

Bryophyte and macrolichen diversity of the *Purdiaea nutans*  
forest in southern Ecuador and its relationship to soil, climate,  
and vegetation structure

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## **I. Chapter**

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### **General Introduction**

### **Tropical Andes – a hotspot of diversity**

One of the most famous features of tropical rain forests is their extreme species richness which has impressed scientists ever since the earliest explorations. The tropical Andes have recently proved as the ‘hottest’ biodiversity hotspot in the world (Brummitt & Lughadha 2003), with an estimated 40.000 species of vascular plants and the highest number of endemic taxa (20.000) recorded worldwide (Churchill et al. 1995, Myers et al. 2000). This high diversity is in particular due to contributions of montane rain forests species (Barthlott et al. 1996). Of about 10.000 vascular plant species occurring in the montane forests of Ecuador, more than one third are endemic to the country (Balslev 1988, Jørgensen & León-Yáñez 1999).

Due to the complex structure of the tropical forests and the resulting variety of micro-habitats suitable for small organisms they generally inhabit many bryophytes and lichens. High precipitation rates and the frequent incidence of clouds in montane areas lead to especially high abundances of bryophytes and lichens (e.g., Grubb et al. 1963, van Reenen & Gradstein 1983, Frahm & Gradstein 1991, Hamilton & Bruijnzeel 2000). Comprehensive studies on bryophyte and lichen assemblages in the Neotropics have mostly focused on lowland, submontane and lower montane forests (e.g., Cornelissen & Ter Steege 1989, Gradstein et al. 2001, Acebey et al. 2003, Zotz et al. 2003, Benavides et al. 2006), less so on upper montane forests (Colombia: Wolf 1995, Costa Rica: Holz et al. 2002, Holz & Gradstein 2005, Venezuela: Kelly et al. 2004). Moreover virtually all of these studies focus on epiphytes; terrestrial assemblages, which are well-developed in upper montane forests (Gradstein 1992), are generally neglected or focus on bryophytes only.

#### **The study area**

The study was carried out in the Reserva Biológica San Francisco (RBSF), Zamora-Chinchipe province southern Ecuador, within the Cordillera Real and ranging from ca. 1800-3100m. In this part of the Andes a distinct depression in the average altitude of the mountain chains is observable and the regular Andean structure is interrupted by many perpendicular valleys cutting deeply into the Cordillera. The Amotape-Huancabamba-depression (Molau, 1988) which stretches from northern Peru to southern Ecuador also acts as a natural connection between the humid Amazon lowlands and the semi-arid to arid

coastal areas and was previously noted as a region of high biodiversity, being home to numerous endemic species (Weigend 2002).

The climate at the RBSF belongs to the “tierra templada” (19-13°C) and extends into the “tierra fria” (13-6°C) (Richter 2003). Annual precipitation averages 2200 mm at 1950 m and increases dramatically with elevation to approx. 6000 mm at 3100m. The period from October to December is relatively dryer than the rest of the year and may experience short but pronounced dry spells induced by foen winds (Emck 2007).

In geological terms the area is characterized by the predominance of crystalline rock (Litherland et al. 1994). The relief is highly structured by deeply incised ravines, steep slopes, narrow ridge tops and some broad ridge plateaux. The steepness of the slopes also promotes an extraordinary frequency of landslides (Hagdorn 2002), often they are triggered by human activities such as logging or slash and burn, but also by natural causes.

Soils in the upper montane belt are described as being very acid humaquepts with hygomorphic properties (Schrumpf et al. 2001). The vegetation of the RBSF was described by Bussmann (2001, 2002), who recognized four elevational belts: lower montane forest (*Ocotea-Nectandra* forest; *Alzateetum verticillatae*) at 1800-2150 m (in ravines up to 2300 m); shrubby upper montane forest (*Purdiaea nutans-Myrica pubescens-Myrsine andina* forest; *Purdiaetum nutantis*) at 2150-2650 m; subpáramo dwarf forest at 2650-3050 m; and treeless páramo vegetation in the summit area at 3050-3150 m. The lower montane and subpáramo forests are well-representative of the zonal vegetation of the northern Andes.

The upper montane belt in southern Ecuador is typically characterized by the abovementioned nutrient-poor acidic soils on underground of crystalline rock, high precipitation and rather strong winds. These abiotic site conditions generally support open forests composed of low-statured trees. At the Reserva Biológica San Francisco (RBSF) they favour a noteworthy forest type, dominated by the otherwise rare treelet *Purdiaea nutans* (Clethraceae) (Bussman 2001, Homeier 2005, Chapter 2) which is exclusive to the northern border of Podocarpus National Park. Paulsch (2002) and Homeier (2004) noted a preference of the *Purdiaea* forests for ridge habitats and suggested that its development was due to very nutrient-poor soils.

### Diversity of *cryptogams* in the study area

The traditional term *cryptogams* comprises a diverse set of unrelated organisms, reproducing by spores. The present thesis focuses mainly on bryophytes (liverworts and mosses) and macrolichens.

Several characteristics make these organism groups particularly useful for vegetation studies in montane tropical forests. Due to their limited size high species densities are possible, allowing for representative sampling in small, ecologically homogeneous plots. Furthermore, they do not interact with animals for fertilization and diaspore dispersal and suffer only minor damage by herbivores compared to seed plants. Their limited biotic interactions as well as their poikilohydric life style lead to a close interrelationship with abiotic environmental factors (climate, soils, etc.). Finally, bryophytes and lichens are distributed worldwide and show parallel development of richness and morphology in the palaeo- and neotropics (e.g., Kürschner & Parolly 1998, Kessler et al. 2001). For these reasons they have been subject of several ecological and biogeographic studies in the study area.

A general inventory of bryophytes and lichens of the RBSF recorded over 500 bryophyte species (320 liverworts, 192 mosses, 3 hornworts), being the highest number ever recorded from a relatively small tropical area of ca. 11 km<sup>2</sup> (Gradstein et al. in press, Kürschner et al. in press), and ca. 200 lichen species (Nöske et al. in press). At least 81 bryophyte species (72 liverworts, 9 mosses) were new to Ecuador and six were new to science. Previous work on the biodiversity of non-vascular epiphytes had so far focused on analyzing the impact of anthropogenic disturbance on bryophyte and lichen diversity in the lower montane forest belt (ca. 1900 m), by inventorying selected trees in one primary and two secondary forest plots (Nöske 2004). Other studies in the area investigated liverwort-fungus interrelationships and provided good evidence for mycorrhiza-like associations (Nebel et al 2004, Kottke & Nebel 2005). Ecosociological studies focused on bryophyte communities of trunks and rotten logs along an elevational gradient between 1200-3000 m (Parolly & Kürschner 2004a, b, 2005). In the upper montane belt two sociological associations were recognized, the *Frullanio serratae*-*Holomitrietum sinuosi*, occurring mainly at lower elevations and the *Macromitrio perreflexi*-*Pleurozietum paradoxae* from higher elevations (Parolly & Kürschner 2004 a, b). The character species of the latter association are rare taxa, *Macromitrium perreflexum* being endemic to southern Ecuador and *Pleurozia paradoxa* and *P. heterophylla* being the only Neotropical members of the small monotypic family Pleuroziaceae. The unique set of character species of this

association probably narrows its range to the southern Ecuadorean Andes. Another noteworthy bryophytic feature of the area is the newly described genus *Physotheca*, belonging to a new subfamily Geocalycaceae subfam. Physothecoideae (Engel & Gradstein 2003).

The abundance of these and other unusual non-vascular plant species in the upper montane forest of the RBSF was one of the main reasons for the present PhD thesis.

### **Research objectives**

The *Purdiaea nutans* forest of the RBSF is the starting point of the present investigation. The central goal of this study was to describe the nature of the monodominant *Purdiaea* forest by analysing vegetation structure, climate, and soil and documenting its diversity in bryophytes and macrolichens. Our investigation was designed to answer the following main questions:

- Is the *Purdiaea* forest an azonal, natural vegetation type of montane ridge tops on very nutrient-poor soils? Why does it only develop on the broad ridges and ridge plateaus of the RBSF and not in other parts of the south Ecuadorian Andes?
- To what extent is the unique setting of the *Purdiaea* forest reflected in the diversity and composition of the non-vascular vegetation, both in the terrestrial and the epiphytic habitat?
- Are diversity and distribution patterns of liverworts, mosses, macrolichens and ferns congruent in different forest and habitat types?

This investigation was part of the multidisciplinary research project ‘Functionality in a tropical mountain forest: diversity, dynamic processes and use-potential under ecosystem aspects’, financially supported by the German Research Foundation (DFG).



## Outline of chapters

The following chapters of this thesis represent either papers published or manuscripts suitable for direct submission. If publication decision has already been made, formatting follows the guidelines of the chosen journal.

In chapter two we search for reasons for the occurrence of the *Purdiaea* forest at the RBSF. We test for the hypothesis that nutrient-poor soils are primarily responsible for the establishment of this unique forest type. For sake of comparison we have studied vegetation structure, climate, and soil characteristics of the *Purdiaea* forest and of other upper montane forests in the region, at mountain pass El Tiro north of Podocarpus National Park and in the Reserva Tapichalaca south of the park. If the closed *Purdiaea* stands were indeed fostered by unusual soil or climate, one would expect striking difference in the prevalent abiotic factors compared to the other two localities. In all three localities, we analyzed 400 m<sup>2</sup> plots in ridge and slope habitats.

Chapter three focuses on the terrestrial bryophyte and macrolichen assemblages of upper montane ridge and slope forests of southern Ecuador. In consideration of the distinctive and unusual features of the monodominant *Purdiaea nutans* forest, this study had two main objectives. On the one hand we compared the terrestrial bryophyte and macrolichen flora of the *Purdiaea nutans* forest with that of upper montane ridge forests of southern Ecuador without *Purdiaea*. On the other hand we analyzed the diversity, composition and habitat requirements of terrestrial assemblages of bryophytes and macrolichens on ridges and slopes in the upper montane belt of southern Ecuador. This is the first study in the tropics dealing in detail with the ecology of terrestrial cryptogamic assemblages. We emphasize the high alpha and beta diversity of terrestrial cryptogams and their distribution in different habitat types in the tropical Andes of southern Ecuador.

In Chapter four we analyzed the non-vascular epiphytic community structure and microclimate in upper montane tropical rain forests in southern Ecuador. Specifically we compared species distributions of epiphytic bryophytes and macrolichens in neighbouring ridge and slope forests and within vertical tree zones. In order to test whether non-vascular species richness reflects the unusual site conditions at the RBSF a comparison was made with two other upper montane forest sites of southern Ecuador and literature data of other Neotropical montane rain previously investigated.

Our interest in Chapter five was to test for congruence in diversity and distribution patterns of lichens, liverworts, mosses, and pteridophytes in tropical mountain rainforests.

We also compared for difference in patterns between epiphytes and terrestrials. The main objective was to assess whether one of our study groups may be used as a surrogate for one or more of the other groups in order to facilitate predictions on the diversity state of tropical montane forests.

## References

- Acebey, A., Gradstein, S.R. & Krömer, T. (2003) Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *Journal of Tropical Ecology*, 19, 9-8.
- Balslev, H. (1988) Distribution patterns of Ecuadorean Plant Species. *Taxon*, 37, 567-577.
- Barthlott, W., Lauer, W. & Placke, A. (1996) Global distribution of species diversity in vascular plants: towards a world map of phytodiversity. *Erdkunde*, 50, 317-327.
- Benavides, J.C., Duque M., A.J., Duivenvoorden, J.F. & Cleef, A.M. (2006) Species richness and distribution of understorey bryophytes in different forest types in Columbian Amazonia. *Journal of Bryology*, 28, 182-189.
- Bruijnzeel, L.A. & Veneklaas, E.J. (1998) Climatic condition and tropical montane forest productivity: The fog has not lifted yet. *Ecology*, 79, 3-9.
- Brummitt N. & Lughadha E.N. (2003) Biodiversity: Where's hot and where's not. *Conservation Biology*, 17, 1442-1448.
- Bussmann, R.W. (2001) The montane forests of Reserva Biológica San Francisco (Zamora-Chinchipec, Ecuador), vegetation zonation and natural regeneration. *Die Erde*, 132, 9-25.
- Bussmann R.W. (2002) Estudio fitosociológico de la vegetación en la Reserva Biológica San Francisco (ECSF) Zamora Chinchipec. Herbario Loja, Loja.
- Churchill, S., Forero, E., Balslev, H. & Luteyn, J., eds. (1995) Biodiversity and Conservation of Neotropical Montane Forests. Bronx, NY, USA: The New York Botanical Garden: 702 pp.

- Cornelissen, J.H.C. & Ter Steege, H. (1989) Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *Journal of Tropical Ecology*, 5, 131-150.
- Emck, P. (2007) Klimadifferenzierung in Süd-ecuador. Dissertation, University of Erlangen, Germany.
- Engel, J.J. & Gradstein, S.R. (2003) Studies on Geocalycaceae XIV. *Physotheca* J.J. Engel & Gradst., a new genus of hepaticae from Ecuador, belonging to a new subfamily, Geocalycaceae subfam. Physothecoideae J.J. Engel & Gradst. *Taxon*, 52, 763-773.
- Frahm, J.-P. & Gradstein, S.R. (1991) An altitudinal zonation of tropical rain forests using bryophytes. *Journal of Biogeography*, 18, 669-678.
- Gomez, E. N. (1989) Elementos de Geografía del Ecuador. Ediguías, Quito
- Gradstein, S.R. (1992) The vanishing tropical rain forest as an environment for bryophytes and lichens. In: Bates, J. W. & Farmer, A.R. (eds.), *Bryophytes and lichens in a changing environment*, pp. 232-256. Oxford University Press.
- Gradstein, S.R., Griffin, D., Morales, M.I. & Nadkarni, N.M. (2001) Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. *Caldasia*, 23, 203-212.
- Gradstein, S.R., Bock, C., Mandl, N.A. & Nöske, N.M. (in press) Bryophytes of the Reserva Biológica San Francisco, Ecuador. Part 1. Introduction; Liverworts and Hornworts. In: Breckle, S. & Liede, S. (eds), *Checklist of plants and animals of the Reserva Biológica San Francisco. Ecotropica Monographs*.
- Grubb, P.J., Lloyd, J.R., Pennington, T.D., & Whitmore, T.C. (1963) A comparison of montane and lowland rain forest in Ecuador 1. The forest structure, physiognomy, and floristics. *The Journal of Ecology*, 51, 567-601.
- Hamilton, L.S. & Bruijnzeel, L.A. (2000) Decision time for cloud forests. IHP humid tropics programme series 13, 1-40.
- Hagedorn, A. (2002) Erosionsprozesse in Südecuador unter der besonderen Berücksichtigung des Oberflächenabtrags. PhD-thesis, Inst. F. Geographie Univ. Erlangen.

- Holz, I., Gradstein, S.R., Heinrichs, J. & Kappelle, M. (2002) Bryophyte Diversity, Microhabitat Differentiation, and Distribution of Life Forms in Costa Rican Upper Montane *Quercus* Forest. *The Bryologist*, 105, 334-348.
- Holz, I. & Gradstein, S.R. (2005) Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica - species richness, community composition and ecology. *Plant Ecology*, 178, 89-109.
- Homeier, J. (2005) *Purdiaea nutans* Planch. In: P. Schütt, H.J. Schuck, U. Lang & A. Roloff (Eds.), *Enzyklopädie der Holzgewächse* 42 (1-4). Landsberg/Lech: Ecomed.
- Jørgensen P.M. & Leon-Yanez S. (1999) *Catalogue of the Vascular Plants of Ecuador*. Missouri Botanical Garden Press.
- Kelly, D.L., O'Donovan, G., Feehan, J., Murphy, S., Drangeid, S.O. & Marcano-Berti, L. (2004) The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora. *Journal of Tropical Ecology*, 20, 643-666.
- Kessler, M., Parris, B.S. & Kessler, E. (2001). A comparison of the tropical montane pteridophyte communities of Mount Kinabalu, Borneo, and Parque Nacional Carrasco, Bolivia. *Journal of Biogeography*, 28, 611-622.
- Killeen T.J., Douglas M., Consiglio T., Jørgensen P.M. & Mejia J. (2007) Dry spots and wet spots in the Andean hotspot. *Journal of Biogeography*, 34, 1357-1373.
- Kottke, I. & Nebel, M. (2005) The evolution of mycorrhiza-like associations in liverworts: an update. *New Phytologist*, 167, 321-323.
- Kürschner, H. & Parolly, G. (1998) Syntaxonomy of trunk-epiphytic bryophyte communities of tropical rain forests. A first pantropical approach. *Phytocoenologia* 28, 357-425.
- Kürschner, H. & Parolly, G. (in press). Bryophytes of the Reserva Biológica San Francisco, Ecuador Part 2. Mosses. *Ecotropica*. Monographs.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.
- Molau, U. (1988) *Scrophulariaceae*. Part 1. *Calceolarieae*. *Fl. Neotr. Monogr.*, 47, 1-291.

- Nebel, M., Kreier, H.P., Preußing, M., Weiß, M. & Kottke, I. (2004) Symbiotic fungal associations of liverworts are the possible ancestors of mycorrhizae. In: Agerer, R. Piepenbring, M., Blanz, P. (eds). *Frontiers in Basidiomycote Mycology*, pp. 339-360. Eching, Germany: IHW-Verlag.
- Nöske, N.M., Gradstein, S.R., Kürschner, H., Parolly, G., & Torrachi, S. (2003) Cryptogams of the Reserva Biológica San Francisco (Province Zamora-Chinchipe, Southern Ecuador). I. Bryophytes. *Cryptogamie, Bryologie*, 24, 15-32.
- Nöske, N.M. & Sipman, H.J.M. (2004) Cryptogams of the Reserva Biológica San Francisco (Province Zamora-Chinchipe, Southern Ecuador). II. Cryptogamie, *Mycologie*, 25, 91-100.
- Nöske N.M.(2004) Effekte anthropogener Störung auf die Diversität kryptogamischer Epiphyten (Flechten, Moose) in einem Bergregenwald in Südecuador. Dissertation; University of Göttingen, Germany.
- Nöske , N.M., Mandl N. & Sipman H.J.M. (in press) Lichens of the Reserva Biológica San Francisco, Ecuador. *Ecotropica Monographs*.
- Parolly, G. & Kürschner, H. (2004a) Ecosociological studies in Ecuadorian bryophyte communities I. Syntaxonomy, life strategies and ecomorphology of the orealepiphytic vegetation of S Ecuador. *Nova Hedwigia*, 78, 1-43.
- Parolly, G. & Kürscher, H. (2004b) Ecosociological studies in Ecuadorian bryophyte communities. II. Syntaxonomy of the submontane and montane epiphytic vegetation of S Ecuador. *Nova Hedwigia*, 79, 377-424.
- Parolly, G., Kürschner, H., Schäfer-Verwimp, A., & Gradstein, S.R. (2004) Cryptogams of the Reserva Biológica San Francisco (Province Zamora-Chinchipe, Southern Ecuador) III. Bryophytes - Additions and new species. *Cryptogamie, Bryologie*, 25, 271-289.
- Parolly, G. & Kürscher, H. (2005) Ecosociological studies in Ecuadorian bryophyte communities. V. Syntaxonomy, life forms and life strategies of the bryophyte vegetation on decaying wood and tree bases in S Ecuador. *Nova Hedwigia*, 81, 1-36.
- Paulsch, A. (2002). Development and application of a classification system for undisturbed and disturbed tropical montane forests based on vegetation structure. Dissertation, University of Bayreuth.

- Sarmiento, F.O. (2001) Ecuador. In: Cappelle, M. & Brown, A. D. (eds.), Bosques nublados del neotrópico. Santo Domingo de Heredia, Costa Rica. Instituto Nacional de Biodiversidad, INBio, S. 497-548.
- Schrumpf, M., Guggenberger, G., Valarezo, C., & Zech, W. (2001) Tropical montane rain forest soils: Development and nutrient status along an altitudinal gradient in the South Ecuadorian Andes. *Die Erde, Themenheft: Tropische Wald-Ökosysteme*, 132, 43-59.
- Van Reenen, G.B.A. & Gradstein, S.R. (1983) A transect analysis of the bryophyte vegetation along an altitudinal gradient on the Sierra Nevada de Santa Marta, Colombia. *Acta Botanica Neerlandica*, 32, 163-175.
- Weigend M (2002) Observations on the Biogeography of the Amotape-Huancabamba Zone in Northern Peru. *The Botanical Review*, 68, 38-54.
- Wolf, J.H.D. (1995) Non-vascular epiphyte diversity patterns in the canopy of an montane rain forest (2550-3679m), Central Cordillera, Colombia. *Selbyana*, 16, 185-195.
- Zotz, G., Schultz, S. & Rottenberger, S. (2003) Are tropical lowlands a marginal habitat for macrolichens? Evidence from a field study with *Parmotrema endosulphureum* in Panama. *Flora*, 198, 71–77.

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## **II. Chapter**

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### **The unique *Purdiaea nutans* Forest of Southern Ecuador - Abiotic Characteristics and Cryptogamic Diversity**

N. Mandl, M. Lehnert, S.R. Gradstein, M. Kessler, M. Abiy and M. Richter

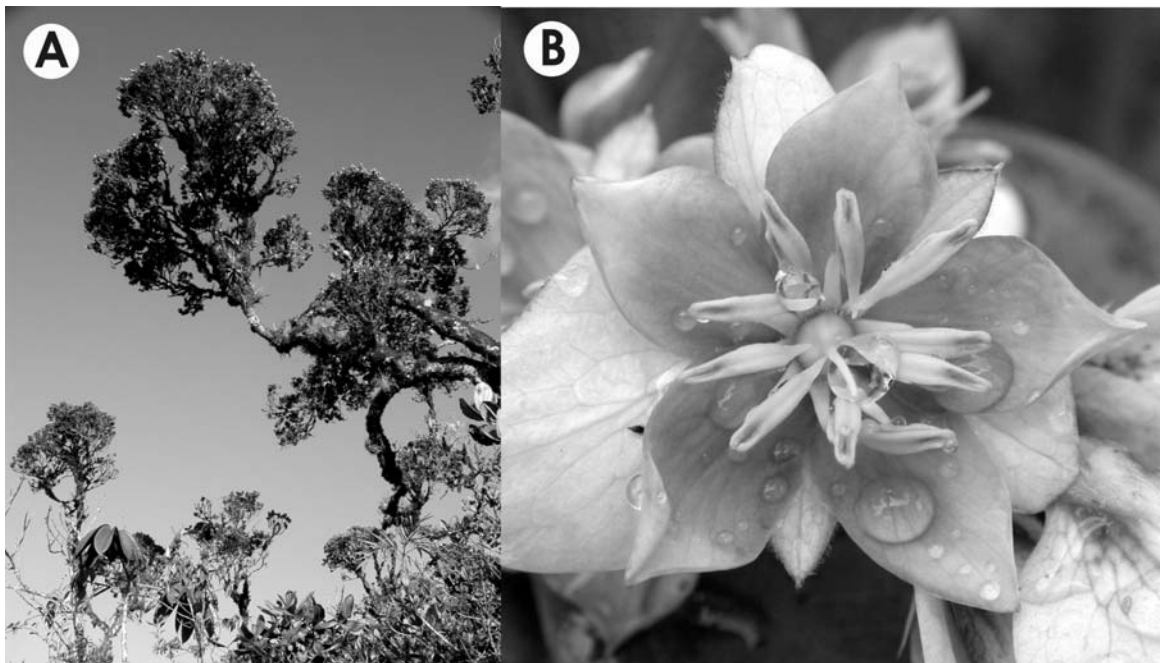
In: E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl (Eds.)

Gradients in a tropical mountain ecosystem of Ecuador.

Ecological Studies (in press)

## Introduction

The genus *Purdiaea* is a Neotropical genus of bushes and small trees belonging to the Ericales or heath alliance (Anderberg and Zhang 2002; Ståhl 2004). *P. nutans* Planch. is the only species of the genus in continental South America, occurring sporadically on nutrient-poor ridges or highly exposed areas in the Venezuelan Guyana Highlands and in the northern Andes from Colombia to northern Peru (Homeier 2005b; Figs. 19.1, 19.2). In all known localities it appears as isolated tree or shrub within mixed forest stands, except in the Rio San Francisco valley, southern Ecuador (Prov. Zamora--Chinchi), where the only known forests dominated by *P. nutans* occur (Bussmann 2001, 2002; Paulsch 2002; Chapter 10.1 in this volume). These *Purdiaea* forests (*Purdiaeaetum nutantis* Bussmann 2002) cover about 200 ha of upper mountain forest, more than half of which are located within the RBSF (Mandl et al., unpublished data).

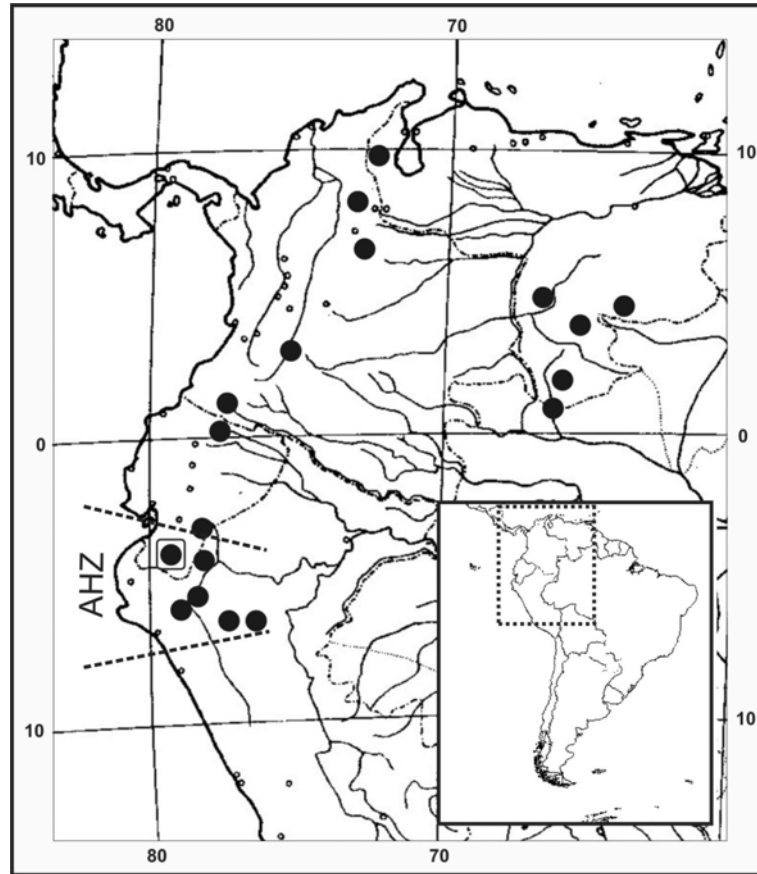


**Fig. 19.1.** *Purdiaea nutans*. **a** Habit. **b** Detail of flower. Images by N. Mandl

Reasons for the occurrence of this forest type in the Río San Francisco valley are unclear. Our hypothesis is that the nutrient-poor soils of the upper montane area of the RBSF might foster the development of the unique *Purdiaea* forest. Phytogeographically, the study area is part of the Amotape--Huancabamba Zone (AHZ) between the Río Jubones system in Ecuador and the Río Chamaya system in Peru, characterized by predominance of

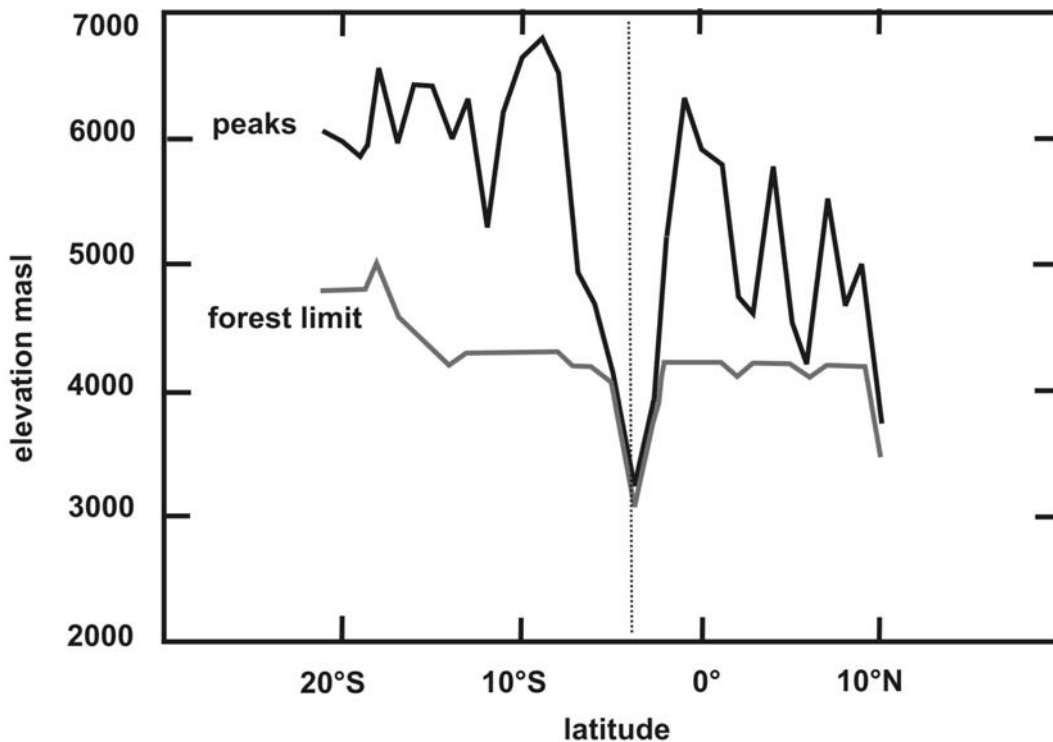


crystalline rock and relatively low mountain peaks (Figs. 19.2, 19.3). This zone has a high level of biodiversity and is home to numerous endemic species (Weigend 2002).



