Diversity and Ecology of Bryophytes and Macrolichens in Primary and Secondary Montane *Quercus* Forests, Cordillera de Talamanca, Costa Rica

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Table of contents

Index of Tables

Index of Figures

CHAPTER 1

General Introduction

Tropical Montane Forests

With increasing elevation on tropical mountains, distinct changes in forest appearance and structure occur (Richards 1952). In montane rain forests a purely tropical flora is left behind, and many of the species are derived from temperate plant groups. The trees get smaller as higher zones are reached and tree species diversity is generally reduced (Grubb et al. 1963). Tree trunks become twisted and gnarled and overgrown with filmy ferns, liverworts, mosses and lichens which enjoy a mist or cloud-like environment around them (Richards 1984).

The specific atmospheric humidity regime of tropical montane forests together with their strong diurnal temperature oscillations are the main environmental factors which cause the large array of differences in the forest structure and composition when compared to tropical lowland forests (Grubb et al. 1963, Grubb & Whitmore 1966). Montane rain forest can be found between lowland rain forest (including submontane rain forest), which reaches to about 1,000-1,500 m (3,300-4,950 ft), and at least 3,000 m (10,000 ft) in many cases where elevation permits. There is great variability in these upper limits because of local climates and soil conditions.

Definitions, names and classification of tropical forest types are myriad, as well as frustratingly overlapping and, at times contradictory (Stadtmüller 1987, Churchill et al. 1995). With increasing elevation we distinguish the following forest belts: lowland rain forest, submontane rain forest, lower montane rain forest, upper montane rain forest, and subalpine rain forests (Frahm & Gradstein 1991, Grubb 1974, 1977, Webster 1995). The most confusing term in literature are cloud forests (Stadtmüller 1987). Some authors use this term to describe montane rain forest in general (e.g. Bruijnzeel & Hamilton 2000), others use it as synonym to subalpine forests (elfin forests) as a zonal forest type. In this paper we define “cloud forest” as a forest type with great influence of mist and clouds on forest structure and species composition (Stadtmüller 1987, Hamilton, Juvik & Scatena 1994). In this sense cloud forests are an a-zonal forest type found in tropical lowland, submontane, montane and subalpine locations. However cloud forest are most common in upper montane and subalpine altitudes.

A special type of tropical and subtropical forests frequently found in montane regions is one in which the canopy layer is dominated by Fagaceae and the understorey layer by woody bamboos. One example of tropical montane fagaceous forests is the *Quercus* dominated forest found above 2000 m altitude in the Costa Rican Cordillera de Talamanca. These forests are almost exclusively dominated by the genus *Quercus* and are about 25 to 40 m tall, with some stands reaching 50 m of height (Blaser 1987). The present study focuses on cryptogams, especially epiphytic bryophytes and macrolichens in these forests.

Bryophytes and Macrolichens in Tropical Forests

Because of their complexity and variety of microhabitats, lowland and montane tropical rain forests are habitat of many bryophytes and lichens. In the Neotropics some 50% of the 2600 mosses and more than 70% of the 1400 liver- and hornworts occur in these forests. Most of the bryophytes and lichens of tropical rain forests are epiphytes (Gradstein et al. 2001). Even though they are often small and inconspicuous, bryophytes and lichens are an important component of tropical forests, especially montane ones, both in terms of ecosystem functioning, biomass and biodiversity (Pócs 1980, Nadkarni 1984, 1986, Coxson 1990, Veneklaas & Van Ek 1990, Veneklaas et al. 1990, Hofstede et al. 1993, Clark et al. 1998a, 1998b).

However, non-vascular epiphytes have received less attention than vascular epiphytes. Early exceptions in the tropics are the contributions by Giesenhagen (1910) on growth forms, by Jovet-Ast (1949) on epiphylls and by Seifritz (1924) on altitudinal zonation in Java. For reviews on tropical rain forest bryophytes, see Pócs (1982), Richards (1984), and Gradstein & Pócs (1989). For tropical lichens see Sipman & Harris (1989) and Galloway (1991).

Richards (1954) was the first to describe shade and sun bryophytic communities from the Neotropics. Work on epiphytic bryophytes in the Neotropics has been done in the Guianas (Cornelissen & Gradstein 1990, Cornelissen & ter Steege 1989, Florschütz-de Waard & Bekker 1987, Gradstein et al. 1990; Richards 1954), Brazil (Lisboa 1976; Pôrto 1992), Colombia (Wolf 1993a, b, c, 1994), Peru (Frahm 1987a, b, Frey 1987), Costa Rica (Sillet et al. 1995, Gradstein et al. 2001), Southern Mexico (Equihua & Gradstein 1995), and Bolivia (Acebey et al. 2003).

World-wide altitudinal transect studies in the ECOANDES and BRYOTROP I-III projects have greatly contributed to our knowledge on cryptogam communities in the understorey of tropical forests (Frahm 1987a, 1987b, 1990a, 1990b; Gradstein & Frahm 1987; Gradstein et al., 1989; Kürschner 1990, Van Reenen 1987, Van Reenen & Gradstein 1983) and showed that diversity of bryophytes and lichens varies considerably in the different rain forests belts (Frahm & Gradstein 1991).

Interest in cryptogamic epiphytes especially in the Neotropics has increased greatly during the past 25 years. The introduction of rope-climbing techniques (Perry 1978; Ter Steege & Cornelissen 1988) overcame the limitations posed by distant observation of the canopy. Cryptogamic canopy communities have been described in detail from lowland rain forests in Guyana and French Guyana (Cornelissen & Ter Steege 1989; Gradstein et al. 1990; Montfoort & Ek 1990). Wolf's (1993a, b, c, 1994) detailed study in Colombia was the first to describe and analyze canopy communities in tropical montane forests.

Epiphytic Bryophytes and Macrolichens in Tropical Montane forests

According to Barkman (1958) epiphytes are organisms living on a plant or in the dead outer tissues of a plant without drawing water or nutrients from its living tissue. Epiphytes are a characteristic and distinctive component of tropical rain forests and have attracted scientific attention since A.F.W. Schimper's (1888) extensive monograph on neotropical epiphytes. The epiphytic habit appears to be a successful adaptation to the canopy habitat since the number of epiphytic vascular and non-vascular plant species is great.

As mentioned above, tropical montane rain forests are especially rich in cryptogamic epiphytes, which contribute significantly to their total biomass, species diversity and nutrient cycling. It has been suggested that epiphytes can be used as bioindicators of climatic change, pollution and ecological damage. However, little is known about epiphytic bryophytes and macrolichens and their communities in these ecosystems.

There are only a few studies dealing with the epiphytic cryptogams in montane rainforests. Frahm (1987a) presented information on the structure and composition of tree base and lower trunk epiphytic bryophyte vegetation in montane rain forest of northeastern Peru. A detailed phytosociological description of these communities, along an altitudinal range from 280 m to 3330 m was given by Kürschner & Parolly (1998a, b).

Wolf (1993a, b, c, 1994) presented a detailed transect study of the epiphytic cryptogams of canopy trees from 1000 m to 4130 m in Colombia. He was the first to use rope climbing techniques to study epiphytic cryptogams in montane rain forests. His description of lower and upper montane communities (Wolf 1993a, b) provided the basis for an analysis of the ecological factors controlling the distribution of non-vascular epiphytes using multivariate statistics (Wolf 1994).

Sillet et al. (1995) studied bryophyte diversity of inner crowns of *Ficus* trees in primary forest of Monteverde (Costa Rica) and compared it to trees from nearby pastures. Gradstein et al. (2001) studied the bryophytes of whole standing trees and logs in Monteverde and described their microhabitat differentiation.

One of the most bryophyte-rich forest types is montane forest located in the cloud zone (Tropical montane cloud forest). This habitat is extremely humid and is cooler than lowland forest. Epiphytic bryophytes are dominant and reach their maximum species diversity and coverage in this habitat. Beside humidity and temperature, the age of the trees within the forest and the area of tree coverage also determine the level of epiphyte and epiphyll diversity.

Bryophytes in Secondary Tropical Forests – Recovery of the forest

Tropical forests make up about half of the world’s closed forests, yet they are rapidly being destroyed as a result of land clearing for pasture and other agricultural uses. In Central America the forest resources are being destroyed at a rate of 416.000 ha per year (Chaverri & Hernández 1995).

Increasingly, these lands are being abandoned because of decreasing productivity and changing economic incentives. Secondary forests are those resulting from human disturbance, such as forests regenerating from logging, clearing for agriculture and abandoned pastures. Secondary ecosystems, especially secondary forests, are rapidly becoming the most important repository of biodiversity in the Neotropics (Brown & Lugo 1990, Chazdon 1994, Holl & Kappelle 1999). Trends in tropical forest conversion have principally been studied in lowland rain forest areas. On the contrary, little is known about whether forests will ever fully recover on abandoned crop fields and pastures at high elevation.

Forest management of secondary forests may be a worthwhile alternative in sustainable land-use. Therefore research on the regeneration processes and features of tropical secondary forests is needed.

While increasing attention has been paid to the taxonomy of tropical bryophytes and lichens, very little is known about their ecology and the impact on them of forest destruction in the tropics. Relevant aspects are degradation of biomass, loss of species diversity and change in microclimate associated with forest fragmentation.

Deforestation is generally considered to have a deleterious effect on the bryophyte flora of the primary forest and may lead to a considerable loss of species. Gradstein (1992a, b) reviewed this topic and concluded that especially ‘shade epiphytes’ are affected by the disappearance of mature forest habitats. Those species surviving in clearings and secondary forests are mainly the desiccation tolerant ‘sun epiphytes’ of the canopy and the weedy ‘generalists’. The comparisons he used were between mature forests and mostly man-made vegetation types (plantations, road sides, etc.). He recommended that “careful comparison of rain forest stands of different ages would have to be carried out to obtain more insight into the recovery of the cryptogamic flora after clearing of the forest” (Gradstein 1992a).

Hyvönen et al. (1987) described the human influence on the moss flora of tropical rain forest in Papua New Guinea and Sillet et al. (1995) compared epiphytic bryophytes from the inner canopy of standing trees in primary forest and pastures in Monteverde (Costa Rica).

Pinheiro da Costa (1999) compared epiphytic bryophytes diversity in primary and secondary lowland rainforests in Southeastern Brazil and Acebey et al. (2003) analyzed species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. Both studies showed a significantly decreased diversity of bryophyte species in the secondary vegetation and supported Gradsteins (1992) suggestion that shade epiphytes are more seriously effected by clearings.

However, recent work on vascular plant diversity in neotropical rain forests indicated that forest degradation does not always lead to a reduction of species richness (e.g. Kappelle 1996, Barthlott et al. 2001).

Study area

The study was conducted in the “Los Santos” forest reserve near San Gerardo de Dota (83°51’W 09°32’N), situated on the Pacific-facing slope of the western Talamanca Mountain Range, Costa Rica (Figs. 1-1 and 5-1). “Los Santos” serves as a buffer zone to the Amistad Biosphere Reserve, recognized as a World Heritage Site by the UNESCO in 1983 (Kappelle & Juárez 1994). Today, it harbours the last remaining large and unfragmented part of undisturbed neotropical montane forest in Central America.

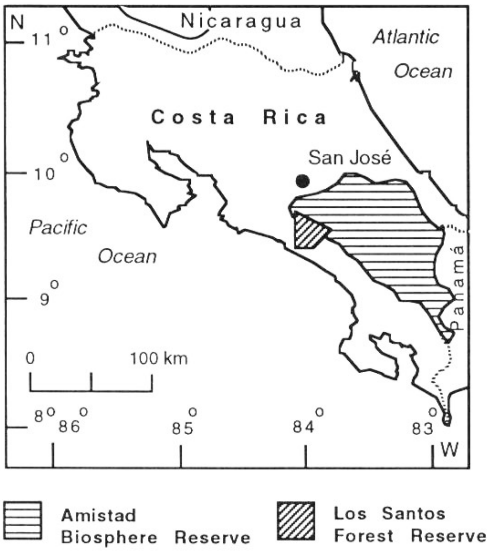

Fig. 1-1. Location of the study area showing the Los Santos Reserve and the La Amistad Biosphere Reserve (from Kapelle et al. 1994)

Geology, geomorphology and soils

The Cordillera de Talamanca stretches in a NW-SE direction, and is made up of intrusive and volcanic rocks, alternated with marine sediments. These oceanic sediments and volcanic rocks were formed as a result of the rifting of the Cocos and Caribbean plates. The uplifting of the Talamanca range occurred 35-15 million years ago, mainly during the Oligocene and Miocene, with folding and intrusive events (Weyl 1980, Castillo 1984).

The geomorphology of the Cordillera de Talamanca is dominated by the contrast between steep, deeply fluvially dissected valleys and extensive remains of flattish Pliocenic formes at rugged crests, which is the result of the violent young uplift of the Cordillera (Bergoeing 1998). Pleistocene glaciations have left their traces such as fossil periglacial phenomena on the Cerro de la Muerte at the near-by Buenavista massif (Weyl 1956).

Soils in higher parts of the Cordillera de Talamanca mainly developed in volcanic ash deposits and are humic (mollic or umbric) andosols, containing dark, deep, rich organic matter, which is medium textured, moderately fertile and excessively drained. Soils of the upper montane *Quercus* forests are very acid: pH values range from 3.7 to 5.0 at a depth of about 15 cm below soil surface and may differ largely over short distances (Kappelle 1995).

Climate

The study area has a Cf climate, according to the Köppen Climate System. In general a short dry and a long wet season can be distinguished. Climatic conditions within the Cordillera de Talamanca are very diverse, due to the region's large expanse, its geographic location which includes both the Pacific and Caribbean watersheds, the great altitudinal differences, and its irregular and abrupt topography.

The local climate on the Pacific-facing slope at 2800-3000 m altitude is cool and humid, annual precipitation averages 2600-2800 mm and the mean daily temperature 11 °C (Instituto Meteorológico Nacional 1988). There is a pronounced dry season from early January to the end of April (Figs. 1-2 and 5-1c). January is the coldest month with an average temperature of 10°C and frost may occur during clear nights with temperatures down to 2-3°C below zero (Herrera 1986). For detailed information on climate of the study area see also Köhler (2002).

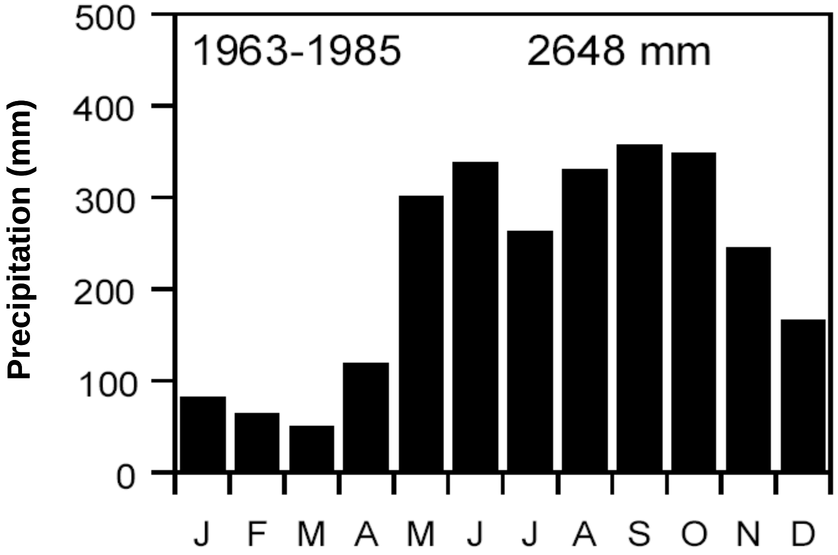

Fig. 1-2. Rainfall diagramm of Ojo de Agua (2960 m), located in the upper montane rain forest region, on the Pacific slope of the Cordillera de Talamanca, Costa Rica (Instituto Meteorológico Nacional 1988).

Vegetation and land use

Originally, the upper Río Savegre watershed at altitudes between 2000 and 3000 m has been totally covered with primary forest. The forest is a montane rainforest (“robledal de altura”) dominated by 30-40 m tall trees of two species of *Quercus*, *Q. copeyensis* C.H.Müll. and *Q. costaricensis* Liebm. Understorey vegetation is characterized by bamboo, tree ferns, dwarf palms, shrubs and herbs. Canopy and subcanopy branches are festooned with vascular and non-vascular epiphytes including orchids, bromeliads, aroids, ericads, ferns, mosses, liverworts and lichens. The forest is dissected by a number of small brooks. A comprehensive description of vegetation structure and secondary succession of these oak forests has been given by Kappelle (1995, 1996).

An unpaved minor road is running from the Pan American Highway down south into the river valley. Two small settlements are located along this road. Jaboncillo is located in the northern part at an altitude of approximately 2800 m and is inhabitated by five families. San Gerado de Dota is located at an altitude of approximately 2000 m and is inhabited by a dozen families. Traditionally, animal husbandry with dairy cattle is practised, as is the cultivation of perennial crops such as apple, peach and to a lesser extent, plum trees (Kappelle & Juárez 1995). Charcoal production serves as a source of income, whereas on-farm production of trout and blackberry-gathering can also serve as a food source. Ecotourism is a recent and growing activity, exploited by some people in the watershed area, and has become a major source of income to few families (Kappelle & Juárez 1995).

Clearing of montane forests for pasture or agriculture began with construction of the Inter-American Highway in the 1940s. However most deforestation in the study region occurred between 1950 and the early 1970s, when small settlements developed into villages following the construction of the Inter-American Highway.

In an aerial photo interpretation study, Van Omme (1998) recognized the following land cover types in the Rio Savegre watershed area: Bamboo paramo (4.2 %), shrub paramo (6.4 %), subalpine dwarf forest (7.7 %), primary montane forest (70.8 %), secondary forest (5.3 %), secondary shrub vegetation (1.1 %), pasture land (3.3 %), orchards (1.0 %), timber plantations and others (roads, bare ground etc., 1.0 %). Secondary forests and secondary shrub vegetation contributes to about 60 % cover of the deforested areas. As Helmer (2000) pointed out, the spatial distribution of secondary forest in tropical landscapes has important implications for biodiversity, watershed processes and biogeochemical pools and fluxes, such as forest carbon budgets.

The oak forest

Thus far, 253 genera of vascular plants, belonging to 114 families, have been recorded from the *Quercus* forests of the Cordillera de Talamanca. A total of 166 genera are woody ones, including 80 tree genera (Kappelle 1995). About 75 % of all genera are tropical (46 % neotropical) in distribution, the remaining 25 % are temperate (17 %) and cosmopolitan (8 %) genera.

The most important species observed in the canopy layer are *Quercus copeyensis* Mueller, *Q. costaricensis* Liebmann und *Q. seemannii* Liebmann, each with its specific altitudinal range (Burger 1977, Kapelle et al. 1989).

Tree density in a typical primary Talamancan upper montane *Quercus* forest at 2650 m is about 500 stems per ha (DBH > 10 cm), of which almost 80 % are individuals belonging to the genus *Quercus* (Jiménez et al. 1988). In general, these *Quercus* forests comprise stands over 40 m tall and consist of up to five layers. These layers are: i) the rather uniform canopy layer, made up of mere *Quercus* trees sometimes intermingled with a few other tree species; ii) the quite diverse 10 to 25 m tall subcanopy layer with common trees like *Weinmannia, Ilex, Zanthoxylum, Viburnum, Vaccinium, Styrax, Symplocos, Clusia*, Araliaceae, Lauraceae, Melastomataceae, and Myrsiniaceae, all together covering 30-50 % of the surface; iii) the shrub layer, which is mainly composed of *Chusquea* bamboos, Cyatheaceae tree ferns, *Geonoma* dwarf palms, *Sphaeradenia* cyclanths and numerous shrubs belonging to Acanthaceae, Ericaceae, Rubiaceae and Solanaceae; iv) the herb layer, mainly consisting of terrestrial aroids, gesneriads and ferns; v) the bryophyte and lichen layer (Kappelle 1995).

Although canopy and especially subcanopy branches are usually festooned with vascular and non-vascular epiphytes there is only limited influence of mist and clouds on forest structure and species composition of the forest (Köhler 2002). The oak forests on the pacific facing slope of Cordillera de Talamanca are thus better termed ‘upper montane rain forests’ instead of ‘cloud forests’. An important factor limiting the epiphytic vegetation is the pronounced dry season from January to April.

Aims, outline and contents of the present study

The purpose of this thesis is to describe and analyze the bryophyte and macrolichen communities in *Quercus* dominated upper montane rain forests of Cordillera de Talamanca, Costa Rica. Biogeographic, ecological and phytosociological aspects of the epiphytic vegetation are the subject of this study. Rope climbing techniques were used to obtain access to the canopy (Perry 1978; ter Steege & Cornelissen 1988).

In addition to describing epiphyte communities of the primary upper montane oak forests, spatial and environmental relationships are also analyzed. Special attention is paid to the epiphyte communities in the canopy of the dominant tree species *Quercus copeyensis* and *Q. costaricensis*. The study also aims to get insight into secondary succession of the epiphyte communities and their regeneration in secondary forests after forest clearance.

The main objective of this study is thus to quantify botanical diversity of primary forests and analyze the impact of disturbance, and in particular forest clearance, on species diversity and functional diversity of epiphytic cryptogam communities (bryophytes and macrolichens). Apart from quantification of the species composition of undisturbed oak forests, an evaluation will be made of the development of plant diversity in regenerating oak forest through time. Special emphasis will be laid on the spatial component of diversity.

The present study is the first to compare diversity and species composition of both epiphytic bryophytes and epiphytic lichens in primary und secondary forest plots in a tropical rain forest. It is structured in the following chapters:

Chapter 2 – focuses on the phytogeography of bryophytes of Costa Rica's Talamancan montane *Quercus* forests within the Neotropical realm. Bryogeographical spectra are presented for primary and secondary oak forests on the basis of extended checklists. These are compared to spectra from Costa Rican páramo vegetation and Costa Rican hepatic flora.

Chapter 3 – deals with bryophyte diversity, microhabitat differentiation and distribution of live forms in Costa Rican upper montane *Quercus* forest and gives full account of the bryophyte flora of all microhabitats in montane oak forest, including forest floor habitats and the understorey of the forest.

Chapter 4 – pays attention to the epiphytic cryptogam communities on the dominant host tree species (*Quercus copeyensis* and *Q. costaricensis*) of upper montane oak forests in Costa Rica. It will be shown that epiphytic bryophyte and lichen species and their communities show a strong host preference in these tropical forest ecosystems.

Chapter 5 – compares species richness, community composition and ecology of cryptogamic epiphytes in primary and recovering upper montane *Quercus* forests of Costa Rica. Concluding remarks are given in this final chapter on recovery times and bryophytes as indicators for recovery of upper montane *Quercus* forests. These results may prove useful for a sustainable management of upper montane oak forests in the future.

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CHAPTER 2

Bryogeography of Talamancan montane *Quercus* forests, Costa Rica

Abstract

Phytogeographical patterns of the bryophyte flora of the montane *Quercus* forests and páramo of the Cordillera de Talamanca, Costa Rica, are compared in the present study. A total of 191 hepatics (29 families), one hornwort and 209 mosses (46 families) bryophytes are recorded. Of these, 251 species (128 hepatics, one hornwort and 122 mosses) are found in the oak forests. 93 % of all oak forest species are tropical in distribution, the remaining 7 % are temperate (4 %) and cosmopolitan (3 %) species. The neotropical element is the best represented and contributes to almost 74 % of the species, whereas the wide tropical element (pantropical, amphi-atlantic, amphi-pacific) is only presented with 19 % of the species. A significant part of the neotropical bryophyte species from oak forests show a tropical Andean-centered distribution (27 %). In contrast, vascular plant genera in the study region are represented by fewer neotropical, more temperate and more amphi-pacific species. Total oak forest bryophyte flora, bryophyte floras of different microhabitats within oak forest, and epiphytic bryophyte floras on Quercus copeyensis of primary, early secondary and late secondary oak forest all show similar phytogeographical make-up.

The comparison of the oak forest spectrum with that of Costa Rican páramo reveals a greater affinity of the páramo bryoflora to temperate regions and the importance of the páramo element. Surprisingly, oak forests have a high percentage of Central American endemics, which are lacking in the páramo.

Compared with the entire Costa Rican hepatic flora, the oak forests have fewer temperate and more Central American species.

Resumen

En la Cordillera de Talamanca, Costa Rica, fueron comparados los patrones fitogeográficos de la flora briofítica de bosques montanos de Quercus con vegetación del páramo. En la lista de briofitas montanas para esta área se registraron en total 191 hepáticas (29 familias), 1 antocerota y 209 musgos (46 familias).

De estos taxa, 251 (128 hepáticas, 1 antocerota, 122 musgos) fueron hallados en bosques de robles. El 93 % de las especies de estos bosques poseen una distribución tropical, el 7 % restante se distribuye en zonas templadas (4 %) o son cosmopolitas (3 %). El elemento neotropical es el mejor representado y contribuye con casi el 74 % de las especies, mientras que solamente un 19 % representa el elemento ampliamente tropical (pantropical, anfi-atlántico, anfi-pacífico). Una parte significativa de las especies de briofitas neotropicales de los bosques de robles muestra una distribución tropical andina (27 %). Los géneros de plantas vasculares poseen menos elementos neotropicales, pero más templados y anfi-pacíficos. Un espectro de briofitas similar al del bosque de robles en su conjunto fue hallado en diferentes microhábitats de 6 ha de bosque montano de robles, y para las especies de briofitas epífitas sobre Quercus copeyensis en bosques primarios, secundarios tempranos y secundarios adultos.

La comparación del espectro hallado entre bosques de roble y el páramo, en Costa Rica, demuestra una gran afinidad de la brioflora del páramo con la región templada y la importancia del elemento del páramo. Sin embargo, y en forma inesperada, los bosques de roble poseen un alto porcentaje de especies endémicas de América Central las cuales faltan en el páramo.

En comparación con datos sobre la fitogeografía de las hepáticas de Costa Rica, en los bosques de roble encontramos menos especies de distribución templada y más especies de América Central.

Introduction

A first description of the montane vegetation in Costa Rica was provided by Wercklé (1909). Since this early work, knowledge of the Talamancan high-altitude flora, vegetation and ecosystems has increased considerably (Weber 1958, Holdridge et al. 1971, Janzen 1983, Gómez 1986, Graham 1989).

Recently, the montane oak forests of Cordillera de Talamanca have been subject of detailed studies focusing on ecological and silvicultural aspects (Blaser 1987, Chaverri et al. 1986, Jiménez 1984, Jiménez et al. 1988, Jiménez & Chaverri 1991 and, especially, Kappelle 1995, 1996). The latter author provided a detailed analysis of the ecology and diversity of mature and recovering *Quercus* forests in Cordillera de Talamanca, including the phytogeography of vascular plant genera (Kappelle et al. 1992). However, little is known about the bryophyte flora and vegetation in this region.

Costa Rica has a remarkable diverse bryophyte flora, which may even be the richest of any Central American country. Roughly 80 percent of the mosses from Central America are known from Costa Rica (Allen 1994, 2002, Holz et al. 2002), this number being similar or even higher for liverworts.

To date, about 690 mosses, 575 hepatics and about 10 hornworts have been recorded from Costa Rica (Bowers 1974, Allen 1994, 2002, Holz et al. 2002, Morales 1991, Gradstein et al. 1994, Dauphin et al. 1998, Holz et al. 2001). Although the bryophyte flora of Costa Rica may be regarded as the best known of any Central American country, the likelihood is high to find species which have not yet been reported from this country. This is partly due to the fact that compared to the total area of the country, only few sites have been studied in larger detail by bryologists. At the same time, many of the previous records may prove to be synonyms or misidentifications. Great parts of the moss flora have recently been reviewed in the ‘Moss Flora of Central America’ (Allen 1994, 2002). It has to be noted, however, that there is still a great need for a critical revision of the hepatic flora.

A first description of the montane moss flora of Costa Rica was provided by Bowers (1970) based on literature data and personal collections. A list of 178 moss species known from high elevations (> 2500 m) of Costa Rica was presented in that study. The list included many species, which were not known from Cordillera de Talamanca but from one of the high volcanos in Cordillera Central (Poás, Barba, Turrialba, Irazú). Species richness of páramo vegetation (63 moss species), secondary (84 moss species) and primary montane forests (57 moss species) were compared and basic geographic relationships discussed. The discussion of geographic relationships of the mosses was largely based on outdated geological and paleoecological literature, however. Later, Kappelle (1996) compiled a checklist of 294 bryophytes (hepatics and mosses) known from high elevations of Cordillera de Talamanca, based on Bowers (1970), Morales (1991), Gradstein et al. (1994), personal collections and herbarium specimens from AMD, CR, FLAS, FULF, JE, LITTLE, MO, NY, PC, TENN, U, USE and USJ. Although presented as a checklist of the bryophytes of the oak forests of the Cordillera de Talamanca, the list also contains many species from páramo, rock outcrops, mires and other habitats. In addition, the list shows some errors in identification, nomenclature and taxonomy of some groups.

The present study is the first attempt to determine the phytogeographical patterns of bryophytes of the Talamancan montane oak forests. It will compare these with patterns from vascular plants of these forests, bryophytes from Costa Rican páramo and parts of the hepatic flora of Costa Rica.

Flora History and Paleogeography

The outstanding richness of Costa Ricas bryophyte flora is apparently due to the country’s highly variable topography (discontinuous mountain chains), climate (differing seasonal patterns of rain fall), geological history (rich mineral volcanic soils, past history as an archipelago, influence of glaciations) and its geographical location between the tropical and subtropical areas of the Americas (Burger 1980). Immigration of taxa from both the North (Guatemala and Mexico) and the South (Colombia) must have played an important role in the origin of the rich floristic diversity of the Talamancan mountain vegetation.

Until the Upper Cretaceous, South America and Africa and perhaps even some of the fragments of Central America have constituted a region of evolutionary importance in which much of the earth's tropical lowlands were concentrated. During this time South America was more accessible to interchange with Africa than with Northern America (Raven 1979). From the late Cretaceous onwards, Africa and South America separated and about 5 to 4 million years ago the Panamanian Isthmus has been formed closing the inter-oceanic connection between the Americas. From the Eocene onwards, floristic interchanges of taxa between the Americas has become common and occurred most intensively during the late Pliocene and Quaternary (Raven 1979, Webb 1985, Stehli & Webb 1985). By the late Pliocene, some 2-3 million years ago, the tectonic activities had created mountains high enough to provide a reliable corridor for montane-adapted plants. Cool climates during the Pleistocene further promoted the dispersal of montane species (Raven & Axelrod 1974).

The summary of Pleistocene climatic changes presented by Buck (1990) indicated that sea level has fluctuated dramatically. Beside the changing land availability, the climatic succession of drier and wetter cycles during the Pleistocene certainly contributed to depauperate the moss flora (Delgadillo 1992).

Distributional data for mosses, liverworts and various other groups of organisms suggest that the Antillean Arc together with the ability for long range dispersal in these species have also favored the interchange between North and South America (Buck 1990, Delgadillo 1987, 1992, 1993, Gradstein & Váňa 1987, Gradstein et al. 1994, Pócs 1988, Steere 1984, 1985).

Quercus, the dominant canopy tree genus in the Talamancan upper montane forest belt, migrated in the past from the holarctic region via Mexico into the mountains of Central and NW South America. Palynological evidence shows the arrival of *Quercus* about 340,000 yr B.P. at the plain of Bogotá in the Eastern Cordillera of Colombia (Hooghiemstra & Ran 1994).

Study area

In Costa Rica, upper montane *Quercus* forests are found in the Cordillera de Talamanca, the geological backbone of Southern Central America. The evergreen high-elevation tropical oak forests occur in the upper montane forest belt *sensu* Grubb (1974) or montane belt *sensu* Holdridge (1967) and are situated between the lower montane forest belt, which has its upper limit at about 2100 m asl and the subalpine dwarf forest belt present above 3100 m asl (see Fig. 2-1).

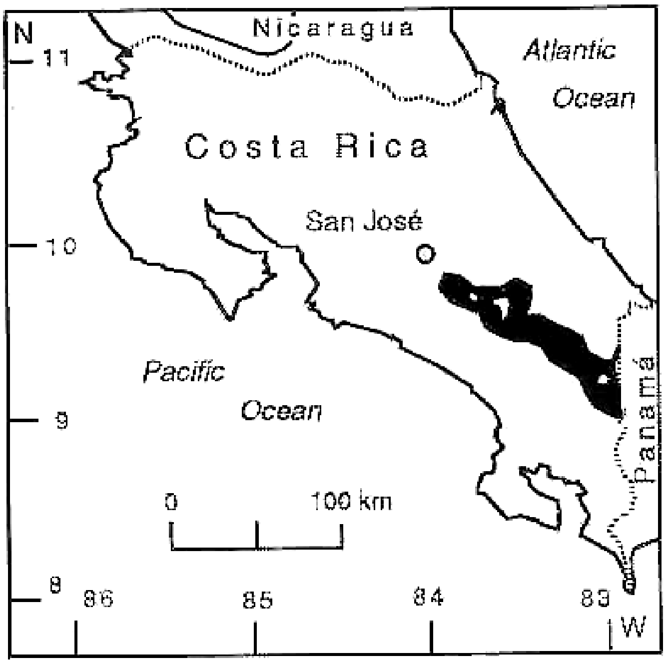

Fig. 2-1. Map of Costa Rica, showing the Talamancan upper montane Quercus forests (black area). White areas in the forest zone represent subalpine forest and paramo vegetation (from Kappelle et al. 1992).

The study area has a Cf climate, according to the Köppen Climate System. In general, a short dry season and a long wet season can be distinguished. At 3000 m a.s.l. (meteorological station Villa Mills) the dry season starts in December and ends in April. Climatic conditions within the Cordillera de Talamanca are very diverse, due to the region’s large expanse, its geographic location, which includes the Pacific and Caribbean watersheds, the great altitudinal differences, and its irregular and abrupt topography. Table 2-1 summarizes the most important climatic parameters from meteorological stations in the Talamancan *Quercus* forest belt.

Table 2-1. Climate parameters at different locations in the Talamancan oak forest zone (from Kappelle et al. 1992)

Location	Altitude (m)	Average annual temperature (°C)	Average annual rain fall (mm)
Crestones (Chirripo)	3670		>2300
Villa Mills	3000	10,9	2812
Ojo de Agua	2960	11,2	
Tres de Junio	2660		3000
Cañón	2500		2144
Cañón	2300	14,5	
Provindencia	1600		2980

In general, the *Quercus* forests under study comprise stands over 40 m tall and consist of about five vegetation layers. These layers are: i) the rather uniform canopy layer, made up of mere *Quercus* trees sometimes intermingled with a few other trees; ii) the diverse 10 to 25 m tall subcanopy layer covering 30-50 % of the surface; iii) the shrub layer, iv) the herb layer and v) the bryophyte layer. Detailed information on vegetation, structure and physiognomy of the forests is given by Kappelle et al. (1989, 1995, 1996).

The geomorphology of Cordillera de Talamanca is dominated by the contrast between steep, deeply fluvially dissected valleys and extensive remains of flattish Pliocene forms of rugged crests, which is the result of the young uplift of the Cordillera. Pleistocene glaciations only influenced the highest peaks (Chirripo, Cerro de la Muerte).

Phytogeography

Methods

For the present study extensive field work in the Río Savegre watershed area (2000 m – 3400 m a.s.l.) has been the basic reference. Additionally, field work in oak forests of other parts of Cordillera de Talamanca was performed and revised herbarium specimens from CR, INB, GOET (U) have been included.

However, the study of the bryophyte flora is certainly biased to the pacific-facing slope of Cordillera de Talmanca.

A checklist of montane bryophyte species of Cordillera de Talamanca (Tab. 2-2) has been compiled, which includes bryophytes from Costa Rican páramo (Gradstein & Holz, in press, with recent updates) and montane *Quercus* forests above 2200 m. Previous checklists of bryophytes of montane oak forest (Bowers 1970, Kappelle 1996) have not been included. In many cases these checklists include specimens from páramo vegetation (above 3000 m) and non-oak forest vegetation from altitudes between 2000 and 3000 m. (e.g. mire vegetation, open rock outcrops, other (azonal) forest types, etc.).

An inventory of bryophytes of six hectare primary oak forest (Chapter 3, Table 3-1) has been used to compare the bryogeographic spectra of different microhabitats within an upper montane *Quercus* forest.

In addition, checklists of epiphytic bryophytes from five *Quercus copeyensis* trees from primary, young secondary and late secondary oak forests have been included to compare the bryogeographic spectra of these forest types (see Table 5-2 in Chapter 5, only bryophytes).

Nomenclature follows Allen (1994, 2002), Buck (1998) and Sharp et al. (1994) for mosses and Uribe & Gradstein (1998) for liverworts. The arrangement of genera and families follows Buck & Goffinet (2000) for mosses and Yano & Gradstein (1997) for liverworts.

If possible, for each bryophyte species listed the present geographical distribution has been determined using the following floras: Allen (1994, 2002), Buck (1998), Sharp et al. (1994) and Churchill & Linares (1995) for mosses and Fulford (1963-1976), Gradstein et al. (2001), Gradstein & Pinheiro da Costa (2003) for liverworts. In addition, many taxonomic papers and monographs have been consulted.

Geographical elements (Table 2-3)

Species belonging to the wide temperate element (T) are limited to the cool and cold areas of both the northern and the southern hemisphere. Species of the northern temperate element (nT) are limited to the extra-tropical northern hemisphere (holarctic). Those with a southern temperate distribution (sT) are distributed over the cool and cold regions of southern South America, Antarctica, Australia, New Zealand and Tasmania, respectively (sub-)antarctic (pacific) islands, with northern extensions to Indonesia, New Guinea and Taiwan (austral-antarctic element).

Table 2-3. Definition of the phytogeographical elements of bryophytes found in Cordillera de Talamanca, Costa Rica.

Acronym	Phytogeographical element	Altitude
Cos	= cosmopolitan	
T	= wide temperate	
nT	= northern temperate	
sT	= southern temperate	
PT	= pantropical (wide tropical)	
A-P	= (tropical) amphi-pacific	
A-A	= tropical amphi-atlantic	
N	= (lowland) neotropical	lowland and submontane (mainly below 1000-1300 m)
A	= Andean (Mexico to Chile)	montane (above 1000-1300 m)
nA	= northern Andean (not known South of northern Peru)	
P	= páramo	alpine (above 3200 m in the Andes, above 3000 m in Central America)
nP	= northern páramo (not known South of Colombia)	
CA	= Central America (“endemic”)	
+ wi	= West Indies	
+ m	= Southern Mexico	

Tropical amphi-pacific (tropical malayo-american) (A-P) species are basically limited to the warm to cool areas of SE Asia and tropical America, while tropical amphi-pacific (tropical afro-american) (A-A) species are restricted to Africa south of the Sahara and tropical America. Many species of the amphi-pacific element are not restricted to the tropics alone, but are also found in very humid extra-tropical areas surrounding the Pacific Ocean. Species with a pantropical (PT) distribution are shared with the African and Asian (paleo)tropics.

Neotropical species are confined to tropical America from Southern Mexico (tropic of Cancer) to northern Argentina and southeastern Brazil (tropic of Capricorn). From the neotropical species (N) the strictly montane species of the Andes (andean, A) and the alpine páramo species (P) may be separated. Definition of the páramo element follows Churchill & Griffin and Gradstein in Luteyn (1992). It is difficult to define the lower altitudinal border of páramo species, as forest elements may be a typical component of páramo vegetation even above 4000 m and alpine-like open-grassy vegetation may be found azonally lower than 3000 m. Many montane species of the Andes (Andean species) are commonly also found in the mountains of SE Brazil and in the Guiana Highlands. Andean species are usually not strictly restricted to tropical America and can also be found in the humid parts of the Rocky Mountains or the southern most parts of the Andeas in Chile and Argentina. Neotropical species restricted (endemic) to Central America (CA) are usually also found in the West Indies (wi) or in southern (tropical) Mexico (m).

The distribution of cosmopolitan species (Cos) is almost world wide, from the warm lowlands and the cool mountains in the tropics to the temperate areas of the northern and southern hemisphere.

Results

Bryophyte Diversity

The list of montane bryophytes of the Cordillera de Talamanca contains 401 species (191 hepatics, one hornwort and 209 mosses) (Tab. 2-2). Two hundred thirty two of these (111 hepatics, 121 mosses) occur in the páramo above 3000 m and 251 (128 hepatics, one hornwort, 122 mosses) are found in oak forests between 2000 and 3000 m. Eighty two species are known from both vegetation types, occurring mainly as epiphytes on shrubs or in small elfin forest islands in the páramo zone. This list is probably far from being complete and should be considered as preliminary. Future work on the perhumid Atlantic slope of the Cordillera de Talamanca may reveal many additional species.

