans. For upright plants mean absolute and relative values are presented for each primary compass point. In each case, means are based on 120 plants.

Side	**Absolute soil compaction (g cm^{-2})**	**Relative soil compaction**
Leaning	1621 ± 455	0.21 ± 0.34
N	1785 ± 403	0.42 ± 0.44
S	1855 ± 394	0.49 ± 0.44
W	1870 ± 392	0.49 ± 0.43
E	1891 ± 406	0.53 ± 0.44

Table 5. Exposure scores for paired leaning and upright plants at four altitudes (means ± standard deviation). Positive scores are more sheltered, negative scores are more exposed, and zero indicates flat terrain.

Altitude (m)	**Exposure score**		***p*-value**
	Leaning	**Upright**	
3600	2.2 ± 5.9	2.5 ± 5.4	0.435
3800	-1.3 ± 3.0	0.5 ± 4.3	0.027
4000	0.6 ± 3.9	3.9 ± 5.9	0.020
4200	0.8 ± 5.4	3.5 ± 6.5	0.028

Soil loosening

If the soil around a plant is loose, the plant may be more susceptible to leaning. Goldstein et al (1985) found that soil was loosened by the daily freeze-thaw cycle in a Venezuelan páramo and this caused large giant rosette plants to lean, leading eventually to their death. Solifluction is not a major influence on the páramo vegetation of Volcán Chiles, at least at the altitudes where *Espeletia pycnophylla* grows. The soil is not subject to regular freezing to depth at these altitudes. Nevertheless, if variability in soil compaction exists, this may promote leaning in plants subjected to differential compaction around the roots.

There was certainly a very clear link between loose soil and leaning: plants leaned into looser soil. However, it is not clear that differences in soil compaction around plants caused them to lean. Another possibility is that the soil was loosened as the plant leaned, pushing up the soil in the direction in which it leaned. If soil variability was causing leaning, one might expect to see the precursors of this process in the form of variability in soil compaction around upright plants, following the same pattern as in leaning plants, but this was not evident. It is more likely, then, that leaning causes differences in relative soil compaction rather than *vice versa*.

It is suggested, tentatively, on the basis of these data that *Espeletia* plants are sometimes tilted by repeated exposure to strong winds. Taller plants may be more susceptible to wind than shorter plants. As a result of tilting, the soil is loosened on the side away from the prevailing wind.

Consequences of leaning

The consequences of leaning can only be speculated about here, since too few data were collected to conduct a meaningful statistical examination. Several consequences of leaning may occur, both sub-lethal effects which reduce growth and reproduction rates without causing mortality , and lethal effects which kill the plant .

- Competition
  The rosette may descend into the tussock grasses as the stem leans. In such cases, it would be expected that the rosette must compete for light with the surrounding vegetation and loses the advantage that its height had provided. Plants can be observed in this condition, but rarely, and this may accurately reflect the frequency of such events or may suggest that the severity of competion results in very rapid death.
- Temperature relations
  Temperature measurements in *Espeletia* rosettes at 4000 m on Volcán Chiles suggest that rosettes close to the ground experience lower temperatures during the day and at night (Ramsay 2001a). Therefore, if tilting lowers the rosette into this zone, the plant may experience lowered growth rates during the day and a higher probability of frost damage at night. However, Ramsay's (2001a) data also showed that a 2.2 m tall plant experienced cooler daytime temperatures than a plant 1.4 m tall. If tall plants tilt slightly, lowering their height but not bringing them close to the ground, this may have a positive effect on growth rates.
- Fire damage
  Ramsay & Oxley (1996) showed that the hottest temperatures during páramo fires occur in the upper part of the tussock structure, about 1 m above ground. This is the zone where lethal temperatures are most likely. Even if a fire does not kill the plant immediately, death may result from the loss of marcescent leaves which insulate the plant during very cold nights (Ramsay 2001a). The current study did show that leaning plants had more stem with no leaf cover than upright plants, though the sample was very small.
- Herbivory
  Predation of *Espeletia pycnophylla* leaves is not common and the plant is strongly resinous (Smithers *et al*. 2001). There is no evidence that predation, by invertebrates or vertebrates, is a significant factor in regulating *Espeletia* populations, nor that it is increased closer to the ground. Leaning would not be expected to increase herbivory.

It is clear that leaning in *Espeletia* on Volcán Chiles is not a simple matter. Leaning is related to exposure and soil compaction—the most likely explanation is that plants are blown over and this loosens the soil on one side of the plant. Although there was no difference between rosette size of leaning and upright plants, the height of a plant may be an important factor in susceptibility to leaning. The consequences of leaning may include changes in the light and temperature regimes and increased damage by fire, though no data are presented here to support such speculation.

Additional work is required to determine if taller plants do lean more than shorter ones, if leaning plants exhibit lower rates of growth, reproduction or mortality , and if leaning plants experience greater mortality after fires. Such information would contribute greatly to the understanding of the structure of *Espeletia pycnophylla* populations and the factors regulating them.

REFERENCES

Cuatrecasas, J. (1986) Speciation and radiation of the Espeletiinae in the Andes. *In:* Vuilleumier, F. and Monasterio, M. (Eds) *High Altitude Tropical Biogeography,* pp. 267–303. Oxford: Oxford University Press.

Goldstein, G., Meinzer, F., and Monasterio, M. (1985) Physiological and mechanical factors in relation to size-dependent mortality in an Andean giant rosette species. *Acta Oecologia/Oecologia Plantarum,* **6***:* 263–275.

Kovář, P. (2001) Effects of burning on *Espeletia pycnophylla* stands in the páramo of Volcán Chiles, Ecuador—a short-term case study. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: High-altitude Ecosystems on the Ecuador-Colombia Border*, pp. 113–118. Plymouth: Pebble & Shell.

Ramsay, P.M. (2001a) Diurnal temperature variation in the major growth forms of an Ecuadorian páramo plant community. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: High-altitude Ecosystems on the Ecuador-Colombia Border*, pp. 101–112. Plymouth: Pebble & Shell.

Ramsay, P.M. (2001b) The zonal páramo vegetation of Volcán Chiles. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: High-altitude Ecosystems on the Ecuador-Colombia Border*, pp. 27–38. Plymouth: Pebble & Shell.

Ramsay, P.M. and Oxley, E.R.B. (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetatio*, **124**: 129–144.

Rundel, P.W. (1994) Tropical alpine climates. *In:* Rundel, P. W., Smith, A. P., and Meinzer, F. C. (Eds) *Tropical Alpine Environments: Plant Form and Function,* pp. 21–44. Cambridge: Cambridge University Press.

Smith, A.P. (1981) Growth and population dynamics of *Espeletia* (Compositae) in the Venezuelan Andes. *Smithsonian Contributions to Botany,* **48***:* 1–45.

Smith, A.P. (1994) Introduction to tropical alpine vegetation. *In:* Rundel, P. W., Smith, A. P., and Meinzer, F. C. (Eds) *Tropical Alpine Environments: Plant Form and Function,* pp. 1–19. Cambridge: Cambridge University Press.

Smith, A.P., and Young, T.P. (1987) Tropical alpine plant ecology. *Annual Review of Ecology and Systematics,* **18***:* 137–158.

Smithers, P., Ramsay, P.M., Bond, A.N., and Burne, M.E. (2001) Macro-arthropod communities of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis*. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: High-altitude Ecosystems on the Ecuador-Colombia Border*, pp. 169–175. Plymouth: Pebble & Shell.

The ground beetles of the Chiles area (Coleoptera, Carabidae): a taxonomic and ecological overview

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SUMMARY

The 19 species of Coleoptera Carabidae that are known from Volcán Chiles and surrounding area (Ecuador, province Carchi) are reviewed taxonomically. A key is provided for identification of genera and species. One species is described as new in the genus *Oxytrechus* JEANNEL (*O. ramsayi* n. sp.), and seven more in the genus *Dyscolus* DEJEAN (*D. atkinsi* n. sp., *D. breviculus* n. sp., *D. cachectes* n. sp., *D. lubricus* n. sp., *D. nubilus* n. sp., *D. riveti* n. sp. and *D. smithersi* n. sp.). The available biogeographic and ecological data are then summarized and discussed. Three species belonging to the genera *Pelmatellus* and *Sericoda* have overlapping ranges both in the montane forest and the subpáramo. *Sericoda bembidioides* KIRBY is a pyrophilous species, occasionally attracted in the páramo by grass fires. The sixteen other species are restricted to páramo habitats. They are all flightless nocturnal predators. A specialised riparian habitat has been observed in three species. Specific diversity is the highest at medium elevations (3800–4100 m), though more information would be needed to reconstruct the altitudinal distribution of every species. The composition of this carabid community suggests that the microclimate of the Chiles area is among the wettest in Ecuadorian páramos. None of the seventeen flightless species found on Volcán Chiles has been recorded from other páramos at the south of the Mira River. These distributional data point to the Mira xeric depression, south of Carchi, as a major biogeographic barrier in the Northern Andes.

RESUMEN

Se presenta una revisión taxonómica de las 19 especies de Coleoptera Carabidae que se conocen del Volcán Chiles y áreas circundantes (Ecuador, provincia Carchi). Una clave dicotómica permite su identificación al nivel genérico y específico. Se describen como nuevas una especie del género *Oxytrechus* JEANNEL (*O. ramsayi* n. sp.) y siete especies del género *Dyscolus* DEJEAN (*D. atkinsi* n. sp., *D. breviculus* n. sp., *D. cachectes* n. sp., *D. lubricus* n. sp., *D. nubilus* n. sp., *D. riveti* n. sp. y *D. smithersi* n. sp.). Se presentan luego los escasos datos ecológicos de los que se dispone sobre estas especies. Tres de ellas, pertenecientes a los géneros *Pelmatellus* y *Sericoda*, se distribuyen en una zona de transición entre el bosque altoandino y el subpáramo. *Sericoda bembidioides* KIRBY es una especie pirófila, ocasionalmente atraída en el páramo por la quema del pajonal. Las dieciséis especies restantes son propias del medio ambiente páramo. Todas son incapaces de volar y son depredadores nocturnos. Una especialización ripícola se ha observado en tres especies. La diversidad específica es mayor en altitudes medianas (3800–4100 m), aunque hacen falta más informaciones para reconstruir la distribución altitudinal de todas las especies. La composición de esta comunidad de Carábidos sugiere que el microclima del Chiles es uno de los más húmedos entre los páramos ecuatorianos. Ninguna de las diecisiete especies micrópteras del Chiles se conoce de otros páramos al sur del Río Mira. Se desprende de estos datos corológicos que la depresión árida del Mira, al sur de la provincia del Carchi, constituye una barrera biogeográfica importante en los Andes septentrionales.

Key words: Systematics, Oxytrechus, Dyscolus, *new species, ecology, Ecuador*

INTRODUCTION

Carabidae or ground beetles are the largest predatory family of Coleoptera after the Staphylinidae. They live in almost all habitats and are a major component of the terrestrial invertebrate communities in montane open lands. Carabids have been the subject of numerous ecological and biogeographic studies during the past fifty years. This can be explained by:

1. a high taxonomic diversity, correlated with diversity in ecological adaptations and specializations;
2. high rates of endemism in mountains and islands, thus providing useful information for biogeographic reconstructions;
3. easy sampling by means of pitfall traps; and
4. the fact that identification at specific level is easier in Carabidae than in most other soil Arthropoda.

The taxonomic treatment of South American carabids is still far from being satisfactory when compared with holarctic faunas, yet preliminary keys by Reichardt (1977) and Erwin (1991) allow identification at generic or tribal level. 167 species arrayed in 15 genera of Carabidae have been so far observed in Ecuadorian páramos above 3500 m, only 59% of which are described (Table 1). The state of knowledge is highly variable from one páramo area to the other. Easily accessible volcanoes like Pichincha and Cotopaxi have been adequately surveyed, whilst other mountains remain almost totally unknown as to their entomological fauna. Regarding Volcán Chiles, the faunistic data are rather abundant and generally precise, but research has focused on the basal slopes of the volcano, neglecting the superpáramo zone.

My purpose in this contribution is two-fold. On the one hand, I will present a taxonomic review of the carabid species so far known from the Chiles area. On the other hand, I will interpret the few biogeographic and ecological data that are available at this time.

MATERIAL AND METHODS

This study is based on the examination of 571 specimens from the high-altitude carabid communities of the Chiles area, kept in the following institutions or private collections: Carnegie Museum of Natural History, Pittsburgh (CMNH); Joaquín Mateu's collection, Barcelona (JM); Muséum National d'Histoire Naturelle, Paris (MNHN); Natural History

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 125-135.

Museum, London (NHM); Author's collection, Toulouse (PM); Universidad Católica del Ecuador, Departamento de Zoología, Quito (QCAZ); University of Plymouth, Department of Biological Sciences (UPBS).

Table 1. Genera of Carabidae found in Ecuadorian páramos above 3500 m. The number of species known and described for Ecuador and the Volcán Chiles area is presented, as well as the maximum altitude at which each genus has been found.

Tribe and genus	**Number of species**			**Max altitude (m)**
	Known Ecuador	**Described Ecuador**	**Known Chiles**	
Migadopini				
Aquilex	1	1		4300
Trechini				
Oxytrechus	12	10	2	4800
Trechisibus	1			3800
Paratrechus	12	2	1	4600
Bembidiini				
Bembidion	17	3	1	5070
Harpalini				
Notiobia	2	2		3850
Bradycellus	2	2		3800
Pelmatellus	11	3	2	4800
Pterostichini				
Blennidus	24	24		4900
Platynini				
Incagonum	1	1		3800
Sericoda	1	1	1	4000
Dyscolus	75	42	12	4970
Dercylini				
Dercylus	5	5		4200
Lebiini				
Mimodromius	2	2		4000
Lebia	1	1		3850
Total	**167**	**99**	**19**	**—**

The first insects collections on Volcán Chiles were made as early as 1870 by the German geologist Alfons Stübel (Kirsch 1889), followed in 1903 by the French anthropologist Paul Rivet, at that time an accompanying member of a geodesic mission. Eighty years later, new collections were obtained at lower and medium elevations, up to 4100 m, by Robert L. Davidson (1983 and 1987), P. Moret (1985), Giovanni Onore (1986), P. Ponce (1986) and C. Young (1987). Additional data were recently gathered by ecologists from the University of Plymouth (Nicholas Atkins, Brian Pickett and Peter Smithers, 1997). There has been only one attempt at entomological survey of the upper part of the volcano, from the south-west ridge at 4200 m to the south crater zone at 4730 m (P. Moret, 1985). Five localities were visited during these expeditions:

1. Páramo 5 km west of Tufiño and 7 km east-south-east of Volcán Chiles, area of the Cueva del Zorro, 3500–3600 m (P. Moret, G. Onore). Wet *Espeletia* páramo. 11 specimens collected.
2. Cerro El Pelado, 10 km south of Chiles, 4150 m (P. Rivet). Biotope undescribed. 15 specimens collected.
3. South slope of Volcán Chiles, near the road from Tufiño to Maldonado, 3400 to 4150 m (R. Davidson, P. Moret, P. Ponce, N. Atkins, B. Pickett, P. Smithers, C. Young). Wet *Espeletia* páramo, cushion bogs, lake shores and stream banks. 519 specimens collected.
4. South-west ridge of the volcano, 4270 to 4400 m (P. Moret). Rocky páramo with cushion plants. 15 specimens collected.
5. Near the south crater and at the base of the summit rocks, 4600 to 4730 m (P. Moret). Rocky superpáramo, patchy and scanty vegetation, abundant sulphur emanations. 11 specimens collected.

As shown by this short list of localities, distribution data are far from complete. Only one zone (3, south slope of Volcán Chiles at low and medium elevations) has been thoroughly explored, to such a point that collections made in that area amount to 91% of the total number of specimens. Faunal associations on the other faces of the mountain are totally unknown, and only a glimpse has been caught of the fauna of the superpáramo zone.

Furthermore, different methods of collecting insects can introduce bias in the data set, as far as relative and absolute frequency of the species is concerned. Pitfall traps were used only by the team from the University of Plymouth in zone 3. This method is the most suitable for ecological purposes since it prevents underestimation of the smallest species (especially that of the genera *Oxytrechus* and *Bembidion*) which may readily be overlooked by active searching. Nonetheless, the low rate of nocturnal activity in páramo carabids has a negative influence on pitfall captures, for at high elevations the beetles are so slow that there is little chance for them to fall in a pit, unless their day-time shelter is very close to it.

Other entomologists and I have searched simply by turning over stones or, where these are lacking, by tearing up the roots of tussocks and cushion plants. A third method, consisting of looking around on the soil surface with a head torch during the first hours of the night, when carabids are hunting, has not been tried on Chiles but could yield good results for future investigations.

SYSTEMATICS

19 species of Carabidae have been so far collected on Volcán Chiles and in surrounding areas, thus representing 11.4% of all the carabid species known from Ecuadorian páramos (Table 1). Six genera are represented in this community, belonging to four tribes: Trechini, Bembidiini, Harpalini and Platynini. Presence of the genus *Blennidus* (Pterostichini) at low elevations at the base of the volcano is expected but has not been confirmed.

11 of these species are new. One species of the genus *Oxytrechus* and seven species of the genus *Dyscolus* are described below. Three new species of *Paratrechus*, *Bembidion* and *Pelmatellus* are quoted, but not described, because the Andean species groups they belong to have not been adequately revised. Descriptions in such an early stage of knowledge could not but cause confusion in the taxonomy.

Identification key

This key is intended to be accessible to non-specialists, by introducing easily observable characters whenever it is possible. As a consequence, it is valid only for the species treated here and cannot be used for identifying tribes or genera in other contexts. Body size is measured from the apex of the mandibles to the apex of the elytra.

1 Body size small (less than 4 mm) 2

— Body size bigger (more than 5 mm)............................4

2 (1) Pronotum cordate with acute hind angles. Elytral striae deeply impressed and punctuated. 3.4–3.8 mm.................. *Bembidion* sp.

— Pronotum rounded with very obtuse hind angles. Elytral striae obsolete. 2.6–3.2 mm 3

3 (2) Bigger (3–3.2 mm). Eyes almost flat, temples bulging. Elytra broad (length/width = 1.33), rounded............................*Oxytrechus vulcanus* MATEU

— Smaller (2.6–2.8 mm). Eyes prominent, temples not bulging. Elytra narrow (length/width = 1.45), subparallel .... *Oxytrechus ramsayi* n. sp.

4 (1) Head with deep and long sulci, arc-shaped around the eyes. Two setae on the fifth interval of the elytra. 5.8 mm............... *Paratrechus* sp.

— Head with short sulci limited to the forehead. No setae on the fifth interval of the elytra........................5

5 (4) Head with one pair of supra-orbital setae. Body broad, stout and convex 6

— Head with two pairs of supra-orbital setae. Body more slender, depressed or moderately convex 7

6 (5) Pronotum with acute hind angles. Fully winged. 6.7–8 mm .... *Pelmatellus columbianus* (REICHE)

— Pronotum with rounded hind angles. Wings reduced. 6.2–6.5 mm............................*Pelmatellus* sp. 2

7 (5) Elytral surface alternately iridescent and granulate, with broad foveate punctures. Fully winged. Size small (5.3–7 mm)...............*Sericoda bembidioides* KIRBY

— Elytra not iridescent, with minute punctures on third interval. Wings reduced. Size bigger (with the exception of *Dyscolus breviculus* n. sp.). Genus *Dyscolus* DEJEAN...8

8 (7) Hind angles of the pronotum sharp 9

— Hind angles of the pronotum rounded....................14

9 (8) Lateral margins of the pronotum with one seta (laterobasal seta lacking). Third interval of the elytra without setae. 10.2–10.6 mm...........................*Dyscolus onorei* MORET

— Lateral margins of the pronotum with two setae. Third interval of the elytra with at least one seta 10

10 (9) Bigger size (9.5–11 mm) .... *Dyscolus (Hydrodyscolus) smithersi* n. sp.

— Smaller size (6.5–8.6 mm)...11

11 (10) Base of elytra broader, humeral angles right and sharp. 6.5–7.2 mm........ *Dyscolus breviculus* n. sp.

— Base of elytra narrower, humeral angles very obtuse or completely rounded 12

12 (11) Laterobasal depressions of pronotum divided by an oblique carina; smaller size (6.7–7.1 mm) (Fig. 10).............*Dyscolus cachectes* n. sp.

— Laterobasal depressions of pronotum simple, not carinate; bigger size (more than 7 mm) 13

13 (12) Lateral margins of elytra sinuate before apex; pronotum cordate. 7–8 mm (Fig. 3).........................*Dyscolus lubricus* n. sp.

— Lateral margins of elytra regularly arcuate before apex; sides of pronotum feebly sinuate basally, not cordate. 7.5–8.6 mm (Fig. 9)..........*Dyscolus montivagus* MORET

14 (8) Third interval of the elytra without setae. Elytral striae obsolete. 9.4–10.1 mm..........................*Dyscolus defrictus* MORET

— Third interval of the elytra with at least one seta...15

15 (14) Dorsal face of metatarsi depressed and rugulose. Lateral margins of the pronotum with one seta (laterobasal seta lacking). 9.5–10.3 mm (Fig. 1)..................*Dyscolus nubilus* n. sp.

— Dorsal face of metatarsi convex and smooth. Lateral margins of the pronotum with two setae 16

16 (15) Neck broad, not constricted dorsally. Temples extremely bulging, as big as the eyes. Antennae very short, one article exceeding the base of the pronotum when extended backwards. 10–11.5 mm .... *Dyscolus crassus* MORET

— Neck constricted dorsally. Eyes bigger than the temples. Antennae longer, two or three articles exceeding the base of the pronotum.........................17

17 (16) Smaller size (7.2–8.4 mm); body convex, pronotum subquadrate (Fig. 2) ....*Dyscolus riveti* n. sp.

— Bigger size (more than 8.5 mm) 18

18 (17) Fifth article of the tarsi with distinct setation on ventral face. Head nearly as broad as pronotum (WP/WH = 1.12). 9.5–11 mm (Fig. 6).................... *Dyscolus fronto* MORET

— Fifth article of the tarsi glabrous on ventral face. Head markedly narrower than pronotum (WP/WH = 1.28). 8.7–10.6 mm (Fig. 11) .... *Dyscolus atkinsi* n. sp.

Trechini

Oxytrechus vulcanus Mateu 1988 (Fig. 5)

Literature: Mateu 1988: 309.

Volcán Chiles SW, 4270–4600 m, 13.I.1985, P. Moret leg. (JM and PM, 4); Volcán Chiles, 4150 m, pitfall, area 284, 10.VIII.1997, N. Atkins leg. (UPBS, 1); Volcán Chiles, 3890 m, páramo, riparian gully n° 1, 25.VIII.1997, IDSPO1, P. Smithers leg. (PM and UPBS, 2).

Twelve species of the genus *Oxytrechus* Jeannel have been found in Ecuador, exclusively in páramos and superpáramos (Mateu 1991). *O. vulcanus* and the following new species probably are endemics of the Carchi highlands.

Oxytrechus ramsayi n. sp. (Fig. 4)

Holotype male: Volcán Chiles, 3700 m, pitfall, area B-middle (298), 12.VIII.1997, B. Pickett leg. (MNHN). 1 paratype: Volcán Chiles, 3700 m, pitfall, area B-3 (298), 10.VIII.1997, B. Pickett leg. (NHM). 1 paratype: Volcán Chiles, 3650 m, pitfall, area A-Q-7 (299), VIII.1997, N. Atkins & B. Pickett leg. (PM).

Overall body length: 2.6–2.8 mm. Colour of the body piceous brown; legs, antennae and mouth parts reddish-testaceous. Head broad; eyes big and moderately prominent; temples very short, oblique, not bulging. Sides of the pronotum rounded apically and feebly arcuate basally; hind angles very obtuse; lateral margins broad. Elytra markedly narrow (length/width = 1.45), subparallel. Striae 1 and 2 very faintly impressed, 3 to 7 obsolete. Aedeagus bigger than average size in the genus, its apex elongate and strongly curved upwards (Fig. 4).

Morphological differences are very weak in the genus *Oxytrechus*, so that a long description of the external habitus of this new species would have been unnecessary. The only reliable way of discriminating species is the examination of the male aedeagus. Nevertheless, *Oxytrechus ramsayi* can be easily distinguished from *O. vulcanus* by its smaller size, narrower elytra and more prominent eyes. Its aedeagus is much bigger (proportionally to the body length) and has a completely different apex (compare Figs. 4 and 5). Owing to the aedeagus morphology, *O. ramsayi* belongs to the same group as *O. moreti* Mateu and *O. zoiai* Casale & Sciaky from the provinces of Pichincha and Cotopaxi, but it is smaller than the latter two, with bigger eyes and broader pronotal margins.

Paratrechus sp.

Volcán Chiles, 3890 m, páramo, riparian gully n° 1, 25.VIII.1997, IDSPO2, P. Smithers leg. (UPBS, 1 female).

The Ecuadorian representatives of *Paratrechus* Jeannel are in the course of revision by Joaquín Mateu (Museo de Zoología, Barcelona). This species is probably new; it resembles a species from mount Cayambe in the Pichincha province.

Bembidiini

Bembidion sp.

Volcán Chiles, 4050 m, pitfall, samples 285 and 286, 10.VIII.1997, N. Atkins leg. (UPBS, 54); 3850 m, pitfall, samples 289 and 290, 11.VIII.1997, N. Atkins leg. (UPBS, 6).

The numerous Andean species of the genus *Bembidion* need revision and reclassification. The species collected on Volcán Chiles is certainly new for science. It shares many derived characters with *Bembidion fulvocinctum* Bates from central Ecuador, and probably belongs to the same species group.

Harpalini

Pelmatellus columbianus (Reiche 1843)

Literature: Perrault 1993: 20 and 22.

Volcán Chiles, 3500 m, riparian gully, under stones, 15.VIII.1997, P. Smithers leg. (UPBS, 5); Volcán Chiles, 3700 m, páramo, under stones, 9.VIII.1997, P. Smithers leg. (UPBS, 2).

This is a very common species, present in most parts of Northern Andes form Venezuela to Perú. It ranges in Ecuador from 2100 to 4150 m and has been collected in almost all provinces: Carchi, Sucumbíos, Imbabura, Pichincha, Napo, Cotopaxi, Tungurahua, Chimborazo, Bolívar, Cañar, Azuay, Zamora-Chinchipe, Loja. It is equally common in montane forest, subpáramo and disturbed anthropogenic grassland.

Pelmatellus sp. 2

Carchi, 5 km W Tufiño, Cueva del Zorro, 3600 m, 13.I.1985, P. Moret leg. (PM, 3).

A micropterous species, undoubtly new for science. It is closely allied with *Pelmatellus variipes* Bates which lives farther south in the Pichincha province.

Platynini

Sericoda bembidioides Kirby 1837

Literature: Kirsch 1889: 48; Liebherr 1991: 82.

Carchi: páramo de Chiles, 4000 m, III.1870, A. Stübel leg. (according to Kirsch 1889: 48, material probably in the Museum für Naturkunde der Humboldt-Universität, Berlin); Tulcán, 1902, P. Rivet leg. (MNHN, 2).

This interesting pyrophilous species is one of the few macropterous carabids that occasionnally occur in the páramo (see below). It has a wide distributional range in North America, Central America and in the Andes. In Ecuador it has also been reported from the provinces of Imbabura, Pichincha, Cotopaxi, Tungurahua, Bolívar, Chimborazo, Cañar and Loja, at elevations from 2300 to 3900 m (Liebherr 1991 and unpublished data).

Genus *Dyscolus* Dejean 1831

The last twelve species of this checklist belong to *Dyscolus* Dejean, a neotropical genus with hundreds of species in Central and South America (Moret 1996, Moret in press). All the species found on Chiles are micropterous and exhibit derived characters that are shared by many orobiont carabids: dull teguments, brownish or piceous colour, inflated head but small eyes, *etc.* It is highly probable that they all are endemics of the Carchi páramos.

Dyscolus crassus Moret 1990

Literature: Moret 1990: 276.

Carchi: Volcán Chiles, 4400 m, 13.I.1985, P. Moret leg. (MNHN and PM, 2); Volcán Chiles, 4150 m, pitfalls, samples 283 and 284, 10.VIII.1997, N. Atkins leg. (PM, QCAZ and UPBS, 6); El Pelado, 4150 m, 1903, P. Rivet leg. (MNHN and PM, 3).

This species belongs to the *bucculentus* group (Moret 1990), a highly specialized orophilous group restricted to southern Colombia and northern half of Ecuador. *D. crassus* is related with the Colombian species *D. quadricollis* (Chaudoir).

Dyscolus defrictus Moret 1993

Literature: Moret 1993: 7.

Volcán Chiles, southern slopes, Laguna Verde, 4010 m, 13.I.1985, P. Moret leg. (MNHN, 1); Tulcan-Maldonado road, 35 ml. SE Maldonado, 3800–3900 m, sulphur lakes, 6.VIII.1983, R. Davidson leg. (CMNH, 1).

Dyscolus onorei Moret 1993

Literature: Moret 1993: 11.

Tufiño, VIII.1986, G. Onore leg. (MNHN, 1); 5 km W Tufiño, Cueva del Zorro, 3600 m, 13.I.1985, P. Moret leg. (PM, 1); Volcán Chiles, 3900 m, II.1986, P. Ponce leg. (QCAZ and PM, 2); km 18–25 Tufiño-Maldonado, 3500–4070 m, 6.VIII.1983 and 18–20.XI.1987, R. Davidson & C. Young leg. (CMNH, 5); Volcán Chiles, 3500 m, riparian gully, 25.VIII.1997, IDSPO7, P. Smithers leg. (PM and UPBS, 2); Volcán Chiles, 4050 m, pitfall, sample 286, 10.VIII.1997, N. Atkins leg. (UPBS, 2).

Dyscolus fronto Moret 1998 (Fig. 6)

Literature: Moret 1998: 17.

Volcán Chiles, 4070 m, 18.XI.1987, R. Davidson & C. Young leg. (CMNH, MNHN, PM, 16); Volcán Chiles, 4050–4150 m, pitfalls, samples 283, 284 and 285, 10.VIII.1997, N. Atkins leg. (PM, QCAZ and UPBS, 72); Volcán Chiles, Laguna Verde, 4010 m, 13.I.1985, P. Moret leg. (PM, 3). Volcán Chiles, south crater, 4730 m, 13.I.1985, P. Moret leg. (PM, 1); Tulcán-Maldonado road, 35 ml. SE Maldonado, 3800–3900 m, sulphur lakes, 6.VIII.1983, R. Davidson leg. (CMNH and PM, 19).

D. fronto is the northern vicariant of *D. megacephalus* (Bates) that lives in various páramos of the Pichincha and Cotopaxi provinces.

Dyscolus montivagus Moret 1998 (Fig. 9)

Literature: Moret 1998: 19.

Volcán Chiles, 4070 m, 18.XI.1987, R. Davidson & C. Young (CMNH, MNHN, PM, 99); Volcán Chiles, 4150 m, pitfalls, samples 283 and 284, 10.VIII.1997, N. Atkins leg. (PM, QCAZ and UPBS, 67); Volcán Chiles, 3890 m, riparian gully, 25.VIII.1997, P. Smithers leg. (UPBS, 1); Volcán Chiles, SW slope, 4270–4400 m, 13.I.1985, P. Moret leg. (PM, 9); Volcán Chiles, south crater, 4600–4730 m, 13.I.1985, P. Moret leg. (PM, 9); Tulcán-Maldonado road, 35 ml. SE Maldonado, 3800–3900 m, sulphur lakes, 6.VIII.1983, R. Davidson leg. (CMNH and PM, 103); El Pelado, 4150 m, I.1903, P. Rivet leg. (MNHN and PM, 6).

Dyscolus atkinsi **sp. nov. (Fig. 11)**

Holotype male: Volcán Chiles, 3850 m, páramo, sample 289, 11.VIII.1997, N. Atkins leg. (MNHN). 7 paratypes: same data as the holotype (PM, QCAZ and UPBS). 10 paratypes: Volcán Chiles, 3850 m, páramo, sample 290, 11.VIII.1997, N. Atkins leg. (NHM, CMNH and PM). 1 paratype: 18–23 km Tufiño-Maldonado, 4070 m, 18–21.XI.1987, R. Davidson & C. Young leg. (CMNH).

Overall body size: 8.7–10.6 mm. Micropterous. Body elongate, the general form recalling *Dyscolus denigratus* (BATES). Colour of the body piceous black; tarsi, antennae and mouthparts brownish. Elytral microsculpture isodiametric. Head convex with a long and dorsally constricted neck, temples oblique, slightly bulging, shorter than the eyes; mandibles long and acute. Sides of the pronotum feebly arcuate distally, rectilineous or feebly sinuate basally; two pairs of lateral setae; hind angles obtusely rounded. Elytra elongate-ovate, very narrowed at their base, with rounded humeri; preapical sinuation weakly marked. Striae entire, well impressed; intervals flat. Third elytral interval normally with 3 setae, the middle one nearer to the basal seta than to the apical seta. Loss of the basal seta, in one elytron or in both, has been observed in three specimens. Umbilicate series consisting in 16 or 17 setae. Abdominal apex bisetose in the males, quadrisetose in the females. Metafemora with two setae on their ventral face and one preapical seta on their anterior edge. External lobe of the fourth metatarsomere as long as the basal part of the article and two times longer than the internal lobe; fifth metatarsomere asetose ventrally. Male aedeagus relatively short, bluntly acuminate at apex.

Dyscolus nubilus **sp. nov. (Fig. 1)**

Holotype male: Carchi, 5 km W Tufiño, Cueva del Zorro, 3600 m, 13.I.1985, P. Moret leg. (MNHN). 1 paratype, same data as the holotype (PM). 3 paratypes: Carchi, Tufiño, VIII.1986, G. Onore leg. (QCAZ and PM).

Overall body size: 9.5 to 10.3 mm. Micropterous. Body black; apex of the femora, tibiae and base of the antennae brownish; tarsi, antennae and mandibles reddish brown; labrum and palpi testaceous. Teguments shiny on the head and the pronotum, sericeous on the elytra due to a granulous isodiametric microsculpture in both sexes. Head broad and convex; frontal furrows short and shallow; eyes moderately prominent preceded by long and oblique temples; labrum deeply emarginate; mandibles long and strong. Pronotum proportionally big, elongate (W/L = 1.14); latero-apical lobes small; sides rectilineous or weakly sinuate in their basal half; hind angles obtusely rounded; lateroposterior seta lacking. Elytra elongate; base very narrow, humeri rounded; basal groove markedly curved; juxtascutellar seta present; scutellar striole obsolete; striae weakly impressed, intervals flat, the third one with 1 to 4 setae; sides sinuate before apex. Second to fourth metatarsomeres with a vestigial median sulcus on basal half; fourth metatarsomere moderately bilobed, the external lobe 1.5 x longer than the internal lobe; fifth metatarsomere asetose ventrally, depressed and rugulose dorsally. Male aedeagus: median lobe arcuate, abruptly narrowed at apex and ending needle-like.

Dyscolus riveti **sp. nov. (Fig. 2)**

Holotype male: Carchi, El Pelado, 4150 m, 1903, P. Rivet leg. (MNHN). 6 paratypes, same data as the holotype (MNHN and PM). 9 paratypes: 18–23 km W Tufiño, Volcán Chiles, 4070 m, 18.XI.1987, R. Davidson & C. Young leg. (CMNH and PM). 1 paratype: Carchi, 34 miles ENE Maldonado, 3775 m (CMNH). 19 paratypes: Volcán Chiles, 4050 m, pitfall, sample 285, 10.VIII.1997, N. Atkins leg. (NHM, PM, QCAZ and UPBS). 5 paratypes: same date and collector, 4150 m, samples 283 and 284 (PM, QCAZ and UPBS).

Overall body size: 7.2 to 8.4 mm. Micropterous. Body piceous; legs, antennae and mouth parts reddish to reddish brown. Elytral microsculpture isodiametric in both sexes. Head broad and rather small; neck strongly constricted; vertex very convex; frontal furrows short, arcuate; eyes little, weakly bulging; temples convex, as long as the eyes. Pronotum subquadrate (W/L = 1.20); sides feebly rounded; latero-apical lobes prominent and rounded; hind angles obtuse; lateroposterior depressions deep, with a pustule-like bulge in middle. Elytra broad and ovate; base broader than that of the pronotum, humeri well marked, obtuse; basal groove feebly curved; juxtascutellar seta present; scutellar striole short; striae strongly impressed, intervals flat to subconvex; third interval with 3 setae (rarely with 2 to 4 setae); sides entirely arcuate, not sinuate before apex. Abdominal apex bisetose in the males, quadrisetose in the females. All metatarsomeres convex dorsally, the fourth one deeply bilobed with asymetric lobes (external lobe = 1.5 x internal lobe); fifth metatarsomere asetose ventrally. Male aedeagus: median lobe small, curved downwards at apex which is acuminate.

Dyscolus lubricus **sp. nov. (Fig. 3)**

Holotype male: Carchi, Tufiño, VIII.1986, G. Onore leg. (QCAZ). 2 paratypes, 35 ml. SE Maldonado, 3800–3900 m, sulphur lakes, 6.VIII.1983, R. Davidson leg. (CMNH). 4 paratypes: 18–23 km Tufiño-Maldonado, 4070 m, 18–21.XI.1987, R. Davidson & C. Young leg. (CMNH, MNHN and PM). 4 paratypes: Volcán Chiles, 3850 m, páramo, samples 289 and 290, 11.VIII.1997, N. Atkins leg. (NHM, PM and UPBS).

Overall body size: 7 to 8 mm. Micropterous. Body shiny black, except the margins of the pronotum and of the elytra which are more or less brownish-piceous; legs and antennae brownish-piceous to reddish-brown; mouth parts reddish-brown. Elytral microsculpture made of transverse meshes in both sexes. Head proportionally big; neck strongly constricted; vertex very convex; frontal furrows oblique and rectilineous; eyes standing out rather prominently; temples long, narrowing obliquely behind the eyes, slightly convex. Pronotum cordate and narrow (W/L = 1.12); latero-apical lobes small and triangular; sides regularly arcuate in their apical two thirds, strongly sinuate near the hind angles which are sharply cut, right or slightly acute; laterobasal depressions deep. Elytra moderately ovate; base narrow, though broader than the base of the pronotum; humeri forming obtuse angles; juxtascutellar seta and scutellar striole present; striae fine but well impressed; intervals flat to feebly convex; third interval with 3 or 4 setae; sides markedly sinuate before apex. Abdominal apex bisetose in the males, quadrisetose in the females. Fourth metatarsomere strongly bilobed, its external lobe 2 x longer than the internal lobe; fifth metatarsomere asetose ventrally. Male aedeagus: median lobe with a short and blunt apex, triangle-shaped in dorsal view.

Dyscolus breviculus **sp. nov. (Fig. 8)**

Holotype male: Volcán Chiles, 3850 m, páramo, sample 290, 11.VIII.1997, N. Atkins leg. (MNHN). 3 paratypes: same data as the holotype (PM, QCAZ and NHM). 2 paratypes: 18–23 km Tufiño-Maldonado, 4070 m, 18–21.XI.1987, R. Davidson & C. Young leg. (CMNH).

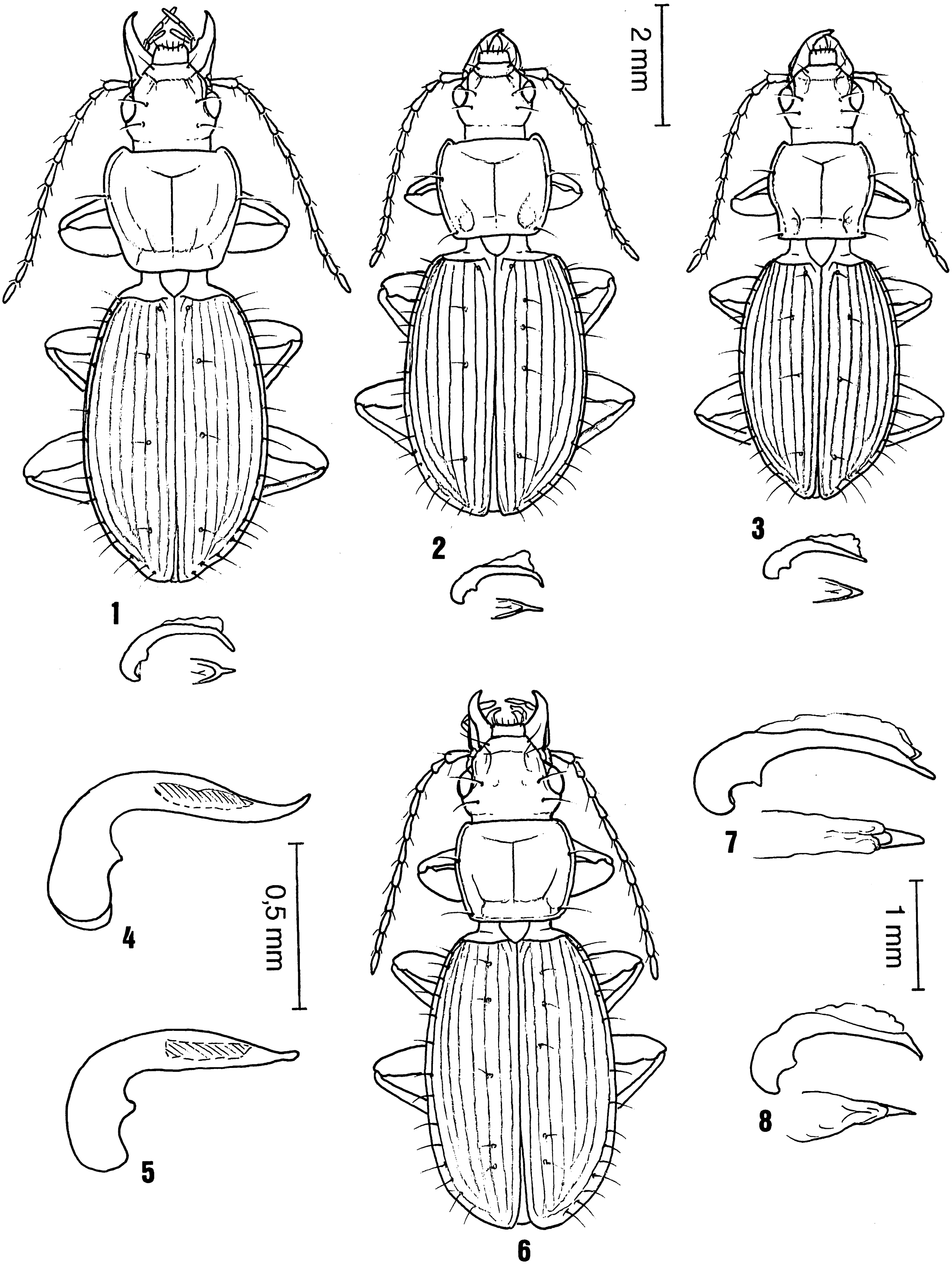
Overall body size: 6.5 to 7.2 mm. Micropterous. Similar to *D. lubricus* n. sp., but the size is smaller, the legs and antennae are reddish, the sides of the pronotum are less sinuate in their basal half, the base of the elytra is much broader, the humeri are more salient with lateral margins broader near the base, the sides of the elytra are regularly arcuate before their apex, not sinuate. Third elytral interval with 4 or 5 setae; fifth interval normally asetose, but the left elytron of one female paratype bears one seta near the base of the fifth interval. Male aedeagus: apex of the median lobe acuminate (Fig. 8).

Dyscolus cachectes **sp. nov. (Fig. 10)**

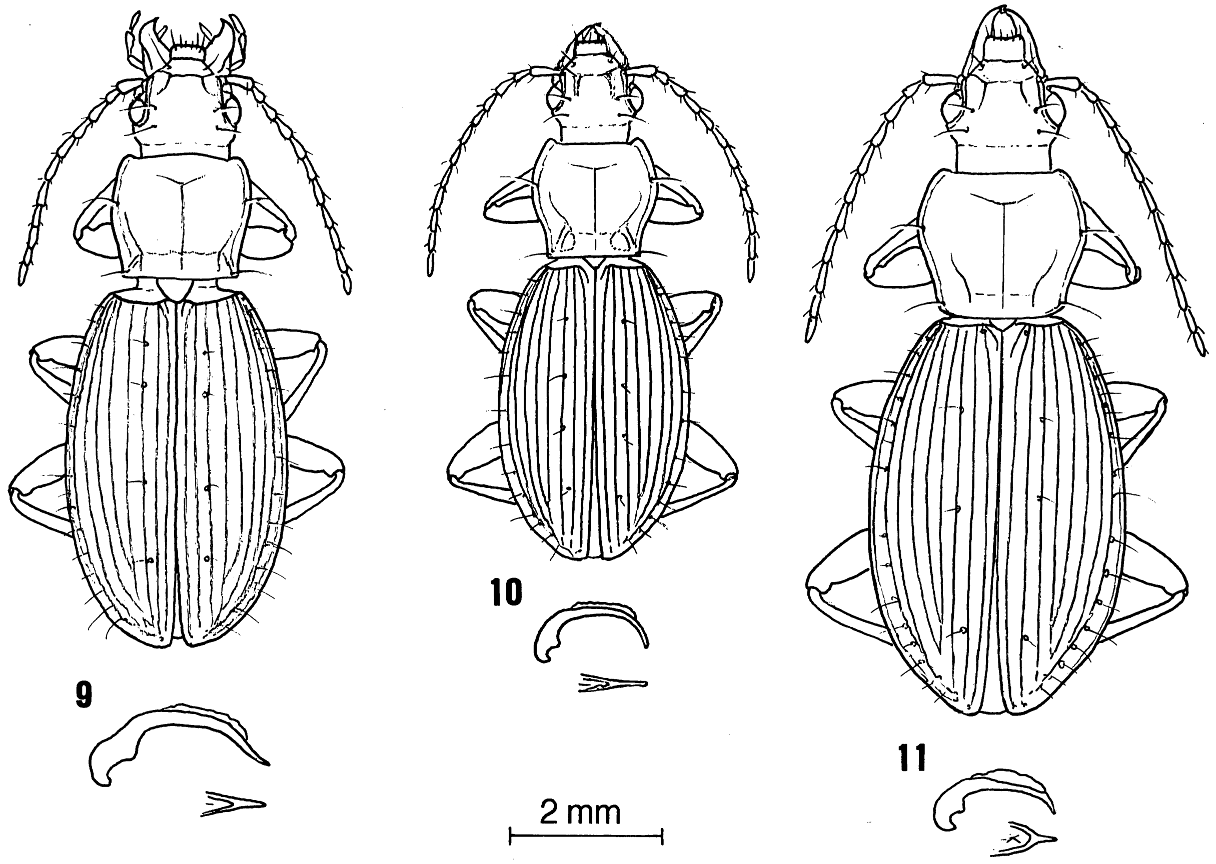
Holotype male: Volcán Chiles, páramo, 3890 m, riparian gully n° 1, IDSPO1, 25.VIII.1997, P. Smithers leg. (MNHN). 1 paratype: same data as the holotype, IDSPO2 (PM).

Overall body size: 6.7 to 7.1 mm. Micropterous. Similar to *D. lubricus* n. sp. and *D. breviculus* n. sp. Microsculpture variable, distinctly isodiametric in the holotype, partly erased in the paratype; colour as in *breviculus*. Form of the pronotum intermediate between *lubricus* and *breviculus*, with sharp and right hind angles; laterobasal depressions divided by an oblique carina. Sides of the elytra rectilineous in the preapical zone. Juxtascutellar seta absent. Elytral striae deep and broad; intervals convex, the third one with 4 or 5 setae; 13 to 14 setae in the umbilicate series. Metafemora with 2 setae on their ventral face and 2 or 3 preapical setae on their anterior edge. Legs and antennae slightly more slender and more elongate than in *lubricus* and *breviculus*. Male aedeagus highly distinctive, big and strongly curved, with a very long apex.

Figs. 1–3. *Habitus and median lobe of male aedeagus in lateral and dorsal views. 1.* Dyscolus nubilus *n. sp.; 2.* Dyscolus riveti *n. sp.; 3.* Dyscolus lubricus *n. sp.* ***Figs. 4–5.*** *Median lobe of male aedeagus, lateral view. 4.* Oxytrechus ramsayi *n. sp.; 5.* Oxytrechus vulcanus *Mateu.* ***Fig. 6.*** *Habitus of* Dyscolus fronto *Moret.* ***Figs. 7–8.*** *Median lobe of male aedeagus, lateral and dorsal views. 7.* Dyscolus (Hydrodyscolus) smithersi *n. sp.; 8.* Dyscolus breviculus *n. sp.*



Figs. 9–11. *Habitus and median lobe of male aedeagus in lateral and dorsal views. 9.* Dyscolus montivagus *Moret; 10.* Dyscolus cachectes *n. sp.; 11.* Dyscolus atkinsi *n. sp.*



Dyscolus (Hydrodyscolus) smithersi **n. sp. (Fig. 7)**

Holotype male: Volcán Chiles, 3400 m, páramo, under stones at stream side, VIII.1997, IDSPO8, P. Smithers leg. (MNHN). 2 paratypes: same data as the holotype (NHM and QCAZ). 3 paratypes: Volcán Chiles, 3620 m, páramo, riparian gully n° 3, 25.VIII.1997, IDSPO3, P. Smithers leg. (PM and UPBS).