**Fig. 19.2.** Distribution of *Purdiaea nutans* in South America, with delimitation of the Amotape--Huancabamba zone (AHZ). The RBSF study area is marked with a *frame*

The purpose of our study was to characterize the abiotic environment (climate, soil) of the *P. nutans* forest and analyze its cryptogamic plant diversity. Cryptogams (ferns, bryophytes, lichens) do not interact with animals for fertilization and diaspore dispersal and suffer only minor damage by herbivores compared with seed plants. Therefore, their occurrence may reflect prevalent local abiotic factors more directly than do seed plants. If the closed *P. nutans* stands at the RBSF were caused by unusual soil or climate, one would expect a significant difference in the abiotic conditions as well as in the cryptogamic community composition and abundance compared with nearby forest stands where *P. nutans* is scarce or lacking. For the sake of comparison, upper montane forest stands in two other localities, El Tiro and Tapichalaca, were included in this study. In all three localities, we analyzed 400 m<sup>2</sup> plots in ridge and slope habitats.



**Fig. 19.3.** Maximum elevation of mountain peaks and upper forest limit along the latitudinal gradient in the tropical Andes. Note the deep dent at ca. 4 °S (study area)

## Results and Discussion

### Abiotic Characteristics

The recorded macroclimate of all three study areas is permanently cool and perhumid, with a relative drier period from September until December. Mean daily courses of temperature and air humidity taken over a period of one year show similar curves at all locations. In the investigated ridge and slope forest stands temperatures rarely rise above 17 °C (RBSF) and relative humidity hardly drops below 82%. However, daily courses of temperature and air humidity fluctuate more strongly on the rather open and heterogenic ridges than in the dense slope stands. The *Purdiaea* forest at RBSF receives up to 5000 mm annual precipitation, which is about 2000 mm more than at El Tiro and 1000 mm more than at Tapichalaca. This difference might cause stronger leaching of minerals at RBSF than at the other study sites and therefore poorer soils in terms of available nutrients were expected. A comparison of soils in the three study sites, however, did not reveal significant differences (Mandl et al., unpublished data). At all three sites soils were acidic, dystic

cambisols and gleysols, with organic layers made up of moor-like wet humus followed by thin Ai and thick Ae and Aa horizons. Organic carbon contents in the organic layer were similar in all sites, nitrogen contents increased slightly from El Tiro to Tapichalaca, and total N was higher on slopes than on ridges. In general, soils of Tapichalaca slopes were slightly richer in nutrients, with higher K, Ca and Mg values and higher C, N and P turnover rates. Ridge soils at Tapichalaca, however, were not different from those at the other sites.

The low and open canopy is a striking structural feature of ridge-top forests in this part of southern Ecuador. Differences in canopy height between ridge and slope forests were less pronounced at RBSF than at the other sites. A crucial finding of our investigation was that *P. nutans* occurred mainly on ridges. *Purdiaea*-dominated stands with 80--100% prevalence among trees with  $\geq 10$  cm dbh were found only along crests and broad ridge plateaus of the Río San Francisco valley. Downhill, the share of *Purdiaea* diminished to 40--60% and about 100 m below the crest only scattered, isolated mature trees occurred. Studies of seedlings in the RBSF have shown that *Purdiaea* seeds may germinate on lower slopes but soon die in these habitats (Knörr 2003) where the substrate is enriched by the downhill flow of nutrients (Silver et al. 1994). Apparently the species is competitively inferior to others for light due to its slow growth (Homeier 2005b).

All these abiotic features cannot explain the dominance of *P. nutans* at the RBSF. However, there is evidence for fire events at the RBSF dating back to about 850 years ago. Records of maize (*Zea*) pollen following those fires lead us to suspect that fires may have been related to human agricultural practices. Personal field observations suggest that *Purdiaea* is highly fire-resistant and even indicate that germination may be triggered by fire. Consequently, it seems likely that *Purdiaea* may have survived pre-Colombian fire events better than other tree species and may have been able to take advantage of the resulting open vegetation structure to achieve extensive regeneration. Slow growth rates of *Purdiaea* and a dense terrestrial herbaceous vegetation cover may limit the establishment of new tree seedlings and hereby preserve the dominance of *P. nutans*.

### Cryptogamic Diversity

Almost 250 species of pteridophytes were recorded in the RBSF (Lehnert et al. in press) which is one of the highest numbers of fern species recorded from such a small area (approx. 11.2 km<sup>2</sup>) in the Andes. About 45 occur on the ridges dominated by *P. nutans*.

Although endemic species are lacking, the fern flora of the *Purdiaea* forest stands out by the common occurrence of several rare species such as *Pterozonium brevifrons* (A.C. Sm.) Lellinger, with a range similar to that of *Purdiacaea nutans* (Guyana Highlands and scattered occurrences in the northern Andes, Fig. 19.2; Tryon and Tryon 1982), the northern Andean species *Blechnum schomburgkii* (Klotzsch) C. Chr. and *Cyathea peladensis* Hieron. The *Purdiaea* forest has no extraordinary accumulation or deficiency of certain fern groups, although typical terrestrial groups (Thelypteridaceae, Dryopteridaceae, Aspleniaceae) are poorly represented. The same was observed on ridges in the other study sites. In terms of species numbers, the pteridophyte flora at the three study sites did not differ significantly, although slopes were significantly richer than ridges (Table 19.1).

**Table 19.1.** Number of pteridophyte species on ridges and slopes in the three study sites.

	RBSF	El Tiro	Tapichalaca
Ridge	49	48	56
Slope	81	91	87
Total	93	94	102

A bryophyte inventory of the RBSF yielded 505 bryophyte species (Gradstein et al. submitted), one of the highest numbers ever recorded from such a rather small tropical area. The species list underscores the richness of the northern Andes as one of the world's main hotspots of biodiversity. Interestingly, species with smaller ranges gain in importance towards higher elevations in the RBSF (Nöske et al. 2003). About 30% of the species from above 2150 m a.s.l., from the *Purdiaea* forest and the páramo have restricted range sizes (endemic, northern Andean, Andean taxa), twice as many as at lower elevation. This trend is noteworthy as two-third of all species occur below 2150 m a.s.l. The increase in species with smaller ranges towards higher elevation has also been observed in vascular plants and other organisms (Balslev 1988; Kessler 2002) and is explained by the reduced and often fragmented habitat surface area available in mountains as compared with lowlands.

With 55 terrestrial bryophyte species the *Purdiaea* forest is similar to other South Ecuadorian ridge forests in terms of bryophyte diversity (Table 19.2). A 1:2 or 1:3 ratio between mosses and liverworts appears to be characteristic for the terrestrial habitat. Towards the forest canopy species richness decreases and the moss/liverwort ratio shifts dramatically in favor of liverworts (mainly Lejeuneaceae and Frullaniaceae). In the outer

*Purdiaea* crowns the percentage of mosses is reduced to 4%. Similar trends were observed on slopes and ridges of the other study sites.

**Table 19.2.** Bryophytes in the *Purdiaea* forest and nearby slopes: species numbers and ratio of mosses to liverworts growing terrestrially, on stem bases or in the canopy.

	Slopes	Ridges -- <i>Purdiaea</i> forest			
	Terrestrial	Terrestrial	Stem base	Inner canopy	Outer canopy
Species numbers	55	55	51	43	33
Mosses:liverworts	1:3	1:2	1:5	1:11	1:24

Bryophyte communities of RBSF and El Tiro were described in detail by Parolly and Kürschner (e.g. 2004a, b, 2005). A notable floristic feature of the *Purdiaea* forest separating it from the two other study sites is the abundant occurrence of the very rare liverwort *Pleurozia heterophylla* Steph. ex Fulf., worldwide known only from three localities (RBSF, Mt. Roraima in the Guyana Highlands, Honduras; Gradstein et al. 2001). It is a character species of the *Frullanio serratae*--*Holomitrietum sinuosi* subassociation *pleurozietum heterophyllae* (Parolly and Kürschner 2004a). Another rare species is *Pleurozia paradoxa* Jack, having the same general range as *Purdiaea nutans* (Fig. 19.3). Further noteworthy floristic records from the *Purdiaea* forest are the liverwort *Fuscocephaloziaopsis subintegra* Gradst. and Vána (which is new to science) and the rare moss *Macromitrium perreflexum* Steere. The latter is only known from southern Ecuador and occurs in all sites but with greatest abundance in the *Purdiaea* forest and subpáramo vegetation. According to Parolly and Kürschner (2004a), *Macromitrium perreflexum* and *Pleurozia paradoxa* are characteristic species of the high montane epiphytic bryophyte community (*Macromitrio perreflexi*--*Pleuroziaetum paradoxae*) endemic to the RBSF, the Podocarpus National Park and surrounding areas.

## Conclusions

The *Purdiaea nutans* forest in southern Ecuador should be considered an azonal ridge vegetation type. Its dominance on mountain crests and exposed plateaus in the San Francisco valley of southern Ecuador cannot be explained by a single factor but is apparently caused by a unique combination of abiotic features, related to the topography,

geology, pedology and macroclimate. The gap in the cordillera presumably functions as a funnel for trade winds and may have caused the very wet climate of the RBSF. The very broad ridges and plateaus and the poor soils offer a suitable environment for the development of *P. nutans* on the southern slopes of the Río San Francisco valley. From our point of view, historical fire events are the most likely cause for the massive occurrence and dominance of this species.

The pteridophyte and bryophyte compositions of the *Purdiaea* forest underscore the ridge-top characteristics of the forest. However, the species richness and composition of this forest in terms of cryptogams do not differ significantly from those of the two other investigated ridge sites.

## References

- Anderberg AA, Zhang X (2002) Phylogenetic relationships of Cyrillaceae and Clethraceae (Ericales) with special emphasis on the genus *Purdiaea* Planch. *Organisms, Diversity and Evolution* 2: 127-137
- Balslev H (1988) Distribution patterns of Ecuadorian plant species. *Taxon* 37: 567-577
- Bussmann R (2001) Epiphyte diversity in a tropical Andean forest- Reserva Biológica San Francisco, Zamora Chinchipe, Ecuador. *Ecotropica* 7: 43-59
- Bussmann R (2002) Estudio fitosociológico de la vegetación en la reserva Biológica San Francisco (ECSF) Zamora- Chinchipe. *Herbario Loja* 8: 1-106
- Gradstein SR, Bock C, Mandl NA, Noeske NM (accepted) Bryophytes of the Reserva Biológica San Francisco, Ecuador. Part 1. Introduction; Liverworts and Hornworts. In: Liede-Schumann S (ed), Checklist of plants and animals of the Reserva Biológica San Francisco. *Ecotropica Monographs*
- Gradstein SR, Churchill SP, Salazar Allen N (2001) A Guide to the Bryophytes of Tropical America. *Memoirs of the New York Botanical Garden* 86: 1-577
- Homeier J (2005) *Purdiaea nutans* Planch In: Schütt P, Schuck HJ, Lang U and Roloff A (eds) *Enzyklopädie der Holzgewächse* 42 (1-4). Landsberg/Lech: Ecomed
- Kessler M (2002) Environmental patterns and ecological correlates of range size among bromeliad communities of Andean forests in Bolivia. *The Botanical Review* 68: 100-127
- Knörr U (2003) Populationsökologie von *Graffenrieda emarginata* (Melastomataceae) und *Purdiaea nutans* (Cyrillaceae) im Höhengradienten eines südecuadorianischen Bergregenwaldes. Diplomarbeit, University of Essen

- Lehnert M, Kessler M, Salazar LI, Navarrete H, Gradstein SR (in press) Checklist to the Pteridophytes of the Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, Ecuador). In: Liede-Schumann S. (ed), Checklist of plants and animals of the Reserva Biológica San Francisco. Ecotropica Monographs
- Litherland M, Aspen JA, Jemielita RA (1994) The metamorphic belts of Ecuador. Overseas Memoir of the British Geological Survey 11: 1-147
- Nöske NM, Gradstein SR, Kürschner H, Parolly G, Torrachi S (2003) Cryptogams of the Reserva Biológica San Francisco (Province Zamora-Chinchipe, Southern Ecuador). I. Bryophytes. Cryptogamie, Bryologie 24, 15-32
- Parolly G, Kürschner H (2004a) Ecological studies in Ecuadorian bryophyte communities I. Nova Hedwigia 78:1-43
- Parolly G, Kürschner H (2004b) Ecological studies in Ecuadorian bryophyte communities II. Syntaxonomy of the submontane and montane epiphytic vegetation of S Ecuador. Nova Hedwigia 79: 377-424
- Parolly G, Kürschner H (2005) Ecological studies in Ecuadorian bryophyte communities V. Syntaxonomy, life forms and life strategies of the bryophyte vegetation on decaying wood and tree bases in S Ecuador. Nova Hedwigia 81: 1-36
- Paulsch A (2002) Development and application of a classification system for undisturbed and disturbed tropical montane forests based on vegetation structure. Dissertation, University of Bayreuth
- Silver WL, Scatena FN, Johnson AH, Siccima TG, Sanchez MJ (1994) Nutrient availability in a montane wet tropical forest: Spatial patterns and methodological considerations. Plant and Soil 164: 129-145
- Stáhl B (2004) Cyrillaceae. In: Smith N, Mori SA, Henderson A, Stevenson DW, Heald SV (eds) Flowering plants of the Neotropics. Princeton Univ. Press, U.S.A
- Tryon RM, Tryon AF (1982) Ferns and allied plants, with special reference to tropical America. Springer, New York
- Weigend M (2002) Observations on the Biogeography of the Amotape-Huancabamba Zone in Northern Peru. The Botanical Review 68: 38-54

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### **III. Chapter**

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## **Effects of Environmental Heterogeneity on Floristic Diversity and Composition of Terrestrial Bryophyte and Macrolichen Assemblages in Southern Ecuador**

N. Mandl, M. Kessler, S. R. Gradstein



## ABSTRACT

Here we present the first study in the tropics dealing in detail with the ecology of terrestrial bryophyte and macrolichen assemblages. For our investigation we chose three different upper montane ridge and slope forests in southern Ecuador. In plots of 400m<sup>2</sup> we investigated (1) terrestrial bryophyte and macrolichen diversity and composition (2) forest structure and (3) microclimatic conditions. We used Detrended correspondence analysis to group relevés by study location, habitat types and canopy closure levels. Species indicator values were calculated and compared for different habitats.

In total 140 species were recorded, the majority being liverworts followed by mosses and lichens. Mosses tended to be more prominent on open ridges than on slopes under a dense canopy. Detrended correspondence analysis clearly separated between slope and ridge relevés and within the ridge habitat between sunny and shaded microhabitats. Life-forms of bryophytes also showed different distribution patterns in slope and in ridge habitats.

Habitat differentiation between ridges and slopes and small scale variation in light and moisture regimes had greater influence on species diversity and composition than geographical distance between study localities.

Keywords: Bryophyte life-forms; indicator species; ridge forest; slope forest; montane tropical forest

STUDIES ON BRYOPHYTES AND LICHENS IN TROPICAL RAIN FORESTS usually deal with epiphytic species and assemblages on tree trunks or in the canopy (*e.g.*, Cornelissen & Ter Steege 1989; Frahm 1987, Gradstein *et al.* 2001a, Holz & Gradstein 2005a, b, Parolly & Kürschner 2004, Wolf 1994, 1995). In contrast, little attention has been paid so far to bryophyte and macrolichen assemblages of the forest floor. Most studies on the ecology of terrestrial bryophytes and lichens are from temperate regions (*e.g.*, During & Verschuren 1988, Mäkipää & Heikkinen 2003, Pfeiffer 2003, Gabriel & Bates 2005, Nelson & Halpern 2005). The very few studies from the Tropics dealing with terrestrial species (Holz *et al.* 2002, Benavides *et al.* 2006) treat them together with the epiphytic taxa and do not discuss them independently. One reason for this is that the terrestrial habitat of lowland rain forests is not particularly suitable for bryophytes and macrolichens. The low light levels and a permanent layer of fallen leaves impede the establishment and growth of these organisms (Pócs 1982, Richards 1984). Lowland rainforests therefore lack a well-developed terrestrial layer of bryophytes and lichens. This situation changes drastically towards higher elevations; the striking increase in the abundance of both epiphytic and terrestrial bryophytes and lichens with increasing elevation in the tropics has been described by numerous authors (*e.g.*, Richards 1984, Gradstein & Pócs 1989, Sipman & Harris 1989, Aptroot 1997). The conspicuous terrestrial bryophyte layer in montane regions correlate with the presence of humus-rich soils that develop at these elevations due to the lower temperature and the plentiful availability of water (van Reenen & Gradstein 1983, Richards 1984, van Reenen 1987), the more irregular canopy layer on steep mountain slopes, and the very complex microtopography so that the leaf litter is spatially unevenly distributed on the forest floor.

Numerous studies have shown that tropical forests are characterized by marked small- and meso-scale variations in plant assemblages as a result of topographical and soil differences (*e.g.*, Tuomisto 2003, Jones 2006). However, most of these studies were conducted in lowland rain forests whereas mountain forests have received little attention in this regard. Unlike lowland forests, mountain forests typically show a conspicuous differentiation of zonal slope and azonal ridge forests. In slope forests, tree density and canopy closure are relatively high, the forest floor is strongly shaded, and terrestrial species experience extended humid periods. Most of these species have evolved a relatively narrow spectrum in physiological tolerances to drought, insolation, and temperature extremes that limit their growth to geographically restricted areas or specific habitats (Proctor 2000). In contrast, ridge forests often show a more open and stunted

structure (Grubb 1977, Tanner *et al.* 1998, Mandl *et al.* in press), resulting in a mosaic of terrestrial microhabitats differing in light and temperature regimes. Accordingly, bryophyte and lichen species growing on ridges are likely to be more drought resistant than those on slopes. Longton (1982) proposed that bryophytes are fairly independent of the macroclimatic conditions of a region, because they are able to exploit microclimatic niches. Consequently one might expect terrestrial bryophyte and macrolichen assemblages to reflect the variety of available microhabitats of regional ridge and slope forests.

This paper focuses on the terrestrial bryophyte and macrolichen assemblages of upper montane ridge and slope forests of southern Ecuador. In the Reserva Biológica San Francisco (RBSF), one of our principal study areas, upper montane forests on ridges and upper slopes are dominated by a single treelet, *Purdiaea nutans* (Clethraceae) (Parolly & Kürschner 2004, Homeier 2005, Mandl *et al.* in press). The monodominant *Purdiaea* forest of the RBSF is unique and not known to occur elsewhere (Mandl *et al.* in press). At all other known localities of *P. nutans*, this species occurs as a few individuals only (Foster *et al.* 2001, 2002, Gradstein *et al.* unpublished data). High precipitation, very poor soils, and presence of broad ridges and plateaus at elevations between 2150 m and 2600 m at the RBSF apparently create extensive areas suitable for the growth of *Purdiaea nutans*.

The purpose of this study was: (1) to analyze the diversity, composition and habitat requirements of terrestrial bryophytes and macrolichen assemblages on ridges and slopes in the upper montane belt of southern Ecuador; and (2) to investigate whether the dominance of the treelet *Purdiaea nutans* at the RBSF is reflected by the terrestrial bryophyte and macrolichen flora.

This is the first study in the tropics dealing in detail with the ecology of these organisms. We emphasize the high alpha and beta diversity of terrestrial bryophytes and their distribution in different microhabitat types in the tropical Andes of southern Ecuador.

## METHODS

**STUDY AREA.**—We studied primary upper montane forests on ridges and slopes at 2400 – 2650 m in three different localities in southeastern Ecuador: Reserva Biológica San Francisco (RBSF), mountain pass El Tiro, and Cerro Tapichalaca Reserve (Fig. 1).

**RBSF** is situated on the southern slope of the San Francisco river valley north of the Cordillera El Consuelo. Ranging between 1800 m and 3140 m, RBSF preserves 1000

ha of humid evergreen mountain rainforest and páramo vegetation (Beck & Müller-Hohenstein 2001). On ridges at 2150-2650 m the shrubby upper montane forest is dominated by *Purdiaea nutans* (Table 1).

**Mountain pass El Tiro** is situated at approx. 2800 m along the Loja-Zamora road, 15 km W of the RBSF and on the border of Loja and Zamora-Chinchipe provinces, on the crest of the cordillera. The mountain slopes at El Tiro pass have a very rugged profile with many small ravines overgrown by low-statured, shrubby cloud forest with a wind-sheared canopy. *Purdiaea nutans* occurs scattered and is nowhere dominant.

**Cerro Tapichalaca Reserve** is situated at approx. 2000-3400 m along the Loja-Zumba road in the Cordillera Real, ca. 90 km south of the town of Loja and just south of Podocarpus National Park. The area supports very wet montane cloud forest and páramo (Simpson 2004). *Purdiaea nutans* has not been recorded in the area.

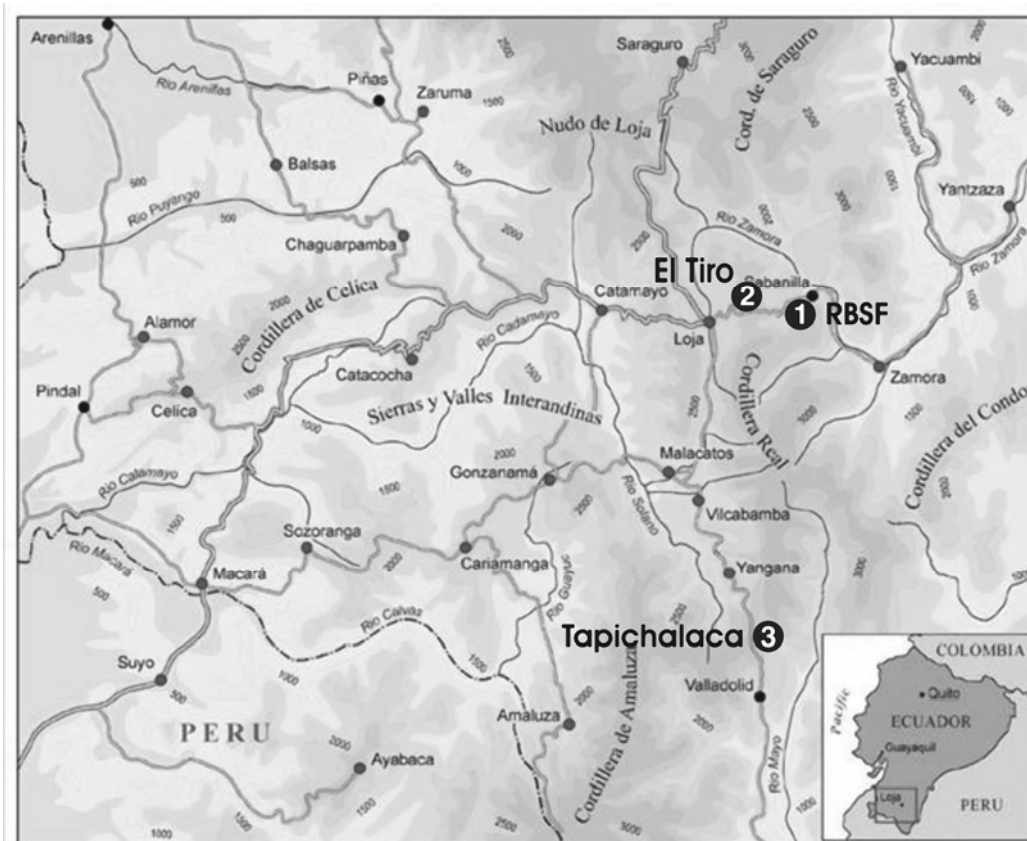


FIGURE 1. Topographic map of the study area in southern Ecuador with indication of the three study localities, RBSF, El Tiro and Tapichalaca.

The climate at all three localities is cool and perhumid with precipitation ranging from ca. 3000 mm annually at El Tiro to ca. 4000 mm at Tapichalaca and over 5000 mm at RBSF (Richter 2003). Temperature maxima occasionally rise up to 25°C and air humidity drops down to 25 percent at all three locations in the period mid October – mid December, when monsoon-induced north-western air streams interrupt the semi-permanent easterly air flow. Soils at all three study sites are poor, acidic (pH 4.6 - 4.1) cambisols and gleysols (Gradstein *et al.* unpublished data).

	Number of plots	Elevation	Inclination	Canopy height	Canopy closure (S.D.)	<i>Purdiaea nutans</i> abundance
RBSF						
Ridge forest	6	2450-2660m	0-25%	4-12m	54% (6)	(40-)80-100%
Slope forest	4	2500-2545m	30-45%	8-20m	88% (2)	(5-)20-40(-60)%
El Tiro						
Ridge forest	3	2550-2600m	0-15%	2-10m	41% (13)	< 5%
Slope forest	6	2430-2575m	30-50%	5-12m	89% (1)	< 5%
Tapichalaca						
Ridge forest	3	2550-2630m	0-25%	3-10m	74% (15)	-
Slope forest	6	2520-2600m	30-50%	10-20m	88% (1)	-

TABLE 1. Comparison of plot parameters at the three study locations.

SAMPLING METHODS.—In each study site, terrestrial bryophyte assemblages were investigated in plots of 400 m<sup>2</sup> (Table 1). Extremely steep or disturbed forest parts (*e.g.*, former landslides) and areas with a high cover of decomposing wood were avoided. Ten plots (six on ridges, four on slopes) were sampled at RBSF, and nine (three on ridges, six on slopes) each at Tapichalaca and El Tiro. Ridges (including ridge plateaus) and slopes were distinguished by their topographical position and by their average inclination, with ridges ranging from 0-25% and slopes from 30-50 % (Table 1). Within each plot, terrestrial bryophytes and macrolichens were sampled in four relevés of 20 x 30 cm, each by completely removing the organism layer and drying it for later analysis. Voucher specimens of all species were deposited in the herbarium LOJA with duplicates in GOET (bryophytes) and B (lichens). As the distribution of the terrestrial bryophytes and macrolichens was highly patchy, relevés were chosen to represent the visually observed

variation in terrestrial microhabitats due to differences in canopy cover and microtopography.