The 401 bryophyte species belong to 29 families of hepatics, 46 families of mosses and one is a hornwort. The following families are represented by five and more genera: Jungermanniaceae (7), Lejeuneaceae (27), Lepidoziaceae (6), Bartramiaceae (5), Brachytheciaceae (7), Bryaceae (5), Dicranaceae (11), Hypnaceae (5), Orthotrichaceae (5), Polytrichaceae (7), Pottiaceae (9), Sematophyllaceae (5). Lejeuneaceae are the most specious family with 46 species in 27 genera. Twenty seven of the 401 species (7%) are Central American endemics. They are restricted to Central America, the West Indies and tropical Southern Mexico.

Phytogeographical trends in the Oak Forest flora compared to the páramo flora

Of the 251 bryophytes found in oak forests of Cordillera de Talamanca, 232 (93 %) have a tropical distribution (PT, A-A, A-P, N, A, nA, P, nP, CA). With 185 species (74 %) the neotropical species (N, A, nA, P, nP, CA) are most important. 69 (27 %) of these neotropical species are tropical Andean-centered (A, nA, P, nP, see Table 2-4). Of the tropical Andean-centred species (montane and alpine distribution) 18 (7 %) are restricted to the northern Andes (nA, nP). These species are not known south of northern Peru. Twenty one species (8 %) are

Central American ‘endemics’. Many of these species are also found in the West Indies and in tropical southern Mexico.

There are no less than 47 wide tropical species (19 %), 24 are pantropical, 21 are tropical amphi-atlantic and only three are amphi-pacific.

Of the ten temperate species five are northern temperate, three are southern temperate and two are bipolar. Only seven species are cosmopolitan in distribution.

Table 2-4. Phytogeographical elements (species numbers and percent of total) of páramo and oak forest bryophytes from Cordillera de Talamanca. Analysis is based on Table 2-2. 1) column refers to 392 hepatic species of Costa Rica studied by Gradstein et al. (1994). 2) column refers to vascular plants studied by Kappelle et al. (1992). For definition of the phytogeographical elements see Table 2-3.

	Phytogeographical element	Páramo	*%*	Oak forest	*%*	*hepatic species of Costa Rica % 1)*	*vascular plant genera % 2)*
1	PT	20	*9*	24	*10*	*-?-*	*15*
2	A-A	12	*5*	21	*8*	*-?-*	*3*
3	A-P	3	*1*	3	*1*	*-?-*	*10*
4	N	46	*20*	95	*38*	*-?-*	*-?-*
5	A	54	*23*	51	*20*	*-?-*	*-?-*
6	NA	28	*12*	18	*7*	*-?-*	*-?-*
7	P	6	*3*	0	*0*	*-?-*	*-?-*
8	NP	10	*4*	0	*0*	*-?-*	*-?-*
9	CA “*endemic*”	8	*3*	21	*8*	*14.5*)*	*0 ?*
10	T	13	*6*	3	*1*	*-?-*	*4*
11	NT	12	*5*	5	*2*	*3.5*	*8*
12	ST	9	*4*	3	*1*	*2.5*	*6*
13	Cos	11	*5*	7	*3*	*1.5*	*8*
	Total (1-13)	**232**	***100***	**251**	***100***	***100***	***100***
	Wide tropical (1-3)	35	*15*	47	*19*	*-?-*	*28*
	Neotropical (4-9)	152	*66*	185	*74*	*-?-*	*46*
	Neotropical montane (5-8)	98	*42*	69	*27*	*17**)*	*-?-*
	Tropical (1-9)	188	*81*	232	*93*	*92.5*	*74*
	Temperate (10-12)	34	*15*	10	*4*	*7.5*	*18*

*) Mesoamerican, Caribbean, endemic and subendemic elements **) Andean element

Compared to the ***páramo*** (see Tab. 2-4) there are slightly more neotropical species in the oak forests (74 % vs. 66 %), but fewer of them are restricted to montane or alpine areas (27 % vs. 42 %). Like in the oak forest most species with a wide tropical range are pantropical or tropical amphi-atlantic. Only 7 % of the species found in Costa Rican páramo are restricted to páramo vegetation (páramo element). The temperate element is represented by no less than 34 species (15 %) in Costa Rican páramo, this being more than three times the number of temperate species in the oak forests. Only 3 % (8 species) of the species found in Costa Rican páramo are Central American endemics, a surprisingly small number compared to the 21 Central American endemics in the oak forest. For a detailed discussion of the phytogeographical relationship of Costa Rican páramo compared to other neotropical páramo areas see Gradstein (1998, 1999) and Gradstein & Holz, in press.

Phytogeographical trends in forest microhabitats

Different microhabitat types have been analysed phytogeographically in order to search for a correlation between habitat type and phytogeographical element. Table 2-5 shows the geographical distribution of bryophyte species found in different microhabitats of an upper montane oak forest (Los Robles, near San Gerardo de Dota, see Chapter 3). Of the 206 species found in six hectare of this type of forest, 199 could be designated to a phytogeographical element. 12 of these species are found on twigs in the outer canopy and 34 on bigger branches in the inner canopy of canopy and subcanopy trees. 58 species are found on trunks and 65 on tree bases of big trees, whereas 61 are found on shrubs and 12 on living leaves in the understorey of the forest. Many species are found on the forest floor, 67 on rotten wood and logs, 69 on open soil and 36 on stones (for a detailed description of this site, see Chapter 3).

Of the classified 199 species, 50 % (100 species) are neotropical species (N) and 19 (37 species) are tropical Andean centred (A, nA). Fifteen species (8 %) are Central American endemics (CA). Thirty five species (18 %) are wide tropical (PT, A-A and A-P). Only seven temperate species are found of which one is bipolar temperate, three are northern temperate, and three are southern temperate. Five species are cosmopolitan in distribution.

When comparing phytogeographical spectra of the microhabitat types (Tab. 2-5), several trends may be observed. Neotropical and wide tropical species are found in all forest microhabitats. While Andean and northern Andean species are not present on living leaves, northern Andean species are also absent on twigs of the outer canopy and stones on the forest floor. The analysis also shows, that temperate species are only found on forests floor habitats (logs, soil, stones), including the base of trees. Also the cosmopolitan species are mainly restricted to the forest floor.

Table 2-5. Geographical distribution of bryophyte species in different microhabitats of an upper montane oak forest in Costa Rica. a) absolute numbers of species b) percentages in a microhabitat. W = wide tropical including A-A, A-P and PT, for definition of phytogeographical elements see Table 2-3. Analysis based on Table 3-1, Chapter 3.

a)

	twigs	branches	trunks	tree bases	shrubs	leaves	logs	soil	stones	all habitats
W	5	6	9	13	16	2	10	8	6	35
N	5	14	32	34	31	9	34	37	20	100
A	2	9	10	10	9		8	12	3	31
nA		2	2	1	2		2	2		6
CA		2	4	4	3	1	7	5	4	15
T								1		1
nT			1	1			2	1		3
sT				2			2	1	1	3
Cos		1					2	2	2	5
Sum	12	34	58	65	61	12	67	69	36	199

b)

	twigs	branches	trunks	tree bases	shrubs	leaves	logs	soil	stones	all habitats
W	42	18	16	20	26	17	15	12	17	18
N	42	41	55	52	51	75	51	54	56	50
A	17	26	17	15	15		12	17	8	16
nA		6	3	2	3		3	3		3
CA		6	7	6	5	8	10	7	11	8
T								1		1
nT			2	2			3	1		2
sT				3			3	1	3	2
Cos		3					3	3	6	3

Table 2-6. Geographical range of bryophyte species in different epiphytic habitats of five standing *Quercus copeyensis* canopy trees in primary, early secondary and late secondary montane oak forest in Costa Rica. a) absolute numbers of species b) percentages in a habitat or forest type. PF = primary forest, ESF = early secondary forest and LSF = late secondary forest. For definition of phytogeographical elements see Table 2-3. Comparison of primary and secondary forest based on Table 5-2.

a) Forest type	PF	PF	PF	PF	PF	ESF	LSF	all
Epiphytic habitat	tree base	trunk	inner canopy	outer canopy	all	all	all	all
PT	4	5	1	4	9	7	9	12
A-A	4	1	1	0	3	5	8	10
A-P	0	0	0	1	1	1	0	1
N	11	10	8	7	20	22	31	42
A	3	3	3	4	8	9	13	17
nA	4	3	3	3	9	6	7	12
CA	0	1	1	1	3	3	4	6
T	0	0	0	0	0	0	0	0
nT	1	1	1	1	2	0	0	2
sT	1	0	0	0	1	0	1	1
Cos	0	0	0	0	1	1	0	2
Sum	28	24	18	21	57	54	73	105

b) Forest type	PF	PF	PF	PF	PF	ESF	LSF	all
Epiphytic habitat	tree base	trunk	inner canopy	outer canopy	all	all	all	all
PT	14	21	6	19	16	13	12	11
A-A	14	4	6	0	5	9	11	10
A-P	0	0	0	5	2	2	0	1
N	39	42	44	33	35	41	42	40
A	11	13	17	19	14	17	18	16
nA	14	13	17	14	16	11	10	11
CA	0	4	6	5	5	6	5	6
T	0	0	0	0	0	0	0	0
nT	4	4	6	5	4	0	0	2
sT	4	0	0	0	2	0	1	1
Cos	0	0	0	0	2	2	0	2

Phytogeographical trends in epiphytic species of primary and secondary oak forests

In a comparative study of primary and secondary oak forests five standing canopy trees of *Quercus copeyensis* were investigated in a primary, an early secondary and a late secondary forest each (Tab. 2-6 and Table 5-2). In total, 105 bryophyte species were found on the 15 investigated trees; 57 occur in the primary forest, 54 in the early secondary forest and 73 in the late secondary forest.

The most common geographical elements of epiphytic bryophyte species on *Quercus copeyensis* in both primary and secondary forests were the neotropical (N) and tropical Andean-centred species (71 species, 68 %). They were followed by 23 wide tropical species (22 %), including 12 pantropical (PT), 10 amphi-atlantic (A-A) and one amphi-pacific (A-P) species. There are only three temperate (T, nT, sT) and two cosmopolitan species. The phytogeographical spectra of the investigated primary, early and late secondary forests showed no significant differences; also Central American endemics are found in all forest types.

Of the 57 epiphytic species on *Quercus copeyensis* in the primary forest, 28 are found on the tree base, 24 on the trunk, 18 on big branches in the inner canopy and 21 on twigs in the outer canopy. All epiphytic microhabitats show similar phytogeographical spectra.

Discussion

The applied approach gives first insights into the present-day phytogeographical pattern of bryophytes of the Talamancan *Quercus* forests and the páramo vegetation in Cordillera de Talamanca, Costa Rica. Overall, the investigation suggests that Costa Rica received much of its bryophyte flora from South America and from Mexico, in the later case through adjacent Central America. It can also be noted, that he bryophyte floras of the northern Andes and montane Central America are very similar (Gradstein et al. 1994). They are a blend of tropical elements, which have adapted to cooler temperatures with temperate elements invading from both boreal and austral regions. As the Andean uplift occurred from the late Miocene to mid-Pliocene the resulting large areas of montane climate were populated initially by lower montane flora, but later invaded by austral elements. Only later in the Pliocene and early Pleistocene, Laurasian taxa may have arrived, mainly by crossing the newly formed isthmus of Panama (Good 1974, Gentry 1982, Gradstein & Váña 1987). Subsequent climatic changes associated with the glaciations were important to the further development of the flora. During the glacials, the tree line was lowered and the montane climate was relatively continuously distributed, facilitating migration and exchange of taxa adapted to montane climates (Van der Hammen 1982).

In total, 93 % of the bryophytes of Talamancan oak forests are tropical (compared to only 81 % of the páramo flora), this is the same number as reported for 392 hepatics from the whole of Costa Rica by Gradstein et al. (1994). The amphi-atlantic and the pantropical elements show the close relationship to the floras of tropical South America and Africa, while both are less closely related to the tropical Asian flora.

Nevertheless, the bryophyte flora of the oak forests is dominated by neotropical elements, many of the species being tropical Andean-centred (A) and restricted to the northern Andes and Central America (nA). Together with the high percentage of Central American endemics this confirms the importance of Pleistocene glacials, when tree line was lowered facilitating migration and exchange of taxa in a north-south direction. In the interglacials the montane flora retreated to more isolated areas at higher elevations, promoting allopatric speciation.

The Andean species are a particular noteworthy element in the flora of Costa Rica. Many of them reach their northernmost limit in the mountains of Costa Rica; some even managed to cross the Nicaraguan depression and extend into Guatemala and southern Mexico (Gradstein et al. 1994). The proportion of montane bryophytes decreases from the páramo (42% of the species) over oak forests (27 %) to 17 % for the hepatic flora of whole Costa Rica (based on a total of 392 species).

Surprisingly, the bryophyte flora of the oak forest has more Central American endemics as the páramo. This may indicate that not only plant migration but also speciation has been an important factor in the development of the Central American bryophyte flora. However, many of the Central American endemics show very close relationships to the flora of tropical southeastern Mexico and the West Indies. These relationships have been discussed in detail by Buck (1990), Crosby (1969), Delgadillo (1986, 1992, 1993, 1995, 2000), Duarte (1982), Pócs (1988) and Steere (1984, 1985) for mosses. No attempt has however been made to distinguish between a Mesoamerican element and a Caribbean element in the present paper. Most species of the Mesoamerican element seem to be montane species, which limits their distribution in the West Indies.

Gradstein et al. (1994) reported 14.5 % of Mesoamerican, Caribbean, endemic and subendemic elements in the hepatic flora of Costa Rica. This is by far more than observed in páramo or oak forest vegetation of Cordillera de Talamanca (Tab. 2-4). Narrow endemism among Costa Rican bryophytes is very low, like in bryophytes in general and the few endemic species known from Cordillera de Talamaca may be artificial due to a insufficient taxonomic knowledge or undercollecting in other parts of Central America, Southern Mexico and the Northern Andes.

Only 26 % of the bryophytes reported from Talamancan oak forests and only 35 % of the bryophytes reported from Costa Rican páramo also occur outside of Latin America (W, A-A, A-P, T, nT, sT, Cos). Temperate species (bipolar, northern temperate and southern temperate) are less common in the oak forests than in the páramo vegetation. As to their habitats, it appears not unexpectedly, that most temperate species are found in high montane and alpine regions and some species are restricted to the latter (Gradstein & Váña 1987). The occurrence of northern temperate hepatics in the tropics has also been discussed in detail by the two authors.

Interestingly, although the dominating tree genus in Talamancan oak forests is of temperate origin, the bryophyte flora in these forests, and especially the epiphytic one, is more tropical in character than the local vascular plant flora. However, *Quercus copeyensis* and *Quercus costaricensis* are restricted to the

Neotropics and are not known north of tropical southeastern Mexico. Temperate bryophyte species are mainly found in the understorey of the oak forests, because microclimatic conditions in the lower layers favour their occurrence.

When the phytogeographical elements of the bryophytes are compared with those of vascular plant genera (Kappelle et al. 1992; Tab. 2-4) similar trends are observed. However, those of the oak forests have more temperate and amphi-pacific, and fewer amphi-atlantic vascular plant genera. One of the reasons for this may be the use of genera of vascular plants instead of species in the study of Kappelle et al. (1992). We suggest that an analysis of the phytogeography of vascular plants at the species level might confirm the trends found in the bryophytes. We also hypothesise that differences in migration rates and speciation between vascular and bryophyte species have played only a minor role.

It would be worthwhile to compare the phytogeographic spectra of the bryophyte floras of the oak forests from Mexico and Colombia with that of Costa Rica but, unfortunately, checklists for these forests are not available to allow for a detailed comparison. Delgadillo & Cárdenas (1989) reported 155 species of mosses based on collections from the coniferous and oak forests of high elevations of Chiapas. Their definition of phytogeographical elements is not fully comparable to our approach, but largely in line with our findings. The authors report 2 % of boreal species (+/- nT), 34 % of Meso-American species, 24 % of Carribean South American, 39 % of species with a wide distribution (wide tropical, cosmopolitan and temperate species) and 2 % of endemic species.

Kappelle et al. (1992, vascular plant genera of oak forests) and Gradstein et al. (1994, hepatics of Costa Rica as a whole) found a stronger floristic affinity with the northern Andes than with tropical southeastern Mexico. In fact, the bryophyte floras of the northern Andes and montane Central America are very similar, but the occurrence of many species which are found in Central America and have there only other occurrence in southeastern Mexico (see Tabl. 2-2 and 2-4) indicates a strong affinity between these two bryophyte floras. The same is suggested by recent findings of *Brachymitrion cochabambae (Müll. Hal.) A.K. Kop., Diphyscium chiapense D.H. Norris, Tayloria chiapensis H.A. Crum* in Costa

Rica (Holz et al. 2002). Other support for this notion comes from Mueller & Halling (1995), who recorded great affinity of ectomycorrhizal fungi (Agricales) of the Costa Rican oak forests to those of North America.

Future research in tropical forests of southeastern Mexico and Central America and the Northern Andes may help to corroborate the continuity of bryophyte distributional patterns from South America to North America through the Central American bridge and the Antillean Arc. More information and other scientific tools will be necessary to determine intensity, direction and routes of major floristic interchanges.

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Table 2-2. Phytgeographical elements of the bryophytes of montane Cordillera de Talmanaca. For definition of phytogeographical elements see Table 2-1.

	phyto-geographical element	***páramo***	***oak forest***
Liverworts (Hepaticae)			
ACROBOLBACEAE			
Acrobolbus Nees			
antillanus R.M.Schust.	nA	*x*	
Lethocolea Mitt.			
glossophylla (Spruce) Grolle	A	*x*	
Tylimanthus Mitt.			
laxus (Lindenb.) Spruce	N	*x*	*x*
ADELANTHACEAE			
Adelanthus Mitt.			
crossii Spruce	nP	*x*	
decipiens (Hook.) Mitt.	PT	*x*	*x*
lindenbergianus (Lehm.) Mitt.	sT	*x*	
pittieri (Steph.) Grolle	A	*x*	*x*
ANEURACEAE			
Cryptothallus Malmb.			
hirsutus Crum	CA	*x*	
Riccardia Gray			
andina (Spruce) Herzog	N		*x*
spp.	-	*x*	*x*
ARNELLIACEAE			
Gongylanthus Nees			
liebmanianus (Lindenb. & Gott.) Steph.	A	*x*	
AYTONIACEAE			
Asterella P.Beauv.			
macropoda (Spruce) Evans	A	*x*	
BALANTIOPSIDACEAE			
Isotachis Mitt.			
lopezii (Schust.) Gradst.	P	*x*	
multiceps Gott.	N	*x*	
serrulata (Sw.) Gottsche	N		*x*
Ruizanthus R.M.Schust.			
venezuelanus R.M.Schust.	nP	*x*	
CALYPOGEIACEAE			
Calypogeia Raddi			
peruviana Nees & Mont.	N	*x*	*x*
CEPHALOZIACEAE			
Cephalozia (Dumort.) Dumort.			
crassifolia (Lindenb. & Gottsche) Fulf.	N		*x*
crossii Spruce	N	*x*	*x*
Iwatsukia N.Kitag.			
jishibae (Steph.) N.Kitag.	A-A		*x*
Nowellia Mitt.			
curvifolia (Dicks.) Mitt.	nT		*x*
CEPHALOZIELLACEAE			
Cephaloziella (Spruce) Schiffn.			
granatensis (Jack) Fulf.	N	*x*	
FOSSOMBRONIACEAE			
Fossombronia Raddi			
sp.	-	*x*	

Table 2-2 (cont’d).

	phyto-geographical element	***páramo***	***oak forest***
GEOCALYCACEAE			
Clasmatocolea Spruce			
vermicularis (Lehm.) Grolle	sT	*x*	*x*
Heteroscyphus Schiffn.			
marginatus (Steph.) Fulf.	A		*x*
polyblepharis (Spruce) Schiffn.	nA		*x*
Leptoscyphus Mitt.			
amphibolius (Nees) Grolle	N	*x*	*x*
cuneifolius (Hook.) Mitt.	N	*x*	
physocalyx (Hampe & Gott.) Gott.	A	*x*	
porphyrius (Nees) Grolle	N	*x*	*x*
Lophocolea (Dumort.) Dumort.			
bidentata (L.) Dumort.	T		*x*
muricata (Lehm.) Nees	sT	*x*	*x*
trapezoidea Mont.	N	*x*	*x*
GYMNOMITRIACEAE			
Gymnomitrion Corda			
andinum (Herz.) Herz.	P	*x*	
setaceum Grolle & Vána	nP	*x*	
truncato-apiculatum Herz.	nP	*x*	
Marsupella Dumort.			
miniata (Lindenb. & Gottsche) Grolle	CA + m	*x*	
*Stephaniella J.B.*Jack			
*paraphyllina J.B.*Jack	A	*x*	
rostrata Schmitt	nP	*x*	
HERBERTACEAE			
Herbertus Gray			
acanthelius Spruce	A	*x*	
divergens Steph.	N		*x*
juniperoides (Sw.) Grolle	N	*x*	
pensilis (Taylor) Spruce	N		*x*
subdentatus (Steph.) Fulf.	A-A	*x*	*x*
Triandrophyllum Fulf. & Hatch.			
subtrifidum (Hook. & Tayl.) Fulf. & Hatch.	sT	*x*	
JUBULACEAE			
Frullania Raddi			
arecae (Spreng.) Gottsche	PT		*x*
brasiliensis Raddi	N	*x*	*x*
caulisequa (Nees) Nees	N		*x*
convoluta Lindb. & Hampe	A	*x*	*x*
ecklonii (Spreng.) Spreng.	PT		*x*
peruviana Gottsche	A		*x*
planifolia Steph.	nP	*x*	
sphaerocephala Spruce	A	*x*	
stenostipa Spruce	A		*x*
JUNGERMANNIACEAE			
Anastrophyllum (Spruce) Steph.			
auritum (Lehm.) Steph.	PT	*x*	*x*
nigrescens (Mitt.) Steph.	A	*x*	
stellatum R.M.Schust.	P	*x*	
Andrewsianthus R.M.Schust.			
jamesonii (Mont.) Vána	PT	*x*	
Cryptochila R.M.Schust.			
grandiflora (Lindb. & Gottsche) Grolle	sT	*x*	
Jamesoniella (Spruce) F.Lees			
rubricaulis (Nees) Grolle	N	*x*	*x*

Table 2-2 (cont'd).

	phyto-geographical element	***páramo***	***oak forest***
Jungermannia L.			
sphaerocarpa Hook.	nT	*x*	
Lophozia (Dumort.) Dumort.			
incisa (Schrad.) Dumort.	nT	*x*	
laxifolia (Mont.) Grolle	P	*x*	
Syzygiella Spruce			
anomala (Lindenb. & Gott.) Steph.	A	*x*	*x*
campanulata Herz.	nA	*x*	
liberata Inoue	nA	*x*	
perfoliata (Sw.) Spruce	N		*x*
LEJEUNEACEAE			
Amphilejeunea R.M.Schust.			
patellifera (Spruce) Schust.	nA	*x*	*x*
Anoplolejeunea (Spruce) Schiffn.			
conferta (Meissn.) Evans	N	*x*	*x*
Aphanolejeunea A.Evans			
crenata Evans	CA +wi		*x*
exigua Evans	A-A		*x*
gracilis Jovet-Ast	N		*x*
Aureolejeunea R.M.Schust.			
aurifera R.M.Schust.	nP	*x*	
fulva R.M.Schust.	nA	*x*	*x*
Blepharolejeunea S.W.Arnell			
incongrua (Lindenb. & Gott.) van Slag. & Kruijt	A	*x*	*x*
securifolia (Spruce) Schust.	A	*x*	
Brachiolejeunea (Spruce) Schiffn.			
laxifolia (Tayl.) Schiffn.	N	*x*	*x*
Bryopteris (Nees) Lindenb.			
filicina (Sw.) Nees	N		*x*
Ceratolejeunea (Spruce) Schiffn.			
cornuta (Lindenb.) Schiffn.	N		*x*
Cheilolejeunea (Spruce) Schiffn.			
inflexa Hampe ex Lehm. & Lindenb.	N		*x*
laevicalyx (J.B.Jack & Steph.) Grolle	A		*x*
Cololejeunea (Spruce) Schiffn.			
vitalana Tixier	N		*x*
Colura (Dumort.) Dumort.			
naumannii (Schiffn. & Gottsche) Steph.	A	*x*	
tenuicornis (A. Evans) Steph.	PT	*x*	*x*
Cyclolejeunea A.Evans			
accendens (Gott.) Evans	N		*x*
Dicranolejeunea (Spruce) Schiffn.			
axillaris (Nees & Mont.) Schiffn.	N		*x*
Diplasiolejeunea (Spruce) Schiffn.			
brunnea Steph.	N		*x*
cavifolia Steph.	PT		*x*
involuta S. Winkl.	nA	*x*	*x*
pluridentata Schäfer-Verwimp	nA	*x*	*x*
replicata(Spruce) Steph.	A	*x*	*x*
Drepanolejeunea (Spruce) Schiffn.			
anoplantha Evans	N		*x*
inchoata (Meissn.) Steph.	N		*x*
lichenicolea (Spruce) Steph.	N	*x*	*x*
Echinocolea R.M.Schust.			
asperrima (Spruce) R.M.Schust.	nA		*x*
Frullanoides Raddi			
densifolia Raddi	N	*x*	*x*

Table 2-2 (cont'd).

	phyto-geographical element	***páramo***	***oak forest***
Harpalejeunea (Spruce) Schiffn.			
stricta (Lindenb. & Gottsche) Steph.	N		*x*
Lejeunea Lib.			
flava (Sw.) Nees	PT		*x*
halei H.Rob.	N		*x*
intricata J.B. Jack & Steph.	A		*x*
laetevirens Nees & Mont.	N		*x*
lepida Lindenb. & Gottsche	A		*x*
phyllobola Nees & Mont.	N		*x*
ramulosa Spruce	A		*x*
Leucolejeunea A.Evans			
xanthocarpa (Lehm. & Lindenb.)	PT	*x*	*x*
Lindigianthus Kruijt & Gradst.			
cipaconeus (Gott.) Kruijt & Gradst.	nA	*x*	*x*
Macrolejeunea (Spruce) Schiffn.			
lancifolia (Steph.) Herzog	A		*x*
pallescens (Mitt.) Schiffn.	A	*x*	*x*
Marchesina Gray			
robusta (Mitt.) Schiffn.	A		*x*
Microlejeunea Steph.			
bullata (Tayl.) Steph.	N	*x*	*x*
capillaris (Gottsche) Steph.	N		*x*
Odontolejeunea (Spruce) Schiffn.			
lunulata (Web.) Schiffn.	A-A		*x*
Omphalanthus Lindenb. & Nees			
filiformis (Sw.) Nees	N	*x*	*x*
Taxilejeunea (Spruce) Schiffn.			
spp.	-		*x*
LEPICOLEACEAE			
Lepicolea Dumort.			
ochroleuca (Spreng.) Spruce	sT	*x*	
pruinosa (Tayl.) Spruce	N	*x*	*x*
LEPIDOZIACEAE			
Bazzania Gray			
arcuata (Lindenb. & Gottsche) Trevis.	N	*x*	
denticulata (Lindenb. & Gottsche) Trevis.	N		*x*
hookeri (Lindenb.) Trevis.	N		*x*
jamaicensis (Lehm. & Lindenb.) Trevis.	N	*x*	
longistipula (Lindenb.) Trevis.	N		*x*
stolonifera (Sw.) Trevis.	N		*x*
Kurzia G.Martens			
capillaris (Sw.) Grolle	N	*x*	
flagellifera (Steph.) Grolle	A-A		*x*
Lepidozia (Dumort.) Dumort.			
cupressina (Sw.) Lindenb.	PT	*x*	*x*
patens Lindenb.	N		*x*
squarrosa Steph.	CA		*x*
Paracromastigum Fulf. & J.Taylor			
granatense (Gott.) Schust.	nA	*x*	
Pseudocephalozia R.M.Schust.			
quadriloba (Steph.) Schust.	sT	*x*	
Telaranea Spruce ex Schiffn.			
nematodes (Gott. ex Aust.) Howe	PT	*x*	*x*
MARCHANTIACEAE			
Dumortiera Nees			
hirsuta L.	PT	*x*	*x*

Table 2-2 (cont'd).

	phyto-geographical element	***páramo***	***oak forest***
Marchantia L.			
berteroana Lehm. & Lindenb.	sT	*x*	
plicata Nees & Mont.	A	*x*	
METZGERIACEAE			
Metzgeria Raddi			
agnewii Kuwah.	A-A		*x*
albinea Spruce	PT		*x*
aurantiaca Steph.	N	*x*	
gigantea Steph.	A	*x*	
liebmanniana Lindenb. & Gottsche	A	*x*	*x*
leptoneura Spruce	Cos	*x*	*x*
MONOCLEACEAE			
Monoclea Hook.			
gottschei Lindb.	N	*x*	*x*
PALLAVICINIACEAE			
Jensenia Lindb.			
erythropus (Gott.) Grolle	N	*x*	
Symphyogyna Nees & Mont.			
brasiliensis Nees & Mont.	A-A	*x*	*x*
brogniartii Mont.	N		*x*
PELLIACEAE			
Noteroclada Tayl. ex Hook. & Wils.			
confluens Tayl. ex Hook. & Wils.	A-A	*x*	
PLAGIOCHILACEAE			
Plagiochila (Dumort.) Dumort.			
adiantoides (Sw.) Lindenb.	A		*x*
aerea Taylor	N	*x*	*x*
alternans Lindenb. & Gottsche	A		*x*
amicta	N		*x*
bicuspidata Gottsche	CA		*x*
bifaria (Sw.) Lindenb.	A-A	*x*	*x*
loriloba Herzog	A		*x*
deflexa	CA	*x*	*x*
deflexirama Taylor	A		*x*
dimorpha var. ecuadorica (Inoue) J.Heinrichs	A	*x*	
diversifolia Lindenb. & Gottsche	A		*x*
fuscolutea Taylor	nA	*x*	
heterophylla Lindenb. ex Lehm.	A-A		*x*
jaramillii Robins.	nP	*x*	
kroneana Steph.	N		*x*
longispina Lindenb. & Gott.	A	*x*	
cf. montagnei Nees	N		*x*
oresitropha Spruce	N		*x*
ovata Lindenb. & Gott.	A	*x*	
pachyloma Taylor	A		*x*
papillifolia Steph.	A-A		*x*
cf. patula (Sw.) Lindenb.	N		*x*
patzschkei Steph.	A	*x*	*x*
pittieri Steph.	CA		
raddiana Lindenb.	N		*x*
retrorsa Gottsche	A-A	*x*	*x*
stolonifera Lindenb. & Gott.	A	*x*	
stricta Lindenb.	A		*x*
superba (Nees ex Spreng.) Mont. & Nees	N		*x*
tabinensis Steph.	A	*x*	
tocarema Gottsche	N		*x*
trichostoma Gottsche	A		*x*

Table 2-2 (cont'd).

	phyto-geographical element	*páramo*	*oak forest*
PORELLACEAE			
Porella L.			
leiboldii (Lehm. & Lindenb.) Trevis.	N	*x*	*x*
liebmanniana (Lindenb. & Gottsche) Trevis.	CA		*x*
swartziana (Web.) Trevis.	N		*x*
PSEUDOLEPICOLEACEAE			
Blepharostoma (Dumort.) Dumort.			
trichophyllum (L.) Dumort.	nT	*x*	
RADULACEAE			
Radula Dumort.			
javanica Gottsche	PT		*x*
laxiramae Steph.	N		*x*
nudicaulis Steph.	A-A	*x*	*x*
quadrata Gottsche	N		*x*
tectiloba Steph.	N	*x*	
tenera Mitt. ex Steph.	N	*x*	
voluta Tayl.	A-A	*x*	*x*
SCAPANIACEAE			
Diplophyllum (Dumort.) Dumort.			
obtusatum (R.M.Schust.) R.M.Schust.	nT	*x*	*x*
Scapania (Dumort.) Dumort.			
portoricensis Hampe & Gott.	N	*x*	*x*
TRICHOCOLEACEAE			
Trichocolea Dumort.			
floccosa Herzog & Hatcher	CA		*x*
tomentosa (Sw.) Gott.	N	*x*	*x*
Hornworts (Anthocerotae)			
DENTROCEROTACEAE			
Megaceros Campb.			
vincentianus (Lehm. & Lindenb.) Campb.	N		*x*
Mosses (Bryopsida)			
ADELOTHECIACEAE			
Adelothecium Mitt.			
bogotense (Hampe) Mitt.	A-A	*x*	*x*
ANDREAEACEAE			
Andreaea Hedw.			
alpestris (Thed.) Schimp.	T	*x*	
rupestris Hedw.	T	*x*	
BARTRAMIACEAE			
Bartramia Hedw.			
angustifolia Mitt.	A		*x*
brevifolia Brid.	A	*x*	*x*
longifolia Hook.	A	*x*	
potosica Mont.	A	*x*	
strumosa (Hampe) Mitt.	nA	*x*	
Breutelia (Bruch & Schimp.) Schimp.			
tomentosa (Brid.) A.Jaeger	A	*x*	*x*
Conostomum Sw.			
tetragonum (Hedw.) Lindb.	nT	*x*	
Leiomela (Mitt.) Broth.			
bartramioides (Hook.) Paris	PT	*x*	*x*
Philonotis Brid.			
longiseta (Michx.) E.Britton	N	*x*	

Table 2-2 (cont'd).

	phyto-geographical element	***páramo***	***oak forest***
BRACHYTHECIACEAE			
Aerolindigia M.Menzel			
capillaceae (Hornsch.) M.Menzel	A-A		*x*
Eurhynchium Bruch & Schimp.			
clinocarpum (Taylor) Paris	N	*x*	
Meteoridium (Müll.Hal.) Manuel			
remotifolium (Müll.Hal.) Manuel	N		*x*
tenuissima (Hook. & Wilson) M.A.Lewis	N		*x*
Palamocladium Müll.Hal.			
leskeoides (Hook.) E.Britton	Cos		*x*
Platyhypnidium M.Fleisch.			
aquaticum (A.Jaeger) M.Fleisch.	N	*x*	*x*
Rhynchostegium Bruch & Schimp.			
serrulatum (Hedw.) A.Jaeger	A		*x*
Squamidium (Müll.Hal.) Broth.			
leucotrichum (Taylor) Broth.	N	*x*	*x*
BRYACEAE			
Acidodontium Schwägr.			
megalocarpum (Hook.) Renauld & Cardot	A		*x*
Anomobryum Schimp.			
julaceum (P.Gaertn., B.Mey. & Scherb.) Schimp.	A	*x*	
plicatum Cardot	nP	*x*	
Brachymenium Schwägr.			
systylium (Müll.Hal.) A.Jaeger	PT		*x*
Bryum Hedw.			
argenteum Hedw.	T	*x*	
billardii Schwägr.	Cos		*x*
capillare Hedw.	T	*x*	
chryseum Mitt.	A	*x*	
procerum Schimp.	A		*x*
Rhodobryum (Schimp.) Limpr.			
beyrichianaum (Hornsch.) Müll. Hal.	N		*x*
ontariense (Kindb.) Paris	Cos	*x*	
CAMPYLIACEAE			
Hygrohypnum Lindb.			
reduncum (Schimp. ex Mitt.) N.Nishim.	A		*x*
CALYMPERACEAE			
Syrrhopodon Schwägr.			
gardneri (Hook.) Schwägr.	PT		*x*
lycopodioides (Sw. ex Brid.) Müll.Hal.	N		*x*
prolifer Schwägr.	PT		*x*
CRYPHAEACEAE			
Cryphaea D.Mohr			
apiculata Schimp.	A	*x*	
attenuata Schimp.	CA +m		*x*
Dendropogonella E.Britton			
rufescens (Schimp.) E.Britton	nA		*x*
DALTONIACEAE			
Calyptrochaeta Desv.			
haitensis (H.A. Crum & Steere) Crosby	CA +m +wi		*x*
Daltonia Hook. & Taylor			
gomezii Crosby	CA	*x*	
gracilis Mitt.	N	*x*	
lindigiana Hampe	nA	*x*	
longifolia Taylor	N		*x*
pulvinata Mitt.	A	*x*	
stenophylla Mitt.	nA		*x*

Table 2-2 (cont'd).

	phyto-geographical element	***páramo***	***oak forest***
Leskeodon Broth.			
cubensis (Mitt.) Thér.	CA +m +wi		x
DICRANACEAE			
Anisothecium Mitt.			
vaginatum (With.) Lindb.	nA	x	
Aongstroemia Bruch & Schimp.			
filiformis (P.Beauv.) Wijk & Marg.	PT	x	
julacea (Hook.) Mitt.	Cos	x	
Campylopodiella Cardot			
stenocarpa (Wils.) P.Müll. & Frahm	nT	x	x
Campylopus Brid.			
albidovirens Herz.	A	x	
areodictyon (C.Müll.) Mitt.	nA	x	
asperifolius Mitt.	nA	x	
cavifolius Mitt.	nA	x	
densicoma (C.Müll.) Par.	A	x	
flexuosus (Hedw.) Brid.	Cos	x	
fragilis (Brid.) Bruch & Schimp.	Cos	x	
jamesonii (Hook.) A.Jaeger	PT	x	x
nivalis (Brid.) Brid.	PT	x	x
paramoensis F.D. Bowers	CA	x	
pilifer Brid.	Cos	x	
richardii Brid.	N	x	
standleyi Bartr.	CA	x	
Chorisodontium (Mitt.) Broth.			
setaceum (E.B.Bartram) E.B.Bartram	CA		x
Dicranodontium Bruch & Schimp.			
longisetum (Hook.) Williams	nA	x	x
meridionale E.B.Bartram	nA		x
Dicranum Hedw.			
flagellare Hedw.	Cos		x
frigidum Müll.Hal.	A	x	x
peruvianum Robins.	A	x	
Holomitrium Brid.			
arboreum Mitt.	N		x
flexuosum Mitt.	A		x
pulchellum Mitt.	N	x	x
Microcampylopus (Müll.Hal.) M.Fleisch.			
curvisetus (Hampe) Giese & J.-P.Frahm	N		x
Pilopogon Brid.			
guadeloupensis (Brid.) J.-P.Frahm	N	x	x
laevis (Tayl.) Thér.	A	x	
Symblepharis Mont.			
lindigii Hampe	A	x	
DITRICHACEAE			
Ceratodon Brid.			
stenocarpus Bruch & Schimp.	PT	x	
Tristichium Müll.Hal.			
mirabile (Müll.Hal.) Herzog	A-A	x	
ENTODONTACEAE			
Entodon Müll.Hal.			
jamesonii (Taylor) Mitt.	nA	x	
EUSTICHIACEAE			
Eustichia (Brid.) Brid.			
longirostre (Brid.) Brid.	PT	x	

Table 2-2 (cont'd).

	phyto-geographical element	***páramo***	***oak forest***
FISSIDENTACEAE			
Fissidens Hedw.			
polypodioides Hedw.	Cos		*x*
wallisii Müll.Hal.	A		*x*
weirii var. hemicrapedophyllus (Cardot) Pursell	N		*x*
weirii Mitt. var. *weirii*	N		*x*
FUNARIACEAE			
Entosthodon Schwägr.			
attenuatus (Dicks.) Bryhn	A-A		*x*
bonplandii (Hook.) Mitt.	N	*x*	
jamesonii (Taylor) Mitt.	A-P	*x*	
Funaria Hedw.			
calvescens Schwägr.	PT	*x*	
GRIMMIACEAE			
Grimmia Hedw.			
longirostris Hook.	A	*x*	
ovalis (Hedw.) Lindb.	nT	*x*	
trichophylla Grev.	T	*x*	
Racomitrium Brid.			
crispipilum (Taylor) A.Jaeger	A	*x*	
lanuginosum (Hedw.) Brid.	T	*x*	
Schistidium Bruch & Schimp.			
apocarpum (Hedw.) Bruch & Schimp.	T	*x*	
HEDWIGIACEAE			
Braunia Bruch & Schimp.			
squarrulosa (Hampe) Müll.Hal	CA +m		*x*
Hedwigidium Bruch & Schimp.			
integrifolium (P.Beauv.) Dixon	Cos	*x*	
HOOKERIACEAE			
Hookeria J.E.Sm.			
acutifolia Hook. & Grev.	A-P		*x*
HYPNACEAE			
Ctenidium (Schimp.) Mitt.			
malacodes Mitt.	A		*x*
Ectropothecium Mitt.			
leptochaeton (Schwägr.) W.R. Buck	N		*x*
Hypnum Hedw.			
amabile (Mitt.) Hampe	N	*x*	*x*
polypterum (Mitt.) Broth.	CA +m +wi		*x*
Mittenothamnium Henn.			
lehmannii (Besch.) Cardot	nA	*x*	
reptans (Hedw.) Cardot	PT		*x*
Pylaisiella Grout			
falcata (Schimp.) Ando	A-P	*x*	
HYPOPTERYGIACEAE			
Hypopterygium Brid.			
tamariscinum (Hedw.) Brid.	PT		*x*
LEMBOPHYLLACEAE			
Orthostichella Müll.Hal.			
pentasticha (Brid.) W.R.Buck	A-A		*x*
Pilotrichella (Müll.Hal.) Besch.			
flexilis (Hedw.) Ångström	N		*x*
LEPYRODONTACEAE			
Lepyrodon Hampe			
tomentosus (Hook.) Mitt.	A	*x*	*x*