Overall body size: 9.5–11 mm. Micropterous. Body slender with elongate legs and antennae. Colour brownish-piceous, the pronotum and the head somewhat darker than the elytra; legs, antennae and mouthparts reddish-brown. Elytral microsculpture consisting in transverse meshes in both sexes. Head convex, fused anteriorly; eyes moderately salient; temples oblique, not bulging, nearly as long as the eyes; two pairs of lateral setae at the base of the submentum. Pronotum slightly broader than long, cordate, with a long sinuation in the basal half of the sides; hind angles right and sharp; laterobasal depressions simple, arcuate. Prosternal apophysis rounded, not margined. Elytra elongate-ovate, depressed; base narrow, humeri fused; all striae well impressed; intervals flats or even depressed; third interval with three setae; sides markedly sinuate before apex. Abdominal apex bisetose in the males, quadrisetose in the females. Metafemora with two setae on their ventral face, anterior edge asetose. Apical lobes of the fourth metatarsomere very long, lacking the latero-apical setae; external lobe two times longer than the internal lobe and longer than the basal part of the article; fifth metatarsomere asetose ventrally. Male aedeagus: median lobe regularly narrowed, rounded at apex (Fig. 7).

This species belongs to the subgenus *Hydrodyscolus* MORET (1996), whose major distinctive character is the absence of both apico-lateral setae on the fourth article of the metatarsi. Another conspicuous feature of this subgenus is the riparian habitat of most of its species (see below).

ECOLOGICAL AND BIOGEOGRAPHIC OVERVIEW

Life history data

Very little can be said about the ecology of the Carabidae found on Volcán Chiles. Like all páramo carabids, they are terrestrial, nocturnal predators and/or scavengers. They go out soon after sunset and run around on the ground surface in search of living or dead prey. Most of them are cold stenotherms, normally active at temperatures between 0°C and 5°C. Their activity is therefore not impeded by the rapid decrease of temperature at the beginning of the night, but I never observed carabids on open ground at freezing temperatures. It may be presumed that they return to their shelters when the temperature falls below 0°C. Cold tolerance and resistance to desiccation were recently measured for three carabid species of the genera *Bembidion*, *Pelmatellus* and *Blennidus*, caught on the Chimborazo between 4250 and 4800 m (Sømme, Davidson & Onore, 1996). They proved neither to be physiologically adapted to aridity, nor to temperatures below 0°C. Andean carabids are therefore compelled to find shelters under stones, in rock crevices or in micro-cavities of the soil, during the day as well as during the coldest hours of the night.

Nothing is known regarding reproduction habits and duration of the larval development. There is no evidence of seasonal rhythm in the breeding behaviour of páramo carabids. On the Volcán Cotopaxi—probably the best explored mountain in Ecuador—adult carabids were caught at almost every months of the year. In the Chiles area, *Dyscolus onorei* was collected in January, February, August and november; *D. fronto* and *D. montivagus* were obtained in January, August and November. It is probable that adults of all the Chiles carabids are active throughout the year.

Information about habitat preferences are partial and vary greatly from one species to another. Though any detailed conclusion on this point is out of our reach at present, it is possible to distinguish two main groups (Table 2):

- The first group includes three species inhabiting the high Andean montane forest and the transition zone towards the páramo. *Pelmatellus columbianus* (Harpalini) is one of the most common carabids of that altitudinal zone. It has a very broad ecological tolerance, thus being a typical component of the synanthropic fauna of Andean cultivated highlands. The habitat requirements of the second *Pelmatellus* species are unknown. *Sericoda bembidioides* (Platynini) is one of the few carabids that have been reported to be strictly pyrophilous (Liebherr 1991; Dajoz 1998). *Sericoda* adults arrive at a fire site immediately after burning and stay there for a short period of time; their larvae are supposed to feed on small xylophagous Arthropoda. Liebherr reared this species from adults collected in Mexico. Under laboratory conditions, the total generation time, from egg to adult, is approximately four weeks. Occasional occurrence of *S. bembidioides* in the páramo is due to attraction by grass fires, but it is unknown whether this species is able to breed in this ecosystem. Other reports of *S. bembidioides* in Ecuador refer to montane forest habitats and xeric subpáramos.
- The second group includes 16 species, all of them restricted to the páramo ecosystem. No species occurs over the whole altitudinal range of the páramo. The broadest altitudinal ranges, those of *Oxytrechus vulcanus*, *Dyscolus fronto* and *Dyscolus montivagus*, are less than 1000 m. Twelve species are restricted to the lower zone of the páramo, approximately between 3400 and 4100 m. The remaining four species are more specialized orobionts, adapted to the highest altitudes and to the adverse conditions of the superpáramo (Moret 1998). They are absent below 3800 m, probably because of their cold stenothermy.

As far as we know, most páramo carabids are eurytopic. They are apparently indifferent to the structure and the density of the vegetation. The only carabids that are likely to be stenotopic in the Chiles area are three riparian species: *Paratrechus sp.* (Trechini), *Dyscolus cachectes* and *Dyscolus smithersi* (Platynini). The latter belongs to the subgenus *Hydrodyscolus* that comprises a number of markedly hygrophilous species (Moret 1996). The six syntypes were collected from under stones at the very edge of a stream, three of them at 3620 m from stones on the bank, the three others at 3400 m from under stones that were in the water (P. Smithers, personal communication). Riparian habitats have been recorded for *D. (Hydrodyscolus) capito* (BATES), *D. (Hydrodyscolus) brocchus* MORET and many other undescribed species of the subgenus. It is worth to recall that the riparian hygrobiont communities of Ecuadorian páramos also include *Aquilex diabolicola* MORET (MIGADOPINI), a very distinctive and taxonomically isolated beetle with austro-american and antarctic affinities (Moret 1989).

The composition of this carabid community suggests that the microclimate of the Chiles páramo is among the wettest in Ecuador. The absence of the genus *Blennidus* (Pterostichini), the presence of *Paratrechus* (Trechini) and the high proportion of *Dyscolus* species (Platynini) to the rest of the carabids are remarkable facts that point to Volcán Chiles as a mountain far more humid than any other in the Cordillera Occidental. *Paratrechus* are highly hygrophilous beetles, with previous records in Ecuador being restricted to the rainiest mountains of the Cordillera Oriental and to the very wet east slope of the Chimborazo. On the contrary, *Blennidus* are typical inhabitants of the semi-arid puna in Bolivia and Perú, whilst their distributional area in Ecuador reveals a preference for xeric páramos in rain-shadow areas. As in all Colombian and Ecuadorian páramos, *Dyscolus* much preponderates over other genera, but the proportion varies according to a number of factors among which the climatic one appears to be crucial. *Dyscolus* includes less than 50% of the total number of species in the dry páramos of the west face of the Chimborazo (36%) and of the north face of the Cotopaxi (45%), whereas it reaches very high proportions in humid páramos of the Cordillera Oriental, especially on mounts Ayapungu (64%) and Cayambe (65%). With a *Dyscolus* proportion of 63%, the Chiles area ressembles more the humid eastern edge of the Cordillera Oriental than other páramos of the Cordillera Occidental (Table 3).

Biodiversity

Diversity in the carabid communities of Andean páramos depends mostly on the following three parameters: surface area of the páramo ecosystem, distance to other páramos, and climatic conditions of the mountain. A vast páramo, surrounded by other páramo-islands nearby, with a variety of microclimates on the different slopes of the mountain, is expected to exhibit the maximum faunal richness.

Table 2. Ecological preferences of the carabid species found in the Volcán Chiles area. The altitudinal range of each species is indicated in the last column; brackets suggest that actual range may be significantly broader as the available data are insufficient.

páramo: medium zone and superpáramo	eurytopic	*Oxytrechus vulcanus*	3890–4600 m
		Dyscolus fronto	3800–4730 m
		Dyscolus montivagus	3800–4730 m
		Dyscolus crassus	4150–4400 m
páramo: low and medium zones	eurytopic	*Oxytrechus ramsayi*	[3650–3700 m]
		Bembidion sp.	3850–4050 m
		Dyscolus atkinsi	3850–4070 m
		Dyscolus onorei	3500–4000 m
		Dyscolus defrictus	3800–4000 m
		Dyscolus nubilus	[3600 m]
		Dyscolus lubricus	3800–4070 m
		Dyscolus breviculus	3850–4070 m
		Dyscolus riveti	3770–4150 m
	riparian hygrobiont	*Paratrechus* sp.	[3890 m]
		Dyscolus cachectes	[3890 m]
		Dyscolus smithersi	3400–3620 m
montane forest/ subpáramo	eurytopic	*Pelmatellus columbianus*	2100–3700 m
	?	*Pelmatellus* sp.	[3600 m]
	pyrophilous	*Sericoda bembidioides*	2300–4000 m

Table 3. Number of species per genera in 8 Ecuadorian mountains (checklist restricted to open páramos above 3500 m), based on partially unpublished data. The province of each mountain is shown in brackets.

Genus	**Chiles (Carchi)**	**Cayambe (Pichincha)**	**Guamaní (Pichincha)**	**Pichincha (Pichincha)**	**Illiniza (Pichincha)**	**Cotopaxi (Cotopaxi)**	**Chimborazo (Chimborazo)**	**Ayapungu (Chimborazo)**
Aquilex								1
Trechisibus							1	
Oxytrechus	2	1	4	1		1		
Paratrechus	1	1					1	1
Bembidion	1	1	2	2	2	1	4	1
Notiobia					1	1	1	
Bradycellus						1		
Pelmatellus	2	1	1	1	1	2	2	1
Blennidus		1	3	2	2	3	6	1
Incagonum		1		1			1	
Sericoda	1			1				
Dyscolus	12	11	13	9	7	10	9	9
Dercylus				1	1	1		
Mimodromius						1		
Lebia						1		
Total genera	6	7	5	8	6	10	8	6
Total species	19	17	23	18	14	22	25	14

Though far from comprehensive, the collections obtained from the Chiles area can be compared with those of other Ecuadorian mountains which have been explored approximately to the same degree (Table 3). The isolated position of the Carchi area (separated from the huge páramo area of Central Ecuador by a xeric barrier) and its uniformly humid microclimate, can explain its relatively low biodiversity. Six genera are represented in this community, placing Volcán Chiles at a rather low rank of generic diversity, below Volcán Cotopaxi (10 genera), Volcán Chimborazo (8 genera) and Volcán Pichincha (8 genera).

Furthermore, the diversity of a páramo insect community cannot be properly estimated if altitudinal zonation is not taken into account. Regarding generic diversity, the number of carabid genera is the highest in the basal zone of the páramo. Five genera are recorded from altitudes around 3600/ 3800 m, whilst from 4100 m upwards only two genera, *Oxytrechus* and *Dyscolus*, are represented by a few specialized orobiont forms.

With regard to the number of species, maximum diversity occurs between 3800 and 4100 m, where the upper limit of the species that are restricted to the lower zone of the páramo overlaps with the lower limit of the high altitude orobionts. This is where almost all the flightless carabid species of Volcán Chiles are likely to be found. The absolute abundance of species begins to decrease drastically above 4100 / 4200 m, but more investigations in the superpáramo are needed to know the actual number of species that live in the perinival zone.

Biogeography

The flightless condition of most high-Andean carabids implies reduced dispersal ability, and therefore has led to a proliferation of geographically restricted species in the fragmented habitats formed by each island-like páramo area. Based on evidence derived from the distribution of flightless carabids, three main areas of endemism were recognized in the Andes of Ecuador: the Carchi area, the Pichincha-Chimborazo area and the Azuay-Cajas area (Moret 1998).

The carabid fauna of the Carchi páramos is completely different, at specific level, from that of any other Ecuadorian highland area. None of the 17 flightless species found there has been recorded from other páramos at the south of the Mira River. These distributional data point to the Mira xeric depression, south of Carchi, as a major biogeographic barrier in the Northern Andes. In the opposite direction, connections are likely to exist with the carabid communities of Cumbal and other volcanoes across the Colombian border. Unfortunately, the fauna of the southern highlands of Colombia is poorly known. All in all, the Carchi páramo area can be considered as the southern extremity of an area of endemism that extends northwards into the Cordillera Central of Colombia.

ACKNOWLEDGEMENTS

My most sincere thanks are due to Paul M. Ramsay for his invitation to participate in this volume. I am also grateful to the institutions and persons that made material available for this study: R.L. Davidson (CMNH), T. Deuve (MNHN), G. Onore (QCAZ) and P. Smithers (UPBS).

REFERENCES

Dajoz, R. (1998) Le feu et son influence sur les insectes forestiers. Mise au point bibliographique et présentation de trois cas observés dans l'ouest des Etats-Unis. *Bulletin de la Société entomologique de France*, **103**: 299–312.

Erwin, T.L. (1991) Natural history of the carabid beetles at the BIOLAT Biological Station, Rio Manu, Pakitza, Peru. *Revista Peruana de Entomología*, **33**: 1–85.

Kirsch, T. (1889) Coleopteren gesammelt in den Jahren 1868–1877 auf einer Reise durch Süd-Amerika von Alphons Stübel. *Abhandlungen und Berichte des Königl. zoologischen Museums zu Dresden*, **4**: 1–58.

Liebherr, J.K. (1991) Phylogeny and revision of the *Anchomenus* clade: the genera *Tetraleucus*, *Anchomenus*, *Sericoda*, and *Elliptoleus* (Coleoptera: Carabidae: Platynini). *Bulletin of the American Museum of Natural History*, **202**: 1–163.

Mateu, J. (1988) Nouvelles espèces du genre *Oxytrechus* Jeannel récoltées en Equateur (Coleoptera, Carabidae). *Nouvelle Revue d'Entomologie* (N.S.), **5**: 305–313.

Mateu, J. (1991) Sur le genre *Oxytrechus* Jeannel, 1927, avec la description de nouvelles espèces de l'Equateur et de la Colombie (Coleoptera, Carabidae, Trechinae). *Eos*, **67**: 71–83.

Moret, P. (1989) Un Migadopidae sans strie surnuméraire des Andes de l'Equateur: *Aquilex diabolicola* gen. nov., sp. nov. (Coleoptera, Caraboidea). *Nouvelle Revue d'Entomologie* (N.S.), 6: 245–257.

Moret, P. (1990) Les *Dyscolus* équatoriens du groupe *bucculentus* sp. nov. (Coleoptera, Harpalidae). *Nouvelle Revue d'Entomologie* (N.S.), **7**: 271–281.

Moret, P. (1993) Les *Dyscolus* de l'Equateur: révision des espèces à élytres achètes (1ère partie) [Coleoptera, Harpalidae, Platyninae]. *Revue française d'Entomologie* (N.S.), **15**: 1–13.

Moret, P. (1996) Mise au point taxinomique sur le genre *Dyscolus* Dejean et description de cinq espèces nouvelles (Caraboidea, Harpalidae, Platynini). *Bollettino del Museo regionale di Scienze naturali – Torino*, **14**: 491–503.

Moret, P. (1998) Les *Dyscolus* de la zone périglaciaire des Andes équatoriennes (Coleoptera, Harpalidae, Platyninae). *Bulletin de la Société entomologique de France*, **103**: 11–28.

Moret, P. (in press) A contribution to the systematics of Neotropical Platynina. The supra-specific taxa of the *Dyscolus* complex (Coleoptera, Carabidae, Platynini). *In:* R. Sciaky and D. Zamotajlov ed., *Studies in homage to O.L. Kryzhanovskji*.

Perrault, G. (1993) Etudes sur les Carabidae des Andes septentrionales. XV- Le genre *Pelmatellus* Bates, 1882 (Coleoptera, Harpalini). *Revue française d'Entomologie* (N.S.), **15**: 19–23.

Reichardt, H. (1977) A synopsis of the genera of Neotropical Carabidae (Insecta: Coleoptera). *Quaestiones Entomologicae*, **13**: 346–493.

Sømme, L., Davidson, R.L. and Onore, G. (1996) Adaptations of Insects at high altitudes of Chimborazo, Ecuador. *European Journal of Entomology*, **93**: 313–318.

Whymper, E. (1892) *Travels amongst the Great Andes of the Equator*, London: Murray.

A draft key to the spider families of northern Ecuadorian páramos

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SUMMARY

Spiders are generalist predators that form an important element of the ground fauna in páramo habitats, and can exert a significant top-down control on populations of other invertebrates. A provisional key to spider families of the páramo of Volcán Chiles is provided here to stimulate co-operation between biologists working on the ecology of páramos. It is hoped this will enable the key to be refined. This key is also published on the Internet. This provisional key includes 14 families (Agelenidae, Anyphenidae, Araneidae, Clubionidae, Dictynidae, Linyphiidae, Lycosidae, Ochyroceratidae, Pholcidae, Salticidae, Theridiidae, Cyrtaucheniidae, Paratropididae). A brief, generalised description of the biology and habitat of each family is also provided.

RESUMEN

Las arañas son depredadores generalizados que forman un elemento importante de la fauna terrestre en hábitats paramunos, y puedan ejercer un control significativo (“de arriba hacia abajo”) en las poblaciones de otros invertebrados. Con objeto de estimular la cooperación entre biólogos que trabajan sobre la ecología de los páramos, se presenta una clave provisional de las familias de arañas presentes en el volcán Chiles. Se espera que este primer trabajo promueva el perfeccionamiento de la clave, la cual estará también disponible en Internet. Este clave provisional incluye 14 familias (Agelenidae, Anyphenidae, Araneidae, Clubionidae, Dictynidae, Linyphiidae, Lycosidae, Ochyroceratidae, Pholcidae, Salticidae, Theridiidae, Cyrtaucheniidae, Paratropididae). Se proporciona además una descripción breve y generalizada de la biología y hábitat de cada familia.

Key words: Systematics, high-altitude, Ecuador, Araneae, tropical alpine

INTRODUCTION

Spiders are generalist predators that form an important element of the ground fauna in most terrestrial habitats, they are often occur at extremely high population densities and exert a significant controlling influence on the invertebrate communities in which they exist.

Little information is readily available that refers to Ecuadorian spiders or spiders from Andean páramos. Roth (1997) produced a list of spiders recorded from Ecuador excluding the Galapagos Islands. This listed 315 species from 46 families, giving the province in which the specimen was collected but with no habitat data. Silva (1992) listed families she had recorded from cloud forests and high altitude grasslands in Peru, but did not differentiate between these habitats. The few keys that do exist begin at the family or sub-family level and are therefore of little assistance if the family is unknown. The Theridiidae of Chile are keyed out to family by Levi (1967), Ecuadorian and Peruvian genera of the Theridiidae subfamily Conopisthine are keyed out by Exline (1950), and Roth (1967) has produced a key to the genera of South American Agelenidae. Millidge (1985, 1991) has described Linyphiidae collected from South America. Whist the genitalia of each of the species described are illustrated, no keys are provided. Millidge points out in his text that the South American Linyphiidae lack any morphological characters that enable a key to be generated and therefore species determination relies solely on the structure of the genitalia. Ravens key to the sub-order Myglomorphae (1985) is however global in its coverage and will key specimens down to genera.

Without a simple taxonomic access point any ecological studies are severely hampered, and workers have to enlist the help of the handful of specialist that are working on the fauna of this region to ascertain even simple taxonomic criteria. A simple introductory key would be of great benefit to ecologist working on Andean páramos, as it would allow them to take these initial steps themselves.

MATERIAL AND METHODS

The material utilised in this study was collected from the páramos of Volcán Chiles, a volcano situated in Carchi Province, close to the Ecuador -Colombia border. The páramo was typical of this region: dominated by the tussock grass *Calomogrostis*, cushion plants, and giant rosette plants belonging to the genera *Puya* and *Espletia*. The material was collected over the summer months of 1997 and 1999 as part of a series of ecological investigations, some of which which are reported in other chapters of this volume (Oxbrough and Ramsay 2001, Pickett 2001, Smithers and Atkins, 2001, Smithers *et al*. 2001). Three forms of collection were used (pitfall traps, hand searches of individual grass tussocks, and more general searches of specific habitats) and the specimens examined in compiling this key were derived from all three sources.

RESULTS

Material collected by members of University of Plymouth expeditions has been assigned to 14 families (Table 1). Comparing this list with that compiled by Silva (pers. comm.) for high-altitude grasslands in Peru, there are significant differences along the Andean chain: only 8 of 19 families were shared (Table 1). This demonstrates how much more work is required to provide an adequate picture of the distribution of spider families in this region.

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 137-143.

Fig. 1. Josa riveti *(*B*ERLAND 1913) (a) Dorsal surface. (b) Ventral surface.*

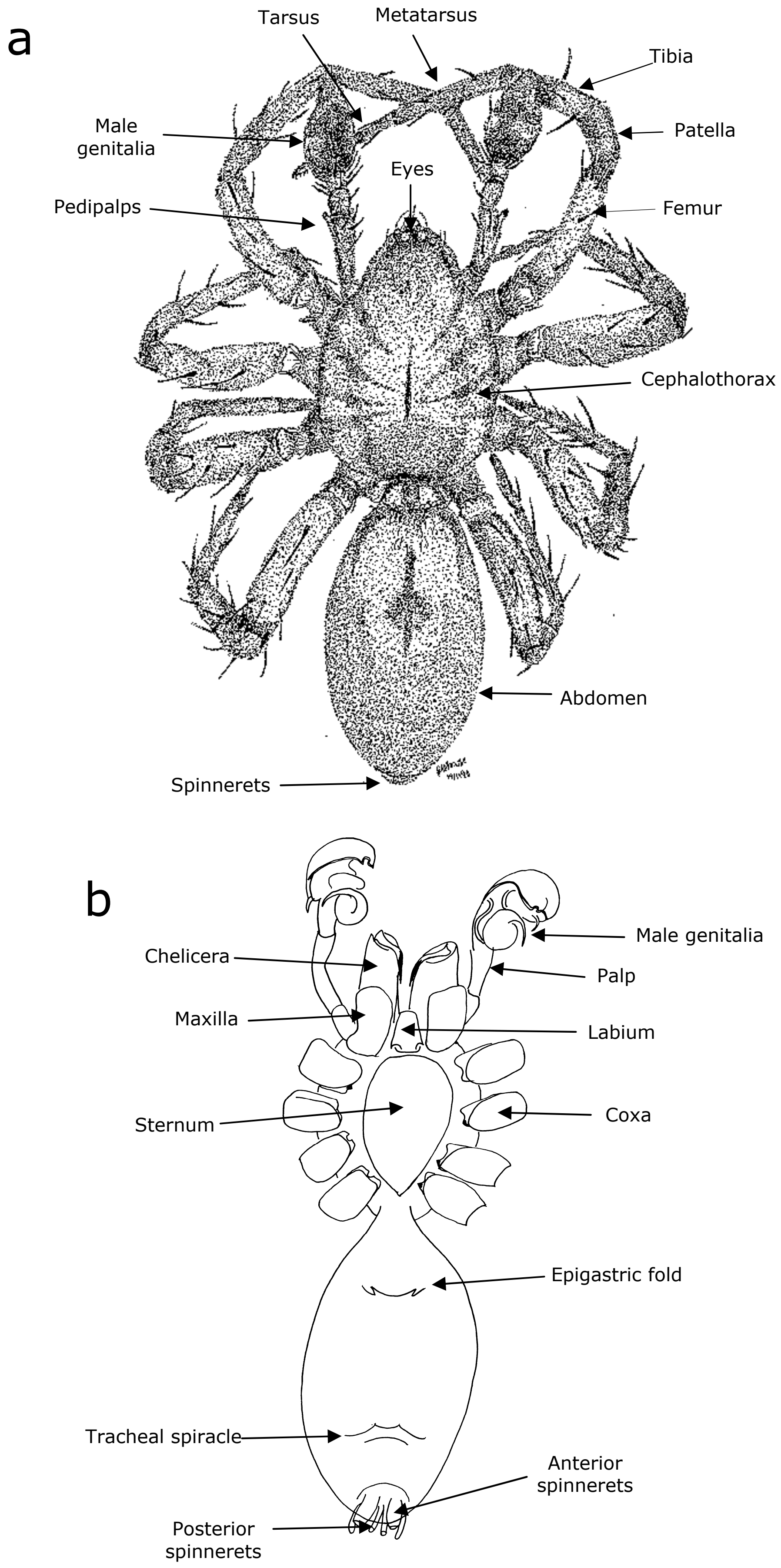


Table 1. Spider families identified from collections made at high altitudes in Ecuador (Volcán Chiles) and Peru (grasslands over 2000 m altitude in Manu National Park & Río Abiseo). The Peruvian data were provided by Diana Silva (American Museum of Natural History, New York).

Family	Ecuador	Peru
Araneomorphaa		
Agelenidae	+	
Anyphenidae	+	+
Araneidae	+	
Amaurobiidae	+	
Clubionidae	+	+
Cybaeidae		+
Dictynidae	+	+
Gnaphosidae		+
Hahniidae		+
Linyphiidae	+	+
Lycosidae	+	+
Mitergidae	+	
Ochyroceratidae	+	
Pholcidae	+	+
Salticidae	+	+
Tetragnathidae		+
Theridiidae	+	+
Thomisidae		+
Myglomorphae		
Cyrtaucheniidae	+	
Paratropididae	+	

PROVISIONAL KEY TO THE SPIDER FAMILIES OF THE PÁRAMOS OF VOLCÁN CHILES

This initial version of the key cannot provide comprehensive coverage of all páramo families because it is based on limited collection. However, it is hoped that this draft key will stimulate co-operation between biologists working on páramo spiders to develop a more comprehensive key in the future.

Workers who would like to contribute to the key are invited to contact the author directly. Preferably, requests to amend the key should be supported by loans of specimens or appropriate drawings of the taxa to be added. Where possible, other supporting material (*e.g.*, published papers covering these taxa) would also be welcome. All contributions will be fully acknowledged and materials sent will be returned if required. The most recent version of the key can be accessed on the web through the author's personal web page at the University of Plymouth, Department of Biological Sciences.

The following key is mostly composed of couplets, but in some cases triplets have been used to allow for families that have not yet been discovered in the páramos of Ecuador. The author would be grateful for notification of specimens that would require the key to be amended.

1 Chelicerae articulate parallel to each other, fangs directed along the length of the body (Fig. 2). Sub Order **Myglomorphae** 2

– Chelicerae articulate in opposition to each other. Sub Order **Araneomorpha**..3

2 Claw tufts absent, trichobothria present on all tarsi, book lung apertures narrow. Eyes in a compact group on a raised tubercle, occupying one-third of the width of the front of the cephalothorax (Fig. 3). ....Family **Paratropididae**

– Claw tufts absent, trichobothria present on all tarsi, book lung apertures narrow, tarsal claws with teeth on inner and outer margins. Terminal segment of posterior lateral spinnerets finger like. Eyes occupy at least half of the front of the cephalothorax, not on a raised tubercle (Fig. 4)......Family **Cyrtaucheniidae**

– Not as above............................new family for this key

3 Carapace with six eyes (Figs 5 & 6). 4

– Carapace with eight eyes (Fig. 7). When counting eyes look on top of the cephalothorax as well as the face..5

Fig. 2.

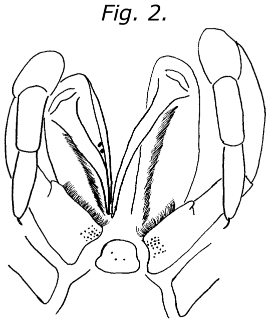


Fig. 3.

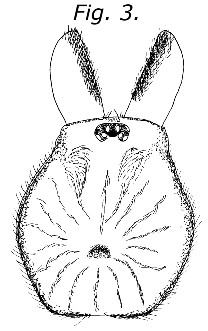


Fig. 4.

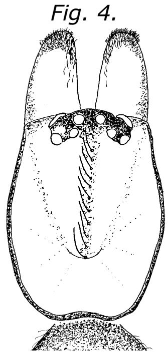


Fig. 5.

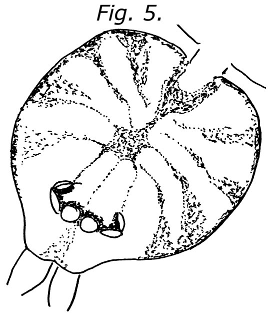


Fig. 6.

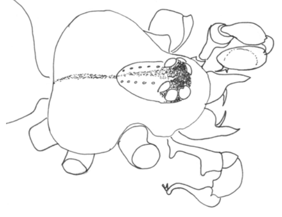


Fig. 7.

Fig. 8.

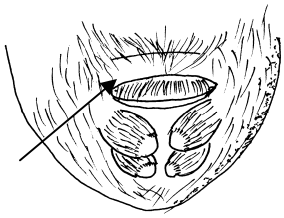


Fig. 9.

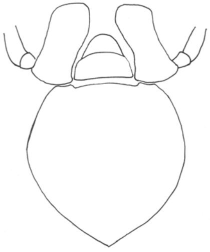


Fig. 10.

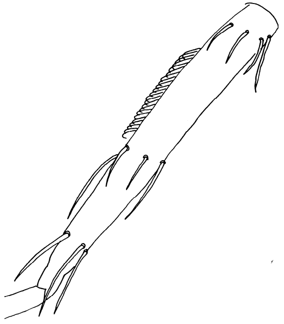


Fig. 11.

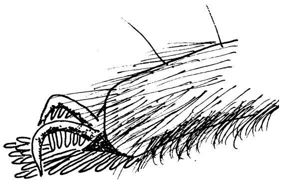


Fig. 12.

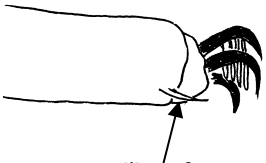


Fig. 13.

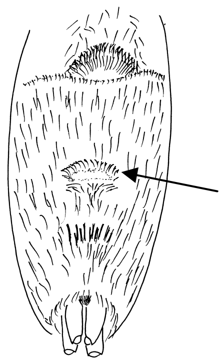


Fig. 14

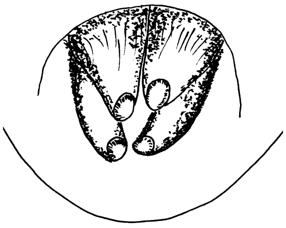


Fig. 15.

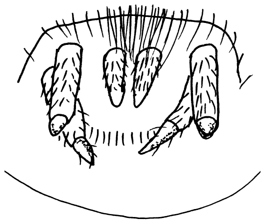


Fig. 16.

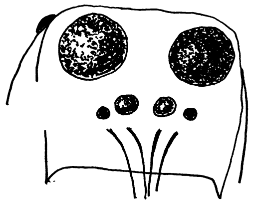


Fig. 17.

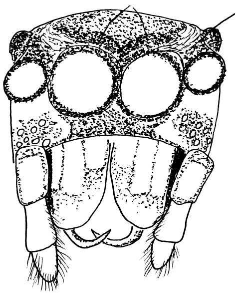
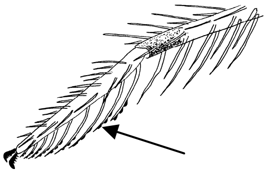


Fig.18.



4 Eyes in a single group at the front of the cephalothorax (Fig. 5). Very small body less than 5 mm. Tarsi comprised of a single segment with three claws. Cephalothorax not domed ....Family **Ochyroceratidae**

– Eyes in two groups of three (Fig. 6). Legs very long and slender. Tarsi flexible, composed of many small segments ....Family **Pholcidae**

– Not as above .... new family for this key

5 Cribellum (an extra plate of silk gland spigots) present (Fig. 8)...6

– Cribellum absent..7

6 Less than 5 mm in body length. Eyes in two rows, maxilla converging (Fig. 9) Calamistrum (a row of hooked seta) runs almost the entire length of metatarsi 4 (this may be difficult to see, look carefully from all angles). ....Family **Dictynidae**

– Body length greater than 5mm. Eyes in two rows. Calamistrum extends over only part of the length of metatarsi 4 (Fig. 10). ....Family **Amaurobiidae**

– Not as above .... new family for this key

7 Tarsi with 2 claws (Fig. 11)..8

– Tarsi with 3 claws (Fig. 12)..10

8 Tracheal spiracles situated between the epigastric fold and the spinnerets at least one-third the distance in front of the spinnerets (Fig. 13)..................Family **Anyphaenidae**

– Tracheal spiracle not obvious or situated adjacent to spinnerets..9

Fig.19.

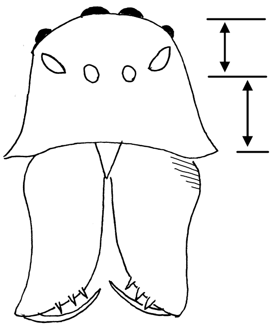


Fig. 20.

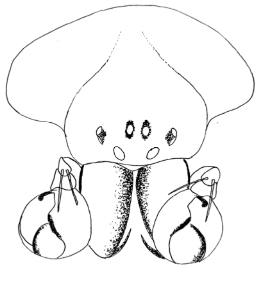


Fig. 21.

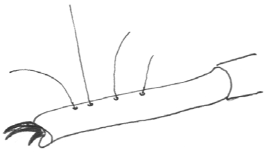
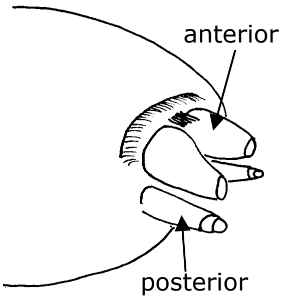


Fig. 22.



9 Anterior spinnerets conical in shape and close together (less than the width of the base of a single spinneret between them, (Fig. 14). Tarsi with two claws. Abdomen longer than cephalothorax .... Family **Clubionidae**

– Anterior spinnerets cylindrical and separated by a distance greater than the width of a single spinneret ....Family **Gnaphosidae**

– Not as above .... new family for this key

10 Posterior spinnerets longer than first two pairs and with two segments (Fig. 15) .... Family **Agelenidae**

– Posterior spinnerets not composed of two distinct segments, posterior spinnerets not longer than the others 11

11 Two of the eight eyes at least twice the diameter of the others (Figs 16 & 17)........................12

– All eyes approximately equal diameter...................13

12 Posterior median eyes much larger than anterior eyes (Fig. 16) ....Family **Lycosidae**

– Anterior median eyes much larger than the rest (Fig. 17) .... Family **Salticidae**

13 Tarsi four with a comb of serrated bristles (Fig. 18) ....Family **Theridiidae**

– Tarsi without comb of serrated bristles 14

14 Small spiders less than 4mm body length when mature. Clypeus as wide or wider than distance between first and second rows of eyes (Fig. 19). Chelicera often with a series of horizontal ridges on the outside surface.......................Family **Linyphiidae**

– Lager spiders. Clypeus narrow, less than distance between anterior and posterior rows of eyes (Fig. 20)..15

15 Tarsi without auxiliary foot claw, but with trichibothria on dorsal surface of tarsi (Fig 21). Posterior spinnerets conical and half the diameter of the anterior spinnerets which are cylindrical (Fig 22). ....Family **Mitergidae**

– Tarsi with an auxiliary foot claw (Fig. 10), tarsi without trichobothria (very fine sensory hairs). .... Family **Araneidae**

– Not as above .... new family for this key

BIOLOGY AND HABITAT OF THE FAMILIES

Whilst little information exists regarding the biology of spider families from South American páramos, there is a body of information from other continents and habitats. Roberts (1995) describes the fauna of Britain and northern Europe, and Dippenaar-Schoeman and Jocque (1997) offer an outline of the African fauna. Most of the generalised information on each of the spider families presented here was compiled from these two sources. Where available, collection details for the páramo specimens examined are provided. Oxbrough and Ramsay (2001) report one specimen each of the Oonopidae and Corrinidae, but these specimens were in poor condition and have not been included in the key at present.

Sub Order Araneomorpha

Family Araneidae

This family produces orb webs that have the centre filled with an unstructured lattice of silken threads. The spiral thread is coated with droplets of sticky glue to which prey items adhere.

They construct their webs in a wide variety of situations but are most frequently found amongst vegetation. As a result they are dependent on the structure of the vegetation for suitable web sites. Araneids are sit-and-wait predators that tend to intercept flying and jumping prey with their webs. The Araneidae mash their prey using a series of teeth on the chelicera; the resultant lump of chitenous debris is quickly cut free of the web.

Collected from the flower heads of the giant rosette plant, *Espeletia pycnophylla*. A single male was also caught in a pitfall trap on the open páramo.

Family Anyphaenidae

Members of this family are active hunters that forage amongst the foliage of trees, vegetation or the litter layer. They construct silken retreats on the undersides of leaves (Nentwig 1993).

They were abundant amongst the vegetation of the open páramo where they were caught in pitfall traps. They were also recorded from the dead leaf sheaths of the giant rosette plant, *Espeletia pycnophylla.*

Family Agelenidae

This family construct horizontal sheet webs with a tubular retreat at on edge. The retreat is open at both ends to facilitate the spider's escape should danger threaten. The web has no glue and the spiders rely on speed to retrieve the prey before it can escape. Webs are constructed in rock crevices, under stones or fallen timber or in undisturbed man-made structures. They are relatively sedentary but males become nomadic when searching for a mate.

They were extremely abundant on the open páramo were they were caught in pitfall traps.

Family Amaurobiidae

These are nocturnal hunters that spend the day under stones and logs or in holes in trees. They construct an untidy tangle web that has a bluish tinge when the silk is fresh. They prey on ground dwelling invertebrates or occasional flying insects that land in their webs.

They were recorded from within the leaf sheaths of the giant rossett plant *Espeletia pycnophylla*.

Family Clubionidae

This family are free-living nocturnal hunters that spend the day in silken retreats under stones, loose bark or amongst vegetation. These retreats are frequently constructed from folded leaves, held together with silk. They hunt throughout vegetation and use their long, first pair of legs to capture prey.

Collected from the flower heads of *Espeletia pycnophylla* and caught in pitfall traps on the open páramo.

Family Dictynidae

The Dictynidae belong to the group of spiders known as cribellates, which posses an extra set of silk producing glands that generate very fine multi-stranded silken threads. The many fine threads easily entangle the spiny limbs of many insects. They tend to construct their webs on the upper surface of the vegetation but some occur at ground level under stones.

Collected from the dead leaf sheaths of *Espeletia pycnophylla* and caught in pitfall traps on the open páramo.

Family Gnaphosidae

These are ground dwelling nocturnal hunters that spend the day in a silken retreat beneath surface debris. Some members of this family have formed associations with ants.

This family does not comprise a large proportion of the Ecuadrian fauna, Roth (1997) lists only 4 species from this family. No members of this family were collected from the sites sampled but it is included in this key as this family is easily confused with the Clubionidae

Family Linyphiidae

Most members of this family are small—less than 4 mm in length. They construct small sheet webs amongst the vegetation or across indentations in the ground and hang beneath them whilst waiting for prey. Other members of this family live in the litter layer. This family becomes dominant at higher latitudes and altitudes. In recent studies of the spiders of Volcán Chiles the number of morphotypes assigned to this family comprised 38% of the total.

Collected from grass tussocks, under stones in riparian gullies and caught in pitfall traps on the open páramo.

Family Lycosidae

These are ground dwelling spiders that hunt by day. Some actively hunt their prey, but most adopt a sit-and-wait strategy. Females carry the egg sac attached to their spinnerets; when the eggs hatch the spiderlings climb onto their mother's back and are carried until they undergo the first moult.

This family was caught in pitfall traps on the open páramo where it was abundant between the altitudes of 3850 and 3950 m.

Family Mitergidae

Most members of this family are nocturnal and are found in the litter layer of forests. Little information is available regarding their natural history.

Collected from the litter layer in *Polylepis* woodlands and riparian gullies.

Family Ochyroceratidae

Only one specimen from this family appears in Roth's (1997) list. It is a small family with only 54 species known globally to date. They have been recorded from deep litter in forests and caves where they construct an irregular space web; little is known of their biology.

A single specimen was collected from under stone on the open páramo at 3600 m.

Family Pholcidae

This family construct a tangled space web in a variety of situations but often close to the ground. Some species are found in caves whist a few small species occur under stones and in rock fissures. They feed on invertebrates caught in their web but often invade the webs of other spiders and consume the occupants.

Two individuals were caught in a pitfall trap on the floor of a *Polylepis* woodland at about 3900 m.

Family Salticidae

Members of this family are diurnal hunters with very good eyesight. They stalk their prey using visual cues and leap on them when close enough. They construct silken cells in which to moult and produce eggs. They are extremely dependant on temperature and will remain hidden in a suitable retreat until it is warm enough to forage.

Collected from under stones in wooded and non-wooded riparian gullies, also caught in pitfall traps on the open páramo.

Family Theridiidae

This is a diverse family in which most posses a tarsal comb of serrated bristles on the fourth tarsi. This is used to cast strands of silk over their prey once they have become entangled in their web. The webs are extremely variable ranging from a simple h-like structure on which the spider sits to a combination of an untidy sheetweb with a maze of vertical threads fixed to the upper surface.

Collected from the flower heads and dead leaf sheaths of *Espeletia pycnophylla;* also from grass tussocks.

Sub Order Myglomorpha

Family Cyrtaucheniidae

This family constructs silk-lined burrows that are often beneath stones or fallen timber.

Collected from under stones on the open páramo

Family Paratropididae

Little information is available for this family in South America.

Collected from grass tussocks on the open paramo.

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REFERENCES

Dippenaar-Schoeman, A.S. and Jocque, R. (1997) *African Spiders: an identification manual,* Pretoria: ARC Plant Protection Division.

Exline, H. (1950) Conopisthine Spiders (Theridiidae) from Peru and Ecuador. In, *Studies Honouring Trevor Kincaid.* pp. 107–167. Washington (DC): University of Washington.

Levi, H.W. (1967) The Theridiid spider fauna of Chile. *Bulletin of the Museum of Comparative Zoology,* **136**: 1–20.

Millidge, A.F. (1985) Some Linyphiid spiders from South America (Araneae, Linyphiidae). *American Museum Novitates,* **2836**: 1–78.

Millidge, A.F. (1991) Further Linyphiid spiders (Araneae) from South America. *Bulletin of the American Museum of Natural History,* **205**: 1–199.

Nentwig, W. (1993) *Spiders of Panama.* Gainsville, Florida: Sanhill Crane.

Oxbrough, A.G. and Ramsay, P.M. (2001) Páramo spiders of Volcán Chiles, Ecuador. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 159–168. Plymouth: Pebble & Shell.

Pickett, B.R. (2001) Comparison of terrestrial invertebrate communities in páramo areas with different recent fire histories. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 153–158. Plymouth: Pebble & Shell.

Raven, R.J. (1985) The spider infraorder Myglomorphae. *Bulletin of the American Museum of Natural History,* 182: 1–182.

Roberts, M.J. (1995) *The Spiders of Britain and Northern Europe.* London: Harper Collins.

Roth, V.D. (1967) A review of the South American spiders of the family Agelinidae (Arachnida, Araneae). *Bulletin of the American Museum of Natural History,* **134**: 299–345.

Roth, V.D. (1997) Working List of Spiders of Ecuador (excluding the Galapagos Islands). Internet (http://spiders.arizona.edu/roth/ECUALIST.html).

Smithers, P. and Atkins, N. (2001) Altitudinal variation in páramo invertebrate communities on Volcán Chiles, with particular reference to Carabidae (Coleoptera). In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 145–151. Plymouth: Pebble & Shell.

Smithers, P., Ramsay, P.M., Bond, A.N. and Burne, M.E. (2001) Macroarthropod communities of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis.* In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 169–175. Plymouth: Pebble & Shell.

Silva, D. (1992) Observations on the diversity and distribution of the spiders of Peruvian montane forests. *Memorias del Museo de Historia Natural, U.N. (Lima),* **21**: 31–37.

Altitudinal variation in páramo invertebrate communities on Volcán Chiles, with particular reference to Carabidae (Coleoptera)

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SUMMARY

The invertebrate community of zonal páramo grassland was sampled at five altitudes on Volcán Chiles (Ecuador-Colombia border) using pitfall trap arrays. Most specimens were identified to order level, but Coleoptera were determined to family level. Six new species of carabid were discovered in this study, described by Moret (2001). A discontinuity in distributions was apparent at around 4000 m altitude: there was greater species diversity and a different composition of species in samples from above this altitude compared with lower altitude samples. This pattern may be related to a discontinuity in vegetation at a similar altitude, observed on Volcán Chiles and in páramos elsewhere in Ecuador. It appears to be associated with reduced density of *Calamagrostis* tussock grass at higher altitudes, which results in significant changes in physiognomy, vegetation composition and microclimate. The Carabidae were more diverse above 4000m and appeared to display partitioning over the altitudinal range sampled. The distinctiveness of the invertebrates of Volcán Chiles highlights the need for more research on high altitude invertebrates here and in other páramo areas.

RESUMEN

Se realizaron muestreos de la comunidad de invertebrados del pastizal zonal del páramo del Volcán Chiles (frontera Ecuador-Colombia) utilizando conjuntos de trampas de fosa ("pitfall traps") en cinco altitudes. La mayoría de los especimenes se determinaron al nivel de orden, con excepción de los Coleoptera, los cuales se identificaron a nivel de familia. Se descubrieron seis especies nuevas de carábidos en este estudio, las cuales han sido descritas por Moret (2001). Una discontinuidad en la distribución de las especies fue aparente alrededor de los 4000 m de altitud: la diversidad de especies fue mayor y la composición de especies cambió drásticamente en las muestras por arriba de esta altitud. Este patrón pueda estar relacionado con una discontinuidad en la vegetación a altitudes parecidas, observada en el Volcán Chiles y otros páramos en Ecuador. Esta discontinuidad parece estar asociada con una reducción en la densidad de macollos de *Calamagrostis* en las mayores altitudes, la cual resulta en cambios significativos en la fisonomía, la composición de la vegetación y el microclima. Los Carabidae fueron más diversos por encima de los 4000 m y parecieron manifestar una repartición del rango altitudinal. La peculiaridad de los invertebrados del Volcán Chiles subraya le necesidad de investigar los invertebrados de grandes altitudes tanto aquí como en otras áreas de páramo.

Key words: arthropods, tropical alpine, beetles, species diversity

INTRODUCTION

Climate has been shown to have a dramatic effect on invertebrate populations (Speight *et al.* 1999) and varies along altitudinal gradients—temperatures are lower at high altitudes. In temperate regions these lowered temperatures have a profound effect on the life cycle of high altitude invertebrates. Recent work on carabid beetles has shown that species occurring at low altitudes possess an annual life cycle whilst those found at higher altitudes have a biannual life cycle (Sparks et al. 1995, Butterfield 1996, Sota 1996). The responses of terrestrial invertebrates to altitudinal gradients in tropical mountains, where seasonality is less pronounced or lacking altogether, are poorly understood.

The páramo grasslands of the High Andes of Ecuador and Colombia provide a natural laboratory for studying tropical mountain gradients. Temperatures decrease by 0.6°C for every 100 m increase in altitude (Rundel 1994). However, daily variation in temperature can be extreme: daily air temperatures range from 21°C to -2°C and soil temperatures at 0.5 cm depth from 52°C to – 2°C (Sømme *et al.* 1996). Hedberg (1964) summed up this climatic regime as "summer every day, winter every night".

The invertebrates of Andean páramos are little collected and poorly described; keys or species lists are unavailable for most groups. However, progress is being made with some invertebrate taxa—the carabid beetles, for example, have been the subject of recent work by Moret (1998, 2001). The lack of taxonomic treatments for most invertebrate groups results in considerable difficulties for ecological studies because many of the taxa involved may be new to science. Therefore, few community-level investigations of páramo invertebrates have been attempted. Pickett (2001) collected samples of invertebrate communities in areas with differing fire histories, and Smithers *et al.* (2001) described invertebrate communities in the giant rosette plant, *Espeletia pycnophylla*. Other work has concentrated on the adaptations of particular invertebrate species to low temperatures and desiccation at high altitudes in the páramo (Sømme 1986, Sømme *et al.* 1996).

Elsewhere, studies of invertebrate biodiversity and altitude have indicated that diversity declines as altitude increases (Speight *et al.* 1999), but there are no data available for tropical alpine mountains.

The current study describes invertebrate community composition across an altitudinal gradient in an Ecuadorian páramo grassland. As the Carabidae of this region are relatively well documented (Moret 2001), this group was examined in more detail.

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 145-151.

METHODS

Study areas

Invertebrate communities were sampled in five sites on the south-western side of Volcan Chiles on the Ecuador-Colombia border, covering an altitudinal range from 3730 to 4150 m (Fig. 1). The lower sites were located in grassy paramo vegetation, dominated by *Calamagrostis* grass tussocks and giant rosettes of *Espeletia pycnophylla* subsp. *angelensis*. The vegetation physiognomy changed between 4000 and 4100 m: above the transition zone, there were fewer giant rosette plants and smaller, dispersed tussock grasses and large cushions of *Plantago rigida* and *Werneria humilis* dominated the vegetation. Cattle and horses grazed in the area, and small sections of the páramo were often burned by farmers to generate fresh growth for the livestock.

Fig. 1. The location of the five study sites.

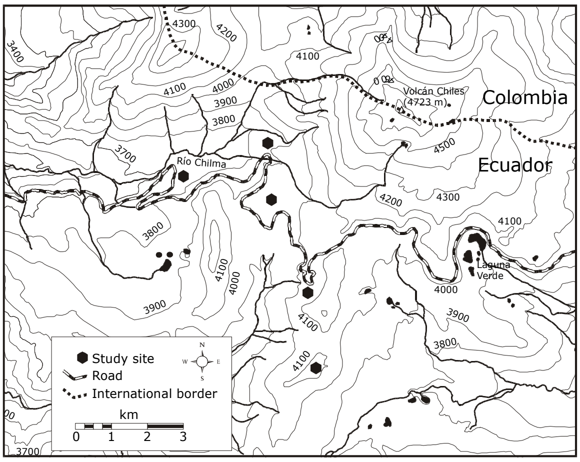
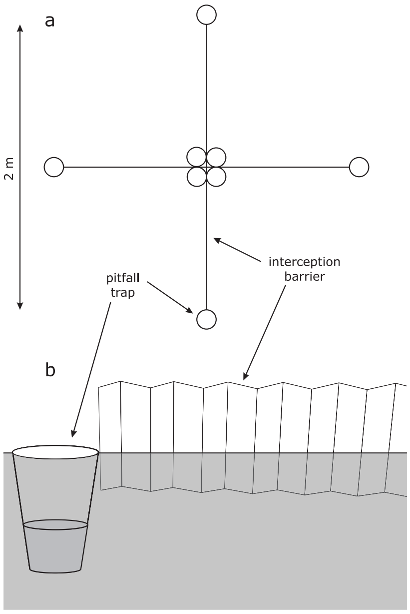


Fig. 2. Trap design for sampling terrestrial invertebrate communities. a. plan view. b. side view.