Additional parameters analyzed within each plot were average canopy height, canopy closure and abundance of *Purdiaea*. Canopy closure, as the percentage of the area shaded by vegetation cover of all plants forming the canopy, was measured with a spherical densiometer on four randomly chosen spots within each plot. On each spot four estimates were taken, one in each cardinal direction. These values were averaged to estimate percent canopy closure on the plot. *Purdiaea* abundance was estimated by counting stems above 10 cm diameter.

On ridges, we visually distinguished between three microhabitats according to the degree of shading of the forest layer. Areas with ca. 0-25 percent canopy closure were referred to as sunny, those with canopy closure ranging from ca. 25-75 percent as intermediate, and those with ca. 75-100 percent as shaded.

Cover of each species per relevé was estimated in percentages using the slightly modified Braun-Blanquet scale (Braun-Blanquet 1964):

+	<1 %	3	25.1 - 50.0 %
1	1.1 -6.0 %	4	50.1 - 75.0 %
2a	6.1 – 12.5 %	5	75.1 - 100.0 %
2b	12.6 – 25.0 %		

Nomenclature follows Kürschner & Parolly (in press) for mosses, León *et al.* (2006) for liverworts, and Nöske *et al.* (in press) for lichens.

At all three sites, air temperature and air humidity were measured in two plots in ridge and slope forest during 12 months (Nov. 2004 – Nov. 2005), using HOBO data-loggers. Measurements were carried out at stem bases, ca. 1 m above the ground. Parameters analyzed in each plot were average canopy height, canopy closure (measured with spherical densiometer on four randomly chosen spots within each plot – four estimates were taken, one in each direction. These estimates were averaged to estimate percent canopy closure on the plot) and *Purdiaea* abundance was estimated by counting stems above 10 cm diameter

STATISTICAL ANALYSES.—Because the number of study plots differed between sites and habitats, total species numbers for these categories were not comparable. Therefore, we used rarefaction, carried out with EstimateS (Colwell 1994-2004) to adjust for the

differences in sampling intensity (Tab. 2). The other statistical analyses were performed with the program package PC-ORD for Windows- Version 4.17 (McCune & Mefford 1999). Community relationships and correlation with their canopy closure were analyzed with *Detrended correspondence analysis* (DCA, Hill & Gauch 1980), employing non-linear rescaling (26 segments). Habitat variables were superimposed on the resulting ordinations using a joint plot, based on correlations of variables with the axes of the community ordination. In a second run of DCA, only relevés from the ridge habitat were included. Habitat variables superimposed on this new ordination contained information about different microhabitats.

Species indicator values for different habitats and exposure levels were calculated using Dufrene & Legendre's (1997) method, which combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group. Indicator Values (IV) were tested for statistical significance using a Monte Carlo technique with 1000 replicates. Indicator values range from zero (no indication) to 100 (perfect indication). Perfect indication means that presence of a species points to a particular group without error, at least with the data set in hand.

## RESULTS

**ABIOTIC CHARACTERISTICS OF STUDY LOCALITIES.**—At all three localities, forest canopies on ridges were ca. 2-12 m high and were generally higher in the RBSF than at El Tiro and Tapichalaca (Table 1). On slopes, forest canopies were highest at Tapichalaca, lowest at El Tiro, and intermediate at RBSF. Canopy height at RBSF increased by about 30 percent on the slopes, but in the other two localities the increase was about 80-90 percent on the slopes compared to the ridges. Canopy closure on ridges varied between 41 percent and 74 percent and was higher at RBSF than at El Tiro, but conspicuously lower than at Tapichalaca (Table 1). On slopes, canopy closure was much higher than on ridges and uniformly ca. 88 percent in all study sites.

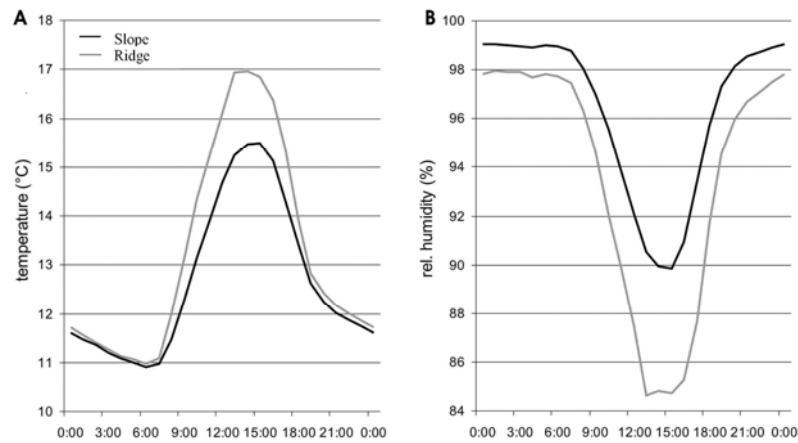


FIGURE 2. Daily course of relative humidity and air temperature at stem bases in ridge and slope forests in investigated plots at the RBSF (means of one year measurement period).

The daily courses of air humidity and temperature, measured the stem bases of trees inside the forest stand, fluctuated much more strongly in ridge forests with a rather open canopy than in slope forests with a dense canopy (data shown for RBSF, Fig. 2).

**SPECIES DIVERSITY AND COMPOSITION.**—We recorded a total of 140 species in 112 relevés, including 7 lichens, 87 liverworts, and 46 mosses (Table 2). Eighty one species were found at RBSF, 72 at Tapichalaca, and 97 at El Tiro (Table 2). Liverworts were the dominant group in all localities and both habitats, counting for about two-thirds of the species. The most species-rich liverwort family was Lepidoziaceae with 31 species, 20 of them belonging to the genus *Bazzania*. Other species-rich liverwort families were Lejeuneaceae (nine spp.) and Geocalyceae (nine spp.). Among mosses, Dicranaceae was the only family of relevance in the terrestrial habitat, with nine species growing on ridges and four of them sporadically on slopes. Mosses were more prominent in the open ridge habitat where their total coverage reached to over 50 percent in single relevés. On slopes, mosses were generally scarce, growing scattered among liverworts. At Tapichalaca and El Tiro terrestrial bryophyte species were more numerous on slopes than on ridges, whereas at RBSF both habitats were more or less equally rich in bryophyte species. Lichens were generally restricted to ridges.

Species density was highly variable with an overall mean of  $11.2 \pm 3.5$  (S.D.) species per relevé (8.3 liverworts, 2.6 mosses, 0.4 lichens; Table 2). Average species density in ridge relevés was 9.6 species, ranging from 6.5 in sunny places (canopy closure < 25%) to 12.3 in shaded places (canopy closure > 75%). Species density was more



homogeneous in slope relevés, averaging 12.4 species. Comparing only sunny and shaded ridge places (34 relevés) species density was significantly higher under a dense canopy (t-test,  $p < 0.0001$ ).

Species composition at the three localities differed considerably. About 36 percent of all species occurred both in ridge and in slope habitats, the remaining species grew exclusively on ridges (26%) or on slopes (38%). In total, only 27 terrestrial bryophyte species were found on the slopes and 18 on the ridges at all three localities. Only 13 species were found in all localities (sites) and habitats. Beta diversity was highest in lichens, followed by mosses and liverworts (Table 2). According to the DCA, species assemblages from the *Purdiaea nutans* forest at the RBSF did not differ from the other two sites and appear more or less clumped together with them (Fig. 3, A). DCA, however, clearly separated between slope and ridge relevés, with those of slope forming a homogenous group and those of ridges a very loose, heterogeneous one (Fig. 3, B). Among ridge relevés, DCA separated the sunny microhabitats (canopy closure  $< 25\%$ ) from those with a denser canopy (Fig. 3, C).

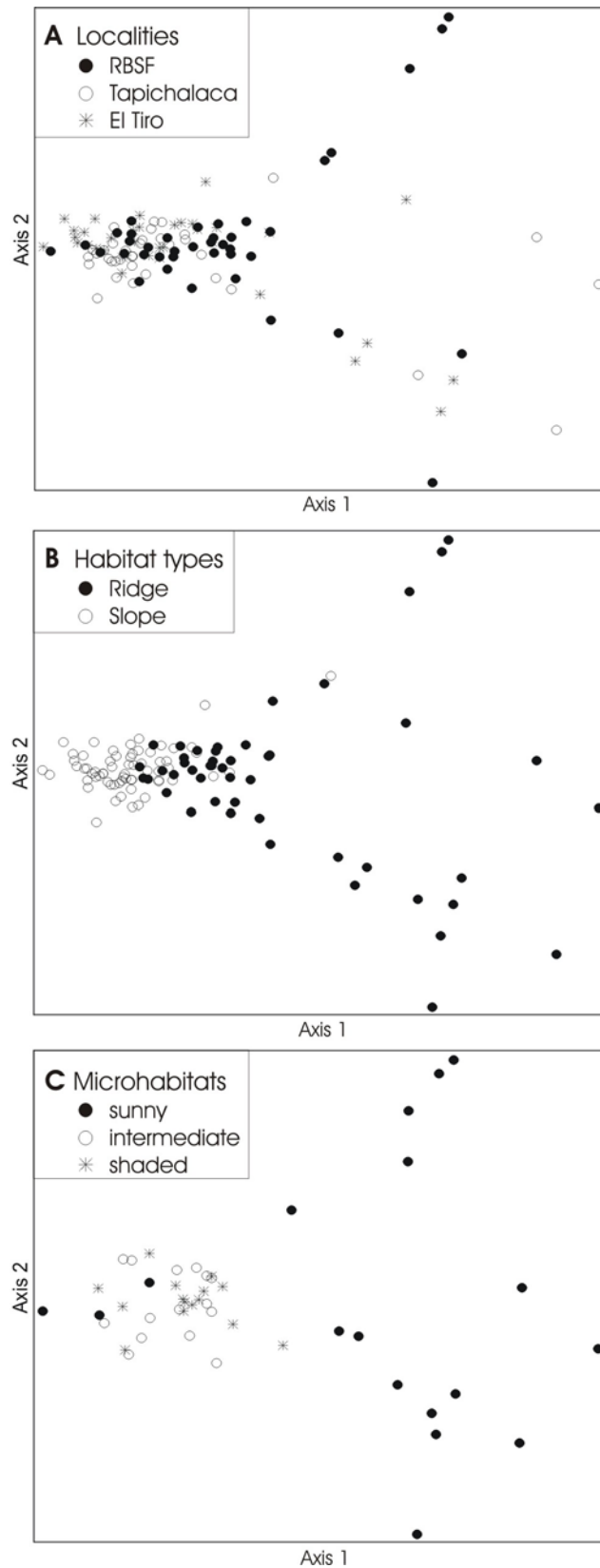


FIGURE 3. DCA ordination diagrams of species composition and abundance. **A** according to study localities, **B** according to habitat types (ridge and slope relevés), and **C** according to microhabitats on ridges.

Species group	Alpha diversity (S.D.)			Beta diversity			Gamma diversity		
	ridges	slopes	total	ridges	slopes	total	ridges	slopes	total
<b>Overall</b>	9.6 (3.8)	12.3 (3.5)	11.2 (3.9)	9.9	7.8	12.5	95	96	140
Bryophytes	9.2 (4.0)	12.3 (3.5)	11.0 (4.0)	9.6	7.8	12.1	88	96	133
Liverworts	6.9 (4.0)	9.5 (3.1)	8.3 (3.8)	8.6	7.0	10.4	59	66	87
Mosses	2.4 (1.0)	2.8 (1.1)	2.6 (1.1)	12.3	10.8	17.7	29	30	46
Lichens	0.4 (0.7)	-	0.2 (0.4)	17.7	-	35.0	7	-	7
<b>RBSF</b>	9.5 (3.7)	11.6 (2.8)	10.3 (3.5)	5.5	4.2	7.5	52	49	78
Bryophytes	9.1 (4.1)	11.6 (2.8)	10.1 (3.8)	5.4	4.2	7.4	49	49	75
Liverworts	6.8 (4.1)	9.2 (2.5)	7.8 (3.7)	4.9	3.9	6.5	33	36	51
Mosses	2.3 (1.0)	2.3 (0.9)	2.3 (1.0)	7.1	5.6	10.4	16	13	24
Lichens	0.4 (0.6)	-	0.2 (0.3)	8.0	-	15.0	3	-	3
<b>El Tiro</b>	10.9 (3.7)	12.0 (3.2)	11.7 (3.4)	4.9	5.6	8.3	54	67	97
Bryophytes	10.3 (3.2)	12.0 (3.2)	11.5 (3.3)	4.7	5.6	8.0	49	67	92
Liverworts	7.8 (3.7)	9.3 (3.1)	8.8 (3.3)	4.6	5.1	7.2	36	47	63
Mosses	2.5 (0.9)	2.8 (1.1)	2.7 (1.1)	5.2	7.1	10.8	13	19	29
Lichens	0.6 (0.9)	-	0.2 (0.4)	8.6	-	25	5	-	5
<b>Tapichalaca</b>	8.6 (3.9)	13.0 (4.0)	11.7 (4.6)	5.1	3.9	6.2	44	51	72
Bryophytes	8.3 (4.2)	13.0 (4.0)	11.6 (4.7)	5.0	3.9	6.0	42	51	70
Liverworts	6.0 (4.4)	9.8 (3.6)	8.7 (4.2)	4.8	3.7	5.4	29	36	47
Mosses	2.3 (1.1)	3.3 (1.3)	2.8 (1.2)	5.6	4.5	8.1	13	15	23
Lichens	0.3 (0.5)	-	0.1 (0.3)	8.0	-	20.0	2	-	2

TABLE 2. *Terrestrial species diversity broken down by groups of sample units. Alpha diversity refers to the average species richness per relevé; Beta diversity was measured as the total number of species per site divided by the average number of species per relevé; Gamma diversity comprises total species richness per group adjusted for the different plot numbers investigated at the study sites.*

DISTRIBUTION OF LIFE-FORMS AND INDICATOR SPECIES.—Life-forms of bryophytes showed different distribution patterns in slope and in ridge habitats (Fig. 4). Slopes were dominated by mat forming species (42%), followed by weft forming species (18%) and species forming tall turfs (14%). On ridges, the frequency of mats decreased to 31 percent whereas tall turfs clearly gained in importance (33%). The importance of the latter was particularly striking in the sunny microhabitat of ridges where almost half of the bryophyte species formed tall turfs (44%). Dendroid life-forms as well as fans, short turfs, and threads were rare in both habitats (Fig. 4).

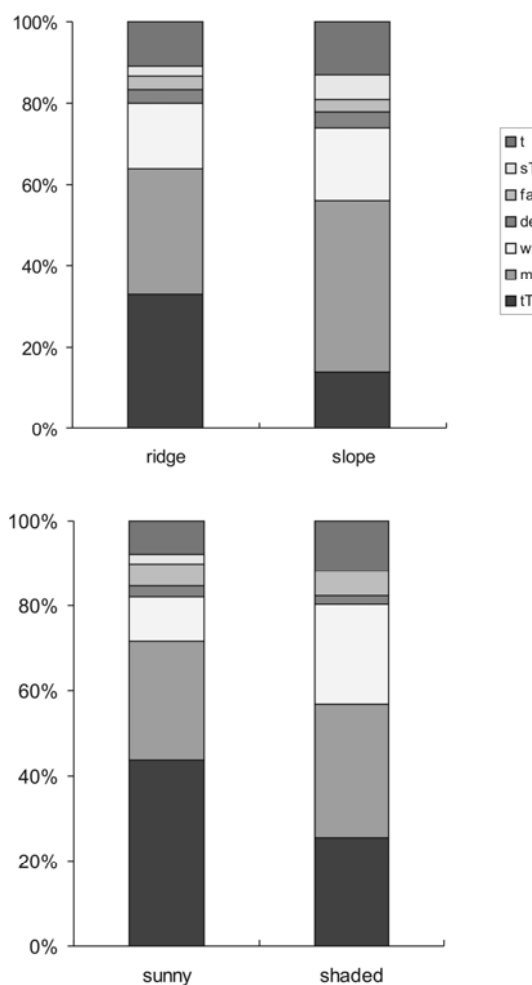


FIGURE 4. Percentages of species number of different bryophyte life-forms on ridges and slopes and in sunny and shaded ridge microhabitats. Abbreviations for life-forms: *tT* tall turfs, *m* mats, *w* wefts, *de* dendroids, *fa* fans, *st* short turfs, *t* threads.

Twenty species of the slope habitat were resolved as indicator species, 15 of them with high significance. Percentage of indication on slopes ranged from 9.4 to 49.7 percent (Table 3). The ridge habitat only had nine indicator species, five of them being highly significantly supported. Indicator values on ridges ranged from 8.3 to 38.6 percent. Because of the heterogeneity of the terrestrial ridge habitat, relevés from sunny and shaded microhabitats on ridges were separated in a further step of the analysis. Three species were resolved as indicators of the sunny microhabitat (*Atractylocarpus longisetus*, *Breutelia polygastrica*, *Jamesoniella rubicaulis*) and 11 of the shaded one. The indicator species of the shaded microhabitat are composed of two ridge indicators (*Lepidozia incurvata*, *Scapania portoricensis*), four slope indicators (*Cephalozia crassifolia*, *Leucobryum giganteum*, *Mnioloma cyclostipa*, *Odontoschisma denudata*), and five common species that were not resolved as indicator species before the division into microhabitats (*Arachniopsis diacantha*, *Calypogeia peruviana*, *Kurzia capillaris*, *Lophocolea trapezoidea*, *Riccardia fucoidea*).

Ridge indicator species	Life-form	Indicator value IV	Slope indicator species	Life-form	Indicator value IV
<i>Campylopus huallagensis</i>	tT	38.6 **	<b>Cephalozia crassifolia</b>	t	49.7 **
<i>Scapania portoricensis</i>	tT	35.1 **	<b>Odontoschisma denudata</b>	m	43.7 **
<i>Lepidozia incurvata</i>	w	30.0 *	<b>Mnioloma cyclostipa</b>	m	43.2 **
<u>Jamesoniella rubicaulis</u>	tT	21.6 **	<b>Leucobryum giganteum</b>	tT	42.3 **
<u>Atractylocarpus longisetus</u>	tT	14.6 **	Bazzania hookeri	w	40.1 **
<u>Breutelia polygastrica</u>	tT	14.6 **	Symphyogyna brasiliensis	m	34.2 **
Sematophyllum cf. subsimplex	m	10.4 *	Telaranea nematodes	t	32.1 **
Frullania brasiliensis	m	8.3 *	Plagiochila aerea	w	28.8 **
Syzygiella anomala	tT	8.3 *	Hypnella pilifera	m	26.0 *
<hr/>			Trichocolea tomentosa	w	25.1 **
Sunny microhabitat			Leptoscyphus spectabilis	m	25.0 **
<hr/>			Rhizogonium novae-hollandiae	m	23.3 **
<u>Jamesoniella rubicaulis</u>	tT	47.1 **	Lophocolea martiana	m	20.3 **
<u>Atractylocarpus longisetus</u>	tT	32.6 *	Bazzania diversicuspis	w	18.8 *
<u>Breutelia polygastrica</u>	tT	29.4 *	Syrrhopodon sp.	sT	15.6 **
<hr/>			Lophocolea sp. A	m	14.1 **
Shaded microhabitat			Lepidozia caespitosa	w	14.1 **
<hr/>			Symphyogyna brogniartii	m	12.7 *
<b>Cephalozia crassifolia</b>	t	77.4 **	Zoopsidella cf. caledonica	t	10.9 *
<i>Calypogeia peruviana</i>	m	67.1 **	Phyllogonium fulgens	m	9.4 *
<i>Lepidozia incurvata</i>	w	63.9 **			
<i>Riccardia fucoidea</i>	de	61.0 **			
<b>Mnioloma cyclostipa</b>	m	58.0 **			
<b>Odontoschisma denudata</b>	m	54.2 *			
<i>Scapania portoricensis</i>	tT	50.4 *			
<i>Arachniopsis diacantha</i>	t	48.3 **			
<i>Kurzia capillaris</i>	w	46.4 *			
<b>Leucobryum giganteum</b>	tT	28.6 *			
<i>Lophocolea trapezoidea</i>	m	28.6 *			

TABLE 3. Life-forms and indicator values (IV) in percent of perfect indication for selected ridge and slope species. On the left in separate boxes IV for different ridge microhabitats. Indicator species of the sunny ridge-microhabitat also resolved for the entire ridge habitat are underlined, those of the shaded microhabitat also resolved for the entire ridge habitat are in italics, and those also resolved for the slope habitat are in **bold**.

## DISCUSSION

GENERAL PATTERNS.—Our analysis of the terrestrial bryophyte and macrolichen layer of upper montane forests in southern Ecuador yielded 140 species, the great majority of these being bryophytes (133 species). El Tiro was the richest locality with 97 species, fewer species were found in the RBSF (75) and Tapichalaca (72). The only comparable study from the Neotropics was that of Holz *et al.* (2002), dealing with both epiphytic and terrestrial bryophytes. In this study 70 terrestrial bryophyte species were recorded in six hectares of 30-40 m tall upper montane oak forest of Costa Rica. In spite of the very different structure of the Costa Rican oak forest and forests of the study region, species richness of terrestrial bryophytes and macrolichens in these two montane forests areas is very similar.

In our study, liverworts play by far the most important role in the species composition of the terrestrial bryophytic layer at all localities, accounting for about two thirds of the species. In comparison, mosses clearly dominate over liverworts on forest floors of temperate rainforests in, *e.g.*, New Zealand (Pfeiffer 2003), Finland (Mäkipää & Heikkinen 2003), and Washington/USA (Nelson & Halpern 2005). In the Costa Rican oak forest, Holz *et al.* (2002) recorded equal rates for terrestrial liverworts and mosses, with liverworts gaining in importance in the epiphytic habitat. Dominance of liverworts in the epiphytic layer seems to be typical for Neotropical moist forests (Richards 1984, Cornelissen & Ter Steege 1989, Gradstein *et al.* 2001a). Lichens, on the other hand, occur scattered only except at open sites where they may become locally dominant.

RIDGES AND SLOPES.—Contrary to our expectations, diversity and composition of the terrestrial bryophyte and macrolichen assemblages of the monodominant *Purdiaea* forest did not differ significantly from those at the other two localities where *Purdiaea nutans* was either lacking (Tapichalaca) or very scarce (El Tiro). Apparently, tree species composition on ridges in the study area did not play a major role in determining the species composition of the terrestrial bryophyte and macrolichen layer. Furthermore, our DCA analyses revealed that the composition of terrestrial bryophyte and macrolichen assemblages was more strongly determined by habitat conditions (ridges versus slopes) than by the geographical distance between the sites.

The slope forest floor habitat was more or less equally shaded and moist at all three localities (Tab. 1, Fig. 2). Ridges, in contrast, were characterized by up to 50 % lower and spatially more variable canopy closure, and by higher fluctuations in the daily course of temperature and air humidity. Our microclimatic measurements were taken at stem bases and thus only reflected conditions in the shaded microhabitat under a dense canopy. Microclimatic conditions in the sunny microhabitat were not measured, but in lowland rain forests tree-fall gaps are known to have significantly higher photon flux density and significantly lower air humidity than adjacent closed forests (*e.g.*, Barik *et al.* 1992, Brokaw & Busing 2000). Accordingly, fluctuations in the daily courses of temperature and air humidity in the sunny ridge microhabitats can be assumed to be even more dramatic than indicated by our measurements.

Species composition and abundance differed clearly between ridge and slope habitats (Fig. 3, B). This suggests that abiotic habitat conditions have greater impact on the bryophyte and macrolichen vegetation than composition of the surrounding tree vegetation, even though former observations point out that throughfall and associated nutrient supply influence the composition of bryophytes assemblages (During & Verschuren 1988). Separating the ridge habitat into microhabitats characterized by different light or canopy closure levels confirms this observation. Small-scale differences in habitat properties, especially microclimatic conditions, appear to have great influence on the composition of terrestrial bryophyte and macrolichen assemblages. Ridge sites which were as shaded and moist as typical slope forest floors were inhabited by the same assemblages as those found on the slopes. In contrast, completely different assemblages of bryophyte and macrolichens were found in open ridge sites (Fig. 3, C) which were less shaded by the tree canopy and, consequently, received more direct sunlight. In these open sites, fewer species co-occur and different species (frequently mosses or lichens) may dominate the bryophyte and macrolichen layer at different sites.

The strong correlation of life-forms of bryophytes with moisture and light condition has been repeatedly demonstrated (Bates 1998, Proctor 1990). Not surprisingly, the distribution of life-forms varied between ridges and slopes in the study area. These differences reflect the permanently humid conditions under the dense slope canopies and the more variable moisture conditions on ridges. On slopes, bryophyte assemblages consisted of dense, thin, interwoven mat and weft-forming species as described for



lignicolous montane communities elsewhere (Pócs 1982). On ridges, however, especially in the open ridge microhabitats, tall turfs played the most important role. According to Mägdefrau (1982), tall turfs are able not only to hold water by capillary action but also to conduct it, making them well adapted to the variable moisture conditions typical for ridges. An investigation of Colombian understory bryophytes also found life-forms of moss species to be significantly associated with particular landscape units (Benavides *et al.* 2006).

Species frequently occurring in a particular habitat can be regarded as indicator species and may provide insight into the state of an ecosystem (Hietz 1999; Gradstein *et al.* 2001b). Their distribution generally reflects microclimatic and substrate conditions (*e.g.*, pH). In this study, more species were resolved as indicators on slopes than on ridges. Moreover, slope indicators were more highly supported statistically than ridge indicators. This may be explained by the more homogenous slope habitat and the patchiness of the ridge habitat. Indeed, statistical support of the indicator values increased after subdivision of ridges into microhabitats. Shaded ridge microhabitats shared four indicator species (*Cephalozia crassifolia*, *Leucobryum giganteum*, *Mnioloma cyclostipa* and *Odontoschisma denudata*) with slopes and two indicator species (*Lepidozia incurvata*, *Scapania portoricensis*) with ridges before the division into microhabitats. Hence, shaded ridge microhabitats form a transition zone between slopes and sunny ridges. The sunny ridge microhabitat, characterized by lesser canopy closure and spatially and temporally less even microclimatic conditions has only three indicator species (*Atractylocarpus longisetus*, *Breutelia polygastrica*, and *Jamesoniella rubicaulis*). All of them form tall turfs and were also resolved as indicator species of the undivided ridge habitat. The sunny ridge microhabitat also shared several bryophytes with the treeless páramo vegetation of higher elevation, for example the indicator species *Breutelia polygastrica* (Gradstein *et al.* 2001b). Thus it appears that ridges of the area share floristic and ecological features with adjoining slopes and with the páramo of higher elevation.

## CONCLUSIONS

Habitat differentiation between ridges and slopes had the strongest impact on species richness and assemblage composition of terrestrial bryophyte and macrolichens in montane forests of southern Ecuador. Further, on ridges the small-scale habitat heterogeneity

determined by variations in canopy density had a marked influence. In contrast, our study did not reveal significant differences of the studied plant assemblages between the three geographically distant study localities, nor between the monodominant *Purdiaea nutans* forest at the RBSF compared to other ridge forest types.

Comparable small-scale habitat and plant community differentiation has previously been documented for tropical lowland forests (*e.g.*, Tuomisto *et al.* 2003) but this is the first study demonstrating the importance of habitat heterogeneity in determining the distribution and diversity of terrestrial bryophyte and macrolichen assemblages in tropical montane areas. It has been suggested that differentiation of plant assemblages decreases towards more extreme environmental conditions because species have less opportunity to fine-tune their ecological specialization (Stevens 1989, 1992). Nevertheless, our results suggest that at least in terrestrial bryophyte and macrolichen assemblages, habitat heterogeneity has a pronounced effect also at higher elevations.