Table 2-2 (cont'd).

	phyto-geographical element	***páramo***	***oak forest***
LEUCOBRYACEAE			
Leucobryum Hampe			
antillarum Schimp. ex Besch.	N		*x*
martianum (Hornsch.) Hampe ex Müll.Hal.	N		*x*
LEUCODONTACEAE			
Leucodon Schwägr.			
curvirostris Hampe	A	*x*	*x*
LEUCOMIACEAE			
Rhynchostegiopsis Müll.Hal.			
tunguraguana (Mitt.) Broth.	A		*x*
METEORIACEAE			
Meteorium (Brid.) Dozy & Molk.			
deppei (Hornsch. ex Müll.Hal.) Mitt.	N		*x*
Toloxis W.R.Buck			
imponderosa (Taylor) W.R.Buck	N		*x*
MNIACEAE			
Epipterygium Lindb.			
mexicanum (Besch.) Broth.	CA +m +wi		*x*
Plagiomnium T.J.Kop.			
rhynchophorum (Hook.) T.J.Kop.	N	*x*	*x*
Pohlia Hedw.			
richardsii A.J.Shaw	nT	*x*	
Schizymenium Harv.			
campylocarpum (Hook. & Arnott) A.J.Shaw	A	*x*	
NECKERACEAE			
Neckera Hedw.			
ehrenbergii Müll.Hal.	CA +m		*x*
urnigera Müll.Hal.	A		*x*
Porotrichodendron M.Fleisch.			
superbum (Taylor) Broth.	A	*x*	*x*
Porotrichum (Brid.) Hampe			
korthalsianum (Dozy & Molk.) Mitt.	N		*x*
lancifrons (Hampe) Mitt.	A		*x*
longirostre (Hook.) Mitt.	A		*x*
mutabile Hampe	N		*x*
ORTHODONTIACEAE			
Orthodontium Wilson			
pellucens (Hook.) Bruch, Schimp. & W.Gümbel	Cos	*x*	*x*
ORTHOTRICHACEAE			
Amphidium Schimp.			
tortuosum (Hornsch.) Cufod.	PT	*x*	
Groutiella Steere			
chimborazensis (Spruce ex Mitt.) Florsch.	N		*x*
Macrocoma (Müll.Hal.) Grout			
tenue ssp. sullivantii (Müll.Hal.) Vitt	A-P		*x*
Macromitrium Brid.			
aureum Müll.Hal.	nA	*x*	*x*
cirrosum (Hedw.) Brid.	N	*x*	*x*
crosbyorum B.H.Allen & Vitt	CA	*x*	
greenmanii Grout	CA		*x*
longifolium (Hook.) Brid.	A		*x*
oblongum (Taylor) Mitt.	nA	*x*	
Orthotrichum Hedw.			
pariatum Mitt.	nA	*x*	
sharpii H.Rob.	CA +m		*x*
Zygodon Hook. & Taylor			
campylophyllus Müll.Hal.	A	*x*	

Table 2-2 (cont'd).

	phyto-geographical element	***páramo***	***oak forest***
ehrenbergii Müll.Hal.	nA	*x*	*x*
liebmannii Schimp.	P	*x*	
obtusifolius Hook.	A-P		*x*
reinwardtii (Hornsch.) Braun	PT	*x*	*x*
PHYLLOGONIACEAE			
Phyllogonium Brid.			
viscosum (P.Beauv) Mitt.	nA		*x*
PILOTRICHACEAE			
Callicostella (Müll.Hal.) Mitt.			
pallida (Hornsch.) Ångström	N		*x*
Cyclodictyon Mitt.			
albicans (Hedw.) Kuntze	N		*x*
roridum (Hampe) Kuntze	A		*x*
Hypnella (Müll.Hal) A.Jaeger			
pilifera (Hook.f. & Wilson) A.Jaeger	N		*x*
Trachyxiphium W.R.Buck			
guadalupense (Spreng.) W.R.Buck	N		*x*
subfalcatum (Hampe) W.R.Buck	nA		*x*
PLAGIOTHECIACEAE			
Plagiothecium Bruch & Schimp.			
drepanophyllum Renauld & Cardot	A		*x*
lucidum (Hook.f. & Wilson) Paris	A	*x*	*x*
POLYTRICHACEAE			
Atrichum P.Beauv.			
oerstedianum (Müll.Hal.) Mitt.	CA +m		*x*
Oligotrichum Lam. & DC.			
aligerum Mitt.	A-P	*x*	
Pogonatum P.Beauv.			
campylocarpum (Müll.Hal.) Mitt.	nA	*x*	
procerum (Lindb.) Schimp.	CA +m +wi		*x*
Polytrichadelphus (Müll.Hal.) Mitt.			
peruvianus Broth.	A	*x*	*x*
Polytrichastrum G.L.Sm.			
alpiniforme (Cardot) G.L.Sm.	P	*x*	
Polytrichum Hedw.			
juniperinum Hedw.	T	*x*	
Steereobryon G.L.Sm.			
subulirostrum (Schimp. ex Besch.) G.L.Sm.	nA		*x*
POTTIACEAE			
Anoectangium Schwägr.			
aestivum Hedw.	Cos	*x*	
Bryoerythrophyllum P.C.Chen			
jamesonii (Taylor) H.A.Crum	A	*x*	
Didymodon Hedw.			
ferrugineus (Schimp. ex Besch.) Hill	Cos	*x*	
laevigatus (Mitt.) R.H.Zander	A	*x*	
nigrescens (Mitt.) Saito	nT	*x*	
Hymenostylium Brid.			
recurvirostrum (Hedw.) Dixon	T	*x*	
Leptodontium (Müll.Hal.) Lindb.			
exasperatum Cardot	A		*x*
flexifolium (Dicks. ex With.) Hampe	nT	*x*	*x*
longicaule Mitt.	PT	*x*	
stoloniferum R.H.Zander	nP	*x*	
ulocalyx (Müll.Hal.) Mitt.	A	*x*	*x*
wallisii (Müll.Hal.) Kindb.	A-A	*x*	

Table 2-2 (cont'd).

	phyto-geographical element	***páramo***	***oak forest***
Mironia R.H.Zander			
ehrenbergiana (Müll.Hal.) R.H.Zander	A	*x*	
stenotheca (Thér.) R.H. Zander	CA +m	*x*	
Pseudosymblepharis Broth.			
bartramii Thér. ex E.B.Bartram	CA		*x*
Streptopogon Mitt.			
erythrodontus (Spruce) Spruce ex Mitt.	PT	*x*	*x*
Trichostomum Bruch			
brachydontium Bruch	T	*x*	
crispulum Bruch	Cos	*x*	
PRIONODONTACEAE			
Prionodon Müll.Hal.			
densus (Sw. ex Hedw.) Müll.Hal.	A-A	*x*	*x*
fusco-lutescens Hampe	A		*x*
PTEROBRYACEAE			
Pterobryon Hornsch.			
densum Hornsch.	N		*x*
Renauldia Müll.Hal.			
mexicana (Mitt.) H.A.Crum	CA +m		*x*
RACOPILACEAE			
Racopilum P.Beauv.			
tomentosum (Hedw.) Brid.	A-A	*x*	*x*
RHABDOWEISIACEAE			
Rhabdoweisia Bruch & Schimp.			
fugax (Hedw.) Bruch & Schimp.	nT	*x*	
RHACOCARPACEAE			
Rhacocarpus Lindb.			
purpurascens (Brid.) Paris	PT	*x*	
RHIZOGONIACEAE			
Leptotheca Schwägr.			
boliviana Herzog	A	*x*	
Pyrrhobryum Mitt.			
mnioides (Hook.) Manuel	sT	*x*	*x*
spiniforme (Hedw.) Mitt.	PT		*x*
Rhizogonium Brid.			
lindigii (Hampe) Mitt.	A		*x*
RIGODIACEAE			
Rigodium Schwägr.			
toxarium (Schwägr.) A.Jaeger	A-A		*x*
SEMATOPHYLLACEAE			
Acroporium Mitt.			
pungens (Hedw.) Broth.	N		*x*
Aptychella (Broth.) Herzog			
proligera (Broth.) Herzog	N	*x*	*x*
Heterophyllum (Schimp.) Kindb.			
affine (Hook.) M.Fleisch.	Cos		*x*
Pylaisiadelpha Cardot			
tenuirostris (Sull.) W.R.Buck	nT		*x*
Sematophyllum Mitt.			
aureosulphureum (Müll. Hal.) Broth.	A	*x*	
dimorphum (Renauld & Cardot) F.D.Bowers	N		*x*
subsimplex (Hedw.) Mitt.	A-A		*x*
swartzii (Schwägr.) W.H.Welch & H.A.Crum	N	*x*	*x*
SPHAGNACEAE			
Sphagnum L.			
cuspidatum Ehrh.	T	*x*	
limbatum Mitt.	nA	*x*	

Table 2-2 (cont'd).

	phyto-geographical element	***páramo***	***oak forest***
magellanicum Brid.	T	*x*	*x*
meridense (Hampe) Müll.Hal.	nA		*x*
sancto-josephense H.A.Crum & Crosby	nA	*x*	
sparsum Hampe	nA	*x*	
subsecundum Nees	T	*x*	
SPLACHNACEAE			
Brachymitrion Taylor			
moritzianum (Müll.Hal.) A.Kop.	nA	*x*	*x*
Tetraplodon Bruch & Schimp.			
mnioides (Hedw.) Bruch & Schimp.	nT	*x*	
THUIDIACEAE			
Cyrto-hypnum (Hampe) Hampe & Lorentz			
mexicanum (Mitt.) W.R.Buck & H.A.Crum	CA +m		*x*
sharpii (H.A.Crum) W.R.Buck & H.A.Crum	CA +m +wi		*x*
Thuidium Bruch & Schimp.			
pseudoprotensum (Müll.Hal.) Mitt.	N	*x*	*x*

CHAPTER 3

Bryophyte diversity, microhabitat differentiation and distribution of life forms in Costa Rican upper montane *Quercus* forest

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Abstract

Upper montane oak forests in the Cordillera de Talamanca show a high diversity of bryophyte species and great diversification of microhabitats. A complete bryophyte inventory of six hectare of forest yielded 206 species: 100 mosses, 105 hepatics and one hornwort. Based on similarities in species composition the forest microhabitats cluster into three main groups: i) forest floor habitats (including tree base), ii) phyllosphere and iii) other epiphytic habitats. The contribution of forest floor habitats to total bryophyte species richness is much higher than in forests of lower elevational belts. Distribution of species and life forms in different microhabitats reflect the vertical variation of humidity and light regimes. At the same time they show the impact of the pronounced dry season and the structural characters (tree height, stratification, number of host tree species) of these oak forests on epiphytic bryophytes compared to more humid forests and upper montane forests of lower stature.

Resumen

Los bosques montano-altos de roble en la Cordillera de Talamanca muestran una gran diversidad de especies de briofitas y una considerable diversificación de microhábitats. El inventario total de las briofitas registra 206 especies: 100 musgos, 105 hepáticas y una antocerota. Con base en similitudes en la composición de especies, los microhábitats del bosque pueden ser clasificados en tres grupos principales: i) suelo del bosque (incluyendo la base de los árboles), ii) filosfera y iii) otros hábitats epífitos. La contribución de los hábitats del suelo del bosque a la diversidad total de especies de briofitas es mucho más importante que en bosques a menor altura. La distribución de especies y formas de vida en diferentes microhábitats reflejan la variación vertical de los regímenes hídrico y lumínico. Al mismo tiempo, muestran el impacto de la pronunciada época seca y de los caracteres estructurales de estos bosques de roble (altura de los árboles, estratificación, número de especies de forófitos) sobre las briofitas epífitas, en comparación con bosques más húmedos y bosques montano-altos de menor estatura.

Introduction

Tropical montane forests have great value as protective cover on steep slopes of headwater catchments. Soil erosion and occurrence of landslides are minimized by the presence of a natural healthy forest cover. It is supposed that these forests exert a sponge effect, soaking up rain water and storing it before releasing it in regular amounts over an extended period (Bruijnzeel & Hamilton 2000). Bryophytes are an important component of tropical montane forests, both in terms of ecosystem functioning, biomass and biodiversity. The large variety of substrates, the low temperatures and the plentiful availability of water favour the growth of epiphytic and terrestrial bryophytes (Wolf 1993). This is reflected by high biomass and the high diversity of species and communities in these forests (Frahm 1990, Gradstein 1995, Gradstein & Pócs 1989, Kürschner & Parolly 1998a).

Our understanding of bryophyte diversity of montane rain forests in Central America and other parts of the Neotropics is still fragmentary. Complete inventories are very scarce. Most studies only deal with part of the bryophyte flora or with selected habitats (e.g. tree bases, logs, living leaves). The most comprehensive investigation of epiphytic bryophyte diversity in neotropical montane rainforests dealing with canopy as well as understorey communities has been presented by Wolf (1993). A synopsis of trunk-inhabiting communities was presented by Kürschner & Parolly (1998a). The only complete bryophyte inventory, dealing with a lower montane cloud forest in Costa Rica, has been conducted by Gradstein et al. (2001).

This paper presents the first complete bryophyte inventory of a neotropical upper montane forest. It explores relationships between species, microhabitats, life forms and environmental factors in an upper montane *Quercus* forest in Costa Rica. The study was carried out within the framework of the project "Changes in the diversity and ecology of cryptogamic epiphytes in tropical montane rain forest canopies along gradients of human-induced disturbance" financed by the German Research Foundation (DFG). A more detailed analysis of the epiphytic bryophyte and lichen vegetation of Costa Rican oak forest will be presented in upcoming publications.

Material and Methods

The study was conducted in the private forest reserve “Los Robles” near San Gerardo de Dota (Los Santos Forest Reserve, 83°51’W 09°32’N), situated on the Pacific-facing slope of the western Talamanca Mountain Range, Costa Rica.

The local climate is cool and humid, annual precipitation averages 2800 mm and the mean daily temperature 14 °C (Instituto Meteorológico Nacional 1988, compare Chapter 1, Fig. 1-2). There is a pronounced dry season from early January to the end of April. The forest is a upper montane rainforest (“robledal de altura”) dominated by 30-40 m tall trees of two species of *Quercus*, *Q. copeyensis* C.H.Müll. and *Q. costaricensis* Liebm. Understory vegetation is characterized by bamboo, tree ferns, dwarf palms, shrubs and herbs. Canopy and subcanopy branches are festooned with vascular and non-vascular epiphytes including orchids, bromeliads, aroids, ericads, ferns, mosses, liverworts and lichens. The forest is dissected by a number of small brooks. A comprehensive description of vegetation structure, vascular plant diversity and secondary succession of these oak forests has been given by Kappelle (1995, 1996).

Field work was carried out during September 1999 and May 2000 within an 8 m wide buffer along a forest trail of 7 km length, between 2200 and 2500 m asl. The total area sampled is about 6 ha. Bryophytes were sampled in all microhabitats along the trail and species abundance of bryophytes in each microhabitat was estimated (rare < 5 observations, frequent < 20 observations, common > 20 observations). Microhabitats inventoried included soil, rock, logs, shrubs, living leaves, tree bases, trunks, and tree crowns (branches, twigs). Sampling of epiphytes on upper portions of trunks and in the canopy was done from seven freshly fallen trees (*Q. copeyensis* and *Q. costaricensis*). In general, sampling in the canopy was less detailed than in the understorey, but recent studies have shown, that complete sampling of 4-5 trees may yield over 75 % of the epiphytic flora of a homogeneous forest stand (Gradstein et al. 1996). Our inventory, which included the two species of oak, should therefore be representative. Voucher specimens were deposited at INB with duplicates in GOET, MO (some) and NY (some).

Eight types of bryophyte life forms were recognized: cushions, feathers, mats, pendants, tails, treelets, turfs and wefts (Bates 1998, Mägdefrau 1982, Richards 1984). Several species showed plasticity of life form and could be assigned to more than one type.

Descriptive statistics was used to describe presence, frequency and distribution of species in different microhabitats of the forest. Similarity in species diversity between microhabitats was calculated using the Jaccard Index (Jaccard 1912). Principal Components Analysis (PCA) of presence / absence data was used to determine main patterns of species distribution and to identify factors affecting species composition. The program packages BIODIVERSITY PROFESSIONAL (version 2) and SYSTAT were used to perform the analysis.

Nomenclature follows Allen (1994), Buck (1998) and Sharp et al. (1994) for mosses and Uribe & Gradstein (1998) for liverworts.

Results and Discussion

Species richness and microhabitats

In total, 206 bryophyte species (101 mosses, 105 hepatics including 1 hornwort) were recorded (Table 1). Tree bases (69 species), rotten logs (70 species) and soil (70 species) are the richest habitats for bryophytes followed by trunks (61 species), branches of the inner canopy (35 species), twigs of the outer canopy (14 species), and leaves in the understorey (14 species) (Fig. 3-1). Canopy leaves were devoid of bryophytes. Sixty five species were associated with lianas, poles and twigs on shrubs, ferns and palms in the forest understorey. Canopy habitats (twigs, branches and upper portions of trunks) had less than twice the number of species (73) as the forest understorey (all other habitats; 184 species). Twenty five percent of the species occurred both in the canopy and the understorey.

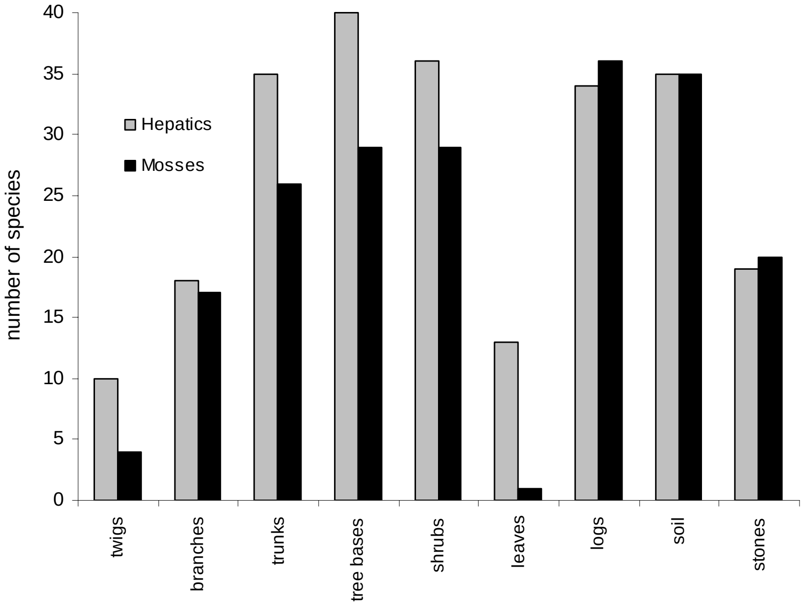


Fig 3-1. Number of mosses and hepatics in different microhabitats at Los Robles.

Species richness of hepatics and mosses was equal on logs, soil and stones, but epiphytic habitats were richer in hepatics (Fig. 3-1). Lejeuneaceae (31 species), Plagiochilaceae (13 species) and Lepidoziaceae (9 species) were the most important liverwort families in terms of number of species; Dicranaceae (9 species), Neckeraceae (7 species), Meteoriaceae (7 species) and Orthotrichaceae (7 species) were the most species rich families of mosses (Fig. 3-3).

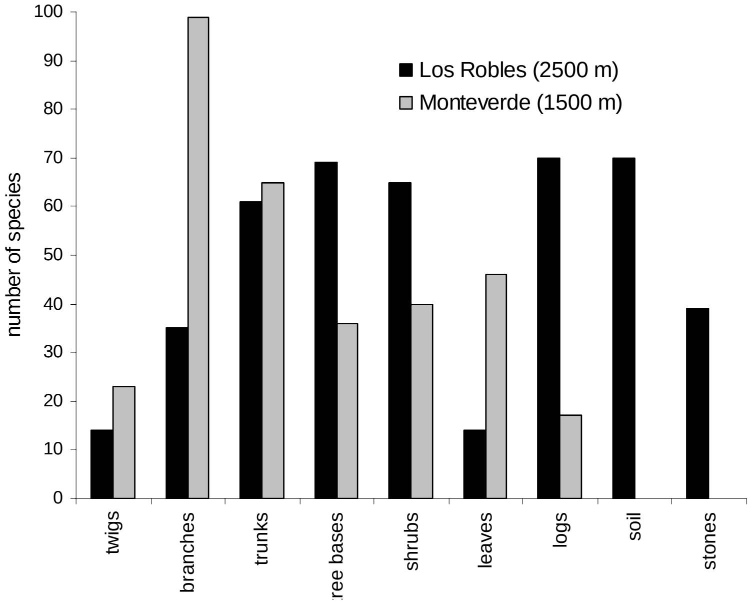


Fig 3-2. Number of bryophytes in different microhabitats in Los Robles and Monteverde.

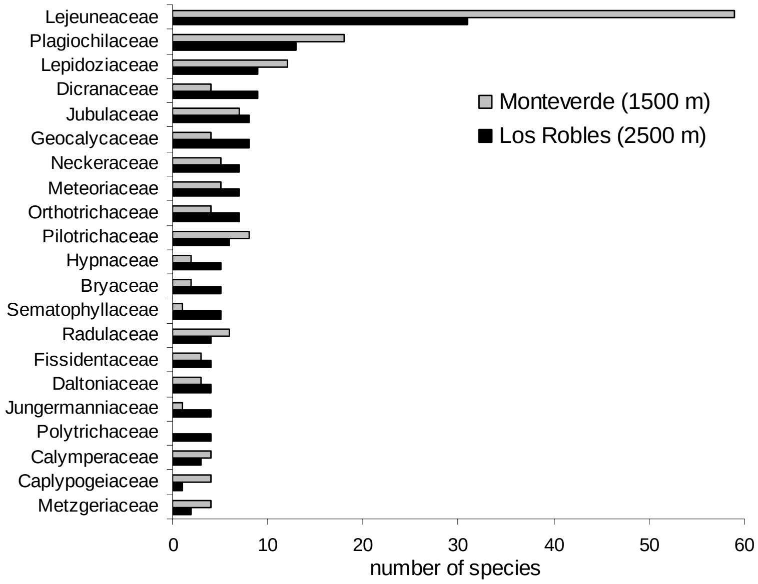


Fig 3-3. Number of species in the most speciose bryophyte families in Los Robles and Monteverde.

A Jaccard similarity calculation (Table 3-2), determining the proportion of species out of the total species list for two habitats which is common to both, revealed that logs and tree bases are most similar in terms of species composition (42 %), followed by trunks and branches (39 %) and stones and soil (31 %).

Tree bases are a transition zone between the species of the forest floor (logs, soil, stones) and the species growing on trunks of large trees. Similarities in species composition of twigs, shrubs, branches and trunks reflect the importance of the stem diameter for the composition of epiphytic cryptogam communities. Tree bases share 37% of their species with trunks and trunks share 39% of the species with branches, but branches have only 10% of their species in common with tree bases. Twigs share 26% of their species with branches. Similarity of twigs to shrubs (15%) and leaves (16%) is low. None of these microhabitats shows a relation to the tree bases, logs, soil and stones in terms of bryophyte species composition.

Table 3-2. Jaccard Index (similiarity matrix) of bryophytes for different microhabitats in a Costa Rican upper montane oak forest.

Habitats	BRAN	TRUN	BASE	SHRU	LEAV	LOGS	SOIL	STON
TWIGS	26	9	5	15	16	1	1	2
BRANCHES		39	9	15	4	5	2	1
TRUNKS			37	28	3	13	9	10
TREE_BASES				20	1	42	26	15
SHRUBS					8	6	9	10
LEAVES						0	0	0
LOGS							32	17
SOIL								31
STONES								

Shrubs form a heterogeneous habitat, showing a species composition similar to that of tree bases and trunks (the species in the lower part of the shrubs). Their species composition is also similar to that of branches and twigs (the species on the upper part of the shrubs). Living leaves are a very distinct microhabitat with very little floristic similarity to other microhabitats except shrubs and twigs.

Table 3-3. Species richness of bryophytes in different microhabitats at Los Robles (2500 m) and Monteverde (1500 m; GRADSTEIN et al., 2001). * = logs only

	Los Robles		Monteverde	
	species number	%	species number	%
Epiphytic	143	58	179	94
Exclusively epiphytic	89	43	173	91
Exclusively not epiphytic	63	31	11*	6*
In canopy (twigs, branches, trunks)	73	35	117	62
Exclusively in canopy (“sun epiphytes”)	22	11	68	36
On forest floor (logs, soil, stones)	117	57	17*	9*
In understory (incl. forest floor)	184	89	121	64
In canopy and in understory	51	25	48	25
Total number of species	206		190	

A comparision of the study site (2500 m) with 4 ha of lower montane cloud forest (1500 m) at Monteverde, Costa Rica (Gradstein et al. 2001) shows that total numbers of species at the two sites are rather similar (Tab. 3-3), but distribution of species in microhabitats differs significantly (Fig. 3-2). Large branches of the inner canopy were richest in species at Monteverde, whereas at Los Robles tree bases, trunks and logs are the richest microhabitats. At Monteverde 179 species (94%) are epiphytic and 68 (36 %) species are restricted to the canopy; at Los Robles only 58 % are epiphytic and only 11 % are restricted to the canopy.

The forest floor at Los Robles plays a much more important role as a habitat for bryophytes than at Monteverde. At Los Robles 117 species (57 %) were found growing on rotten logs, soil and stones and 63 of them were not found epiphytically; at Monteverde only 11. The understory (incl. the forest floor) at Los Robles harbors 89 % (184 species) of the total bryophyte flora (Tab. 3-3); at Monteverde only 64% (121 species).

Lejeuneaceae, Plagiochilaceae and Lepidoziaceae are the largest families at both sites in terms of numbers of species, but the total number of families at Los Robles (59) is significantly higher than at Monteverde (39). Lejeuneaceae contribute more than 30 % to the bryophyte flora of Monteverde and 15 % to Los Robles (Fig. 3-3). The lower figure for Lejeuneaceae at Los Robles fits the notion that importance of this family in terms of number of species generally decreases with elevation (Gradstein 1995).

The differences between Los Robles (upper montane *Quercus* forest) and Monteverde (lower montane cloud forest) in terms of species richness and microhabitat differentiation of bryophytes match with differences in climate and forest composition at the two sites. Mean annual temperature at Los Robles (ca 14 °C) is about 5 °C lower and clouds are less frequent than at Monteverde. Moreover, the forest at Monteverde is much richer in host tree species than at Los Robles (Nadkarni & Wheelwright 1999).

Bryophyte sinusia

Tree bases. Bases of large trees represent the most shady habitat for epiphytes and air humidity is relatively high. Furthermore tree bases accumulate much soil and detritus. The most abundant hepatics in this habitat are *Bazzania hookeri, B. stolonifera, B.* spp*., Lepidozia cupressina. Syrrhopodon prolifera, Plagiochila subtrinitensis* and *P. trichostoma. Plagiochila aerea* and *Rhizogonium lindigii* are usually restricted to somewhat overhanging places or small caves. Common mosses are *Heterophyllium affine, Leucobryum martianum, Sematophyllum subsimplex*, *Rigodium toxarium* (only on *Quercus costaricensis*, see Chapter 4, host preference) and *Thuidium pseudoprotensum*.

Trunks. Trunks are shady, but much drier than the tree base. Dominant bryophyte species are *Adelanthus pittieri, Herbertus divergens, Leptoscyphus porphyrius, Aphanolejeunea conferta, Holomitrium pulchellum, Groutiella chimborazensis, Macromitrium longifolium* and *Zygodon ehrenbergii*.

Branches. In this oak forests large branches of the inner canopy are a very exposed habitat. They are one of the first layers to receive rain, but they are also exposed to direct radiation and desiccation. Many bryophytes in this habitat build big mats or turfs, suitable for accumulating detritus and storing of water, for example *Frullania brasilensis, Leptodontium ulocalyx, Leucodon curvirostris, Macromitrium* spp., *Braunia squarrulosa* and *Holomitrium* spp.

Twigs. The thin twigs of the outer canopy are even more exposed to direct radiation and desiccation. Species in this habitat are small, do not accumulate much detritus and store little water. Hepatics (especially Lejeuneaceae) are more common in this habitat than mosses. Typical species are *Brachiolejeunea laxifolia, Microlejeunea bullata, Drepanolejeunea* spp*. Diplasiolejeunea* spp*., Colura tenuicornis, Leucolejeunea xanthocarpa, Daltonia longifolia* and *Zygodon reinwardtii*

Shrubs. Branches and stems of shrubs and ferns are a very heterogeneous substrate for bryophytes. On the base and lower stems of shrubs characteristic species are *Plagiochila* spp*. (*Sect*. Contiguae), P. subtrinitensis, Radula* spp*., Syrrhopodon lycopodioides, Neckera urnigera, Porotrichodendron superbum, Porotrichum* spp*., Prionodon densus, Pterobrion densum*. On the upper trunk and on fine twigs small Lejeuneaceae and pendant bryophytes are more common: *Frullania convoluta, Frullania brasilensis, Diplasiolejeunea cavifolia, Denropogonella rufescens, Pilotrichella flexilis, Meteoridium* spp., *Toloxis imponderosa. Zygodon reinwardtii* and Lejeuneaceae div. spec.

Leaves. Epiphyllous bryophytes are rather poorly presented, which is characteristic for upper montane rain forests. They are restricted to leaves in the understorey at microsites with a very high air humidity. Allmost all of them are Lejeuneaceae: *Aphanolejeuna crenata, Aphanolejeunea gracilis, Cololejeunea vitalana, Cyclolejeunea accendens, Diplasiolejeunea cavifolia, Drepanolejeunea* spec., etc. Only one moss species, *Daltonia stenophylla*, was found growing on living leaves.

Logs. Dead and decomposing wood (fallen trees and branches, rotting logs and stumps) is a very common and important habitat for bryophytes in the studied forest, probably due to its capability to absorb much water. Common hepatics are *Riccardia* spec., *Cephalozia crassifolia, Syzygiella anomala, Bazzania* spp., *Lepidozia* spp. Pleurocarpous mosses growing in loose mats such as *Mittenothamnium reptans*, *Trachyxiphium guadalupense* and *Thuidium pseudoprotensum* are also typical components of this microhabitat.

Soil. Soil and especially disturbed soil on banks along brooks, erosion gullies and the hollows at the base of fallen trees are a species rich microhabitat at

Los Robles. Many mosses especially Dicraneaceae, are common in this habitat, e.g. *Pilopogon guadalupensis, Atrichum oerstedianum, Pogonatum procerum, Dicranum frigidium, Rhodobryum beyrichianum, Bryum procerum, Fissidens* spp., *Plagiomnium rhynchophorum*. Common terricolous hepatic species are *Calypogeia peruviana*, *Isotachis serrulata, Monoclea gottschei* and *Symphyogyna* spp.

Stones. There are not many rocks in Los Robles, but shady boulders and wet stones near brooks and in small valleys are usually covered by bryophytes, including *Riccardia andina, Clasmatocolea vermicularis, Monoclea gottschei, Symphyogyna* spp., *Megaceros vincentinanus, Hygrohypnum reduncum, Cyclodictyon albicans* and *Cyclodiction roridum.*

Life forms and microhabitats

The distribution of life forms over the different microhabitats is shown in Fig. 3-4. Mats and turfs are the most common types of life form, occurring in high frequencies in all microhabitats, but turfs are lacking on living leaves and canopy twigs and are rare on shrubs. Pendants, feathers and tails are most common on shrubs and constitute more than 50 % of the species in this habitat. Feathers also occur on branches, trunks, soil and stones. Cushions are only represented by a few species (*Zygodon species, Daltonia species*) and are restricted to twigs, branches, shrubs and leaves. *Hypopterygium tamariscinum* is the only treelet and grows on soil and stones in humid hollows and close to running water.

The strong correlation of life forms with moisture and light conditions has been repeatedly demonstrated (Bates 1998, Proctor 1990, Schofield 1981, Thiers 1988). Bates (1998) showed the correlation of feathers, tails, pendants and wefts with a high atmospheric moisture availability. The data presented here clearly reflect the humid conditions in the understory and the much drier conditions on trunks, branches and twigs in the canopy of the forest. Moreover, the high percentage of mats and the fact that there are nearly no feathers, tails or pendants in the inner and outer canopy are indicative of the pronounced dry season in these upper montane oak forests.

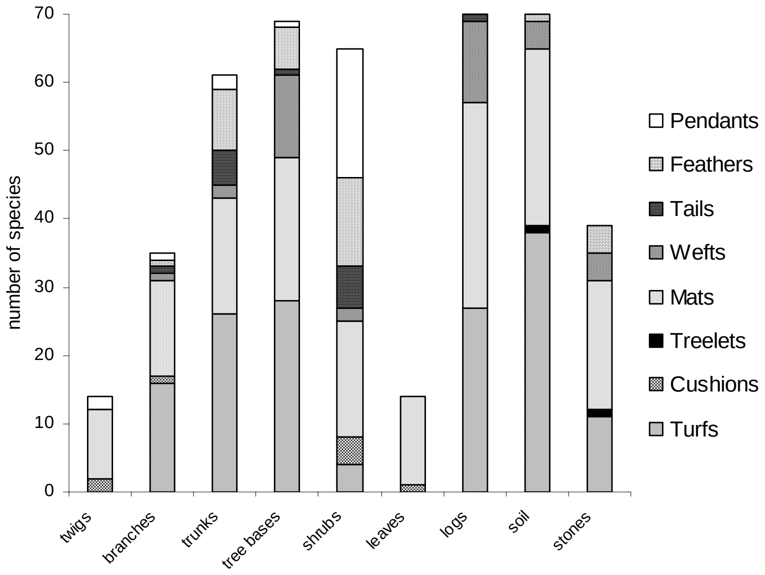


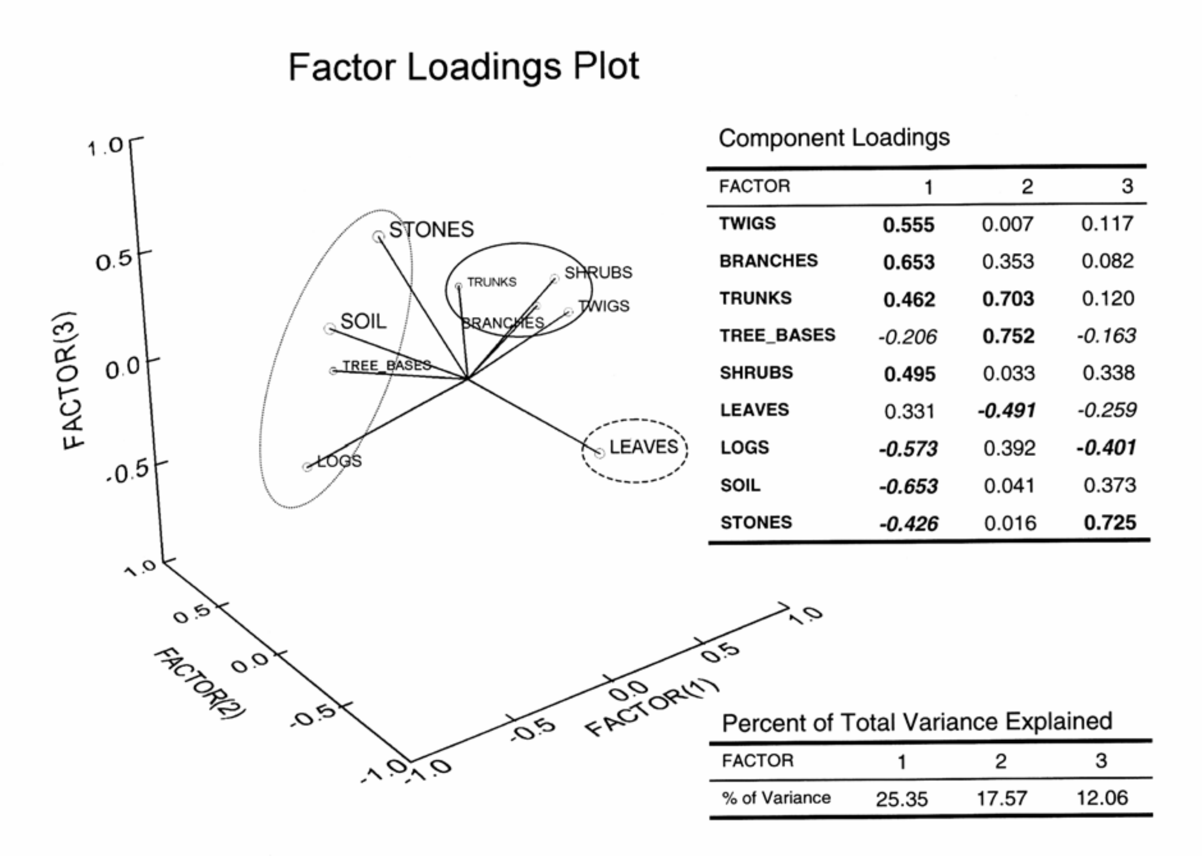
Fig. 3-4. Distribution of life forms of bryophytes in different microhabitats at Los Robles.

A comparison with upper montane forests in Northern Peru (Kürschner & Parolly 1998b) reveals much higher percentages of pendants, wefts, tails and feathers in the Peruvian forests than at Los Robles. Reasons for these differences are not quite clear but may be caused by the lower height of the trees in the Peruvian forests.

Factors controlling the microhabitat differentiation of bryophytes

Principal components analysis (PCA) of microhabitat differentiation of bryophytes reveals that more than 55 % of the observed variation is explained by three factors (Fig. 3-5). Twigs, branches, trunks and shrubs show high positive loadings on factor 1, whereas tree bases, logs, soil and stones load negatively. This factor clearly separates epiphyte habitats (incl. epiphylls) from forest floor habitats (incl. tree bases) and explains 25 % of total variation. As twigs and branches of large trees show highest positive loadings, even higher than trunks, shrubs and leaves factor 1 is probably related to light intensity.

Factor 2 still explains about 18 % of the total variation. Tree bases, trunks, branches and logs show highly positive and leaves highly negative loadings on this factor. Twigs, shrubs and soil do not show any association with factor 2. The identity of factor 2 remains unclear, but could be related to water storage during the dry season. The third factor explains 12 % of the total variation. Logs, leaves and tree bases load negatively on this factor, all other habitats positively, with stones, soil and shrubs showing the highest positive loadings. We speculate that this factor represents high availability of cations, because rocks and soils at Los Robles are generally base rich microhabitats and bark of shrubs has higher pH values than other epiphytic habitats or logs (Holz, unpubl. obs.).



Component Loadings

FACTOR	1	2	3
TWIGS	**0.555**	0.007	0.117
BRANCHES	**0.653**	0.353	0.082
TRUNKS	**0.462**	**0.703**	0.120
TREE_BASES	*-0.206*	**0.752**	*-0.163*
SHRUBS	**0.495**	0.033	0.338
LEAVES	0.331	***-0.491***	*-0.259*
LOGS	***-0.573***	0.392	***-0.401***
SOIL	***-0.653***	0.041	0.373
STONES	***-0.426***	0.016	**0.725**

Percent of Total Variance Explained

FACTOR	1	2	3
% of Variance	25.35	17.57	12.06

Fig. 3-5. Factor Loadings Plot, Component Loadings and Percent of Total Variance Explained derived by a Principal Component Analysis (PCA) of species composition in different microhabitats in the upper montane oak forest at Los Robles.

In conclusion, the ecological interpretation of the first factor is rather straight forward, but that of factors 2 and 3 remain unclear. Taken together the three factors separate the microhabitats in the forest at Los Robles into three groups: forest floor habitats (stones, soil, logs, tree bases), epiphytic habitats (trunks, branches, twigs, shrubs), and phyllosphere (living leaves) (Fig. 3-5).

Wolf (1994) used canonical correspondence analysis (CCA) in a study of the relations between epiphyte distribution and environmental factors in the northern Andes. He found that altitude and relative height in the host tree showed highest correlations with the deduced axes. However, a significant relation between environmental parameters and species composition could not be expected since only 4.3 % of the variation in species distribution could be explained by the first three constrained axes.