Sampling and identification of specimens

The work took place during August 1997. Invertebrate communities were sampled using a pitfall trap array with interception barriers (Fig. 2). These consisted of two 2 m lengths of 15 cm wide corrugated lawn edging which were arranged at right angles to each other and buried to a depth of approximately 5 cm in the soil. Plastic cups were buried in the soil at the ends of each length of lawn edging and in each of the right angles formed by the central intersection, giving a total of eight pitfall traps. The cups were part filled with antifreeze (ethylene glycol) in order to kill and preserve the catch. They were left in place for two weeks after which the traps were emptied and the catch preserved in 70% ethanol. Two trap arrays were established in each location, but cattle destroyed one of these at the lowest altitude. Therefore, a total of nine samples were collected.

Preserved material was identified at the University of Plymouth to order level. The Coleoptera were sorted from the other specimens and identified to family using Unwin (1988), representative specimens of Carabidae were determined by Pierre Moret (Toulouse) and a working key, provided by Moret, was used to identify the remaining specimens (see Moret 2001 for a full key partly based on specimens from this study).

Data analysis

Species diversity was examined using four different measures. The first was the number of species in each 25 m² sample (species richness, S). Shannon's index of information content, was calculated according to the formula:

$$H' = \sum_{i=1}^{S} p_i \log p_i$$

where p_i is the proportional abundance of species i in the sample. The evenness of non-zero species abundances (equitability) was calculated by:

$$E = \frac{H'}{\ln S}$$

Finally, the complement of Simpson's original index for a finite population was calculated as follows:

$$D = 1 - \sum_{i=1}^{S} p_i^2$$

It represents the likelihood that two randomly chosen individuals will be different species, reaching maximal values for a sample with all species present in equal abundance.

The samples were grouped by cluster analysis, using relative Sørensen's distance measure and Ward's method of group linkage. The invertebrate samples and species were ordinated (using the Bray-Curtis method, modified to use relative Sorensen's distance measure and endpoint selection by variance-regression). All of these analyses were performed with the PC-ORD package (McCune and Mefford 1999).

RESULTS

There were 49 taxa in the nine samples (Table 1). The commonest invertebrate taxa were Araneae, Diptera, Collembola, Opilliones, Hymenoptera, Lepidoptera, Dermaptera and Coleoptera. Within the Coleoptera, the dominant families were Carabidae, Curculionidae and Chrysomelidae. Of the ten named species of carabid, five were new to science (*Dyscolus riveti, Dyscolus lubricus, Dyscolus atkinsi, Dyscolus breviculus, Dyscolus smithersi*—Moret 2001), and the presently undescribed *Bembidion* species is also new (Moret 2001).

The number of taxa caught in any one trap array varied from 15 to 25 (Table 2). At 4050 m and above, species diversity was higher than at altitudes at 3950 m and below.

The distinction between the two highest sample areas and the rest was also evident from the cluster analysis (Fig. 3). Pitfall trap arrays at and above 4050 m were separated from those at lower altitudes on the basis of their species composition. Furthermore, while the higher altitude traps showed clear altitudinal separation, the lower altitudinal samples showed less consistency within replicate samples. The separation of the samples at 4050 and 4150 m from the rest, and the variability within the samples from 3950 m, is clear in the Bray-Curtis ordination of sites (Fig. 4).

The Bray-Curtis ordination of taxa is shown in Fig. 5. Species plotted close together tend to have similar distributions among the pitfall trap samples. Furthermore, this ordination is constructed in the same ordination space as Fig. 4—species occupying a similar position in Fig. 5 to a sample in Fig. 4 tend to characterise this sample. Axis 1, represents at a crude level the altitudinal gradient, with species on the left side characteristic of lower altitude samples, and those on the right characteristic of higher altitude samples. Axis 2 represents an additional source of variability more or less independent of altitude.

Interestingly, the majority of carabid species are located at the fringes of the ordination—their distributions are distinct and confined to particular samples. The partitioning of the páramo between species of carabid is clear from Fig. 6. There appear to be three groups of carabids occurring at different altitudes: 4150 m (*Dyscolus montivagus, D. fronto, D. carassus, D. smithersi* and *Oxytrechus vulcanus*), 4050 m (*D. onore, D. riveti* and *Bembidion* sp.), and 3850 m (*D. atkinsi, D. breviculus* and *D. lubricus*).

DISCUSSION

The invertebrate communities described in this study were composed of orders and families characteristic of grassland ecosystems, with the exception of ants (Formicidae), which were not present at all. Ants are strongly thermophilic, and they function poorly below 20°C and not at all below 10°C—they disappear from tropical mountains at altitudes of approximately 2500 m (Hölldobler and Wilson 1990).

The main distributional pattern found in this study was the distinction between communities above 4000 m and those below. Invertebrate diversity was higher above 4000 m than below. However, this may be an artefact of the level of identification to which different groups of invertebrates were taken. The Coleoptera, more abundant at higher altitudes, were identified to species level whereas other taxa were often determined only to the level of order. Carabids belonging to the genus *Dyscolus* also tend towards a distribution at higher altitudes in other Ecuadorian páramos (Moret 1998).

Nevertheless, the distinction between the two zones of the páramo of Volcán Chiles is confirmed in the abundances of other invertebrate orders. Lower altitude samples were indicated by high abundances of Araneae, Diptera, Hemiptera and Chalcidoidea, whilst the higher altitude samples were characterised by Opilliones as well as the taxa of Coleoptera referred to earlier.

With such a small set of data and with no environmental measurements, it is only possible to speculate on the factors responsible for these differences.

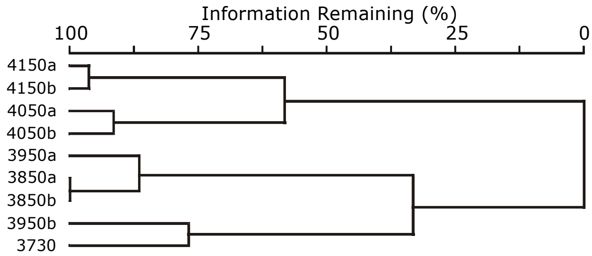


Fig.3. Cluster analysis of the nine samples of terrestrial invertebrates.

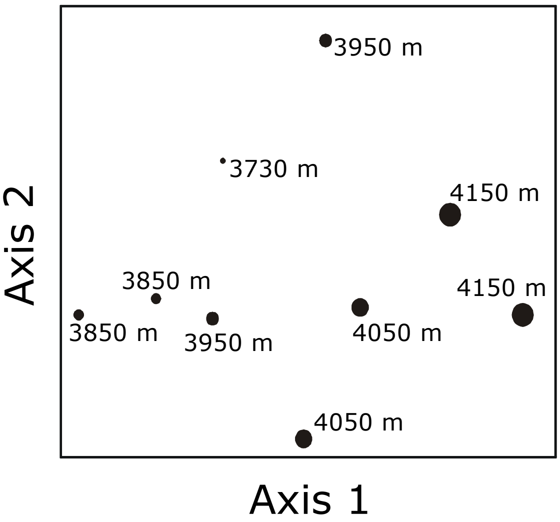


Fig. 4. Bray-Curtis ordination of the nine samples of terrestrial invertebrates.

Table 1. Invertebrate taxa collected in nine pitfall trap arrays.

	Altitude (m)								
	4150	**4150**	**4050**	**4050**	**3950**	**3950**	**3850**	**3850**	**3730**
Sample number	***283***	***284***	***285***	***286***	***287***	***288***	***289***	***290***	***291***
Dyscolus fronto	18	31	3	1					
Dyscolus riveti	5	3	19	7					
Dyscolus montivagus	17	26							
Dyscolus carassus	4	1							
Oxytrechus vulcanus		1							
Bembidion sp.			7	48	3		1	5	
Dyscolus onorei				2					
Dyscolus lubricus							3	3	
Dyscolus atkinsi							8	15	
Dyscolus breviculus			1				4	4	
Dyscolus smithersi		8							
Unidentified Beetle		1							
Curculionidae A	1	6		4	1		3	1	
Curculionidae B		1	1						
Curculionidae C	4	2	4	3					1
Curculionidae D	4	2	2	2			1	2	
Curculionidae E					1				
Curculionidae F	2		2	1			2		
Chrysomelidae A	1		3	2	1	2			3
Chrysomelidae B			1		1	2	2	1	
Chrysomelidae C						5			8
Chrysomelidae D		1							
Chrysomelidae E			3				1		
Elateridae A			1						
Elateridae B						3			
Staphylinidae					1				
Pselaphide			1	2			5	1	2
Haliplidae		1							
Sicadelidae				1			6	1	4
Dytiscidae				1		6			1
Leiodidae			1				16	3	
Scaphidae									
Araneae	7	18	8	5	31	55	45	45	50
Diptera	5	18	38	51	27	56	66	88	77
Hemiptera		1		1	1	10	4		124
Collembola	21	38	46	23	9	164	19	2	19
Opilione	12	7	20	18	8	5	6	11	1
Hymenoptera	8		8	8	6	20	5	5	20
Lepidoptera	4	3	8	3	2	4	6	1	2
Phasmida	1	2					1	1	
Acari		1				7	1	3	12
Isopoda	7	3	2	2			2		1
Dermaptera	3	1	3	2	6	8	1		11
Thysanura							2		
Chilopoda				1		3			
Annalida				1			1		1
Orthoptera					1	1			
Chalcidoidea						133			40
Thysanoptera						7			5

Fig. 5. Bray-Curtis ordination of invertebrate taxa collected in nine pitfall trap arrays.

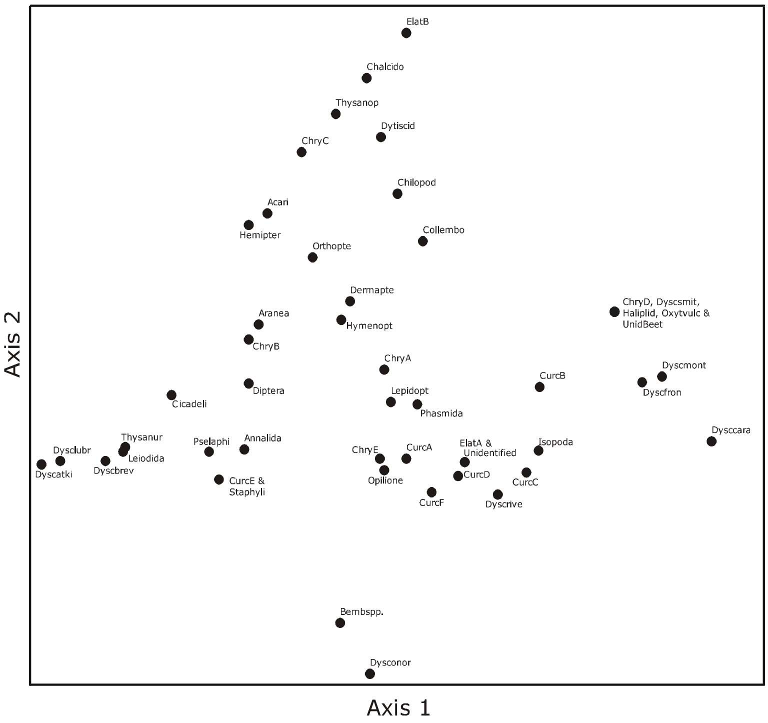


Fig.6. Altitudinal distribution of carabid species collected in nine pitfall trap arrays.

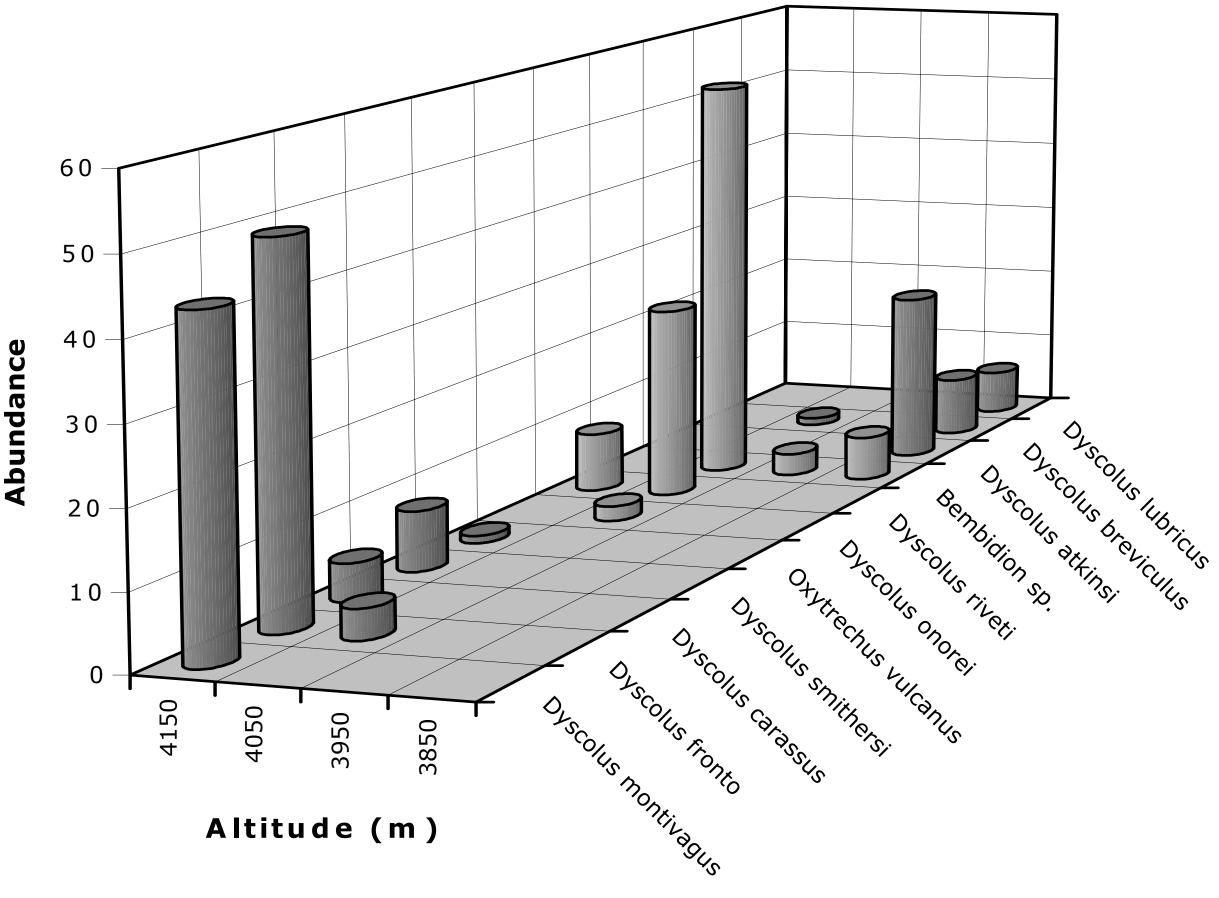


Table 2. Species diversity in the nine pitfall samples.

Altitude	S	E	H′	D
4150a	18	0.884	2.556	0.9031
4150b	23	0.764	2.395	0.8733
4050a	23	0.763	2.391	0.8624
4050b	23	0.711	2.230	0.8331
3950a	15	0.734	1.989	0.8034
3950b	18	0.663	1.917	0.7862
3850a	25	0.726	2.336	0.8362
3850b	18	0.618	1.786	0.7227
3730	19	0.700	2.061	0.8180
Overall	20.2	0.729	2.184	0.8265

Invertebrate populations may be responding to changes in the structure of vegetation at this altitude. Important changes in plant community composition at around 4000 m have been found for Volcán Chiles (Ramsay 2001b), Ecuadorian páramos in general (Sklenář and Ramsay, in press), and even beyond the Andes in the Mexican volcanoes (Ramsay and Almeida-Leñero, unpublished manuscript). Since many invertebrate species depend on particular plants for food and shelter, it is not surprising to find rapid changes in invertebrate community structure where plant community structure changes rapidly—such as at the grassy páramo to superparamo transition zone located at around 4000 m on Volcán Chiles.

Some carabids are well known as seed predators feeding on a range of seeds. A change in the diversity of plant species above 4,000 m could alter the range of seed size and morphology allowing the partitioning of this potential food resource between carabid species. As seeds require larger muscles to break them open, the muscles of the mandibles occupy a larger proportion of the head capsule and the muscles for the maxilla are subsequently smaller, with associated morphological characters (Forsyth 1982)—but none of the carabid species from Volcán Chiles exhibited these characteristics. Therefore, a link between these carabids and plant seed resources must be ruled out, but does not preclude other dependent interactions between carabids, or other invertebrate taxa, and plants.

Invertebrate taxa are susceptible to freezing and some species from cold environments have evolved the ability to produce glycerol in their haemolymph and other body fluids, a process known as supercooling (Speight *et al*. 1999). The glycerol acts as antifreeze and prevents the formation of ice crystals which can damage cells and tissues. Studies of Coleoptera from high altitude environments indicate that supercooling is not a common adaptation. Rossolimo (1994) examined 41 species of beetle from the Khybiny Mountains and Pola Urals and found only two species that exhibited supercooling. Only a few species of carabids have been shown to exhibit supercooling in the páramo (Sømme *et al*. 1996). The main strategy of páramo invertebrates appears to be the behavioural avoidance of cold temperatures. Some seek shelter from the low temperatures in the soil, others under stones, and many move into the vegetation which maintains warmer temperatures at night. In addition, there appears to be a community of páramo invertebrates that spend the majority of their lives inside the giant rosette plant, *Espeletia pycnophylla* (Smithers *et al*. 2001).

The shift in plant species composition on Volcán Chiles is also reflected in significant physiognomic changes: below 4000 m the tussock grass *Calamagrostis* is the dominant plant while it is far less abundant above. There is also an increase in cushion plants above 4000 m. Dense tussock cover at lower altitudes provides a relatively uniform microclimate at ground level, with dense shade and buffered temperature regimes (Ramsay 2001a). The more fragmented tussock cover above 4000 m may allow direct sunlight to warm the ground by day, but radiate heat faster at night—as well as providing a more spatially variable environment. At the same time, the interior of cushion plants can be 4–5°C warmer than the air temperature at night (Ramsay 2001a). The higher spatial variability in microclimate at higher altitudes might provide a greater opportunity for coexistence between invertebrate species at these altitudes, an effect which has been demonstrated in other ecosystems (Strong *et al*. 1984). The same effect was evident in the Carabidae, where there was clear partitioning between three groups of species at distinct altitudes: 4150 m (*Dyscolus montivagus, D. fronto, D. carassus, D. smithersi* and *Oxytrechus vulcanus*), 4050 m (*D. onore, D. riveti* and *Bembidion* sp.), and 3850 m (*D. atkinsi, D. breviculus* and *D. lubricus*). Other taxa may share similar patterns but since only the Coleoptera were identified to the level of species, such patterns cannot be determined from these data.

The more or less continuous cover of tussock grasses below 4000 m also influences the disturbance regime—burning, trampling and grazing are commonest in this zone because tussocks provide the principal fuel for páramo fires and cattle graze preferentially in recently burned patches (Ramsay 2001b). Invertebrate communities are distinct in areas of Volcán Chiles with different fire histories, presumably because of differential responses to the fires themselves and the changing resource base characteristic of post-fire vegetation succession (Pickett 2001). Some species even appear to be pyrophilous and are associated with areas which have been recently burned (*e.g*., *Sericoda bembidioides*—Moret 2001). The high variability between sample areas at 3950 m, and the overall differences in invertebrate composition between the grassy páramo and the superpáramo, may be explained in terms of these responses to disturbance regimes.

This study has shown that invertebrate communities do vary with altitude in the páramo of Volcán Chiles. Despite a low number of samples, six new species of carabid beetles were discovered, with the potential for many other new species among the other families and orders. This illustrates our poor knowledge of páramo invertebrates and highlights the need for more studies in the future. Moret (2001) notes that the carabids of Volcán Chiles are distinct from those of the rest of Ecuador, to the south of the Mira Depression, and more ecological studies in these other areas would be useful. On Volcán Chiles, more detailed ecological investigations with invertebrate communities are underway, alongside taxonomic studies of the specimens collected (directed from the University of Plymouth). This partnership between taxonomists and ecologists is vital for progress in this area in the future.

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REFERENCES

Butterfield, J. (1996) Carabid life cycle strategies and climate change: a study on an altitudinal transect. *Ecological Entomology*, **21**: 9–16.

Forsyth, T.G. (1982) Feeding mechanisms of certain ground beetles (Coleoptera: Carabidae). *Coleopterist Bulletin*, **36**: 26–73.

Hedberg, O. (1964) Features of Afroalpine Plant Ecology. *Acta Phytogeographic Suecica*, **49**: 1–144.

Hölldobler, B. and Wilson, E.O. (1990) *The Ants,* Berlin: Springer.

McCune, B. and Mefford, M.J. (1999) *PC-ORD: multivariate analysis of ecological data. Version 4.* Gleneden Beach (Oregon): MjM Software.

Moret, P. (2001) The ground beetles of the Chiles area (Coleoptera, Carabidae): a taxonomic review and ecological overview. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 125–135. Plymouth: Pebble & Shell.

Pickett, B.R. (2001) Comparison of terrestrial invertebrate communities in páramo areas with different recent fire histories. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 153–158. Plymouth: Pebble & Shell.

Ramsay, P. M. (2001a) Diurnal temperature variation in major growth forms of an Ecuadorian páramo plant community. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 101–112. Plymouth: Pebble & Shell.

Ramsay, P.M. (2001b) The zonal paramo vegetation of Volcan Chiles. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 27–38. Plymouth: Pebble & Shell.

Rossolimo, T.E. (1994) Cold-hardiness of Coleoptera from the Subarctic region (comparative analysis). *Zoologichesky Zhurnal*, **73**: 101–113.

Rundel, P.W. (1994) Tropical alpine climates. In: Rundel, P.W., Smith, A.P. and Meinzer, F.C. (Eds.) *Tropical Alpine Environments: Plant Form and Function*, pp. 21–44. Cambridge: Cambridge University Press.

Sklenář, P. and Ramsay, P.M. (in press) Diversity of zonal páramo plant communities in Ecuador. *Diversity and Distributions.*

Smithers, P., Ramsay, P.M., Bond, A.N. and Burne, M.E. (2001) Macroarthropod communities of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis*. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 169–175. Plymouth: Pebble & Shell.

Sømme, L., Davidson, R.L. and Onore, G. (1996) Adaptations of insects at high altitudes of Chimborazo, Ecuador. *European Journal of Entomology*, **93**: 313–318.

Sota, T. (1996) Altitudinal variation in life cycles of carabid beetles: life cycle strategy and colonisation in alpine zones. *Artic and Alpine Research,* **28**: 441–447.

Sparks, T.H., Buse, A. and Gadsden, R.H. (1995) Life strategies of *Carabus problematicus* (Coleoptera, Carabidae) at different altitudes on Snowdon, North Wales. *Journal of Zoology*, **236**: 1–10.

Speight, M.R., Hunter, M.D. and Watt, A.D. (1999) *Ecology of Insects,* Oxford: Blackwell Science.

Strong, D.R., Lawton, J.H. and Southwood, R. (1984) *Insects on Plants,* Oxford: Blackwell Scientific.

Unwin, D.M. (1988) *A Key to the Families of British Beetles,* Preston Montford: Field Studies Council.

Comparison of terrestrial invertebrate communities in páramo areas with different recent fire histories

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SUMMARY

Terrestrial invertebrate communities were sampled from four páramo grassland areas on Volcán Chiles, Ecuador, with different recent fire histories. The sites were burned two weeks, three months, six months and two years prior to sampling with pitfall trap arrays and hand searches of individual tussocks. The commonest taxa were Collembola, Acari, Chalcidoidea, Hemiptera, Diptera, Araneae and Coleoptera. Community composition was distinct in each of the four sites, perhaps reflecting differential mortality during fires and the changing resource base associated with the successional recovery of páramo vegetation after fire. Detritivores were the dominant element in all sites, though detritivore orders followed a successional pattern with Acari the most abundant taxon in the initial stages of recovery and Collembola the most abundant two years after burning. Herbivores reached their peak abundance in the intermediate stages (at a time when tussock shoot growth would be most productive). Predators represented 16–18% of the catch in all pitfall samples. The significance of burned patches in various stages of recovery from variable intensity fires is discussed in relation to invertebrate species diversity.

RESUMEN

Se realizaron muestreos de comunidades de invertebrados terrestres en cuatro áreas de páramo con diferentes historias recientes de fuego en Volcán Chiles, Ecuador,. Estos sitios fueron quemados dos semanas, tres meses, seis meses y dos años antes del inicio del muestreo. El muestreo se realizó con conjuntos de trampas de fosa ("pitfall traps") y busquedas a mano sobre macollos. Los taxa más comunes fueron Collembola, Acari, Chalcidoidea, Hemiptera, Diptera, Araneae y Coleoptera. La composición de la comunidad fue distinta en cada uno de los cuatro sitios, reflejando quizá la mortalidad diferencial durante los fuegos y los cambios en la base de recursos asociados con la recuperación sucesional de la vegetación del páramo después del fuego. Los detritívoros fueron el elemento dominante en todos los sitios, pero los ordenes de los detritívoros siguieron un patrón succesional siendo los ácaros el taxón más abundante en las etapas iniciales de recuperación y los colémbolos el más abundante dos años después de la quema. Los herbívoros alcanzaron su mayor abundancia en las etapas intermediadas (justo en el momento cuando la producción de brotes de los macollos fue mayor). Los depredadores representaron 16-18% de la captura en todas las trampas. Se discute la importancia de la existencia de un mosaico de parches quemados en varias etapas de recuperación, producto de fuegos de diferentes intesidades, en relación a la diversidad de especies de invertebrados.

Key words: burning, feeding guilds, succession, tropical alpine

INTRODUCTION

The páramos are alpine grasslands between 3000 m and 4800 m in the northern Andes. In Ecuador, the area covered by páramo has been estimated at around 20000 km^2 (Bonifaz 1961; Encalada 1986). These páramos are dominated by grass tussocks, mostly belonging to the genera *Calamagrostis* and *Festuca* (Ramsay and Oxley 1996), and in the north of Ecuador, giant stem rosette plants (*Espeletia pycnophylla*) are co-dominant. The climate of these tropical alpine areas is charcterised by cold nights and cool to warm days (Rundel 1994).

Local farmers burn the grassy páramo to encourage nutritious young shoots for their livestock to graze (Ramsay and Oxley 1996). Consequently, the grass páramo usually consists of a mosaic of burned patches of different ages and in different phases of recovery (Ramsay 1999). It has also led to questions about the naturalness of the grassland: that native forest has been displaced because of regular human-induced fires (Laegaard 1992).

Few ecological studies of terrestrial invertebrates in the Ecuadorian páramos have been carried out, and none of these have focused on the effects of burning on community structure. Moret (1998, 2001) describes the ecology of carabids in the Ecuadorian Andes, as part of his work on this group's taxonomy. Smithers and Atkins (2001) provide an account of altitudinal variation in beetle community composition on Volcán Chiles, while Smithers *et al.* (2001) describe the invertebrate communities inhabiting the giant rosettes of *Espeletia pycnophylla* on the same mountain.

This study, also conducted on Volcán Chiles, examines the composition of terrestrial invertebrate communities in areas at different stages in the recovery process after burning.

METHODS

Study Areas

Invertebrate communities were sampled at four sites in grassy páramo between 3700 and 3950 m (Fig. 1) that represented a chronosequence of time since burning:

- *two weeks after fire (3880 m)*
  The ground was covered in black ash, with green shoots regrowing from the burned tussock bases. The stems of *Espeletia* plants were charred, but the withered rosettes were showing signs of recovery. The burning of this site took place during the fieldwork period and its timing could be confirmed directly.
- *three months after fire (3700 m)*
  Regrowth of tussock-forming species, giant rosette species and cushion plants was evident, but large

patches of bare ground were common. The burning age of this site was estimated and verified by a local farmer.

- *six months after fire (3730 m)*
  The principal plant growth forms at this site were tussocks, giant rosettes, shrubs and cushion plants. Vegetation recovery was more advanced than the nearby site at 3700 m, and patches of bare ground were less extensive, but still common. The burning age of this site was estimated and verified by the local farmer.
- *two years after fire (3950 m)*
  Dense vegetative cover consisted of tussocks, giant rosettes, shrubs, herbs and cushion plants. Bare ground was infrequent and consisted of small patches in heavy shade. The burning age of this site was estimated and could not be verified precisely by the local farmer.

These sites were chosen for relatively easy access from the road and because, in all but one case, their recent fire histories were known.

Invertebrate community sampling

Two methods were used to sample terrestrial invertebrate communities at each site:

1. For active species, two pitfall trap arrays were established at each site. Each trap array consisted of eight white plastic cups sunk into the ground in the arrangement shown in Fig.2. Lawn edging was used to increase trapping efficiency. Each trap contained antifreeze (ethylene glycol) as a non-volatile killing agent and preservative. The traps were left for two weeks before the contents were collected and preserved in 70% ethanol.
2. For less active species, hand searches were made of whole tussocks of *Calamagrostis intermedia.* Six replicate tussocks of approximately 30 x 30 cm basal area were cut with a saw at their bases. For each tussock, the harvested leaf material and any invertebrates contained within it were placed in a polythene bag and sealed. The tussock base was then searched throughly, before sifting through the harvested material in the bag. All invertebrates encountered in the searches were killed and preserved in 70% alcohol. Specimens found in the tussock bases were kept separate from those found in the tussock leaves.

The sampling was carried out in July and August 1997. Preserved invertebrate specimens were identified to order using Tillings (1987) at the University of Plymouth, and counts made of each taxon.

Soil measurements

One soil sample was also taken from each site and air dried for measurements of soil acidity (with a Phillips PW9409 pH meter) and organic matter content (by heating in an oven at 430ºC for 22 hours).

Data analysis

The DIVERSE programme, part of Clarke and Warwick's (1994) PRIMER package, was used to calculate two measures of species diversity. The Shannon-Weiner diversity index was calculated as:

$$H' = \sum_i p_i (\log p_i)$$

Fig. 1. The location of the four study sites.

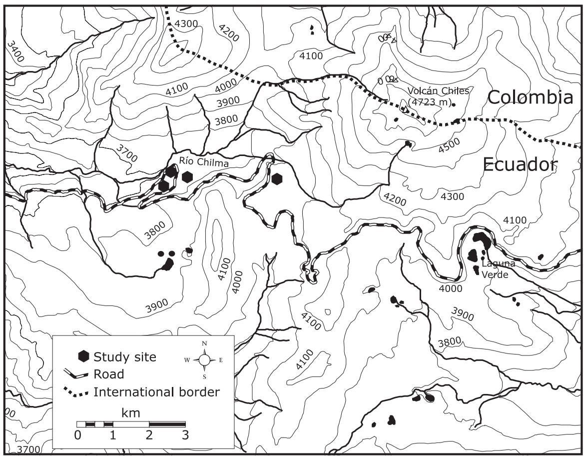
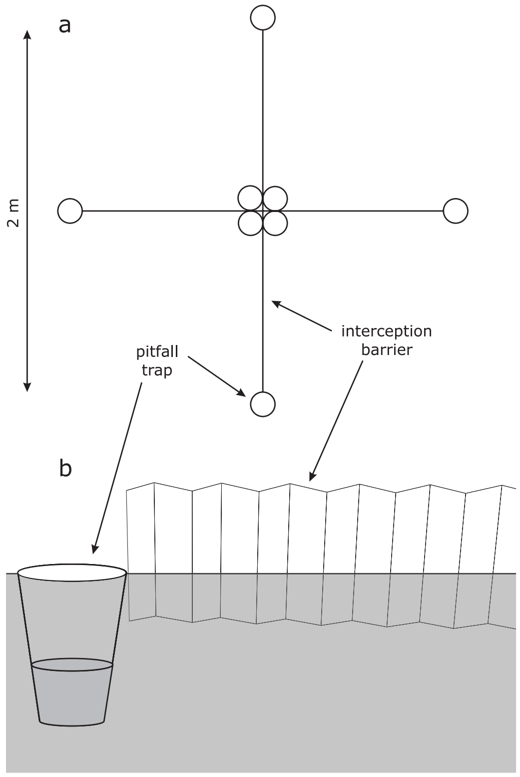


Fig. 2. The design of the pitfall trap arrays. a. plan view, b. side view.



and Simpson's dominance index as:

$$SI = \sum_i (p_i)^2$$

where p_i is the proportion of the total count arising from the ith species.

RESULTS

The pitfall trap array established in the two-weeks-since-fire site was destroyed by cattle—no pitfall data are available for this site. The remaining pitfall samples provided 1530 individual invertebrates (Table 1). The commonest taxa were Collembola (291), Acari (216), Chalcidoidea (209), Hemiptera (207), Diptera (195), Araneae (141), and Coleoptera (100). Several taxa increased in number through the chronosequence (Collembola, Chalcidoidea, Araneae, Coleoptera), others were associated with the early recovery phase after burning (Acari, Diplopoda), and others with the intermediate phase (Hemiptera, Diptera, Dermaptera). Overall, the number of invertebrates was higher as the time since burning increased.

Hand searching of tussocks provided 181 animals in total (Table 2), the commonest taxa being Collembola (45), Araneae (32), Diplura (20), Coleoptera (20), Diplopoda (15), and Dermaptera (14). The Isopoda and Araneae were most abundant in the searches conducted in the plot two weeks after burning. Other taxa were characteristic of the samples with most recovery time (Collembola, Diplura, Lepidoptera), while the highest numbers of Diptera were found in samples with an intermediate time since fire. Several taxa were equally abundant in the tussocks throughout the chronosequence (Coleoptera, Diplopoda, Dermaptera).

The most invertebrates were found in tussocks burned two weeks previously. There were fewer organisms in the three- and six-month sites, but numbers were higher again in the two-year plot. With the exception of tussocks burned three months earlier, more invertebrates were found in the bases of the tussocks compared with the leaves (Fig. 3).

Species richness was similar for pitfall and hand-search samples and across the sites, between 2.2 and 2.4 (Table 3). The Shannon and Simpson indices were more variable in the hand-search samples.

The taxa were crudely assigned to feeding guilds (Table 4). In the pitfall samples detritivores dominated the community, and the numbers of predators, detritivores and parasites rose with increased recovery time. Herbivores were most abundant in the site burned six months earlier. Patterns were less clear in the hand samples. Predators were co-dominant with detritivores. Numbers of detritivores, herbivores and predators were relatively high in the two-weeks-after-fire site. The site burned two weeks before sampling took place had the highest soil pH and organic matter content (Table 5).

Fig. 3. The number of invertebrates found in the base and leaf portions of grass tussocks in sites burned two weeks, three months, six months, and two years previously.

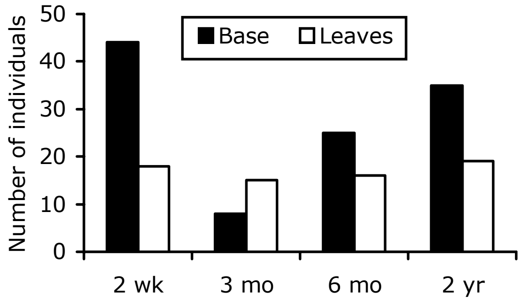


Table 1. Number of invertebrates collected at each site from the pitfall trap arrays.

Taxon	Time since burning		
	3 mo	**6 mo**	**2 yr**
Collembola	57	71	163
Acari	80	80	56
Chalcidoidea	20	56	133
Hemiptera	60	123	24
Diptera	62	77	56
Araneae	36	50	55
Coleoptera	25	35	40
Hymenoptera	26	24	21
Diplopoda	16	10	6
Dermaptera	5	11	7
Thysanoptera	8	6	7
Lepidoptera	3	3	4
Opilione	3	1	6
Isopoda	1	1	
Orthoptera			1
Annelida		1	
Total	402	549	579

Table 2. Number of individual invertebrates collected at each site from the hand sampling method

Taxon	Time since burning			
	2 wk	**3 mo**	**6 mo**	**2 yr**
Collembola	3	10	8	24
Araneae	17	5	6	4
Diplura	7		8	5
Coleoptera	8	1	3	8
Diplopoda	5	1	5	4
Dermaptera	9	1		4
Isopoda	6		1	1
Hemiptera	3	2		1
Diptera		1	5	
Acari		2	2	1
Lepidoptera			2	2
Opilione	1		1	
Chilopoda	2			
Annelida	2			
Total	63	23	41	54

DISCUSSION

The páramo grasslands of Ecuador and Colombia have been regularly burned by farmers to encourage the growth of young grass shoots for cattle grazing, and for hunting, climate control (to encourage rain), and vandalism (Ramsay 2001). The fuel for these páramo fires largely comprises the dead leaves of tussock grasses, most of which remain attached to the tussock after death. Fires can only burn when there has been sufficient build-up of this combustible material—usually restricting fires to a burning cycle of 2–4 years (Ramsay and Oxley 1996).

The continued burning of the grassland has resulted in a landscape mosaic of patches with different fire histories (Ramsay 1999). Before burning, grassy páramo usually consists of dense cover of tussock grasses up to 1 m tall and casting heavy shade on the ground below. Fire removes the leaves of the tussocks, allowing sunlight to penetrate to the ground. It also consumes leaf litter, and releases phosphorus, potassium, calcium and other elements into the soil (Smith 1980, Hofstede 1995). The diversity of plants is reduced—many are killed by fire—and recolonisation and regrowth can be slow (Ramsay and Oxley 1996; Keating 1998; Ramsay 2001).

The profound changes to vegetation and soil that follow fires would be expected to drive shifts in invertebrate community composition, but there has been little work in this area. Suárez and Toral (1996) reported no significant differences in earthworm populations between páramo areas with differing fire histories, though fire temperatures in the soil would be unlikely to reach lethal levels (Ramsay and Oxley 1996).

The present study demonstrated differences in soil conditions in areas with varying recent fire histories. The area subjected to burning two weeks earlier had a higher pH than the other sites, a consequence of the alkaline ash released by the fire (Forgeard and Frenot 1996). Similarly, organic matter content in the soil was highest soon after the fire—normally leaf litter from the tussocks remains attached to the plants and only reaches the soil in quantity after a fire, when some material escapes combustion. However, the relative differences between the sites were small.

Both pitfall trapping and hand searching showed that invertebrate communities, even when identified to broad taxonomic groups, were substantially different from each other in the four sites. Since the four sites were geographically close and represent a chronosequence, it seems likely that the main factors responsible for these differences were related to fire history.

The main changes can be expressed in terms of feeding guilds. The pitfall trap samples were dominated by detritivores, which increased only slightly alongside the recovery of the vegetation. A similar pattern was observed in the hand search samples. However, the relative constancy in detritivore numbers conceals significant shifts in the taxa comprising this group. The early stages after a fire were dominated by Acari, but their number had declined by the two-year site. Diptera were most abundant six months after burning, while Collembola numbers were much higher in the two-year site compared with the others. These community shifts probably reflect the changing nature of their food supplies as the vegetation recovers with time: from fragments of unburned litter on the ground to standing dead biomass in the form of dead tussock leaves.

Table 3. Three measures of species diversity for terrestrial invertebrate samples from four sites with different times since burning. PT = pitfall trap sample, HS = hand search sample.

Time since burning	Sampling method	Species richness	Shannon index	Simpson index
2 wk	PT	—	—	—
	HS	2.4	2.1	0.13
3 mo	PT	2.2	2.2	0.13
	HS	2.2	1.7	0.23
6 mo	PT	2.4	2.3	0.12
	HS	2.4	2.1	0.12
2 yr	PT	2.3	2.1	0.16
	HS	2.3	1.8	0.23

Table 4. Number of individuals assigned to crude feeding guilds from pitfall trap and hand-search samples.

Feeding Guild	Time since burning			
	2 wk	3 mo	6 mo	2 yr
Pitfall samples				
Detritivores	—	232.3	257.7	301.3
Herbivore	—	76.3	148.7	49.3
Parasites	—	20.0	56.0	133.0
Predators	—	73.3	86.7	95.3
Hand-search samples				
Detritivores	18.7	14.3	22.0	32.7
Herbivore	14.7	3.3	3.0	9.7
Parasites	0.0	0.0	0.0	0.0
Predators	29.7	5.3	16.0	11.7

Table 5. Altitude and soil measurements in the four sampling areas.

	Time since burning			
	2 wk	3 mo	6 mo	2 yr
Altitude (m)	3650	3700	3750	3950
Soil pH	5.5	4.7	4.7	4.9
Soil organic content (%)	24.6	21.6	22.2	17.0

Herbivores were most numerous in the site burned six months earlier. This was the time when tussocks were composed almost entirely of dense green shoots—attractive to cattle as well as invertebrate grazers.

Only one taxon was assigned to the parasitic guild: the Chalcidoidea, a super family of Hymenoptera parasitic on the eggs and larvae of Coleoptera, Hemiptera, Lepidoptera, Diptera and Araneae (Gillot 1980). The parasitic lifestyle was most successful in the site burned two years before sampling. The increase in parasite numbers does not appear to correlate with the numbers of its hosts, suggesting that either the parasites specialise on particular hosts that are more abundant in the later stages of vegetation recovery, or else their numbers lag behind those of their hosts.

In the pitfall samples, predators increased in number, though the proportion of the total invertebrate catch changed little (representing 16–18%).

These changes were evident using very crude approximations to feeding guilds or at very general taxonomic groups (orders and super-families). It was not possible to identify specimens to species level because the taxonomy of many of these groups is poorly developed for High Andean species. Nevertheless, it was clear during the sorting of the specimens that were the data available at species level, there would be very clear differences between the communities of each site.

Both sampling strategies used in this study produce biased estimate of invertebrate communities. Pitfall traps are useful only for active species which roam into the traps. Relatively inactive species would be underrepresented, if they were caught at all. The pitfalls were also located in the ground between tussocks and would not catch species that do not venture out of the tussocks or the soil-like tussock bases (*e.g.*, Diplura and Chilopoda). The hand searching of tussocks would be expected to yield some of these animals, but it is easier to overlook small and inactive species (perhaps explaining the low numbers of Acari and Chalcidoidea in these samples).

Clearly, food supplies for detritivores and herbivores—related to the recovery of vegetation after a fire—and the availability of prey and hosts for predators and parasites, help to explain the differences in community composition between the study sites. However, there may be other important factors too.

Ramsay and Oxley (1996) showed that fire temperatures in the grass tussock canopy could be as high as 600ºC. At the same time, temperatures of less than 65ºC were measured in the base grass tussocks and 2 cm below ground. The result of these lower ground temperatures in the páramo allows tussocks to regrow from the bases, and other plants to regenerate from roots or rhizomes (Ramsay and Oxley 1996). Invertebrates that live at the base of tussocks or below the surface also have a potentially greater chance of surviving through the fire. Suárez and Toral (1996) showed that earthworm populations were similar in areas with different burn history, suggesting that the soil environment offers protection from lethal fire temperatures. Most of the organisms collected during the searches of tussock plants came from the tussock bases (62%). Invertebrates in this part of the plant may survive a páramo fire unharmed. Similarly, organisms which are more active and forage outside the tussock bases may retreat into the tussocks or soil when fires occur.

Therefore, resulting from a combination of changing resource availabilities after burning and differential species survivorship of the fires themselves, the páramo is a mosaic of burned patches, each with its own invertebrate community composition. Thus fire, taken at the landscape level, would be expected to generate high invertebrate diversity through the creation of gaps, new successions and patchwork mosaics in communities (Begon *et al*. 1996). Connell's (1978) intermediate disturbance hypothesis suggests that the highest diversity might result from intermediate frequencies and intensities of burning. Infrequent or low intensity fires would not alter the dominance of species associated with mature tussock vegetation. On the other hand, continual or high intensity burning would result in an invertebrate community consisting only of species which are tolerant of fires or with good dispersal abilities. The combined diversity of a range of patches with different fire histories, at different stages of recovery, would provide the highest invertebrate diversity.

Nevertheless, the impact of regular burning on the páramo may have resulted in the loss of certain species which are highly intolerant of fire disturbance. The fire return time of 2–4 years may be insufficient to permit these species to return to areas where they have been lost. In the present study, the species in the samples may represent only a sub-set of the total species pool: the ones which are able to maintain viable populations in páramo which is regularly burned.

This study has shown that invertebrate communities do respond to the changing resource base that follows the successional recovery of vegetation after burning. These differences are evident using basic taxonomic treatments at order or super-family level or with crude feeding guild assemblages. However, more observational data are required to verify the nature of the effects and their longer-term consequences. In particular, experimental fires may offer insights into the changes in community structure by direct observation of changes through time, as well as the behavioural responses of invertebrates to fire. It is important that areas of páramo which have not been burned for many years are included in such studies.

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REFERENCES

Begon, M., Harper, J.L. and Townsend, C.R. (1996) *Ecology,* Oxford: Blackwell Science.

Bonifaz, E. (1981) Agricultura y población de los Andes. *Revista Geográfica (Quito),* **14**: 31–42.

Clarke, K.R. and Warwick, R.M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation,* Plymouth: Plymouth Marine Laboratory.

Connell, J.H. (1978) Diversity in tropical rainforests and coral reefs. *Science*, **199**: 1302–1310.

Encalada, M. (1986) *Evidencias del Deterioro Ambiental en el Ecuador,* Quito: Gangotena & Ruiz Editores.

Foregeard, F. and Frenot, Y. (1996) Effects of burning on heathland soil chemical properties: an experimental study on the effect of heating and ash deposits. *Journal of Applied Ecology,* **33**: 803–811.

Gillott, C. (1980) *Entomology,* New York: Plenum Press.

Hofstede, R.G.M. (1995) The effects of grazing and burning on soil and plant nutrient concentrations in Colombian páramo grasslands. *Plant and Soil,* **173***:* 111–132.

Keating, P.L. (1998) Effects of anthropogenic disturbances on páramo vegetation in Podocarpus National Park, Ecuador. *Physical Geography,* **19***:* 221–238.

Laegaard, S. (1992) Influence of fire in the grass páramo vegetation of Ecuador. In: Balslev, H. and Luteyn, J.L. (Eds) *Páramo: An Andean Ecosystem under Human Influence,* pp. 151–170, London: Academic Press.

Moret P. (1998) Les *Dyscolus* de la zone périglaciaire des Andes équatoriennes (Coleoptera, Harpalidae, Platyninae). *Bulletin de la Société entomologique De France*, **103**: 11–28.

Moret, P. (2001) The ground beetles of the Chiles area (Coleoptera, Carabidae): a taxonomic and ecological overview. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 125–135. Plymouth: Pebble & Shell.

Ramsay, P.M. (1999) Landscape mosaics in the High Andes: the role of fire in páramo communities. In: Kovář, P. (editors), *Nature and Culture in Landscape Ecology: Experiences for the 3rd Millennium*, pp. 192–199. Prague: The Karolinum Press.

Ramsay, P.M. (2001) Páramo vegetation recovery in the first two years after a fire on Volcán Chiles, Ecuador. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 65–73. Plymouth: Pebble & Shell.

Ramsay, P. M., and Oxley, E.R.B. (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetatio,* **124**: 129–144

Rundel, P.W. (1994) Tropical alpine climates. In: Rundel, P.W., Smith, A.P., and Meinzer, F.C. (Eds) *Tropical Alpine Environments: Plant Form and Function,* pp. 21–44. Cambridge: Cambridge University Press.

Smith, R. L. (1980) *Ecology and Field Biology,* New York: Harper & Row.

Smithers, P., and Atkins, N. (2001) Altitudinal variation in páramo invertebrate communities on Volcán Chiles, with particular reference to Carabidae (Coleoptera). In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 145–151. Plymouth: Pebble & Shell.

Smithers, P., Ramsay, P.M., Bond, A.N., and Burne, M.E. (2001) Macro-arthropod communities of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis.* In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 169–175. Plymouth: Pebble & Shell.

Suárez, E., and Toral, C. (1996) *Abundancia y biomasa de lombrices de tierra en páramos con distinto uso del suelo en el Ecuador: evaluación preliminar de los efectos de las quemas.* Quito: EcoCiencia.

Tillings, S.M. (1987) *A Key to the Major Groups of British Terestrial Invertebrates.* Preston Montford: Field Studies Council.

Páramo spiders of Volcán Chiles, Ecuador

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SUMMARY

Spiders were collected from the páramo using pitfall traps to investigate the relationship between species diversity and abundance with habitat type and altitude. An altitudinal range of 3300–4300 m was used with traps being set in various habitat types: zonal páramo grassland, riparian zone, *Polylepis* woodland, mire, and scree (talus). The body length of spiders from the zonal grassland was also measured. Páramo spiders employed a wide range of hunting strategies and exhibited differences in body size that may restrict competitive interactions and permit coexistence. However, there is some evidence that certain groups may be negatively associated. Specialisation to particular habitat types appears to be limited to a relatively large number of rare species, and common spiders were not habitat-restricted. *Polylepis* woodland assemblages were most distinct from those of the other habitat types. In the zonal páramo, a significant decline in spider abundance and diversity coincided with the change from grassy páramo to cushion páramo (superpáramo) at around 4000–4100 m. The reduced structural complexity of vegetation above this transition zone provides fewer potential niches for the spiders and prey. The species diversity of vegetation decreases with altitude and may limit the range of prey (herbivorous invertebrates) and therefore spiders. Assemblage body size distributions were explained in terms of prey availability, again related to the decline in the diversity and structural complexity of vegetation at higher altitudes. It is suggested that future studies should define morphospecies and focus on functional attributes of spiders (*e.g.*, feeding strategies, body size): this would provide useful ecological information as well as specimens for taxonomic work in developing keys for páramo spiders.