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**LITERATURE CITED**

- APTROOT, A. 1997. Lichen biodiversity in Papua new Guinea, with report of 173 species on one tree. *Bibl. Lichenol.* 68: 203-213.
- BAKIK, S.K., H.N. PANDEY, R.S. TRIPATHI, AND P. RAO. 1992. Microenvironmental variability and species diversity in treefall gaps in a sub-tropical broadleaved forest. *Vegetatio* 103: 31-40.
- BATES, J.W. 1998. Is "lifeform" a useful concept in bryophyte ecology? *Oikos* 82: 223-237.
- BECK, E., AND K. MÜLLER-HOHENSTEIN. 2001. Analysis of undisturbed tropical mountain forest ecosystems in Southern Ecuador. *Die Erde* 132: 1-8.
- BENAVIDES, J.C., A.J. DUQUE M., J.F. DUIVENVOORDEN, AND A.M. CLEEF. 2006. Species richness and distribution of understory bryophytes in different forest types in Colombia Amazonia. *J. Bryol.* 28: 182-189.
- BRAUN-BLANQUET, J. 1964. *Pflanzensoziologie: Grundzüge der Vegetationskunde*. pp. 865. Springer, Vienna.
- BROKAW, N., AND R.T. BUSING. 2000. Niche versus chance and tree diversity in forest gaps. *TREE* 15: 183-188.
- COLWELL, R.K. 1994-2004. EstimateS: Statistical estimating species richness and shared species from samples. Version 7. Persistent URL <[purl.oclc.org/estimates](http://purl.oclc.org/estimates)>.
- CORNELISSEN, J.H.C., AND H. TER STEEGE. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *J. Trop. Ecol.* 5: 131-150.
- DUFRENE M., AND P. LEGENDRE. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67: 345-366.
- DURING, H.J., AND G.A.C.M. VERSCHUREN. 1988. Influence of the tree canopy on terrestrial bryophyte communities: microclimate and chemistry of throughfall. *In* J. J. Barkman, and K.V. Sýkora (Eds.) *Depending plant communities*, pp. 99-110. SPB Academic Publishing, The Hague.
- FOSTER, R., H. BELTRÁN, AND W.S. ALVERSON. 2001. Flora and Vegetation. *In* W.S. Alverson, L.O. Rodríguez, and D.K. Moskovits (Eds.) *Rapid biological inventories 2*, pp. 124-137. Chicago: Field Museum.
- FOSTER, R., N. PITMAN, AND R. AGUINDA. 2002. Flora and Vegetation. *In* N. Pitman, D.K. Moskovits, W.S. Alverson, and R. Borman (Eds.) *Rapid biological inventories 3*, pp. 122-135. Chicago: Field Museum.

- FRAHM, J.-P. 1987. Ökologische Studien über die epiphytische Moosvegetation in Regenwäldern NO-Perus. *Beih. Nova Hedwigia*. 88: 143-158.
- GABRIEL, R., AND J.W. BATES. 2005. Bryophyte community composition and habitat specificity in the natural forests of Terceira, Azores. *Plant Ecology* 177: 125-144.
- GRADSTEIN, S.R., AND T. PÓCS, 1989. Bryophytes. *In* H. Lieth, and M.J.A. Werger (Eds.) *Tropical rain forest ecosystems*, pp.311-325. Elsevier Science Publishers B.V., Amsterdam, The Netherlands.
- GRADSTEIN, S.R., D. GRIFFIN, M.I. MORALES, AND N.M. NADKARNI. 2001a. Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. *Caldasia* 23: 203-212.
- GRADSTEIN, S.R., S.P. CHURCHIL, AND A.N. SALAZAR. 2001b. Guide to the bryophytes of tropical America. *Mem. N.Y. Bot. Garden* 86: 1-590.
- GRUBB, P.J. 1977. Control of forest growth and distribution on wet tropical mountains, with special reference to mineral nutrition. *Annu. Rev. Ecol. Syst.* 8: 83-107.
- HIEZT, P. 1999. Diversity and Conservation of Epiphytes in a Changing Environment. *Pure Appl. Chem.* 70: 2114. URL: <http://www.iupac.org/symposia/proceedings/phuket97/hietz.html>.
- HILL, M.O., AND H.G. GAUCH. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.
- HOLZ, I., S.R. GRADSTEIN, J. HEINRICHS, AND M. KAPPELLE. 2002. Bryophyte Diversity, Microhabitat Differentiation, and Distribution of Life-forms in Costa Rican Upper Montane Quercus Forest. *The Bryologist* 105: 334-348.
- HOLZ, I., AND S.R. GRADSTEIN. 2005a. Phytogeography of the bryophyte floras of oak forests and páramo of the Cordillera de Talamanca, Costa Rica. *J. Biogeogr.* 32: 1591-1609.
- HOLZ, I., AND S.R. GRADSTEIN. 2005b. Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica - species richness, community composition and ecology. *Plant Ecol.* 178: 89-109.
- HOMEIER, J. 2005. *Purdiaea nutans* Planch. *In* P. Schütt, H.J. Schuck, U. Lang, and A. Roloff (Eds.) *Enzyklopädie der Holzgewächse* 42 (1-4), Landsberg/Lech: Ecomed.
- JONES, M.M., H. TUOMISTO, D.B. CLARK, AND P. OLIVAS. 2006. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *J. Ecol.* 94: 181-195.

- KÜRSCHNER, H., AND G. PAROLLY. in press. Bryophytes of the Reserva Biológica San Francisco, Ecuador Part 2. Mosses. Ecol.Monogr.
- LEON-YANEZ, S., S.R. GRADSTEIN, AND C. WEGNER. 2006. Catalogue of the liverworts and hornworts of Ecuador. Herbario QCA, Quito.
- LONGTON, R.E. 1982. Physiological ecology of mosses. In: Taylor, R.J., and Leviton, A.E. (eds.) pp. 77-113, The mosses of North America. Pacific association for the advancement of science, San Francisco, CA.
- MANDL, N., M. LEHNERT, S.R. GRADSTEIN, M. KESSLER, M. ABIY, AND M. RICHTER. in press. The unique *Purdiaea nutans* forest of southern Ecuador - abiotic characteristics and cryptogamic diversity. *In* E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl (Eds.). Gradients in a tropical mountain ecosystem of Ecuador. Ecological Studies, Springer Verlag, Berlin, Heidelberg.
- MÄGDEFRAU, K. 1982. Life-forms of bryophytes. *In* A. J. E. Smith (Ed) Bryophyte Ecology, pp. 45-58. Capman and Hall, London.
- MÄKIPÄÄ, R., AND J. HEIKKINEN. 2003. Large-scale changes in abundance of terricolous bryophytes and macrolichens in Finland. *J. Veg. Sci.* 14: 497-508.
- MC CUNE, B., AND M.J. MEFFORD. 1999. PC-ORD Multivariate analysis of ecological data. Version 4. MjM Software Design, Gleneden Beach OR.
- NELSON, C.R., AND CH.B. HALPERN. 2005. Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. *Can. J. Bot.* 83 (6): 610-620.
- NÖSKE, N.M., S.R. GRADSTEIN, H. KÜRSCHNER, G. PAROLLY, AND S. TORRACHI. 2003. Cryptogams of the Reserva Biológica San Francisco (Province Zamora-Chinchipec, Southern Ecuador). I. Bryophytes. *Cryptogamie, Bryol.* 24: 15-32.
- NÖSKE, N.M., N. MANDL, AND H.J.M. SIPMAN. in press. Lichens of the Reserva Biológica San Francisco, Ecuador. Ecol. Monogr.
- PAROLLY, G., AND H. KÜRSCHNER. 2004. Ecosociological studies in Ecuadorian bryophyte communities II. Syntaxonomy, life strategies and ecomorphology of the submontane and montane epiphytic vegetation of S Ecuador. *Nova Hedwigia* 79: 377-424.
- PFEIFFER, T. 2003. Terricolous bryophyte vegetation of New Zealand temperate rain forests. *Bryophyt. Bibl.* 59.
- PÓCS, T. 1982. Tropical forest bryophytes. *In* A. J. E. Smith (Ed). Bryophyte Ecology, pp. 59-104. Capman and Hall, London.
- PROCTOR, M.C.F. 2000. The bryophyte paradox: tolerance of desiccation, evasion and drought. *Plant Ecol.* 151:41-49.

- PROCTOR, M.C.F. 1990. The physiological basis for bryophyte production. *Bot. J. Linn. Soc.* 104: 61-77.
- REENEN, G.B.A. VAN 1987. "Altitudinal bryophyte zonation in the Andes of Columbia: A preliminary report." *Symbiosia biologica Hungarica* 35: 631-637.
- REENEN, G.B.A. VAN, AND S.R. GRADSTEIN. 1983. "Studies on Colombian Cryptogams XX: A transect analysis of the bryophyte vegetation along an altitudinal gradient on the Sierra-Nevada de Santa-Marta, Colombia." *Acta Bot. Neerl.* 32 (3): 163-175.
- RICHARDS, P.W. 1984. The ecology of tropical forest bryophytes. *In* R.M. Schuster (Ed) *New Manual of Bryology Vol. 2.*, pp. 1233-1270 The Hattori Botanical Laboratory, Nichinan, Miyazaki.
- RICHTER, M. 2003. Using epiphytes and soil temperature for eco-climatic interpretations in Southern Ecuador. *Erdkunde* 57: 161-181.
- SIMPSON, N. 2004. Saving threatened plants and birds in the Andes of Ecuador. *Plant Talk* 37: 17- 21.
- SIPMAN, H.J.M., AND R.C. HARRIS. 1989. Lichens. *In* H. Lieth, and M.J.A. Werger (Eds.) *Tropical rain forest Ecosystems, Ecosystems of the world*, pp. 303-309, Elsevier, Amsterdam.
- STEVENS, G.C. 1989. The latitudinal gradient in geographical range: How so many species coexist in the tropics. *Am. Nat.* 133: 240-256.
- STEVENS, G.C. 1992. The elevational gradient in altitudinal range: An extension of Rapoport's latitudinal rule to altitude. *Am. Nat.* 140: 893-911.
- TANNER, E.V.J., P.M. VITOUSEK, AND E. CUEVAS. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79: 10-22.
- TUOMISTO, H., K. RUOKOLAINEN, M. AGUILAR, AND A. SARMIENTO. 2003. Floristic patterns along a 43-km long transect in an Amazonian rain forest. *J. Ecol.* 91: 743–756.
- WOLF, J.H.D. 1994. Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio* 112: 15-28.
- WOLF, J.H.D. 1995. Non-vascular epiphyte diversity patterns in the canopy of a montane rain forest, Central Cordillera, Colombia. *Selbyana* 16: 185-195.

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## **IV. Chapter**

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### **Diversity and ecology of epiphytic bryophytes and macrolichens in Andean montane forest habitats**

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**ABSTRACT**

We analyse non-vascular epiphytic community structure and microclimate in three different upper montane tropical rain forests in southern Ecuador. On 34 trees (17 on ridges, 17 on slopes) we compared species distribution of epiphytic bryophytes and macrolichens in neighbouring ridge and slope forests and within vertical tree zones. Furthermore we determined the influence of the unusual site conditions in the study area on species diversity of epiphytic bryophytes and macrolichens, by comparing our results with previous studies on non-vascular epiphytes in montane rain forests of the Neotropics. We used Detrended correspondence analysis to group relevés by study locality, forest type and zone within the tree. Species life forms were recorded and species indicator values were calculated and compared for different habitats.

In total 211 taxa were recorded, the majority being liverworts followed by lichens and mosses. Mosses tended to be more prominent in the understorey, whereas lichens only were abundant in the canopy; liverworts were equally distributed in all tree zones.

Vertical distribution patterns play an important role even on small trees and in relatively open forest types. High precipitation rates in the study area favour liverworts and constrain mosses and macrolichens.



## INTRODUCTION

Tropical montane rain forests are rich in epiphytic bryophytes and lichens, which contribute significantly to total biomass and species diversity (Pócs 1982, Richards 1984, Sipman 1995) and play a key role in ecosystem processes by affecting water balance and nutrient cycling (e.g., Veneklaas & van Ek 1990, Coxson & Nadkarni 1995, Clark et al. 1998). Despite their importance, studies on the diversity and ecology of non-vascular epiphytes have been scarce in the Tropics (Gradstein 1992). During the past 20 years this has changed due to an increased interest in tropical biodiversity caused by the rapid loss of forested areas in this part of the world. Nevertheless, most studies on epiphytic bryophytes and lichens only deal with selected epiphytic habitats, such as tree bases and the lower, more reachable part of the trunk (e.g., Frahm 1987; Parolly & Kürschner 2004a, 2004b; Benavides et al. 2006). Fewer studies include the forest canopy (e.g., Cornelissen & ter Steege 1989, Montfoort & Ek 1990). The first comprehensive investigation of non-vascular epiphytes in montane tropical rain forests including whole trees was conducted in Colombia by Wolf (1994), followed by studies in Costa Rica (Gradstein et al. 2001, Holz et al. 2002, 2005) and Ecuador (Nöske 2004). These studies observed either an altitudinal gradient or a succession gradient. Another study in Venezuela attempted an integrated account of climbing and epiphytic, vascular and non-vascular species in upper montane rain forests (Kelly et al. 2004). The present study assesses the diversity of epiphytic bryophytes and macrolichens on whole trees in mature, undisturbed forests of the upper montane belt (2450-2650 m altitude) of southern Ecuador.

Southern Ecuador is characterized by relatively low mountain peaks paired with an unusual low altitude of the timberline as compared with other Andean areas (Weigend 2002, Mandl et al. in press). The upper montane belt at our main study site, the Reserva Biológica San Francisco, is also quite unique, as the frequently broad ridges are dominated by a single treelet, *Purdiaea nutans* (Clethraceae) (Parolly & Kürschner 2004a, Homeier 2005, Mandl et al. in press). Ecosociological studies on trunk epiphytic bryophyte communities of the *Purdiaea* forest by Parolly & Kürschner (2004 a, b) showed the occurrence of two associations, the *Frullanio serratae*-*Holomitrium sinuosi* at lower elevations and the *Macromitrium perreflexi*-*Pleurozietum paradoxae* at higher elevations. The character species of the latter association are rare taxa, *Macromitrium perreflexum* being endemic to southern E Ecuador and *Pleurozia paradoxa* being only known from

northern South America and Patagonia. The unique set of character species of this association probably narrows its range to the southern Ecuadorean Andes.

In order to test whether non-vascular epiphyte diversity and composition of this forest type are representative for the region of southern Ecuador, a comparison was made with two other upper montane forest sites of that region.

In both temperate and tropical forests vertical profiles of non-vascular epiphyte assemblages have been documented (e.g., McCune et al. 1997, Wolf 1994, Holz 2003). In tropical rain forests, the vertical stratification of epiphytes within the forest is generally correlated with gradients in air humidity and moisture availability (e.g., Wolf 1993a, Hietz & Briones 1998, Zotz & Hietz 2001, Acebey et al. 2003, Nöske 2004). In the southern Ecuadorian Andes, upper montane forests appear to be lower, and on ridges also more open than in more typical tropical forests of the same altitude (Mandl et al. in press). As a consequence the vertical microclimatic gradient within these upper montane forest stands may be less pronounced, and epiphytic species of these forests adapted to persist prolonged periods of drought. Under these conditions, we hypothesise lower species diversity in these forests than in taller, more typically shaped upper montane forests.

The aims of the present study were: (a) to analyse non-vascular epiphytic community structure and microclimate in upper montane tropical rain forests in southern Ecuador. Specifically we compared species distributions of epiphytic bryophytes and macrolichens in neighbouring ridge and slope forests and within vertical tree zones. (b) To determine the influence of the unusual site conditions in the study area on species diversity of epiphytic bryophytes and macrolichens, by comparing our results with previous studies on non-vascular epiphytes in montane rain forests of the Neotropics.

## **METHODS**

### **Study area**

We studied undisturbed upper montane ridge and slope forests at 2400 – 2650 m in three different localities in the Cordillera Real de Loja, southeast Ecuador: The Reserva

Biológica San Francisco (RBSF), the mountains pass El Tiro, and the Tapichalaca Reserve (Fig. 1).

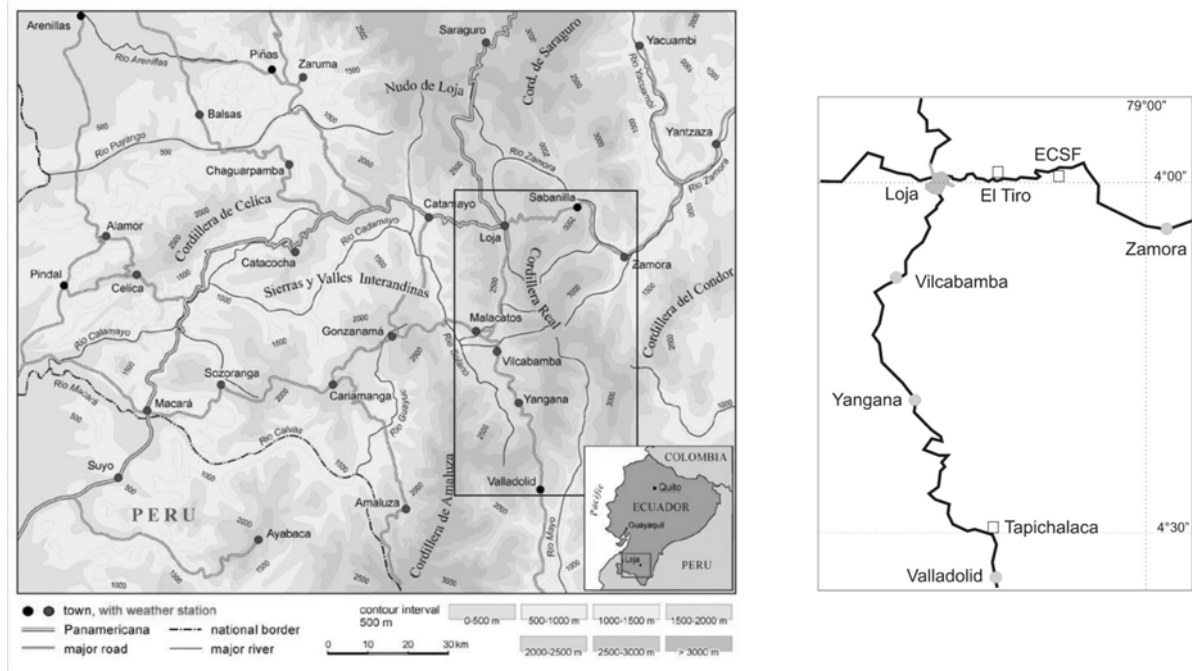


FIGURE 1. Map of southern Ecuador, frame indicates study area; location of study sites in extra frame.

### Study sites

The **RBSF** is located west of Loja and preserves about 1000 ha of mountain rain forest and Páramo vegetation (Beck & Müller-Hohenstein 2001) between 1800 and 3140 m. The high relief energy with steep and instable slopes, causing many landslides in even intact forest stands, is a striking feature of the area. On ridges at 2150-2650 m, the shrubby upper montane forest is dominated by *Purdiaea nutans* (Busmann 2001) (abundance averaging 80-100%, Table 1). Accompanying tree species on ridges are *Ilex rimbachii*, *I. scopulorum* and *I. weberlingii* (Aquifoliaceae), *Weinmannia elliptica*, *W. fagaroides* and *W. loxensis* (Cunoniaceae), *Clusia* spp. (Clusiaceae), *Cybianthus marginatus* (Myrsinaceae), *Calyptranthes pulchella* (Myrtaceae), and *Myrcia* sp. (Myrt.) In slope forest *P. nutans* is still dominant, but to a lesser degree (abundance averaging 20-40%, Mandl et al. in pres) and accompanied by different tree species, e.g. *Hedyosmum* spp. (Chloranthaceae), *Clusia* spp., *Licaria subsessilis* (Lauraceae), *Meriania rigida* (Melastomataceae), *Miconia* spp. (Melast.), *Podocarpus oleifolius* (Podocarpaceae), *Dioicodendron dioicum* (Rubiaceae), and *Drimys granadensis* (Winteraceae).

The mountain pass **El Tiro** is situated along the Loja-Zamora road at approx. 2800 m, 15 km west of the RBSF and on the border of Loja and Zamora-Chinchipe provinces, on the crest of the cordillera. The mountain slopes at El Tiro pass have a very rugged profile with many small ravines overgrown by low-statured, shrubby forest with a wind-sheared canopy, and abundant terrestrial bromeliads. *Purdiaea nutans* occurs scattered and is nowhere dominant. In ridge and slope forests of El Tiro *Purdiaea* is very scarce (Mandl et al. in press). Most important woody taxa on ridges are *Ilex rimbachii*, *Schefflera* spp. (Araliaceae), *Clusia* spp., *Weinmannia elliptica*, *W. fagaroides*, *Miconia* spp., *Calyptranthes pulchella*, *Siphoneugena* sp. (Myrt.), and *Ternstroemia jelskii* (Theaceae). On slopes *Ilex hippocrateoides*, *Clusia* spp., *Miconia* spp., *Calyptranthes pulchella*, *Podocarpus oleifolius*, and *Elaeagia ecuadorensis* (Rub.) are the principal tree species.

The **Tapichalaca** Reserve is situated along the Loja-Zumba road in the Cordillera Real at approx. 2000-3400 m, ca. 90 km south of Loja and on the southern end of Podocarpus National Park. The area supports very wet montane cloud forest and páramo (Simpson 2004). *Purdiaea nutans* has not been recorded in the area. Common tree species on ridges are *Ilex gabinetensis*, *Hedyosmum translucidum*, *Weinmannia fagaroides*, *Miconia* spp., *Myrica pubescens* (Myricaceae), and *Myrsine coriacea*; on slopes *Hedyosmum* sp., *Clusia ducu*, *C. sp.*, *Weinmannia fagaroides*, *Miconia* spp., *Myrsine coriacea*, *Myrcia fallax*, *Podocarpus oleifolius* and *Drimys granadensis*. *Graffenrieda harlingii* (Melast.) is common in ridge and slope forests at all three study sites. The frequent presence of palms (*Geonoma* spp., *Ceroxylon parvifrons*) is a striking feature of the Reserva.

The climate at all three localities is cool and perhumid. Precipitation ranges from approx. 3000 mm annually at El Tiro to approx. 4000 mm at Tapichalaca and over 5.000 mm at the RBSF (Richter 2003). Temperature maxima occasionally rise to 25°C and air humidity drops to 25% at all three locations in the period mid October – mid December, when monsoon-induced north-western air streams interrupt the semi-permanent easterly air flow (Gradstein et al. in prep.). Soil characteristics do not differ significantly among the three study sites and generally consist of poor, acidic (pH 4.6 - 4.1) cambisols and gleysols (Schrumpf et al. 2001, Mandl et al. in press).

At all three study sites, air temperature and air humidity were measured in two plots per ridge and slope forest during a period of 12 months (Nov. 2004 – Nov. 2005), using

HOBO data loggers. Microclimatic measurements were carried out at stem base (ca. 1 m above the ground) and in the canopy.

### Sampling methods and species identification

Fieldwork was carried out during two main sampling periods in August 2003 - January 2004 and August 2004 – January 2005. In the forest, vegetation analysis was carried out in 28 plots of 400 m<sup>2</sup> randomly placed plots in ridge (12 plots) and slope forests (16 plots) in the three study localities described above. Ridge and slope forests were distinguished by their topographic position and their mean inclination; ranging from 0-25% on ridges and 30-50% on slopes (Table 1). To ensure habitat homogeneity, extremely steep or disturbed forest parts (e.g., former landslides) and areas with a high cover of decomposing wood were avoided.

TABLE 1. Comparison of plot parameters of the three study sites. S.D. = standard deviation

	Number of plots/ trees	Elevation	Inclination	Canopy height	Canopy closure (S.D.)	Average diameter of trees (S.D.)
<b>RBSF</b>						
Ridge forest	6 / 6	2450-2660 m	0-25%	4-12 m	54% (6)	12 cm (0.6)
Slope forest	4 / 6	2500-2545 m	30-45%	8-20 m	88% (2)	16.3 cm (6.0)
<b>El Tiro</b>						
Ridge forest	3 / 5	2550-2600 m	0-15%	2-8 m	41% (13)	6.7 cm (4.2)
Slope forest	6 / 6	2430-2575 m	30-50%	5-15 m	89% (1)	15.2 cm (1.8)
<b>Tapichalaca</b>						
Ridge forest	3 / 6	2550-2630 m	0-25%	3-10 m	74% (15)	9.0 cm (4.5)
Slope forest	6 / 5	2520-2600 m	30-50%	10-20 m	88% (1)	24.2 cm (3.7)

Vegetation parameters analyzed in each plot included tree species composition, size and number of trees (dbh  $\geq$  10 cm), estimated average canopy height, and estimated average canopy closure (Table 1). Canopy closure measurements were performed using a

spherical densiometer; on four randomly chosen spots within each plot four estimates were taken, one in each exposition. These estimates were averaged to estimate percent canopy closure in the plot. All plots were mapped by GPS and were located at a considerable distance from each other.

For investigation of epiphytic bryophytes and macrolichens within each plot, randomly chosen trees were rigged and climbed using single rope technique (Perry 1978, ter Steege & Cornelissen 1988). Preventing host specific community effects, selected canopy trees had similar bark type and trees with excessively smooth, coarse or scaling bark were avoided. To analyze species richness and abundance, we subdivided trees into the following five vertical zones, relative to their position within the host tree (Johansson 1974): zone 1 (Z1) - stem base (0-0.5 m), zone 2 (Z2) - trunk, zone 3 (Z3) - inner canopy, zone 4 (Z4) - middle canopy, zone 5 (Z5) - outer canopy (twigs of ca. 1 cm in diameter). On slopes all five height zones were sampled, whereas on ridges, because of the limited tree height, only Z1, Z3 and Z5 were available for study. In total 34 trees were inventoried (Table 1). All sub-samples were taken from the 'weather side'. Crustose lichens and epiphylls were not included in the study. For species identifications the samples were examined microscopically in the laboratory. About 85% of the bryophytes were identified to species level. Most of the unidentified bryophyte species were scarce and plant material insufficient for reliable identification work. Identification of lichens was problematic due to lack of adequate keys or sporulating material. Consequently, 37% of macrolichens were not identified to species level.

Relevés were 600 cm<sup>2</sup> (mostly 20 x 30 cm), except for those taken from the middle and outer canopy where 60 cm long branches or twigs were sampled. In the middle canopy only the upper half-cylinder was considered. Percentage cover of species was estimated relative to relevé area, using the slightly modified Braun-Blanquet scale (Braun-Blanquet 1964).

+	<1 %	3	25.1 - 50.0 %
1	1.1 - 6.0 %	4	50.1 - 75.0 %
2a	6.1 - 12.5 %	5	75.1 - 100.0 %
2b	12.6 - 25.0 %		

Eight different life forms were recognized: dendroids (de), fans (fa), mats (ma), pendants (pd), tails (ta), short turfs (sT), tall turfs (tT) and wefts (w) (Mägdefrau, 1982).

Nomenclature follows Kürschner & Parolly (in press) for mosses, León et al. (2006) for liverworts, and Nöske et al. (in press) for lichens. Voucher specimens were deposited in the herbarium LOJA, with duplicates in GOET and for lichens also in B.

### **Data analyses**

Rarefaction, carried out with EstimateS (Colwell 1994-2004), was used to adjust for the different sample numbers in different tree zones.