Conclusion

Upper montane oak forests in Cordillera de Talamanca ("robledal de altura") show a high diversity of bryophyte species and a great diversification of microhabitats. Tree bases, rotten logs, soil and trunks are the richest habitats for bryophytes in these forests. Only 58 % of the species are epiphytes and, only 11 % are restricted to the canopy. In comparison, more than 90 % of the bryophytes of lowland and lower montane rain forests are epiphytes and 35 - 50 % of the species are canopy dwellers (Cornellissen & Gradstein 1990, Cornelissen & ter Steege 1989, Gradstein et al. 2001, Montfoort & Ek 1990). Thus the forest floor plays a more important role as a habitat for bryophytes in upper montane forest than in forests of lower elevational belts. While hepatics and mosses are equal in forest floor habitats in terms of number of species, hepatics are dominant in epiphytic habitats. Like in other tropical rain forests Lejeuneaceae, Plagiochilaceae and Lepidoziaceae are the dominant hepatic families. The upper montane forest, however, is much richer in number of bryophyte families than lower montane and lowland forests.

Similarities in species composition show a strong relationship between forest floor habitats (including the tree base) in contrast to epiphytic habitats. The bryophytes of living leaves (the phyllosphere) are a distinct group with not much relation to those of other epiphytic microhabitats. Distribution of species and life forms in different forest microhabitats are correlated with humidity and light regimes and show the importance of the pronounced dry season in the oak forest of Los Robles for epiphytic bryophytes. Beside humidity and light conditions, which show clear vertical variation patterns in the forest, stem diameter is also an important factor determining the composition of epiphytic bryophyte communities.

The different species numbers, species composition and niche differentiation in Los Robles and Monteverde correlate with the climatic differences and the differences in forest composition at the two sites.

In contrast to most upper montane forests, especially true cloud forests, in which it is not possible to distinguish as many different epiphytic habitats on any one tree as in lowland forests (Pócs 1982), the microhabitats of the oak forest at Los Robles show remarkably distinct bryophyte synusiae and a clear differentiation between tree bases, trunks, branches and twigs in terms of their bryophyte assemblages. This is due to differences in the structural characters of the oak forest, especially the unusually large height of the trees, and to the pronounced dry season in the study area (Kappelle 1996).

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Table 3-1. Species, microhabitat distribution and life form of bryophytes in upper montane oak forest in Costa Rica. Life forms: Cu = Cushions; Fe = Feathers; Ma = Mats; Pe = Pendants; Ta = Tails; Tr = Treelets; Tu = Turfs; We = Wefts. Frequencies: 1 = rare; 2 = frequent; 3 = common.

Taxa	twigs	branches	trunks	tree bases	shrubs	leaves	logs	soil	stones	*close to a brook*	*close to the trail*	Life form
HEPATICAE												
ACROBOLBACEAE												
Tylimanthus laxus (Lehm. & Lindenb.) Spruce				1								Tu
ADELANTHACEAE												
Adelanthus decipiens (Hook.) Mitt.			2									Tu
Adelanthus pittieri (Steph.) Grolle		3	3	2			2					Tu
ANEURACEAE												
Riccardia andina (Spruce) Herzog								1	2	*x*		Tu
Riccardia spp.				2			3		2	*x*		Ma
BALANTHIOPSACEAE												
Isotachis serrulata (Sw.) Gottsche								2	2	*x*	*x*	Tu
CALYPOGEIACEAE												
Calypogeia peruviana (Nees. & Mont.) Steph.								2	2	*x*	*x*	Ma
CEPHALOZIACEAE												
Cephalozia crassifolia (Lindenb. & Gott.) Fulf.				1			3	2				Ma
Cephalozia crossi Spruce								1			*x*	Ma
Nowellia curvifolia (Dicks.) Mitt.			2	1			2					Ma
GEOCALYCACEAE												
Clasmatocolea vermicularis (Nees) Grolle									2	*x*		Ma
Heteroscyphus marginatus (Steph.) Fulf.							2					Ma
Heteroscyphus polyblepharis (Spruce) Schiffn.							2	1				Ma
Leptoscyphus amphibolius (Nees) Grolle				2			2	1				Ma
Leptoscyphus porphyrius (Nees) Grolle		3	2									Ma
Lophocolea bidentata (L.) Dumort.							1					Ma
Lophocolea muricata (Lehm.) Nees				2			2					Ma
Lophocolea trapezoidea Mont.							2	2				Ma
HERBERTACEAE												
Herbertus divergens Steph.		3	3	2								Tu, Ta
Herbertus pensilis (Taylor) Spruce		2	2									Ta
Herbertus subdentatus (Steph.) Fulf.		1	1	2			2	2				Tu, Ta
JUBULACEAE												
Frullania arecae (Spreng.) Gottsche					2							Ma
Frullania brasiliensis Raddi	2	3	2	2	3							Pe, Tu, Ma
Frullania caulisequa (Nees) Nees					2							Ma
Frullania convoluta Lindenb. & Hampe					3							Pe
Frullania ecklonii (Spreng.) Spreng.	2	2			2							Ma
Frullania stenostipa Spruce	1	1	1									Ma
Frullania peruviana Gottsche					1							Pe
JUNGERMANNIACEAE												
Anastrophyllum auritum (Lehm.) Steph.		2	2				2					Tu
Jamesoniella rubicaulis (Nees) Grolle		1	1									Tu, Ma
Syzygiella anomala (Lindenb. & Gottsche) Steph.				2			3	1				Ma

Table 3-1. (cont'd)

	twigs	branches	trunks	tree bases	shrubs	leaves	logs	soil	stones	*close to a brook*	*close to the trail*	Life form
Syzygiella perfoliata (Sw.) Spruce							2	2				Tu
LEJEUNEACEAE												
Anoplolejeunea conferta (Meissn.) Schiffn.	2	3	3	1	3							Ma
Aphanolejeunea crenata Evans						2						Ma
Aphanolejeunea gracilis Jovet-Ast						1						Ma
Brachiolejeunea laxifolia (Taylor) Schiffn.	3				2							Ma, Pe
Bryopteris filicina (Sw.) Nees				1								Fe
Ceratolejeunea maritima (Spruce) Steph.			1	1								Ma
Cheilolejeunea inflexa Hampe ex Lehm. & Lindenb.					1	1						Ma
Cololejeunea vitalana Tixier						2						Ma
Colura tenuicornis (Evans) Steph.	2											Ma
Cyclolejeunea accedens (Gott.) Evans						2						Ma
Dicranolejeunea axillaris (Nees & Mont.) Schiffn.				1				1				Tu
Diplasiolejeunea cavifolia Steph.					3	2						Ma
Diplasiolejeunea brunnea Steph.						1						Ma
Diplasiolejeunea sp.	2				2	1						Ma
Drepanolejeunea anoplantha Evans							1					Ma
Drepanolejeunea inchoata (Meissn.) Steph.						1						Ma
Drepanolejeunea lichenicola (Spruce) Steph.						1						Ma
Drepanolejeunea spp.	2	2	2		2	1						Ma
Frullanoides densifolia Raddi					2							Ta
Harpalejeunea stricta (Lindenb. & Gottsche) Steph.					1							Ma
Lejeunea flava (Sw.) Nees			2	1	2							Ma
Lejeunea intricata J.B. Jack & Steph.		2	2		2							Ma
Lejeunea lepida Lindenb. & Gottsche					1							Ma
Leucolejeunea xanthocarpa (Lehm. & Lindenb.) Evans	2	2			2							Ma
Lindigianthus cipaconeus (Gottsche) Kruijt & Gradst.		2	1	1	2							Ma
Macrolejeunea pallescens (Mitt.) Schiffn.					1			1				Pe, Ma
Marchesinia robusta (Mitt.) Schiffn.					2							Pe, Ma
Microlejeunea bullata (Taylor) Steph.	3	3	2	1	2	1						Ma
Microlejeunea capillaris (Gott.) Steph.							1					Ma
Odontolejeunea lunulata (Web.) Schiffn.					2	2						Ma
Omphalanthus filiformis (Sw.) Nees				1	2			1				We, Pe, Ma
Taxilejeunea sp.			1	1	2		2	1	1			Pe, Ma
LEPICOLEACEAE												
Lepicolea pruinosa (Taylor) Spruce				2			2	1				Tu
LEPIDOZIACEAE												
Bazzania denticulata (Lindenb. & Gottsche) Trevis.				2								Tu
Bazzania hookeri (Lindenb.) Trevis.			1	3			2					Tu
Bazzania longistipula (Lindenb.) Trevis.		2	2	2			3					Tu
Bazzania stolonifera (Sw.) Trevis.			2	3			2	1				Tu
Kurzia flagellifera (Steph.) Grolle				1			1	1				Ma
Lepidozia cupressina (Sw.) Lindenb.			2	3			3	2	2			Tu
Lepidozia patens Lindenb.							1					Ma
Lepidozia squarrosa Steph.							2					Ma
Telaranea nematodes (Aust.) Howe				1			2					We

Table 3-1. (cont'd)

	twigs	branches	trunks	tree bases	shrubs	leaves	logs	soil	stones	*close to a brook*	*close to the trail*	Life form
MARCHANTIACEAE												
Dumortiera hirsuta (Sw.) Nees								2	2	*x*		Ma
METZGERIACEAE												
Metzgeria leptoneura Spruce					2			2				Pe, Ma
Metzgeria albinea Spruce									1			Ma
MONOCLEACEAE												
Monoclea gottschei Lindb.							1	3	3	*x*		Ma
PALLAVICINIACEAE												
Symphyogyna brasiliensis Nees								1	2	*x*		Ma
Symphyogyna brogniartii Mont.								2	2	*x*		Ma
PLAGIOCHILACEAE												
Plagiochila adiantoides (Sw.) Lindenb.			2	2								Tu
Plagiochila aerea Taylor			2	3								We
Plagiochila alternans Lindenb. & Gottsche								2				Tu
Plagiochila bifaria (Sw.) Lindenb.		1	2									Tu
Plagiochila deflexirama Taylor			1	1	2			1				Fe
Plagiochila diversifolia Lindenb. & Gottsche				1			1	1	2	*x*		Tu
Plagiochila raddiana Lindenb.			1	1								Tu
Plagiochila stricta Lindenb.			1		2							Tu
Plagiochila subbiloba Herzog								1				Tu
Plagiochila subtrinitensis Herzog			2	3	3		2	1				Tu, Pe
Plagiochila superba (Spreng.) Mont. & Nees								2				Tu
Plagiochila trichostoma Gottsche				3			2	2				Tu
Plagiochila spp. (sect. Vagae)			1	2	3				2			Tu, Fe
PORELLACEAE												
Porella leiboldii (Lehm.) Trevis.									1	*x*		Fe
Porella liebmanniana (Lindenb. & Gottsche) Trevis.			1									Fe
Porella swartziana (Web.) Trevis.			1						2			Fe
RADULACEAE												
Radula javanica Gottsche			1	2	3							Ma
Radula laxiramea Steph.					2				2	*x*		Fe, Ma
Radula quadrata Gottsche					2							Fe
Radula voluta Gottsche et al.					3							Fe
SCAPANIACEAE												
Diplophyllum obtusatum (R.M.Schust.) R.M.Schust.								2		*x*	*x*	Tu
Scapania portoricensis Gott.			1	2	2		2	1	1			Tu
TRICHOCOLEACEAE												
Trichocolea floccosa Herzog & Hatcher				2			1					We
Trichocolea tomentosa (Sw.) Gottsche				1	2		2	1				Tu, We, Fe
ANTHOCEROTAE												
ANTHOCEROTACEAE												
Megaceros vincentianus (Lehm. & Lindenb.) Campb.							1	1	3	*x*		Ma
MUSCI												
ADELOTHECIACEAE												
Adelothecium bogotense (Hampe) Mitt.					2							Ta

Table 3-1. (cont'd)

	twigs	branches	trunks	tree bases	shrubs	leaves	logs	soil	stones	*close to a brook*	*close to the trail*	Life form
AMBLYSTEGIACEAE												
Hygrohypnum reduncum (Mitt.) N.Nishim.									2	*x*		Ma
BARTRAMIACEAE												
Bartramia brevifolia Brid.								2				Tu
Breutelia tomentosa (Brid.) Jaeg.								1		*x*		Tu
Leiomela bartramioides (Hook.) Par.			1		2							Tu
BRACHYTHECIACEAE												
Palamocladium leskeoides (Hook.) E.Britton		1										We
Platyhypnidium aquaticum (A. Jaeger) M.Fleisch.									2	*x*		Tu
BRYACEAE												
Acidodontium megalocarpum (Hook.) Renauld & Cardot			1									Tu
Bryum billarderi Schwägr.							2					Tu
Bryum procerum Schimp.				1				2				Tu
Epipterygium mexicanum (Besch.) Broth.								2	2		*x*	Tu
Rodobryum beyrichianum (Hornsch.) Müll.Hal.							2	3		*x*		Tu
CALYMPERACEAE												
Syrrhopodon gardneri (Hook.) Schwägr.				1			2					Tu
Syrrhopodon lycopodioides (Brid.) Müll.Hal.			1		3							Ta
Syrrhopodon prolifer Schwägr.				3			1					Tu
CRYPHAEACEAE												
Dendropogonella rufescens (Schimp.) E.Britton					3							Pe
DALTONIACEAE												
Calyptrochaeta haitensis (H.A.Crum & Steere) Crosby							1			*x*		Ma
Daltonia longifolia Taylor	2				2							Cu
Daltonia stenophylla Mitt.					2	1						Cu
Leskeodon cubensis (Mitt.) Thér.			1	2						*x*		Tu
DICRANACEAE												
Campylopodiella stenocarpa (Wilson) P.Muell. & J.-P.Frahm							2					Tu
Campylopus jamesonii (Hook.) A.Jaeger								1			*x*	Tu
Campylopus nivalis (Brid.) Brid.							1					Tu
Dicranum frigidum Müll.Hal.								3				Tu
Holomitrium arboreum Mitt.		2	1									Tu
Holomitrium flexuosum Mitt.		2										Tu
Holomitrium pulchellum Mitt.		2	2									Tu
Microcampylopus curvisetus (Hampe) Giese & J.-P.Frahm								2				Tu
Pilopogon guadelupensis (Brid.) J.-P.Frahm								3			*x*	Tu
FISSIDENTACEAE												
Fissidens polypodioides Hedw.								2	2			Tu
Fissidens wallisii Müll.Hal.								1				Tu
Fissidens weirii var. hemicraspedophyllus (Cardot) Pursell								2				Tu
Fissidens weirii Mitt. var. weirii							1					Tu
HEDWIGIACEAE												
Braunia squarrulosa (Hampe) Müll.Hal.		2										Ma
HOOKERIACEAE												
Hookeria acutifolia Hook. & Grev.								2	2	*x*		Ma

Table 3-1. (cont'd)

	twigs	branches	trunks	tree bases	shrubs	leaves	logs	soil	stones	*close to a brook*	*close to the trail*	Life form
HYPNACEAE												
Ctenidium malacodes Mitt.				1			2			*x*		Ma
Ectropothecium leptochaeton (Schwägr.) W.R.Buck							2					Ma
Hypnum amabile (Mitt.) Hamp.				1			2	2				We
Hypnum polypterum (Mitt.) Broth.							2					We
Mittenothamnium reptans (Hedw.) Cardot				2			3					We
HYPOPTERYGIACEAE												
Hypopterygium tamariscinum (Hedw.) Brid								2	1	*x*		Tr
LEMBOPHYLLACEAE												
Rigodium toxarium (Schwägr.) A.Jaeger			1	3	2							We
LEPYRODONTACEAE												
Lepyrodon tomentosus (Hook.) Mitt.		2	1									Ma
LEUCOBRYACEAE												
Leucobryum martianum (Hornsch.) Müll.Hal.			1	2			2	1				Tu
LEUCODONTACEAE												
Leucodon curvirostris Hampe		3	2									Ma
LEUCOMIACEAE												
Rhynchostegiopsis tunguraguana (Mitt.) Broth.				1			2					Ma
METEORIACEAE												
Aerolindigia capillaceae (Hornsch.) M.Menzel					2							Ta
Meteoridium remotifolium (Müll.Hal.) Manuel					2							Pe
Meteoridium tenuissima (Hook. & Wilson) M.A.Lewis					2							Pe
Orthostichella pentasticha (Brid.) W.R.Buck					1							Pe
Pilotrichella flexilis (Hedw.) Ångstr.		2	2		3							Pe
Squamidium leucotrichum (Taylor) Broth.					2							Pe
Toloxis imponderosa (Taylor) W.R.Buck			1	2	3		3	1	1			Pe, We
MNIACEAE												
Plagiomnium rhynchophorum (Hook.) T.J.Kop.				1			1	2	2	*x*		We
NECKERACEAE												
Neckera ehrenbergii Müll.Hal.		1	1		2							Fe
Neckera urnigera Müll.Hal.					3							Fe
Porotrichodendron superbum (Taylor) Broth.			1	2	3							Fe
Porotrichum korthalsianum (Dozy & Molk.) Mitt.			1	2	3				2	*x*		Fe
Porotrichum longirostre (Hook.) Mitt.			1									Fe
Porotrichum lancifrons (Hampe) Mitt.					2							Fe
Porotrichum mutabile Hampe			1	1	2				1	*x*		Fe
ORTHOTRICHACEAE												
Groutiella chimborazensis (Mitt.) Florsch.		2	2									Tu
Macrocoma tenue ssp. sullivantii (Müll.Hal.) Vitt.	2	2										Ma
Macromitrium aureum Müll.Hal.		2										Tu
Macromitrium cirrosum (Hedw.) Brid.		1	1									Tu
Macromitrium longifolium (Hook.) Brid.		3	2		2							Tu
Zygodon reinwardtii (Hornsch.) A.Braun	3	2			3							Cu
Zygodon ehrenbergii Müll.Hal.		2	3									Tu
PHYLLOGONIACEAE												
Phyllogonium viscosum (P.Beauv.) Mitt.					2							Pe

Table 3-1. (cont'd)

	twigs	branches	trunks	tree bases	shrubs	leaves	logs	soil	stones	*close to a brook*	*close to the trail*	Life form
PILOTRICHACEAE												
Callicostella pallida (Hornsch.) Ångstr.									1	*x*		Ma
Cyclodictyon albicans (Hedw.) Kuntze								2	3	*x*		Ma
Cyclodictyon roridum (Hampe) Kuntze								1	2	*x*		Ma
Hypnella pilifera (Hook.f. & Wilson) A.Jaeger							2	1				We, Ma
Trachyxiphium guadalupense (Spreng.) W.R.Buck							3	2	2			Ma
Trachyxiphium subfalcatum (Hampe) W.R.Buck							1					Ma
PLAGIOTHECIACEAE												
Plagiothecium drepanophyllum Renauld & Cardot				1			1	1				Ma
Plagiothecium lucidum (Hook. f. & Wilson) Paris				1			2					Ma
POLYTRICHACEAE												
Atrichum oerstedianum (Müll.Hal.) Mitt.				2			1	3	2	*x*	*x*	Tu
Pogonatum procerum (Lindb.) Schimp.							1	3	1			Tu
Polytrichadelphus peruvianus Broth.								2				Tu
Steereobryon subulirostrum (Besch.) G.L.Sm.								1				Tu
POTTIACEAE												
Leptodontium ulocalyx (Müll.Hal.) Mitt.	2	3	2	1	2		2	1	1			Pe, Ma, Tu
Pseudosymblepharis bartramii E.B.Bartram								1				Tu
Streptopogon erythrodontus (Taylor) Wilson					1							Cu
PRIONODONTACEAE												
Prionodon densus (Hedw.) Müll.Hal.			2	2	3							Ta
Prionodon fusco-lutescens Hampe					2		1			*x*		Ta
PTEROBRYACEAE												
Pterobryon densum Hornsch.			1	2	3							Fe
RACOPILACEAE												
Racopilum tomentosum (Hedw.) Brid.				2			2	2	1	*x*		Ma
RHIZOGONIACEAE												
Phyrrhobryum mnioides (Hook.) Manuel				2			1	2				Tu
Phyrrhobryum spiniforme (Hedw.) Mitt.				2								Tu
Rhizogonium lindigii (Hampe) Mitt.			1	2								Tu
SEMATOPHYLLACEAE												
Aptychella proligera (Broth.) Herzog							1					Tu
Heterophyllum affine (Hook.) M.Fleisch.				2			2					We
Sematophyllum dimorphum (Renauld & Cardot) F.D. Bowers							1					Ma
Sematophyllum subsimplex (Hedw.) Mitt.				2			2					We
Sematophyllum swartzii (Schwägr.) W.H.Welch & H.A.Crum			1	2			2	1				Ma
SPHAGNACEAE												
Sphagnum magellanicum Brid.								1		*x*		Tu
Sphagnum meridense (Hampe) Müll.Hal.								3				Tu
SPLACHNACEAE												
Brachymitrion moritzianum (Müll.Hal.) A.K.Kop.							1					We
THUIDIACEAE												
Cyrto-hypnum sharpii (H.A.Crum) W.R.Buck & H.A.Crum							2		1	*x*		We
Thuidium pseudoprotensum (Müll. Hal.) Mitt.				2	2		3	2	1			We

CHAPTER 4

Host preference, vertical distribution and community composition of cryptogamic epiphytes on two species of oak in upper montane forest of Costa Rica

Abstract

A study of epiphytic bryophytes and macrolichens on standing mature *Quercus copeyensis* and *Q. costaricensis* trees was carried out in an upper montane rain forest of the Cordillera de Talamanca, Costa Rica. Trees were sampled from the base up to the twigs of the outer canopy, using a single rope technique. Coverage of corticolous bryophyte and macrolichen species was estimated and compared using Detrended Correspondence Analysis (DCA) and non-metric Multi-response Permutation Procedure (MRPP).

Of the 153 taxa found in this study, 57 were lichens, 56 hepatics and 40 mosses. Beside the vertical gradient the two host tree species proved to be the most important factor in community differentiation of epiphytic cryptogams as indicated by DCA. Many of the species are preferential or exclusive to either *Quercus copeyensis* or *Q. costaricensis*, the dominant tree species in the studied forest area. Also, non-metric MRPP confirmed the significant differences in community composition of individual height zones on different host trees. Furthermore, bark pH, water capacity and bark hardness differ significantly among host species and may well explain host-epiphyte relations.

For the first time, a detailed description of epiphytic cryptogam communities of whole standing canopy trees in an upper montane oak forest is given. Species indicator values are calculated, ecological species groups are described and factors controlling the vertical and horizontal distribution of species are discussed. Changes in species richness, community composition and community structure along the vertical gradient are further aspects of the study.

Resumen

En un bosque de alta montaña en la Cordillera de Talamanca, Costa Rica, fue llevado a cabo un estudio sobre briofitas y macrolíquenes epífitos sobre árboles adultos de *Quercus*. Se realizaron muestreos en los árboles desde la base hasta las ramas externas del dosel, utilizando técnicas de cuerda simple. La cobertura de las especies de briofitas y macrolíquenes corticícolas fue estimada y comparada por medio del ‘análisis correspondiente intendenciado (detrended correspondence analysis, DCA)’ y por ‘non-metric multi-response permutation procedure (MRPP)’.

En este estudio se encontraron 153 taxa, distribuídos en 57 líquenes, 56 hepáticas y 40 musgos. Además de un gradiente vertical, el factor más importante en la diferenciación de las comunidades de criptógamas epífitas, tal como fue indicado por el DCA, es la presencia de dos especies de forofitos. Muchas de las criptógamas crecen con preferencia, o en forma exclusiva, sobre *Quercus copeyensis* o sobre *Q. costaricensis*, las especies arbóreas dominantes en el área de investigación. Los estudios no métricos, MRPP, también confirmaron las diferencias significativas en composición de comunidades en zonas altitudinales individuales, sobre diferentes árboles forofitos. El pH de la corteza, la capacidad de retención de agua y la dureza de la corteza difieren significativamente entre las especies de forofitos y podrían explicar muy bien las relaciones epífito-forofito.

Por primera vez se describen en forma detallada las comunidades de criptógamas epífitas en arboles del estrato arbóreo del dosel en un bosque montano de *Quercus*. Se calculan valores para especies indicadoras, se describen grupos ecológicos de especies y se discuten factores que controlan la distribución vertical y horizontal de las especies. Otros aspectos considerados en este estudio son los cambios en la riqueza de especies, la composición y la estructura de las comunidades a lo largo del gradiente vertical.

Introduction

Epiphytic cryptogams play an important role in montane tropical forests, both in terms of species diversity and ecosystem functioning (Clark et al. 1998, Hofstede et al. 1993, Pócs 1982, Richards 1984, Wolf 1993b). Our understanding of the diversity of montane rain forests in Central America and other parts of the Neotropics is still fragmentary. Despite their importance, there is only little information on species richness, community composition and ecology of bryophytes and lichens in these forests (Gradstein 1992). Studies in temperate and tropical zones have shown that certain species of bryophytes and lichens require primary or old growth forests for their survival. This fact and the important ecological role of cryptogamic epiphytes in water balance, nutrient cycling and environmental monitoring of montane tropical forests makes describing and analysing these epiphytic communities a research priority for conserving biodiversity (Gradstein et al. 2001a, Porembski & Barthlott 2000).

Host specificity or host preference of cryptogamic epiphytes in the tropics is widely believed to be of minor importance (e.g., Pócs 1982, Richards 1984, Kürschner 1990, Kürschner & Parolly 1998). However, Cornelissen & ter Steege (1989) demonstrated that in tropical lowland forests host specificity may occur and Smith (1982) suggested that host preference is common among tropical bryophytes except in very humid montane forests. Quantitative data to support this assumption is still lacking, especially concerning montane rain forests and canopy species.

Vertical profiles of epiphytic lichens and bryophytes on trees have been described in many temperate areas, including temperate rainforests (e.g. Kantvilas & Michin 1989, McCune et al. 1997, McCune et al. 2000). In the tropics, most studies have been limited to the tree base and the lower part of the trunk (e.g. Frahm 1987, Kürschner 1990, Kürschner & Parolly 1998a, 1998b) but neglected the richness of the canopy flora. However, the epiphytic vegetation of the tree base is often heterogeneous and more similar to the surrounding terrestrial vegetation than to the trunk and canopy flora. This limits the usefulness of the tree base flora and communities as an indicator of epiphytic diversity or to predict that of the canopy (Clement et al. 2001, Hietz & Hietz-Seifert 1995, Holz et al. 2002).

In tropical lowland forests Richards (1954) and Florschütz-de Waard & Bekker (1987) distinguished skiophilous (shade epiphytes) and photophilous species (sun epiphytes). Vertical gradients in the distribution of bryophyte and lichen species on their host trees in the tropics were also demonstrated by Cornelissen & ter Steege (1989), Montfoort & Ek (1990), Wolf (1994), Gradstein et al. (2001b), Holz et al. (2002), and Acebey et al. (2003). However, a detailed analysis of the vertical distribution of cryptogamic epiphytes on trees in upper montane tropical rain forests is still lacking. Pócs (1982) recognized four height zones in lowland rain forests: tree base, trunk, main branches and terminal twigs, which were considered rather similar in their floristic composition and life form spectrum throughout the tropics. Other authors differentiated between lower and upper trunk, inner canopy, middle canopy and outer canopy and recognized five or six height zones (e.g., Cornelissen & ter Steege 1989, Johansson 1974, Hietz & Hietz-Seifert 1995, Longman & Jeník 1987, Montfoort & Ek 1990). In montane and upper montane tropical rain forests this vertical differentiation is believed to be less distinct (Pócs 1982, Richards 1984).

In addition to single species, *community composition* and changes in community composition along ecological gradients may provide important information on the ecology of ecosystems. In tropical forests, conservation concepts based on single species (indicator species) may be inadequate to access the vulnerability of the ecosystem due to the complex niche diversification of these forests. However, beside the study of Wolf (1993a, 1994) in Colombia, there is hardly any information on community compositon of epiphytic bryophytes and lichens in tropical montane forests, especially with respect to the canopy.

So far, little work has been done on the ecology of epiphytic bryophytes and macrolichens in rain forests of Costa Rica, despite the high diversity in bryophytes and lichens and the high number of taxonomic and floristic studies from this easily accessible region. In Monteverde National Park, Sillet et al. (1995)

analysed the epiphytic bryophyte flora in the inner canopy of six *Ficus* trees, three in the dense forest and three isolated trees in adjacent pastures and demonstrated their different species assemblages. Recently, Gradstein et al. (2001b) and Holz et al. (2002) analysed the diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde (Cordillera de Tilaran, 1500 m) as well as in the upper montane oak forest of Los Robles (Los Santos Forest Reserve, Cordillera de Talamanca, 2500 m).

The present study deals with epiphytic bryophytes and macrolichens on tall canopy trees in a primary upper montane oak forest in the Cordillera de Talamanca (Costa Rica, 2900 m asl) and presents a description of host preference, vertical distribution and community composition of cryptogamic epiphyte communities of these oak forests. In addition, the use of cryptogamic epiphytes as indicator species is discussed and indicator values (IV) for species in different height zones on the studied host tree species are calculated.

Study Site

The study was conducted in a primary upper montane oak forest near San Gerardo de Dota in the Los Santos Forest Reserve (83°47’W 09°35’N), situated at an altitude of about 2900 m on the Pacific-facing slope of the western Talamanca Mountain Range, Costa Rica.

The local climate is cool and humid, with a mean daily temperature of 11 °C and annual precipitation averaging 3000 mm (Instituto Meteorológico Nacional, 1988). There is a pronounced dry season from early January to the end of April. The forest is an upper montane rainforest (“robledal de altura”) dominated by 30 to 40 m tall trees of two species of *Quercus*, *Q. copeyensis* C.H.Müll. and *Q. costaricensis* Liebm. Understory vegetation is characterized by bamboo, tree ferns, dwarf palms, shrubs and herbs. Canopy and subcanopy branches are festooned with vascular and non-vascular epiphytes including orchids, bromeliads, aroids, ericads, ferns, mosses, liverworts and lichens. A comprehensive description of the vegetation structure, vascular plant diversity and secondary succession of these oak forests has been given by Kappelle (1995, 1996). The study site and the forest structure are characterised by the following supplementary parameters: inclination – 30,9°, stem number per 1 ha (DBH > 3cm) – 3460, canopy height – 35-40 m, vegetation strata – 3, leaf area index (LAI) – 3.8 m^2 m^{-2} (Köhler 2002). The forest is a primary forest with very little human impact, the studied trees are at least 200 years of age (Kappelle, pers. com.).

Methods

Ten mature trees belonging to the two dominating species of oak, *Quercus copeyensis* (5) and *Q. costaricensis* (5) were randomly selected in a primary forest. Cryptogamic epiphytes (bryophytes and macrolichens) were sampled in the outer canopy, the inner canopy, on the trunk and on the tree base. The canopy trees (30-35 m height, 90-170 cm DBH) were rigged and climbed using a crossbow and a single rope technique (Perry 1978, ter Steege & Cornelissen 1988). Major parts of the field work, were carried out during January to May 2000.

In total, 391 relevés were taken on the ten studied trees (177 on *Q. copeyensis* and 214 on *Q. costaricensis*). Relevés represented the variation in the epiphytic vegetation. Several relevés were taken from each tree and in each height zone of the tree (according to Johansson 1974, slightly modified); 62 relevés were taken from the tree bases, 118 from the trunks, 109 from the inner canopy and 102 from the outer canopy (see Table 4-1).

Relevé size was 600 cm^2 (20 cm x 30 cm; 15 cm x 40 cm on smaller branches) on tree bases, trunks and branches of the inner canopy. In the outer canopy complete twigs were sampled over a length of up to 1 m. Depending on the diameter of the twigs, total area sampled in this relevés was between 500 and 800 cm^2. Species abundance in each relevé was determined by estimating percentage cover rather than by using a combined cover/number of individuals scale (e.g. Braun-Blanquet scale) because the small size of the sample area made accurate estimation of percentage cover possible. Moreover, counting of individuals of species with a gregarious growth habit, as commonly observed in bryophytes and lichens, is impractical.

Bark samples from the investigated trees were extracted with deionized H_2O and analysed for pH. One tree of each species (*Q. copeyensis, Q. costaricencis*) was subdivided into tree base, middle trunk, upper trunk, inner canopy and outer canopy and sampled within these zones. Four samples of bark were taken from each of the sectors in the tree. From the other trees only two samples were taken from a height of about 2 m above the ground.

All bryophytes and macrolichens within each relevé were collected and identified to species level. Voucher specimens were deposited at INB with duplicates in GOET, MO (some) and NY (some). Nomenclature follows Allen (1994, 2002), Buck (1998) and Sharp et al. (1994) for mosses and Uribe & Gradstein (1998) for liverworts.

The *main data matrix* (species cover) used consisted of 391 rows (relevés) and 153 columns (species). There were 59.823 cells in this matrix and 93.6 percent of these cells were zero. The *second data matrix* consisted of 391 rows (relevés) and 12 columns representing the following variables: host tree number, host tree species, height zone, height in tree, stem diameter, total number of species (richness), hepatic richness, moss richness, lichen richness, Shannon Index, Simpson Index and total cover.

All statistical analyses were performed using the program package PC-ORD for Windows - Version 4.17 (McCune & Mefford 1999). Groups defined by height zone and/or host tree species and host tree number were compared with non-metric MRPP (*Multi-response Permutation Procedures*). These analyses provided a nonparametric multivariate test of differences between groups. The A statistic from MRPP describes effect size, the chance-corrected within-group agreement. When all items are identical within groups, then the observed delta = 0 and A = 1; when A = 0, the groups are no more different than expected by chance. In community ecology values for A are commonly below 0.1, even when differences between groups are apparent; A > 0.3 may be regarded as high, showing that groups are significantly different from each others.

Detrended correspondence analysis (DCA) provided a graphical depiction of community relationships and habitat variables. For DCA, species with fewer than three occurences were removed from the main matrix, resulting in an updated matrix of 391 relevés and 117 species. This strengthened the apparent differences among habitats by reducing random noise from infrequent species. Two forms of the main data matrix were used in multivariate analyses: one containing the untransformed abundance data (in percent cover) and one containing data transformed by the sociological favorability index of Beals (Beals Index). The purpose of this transformation is to relieve the "zero-truncation problem" (Beals 1984; McCune 1994). It tends to reduce the noise in the data by enhancing the strongest patterns in the data. Presence/absence data are replaced with quantitative values (range 0-1) that represent the probability of a species occurring in a particular relevé based on other species that were present as well in that relevé. In the DCA, ordination standard downweighting, segment detrending (26 segments) and non-linear rescaling were employed. Habitat variables were superimposed on the resulting ordination using a joint plot, based on the correlations of those variables with the axes of the community ordination. Variance explained was expressed by the coefficient of determination between Euclidian distances in the ordination space and the Relative Euclidian distances in the original species space, as recommended to users of DCA by McCune & Mefford (1999).

We calculated species indicator values for the different height zones on the two host tree species using Dufrene and Legendre’s (1997) method, wich 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 test with 1000 replicates.

Results

Species diversity

In total, 153 taxa, including 57 lichens, 56 hepatics and 40 mosses, were found in the 391 relevés from 10 trees (Table 4-2). More than 90 % of these taxa could be identified to species level. The relative abundance of a species on the studied host tree species or in one of the height zones is shown in Table 4-1. The average abundance of a given species in a given group of relevés (host tree species, height zone) over the average abundance of that species in all relevés expressed as percent is given in the table.

Table 4-2 summarizes the overall species diversity broken down by host tree species, taxonomy and height zones. In total, 100 species were found on *Quercus copeyensis* and 122 on *Quercus costaricensis*. Sixty nine species were found on only one of the host trees. Overall species richness was highest on trunks (91 species), followed by the inner canopy (85 species), the outer canopy (79 species) and the tree base (57 species). On *Quercus copeyensis* the outer canopy (55 species) appeared to be the species richest zone, whereas on *Quercus costaricensis* the inner canopy (74 species) and the trunk (71 species) were the richest zones.

Figure 4-1 shows species area curves for the accumulated relevés in different height zones on the two host tree species. The form of the curves indicate that for all habitats more than 80 % of the species were found. Total number of species and species area curves were very similar for tree base, trunk and inner canopy of *Quercus copeyensis* and tree base of *Quercus costaricensis*. The outer canopy of *Quercus copeyenis* has more species than the other height zones on this tree species. In contrast, trunk, inner canopy and outer canopy are species rich habitats on *Quercus costaricensis* (Fig. 4-1).

Species richness per relevé was highly variable, with a mean of 9.7 species (4.7 hepatics, 2.7 lichens and 2.3 mosses) and a high standard deviation of 3.5 species. There was no difference between the average number of species per relevé on the two host tree species, but species richness generally increased with height in the tree. This was also true for the richness of lichens, whereas richness of mosses generally decreased (see Fig. 4-2). There was no general trend for hepatics.

Table 4-2. Species diversity overall and broken down by groups of sample units. Beta diversity was measured as the total number of species divided by the average number of species.

Group (sample size)	Average species richness (S.D.)	Beta diversity	Total number of species
Overall (391)			
Hepatics	4.7 (2.1)	11.9	56
Mosses	2.3 (1.4)	17.4	40
Lichens	2.7 (2.5)	21.1	57
Bryophytes + Lichens	9.7 (3.5)	15.8	153
Tree base (62)	7.1 (2.2)	8.0	57
Trunk (118)	9.2 (2.6)	9.9	91
Inner canopy (109)	9.0 (3.0)	9.4	85
Outer canopy (102)	12.8 (3.1)	6.2	79
***Quercus copeyensis* (177)**			
Hepatics	4.8 (2.3)	8.3	40
Mosses	2.2 (1.1)	9.5	21
Lichens	2.7 (2.4)	14.4	39
Bryophytes + Lichens	9.7 (3.7)	10.3	100
Tree base (29)	7.0 (1.7)	5.4	38
Trunk (48)	9.6 (2.8)	4.3	41
Inner canopy (48)	8.3 (3.4)	4.8	40
Outer canopy (52)	12.7 (3.5)	4.3	55
***Quercus costaricensis* (214)**			
Hepatics	4.6 (1.9)	9.8	45
Mosses	2.3 (1.6)	12.2	28
Lichens	2.8 (2.7)	17.5	49
Bryophytes + Lichens	9.7 (3.4)	12.6	122
Tree base (33)	7.2 (2.5)	5.1	37
Trunk (70)	8.9 (2.4)	8.0	71
Inner canopy (61)	9.5 (2.5)	7.8	74
Outer canopy (50)	12.9 (3.9)	4.7	61

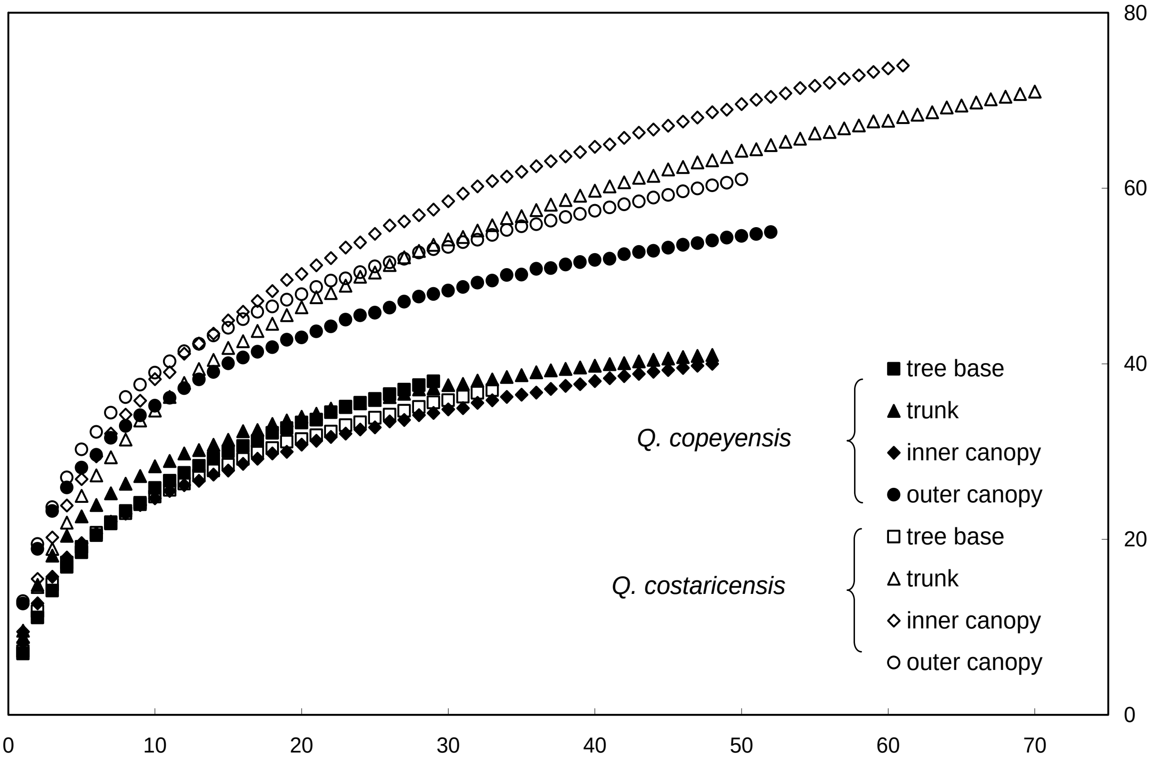

Fig. 4-1. Species area curves of cryptogamic epiphytes (bryophytes and macrolichens) in different height zones on mature *Quercus copeyensis* and *Quercus costaricensis* trees in an oak dominated upper montane rain forest of Cordillera de Talamanca (Costa Rica). X-axis: number of relevés pooled, y-axis: number of species.