RESUMEN

Se recolectaron arañas del páramo utilizando trampas de caida para investigar la relación entre la diversidad de especies y la abundancia con el tipo de hábitat y la altitud. El intervalo altitudinal fue 3300–4300 m y las trampas fueron colocadas en varios tipos de hábitat: pastizal zonal de páramo, zona riparia, bosque de *Polylepis*, turbera, y pedregal (talus). Se medió el largo del cuerpo de las arañas del pastizal zonal del páramo. Las arañas del páramo emplearon un amplio intervalo de estrategias de caza y manifestaron diferencias en el tamaño del cuerpo que pueden restringir las interacciones competitivas y permitir la coexistencia. Sin embargo, hubo evidencia de que ciertos grupos se asociaron negativamente. La especialización a hábitats particulares parece ocurrir en un número relativamente grande de especies raras, y las arañas comunes no estuvieron restringidas a hábitats particulares. Los ensambles de arañas en el bosque de *Polylepis* fueron distintos de aquellos en otros hábitats. En el páramo zonal, una disminución significativa en la abundancia y diversidad de arañas coincidió con el cambio de pastizal a páramo de cojines (superpáramo) alrededor de 4000–4100 m. La reducida complexidad estructural de la vegetación por encima de esta zona de transición provee menos nichos potenciales para las arañas y sus presas. La diversidad de especies de la vegetación, la cual disminuye con la altitud, puede limitar el intervalo de presas (invertebrados herbívoros) y, por lo tanto, de arañas. Las distribuciones del tamaño del cuerpo de los ensambles fueron explicados en términos de la disponibilidad de presa, relacionada ésta, una vez mas, a la disminución en la estructura y diversidad de la vegetación con la altitud. Se sugiere que estudios futuros deberán definir morfoespecies y enfocarse en los atributos funcionales de las arañas (por ejemplo, estrategias de alimentación, tamaño de cuerpo): ello proporcionaría información ecológica útil, así como especimenes para estudios taxonómicos que permitan desarrollar claves de identificación de las arañas del páramo.

Key words: Araneae, tropical alpine, body size, Polylepis, altitude

INTRODUCTION

The páramo grasslands of the equatorial High Andes represent a challenge for most invertebrate taxa. Although there is little seasonal variation in climatic conditions, daily oscillations in temperature can be extreme. Daytime temperatures on the ground may be very high as sunlight penetrates the thin atmosphere. At night, radiative losses of heat are significant and temperatures can drop below to freezing (Ramsay 2001a). Invertebrates living in this environment must be capable of surviving these temperature extremes.

Spiders are the most common predators in terrestrial systems and seem well adapted to living in harsh environments—their low metabolic rates allow them to reproduce in situations of low prey abundance (Dippenaar-Schoeman and Jocqué 1997). This starvation resistance has allowed them to colonize and flourish in many inhospitable areas of the world.

Nevertheless, spiders also take advantage of the shelter provided by a range of microhabitats, which may permit the coexistence of several species (de Keer and Maelfait 1988). For example, a small spider may construct a web on the under surface of a leaf and a larger spider may be an active hunter over the surface of a plant. Spiders may also specialise on different prey (Nentwig 1987), which may also enable spider species to coexist (Enders 1975). There is often variation in behavioural strategies from orb web weavers (Araneidae) and sheet web weavers (Agelenidae) to active nocturnal hunters (Clubionidae) and sit and wait spiders (Lycosidae) (Marc *et al.* 1999). Some spiders also show more specific adaptations such as the use of abdomen markings to reflect UV radiation (Humphrey 1987). Niche differentiation between spiders may often be

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 159-168.

reflected in body size variation between coexisting species of spider (Enders 1975, 1976).

The páramo zone (which covers an altitudinal range from 3200 to 4800 m in Ecuador) may provide further scope for specialisation among spiders because it is made up of several different habitat types. Zonal páramo grassland consists of tussock grasslands at lower altitudes (with *Espeletia* giant rosette plants in the north of Ecuador), which is replaced by more open cushion páramo at altitudes above 4000 m and scattered, isolated plants at the highest altitudes. However, there are also several azonal habitat types occurring within the páramo zone. Areas along streams and rivers (riparian zones) may provide different temperature and humidity regimes from the surrounding páramo. Patches of woodland, dominated by trees belonging to the genus *Polylepis*, are common above the forest line in Ecuadorian páramos. These provide very different climatic and structural habitats from neighbouring grassland. Mires, often dominated by cushion plants, and rocky scree or talus slopes also provide further heterogeneity at the landscape level.

A decrease in species diversity and abundance as altitude increases has been well documented for many taxa: millipedes in Czech and Slovak mountains (Tajovsky 1997), leaf litter invertebrates of Panama cloud forest (Olson 1994), birds and mammals of Nepal (Hunter and Yonzon 1992), stream invertebrates from Ecuador (Jacobsen *et al*. 1997), and vascular plants in the páramo (Sklenář and Ramsay, in press). Similarly, there is likely to be a decrease in the abundance of individual spiders and species diversity with increasing altitude (Rollard 1993). There are three main reasons to expect this. Firstly, the environmental conditions at high altitudes may filter out those species that do not possess appropriate physiological and behavioural adaptations. Secondly, the thinning of plant cover and the reduction in structural complexity of vegetation with altitude reduces the opportunities for avoidance strategies in spiders (*e.g.*, sheltering in dense vegetation) and niche differentiation (which may lead to local extinctions of competing species). The relationship between habitat structure and species richness has been well documented for arthropods in general (Mühlenberg *et al*. 1977, Dennis *et al.* 1998) and spiders (Curtis and Morton 1974, Otto & Svensson 1982, Docherty and Leather 1997). Lower structural diversity of a habitat may not be able to support as diverse a range of body sizes as lower altitudes (Otto and Svensson 1982). Thirdly, high altitude plants tend to be tougher and less palatable to herbivorous invertebrates (Mani 1962), supporting smaller populations, and consequently smaller population sizes of predatory species like spiders, despite their high resistance to starvation.

While spider studies in some parts of the world have begun to focus on more complex ecological interactions, many regions still lack the preliminary data with which to identify simple aspects of community structure (Rollard 1993). South America is one of these areas with very little published information, and information on páramo species is very limited. Nentwig (1987) has produced a relatively comprehensive guide to the spiders of Panama, but few Central American spiders are shared with South America (Nentwig 1987). Keys do exist for South American Agelenidae (Roth 1967) and Linyphiidae (Millidge 1991), but these are far from complete.

The current study surveys the spiders of Volcán Chiles, a páramo area on the border between Ecuador and Colombia. Ultimately, the specimens collected can contribute to a taxonomic treatment of páramo spiders, but this is a long-term objective. For the purposes of this article, the survey allows spider distribution patterns with respect to altitude and habitat type to be described, and patterns in spider body size to be examined.

METHODS

Study area and sampling sites

The study area was located on Volcán Chiles (0°49′25″N 77°56′35″W) in northern Ecuador on the Colombian border. The páramo landscape is found above 3000 m and characterized by tussock grass (*Calamagrostis* spp) and giant rosette plants (*Espeletia pycnophylla*). Ramsay (2001b) and Sklenář (2001) provide more detailed treatments of the vegetation of the zonal páramo of the area.

Five habitats were chosen for sampling within the páramo zone:

- **zonal páramo grassland (3300–4300 m; 11 sites)** The grass sites were characterised by widespread tussock grass (*Calamagrostis* spp) which was frequently interspersed with giant rosette plants (*Espeletia pycnophylla* subsp. *angelensis*), and to a lesser degree *Puya* (*Puya humata* and *Puya clava-herculis*). The average grass height for these sites was approximately 30 cm, although at higher altitudes grass height was significantly reduced.
- **riparian grassland (3300–4300 m; 10 sites)** Riparian sites (defined here as the land within 0.5 m of a river or stream) comprised a mixture of tussock grass, shrubs and bare, partially saturated ground. The riparian sites were paired with the zonal páramo grassland sites.
- ***Polylepis* woodland (3550, 3700, 3900 m; 3 sites)** These woodlands were confined to sheltered areas (*e.g.*, steep valleys or gullies below cliffs) and occupied relatively limited areas of the páramo landscape. They were dominated by *Polylepis* trees (*P. sericea, P.pauta* and *P. incana*), approximately 1.5–2.0 m in height. The woodland at 3900 m was 1875 m x 250 m, the one at 3700 m covered an area of approximately 2250 x 125 m, and that at 3550 m was much smaller than the others, 15 m x 15 m in area (less dense and with significantly more shrubs around the edges).

- **mire (3700, 3750, 4100 m; 3 sites)**
  The mire at 4100 m was 75 m x 50 m in area, and was characterised by cushion plants (*Plantago rigida* and *Oreobolus obtusangulus*), generally less than 2 cm in height with water-filled pools between. The mire at 3700 m (75 m x 50 m) consisted of similar vegetation to the first mire, but some tussock grass and several small *Puya* plants were present. At 3750 m the mire was characterised by short grass (less than 20 cm high), which was waterlogged in many places. Only a few scattered patches of cushion plant were present. It measured 15 m x 10 m in area.

- **scree or talus (3900, 4200, 4400 m; 3 sites)**
  The scree area at 3900 m was approximately 10 x 20 m in area with a varied rock size of 20–200 cm in diameter, interspersed with smaller stones. No vegetation was present within the scree. The scree slope at 4200 m was approximately 2 m x 20 m in area and characterised by rocks varying in size from 30–200 cm in diameter. Many of these were lichen covered with small patches of tussock grass present between the boulders. At 4400 m scree was the predominant element in the landscape. Boulders were often more than 2 m in diameter, interspersed with smaller rocks of 30 cm in diameter. No vegetation was present.

The location of each site was determined with a Magellan ColorTrak GPS, and is shown in Fig. 1.

Spider sampling

The study was carried out in July 1999. At each site in the zonal páramo grassland, *Polylepis* woodland, and mire, four replicate pitfall trap arrays (16 pitfalls within a 2 x 2 m area) were established. The replicate trap arrays were subsequently pooled to provide sufficient numbers for analysis. Plastic cups (approximately 90 cm^3 volume) were used as pitfalls, with approximately 2 cm depth of ethylene glycol added to the each to act as a non-evaporating preservative and killing agent. At riparian sites traps were placed in an area of 0.5 m x 8 m (equivalent to 2 m x 2 m).

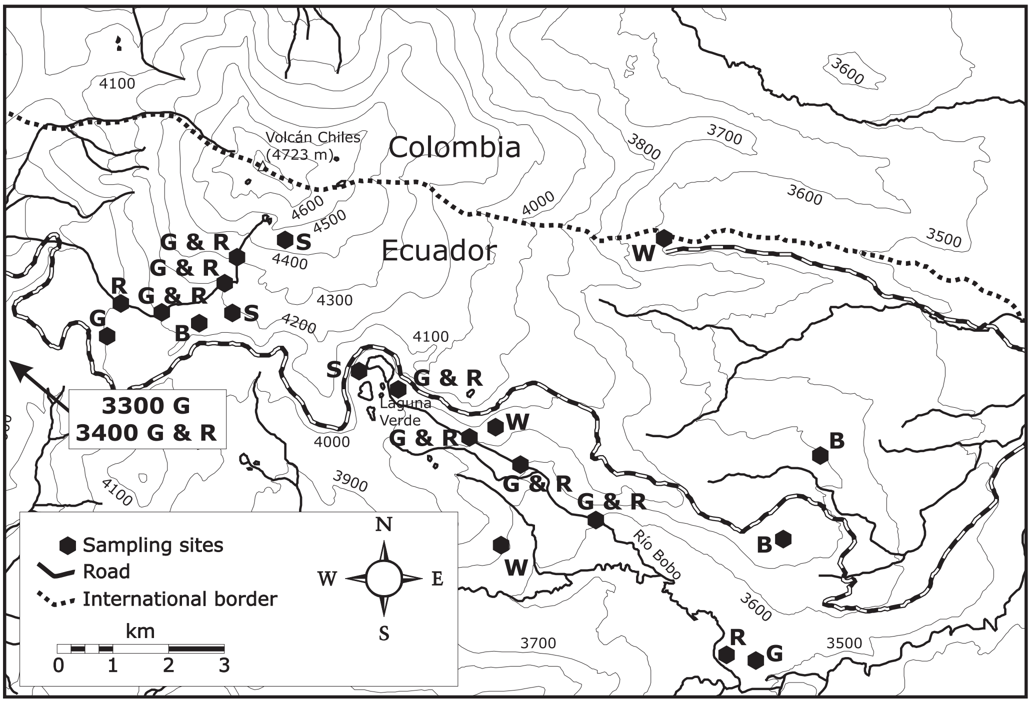
It was not possible to lay pitfalls in scree fields because of the rocky nature of this habitat. Therefore, pitfall traps were set in perspex platforms (15 x 15 cm in area, sand-papered to provide a rough surface for invertebrates to walk on). At each site, 25 of these traps were placed among the rocks.

All the traps were left for 12–16 days before retrieval, and all animals were preserved in alcohol (70% ethanol).

Identification of spiders

The preserved spiders were sorted and identified in the laboratory at the University of Plymouth. Identification to family level was carried out using Dippenaar-Schoeman and Jocqué's (1997) key to African spiders. Comprehensive keys to North American spiders were less useful because there are fewer similarities between North and South America (Nentwig 1993). More detailed, South American keys

Fig. 1. Location of the sampling sites on Volcán Chiles. Codes: G, páramo grassland; R, riparian grassland; W, woodland; S, scree; B, mire. The grassland and riparian grassland samples from 3300and 3400 m were located near the road, but off the map to the west.



to the Linyphiids (Millidge 1991) and Agelenids (Roth 1967) were used for these taxa, but only about one-quarter of the species collected during the survey were covered in these keys. This highlights our poor knowledge of spiders from this region, and the need for a key for páramo spiders—a project now underway, based partly on specimens from this study (Smithers 2001). In the absence of formal taxonomic identification, specimens were assigned to morphospecies, operational identifications to "species" level. It was often difficult to match males and females of the same species, so the sexes were assigned to different morphospecies. Immature spiders were placed in family groups rather than attempting an imprecise assignment to one of the adult morphospecies.

The body length of all adult spiders from grass habitats at 3300 m, 3500 m, 3700 m, 3900 m, 4100 m, 4300 m were measured. Body length was measured from the anterior tip of the carapace to the posterior tip of the abdomen (excluding the spinnerets).

Data Analysis

All analyses were carried out using PC-ORD version 4 (McCune and Meffod 1999). Species diversity was examined using four different measures. The first was the number of species in each sample (species richness, *S*). In addition, Shannon's index of information content, was calculated according to the formula:

$$H' = \sum_{i=1}^{S} p_i \log p_i$$

where p_i is the proportional abundance of species i in the sample. The evenness of non-zero species abundances (equitability) was calculated by:

$$E = \frac{H'}{\ln S}$$

Finally, the complement of Simpson's original index for a finite population was calculated as follows:

$$D = 1 - \sum_{i=1}^{S} {p_i}^2$$

Outlier analysis was used to identify rare species that might bias subsequent analyses and these were removed before carrying out cluster analysis to compare the similarity in composition of spider samples at each site. Ward's linkage method and the relative Sørensen (Kulcynski) distance measure were employed. Finally, Dufrêne and Legendre's (1997) indicator analysis was used to determine key species in defining each of the groups produced by cluster analysis.

RESULTS

Unfortunately, no specimens were caught in the pitfall arrays located in riparian sites at 3600, 3700 and 3925 m because the pitfalls were filled with water following heavy rainfall. Therefore, all the results that follow do not include these samples, and are derived from 27 sampling sites in total.

Altogether, 483 spiders were collected from the traps, belonging to 67 morphospecies and 15 families (Table 1). Only 36 of the morphospecies occurred in more than one site, and 55% of all morphospecies were represented by three or less specimens. Just three morphospecies were present in more than ten sites (LC1, L Li22 and LA5). The most abundant morphospecies were LL1 (55 individuals), LC1 (47 individuals) and LA5 (42 individuals).

The most abundant family on the páramo was the Linyphiidae (Table 2). Although other families did not exhibit as many different species as the Linyphiids, some were relatively more abundant in terms of individuals compared to the number of species identified. Agelenidae and Lycosidae had the lowest ratio of species to individuals indicating that their few species are more widely abundant on the páramo than those of the Linyphiidae. The grassland samples contained the most morphospecies and families (Fig. 2). The fewest number of morphospecies were associated with the scree samples, and the fewest families were found in the mire samples.

Table 1. Morphospecies abundance and distribution in the samples. For each morphospecies the number of sites in which it was found is given, along with the total number of individuals collected and a breakdown of their distribution in the samples from the five habitat types (G, zonal páramo grassland; R, riparian páramo grassland; W, Polylepis *woodland; B, mire; S, scree). Where specimens have been identified to genus and species level, the names are given next to the code. (Continued on next page)*

Morphospecies	**No of sites**	**Total no of individuals**	**Zonal grassland**	**Riparian grassland**	***Polylepis* woodland**	**Mire**	**Scree**
Sub-order Labidiognatha (L)							
Family Clubionidae (C)							
LC1	10	47	18	4	23		1
LC2	3	3	3				
LC3	4	6	1	2			3
LC5	2	7	1		7		
LC6	3	5			5		
LC7	1	1	1				
LC8	1	2	2				
LC9	1	1		1			
LC immature	3	9			6		2
Family Ochyroceratidae (O)							
LO1 *Drymusa* sp.	2	3	2		1		

Table 1. Continued.

Morphospecies	**No of sites**	**Total no of individuals**	**Zonal páramo grassland**	**Riparian grassland**	***Polylepis* woodland**	**Mire**	**Scree**
Family Linyphiidae (Li)							
L Li4 *Erigone clavipalpis*	5	13	2	1		10	
L Li5 *Labicymbium* sp. 1	3	8	3			5	
L Li6	1	1	1				
L Li7	3	5	1	4			
L Li8 *Fissiscapus* sp. 1	6	7	5		1		
L Li 9 *Labicymbium* sp. 2	5	10	2		8		
L Li10 *Fissiscapus* sp. 2	1	1	1				
L Li11 *Erigone palustris*	1	1	1				
L Li12	5	8	3	5			
L Li13	4	4	4				
L Li14 *Laminacauda* sp. 1	2	2	1			1	
L Li15 *Labicymbium* sp. 3	4	6	1	1		2	
L Li17	7	11	4	3		4	
L Li18 *Laminacauda* sp. 2	5	20	8	9		3	
L Li19	1	2	2				
L Li20	1	1	1				
L Li22	5	18	3	13		2	
L Li23 Dubiceranea sp. 1	1	1			1		
L Li24 *Fissiscapus* sp. 3	2	5			5		
L Li25 Dolabritor sp. 1	1	1			1		
L Li26	1	1			1	1	
L Li27	1	1	1				
L Li28 *Eperigone obscura*	1	1				1	
L Li29	1	2			1		
L Li30	1	1			1		
L Li immature	12	42	12	7	17	5	1
Family Agelenidae (A)							
LA1	6	17	10	3	4		
LA2 Neoporteria sp. 1	8	15	10	4	1		
LA3 Naevius sp. 1	7	17	2	4	5		4
LA4	1	1		1			
LA5 Hiconodon sp. 1	13	42	16	7	19		
LA6	1	1	1				
LA7 Hiconodon sp. 2	3	5	1		4		
LA immature	5	13		2	6		5
Family Araneidae (Ar)							
L Ar 1	1	1	1				
L Ar 4	1	1		1			
Family Anyphaenidae (A)							
L An 2 immature	1	1	1				
L An 3 *Josa riveti* ♀	2	2				1	1
L An 4 *Josa riveti* ♂	1	1					1
L An 5 ♀	1	1	1				
Family Prodidomidae (Pr)							
L Pr 1	1	1	1				
Family Pholcidae (P)							
L P 1	1	2			2		
Family Miturgidae (M)							
LM1	1	2			2		
LM3	1	1		1			
LM4	1	1		1			
Family Corrinidae (Co)							
L Co 1	1	1					1
Family Lycosidae (L)							
L L 1	7	55	42	8		5	
L L 3	8	19	13	5		1	
L L 4	2	2				2	
L L immature	2	4	4				
Family Theridiidae (T)							
LT1	1	1					1
Family Tetragnathidae (Te)							
L Te 1 *Meta* sp. 1	4	7		3	2		
Family Oonopidae (O)							
L O 1	1	1	1				
Family unknown (unk)	1	1	1				
Sub-order Myglomorpha (M)							
Family Paratropididae (P)							
MP1 *Anisaspoides* sp. ♀	5	7	4		3		
MP2 *Anisaspoides* sp. ♂	1	1		1			
MP immature	3	3	3				

Table 2. The number of morphospecies (S) and the number of individuals (I) found in the most abundant páramo spider families.

Family	*S*	*I*	Ratio *S*:*I*
Linyphiidae	25	82	0.30
Clubionidae	8	28	0.29
Agelenidae	7	44	0.16
Anyphaenidae	4	5	0.80
Lycosidae	3	17	0.18
Miturgidae	3	8	0.38

Fig. 2. The number of morphospecies and families found in each páramo habitat type.

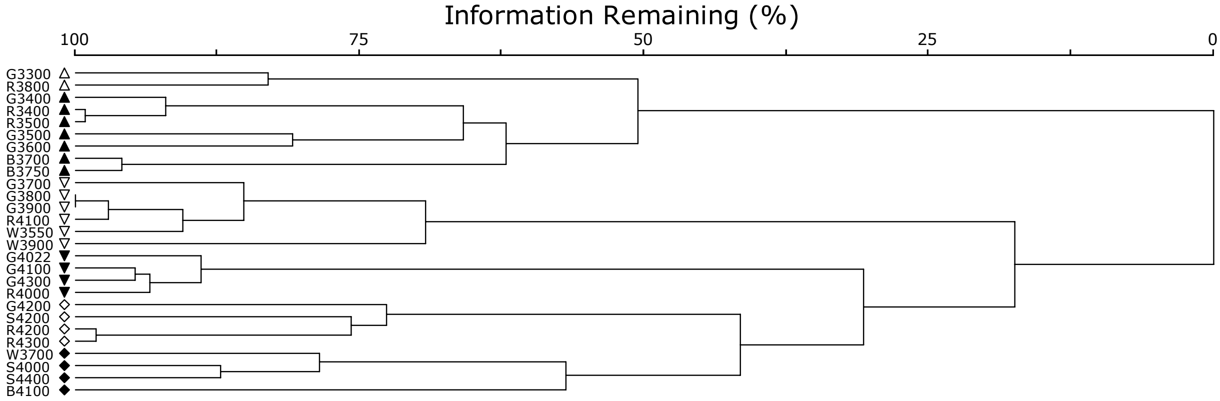
Table 3. Number of individuals and species found at each site with Evenness (E), Shannon diversity (H) index and Simpson diversity (D) index calculated.

Site	Trap days	Total no of individuals	Total no of species	Evenness	Shannon index	Simpson index
Zonal páramo grassland						
G3300	12	26	15	0.9	2.4	0.9
G3400	14	36	11	0.9	2.1	0.8
G3500	14	38	10	0.6	1.3	0.5
G3600	14	20	10	0.9	2.1	0.8
G3700	12	13	9	1.0	2.1	0.9
G3800	12	26	8	0.9	1.8	0.8
G3900	12	15	8	0.9	1.8	0.8
G4000	14	11	7	0.9	1.8	0.8
G4100	14	2	2	1.0	0.7	0.5
G4200	15	6	5	1.0	1.6	0.8
G4300	15	4	3	1.0	1.0	0.6
Overall		197 (av. 18)	40	0.9	1.7	0.7
Riparian grassland						
R3400	14	24	7	0.9	1.7	0.8
R3500	14	11	5	0.9	1.5	0.7
R3800	12	27	13	0.9	2.3	0.9
R4000	14	1	1	—	—	—
R4100	14	18	8	0.9	1.8	0.8
R4200	15	10	5	0.9	1.5	0.8
R4300	15	4	2	0.8	0.6	0.4
Overall		95 (av. 14)	22	0.9	1.6	0.7
***Polylepis* woodland**						
W3550	12	71	16	0.8	2.3	0.9
W3700	11	18	8	0.9	1.8	0.8
W3900	11	40	15	0.9	2.5	0.9
Overall		129 (av. 43)	21	0.9	2.2	0.9
Mire						
B3700	16	17	7	0.9	1.7	0.8
B3750	12	22	11	0.9	2.3	0.9
B4100	12	4	3	1.0	1.0	0.6
Overall		43 (av. 14)	13	0.9	1.6	0.8
Scree (talus)						
S3900	14	6	5	1.0	1.6	0.8
S4200	16	8	4	1.0	1.3	0.7
S4400	16	6	3	0.9	1.0	0.6
Overall		20 (av. 7)	7	1.0	1.3	0.7

In all cases, measures of evenness and dominance (Simpson's Index) were relatively constant across the sites (Table 3). The main differences reflect variations in the species richness component of divesity (total number of species and the Shannon index). Overall, the highest diversity of morphospecies was found in the *Polylepis* woodlands, the lowest diversity in the scree, with the grassland, riparian and mire samples intermediate. The woodland samples also yielded the highest number of individuals per site, and the scree samples lowest (43 and 7, respectively). An altitudinal trend in diversity was only clearly evident in the zonal páramo grassland samples: diversity tended to decline as altitude increased.

At a 55% level of similarity six groups were identified from the cluster analysis as having similar community composition (Fig 3). Groups 1–3 contain samples from low to medium altitudes that include representatives from all the habitats except scree. Groups 4–6 contain mixed habitat sites from high-altitude, with the exception of one intermediate altitude site in Group 6 (W3700 m). Throughout, there is no clear division between habitat types according to spider assemblage composition.

Fig. 3. Cluster analysis identifying percentage similarity in community composition between sites. Six groups were identified at 55% level of similarity. Group 1(⇖) indicator species: LC3, L Li18, LA1, LL3. Group 2 ( ) indicator species: LC1, L Li5, L Li22, L4imm, LL1, MH1. Group 3 (↗) indicator species: none. Group 4 (➚) indicator species: none. Group 5 (🡐) indicator species: LC3. Group 6 (⇦) indicator species: Lan3.



The distribution of spider body length in relation to altitude in the zonal páramo grassland samples is shown in Fig. 4. Spiders from the lower altitude sites (3300, 3500, 3700, 3900 m) showed a bimodal distribution in body size, within a range of about 8 mm. At higher altitudes (4100 and 4300 m), the range of body size was much lower: approximately 4 mm.

DISCUSSION

The azonal páramo habitat types (riparian zone, woodland, mire, and scree) did not show a clear altitudinal decline in diversity or abundance. This may be related to the island-like nature of these habitats, which provide conditions that are less dependent on altitude. However, the samples from the zonal páramo grassland did show a clear decrease in spider diversity and abundance with increasing altitude. This is likely to be strongly related to the decrease in vegetation diversity and structure along altitudinal gradients on the páramo (Luteyn 1999, Ramsay 2001b, Ramsay & Sklenář 2001).

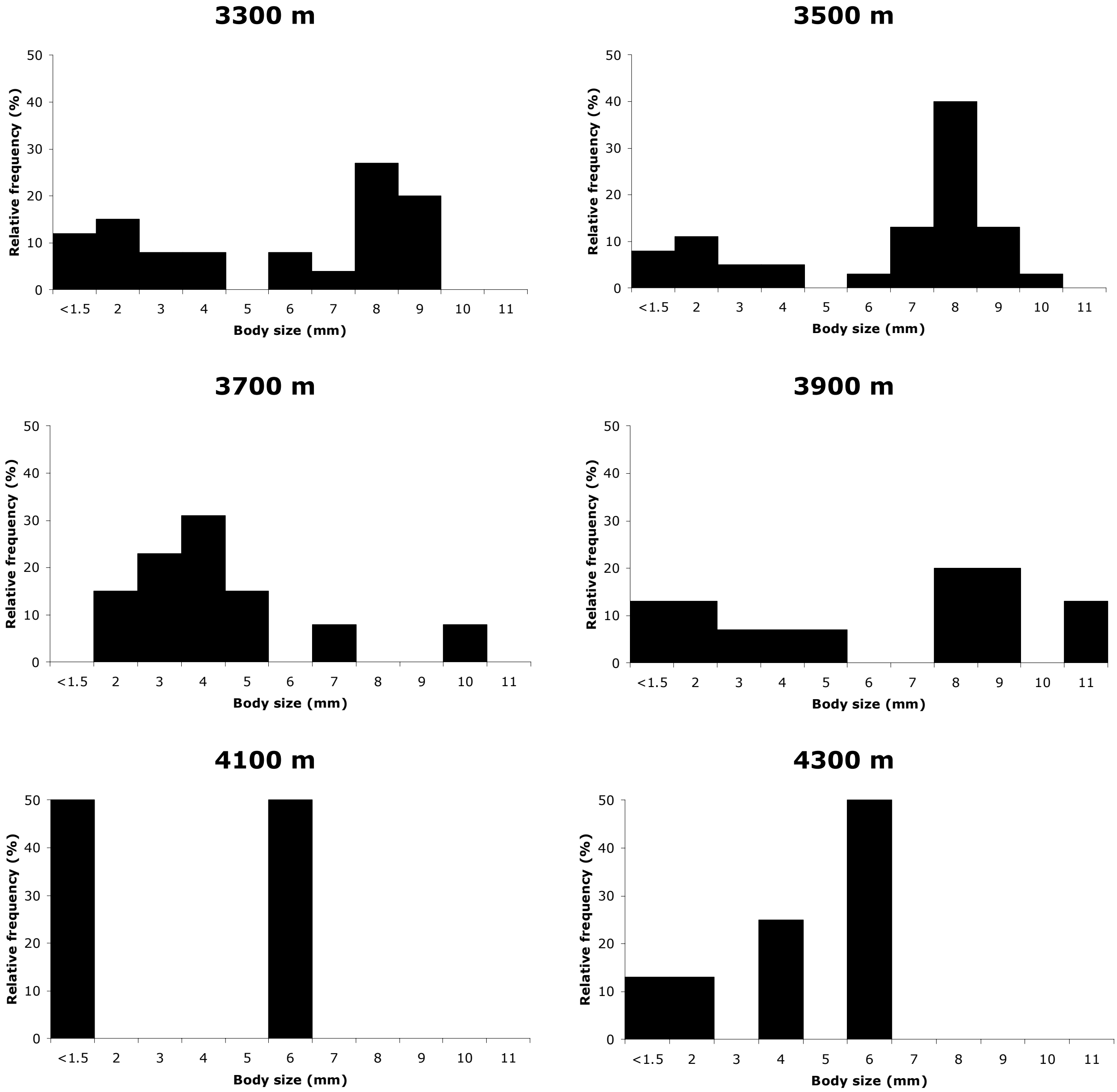
At lower altitudes the increased ground cover can promote higher temperatures and humidity (Rypstra *et al.* 1999). In the páramo at 4000 m on Volcán Chiles, the bases of tussock grasses can be up to 8°C warmer than ambient air temperatures during the day and up to 4.5°C warmer during the night (Ramsay 2001a). The thermal advantages of such microhabitats are evident. *Espeletia* species are codominant in the páramo on this mountain below 4100 m (Ramsay 2001b), and their marcescent (dead) leaves and rosettes provide habitat for many spider species (Smithers *et al.* 2001). Physiological or behavioural avoidance strategies may be employed by spiders to survive low temperatures and desiccation. For example, some species may have the ability to supercool (Speight *et al.* 1999); supercooling points of -4 to –34°C have been recorded in some spider species (Kirchner 1987). However most invertebrates cannot supercool and generally survive by sheltering under stones or in vegetation (Sømme and Zachariassen 1981). At higher altitudes, where dense vegetation is lacking, the opportunities for behavioural avoidance may be limited and could contribute to the reduction in diversity and abundance of spiders.

The reduction in plant species diversity with altitude in the páramo is also likely to reduce spider diversity indirectly through prey numbers. The numbers of several prey groups for spiders are reduced above 4000 m in these samples including Collembola, Hymenoptera, Diptera, Coleoptera and Hemiptera (Simpkins, unpublished data).

There is a key change in vegetation structure at 4000 m in the páramo of Volcán Chiles, with tussock grassland giving way to more open cushion páramo and scattered plants (Ramsay 2001b). Given that Halaj *et al.* (1998) found higher spider species richness in trees with more complex structures, it seems likely that the more complex habitat structure at lower altitudes in the páramo is likely to provide more niches and therefore support a wider variety of species.

This may also explain why the most diverse samples came from *Polylepis* woodlands: there are more niches available for specialisation and coexistence. The presence of an enhanced leaf litter layer in woodlands promotes the survival of soil dwelling spiders (Rypstra *et al.* 1999). This is reflected in the relatively high diversity of Linyphiid species found in the woodlands—their most important source of food is soil dwelling Collembola (Danilov 1972). There was also a greater proportion of the families with cryptic life strategies in the woodlands (*e.g.*, Tetragnathidae, Pholcidae, Ochyroceratidae and Paratropididae). Within the woodlands it is likely that temperature and humidity are not as extreme as on the open páramo and diurnal fluctuations will not be as great.

Figure 4. Body length distributions of spiders at different altitudes from the zonal páramo grassland.



3300 m

3500 m

3700 m

3900 m

4100 m

4300 m

By contrast, the vegetation-poor scree sites had the lowest spider diversity of the habitats surveyed. This was probably due to the lack of vegetation at these sites affecting the density of prey. The species found in the scree slopes were common to the surrounding páramo, suggesting that these species are not specialists to this habitat. There was no dominant life strategy in scree as families range from Clubionids and Lycosids (active hunters) to Agelenids (sheetwebs with funnel shaped retreats) and Linyphiids (sheetwebs close to the ground).

Mire sites, although containing more species than scree habitats, had half the number of families. This indicates that mires may not be able to support as wide a range of life strategies as the other habitat types, and therefore might be the most homogenous in terms of vegetation structure. The most abundant family on the mire habitats were the Linyphiids which are very small and so could live within the structure of the cushions plants. The only alternative strategy would be too live on top of the cushion plants (explaining the presence of Lycosids and Anyphaenids). However this would put them at great risk from predation and may explain why these species are at low abundances.

Although zonal páramo grassland yielded the most morphospecies (24% more than woodland sites), it was subjected to greater sampling intensity (73% more samples than woodland) covering a greater altitudinal range. The families identified from grass and riparian habitats are in two main classes: sit and wait predators (Linyphiidae, Agelenidae, Paratropididae, Araneidae, Tetragnathidae) and active hunters (Clubionidae, Lycosidae, Oonopidae, Anyphaenidae). The higher incidence of sit and wait predators at these habitats is due to the more complex vegetation structure which provides for sheet and orb webs.

Cluster analysis did not produce habitat-related groups, suggesting that many of the dominant spider species have a widespread distribution throughout the páramo zone. Nevertheless, the high proportion of rare species in the samples does leave room for the presence of specialist, habitat-restricted species in the páramo.

Employing a non-taxonomic approach of body size distribution, there was an evident reduction in the range of body sizes at higher altitudes. This may reflect the same changes in environmental conditions, habitat structure and prey availability associated with altitudinal changes in vegetation structure that were discussed earlier. There is also a tendency towards a bimodal body size distribution in páramo spider assemblages. This is in agreement with Otto and Svensson's (1982) study of body sizes of ground dwelling spiders in Norway. They explained the bimodal pattern in terms of prey availability: small prey support small spiders, and these spiders in turn provide food for the second group of larger spiders.

This bimodal pattern is also evident in the mires where the dominant species are Linyphiids (2–4 mm in size) and a few Lycosids and Anyphaenids (8–10 mm). A larger body size at the upper limit may be permitted as the mire sites were not at the very high altitudes and so other forms of prey and shelter may have been available.

Clubionids and Lycosids have similar body sizes and, since body size is strongly correlated to prey size in spiders (Enders 1975), representatives of these two families may be in competition for prey when occurring together. Ordinarily Clubionids and Lycosids are separated by niche: Clubionids actively hunt in the vegetation and Lycosids actively hunt on the ground. The low stature of the vegetation at high altitudes in the páramo may bring these two taxa into competition and explain their negative association in these grasslands. Lycosids are abundant at 3300–3700 m and Clubionids at 3700–4000 m. Above 4000 m, neither group is present in significant numbers.

Otto and Svensson (1982) indicate that at high altitudes as much as 84–99% of all terrestrial predators are spiders. Páramo spiders employ a wide range of hunting strategies and exhibit differences in body size that may restrict competitive interactions and permit coexistence. However, there is some evidence that certain groups may be negatively associated. Specialisation to particular habitat types appears to be limited to a relatively large number of rare species, and common spiders were not habitat-restricted. *Polylepis* woodland assemblages were most distinct from those of the other habitat types. In the zonal páramo, a significant decline in spider abundance and diversity coincided with the change from grassy páramo to cushion páramo (superpáramo) at around 4000–4100 m.

The taxonomy of páramo spiders is poorly understood at present, and this situation is unlikely to change in the near future. Despite this, using a morphospecies approach and defining functional types in terms of body size or feeding strategies (*e.g.*, Uetz 1999) can reveal interesting ecological relationships which help to explain distribution patterns. It is suggested that this type of study can contribute to our understanding of páramo spider ecology and at the same time provide valuable collections of specimens for taxonomists. Collaborative work of this kind will be vital if spider ecology is to progress at high altitudes in the Andes.

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REFERENCES

Curtis, D.J. and Morton, E. (1974) Notes on spiders from tree trunks of different bark texture; with indices of diversity and overlap. *Bulletin of the British Arachnological Society*, **3**: 1–5.

Danilov, N.N. (1972) Birds and arthropods in the tundra biogeocenosis. In Wielgolaski, F.E. and Rosswall, T. (Eds.) *Tundra Biome*, pp. 117–212. Proceedings of the IV International meeting of Biological Productivity in Tundra, Leningrad, USSR.

de Keer, R. and Maelfait, J.P. (1988) Observations on the life cycle of *Erigone atra* (Araneae: Erigoninae) on a heavily grazed pasture. *Pedobiologia*, **32**: 201–212.

Dennis, P., Young, M.R. and Gordon, I.J. (1998) Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology*, **23**: 253–264

Dippenaar-Schoeman, A. S. & Jocqué, R. (1997) *African spiders: an identification manual,* Pretoria: Plant Protection Research Institute.

Docherty, M. and Leather, S.R. (1997) Structure and abundance of arachnid communities on Scots and Lodgepole pine plantations. *Forest Ecology and Management,* **95:** 197–207

Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs,* **67**: 345–366.

Enders, F. (1975) The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae, Salticidae). *American Naturalist,* **109**: 737–763.

Enders, F. (1976) Size, food finding and Dyar's constant. *Environmental Entomology,* **5:** 1–10.

Halaj, J., Ross, D.W. and Moldenke, A.R. (1998) Habitat structure and prey availability as predictors of the abundance and community organization of spiders in western Oregon forest canopies. *Journal of Arachnology*, **27:** 371–377.

Humprey, W.F. (1987) Behavioural temperature regulation. In: Nentwig, W. (Ed.) *Ecophysiology of Spiders,* pp. 187–202. Berlin: Springer.

Hunter, M.L. & Yonzon P. (1992) Altitudinal distributions of birds, mammals, people, forests and parks in Nepal. *Conservation Biology*, **7**: 420–423.

Jacobsen, D., Schultz, R. and Encalada, A. (1997) Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology*, **38**: 247–261.

Kirchner, P. (1987) Behavioural and physiological adaptations to cold. In Nentwig, W. (Ed.) *Ecophysiology of Spiders*, pp. 66–77. Berlin: Springer.

Luteyn, J.L. (1999) *Páramos: a checklist of plant diversity, geographical distribution, and botanical literature,* New York: New York Botanical Garden Press.

Mani, M.S. (1962) *Introduction to High Altitude Entomology*, London: Methuen.

Marc, P., Canard, A. and Ysnel, F. (1999) Spiders (Araneae) useful for pest limitation and bioindication. *Agriculture, Ecosystems and Environment,* **75**: 229–273.

McCune, B. and Mefford, M.J. (1999) *PC-ORD: multivariate analysis of ecological data, Version 4,* Gleneden Beach (Oregon): MjM Software.

Millidge, F. (1991) Further Linyphiid spiders (Araneae) from South America. *Bulletin of the American Museum of Natural History*, **205**.

Mühlenberg, M., Leipold, D., Mader, H.J. and Steinauer, B. (1977) Island ecology of arthropods I. Diversity, niches and resources on some Seychelles islands. *Oecologia* **29**: 117–134.

Nentwig, W. (1987) The prey of spiders. In Nentwig, W. (Ed.) *Ecophysiology of Spiders,* pp. 249–263. Berlin: Springer.

Nentwig, W. (1993) *Spiders of Panama,* Gainsville (FL): Sanhill Crane.

Olson, D.M. (1994) The distribution of leaf litter invertebrates along a neotropical altitudinal gradient. *Journal of Tropical Ecology*, **10:** 129–150.

Otto, C. and Svensson, B.S. (1982) Structure of Communities of ground living spiders along altitudinal gradients. *Holarctic Ecology,* **5:** 35–47.

Ramsay, P. M. (2001a) Diurnal temperature variation in the major growth forms of an Ecuadorian páramo plant community. In: Ramsay, P.M. (Ed.), *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 101–112. Plymouth: Pebble & Shell.

Ramsay, P. M. (2001b) The zonal páramo vegetation of Volcán Chiles. In: Ramsay, P.M. (Ed.), *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 27–38. Plymouth: Pebble & Shell.

Rollard, C. (1993) The spiders of the high altitude meadows of Mount Nimba (West Africa); a preliminary report. *Memoirs of the Queensland Museum,* **33:** 629 –634.

Roth, V.D. (1967) A review of the South American spiders of the family Agelenidae (Arachnida, Araneae). *Bulletin of the American Museum of Natural History*, **134**.

Rypstra, A.L., Carter, P.E., Balfour, R.A. and Marshall, S.D. (1999) Architectural features of agricultural habitats and their impact on spider inhabitants. *Journal of Arachnology*, **27**: 371–377.

Sklenář, P. (2001) Superpáramo flora and vegetation of Volcán Chiles. In: Ramsay, P. M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*, pp. 39–45. Plymouth: Pebble & Shell.

Sklenář, P. & Ramsay, P.M. (in press) Diversity of zonal páramo plant communities in Ecuador. *Diversity and Distributions.*

Smithers, P. (2001) A draft key to the spider families of northern Ecuadorian páramos. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 137–143. Plymouth: Pebble & Shell.

Smithers, P., Ramsay, P.M., Bond, A.N. and Burne, M.E. (2001) Macroarthropod communities of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis*. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 169–175. Plymouth: Pebble & Shell.

Sømme, L. and Zachariassen, K.E. (1981) Adaptations to low temperature in high altitude insects from Mount Kenya. *Ecological Entomology,* **16:** 199–204.

Speight, M.R., Hunter, M.D. and Watt, A.D. (1999) *Ecology of Insects: concepts and application*, Oxford: Blackwell Science.

Tajovsky, K. (1997) Distribution of Millipedes along an altitudinal gradient in three mountain regions in the Czech and Slovak republics (Diplopoda). *Entomologica Scandinavica,* **S51:** 225–233.

Uetz, G.W., Halaj, J. and Cady, A.B. (1999) Guild structure of spiders in major crops. *Journal of Arachnology*, **27**: 270–280.

Macro-arthropod communities of the giant rosette plant, *Espeletia pycnophylla* subsp. *angelensis*

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SUMMARY

Giant rosette plants of *Espeletia pycnophylla* subsp. *angelensis* may provide shelter and food for a range of macro-arthropods in the high-altitude páramos of Ecuador, particularly at night. Older plants may provide greater habitat diversity than younger plants, and therefore their fauna may also be expected to be more diverse. Plants of three sizes were collected (1, 1.5 and 2 m tall), and their macro-arthropod fauna were examined in 0.5 m sections of the stem. *Espeletia* plants contained a community of macro-arthropods dominated by Araneae, Coleoptera adults, Lepidoptera larvae, Pseudoscorpionidea and Diptera. Most of the animals occupied the living leaf rosette and the dead-leaf-covered stem just below it. Few individuals were found in the lower, older sections of the stem. Older plants did not contain more diverse communities than younger plants, suggesting that the additional habitat provided at the base of older plants was not utilised by specialist fauna. Although there was some evidence for the plants being used as night-time refugia, the populations of arthropods were highly variable from plant to plant.

RESUMEN

Las rosetas gigantes de *Espeletia pycnophylla* subsp. *angelensis* puedan proporcionar protección y alimentación a una amplia gama de macro-artrópodos, particularmente durante la noche, en los altos páramos andinos de Ecuador. Las plantas de mayor edad puedan proporcionar una mayor diversidad de hábitats que las más jóvenes, y por lo tanto, es de suponer que la fauna sería también más diversa. Se recolectaron plantas de tres tamaños (1, 1.5 y 2 m de altura) y se examinó su fauna de macro-artrópodos en secciones del tallo de 0.5 m. Las plantas de *Espeletia* contuvieron una comunidad de macro-artrópodos dominado por Araneae, adultos de Coleoptera, larvas de Lepidoptera, Pseudoscorpionidea y Diptera. La mayoría de los animales se localizaron en la roseta terminal de hojas vivas y en el tallo cubierto en hojas muertas inmediatamente por abajo de la roseta. Pocos individuos fuero encontrados en las secciones más bajas y viejas del tallo. Las plantas más viejas no tuvieron comunidades más diversas que las plantas más jóvenes, sugiriendo que el hábitat adicional proporcionado por la base de las plantas viejas no fue utilizado por la fauna especialista. Aunque hubo cierta evidencia de que las plantas fueron utilizadas como refugio por la noche, las poblaciones de artrópodos variaron fuertemente de planta a planta.

Key words: invertebrates, páramo, plant height, diurnal, nocturnal, Ecuador

INTRODUCTION

The páramos are relatively inhospitable environments which are dominated by tussock forming grasses, bamboos, cushion plants and composites (Luteyn 1999). There is little seasonal change in the climate, but there are enormous variations on a daily basis with fluctuations in temperature from 25°C in the day to below freezing at night (Sømme, Davidson and Onore 1996).

Páramos at the northern end of the Andean chain are dominated by Compositae of the genus *Espeletia* (Luteyn 1999). These plants can grow to a height of 3 m and cover huge areas of the páramo. They possess an apical rosette on top of a stem that is sheathed in marcescent leaves. As the plant produces new leaves at the growing point the older leaves in the lower part of the rosette senesce but are retained on the stem as a thick sheath, which insulates the stem from the extremes of temperature experienced during the night (Smith 1979, Beck 1994, Ramsay 2001). This sheath prevents the water in the plant stem from freezing thus avoiding tissue damage and thus providing a reservoir of available water. This can then be utilised in the early hours of the morning so that the leaves in the rosette are able to begin transpiration as soon as the light levels are high enough, rather than waiting for the ground water in the surrounding soil to thaw (Smith 1979). Thus the plant is able to increase the time available for photosynthesis and growth. This growth form has evolved independently in many tropical mountain habitats across the globe (Smith 1994).

Espeletia pycnophylla has been observed to add height at around 1.5–2 cm yr^{-1} on average (Ramsay, unpublished data), consistent with reports for other species from this genus (Smith 1981, Monasterio and Lamotte 1989, Cavalier *et al.* 1992, Estrada 1995). Therefore, the leaves at the base of a 2 m high plant could be in the order of 100 years old. It is thought that the very slow rate of decomposition of these leaves is due to the low environmental temperatures and the presence of terpenic resins in the leaves (Smith 1979). The structure of the marcescent leaf sheath alters with age. Younger dead leaves are entire and firmly attached to the stem forming a series of compact layers, whilst older leaves at the bases of tall plants (*i.e.*, >2m high) are highly fragmented and form a dense matrix that is only loosely attached to the stem.

Invertebrates living on the páramos have evolved a number of strategies to deal with very low nocturnal temperatures. Some can with stand subzero temperatures by supercooling their tissues whilst others avoid the low temperatures by seeking shelter in either the soil or within the vegetation (Sømme 1986).

The sheaths of marcescent leaves on the stems of *Espeletia* plants would appear to offer invertebrates a complex structural matrix and provides an ideal refuge from the low nocturnal temperatures of the open páramo. Thus the *Espeletia* plants could possess two distinct invertebrate communities, a permanent community and a temporary nocturnal assemblage of species that use the *Espeletia* plants as a refuge.

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 169-175.

Individual plants could be considered as islands within the tussock páramo, with habitat variability increasing with the age of the plant. Older and taller plants would be expected to have more habitat heterogeneity and, thus, higher diversity of invertebrates.

Previous workers have examined the invertebrates associated with *Espeletia* species and found a wide range of taxonomic groups present. Sturm and Abouchaar (1981) investigated *Espeletia* plants on Colombian páramos using Berlese funnels to extract the fauna and found 20 taxonomic groups of insects, two myriopods, one isopod, and four arachnids. In terms of the numbers present the Acari and Collembola dominated the community. The stem sheath comprised 90% Acari, 3% Collembola, the rosette base was 100% Acari and the rosette leaves were 94% Acari and 5% Collembola. Only the flowers were dominated by other groups having only 19% Acari. Venezuelan *Espeletia* species are also dominated by micro-arthropods, with flies, beetles, crickets and spiders (Garay and Lamotte 1989, Monasterio and Lamotte 1989). Lamotte (1998) studied *Espeletia* plants in Venezuela where he found large numbers of micro arthropods and few phytophagus, detritivorous or carnivorous invertebrates. He speculated that the high concentrations of terpenic resin found in the plants lead to the inability of most invertebrates to metabolise the leaves successfully. Other workers have concentrated on the rosettes, dividing the invertebrates into residents and visitors. Sturm (1989) recorded a resident fauna of Thysanoptera, Hemiptera, Coleoptera (Chrysomelidae, Curculionidae, Staphylinae, Melyridae, Lathridiidae, Corylophidae), Lepidoptera (Gelechiiidae), and Diptera (Boridae, Bibionidae). He considered the following to be visitors: Hymenoptera (bombus), Diptera (Tachinidae, Syrphidae), Coleoptera (Lampyridae, Elatridae, Curculionidae), and Lepidoptera (Noctuidae, Sphingiodae). Klimaszewski and Sturm (1991) reported four new species of Staphylinid beetle collected from the rosettes of *Espeletia* species in Colombia and northern Ecuador. They also reported the presence of four other Coleoptera families (Curculionidae, Melyridae, Chrysomelidae and Lathridiidae), along with Thysanaptera, Rynchota, Lepidoptera, Diptera and Acari.