Further statistical analyses were performed with the program package PC-ORD for Windows - Version 4.17 (McCune & Mefford 1999). Patterns in species composition according to study locality, forest type and tree zone were explored by Detrended correspondence analysis (DCA, Hill & Gauch 1980), employing non-linear rescaling (26 segments). Habitat variables were superimposed on the resulting ordinations using a joint plot, based on correlations of variables with the axes of the community ordination.

We calculated species indicator values for the different height zones using Dufrene & Legendre's (1997) method, which combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group. It produces indicator values (IV) for each species in each group. When more than two groups are defined, the IV for a particular species in a particular group is dependent on the set of sample units belonging to other groups. Groups are defined by height zone within the tree. These are tested for statistical significance using a Monte Carlo technique. Indicator values range from zero (no indication) to 100 (perfect indication). Perfect indication means that presence of a species points to a particular group without error, at least with the data set in hand.

## RESULTS

### Microclimate

Microclimatic measurements showed distinct differences between slope and ridge habitats. The daily course of air humidity and temperature fluctuated much stronger in ridge forests with a rather open canopy than in slope forest with a closed canopy (Fig. 2). At the RBSF and at Tapichalaca, fluctuations of air humidity during the day increased from the stem base of slope trees over the canopy of slope trees and stem base of ridge trees to the canopy of ridge trees (data shown for RBSF, Fig. 2). At El Tiro this trend was not as clear. Microclimatic differences between stem base and canopy climate were not pronounced in daily course of temperature.

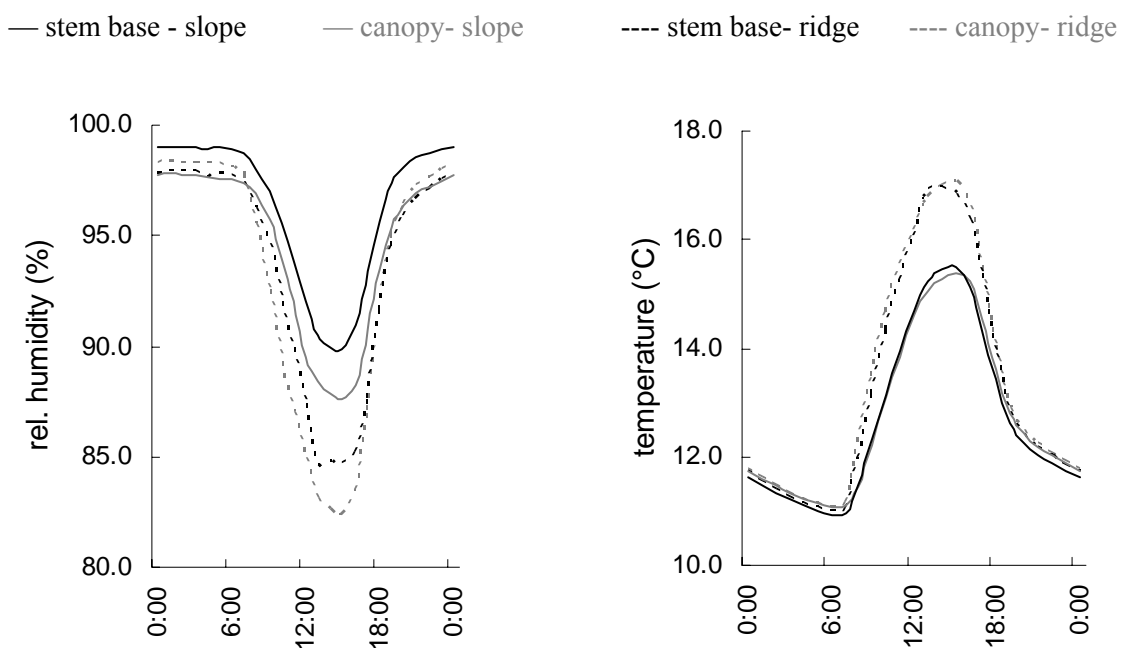


FIGURE 2. RBSF: daily courses of air humidity and temperature at stem bases and in the canopy in ridge and slope forests (means of one year measurement period).

### Species richness and composition

In total, 211 taxa were recorded, including 144 bryophytes (112 liverworts, 32 mosses) and 67 lichens (Table 2; Appendix 1). Total species richness, including ridge and slope forests was remarkably similar in the three study sites, with highest numbers found at Tapichalaca (140) and lowest in RBSF (127, Table 2). Seventy-six percent (116 taxa) were found in



more than one relevé and 55% in more than one locality. In total, 35% of all bryophytes species were shared by all localities, while only few bryophytes were exclusive to the RBSF (10%), Tapichalaca (15%) and El Tiro (17%).

In all three forest localities liverworts were dominant, accounting for about 54% of all recorded species, followed by lichens (32%) and mosses (15%). At single sites these percentages shift slightly (Table 2). At all three study sites percentages of liverworts were very similar (57%), whereas macrolichens were most important at the RBSF and mosses at El Tiro (Table 2).

In terms of number of families, El Tiro (48) is the most diverse forest locality, followed by Tapichalaca (42), and RBSF (38). For bryophytes, Lejeuneaceae was the family richest in species (31 spp., 28%), followed by Lepidoziaceae (22 spp., 20%), Plagiochilaceae (12 spp., 11%), and Frullaniaceae (9 spp., 8%). The best represented moss families were Dicranaceae (7 spp., 21%) and Macromitriaceae (6 spp., 18%). In lichens Parmeliaceae clearly dominated (31 spp., 46%), followed by Physciaceae (9 spp., 13%), and Cladoniaceae (7 spp., 8%).

Species richness per relevé was variable and ranged from 8 to 12 species per plot. No significant difference was found in species density along the vertical distribution within the tree. Overall, however, in the inner and middle canopy more species tended to coexist in one relevé.

### **Vertical distribution of epiphytic bryophytes and macrolichens**

Species accumulation curves for pooled relevés indicated that different height zones have different non-vascular species richness (Fig. 3). Species richness was highest in the inner canopy and lowest in the middle and outer canopy. The form of the curves of Z2 and Z4 demonstrated that even though fewer relevés ( $n=17$ ) were sampled than in the other zones ( $n=34$ ) species sampling completeness was comparable to that of other zones.

TABLE 2. Absolute and relative species richness per tree zone for all taxa and all study sites.

	group	all sites	%	RBSF	%	Tapichalaca	%	El Tiro	%
<b>Zone 1</b>	<b>all taxa</b>	<b>106</b>		<b>56</b>		<b>55</b>		<b>58</b>	
	liverworts	73	68.9	42	75.4	43	78.2	37	63.8
	mosses	21	19.8	7	12.3	12	21.8	14	24.1
	macrolichens	12	11.3	7	12.3	0	0.0	7	12.1
<b>Zone 2</b>	<b>all taxa</b>	<b>82</b>		<b>48</b>		<b>39</b>		<b>39</b>	
	liverworts	50	61.0	37	77.1	27	69.2	22	56.4
	mosses	16	19.5	4	8.3	8	20.5	9	23.1
	macrolichens	16	19.5	7	14.6	4	10.3	8	20.5
<b>Zone 3</b>	<b>all taxa</b>	<b>122</b>		<b>61</b>		<b>69</b>		<b>74</b>	
	liverworts	66	52.5	39	63.9	40	58.0	41	55.4
	mosses	15	12.7	3	4.9	10	14.5	10	13.5
	macrolichens	41	34.7	19	31.1	19	27.5	23	31.1
<b>Zone 4</b>	<b>all taxa</b>	<b>72</b>		<b>40</b>		<b>34</b>		<b>41</b>	
	liverworts	45	62.5	30	75.0	22	65.7	28	65.9
	mosses	6	8.3	2	5.0	3	8.6	5	12.2
	macrolichens	21	29.2	8	20.0	9	25.7	9	22.0
<b>Zone 5</b>	<b>all taxa</b>	<b>84</b>		<b>52</b>		<b>51</b>		<b>53</b>	
	liverworts	45	53.6	31	59.6	31	60.8	29	54.7
	mosses	3	3.6	1	1.9	2	3.9	3	5.7
	macrolichens	36	42.9	20	38.5	18	35.3	21	39.6
<b>all zones</b>	<b>all taxa</b>	<b>211</b>		<b>127</b>		<b>140</b>		<b>134</b>	
	bryophytes	144	68.2	85	66.9	103	73.6	103	76.9
	liverworts	112	53.1	74	56.7	79	56.4	76	56.7
	mosses	32	15.2	11	8.7	21	15.0	24	17.9
	macrolichens	67	31.8	44	34.6	40	28.6	34	25.4

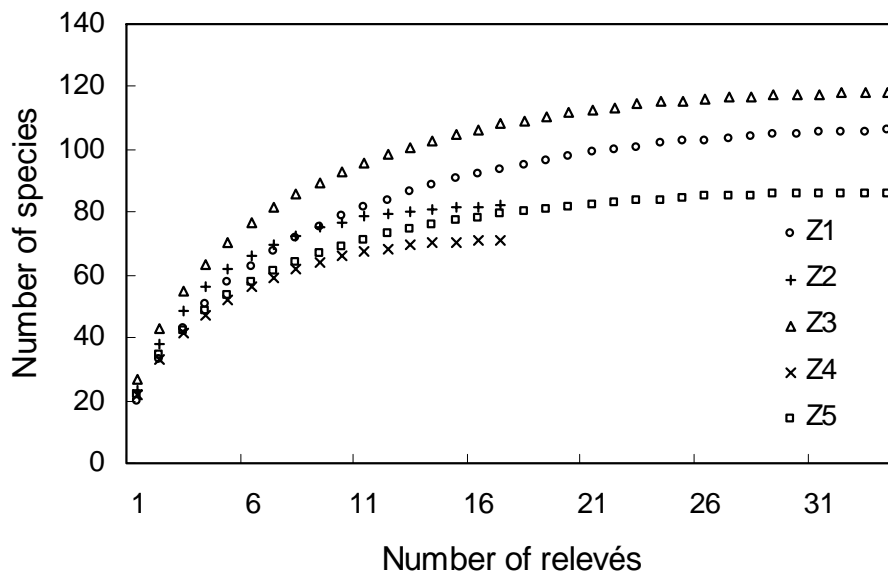


FIGURE 3. Species accumulation curves of non-vascular epiphytes in different height zones. X-axis: number of relevés pooled, y-axis: number of species, Z2, Z4.

The general pattern of vertical species distribution was very similar at all three study sites. The inner canopy was not only the most divers zone but also the zone with highest variability between the study sites, with species numbers ranging from 61 (RBSF) to 74 (El Tiro) species. In comparison total species richness at the stem base (55-58 spp.) and in the outer canopy (51-53 spp.) was very uniform. Macrolichen richness increased from the trunk to the canopy. In contrast, richness of liverworts and especially of mosses decreased (Table 2).

In slope forests Z1, Z3 and Z5 together accounted for about 91% of total species richness, only 9% were added by Z2 and Z4.

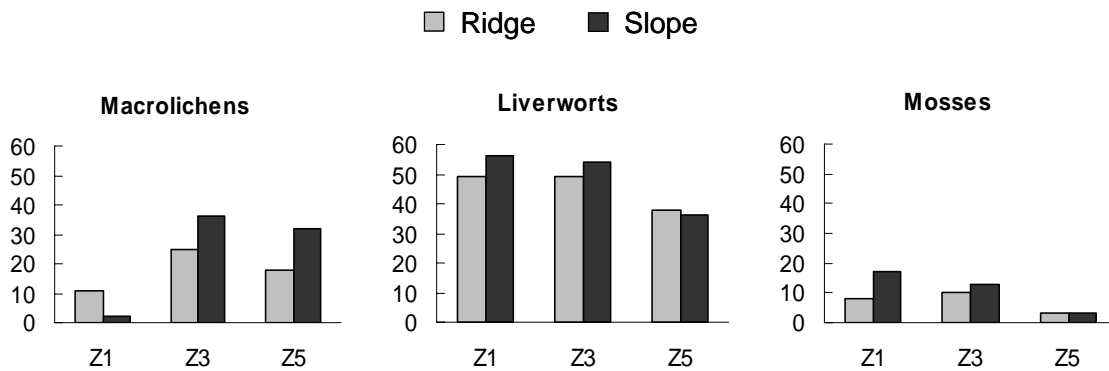


FIGURE 4. Species numbers of macrolichens, liverworts and mosses according to different height zones within the host trees in ridge and slope forests.

Comparing ridge and slope forests according to the vertical distribution of non-vascular taxa we found liverworts dominating both forest types, from stem base to outer canopy (referring only to Z1, Z3, and Z5; Fig. 4). Macrolichens hardly occurred at the stem base of slope trees, however increased in species number towards the outer canopy, more dramatically than on ridge trees (Fig. 4). On slope trees species number of mosses declined from stem base to tree crown, whereas on ridge trees this trend was not as clear (Fig. 4). Generally, slopes were richer in species than ridges. Overall, 109 species (52%) were shared between ridge and slope assemblages. The percentage of species shared between both forest types, however, varied between taxonomic groups and height in the tree. While stem base of ridge and slope trees had about 34% of all species in common, this amount increased in the middle and outer canopy to over 50%. For liverworts and mosses separately these figures were even higher, 60% and 100 % respectively.

### Vertical distribution of life forms and indicator species

Life forms of bryophytes showed a clear vertical distribution pattern (Fig. 5). The number of life forms was reduced from the stem base towards the outer canopy. In all five tree zones the majority of bryophyte species occurred as mats, reaching a maximum in the outer canopy with 57% of all species. Tall turfs were the second most common life forms in Z2 to Z4 and wefts were more important from Z1 to Z4 than in Z5. Fans showed a strong preference for tree bases and trunks, whereas pendants and short turfs increased with height within the host tree. Dendroids were only found at the tree base.

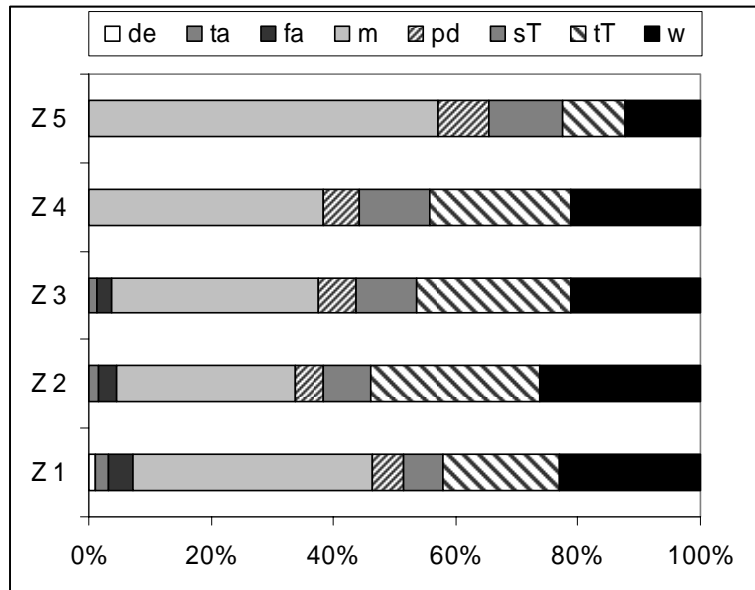


FIGURE 5. Vertical distribution of the eight recognized bryophyte life forms in percentages of total number of bryophytes; dendroids (de), fans (fa), mats (ma), pendants (pd), tails (ta), short turfs (sT), tall turfs (tT) and wefts (w).

Liverworts also proved to be the principal indicator taxa for the different height zones on the trees. Forty-one epiphytic bryophyte and macrolichen species were resolved as indicator species, including 36 liverworts, four mosses and one macrolichen (Table 3). Z1 to Z3 had five to seven indicator species, while Z4 and Z5 had eight and 12, respectively, including three groups of taxa (*Cheilolejeunea* spp., *Drepanolejeunea* spp., *Metzgeria* spp.). Percentage of indication ranged from about 10% to 49%. Highest indicator values were obtained for *Rhizogonium novae-hollandiae*, *Scapania portoricensis*, and *Campylopus hualagensis* in Z1, *Plagiochila aerea*, *Bazzania roraimensis*, and *Lepicolea pruinosa* in Z2, *Jamesoniella rubricaulis* and *Frullania intumescens* in Z3, *Ceratolejeunea grandiloba*, *Frullania brasiliensis* and *Lejeunea inflexiloba* in Z4, and *Aureolejeunea fulva*, *Diplasiolejeunea pauckertii*, *Frullania apiculata*, *Frullania cuencensis*, *Leucolejeunea xanthocarpa* and *Metzgeria* spp. in Z5 (Table 3).

TABLE 3. Relative abundance and indicator values (IV) of most significant bryophyte and macrolichen species in different tree zones.

	Indicator species	Life form	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	IV	p *
Zone 1	<i>Rhizogonium novae-hollandiae</i>	tT	83	17	0	0	0	17.2	0.004 **
	<i>Scapania portoricensis</i>	tT	49	22	29	0	0	18.8	0.005 **
	<i>Campylopus hualagensis</i>	tT	56	31	13	0	0	18.0	0.010 *
	<i>Cephalozia crassifolia</i>	m	100	0	0	0	0	11.8	0.021 *
	<i>Plagiochila stricta</i>	fa	85	0	15	0	0	10.0	0.047 *
Zone 2	<i>Plagiochila aerea</i>	w	30	59	7	4	0	27.9	0.001 ***
	<i>Bazzania roraimensis</i>	w	18	53	11	10	8	18.8	0.008 **
	<i>Lepicolea pruinosa</i>	tT	29	35	24	12	0	26.8	0.003 **
	<i>Campylopus fragilis</i>	tT	7	93	0	0	0	11.0	0.026 *
	<i>Lepidozia caespitosa</i>	w	0	84	16	0	0	14.9	0.011 *
	<i>Prionodon densus</i>	fa	13	88	0	0	0	10.3	0.030 *
Zone 3	<i>Schoenobryum rubricaulae</i>	m	0	100	0	0	0	11.8	0.036 *
	<i>Adelanthus lindenbergianus</i>	sT	4	45	46	0	5	15.8	0.026 *
	<i>Anastrophyllum auritum</i>	tT	0	0	100	0	0	11.8	0.022 *
	<i>Cheilolejeunea inflexa</i>	m	4	26	43	26	0	12.8	0.048 *
	<i>Frullania intumescens</i>	pd/m	7	22	51	7	12	18.1	0.015 *
	<i>Jamesoniella rubicaulis</i>	tT	15	13	33	27	12	23.2	0.020 *
	<i>Pleurozia paradoxa</i>	tT	0	0	100	0	0	11.8	0.024 *
Zone 4	<i>Ceratolejeunea grandiloba</i>	m	0	6	8	58	28	30.9	0.001 ***
	<i>Frullania brasiliensis</i>	pd/m	2	4	14	48	32	30.8	0.001 ***
	<i>Lejeunea inflexiloba</i>	m	4	0	9	62	25	36.3	0.001 ***
	<i>Ceratolejeunea patentissima</i>	m	0	6	19	54	21	22.2	0.003 **
	<i>Plagiochila bifaria</i>	w	0	0	14	49	36	26.2	0.002 **
	<i>Herbertus divergens</i>	tT	6	22	24	38	11	17.7	0.035 *
	<i>Plagiochila cristata</i>	w	9	0	41	50	0	11.8	0.037 *
	<i>Radula fendleri</i>	m	6	8	0	45	42	16.0	0.021 *
Zone 5	<i>Aureolejeunea fulva</i>	m	0	0	9	9	81	35.9	0.001 ***
	<i>Diplasiolejeunea pauckertii</i>	m	0	0	0	16	84	42.0	0.001 ***
	<i>Frullania apiculata</i>	m	0	0	15	34	51	40.2	0.001 ***
	<i>Frullania cuencensis</i>	m	0	0	0	0	100	20.6	0.001 ***
	<i>Leucolejeunea xanthocarpa</i>	m	0	0	8	9	83	48.9	0.001 ***
	<i>Metzgeria spp.</i>	m	10	14	3	0	72	36.2	0.001 ***
	<i>Cheilolejeunea spp.</i>	m	0	0	7	29	64	17.0	0.009 **
	<i>Drepanolejeunea spp.</i>	m	15	11	23	19	33	25.4	0.005 **
	<i>Frullania kunzei</i>	m	0	0	9	27	64	22.7	0.004 **
	<i>Anoplolejeunea conferta</i>	m	2	15	16	31	36	18.2	0.043 *
	<i>Omphalanthus filiformis</i>	pd/m	14	24	19	6	37	21.8	0.012 *
<i>Usnea spp.</i>	-	8	7	26	26	34	18.1	0.038 *	

The number of indicator species resolved for single height zones and indication values generally increased from the stem base to the outer canopy (Table 3). In the transition zone (Z3) between the trunk habitats and the crown habitats no highly significant indicator species were found.

DCA was performed to visualize the similarity between certain groups of relevés. The ordination diagrams revealed no separation of the three study sites (Fig 6B) or the two forest types (Fig. 6A). However, ridges assemblages tended to be more variable than slopes assemblages, as indicated by the more scattered ridge symbols. In contrast, the importance of height zone for community differentiation is clearly demonstrated by the separation of relevés in the ordination by DCA (Fig. 6 C). Species assemblages from the crown zones (Z4 and Z5) did not overlap with assemblages from the trunk (Z1 and Z2, Fig 4A).

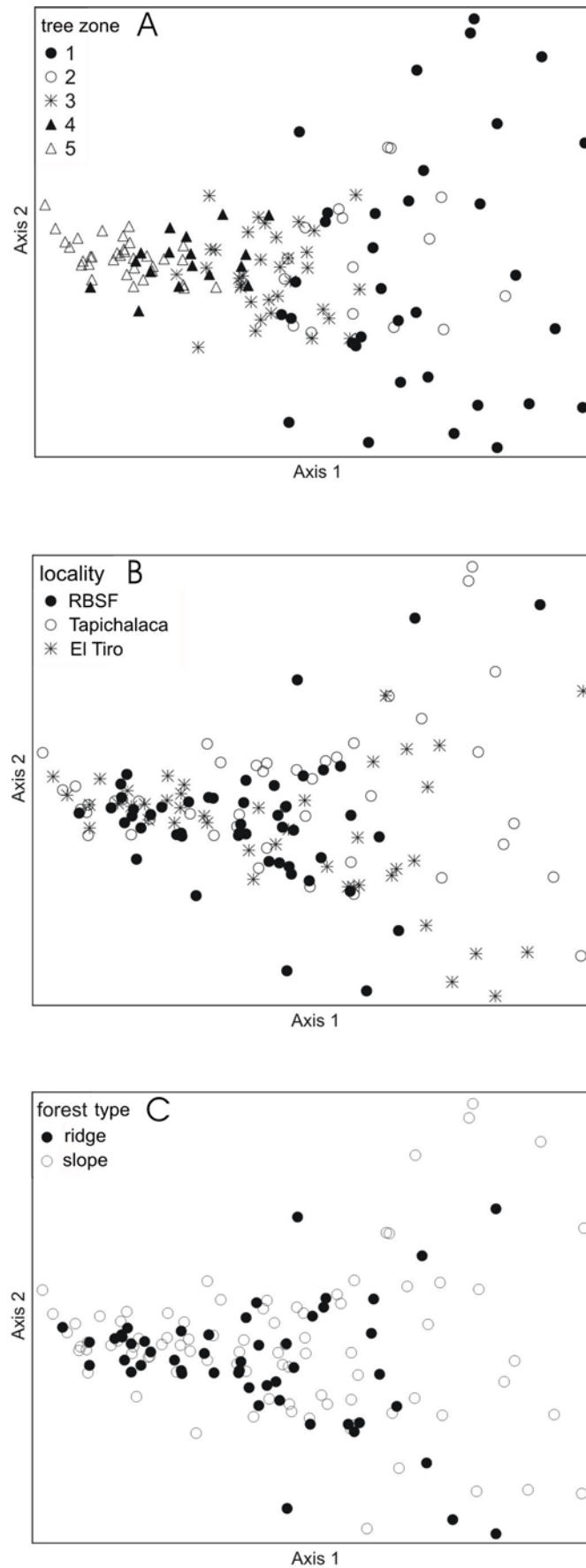


FIGURE 6. DCA ordination diagrams of species composition and abundance. **A** according to tree zones, **B** study localities, and **C** forest types.



## DISCUSSION

### **Diversity and distribution of non-vascular epiphytes in tropical montane forests - a comparison**

In terms of species richness our analysis reveals epiphytic assemblages of tropical montane forests in southern Ecuador dominated by liverworts, followed by macrolichens, and mosses. This absolute dominance of liverworts over mosses is in accordance with the general picture presented by other studies on non-vascular epiphytes in the Neotropics, e.g. for upper montane rain forests in Colombia (Wolf 1993b), in Costa Rican (Holz et al. 2003), and in Venezuela (Kelly et al. 2004) and for lower montane rain forests in Ecuador (Nöske 2004) (Table 4). In palaeotropical forests, mosses generally tend to be more abundant (Gradstein & Pocs 1989), Sporn unpubl. data).

To gain better knowledge about general trends in the species distribution of non-vascular epiphytes in the montane belt of the Neotropics we compare previous studies from Colombia, Costa Rica, Venezuela and Ecuador with our findings (Table 4). Site characteristics, e.g. macroclimate, forest structure and altitude, and the number of sample trees vary between the different investigations. Nevertheless, total species richness of non-vascular epiphytes is rather similar and ranges from 129 - 147 species in forest with canopy trees up to 20 m and 153 - 186 species in forests with a canopy level of about 30 m (Table 4). The available data thus suggest that there is a correlation between species richness and canopy height of the forest, with increase of canopy height resulting in higher species numbers. Canopy closure, found to be an important correlate with epiphyte richness in Costa Rican upper montane forest (Holz & Gradstein, 2005), was rather similar in our study sites and slightly higher than in Venezuela and Costa Rica. A comparison between the three areas in terms of species richness and canopy closure in undisturbed upper montane forest forests did not yield significant differences (data not shown). A possible bias of the results due to different methods of canopy closure estimation employed in the three areas cannot be ruled out, however.

Compared to most other tropical montane forests investigated, the study sites in upper montane forests of southern Ecuador are characterized by a lower proportion of macrolichens and, with the exception of the upper montane forests in Venezuela, also in mosses (Table 4). A striking pattern within our three study sites is the decrease in moss diversity with increasing precipitation, whereas species numbers of liverworts and lichens

remain unchanged. A similar gradient appears to exist within the entire RBSF area (1800-3100m), where moss species are much more numerous in lower montane forests (Nöske 2004) than in the upper montane belt (this study), correlating with a dramatic increase of precipitation with elevation. While at around 1900 m a.s.l. annual precipitation averages 2500 mm, at 2500 m a.s.l. over 5000 mm of annual precipitation is reached. Hence, these results are in support of the notion humidity is reflected in the moss-liverwort ratio and that liverworts are less tolerant to drought than mosses (van Reenen & Gradstein 1983, Frahm & Gradstein 1991, Wolf 1993c). On the other hand, the relatively reduced diversity of macrolichens may be linked to the strong competition with liverworts, which are favoured by the humidity conditions.

Best represented liverwort families in terms of species numbers were the same in all compared studies, namely Lejeuneaceae, Frullaniaceae, Lepidoziaceae, and Plagiochilaceae (in varying proportions). Macromitriaceae is the only moss family frequently mentioned as species rich. In lichens Parmeliaceae, Physciaceae, and Lobariaceae generally play the most important role.

TABLE 4. Epiphytic bryophyte and macrolichen richness in an upper montane oak forest (Cost Rica), an Andean montane rain forest (Venezuela), a montane tropical rain forest (Colombia), three upper montane rain forests (Ecuador), lower montane rain forest (Ecuador). (1) from Holz (2003), (2) from Kelly et al. (2004), (3) from Wolf (1993c), (4) slope forests of this study, (5) from Nöske (2004). In all studies whole trees were sampled. All data refer to undisturbed forests.