Species turnover rates, as measured by beta diversity, were different for lichens, hepatics and mosses. Overall and broken down by host tree species, beta diversity was highest for lichens, followed by mosses and hepatics. Overall beta diversity of non-vascular epiphytes was very high (15.8), reflecting the wide range of habitats sampled. When the relevés were divided into more homogenous groups (different host tree species, different height zones), beta diversity of non-vascular epiphytes was much lower. The large number of infrequent species (36 species occurred only once or twice) also contributed to the high beta diversities. Overall beta diversity was similar on tree bases, trunks and in the inner canopy, but lower in the outer canopy.

Differences among host trees and height zones

Multi-response permutation procedure analyses (MRPP) were performed to test the differences between groups of relevés. There was no significant difference between between the relevés from each of the studied *Quercus* *copeyensis* trees or between each of the studied *Q. costaricensis* trees in this study (A = 0.03). In contrast, differences between different height zones (A = 0.39) and between height zones from different host trees (A = 0.54) were marked (Tab. 4-3).

Table 4-3. Comparison of differences in community composition on *Quercus copeyensis* and *Q. costaricensis* using non-metric MRPP, based on Sørensen distances; G = number of groups; A = chance-corrected within-group agreement; p = probability of Type I error for H_0: no difference between groups.

Grouping variable	G	A raw data	p
Q. copeyensis trees	5	0.03	0.0014
Q. costaricensis trees	5	0.03	0.0004
height zone	4	0.39	$< 10^{-8}$
Combination of height zone and host tree species	8	0.54	$< 10^{-8}$

Table 4-4. Comparison of differences in community composition of height zones on *Quercus copeyensis* and *Quercus costaricensis* (before and after Beals smoothing) using non-metric MRPP, based on Sørensen distances; A = chance-corrected within-group agreement; p = probability of Type I error for H_0: no difference between groups.

height zone	A raw data	A Beals smoothing	p
Tree base	0.25	0.42	$< 10^{-8}$
Trunk	0.16	0.35	$< 10^{-8}$
Inner canopy	0.11	0.23	$< 10^{-8}$
Outer canopy	0.34	0.16	$< 10^{-8}$

Table 4-5. Comparison of differences in community composition of height zones using non-metric MRPP, based on Sørensen distances; A = chance-corrected within-group agreement; $p < 10^{-8}$ for all values (p = probability of Type I error for H_0: no difference between groups).

	Tree base	Trunk	Inner Canopy
Trunk	0.15	-	-
Inner canopy	0.27	0.13	-
Outer canopy	0.36	0.37	0.25

Chance-corrected within group agreement (A) for comparison of differences in community composition between height zones is presented in Table 4-5. Differences are significant for comparisons of all zones. A was low when trunk and inner canopy were compared (0.13). Differences in community composition of the same height zone from different host trees were significant, suggesting that communities show host preference, with the biggest differences in the outer canopy and on the tree base (Table 4-4, raw data).

The importance of height zone and host tree species for community differentiation is also demonstrated by the separation of relevés in the ordination by DCA after Beals smoothing (Fig. 4-2). Ordination of raw data is shown in the insert of the diagram and lines indicate habitat descriptors.

The first three axes in the ordination of the raw data explained 37 % of the community variation and 92 % after Beals smoothing (Fig. 4-2). The most important descriptor, axis 1, representing 23 % of the variation before and 84 % after Beals smoothing, was closely related to height in the tree and stem diameter. The second axis representing 9 % of the variation before and 8 % after Beals smoothing, separated the two host tree species, especially in the lower part of the tree. The third axis, representing 5 % of the variation before and only 0.5 % after Beals smoothing, differentiated between the canopy communities of the two host species. In general, Beals smoothing showed a tendency to increase the differences between the two host trees with regard to the lower part of the trunk and it decreased the differences with regard to their canopy (see Table 4-4).

Lichen richness, species richness per relevé and Shannon Index increased with the first ordination axis (height in the tree), while moss richness and total cover decreased with height on the tree (Fig. 4-2). The results from the DCA closely paralleled the results from MRPP. Cryptogamic epiphyte communities were differentiated by height zone, height in tree, stem diameter and host tree species. The first three variables were strongly intercorrelated.

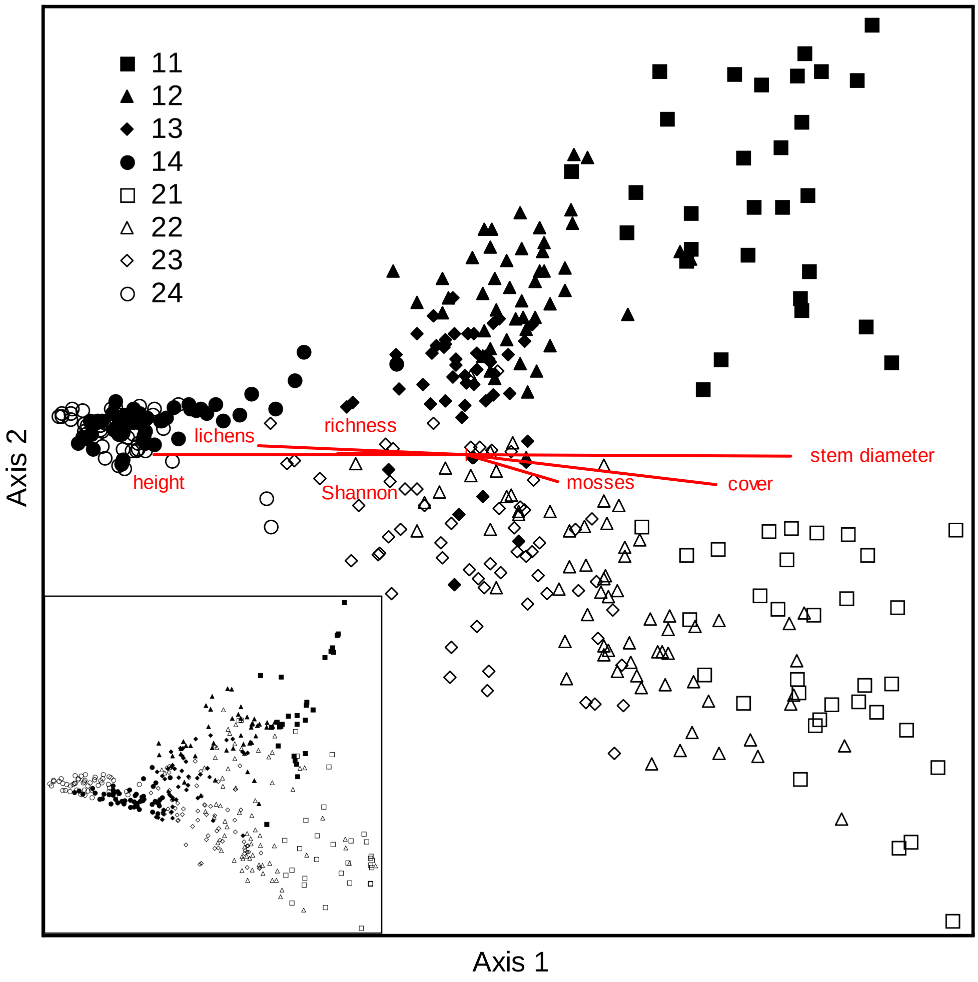

Fig. 4-2. Ordination of relevés (plots) in epiphyte species space using DCA and Beals smoothing. Diagram insert indicates the ordination without Beals smoothing. Symbols indicate host tree and height zone where relevés were taken. *Quercus copeyensis* (open symbols): 11 = tree base, 12 = trunk, 13 = inner canopy, 14 = outer canopy. *Quercus costaricensis* (closed symbols): 21 = tree base, 22 = trunk, 23 = inner canopy, 24 = outer canopy.

Ecological species groups

The main reason to use Beals smoothing for the DCA was to find and depict characteristic species groups for the different host tree species and the different height zones. Fig. 4-3 shows the ordination of the species along the two main axes. The figure should be interpretated with caution and absolute figures given in Table 4-1 should be taken into account to avoid misinterpretation. Widespread species like *Frullania brasiliensis*, *Usnea* spec. or *Zygodon ehrenbergii* are ordinated to the metric centre of their distribution range despite their wide ecological amplitude.

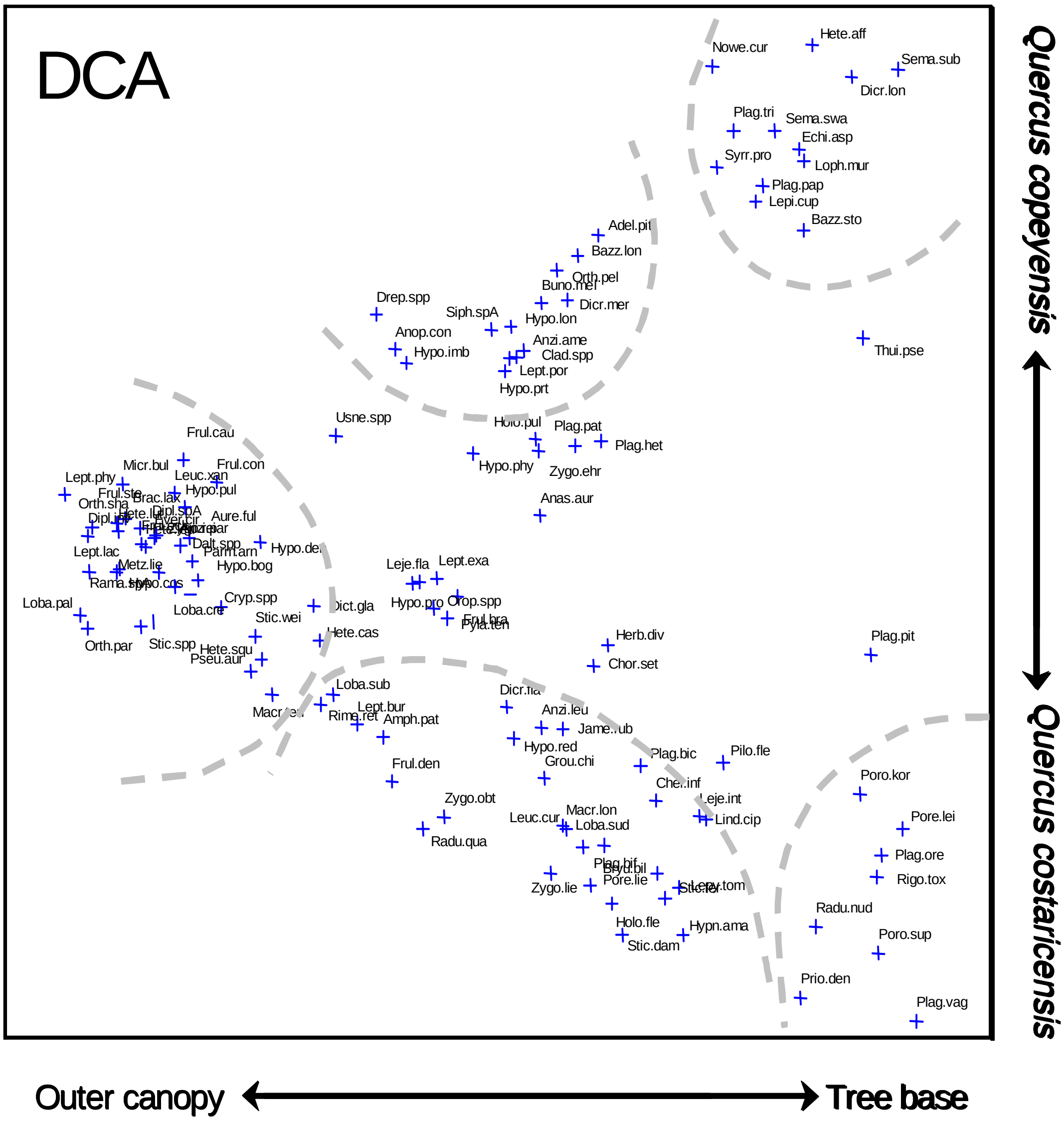

Fig. 4-3. Ordination of species in the epiphyte species space using DCA and Beals smoothing. X-axis: Axis 1, y-axis: Axis 2. Broken lines indicate main ecological species groups. For explanation of acronyms see Table 4-1.

The data allow the distinction of the following nine species groups:

i) Tree base species on *Quercus copeyensis*: *Dicranodontium longisetum, Echinocolea asperrima, Heterophyllium affine, Lepidozia cupressiana, Nowellia curvifolia, Plagiochila papillifolia, Plagiochila trichostoma, Sematophyllum subsimplex, Sematophyllum swartzii, Syrrhopodon prolifer*.

ii) Tree base species on *Quercus costaricensis*: *Plagiochila oresitropha, Plagiochila cf. vagae, Porella leiboldii, Porotrichodendron superbum, Porotrichum korthalsianum, Prionodon densus, Radula nudicaulis, Rigodium toxarium*.

iii) Tree base species common on both host trees: *Bazzania stolonifera* (more common on *Q. copeyensis*), *Plagiochila pittieri, Thuidium* *pseudoprotensum*. Most tree base species are restricted to this epiphytic habitat and are more common on rotten logs, soil and the lower parts of shrubs in the understory of the forest.

iv) Trunk and inner canopy species on *Quercus copeyensis*: *Adelanthus pittieri, Bazzania longistipula, Dicranodontium meridionale, Leptoscyphus porphyrius, Orthodontium pellucens, Anzia americana, Bunodophorum melanocarpum, Cladonia spp., Hypotrachyna imbricatula, Hypotrachyna longiloba, Hypotrachyna protoboliviana, Siphula spec. A*.

v) Trunk and inner canopy species on *Quercus costaricensis*: *Cheilolejeunea inflata, Dicranum flagellare, Groutiella chimborazensis, Holomitrium flexuosum, Hypnum amabile, Jamesoniella rubicaulis, Lepyrodon tomentosus, Leucodon curvirostris, Macromitrium longifolium, Plagiochia bifaria, Porella liebmanniana, Radula quadrata, Zygodon liebmannii, Zygodon obtusifolius, Anzia leucobates, Hypotrachyna reducens, Lobaria subdissecta, Lobaria subexornata, Sticta damaecornis, Sticta ferax*.

vi) Trunk and inner canopy species on both host trees: *Anastrophyllum auritum, Chorisodotium setaceum, Holomitrium pulchellum, Leptodontium exasperatum* (mainly in the inner canopy), *Pylaisiadelpha tenuirostris, Hypotrachyna physioides, Hypotrachyna prolongata, Oropogon spp.*.

vii) Species of the inner and outer canopy on both host trees: *Macrocoma tenuis* (mainly on *Q. costaricensis*), *Dictyonema glabratum, Heterodermia squamulosa, Pseudocyphellaria aurata, Sticta spp., Cryphaea spp., Daltonia spp., Hypotrachyna densirhizinata, Parmotrema arnoldii, Aureolejeunea fulva, Anzia parasitica* (on *Q. costaricensis*), *Everniastrum cirrhatum* (on *Q. costaricensis*).

viii) Species mainly in the outer canopy on both host trees: *Brachiolejeunea laxifolia, Diplasiolejeunea spec. A, Diplasiolejeunea involuta* (on *Q. costaricensis*), *Frullania caulisequa, Frullania convoluta, Frullania ecklonii, Frullania stenostipa, Leptogium phyllocarpum, Leucolejeunea xanthocarpa, Metzgeria liebmanniana, Microlejeunea bullata, Orthotrichum pariatum, Orthotrichum sharpii, Zygodon reinwardtii, Hypotrachyna costaricensis,* *Hypotrachyna pulvinata, Heterodermia leucoma, Heterodermia lutescens, Leptogium laceroides, Lobaria pallida* (on *Q. costaricensis*). *Ramalina spec. A*.

ix) Species common in at least three height zones (generalists) on both host trees: *Anoplolejeunea conferta* (mainly on *Q. copeyensis*), *Frullania brasiliensis, Herbertus divergens, Lejeunea flava, Lejeunea intricata, Lindigianthus cipaconeus* (mainly on *Q. costaricensis*), *Pilotrichella flexilis* (mainly on *Q. costaricensis*), *Plagiochila heterophylla, Plagiochila patzschkei, Zygodon ehrenbergii, Heterodermia casarettiana* (mainly on *Q. costaricensis*), *Sticta weigelii* (mainly on *Q. costaricensis*), *Usnea spp.* (most frequent in the outer canopy of *Q. costaricensis*).

Some of the species that are restricted to the outer canopy of *Quercus copeyensis* are more common on *Q. costaricensis* and show a wider vertical amplitude on this host tree species (e.g. *Cryphaea* spp*.*, *Daltonia* spp., *Dictyonema glabratum, Heterodermia cassaretiana, Sticta weigelii*).

Table 4-6. pH values of bark samples taken from *Quercus copeyensis* and *Q. costaricensis* (S.D. < 0.2 pH units)

	N	Q. copeyensis	Q. costaricensis
2 m above ground	2 x 5	4.1	5.5
Outer Canopy	4	4.5	5.4
Inner Canopy	4	4.3	5.2
Upper Trunk	4	4.1	5.4
Middle Trunk	4	4	5.4
Tree base	4	3.6	5.3

Bark pH

pH values of bark relevés from *Quercus copeyensis* and *Q. costaricensis* are presented in Table 4-6. There is a marked difference of 1.5 pH units between bark from 2 m above ground from the two host tree species. The pH values and differences between the two host species are comparable to those measured in stemflow from the two host tree species (Köhler 2002). Bark pH values on

Quercus costaricensis were rather similar along the height gradient with slightly lower values in the inner canopy and the tree base. On *Quercus copeyensis* bark pH values grade from 4.5 in the outer canopy to a minimum of 3.6 at the tree base.

Discussion

Species richness

There has been much discussion on the differences in species numbers between lowland, submontane, montane and upper montane forests in the tropics (Cornelissen & ter Steege 1989, Florschütz-de Waard & Bekker 1987, Frahm 1987, Gradstein & Pócs 1989, Gradstein 1995, Wolf 1993b). Table 4-7 provides a literature overview on epiphytic bryophyte and macrolichen richness in lowland and montane rain forests in the Neotropics. General trends in species richness can hardly be derived as most of the studies on species richness are biased to a single habitat (e.g. the understory) or the climatic conditions in a special study area. It is furthermore difficult to directly compare these species numbers as they vary in many factors such as (1) number of trees sampled, (2) number of host tree species sampled, (3) number and size of relevés taken from each tree and height zone, (4) forest structure (height of trees, tree density), (5) height above see level, (6) climate (precipitation, frequency of mist, length of dry seasons, etc.), etc.

The only study to date comparing explicitly species diversity of epipyhtic bryophytes and macrolichens on two different host tree species is by Cornelissen & ter Steege (1989) in dry evergreen lowland forest in Guyana. The total number of species recorded is higher in the present study (153 species on ten trees) than in Guyana (114 species on 11 trees). However, the forest in Costa Rica has been sampled more intensively (391 relevés, compared to 90 in Guyana), whereas relevé size was larger in Guyana, varying from a few to over 35 dm^2 (6 dm^2 in present study). An extremely high number of species (186 species) has been reported by Wolf (1993b) from four sampled trees (10 relevés per tree) in upper montane rain forests of Colombia (2550 m). Relevé size in his study varied from a few to over 20 dm^2. The high number of species recorded was due to the high proportion of liverworts (especially Lejeuneaceae). The area studied by Wolf was characterized by a very humid climate troughout the year and many species normally restricted to wet habitats of the forest floor, usually close to brooks, occurred as epiphytes (e.g., *Monoclea gottschei* Lindb., *Symphyogyna brogniartii* Mont., *Aneura* spec.).

Table 4-7. Epiphytic bryophyte and macrolichen richness in lowland and montane rain forests in Central and South America. (1) Cornelissen & ter Steege (1989), (2) Montfoort & Ek (1990), (3) Acebey et al. (2003), (4) Wolf (1993b), (5) Sillet et al. (1995), (6) this study. *) (?) = number estimated from description of methods

	trees sampled	host tree species*)	mosses	liver-worts	Macro-lichens	total
lowland rain forest						
Eperua forest, Guyana (1)	11	2	28	53	33	114
mixed forest, Guyana (1)	5	5 (?)	28	60	19	107
200 m, French Guiana (2)	4	4 (?)	43	61	21	125
submontane rain forest						
600 m, Bolivia	6	4-5 (?)	32	48	(?)	-
montane rain forest, Colombia (4)						
1500 m	4	4 (?)	22	36	49	107
2550 m	4	4 (?)	33	102	51	186
3510 m	4	4 (?)	19	63	37	119
montane rain forest, 1500 m, Costa Rica (5)						
Ficus tuerkheimii (inner canopy)	3	1	41	67	(?)	
upper montane rain forest, 2900 m, Costa Rica (6)						
Quercus copeyensis	5	1	21	40	39	100
Quercus costaricensis	5	1	28	45	49	122
both *Quercus* species	10	2	40	56	57	153

Sample heterogenity and minimum area

A high within-habitat variability has often been reported for non-vascular epiphyte communities (Oksanen 1988, Wolf 1994, McCune et al. 2000), which is due to the occurrence of many low frequency or high abundance species. It may also occur when the general species abundance distribution is skewed. Both is true for this study, as 56 (37 %) of the species found in 391 relevés had less than 5 occurrences and 121 species (79 %) were found in less than 10 % of all relevés. These numbers and the species area curves for different microhabitats (Fig. 4-1) indicate that the minimum area for epiphytic cryptogam communities is large, sometimes up to one square meter. In most cases, however, it is not possible to get homogenous relevés of that size on a tree. Even on the trunk and the tree base of a large tree there are very distinct changes in community composition within small patches, which are caused by changes in exposition and microniches produced by the larger vascular epiphytes. This generally limits the use of a classical phytosociological approach (e.g. BRAUN-BLANQUET) to study cryptogamic epiphyte communities in the tropics (e.g. Kürschner & Parolly 1998b).

Host specificity or host preference

Out of the 153 species recorded, 69 (45 %) were found on only one of the host tree species and an even larger number of species shows clear host tree preference (Tab. 4-1). Beside the vertical gradient the two host tree species are the most important factor in community differentiation of epiphytic cryptogams as indicated by DCA (Fig. 4-2). Also, non-metric MRPP confirmed the significant differences in community composition of individual height zones on different host trees (Tab. 4-4). Furthermore, bark pH (Tab. 4-6), water capacity and bark hardness (Köhler 2002 and pers. comm.) differ significantly among host species and may well explain host-epiphyte relations.

The pH value of the bark is known to be an important factor for host preference in temperate areas (e.g. Barkman 1958, Palmer 1986), but had been believed to be of minor importance in the tropics (Frahm 1990). Palmer (1986) showed for forests in North Carolina that bryophyte species in different areas segregate along the same gradients to tree bark chemistry and physics, even if the sites do not have tree species in common. Our observation (Holz, unpubl.) that many species restricted to mature *Q. costaricensis* trees (high pH values) also occur on young understory trees of *Q. copeyensis* (with higher pH values than mature *Q. copeyensis* trees) indicates the importance of pH as an ecological parameter in the study area. With regard to the vertical differentiation of epiphyte communities age-dependent tree base acidification could be a reason for the differences in community composition at least on *Quercus copeyensis*.

Following Slack (1976) host specificity may be considered a special case of host preference, and concerns epiphytes occurring exclusively on one host species studied. However, as Wolf (1994) pointed out, host specificity is a misleading concept in the sense that it is not the identity of the host tree that is responsible for specific tree-epiphyte relationships, but the ecological conditions prevailing on its branches and trunk. The conditions on a host tree species are bound less unique when more tree species with intermediate bark properties are investigated. This also explains why studies in the tropics, with many different host tree species and few sampled trees, usually do not show any host specificity or preference of epiphytic cryptogams.

An open question, is whether the observed differences in host preference are similar or less prominent in the oak forests of the Atlantic side of Cordillera de Talamanca, where precipitation is higher and the dry season less pronounced.

Ecological factors controlling vertical distribution

The data presented in this paper indicate that the majority of cryptogamic epiphytes show a clear preference for a certain tree height zone in upper montane oak forests (Tab. 4-1, Fig. 4-2). This has before been shown by Cornelissen & ter Steege (1989) for a lowland rain forest in Guyana. Based on vertical distribution two categories of epiphytic species can be distinguished: ‘specialists’ with a narrow vertical distribution and ‘generalists’ with a broad vertical distribution (Cornelissen & ter Steege 1989, Wolf 1994). Even ‘generalists’ usually show a height preference in avoiding a special height zone (e.g. the outer canopy or the tree base).

As to the vertical distribution of epiphytic bryophytes in tropical forests, Richards (1954, 1984) distinguished a low (skiophilous, shade epiphytes) and a high (photophilous, sun epiphytes) community. In our study 37 % of the variation in the species data was explained by the first axis of the DCA and the value rises to 92 % after Beals smoothing (Fig. 4-2). The axis is strongly correlated to height in the tree and stem diameter, which are clearly interdependent. Height in the tree and stem diameter are not ecological factors in the strict sense determining species distribution in forests but they are good indicators for the combination of ecofactors in a vertical gradient (e.g. humidity and light intensity).

Assuming that the underlying model of unimodal species response along gradients is correct, the remaining variation has to be attributed to unmeasured ecological factors, which are independent from the position in the host tree. Microclimatic factors like light, humidity and temperature conditions are clearly determined by the height in the tree and so are the substrate depending factors like age of substrate, structure of bark and pH of bark (see Tab. 4-6). Our observations indicate that several ramicolous species of the outer canopy also occur on branches and twigs in the understory of the forests (Holz et al. 2002), which has also been demonstrated by Cornelissen & ter Steege (1989) for lowland forests. Such species may best be characterized as pioneer species, some of them are facultative epiphylls. Studying only small twigs at different heights could thus be a promising approach to obtain more information on the relative importance of microclimatic factors, substrate factors or competition for the vertical differentiation of cryptogamic epiphytes.

When comparing species distribution on the two studied host trees (see Tab. 4-1), it may be recognized that most species occupy the same height zone on the different host trees. However, many of these species show a broader height spectrum on one tree than on the other tree species (e.g. many of the species restricted to the outer canopy of *Q. copeyensis* are common in the outer canopy, the inner canopy or even the upper trunk of Q. costaricensis). It seems that substrate factors (bark chemistry or bark physics) are more important for the distribution of these species than the microclimatic factors, including light conditions. Physiological and transplant experiments might help to resolve the factors responsible for stratification with height.

Using tree trunk relevé data, it appears that part of the variation in species distribution is explained by exposition. It also seems obvious that inclination in the inner canopy and on the tree base are important for humus accumulation and water retention.

Community composition and structure

Community composition of cryptogamic epiphytes on *Quercus copeyensis* and *Q. costaricensis* is significantly different and changes gradually with height in the tree (Fig. 4-2, Tabs. 4-4, 4-5). The largest differences are observed in the tree base communities of the two host tree species. Micro-niche differentiation, exposition, and invasion of terrestrial species are important factors determining the composition of tree base communities, which are more similar to the surrounding terrestrial vegetation than to that of the tree trunk and canopy in the study area (Holz et al. 2002). Similar observations were made in conifer forests of southern Chile dominated by *Fitzroya cupressoides* (Clement et al. 2001).

Based on 219 relevés taken over a 3500 m elevational gradient, Kürschner & Parolly (1998b) classified the trunk-epiphytic bryophyte communities of Central and South America orders, alliances, associations and subassociations, using a classical phytosociological approach (Kürschner & Parolly 1998b, Tab. 5 - 7). Species groups on tree bases and trunks in the studied oak forest weakly coincide with the order '*Prionodontetalia fusco-lutescentis*' and the alliance '*Herberto divergentis-Plagiochilion compressulae*', but not with the associations or subassociations described by Kürschner & Parolly (1998a, 1998b). In fact, many of the character species of these associations and subassociations show a wide ecological amplitude in the investigated oak forest or preferences to microhabitats other than tree bases and trunks (Holz et al. 2002).

In a study of epiphytic cryptogam communities in upper montane forests of Colombia, Wolf (1993a, 1994) distinguished five canopy and five tree base communities using TWINSPAN for classification of relevés. However, TWINSPAN has been reported to perform poorly when there is more than one important underlying ecological gradient (van Groenewoud 1992, Belbin & McDonald 1993).

Unlike cluster analysis which has no inherent reduction in dimensionality, TWINSPAN cannot effectively represent complex data sets in its one-dimensional framework. Nevertheless, species groups of the present study partially coincide with the communities described by Wolf. Both studies reveal distinct canopy and tree base communities, and discrete differences in species composition of the communities of the outer canopy, the inner canopy and the trunk. Differences between trunk and inner canopy communities are less distinct in the present investigation than in the Colombian one, however. Moreover, in the present study the tree base, trunk and inner canopy communities of the two investigated tree species are clearly different. In the Colombian study, host specificity was not detected.

Furthermore, many of the species occurring widely from the tree base up to the canopy or exclusively in the canopy in the Colombian study (e.g., *Anoplolejeunea conferta, Prionodon fusco-lutescens, Trichocolea tomentosa, Lepicolea pruinosa, Lepidozia* spec*., Lophocolea trapezoidea, Bazzania hookeri*) are restricted to the lower, shaded part of the forest understory in the investigated oak forest. These differences in species distribution may possibly be due to the higher and more evenly distributed rainfall in the area studied by Wolf, exceeding 100 mm per month even during the “dry” season (Wolf 1993a). The moister climate may also explain the occurrence of hygrophytic terrestrial species on the tree trunks in the Colombian forests noted earlier (see above). Other factors explaining the different community compositions of the upper montane forests of Colombia (Wolf 1993a) and of Costa Rica (this study) may be the different structure and different host tree species of the forests and differences in the methodological approach.

Kürschner & Parolly (1998c) showed that perennials are the predominant life strategy of epiphytic bryophytes on tree bases and lower parts of the trunks. As adaptation to promote interspecific competition for space and light many species on the tree base tend to grow in pure patches due to their growth form and vegetative reproduction (e.g. *Bazzania* spp., *Rigodium toxarium*, *Thuidium* spp., *Plagiochila* spp.). This is also the case in many lichens growing on the trunk and in the inner canopy (e.g. *Hypotrachyna* spp., *Lobaria* spp.).

In the outer canopy, community structure and ecological strategies of species are very different (Fig. 2). Many species are restricted to this height zone (Tab. 1) and are early-successional ‘sun epiphytes’ or pioneers occurring also on twigs in the understory (Cornelissen & ter Steege 1989). Average species richness per plot and species frequency are higher in the outer canopy than on the tree base and tree trunk and beta diversity is low (Tab. 2). Similar observations have been reported by McCune et al. (2000) in an old-growth conifer forest in Western Washington and is apparently a general characteristic of the twig community. Outer canopy twigs are a relatively young habitat and light and humidity conditions in this habitat are more extreme than in the understory.

Species of this community are characterized by small stature, low cover, and copious production of diaspores to allow for fast establishment (Cornelissen & ter Steege 1989, Van Leerdam, Zagt & Veneklaas 1990). They are r strategists, while those of the tree base and trunk are k strategists (MacArthur & Wilson 1967). McCune et al. (2000) hypothesized the importance of birds for the development of epiphyte communities in the tree tops of old conifer forests in Western Washington, by transport of propagules (on their feet) and by increasing local nutrient availability through deposition of faeces. The principles of dispersal and life strategies of the rain forest bryophytes and lichens remain poorly understood (Schuster 1989, Gradstein 1992), however, and require long-term observations on succession and colonization. Van Dunné’s (2001) study on the establishment of epiphytes in secondary forests and plantations constitutes a first approach to this subject.

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Table 4-1. Relative abundance of bryophytes and macrolichens in a group of relevés in primary upper montane *Quercus* forest of Costa Rica. Abundance of a species in a group of relevés over the abundance of that species in all relevés expressed as a %. **N** = number of relevés (plots) or observations of a species. IV = indicator value (Dufrene & Legendre 1997). MaxGroup = height zone with highest number of observations. p = statistical significance using a Monte Carlo test with 1000 replicates.

Hosttree			***Q. copeyensis***					***Q. costaricensis***					Indicator Value		
Group (height zone)			total	tree base	trunk	inner canopy	outer canopy	total	tree base	trunk	inner canopy	outer canopy	MaxGroup	IV	p
Group Identifier				11	12	13	14		21	22	23	24			
Taxon	acronym	***N***	***177***	***29***	***48***	***48***	***52***	***214***	***33***	***70***	***61***	***50***			
Adelanthus decipiens (Hook.) Mitt.	Adel.dec	***1***	100	0	100	0	0	0	0	0	0	0	12	2,1	0,402
Adelanthus pittieri (Steph.) Grolle	Adel.pit	***23***	88	31	59	0	0	12	0	9	0	0	12	18,6	0,001 **
Amphilejeunea patellifera (Spruce) R.M.Schust.	Amph.pat	***22***	30	0	0	11	17	70	0	0	34	38	23	6,1	0,035 *
Anastrophyllum auritum (Lehm.) Steph.	Anas.aur	***40***	66	0	18	51	0	34	0	14	17	0	13	17,9	0,001 **
Anoplolejeunea conferta (C.F.W.Meissn.) A.Evans	Anop.con	***86***	96	2	27	7	60	4	1	0	0	3	14	42,4	0,001 **
Anzia americana Yoshim. & Sharp	Anzi.ame	***32***	61	6	35	26	0	39	0	31	3	0	12	9,4	0,003 **
Anzia leucobates (Nyl.) Müll.Arg.	Anzi.leu	***8***	0	0	0	0	0	100	0	64	36	0	23	3	0,222
Anzia masonii Yoshim.	Anzi.mas	***1***	0	0	0	0	0	100	0	100	0	0	22	1,4	1
Anzia parasitica (Fée) Zahlbr.	Anzi.par	***23***	0	0	0	0	0	100	0	11	15	74	24	28,3	0,001 **
Aureolejeunea fulva R.M.Schust.	Aure.ful	***38***	51	0	0	0	47	49	0	0	14	39	14	15,3	0,001 **
Bazzania longistipula (Lindenb.) Trevis.	Bazz.lon	***19***	100	1	99	0	0	0	0	0	0	0	12	37	0,001 **
Bazzania stolonifera (Sw.) Trevis.	Bazz.sto	***52***	69	70	2	0	0	31	23	5	0	0	11	64,8	0,001 **
Brachiolejeunea laxifolia (Taylor) Schiffner	Brac.lax	***53***	62	0	0	5	52	38	0	0	0	44	24	24,5	0,001 **
Brachymenium systylium (Müll.Hal.) A. Jaeger	Brac.sys	***1***	0	0	0	0	0	100	0	0	100	0	23	1,6	0,83
Braunia squarrulosa (Hampe) Müll.Hal.	Brau.squ	***1***	0	0	0	0	0	100	0	100	0	0	22	1,4	1
Bryum billarderi Schwägr.	Bryu.bil	***4***	0	0	0	0	0	100	88	1	11	0	21	2,7	0,355
Bunodophoron melanocarpum (Sw.) Wedin	Buno.mel	***53***	100	1	61	38	0	0	0	0	0	0	12	39,2	0,001 **
Cheilolejeunea inflexa Hampe ex Lehm. & Lindenb.	Chei.inf	***25***	0	0	0	0	0	100	10	73	17	0	22	18,7	0,001 **
Chorisodontium setaceum (E.B.Bartram) E.B.Bartram	Chor.set	***8***	57	0	0	61	0	43	0	35	4	0	13	5,1	0,035 *
Cladonia spp.	Clad.spp	***25***	71	0	10	64	0	29	0	13	13	0	13	11,9	0,002 **
Coccocarpia erythroxyli (Spreng.) Swinscow & Krog	Cocc.ery	***1***	0	0	0	0	0	100	0	0	0	100	24	2	0,545
Cryphaea spp.	Cryp.spp	***9***	50	0	0	0	47	50	0	0	30	23	14	5,4	0,021 *

Table 4-1 (cont'd).

Group (height zone)			***Q. copeyensis***					***Q. costaricensis***					Indicator Value		
			total	tree base	trunk	inner canopy	outer canopy	total	tree base	trunk	inner canopy	outer canopy	MaxGroup	IV	p
Group Identifier				11	12	13	14		21	22	23	24			
Daltonia spp.	Dalt.spp	***5***	64	0	0	0	61	36	0	0	17	21	14	3,5	0,093
Dicranodontium longisetum (Hook.) R.S.Williams	Dicr.lon	***14***	100	100	0	0	0	0	0	0	0	0	11	48,3	0,001 **
Dicranodontium meridionale E.B.Bartram	Dicr.mer	***61***	98	5	72	19	1	2	2	0	1	0	12	58,8	0,001 **
Dicranum flagellare Hedw.	Dicr.fla	***3***	0	0	0	0	0	100	0	18	82	0	23	2,7	0,21
Dictyonema glabratum (Spreng.) D.L.Hawksw.	Dict.gla	***4***	32	0	0	0	29	68	0	0	26	45	24	0,9	0,884
Diplasiolejeunea involuta S. Winkl.	Dipl.inv	***12***	0	0	0	0	0	100	0	0	0	100	24	24	0,001 **
Diplasiolejeunea replicata (Spruce) Steph.	Dipl.rep	***2***	100	0	0	0	100	0	0	0	0	0	14	3,8	0,085
Diplasiolejeunea spec. A	Dipl.spA	***89***	48	0	0	0	43	52	0	0	0	57	24	54,7	0,001 **
Drepanolejeunea spp.	Drep.spp	***34***	33	4	27	0	0	67	0	0	0	69	24	25	0,001 **
Echinocolea asperrima (Spruce) R.M.Schust.	Echi.asp	***4***	100	89	11	0	0	0	0	0	0	0	11	9,2	0,001 **
Erioderma mollissimum (Samp.) DR.	Erio.mol	***2***	97	0	0	0	97	3	0	0	0	3	14	1,9	0,669
Everniastrum cirrhatum (E.Fr.) Hale ex Sipman	Ever.cir	***8***	0	0	0	0	0	100	0	0	26	74	24	10,4	0,002 **
Frullania brasiliensis Raddi	Frul.bra	***280***	52	3	5	24	21	48	3	10	30	5	23	29	0,001 **
Frullania caulisequa (Nees) Nees	Frul.cau	***3***	100	0	0	0	100	0	0	0	0	0	14	5,8	0,01 **
Frullania convoluta Lindenb. & Hampe	Frul.con	***8***	100	0	0	7	93	0	0	0	0	0	14	12,5	0,001 **
Frullania ecklonii (Spreng.) Spreng.	Frul.eck	***55***	52	0	0	0	46	48	0	0	4	50	14	26,7	0,001 **
Frullania stenostipa Spruce	Frul.ste	***53***	22	0	0	0	19	78	0	0	0	81	24	57	0,001 **
Frullanoides densifolia Raddi ssp. densifolia	Frul.den	***4***	6	0	0	0	6	94	0	28	65	1	23	1,1	0,887
Groutiella chimborazensis (Spruce ex Mitt.) Florsch.	Grou.chi	***31***	0	0	0	0	0	100	0	30	69	1	23	23,8	0,001 **
Harpalejeunea stricta (Lindenb. & Gottsche) Steph.	Harp.str	***1***	0	0	0	0	0	100	0	100	0	0	22	1,4	1
Herbertus divergens (Steph.) Herzog	Herb.div	***140***	22	7	10	9	0	78	11	36	27	0	22	27,3	0,001 **
Heterodermia casarettiana (Massal.) Trevis.	Hete.cas	***9***	5	0	0	0	5	95	0	54	9	32	24	2,6	0,301
Heterodermia leucomela (Fée) Swinsc. & Krog	Hete.leu	***67***	44	0	0	0	39	56	0	0	0	61	24	45	0,001 **
Heterodermia lutescens (Koruk.) Follm. & Redon	Hete.lut	***25***	44	0	0	0	39	56	0	0	0	61	24	17,2	0,001 **
Heterodermia obscurata (Nyl.) Trev.	Hete.obs	***2***	100	0	0	0	100	0	0	0	0	0	14	3,8	0,077
Heterodermia squamulosa (Degel.) W.Culb.	Hete.squ	***15***	41	0	0	12	26	59	0	5	6	50	24	8,1	0,005 **
Heterodermia vulgaris (Vain.) Follmann & Redon	Hete.vul	***2***	55	0	0	51	0	45	0	0	0	49	13	1,1	0,846

Table 4-1 (cont'd).