Although a diverse assemblage of invertebrates has been recorded from *Espeletia* species, there are few studies of the ecology of this association. The aim of the present study was to investigate the invertebrate community living in *Espeletia pycnophylla* plants to explore the hypothesis that older plants contain a greater diversity of invertebrates and to examine the role of these plants as nocturnal refuges.

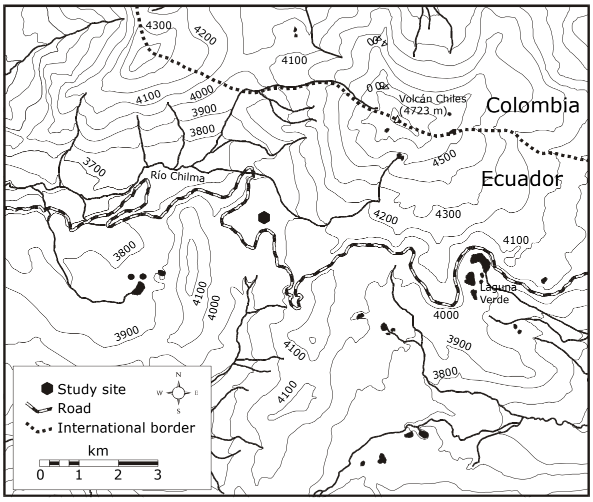
METHODS

Study Area

The work took place at an altitude of 3,850 m, on the western slopes of Volcan Chiles (Fig. 1), an extinct volcano 15 km north of Tulcán (Carchi province, northern Ecuador). Giant stem rosettes of *Espeletia pycnophylla* subsp. *angelensis* and tussock grasses (principally *Calamagrostis intermedia* and *C. effusa*) dominate the area, with occasional giant basal rosettes of *Puya hamata*. The dense sward of *Calamagrostis* was interspersed with *Lachemilla hispidula, Hypochaeris sonchoides, H. sessiliflora, Loricaria ilinissae, Hypericum larcifolium, Pentacalia andicola, P. peruviana, P. vaccinioides, Disterigma empetrifolium, Lycopodium clavatum, Gentianella nummulariifolia, Castilleja fissifolia, Rhynchospora macrochaeta, Cortaderia nitida, Lupinus sarmentosus, Oreobolus obtusangulus, O. goeppingeri* and *Plantago rigida*.

Local farmers graze cattle and horses in the area, and parts of the páramo are burned to generate fresh growth for the livestock.

Fig. 1. Sampling location of the Espeletia pycnophylla *plants.*



Sampling Protocol

In order to assess the effect of plant age on the macro-invertebrate community three height classes of *Espeletia* plants were selected: 1 m, 1.5m and 2m tall. Assuming an estimated growth rate of about 2 cm yr^{-1}, *E. pycnophylla* plants of these heights would be approximately 30, 55 and 80 years old, respectively. Though the rosettes of tall and short plants are similar, the characteristics of the stem vary with age. The difference between a tall and short plant is the presence of additional stem, which is much older and of a different character to that found on younger plants. The sampling procedure, therefore, attempted to collect material which would allow comparison between different sized plants; by sampling the *Espeletia* plants in 0.5 m sections (the approximate size of the rosette, and a manageable size for processing).

Plants were selected that had been unaffected by burning, *i.e.*, they had a full sheath of marcescent leaves. Selected plants were divided into 0.5 m sections of stem and the rosette. Each section was covered with a large plastic bag to prevent the escape of invertebrates. The bag was held tightly around the stem whilst the section was sawn off. This process was started from the top of the plant and repeated until all sections of the plant were sealed in bags.

Daytime samples were collected in late July 1997 over two warm, sunny days beginning at 10:00 on each occasion, whilst the nocturnal samples were collected on a single clear and cold night beginning at 22:00.

Ten replicate plants for the 1 m height class were collected, but only three replicates of the 1.5 m and 2 m plants were sampled (owing to logistical constraints). Later, each section was placed on a white sheet, and carefully dissected whilst searching for invertebrates. Any invertebrates found were preserved in 70% alcohol, and subsequently identified to order using a basic key (Tillings 1987).

RESULTS

Table 1 shows the mean number of individuals from each taxon recorded from each of the plant size classes. 1 m tall plants had fewer individuals than the other plants. Daytime and night-time samples were dominated by similar groups of invertebrates: Araneae were the most abundant followed by the Coleoptera, Lepidoptera larvae, Pseudoscorpionidea, Diptera and insect pupae. There were very few representatives of the Acari and Collembola. In all cases, there was high variability in the abundance of the taxa from plant to plant.

Table 2 shows species diversity for each of the 0.5 m height sections for each of the plant size classes for both day and night samples. There are more taxa in the night-time samples than in the ones collected during the day. In conjunction with reduced numbers of representatives of the dominant taxa, this helps to explain the higher diversity values at night. 1 m tall plants have more taxa than the taller plants, and have higher species diversity both diurnally and nocturnally.

Lepidoptera larvae and Coleoptera adults were most abundant in the rosette and the section of stem just below it (Table 3). There were fewer Coleoptera adults present at night. By contrast, there were more Diptera in the plants at night than by day. Araneae, Pseudoscorpionidea and Hymenoptera were most abundant in the marcescent leaf zone just below the rosette, especially by day.

DISCUSSION

The dominant groups of macro-arthropods collected were the Araneae, Coleoptera and Lepidoptera larvae, which together comprised approximately 72% (by day) and 65% (by night) of the fauna. The Lepidoptera larvae and some of the Coleoptera are herbivores that feed on the younger tissues of the plants. The concentration of Coleoptera in the rosettes suggests that the majority of this group may be herbivores and some individuals were observed feeding when collected. The Lepidoptera larvae were concentrated in the both the rosette and the top stem section. Whilst many larvae were observed feeding on the flower heads and young leaves in the rosette there is little of nutrient value in the sheath. However the top of the leaf sheath provides an ideal environment for larvae about to pupate, therefore the larvae recorded from the leaf sheath were probably seeking pupation sites rather than feeding on the older leaves.

The Araneae were the most abundant taxa recorded which is not unusual as the Araneae are often the dominant macro-arthropod in grassland ecosystems. Examination of the Araneae from the diurnal samples reveals that the group is dominated by the family Anyphenidae. This family is made up of nomadic hunters and they are often abundant in the ground vegetation of the surrounding páramo (Oxbrough, unpublished data), which suggests that the Anyphenidae are constantly moving in and out of the *Espeletia* plants. They were more abundant in the top section of the leaf sheath as the highest density of other invertebrates was found in this section, providing a concentration of potential prey.

The Diptera displayed a greater abundance in the 1 m plants. This represents a good strategy for small flying insects living in an environment where high wind speeds are frequently experienced. By keeping close to the ground where wind speeds are lower and temperatures are higher, they are able to forage more effectively without being blown out of suitable patches of habitat as well as avoiding physical damage.

The Pseudoscorpionidae also display a maximum abundance in the centre sections of the leaf sheath. These are sit and wait predators which feed on micro arthropods indicating the presence of a significant microarthropod community in the leaf sheath.

The majority of the Hymenoptera recorded were from the family Ichneumonidae, all of which are parasitic. This family has been recorded from a variety of hosts including Coleoptera, Lepidoptera larvae and the Araneae, all of which were abundant in the giant rosette plants. Thus the Ichneumonidae were most abundant in the section of stem just below the leaf rosette where their potential hosts were in highest numbers.

Table 1. Mean number of individuals (± sd) from three heights of Espeletia *plants collected by day and by night.*

Taxon	**Height of giant rosette plant**			**Total number of individuals**	**Percentage of total**
	1 m	**1.5 m**	**2 m**		
n=	10	3	3		
Daytime samples					
Araneae	20 ± 4.7	36 ± 21.5	38.0 ± 6.0	422	33.4
Coleoptera adult	18.5 ± 25.1	24.3 ± 24	22.7 ± 12.7	326	25.8
Lepidoptera larvae	11.5 ± 10.2	2.7 ± 2.5	16.3 ± 10.0	172	13.6
Pseudoscorpionidea	5.4 ± 11.3	19.3 ± 29.3	4.3 ± 4.0	125	9.9
Diptera adult	5.1 ± 3.9	1.3 ± 1.5	3.3 ± 2.5	65	5.1
Insect Pupae	2.5 ± 2.2	1.0 ± 1.0	5.3 ± 4.9	44	3.5
Hymenoptera	1.8 ± 2.3	2.7 ± 3.1	2.0 ± 1.0	32	2.5
Acari	2.0 ± 5.6	—	1.0 ± 1.0	23	1.8
Coleoptera larvae	1.4 ± 2.5	0.3 ± 0.6	—	15	1.2
Hemiptera	0.6 ± 0.5	1.0 ± 1.0	1.0 ± 1.0	12	1.0
Lepidoptera imago	0.7 ± 1.3	—	1.3 ± 2.3	11	0.9
Psocoptera	0.1 ± 0.3	0.7 ± 1.2	2.7 ± 1.2	11	0.9
Collembola	0.4 ± 0.5	—	—	4	0.3
Diplopoda	0.1 ± 0.3	—	—	1	0.1
Mean no of individuals per plant	70.1	89.3	98.0		
Night-time samples					
Araneae	13.3 ± 9.8	19.0 ± 26.0	9.3 ± 6.7	218	32.3
Lepidoptera larvae	2.7 ± 2.2	18.7 ± 22.8	9.3 ± 5.8	111	16.4
Coleoptera adult	4.5 ± 3.9	17.0 ± 19.9	4.0 ± 2.6	108	16.0
Insect pupae	2.9 ± 3.5	7.0 ± 6.6	7.7 ± 4.7	73	10.8
Diptera adult	3.9 ± 3.3	3.7 ± 6.4	6.0 ± 5.3	68	10.1
Pseudoscorpionidea	3.5 ± 8.7	3.7 ± 2.1	6.0 ± 4.4	64	9.5
Hymenoptera	0.8 ± 0.8	1.3 ± 1.2	1.7 ± 0.6	17	2.5
Hemiptera	0.5 ± 1.0	—	0.7 ± 0.6	7	1.0
Lepidoptera imago	0.2 ± 0.4	—	0.7 ± 1.2	4	0.6
Acari	0.2 ± 0.4	0.3 ± 0.6	—	3	0.4
Collembola	0.2 ± 0.4	—	—	2	0.3
Mean no of individuals per plant	32.7	70.67	45.33		

Table 2. Species diversity scores for three heights of Espeletia *plants, divided into 0.5 m sections down the stem, by day and by night. Species richness (the number of taxonomic groups) and two diversity indices are shown; in each case, "Σ" is the calculation for all invertebrates collected from a particular section of plant. The maximum age of each section has been estimated assuming a growth rate of 2 cm yr^{-1}; thus the first 0.5 section represents the rosette, the next 0.5 m section 5–30 years,* etc.

		No of Taxonomic Groups				**Margalef Index**				**Pielou Index**			
	Plant height:	**1.0m**	**1.5m**	**2.0m**	Σ	**1.0m**	**1.5m**	**2.0m**	Σ	**1.0m**	**1.5m**	**2.0m**	Σ
	***N*=**	**10**	**3**	**3**		**10**	**3**	**3**		**10**	**3**	**3**	
Daytime samples													
	Rosette	9.02	4.33	4.67	6.01	2.63	1.03	1.56	1.74	1.51	0.86	0.88	1.08
Approx age (yr)	5–30	4.20	3.67	5.00	4.29	1.19	0.76	1.53	1.16	0.64	0.54	0.92	0.70
	30–55		3.67	3.67	3.67		1.07	1.45	1.26		0.54	0.92	0.73
	55–80			2.67	2.67			0.92	0.92			0.63	0.63
	Overall	6.61	3.89	4.00		1.91	0.95	1.37		1.08	0.65	0.84	
Night-time samples													
	Rosette	10.00	7.00	7.00	8.00	1.02	0.84	0.96	0.94	0.65	0.43	0.67	0.58
Approx age (yr)	5–30	8.00	7.00	7.00	7.33	1.33	1.35	1.60	1.43	0.74	0.62	0.74	0.70
	30–55		6.00	7.00	6.50		1.02	1.45	1.24		0.49	0.76	0.63
	55–80			6.00	6.00			0.24	0.24			0.33	0.33
	Overall	9.00	6.67	6.75		1.18	1.07	1.06		0.70	0.51	0.63	

Table 3. Mean number of individuals from selected taxa occurring in 0.5 m sections of Espeletia *plants of three heights. See Table 2 for an explanation of the age estimates.*

	Plant height:	**1.0m**	**1.5m**	**2.0m**	**1.0m**	**1.5m**	**2.0m**	**1.0m**	**1.5m**	**2.0m**
	***n*=**	**10**	**3**	**3**	**10**	**3**	**3**	**10**	**3**	**3**
		Lepidoptera Larvae			**Coleoptera Adults**			**Diptera Adults**		
Daytime samples										
	Rosette	7.9 ± 8.4	1.3 ± 1.2	4.7 ± 3.1	7.7 ± 14.6	19 ± 16.5	16.7 ± 11.4	1.6 ± 1.3	1.3 ± 1.5	0.3 ± 0.6
Approx age (yr)	5–30	3.6 ± 2.6	1.3 ± 1.5	9.3 ± 8.5	10.8 ± 12.4	4.3 ± 5.8	4.3 ± 0.6	3.5 ± 3.3	—	2.0 ± 1.0
	30–55		—	2.3 ± 2.1		1.0 ± 1.7	1.7 ± 1.2		—	1.0 ± 1.0
	55–80			—			—			—
Night-time samples										
	Rosette	1.6 ± 1.4	13.7 ± 15	1.7 ± 2.1	3.5 ± 3.4	14.0 ± 14.7	0.7 ± 1.2	3.5 ± 3.2	3.0 ± 5.2	1.3 ± 1.5
Approx age (yr)	5–30	1.1 ± 1.2	4.3 ± 7.5	6.3 ± 4.5	1.0 ± 1.3	2.0 ± 3.5	2.0 ± 3.5	0.4 ± 0.7	0.3 ± 0.6	1.0 ± 1.0
	30–55		0.7 ± 0.6	0.0 ± 0.0		1.0 ± 1.7	0.3 ± 0.6		0.3 ± 0.6	0.7 ± 1.2
	55–80			1.3 ± 2.3			1.0 ± 1.7			3.0 ± 5.2
		Hymenoptera			**Araneae**			**Pseudoscorpionidae**		
Daytime samples										
	Rosette	0.4 ± 1.3	—	—	0.9 ± 0.6	4.0 ± 4.6	1.7 ± 0.6	0.4 ± 1.3	1.0 ± 1.7	—
Approx age (yr)	5–30	1.4 ± 2.2	2.3 ± 2.5	1.7 ± 0.6	19.1 ± 4.6	24.7 ± 19.9	22.3 ± 11.0	5.0 ± 10.3	13.3 ± 20.6	1.0 ± 1.7
	30–55		0.3 ± 0.6	0.3 ± 0.6		7.3 ± 6.1	11.7 ± 6.5		5.0 ± 7.0	3.3 ± 2.9
	55–80			—			2.3 ± 0.6			—
Night-time samples										
	Rosette	0.3 ± 0.5	—	—	3.2 ± 5.1	4.0 ± 5.3	3.7 ± 1.5	0.5 ± 1.6	0.7 ± 1.2	1.0 ± 1.0
Approx age (yr)	5–30	0.5 ± 0.7	1.3 ± 1.2	1.0 ± 1.0	10.1 ± 9.7	12.3 ± 17	4.7 ± 6.4	3 ± 7.1	2.3 ± 3.2	1.7 ± 2.1
	30–55		—	0.7 ± 0.6		2.7 ± 3.8	1.0 ± 1.0		0.7 ± 0.6	2.0 ± 2.6
	55–80			—			—			1.3 ± 2.3

There were very few representatives of the micro-arthropods, which have been recorded in great numbers in previous studies of the invertebrate fauna of *Espeletia* plants (Sturm and Abouchaar 1981, Sturm 1989, Garay and Lamotte 1989, Monasterio and Lamotte 1989, Lamotte 1998). Only 26 Acari and six Collembola were collected from the 32 plants, compared with thousands of individuals in other studies. This difference may be explained by the extraction procedure. The current study used hand searching whereas the previous investigations used funnel extraction techniques. Nevertheless, the low incidence of these taxa in the hand searches suggests that their numbers may be considerably lower than in other species of *Espeletia* in Colombia and Venezuela.

Although there were more individual invertebrates in taller plants compared with 1 m ones, there were fewer taxa and lower species diversity. It appears that the additional habitat provided by older *Espeletia* plants at the base of the stems is not attracting more taxa into these plants. In other words, the very old leaf remains attached to the base of the stems is not being utilised by specialist macro-arthropods. In fact, these sections of the stem supported very low numbers of invertebrates, perhaps explained by the dry, corky nature of the leaf material, and their impregnation with terpenes. In a way, this part of the plant is the equivalent of an inhospitable desert with very little food resources. Furthermore, this zone may act as a barrier to the migration of animals from the ground into the rosette. The poor development of this zone in young *Espeletia* plants may explain the higher number of taxa and greater species diversity in their rosettes, when compared with taller plants. The presence of vegetation "bridges" connecting the rosettes directly with neighbouring plants may allow invertebrates to bypass the stem altogether.

There was some evidence to support the theory that *Espeletia* plants may provide night-time refuge for invertebrates which are active outside the plants during the day. In particular, the number of arthropod taxa increased at night in the plant sections—although the arthropod community in the *Espeletia* plants was highly variable from plant to plant. It may be the case that invertebrates take full advantage of the insulating properties of the *Espeletia* stem on the coldest nights when temperatures drop below freezing. The night-time samples in this study were collected when the ambient air temperature was around 2°C.

Although several of the dominant groups inside the *Espeletia* plants are predators, they are also abundant in the tussock grasses and on the ground of the páramo. Visiting arthropods may not, therefore, experience greater predation rates inside the plants. Furthermore, the numbers of spiders inside *Espeletia* plants is lower at night than during the day, suggesting that some of them may forage outside at night.

Nevertheless, the plant's terpenes act as a deterrent to some visiting arthropods, in spite of the insulation from cold temperatures the stem affords.

Espeletia pycnophylla subsp. *angelensis* did contain a community of macro-arthropods, dominated by Araneae, Coleoptera adults, Lepidoptera larvae, Pseudoscorpionidea and Diptera. Most of the macro-arthropods were present in the living leaf rosette and the dead-leaf-covered stem just below it. Few individuals were found in the lower, older sections of the stem. Older plants were not more diverse than younger plants, suggesting that the additional habitat provided at the base of older plants was not utilised by specialist fauna. Although there was some evidence for the plants being used as night-time refugia, the populations of arthropods were highly variable from plant to plant. A large number of replicate samples would be required to provide reliable indications of shifts in abundance between day and night. The development of *in situ* trapping techniques may provide better insight into these community changes.

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REFERENCES

Beck, E. (1994) Cold tolerance in tropical alpine plants. In: Rundel, P.W., Smith, A.P. and Meinzer, F.C. (Eds.) *Tropical Alpine Environments: Plant Form and Function*, pp. 77–110. Cambridge: Cambridge University Press.

Cavalier, J., Machado, J.L., Valecia, D. Monton, J., Laignelet, A., Varela, A. and Mejía, C. (1992) Leaf demography and growth rates of *Espeletia barclayana* Cuatr. (Compositae), a caulescent rosette in a Colombian páramo. *Biotropica*, **24**: 52–63.

Estrada, C.A. (1995) *Procesos productivos en poblaciones de* Espeletia timotensis *en el páramo desértico.* PhD thesis, Universidad de los Andes, Mérida, Venezuela.

Lamotte, M., Garay, I. and Monasterio, M. (1989) Les grands traits du functionnement d'un écosystème tropical d'altitude. *Societa Italiana di Ecologia Atti (Sienne),* **3**: 61–66.

Garay, I. and Lamotte, M. (1989) Le peuplement animal des rosettes d'*Espeletia* dan le páramo désertique des Andes du Venezuela. *Societa Italiana di Ecologia Atti (Sienne),* **7**: 55–59.

Klimaszewski, J. and Sturm, H. (1991) Four New Species of the Oxypodine Genus *Polylobus* Solier (Coleoptera: Staphylinidae: Aleocharinae) collected on the flower rosettes of some high Andean giant rosette plants (Espeletiinae: Asteraceae). *The Coleopterist Bulletin*, **45:** 1–13.

Lamotte, M. (1998) La Zoocenose du Páramo Desertique des Andes de Merida (Venexuela). *Bulletin de la Société zoologique de France,* **123**: 395–400.

Luteyn, J.L. (1999) *Páramos: a checklist of plant diversity, geographical distribution, and botanical literature,* New York: New York Botanical Garden Press.

Monasterio, M. and Lamotte, M. (1989) Les populations d'*Espeletia timotensis* dans le páramo désertique des Andes du Venezuela. *Revue Ecologique,* **44**: 201–227.

Ramsay, P. M. (2001) Diurnal temperature variation in the major growth forms of an Ecuadorian páramo plant community. In: Ramsay, P.M. (Ed.), *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 101–112. Plymouth: Pebble & Shell.

Smith, A.P. (1979) Function of the Dead Leaves in *Espeletia schultzii* (Compositie)an Andean Caulescent Rosette Species. *Biotropica,* **11**: 43–47.

Smith, A.P. (1981) Growth and population dynamics of *Espeletia* (Compositae) in the Venezuelan Andes. *Smithsonian Contributions to Botany*, **48**: 1–45.

Smith, A.P. (1994) Introduction to tropical alpine vegetation. In: Rundel, P.W., Smith, A.P. and

Meinzer, F.C. (Eds.) *Tropical Alpine Environments: Plant Form and Function*, pp. 1–19. Cambridge: Cambridge University Press.

Snow ,D.W. (1983) The use of *Espeletia* by páramo humingbirds in the eastern Andes of Colombia. *Bulletin of the British Ornithologists' Club*, **103**: 89–94.

Sømme, L. (1986) Tolerences to Low Temperatures and Desication in Insects from Andean Páramos. *Artic and Alpine Research,* **18**: 253–257.

Sømme, L., Davidson, R.L. and Onore, G. (1996) Adaptations of Insects at high altitudes of Chimborazo, Ecuador. *European Journal of Entomology*, **93**: 313–318.

Sturm, H. and Abouchaar, A. (1981) Obsevaciones sobre la ecología del páramo andino de Monserrate. *Caldasia*, **62**: 223–256.

Sturm, H. (1989) Beziehungen zwischen den Bluten einiger hochandiner Wollschopfpflanzen (Espeletiinae, Asteraceae) und Insekten. *Studies on Neotropical Fauna and Environment*, **24**: 137–155.

Tillings, S.M. (1987) *A Key to the Major Groups of British Terestrial Invertebrates*, Preston Montford: Field Studies Council.

The influence of physicochemistry on macroinvertebrate community assemblages in the upper Río Chilma

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SUMMARY

Macroinvertebrates were sampled from 20 sites in four high-altitude tributary streams of the Río Chilma, northern Ecuador, to assess the influence of altitude and various physicochemical variables on community composition and diversity. The most abundant families were Baetidae, Leptophelebiidae, Sericostomatidae, Chironomidae and Limnephilidae. There was a significant negative relationship between total family richness and altitude and the abundance of several families was also significantly correlated with altitude. Altitude itself is unlikely to govern the distribution of aquatic animals directly, but is correlated with physicochemical parameters that may determine distribution patterns. However, the measured environmental parameters explained only a part of the variability in composition. Undoubtedly, other environmental factors may be responsible for some of the remainder, but interactions between species and chance colonisation events may also be important.

RESUMEN

Se realizaron muestreos de macroinvertebrados en 20 sitios de cuatro riachuelos afluentes de gran altitud del Río Chilma, en el norte del Ecuador, con objeto de evaluar la influencia de varias variables fisicoquímicas sobre la composición y diversidad de las comunidades. Las familias mas abundantes fueron Baetidae, Leptophelebiidae, Sericostomatidae, Chironomidae y Limnephilidae. Hubo una relación negativa significativa entre la riqueza total de familias y la altitud y, asimismo, la abundancia de varias familias estuvo también relacionada con la altitud. Es improbable que la altitud misma determine directamente la distribución de estos animales acuáticos, sino que sea la correlación entre la altitud y diversos parámetros fisicoquímicos la responsable de estos patrones. Sin embargo, los parámetros ambientales medidos solo explicaron parte de la variabilidad en la composición de la comunidad. Indudablemente, otros factores ambientales podrían ser responsables de al menos parte de la variabilidad no explicada, pero las interacciones entre las especies y eventos fortuitos de colonización podrían también ser importantes.

Key words: streams, páramo, tropical alpine, aquatic invertebrates

INTRODUCTION

The ecology of high-altitude, tropical streams is poorly understood and, as these ecosystems may be highly vulnerable to anthropogenic impacts, there is a pressing need for studies that provide fundamental information on the communities that inhabit these streams. Moreover, recent studies that have focused on such ecosystems (Rundle and Omerod 1995, Omerod *et al.* 1994), suggest that they do not conform to the general models developed for streams, such as the River Continuum Concept (Vannote *et al.* 1980). Hence, studies that aim to assess the relationship between biota and physicochemistry in such systems will greatly enhance our knowledge on how these systems function and aid the development of more relevant models.

In Ecuador, high-altitude streams are often located many kilometres from human habitation and are mostly unaffected by direct anthropogenic disturbance. Such systems allow the generation of important baseline information in pristine conditions, against which impacts from anthropogenic activities can be gauged. There have been several studies published on South American highland stream systems, including an early study by Illes (1964), monthly data from a single stream site at 3300 m by Turcotte & Harper (1982a), a study of invertebrate drift in a Peruvian tributary of the Amazon (Turcotte and Harper 1982b), and a more recent study by Jacobsen *et al.* (1997). The latter study focused upon the influence of temperature on the structure and diversity of stream macroinvertebrate assemblages in contrasting stream systems (high and low altitude in Ecuador and low altitude in Denmark). Here we take a more extensive approach to assessing between-stream variation in macroinvertebrate assemblages at high altitudes in the páramo of northern Ecuador. Our main aim was to assess the importance of altitude and other physicochemical variables in correlations with the diversity and structure of macroinvertebrate community assemblages.

METHODS

Study area and sampling sites

Four first-order tributaries (<2 m wide) in the Río Chilma catchment were sampled between 3400 and 4200 m on Volcán Chiles, on the Ecuador-Colombia border (Fig. 1). Each tributary was fast-flowing with a coarse substratum, and is referred to here by code (H, VC, RT or SN) because only one has been formally named (Quebrada de Santo Negro—SN). All of these tributaries flow into the Río Chilma and then into the Río Mira, which enters the Pacific Ocean near San Lorenzo.

The geology in this area was typically Andean, comprising mainly crystalline formations of gneiss, diorites and mica schists (Butland 1972). The surrounding páramo vegetation was dominated by tussock grasses (especially *Calamagrostis intermedia*) and the giant rosettes of *Espeletia pycnophylla* subsp. *angelensis* (Ramsay 2001). Above 4000 m vegetation cover was sparse. An annual rainfall average of 1050 mm of rain per year has been recorded at 3100 m

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 177-183.

Fig. 1. Location of sampling sites on Volcán Chiles.

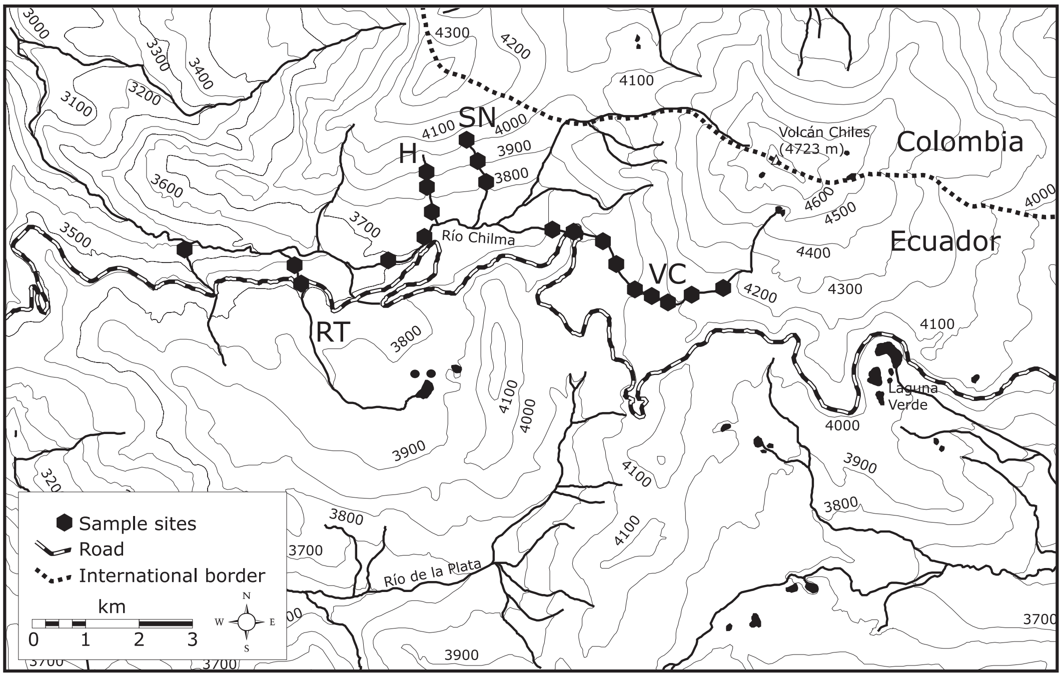

Table 1. Mean (and range) of physico-chemical variables for sample sites in four tributaries of the Río Chilma.

	H	**VC**	**RT**	**SN**
***n*=**	**5**	**10**	**2**	**3**
Temperature (ºC)	10.2 (9.5–11.7)	7.7 (7.0–10.2)	10.2 (9.9–10.6)	10.55 (10.5–10.6)
Conductivity (µS)	447.00 (273–923)	101.00 (12.52–416.00)	318.00 (248–354.00)	507.5 (259– 756)
pH	7.34 (5.95–7.85)	7.70 (7.5–7.98)	7.00 (6.6–7.6)	7.65 (7.5–7.8)
Dissolved Oxygen (%)	50.08 (39.2–57.4)	56.0 (40.8–61.2)	51.3 (50.0–53.0)	55.0 (52.0–58.0)
Copper (mg l^{-1})	0.00 (0.00–0.02)	0.05 (0.01–0.11)	0.01 (0.00–0.03)	0.03 (0.02–0.03)
Zinc (mg l^{-1})	0.00 (0.00–0.02)	0.02 (0.00–0.04)	0.00 (0.00–0.01)	0.01 (0.01)
Aluminium (mg l^{-1})	1.67 (1.51–1.93)	0.76 (0.04–1.17)	0.77 (0.76–0.79)	0.93 (0.81–1.04)
Magnesium (mg l^{-1})	7.14 (1.93–18.80)	1.17 (0.23–6.00)	3.04 (0.61–4.67)	2.72 (2.19–3.24)
Calcium (mg l^{-1})	40.10 (21.60–94.60)	6.19 (0.01–38.80)	28.40 (22.00–33.70)	20.85 (19.69–22.00)
Lead (mg l^{-1})	0.16 (0.05–0.20)	0.01 (0.00–0.04)	0.00 (0.00–0.00)	0.05 (0.05–0.06)
Iron (mg l^{-1})	0.14 (0.06–0.26)	0.15 (0.01–0.63)	0.02 (0.00–0.05)	0.13 (0.12–0.13)
Sodium (mg l^{-1})	8.35 (3.49–15.63)	1.62 (0.44–5.49)	2.83 (2.10–3.48)	3.76 (3.70–3.82)
Potassium (mg l^{-1})	2.45 (1.64–4.31)	1.15 (0.17–2.44)	1.52 (1.11–2.05)	1.64 (1.60–1.68)
Width Riffle (m)	0.7 (0.30–2.0)	0.5 (0.25–0.85)	0.32 (0.31–0.34)	0.42 (0.29–0.54)
Width Pool (m)	1.7 (0.35–3.80)	1.4 (0.32–3.10)	0.8 (0.58–1.05)	0.5 (0.15–0.76)
Depth Pool (cm)	35.8 (5.0–63.0)	27.9 (10.0–20.0)	25.0 (19.0–28.0)	60.5 (27.0–94.5)
Depth Riffle (cm)	20.6 (6.0–57.0)	16.75 (4.0–35.0)	22.0 (16.0–31.0)	10.5 (7.0–14.0)

on the Colombian side of Volcán Chiles, with wetter periods from March-May and October-December (Rangel-Ch. & Ariza-N. 2000). Air temperatures vary considerably during the 24-hour cycle. Occasionally the daytime maximum may reach 20°C, falling to below zero at night. Surrounding land use was largely extensive pastoral agriculture, with most disturbances resulting from fires set to encourage the growth of green fodder for livestock.

An attempt was made to sample each tributary at approximately 50 m intervals of altitude. However, due to topographic restrictions in some areas, this was often not possible. Also, each tributary covered a different range of altitude Thus the number of samples per tributary varied (H=5, VC=10, SN=2, RT=3).

Physicochemical measurements

At each site the width, depth and altitude were recorded. pH, dissolved oxygen and stream temperature were measured in the field using a portable Solomat Water Quality Monitoring System. A water sample was also taken in an acid-washed plastic bottle for analysis of major ions at the University of Plymouth using a Varian Spectra AA-600 flame atomic absorption spectrophotometer: copper, iron, zinc, lead, calcium, magnesium, sodium, potassium and aluminium.

Macroinvertebrates

Macroinvertebrates were sampled from each location by taking two-minute kick samples (net mesh size 250 µm), one from a pool and another from a riffle habitat. In each case the entire width of the habitat was sampled. Invertebrates were then separated in the field from substratum and debris in a white tray and preserved in 70% alcohol.

In the laboratory, individuals were identified to family level using Merritt and Cummins (1996). Family level identification was used because it maintained a greater degree of consistency than would have resulted if a mixture of family, species and genus had been adopted.

Data analysis

Analyses were carried out using the computer package PRIMER (Clarke and Warwick 1994). Diversity indices were calculated using the DIVERSE function in PRIMER. Family richness was represented by Margalef's Index and equitability by Pielous' Evenness Index. The Shannon-Weiner Index, which incorporates aspects of both family richness and evenness, was also calculated. The relationship between family richness measures and environmental variables was investigated using simple, linear regression and between abundances of each family and environmental variables using the product-moment correlation coefficient.

Similarities in macroinvertebrate community composition between streams were investigated using cluster analysis (CLUSTER programme in PRIMER) following square root transformation of data. Non-metric multidimensional scaling ordination (MDS) was then used to provide a two-dimensional representation of the similarities between sites. BIOENV was then used to assess which environmental variables (either alone or in combination) best explained differences between sites in community composition.

Table 2. Macroinvertebrate families from 20 sites in four tributaries of the Río Chilma. Microhabitat preferences for pools or riffles are shown as the percentage of the total macroinvertebrates collected.

Family	Overall total	Riffles (%)	Pools (%)
Order Ephemeroptera			
Baetidae	1099	47.2	52.8
Leptophelebiidae	1033	57.4	42.6
Order Trichoptera			
Sericostomatidae	579	54.6	45.4
Limnephilidae	233	28.8	71.2
Psycomyiidae c.l.	44	56.8	43.2
Leptoceridae	43	16.3	83.7
Hydropsychidae c.l.	9	55.6	44.4
Hydroptilidae	3	33.3	66.7
Glossosomatidae	2	0.0	100.0
Heliopsychidae	1	0.0	100.0
Order Coleoptera			
Elmidae (larvae)	78	42.3	57.7
Elmidae (adults)	20	85.0	15.0
Hydrophilidae (larvae)	37	48.6	51.4
Scirtidae (larvae)	3	100.0	0.0
Scirtidae (adults)	1	0.0	100.0
Hydrophilidae (adults)	1	0.0	100.0
Order Diptera			
Chironomidae	494	68.2	31.8
Simuliidae	76	55.3	44.7
Tipulidae	11	9.1	90.9
Tabanidae	3	66.7	33.3
Muscidae	6	100.0	0.0
Empididae	2	50.0	50.0
Culicidae	1	100.0	0.0
Order Meagaloptera			
Corydalidae (larvae)	1	0.0	100.0
Order Plecoptera			
Nemouridae	22	68.2	31.8
Perlidae	4	100.0	0.0
Order Amphipoda			
Hyalidae	248	207	41
Order Collembola			
Isotonimidae	2	100.0	0.0
Class Hirudinea			
Glossiphonidae	13	0.0	100.0
Order Hydracarina	18	11.1	88.9

RESULTS

Stream chemistry and physiography

Physicochemical conditions for each tributary are given in Table 1. Regression analysis revealed significant negative relationships between altitude and three chemical variables: sodium, ($r = -0.62$, $p<0.01$), magnesium ($r=-0.55$, $p<0.05$) and aluminium ($r=-0.11$, $p<0.05$). There was also a significant negative correlation between altitude and conductivity ($r=-0.62$, $p<0.01$). There were also highly significant positive relationships between conductivity and concentrations of magnesium, calcium and ($r=0.936$, $r=0.951$ and $r=0.906$, respectively—all $p<0.001$). Dissolved oxygen was positively correlated with altitude, ($r=0.616$, $p<0.01$). pH was not correlated with any other variables.

Macroinvertebrates communities

Altogether, 25 macroinvertebrate families were identified, including eight trichopteran and seven dipteran families (Table 2). Family richness ranged from 2 to 12 across sites (Table 3). The four most abundant taxa were the baetid and leptophlebid mayflies, the chironomids and the limnephilid caddis. Of these taxa, only the Limnephilidae showed a clear difference in their microhabitat distribution, being more abundant in pools compared with riffles. The relative abundance of macroinvertebrate families at each of the sites is shown in Table 4.

Regression analysis demonstrated a significant negative correlation between the number of families and altitude for pool and riffle samples combined (Fig. 2); no relationship was evident for pools and riffles separately. The abundance of several families was also correlated with altitude. Limnephilidae and Sericostomatidae were more abundant at higher altitudes, whereas the abundance of psychomyid caddis and perlid stoneflies was higher at low altitudes (Table 5).

Cluster analysis for combined riffle and pool data indicated low similarities between samples from the same tributary, and between riffle and pool samples from the same site (Fig. 3), and this was reflected in the MDS ordination (Fig. 4). BIOENV indicated that altitude was the most important single variable in correlations with community composition variation; the best relationship was with altitude, iron and zinc in combination (Table 6).

Fig. 2. The relationship between family richness and altitude for stream invertebrates from 20 sites from four tributaries of the Río Chilma ($r=-0.870$, $r^2=76\%$, $p<0.01$).

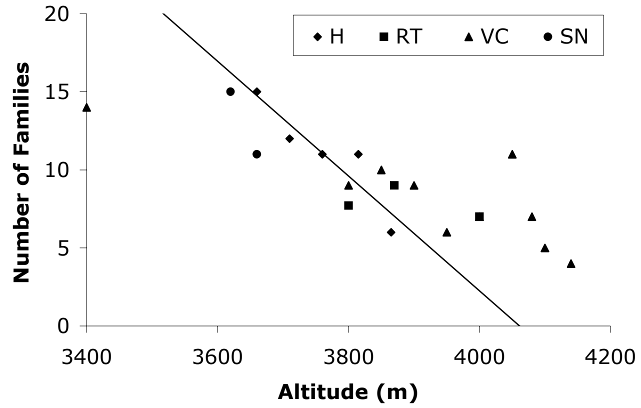

Fig 3. Cluster analysis of macroinvertebrate community data from pools (P) and riffles (R) from four tributaries of the Río Chilma.

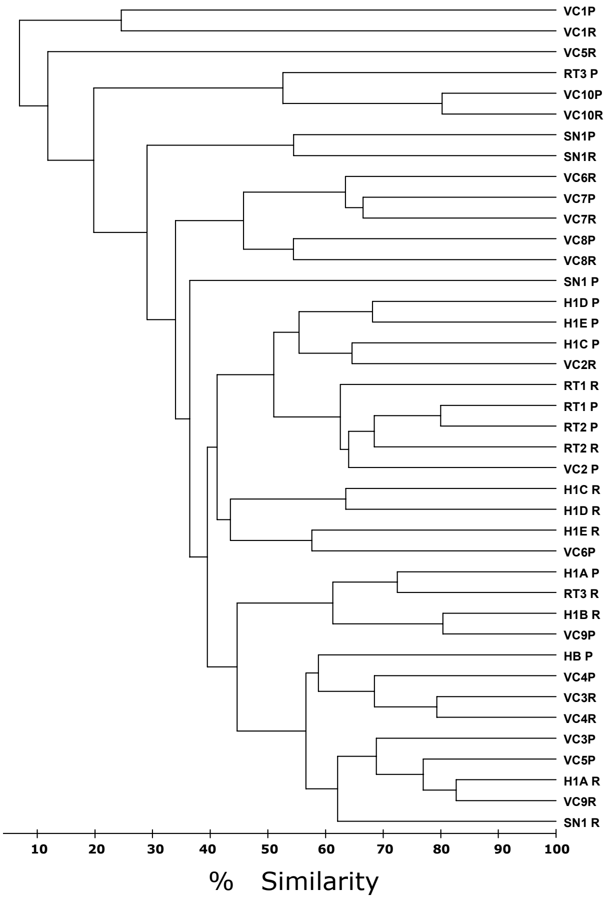

Table 3. The number of individuals and families of macroinvertebrates collected from 20 sites from four tributaries of the Río Chilma. Values for Margalef richness, Pielou's evenness and the Shannon-Weiner index were calculated using family level data. Values are means (ranges in parentheses).

Stream	**H**	**RT**	**VC**	**SN**
Number of Individuals	64.2 (13–130)	133.5 (38–244)	106.0 (4–304)	131.0 (29–298)
Number of Families	6.0 (5–11)	6.6 (6.0–8.0)	5.4 (2–8)	8.5 (6–12)
Margalef's Index	1.48 (0.39–2.36)	1.20 (0.85–1.37)	1.03 (0.30–1.62)	1.66 (1.40–2.34)
Pielou's Index	0.69 (0.49–0.85)	0.74 (0.72–0.86)	0.63 (0.20–0.91)	0.63 (0.45–0.78)
Shannon-Weiner Index	1.26 (0.54–2.03)	1.39 (1.19–1.53)	0.99 (0.219–1.58)	1.34 (0.98–1.77)

Table 4. The relative abundance within sites (pool and riffle samples combined) of macroinvertebrate families.

Altitude (m)	**3400**	**3620**	**3660**	**3710**	**3760**	**3800**	**3815**	**3850**	**3865**	**3870**	**3900**	**3950**	**4000**	**4050**	**4080**	**4100**	**4140**
Baetidae	49.5	4.9	9.2	58.5	32.5	32.9	31.5	11.0	20.2	15.0	13.3	21.6	18.7	23.0	6.4	53.1	37.9
Chironomidae		11.5	11.3		0.7	30.5	1.4		3.8	1.7			2.0	3.0	8.5	38.1	30.8
Corydalidae (larvae)											6.7						
Elmidae (adults)			0.3	0.7								1.9	2.0	1.0			
Elmidae (larvae)		5.9	5.6	4.1	0.7							3.3	2.0	1.6	10.6	1.9	
Glossiphonidae		1.2	1.8														0.4
Hyalidae	15.1		3.7	6.1		15.2						9.4				1.3	15.5
Hydracarina			0.6	2.0	1.3		2.8							1.0			
Hydrophilidae			0.6	2.0	1.3	1.4	2.1	3.4	3.8	0.8			1.5				0.2
Hydrophilidae (adults)						0.2											
Isostomidae	0.9																
Leptoceridae		3.9	3.7	5.4	1.3		4.2				26.7						
Leptophelebiidae	13.7		9.2	3.4	4.0	4.7	46.2	21.4	69.2	80.8		23.5	41.1	67.7	70.2	1.3	3.3
Limnephilidae						1.4	8.4	41.4					25.2				10.8
Mycetophilidae			0.2														
Nemouridae	1.4			3.4	0.7	0.4		0.7				1.9	0.7		3.2		
Perlidae		2.5									26.7						
Psycomyiidae	0.9	2.5	2.6		4.0	0.7	1.4		1.0				1.0	0.6	1.1	2.5	0.2
Sericostomatidae	9.9	65.2	46.1	10.9	52.3	9.3	0.7	16.6	1.9			31.0	4.7	1.8		0.6	0.4
Simuliidae	8.5	0.5	1.3	2.7	1.3	2.8	0.7	5.5				7.0	0.5	0.4			
Tipulidae		1.5	1.6														0.2

*Table 5. Matrix of correlations between physiochemical variables, and the nine most abundant macroinvertebrate taxa, to illustrate the significance of relationships between taxa and environmental variables. Significance levels: NS, p>0.10; *, p≤0.10; **, p≤0.05; ***, p≤0.01.*

	Altitude	**Temperature**	**Dissolved O2**	**pH**	**Conductivity**
Baetidae	0.211 *	0.135 NS	0.239 NS	0.022 NS	-0.036 NS
Chironomidae	0.141 NS	0.078 NS	0.034 NS	-0.257 NS	-0.055 NS
Hyalidae	0.133 NS	0.046 NS	0.09 NS	-0.047 NS	0.086 NS
Leptophelibidae	0.119 *	0.261 NS	0.263 NS	0.159 NS	-0.243 NS
Limniphilidae	0.451 ***	-0.407 ***	0.399 ***	-0.077 NS	-0.366 **
Nemouridae	-0.075 NS	0.013 NS	0.55 NS	0.172 NS	0.115 NS
Perlidae	-0.398 **	0.128 NS	-0.44 ***	0.149 NS	0.003 NS
Psycomyidae	-0.276 *	0.361 **	-0.069 NS	-0.113 NS	0.174 NS
Seriostomatidae	0.318 *	0.282 *	-0.075 NS	-0.014 NS	0.097 NS

Fig. 4. MDS ordination for macroinvertebrate communities from four tributaries of the Río Chilma. Pool (P) and riffle (R) samples are indicated by the final letter. Stress = 0.17.

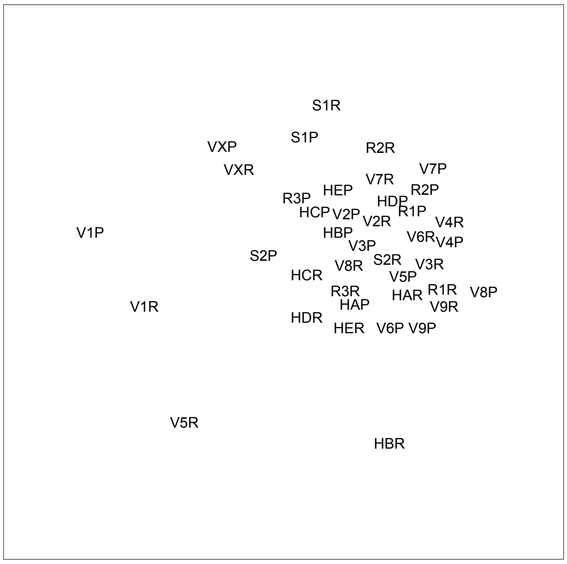

Table 6. BIOENV analysis indicating relationships between environmental variables and community composition of macroinvertebrate communities.

	Number of variables		
	1	2	3
Highest correlation	Altitude 0.379	Altitude, Fe 0.391	Altitude, Fe, Zn 0.403
Second	Dissolved O2 0.222	Altitude, Conductivity 0.326	Altitude, Conductivity , Fe 0.370
Third	Zn 0.093	Altitude, K 0.313	Altitude, Fe, Ca 0.356

DISCUSSION

Despite the relatively small altitudinal range sampled in this study several findings indicated that altitude played an important role in shaping macroinvertebrate communities in these high altitude páramo streams. There was a clear significant negative correlation between macroinvertebrate family richness and altitude. Furthermore, the multivariate BIOENV procedure indicated that altitude was the predominant factor responsible for the variation in faunal composition between sites. Previous studies have also demonstrated a relationship between macroinvertebrate assemblages and altitude (Hynes 1970, Malmquist *et al*. 1993, Rundle *et al*. 1994, Ormerod *et al*. 1994, Jacobsen *et al*. 1997). However, such studies have concluded that any relationship between macroinvertebrate assemblages and altitude is often confounded by the influence of other variables that also change altitudinally. Stream hydraulics (Statzner and Higler 1986), temperature (Jacobsen et al 1997), substrate size and composition (Willard and Kevern 1973), nutrient levels (Dudgeon 1984) and food availability (Hynes 1970) are all variables that vary along the length of rivers and thus with altitude.

The strong significant relationships between altitude and several chemical variables (sodium, magnesium, aluminium and conductivity) in this study also suggest that altitude may act in conjunction with these variables in influencing communities. In this case, the general decrease in the ionic content of stream water with altitude was not unexpected considering that inputs of major ions tend to increase with distance downstream and an increased influence from erosion. The correlations between environmental variables and the abundance of certain families also suggested a combined influence from altitude and stream chemistry, as did the correlation of altitude, Mg and Fe with variation in community composition.