	Elevation	mean temp	mean annual precipitation	number of trees sampled	tree height	canopy closure (%)	Mosses (%)	Liverworts (%)	Macrolichens (%)
Costa Rica (1)	2900 m	11°C	3000 mm	10	30-35 m	65-80	40 (26)	56 (37)	57 (37)
Venezuela (2)	2500 - 2650 m	13°C	2500 mm	12 (8)	11-18m	73	22 (16)	66 (49)	46 (34)
Colombia (3)	2550 m	-	2000 mm	4	20-30 m	-	33 (18)	102 (55)	51 (27)
<b>Tapichalaca (4)</b>	2520 - 2600 m	13°C	4000 mm	5	10-20 m	89	18 (15)	69 (58)	33 (28)
<b>El Tiro (4)</b>	2430 - 2575 m	10°C	3000 mm	6	5-15 m	88	22 (18)	67 (56)	30 (25)
<b>RBSF (4)</b>	2500 - 2545 m	11°C	5000 mm	6	10-20 m	88	8 (7)	67 (61)	34 (31)
RBSF (5)	1850 - 1930 m	16°C	2200 mm	10	16-21 m	89	31 (21)	61 (41)	55 (37)

Even though tree species composition and forest structure varied conspicuously between our study sites, we found rather little variability in the distribution of species

assemblages amongst them (Table 2, Fig. 5B). In terms of absolute species richness and the number of families contributing to total species richness, the RBSF is outstripped by the other two study localities. This may be explained by the less pronounced structural differences between ridge forest and slope forest (Table 2).

Host-tree specificity, as reported from other Neotropical montane forests (e.g. Wolf 1994, Holz 2003), was not observed for non-vascular epiphytic species in our study area. Due to the monodominance of *Purdiaea nutans*, most of the trees sampled at the RBSF site belonged to the same species; yet, species assemblages from that site are distributed evenly within assemblages from the other two sites (Fig. 6B).

Slopes generally harbour more non-vascular epiphytes than ridges, both on whole trees and on individual tree zones (Fig. 3). This may be explained by the taller size of trees on slopes and the less pronounced daily fluctuations of air humidity.

### **Microclimate and vertical gradients**

Microclimatic measurements define the humidity conditions under which epiphytic taxa thrive. These conditions are particularly important for the poikilohydric bryophytes and macrolichens, which are highly dependent on atmospheric water and nutrient supply (Richards 1984, Scott 1994). At our study sites microclimatic measurements indicate that the intensity of daily fluctuations of air humidity increases from stem base to canopy and from dense forests with higher canopy (slope forests) to open low-statured forests (ridge forests). Daily courses of air temperature, on the contrary, appear steadier within one forest stand and only show clear differences between ridge and slope forests.

Compared to other tropical montane forest sites (Wolf 1993, León-Vargas et al. 2006, Zotz 2007), the structure of the investigated forests stands out by the non-stratified, simple canopy with all mature trees contributing to a single canopy layer. Consequently, fluctuations in air humidity in the investigated forests are more severe than measured in a multilayered montane rain forest of Venezuela, where the more complex vegetation structure buffers microclimatic conditions (León-Vargas et al. 2006). According to a recent study on the desiccation tolerance of epiphytic bryophytes, photosynthesis stops completely beyond a humidity level of 95% (León-Vargas et al. 2006). For our study sites this means that both stem and canopy inhabitants have to cope with photosynthetically unfavorable conditions for a long period of the day. However, the quantity of hours in which humidity levels below 95% are reached, differs between ridge and slope and stem

and canopy habitats and we presume that these differences are relevant (Fig. 2). Similar harsh conditions have so far only been reported from the outer canopy of tropical forests (Buckley et al. 1980, Nadkarni & Longino 1990, Freiberg 1997, 2001).

Nevertheless, we observed a clear vertical gradient in the distribution of species assemblages (Fig. 4), and a significant preference of various species for a specific tree zone. In accordance with observations by Wolf (1995), Holz (2004), Nöske (2004) and Kelly et al. (2004), trunk and canopy communities were distinctly different. The proportion of canopy specialists was 13% at our study sites. This percentage is rather low compared to findings in lower montane rain forests of Costa Rica (Gradstein et al. 2001), in lowland rain forests in Guyana (Cornelissen & Gradstein 1990), with 52% and 50% respectively. Kelly et al. (2004) recorded 31% of the corticolous bryophyte restricted to the canopy. They argued that the less extreme contrast in microclimatic conditions between canopy and understorey may cause the lower proportion of exclusive species in the canopy of rather open tropical rain forests of higher altitudes. Our study confirms that the less extreme contrast in microclimatic conditions between canopy and understorey may result in a lower proportion of species exclusive to the canopy. In contrast, the percentage of understorey specialist, being exclusive to tree base and tree trunk was much higher (27%) in the investigated forests and close to the 20% recorded for lower montane forest in Costa Rica (Gradstein et al. 2001). Apparently, the microclimatic conditions at the stem base and on trunks favored a relatively high number of shade specialists.

### **Indicator species and life forms**

Some bryophyte life forms, such as pendants, tails, and fans, which in our study only have been observed from the stem base to the inner canopy, are associated with high humidity and low light levels in literature (Mägdefrau 1982). Larger species forming abundant patches of tall turfs and wefts are common on trunks, inner and middle canopy. Our observations are in agreement with those of Parolly & Kürschner (2004a), who recorded weft and tall turfs as the predominating life forms in the *Purdiaea* forest. According to the latter authors, vegetative reproduction is the principal reproductive strategy in these montane bryophyte communities.

In contrast, mat forming bryophytes grow interwoven among these patches of tall turf and wefts. They gain importance with increasing height in the tree due to the many pioneer species of the canopy twigs microhabitat belonging to this life form. These outer

canopy species are mostly small leafy liverworts growing closely appressed to the substrate with their specialized lobules (Lejeuneaceae) or watersacs (*Frullania*). In our study about 70% of bryophyte species, restricted to the canopy belong this group. Consequently, the exposed canopy also harbours the lowest diversity of bryophyte life forms. Similar findings have been reported from Costa Rica (Holz et al. 2002, Sillett et al. 1995). These leaf modifications seem to be related to water retention and enable species to colonize exposed epiphytic substrata by avoiding hydric stress (Thiers 1988, Gradstein & Pócs 1989). The vertical distribution of bryophyte life forms at our study sites confirms results by Holz (2002) and Nöske (2004). The proportion of macrolichens in the canopy, however, is much higher in other montane rain forests than at our study sites. The very high humidity and strong winds, reaching peak velocities of about 20 m/sec at El Tiro, may be the cause of predominance of appressed growth forms in the canopy and the lack of projecting and pendulous ones.

TABLE 5. List of characteristic species for certain tree zones in common with other Neotropical montane rain forests. (1) This study, (2) lower montane rain forest (Ecuador, Nöske (2004), (3) upper montane oak forest (Cost Rica, Holz 2004), (3) Andean montane rain forest (Venezuela, Kelly et al. 2004). UP= *Usnea-Parmotrema* group, outer canopy; OM = *Omphalanthus filiformis-Maxilaria miniata* group, middle canopy

	Ecuador - this study (1)	Ecuador (2)	Cost Rica (3)	Venezuela (4)
<i>Campylopus hualagensis</i>	Z1	Z3		
<i>Campylopus fragilis</i>	Z2	Z2		
<i>Prionodon densus</i>	Z2	Z2	Z1	
<i>Jamesoniella rubricaulis</i>	Z3	Z3	Z2,Z3	up+om
<i>Frullania brasiliensis</i>	Z4	Z4		up+om
<i>Plagiochila bifaria</i>	Z4	Z3	Z2,Z3	
<i>Radula fendleri</i>	Z4	Z2		
<i>Aureolejeunea fulva</i>	Z5	Z5	Z3,Z5	
<i>Diplasiolejeunea pauckertii</i>	Z5	Z5		
<i>Leucolejeunea xanthocarpa</i>	Z5		Z5	up+om
<i>Drepanolejeunea spp.</i>	Z5	Z5		
<i>Frullania kunzei</i>	Z5	Z5		
<i>Anoplolejeunea conferta</i>	Z5	Z3		up+om
<i>Omphalanthus filiformis</i>	Z5	Z3		om
<i>Usnea spp.</i>	Z5	Z5		up

Abundant species within a narrow distribution range are suitable indicator species for a special habitat type, as they give insight in the predominating conditions (Hietz 1999, Gradstein et al. 2001). Because exclusiveness of species to certain tree zones increases slightly with height in the tree, more indicator species resolve for the outer and middle canopy than for the other tree zones. Nevertheless at least five species resolve as indicator species for stem bases.

Not surprisingly nearly all indicator species of the outer canopy and most of the middle canopy are small liverworts (Lejeuneaceae, Frullaniaceae) and have mat life form. At the inner canopy and on trunks other life forms, especially tall turfs and wefts (e.g. Lepidoziaceae, Plagiochilaceae, and mosses), gain importance as indicator species.

The attempt to create a list of general indicator species for different height zones in intact montane rain forests only reveals few species in common (Table 5). Of 41 indicator species only 15 have been found mentioned as characteristic for a similar zone in other studies. *Prionodon densus* is a characteristic species of trunk habitats, *Jamesoniella rubricaulis*, *Frullania brasiliensis* and *Plagiochila bifaria* for the inner and middle canopy, and *Anoplolejeunea conferta*, *Omphalanthus filiformis*, *Leucolejeunea xanthocarpa* and *Usnea spp.* for the outer canopy. Neotropical montane forests have more characteristic species in common in canopy habitats than at the stem base or on the trunk.

A direct comparison of lower and upper montane forests at the RBSF which reveals far more characteristic species in common also indicates that geographical distance is the main constraint for generally valid indicator species for specific microclimate and microhabitat conditions.

## CONCLUSION

- Our assumption that other upper montane rain forests in the Neotropics harbour more non-vascular epiphytes than the low-statured forests in southern Ecuador are partly met. An increase of total species numbers with canopy height in montane neotropical rain forests is observed. Higher species richness in other forests is mostly due to an increase in mosses and macrolichens. Liverworts, however, show similar or even higher species numbers in our study sites.

- Although canopy height in our study sites is rather low compared to montane rain forests in Costa Rica and Columbia (Holz 2004, Wolf 1993c) we still observe a clear vertical gradient in terms of the distribution of species assemblages, indicator species and predominance of life forms. These results indicate that vertical distribution patterns play a relevant role even on small trees and in relatively open forest types.
- The elevation gradient in the distribution of macrolichens and mosses found at the RBSF is probably caused by a dramatic increase in humidity with altitude and the strong winds at higher elevations constraining the growth of projecting or hanging species.
- Species assemblages show fewer differences among our three study sites and among ridge and slope forests than between different height zones within the forest. We conclude that microclimatic conditions as well as microsite characteristics determine the distribution of non-vascular epiphytes according to their life form and drought tolerance.

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## REFERENCES

- Acebey, A., Gradstein, S.R. & Krömer, T. (2003) Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *Journal of Tropical Ecology*, **19**, 9-8.

- Beck, E. & Müller-Hohenstein, K. (2001) Analysis of undisturbed tropical montain forest ecosystems in Southern Ecuador. *Die Erde*, Themenheft: Tropische Wald-Ökosysteme, **132**, 1-8.
- Benavides, J.C., Duque M., A.J., Duivenvoorden, J.F. & Cleef, A.M. (2006) Species richness and distribution of understorey bryophytes in different forest types in Columbian Amazonia. *Journal of Bryology*, **28**, 182-189.
- Braun-Blanquet, J. (1964) Pflanzensoziologie: Grundzüge der Vegetationskunde. pp. 865. Springer, Vienna.
- Brehm, G., Pitkin, L.M., Hilt, N. & Fiedler, K. (2005) Montane Andean rain forests are a global diversity hotspot of geometrid moths. *Journal of biogeography*, **32**, 1621–1627
- Bussmann, R. W. (2001) Epiphyte diversity in a tropical Andean forest- Reserva Biológica San Franzisco, Zamora Chinchipe, Ecuador. *Ecotropica*, **7**, 43-59.
- Clark, K.L., Nadkarni, N.M. & Gholz H.L. (1998) Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytes in a tropical montane forest. *Biotropica*, **30**, 12-23.
- Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.*, **67**, 345–366.
- Cornelissen, J.H.C. & Gradstein, S.R. (1990) On the occurrence of bryophytes and macrolichens in different lowland rain forest types at Marabu Hill, Guyana. *Tropical Bryology*, **3**, 29-35
- Cornelissen, J.H.C. & Ter Steege, H. (1989) Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *Journal of tropical ecology*, **5**, 131-150.
- Coxson, D.S. & Nadkarni, N.M. (1995) Ecological roles of epiphytes in nutrient cycles of forest ecosystems. In: Lowman, M. & Nadkarni, N. (eds), *Forest canopies*. Academic Press, San Diego. pp. 495–546.
- Frahm J.-P. (1987) Struktur und Zusammensetzung der epiphytischen Moosvegetation in Regenwäldern No-Perus. Beihefte zur *Nova-Hedwigia*, **88**, 115-141.



- Gradstein, S.R. & Pocs, T. (1989) Bryophytes. In: Lieth, H. & Werger, M.J.A. (eds), Tropical rain forest ecosystems. Elsevier Science Publishers B.V., Amsterdam. pp. 311-325.
- Gradstein, S.R., Montfoort, D. & Cornelissen J.H.C. (1990) Species richness and phytogeography of the bryophyte flora of the Guianas, with special references to the lowland forest. *Tropical Bryology*, **2**, 117-126.
- Gradstein, S.R. (1992) The vanishing tropical rain forest as an environment for bryophytes and lichens. In: Bates, J.W. & Farmer, A.R. (eds.), Bryophytes and lichens in a changing environment. Oxford University Press. pp. 232-256.
- Gradstein, S.R., Griffin, D., Morales, M.I. & Nadkarni, N.M. (2001) Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. *Caldasia*, **23**, 203-212.
- Gradstein, S.R., Nadkarni, N.M., Krömer, T., Holz, I. & Nöske, N. (2003) A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. *Selbyana*, **24**, 105-111.
- Hietz, P. & Briones, O. (1998) Correlation between water relations and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. *Oecologia*, **114**, 305-316.
- Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetatio*, **42**, 47-58.
- Hilt, N., Brehm, G. & Fiedler, K. (2006) Diversity and ensemble composition of geometrid moths along a successional gradient in the Ecuadorian Andes. *Journal of tropical Ecology*, **22**, 155-165.
- Holz, I., Gradstein, S.R., Heinrichs, J. & Kappelle, M. (2002) Bryophyte Diversity, Microhabitat Differentiation, and Distribution of Life Forms in Costa Rican Upper Montane *Quercus* Forest. *The Bryologist*, **105**, 334-348.
- Holz, I. (2003) Diversity and Ecology of Bryophytes and Macrolichens in Primary and Secondary Montane *Quercus* forests, Cordillera de Talamanca, Costa Rica. Dissertation, University of Göttingen.
- Holz, I. & GRADSTEIN, S.R. (2005) Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica - species richness, community composition and ecology. *Plant Ecology*, **178**, 89-109.

- Homeier J. (2005) *Purdiaea nutans* Planch. In: Schütt, P., Schuck, H.J., Lang, U. & Roloff, A. (eds), Enzyklopädie der Holzgewächse, 42, (1-4). Landsberg/Lech: Ecomed.
- Johansson, D. (1974) Ecology of vascular epiphytes in West African rain forest, Uppsala.
- Kelly, D.L., O'Donovan, G., Feehan, J., Murphy, S., Drangeid, S.O., & Marcano-Berti, L. (2004) The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora. *Journal of Tropical Ecology*, **20**, 643-666.
- Kürschner, H. & Parolly, G. (in press). Bryophytes of the Reserva Biológica San Francisco, Ecuador Part 2. Mosses. Ecol.Monogr.
- León-Vargas, Y., Engwald, S., & Proctor, C.F. (2006) Microclimate, light adaptation and desiccation tolerance of epiphytic bryophytes in two Venezuelan cloud forests. *Journal of Biogeography*, **33**, 901-913.
- León-Yanez, S., Gradstein, S.R. & Wegner, C. (2006) Hepáticas y antoceros del Ecuador. Herbario QCA, Quito.
- Mägdefrau, K. (1982) Life-forms of bryophytes. In: Smith, A. J. E. (ed), *Bryophyte Ecology*. London.
- Mc Cune, B., Amsberry, K.A., Camacho, F.J., Clery, S., Cole, C., Emerson, C., Felder, G., French, P., Greene, D., Harris, R., Hutten, M., Larson, B., Lesko, M., Majors, S., Markwell, T., Parker, G., Pendergrass, K., Peterson E.B., Peterson E.T., Platt, J., Proctor, J., Rambo, T., Rosso, A., Shaw, D., Turner, R. & Widmer, M. (1997) Vertical profile of epiphytes in a Pacific northwest old-growth forest. *Northwest Science*, **71**, 145-152.
- Mc Cune, B. & Mefford, M.J. (1999) PC-ORD Multivariate analysis of ecological data. Version 4. MjM Software Design, Gleneden Beach OR.
- Montfoort, D. & van Ek, R.C. (1990) Vertical distribution and ecology of epiphytic bryophytes and lichens in a lowland rain forest in French Guiana. Dissertation, Institute of Systematic Botany, Utrecht, 61 S.
- Nöske N. (2004) Effekte anthropogener Störung auf die Diversität kryptogamischer Epiphyten (Flechten, Moose) in einem Bergregenwald in Südecuador. Dissertation; University of Göttingen, 145 S.

- Nöske, N.M., Mandl N. & Sipman H.J.M. (in press) Lichens of the Reserva Biológica San Francisco, Ecuador. *Ecol. Monogr.*
- Parolly, G. & Kürschner, H. (2004a) Ecosociological studies in Ecuadorian bryophyte communities I. Syntaxonomy, life strategies and ecomorphology of the oreal epiphytic vegetation of S Ecuador. *Nova Hedwigia*, **78**, 1- 43.
- Parolly, G. & Kürschner, H. (2004b) Ecosociological studies in Ecuadorian bryophyte communities. II. Syntaxonomy of the submontane and montane epiphytic vegetation of S Ecuador. *Nova Hedwigia*, **79**, 377-424.
- Perry, D. R. (1978) A method of access into the crowns of emergent and canopy trees. *Biotropica*, **10**, 155-157.
- Pócs, T. (1982) Tropical forest bryophytes. In: Smith, A. J. E. (ed), *Bryophyte Ecology* London.
- Richards, P.W. (1984). The ecology of tropical forest bryophytes. In: Schuster R.M. (ed.), *New Manual of Bryology* Vol. 2. Nichinan. pp. 1233-1270.
- Richter, M. (2003) Using epiphytes and soil temperatures for eco-climatic interpretations in southern Ecuador. *Erdkunde*, **57**, 161-181.
- Rhoades F.M. (1995) Nonvascular epiphytes in forest canopies: worldwide distribution, abundance, and ecological roles. In: Lowerman M. D. & Nadkarni N.M. (eds), *Forest canopies*. Academic press, USA, New York, London.
- Schrumpf, M., Guggenberger, G., Valarezo, C., & Zech, W. (2001) Tropical montane rain forest soils: Development and nutrient status along an altitudinal gradient in the South Ecuadorian Andes. *Die Erde*, Themenheft: Tropische Wald-Ökosysteme, **132**, 43-59.
- Scott, G. A. M. (1994) Elementary reflections on the biology of bryophytes. *The Victorian Naturalist*, **111**, 112-115.
- Sillett, S.C., Gradstein, S.R., & Griffin, D. (1995) Bryophyte diversity of *Ficus* crowns from cloud forest and pasture in Costa Rica. *The Bryologist*, **98**, 251-260.
- Simpson, N. (2004) Saving threatened plants and birds in the Andes of Ecuador. *Plant Talk*, **37**, 17- 21.

- Sipman, H.J.M. (1995) Preliminary review of the lichen biodiversity of the Colombian montane forests. In: Churchill, S.P. (ed), Biodiversity and conservation of Neotropical montane forests. Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium. The New York Botanical Garden, pp. 313-320.
- Ter Steege, H. & Cornelissen, H.J.C. (1988) Collecting and studying bryophytes in the canopy of standing rain forest trees. In: Glime, J. M. (ed.), Method in bryology. Proceedings of the Bryological Methods Workshop, Mainz, pp. 285-290.
- Thiers, B. M. (1988) Morphological adaptations of the Jungermanniales (Hepaticae) to the tropical rainforest habitat. *Journal of the Hattori Laboratory*, **64**, 5-14
- Van Reenen, G.B.A. & Gradstein, S.R. (1983) Studies on Colombian Cryptogams XX: A transect analysis of the bryophyte vegetation along an altitudinal gradient on the Sierra-Nevada de Santa-Marta, Colombia. *Acta Botanica Neerlandica*, **32**, 163-175.
- Veneklaas, E.J. & van Ek, R. (1990) Rainfall interception in two tropical montane rain forests, Colombia. *Hydrological Processes*, **4**, 311-326.
- Weigend M (2002) Observations on the Biogeography of the Amotape-Huancabamba Zone in Northern Peru. *The Botanical Review*, **68**, 38-54
- Wolf, J.H.D. (1993a) Epiphyte communities of tropical montane rain forests in the northern Andes. Lower montane communities. *Phytocoenologia*, **22**, 1-52
- Wolf, J.H.D. (1993b) Epiphyte communities of tropical montane rain forests in the northern Andes. Upper montane communities. *Phytocoenologia*, **22**, 53-103
- Wolf, J.H.D. (1993c) Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annals of the Missouri Botanical Garden*, **80**, 928-960
- Wolf, J.H.D. (1994) Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio*, **112**, 15-28.
- Zotz, G. & Hietz, P. (2001) The physiological ecology of vascular epiphytes: current knowledge, open questions. *J. Exp. Bot.*, **52**, 2067-2078.
- Zotz, G. (2007) Johansson revisited: the spatial structure of epiphyte assemblages. *Journal of Vegetation Science*, **18**, 123-130.

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## **V. Chapter**

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### **A comparison of diversity and distribution patterns of lichens, liverworts, mosses, and ferns in an Andean montane rainforest**

Nicole Mandl, Marcus Lehnert, Michael Kessler and S. Robbert Gradstein

**ABSTRACT**

We present the first comparison of diversity and distribution patterns of lichens, liverworts, mosses, and ferns, in tropical montane rainforests. We analyzed the patterns of both alpha diversity (i.e., species richness) and beta diversity (i.e., species turnover) and asked if specific taxa may be used as surrogates for other taxa. At three localities in southern Ecuador, we surveyed terrestrial and epiphytic assemblages on ridge and slope forests in 28 plots of 400m<sup>2</sup> each.

The epiphytic habitat was significantly richer in ferns, liverworts, and lichens than the terrestrial habitat; only mosses were primarily terrestrial. Patterns of alpha diversity were congruent for ferns and liverworts in both habitat types, whereas mosses only showed similarities with ferns and liverworts in the epiphytic habitat and lichens did not share patterns with any other group. Beta diversity of all studied plant groups (lichens not included due to low species richness) was similar in the terrestrial habitat, but not in the epiphytic habitat. Our results demonstrate that patterns of alpha diversity of the four plant groups can not be used to predict patterns of beta diversity. Moreover diversity patterns observed in epiphytes are not the same as in terrestrials. There appears to be good evidence for a general coincidence in species patterns of liverworts and ferns. Diversity patterns of macrolichens on the other hand are completely independent from any other taxonomic group studied.

## INTRODUCTION

Tropical forests are well known for their high species richness. While fascinating, this richness poses enormous problems to biologists aiming to survey plant and animal communities. Complete biological inventories of tropical vegetation types are impossible for animals and very rare for plants, where researchers have usually focused on selected taxonomic or ecological taxa (e.g., Valencia et al. 2004). One of the crucial questions arising from this approach is to which degree the spatial patterns of species richness and community composition agree between different groups of organisms, i.e., to which degree selected taxa can be used as surrogate taxa for others. In the tropics, such studies on plants have mostly focused on lowland forests (e.g., Duivenvoorden, 1994, 1996, Tuomisto & Ruokolainen 2005) and have usually excluded most or all non-flowering plants as well as lichens. Nevertheless, tropical forests often favor rich diversities of ferns, bryophytes and lichens. Especially in tropical montane rain forests a continuous layer of these organism groups may be observed on trunks and branches of trees (Pócs 1982, Gradstein 1992, Sipman 1995) and even be abundant on the forests floor. Due to their importance for the tropical montane ecosystems these organism groups should not be neglected as possible indicator species for the diversity state of an area.

Lichens, liverworts, mosses, and ferns have traditionally been grouped under the term cryptogams referring to all taxa which reproduce by spores rather than seeds (Scott 1994). This classification is not a natural one, but ecological and physiological similarities between the four groups are undeniable. Most importantly, they all show a close interrelationship with abiotic environmental factors. Especially air humidity is constraining the poikilohydric bryophytes, lichens and some fern families (e.g. Hymenophyllaceae). Another good reason for combining all these taxonomic groups in one survey is their frequent and abundant occurrence within the same habitat types, as is the case in the abovementioned tropical montane forests.

Unfortunately, species of these diverse taxonomic groups are mostly difficult to identify in the field and generally require time-consuming identification work. As a consequence, datasets that include all four groups are rare. Most studies deal with only one or two groups at a time (e.g., Gradstein 2001, Kessler 2002, Holz 2005, Tuomisto et al. 2002, Ruokolainen et al. 2007, Kluge & Kessler in press). In the Andes of Venezuela, Kelly et al. (2004) studied epiphytic communities of vascular and non-vascular plant groups, and in

Australian dry forests Pharo et al. (1999) surveyed vascular plant diversity as a surrogate for bryophyte and lichen diversity. To our knowledge, this is the first study on diversity and distribution patterns of lichens, liverworts, mosses, and ferns that separates in terrestrial and epiphytic taxa.

In this study, we therefore link alpha and beta diversity of all four taxonomic groups in two forest types (ridge forest, slope forest) and two habitat types (terrestrial, epiphytic) at three different study sites in the Andes of southern Ecuador. The principal goal of this survey was to test whether one of our study groups may be used as a surrogate for one or more of the other groups in order to facilitate predictions on the diversity state of an area.

## METHODS

### Study area and study sites

This study took place at three different study sites, the Reserva Biológica San Francisco (RBSF), the mountain pass El Tiro, and the Tapichalaca Reserve, all situated in the surroundings of Podocarpus National Park in southeastern Ecuador (Fig. 1). We studied undisturbed upper montane ridge and slope forests at 2400 – 2650 m. Fire events and human agriculture has been recorded in the area dating back to about 800 years (Nieder & Behling in press). The regional climate is cool and perhumid with precipitation ranging from ca. 3000 mm annually at El Tiro to ca. 4000 mm at Tapichalaca and over 5000 mm at RBSF (Richter 2003). At all three localities temperature maxima occasionally rise up to 25°C and air humidity drops down to 25% in late autumn. Soils do not differ significantly among the three study sites and consist of poor, acidic (pH 4.6 - 4.1) cambisols and gleysols (Mandl et al. in press).

The **RBSF** is situated on the southern slope of the San Francisco river valley north of the Cordillera El Consuelo. The reserve covers ca. 1000 ha of mountain rainforest and páramo vegetation, ranging between 1800 m and 3140 m (Beck & Müller-Hohenstein 2001). At 2150-2650 m the shrubby upper montane forest is mono-dominated by *Purdiaea nutans* (Clethraceae).

The mountain pass **El Tiro** is situated at ca. 2800 m along the Loja-Zamora road, 15 km W of the RBSF and on the border of Loja and Zamora-Chinchi provinces, on the crest



of the cordillera. Our study site was located some 200-450 m below the actual pass towards the east, in an area of very topography with many small ravines and ridges overgrown by low-statured, shrubby cloud forest.