			Q. copeyensis					***Q. costaricensis***					Indicator Value		
Group (height zone)			total	tree base	trunk	inner canopy	outer canopy	total	tree base	trunk	inner canopy	outer canopy	MaxGroup	IV	p
Group Identifier				11	12	13	14		21	22	23	24			
Heterophyllium affine (Hook.) M.Fleisch.	Hete.aff	***9***	100	90	10	0	0	0	0	0	0	0	11	21,7	0,001 **
Holomitrium flexuosum Mitt.	Holo.fle	***4***	0	0	0	0	0	100	0	0	100	0	23	6,6	0,013 *
Holomitrium pulchellum Mitt.	Holo.pul	***75***	24	0	10	16	1	76	0	34	40	0	22	9,6	0,063
Hypnum amabile (Mitt.) Hampe	Hypn.ama	***3***	0	0	0	0	0	100	0	69	31	0	22	2	0,291
Hypotrachyna bogotensis (Vain.) Hale	Hypo.bog	***10***	32	0	0	0	32	68	0	39	0	29	14	2,4	0,339
Hypotrachyna costaricensis (Nyl.) Hale	Hypo.cos	***5***	0	0	0	0	0	100	0	0	0	100	24	10	0,001 **
Hypotrachyna densirhizinata (Kurok.) Hale	Hypo.den	***6***	23	0	0	21	0	77	0	0	0	79	24	7,9	0,007 **
Hypotrachyna ducalis (Jatta) Hale	Hypo.duc	***1***	100	0	100	0	0	0	0	0	0	0	12	2,1	0,404
Hypotrachyna ensifolia (Kurok.) Hale	Hypo.ens	***1***	100	0	0	0	100	0	0	0	0	0	14	1,9	0,661
Hypotrachyna imbricatula (Zahlbr.) Hale	Hypo.imb	***56***	100	0	18	67	15	0	0	0	0	0	13	34,9	0,001 **
Hypotrachyna longiloba (H.Magn.) Hale	Hypo.lon	***7***	100	0	52	48	0	0	0	0	0	0	13	4	0,05 *
Hypotrachyna monilifera (Kurok.) Hale	Hypo.mon	***2***	100	0	0	100	0	0	0	0	0	0	13	4,2	0,04 *
Hypotrachyna physcioides (Nyl.) Hale	Hypo.phy	***99***	51	0	27	26	0	49	0	11	31	5	12	16,6	0,003 **
Hypotrachyna prolongata (Kurok.) Hale	Hypo.pro	***11***	24	0	0	26	0	76	0	50	16	8	22	2,8	0,305
Hypotrachyna protoboliviana (Hale) Hale	Hypo.prt	***11***	100	0	50	49	1	0	0	0	0	0	13	7,1	0,01 **
Hypotrachyna pulvinata (Fée) Hale	Hypo.pul	***73***	48	0	2	5	36	52	0	2	3	52	24	31,1	0,001 **
Hypotrachyna reducens (Nyl.) Hale	Hypo.red	***5***	0	0	0	0	0	100	0	32	68	0	23	4,4	0,052
Hypotrachyna rockii (Zahlbr.) Hale	Hypo.roc	***2***	0	0	0	0	0	100	0	0	96	4	23	1,6	0,81
Iwatsukia jishibae (Steph.) N.Kitag.	Iwat.jis	***1***	100	100	0	0	0	0	0	0	0	0	11	3,4	0,067
Jamesoniella rubricaulis (Nees) Grolle	Jame.rub	***15***	2	0	0	3	0	98	0	44	53	0	23	5,2	0,072
Lejeunea flava (Sw.) Nees	Leje.fla	***30***	75	10	6	0	50	25	27	6	0	0	14	18,4	0,001 **
Lejeunea intricata J.B.Jack & Steph.	Leje.int	***35***	0	0	0	0	0	100	37	46	18	0	21	14,4	0,001 **
Lejeunea laetevirens Nees & Mont.	Leje.lae	***2***	0	0	0	0	0	100	100	0	0	0	21	6,1	0,014 *
Lepidozia cupressina (Sw.) Lindenb.	Lepi.cup	***31***	97	93	4	0	0	3	4	0	0	0	11	64	0,001 **
Leptodontium exasperatum Cardot	Lept.exa	***167***	72	0	1	65	7	28	0	1	25	1	13	57,8	0,001 **
Leptodontium flexifolium (Dicks.) Hampe	Lept.fle	***1***	0	0	0	0	0	100	0	0	100	0	23	1,6	0,83
Leptogium burgessii (L.) Mont.	Lept.bur	***7***	1	0	0	0	1	99	0	0	45	54	24	3,2	0,172

Table 4-1 (cont'd).

			Q. copeyensis					*Q. costaricensis*					Indicator Value		
Group (height zone)			total	tree base	trunk	inner canopy	outer canopy	total	tree base	trunk	inner canopy	outer canopy	MaxGroup	IV	p
Group Identifier				11	12	13	14		21	22	23	24			
Leptogium coralloideum (Mey. & Flot.) Vain.	Lept.cor	***1***	100	0	0	0	100	0	0	0	0	0	14	1,9	0,687
Leptogium laceroides Bouly de Lesd.	Lept.lac	***16***	52	0	0	0	46	48	0	0	0	54	24	8,6	0,001 **
Leptogium phyllocarpum (Pers.) Mont.	Lept.phy	***3***	0	0	0	0	0	100	0	0	0	100	24	6	0,019 *
Leptoscyphus amphibolius (Nees) Grolle	Lept.amp	***2***	29	27	0	0	0	71	73	0	0	0	21	2,2	0,263
Leptoscyphus porphyrius (Nees) Grolle	Lept.por	***78***	94	1	14	70	9	6	0	0	6	0	13	43,8	0,001 **
Lepyrodon tomentosus (Hook.) Mitt.	Lepy.tom	***7***	0	0	0	0	0	100	0	100	0	0	22	10	0,002 **
Leucobryum antillarum Schimp. ex Besch.	Leuc.ant	***1***	100	100	0	0	0	0	0	0	0	0	11	3,4	0,074
Leucodon curvirostris Hampe	Leuc.cur	***30***	3	0	0	3	0	97	0	25	72	0	23	21,2	0,001 **
Leucolejeunea xanthocarpa (Lehm. & Lindenb.) A.Evans	Leuc.xan	***32***	75	0	0	0	70	25	0	0	0	30	14	29,6	0,001 **
Lindigianthus cipaconeus (Gottsche) Kruijt & Gradst.	Lind.cip	***52***	0	1	0	0	0	100	35	30	35	0	21	13,8	0,002 **
Lobaria crenulata (Hook. in Kunth) Trev.	Loba.cre	***29***	45	0	0	0	41	55	0	0	17	42	14	10,1	0,003 **
Lobaria pallida (Hook. in Kunth) Trevis.	Loba.pal	***3***	0	0	0	0	0	100	0	0	0	100	24	6	0,015 *
Lobaria pulmonaria (L.) Hoffm.	Loba.pul	***1***	0	0	0	0	0	100	0	0	100	0	23	1,6	0,821
Lobaria subdissecta (Nyl.) Vain.	Loba.sud	***52***	0	0	0	0	0	100	2	47	51	0	22	20,9	0,001 **
Lobaria subexornata Yoshim.	Loba.sub	***28***	3	0	0	0	3	97	0	31	58	9	23	9,5	0,009 **
Lophocolea muricata (Lehm.) Nees	Loph.mur	***3***	71	69	0	0	0	29	31	0	0	0	11	4,8	0,028 *
Macrocoma tenuis subsp. sullivantii (Müll.Hal.) Vitt	Macr.ten	***7***	9	0	0	0	8	91	0	0	69	23	23	3,4	0,192
Macromitrium longifolium (Hook.) Brid.	Macr.lon	***50***	0	0	0	0	0	100	0	44	56	0	23	23,1	0,001 **
Metzgeria liebmanniana Lindenb. & Gottsche	Metz.lie	***56***	86	0	0	0	83	14	0	0	0	17	14	60,9	0,001 **
Microlejeunea bullata (Tayl.) Steph.	Micr.bul	***87***	35	0	0	0	30	65	0	0	0	70	24	66,8	0,001 **
Mittenothamnium reptans (Hedw.) Cardot	Mitt.rep	***1***	0	0	0	0	0	100	100	0	0	0	21	3	0,175
Nephroma helveticum Ach.	Neph.hel	***1***	0	0	0	0	0	100	0	0	0	100	24	2	0,527
Nowellia curvifolia (Dicks.) Mitt.	Nowe.cur	***3***	100	100	0	0	0	0	0	0	0	0	11	10,3	0,001 **
Omphalanthus filiformis (Sw.) Nees	Omph.fil	***1***	0	0	0	0	0	100	100	0	0	0	21	3	0,176
Oropogon loxensis (Fée) Th.Fr.	Orop.lox	***1***	0	0	0	0	0	100	0	0	0	100	24	2	0,554
Oropogon spp.	Orop.spp	***55***	35	0	10	24	2	65	0	22	33	8	23	9,3	0,018 *
Orthodontium pellucens (Hook.) B.S.G.	Orth.pel	***4***	100	0	100	0	0	0	0	0	0	0	12	8,3	0,005 **

Table 4-1 (cont'd).

Group (height zone) Group Identifier			*Q. copeyensis*					*Q. costaricensis*					Indicator Value		
			total	tree base 11	trunk 12	inner canopy 13	outer canopy 14	total	tree base 21	trunk 22	inner canopy 23	outer canopy 24	MaxGroup	IV	p
Orthotrichum pariatum Mitt.	Orth.par	***4***	0	0	0	0	0	100	0	0	0	100	24	8	0,003 *
Orthotrichum sharpii H.Rob.	Orth.sha	***6***	100	0	0	0	100	0	0	0	0	0	14	11,5	0,002 *
Pannaria spec. A	Pann.spA	***1***	0	0	0	0	0	100	0	0	100	0	23	1,6	0,8
Parmeliopsis venezuelana (Hale) DePriest & Hale	Parm.ven	***1***	100	0	100	0	0	0	0	0	0	0	12	2,1	0,371
Parmotrema arnoldii (DR.) Hale	Parm.arn	***70***	46	0	0	3	39	54	0	4	17	37	24	22,9	0,001 **
Physcia lopezii Moberg	Phys.lop	***1***	0	0	0	0	0	100	0	0	0	100	24	2	0,523
Pilotrichella flexilis (Hedw.) Ångström	Pilo.fle	***59***	8	9	1	2	0	92	15	68	5	0	22	28,2	0,001 **
Plagiochila bicuspidata Gottsche	Plag.bic	***4***	0	0	0	0	0	100	89	1	11	0	21	2,7	0,342
Plagiochila bifaria (Sw.) Lindenb.	Plag.bif	***39***	3	0	0	3	0	97	14	37	46	0	23	14,3	0,001 **
Plagiochila cf. vagae (sect. Contiguae)	Plag.vag	***3***	0	0	0	0	0	100	100	0	0	0	21	9,1	0,002 **
Plagiochila heterophylla Lindenb. ex Lehm.	Plag.het	***189***	67	31	30	10	0	33	7	15	7	0	12	24,5	0,001 **
Plagiochila oresitropha Spruce	Plag.ore	***4***	0	0	0	0	0	100	100	0	0	0	21	12,1	0,001 **
Plagiochila pachyloma Tayl.	Plag.pac	***1***	0	0	0	0	0	100	0	100	0	0	22	1,4	1
Plagiochila papillifolia Steph.	Plag.pap	***11***	100	96	4	0	0	0	0	0	0	0	11	29,8	0,001 **
Plagiochila patzschkei Steph.	Plag.pat	***23***	36	5	17	2	1	64	73	1	1	0	21	8,8	0,027
Plagiochila pittieri Steph.	Plag.pit	***23***	21	20	0	0	0	79	79	0	0	0	21	38,4	0,001 **
Plagiochila retrorsa Gottsche	Plag.ret	***2***	94	97	0	0	0	6	0	3	0	0	11	3,3	0,094
Plagiochila stricta Lindenb.	Plag.str	***1***	0	0	0	0	0	100	100	0	0	0	21	3	0,149
Plagiochila trichostoma Gottsche	Plag.tri	***4***	100	85	15	0	0	0	0	0	0	0	11	8,8	0,001 **
Porella leiboldii (Lehm.) Trevis.	Pore.lei	***3***	0	0	0	0	0	100	100	0	0	0	21	9,1	0,001 **
Porella liebmanniana (Lindenb. & Gottsche) Trevis.	Pore.lie	***9***	0	0	0	0	0	100	0	24	76	0	23	6,2	0,03 *
Porotrichodendron superbum (Taylor) Broth.	Poro.sup	***14***	0	0	0	0	0	100	95	5	0	0	21	31,7	0,001 **
Porotrichum korthalsianum (Dozy & Molk.) Mitt.	Poro.kor	***22***	5	7	0	0	0	95	40	52	0	0	21	13,5	0,002 **
Prionodon densus (Sw. ex Hedw.) Müll.Hal.	Prio.den	***14***	0	0	0	0	0	100	70	30	0	0	21	14,9	0,001 **
Pseudocyphellaria aurata (Ach.) Vain.	Pseu.aur	***6***	46	0	0	0	45	54	0	0	52	3	14	1,7	0,429
Pseudocyphellaria crocata (L.) Vain.	Pseu.cro	***2***	0	0	0	0	0	100	0	30	70	0	23	1,1	0,82
Pylaisiadelpha tenuirostris (Sull.) W.R.Buck	Pyla.ten	***11***	70	0	67	3	3	30	0	21	6	0	12	2,8	0,404

Table 4-1 (cont'd).

Group (height zone)			***Q. copeyensis***					***Q. costaricensis***					Indicator Value		
			total	tree base	trunk	inner canopy	outer canopy	total	tree base	trunk	inner canopy	outer canopy	MaxGroup	IV	p
Group Identifier				11	12	13	14		21	22	23	24			
Radula nudicaulis Steph.	Radu.nud	***34***	0	0	0	0	0	100	70	29	1	0	21	36,2	0,001 **
Radula quadrata Gottsche	Radu.qua	***16***	0	0	0	0	0	100	0	0	86	14	23	15,5	0,001 **
Ramalina spec. A	Rama.spA	***24***	57	0	0	0	51	43	0	0	0	49	14	11,8	0,002 **
Renauldia mexicana (Mitt.) H.A.Crum	Rena.mex	***2***	0	0	0	0	0	100	0	100	0	0	22	2,9	0,216
Rigodium toxarion (Schwägr.) A.Jaeger	Rigo.tox	***39***	0	0	0	0	0	100	81	19	0	0	21	68,6	0,001 **
Rimelia cetrata (Ach.) Hale & A.Fletcher	Rime.ret	***9***	79	0	0	78	0	21	0	2	5	14	13	1,6	0,765
Sematophyllum subsimplex (Hedw.) Mitt.	Sema.sub	***5***	100	100	0	0	0	0	0	0	0	0	11	17,2	0,001 **
Sematophyllum swartzii (Schwägr.) W.H.Welch & H.A.Crum	Sema.swa	***7***	100	69	31	0	0	0	0	0	0	0	11	14,3	0,001 **
Siphula spec. A	Siph.spA	***4***	100	0	23	77	0	0	0	0	0	0	13	1,6	0,62
Sticta damaecornis agg.	Stic.dam	***11***	0	0	0	0	0	100	0	95	5	0	22	13,6	0,001 **
Sticta ferax Müll. Arg.	Stic.fer	***29***	0	0	0	0	0	100	3	73	24	0	22	22,9	0,001 **
Sticta spp.	Stic.spp	***30***	41	0	0	0	38	59	0	0	32	30	14	9,5	0,013 *
Sticta weigelii (Isert) Ach.	Stic.wei	***13***	15	0	0	0	15	85	0	35	17	33	24	2	0,579
Syrrhopodon prolifer Schwägr.	Syrr.pro	***8***	100	99	1	0	0	0	0	0	0	0	11	20,5	0,001 **
Telaranea nematodes (Austin) M.Howe	Tela.nem	***1***	100	100	0	0	0	0	0	0	0	0	11	3,4	0,075
Teloschistes spec. A	Telo.spA	***1***	100	0	0	0	100	0	0	0	0	0	14	1,9	0,654
Thuidium pseudoprotensum (Müll.Hal.) Mitt.	Thui.pse	***27***	23	22	0	0	0	77	77	0	0	0	21	35,2	0,001 **
Trichocolea floccosa Herzog & Hatch.	Tric.flo	***2***	0	0	0	0	0	100	5	95	0	0	22	1,4	0,982
Usnea spp.	Usne.spp	***105***	16	0	5	8	1	84	0	1	11	74	24	59,1	0,001 **
Zygodon ehrenbergii Müll.Hal.	Zygo.ehr	***119***	48	0	38	9	0	52	18	29	5	0	12	26,9	0,001 **
Zygodon liebmannii Schimp.	Zygo.lie	***14***	0	0	0	0	0	100	0	24	76	0	23	13,6	0,001 **
Zygodon obtusifolius Hook.	Zygo.obt	***5***	0	0	0	0	0	100	0	22	77	2	23	3,8	0,103
Zygodon reinwardtii (Hornsch.) A.Braun	Zygo.rei	***41***	95	0	0	0	95	5	0	0	1	4	14	65,5	0,001 **
	Averages	***24***	41	11	8	7	14	59	12	15	16	17			

CHAPTER 5

Cryptogamic epiphytes in primary and recovering upper montane *Quercus* forests of Costa Rica - Species richness, community composition and ecology

Abstract

Species richness, community composition and ecology of cryptogamic epiphytes (bryophytes, macrolichens) were studied in upper montane primary, early secondary and late secondary oak forests of the Cordillera de Talamanca, Costa Rica. Canopy trees of *Quercus copeyensis* were sampled with the aim of getting insight in patterns and processes of epiphyte succession and recovery of diversity in secondary forest following forest clearing. Species richness of cryptogamic epiphytes in secondary and primary forests were nearly the same, showing that primary forests are not necessarily more diverse than secondary forests. High species richness of secondary forests was presumably due to the closed canopy, resulting in permanently high atmospheric humidity in these forests. Similarity in species composition of secondary and primary forests increases with forest age, but after 40 years of succession one third (46 species) of primary forest species had not re-established in the secondary forest. Community composition in primary and secondary forests differed markedly and indicates that a long time is needed for the re-establishment of microhabitats and re-invasion of species and communities adapted to differentiated niches. Genera and species exclusive to primary forests are relevant as indicator taxa and conservation targets. Forty percent (68 species) of all species recorded are restricted to secondary forests, indicating the important contribution of secondary forest diversity to total species richness of the oak forests of Costa Rica.

Resumen

En bosques montanos primarios y secundarios de *Quercus*, en la Cordillera de Talamanca, Costa Rica, se estudiaron la riqueza de especies, la composición de la comunidad y la ecología de criptógamas epífitas. Se tomaron muestras en árboles adultos de *Quercus copeyensis*, con el fin de obtener una idea sobre el potencial de recuperación, patrones y procesos de sucesión epífita luego de disturbios antropógenas.

Los análisis de la diversidad de briofitas y líquenes revelaron que el total de especies en bosques primarios y secundarios es casi el mismo, demostrando que bosques primarios no son necesariamente más diversos que bosques secundarios. La similitud en composición de especies entre bosques secundarios y bosques primarios aumenta con la edad del bosque, pero incluso después de 40 años, un tercio (46 especies) de las especies del bosque primario no volvieron a invadir el bosque secundario. Géneros y especies exclusivos de bosques primarios son decisivos como especies indicadoras y para fines de conservación. Por el contrario, el 40 % (68 especies) de todas las especies halladas en los todos tipos de bosque está restringido a bosques secundarios, lo cual subraya la importancia de los mismos en cuanto a su aporte a la riqueza total de especies de un área determinada.

Introduction

During the last decades human impact on tropical montane forests has increased at an alarming rate. Clearing and subsequent land degradation have become major threats to these ecosystems (Bruijnzeel & Hamilton 2000, Churchill et al. 1995a). Secondary forest communities are widely distributed and are increasingly becoming the most important repository of biodiversity in tropical uplands (Brown & Lugo 1990, Chazdon 1994, Helmer 2000, Holl & Kappelle

1999). Yet, only little is known about the biodiversity of these forests and the patterns and processes of recovery following clearing. Will tropical forests ever fully recover on abandoned crop fields and pastures?

This paper deals with the biodiversity of epiphytic cryptogams (mosses, hepatics, macrolichens) in primary and secondary montane forests. Tree diversity in these forests is comparatively low, while a high proportion of total species richness is achieved by the cryptogams (Churchill et al. 1995b, Gradstein 1995, Sipman 1995, Wolf 1993a, 1993b). Cryptogams play an important role in these forests, not only in terms of species diversity but also in ecosystem functioning. Dense epiphytic mats of cryptogams hold water, trap seeds, intercept and retain nutrients (e.g., NO3-) from fog, and provide anchorage for seedlings (Clark et al. 1998, Hofstede et al. 1993, Nadkarni 1986, 1992, Pócs 1982, Richards 1984, Veneklaas 1990, Wolf 1993b). They shelter an abundant and diverse fauna (eg. Nadkarni & Matelson 1989, Ingram & Nadkarni 1993) and pendant cryptogamic taxa like *Frullania* sect. *Meteoriopsis*, *Phyllogonium fulgens*, *P. viscosum*, *Pilotrichella flexilis* and *Usnea* spp. are valuable non-timber forest products in Costa Rica (Romero 1999, Holz, unpubl. obs.).

Logging and land use have serious negative impact on epiphytic communities. Because of their important ecological role and usefulness in environmental monitoring, is describing and analysing these communities a research priority for conservation of biodiversity, and a prerequisite for a sustainable management of tropical montane forest (Chaverri & Hernández 1995, Hietz 1999, Gradstein et al. 2001a).

Studies on recovery of cryptogamic communities in secondary tropical forests are very few and focus only on lowland, submontane or lower montane rain forests (e.g., Acebey et al. 2003, Costa 1999, Equihua & Gradstein 1995, Mervin et al. 2001, Sillet et al. 1995), none on upper montane ones. In spite of the use of different field methodologies, the general trend emerging from these studies was that human impact causes loss of biodiversity. Costa (1999) found species richness of secondary lowland rain forests considerably impoverished as compared with primary forests. Acebey et al. (2003) showed a significantly decreased diversity of epiphytic bryophytes in young fallows; after 10-15 years only half of the bryophyte species of rain forest had re-established. They also demonstrated a significant shift of forest canopy species to lower heights in the fallows. Most of the species in young fallows are ecological generalists and sun epiphytes; shade epiphytes are largely lost when the forest is cleared (see also Equiha & Gradstein 1995). The high percentage of smooth mat species in fallows reflected the warmer and drier microclimate in these secondary habitats compared to the primary forest (Acebey et al. 2003).

Most work on species recovery of cryptogams following clearing has focused on agricultural lands abandoned for less than 10-15 years. As for vascular plant diversity, very little is known about late succession in secondary tropical forests, following establishment of an initial canopy (Holl & Kappelle 1999).

The present study for the first time compares cryptogamic epiphyte diversity and species composition in primary and secondary upper montane forests. Two successional stages of secondary forest (young secondary, late secondary) are compared with primary forest, in order to gain insight in recovery potential, general biodiversity patterns and processes of epiphyte succession following human disturbance.

Study Area

The study was conducted during March 1999 – May 2000 in an upper montane oak forest area in Los Santos Forest Reserve, situated at ca. 2900 m elevation on the Pacific-facing slope of the western Talamanca mountain range, Costa Rica (Figs. 5-1a, b). The Los Santos Forest Reserve is part of the buffer zone surrounding the UNESCO La Amistad Biosphere Reserve and World Heritage Site, one of the largest areas of undisturbed montane rain forest in Central America. Local climate at this altitude is cool and humid, annual precipitation averages 3000 mm and mean daily temperature 11 °C (Instituto Meteorológico Nacional, 1988). There is a pronounced dry season from early January to the end of April (Fig. 5-1c). The natural vegetation is an upper montane rain forest dominated by 30-40 m tall trees of two species of oak, *Quercus copeyensis* C.H.Müll. and *Q. costaricensis* Liebm. Understorey vegetation is characterized by bamboo, tree ferns, dwarf palms, shrubs, and herbs. Canopy and subcanopy branches are festooned with vascular and non-vascular epiphytes, including orchids, bromeliads, aroids, ericads, ferns, mosses, liverworts, and lichens (Kappelle 1995, 1996, Holz et al. 2002).

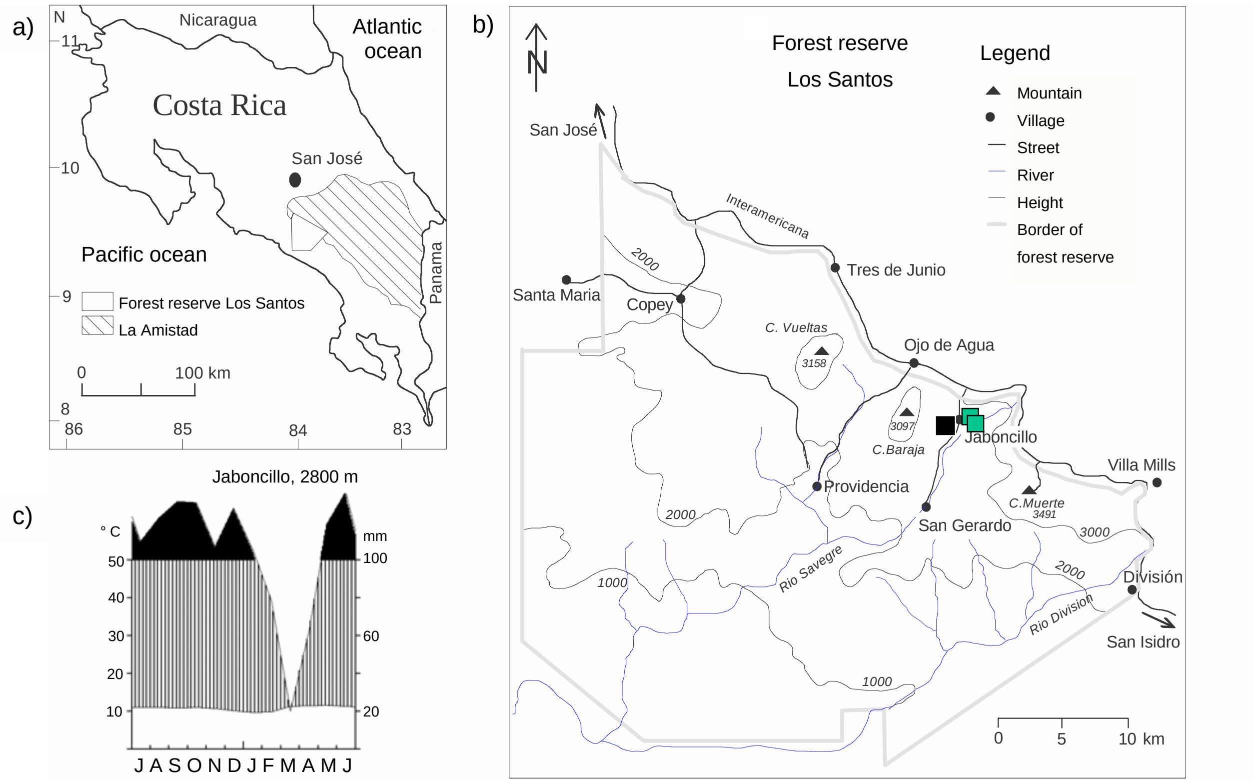

Fig. 5-1. Study area. a) Map of Costa Rica, showing La Amistad Biosphere Reserve and Los Santos Forest Reserve on the Pacific-facing slope of the Cordillera de Talamanca. b) Map of Los Santos Forest Reserve, showing Río Savegre valley and study sites; black square = primary forest, grey squares = secondary forests. c) Climate diagramm from Jaboncillo at about 2850 m elevation (July 1999 – Juni 2000), showing a pronounced dry season during January – April (from Köhler 2002).

Originally, the upper Río Savegre watershead had been entirely covered with these evergreen oak-dominated forest. Following the construction of the Interamerican Highway in the 1940's, clearing of forest stands to meet the increasing demands for charcoal, pasture and arable land by the rural population has occurred frequently. Since the 1980's, these activities have been reduced and the transition of locals to the touristic sector as well as the expansion of less areaconsuming orchards are now accompanied by a secondary forest succession on the cleared land (Kappelle 1995, 1996; Helmer 2000).

Methods

One primary and two secondary upper montane oak forest sites of ca. 1 ha each in the upper part of the Río Savegre valley near Jaboncillo (9°35'N, 83°44'W), were selected for comparison of epiphytic cryptogamic vegetation (Fig. 5-1b). The vascular plant vegetation of the three sites has been described by Kappelle et al. (1995); characteristics of are provided in Table 1. In spite of their different ages and forest structure, all three sites showed clear vertical profiles of humidity (Fig. 5-2) and air temperature (Köhler 2002).

Table 5-1. Description of study sites. Data on leaf area index and biomass from Köhler (2002).

	Primary forest **PF**	Early secondary forest **ESF**	Late secondary forest **LSF**
Altitude	2900 m	2880 m	2900 m
Slope	30,9 °	30,4 °	25,2 °
Age of forest stand	> 200 years	10 – 15 years	ca 40 years
Height of forest stand	30 – 35 m	5 – 9 m	11 – 15 m
Stems * 0.1 ha^{-1} (DBH > 3cm)	346	573	480
leaf area index (LAI) (m^{2} * m^{-2})	3.8	3.8	4.7
% of trunks reaching the canopy	7	94	39
Estimated total biomass of vascular and non-vascular ephiphytes (kg * ha^{-1})	3400	160	520
Dominant canopy tree species	*Quercus copeyensis* *Q. costaricensis*	Mixed forest of shrubs and pioneer tree species	*Quercus copeyensis* *Q. costaricensis*

Primary upper montane oak forest (PF).- The forest canopy is dominated by 35 m tall trees of *Quercus copeyensis* and *Q. costaricensis*. Average cover of the canopy layer is about 65 – 80%, of the subcanopy layer (10 – 15 m) ca. 40 – 50 %. Common subcanopy trees are *Cleyera theaedoides, Didymopanax pittieri, Nectandra salicina, Oreopanax capitatum, Styrax argenteus and Weimannia* *pinnata*. The primary forest canopy is more open, with more light entering the subcanopy and shrub layer, than that of the late secondary forest (see Table 1 and below).

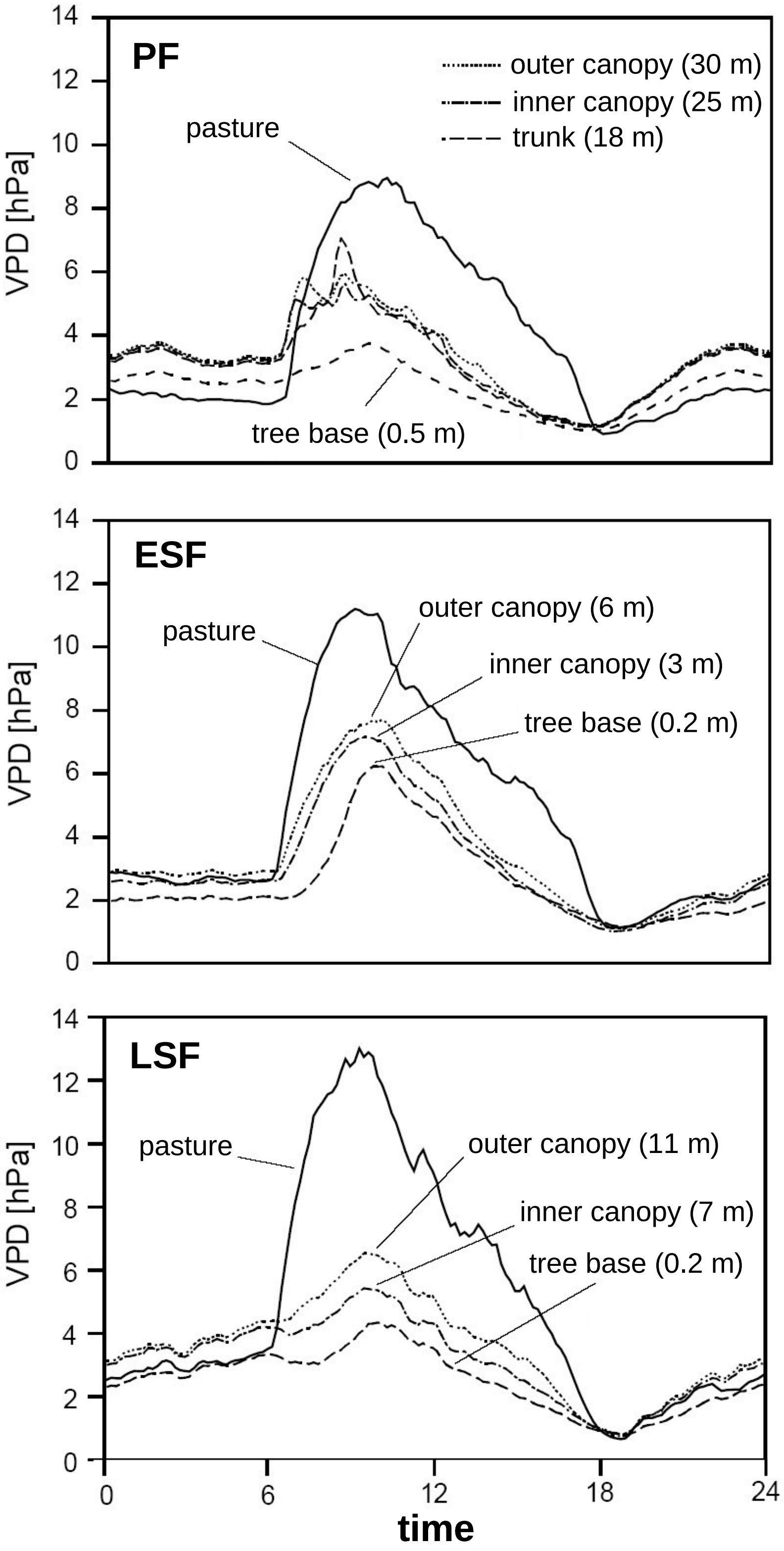

Fig. 5-2. Mean daily course of vapour pressure deficit (VPD) during the dry season (1999/2000) in different tree height zones of the investigated oak forests. PF = primary forest (mean of 49 days), ESF = early secondary forest (mean of 45 days), LSF = late secondary forest (mean of 34 days). Figure modified after Köhler (2002).

Early secondary forest (ESF).- The 5 – 9 m high stand with a recovery age of 10 – 15 years after abandonment is dominated by early secondary trees and shrubs such as *Abatia parviflora, Bocconia frutescens*, *Buddleja nitida, Cornus disciflora, Fuchsia arborescentes, F. paniculata, Monochaete spec., Myrsine coriacea, Oreopanax capitatus, O. xalapensis* and *Virburnum costaricanum*. Tree layer cover is about 75 %, of the shrub layer 40 – 50 %. *Quercus copeyensis* and *Q. costaricensis* attain a total cover of about 20 % and play a minor role in ESF.

Late secondary forest (LSF).- The 12-14 m tall, closed stand, of about 40 years in age is dominated by *Quercus costaricensis* and *Q. copeyensis* trees. Accompanying species with high cover are the tree species *Cornus disciflora, Myrsine coriacea, Weinmannia pinnata* and *Zanthoxylum sheryi* and the climbing liana *Smilax knuthii*. Due to the very dense canopy, the understorey of LSF is rather dark and cover of the shrub layer is less than 30%.

Five *Quercus copeyensis* canopy trees were randomly selected in the primary forest and in each of the two secondary forest stands. From each investigated tree two bark samples were taken at ca. 2 m above ground, extracted with deionised H_2O and analysed for pH. Cryptogamic epiphytes (bryophytes, macrolichens) were sampled in the outer canopy, the inner canopy, on the trunks and on the tree bases. Trees in the PF and the LSF were climbed using the single rope technique (Perry 1978, ter Steege & Cornelissen 1988). In total, 437 relevés were inventoried on 15 trees (177 relevés in PF, 76 in ESF and 184 in LSF). Several relevés were taken on each tree and in each height zone of the tree (Johansson 1974, modified). In PF 29 relevés were taken on tree bases, 48 on trunks, 48 in inner canopy and 52 in outer canopy; in LSF 25 on tree bases, 76 on trunks, 30 in inner canopy and 53 in outer canopy; in ESF 5 on tree bases, 21 on trunks, 25 on lower twigs and 25 relevés on upper twigs. Relevé size was 600 cm^2 (20 cm x 30 cm, on smaller branches 15 cm x 40 cm) except in the outer canopy of the primary forest and in the outer and inner canopy of the late secondary forest where twigs up to 1 m long were fully sampled. In ESF the tree base was defined as the lower 50 cm of the stem and sampled as one relevé, in other tree zones of

ESF complete stems and twigs were sampled over a length of 1 m. Depending on diameter, total area of twigs sampled was 500 – 900 cm^2. Cover of species in each relevé was estimated in percent. A combined cover/number of individuals scale, the “Braun-Blanquet scale” (Braun-Blanquet 1964) was not applied because the small size of the relevé area allowed for estimation of percentage cover. Moreover, counting of individuals of species with a gregarious growth habit, commonly observed in bryophytes and lichens, is impractical. All bryophytes and macrolichens within each relevé were collected and identified to species level. Voucher specimens were deposited at INB with duplicates in GOET, MO (some) and NY (some). Nomenclature follows Allen (1994, 2002), Buck (1998), and Sharp et al. (1994) for mosses, and Uribe & Gradstein (1998) for hepatics.

All statistical analyses were performed using the program package PC-ORD for Windows - Version 4.17 (McCune & Mefford 1999). The main data matrix (species cover) used consisted of 437 rows (relevés) and 168 columns (species). There were 73416 cells in this matrix and 93.6 percent of these cells were zero. The second data matrix consisted of 437 rows (relevés) and 16 columns representing the following variables: host tree number, forest stand, height zone, a combination of forest type and height zone, height of host tree, height of relevé in the tree, relative height of relevé in the tree, stem diameter, total number of species (richness), hepatic richness, moss richness, lichen richness, eveness, Shannon Index, Simpson Index, and total cover.

Groups of relevés defined by height zone and/or host tree species, forest type and host tree number were compared with non-metric MRPP (Multi-response Permutation Procedures). The analyses provided a nonparametric multivariate test of differences between groups. The A statistic from MRPP describes effect size, the chance-corrected within-group agreement. When all items are identical within groups, the observed delta = 0 and A = 1; when A = 0, the groups are no more different than expected by chance. In community ecology values for A are commonly below 0.1, even when differences between groups are apparent; $A > 0.3$ may be regarded as high, indicating that groups are significantly different from each others.

An updated matrix of 437 relevés x 132 species, following removal of species with less than three occurrences, was subject to *Detrended correspondence analysis* (DCA) and *non-metric multidimensional scaling* (NMS), to obtain a graphical depiction of community relationships and habitat variables. Two forms of the main data matrix were then used in multivariate analyses: one containing the untransformed abundance data (in percent cover) and one containing data transformed by the sociological favorability index of Beals (“Beals Index”, Beals 1984, McCune 1994). It tends to reduce the noise in the data by enhancing the strongest patterns in the data. Presence/absence data are replaced with quantitative values (range 0-1) that represent the probability of a species occurring in a particular relevé based on associating species that were present as well in that relevé. In DCA, ordination standard downweighting, segment detrending (26 segments) and non-linear rescaling were employed, in NMS the “slow-and-thorough” autopilot mode of PC-ORD used the best of 40 runs with the real data along with 50 runs of randomized data for a Monte Carlo test of significance. Relative Sørensen distances expressed community resemblances in NMS. DCA has been quite popular in community ecology, but Minchin (1987) found a lack of robustness and erratic performance of DCA as compared to NMS. Habitat variables were superimposed on the resulting ordinations using a joint plot, based on the correlations of those variables with the axes of the community ordination. For DCA, variance explained was expressed by the coefficient of determination between Euclidian distances in the ordination space and the Relative Euclidian distances in the original species space (McCune & Mefford 1999).

To identify and depict characteristic species groups for different forest types and height zones ordination of species by DCA after Beals smoothing was used. As widespread species having a wide ecological amplitude in the analysis are ordinated to the metric centre of their distribution range, the results should be interpreted with caution using the absolute figures provided in Table 2.

Finally, species indicator values (IV) for different forest types were calculated based on abundance and faithfulness values of species (Dufrene & Legendre 1997). Species indicator values were tested for statistical significance using a Monte Carlo procedure with 1000 replicates.