Overall, the community-level analysis suggested, however, that there was a substantial proportion of between-site variation in community composition that could not be explained by the physicochemical variables measured. This could be due to the fact that at least one key variable was missing from the analyses. Substratum composition, for example, was not measured, but has been shown previously to be influential in influencing macroinvertebrate assemblages (Willard and Kevern 1973, Allan 1975). Similarly, the relationship between flow and macroinvertebrate assemblage is also well documented (Illes 1961, Hynes 1970, Whitton 1975, Allan 1995) but, due to low flows in some sites it was impossible to gain sufficient measures of this variable in this study.

The lack of a strong relationship between environmental variables and community composition might also be due to the relatively homogeneous environment offered by páramo streams and the páramo habitat in general. This may lead to the composition of communities being driven more by random colonisation events rather than being determined by local physicochemical conditions. Moreover, the low proportion of taxa that are poor dispersers and likely to be influenced more by stream chemistry suggests that this may be the case. The absence of molluscs from these stream systems is particularly intriguing considering the relatively high hardness values of the streams studied (average Ca^{2+} ion value of 19.3 mg l^{-1}; molluscs and crustaceans require at least 5 mg l^{-1} of calcium to allow proper shell development—Hynes 1970).

Biotic interactions also influence the composition of stream communities. It seems unlikely that predation pressure is that great in these systems, however, as fish are absent or in low abundance and invertebrate predators are also scarce. A lack of predation pressure might increase the chances of competition, although it has also been proposed that such interactions may be weak in streams where high flow events prevent population densities reaching levels where interactions are of importance.

Despite the fact that identification to family level is useful in allowing comparisons with other work (*e.g.*, Jacobsen *et al*. 1997), some species within families may have shown a relationship with altitude or a preference for pools or riffles in their distribution. For example, the Chironomidae is known to contain pool and riffle habitat specialists.

Despite the limitations of this study, and the altitudinal range of only 750 m over which sampling was conducted, it provides important baseline information on patterns of macroinvertebrates in tropical Ecuadorian highland streams. The data suggest that environmental variables associated with altitude explain part of the variability in composition at family level. However, the remaining variability might be related to interactions between species and random colonisation events. More surveys are required along with manipulative experiments to determine the relative importance of these factors.

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REFERENCES

Allan, D.J. (1975) Distributional ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology,* **56:** 1040–1053.

Allan, D.J. (1995) *Stream Ecology: Structure and Function of Running Waters,* London: Chapman and Hall.

Barber, W.N.S. and Kervern, N.R. (1973) Ecological factors influencing macroinvertebrate standing crop distribution. *Hydrobiologia,* **43**: 53–75.

Butland, G.J. (1972) *Latin America: a Regional Geography,* 3rd Edition, Harlow: Longman.

Clarke, K.R. and Warwick, R.M. (1994) *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation,* Plymouth: Plymouth Marine Laboratory.

Fowler, J. and Cohen, L. (1990) *Practical Statistics for Field Biology,* Milton Keynes: Open University Press.

Hawkins, R. (1993) A hierarchical approach to classifying stream habitat features. *Fisheries,* **18**: 3–12.

Hynes, H.B.N. (1970) *The Ecology of Running Waters,* Liverpool: Liverpool University Press.

Merrit, R.W. & Cummins, K.W. 1996. *An Introduction to the Aquatic Insects of North America,* 3rd Edition, Dubuque, Iowa: Kendall/Hunt.

Morris, A.S. (1981) *South America,* 2nd Edition, London: Hodder & Stoughton.

Omerod, S.J., Rundle, S.D., Wilkinson, S.M., Daly, G.P. and Dale, K.M. (1994) Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. *Freshwater Biology,* **32**: 309–322

Ramsay, P.M. (2001) The zonal páramo vegetation of Volcán Chiles. In: Ramsay, P.M. (Ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border,* pp. 27–38. Plymouth: Pebble & Shell.

Rosenberg, D.M. and Resh, V.H. (1984) *The Ecology of Aquatic Insects,* London: Chapman and Hall.

Soderstrom, O. (1987) Upstream movements of invertebrates in running waters—a review. *Archiv für Hydrobiologie.* **111**: 197–208.

Surren, A. (1994) Macroinvertebrate communities of streams in western Nepal: effects of altitude and land use. *Freshwater Biology,* **32**: 323–336.

Statzner, B. and Higler, B. (1986) Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology,* **16**: 127–139

Turcotte, P. and Harper, P. (1982a) Drift patterns in a high Andean stream. *Hydrobiologia,* **89**: 141–151.

Turcotte, P. and Harper, P. (1982b) The macroinvertebrate fauna of a small Andean stream. *Freshwater Biology*. **12**: 411–419.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushings, C.E. (1980) The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences,* **37:** 130–137.

Ward, J.V. (1996) *Aquatic Insect Ecology,* New York: Wiley.

Ward, J.V. (1986) Altitudinal zonation in a Rocky Mountain stream. *Archiv für Hydrobiologie*, **2**: 133–199.

Whitton, B.A. (1975) *River Ecology,* Oxford: Blackwell Scientific.

Wolf, T. (1975) *Geografía y Geología del Ecuador,* Quito: Editores Casa de la Cultura Ecuatoriana.

The stream invertebrate communities of the Río Bobo, Volcán Chiles

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SUMMARY

Páramo macro-invertebrates were sampled over an altitudinal gradient of 420 m from two tributary streams of the Río Bobo, Volcán Chiles. Animals were identified to family level, and then tentatively assigned to morphospecies. Physicochemical parameters were also determined for each of the 22 sample sites (12 pools and 10 riffles), which covered an altitudinal range from 3500 to 3920 m. Insects dominated the aquatic macrofauna of these páramo streams, particularly species belonging to the Ephemeroptera, Trichoptera, Diptera and Coleoptera. Amphipoda (Hyalidae) were also common. Hirudinea, Acari and Collembola were also present in some samples. Variability in the macro-invertebrate composition of páramo streams on Volcán Chiles appears to be driven by habitat heterogeneity within the streams and variability in water chemistry. Disturbance and dispersal events may also influence composition. Within the grassy páramo zone, altitudinal differences are subordinate to these factors.

RESUMEN

Se realizaron muestreos de macroinvertebrados paramunos a lo largo de un gradiente altitudinal de 420 m en dos riachuelos afluentes del Río Bobo, Volcán Chiles. Se identificaron los animales al nivel de familia y posteriormente se asignaron a morfoespecies tentativas. Se determinaron algunos parámetros fisicoquímicos en cada uno de los 22 sitios de muestreo (12 charcas y 10 zonas pedregosas someras de flujo rápido) que se extendieron en un intervalo altitudinal de 3500 a 3920 m. Los insectos dominaron la macrofauna acuática de estos riachuelos paramunos, particularmente especies que pertenecen a las familias Ephemeroptera, Trichoptera, Diptera y Coleoptera. Los Amphipoda (Hyalellidae) fueron también comunes. Los Hirudinea, Acari y Collembola estuvieron presentes en algunas muestras. La variabilidad en la composición de macroinvertebrados pareció estar determinada por la heterogeneidad del hábitat y la variabilidad en la química del agua de estos riachuelos. La perturbación y los eventos de dispersión pudieron también haber influenciado la composición de especies. Dentro de la zona de pastizal paramuno, las diferencias altitudinales parecen entonces estar subordinadas a estos factores.

Key words: community structure, high altitude, macroinvertebrates, tropical alpine

INTRODUCTION

As biodiversity loss and habitat destruction increases, it becomes imperative for ecologists to provide accurate data for communities and develop robust, predictive models for ecosystems. Many ecological ideas have been developed for freshwater ecosystems (*e.g.*, Yodzis 1986, Townsend 1989, Vannote *et al.* 1980), but there are still large gaps in our understanding of these systems. In particular, we have a poor knowledge of polar, high altitude, tropical and sub-tropical streams, and much of the data that has been collected is confounded by anthropogenic influences (*e.g.*, Rundle *et al.* 1993). It is important to obtain sound ecological data from pristine systems so that we have a “base line” with which to compare impacted stream systems.

Few studies of freshwater systems have concentrated on high-altitude streams, those that do often only consider them as part of an entire river system (*e.g.*, Jacobsen *et al.* 1997, Dudgeon 1984). Usually, such studies do not strive to understand the processes that control high-altitude stream communities or consider the variation within such streams. Turcotte and Harper (1982) provided a more thorough study by sampling a high-altitude stream monthly over a one-year period, but was limited because they used only one sample site, which at 3300 m was on the borderline between high-altitude and central valley river sections. Other studies of high-altitude streams have been compounded by the impact of local human land use (Rundle *et al.* 1993, Dudgeon 1984, Zamora-Muñoz *et al.* 1993), overshadowing altitudinal patterns in faunal composition.

The páramo regions of the Andes represent one area where remote and, therefore, more or less pristine streams can still be found. Accordingly, freshwater systems in these areas can provide a valuable insight into the variation of stream macroinvertebrate assemblages with altitude. This study attempts to determine the importance of altitude and other physicochemical variables on the diversity and structure of macroinvertebrate community assemblages.

MATERIALS AND METHODS

Study area and site selection

The study was undertaken on the slopes of Volcán Chiles. Although the volcano is extinct, thermal springs and faults cause localised increases in stream temperature and the concentrations of metallic and sulphurous compounds in the water.

The surrounding páramo vegetation is dominated by tussock grass (*Calamagrostis intermedia*) and giant rosettes of *Espeletia pycnophylla* subsp. *angelensis*. Occasionally, in sheltered areas, small woodlands of *Polylepis* occur. The páramo grasslands are subjective to extensive grazing by cattle and horses. However, the main form of human disturbance is burning, carried out for a variety of reasons but mainly to encourage better forage for the livestock (Ramsay 2001).

Three streams and their associated tributaries were sampled from the Río Bobo catchment: Quebrada de Los Colorados, Quebrada de Los Piedros and the Río

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 185-191.

Verde (Fig. 1). Samples were taken over the space of two weeks in July 1997, during the dry season assuring that streams sampled were permanent. For each stream samples were taken at approximately 100 m altitudinal intervals, though topography sometime prevented exact replication of altitudes.

Physicochemistry

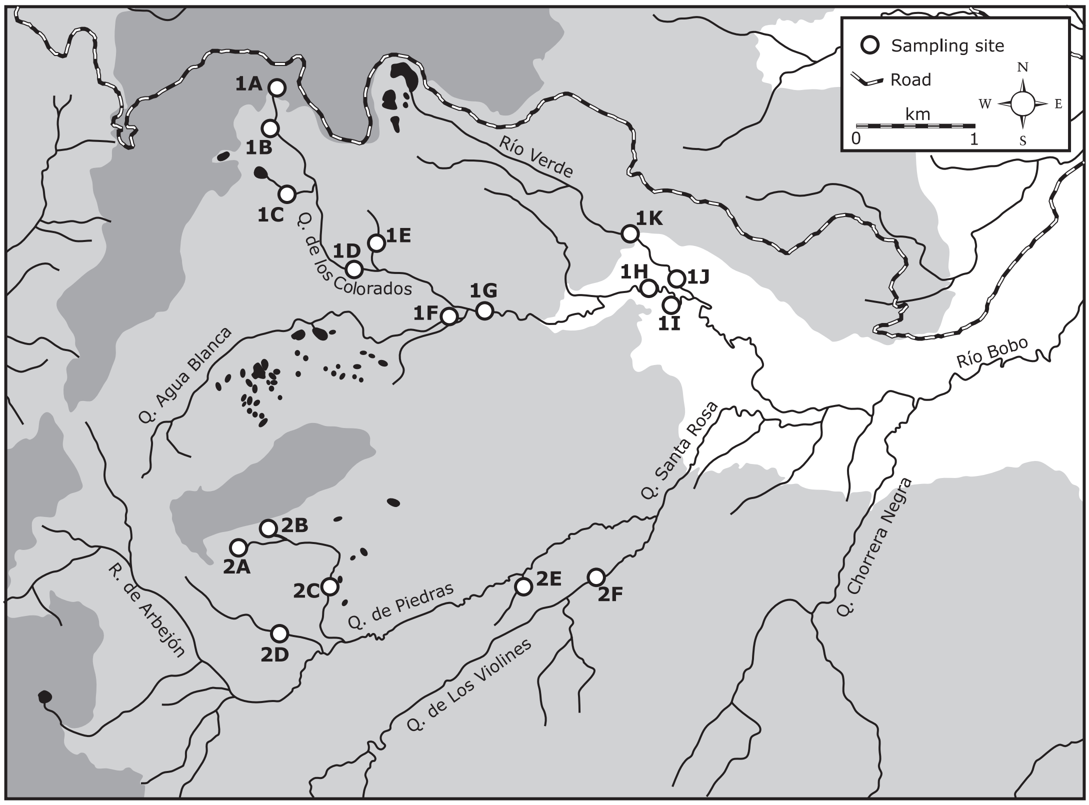
Physical variables

The width, depth, flow and substratum composition of each site was measured *in situ*, the latter being determined by assessing the proportional composition of five major components (as defined by Rutt *et al*. 1989) in the section of stream to be sampled: Bedrock/Boulders (>25 cm), Cobbles/Pebbles (1.5–25 cm), Gravel (0.06–1.5 cm), Silt/Mud (<0.06 cm) and macrophytes. The average width and depth of the riffle or pool was measured by taking three measurements along its length for each variable. Mean flow (m s^{-1}) for the riffle was recorded using a portable meter (Solomat 520c) over a one minute period and altitude was determined with an analogue altimeter (Thommen 0–6000 m).

Chemical Variables

Dissolved oxygen and pH were measured on site using portable meters (YSI 51B and pHox 42E, respectively) and a water sample was collected in an acid washed plastic bottle for the measurement of major ions (Al, Ca, Cu, Fe, K, Mg, Na, Pb, Zn) using a Varian SpectrAA-600 flame atomic absorption spectrophotometer.

Fig. 1. The sampling sites for aquatic invertebrates on the Río Bobo and its tributaries, Volcán Chiles. Shading indicates land above 3600 m, with the darker shading representing land above 4000 m. See Table 4 for the altitudes of these sample sites.



Macroinvertebrates

A semi-quantitative method of sampling was used to assess macroinvertebrate community structure. Animals were collected from riffles using a one-minute kick sample (net mesh 0.9 mm), and pool samples were taken by vigorous sweep netting for a one-minute period. In both cases the whole width of the habitat was sampled. The organisms were then separated from the substrate by elutriation and placed in a white sorting tray. Due to the relatively low abundances all the organisms were transferred into tubes and preserved in 70% alcohol in the field. Due to the limited accessibility of South American keys, animals were identified to family level using a key for North American invertebrates (Merrit and Cummings 1996), and then pseudospecies were defined within each family. Previous studies have shown that family level identification is appropriate for determining important ecological patterns at the community level (*e.g.*, Furse *et al*. 1984, Corkum 1989, Rutt *et al*. 1990).

Statistical analysis

Most statistical analyses were carried out using the PRIMER computer package (Clarke and Warwick

1994). Diversity indices were calculated using the DIVERSE function within the package. A Margalef index was used to illustrate species richness and Pielous' evenness index was used as an equitability value. The Shannon-Weiner diversity index, which includes aspects of both species diversity and equitability, was also calculated.

Similarities in macroinvertebrate communities between sites and habitats (pools and riffles) was investigated using CLUSTER analysis in PRIMER, following a fourth root transformation to downweight rare species. Non-metric multidimensional scaling was employed to ordinate the similarities graphically. CCA in CANOCO (ter Braak and Šmilauer 1998) was used to assess the environmental factors that correlated best with the variation in community composition between sites. A Monte Carlo permutation test (part of CANOCO) was conducted in order to determine if the distribution of species within the samples was related to the measured environmental variables.

Substratum data for each site was reduced to facilitate regression analyses using Principle Components Analysis (PCA in PRIMER).

RESULTS

In total, 22 samples were taken from the catchment: 12 from pools and 10 from riffles (it was not always possible to find both habitats close together). The samples covered an altitudinal range of 420 m (3500–3920 m).

Physicochemistry

Despite the relative uniformity of the páramo environment over the altitudinal range studied, stream physicochemistry proved highly variable (Table 1). Negative correlations were found between altitude and temperature (r=-0.53, p=0.012), conductivity (r=-0.45, p=0.034), and magnesium (r=-0.44. p=0.039). Positive correlations were found between conductivity and magnesium (r=0.70, p=0.0003), calcium (r=0.68, p=0.0005), sodium (r=0.68, $p < 0.0001$) and aluminum (r=0.57, p=0.005). The principal component derived from the substratum data was not correlated with any of the other environmental data.

Macroinvertebrates

Insects dominate the aquatic macrofauna of these páramo streams (Table 2). They contributed 80% of the morphospecies and 76% of the individuals in the samples. Amphipods were also common (22% of all individuals found), belonging to the family Hyalidae. Leeches (Hirudinea) were present in some samples, but Acari and Collembola were rarely encountered. Within the insects the Diptera were most diverse and contained seven morphospecies. The Ephemeroptera were numerically dominant, however, accounting for 38% of individual animals found. The Trichoptera (16% of individuals), Diptera (10%) and Coleoptera (10%) were also relatively common.

Few families were specific to either pools (Hydracarinae, Muscidae and Isopoda) or riffles (Entomobyridae, Blephariceridae, Canaceidae, Leutridae and Psychomyiidae). Of these families, most were rarely encountered—only the Psychomyiidae were found in higher densities.

When subjected to an analysis of medians using a Kruskal-Wallis test, no significant difference was detected between pools and riffles either in terms of the number of morphospecies or the total number of individuals. Furthermore, there were no significant differences between diversity scores between the two habitats. Combined pool and riffle diversity scores at each altitude (Table 2) showed no statistical differences, with relatively uniform diversity scores throughout.

Cluster analysis showed that there was some differentiation between pools and riffles in terms of species composition (Fig. 2). A group of five riffle samples and another of eight pool samples (plus one riffle) are evident, with only about 40% similarity between them. None of the groupings were associated with altitudinal trends or differences between the two tributary stream systems (Q. Santa Rosa and Río Verde). Similarly, in separate cluster analyses for pools and riffles, no patterns are evident in relation to altitude or stream system.

The CCA biplot is shown in Fig. 4. The closer samples are to each other, the more similar they are in composition. The environmental variables are shown as arrows: the direction of the arrow indicates the direction of its increase across the ordination space; and the longer the arrow, the more important the variable is in explaining the distribution patterns of the morphospecies. There was a significant relationship between the distribution of species in the samples and the environmental variables (Monte Carlo test, p=0.01). The first two axes of this ordination explain about 70% of the variation in species abundance. There is a general separation of pool and riffle samples (accounting for the importance of flow in explaining species distributions in the samples). Copper and lead concentrations in the water also correlate well with the major patterns of species abundance. Altitude shows low correlation with community structure.

Table 1. Average values of 16 physicochemical variables recorded for pools and riffles over the altitudinal gradient studied. Altitudes are rounded to the nearest 100 m. Substratum PC refers to the principal component score derived from substrate category proportions at each site.

	3500		**3600**		**3700**		**3800**		**3900**	
Abiotic Factor	**Pool *n*=3**	**Riffle *n*=2**	**Pool *n*=3**	**Riffle *n*=2**	**Pool *n*=1**	**Riffle *n*=1**	**Pool *n*=3**	**Riffle *n*=2**	**Pool *n*=2**	**Riffle *n*=3**
Width (m)	1.41	1.64	1.49	0.57	0.76	0.43	0.74	0.63	0.30	0.54
Depth (m)	0.50	0.13	0.54	0.13	0.35	0.11	0.23	0.25	0.11	0.14
Cu ppm	0.04	0.02	0.03	0.02	0.05	0.05	0.06	0.03	0.01	0.01
Zn ppm	0.29	0.01	0.03	0.03	0.06	0.06	0.05	0.04	0.00	0.00
Al ppm	0.36	0.49	1.86	1.69	0.41	0.41	1.39	0.87	0.52	0.61
Mg ppm	4.84	6.25	3.57	2.97	1.37	1.37	2.11	2.44	1.78	1.94
Ca ppm	7.26	10.50	8.01	8.07	0.44	0.44	5.47	6.15	3.93	4.39
Pb ppm	0.06	0.09	0.08	0.11	0.00	0.00	0.07	0.10	0.12	0.13
Fe ppm	0.01	0.02	0.01	0.01	0.00	0.00	0.06	0.04	0.03	0.04
Na ppm	4.94	4.03	4.47	2.83	2.97	2.97	3.39	3.25	2.42	2.77
K ppm	1.74	1.71	1.71	1.46	4.42	4.42	2.83	1.40	0.96	1.21
Conductivity (µS)	173	182	224	136	71	70	146	118	65	72
pH	5.9	5.55	5.66	5.71	5.68	5.61	5.61	5.40	3.97	5.91
Temperature (°C)	8.53	8.50	8.73	9.30	11.20	11.20	7.93	8.05	4.23	5.97
DO (%)	50.9	53.4	51.2	58.9	75.4	84.3	55.3	63.6	33.5	56.5
Substratum PC	1.4	-2.1	-0.7	-0.5	0.7	0.7	-0.1	-0.1	-0.8	0.91

Table 2. Number of individuals in pool and riffle samples over the altitudinal gradient studied. Altitudes are rounded to the nearest 100 m. The numbers of morphospecies found in each family are also shown.

Order	**Family**	**No of Morpho-species**	**3500**		**3600**		**3700**		**3800**		**3900**	
			Pool n=3	**Riffle n=2**	**Pool n=3**	**Riffle n=2**	**Pool n=1**	**Riffle n=1**	**Pool n=3**	**Riffle n=2**	**Pool n=2**	**Riffle n=3**
Acari	Hydracarinae	1			2				1			
Amphipoda	Hyalidae	1	27	4	6	5	20	19	15	4	16	59
Collembola	Entomobyridae	1										1
Coleoptera	Elmidae	2	5	1	11	9	14	13				
	Helodidae	2	1		4	2		10	1	3	1	
Diptera	Chironomidae	2	6	5		2			2	1	2	8
	Tipulidae	1		1					1			
	Muscidae	1									2	
	Blephariceridae	1				1						
	Canaceidae	1				1						
	Simulidae	1	8	4	8	7	1	1		3	8	4
Plecoptera	Leutridae	1		1								
	Perlidae	1							2	3		
Ephemeroptera	Ephemerellidae	1	41	31	12	105	5		22	20	17	21
	Baetidae	1	1		8	4			4	3		3
Trichoptera	Leptoceridae	2	2	5	1	8			1	3		4
	Hydropsychidae	1		4	1		3	24	1	12		
	Brachyceridae	1				1	7					
	Rhyacophillidae	1			1	2	4					
	Psychomyiidae	1		1		10		10		13		8
Hirudinea		—			4	2	2				2	12
Isopoda		1									1	
Margalef index (richness)			1.29	1.27	1.91	1.99	1.98	1.19	1.65	2.01	1.56	1.24
Pielous' evenness index			0.74	0.44	0.84	0.58	0.81	0.83	0.84	0.82	0.78	0.80
Shannon-Weiner index			1.23	0.80	1.50	1.31	1.78	1.49	1.18	1.71	1.39	1.23

Fig 2. Cluster analysis of all samples. The site code is followed by a code for pools (P) or riffles (R), and the altitude in metres. The data were fourth-root transformed before conducting the analysis.

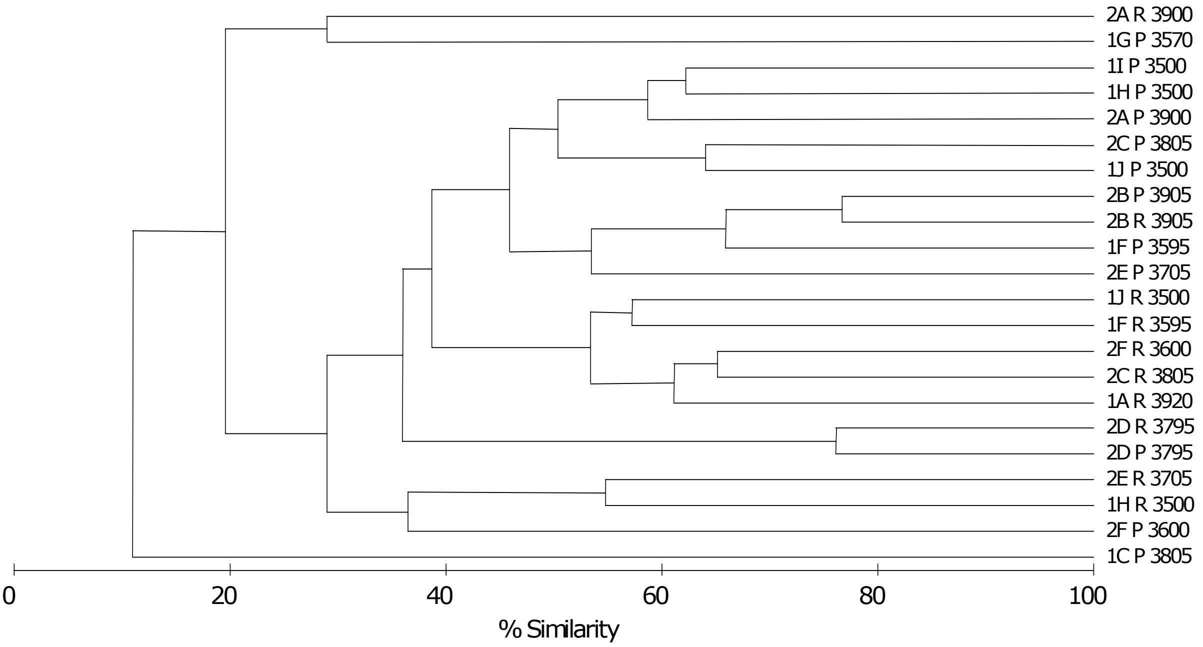


Fig.4. Canonical correspondence analysis biplot for macroinvertebrate samples from the Rio Bobo catchment. Pool (P) and Riffle (R) samples are plotted separately.

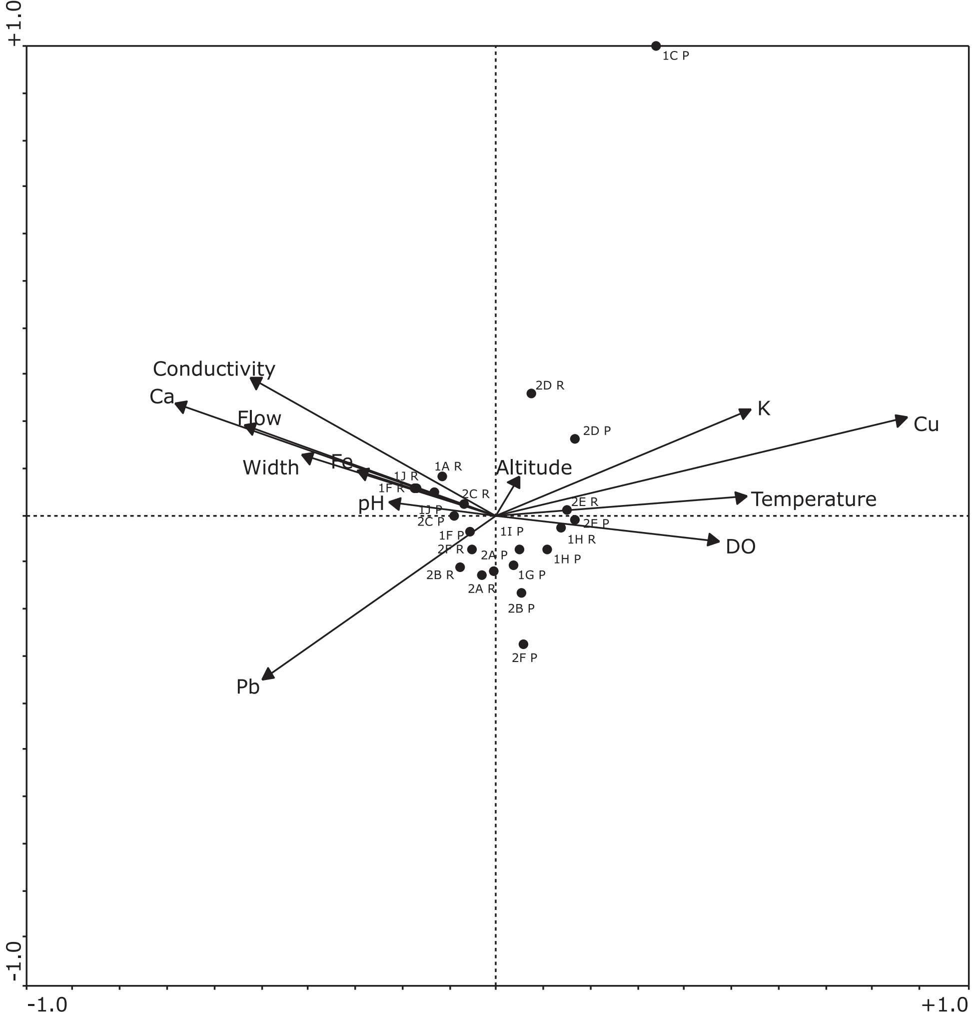


Fig 3. Cluster analyses for riffle and pool data independently. Codes as Fig. 2. The data were fourth-root transformed before conducting the analysis.

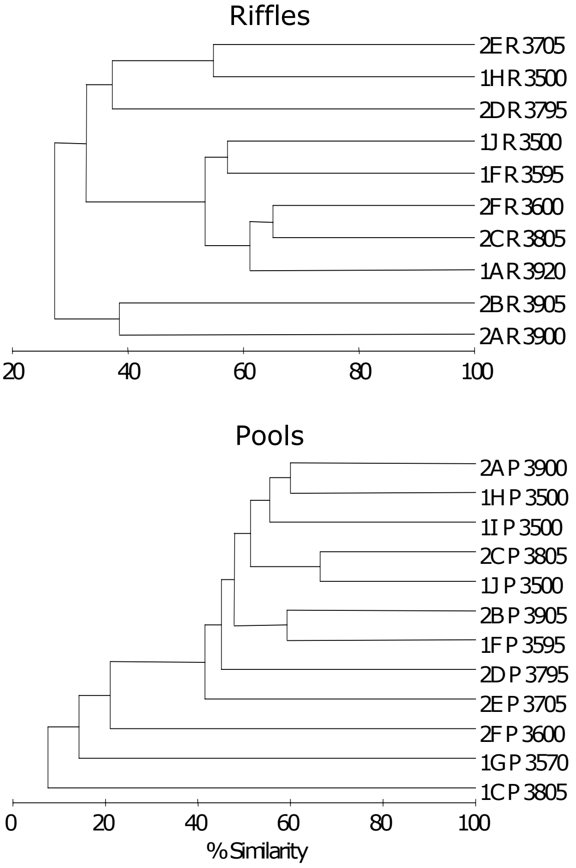
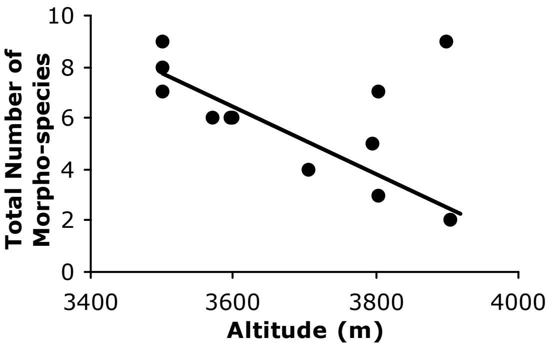


Fig 5. Relationship between altitude and the total number of morphospecies in pools (correlation coefficient=-0.578, r^2=33.49%, p< 0.05).



There were a number of trends in (morpho)species diversity within the samples. Although there was no overall correlation between altitude and the number of morphospecies, there was a general fall in numbers with altitude in pools (Fig. 5). There were also more morphospecies present in pools with higher concentrations of sodium (*r*=0.52, *p*<0.05). There were no significant correlations between riffle diversity and any of the environmental variables. Taking riffle and pool samples together, the species diversity was lower in samples with higher ion concentrations: Shannon-Weiner index with conductivity (*r*=-0.52, *p*=0.01), calcium (*r*=-0.46, *p*=0.03), and magnesium (*r*=-0.47, *p*= 0.0261). There was no relationship between substrate and species diversity.

DISCUSSION

The taxa collected during this survey are largely comparable with other studies from Ecuadorian páramo streams (Jacobsen *et al.* 1997, Turcotte and Harper 1982). However, certain families found in the Volcán Chiles streams were not identified in these other studies: Ephemerellidae, Brachyceridae, Rhyacophilidae, Rhyacophillidae and Psychomyiidae. The Isopoda were also absent from these studies. Faunal composition was also similar to that of streams in Nepal (Rundle *et al.* 1993). Thus, there are similarities with high-altitude stream systems elsewhere, but some differences too.

There were no clear patterns with altitude in this study, except for a fall in species diversity in pools with increasing altitude. The composition of the stream samples was largely independent of altitude within the elevational range of this survey, similar to the findings of Weaver and Rundle (2001). Although various physicochemical parameters vary with altitude (*e.g.*, stream width, conductivity, substratum size and composition), these changes do not appear to influence the distribution and abundance of freshwater macrofauna in these páramo streams. This does not match the results of Weaver and Rundle (2001) for a nearby catchment on the same mountain,

The principal pattern to emerge from the community analyses was a difference between pools and riffles. Therefore, within the grass páramo zone, stream invertebrate assemblages appear to be influenced more by microhabitat differentiation within the watercourse than by altitude. Again, this conflicts with Weaver and Rundle's (2001) findings where pools and riffles had similar community composition.

Interestingly, the number of morphospecies, abundances and diversity indices do not vary greatly between microhabitats, suggesting that the microhabitats support similar amounts of biomass regardless of the species composition.

In addition, there is significant variability in stream water chemistry in this volcanic landscape. There is also a relationship between species distribution patterns and the concentrations of various ions in solution, most notably Ca, Mg and Na. These cations also correlate with the diversity indices.

The absence of strong physicochemical relationships with species distributions suggests that stream composition is partially controlled by random colonisation events (Sale 1977) or disturbances such as flood events (Flecker and Feifarek 1994) leading to variable communities across the altitudinal range, rather than reflecting environmental gradients directly.

In summary, variability in the macro-invertebrate composition of páramo streams on Volcán Chiles appears to be driven by habitat heterogeneity within the streams and variability in water chemistry. Disturbance and dispersal events may also have resulted in variable composition. Within the grass páramo, altitudinal differences are subordinate to these factors.

It is clear that the driving forces in shaping high-altitude stream communities in the Andes are complex and subtle in their influence and have been touched on only superficially in this investigation. A more rigorous and exhaustive programme of investigation in páramo streams is required.

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REFERENCES

Clarke, K.R. and Warwick R.M. (1994) *Change in Marine Communities: an approach to statistical analysis and interpretation*, Plymouth: Plymouth Marine Laboratory.

Corkum, L.D. (1989) Patterns of benthic invertebrate assemblages in rivers of north-western North America. *Freshwater Biology*, **21**: 191–205.

Dudgeon, D. (1984) Longitudinal and temporal changes in functional organization of macroinvertebrate communities in the Lam Tsuen River, Hong Kong. *Hydrobiologia*, **111**:207–217.

Flecker, A.S., and Feifarek, B. (1994) Disturbance and the temporal variability of invertebrate assemblages in two Andean streams. *Freshwater Biology*, **31**: 131–142.

Furse, M.T., Moss, D., Wright, J.F., and Armitage, P.D. (1984) The influence of seasonal and taxonomic factors on the ordination and classification of running-water sites in Great Britain and on the prediction of their macroinvertebrate communities. *Freshwater Biology*, **14**: 257–280.

Jacobsen, D., Schultz, R. and Encalada, A. (1997) Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology*, **38**: 247–261.

Merritt, R.W. and Cummins, K.W. (1996) *An Introduction to the Aquatic Insects of North America*, Third edition, Dubuque: Kendall & Hunt Publishing Company.

Rundle, S.D., Jenkins, A. and Ormerod, S.J. (1993) Macroinvertebrate communities in streams in the Himalaya, Nepal. *Freshwater Biology*, **30**: 169–180.

Rutt, G.P., Weatherley, N.S. and Ormerod, S.J. (1989) Microhabitat availability in Welsh moorland and forest streams as a determinant of macroinvertebrate distribution. *Freshwater Biology*, **22**: 247–261.

Rutt, G.P., Weatherley, N.S., and Ormerod, S.J. (1990) Relationships between the pysicochemistry and macroinvertebrates of British upland streams: the development of a modelling and indicator system for predicting fauna and detecting acidity. *Freshwater Biology*, **24**: 463–480.

Sale, P.F. (1977) Maintenance of high diversity in coral reef fishes. *American Naturalist*, **111**: 337–359.

ter Braak, C.J.F. and Šmilauer, P. (1998) *CANOCO Reference Manual and User's Guide to Canoco for Windows*, Wageningen: Centre of Biometry.

Townsend, C.R. (1989) The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*, **8**: 36–50.

Turcotte, P. and Harper, P.P. (1982) The macro-invertebrate fauna of a small Andean stream. *Freshwater Biology*, **12**: 411–419.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushings, C.E. (1980) The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences,* **37:** 130–137.

Weaver, R.G.S. and Rundle, S.D. (2001) The influence of altitude on macroinvertebrate community assemblages in the Río Chilma and its tributaries, Volcán Chiles. In: Ramsay, P.M. (ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombian border,* pp. 177–183. Plymouth: Pebble & Shell.

Yodzis, P. (1986) Competition, mortality and community structure. In: Diamond, J.M. and Case, T.J. (Eds.) *Community Ecology*, pp. 430–455. New York: Harper and Row.

Zamora-Muñoz, C., Sanchez-Ortega, A. and Alba-Tercedor, J. (1993) Physico-chemical factors that determine the distribution of mayflies and stoneflies in a high-mountain stream in southern Europe (Sierra Nevada, southern Spain). *Aquatic Insects*, **15**: 11–20.

Aquatic invertebrate communities of Ecuadorian waterfall pools: the effects of altitude and associated variables

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SUMMARY

The structure and diversity of the macroinvertebrate fauna of waterfall pools was studied in relation to altitude and seven physicochemical variables in Ecuador. Six páramo waterfall pools were sampled within an altitudinal range of 3540 m to 3940 m. Samples were also collected from two montane forest pools (at 2200 m and 2250 m). Within each pool separate samples were taken from the margin, pool centre and directly under cascade. Physicochemical parameters were also measured at each site. The waterfall pools showed clear differences related to environmental variables represented by altitude (*e.g.*, temperature and flow), but few differences related micro-habitat within the pools. Species composition in páramo waterfall plunge pools differed from that in pools and riffles in other parts of the same stream, though some taxa were shared. Many of the additional taxa living in waterfall pools show adaptations to the high-energy environment found beneath cascades. It is important, therefore, that these pools are not forgotten in surveys of streams and rivers, particularly in the High Andes where cascades are common.

RESUMEN

La estructura y la diversidad de la fauna de macroinvertebrados en pozas bajo cascadas fue estudiada en relación a la altitud y siete variables fisicoquímicas en Ecuador. Los muestreos se realizaron en seis pozas debajo de cascadas en el páramo dentro del intervalo altitudinal 3540-3940 m. Adicionalmente, se recolectaron muestras de dos charcas del bosque nublado (a 2200 y 2250 m). Dentro de cada poza se tomaron muestras independientes de la orilla, del centro y directamente por debajo de la cascada. Los parámetros fisicoquímicos fueron también medidos en cada sitio. Las pozas mostraron claras diferencias relacionadas a variables representadas por la altitud (por ejemplo, la temperatura y el flujo), pero pocas diferencias relacionadas a los tres microhábitats dentro de las pozas. La composición de especies en estas pozas formadas por la caida de agua fue distinta de aquella de las charcas y zonas pedregosas someras de flujo rápido en otras partes del mismo riachuelo. No obstante, algunos taxa fueron compartidos. Muchos de los taxa adicionales que viven en pozas bajo cascadas muestran adaptaciones al ambiente de alta-energía que se encuentra por debajo de estas caidas de agua. Por lo tanto, es importante no olvidar estas pozas en prospecciones de riachuelos y ríos, particularmente en los altos Andes donde estas cascadas son comunes.

Key words: páramo, montane forest, tropical alpine, freshwater invertebrates, macroinvertebrates

INTRODUCTION

There is little information about aquatic insect assemblages in tropical streams, particularly cold tropical and sub tropical streams (Rundle *et al.* 1993, Turcotte and Harper 1982, Ormerod *et al.* 1994). Vuilleumier (1986) suggests that, "All too often, the cold montane tropics are overlooked by students of tropical biology, who focus on the warm lowlands, either the rain forests or the savannas." Nevertheless, there have been a limited number of studies into the ecology of high altitude streams throughout the world. Macroinvertebrate communities of Himalayan streams in Nepal were sampled by Rundle *et al.* (1993), Ormerod *et al.* (1994) and Surren (1996). All three studies showed that taxonomic richness declined with increasing altitude though, as Rundle *et al.* (1993) point out, altitude in itself is unlikely to influence the structure of stream communities. Many environmental variables change with altitude (*e.g.*, nutrient load, successional sequence, temperature and flow) and it is these that are likely to influence invertebrates directly. An inverse correlation between altitude and invertebrate species richness has also been found in streams on Tenerife (Malmqvist *et al.* 1993).

Turcotte and Harper (1982) provided a basic outline of the taxa found in an Andean stream in Ecuador. Jacobsen *et al.* (1997) investigated the influence of temperature in relation to altitude and latitude on the structure and diversity of stream invertebrate assemblages in Ecuador and Denmark. They found that maximum stream temperature explained the most variability in faunal composition. More recently, invertebrate surveys of the páramo streams of Volcán Chiles have been carried out by Prowse (2001) and Weaver and Rundle (2001). In their study of the Río Chilma (on the west side of the volcano), Weaver and Rundle (2001) found that altitude was one of the environmental variables which correlated with species composition in streams from 3400 to 4200 m altitude. In contrast, Prowse (2001) collected samples from the Río Bobo (on the east side of the volcano) and found that altitude was not a particularly important factor in determining taxon diversity over the range studied (3500–3920 m). However, he did find that habitat heterogeneity within the streams (pools and riffles) did influence community composition.

None of these studies considered the specialist habitats of waterfall plunge pools, which can be relatively common at high altitudes where slopes are often very steep. For this reason, a study was carried out to investigate the influence of physico-chemical parameters on the composition of aquatic invertebrate communities in waterfall pools in páramo and montane forest in Ecuador.

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 193-199.

METHODS

Study areas

Two study areas were established in the Ecuadorian Andes: a typical high grade, high-altitude páramo stream (Río Chilma, Volcán Chiles) and a lower altitude stream in montane cloud forest (Bellavista Reserve, western drainage basin of Volcán Pichincha). The location of these sites is shown in Fig. 1.

Volcán Chiles (páramo)

Páramo is a high-altitude open vegetation ecosystem which is found principally in the humid, equatorial Andes of northern South America (Luteyn 1992). The páramo belt is situated between the montane forest and the permanent snowline. Volcán Chiles, on the border between Ecuador and Colombia, provides road access to páramo dominated by giant rosettes of *Espeletia pycnophylla* subsp. *angelensis* CUATREC. and tussock grasses. The Río Chilma arises at an altitude of 4500 m on the south-western side of the volcano and flows west to montane forest and eventually to the Pacific Ocean. In these, its upper reaches, the Río Chilma is a fast flowing, first-order stream with a coarse substratum. Six waterfall plunge pools on the Río Chilma were sampled over an altitudinal range of 3400–3900 m (Fig. 2).

Bellavista (montane forest)

Two pools were sampled from a montane forest stream in the Bellavista Cloud Forest Reserve. The stream arises at an altitude of approximately 2500 m and flows into the Pichincha drainage basin, eventually meeting the Río Mindo. The pools were located at altitudes of 2200 m and 2250 m.

Invertebrate sampling

Sampling was carried out in July and August 1997. The semi-quantitative sampling procedure involved taking standardised two minute kick samples with a net of mesh size 0.8 mm. In each of the six páramo waterfall pools, three samples were collected: one from the margin, another from the centre, and the third from directly under cascade. The smaller size of the two montane forest pools meant that only two samples were possible from each pool, from the margin and under the cascade.

The animals were preserved in the field with 70% alcohol and taken to the University of Plymouth for identification. All insects were identified to family level and non-insects to class, using the keys of Croft (1986) and Merritt and Cummins (1996). More detailed determinations are not easily performed in the absence of specific keys for this part of the Andes. Rundle *et al*. (1993), Corkum (1989), and Rutt *et al*. (1990) recognise family level identification as sufficient in such situations.

Physicochemistry

Physicochemical parameters were measured at each site at the same time as the invertebrate samples were collected. Temperature was measured with a thermometer. Dissolved oxygen and pH were measured on site using portable meters (YSI 51B and pHox 42E, respectively). Pool area was measured, and the water discharge of each pool was calculated using cross sectional area and flow rates for segments of the outfall (Allan 1995). The composition of the substratum was estimated by eye and placed into one of the size categories identified by Hynes (1970): boulders, cobbles, pebbles, gravel, sand and silt.

Fig. 1. The location of the study areas on Volcán Chiles and Bellavista Cloud Forest Reserve, Ecuador.

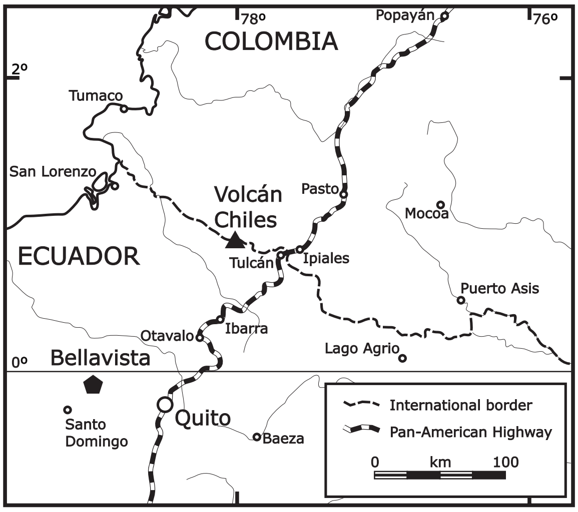
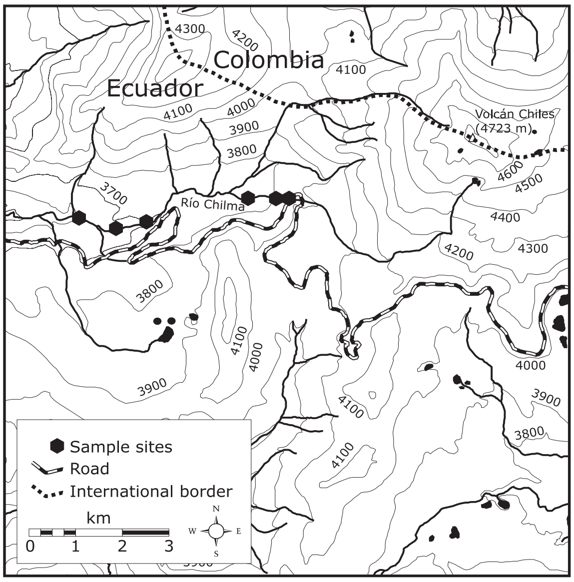


Fig. 2. Location of six waterfall plunge pools sampled on the Río Chilma, Volcán Chiles.



Data analysis

Cluster analysis and multi-dimensional scaling (MDS) was carried out using the PRIMER suite of multivariate analysis programmes (Clarke and Warwick 1994). Also part of the PRIMER package, SIMPER and BIOENV were used to determine indicator taxa for groups of samples and correlations between community composition and environmental variables, respectively.

RESULTS

Physicochemical characteristics

Temperature and pH showed important differences between the páramo and montane pools (Table 1). Páramo pools had a mean temperature of 8.4ºC, compared with 13.6ºC for the lower altitude montane forest pools. The pH of montane forest pools was more acidic (5.0) compared with the circumneutral pools of the páramo (7.7 on average). Dissolved oxygen concentrations were slightly lower in the montane forest pools.

The páramo pools were generally larger than the montane forest ones, with greater discharge rates. Neverthless, some páramo pools had similar sizes and discharges to the montane forest pools.

Cobbles and boulders were the main substratum constituents in all pools, although the montane forest pools had a slightly less coarse substratum, with a higher percentage of gravel and pebbles.

Invertebrate communities

A total of 28 taxa were identified and taxon richness ranged from 10 to 19 in the eight pools sampled (Table 2). Aquatic insect larvae dominated the waterfall plunge pools, accounting for 92% of the fauna in páramo pools and 99% in the montane forest pools. The other components of the páramo communities were Amphipoda (all Hyalellidae), Hydracarina, Hirudinea and Oligochaeta. Apart from the insects, only Amphipoda were found in the montane forest pools.

Within the Insecta, members of the Ephemeroptera and Trichoptera dominated the páramo pools, and were co-dominant in the montane forest pools (with Coleoptera, Diptera and Hemiptera). There were no representatives of the Hemiptera and Odonata in the páramo. Sericostomatidae (Trichoptera) were absent from the montane forest pools, but contributed 24% of the catch in páramo pools. Baetidae (Ephemeroptera) was the most widespread family (found in 100% of samples), but other families were frequent in the samples: Perlidae (Plecoptera), Elmidae (Coleoptera), Sericostomatidae (Trichoptera), Leptoceridae (Trichoptera), Chironmidae (Diptera) and Blephariceridae (Diptera).

Table 3 shows three diversity indices calculated for the eight sites. Samples from montane forest pools were more diverse than those from páramo pools.

Three principal groups of samples were determined by cluster analysis: higher altitude páramo pools, lower altitude páramo pools, and montane forest pools (Fig. 3). The lower altitude páramo pools showed more similarity to montane forest pools than to the páramo pools at higher altitudes. The sub-habitats within pools did vary, but separation of sample groups related primarily to altitude rather than to sub-habitat designation. The MDS plot shows a similar pattern, with the higher altitude páramo samples located towards the lower left corner of the plot, while the remaining two groups are situated towards the opposite corner of the plot (Fig. 4).