The **Tapichalaca** Reserve is situated at ca. 2000-3400 m along the Loja-Zumba road in the Cordillera Real, ca. 90 km south of the town of Loja and just south of Podocarpus National Park. The area supports very wet montane cloud forest and páramo (Simpson 2004). For a more detailed description of the study sites we refer to Mandl et al. (in press) and Gradstein et al. (submitted).



**Fig. 1.** Map of the study region showing the location of the study sites.

### Sampling method

Field research was carried out from July 2003 to January 2003 and from August 2004 to January 2004. Lichens, liverworts, mosses, and ferns were inventoried in 28 plots of 20 m x 20 m or an equivalent surface area, 12 plots in ridge forest and 16 in slope forest. Ridges and slopes were distinguished by their topographic position as well as their mean inclination, never exceeding 25% on ridges and ranging from 30 to 50% on slopes. In each locality we

sampled at least 3 replicates for every forest type. Study plots were selected based on habitat homogeneity, avoiding extremely steep and disturbed sites. Ferns were recorded as distinguishable morpho-species in the field. Abundance and life form (epiphyte, terrestrial) were noted for all species in each plot. Due to the small size of bryophyte and lichen taxa, their presence and abundance was estimated in sub-samples. In each plot four sub-samples were taken from the terrestrial layer. For sampling epiphytic assemblages, one to two trees per plot were rigged and climbed using single rope techniques (Perry 1978). Sub-samples were taken from different height zones, relative to the position in the host tree; zone 1 - stem base, zone 2 - trunk, zone 3 - inner canopy, zone 4 - middle canopy, zone 5 - outer canopy (Johansson, 1974).

On slopes all five zones were sampled, whereas on ridges, according to the smaller tree size, only zone 1, 3 and 5 were considered. Dimension of sub-samples comprised 600 cm<sup>2</sup> (terrestrials, zones 1-3) and 60 cm long branches (upper half cylinder, zone 4) and twigs (zone 5), reflecting differences in the habitat structure and evenness of the assemblages.

### Data analyses

To avoid misinterpretations of data analyses due to differences in sampling completeness for different taxonomic groups, the percentage of the observed species richness relative to the estimated species richness was calculated using Chao 2 richness estimator as recommended by Walter & Moore (2005) (Table 1). Calculations of sampling completeness were done separately for epiphytic and terrestrial species and in a second run for ridge and slope forests.

Additive partitioning (Wagner et al. 2000, Christ et al. 2003, Gering et al. 2003) was used to describe the contribution of different spatial scales to overall species richness per taxonomic group. Alpha 1 was calculated as the mean species density recorded in all sub-samples, alpha 2 as the mean number of species in the 28 plots, alpha 3 as the mean richness per habitat type, alpha 4 as the mean richness per study locality, and alpha 5 as the total richness. Beta diversity was expressed as the difference between the levels of alpha diversity;  $\beta_1 = \alpha_2 - \alpha_1$ ,  $\beta_2 = \alpha_3 - \alpha_2$ , and  $\beta_3 = \alpha_4 - \alpha_3$  (Wagner et al. 2000, Crist et al. 2003).

We used Mantel analyses to calculate the relationship between species richness of the different taxonomic groups, and between species turnover. The correlation of species richness per plot between taxonomic groups was calculated through Mantel analyses with matrices filled with the difference between sites in terms of species richness. Similarities between

species assemblages were estimated with the quantitative Sørensen similarity index (Bray-Curtis index) which also takes into account species abundances (Magurran 2004). All Mantel analyses were conducted with PCOrd 4.5 (McCune & Mefford 1999) applying 9999 randomization runs.

## RESULTS

### Alpha diversity

For the terrestrial habitat we recorded a total of 256 species, with species richness per group varying greatly, ranging from a low of 7 lichen species to a high of 116 fern species (Table 1).

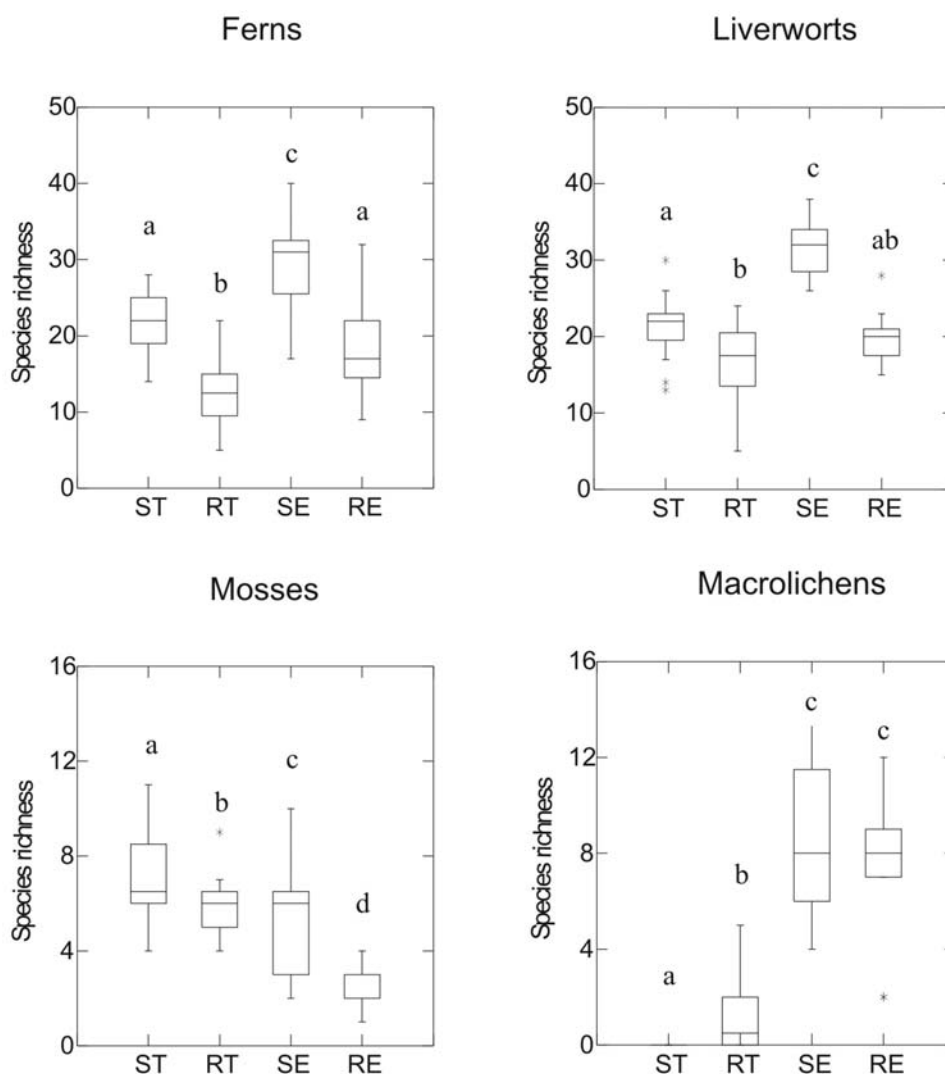
The epiphytic habitat was richer in species with a total of 319 species. Liverworts and especially lichens (67 species) gained in importance, while species richness of ferns and mosses slightly declined (Table 1). Sampling completeness ranged from 54% for terrestrial lichens to 86% for epiphytic liverworts, being generally higher for epiphytes (Table 1).

Within both habitats, sampling completeness was similar for liverworts, mosses and ferns, and lower among macrolichens.

**Table 1.** Number of observed species in 28 plots ( $S_{\text{obs}}$ ), estimated total number of species in the study region (Chao2 estimator,  $S_{\text{est}}$ ), sampling completeness (% $S_{\text{obs}}$  of  $S_{\text{est}}$ )

Terrestrials	$S_{\text{obs}}$	$S_{\text{est}}$ (Chao2)	Sampling completeness (%)
Lichens	7	13	54
Liverworts	87	126	69
Mosses	43	55	78
Ferns	116	147	79
Epiphytes			
Lichens	67	102	66
Liverworts	119	138	86
Mosses	33	39	85
Ferns	100	117	85

Patterns of species richness per site varied strongly between different taxonomic groups (Fig. 2), with the exception of liverworts and ferns. The latter resembled in actual species richness per plot and their patterns of alpha diversity were congruent along different habitat types. In both forest types the epiphytic habitat was significantly richer in ferns, liverworts and lichens. Mosses were the only primarily terrestrial group. Generally, species richness declined from slopes to ridges, with the exception of terrestrial lichens which were completely missing on slopes.



**Fig. 2.** Species richness of four study groups in different habitat types (ST = slopes, terrestrial; RT = ridges, terrestrial; SE = slopes, epiphytic; RE = ridges, epiphytic). Lower case letters designate statistically different means (ANOVAs with post-hoc Tukey tests).

According to a comparison of differences in alpha diversity through the Mantel analyses epiphytic fern species richness was positively related to that of epiphytic liverworts

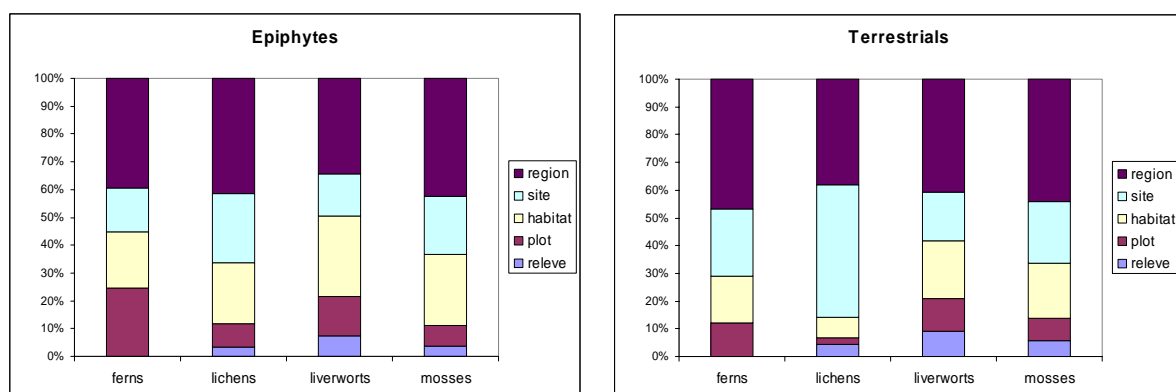
and mosses ( $r=0.64$ ), and liverwort richness to mosses ( $r=0.54$ ), but no correlations with epiphytic lichens were found (Table 2). For terrestrials, only fern and liverwort species richness were significantly correlated to each other. Lichens showed slightly negative correlations with liverworts and ferns. Mantel correlation coefficients were significantly correlated with sampling completeness ( $R= 0.87, P=1$ ).

**Table 2.** Correlations (R values) between the four study groups of E) epiphytic and T) terrestrial species richness per plot. Values obtained by Mantel analyses. \*  $p < 0.05$ , \*\*  $p < 0.001$ , \*\*\*  $p < 0.0001$ .

	Lichens		Liverworts		Mosses	
	E	T	E	T	E	T
Ferns	0.28	-0.32	0.64**	0.53**	0.54*	0.21
Lichens			0.16	-0.24	0.16	0.02
Liverworts					0.53**	0.15

### Beta diversity

Additive partitioning of species on the plot level varied greatly among different taxonomic groups but showed similar patterns for epiphytes and terrestrials (Fig. 3). Ferns were the only group with a significant difference in the relative species richness for the two habitat types ( $t=4.84, p=0.000$ ). The plot level (alpha 2) of the terrestrial habitat only yielded 12% of regional species richness, as compared to 25% in the epiphytic habitat. Additive patterns of species richness for terrestrial macrolichens are not representative due the very low sampling completeness. Overall, epiphytes showed less variation on the regional scale than terrestrials.



**Fig. 3.** Mean percentage of species found in a single sub-samples, forest- or habitat type relative to the total number of species found in the region.

The Mantel test of quantitative Sørensen's indices between taxonomic groups gave significant positive correlations for all groups (lichens excluded) in the terrestrial habitat, whereas only very low correlations were found in the epiphytic habitat (Table 3). The only significant correlation of lichens was with epiphytic ferns.

**Table 3.** Correlations (R values) between similarity matrices of Sørensen's quantitative (Bray Curtis) similarity index of E) epiphytic and T) terrestrial species compositions per plot between the four study groups. \*  $p < 0.05$ , \*\*  $p < 0.001$ , \*\*\*  $p < 0.0001$ .

	Lichens		Liverworts		Mosses	
	E	T	E	T	E	T
Ferns	0.15*	-	0.13*	0.25**	0.18**	0.37***
Lichens			-0.13	-	-0.01	-
Liverworts					0.12	0.50***

## DISCUSSION

This is the first study comparing patterns of alpha and beta diversity among mosses, liverworts, ferns, and lichens in a tropical montane forest. Importantly, we separated between epiphytic and terrestrial assemblages as well as between ridge and slope forests because of the different environmental conditions in these habitats. For bryophytes, it is well known that the most important characteristics of different forest types are those that affect their structure and internal microclimate (Richards, 1984). Similarly, the composition of fern assemblages is strongly determined by soil characters (for terrestrials) and vegetation structure and microclimate (both terrestrials and epiphytes) (Kluge & Kessler in press).

### Alpha diversity

In total, we identified 446 species in our four study groups, of which 127 species were terrestrial, 190 epiphytic, and 129 facultative. The epiphytic habitat was noticeably richer in species than the terrestrial habitat. The different taxonomic groups varied in their occurrence in the different habitat types. Whereas mosses had their focus of distribution in the terrestrial habitat, liverworts, ferns and lichens were best represented in the epiphytic habitat. Slope

forests were generally richer in species than ridges forests. This pattern is presumably linked to the differences in forest structure between the two forest types. Probably, the higher trees in slope forests provide more varied and more favorable microhabitat conditions as well as more space for different species to coexist (Mandl et al. in prep).

Overall, on average only 5% ( $\pm$  31% SD) of the variance in species richness of one taxonomic group could be predicted by species richness of another. Considering only the epiphytic habitat this value increased to 15% ( $\pm$  20%). However, these mean values conceal major variability. Patterns of alpha diversity were highly congruent for ferns, liverworts and mosses in the epiphytic habitat ( $R^2 = 0.28-0.41$ ) and for ferns and liverworts to a lesser degree in the terrestrial habitat ( $R^2 = 0.28$ ). In contrast, macrolichens did not show significant correlations of species richness with any other group. In the terrestrial habitat relatively weak negative correlations were found between macrolichens and ferns respectively bryophytes, in the epiphytic habitat weak positive correlations were recorded. When macrolichens were omitted, however, no less than 32% of the variance in epiphytic species richness of a given group was explained by other taxa.

These results are in accordance with patterns observed in coastal lowland forests of eastern Australia (Pharo et al. 1999), but contradict results from forests of the Azores, in which no correlations between bryophytes, macrolichens and vascular plant cover were found (Gabriel & Bates 2005). Both studies, however, did not separate between liverworts and mosses, and between epiphytic and terrestrial species. Overall, numerous studies have found that patterns of alpha diversity between different higher level taxa usually only show limited correlation (e.g., Lawton et al. 1998, Schulze et al. 2004, Tuomisto & Ruokolainen 2005).

### **Beta diversity**

The variability of beta diversity as revealed by additive partitioning showed that species turnover depends very much on the spatial scale considered. Generally, we have found more variation in species richness between the different taxonomic groups within smaller scales than on the regional scale. Nevertheless, by adding all species of one taxonomic group of one study site we still only reached about 55% - 65% of regional species richness, with the tendency of higher proportions reached in the epiphytic habitat. This marked regional differentiation is noteworthy bearing in mind the spore dispersal of our study groups and the fact that the majority of species are widespread, occurring well beyond the range spanned by our study sites (Gradstein et al. in press, Kürschner & Parolly in press, Lehnert et al. in press,

Nöske et al. in press). Causes for this regional differentiation may involve slight climatic and geological differences between the three study sites (Mandl et al. in press) as well as stochastic events.

Another noteworthy finding was that ferns showed greater differences between terrestrial and epiphytic patterns at the plot level than any other study group. While in the terrestrial habitat about 12% of total diversity was reached by sampling one plot, this amount was more than doubled in the epiphytic habitat. The fact that the majority of terrestrial ferns are relatively large (e.g., Cyatheaceae, Dryopteridaceae) compared to the majority of epiphytic taxa (e.g., Hymenophyllaceae, Polypodiaceae) is a possible explanation for the lower density of terrestrial fern species on the relatively small plots.

Correlations of beta diversity between the studied plant groups (lichens not included due to low species richness) were higher in the terrestrial than in the epiphytic habitat and most pronounced for mosses and liverworts. Overall, congruence of beta diversity patterns between study groups was lower than that of alpha diversity. This implies that at least for our studied taxa the use of an indicator group as a surrogate for others is more applicable for species richness than for community composition. This finding contrasts with studies among vascular plants in lowland Amazonia, where patterns of beta diversity were predicible than those of alpha diversity (Tuomisto & Ruokolainen 2005).

Comparing patterns of alpha and beta diversity, correlations of alpha diversity were stronger in the epiphytic habitat whereas correlations of beta diversity were stronger in the terrestrial habitat. One possible explanation could lie in the differing distribution of spatial heterogeneity in these two habitats. The epiphytic habitat is predominately formed by mature canopy trees, all structured more or less in the same way, with stem base, trunk, inner branches, middle branches and outer twigs (Johansson 1974). This implies that variation in habitat conditions are distributed vertically and by sampling all height zones within a single tree, most of the microhabitat variability of a site is taken into account. In contrast, the terrestrial habitat consists of a mosaic of microhabitats influenced mainly by microtopography, geology, soil, vegetation cover, inclination, and the amount of decaying wood (e.g., Kluge & Kessler in press). These microhabitats are scattered within a given forest habitat over distances exceeding the size of individual plots. In small plot sizes of 20 x 20m it is likely to miss out on some of the ecological variability within the terrestrial habitat. Nevertheless, if spatial heterogeneity of the epiphytic habitat was indeed distributed within a smaller scale we should also expect significantly higher alpha diversities for all taxonomic groups. However, this is only true for ferns and was already explained by differences in the



size of terrestrial and epiphytic species. We are therefore at present unable to explain the conspicuous differences in alpha and beta diversity between the epiphytic and terrestrial habitats.

## CONCLUSIONS

Our data reveal that the four taxonomic categories integrated in the term cryptogams do not share universally valid patterns for neither alpha nor beta diversity. Their response to environmental gradients as observed in different forest and habitat types cannot easily be generalized. Furthermore, our results demonstrate that diversity patterns for epiphytes and terrestrials are distinct and should be treated separately. Ferns and liverworts show most similar patterns of alpha and beta diversity, and are most likely to work as surrogates for one another. Diversity patterns of macrolichens on the other hand are completely independent from those of the other taxonomic groups studied.

## REFERENCES

- Beck, E. & Müller-Hohenstein, K. (2001) Analysis of undisturbed tropical mountain forest ecosystems in Southern Ecuador. *Die Erde, Themenheft: Tropische Wald-Ökosysteme* 132, 1-8.
- Churchill S.T., Balslev H., Forero E. and Luteyn J.L. 1995. Biodiversity and conservation of Neotropical montane forests. *Proceedings of the Neotropical montane forest biodiversity and conservation 131 symposium. The New York Botanical Garden, 21–26 June 1993.* New York Botanical Garden, New York.
- Crist, T.O., Veech, J.A., Gering, J.C. & Summerville, K.S. (2003) Partitioning species diversity across landscapes and regions: A hierarchical analysis of  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity. *The American Naturalist* 162, 734-743.
- Duivenvoorden, J.F. (1994) Vascular plant species counts in the rain forests of the middle Caquetá area, Colombian Amazonia. *Biodiversity and Conservation* 3, 685-715.

- Duivenvoorden, J.F. (1996) Patterns of tree species richness in rain forests of the middle Caquetá area, Colombia, NW Amazonia. *Biotropica* 28, 142-158.
- Favreau, J., Drew, C., Hess, G., Rubino, M., Koch, F. & Eschelbach, K. (2006) Recommendations for Assessing the Effectiveness of Surrogate Species Approaches. *Biodiversity and Conservation* 15, 3949-3969.
- Gabriel, R. & Bates, J. W. (2005) Bryophyte community composition and habitat specificity in the natural forests of Terceira, Azores. *Plant Ecology*, 177, 125-144.
- Gradstein, S.R. (1992) The vanishing tropical rain forest as an environment for bryophytes and lichens. In: *Bryophytes and lichens in a changing environment* (Bates, J. W. & Farmer, A.R. eds.). Oxford University Press. pp. 232-256.
- Gradstein, S.R. (1995) Diversity of Hepaticae and Anrthocerotae in montane forests of the tropical Andes. In: *Biodiversity and conservation of Neotropical montane forests. Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium* (Churchill, S. P. ed). The New York Botanical Garden. pp. 321-334.
- Gradstein, S.R., Griffin, D., Morales, M.I., & Nadkarni, N.M. (2001) Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. *Caldasia*, 23, 203-212.
- Holz, I. & Gradstein, S.R. (2005) Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica - species richness, community composition and ecology. *Plant Ecology* 178, 89-109.
- Johansson, D. (1974) Ecology of vascular epiphytes in West African rain forest, Uppsala.
- Kelly, D.L., O'Donovan, G., Feehan, J., Murphy, S., Drangeid, S.O. & Marciano-Berti, L. (2004) The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora. *Journal of Tropical Ecology* 20, 643-666.
- Kessler, M. (2002) Environmental patterns and ecological correlates of range-size among bromeliad communities of Andean forests in Bolivia. *Bot Rev* 68, 100-127.
- Kluge, J. & Kessler, M. (in press) Microhabitat segregation of pteridophytes along an elevational gradient in Costa Rica. *Journal of Tropical Ecology*.
- Kürschner, H. & Parolly, G. (in press). Bryophytes of the Reserva Biológica San Francisco, Ecuador Part 2. Mosses. *Ecotropica Monographs*.

- Lawton, J.H., Bignell, D. E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R. D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S. & Watt, A.D. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest, *Nature* 391, 72-76.
- Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell, Oxford, UK.
- Mandl, N., Lehnert, M., Gradstein, S.R., Kessler, M., Abiy, M. & Richter, M. (in press) The unique *Purdiaea nutans* forest of southern Ecuador - abiotic characteristics and cryptogamic diversity. In: *Gradients in a tropical mountain ecosystem of Ecuador* (Beck, E., Bendix, J., Kottke, I., Makeschin, F., & Mosandl R. eds.). *Ecological Studies*, Springer Verlag, Berlin, Heidelberg.
- Mc Cune, B. & Mefford, M. J. (1999) *PC-ORD Multivariate analysis of ecological data. Version 4*. MjM Software Design, Gleneden Beach OR.
- Niemann, H. & Behling, H. (in press) Past vegetation and fire dynamics. In: *Gradients in a tropical mountain ecosystem of Ecuador* (Beck, E., Bendix, J., Kottke, I., Makeschin, F., & Mosandl R. eds.). *Ecological Studies*, Springer Verlag, Berlin, Heidelberg.
- Nöske, N.M., Mandl, N. & Sipman, H.J.M. (in press) Lichens of the Reserva Biológica San Francisco, Ecuador. *Ecotropica Monographs*.
- Perry, D.R. (1978) A method of access into the crowns of emergent and canopy trees. *Biotropica*, 10, 155-157.
- Pharo, E.J. & Beattie, A.J. (1997) Bryophyte and lichen diversity: A comparative study. *Austral Ecology* 22, 151-162.
- Pharo, E.J., Beattie, A.J. & Binns, D. (1999) Vascular plant diversity as a surrogate for bryophyte and lichen diversity. *Conservation Biology*. *The Bryologist* 102, 320-326.
- Pharo, E.J., Beattie, A.J. & Pressey, R.L. (2000) Effectiveness of using vascular plants to select reserves for bryophytes and lichens. *Biological Conservation* 96, 371-378.
- Pócs, T. (1982) Tropical forest bryophytes. In: *Bryophyte ecology* (Smith, A. J. E. ed), London. pp. 59-104.
- Richards, P.W. (1954) Notes on the bryophyte communities of lowland tropical rain forest, with special reference to Moraballi Creek, British Guiana. *Vegetatio* 5-6, 319-328.

- Richards, P.W. (1984) The ecology of tropical forest bryophytes. In: *New Manual of Bryology* Vol. 2 (Schuster R.M. ed ). Nichinan. pp. 1233-1270.
- Ruokolainen, K., Tuomisto, H., Macía, M.J., Higgins, M.A. & Yli-Halla, M. (2007) Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae? *Journal of Tropical Ecology* 23, 13-25.
- Schulze, C.H., Waltert, M., Kessler, P.J A., Pitopang, R., Shahabuddin, Veddeler D., Muhlenberg, M., Gradstein, S.R., Leuschner C., Steffan-Dewenter, I. & Tschardtke, T. (2004) Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. *Ecological Applications* 14, 1321-1333.
- Scott, G.A.M. (1994) Elementary reflections on the biology of bryophytes. *The Victorian Naturalist* 111, 112-115.
- Sipman, H.J.M. (1995) Preliminary review of the lichen biodiversity of the Colombian montane forests. In: *Biodiversity and conservation of Neotropical montane forests. Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium* (Churchill, S. P. ed). The New York Botanical Garden. pp. 313-320.
- Tuomisto, H., Ruokolainen, K., Poulsen, A.D., Moran, R.C., Quintana, C., Canas, G. & Celi, J. (2002) Distribution and diversity of pteridophytes and Melastomataceae along edaphic gradients in Yasuni National Park, Ecuadorian Amazonia. *Biotropica* 34, 516-533.
- Tuomisto, H. & Ruokolainen, K. (2005) Environmental heterogeneity and the diversity of pteridophytes and Melastomataceae in western Amazonia. *Biologiske Skrifter* 55, 37-56.
- Valencia R., Foster R.B., Villa G., Condit R., Svenning J.-C., Hernández C., Romoeroux K., Losos E., Magard E. & Balslev H. (2004) Tree species distribution and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology* 92, 214-229.
- Wagner, H.H., Wildi, O. & Ewald, K.C. (2000) Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology* 15, 219-227.
- Walther, B. & Moore, J.L. (2005) The concept of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* 28, 815-829.

Wolf, J.H.D. (1994) Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio* 112, 15-28.

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## Summary

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This study confirms that the unique *Purdiaea nutans* forest in the upper montane belt of the Reserva Biológica San Francisco in southern Ecuador is an azonal ridge vegetation type. Our assumption that the mass occurrence of *Purdiaea* may be caused by extremely poor soils was not confirmed. From our point of view the development of this monodominant forest was more likely triggered by historical fire events and a combination of site specific abiotic factors, related to topography, geology, pedology, and macroclimate.

Neither the terrestrial nor the epiphytic bryophyte and macrolichen species richness or composition were affected by the unusual tree species composition, but instead represent typical upper montane ridge communities of the region.

Distribution of bryophytes and Macrolichens is primarily determined by differences in microclimatic conditions. Habitat differences between slope forest and ridge forest, and small scale habitat heterogeneity within ridges, define microclimatic conditions and are therefore responsible for the variability of terrestrial bryophyte and Macrolichen assemblages in upper montane forests in southern Ecuador. In the epiphytic habitat, microclimatic conditions follow a vertical gradient rather than a horizontal one.

Accordingly, different species assemblages, indicator species and life forms are observed in different positions within the tree. Tree crowns are inhabited by rather small, desiccation-tolerant and wind-approved bryophytes and Macrolichens, whereas on trunks taller, shade tolerant bryophytes predominate.

The higher species richness recorded from other Neotropical upper montane forests is mostly due to high species numbers of mosses and Macrolichens; liverworts are relatively more pronounced in our study sites. The extremely high precipitation of the area favours liverworts and strong winds constrain the growth of projecting or hanging species such as Meteoriaceae and macrolichens typical for outer canopies elsewhere.