Results

Species diversity

In total, 168 species (60 of lichen, 67 of hepatic, 41 of moss) were found in 437 relevés taken on 15 trees in PF, ESF and LSF (Tab. 5-3). More than 90 % of the species could be fully identified. Relative abundance of a species in each forest type or in height zone within forest type is shown in Table 5-2.

Table 5-3. Species diversity overall and broken down by taxonomic groups and forest types. Beta diversity was measured as the total number of species divided by the average number of species. S.D. = standard deviation.

Group (sample size)	Average species richness per relevé (S.D.)	Beta diversity	Total number of species
Overall (437)			
Hepatics	6.0 (2.4)	11.2	67
Mosses	2.3 (1.5)	17.8	41
Lichens	2.5 (2.3)	24.0	60
Bryophytes + Lichens	10.7 (4.4)	15.7	168
Primary Forest - PF (177)			
Hepatics	4.8 (2.3)	8.3	40
Mosses	2.2 (1.1)	9.5	21
Lichens	2.7 (2.4)	14.4	39
Bryophytes + Lichens	9.7 (3.7)	10.3	100
Early secondary forest – ESF (76)			
Hepatics	7.4 (2.5)	4.6	34
Mosses	2.1 (1.9)	10.0	21
Lichens	2.4 (2.2)	13.3	32
Bryophytes + Lichens	11.8 (5.7)	7.4	87
Late secondary forest – LSF (184)			
Hepatics	6.5 (2.0)	7.7	50
Mosses	2.5 (1.5)	9.6	24
Lichens	2.3 (2.3)	13.9	32
Bryophytes + Lichens	11.3 (4.3)	9.4	106

In total, 100 species were found in PF, 87 in ESF and 106 in LSF. In all the three forest types hepatics were the species-richest group followed by lichens and mosses. Fig. 5-3 shows species-accumulation curves of randomly pooled relevés from the three forest types. Total species richness was remarkably similar in the three forest types, with highest numbers found in LSF and lowest in ESF (Tab. 5-3).

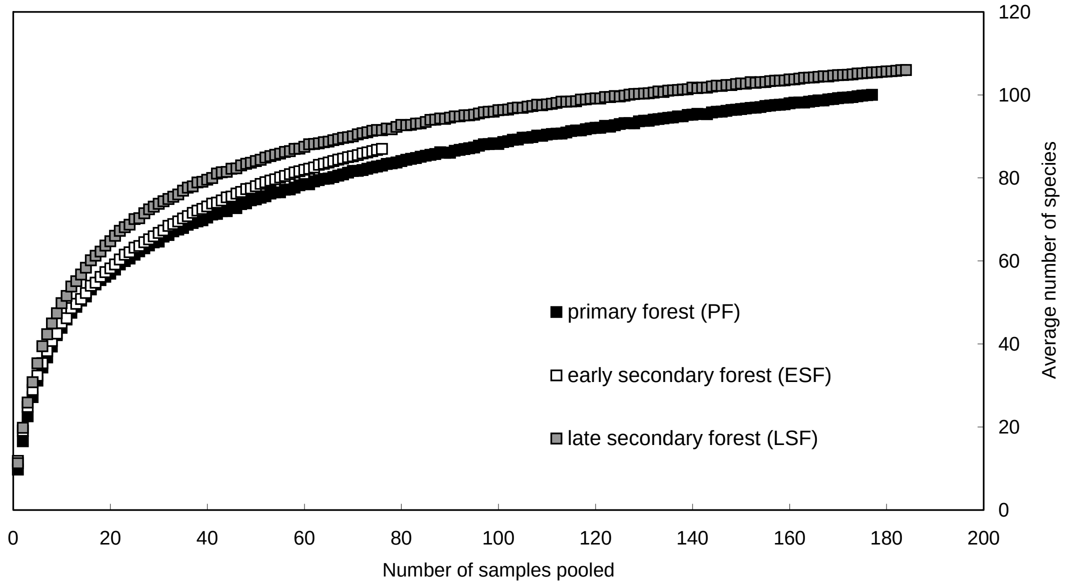

Fig. 5-3. Species-accumulation curves (rarefaction) of cryptogamic epiphyte relevés taken from primary forest (PF), early secondary forest (ESF) and late secondary forest (LSF).

With 36 different families the primary forest is the most diverse of the studied forests, followed by the late secondary forest (34 families) and the early secondary forest (30 families). Distribution of species over families is very similar in all forest types (Fig. 5-3). *Lejeuneaceae* (liverworts), *Parmeliaceae* (lichens), *Plagiochilaceae* (liverworts), *Lobariaceae* (lichens), *Physciaceae* (lichens), *Jubulaceae* (liverworts) and *Orthotrichaceae* (mosses) are the species-richest families. *Collemataceae* (lichens) replace the Jubulaceae in the early secondary forest in terms of species richness.

In the primary forest, *Parmeliaceae* (with the genus *Hypotrachyna*) are the most specious family, being replaced by *Lejeuneaceae* in the secondary forest. The species richest family of mosses in all forest types are the *Orthotrichaceae* (incl. *Macromitriaceae*).

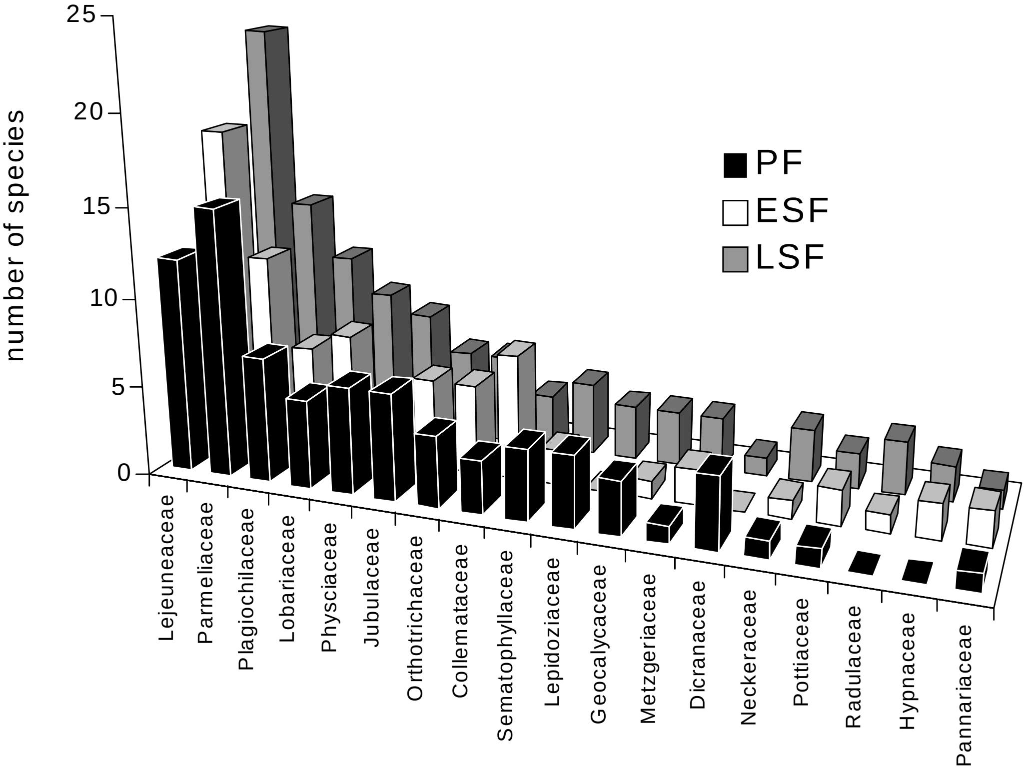

Fig. 5-4. Number of species in lichen, hepatic and moss families within the studied forest types.

Species richness per relevé is variable (Tab. 5-3), with a mean of 10.7 species (6.0 of hepatic, 2.5 of lichen and 2.3 of moss) and a high standard deviation (4.4). Average number of species per relevés is highest in ESF and lowest in PF. Hepatics are the richest group in all zones and in all forest types (Fig. 5-6). Trunks in ESF and the inner canopy of LSF are the species-richest zones, followed by the outer canopy in LSF and PF, and lower twigs in the ESF (Figs. 5-5, 5- 6).

In PF number of species on tree bases, trunks and inner canopy are very similar and are lower than in the outer canopy, which is the richest zone both in terms of species per relevé and total number of species. Tree base in PF had the lowest number of species per relevé.

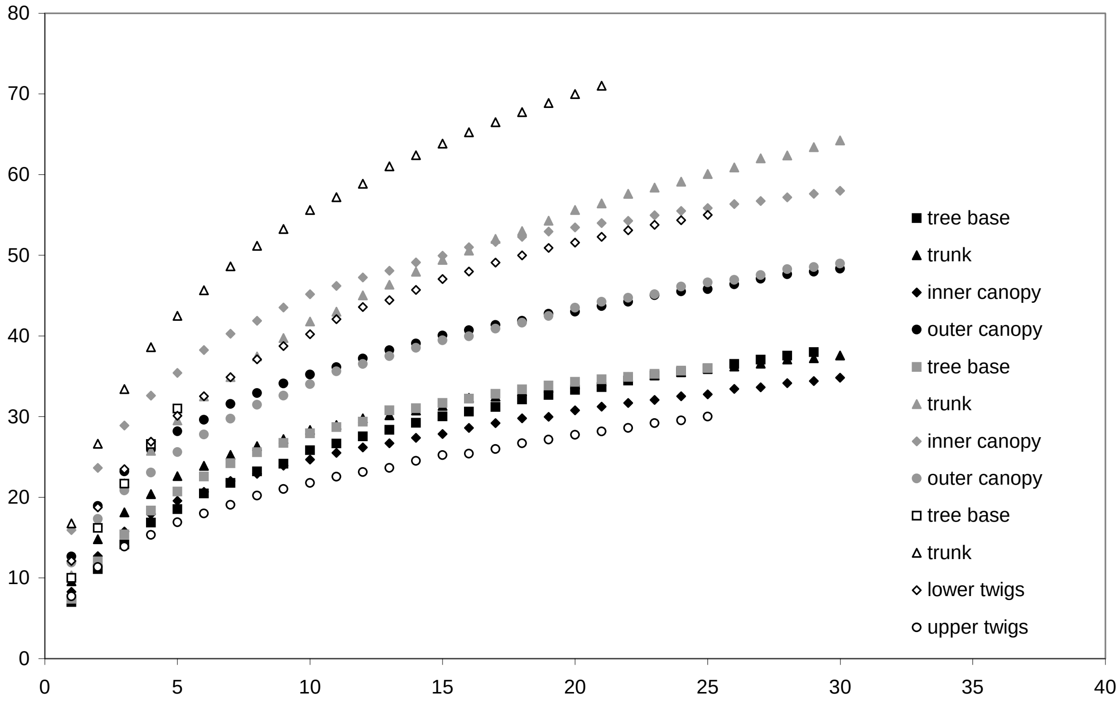

Fig. 5-5. Species-accumulation curves (rarefaction) of relevés taken within different height zones in the primary forest (PF: black symbols), early secondary forest (ESF: white symbols) and late secondary forest (LSF grey symbols).

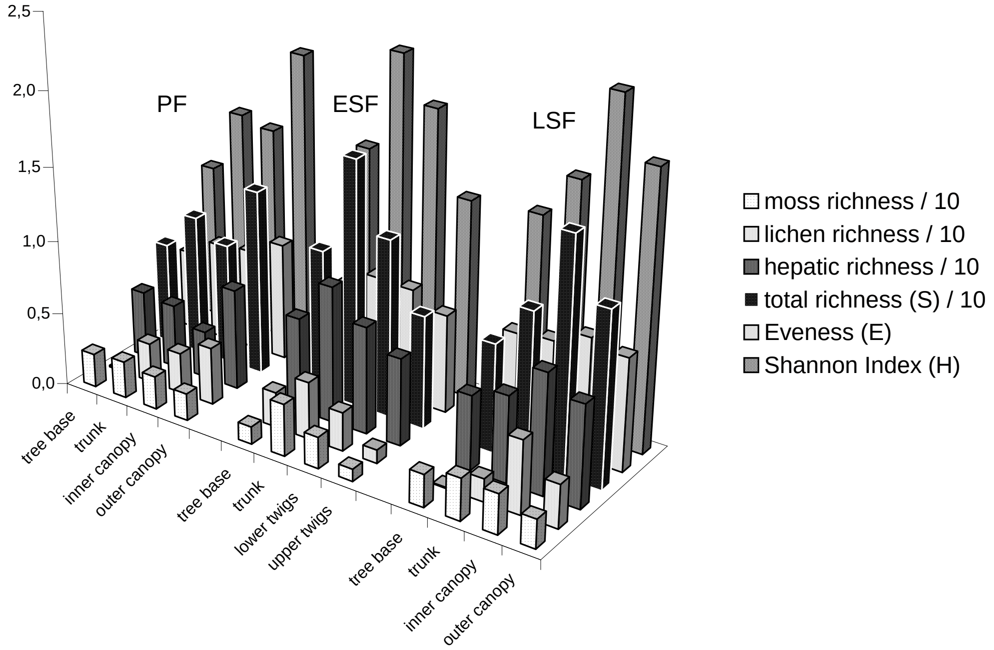

Fig. 5-6. Mean species richness, evenness and Shannon diversity Index per relevé within different height zones in the primary forest (PF), early secondary forest (ESF) and late secondary forest (LSF).

In ESF tree trunks are richest in species, both in total number and number per relevé. More than 80 % of the species in ESF were found on trunks. Lower twigs are the second most rich habitat and upper twigs are the poorest, being the youngest and most rapidly growing portions of the trees. Number of hepatics is very high and contributes to more than 60 % of species recorded per relevé and 40 % of species found in this forest type.

In LSF highest total number of species is found on the trunk and highest number per relevé in the inner canopy. Tree base in LSF are poorest both with regard to total number of species and number per relevé.

It thus appears that diversity in terms of total number of species and number of species per relevé is lowest on trunk in the ESF and highest in the outer canopy of PF. Species turnover rates, as measured by beta diversity, are different for lichens, hepatics and mosses and are highest for lichens, both overall and broken down by forest type (Table 5-3). Overall beta diversity of epiphytic cryptogams is very high (15.7), reflecting the wide range of habitats sampled.

Table 5-4. Habitat preferences of cryptogamic epiphyte species only found in one of the studied forests.

	No.	%
Species only found in the PF	**46**	
Tree base	14	30
Trunk	9	20
Inner canopy	15	33
Outer canopy	8	17
Species only found in the ESF	**10**	
Tree base	3	30
Trunk	4	40
Inner canopy	3	30
Outer canopy	0	0
Species only found in the LSF	**26**	
Tree base	7	27
Trunk	15	57
Inner canopy	2	8
Outer canopy	2	8

Although total number of species in PF is relatively low compared to the two secondary forest types (Figs. 5-3, 5-5), PF has the highest number of species exclusive to one forest type (46 % of all species in PF; 27 % of all species found; Tab. 5-4). Exclusive species of PF are distributed over all height zones with highest numbers on the tree base (14 species) and in the inner canopy (15 species). On the other hand, 68 species (40 % of all species found) are not found in PF. Of these, 26 are restricted to LSF and 10 to ESF.

Community composition of epiphytes

Multi-response permutation procedure analysis (MRPP) revealed no significant difference between the relevés from each of the five *Quercus copeyensis* trees in PF, in ESF or in LSF (Tab. 5-5). In contrast, differences between the three forest types (A = 0.24), height zones of forest types (A > 0.4) and height zones within each forest type (A > 0.3) were marked (Tab. 3). Chance-corrected within-group agreement (A) for the comparison of community composition in height zones showed significant differences between height zones except for inner and outer canopy of LSF and lower twigs and upper twigs of ESF (A > 0.10; Tab. 5-6).

Table 5-5. Comparison of differences in epiphyte community composition using non-metric MRPP, based on Sørensen distances. G = number of habitats in habitat group; A = chance-corrected within-group agreement; p = probability of Type I error for H_0: no difference between groups.

Habitat group	G	A (raw data)	P
Trees in PF	5	0.03	$< 10^{-8}$
Trees in LSF	5	0.03	$< 10^{-8}$
Trees in ESF	5	0.09	$< 10^{-7}$
Forest (PF, ESF, LSF)	3	0.24	$< 10^{-8}$
Tree base (PF, ESF, LSF)	3	0.47	$< 10^{-8}$
Trunk (PF, ESF, LSF)	3	0.43	$< 10^{-8}$
Inner canopy (PF, ESF, LSF)	3	0.51	$< 10^{-8}$
Outer canopy (PF, ESF, LSF)	3	0.45	$< 10^{-8}$
Height zones in PF	4	0.47	$< 10^{-8}$
Height zones in ESF	4	0.47	$< 10^{-8}$
Height zones in LSF	4	0.33	$< 10^{-8}$

Table 5-6. Comparison of differences in epiphyte community composition within height zones using non-metric MRPP, based on Sørensen distances; A = chance-corrected within-group agreement; p < 0.001 for all values (p = probability of Type I error for H_0: no difference between groups).

	Tree base	Trunk	Inner Canopy
	PF		
Trunk	0.18	-	-
Inner canopy	0.34	0.21	-
Outer canopy	0.38	0.42	0.30
	ESF		
Trunk	0.16	-	-
Inner canopy	0.46	0.29	-
Outer canopy	0.39	0.42	0.10
	LSF		
Trunk	0.25	-	-
Inner canopy	0.29	0.19	-
Outer canopy	0.25	0.31	0.06

DCA after Beals smoothing separates between forest types and relative height of relevés on the tree (Fig. 5-7). PF relevés are grouped by: i) tree base, ii) trunk and inner canopy, and iii) outer canopy; LSF relevés by: i) tree base, ii) trunk, and iii) inner and outer canopy. ESF relevés are not as clearly grouped and are closely related to relevés from outer canopy, inner canopy and trunks of LSF. Outer canopy relevés of PF, inner and outer canopy relevés of LSF and twig relevés of ESF are also similar.

The above results are corroborated with less robust support by DCA performed on raw data (not presented). Thus, the first three axes explained 39 % of the community variation in DCA of raw data and 91 % after Beals smoothing (Fig. 7). The first axis explaining 25 % of variation using raw data and 75 % after Beals smoothing, was closely related to stem diameter and percent of total cover, the second on (11 % resp. 17 %), shows highest correlations with absolute and relative height of relevé in the tree. The third axis (not shown), explaining 3 % of variation of raw data and only 1 % after Beals smoothing, has a similar effect on seperation of the relevés like the second one, but emphasizes more the difference between tree base and the rest of the tree than showing a continuous gradient from the tree base to the outer canopy. Correlation of the third axis is higher with absolute height than with relative height of relevé in the tree.

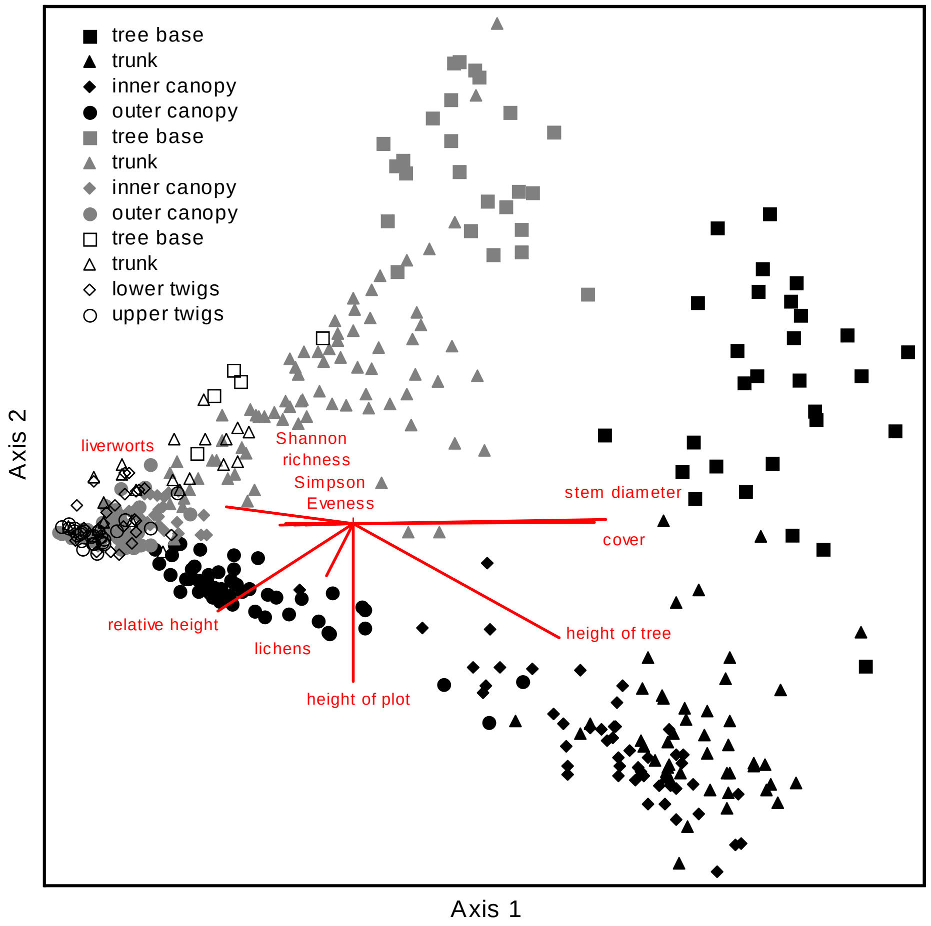

Fig. 5-7. Ordination of relevés in epiphyte species space using DCA after Beals smoothing. Symbols indicate height zones in the different forest types where relevés were taken. Primary forest (PF): black symbols, Early secondary forest (ESF): white symbols, Late secondary forest (LSF): grey symbols.

In NMS ordination of raw cover data (Fig. 5-8), forest stands are separated along the first axis and height zones along the third axis, like in DCA ordination. The first axis shows a high correlation with tree height (separating the three forest types), the third one a high correlation with relative height of relevés in the tree.

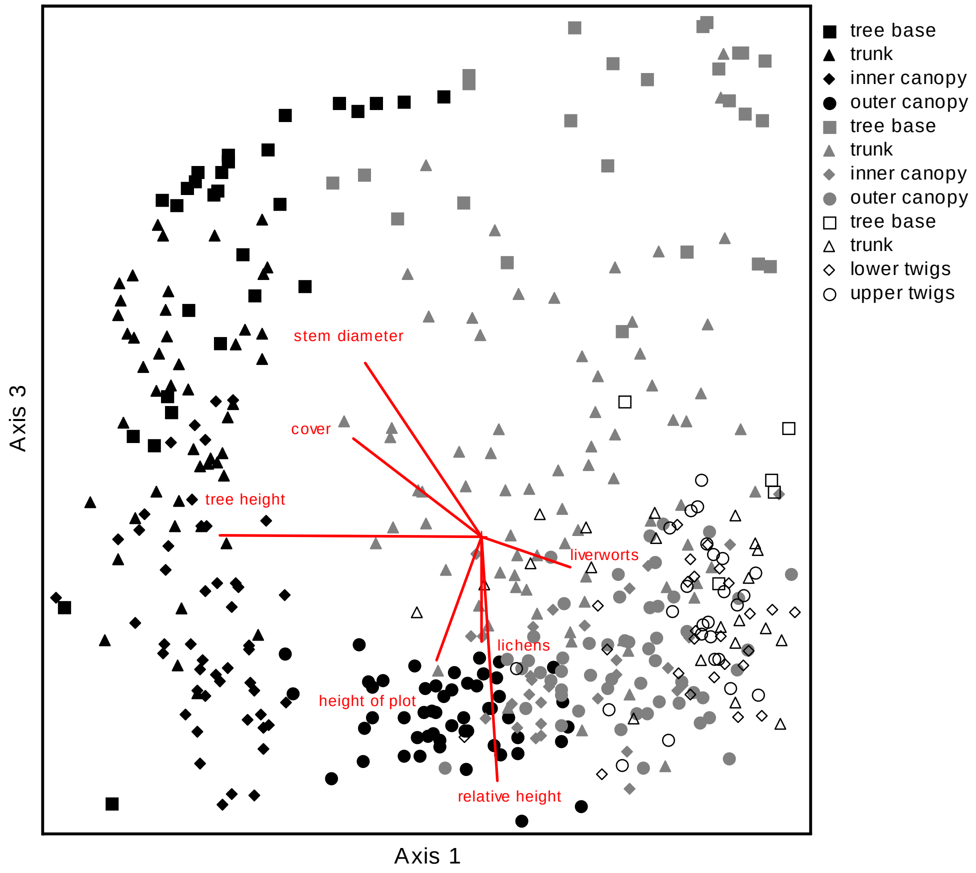

Fig. 5-8. Ordination of relevés in epiphyte species space (raw cover data) using NMS. Symbols indicate height zones in the different forest types where relevés were taken. Primary forest (PF): black symbols, Early secondary forest (ESF): white symbols, Late secondary forest (LSF): grey symbols.

Ecological species groups and indicator species

Ecological species groups and indicator species of forest types and height zones, determined using ordination of species by DCA after Beals smoothing and calculation following Dufrene & Legendre (1997), are shown in Figure 9 and Table 2. It should be pointed out that results are only valid for the investigated forest types and that indicator species may also be common in other habitats of on host trees other than *Quercus copeyensis*. Species with highest calculated indicator values (IV's)for the three forest types are the following (in order of decreasing IV's):

i) Species with highest indicator values for PF: *Leptodontium exasperatum, Frullania brasiliensis, Plagiochila heterophylla, Zygodon ehrenbergii, Dicranodontium meridionale, Hypotrachyna imbricatula, Bunodophoron melanocarpum, Herbertus divergens, Hypotrachyna physcioides* and *Holomitrium pulchellum*.

ii) Species with highest indicator values for ESF: *Microlejeunea bullata, Daltonia longifolia, Metzgeria liebmanniana, Metzgeria agnewii, Brachiolejeunea laxifolia, Heterodermia leucomela, Diplasiolejeunea replicata, Frullania ecklonii* and *Plagiochila bicuspidata*. They are typically pioneer species and may also occur in LSF or (some) in the outer canopy of PF.

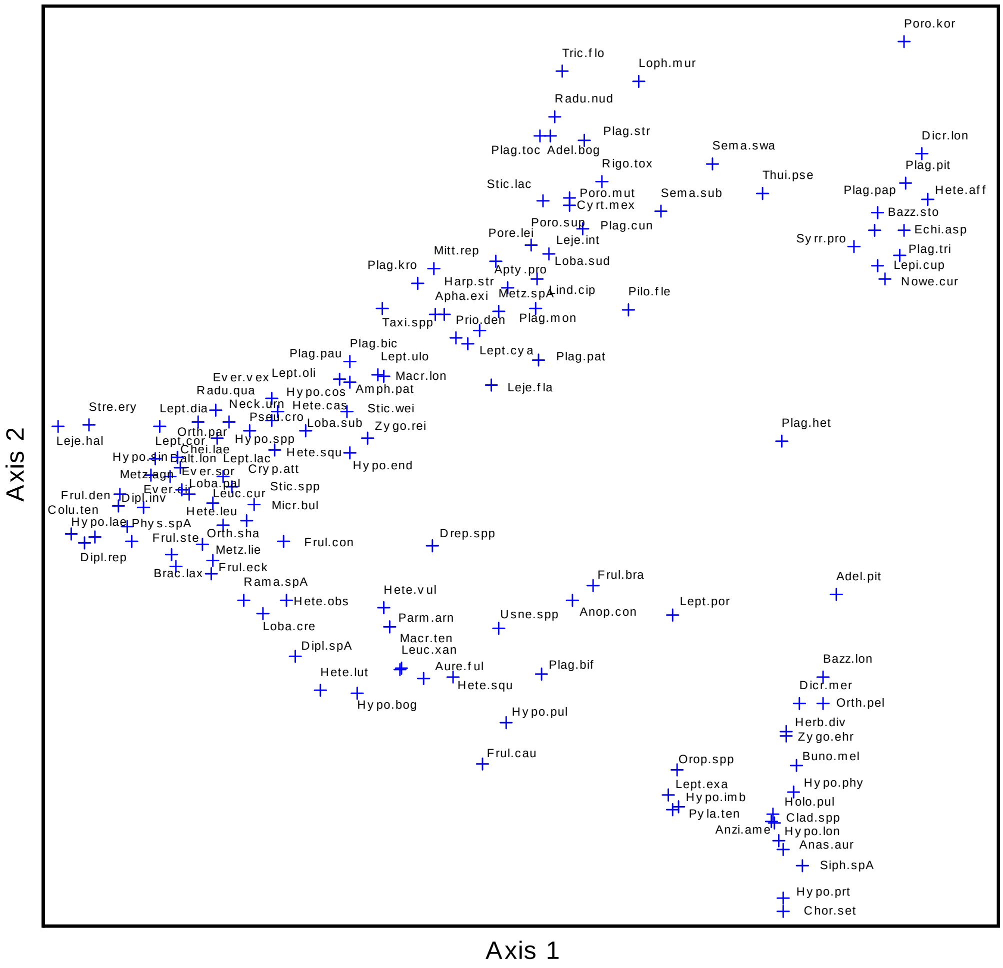

Fig. 5-9. Ordination of species in the epiphyte species space using DCA after Beals smoothing. For acronyms of species see Tab. 5-2.

iii) Species with highest indicator values for LSF: *Lejeunea intricata, Zygodon reinwardtii, Plagiochila patzschkei, Aptychella proligera, Metzgeria spec. A, Hypotrachyna costaricensis, Porotrichum mutabile, Frullania stenostipa* and *Lejeunea flava*. Most of these species can also be found in ESF.

Bark pH

Bark pH decreases significantly with age of tree (Tab. 7) and is paralleled by decreasing pH values with height in the tree in PF (see Chapter 4).

Table 5-7. pH of bark samples of *Quercus copeyensis* from about 2 m above ground. S.D. = standard deviation.

N = 5 x 2 = 10	PF	ESF	LSF
Average	4.1	5.1	4.5
S.D.	0.1	0.15	0.1

Discussion

Species diversity

Recent studies have shown that species richness of epiphytes (vascular, non-vascular) in secondary forests is normally reduced as compared to primary forests (e.g., Turner et al. 1994, Barthlott et al. 2001, Acebey et al. 2002, Costa 1999). However, Kappelle et al. (1995) recorded more vascular plant species (trees, shrubs, herbs) in the secondary than in the primary oak forests of the Cordillera de Talamanca studied here, indicating that forest degradation does not always lead to reduction of plant species richness. The increased diversity in the secondary forest was largely due to down-slope migration of species of the adjacent páramo vegetation. Our results were in agreement with those of Kappelle (l.c.) and revealed that total species richness of cryptogamic epiphytes in secondary and primary forest were nearly the same (with even slightly higher numbers of species being recorded from the secondary forests, Fig. 5-3), in spite of the large differences in tree height and forest structure between the three forest types (Tab. 5-1). Like in vascular plants, many of the cryptogamic epiphyte species found in the investigated secondary forest stands are common in the adjacent páramo vegetation where they occur primarily on twigs and branches of shrubs (Gradstein & Holz, in press).

Previous studies reporting loss of diversity in secondary forests usually focused on secondary forest stands with a more open canopy or compared primary forests with remnant trees in pastures. Opening-up the canopy leads to loss of shade epiphytes, which are adapted to growth in the moist, shaded understorey of the forest (e.g. Gradstein 1992, Hietz-Seifert et al. 1996, Acebey et al. 2003). Loss of shade epiphytes was not observed in the secondary forests investigated in this study. Presumably, the high species richness of these secondary forests is due to their closed canopy, resulting in permanently high atmospheric humidity in these forests. The shadier conditions in this microhabitat are also reflected by its richness in hepatics (Fig. 5-6). In fact, the canopy of LSF was denser and the understorey more shaded than that of PF (Tab. 5-1, Fig. 5-1).

Closed-canopy secondary forests are a common phenomenon in secondary forest succession after clearing of Talamancan upper montane oak forests.

Genera and species exclusive to primary forests are crucial for the purpose of conservation. In present study, species restricted to the primary forest were found in any height zone and not predominantly in shady understorey habitats (Tab. 5-4). Tree bases and large branches of the inner canopy of the primary forest are microhabitats, that need much time to develop their special substrate and microclimatic conditions necessary for the establishment of adapted species. This should be respected, when management practices are sought to increase, restore or maintain biodiversity.

Like species richness, alpha diversity increases with height in the tree in the primary forest and is slightly higher in secondary forest than in primary forest (Figs. 5-6, 5-7). Alpha diversity is highest on trunks and lower twigs in ESF and in the outer canopy of LSF and PF. These habitats correspond with the ‘light transition zone’, represented by the range of heights in which abrupt transitions in light transmittance by the canopy occur (McCune et al. 1997). Alpha diversity is lowest in the more shady, “older” habitats such as tree bases and trunks of LSF and tree bases, trunks and big branches of inner canopy of PF, where the cryptogamic epiphyte vegetation is dominated by rough mats or large turfs of *Bazzania* spp., *Hypotrachyna* spp., *Herbertus divergens* etc. The observations on alpha diversity in PF agree with those of Wolf (1995) who found that alpha diversity of cryptogamic epiphytes in mature montane cloud forests of Colombia decreased with increased age (as expressed by increased diameter) of canopy branches.

Beta diversity, measured as the total number of species in a forest type divided by the average number of species per relevé (Tab. 5-3) shows that hepatics are more evenly distributed in the forest than mosses and, especially, lichens. A sparser distribution of lichens, as compared with bryophytes, has also been observed in tropical lowland forest (Montfoort & Ek 1990, Gradstein 1992) and may therefore be a characteristic feature of tropical rain forests in general.

Cryptogamic epiphytes as indicator species of primary and secondary forests

Species that give clues about the state of an ecosystem are known as indicator species, because they indicate the conditions within the local environment. Epiphytic cryptogams are of great value as ecological indicator species in tropical forest ecosystems (Hietz 1999, Gradstein et al. 2001). Because they do not grow in random fashion, different taxa are found on tree bases, trunks, branches, twigs in the outer canopy, shrubs, living leaves, soil, or on logs in various stages of decay. In most cases their distribution reflects microclimatic and substrate conditions of their microhabitat (Pócs 1982, Richards 1984, Gradstein 1992, Holz et al. 2002, see Chapter 3 and 4).

Floristic changes due to deforestation may be large, depending on the amount and type of damage inflicted upon the forest. Clearcutting results in the immediate loss of epiphytic cryptogams, while selective logging will change forest structure and microclimatic conditions. After secondary forest regeneration on clearcut areas or in plantations (and agroforest ecosystems) at least part of the species may return. The resulting distribution patterns of cryptogamic epiphytes and their communities are diverse, reflecting the progress and speed of succession. If we use cryptogamic epiphytes as indicators of forest disturbance we should keep in mind that these patterns do not directly reflect the type and amount of damage, but rather the microclimatic and substrate conditions in their secondary microhabitat. Generalizations may be misleading, as there are many different kinds of primary forests (differing in structure, climate, etc.) and the richness of cryptogamic epiphytes varies considerably within and between these forests (Gradstein et al. 2001).

The following trends in species distribution can be observed when comparing primary and secondary forest (Tab. 5-2): (1) the species disappears from the forest, (2) the species changes the microhabitat (to compensate for new microclimatic conditions or physical or chemical changes of substrate), (3) the species will be restricted to fewer microhabitats (smaller ecological amplitude), (4) the species will be more widely distributed in different microhabitats (wider ecological amplitude), and (5) new species will be found in the forest. (1) and (5) may be interpreted as special cases of (3) and (4), respectively.

Recovery of cryptogamic epiphyte communities after forest clearance

Chapman & King (1983) showed that in subtropical rain forests of Australia only few bryophyte species were able to return after 25 years and Norris (1987) reported that the bryophyte flora of old-growth secondary forests and of primary forest in North Carolina showed differences even 100 years after cutting of the primary forest. Recently, Acebey et al. (2003) found that about half of the rain forest species, especially liverworts, may re-establish in 10-15 years old fallows in submontane areas of Bolivia. To date, however only few studies dealt with the question how cryptogamic epiphyte communities fit into the secondary succession of tropical rain forests and none of them covered montane or upper montane forests.

Although species richness is high in the secondary forests (both ESF and LSF) studied here, the rate of floristic recovery as expressed by floristic similarity to the primary forest is relatively slow. Similarity in species composition in secondary forests compared to the primary forest increases with age, but still after 40 years of forest succession one third (46 species = 46 %) of primary forest species of cryptogams were not found in the secondary forest. On the contrary, 40 % (68 species) of all species recorded were restricted to secondary forest, which shows the important contribution of secondary forests to total species diversity in the Talamancan oak forests. In order to maintain high cryptogamic biodiversity, management practices maintaining all successional stages of these forests should thus be adopted.

Kappelle et al. (1996) estimated about 85 years as the minimum time needed for structural recovery of upper montane oak forests following clearing. This estimation was based on the development of basal area of trees and canopy height using linear regressions. As the oldest secondary forest included in the calculation was less than 35 years old, the estimation is not very robust and it remains unanswered if all characteristics of the different microhabitats of the forest will recover within this time. The high number of cryptogamic species only found in the primary forest suggests that complete recovery of microhabitat and species diversity requires more than 85 years. We suggest that at least hundred years are needed for the complete recovery of the floristic and community composition and possibly centuries if the recovery follows non-linear trends. Predicting how similar the non-vascular epiphyte vegetation of the mature secondary forest will be compared to the original primary forest remains difficult and requires more work on the reproductive biology of the species (local epiphyte propagule supply, fragments from which species regenerate), their physiological ecology and competition for resources. Future sampling of cryptogamic epiphyte communities in over 40 years old secondary forests would be needed in order to better understand long-term trends in secondary succession in the montane oak forests of Costa Rica.

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Table 5-2. Relative abundance in a group of relevés and Indicator Values (IV) of cryptogamic epiphytes in primary and secondary upper montane *Quercus* forest of Costa Rica. Abundance of a species in a group of relevés over its abundance in all relevés expressed as %. **N** = total number of samples (plots) or observations of a species. MaxGroup = forest type with highest number of observations. p = statistical significance of Indicator Value using a Monte Carlo test with 1000 replicates. PF= primary forest, ESF = early secondary forest, LSF = late secondary forest.

			PF					**ESF**					**LSF**					**Indicator Value (IV)**			
			total	tree base	trunk	inner canopy	outer canopy	**total**	tree base	trunk	lower twigs	upper twigs	**total**	tree base	trunk	inner canopy	outer canopy	**MaxGroup**	% of perfect indication	Monte Carlo Test	significance
Taxon	acronym	***N***	***177***	***29***	***48***	***48***	***52***	***76***	***5***	***21***	***25***	***25***	***184***	***25***	***76***	***30***	***53***		IV	p	
Adelothecium bogotense (Hampe) Mitt.	Adel.bog	***6***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	37	63	0	0	**LSF**	3,3	0,037	*
Adelanthus decipiens (Hook.) Mitt.	Adel.dec	***1***	**100**	0	100	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,581	
Adelanthus pittieri (Steph.) Grolle	Adel.pit	***22***	**100**	35	65	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	12,4	0,001	**
Amphilejeunea patellifera (Spruce) R.M.Schust.	Amph.pat	***79***	**1**	0	0	1	1	**42**	23	35	1	0	**57**	0	34	6	1	**LSF**	16,4	0,004	**
Anastrophyllum auritum (Lehm.) Steph.	Anas.aur	***24***	**100**	0	26	74	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	13,6	0,001	**
Anoplolejeunea conferta (C.F.W.Meissn.) A.Evans	Anop.con	***147***	**23**	0	7	2	14	**27**	17	18	3	1	**50**	2	31	4	0	**LSF**	13,2	0,731	
Anzia americana Yoshim. & Sharp	Anzi.ame	***24***	**99**	9	52	39	0	**1**	0	1	0	0	**0**	0	0	0	0	**PF**	12,9	0,001	**
Aphanolejeunea exigua A.Evans	Apha.exi	***26***	**0**	0	0	0	0	**91**	0	86	2	0	**9**	8	1	0	3	**ESF**	13,2	0,001	**
Aptychella proligera (Broth.) Herzog	Apty.pro	***52***	**0**	0	0	0	0	**4**	0	3	1	0	**96**	36	60	0	0	**LSF**	23,5	0,001	**
Aureolejeunea fulva R.M.Schust.	Aure.ful	***22***	**69**	0	0	0	70	**0**	0	0	0	0	**31**	0	17	12	0	**PF**	6,6	0,011	*
Bazzania longistipula (Lindenb.) Trevis.	Bazz.lon	***19***	**100**	1	99	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	10,7	0,001	**
Bazzania stolonifera (Sw.) Trevis.	Bazz.sto	***39***	**87**	82	2	0	0	**0**	0	0	0	0	**13**	15	0	0	0	**PF**	17,7	0,001	**
Blepharolejeunea incongrua (Lindenb. & Gottsche) Slageren & Kruijt	Blep.inc	***1***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	100	0	0	**LSF**	0,5	1	
Brachiolejeunea laxifolia (Taylor) Schiffner	Brac.lax	***143***	**9**	0	0	1	8	**45**	0	22	13	6	**45**	0	4	23	24	**ESF**	26,9	0,001	**
Bryum billarderii Schwägr.	Bryu.bil	***1***	**0**	0	0	0	0	**100**	0	100	0	0	**0**	0	0	0	0	**ESF**	1,3	0,175	
Bunodophoron melanocarpum (Sw.) Wedin	Buno.mel	***53***	**100**	1	61	38	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	29,9	0,001	**
Cheilolejeunea laevicalyx (J.B.Jack & Steph.) Grolle	Chei.lae	***5***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	91	0	9	**LSF**	2,7	0,063	
Chorisodontium setaceum (E.B.Bartram) E.B.Bartram	Chor.set	***4***	**100**	0	0	100	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	2,3	0,052	
Cladonia spp.	Clad.spp	***17***	**100**	0	13	87	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	9,6	0,002	**
Colura tenuicornis (A.Evans) Steph.	Colu.ten	***34***	**0**	0	0	0	0	**28**	0	4	2	20	**72**	0	0	0	74	**LSF**	7,1	0,069	*
Cryphaea attenuata Schimp.	Cryp.att	***58***	**4**	0	0	0	3	**38**	8	15	14	0	**58**	0	11	35	14	**LSF**	11	0,02	*
Cyclodictyon albicans (Hedw.) Kuntze	Cycl.alb	***1***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	100	0	0	0	**LSF**	0,5	1	
Cyrto-hypnum mexicanum (Mitt.) W.R.Buck & H.A.Crum	Cyrt.mex	***7***	**0**	0	0	0	0	**50**	75	0	0	0	**50**	18	5	2	0	**LSF**	1,6	0,363	

Table 5-2 (cont'd).