The principal taxa associated with each of these groups was determined by SIMPER (part of the PRIMER package). The group of samples from higher altitude páramo pools was charcterised by Baetidae, Sericostomatidae and Hydrocarina; Hydropsychidae were absent. Baetidae, Hydropsychidae, Elimidae adults and Hyalellidae were representative taxa of the group of lower altitude páramo pools. Finally, the montane forest pools were characterised by Baetidae, Elmidae adults, Perlidae and Hydropsychidae. The most significant differences between the páramo groups were the presence of Sericostomatidae in the higher altitude samples, and Elimidae adults in the lower altitude ones. The montane forest pools differed from the lower páramo pools in that they contained members of the Veliidae, Gomphidae, Simuliidae and Leptophlebiidae.

***Table 1**. Physicochemical characteristics of eight waterfall plunge pools. The pools at 2200 m and 2250 m were from Bellavista montane forest, the remainder from the páramo of Volcán Chiles.*

	Páramo (Volcán Chiles)						**Montane forest (Bellavista)**	
Altitude (m)	3940	3920	3850	3720	3650	3540	2250	2200
Temp. (ºC)	7.5	7.5	7.9	9.3	8.0	10.2	13.2	14.0
Dissolved O_2 (%)	89.8	90.0	86.0	88.7	97.5	95.2	83.1	82.3
pH	7.9	7.9	7.9	7.5	7.9	7.3	5.0	5.0
Discharge (m^3 s^{-1})	6.2	1.4	3.5	1.2	5.2	2.5	0.4	1.4
Pool Area (m^2)	19.2	3.6	7.0	1.0	6.1	3.2	2.3	2.5
silt + sand (% cover)	0	0	0	0	0	0	0	0
gravel + pebble (% cover)	10	5	10	10	15	5	30	35
Cobble + boulder (% cover)	90	95	90	90	85	95	70	65

Table 2. Composition of aquatic invertebrates in the samples of páramo (n=6) and montane forest (n=2) pools.

Family	**Páramo**		**Montane forest**	
	N	**% of total**	**N**	**% of total**
Coleoptera	**116**	**8.2**	**43**	**20.4**
Elmidae (adults)	56	4.0	40	18.5
Elmidae (larvae)	60	4.3	2	0.9
Hydrophilliidae			1	0.5
Diptera	**108**	**7.7**	**37**	**17.1**
Blephariceridae	51	3.6	3	1.4
Ceratopogonidae	8	0.6	7	3.2
Chironomidae	22	1.6	5	2.3
Muscidae	8	0.6	8	3.7
Simuliidae	8	0.6	6	2.8
Tabanidae	2	0.1	5	2.3
Tipulidae	9	0.6	3	1.4
Ephemeroptera	**630**	**44.7**	**46**	**21.3**
Baetidae	618	43.9	37	17.1
Leptophlebiidae	12	0.9	9	4.2
Hemiptera			**30**	**13.9**
Veliidae			30	13.9
Odonata			**13**	**6.0**
Aeshnidae			1	0.5
Gomphidae			12	5.6
Plecoptera	**20**	**1.4**	**17**	**7.9**
Leuctridae	2	0.1		
Perlidae	18	1.3	17	7.9
Trichoptera	**423**	**30.0**	**27**	**12.5**
Hydropsychidae	31	2.2	18	8.3
Leptoceridae	27	1.9	6	2.8
Limnephiliidae	11	0.8		
Philopotamidae	2	0.1		
Psychomyiidae	19	1.3	3	1.4
Sericostomatidae	333	23.6		
Amphipoda	**59**	**4.2**	**3**	**1.4**
Hyalellidae	59	4.2		
Xanthidae			3	1.4
Hydracarina	**27**	**1.9**		
Hirudinea	**23**	**1.6**		
Oligochaeta	**3**	**0.2**		
Total	**1409**		**216**	

Table 3: Mean taxon diversity indices for samples from each pool (n=3 for páramo, n=2 for montane forest).

	Margalef's Richness	**Pielou's Evenness**	**Shannon-Wiener**
Páramo pools			
3940 m	2.6	0.56	1.6
3920 m	1.7	0.49	1.1
3850 m	2.6	0.74	2.0
3720 m	2.0	0.60	1.4
3650 m	2.2	0.68	1.7
3540 m	2.3	0.76	2.0
Montane forest pools			
2250 m	3.1	0.85	2.4
2200 m	3.0	0.84	2.2

Fig. 3. Cluster analysis of samples of aquatic invertebrate communities in six páramo (filled symbols) and two montane forest (open symbols) waterfall plunge pools. Symbols indicate samples from below the cascade (⬉↖), pool margins (⬇↓) and pool centre (■).

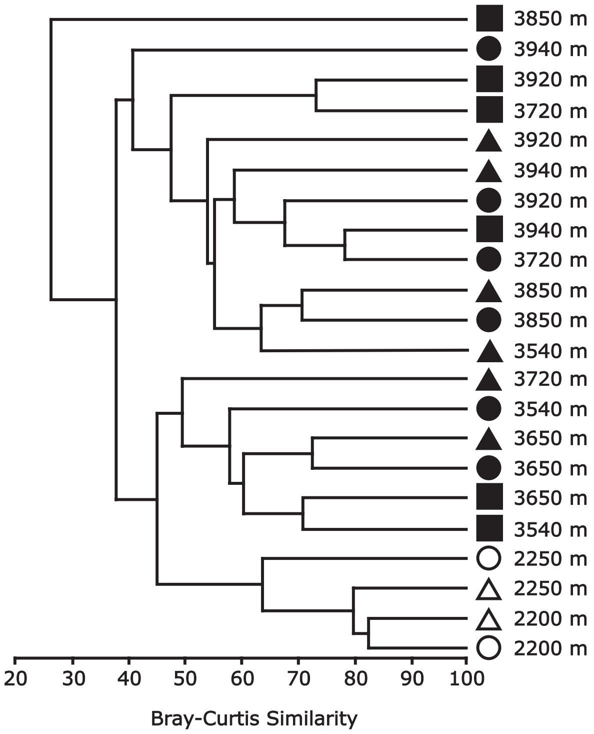
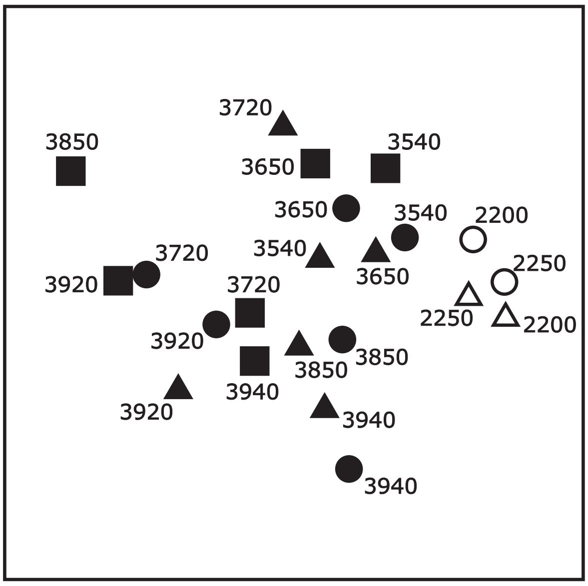


Fig. 4. Multidimensional scaling ordination of samples of aquatic invertebrate communities in six páramo (filled symbols) and two montane forest (open symbols) waterfall plunge pools. Symbols indicate samples from below the cascade (⬉↖), pool margins (⬇↓) and pool centre (■). Each sample is labelled with the altitude of the pool. The stress value was 0.18.



Correlations between community composition and environmental variables were determined using BIOENV (part of the PRIMER package). Altitude showed the highest correlation with community composition (correlation coefficient, r_s=0.73). Temperature (r_s=0.56), pH (r_s=0.54) and substrate (r_s=0.32) were also linked to the faunal assemblages, but the remaining variables showed little correlation.

DISCUSSION

Both the páramo and montane forest waterfall plunge pools were dominated by insect taxa, with Baetidae (Ephemeroptera) very abundant in the páramo samples. Turcotte and Harper (1992), describing the community composition of a small Andean stream in southern Ecuador, also found insects were the most abundant class, but principally belonging to the orders Diptera (64% of the Insecta collected), Trichoptera (14%), Coleoptera (13%) and Ephemeroptera (6%). The most abundant family was Chironomidae. A similar pattern of dominance by Chironomidae was reported by Williams and Hynes (1971) for streams on Mount Elgon, East Africa, and Hynes (1975) for a river in southern Ghana. Only 1.6% of the páramo samples in the current study were Chironimidae (slightly higher for montane forest pools at 2.3%). However, the predominance of Baetidae in the páramo waterfall pools did resemble reports from three Himalayan stream studies (Rundle *et al*. 1993, Ormerod *et al*. 1994, Surren 1994). In one study, Baetidae accounted for 60% of the total numbers identified. The same group was responsible for 45% of animals collected in páramo waterfall pools.

Jacobsen *et al*. (1997) found insect dominance in páramo streams: the most abundant orders were Diptera (27.8%), Ephemeroptera (26.3%) and Coleoptera (10.4%). Amphipoda were responsible for 13.8% of the fauna.

These differences are likely to reflect the environmental conditions prevalent at each of the sites studies. Waterfall pools are particularly turbulent, high-energy environments which may differ significantly from the rest of the stream. The invertebrate communities of páramo waterfall pools might be expected to be more similar to those of Himalayan streams—since these habitats were also turbulent and fast-flowing—than riffle and pool communities from nearby sections of the same stream, or of other Andean streams, like those descibed by Turcotte and Harper (1982).

Weaver and Rundle (2001) described aquatic invertebrate communities from riffle and pools of the Río Chilma, the same stream as the current study. In their survey, the most important insect families were Baetidae, Leptophlebiidae, Sericostomatidae, Limnophilidae and Chironomidae, with Hyalellidae (Amphipoda) also very abundant. The Río Bobo, on the eastern side of Volcán Chiles, was recently surveyed by Prowse (2001). 80% of the morphospecies he collected were insects—Ephemerellidae (Ephemeroptera) were the most abundant family. Both Baetidae and Chironomidae were found in low abundance.

Hydropsychidae were absent from higher altitude communities in Rundle *et al*.'s (1993) Himalayan study (S. Rundle, pers. comm.). Similarly, Hydropsychidae were only present in páramo waterfall pools below 3850 m in the Río Chilma. Hydropsychids are collectors (filter feeders dependent on fine particulate organic matter, FPOM). The abundance of FPOM is determined by inputs of organic matter into the stream, and the processing of this coarse particulate organic matter (CPOM) by shredder activity (Cuffney *et al*. 1990). It might be that FPOM is in short supply in the páramo pools, but approximately 64% of the insects in these pools were also collectors (following Merritt and Cummins 1996), dependent on FPOM. Shredders, processing CPOM into FPOM, were also abundant in the páramo pools (representing approximately 27% of the total number of insects sampled).

Jacobsen *et al*. (1997) reported a distinct increase in the abundance of Hyalellidae with altitude in Ecuadorian streams: total absence of this group in lowland Ecuadorian streams, 3% of the total numbers in the central Andean valley, and 14% in páramo streams. This pattern is supported by this study, where Hyalellidae was absent from the lower altitude (2200–2250 m) montane forest pools, but represented 4% of the fauna collected from the páramo. The absence of Limnephilidae outside the páramo corresponds with similar findings by Jacobsen *et al.* (1997) for Ecuadorian stream communities.

Some of these differences might reflect the relative lack of predators in páramo waterfall pools compared with ones in montane forest—3% and 37%, respectively.

The main differences between samples were related to altitude rather than within-pool habitat differences: the main patterns brought out by multivariate analysis grouped samples by altitude rather than by sub-habitat. This is not to say that differences do not exist between waterfall pool margins, the centre of the pools, and the water below the cascade itself. There may be important differences between sub-habitats, but altitudinal patterns overshadow them in this study. The lack of replication within altitudes makes it impossible to determine the nature of such patterns, if they exist, using the data from these samples.

Three groups of samples were defined by cluster analysis and supported by MDS:

- Higher altitude páramo waterfall pools (mostly 3720 m and above), charcterised by the presence of Baetidae, Sericostomatidae and Hydrocarina, and the absence of Hydropsychidae.
- Lower altitude páramo waterfall pools (mostly below 3720 m), characterised by the presence of Baetidae, Hydropsychidae, Elimidae adults and Hyalellidae.
- Montane forest waterfall pools (2200–2250 m), characterised by the presence of Baetidae, Elmidae adults, Perlidae and Hydropsychidae, with Veliidae, Gomphidae, Simuliidae and Leptophlebiidae.

Altitude was the environmental variable which best explained the differences in invertebrate composition but it is a surrogate variable, summarising changes in other variables which might influence invertebrates directly. In fact, all of the environmental variables measured in this study are interrelated. Water temperature usually falls with an increasing altitude, and flow rate is usually greater at higher altitudes where topography is steeper. Low water temperature and high flow rates promote increased levels of dissolved oxygen which can increase the number of available niches and lead to oxygen-substrate interactions (Ward 1992). High flow rate also influences substrate composition (because of its erosional effects), and food supply for aquatic organisms by affecting the retention of both CPOM and FPOM (Richardson 1991). The hydraulic regime also influences whether dissolved nutrients are stored or exported from the water column (Lancaster and Hildrew 1993).

The complexity of these interactions between environmental variables demonstrates the futility of trying to assess the relative importance of one or a number of combined variables on invertebrate assemblages. Nevertheless, water temperature showed strong correlations with invertebrate composition in waterfall pools, confirming within the páramo-montane forest zone the pattern described by Jacobson *et al.* (1997) for a much greater altitudinal range in Ecuador (100–4000 m).

Given the high discharge and turbulent nature of the waterfall pools in this study, it would be expected that at least some of the predominant families recorded would show specific adaptations to these conditions. In particular, these organisms might respond to the mechanical forces imposed by the movement of water around the animal and collisions with moving objects (Menge and Sutherland 1987). According to Merritt and Cummins' (1996) habitat classification system, approximately two-thirds of the insect families found in the waterfall pool samples typically inhabit erosional habitats (68% for the páramo pools, 63% for montane forest pools). Although nearly all lotic organisms show adaptations to current, some are more adapted to torrential stream habitats than others—though many of these adaptations are behavioural rather than morphological. The dominant mode of existence in these samples was clinging (following Merritt and Cummins 1996)—44% of insects in the páramo samples and 53% in the montane forest ones. Of particular note in the waterfall pool communities, were the elmid beetles and blephariceridfly larvae. Ward (1992) considers Elmidae to be important in habitats with high physical stress levels, and their small size allows them to take refuge in the boundary layer or in crevices (the adults possess large tarsal claws to hold on to the substrate). Blephariceridae were found in low numbers at nearly all sites and are one of the few stream insects to possess hydraulic suckers. According to Ward (1992), they are restricted to mountain streams and maintain their position in fast water by attaching six ventral suckers to smooth rock surfaces.

In summary, the waterfall pools of the páramo and montane forest showed clear differences related to the environmental variables that are reflected in altitude. Species composition in waterfall plunge pools of the Río Chilma differed from the pools and riffles that made up the rest of the stream—though many taxa were shared—and some of these differences relate to the high-energy environment found beneath cascades. Many of the taxa living in these pools show adaptations to these conditions. It is important, therefore, that waterfall pools are considered in surveys of streams and rivers, particularly in the High Andes where cascades are common.

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REFERENCES

Allan, J. (1995) *Stream Ecology: Structure and Function of Running Waters,* London: Chapman & Hall.

Luteyn, J.L. (1992) Páramos: why study them? In: Balslev, H. and Luteyn, J.L. (Eds) *Páramo: An Andean Ecosystem under Human Influence*, pp. 1–14. London: Academic Press.

Clarke, K.R. and Warwick, R.M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation,* Plymouth: Plymouth Marine Laboratory.

Corkum L.D. (1989) Patterns of benthic invertebrate assemblages in rivers of northwestern North America. *Freshwater Biology,* **21:** 191–205.

Croft P. (1986). A key to the major groups of freshwater invertebrates. *Field Studies,* **6:** 695–766.

Cuffney, T., Wallace, J. and Lugthart, G. (1990) Experimental evidence quantifying the role of benthic invertebrates in the organic matter dynamics of headwater streams. *Freshwater Biology.* **23:** 281–299.

Hynes H. (1970) *The Ecology of Running Waters,* Liverpool: Liverpool University Press.

Hynes, J. (1975) Annual cycles of macroinvertebrates in a river in southern Ghana. *Freshwater Biology,* **5:** 71–83.

Jacobsen, D., Schultz, R. and Encalada, A. (1997) Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology,* **38:** 247–261.

Lancaster, J. and Hildrew, A. (1993) Characterising instream flow refugia. *Canadian Journal of Fisheries and Aquatic Sciences,* **50:** 1663–1675.

Malmqvist, B. (1993) Stream macroinvertebrate communities in the island of Tenerife. *Archiv für Hydrobiologie,* **128:** 209–235.

Menge, B. and Sutherland, J. (1987) Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. *American Naturalist,* **130:** 730–757.

Merritt, R.W. and Cummins, K.W. (1996) *An Introduction to the Aquatic Insects of North America,* 3rd edition, Dubuque: Kendall & Hunt.

Ormerod, S.J., Rundle, S.D., Wilkinson, S.M., Daly, G.P. and Dale, K.M. (1994) Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. *Freshwater Biology,* **32:** 309–322.

Prowse, G.M. (2001) The stream invertebrate communities of the Río Bobo, Volcán Chiles. In*:* Ramsay, P.M. (ed.) *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombian border,* pp. 185–191. Plymouth: Pebble & Shell.

Richardson, J. (1991) Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology,* **72:** 873–887.

Rundle, S.D., Jenkins, A. and Ormerod, S.J. (1993) Macroinvertebrate communities in streams in the Himalaya, Nepal. *Freshwater Biology*, **30**: 169–180.

Rutt, G.P., Weatherley, N.S. and Ormerod, S.J. (1990) Relationships between the physicochemistry and macroinvertebrates of British upland streams—the development of modeling and indicator systems for predicting fauna and detecting acidity. *Freshwater Biology*, **24**: 463–480.

Surren, A. (1994) Macroinvertebrate communities of streams in western Nepal: effects of altitude and land use. *Freshwater Biology,* **32:** 323–336.

Turcotte, P. and Harper, P.P. (1982) The macroinvertebrate fauna of a small Andean stream. *Freshwater Biology,* **12:** 411–419.

Vuilleumier, F. and Monasterio, M. (1986) Preface. In: Vuilleumier, F. and Monasterio, M. (Eds.) *High Altitude Tropical Biogeography,* pp. v–vi. Oxford: Oxford University Press.

Ward, J. (1992) *Aquatic Insect Ecology. 1. Biology and Habitat,* London: John Wiley & Sons.

Weaver, R.G.S. and Rundle, S.D. (2001) The influence of altitude on macroinvertebrate community assemblages in the Río Chilma and its tributaries, Volcán Chiles. In*:* Ramsay, P.M. (ed.) *The Ecology of Volcan Chiles: high-altitude ecosystems on the Ecuador-Colombian border,* pp. 177–183. Plymouth: Pebble & Shell.

Williams, T. & Hynes, H. (1971) A survey of the fauna of streams on Mount Elgon, East Africa, with special reference to the Simuliidae (Diptera). *Freshwater Biology,* **1:** 227–248.

Community structure and diversity of Andean pond habitats: the influence of altitude upon community structure and biotic interactions

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SUMMARY

The structure and diversity of macroinvertebrate fauna were studied in relation to altitude in three groups of lentic systems in Ecuador (páramo pools, 3450–4080 m; high-altitude lakes, 4000–3650 m; and cloudforest, 1200–2200 m). Species and family diversity decreased with increasing altitude. Faunal assemblages were compared at family level, and at the maximum resolution of identification within each taxon. The high-altitude páramo sites were more similar to each other than any of the other sites at both levels of analysis. The high-altitude lakes were also more similar to each other than to other samples. The two cloudforest sites were the most diverse in species and families, and were distinct from each other as well as the samples from higher altitudes.

RESUMEN

Se estudiaron la estructura y la diversidad de fauna macroinvertebrada en relación a la altitud en tres grupos de sistemas lénticos en Ecuador (charcas del páramo entre 3450 y 4080 m, lagos de gran altitud entre 4000 y 3650 m y bosque nublado entre 1200 y 2200 m). La diversidad de especies y familias disminuyó con la altitud. Los ensambles de macroinvertebrados fueron comparados tanto a nivel de familia como a la máxima resolución de identificación dentro de cada taxón. Los sitios de gran altitud en el páramo se parecieron más entre si que a cualquiera de los otros sitios a ambos niveles de análisis. Los lagos de gran altitud también se asemejaron entre si más que con el resto de las muestras. Los dos sitios en el bosque nublado fueron los más diversos en especies y familias, y fueron distintos tanto entre si como de las muestras de mayores altitudes.

Key words: páramo, tropical alpine, lentic, aquatic invertebrates, macroinvertebrates

INTRODUCTION

Species richness of both regional and local biotas show a general increase from high to low latitudes, this being true of almost all taxa and ecosystems (Fischer 1960, Rosenzweig 1995). In freshwater biotas, however, there have been few studies that have demonstrated such a latitudinal richness gradient. Whether this is due to a genuine absence of such a gradient in freshwaters or a result of inadequate data is difficult to assess at present. To date, it is only in freshwater fish that greater species richness has been demonstrated in tropical freshwaters (Lowe-McConnell 1987). Studies of aquatic insect diversity to date show an unclear latitudinal pattern; some authors have found higher diversity in the tropics, while others have determined the same diversity in tropical and temperate regions. The further evaluation of this question is limited by the relatively small number of studies available from the tropics and the incomplete knowledge on the systematics of tropical freshwater insects (Jacobsen *et al.* 1997).

Studies on altitudinal zonation of freshwater faunas from tropical and temperate regions have demonstrated clear changes in faunal composition and a decrease in diversity with altitude, for streams at least (Jacobsen *et al.* 1997). There is a distinct lack of data for tropical high-altitude ponds, and altitudinal variation in such systems may be obscured by the wide variety of habitat types and environmental variables. Jacobsen *et al.* (1997) cite temperature as the major abiotic variable related to altitude as well as latitude. In their studies on the composition of Ecuadorian streams, they determined that highland streams bore more resemblance to Danish lowland streams than Ecuadorian lowland streams. This was largely due to the greater number of insect families in the Ecuadorian lowlands. The number of insect orders and families increased linearly with maximum stream temperature and therefore decreased with altitude and latitude. This led them to estimate that small, tropical, lowland streams have a two- to four-fold higher species richness than temperate lowland streams (Jacobsen *et al.* 1997). Ward and Stanford (1982) ascribed temperature as having a major role in determining diversity, distribution and abundance patterns of aquatic insects along altitudinal gradients. However, competition is likely to alter the temperature ranges that a species could inhabit.

In lentic communities, the degree of habitat permanence is of over-riding importance in determining assemblage composition (Williams 1996). For example Collinson *et al.* (1995) undertook a survey of Oxfordshire ponds and assessed the effects of drying out on the macroinvertebrate communities. The results demonstrated that species richness increases with the length of the wet phase of the pond, something which has been demonstrated in subsequent studies (e.g. Bilton *et al.* in press).

The fundamental aim of the present study was to investigate the effect of habitat composition and altitude on the invertebrate assemblages present in stillwaters in the Ecuadorian Andes. The investigation aimed to provide a quantitative description of the habitats sampled in terms of aquatic invertebrate composition and diversity. Therefore, species composition, relative similarity and diversity of aquatic macroinvertebrate faunas from 18 separate sites were analysed. By comparing sites from different altitudes and ecosystems, the possibility of differentiating between altitudinal faunas was examined.

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 201-208.

METHODS

Study areas

Seven different areas were visited in northern Ecuador (Fig. 1):

- *Páramo de Volcán Chiles*
  Samples were taken from an altitudinal range from 3450 to 4080 m (Fig. 2). The ponds varied in depth from 5cm to more than 200cm and in area from $1 m^2$ to $3400 m^2$. The ponds at B5 to B8 were shallow and contained vegetation, but the rest were deep and clear, possessing only marginal vegetation. Substrates for all sites consisted of fine, dark brown sediment.
- *Páramo de Guamaní*
  A series of large ponds at approximately 4000 m were sampled. The vegetation was largely marginal and the pools were generally between 60 and 100 cm in depth.
- *Laguna Mojanda*
  This site consisted of a crater lake approximately 3650 m. Its approximate area was $2 km^2$.
- *Laguna Cuicocha*
  This was another crater lake, at 3700 m, larger than $10 km^2$. Tall stands of macrophytes flanked the margins.
- *Laguna Limpio Pungo (Cotopaxi National Park)*
  This lake was situated at an altitude of 3800 m. It had an area of roughly $0.6 km^2$. The water column was generally less than 100 cm in depth and contained large amounts of macrophytic vegetation.
- *Bellavista*
  A roadside pool, $3.4 m^2$ in area and 7 cm deep, was sampled from this cloudforest site at an altitude of 2200 m. The substrate was fine silt and the habitat was heavily vegetated.
- *Mindo*
  The final cloud forest site (1200 m) consisted of roadside pools ranging from 1–2 m^2 in area and up to 6 cm in depth.

Sampling

Macroinvertebrate samples were collected at all sites between the 21 July and 1 September 1997, in the Ecuadorian dry season, when for streams at least, taxon richness and density of invertebrates are highest (Jacobsen *et al.* 1997).

Páramo bog systems often consisted of ten or more interlinked and individual ponds, in which case a representative sample was taken at random from at least two ponds for that altitude. Invertebrate samples for all sites were collected by standardised sweep net sampling, consisting of a series of five 1 m long sweeps amongst submerged vegetation and surface sediment. A total of five samples were taken per pond. The contents of each sample were emptied into a tray and invertebrates extracted in the field and preserved in 70% ethanol.

Physical measurements

Pond area and depth were measured, although it was only possible to measure depths up to 2 m. The altitude of each site was logged using calibrated altimeters and notes made about the surrounding vegetation. Finally, pH values were tested using indicator paper.

Laboratory techniques

Invertebrates were identified in the laboratory at the University of Plymouth. Insects were identified using Merritt and Cummins (1996) and a variety of additional sources. For some of the aquatic Coleoptera, identification to species and genus was possible, whereas for the majority of invertebrates determination to family or subfamily only were possible.

Data analysis

The PRIMER package (Clarke and Warwick 1994) was used to analyse the similarity in faunal structure (fourth-root transformed abundance data) among the 18 sites through cluster analysis and multi-dimensional scaling (MDS) ordination. One-way analysis of variance was used to determine the influence of area and altitude on species diversity and abundance. Finally, non-parametric diversity indices were calculated (Margalef 's index, Shannon-Weiner Index and Pielous' J statistic).

Fig. 1. Location of the seven sampling areas in northern Ecuador.

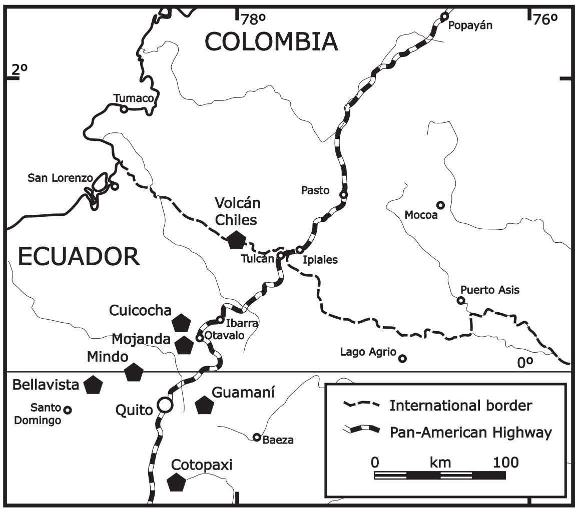
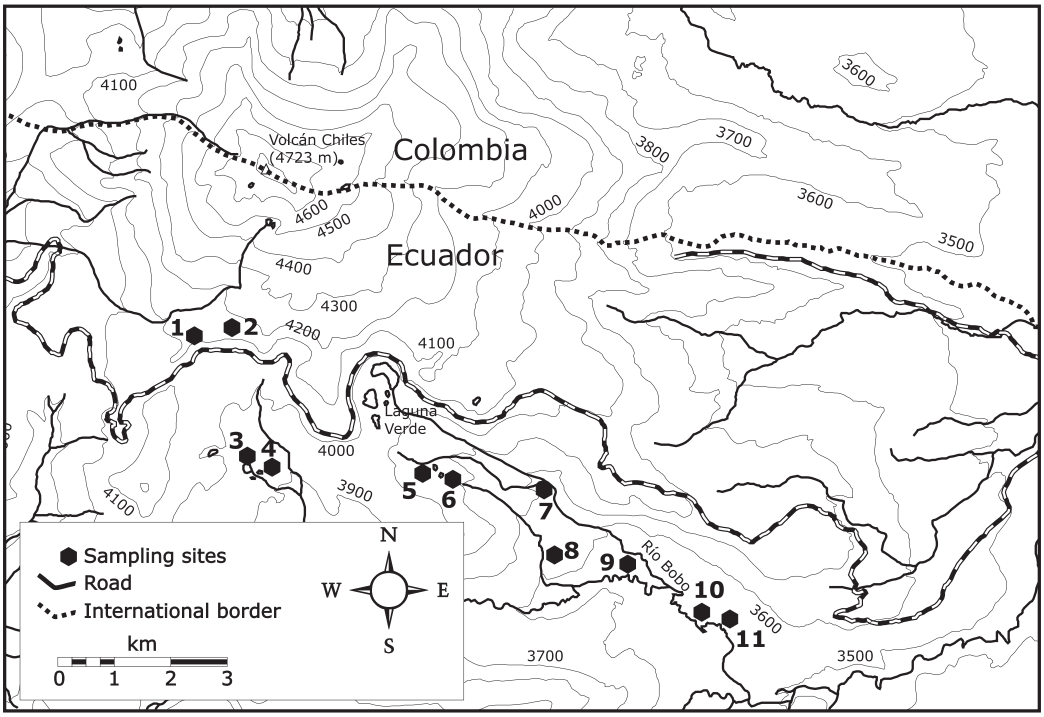


Fig. 2. Location of the sampling sites on Volcán Chiles. The site numbers correspond to those listed in Table 1.



RESULTS

In total, 18 sites were sampled and these are briefly described in Table 1.

The abundance of macroinvertebrates was significantly greater in the highest altitude ponds in the páramo. In particular, the altitudinal range of 3900–4080 m contained the greatest densities of organisms with greatest between site variation (analysis of variance, square root transformed data, $p<0.05$). A significant relationship between diversity and area or altitude was not detected in these sites ($p>0.28$). The number of families was highest in the lowest cloud forest site, as was species diversity.

All three measures of diversity were statistically correlated with altitude ($p<0.05$, though r^2 was less than 40% for Shannon-Weiner and less than 30% for evenness and richness).

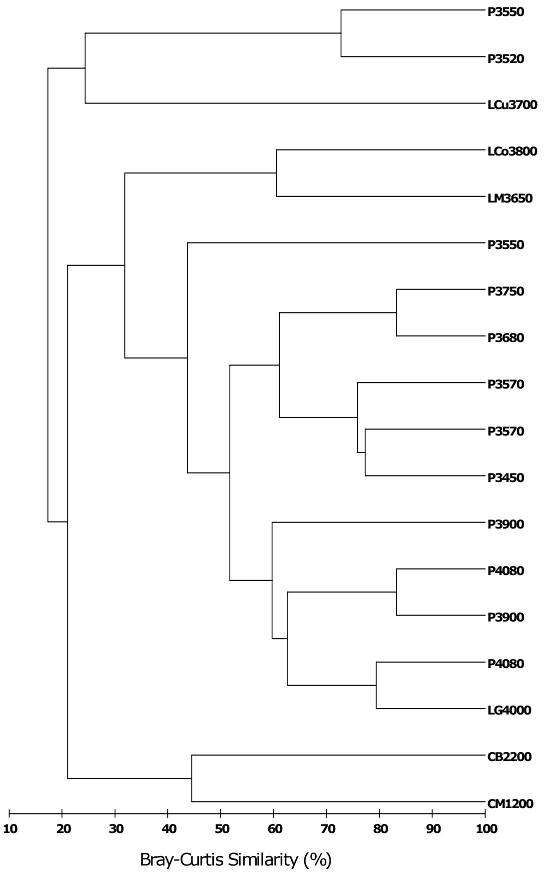
Insects dominated the fauna of the páramo, cloudforest and high-altitude lakes. The Order Coleoptera was present throughout all altitudinal ranges and habitats, whereas hemipteran and odonatan abundances were highest at the middle to lower altitudes. The Amphipoda (Hyalidae) showed a slight increase with altitude, being absent from the lowest sites in the cloudforest.

A total of twenty macroinvertebrate families were found in Ecuador, of which five were exclusively found in the lowest cloudforest site at 1200 m. Three more were present only in the second cloudforest site at 2200 m. No families were restricted solely to páramo. Overall, the páramo pools shared seven families with the high-altitude lake sites and three families with the cloudforest sites, whereas lakes and cloudforest shared just three families. At the generic level for water beetles, the páramo and cloudforest both shared *Rhantus* (Coleoptera, Dytiscidae—*R.cripticus* and *R.calidus*, respectively). A high-altitude lake in the Páramo de Guamaní shared species of *Liodessus* (Coleoptera, Dytiscidae) with most of the páramo pools from the páramo of Volcán Chiles.

Feeding guild composition for the páramo as a whole showed there to be four predator families (Dytiscidae, Aeshnidae, Hirudnea and Apanisagrionidae), two collector gatherers (Chironomidae, Hyalidae) and one herbivore-collector (Corixidae). The high-altitude lake sites were composed of four predatory groups (Dytiscidae, Aeshnidae, Hirudnea and Coenagrionidae), four collector gatherers (Chironomidae, Hyalidae, Corixidae and Platyhelminthes), two grazer/scrapers (Planorbiidae, Hydrobiidae) and one filterer (Ancyclidae). Finally, the cloudforest sites contained six predator families (Dytiscidae, Aeshnidae, Coenagrionidae, Saldidae, Gyrinidae and Nepidae), two detritivores (Hydraenidae and Hydrophilidae), two scraper collectors (Psephenidae, Dryopidae) and one herbivore (Curculionidae).

Distinct groupings of sites were distinguished by cluster analysis of family-level data (Fig. 3). These clusters were more distinct in a similar analysis using the highest possible taxonomic resolution (*i.e.*, groupings at the subfamily, generic and species level where possible; Fig. 4). In essence, there were

Fig. 3. Cluster analysis for all sites using family level data. The sample codes show the altitude preceded by letters denoting the sampling area: P, páramo de Volcán Chiles; LCu, Laguna Cuicocha; LCo, Laguna Limpio Pungo (Cotopaxi National Park); LM, Laguna Mojanda; LG, Laguna de Guamaní; CB, Cloudforest, Bellavista; CM, Cloudforest, Mindo.

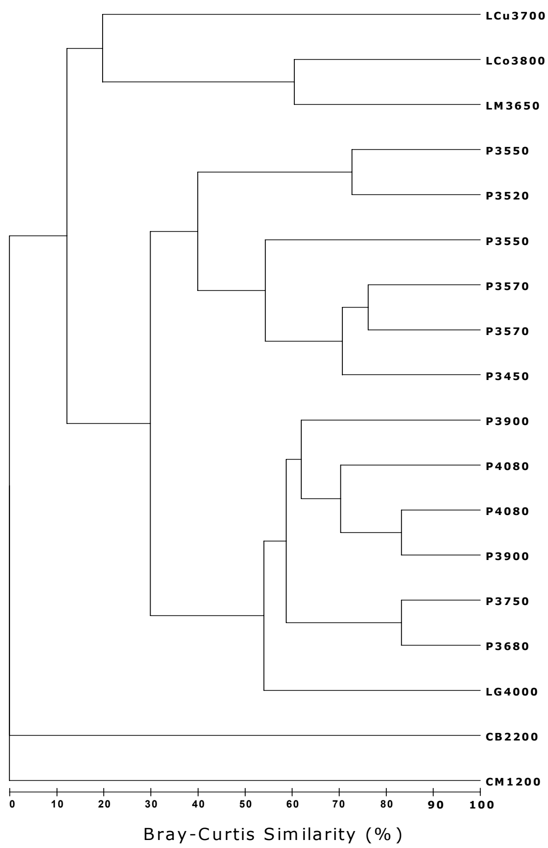


groupings representing the cloudforest sites, the high-altitude lakes, and several groups of páramo pools (which includes the lake from the Páramo de Guamaní). Similar groupings were shown by the MDS ordinations of the same data (Figs. 5 and 6).

DISCUSSION

Faunal diversity in the present study does tend to increase with decreasing altitude. The relationship is not linear and is apparently unrelated to habitat area or pH. Furthermore, species diversity at the high-altitude sites is apparently low, despite their proximity to the equator. According to Rapoport's rule, one of the mechanisms believed to regulate species diversity along the latitudinal continuum from the tropics to the poles, the geographical range of organisms diminishes with declining latitude (Stevens 1989). In a broad context, the rule can be applied to the decreasing diversity observed with increasing altitude. It is further argued that because species living at high latitudes and altitudes are exposed to a wide range of annual climatic conditions, natural selection favours broad climatic tolerances.

Fig. 4. Cluster analysis for all sites using taxonomic determinations to the lowest level (varying amongst taxa). The sample codes are explained in Fig. 3.



In the tropics, climate remains within a narrow range of conditions, but this is not the case at altitude since temperature and relative humidity can vary widely diurnally. Thus, organisms at higher altitudes should generally be less restricted in their habitat use and possess broader geographical ranges. Species at low latitudes and altitudes exist within a narrow range of climatic conditions and are therefore restricted in their habitat use and geographical range.

One possible explanation for the low species diversity observed at high altitude is that Andean montane ecosystems represent temperate habitat islands in a sea of tropical rainforest. Colonising the high-altitude páramo would require substantial evolutionary time for the majority of tropical organisms, since these environments pose a number of physiological challenges. To support this contention further, a thorough understanding of the evolution and development of the High Andes is necessary. Van der Hammen and Cleef (1986) have reviewed of the development of páramo ecosystems. By the beginning of the Pliocene, the sediments of the inter-Andean Magdalena and Cauca Valleys were folded and the Tertiary Geosynclinal sedimentation cycle was practically closed. At that time, the whole Andean region underwent a strong upheaval, which raised the north Andean area to its present altitudes. During the Plio-Pleistocene, an important factor in

Table 1.Characteristic features of the sampling sites. 20-25 samples were taken at each site.

Site	Name and habitat type	Altitude	Dominant taxa	Site descriptions
1	Volcán Chiles, páramo	4080 m	Dytiscidae, *Liodessus* sp.A*,* Chironimidae	Ponds surrounded by vegetation dominated by tussock grasses and giant resoette plants of *Espeletia pycnophylla* subsp. *angelensis* and *Puya hamata*. Depths varied between 5–200+ cm and areas 1–3400 m^2. Aquatic vegetation was limited to filamentous algae around the margins, resulting in a clear water column. Substrates were composed of fine particulate matter that did not support vegetation. Macroinvertebrate species diversity was low (0.2-0.4 Shannon Weiner) and dominated by predators and collector-gatherers. These pools were exposed to the prevailing wind. pH of 6.
2	Volcán Chiles, páramo	4080 m	*Liodessus* sp. A, Hyalidae	
3	Volcán Chiles, páramo	3900 m	*Liodessus* sp.A, Triacanthagyna	
4	Volcán Chiles, páramo	3900 m	*Liodessus* sp. A, Chironomidae, Hyalidae	
5	Volcán Chiles, páramo	3750 m	*Liodessus* sp. A, Chironomidae, Hyalidae, Triacanthagyna	These sites were located amongst similar vegetation to those above. They were less exposed. Pond habitats tended to support macrophytes. Invertebrate species diversity was higher (≤1.2). and communites were composed largely of predators and collector-gatherers.
6	Volcán Chiles, páramo	3680 m	*Liodessus* sp. A, Chironomidae, Hyalidae, Hirudinea	
7	Volcán Chiles, páramo	3570 m	*Liodessus* sp.A, *Rhantus cripticus*, Triacanthagyna, Chironimidae, Graptocorixini	These habitats were generally shallow and apparently drying. They supported macrophytic vegetation and quite diverse macroinvertebrate communities (1.4-1.7). The sites were generally sheltered. Communities were dominated by predators and collector-gatherers, although herbivore-collectors were also abundant. pH of 6.
8	Volcán Chiles, páramo	3570 m	*Liodessus* sp. A, *R. cripticus,* Chironimidae, Hyalidae, Apanisagrionidae, Graptocorixini	
9	Volcán Chiles, páramo	3550 m	Triacanthagyna, Graptocorixini	
10	Volcán Chiles, páramo	3550 m	*Liodessus* sp. A, *R.cripticus.* Graptocorixini, Apanisagrionidae	
11	Volcán Chiles, páramo	3520 m	Triacanthagyna, Hirudinea, Graptocorixini	
12	Volcán Chiles, páramo	3450 m	*Liodessus* sp. A, Triacanthagyna, Apanisagrionidae	The lowest of the Volcán Chiles sites was large, deep (>2m) and full of macrophytes. Species diversity <1.2.
13	Laguna Limpio Pungo (Cotopaxi National Park), high-altitude lake	3800 m	Corixidae, Hyalidae, Chironimidae	An exposed site surrounded by low scrub. Macrophytes abundant. Community dominated by collector gatherers and herbivores. Diversity 0.8. pH of 6.
14	Laguna Cuicocha, high-altitude lake	3700 m	Aeshnidae, Coenagrionidae	Tall macrophytic vegetation. Abundant predators. Diversity 1.3.
15	Laguna Mojanda, high-altitude lake	3650 m	Hyalidae, Hydrobiidae	Short macrophytic vegetation. A collector-gatherer dominated community. Diversity0.9.
16	Guamani, páramo with high-altitude lakes	4000 m	*Liodessus* sp. A, *Liodessus* sp. B, Hyalidae	Vegetation dominated by tussock grasses and *Puya* spp. Abundance of predators and collector-gatherers. Diversity 0.9.
17	Bellavista, cloudforest	2200 m	Hydraenidae, Saldidae’ Hydrophilidae, Coenagrionidae, *Rhantus calidus*	Cloud forest vegetation dominated. The pond habitats consisted mainly of flooded hollows. Communities were dominated by predators and detrivore-shredders. Species diversity was high (1.5-2.3). pH of 5.
18	Mindo, cloudforest	1200 m	*Copelatus spp,* Hydrophilidae, Coenagrionidae	

Fig. 5. MDS plot of all sites at family level (stress value 0.14). The codes refer to the site numbers in Table 1: 1-12, páramo de Volcán Chiles; 13, Laguna Limpio Pungo (Cotopaxi National Park); 14, Laguna Cuicocha; 15, Laguna Mojanda; 16, Laguna de Guamaní; 17, Cloudforest, Bellavista; 18, Cloudforest, Mindo

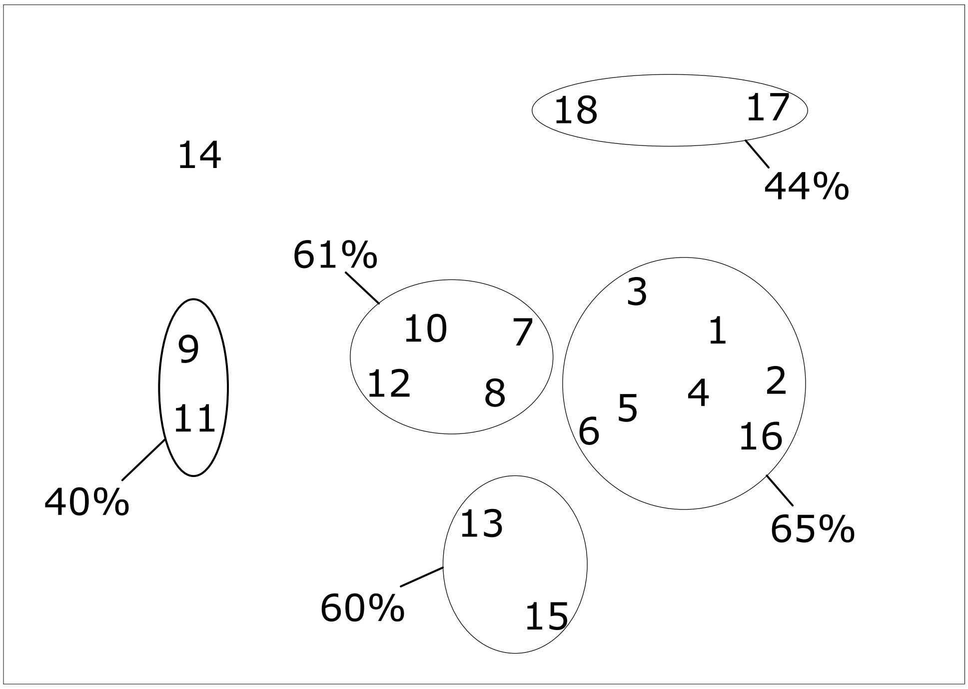
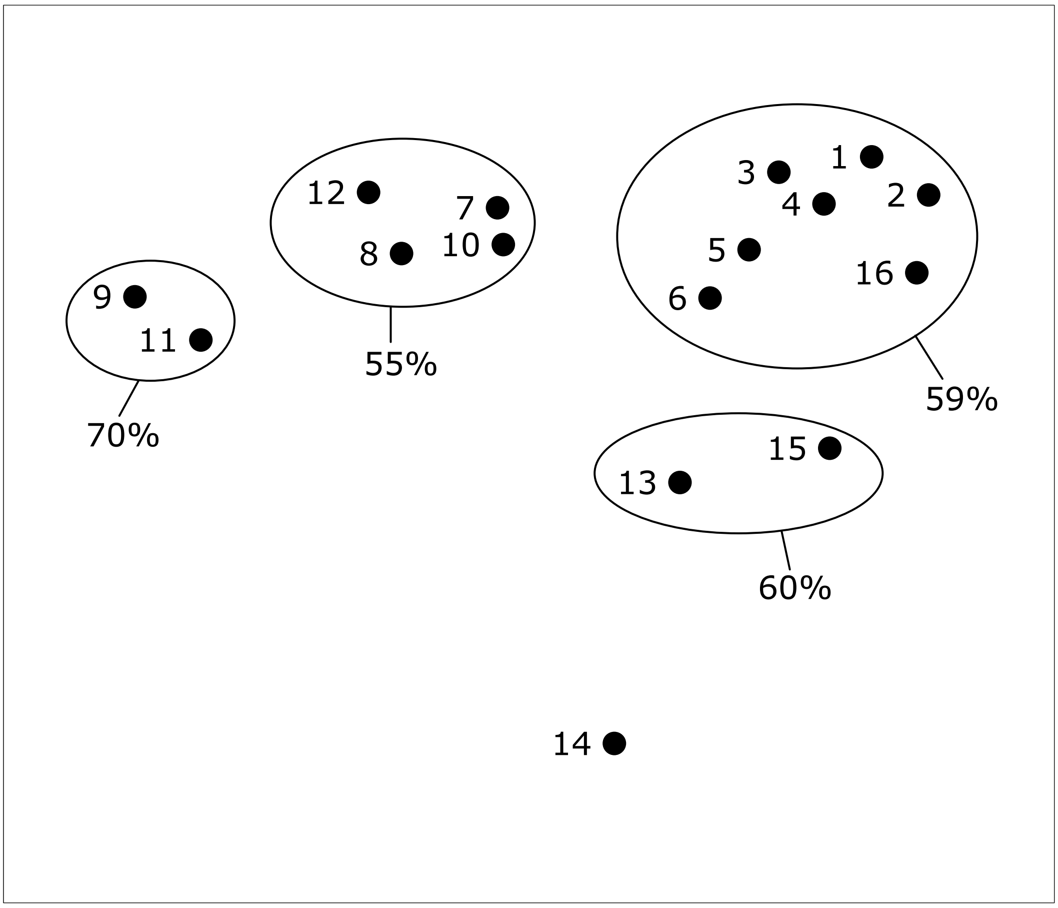


Fig. 6. MDS plot at maximum taxonomic resolution (stress value 0.01). The two cloudforest sites are outliers and are not shown in this plot. The codes refer to the site numbers in Table 1.



Ecuador was volcanic activity and the majority of the higher elevations (>3800 m, above the present forest line) came into being through the accumulation of volcanic rocks, lava and ash. Determining the height of the northern Andes during the different uplift phases of the Tertiary is extremely difficult. However, it is considered inconceivable that areas above 3000 m existed long before the Miocene/Pliocene. It is therefore unlikely that areas with a climate comparable to that of the páramo existed before the Pliocene, or prior to about 5 million years ago (Van der Hammen and Cleef 1986).

Within the páramo, there was a shift in composition in Dytiscidae occurred, from *Liodessus* sp. (dominant at higher altitude) to *Rhantus cripticus* (dominant at lower altitude). These two taxa are morphologically dissimilar, with the *Rhantus* measuring between 0.8 and 1.0cm in length and *Liodessus* typically measuring 0.2cm. As predicted by Wilson (1975) a competitive hierarchy might be present, whereby, environmental constraints (such as permanence) become relaxed enough to enable larger species of predatory arthropod to become competitively dominant over smaller species (Colinson *et al.* 1994).

At intermediate altitudes in the páramo (3750–3450 m), the trophic structure was more complicated with up to five predators present (*R. cripticus, Liodessus sp* A, *Triacanthagyna*, Hirudnea and Apanisagrionidae) and three collector/gatherers/herbivores (Chironomidae, Hyalidae and Graptocorixini). At no point, however, were there more than three predators or collector/gatherers present in an individual pond. In these habitats, it is likely *Rhantus* was not only feeding on the decreasingly abundant chironomids but also upon *Apanisagrion*, since feeding experiments have demonstrated that larger Dytiscidae will readily eat zygopteran nymphs (Deding 1988). It is potentially the greater variety of prey material in these, more diverse, lower altitude ponds that is responsible for the incidence of larger predators, such as *R. cripticus* and *Triacanthagyna*. Juliano and Lawton (1990), however, would advocate from experiments with *Hyphydrous ovatus* (Dytiscidae) that feeding links between predator and prey do not substantially affect population dynamics and are not the sole explanation for observed food web patterns.