A taxonomic comparison of alpha and beta diversities reveals no universally valid pattern for lichens, liverworts, mosses, and ferns. The results indicate that diversity patterns for epiphytic and terrestrial species are distinct and should be treated separately. Among the

studied taxonomic groups, ferns and liverworts show most similar patterns of alpha and beta diversity and therefore are most likely to work as surrogates for one another.

# Appendix

**Table A-1.** Frequencies of mosses, liverworts and macrolichens in the epiphytic and the terrestrial habitat.

**Life forms:** **f** foliose, **fr** fruticose, **sq** squamulose; **de** dendroids, **fa** fans, **ma** mats, **pd** pendants, **ta** tails, **sT** short turfs, **tT** tall turfs and **w** wefts

**Chorotype:** **A** Andean, **A-n** northern Andean (Costa Rica to northern Peru), **A-S** southern Andean, **Am-C** Central American (incl. Caribbean), **Am-S** South American, **Am-Afr** American African, **End** Endemic (Ecuador), **Neotrop** Neotropical, **Pantrop** pantropical, **Temp** Temperate, **Temp-s** southern Temperate, **nE** new to Ecuador, **nS** new species

	epiphytic habitat	terrestrial habitat	Life form	Chorotype
<b>I. Mosses</b>				
<b>Bartramiaceae</b>				
<i>Breutelia polygastrica</i> (Müll. Hal.) Broth.		7	m,tT	A
<b>Brachytheciaceae</b>				
<i>Aerolindigia capillacea</i> (Hornsch.) Menzel	1		ta	Pantrop
<b>Bryaceae</b>				
<i>Bryum</i> sp.		3	sT	-
<i>Bryum</i> sp. A		2	sT	-
<i>Rhodobryum grandifolium</i> (Taylor) Schimp.		1	de	Am-C, S
<b>Calympereaceae</b>				
<i>Syrrophodon lycopodioides</i> (Sw. ex Brid.) Müll. Hal.	1		sT	Am-C, S
<i>Syrrophodon prolifer</i> Schwägr.	10		sT	Pantrop
<b>Crypheaceae</b>				
<i>Schoenobryum rubricaula</i> (Taylor) Manuel	2		?	A-n
<b>Daltoniaceae</b>				
<i>Leskeodon andicola</i> (Spruce ex Mitt.) Broth.		1	m	Am-C, S
<b>Dicranaceae</b>				
<i>Atractylocarpus longisetus</i> (Hook.) Bartr.		7	tT	A-n
<i>Campylopus anderssonii</i> (Müll. Hal.) A.Jaeg.		3	tT	Am-C, S
<i>Campylopus arctocarpus</i> (Hornsch.) Mitt.	13	1	tT	Am-C, S
<i>Campylopus asperifolius</i> Mitt.	1		tT	A-n
<i>Campylopus fragilis</i> (Brid.) Bruch & Schimp.	3	7	tT	Temp-n
<i>Campylopus huallagensis</i> Broth.	17	53	tT	A
<i>Campylopus richardii</i> Brid.		14	tT	Am-C, S
<i>Campylopus</i> sp. A		3	tT	-
<i>Holomitrium arboreum</i> Mitt.	6		tT	Am-C, S
<i>Holomitrium pulchellum</i> Mitt.	4		tT	Am-C, S
<i>Holomitrium sinnosum</i> B.H.Allen	3	1	tT	A-n
<b>Fissidentaceae</b>				
<i>Fissidens steerei</i> Grout		1	ta	Am-C, S
<i>Fissidens</i> sp.	1		sT	-



	epiphytic habitat	terrestrial habitat	Life form	Chorotype
<b>Hypnaceae</b>				
<i>Isopterygium</i> sp.		1	m	-
<b>Leucobryaceae</b>				
<i>Leucobryum antillarum</i> Schimp.	2	1	tT	Am-C, S
<i>Leucobryum giganteum</i> Müll. Hal.	2	1	tT	Am-C, S
<b>Leucomiaceae</b>				
<i>Leucomium</i> cf. <i>strumosum</i> (Hornsch.) Mitt.	1	15	m	Pantrop
<b>Leucophanaceae</b>				
<i>Leucophanes molleri</i> Müll. Hal.	1		m	Am-Afr
<b>Macromitriaceae</b>				
<i>Macromitrium cirrosum</i> (Hedw.) Brid.	2		sT	Am-C, S
<i>Macromitrium perreflexum</i> Steere	1	39	tT	End
<i>Macromitrium</i> sp.	5		sT	-
<i>Macromitrium ulophyllum</i> Mitt.	9		sT	A-n
<i>Schlotheimia torquata</i> (Hedw.) Brid.	1		sT	Am-C, S
<b>Meteoriaceae</b>				
<i>Pilotrichella flexilis</i> (Hedw.) Ångst.	3		pd	Am-C, S
<i>Squamidium leucotrichum</i> (Taylor) Broth.	1		pd	Am-C, S
<b>Phyllogoniaceae</b>				
<i>Phyllogonium fulgens</i> (Hedw.) Brid.	4	6	pd,m	Am-C, S
<b>Pilotrichaceae</b>				
<i>Cyclodictyon rubrisetum</i> (Mitt.) O. Kuntze		3	m	Am-C, S
<i>Hypnella diversifolia</i> (Mitt.) A. Jaeg	3	12	m	Am-C, S
<i>Hypnella pilifera</i> (Hook. f. & Wils.) A. Jaeg.		32	m	Am-C, S
<b>Prionodontaceae</b>				
<i>Prionodon densus</i> Hedw.	4		ta	Pantrop
<b>Pterobryaceae</b>				
<i>Pterobryum densum</i> (Schwägr.) Hornsch.	2		fa	Neotrop
<b>Rhacocarpaceae</b>				
<i>Rhacocarpus purpurascens</i> (Hedw.) Paris		2	w	Pantrop
<b>Rhizogoniaceae</b>				
<i>Rhizogonium novae-hollandiae</i> (Brid.) Brid.	8	17	tT	Pantrop
<b>Sematophyllaceae</b>				
<i>Aptychella prolifera</i> (Broth.) Herzog	17	5	sT	Neotrop
<i>Sematophyllum subsimplex</i> (Hedw.) Mitt.		6	m	Neotrop
<i>Sematophyllum</i> sp. A		4	m	-
<i>Sematophyllum</i> sp. B		5	m	-
<b>Sphagnaceae</b>				
<i>Sphagnum</i> sp.		5	tT	-
<i>Sphagnum</i> sp. A		2	tT	-
<i>Sphagnum</i> sp. B		3	tT	-
<i>Sphagnum</i> sp. C		1	tT	-
<i>Sphagnum</i> sp. D		1	tT	-
<i>Sphagnum</i> sp. E		1	tT	-

	epiphytic habitat	terrestrial habitat	Life form	Chorotype
<b>Thamnobryaceae</b>				
<i>Porotrichum expansum</i> (Taylor) Mitt.	5	3	fa	A-n
<i>Porotrichum korthalsianum</i> (Dozy & Molk.) Mitt.		2	de,fa	Neotrop
<i>Porotrichum longiroste</i> (Hook.) Mitt.		1	de,fa	Neotrop
<b>Thuidiaceae</b>				
<i>Thuidium delicatulum</i> (Hedw.) Schimp.	2	4	w	Temp-n
<i>Thuidium tomentosum</i> Schimp.		2	w	Neotrop
<b>II. Liverworts</b>				
<b>Acrobolbaceae</b>				
<i>Acrobolbus</i> sp.	6		m	-
<b>Adelanthaceae</b>				
<i>Adelanthus decipiens</i> (Hook.) Mitt.	27	4	sT	Pantrop
<i>Adelanthus lindenbergianus</i> (Lehm.) Mitt.	21	7	sT	Temp-s
<b>Aneuraceae</b>				
<i>Aneura pinguis</i> (L.) Dumort.	1		m	Temp
<i>Riccardia fucoidea</i> (Sw.) Schiffn.	1	44	de	Neotrop
<i>Riccardia lepidomitra</i> (Spruce) Gradst.		1	m	A
<i>Riccardia</i> spp.	6	27	m	-
<b>Calypogeiaceae</b>				
<i>Calypogeia lechleri</i> (Steph.) Steph.		3	m	Neotrop
<i>Calypogeia oblata</i> Herzog		6	m	nA
<i>Calypogeia peruviana</i> Nees & Mont.	1	54	m	Neotrop
<i>Mnioloma cyclostipa</i> (Spruce) R.M. Schust.	8	59	m	A
<b>Cephaloziaceae</b>				
<i>Cephalozia bischlerae</i> Fulford		1	m	A
<i>Cephalozia crassifolia</i> (Lindenb. & Gottsche) Fulford	4	66	m	Neotrop
<i>Cephalozia crossi</i> Spruce		1	m	Neotrop
<i>Odontoschisma denudatum</i> (Nees) Dumort.	5	49	m	Temp-n
<b>Frullaniaceae</b>				
<i>Frullania apiculata</i> (Reinw., Blume & Nees) Nees	50		m	Pantrop
<i>Frullania brasiliensis</i> Raddi	35	4	pd	Neotrop
<i>Frullania cuencensis</i> Taylor	7		m	A
<i>Frullania intumescens</i> (Lehm. & Lindenb.) Lehm. & Lindenb.	24	2	m	Neotrop
<i>Frullania kunzei</i> (Lehm. & Lindenb.) Lehm. & Lindenb.	16		m	Neotrop
<i>Frullania montagnei</i> Gottsche	2		m	A
<i>Frullania serrata</i> Gottsche	7		m	Pantrop
<i>Frullania</i> sp.	1		m	-
<b>Geocalyceae</b>				
<i>Heteroscyphus combinatus</i> (Nees) Schiffn.	1	2	m	Neotrop
<i>Heteroscyphus polyblepharis</i> (Spruce) Schiffn.		5	m	A
<i>Leptoscyphus cuincifolius</i> (Hook.) Mitt.	1		m	Neotrop
<i>Leptoscyphus gibbosus</i> (Taylor) Mitt.	11		m	Neotrop
<i>Leptoscyphus porphyrius</i> (Nees) Grolle	22	1	m	Neotrop
<i>Leptoscyphus spectabilis</i> (Stephani) Grolle		16	m	Neotrop
<i>Lophocolea martiana</i> Nees		13	m	Pantrop
<i>Lophocolea</i> sp. A		8	m	-
<i>Lophocolea trapezoidea</i> Mont.	4	20	m	Neotrop
<i>Physotheca autoica</i> J.J.Engel & Gradst.	1		m	End

	epiphytic habitat	terrestrial habitat	Life form	Chorotype
<b>Herbertaceae</b>				
<i>Herbertus acanthelium</i> Spruce	4		tT	A
<i>Herbertus divergens</i> (Steph.) Herzog	36		tT	Neotrop
<i>Herbertus juniperoideus</i> (Sw.) Grolle	1		tT	Pantrop
<i>Herbertus pensilis</i> (Taylor) Spruce	30	26	tT	Neotrop
<i>Herbertus sendtneri</i> (Nees) Nees		2	tT	-
<b>Jungermanniaceae</b>				
<i>Anastrophyllum auritum</i> (Lehm.) Steph.	5		tT	Pantrop
<i>Anastrophyllum piligerum</i> (Reinw. & Blume & Nees) Steph.	7		tT	Pantrop
<i>Jamesionella rubricaulis</i> (Nees) Grolle	63	1	m, tT	Neotrop
<i>Syzygella anomala</i> (Lindenb. & Gotsche) Steph.	2	4	m	A
<i>Syzygiella setulosa</i> Steph.	2	3	m	A
<i>Syzygiella tonduziana</i> Steph.		4	tT	A-n
<b>Lejeuneaceae</b>				
<i>Anoplolejeunea conferta</i> (C.F.W.Meissn. ex. Spreng.)	39		m	Neotrop
<i>Aureolejeunea fulva</i> R.M. Schuster	18		m	A
<i>Blepharolejeunea incongrua</i> (Lindenb. & Gotsche) van Slag. & Kruijt	3		m	A
<i>Blepharolejeunea saccata</i> (Steph.) van Slag. & Kruijt	11		m	Neotrop
<i>Ceratolejeunea dussiana</i> (Steph.) Dauphin	1	9	m	Neotrop
<i>Ceratolejeunea grandiloba</i> J.B.Jack. & Steph.	25		m	A-n
<i>Ceratolejeunea patentissima</i> (Hampe & Gotsche) A.Evans	20	1	m	Neotrop
<i>Ceratolejeunea sp.</i>	3		m	-
<i>Cheilolejeunea holostipa</i> (Spruce) Grolle & Zhu	4		m	Neotrop
<i>Cheilolejeunea inflexa</i> (Hampe ex Lehm.) Grolle	17	4	m	Neotrop
<i>Cheilolejeunea laevicalyx</i> (J.B. Jack & Stephani) Grolle	2		m	Neotrop
<i>Cheilolejeunea oncophylla</i> (Angst.) Grolle & Gradst.	7		m	Neotrop
<i>Cheilolejeunea spp.</i>	12		m	-
<i>Cyclolejeunea luteola</i> (Spruce) Grolle	1	1	m	Neotrop
<i>Diplasiolejeunea pauckertii</i> (Nees) Steph.	19		m	A
<i>Drepanolejeunea spp.</i>	72	4	m	-
<i>Frullanoides densifolia</i> Raddi	4		m	Neotrop
<i>Lejeunea angusta</i> (Lehm. & Lindenb.) Mont.	2		m	Neotrop
<i>Lejeunea cf. catimulifera</i> Spruce	1		m	Neotrop
<i>Lejeunea cf. concinnula</i> Spruce & Stephani	1		m	A
<i>Lejeunea flava</i> (Sw.) Nees	3		m	Pantrop
<i>Lejeunea inflexiloba</i> J.B.Jack & Steph.	23		m	A-n
<i>Lejeunea meridensis</i> Ilkiu-Borges	1		m	nE
<i>Lejeunea ramulosa</i> Spruce	1		m	A
<i>Lepidolejeunea spongia</i> (Spruce) B.Thiers	1	2	m	Neotrop
<i>Leucolejeunea sp.</i>	1		m	-
<i>Leucolejeunea xanthocarpa</i> (Lehm. & Lindenb.) A.Evans	24		m	Pantrop
<i>Lindigianthus cipaconeus</i> (Gotsche) Kruijt & Gradst.	2		m	A-n
<i>Omphalanthus filiformis</i> (Sw.) Nees	46	2	pd,m	Neotrop
<i>Prionolejeunea aemula</i> (Gotsche) A.Evans	1	1	m	Neotrop
<b>Lepicoleaceae</b>				
<i>Lepicolea pruinosa</i> (Taylor) Spruce	63	24	tT	Neotrop
<b>Lepidoziaceae</b>				
<i>Arachniopsis diacantha</i> (Mont.) Howe	4	22	m	Pantrop
<i>Bazzania affinis</i> (Lindenb. & Gotsche) Trevis.	4	1	w	A
<i>Bazzania arcuata</i> (Lindenb. & Gotsche) Trevis.	1		w	A
<i>Bazzania bidens</i> (Gotsche & Lindenb.) Trevis.	1		w	Am-C
<i>Bazzania breuteliana</i> (Lindenb. & Gotsche) Trevis.	2	1	w	A-n
<i>Bazzania canelensis</i> (Steph.) Fulford		1	w	End
<i>Bazzania chilensis</i> (Steph.) Fulford		1	w	Neotrop
<i>Bazzania cuneistipula</i> (Gotsche & Lindenb.) Trevis.	11	2	w	Neotrop

	epiphytic habitat	terrestrial habitat	Life form	Chorotype
<i>Bazzania denticulata</i> (Lindenb. & Gottsche) Trevis.		3	w	Neotrop
<i>Bazzania diversicuspis</i> Spruce	7	17	w	Neotrop
<i>Bazzania cf. falcata</i> (Lindenb.) Trevis.	7	3	tT	Neotrop
<i>Bazzania gracilis</i> (Hampe & Gottsche) Steph.	9	6	w	Neotrop
<i>Bazzania hookeri</i> (Lindenb.) Trevis.	4	39	tT	Neotrop
<i>Bazzania longa</i> (Nees) Trevis.	6		tT	Neotrop
<i>Bazzania longistipula</i> (Lindenb.) Trevis.	38	1	w	Neotrop
<i>Bazzania pallide-virens</i> (Steph.) Fulford		1	w	Neotrop
<i>Bazzania phyllobola</i> Spruce	6	3	w	Neotrop
<i>Bazzania roraimensis</i> (Steph.) Fulford	20		w	Neotrop
<i>Bazzania spruceana</i> Steph.		1	w	Neotrop
<i>Bazzania taleana</i> (Gottsche) Fulford	6	2	w	Neotrop
<i>Bazzania nov. sp.</i>		1	tT	nS
<i>Bazzania spp.</i>	1	8	w	-
<i>Kurzia capillaris</i> (Sw.) Grolle	4	56	w	Neotrop
<i>Lepidozia brasiliensis</i> Steph.	1		w	Am-S
<i>Lepidozia caespitosa</i> Spruce	4	9	w	Neotrop
<i>Lepidozia incurvata</i> Lindenb.	13	41	w	A
<i>Lepidozia squarrosa</i> Steph.	12	6	w	Neotrop
<i>Lepidozia sp.</i>		2	m	-
<i>Micropterygium trachyphyllum</i> Reimers		3	m	Neotrop
<i>Micropterygium sp.</i>		1	m	-
<i>Telaranea nematodes</i> (Gottsche ex Austin) Howe	2	26	w, m	Pantrop
<i>Zoopsidella cf. caledonica</i> (Steph.) Schust.		7	t	-
<b>Marchantiaceae</b>				
<i>Marchantia sp.</i>		1	m	-
<b>Metzgeriaceae</b>				
<i>Austrometzgeria sp.</i>	2		m	-
<i>Metzgeria spp.</i>	22	5	m	-
<b>Palaviciniaceae</b>				
<i>Jensenia erythropus</i> (Gottsche) Grolle		1	m	Neotrop
<i>Symphogyna brasiliensis</i> Nees		29	m	Pantrop
<i>Symphogyna brogniartii</i> Mont.	2	13	m	Neotrop
<b>Plagiochilaceae</b>				
<i>Plagiochila aerea</i> Taylor	21	24	w	Neotrop
<i>Plagiochila bifaria</i> (Sw.) Lindenb.	29		w	Neotrop
<i>Plagiochila fuscolutea</i> Taylor	1		w	A
<i>Plagiochila cristata</i> Lindenb.	10		w	Neotrop
<i>Plagiochila pachyloma</i> Taylor	2		sT	A
<i>Plagiochila punctata</i> (Taylor) Taylor	7	3	w	A
<i>Plagiochila stricta</i> Lindenb.	5	1	fa	Neotrop
<i>Plagiochila superba</i> (Nees ex Spreng.) Mont. & Nees	5	6	fa	Neotrop
<i>Plagiochila tabinensis</i> Steph.	23	1	w	A
<i>Plagiochila sp. (sect. Arectae)</i>	2		w	-
<i>Plagiochila spp.</i>	17	1	w	-
<b>Pleuroziaceae</b>				
<i>Pleurozia heterophylla</i> Steph. ex Fulf.	2		tT	A
<i>Pleurozia paradoxa</i> J.B.Jack	4	2	tT	A-n
<b>Porellaceae</b>				
<i>Porella sp.</i>		2	m	-
<b>Radulaceae</b>				
<i>Radula fendleri</i> Gottsche ex Steph.	19		m	Neotrop

	epiphytic habitat	terrestrial habitat	Life form	Chorotype
<i>Radula sp. A</i>		5	m	-
<i>Radula sp. B</i>	2		m	-
<b>Scapaniaceae</b>				
<i>Scapania portoricensis</i> Hampe & Gottsche	24	31	tT	Neotrop
<b>Trichocoleaceae</b>				
<i>Trichocolea tomentosa</i> (Sw.) Gottsche	17	25	w	Neotrop
<b>III. Macrolichens</b>				
<b>Cladoniaceae</b>				
<i>Cladia aggregata</i>	8	2	fr	Pantrop
<i>Cladia sp.</i>	1		fr	
<i>Cladina arcuata</i> (Ahti) Ahti & Follm.		1	fr	Am-C, S
<i>Cladina confusa</i> (Mull. Arg.) Ahti		7	fr	Pantrop
<i>Cladonia subradiata</i> (Vain.) Sanst.	1		fr	Pantrop
<i>Cladonia cf. symphoriza</i> Nyl.		1	fr	-
<i>Cladonia coccifera</i> (L.) Willd.	1		fr	Temp
<i>Cladonia didyma</i> (Fée) Vain.	7	1	fr	Pantrop
<i>Cladonia lopezii</i> S. Stenroos	1		fr	Am-C, S
<i>Cladonia spp.</i>	13	2	fr	
<b>Coccocarpiaceae</b>				
<i>Coccocarpia domingensis</i> Vain.	2		f	Am-C, S
<i>Coccocarpia palmicola</i> (Spreng.) L. Arvidss. & D.J. Galloway	2		f	Pantrop
<i>Coccocarpia pellita</i> (Ach.) Müll. Arg.	1		f	Pantrop
<i>Coccocarpia sp.</i>	1		f	
<b>Collemataceae</b>				
<i>Leptogium sp.</i>	1		f	
<b>Dictyonemaceae</b>				
<i>Dictyonema sericeum</i> Johow	3		f	Pantrop
<b>Icmadophilaceae</b>				
<i>Siphula sp.</i>	9		fr	
<b>Lobariaceae</b>				
<i>Lobaria subexornata</i> (Yoshim.) Yoshim.	1		f	Am-C, S
<i>Lobaria sp.</i>	1		f	
<i>Sticta fuliginosa</i> (Dicks.) Ach	1		f	Pantrop
<i>Sticta laciniata</i> Ach.	5		f	Pantrop
<i>Sticta spp.</i>	5		f	
<b>Pannariaceae</b>				
<i>Erioderma glabrum</i> P. M. Jørg. & Arv.	1		f	Am-C, S
<i>Erioderma verruculosum</i> Vain.	5		f	Am-C, S
<i>Erioderma sp.</i>	2		f	
<i>Parmeliella pannosa</i> (Sw.) Müll. Arg.	2		f	Pantrop
<b>Parmeliaceae</b>				
<i>Anzia leucobatis</i> (Nyl.) Müll. Arg.	1		f	A-n
<i>Anzia parasitica</i> (Fée) Zahlbr.	1		f	A-n

	epiphytic habitat	terrestrial habitat	Life form	Chorotype
<i>Anzia</i> sp.	4		f	
<i>Bulboxtrix suffixa</i> (Stirt.) Hale	1		f	Pantrop
<i>Everniastrum vexans</i> Hale	21		f	Pantrop
<i>Hypotrachyna</i> cf. <i>dentella</i> (Hale & Kurok.) Hale	2		f	
<i>Hypotrachyna costaricensis</i> (Nyl.) Hale	1		f	
<i>Hypotrachyna imbriculata</i> (Zahlbr.) Hale	11		f	Pantrop
<i>Hypotrachyna immaculata</i> (Kurok.) Hale	1		f	Am-Afr
<i>Hypotrachyna laevigata</i> (Sm.) Hale	1		f	-
<i>Hypotrachyna microblasta</i> (Vain.) Hale	9		f	Temp
<i>Hypotrachyna physcioides</i> (Nyl.) Hale	1		f	
<i>Hypotrachyna reducens</i> (Nyl.) Hale	1		f	Am-C, S
<i>Hypotrachyna singularis</i> (Hale) Hale	1		f	
<i>Hypotrachyna</i> sp.	1		f	
<i>Hypotrachyna</i> spp.	19		f	
<i>Oropogon formosanus</i> Asah.	6		fr	Pantrop
<i>Oropogon lorobic</i> Essl	9		fr	Am-C, S
<i>Parmelinopsis horrescens</i> (T. Tayl.) Elix & Hale	3		f	Temp
<i>Parmelinopsis minarum</i> (Vain.) Elix & Hale	10		f	Temp
<i>Parmelinopsis</i> sp.	3		f	
<i>Parmotrema mellissii</i> (C. W. Dodge) Hale	10		f	Pantrop
<i>Parmotrema</i> sp. A	9		f	
<i>Parmotrema</i> sp. B	1		f	
<i>Usnea</i> spp.	46	1	fr	
<b>Physciaceae</b>				
<i>Heterodermia circinalis</i> (Zahlbr.) W. A. Weber	2		f	Pantrop
<i>Heterodermia galactophylla</i> (Tuck.) W. Culb.	1		f	Pantrop
<i>Heterodermia isidiophora</i> (Vain.) Awas.	1		f	Pantrop
<i>Heterodermia leucomela</i> (L.) Poelt	5		f	Pantrop
<i>Heterodermia squamulosa</i> (Degel.) W. Club.	1		f	Pantrop
<i>Heterodermia vulgaris</i> (Vain) Follmann & Redón	2		f	Am-Afr
<i>Heterodermia</i> sp. A	2		f	
<i>Heterodermia</i> spp.	10		f	
<i>Physcia decorticata</i> Moberg	1		f	Am-S
<b>Placynthiaceae</b>				
<i>Polychidium dendriscum</i> (Nyl.) Henssen	2		fr	Temp
<b>Sphaerophoraceae</b>				
<i>Bundophoron melanocarpum</i> (Sw.) Wedin	10		fr	Pantrop
<b>Verrucariaceae</b>				
<i>Normandina pulchella</i> (Borrer) Nyl	8		sq	Temp
<b>Incertae Sedis</b>				
<i>Leprocaulon arbuscula</i> (Nyl.) Nyl.	2		fr	Pantrop

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## List of Publications

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- Mandl NA, Sipman HJM, Gradstein SR (in prep) Diversity and ecology of epiphytic bryophytes and macrolichens in Andean montane forest habitats.
- Mandl NA, Lehnert M, Kessler M, Gradstein SR (in prep.) A comparison of diversity and distribution patterns of lichens, liverworts, mosses, and pteridophytes in an Andean montane rainforest.
- Gradstein, SR, Kessler M, Lehnert M, Makeschin F, Mandl NA, Abiy M, & Richter M (submitted). Vegetation, climate, and soil of the unique *Purdiaea* forest of southern Ecuador. *Ecotropica*.
- Mandl NA, Kessler M, Gradstein SR (submitted) Effects of environmental heterogeneity on floristic diversity and composition of terrestrial bryophyte and macrolichen assemblages in Southern Ecuador. *Biotropica*.
- Kessler, M, Lehnert, M, Mandl, NA & Gradstein, RS (submitted) Are ridge habitats special sites for endemic plants in tropical montane rain forests? A case study of pteridophytes in Ecuador. *Folia Geobotanica*.
- Gradstein SR, Bock C, Mandl NA and Noeske NM (accepted) Bryophytes of the Reserva Biológica San Francisco, Ecuador. Part 1. Introduction; Liverworts and Hornworts. In: Liede S (ed), Checklist of plants and animals of the Reserva Biológica San Francisco. *Ecotropica Monographs*.
- Nöske NM, Mandl NA & Sipman HJM (accepted) Lichens of the Reserva Biológica San Francisco, Ecuador. In: Liede S (ed), Checklist of plants and animals of the Reserva Biológica San Francisco. *Ecotropica Monographs*.
- Mandl NA, Lehnert M, Gradstein SR, Kessler M, Makeschin F, & Richter M (in press). The unique *Purdiaea nutans* forest of southern Ecuador: abiotic characteristics and cryptogamic diversity. *Ecological Studies*.
- Staudt M, Mandl N, Joffre R, and Rambal S (2001) Intraspecific variability of monoterpene composition emitted by *Quercus ilex* leaves. *Can. J. For. Res./Rev. can. rech. for.* 31(1): 174-180.



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# Curriculum vitae

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