The similarity between the páramo lake in Guamaní (4000 m) and a pool in the páramo of Volcán Chiles (4080 m) was almost 80% at the family level (mostly due to the Hyalidae and Dytiscidae). The same lake showed strong similarity (>50%) at the more detailed taxonomic level with several other pools on Volcán Chiles (3680–4080 m). This suggests that lentic systems at similar altitudes may possess similar compositions of invertebrates, at least within northern Ecuador.

The remaining three high-altitude lake sites (Laguna Limpio Pungo at 3800 m in Cotopaxi National Park, Laguna Cuicocha at 3700 m, and Laguna Mojanda at 3650 m) were largely dissimilar to Guamani and the Volcán Chiles groups. Again, Hyalidae were important indicators of the difference. These three lakes were clustered together when more detailed taxonomic considerations were taken into account, even though it was at the very low 20–50% similarity level. The relative lack of faunistic similarity between these sites and the others in the study can be attributed to a variety of factors ranging from geographical isolation to area of habitat.

The cloudforest site at Mindo was the most diverse sampled in terms of species and families. The two cloudforest sites did not possess any species in common, nor did they share any species with the other sampling sites. Apart from the altitudinal differences, there was a wider variety of macrophyte and marginal vegetation in cloudforest pond habitats, providing greater environmental heterogeneity and a wider variety of microhabitats than was found in páramo pools.

Fundamentally, the habitat along altitudinal gradient shifts from *r* to *K*-selecting, requiring that the faunal assemblages develop alternative survival strategies. By demonstrating a lack of similarity between low altitude (“tropical”) communities and high-altitude (“temperate”) communities, this study tends to support the work of Jacobsen *et al.* (1997), on stream invertebrate communities.

The determination of a single factor governing the observed patterns is unlikely. A more realistic suggestion is that a series of physical and biotic interactions are influencing habitat composition. On the whole, the observations would tend to support Rapoport’s rule, whereby the geographical ranges of aquatic macroinvertebrates decline with declining latitude, or in this case altitude. Further experimental tests of these patterns will be required, and in many respects, the equatorial Andes could provide a useful location for testing hypotheses concerning the determinants of species richness.

In general terms, tropical montane ecosystems would appear to be extremely useful environments in which to test ecological theories, such as the questions posed by island biogeography and species diversity versus latitude and altitude relationships. Furthermore, freshwater bog and pond communities can be separated to a larger extent from the surrounding matrix than terrestrial systems, allowing for a more isolated approach to community analysis.

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REFERENCES

Bilton, D.T., Foggo, A. and Rundle, S.D. (in press). Size, permanence and the proportion of predators in ponds. *Archiv fur Hydrobiologia*.

Collinson, N.H., Biggs, J., Corfield, A., Hodson. M.J., Walker, D., Whitfield, M. and Williams, P.J. (1995). Temporary and permanent ponds: an assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. *Biological Conservation,* **74**: 125–133.

Clarke, K.R. and Warwick, R.M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation,* Plymouth: Plymouth Marine Laboratory.

Deding, J. (1988) Gut Content Analysis of Diving Beetles (Coleoptera, Dytiscidae). *Natura Jutlandica,* **22**: 177-184.

Fischer, A.G. (1960) Latitudinal variations in organisc diversity. *Evolution*, **14**: 64–81.

Jacobsen, D., Schultz, R. and Encalada, A. (1997) Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology,* **38:** 247–261.

Juliano, S. and Lawton, J. (1990) Extrinsic vs. intrinsic food shortage and the strength of feeding links: effects of density and food availability on feeding rate of *Hyphydrous ovatus* . *Oecologia*, **83**: 535–540.

Lowe-McConnell, R.H. (1987) *Ecological Studies in Tropical Fish Communities*, Cambridge: Cambridge University Press.

Merritt, R.W. and Cummins, K.W. (1996) *An Introduction to the Aquatic Insects of North America.* Third edition. Dubuque: Kendall & Hunt Publishing Company.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time,* Cambridge: Cambridge University Press.

Stevens, G.C. (1989) The latitudinal gradient in geographical range—how so many species coexist in the tropics. *American Naturalist*, **133**: 240–256.

Van der Hammen, T. and Cleef, A.M. (1986) Development of the High Andean páramo flora and vegetation. In: Vuilleumier, F. and Monasterio, M. (Eds) *High Altitude Tropical Biogeography,* pp. 153–177. Oxford: Oxford University Press.

Ward, J.V. and Stanford, J.A. (1982) Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology,* **27**: 97–117.

Williams, D.D. (1996) Environmental constraints in temporary freshwaters and their consequences for the insect fauna. *Journal of the North American Benthological Society*, **15**: 634–650.

Wilson, E.O. (1975) *Sociobiology: the new synthesis*. Cambridge (MA): Harvard University Press.

Variability in nectar supply: implications for high-altitude hummingbirds

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SUMMARY

The relationship between hummingbird activity and nectar production by *Puya hamata* was investigated in a high-altitude páramo on the Ecuador-Colombia border. Bird behaviour was recorded and nectar sampled in a small plot containing 16 *Puya* plants. Nectar concentration and sugar mass, but not volume, of *Puya* flowers were temporally variable, with distinct morning and afternoon peaks. Nectar production varied significantly between flowers but not between plants. Perching frequency correlated with nectar sugar concentration, but other aspects of behaviour—including territorial activities like chasing—were unrelated to nectar quality. It is suggested that hummingbirds at high altitudes may be flexible foragers and less dependent on particular nectar sources than hummingbirds at lower altitude, despite being strongly resource-limited overall. Agricultural burning of the páramos may alter the distribution patterns of hummingbird food plants. This, in turn, may change the competitive balance between hummingbird species and the foraging strategies they adopt.

RESUMEN

Se investigó la relación entre la actividad de colibríes y la producción de néctar de *Puya hamata* en un páramo de gran altitud en la frontera Ecuador-Colombia. Se registró el comportamiento de las aves y se realizaron muestreos de néctar en una pequeña parcela que contenía 16 plantas de *Puya*. La concentración, mas no el volumen, del néctar y la cantidad de azúcar variaron con el tiempo, presentándose picos claros de producción en la mañana y en la tarde. La producción de néctar varió significativamente entre flores mas no entre plantas. La frecuencia en encaramado (percheo) estuvo correlacionada con la concentración de azúcar en el néctar, pero otros aspectos del comportamiento—incluyendo actividades territoriales como la persecución—no guardaron ninguna relación con la calidad del néctar. Se sugiere que los colibríes de gran altitud pueden ser forrajeros flexibles y menos dependientes de fuentes particulares de néctar que los colibríes de menores altitudes, a pesar de estar, en general, fuertemente limitados por recursos. La quema agrícola de los páramos puede alterar los patrones de distribución de las plantas de alimentación de los colibríes. Esto, a su vez, puede alterar el balance competitivo entre las diferentes especies de colibrí y las estrategias de forrejeo que éstas adoptan.

Key words: foraging strategies, Colombia, Ecuador, páramo

INTRODUCTION

Hummingbirds (Trochilidae) are often resource limited and feed almost exclusively on nectar, with few alternative sources of food (Feinsinger and Colwell 1978, Wolf and Gill 1986, Wiens 1989). Insects provide an important additional source of vitamins, proteins, fatty acids and other essential elements of their diet (Wolf and Gill 1980, Baltosser 1989), but insect- catching comprises just 3% of time budgets at high altitudes (Hainsworth and Wolf 1976, Wolf *et al.* 1976, Wolf and Gill 1986). Nectar sugar is the primary source of energy for hummingbirds (Wolf and Gill 1986).

This dependence on nectar results in close association between behaviour and nectar availability (Feinsinger and Colwell 1978, Wolf and Gill 1986, Wiens 1989), and hummingbirds are responsive to resource variation (Gass and Lertzman 1980, Wolf and Gill 1986, Wiens 1989). Foraging behaviour is reported to be unaffected by predation which occurs mainly at the nestling stage (Carpenter 1978, Wolf and Hainsworth 1983, Baltosser 1986).

Nectar availability is not uniform but often varies spatially and temporally (Feinsinger 1978, Wolf 1978, Feinsinger 1983, Feinsinger *et al.* 1985, Trevelyan 1995). There is often a bi-modal pattern of diurnal production, with distinct morning and afternoon peaks (Stiles 1975), and consequent variations in the levels of hummingbird activity (Hixon *et al.* 1983, Powers and McKee 1994).

Five principal foraging strategies have been identified in hummingbird communities (Feinsinger and Colwell 1978) which maintain positive energy budgets—where energetic benefits exceed energetic costs. *High-reward trapliners* follow a repeated foraging circuit among successive dispersed flowers (trapline), specializing in nectar-rich flowers but do not defend them. *Territorialists* defend dense clumps of smaller flowers, usually with lower nectar production per flower. *Low-reward trapliners* are excluded from clumped flowers by territorialists and follow a trapline of moderate to low nectar-producing flowers. *Territory parasites* steal nectar from clumped flowers defended by resident territorialists, while *generalists* both trapline and steal nectar from defended flowers. The strategy adopted by a particular individual may be flexible and depends on three factors (Feinsinger and Colwell 1978):

- the distribution and relative abundance of nectar sources
- the morphology of the bird which constrains its feeding options, *e.g.*, high-reward trapliners tend to feed on flowers with distinctive corolla morphology which in turn is reflected in the bill morphology of the birds themselves
- competition from other individuals of the same or different species for the rewards.

Most studies have been performed on lowland hummingbird communities (e.g., Wolf and

P.M. Ramsay (ed.), 2001, *The Ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth: Pebble & Shell. Pp. 209-217.

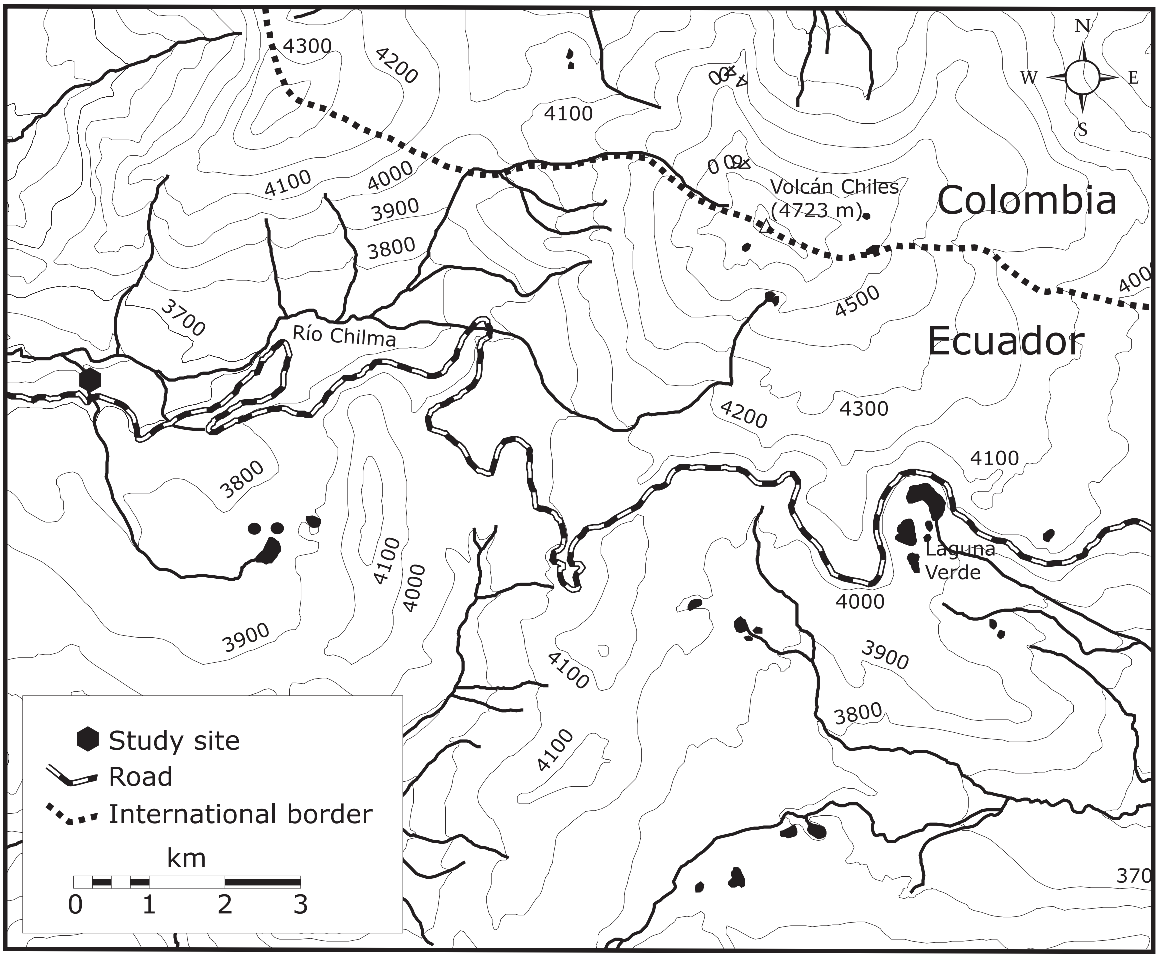
Hainsworth 1971, Feinsinger 1978, Hixon *et al*. 1983, Feinsinger *et al*. 1985). However, high-altitude communities represent "an extreme case of resource limitation" (Carpenter 1978), where energetic costs are higher and nectar volumes and sugar concentrations lower (Wolf and Gill 1986). Thus, high altitude communities may be more strongly influenced by variations in nectar availability compared to lower elevation communities (Carpenter 1978, Wolf and Gill 1986). A change in spatial resource availability, therefore, could be highly influential on the communities at higher altitudes. However, since Wolf and Gill (1986) called for more information on truly high-altitude tropical nectarivores, few new studies have been published (Salaman 1994, Burd 1994, 1995, Evans 1996, Evans and Barnard 1995).

The páramos, high-altitude grasslands of the Andes, represent an appropriate system for studying the effects of resource limitation on hummingbird communities. Páramo covers an area of nearly 78,000 km^2 (Dinerstein *et al*. 1995) with the main expanse in Ecuador, Colombia and Venezuela and additional areas in Peru, Costa Rica and Mexico. It ranges from 3,000 to 5,000 m above sea level from the upper forest line to the snowline (Luteyn 1992).

The páramos are fragile and slow to recover after disturbance (Luteyn 1992) and the conservation status of these high priority ecoregions is vulnerable (Dinerstein *et al*. 1995). Stattersfield *et al*. (1998) have identified the conservation of birds in the Central Andean páramo as an urgent priority. 'This region has suffered great alteration from its natural condition (Stotz *et al*. 1996), and burning, in particular, represents a significant threat to these ecosystems and resource availability within them.

This study examines diurnal variation in bird behaviour and nectar production in *Puya hamata* L.B. Smith (Bromeliaceae), a major supplier of nectar to hummingbirds (Miller 1987), in a páramo system on the Ecuador-Colombia border. Hummingbird strategies are described and the significance of resource patchiness in them is discussed.

Fig. 1. Location of study area on Volcán Chiles.



METHODS

Puya hamata plants are widely distributed throughout the Ecuadorian páramos, occurring between 3,350–3,700 m with a typically patchy local distribution (Gilmartin 1972). This species has a giant basal rosette growth form (Ramsay and Oxley 1997), and produces massive rosettes up to 3.5 m in diameter. In February to April, densely pubescent, cylindrical inflorescences emerge from plants estimated to be 27–28 years old (Miller 1987). On average about 970 flowers are produced per inflorescence from May–July, and seeds develop August–October (Miller 1987). *Puya hamata* is semelparous and each plant senesces and dies within 2–6 months after flowering. Although vegetative reproduction does occur in about 3% of all rosettes (Miller 1987), most new rosettes arise in suitable microsites from seeds with limited dispersal ability, explaining their patchy distribution (Miller and Silander 1991).

A study area (Fig. 1) was established at 3,600 m beside the Quebrada Piedra Negra on the south-western side of Volcán Chiles, on the Ecuador-Colombia border (00°57'N 77°48'W), containing a large number of *Puya hamata* rosettes—many of which were in flower. The inflorescences of 16 plants used in this study, all about 2.5 m tall and within a few metres of other flowering *Puya* plants.

In July and August 1997, 39 hours of observations were made of the activities of the hummingbird community utilizing this clump of *Puya* plants, between 07:00 and 18:00. For each instance of particular types of activity (*i.e.*, chasing, perching, feeding), records were kept on the hummingbird species involved, the *Puya* plant around which the activity was focused, and the commencement time and duration of the activity (with a stopwatch). If a bird was feeding, the number of flowers probed during the visit was also recorded. These observations were made from a vantage point about 20 m away on the opposite side of the stream.

Over a 24-hour period in August 1997, between 07:00 and 18:00, nectar was sampled from the same *P. hamata* inflorescences using 0.5 mm diameter, 75 µl microcapillary tubes. During the entire sampling period, hummingbirds were prevented from feeding on these inflorescences. Nectar volumes were determined immediately and percentage sugar concentration was measured with a hand-held refractometer. From nectar volume and sugar concentration, the sugar content of the flower was also calculated.

RESULTS

Nectar resources

Nectar samples were taken from nine inflorescences, the other plants being inaccessible. The mean volume of nectar in each flower was 10.8 µl (± standard deviation of 9.4 µl). The mean nectar sugar concentration was 18.3 (± 8.2) % (w/w), and the mean mass of sugar 2.2 (± 1.6) mg sucrose equivalents. However, nectar production was highly variable from flower to flower (Table 1) and few statistically significant differences were found between plants—though inflorescences of *Puya* 6 and 7 produced nectars which were significantly different in terms of nectar volume (p=0.0046, Anova).

Sugar mass showed the same diurnal pattern as sugar concentration, but volume differed (Fig. 2). Both sugar concentration and sugar mass (both p<0.0001, Anova) showed peaks at 07–09:00 and 16–17:00 with a trough between. Nectar volume showed no significant difference throughout the day (p=0.4683).

Hummingbird activity

Eight hummingbird species were recorded in the study: *Aglaeactis cupripennis* (Shining Sunbeam), *Pterophanes cyanopterus* (Great Sapphirewing), *Patagona gigas* (Giant Hummingbird), *Chalcostigma herrani* (Rainbow-bearded Thornbill), *Lesbia victoriae* (Black-tailed Trainbearer), *Oreotrochilus estella* (Chimborazo Hillstar), *Eriocnemis vestitus* (Glowing Puffleg) and *Eriocnemis mosquera* (Golden-breasted Puffleg). Two of these species, *P. gigas* and *0. estella* have only recently been discovered this far north (Salaman 1994, Salaman and Mazariegos 1998, Woods *et al.* 1998).

In total, 2323 separate records of hummingbird activity were noted during the study period. In 95% of the 660 chases recorded, the chasing species was *A. cupripennis* (Table 2), confirming its role as the primary territorial species within the study area. *A. cupripennis* was only chased on four occasions by

Table 1. Mean nectar volume, sugar concentration and sugar content per flower for each Puya hamata *sampled. For* Puya *1, 2a, 3a, 7a and 8, measurements are based on 15 observations; for the remainder, 12 observations were made.*

Puya	Volume (µl)	Sugar Content (mg)	Sugar Conc (% sucrose equivalents)
1	12.2 (± 12.5)	2.5 (± 1.6)	20.3 (± 8.7)
2a	12.0 (± 8.3)	2.3 (± 1.6)	16.1 (± 5.9)
3a	11.5 (± 13.8)	2.4 (± 2.9)	16.9 (± 8.0)
4a	10.1 (± 9.0)	1.9 (± 1.0)	20.3 (± 12.9)
6	4.8 (± 3.9)	1.7 (± 0.9)	22.2 (± 7.6)
7	18.3 (± 8.3)	3.0 (± 1.3)	14.6 (± 4.4)
7a	9.0 (± 8.2)	1.9 (± 1.5)	19.3 (± 7.6)
8	10.3 (± 6.1)	1.9 (± 1.0)	16.7 (± 4.4)
8a	8.4 (± 6.0)	1.8 (± 1.0)	19.7 (± 11.9)
Overall	10.7 (± 9.4)	2.2 (± 1.6)	18.3 (± 8.2)

Fig. 2. Diurnal pattern of mean nectar volume (µl ■), sugar concentration (% w/w ▲) and sugar mass (mg ●) for Puya hamata. *Mean values are based on an average of 11 replicates (range 6–18) for each hourly interval.*

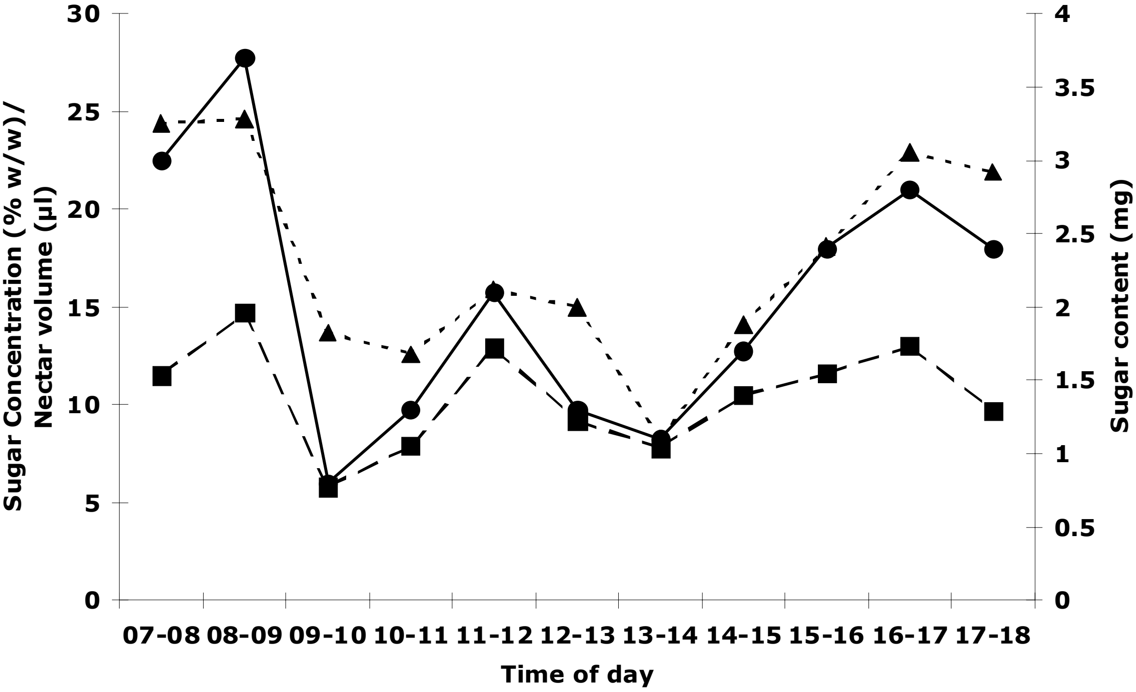
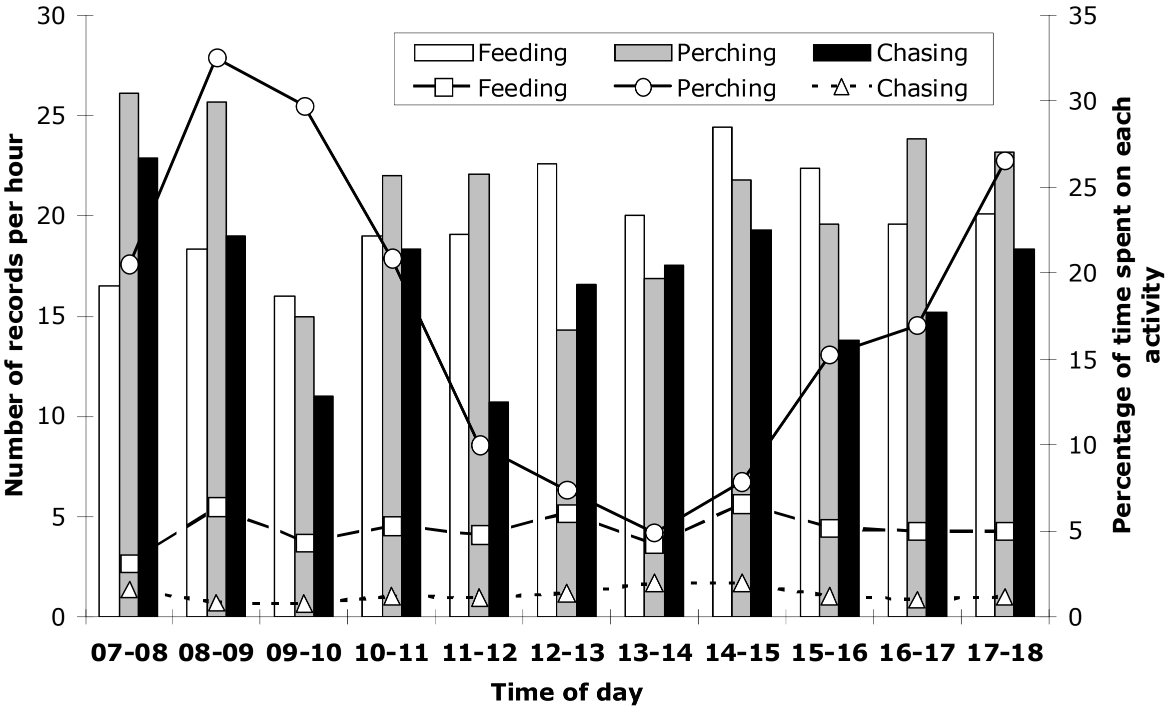


Fig. 3. Frequency of occurrence of each activity (bars) and percentage of time spent on each activity (lines) for hourly intervals throughout the day. All data have been standardized for observation time.



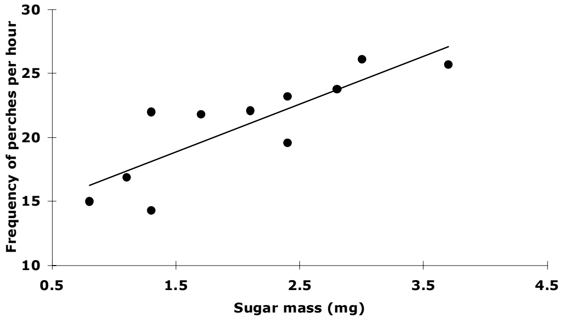
other species, which were responsible for fewer than 2% of chases each. Table 2 also highlights the high number of records of intraspecific territoriality. Intraspecific chases accounted for over 85% of all chases, and at least two-thirds of chases for any one species.

The time birds devoted to perching showed a clear diurnal pattern (Fig. 3) with peaks in early morning and late afternoon. The number of perchings followed a slightly different pattern of three peaks during the course of the day. Feeding and chasing activity did not change much over the course of the day. The time spent feeding and chasing remained more or less constant throughout the day at about 2% and 5% of the time available.

Table 2. Records of chasing activity. Aglaeactis cupripennis *was responsible for 95% of all chases.*

Chasing species **Chased species**	**No of Chases**	**%**
Lesbia victoriae		
Lesbia victoriae	4	67
Aglaeactis cupripennis	2	33
Total	6	
Patagona gigas		
Patagona gigas	2	67
Aglaeactis cupripennis	1	33
Total	3	
Pterophanes cyanopterus		
Pterophanes cyanopterus	8	80
Lesbia victoriae	1	10
Aglaeactis cupripennis	1	10
Total	10	
Chalcostigma herrani		
Chalcostigma herrani	11	92
Lesbia victoriae	1	8
Total	12	
Aglaeactis cupripennis		
Aglaeactis cupripennis	539	88
Lesbia victoriae	4	<1
Oreotrochilus estella	1	<1
Eriocnemis mosquera	2	<1
Patagona gigas	4	<1
Pterophanes cyanopterus	52	9
Chalcostigma herrani	9	1
Total	611	
Overall		
Intraspecific	564	88
Interspecific	78	12
Total	642	

*Fig. 4. Number of perch records compared to mass of sugar (mg sucrose equivalents) in nectar for hourly intervals throughout the day (*p*=0.0014).*



Relationship between bird behaviour and nectar

The only activity that was correlated with patterns of nectar production was the number of perches, which was related to nectar volume (*p*=0.0135) but more strongly to sugar concentration and mass (*p*=0.0097 and 0.0014, respectively). Fig. 4 shows the relationship between the frequency of perches and the sugar mass in nectar—perching occurred more often at times of high sugar content in the nectar. Time spent perching did follow a daily pattern, as noted earlier, but was not correlated with the pattern of nectar production.

Bird activity did focus on particular pairs of *Puya* inflorescences (Table 3). About two-thirds of all chases were associated with plant pairs 5 and 8 (26 and 40%, respectively), and perching was concentrated around these same plants (61% and 17%). Almost 40% of feeding activity centred on *Puya* pair 8.

On average, *Aglaeactis* visited four flowers per feeding visit, whereas the next most frequent visitor, *Pterophanes,* visited 19 flowers on average. However, the mean number of probes per flower was similar for both species (means 1.2 and 1.1 respectively).

DISCUSSION

Mean nectar concentration for *Puya hamata* was 18.3% w/w sucrose equivalents, lower than the 20–25% average for hummingbird-pollinated plants (Baker 1975, Bolten and Feinsinger 1978, Pyke and Waser 1981, Roberts 1996). It falls within Feinsinger *et al.*'s (1985) range of 10–30 µl nectar day^{-1} for a “moderate” reward flower. Plants at high altitudes often produce less concentrated nectar than lower elevations (Wolf and Gill 1986).

Nectar concentration and volume (and therefore total energy) is highly variable from flower to flower in *Puya hamata*. This may make it difficult for birds to assess the quality of nectar rewards between flowers and even inflorescences. This variability may promote high visitation rates by more than one individual bird, and encourages the exploitation of a variety of

Table 3. Number and percentage of records of each activity for each Puya hamata *plant pair.*

***Puya* pair**	**Feeding**		**Perching**		**Chasing**	
	n	**%**	**n**	**%**	**n**	**%**
1	58	7.7	82	10.1	19	4.9
2	76	10.1	7	0.9	13	3.3
3	66	8.7	9	1.1	21	5.4
4	44	5.8	57	7.0	19	4.9
5	37	4.9	497	60.9	101	25.8
6	81	10.7	4	0.5	17	4.4
7	94	12.4	19	2.3	43	11.0
8	300	39.7	140	17.2	158	40.4
Total	756		815		391	

flowers and inflorescences (Burd 1995, Zimmerman and Cook 1985), maximising the chances of pollination and outcrossing.

Hummingbirds have low crop capacity compared with larger birds (Wolf and Gill 1986), requiring them to feed regularly during the day—though recent unpublished studies by Powers and Van Hook have shown that hummingbirds can store nectar amounts equivalent to 25–30% of their body mass (double the predicted crop size). Furthermore, territorial birds tend to feed little and often for energetic reasons (Carpenter *et al.* 1991). Relatively constant feeding effort was observed throughout this study by the dominant, territorial species, *A. cupripennis*. However, energy requirements would be particularly high early in the morning and late in the afternoon (Wolf and Gill 1986), in a climate characterised by “summer every day, winter every night” (Hedberg 1964). The volume of *Puya* nectar did not increase after sunrise and before sunset, but the energy content did—provided by a more concentrated nectar at these times. In the low temperatures typical of sunrise and sunset, it might be more difficult for birds to maintain a positive energy budget, which may explain why the peaks of nectar production are offset by several hours from dawn and dusk to warmer times of day. The role of the intermediate peak of nectar energy content between 11:00–12:00 will be discussed later.

Despite these clear peaks in nectar production, offering higher rewards, there was no increase in the frequency of chasing at these times—an obvious form of territoriality and dominance. A clear relationship between nectar supply and hummingbird behaviour, suggested by studies at lower altitudes (Feinsinger and Colwell1978; Powers 1987; Powers and McKee 1994; Blem *et al.* 1997), was not observed.

However, perching frequency did reflect changes in the quality of nectar, and may represent a form of non-aggressive territoriality. Perching activity is difficult to evaluate in this context because it may serve two, unrelated purposes—a form of rest and also a method of monitoring the territory (Pitelka 1942; Wolf 1978). Birds perched most in the vicinity of *Puya* 5, and over a quarter of all chases originated from here, although very little feeding took place on the inflorescences of this pair of plants. In fact, most of the perching occurred in a non-flowering bush beside these *Puya* plants, and may have represented a good position, on the upper slope of the study area, to monitor intruding birds. Since most perching was located in the centre of this bush, it was not considered to be a form of territory advertisement.

It is possible that the birds are unable to perceive changes in the quality of nectar, but this seems unlikely. Other hummingbird species are capable of distinguishing between nectar concentrations in choice tests, and typically prefer artificially high concentrations of more than 45% (Stiles 1976, Pyke and Waser 1981), but discriminate against very concentrated solutions (Tamm and Gass 1986). More likely, hummingbirds face a different set of circumstances at high altitudes compared with the lowlands, explaining why the birds' behaviour is not so tightly bound to nectar production in *Puya*.

This study focused on diurnal variations in nectar supply, but studies at different temporal scales can provide further insight into the interpretation of hummingbird behaviour (Gass and Roberts 1992; Roberts 1996). The *Puya* nectar resource lasts just three months of the year (Miller 1987), and is consequently patchy temporally as well as spatially. *Puya* is also semelparous, each plant flowers once and dies, making their nectar an unpredictable resource subject to boom and bust years, depending on conditions for their establishment nearly 30 years previously. Therefore, hummingbirds would not be expected to specialise in feeding on *Puya hamata* flowers alone; rather they might take advantage of the resources when and where they occur.

Clearly, this kind of behaviour would require a rapid response to changing resources. Traplining in bumblebees is characterised by learning behaviour which concentrates activity in initially more rewarding areas, even after resources have declined to sub-optimal levels (Thomson 1996). High-altitude hummingbirds would need to be much more sensitive to temporal resource variation to adopt a combination strategy effectively. Certainly, hummingbird territories elsewhere are not static, but respond to changes in resource distribution (Gass and Lertzman 1980; Wiens 1989).

Puya hamata flowers from May to July (Miller 1987), and this study took place at the end of this period. The nectar resource represented by these plants visibly declined as flower numbers fell per inflorescence. During this period, individuals of *A. cupripennis* and *P. cyanopterus* were observed feeding on other nectar sources outside the study area, perhaps indicating a shift away from the *Puya* plants.

This combination of strategies over shorter timescales is significant. Hummingbirds may adopt different strategies over the course of a single day. In this study, some birds may have defended *Puya* inflorescences during times of peak nectar quality and traplined for the remainder of the day. The production of an intermediate peak in nectar quality towards the middle of the day may represent a mechanism which maintains a population of subordinate territorial birds throughout the day. Thus, although feeding and chasing may occur at similar levels throughout the day, the identity of the birds may change. It was impossible to identify individuals in this study and so this scenario remains speculative, but it would also enhance outcrossing in the plants.

In any case, the results support Ingvarson and Lundberg's (1995) view that pollinating hummingbirds may be less dependent on the plants than vice versa. This asymmetrical plant-pollinator relationship explains why a clear match between plant nectar production and bird behaviour is lacking—birds are able to exploit other resources at the same time.

Aglaeactis cupripennis was evidently the dominant territorial species in the study area. It was also dominant and territorial in studies on the Colombian flanks of Volcán Chiles (Salaman 1994), and in the nearby Ecuadorian páramo of El Angel (Miller 1987). *Lesbia victoriae* followed a traplining strategy around the study area. On Volcán Cotopaxi, Ecuador, the same species adopted a traplining strategy when only scattered *Puya clava-herculis* plants were present, but in dense patches of *Puya* it was territorial (Miller 1987). *Aglaeactis cupripennis* was not observed feeding on Cotopaxi at this time, which suggests that strategies change not just in relation to resource availability, but also depend on the other hummingbird species present, perhaps in accordance with a competitive hierarchy among species.

The remaining five species were non-territorial, and followed a low-reward traplining strategy . However, *Patagona gigas, Pterophanes cyanopterus* and *Chalcostigma herrani* may be territory parasites, stealing nectar from defended plants—the morphology of both birds fits with that suggested by Feinsinger and Colwell (1978). The latter two species stole nectar in a very similar situation nearby (Salaman 1994), and were the species chased most of all by *Aglaeactis*. The greater number of flowers visited per feeding visit by *Pterophanes* was in line with expectation for a parasitic forager trying to maximise rewards in the short space of time before being noticed by the owner of the territory. All feeding visits by *Pterophanes* were ended by aggression from *Aglaeactis*.

Oreotrochilus estella chimborazo was previously regarded as a specialist, traplining between isolated shrubs of *Chuquiraga* (Corley Smith 1969). More recently, it has been acknowledged that this bird also feeds on alternative nectar sources such as members of the Malvaceae and *Puya* (Fjeldsa and Krabbe 1990) and introduced Eucalyptus species (Carpenter 1978). Again, a certain plasticity seems to be a prerequisite for survival at high altitudes.

Despite the value of flexible foraging strategies, the páramo is still highly resource limited for hummingbirds. Changes to the distribution of resources could have profound effects on the strategies adopted by different species and their abundance. Although hummingbird communities are rarely affected directly by human disturbance, indirect influences could be very important. Agricultural burning is the most widespread human impact on the páramos (Horn 1997, Laegaard 1992, Luteyn 1992, Ramsay and Oxley 1996, Smith and Young 1987). It is carried out to encourage the production of new green shoots for cattle grazing. One of the clearest impacts of burning on páramo vegetation is the loss of fire sensitive shrubs which hold their buds in the zone where highest fire temperatures occur (Ramsay and Oxley 1996), though in some páramos this loss may be temporary as many shrubs regenerate vegetatively from below ground (Horn 1997).

Given the importance of many shrub species as nectar sources, any decline in abundance of these plants may result in changes in hummingbird communities. Certain strategies, such as traplining by small-bodied birds, may become insupportable, and the ability of some species to adopt alternative strategies may be hampered or encouraged by interactions with other species. Such changes would occur quickly, as hummingbird behaviour and abundances respond rapidly to variations in resource levels (Wiens 1989). Ultimately, localised extinctions of hummingbirds may occur. Once locally extinct, the isolated nature of páramo areas would hinder recolonisation from other areas.

Unfortunately, there is very little information which could inform management practices in the páramos to conserve hummingbirds. Although some plants are known to be hummingbird pollinated, there have been no studies to record the range of plants visited by hummingbird species, the significance of these plants in maintaining hummingbird populations, and the response of hummingbird species to resource changes. Of course, the nature of páramo hummingbird foraging patterns—often travelling rapidly over long distances—makes these studies difficult.

This study suggests that páramo hummingbird foraging behaviour relates to, but is not wholly dependent upon, nectar production in *Puya hamata*. Rather, hummingbirds at high altitudes may be flexible foragers and less dependent on particular nectar sources, despite being strongly resource-limited overall. Changes in nectar resource levels and distribution caused by páramo burning may alter the competitive balance between hummingbird species and the foraging strategies they adopt. However, in the absence of key data on nectar resources for páramo hummingbirds, it is difficult to assess the threat this poses to high-altitude hummingbird communities in the Northern Andes.

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REFERENCES

Baker, H.G. (1975) Sugar concentrations in nectars from hummingbird flowers. *Biotropica,* **7**: 37–41.

Baltosser, W.H. (1986) Nesting success and productivity of hummingbirds in southwestern New Mexico and southeastern Arizona. *Wilson Bulletin,* **98***:* 353–367.

Baltosser, W.H. (1989) Nectar availability and habitat selection by hummingbirds in Guadalupe Canyon. *Wilson Bulletin,* **101***:* 559–578.

Blem, C.R., Blem, L.B. and Cosgrove, C.C. (1997) Field studies of rufous hummingbird sucrose preference: does source height affect test results? *Journal of Field Ornithology,* **68**: 245–252.

Bolten, A.B. and Feinsinger, P. (1978) Why do hummingbird flowers secrete dilute nectar? *Biotropica,* **10**: 307–309.

Burd, M. (1994) A probabilistic analysis of pollinator behavior and seed production in *Lobelia deckenii. Ecology,* **75**: 1635–1646.

Burd, M. (1995) Pollinator behavioral-responses to reward size in *Lobelia deckenii*—no escape from pollen limitation of seed set. *Journal of Ecology,* **83**: 865–872.

Carpenter, F.L. (1978) A spectrum of nectar-eater communities. *American Zoologist,* **18**: 809–819.

Carpenter, F.L., Hixon, M.A., Hunt, A. and Russell, R.W. (1991) Why hummingbirds have such large crops. *Evolutionary Ecology,* **5***:* 405–414.

Corley Smith, G.T.C. (1969) A high altitude hummingbird on the volcano Cotopaxi. *Ibis,* **111**: 17–22.

Dinerstein, E., Olson, D.M., Graham, D.J., Webster, A.L., Primm, S.A., Bookbinder, M.P. and Ledec, G. (1995) *A Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean,* Washington (DC): The International Bank for Reconstruction and Development/The World Bank.

Evans, M.R. (1996) Nectar and flower production of *Lobelia telekii* inflorescences, and their influence on territorial behavior of the scarlet-tufted malachite sunbird (N*ectarinia johnstoni*). *Biological Journal of the Linnean Society,* **57**: 89–105.

Evans, M.R. and Barnard, P. (1995) Variable sexual ornaments in scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*) on Mount Kenya. *Biological Journal of the Linnean Society,* **54**: 371–381.

Feinsinger, P. (1978) Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecological Monographs,* **48**: 269–287.

Feinsinger, P. (1983) Variable nectar secretion in a *Heliconia* species pollinated by hermit hummingbirds. *Biotropica,* **15**: 48–52.

Feinsinger, P. and Colwell, R.K. (1978) Community organisation among neotropical nectar-feeding birds. *American Zoologist,* **18**: 779–795.

Feinsinger, P., Swarm, L.A. and Wolfe, J.A. (1985) Nectar-feeding birds on Trinidad and Tobago: Comparison of diverse and depauperate guilds. *Ecological Monographs,* **55**: 1–28.

Fjeldså, J. and Krabbe, N. (1990) *Birds of the High Andes*, Copenhagen: Museum of Zoology, University of Copenhagen.

Gass, C.L. and Lertzman, K.P. (1980) Capricious mountain weather: a driving variable in hummingbird territorial dynamics. *Canadian Journal of Zoology,* **58**: 1964–1968.

Gass, C.L. and Roberts, W.M. (1992) The problem of temporal scale in optimization: three contrasting views of hummingbird visits to flowers. *American Naturalist,* **140**: 829–853.

Gilmartin, A.J. (1972) The Bromeliaceae of Ecuador. *Phanerogamarum Monographiae Tomus,* **4**: 1–255.

Hainsworth, F.R. and Wolf, L.L. (1976) Nectar characteristics and food selection by hummingbirds. *Oecologia,* **25**: 101–113.

Hedberg, O. (1964) Features of Afroalpine Plant Ecology. *Acta Phytogeographic Suecica,* **49**: 1–144.

Hixon, M.A., Carpenter, F.L. and Paton, D.C. (1983) Territory area, flower density, and time budgeting in hummingbirds—an experimental and theoretical-analysis. *American Naturalist,* **122**: 366–391.

Horn, S.P. (1997) Postfire resprouting of *Hypericum irazuense* in the Costa Rican páramos: Cerro Asunción revisited. *Biotropica,* **29**: 529–531.

Ingvarsson, P.K. and Lundberg, S. (1995) Pollinator functional response and plant population dynamics: pollinators as limiting resources. *Evolutionary Ecology,* **9**: 421–428.

Laegaard, S. (1992) Influence of fire in the grass páramo vegetation of Ecuador. In: Balslev, H. and Luteyn, J.L. (Eds.) *Páramo: An Andean Ecosystem under Human Influence*, pp. 151–170. London: Academic Press.

Luteyn, J.L. (1992) Páramos: why study them? In: Balslev, H. and Luteyn, J.L. (Eds.) *Páramo: An Andean Ecosystem under Human Influence*, pp. 1–14. London: Academic Press.

Miller, G.A. (1987) *The Population Biology and Physiological Ecology of Species of* Puya

(Bromeliaceae) in the Ecuadorian Andes. PhD Thesis, University of Connecticut.

Miller, G.A. and Silander, J.A., Jr. (1991) Control of the distribution of giant rosette species of *Puya* (Bromeliaceae) in the Ecuadorian páramos. *Biotropica,* **23**: 124–133.

Pitelka, F.A. (1942) Territoriality and related problems in North American hummingbirds. *Condor,* **44**: 189–204.

Powers, D.R. (1987) Effects of variation in food quality on the breeding territoriality of the male anna hummingbird. *Condor,* **89**: 103–111.

Powers, D.R. and McKee, T. (1994) The effect of food availability on time and energy expenditures of territorial and non-territorial hummingbirds. *Condor,* **96**: 1064–1075.

Pyke, G.H. and Waser, N.M. (1981) The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica,* **13**: 260–270.

Ramsay, P.M. and Oxley, E.R.B. (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetatio,* **124**: 129–144.

Ramsay, P.M. and Oxley, E.R.B. (1997) The growth form composition of plant communities in the Ecuadorian páramos. *Plant Ecology,* **131**: 173–192.

Roberts, W.M. (1996) Hummingbirds nectar concentration preferences at low-volume: the importance of time-scale. *Animal Behaviour,* **52**: 361–370.

Salaman, P.G.W. (1994) *Surveys and Conservation of Biodiversity in the Chocó, South-West Colombia,* Cambridge: BirdLife International.

Salaman, P.G.W. and Mazariegos, L.H. (1998) The hummingbirds of Nariño, Colombia. *Cotinga*, **10**: 30–36.

Smith, A.P. and Young, T.P. (1987) Tropical alpine plant ecology. *Annual Review of Ecology and Systematics,* **18**: 137–158.

Stattersfield, A.J., Crosby, M.J., Long, A.J. and Wege, D.C. (1998) *Endemic Bird Areas of the World: Priorities for Biodiversity Conservation,* Cambridge: BirdLife International.

Stiles, F.G. (1975) Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology,* **56**: 285–301.

Stiles, F.G. (1976) Taste preferences, colour preferences, and flower choice in hummingbirds. *Condor,* **78**: 10–26.

Stotz, D.F., Fitzpatrick, J.W., Parker, T.A. and Moskovits, D.T. (1996) *Neotropical Birds: Ecology and Conservation,* Chicago: University of Chicago Press.

Tamm, S. and Gass, C.L. (1986) Energy-intake rates and nectar concentration preferences by hummingbirds. *Oecologia,* **70**: 20–23.

Thomson, J.D. (1996) Trapline foraging by bumblebees: I. Persistence of flight-path geometry. *Behavioral Ecology,* **7**: 158–164.

Trevelyan, R. (1995) The feeding ecology of Stephen's lory and nectar availability in its food plants. *Biological Journal of the Linnean Society,* **56**: 185–197.

Wiens, J.A. (1989) *The Ecology of Bird Communities. Volume 2. Processes and Variations*, Cambridge: Cambridge University Press.

Wolf, L.L. (1978) Aggressive social organisation in nectarivorous birds. *American Naturralist,* **18**: 765–778.

Wolf, L.L. and Gill, F.B. (1980) Resource gradients and community organization of nectarivorous birds. *Acta Congressus Internationalis Ornithologici,* **17**: 1105–1113.

Wolf, L.L. and Gill, F.B. (1986) Physiological and ecological adaptations of high montane sunbirds and hummingbirds. In: Vuilleumier, F. and Monasterio, M. (Eds.) *High Altitude Tropical Biogeography*, pp. 103–118. Oxford: Oxford University Press.

Wolf, L.L. and Hainsworth, F.R. (1971) Time and energy budgets of territorial hummingbirds. *Ecology,* **52**: 980–988.

Wolf, L.L., Hainsworth, F.R. and Gill, F.B. (1975) Foraging efficiencies and time budgets in nectar feeding birds. *Ecology,* **56**: 117–128.

Wolf, L.L., Stiles, F.G. and Hainsworth, F.R. (1976) Ecological organisation of a tropical, highland hummingbird community. *Journal of Animal Ecology,* **45**: 349–380.

Woods, S., Ortiz-Crespo, F. and Ramsay, P.M. (1998) Presence of the Giant Hummingbird, *Patagona gigas*, and the Ecuadorian Hillstar, *Oreotrochilus chimborazo jamesoni*, at the Ecuador-Colombia border. *Cotinga*, **10**: 37–40.

Zimmerman, M. and Cook, S. (1985) Pollinator foraging, experimental nectar robbing and plant fitness in *Impatiens capensis. American Midland Naturalist,* **113**: 84–91.

The páramo zone is found between the upper limit of continuous forest and the lower limit of permanent snow in the northern Andes. The páramos are famous for their rugged beauty, and the wealth of plant species that live there. These wet, mountainous areas also provide a reliable source of water for most Andean people of the region, but many have been modified by agricultural practices such as burning and grazing.

Although extensive collections of páramo plants have provided us with a firm basis for plant taxonomy, the ecology of plants at high altitudes in the Andes is still poorly understood. We know even less about páramo animals, especially the invertebrates. Almost every collection turns up species new to science.

This book brings together various studies from the páramo zone of Volcán Chiles, a mountain on the border between Ecuador and Colombia. There is nothing special about this mountain, but it has been the focus for a wide range of research over the last 10-15 years. Some contributions provide a taxonomic basis for ecological work (e.g., checklists of plants, keys to ground beetles and spiders) or describe distribution patterns over an altitudinal gradient in aquatic and terrestrial organisms. Other chapters present treatments of giant rosette plant anatomy and ecophysiology, hummingbird behaviour, and the impact of burning.

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