Taxon	acronym		PF					ESF					LSF					Indicator Value (IV)			
			total	tree base	trunk	inner canopy	outer canopy	**total**	tree base	trunk	lower twigs	upper twigs	**total**	tree base	trunk	inner canopy	outer canopy	**MaxGroup**	% of perfect indication	Monte Carlo Test	significance
Daltonia longifolia Taylor	Dalt.lon	***127***	**0**	0	0	0	0	**69**	0	34	23	8	**30**	0	4	16	14	**ESF**	43,8	0,001	**
Dicranodontium longisetum (Hook.) R.S.Williams	Dicr.lon	***14***	**100**	100	0	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	7,9	0,001	*
Dicranodontium meridionale E.B.Bartram	Dicr.mer	***60***	**98**	5	73	19	1	**0**	0	0	0	0	**2**	1	1	0	0	**PF**	32,2	0,001	**
Dictyonema glabratum (Spreng.) D.L.Hawksw.	Dict.gla	***1***	**100**	0	0	0	100	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,575	
Diplasiolejeunea involuta S.Winkl.	Dipl.inv	***14***	**0**	0	0	0	0	**71**	0	10	26	26	**29**	0	3	22	12	**ESF**	6,5	0,001	**
Diplasiolejeunea replicata (Spruce) Steph.	Dipl.rep	***62***	**1**	0	0	0	0	**60**	0	13	24	16	**40**	0	0	18	29	**ESF**	20,4	0,001	**
Diplasiolejeunea spec. A	Dipl.spA	***71***	**79**	0	0	0	75	**8**	0	1	3	3	**13**	0	1	12	5	**PF**	17,4	0,001	**
Drepanolejeunea spp.	Drep.spp	***90***	**12**	1	10	0	0	**17**	0	8	3	2	**71**	0	0	45	31	**LSF**	17,4	0,004	**
Echinocolea asperrima (Spruce) R.M.Schust.	Echi.asp	***4***	**100**	89	11	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	2,3	0,052	
Erioderma granulosum	Erio.gra	***2***	**0**	0	0	0	0	**83**	0	0	81	0	**17**	0	0	0	19	**ESF**	1,1	0,253	
Erioderma mollissimum (Samp.) DR.	Erio.mol	***1***	**100**	0	0	0	100	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,558	
Everniastrum cirrhatum (E.Fr.) Hale ex Sipman	Ever.cir	***17***	**0**	0	0	0	0	**37**	0	0	20	10	**63**	0	7	31	32	**LSF**	4,5	0,053	
Everniastrum fragile Sipman	Ever.fra	***1***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	100	0	0	**LSF**	0,5	1	
Everniastrum sorocheilum (Vain.) Hale ex Sipman	Ever.sor	***15***	**0**	0	0	0	0	**81**	0	62	11	1	**19**	0	0	20	5	**ESF**	7,5	0,002	**
Everniastrum vexans (Zahlbr.) Hale ex Sipman	Ever.vex	***6***	**0**	0	0	0	0	**63**	0	58	5	0	**37**	0	16	20	1	**ESF**	2,5	0,108	
Frullania brasiliensis Raddi	Frul.bra	***211***	**67**	4	6	31	27	**7**	0	6	1	0	**26**	0	13	10	1	**PF**	46,8	0,001	**
Frullania caulisequa (Nees) Nees	Frul.cau	***3***	**100**	0	0	0	100	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	1,7	0,127	
Frullania convoluta Lindenb. & Hampe	Frul.con	***33***	**42**	0	0	3	39	**33**	0	11	21	0	**25**	0	8	12	7	**ESF**	5,2	0,236	
Frullania ecklonii (Spreng.) Spreng.	Frul.eck	***117***	**14**	0	0	0	13	**44**	7	19	15	3	**41**	0	6	20	18	**ESF**	18,1	0,006	**
Frullania stenostipa Spruce	Frul.ste	***106***	**11**	0	0	0	9	**35**	0	11	12	6	**55**	0	2	31	29	**LSF**	17,5	0,005	**
Frullanoides densifolia Raddi ssp. densifolia	Frul.den	***6***	**14**	0	0	0	12	**3**	0	0	3	0	**83**	0	17	45	24	**LSF**	1,8	0,274	
Harpalejeunea stricta (Lindenb. & Gottsche) Steph.	Harp.str	***28***	**0**	0	0	0	0	**21**	16	19	0	0	**79**	10	50	6	0	**LSF**	9,4	0,002	**
Herbertus divergens (Steph.) Herzog	Herb.div	***50***	**100**	26	40	34	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	27,1	0,001	**
Heterodermia casarettiana (Massal.) Trevis.	Hete.cas	***20***	**2**	0	0	0	1	**39**	40	14	0	0	**59**	0	8	33	4	**ESF**	4,1	0,125	
Heterodermia leucomela (Fée) Swinsc. & Krog	Hete.leu	***144***	**14**	0	0	0	12	**42**	0	20	14	3	**44**	0	7	28	16	**ESF**	21,7	0,006	**
Heterodermia lutescens (Koruk.) Follm. & Redon	Hete.lut	***11***	**100**	0	0	0	100	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	6,2	0,001	**

Table 5-2 (cont'd)

Taxon	acronym		PF					ESF					LSF					Indicator Value (IV)		
			total	tree base	trunk	inner canopy	outer canopy	**total**	tree base	trunk	lower twigs	upper twigs	**total**	tree base	trunk	inner canopy	outer canopy	**MaxGroup**	% of perfect indication	Monte Carlo Test significance
Heterodermia obscurata (Nyl.) Trev.	Hete.obs	*4*	**61**	0	0	0	46	**0**	0	0	0	0	**39**	0	0	54	0	**PF**	0,7	0,672
Heterodermia squamulosa (Degel.) W.Culb.	Hete.squ	*5*	**78**	0	0	26	57	**0**	0	0	0	0	**22**	0	17	0	0	**LSF**	3,3	0,043 *
Heterodermia spec. A	Hete.spA	*6*	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	34	66	0	**PF**	1,8	0,195
Heterodermia vulgaris (Vain.) Follmann & Redon	Hete.vul	*3*	**28**	0	0	29	0	**72**	0	66	0	6	**0**	0	0	0	0	**ESF**	1,9	0,085
Heterophyllium affine (Hook.) M.Fleisch.	Hete.aff	*9*	**100**	90	10	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	5,1	0,006 **
Holomitrium pulchellum Mitt.	Holo.pul	*42*	**100**	0	36	61	3	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	23,7	0,001 **
Hypnum amabile (Mitt.) Hampe	Hypn.ama	*1*	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	100	0	0	**LSF**	0,5	1
Hypotrachyna bogotensis (Vain.) Hale	Hypo.bog	*4*	**100**	0	0	0	100	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	2,3	0,044 *
Hypotrachyna costaricensis (Nyl.) Hale	Hypo.cos	*43*	**0**	0	0	0	0	**3**	0	2	0	0	**97**	0	24	67	7	**LSF**	22,2	0,001 **
Hypotrachyna densirhizinata (Kurok.) Hale	Hypo.den	*1*	**100**	0	0	100	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,602
Hypotrachyna ducalis (Jatta) Hale	Hypo.duc	*1*	**100**	0	100	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,621
Hypotrachyna endochlora (Leight.) Hale	Hypo.end	*3*	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	61	39	0	**LSF**	1,6	0,21
Hypotrachyna ensifolia (Kurok.) Hale	Hypo.ens	*1*	**100**	0	0	0	100	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,582
Hypotrachyna imbricatula (Zahlbr.) Hale	Hypo.imb	*56*	**100**	0	18	67	15	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	31,6	0,001 **
Hypotrachyna laevigata (Smith) Hale	Hypo.lae	*8*	**0**	0	0	0	0	**59**	0	0	37	18	**41**	0	0	0	45	**ESF**	1,5	0,394
Hypotrachyna longiloba (H.Magn.) Hale	Hypo.lon	*7*	**100**	0	52	48	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	4	0,01 *
Hypotrachyna monilifera (Kurok.) Hale	Hypo.mon	*2*	**100**	0	0	100	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	1,1	0,335
Hypotrachyna physcioides (Nyl.) Hale	Hypo.phy	*44*	**100**	0	51	49	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	24,9	0,001 **
Hypotrachyna prolongata (Kurok.) Hale	Hypo.pro	*2*	**100**	0	0	100	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	1,1	0,207
Hypotrachyna protoboliviana (Hale) Hale	Hypo.prt	*11*	**100**	0	50	49	1	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	6,2	0,002 **
Hypotrachyna pulvinata (Fée) Hale	Hypo.pul	*40*	**81**	0	5	10	66	**19**	0	19	0	0	**0**	0	0	0	0	**PF**	17,9	0,001 **
Hypotrachyna sinuosa (Smith) Hale	Hypo.sin	*18*	**0**	0	0	0	0	**25**	0	5	12	0	**75**	0	0	62	20	**LSF**	6,5	0,007 **
Hypotrachyna spp.	Hypo.spp	*23*	**0**	0	0	0	0	**100**	0	66	25	9	**0**	0	0	0	0	**ESF**	30,3	0,001 **
Iwatsukia jishibae (Steph.) N.Kitag.	Iwat.jis	*1*	**100**	100	0	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,568
Jamesoniella rubricaulis (Nees) Grolle	Jame.rub	*1*	**100**	0	0	100	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,578
Kurzia flagillifera (Steph.) Grolle	Kurz.fla	*1*	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	100	0	0	**LSF**	0,5	1

Table 5-2 (cont'd)

			PF					ESF					LSF					Indicator Value (IV)		
Taxon	acronym		**total**	tree base	trunk	inner canopy	outer canopy	**total**	tree base	trunk	lower twigs	upper twigs	**total**	tree base	trunk	inner canopy	outer canopy	**MaxGroup**	% of perfect indication	Monte Carlo Test significance
Lejeunea flava (Sw.) Nees	Leje.fla	***62***	**13**	2	1	0	9	**3**	7	1	0	0	**84**	38	34	7	0	**LSF**	17,3	0,003 **
Lejeunea halei H.Rob.	Leje.hal	***6***	**0**	0	0	0	0	**91**	0	48	42	0	**9**	0	0	0	10	**ESF**	6	0,002 **
Lejeunea intricata J.B.Jack & Steph.	Leje.int	***75***	**0**	0	0	0	0	**3**	1	2	0	0	**97**	72	26	0	0	**LSF**	36	0,001 **
Lejeunea phyllobola Nees & Mont.	Leje.phy	***1***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	0	100	0	**LSF**	0,5	1
Lepidozia cupressina (Sw.) Lindenb.	Lepi.cup	***27***	**100**	96	4	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	15,3	0,001 **
Lepicolea pruinosa (Taylor) Spruce	Lepi.pru	***1***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	100	0	0	**LSF**	0,5	1
Leptodontium ulocalyx (Müll.Hal.) Mitt.	Lept.ulo	***49***	**0**	0	0	0	0	**60**	0	37	27	0	**40**	0	28	6	1	**ESF**	15,1	0,003 **
Leptodontium exasperatum Cardot	Lept.exa	***96***	**100**	0	2	88	10	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	54,2	0,001 **
Leptogium burgessii (L.) Mont.	Lept.bur	***2***	**30**	0	0	0	32	**70**	0	0	68	0	**0**	0	0	0	0	**ESF**	0,9	0,652
Leptogium cochleatum	Lept.coc	***2***	**0**	0	0	0	0	**100**	0	0	100	0	**0**	0	0	0	0	**ESF**	2,6	0,027 *
Leptogium coralloideum (Mey. & Flot.) Vain.	Lept.cor	***23***	**3**	0	0	0	3	**64**	0	47	12	0	**33**	0	2	20	16	**ESF**	7,6	0,004 **
Leptogium cyanescens (Rabenh.) Körb.	Lept.cya	***5***	**0**	0	0	0	0	**80**	0	86	0	0	**20**	0	14	0	0	**ESF**	2,1	0,099
Leptogium diaphanum (Sw.) Nyl.	Lept.dia	***3***	**0**	0	0	0	0	**100**	0	96	4	0	**0**	0	0	0	0	**ESF**	3,9	0,01 **
Leptogium laceroides Bouly de Lesd.	Lept.lac	***26***	**14**	0	0	0	12	**59**	0	34	19	0	**27**	0	3	24	7	**ESF**	8,5	0,005 **
Leptogium olivaceum var. olivaceum (Hook.) Zahlbr.	Lept.oli	***3***	**0**	0	0	0	0	**100**	98	2	0	0	**0**	0	0	0	0	**ESF**	3,9	0,007 **
Leptoscyphus amphibolius (Nees) Grolle	Lept.amp	***2***	**26**	22	0	0	0	**0**	0	0	0	0	**74**	78	0	0	0	**LSF**	0,4	1
Leptoscyphus porphyrius (Nees) Grolle	Lept.por	***100***	**61**	1	10	49	6	**8**	1	8	0	0	**32**	3	22	0	0	**PF**	20,9	0,001 **
Leucobryum antillarum Schimp. ex Besch.	Leuc.ant	***1***	**100**	100	0	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,602
Leucodon curvirostris Hampe	Leuc.cur	***15***	**24**	0	0	25	0	**37**	0	8	24	0	**39**	0	6	20	17	**ESF**	1,9	0,664
Leucolejeunea xanthocarpa (Lehm. & Lindenb.) A.Evans	Leuc.xan	***35***	**59**	0	0	0	52	**15**	0	6	6	0	**26**	0	3	32	0	**PF**	7,4	0,037
Lindigianthus cipaconeus (Gottsche) Kruijt & Gradst.	Lind.cip	***11***	**2**	2	0	0	0	**19**	10	10	0	0	**80**	64	14	0	0	**LSF**	2,6	0,286
Lobaria crenulata (Hook. in Kunth) Trev.	Loba.cre	***31***	**27**	0	0	0	19	**34**	19	9	10	0	**39**	0	0	34	9	**ESF**	3,1	0,797
Lobaria pallida (Hook. in Kunth) Trevis.	Loba.pal	***3***	**0**	0	0	0	0	**44**	66	0	0	0	**56**	0	0	33	1	**LSF**	0,6	0,739
Lobaria subdissecta (Nyl.) Vain.	Loba.sud	***13***	**0**	0	0	0	0	**1**	6	0	0	0	**99**	8	86	0	0	**LSF**	6,4	0,002 **
Lobaria subexornata Yoshim.	Loba.sub	***18***	**7**	0	0	0	4	**77**	61	20	8	0	**16**	0	4	0	3	**ESF**	9,1	0,002 **
Lophocolea muricata (Lehm.) Nees	Loph.mur	***9***	**3**	2	0	0	0	**0**	0	0	0	0	**97**	97	0	0	0	**LSF**	3,7	0,043 *

Table 5-2 (cont'd)

			PF					**ESF**					**LSF**					**Indicator Value (IV)**			
Taxon	acronym		**total**	tree base	trunk	inner canopy	outer canopy	**total**	tree base	trunk	lower twigs	upper twigs	**total**	tree base	trunk	inner canopy	outer canopy	**MaxGroup**	% of perfect indication	Monte Carlo Test	significance
Macrocoma tenuis subsp. sullivantii (Müll.Hal.) Vitt	Macr.ten	***3***	**32**	0	0	0	31	**68**	0	69	0	0	**0**	0	0	0	0	**ESF**	0,9	0,684	
Macrolejeunea lancifolia (Steph.) Herzog	Macr.lan	***1***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	0	0	100	**LSF**	0,5	1	
Macromitrium longifolium (Hook.) Brid.	Macr.lon	***17***	**0**	0	0	0	0	**20**	0	24	0	0	**80**	0	57	18	0	**LSF**	7	0,003	**
Metzgeria agnewii Kuwah.	Metz.agn	***105***	**0**	0	0	0	0	**51**	0	26	8	8	**49**	0	1	37	21	**ESF**	33,9	0,001	**
Metzgeria liebmanniana Lindenb. & Gottsche	Metz.lie	***166***	**13**	0	0	0	11	**47**	7	22	7	9	**40**	0	1	26	17	**ESF**	38,3	0,001	**
Metzgeria spec. A	Metz.spA	***43***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	46	54	0	0	**LSF**	23,4	0,001	**
Microlejeunea bullata (Tayl.) Steph.	Micr.bul	***200***	**9**	0	0	0	9	**57**	0	27	14	12	**34**	0	4	13	20	**ESF**	51,4	0,001	**
Mittenothamnium reptans (Hedw.) Cardot	Mitt.rep	***8***	**0**	0	0	0	0	**27**	31	5	0	0	**73**	64	1	0	0	**LSF**	1,6	0,614	
Neckera urnigera Müll.Hal.	Neck.urn	***4***	**0**	0	0	0	0	**67**	0	74	0	0	**33**	0	20	0	6	**ESF**	0,9	0,528	
Nowellia curvifolia (Dicks.) Mitt.	Nowe.cur	***3***	**100**	100	0	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	1,7	0,122	
Omphalanthus filiformis (Sw.) Nees	Omph.fil	***1***	**0**	0	0	0	0	**100**	0	0	100	0	**0**	0	0	0	0	**ESF**	1,3	0,181	
Oropogon spp.	Orop.spp	***23***	**98**	0	26	65	6	**1**	0	0	0	0	**2**	0	0	3	0	**PF**	11	0,001	**
Orthodontium pellucens (Hook.) B.S.G.	Orth.pel	***4***	**100**	0	100	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	2,3	0,065	
Orthotrichum pariatum Mitt.	Orth.par	***16***	**0**	0	0	0	0	**11**	0	5	4	0	**89**	0	18	44	29	**LSF**	6,8	0,011	*
Orthotrichum sharpii H.Rob.	Orth.sha	***29***	**26**	0	0	0	21	**7**	0	2	3	0	**66**	0	0	47	26	**LSF**	6,5	0,051	
Pameliopsis spumosa (Asah.) Elix & Hale	Parm.spu	***1***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	100	0	0	**LSF**	0,5	1	
Parmeliopsis venezuelana (Hale) DePriest & Hale	Parm.ven	***1***	**100**	0	100	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,578	
Parmotrema arnoldii (DR.) Hale	Parm.arn	***65***	**35**	0	0	3	33	**5**	0	5	0	0	**60**	0	30	21	8	**LSF**	10,8	0,05	*
Physcia spec. A	Phys.spA	***4***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	0	46	54	**LSF**	2,2	0,075	
Pilotrichella flexilis (Hedw.) Ångström	Pilo.fle	***35***	**17**	24	2	5	0	**5**	0	3	2	0	**78**	0	60	4	0	**LSF**	8,9	0,022	*
Plagiochila bicuspidata Gottsche	Plag.bic	***31***	**0**	0	0	0	0	**79**	87	7	1	0	**21**	0	5	0	0	**ESF**	17,7	0,001	**
Plagiochila bifaria (Sw.) Lindenb.	Plag.bif	***4***	**51**	0	0	21	0	**48**	79	0	0	0	**1**	0	0	0	0	**ESF**	0,6	0,965	
Plagiochila cuneata var. loriloba Herzog	Plag.cun	***8***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	98	2	0	0	**LSF**	4,3	0,01	**
Plagiochila heterophylla Lindenb. ex Lehm.	Plag.het	***101***	**92**	39	39	12	0	**0**	0	0	0	0	**8**	8	1	0	0	**PF**	43,2	0,001	**
Plagiochila kroneana Steph.	Plag.kro	***6***	**0**	0	0	0	0	**40**	61	0	0	0	**60**	36	2	1	0	**LSF**	1,6	0,367	
Plagiochila cf. montagnei Nees	Plag.mon	***5***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	100	0	0	**LSF**	2,7	0,046	*

Table 5-2 (cont'd)

			PF					ESF					LSF					Indicator Value (IV)			
Taxon	acronym		**total**	tree base	trunk	inner canopy	outer canopy	**total**	tree base	trunk	lower twigs	upper twigs	**total**	tree base	trunk	inner canopy	outer canopy	**MaxGroup**	% of perfect indication	Monte Carlo Test	significance
Plagiochila papillifolia Steph.	Plag.pap	***11***	**100**	96	4	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	6,2	0,003	**
Plagiochila patzschkei Steph.	Plag.pat	***102***	**4**	1	2	0	0	**24**	50	5	0	0	**72**	12	29	1	0	**LSF**	28,5	0,001	**
Plagiochila cf. patula (Sw.) Lindenb.	Plag.pau	***3***	**0**	0	0	0	0	**100**	99	1	0	0	**0**	0	0	0	0	**ESF**	3,9	0,002	**
Plagiochila pittieri Steph.	Plag.pit	***5***	**100**	100	0	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	2,8	0,048	*
Plagiochila retrorsa Gottsche	Plag.ret	***1***	**100**	100	0	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,576	
Plagiochila stricta Lindenb.	Plag.str	***22***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	98	2	0	0	**LSF**	12	0,001	**
Plagiochila tocarema Gottsche	Plag.toc	***15***	**0**	0	0	0	0	**22**	38	0	0	0	**78**	59	3	0	0	**LSF**	6	0,012	*
Plagiochila trichostoma Gottsche	Plag.tri	***4***	**100**	85	15	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	2,3	0,079	
Porella leiboldii (Lehm.) Trevis	Pore.lei	***9***	**0**	0	0	0	0	**18**	10	12	0	0	**82**	53	25	0	0	**LSF**	2,7	0,157	
Porotrichodendron superbum (Taylor) Broth.	Poro.sup	***6***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	19	81	0	0	**LSF**	3,3	0,017	*
Porotrichum korthalsianum (Dozy & Molk.) Mitt.	Poro.kor	***3***	**100**	100	0	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	1,7	0,175	
Porotrichum mutabile Hampe	Poro.mut	***33***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	84	16	0	0	**LSF**	17,9	0,001	**
Prionodon densus (Sw. ex Hedw.) Müll.Hal.	Prio.den	***16***	**0**	0	0	0	0	**1**	0	2	0	0	**99**	0	94	0	4	**LSF**	7,5	0,003	**
Pseudocyphellaria aurata (Ach.) Vain.	Pseu.aur	***2***	**100**	0	0	0	100	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	1,1	0,181	
Pseudocyphellaria crocata (L.) Vain.	Pseu.cro	***7***	**0**	0	0	0	0	**22**	6	13	0	0	**78**	0	4	77	0	**LSF**	2,1	0,278	
Pylaisiadelpha tenuirostris (Sull.) W.R.Buck	Pyla.ten	***7***	**100**	0	93	4	4	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	4	0,018	*
Racopilum tomentosum (Hedw.) Brid.	Raco.tom	***1***	**0**	0	0	0	0	**100**	100	0	0	0	**0**	0	0	0	0	**ESF**	1,3	0,174	
Radula nudicaulis Steph.	Radu.nud	***14***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	94	6	0	0	**LSF**	7,6	0,003	**
Radula quadrata Gottsche	Radu.qua	***39***	**0**	0	0	0	0	**64**	0	61	7	0	**36**	0	17	5	10	**ESF**	14,4	0,002	**
Radula voluta Taylor	Radu.vol	***1***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	100	0	0	**LSF**	0,5	1	
Ramalina spec. A	Rama.spA	***33***	**58**	0	0	0	46	**2**	0	0	1	0	**40**	0	1	46	5	**LSF**	4,1	0,462	
Rhynchostegium serrulatum (Hedw.) A.Jaeger	Rhyn.ser	***1***	**0**	0	0	0	0	**100**	0	100	0	0	**0**	0	0	0	0	**ESF**	1,3	0,176	
Rigodium toxarion (Schwägr.) A.Jaeger	Rigo.tox	***3***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	100	0	0	0	**LSF**	1,6	0,226	
Rimelia cetrata (Ach.) Hale & A.Fletcher	Rime.cet	***2***	**97**	0	0	97	0	**3**	0	3	0	0	**0**	0	0	0	0	**PF**	0,5	0,729	
Rimelia spec. A	Rime.spA	***2***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	48	0	52	**LSF**	1,1	0,387	
Sematophyllum subsimplex (Hedw.) Mitt.	Sema.sub	***12***	**13**	11	0	0	0	**1**	0	0	0	0	**86**	88	0	0	0	**LSF**	1,4	0,907	

Table 5-2 (cont'd)

			PF					ESF					LSF					Indicator Value (IV)		
Taxon	acronym		**total**	tree base	trunk	inner canopy	outer canopy	**total**	tree base	trunk	lower twigs	upper twigs	**total**	tree base	trunk	inner canopy	outer canopy	**MaxGroup**	% of perfect indication	Monte Carlo Test significance
Sematophyllum swartzii (Schwägr.) W.H.Welch & H.A.Crum	Sema.swa	***18***	**18**	10	4	0	0	**0**	0	0	0	0	**82**	83	3	0	0	**LSF**	4,9	0,113
Siphula spec. A	Siph.spA	***4***	**100**	0	23	77	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	2,3	0,103
Sticta laciniata (Sw.) Ach.	Stic.lac	***4***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	0	100	0	0	**LSF**	2,2	0,073
Sticta spp.	Stic.spp	***47***	**12**	0	0	0	11	**54**	14	33	13	0	**34**	0	13	12	5	**ESF**	11,4	0,009 **
Sticta weigelii (Isert) Ach.	Stic.wei	***14***	**17**	0	0	0	7	**39**	77	0	0	0	**45**	0	11	0	4	**LSF**	2	0,585
Streptopogon erythrodontus (Taylor) Wilson	Stre.ery	***5***	**0**	0	0	0	0	**100**	0	44	56	0	**0**	0	0	0	0	**ESF**	6,6	0,001 **
Syrrhopodon prolifer Schwägr.	Syrr.pro	***8***	**100**	99	1	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	4,5	0,013 *
Taxilejeunea spp.	Taxi.spp	***4***	**0**	0	0	0	0	**66**	9	67	0	0	**34**	0	24	0	0	**ESF**	2,6	0,014 *
Telaranea nematodes (Austin) M.Howe	Tela.nem	***1***	**100**	100	0	0	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,591
Teloschistes spec. A	Telo.spA	***1***	**100**	0	0	0	100	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	0,6	0,581
Thuidium pseudoprotensum (Müll.Hal.) Mitt.	Thui.pse	***14***	**93**	96	0	0	0	**7**	0	4	0	0	**0**	0	0	0	0	**PF**	5,8	0,011 *
Trichocolea floccosa Herzog & Hatch.	Tric.flo	***10***	**0**	0	0	0	0	**0**	0	0	0	0	**100**	80	20	0	0	**LSF**	5,4	0,004 **
Usnea spp.	Usne.spp	***149***	**37**	0	11	19	2	**8**	0	3	2	2	**55**	0	6	42	14	**LSF**	26,7	0,001 **
Zygodon ehrenbergii Müll.Hal.	Zygo.ehr	***58***	**100**	0	80	19	0	**0**	0	0	0	0	**0**	0	0	0	0	**PF**	32,8	0,001 **
Zygodon reinwardtii (Hornsch.) A.Braun	Zygo.rei	***166***	**14**	0	0	0	15	**26**	2	20	6	1	**60**	2	33	14	7	**LSF**	33,4	0,001 **
	Averages		**39**	10	8	10	10	**22**	7	11	5	1	**39**	10	14	9	5			

CHAPTER 6

Summary

The present thesis contains results of a study on the diversity and ecology of bryophytes and macrolichens in upper montane oak forests in the Cordillera de Talamanca, Costa Rica. Aspects dealt with in this study are the diversity and biogeography of bryophytes, the distribution patterns of life forms and species in microhabitats and along ecological gradients, the host preference and community composition of epiphytic bryophytes and macrolichens, the secondary succession of epiphytic vegetation and the selection of indicator species.

The scope of the study is to describe epiphytic cryptogam communities, to analyze their spatial and environmental relationships and to assess changes in the community composition and development after human-induced disturbance of the forest. For the first time recovery of epiphytic cryptogam communities in secondary tropical montane forests receives full attention.

The study took place in the upper Río Savegre watershed area on the Pacific-facing slope of the western Talamanca Mountain Range, Costa Rica.

In **Chapter 1** a general introduction to tropical montane rain forests and to bryophytes and macrolichens as an important component of these ecosystems is presented. Special emphasis is laid on epiphytic cryptogams and their communities in primary and secondary forests. The reader is introduced to the study area, its climate, geology and vegetation. Towards the end of the chapter, aims, outline and contents of the study are concisely presented.

In **Chapter 2** the phytogeographical patterns of bryophytes of Costa Rica’s Talamancan montane oak forests are analysed and discussed. 251

bryophyte species (128 hepatics, one hornwort and 122 mosses) are found in Talamancan *Quercus* forests. 93 % of all species in these forests are tropical in distribution. The remaining 7 % are made up of temperate and cosmopolitan species. The neotropical element is the most pronounced and contributes to almost 74 % of the species, whereas the wide tropical element (pantropical, amphi-atlantic, amphi-pacific) is only presented with 19 % of the species. A significant part of the neotropical bryophyte species in the studied oak forests show a tropical Andean centered distribution. In contrast, vascular plant genera show fewer neotropical species, more temperate and more amphi-pacific elements than the bryophytes. Similar bryogeographical spectra as for the complete oak forest flora have been found in different microhabitats of six hectare of an upper montane oak forest and in epiphytic bryophyte species on *Quercus copeyensis* of primary, early secondary and late secondary forests. The comparison of the oak forest spectrum with that of Costa Rican páramo reveals a greater affinity of the páramo bryoflora to temperate regions and the importance of the páramo element. However, surprisingly oak forests have a high percentage of Central American endemics which are lacking in the páramo. Compared to data on the phytogeography of Costa Rican hepatics there are fewer temperate and more Central American species found in the oak forest flora.

Chapter 3 deals with bryophyte diversity, microhabitat differentiation and distribution of live forms in an Costa Rican upper montane *Quercus* forest. It gives a comprehensive overview on the bryophyte flora of all microhabitats, including forest floor and the understorey of the forest.

A complete bryophyte inventory of six hectare of forest yielded 206 species: 100 mosses, 105 hepatics and one hornwort. Based on similarities in species composition the forest microhabitats cluster into three main groups: i) forest floor habitats (including tree base), ii) phyllosphere and iii) other epiphytic habitats. The contribution of forest floor habitats to total bryophyte species richness is much higher than in forests of lower elevational belts. Distribution of species and life forms in different microhabitats reflect the vertical variation of humidity and light regimes. At the same time they reflect the impact of the pronounced dry season and the forest structural characters (tree height, stratification, number of host tree species) on epiphytic bryophytes compared to more humid forests and upper montane forests of lower stature.

Chapter 2 and 3 are the basis for a more detailed analysis of the epiphytic habitats in the studied upper montane oak forest. **Chapter 4** and **5** contain the description of epiphytic cryptogam communities (bryophytes and macrolichens) in primary and secondary forests. Trees were climbed using a mountaineering-derived single rope technique and were sampled from the base up to the twigs of the outer canopy. The relevés taken in each height zone represented the complete variation of the epiphytic vegetation. Percentage cover of corticolous bryophyte and macrolichen species was estimated and later compared using Detrended Correspondence Analysis (DCA) and non-metric Multi-response Permutation Procedure (MRPP). Bark samples from the investigated trees were extracted with deionized H_2O and analysed for pH.

Chapter 4 pays attention to the epiphytic cryptogam communities on the two dominant host tree species (*Quercus copeyensis* and *Q. costaricensis*) of upper montane oak forests in Costa Rica.

Of the 153 taxa found in this study, 57 were lichens, 56 hepatics and 40 mosses. Beside the vertical gradient the two host tree species proved to be the most important factor in community differentiation of epiphytic cryptogams as indicated by DCA. Many of the species are preferential or exclusive to either *Quercus copeyensis* or *Q. costaricensis*. Also, non-metric MRPP confirmed the significant differences in community composition of individual height zones on different host trees. Furthermore, bark pH, water holding capacity and bark hardness differ significantly among host species and may well explain host-epiphyte relations.

For the first time, a detailed description of epiphytic cryptogam communities of whole standing canopy trees in an upper montane oak forest is given. Species indicator values are calculated, ecological species groups are described and factors controlling the vertical and horizontal distribution of species are discussed. Changes in species richness, community composition and community structure along the vertical gradient are further aspects of this chapter.

Chapter 5 compares species richness, community composition and ecology of cryptogamic epiphytes in primary and recovering upper montane *Quercus* forests of Costa Rica. Canopy trees of *Quercus copeyensis* were sampled with the aim of getting insights into recovery potential, underlying patterns and processes of epiphyte succession following anthropogenic disturbance.

Analysis of bryophyte and lichen diversity revealed that total species richness in secondary and primary forests were nearly the same, showing that primary forests are not necessarily more diverse than secondary forests. Similarity in species composition in secondary forests compared to the primary forest increases with age, but still after 40 years one third (46 species) of the primary forest species had not re-invaded the secondary forest. Genera and species exclusive to primary forests are crucial as indicator species and for the purpose of conservation. On the contrary, 40 % (68 species) of all species found in the studied forest types are restricted to secondary forests alone, which indicates the importance of secondary forests contributing to the total species richness within the area.

In further analyses, species indicator values were calculated, ecological species groups described and ecological factors controlling the distribution of species in epiphytic microhabitats of primary and secondary forests discussed. In the succession of cryptogamic epiphyte communities towards a mature secondary forest, the diversity in microsites due to tree growth is of outmost importance. The high number of species only found in the primary forest indicates that a long time will be needed for the re-establishment of microhabitats and re-invasion of species adapted to differentiated niches.

It may thus be recommended, that in order to maintain a high biodiversity at La Amistad's outer forest margin, management practices should be adopted to maintain all successional stages present in a forest landscape to preserve the diversity of non-vascular epiphytes.

Zusammenfassung

Die vorliegende Dissertation fasst die Untersuchungsergebnisse einer Studie zur Diversität und Ökologie von Moosen und Makroflechten in hochmontanen Eichenwäldern der Cordillera de Talamanca (Costa Rica) zusammen. Folgende Themenkomplexe wurden behandelt: Biogeographie, Pflanzendiversität, Verbreitungsmuster von Lebensformen und Arten in Mikrohabitaten sowie entlang ökologischer Gradienten, Epiphyt-Porophyt-Beziehungen, Vergesellschaftung, Sekundärsukzession und die Auswahl von Indikatorarten.

Ziel der Untersuchung ist es die epiphytischen Kryptogamengesellschaften des Untersuchungsgebietes zu beschreiben, ihre räumlichen und ökologischen Beziehungen zu analysieren und einen Einblick in die Veränderungen der Gesellschaften, sowie ihrer Weiterentwicklung nach menschlicher Zerstörung der Wälder, zu geben. Zum ersten Mal wird bei einer derartigen Untersuchung die sekundäre Sukzession von Kryptogamengesellschaften in tropischen Bergregenwäldern voll berücksichtigt.

Die Untersuchung wurde im Einzugsgebiet des Río Savegre auf der pazifikseitigen Abdachung der westlichen Cordillera de Talamanca (Costa Rica) durchgeführt.

Kapitel 1 gibt eine generelle Einführung in Tropische Bergregenwälder und die Bedeutung von Moosen und Makroflechten als wichtige Komponenten dieser Ökosysteme. Ein besonderes Augenmerk wird auf epiphytische Kryptogamen und ihre Vergesellschaftung in Primär- und Sekundärwäldern gelegt. Der Leser wird in das Untersuchungsgebiet, sein Klima, seine Geologie und seine Vegetation eingeführt. Ziel, Umfang und Inhalt der Studie werden näher ausgeführt.

Im **Kapitel 2** werden die pflanzengeographischen Muster der Moose montaner Eichenwälder der Cordillera de Talamanca dargestellt und diskutiert. 251 Moosarten (128 Lebermoose, 1 Hornmoos, 122 Laubmoose) wurden in den

Eichenwäldern der Talamanca nachgewiesen. 93 % aller Arten dieser Wälder haben eine tropische Verbreitung. Die restlichen 7 % setzen sich aus temperaten und kosmopolitischen Arten zusammen. Das neotropische Element ist am stärksten vertreten und trägt zu 74 % aller Arten bei, während pantropische, amphi-atlantische und amphi-pazifische Arten nur 19 % der Arten ausmachen. Ein signifikanter Teil der neotropischen Arten der Eichenwälder zeigt eine tropisch andin-zentrierte Verbreitung. Bei den Gefäßpflanzengattungen der Eichenwälder finden sich weniger neotropische Arten, jedoch mehr temperate und mehr amphi-atlantische. Ähnliche phytogeographische Spektren wie für die Gesamtmoosflora der Eichenwälder wurden in den einzelnen Mikrohabitaten eines 6 ha umfassenden primären, hochmontanen Eichenwaldes, sowie bei den epiphytischen Moosarten an *Quercus copeyensis* von Primär- und Sekundärwäldern vorgefunden.

Der Vergleich des Eichenwaldspektrums mit dem costaricanischer Paramos zeigt eine größere Affinität der Paramomoosflora zu temperaten Regionen und die Bedeutung des spezifischen Paramoelementes. Überraschenderweise haben die Eichenwälder einen hohen Prozentsatz an mittelamerikanischen Endemiten, die dem Paramo fehlen. Auch im Vergleich zur Phytogeographie der costaricanischen Lebermoosflora findet man in den Eichenwäldern weniger temperate Arten und mehr mittelamerikanische Endemiten.

Kapitel 3 diskutiert Diversität, Mikrohabitatdifferenzierung und Lebensformenspektren der Moose in einem hochmontanen Eichenwald Costa Ricas. Es wurde versucht, die Moosflora aller Mikrohabitate eines Eichenwaldes, inklusive der Strauch- und Bodenschicht zu erfassen.

Eine vollständige Inventarisierung der Moosflora von 6 ha Eichenwald ergab 206 Arten: 100 Laubmoose, 105 Lebermoose und ein Hornmoos. Basierend auf der Ähnlichkeit der Artenzusammensetzung wurden die Mikrohabitate des Bergregenwaldes in drei Hauptgruppen gegliedert: 1. Waldbodenhabitate (inklusive der Stammbasis), 2. Phyllosphäre und 3. andere epiphytische Habitate.

Der Beitrag der Waldbodenhabitate zum Gesamtartenreichtum der Moose in diesen Wäldern ist viel höher als in Regenwäldern tieferer Lagen. Die Verbreitung der Arten und Lebensformen in den einzelnen Mikrohabitaten spiegelt vor allem die vertikale Variation des Feuchte- und Lichtregimes in den Wäldern wieder. Gleichzeitig zeigen sie den Einfluss der ausgeprägten Trockenzeit und der strukturellen Parameter (Baumhöhe, Schichtung, Anzahl der Porophytenarten) der Eichenwälder, im Vergleich zu feuchteren, weniger hochwüchsigen hochmontanen Bergregenwäldern.

Kapitel 2 und 3 bilden die Grundlage einer detaillierten Analyse der epiphytischen Habitate eines hochmontanen Bergregenwaldes. Kapitel 4 und 5 beinhalten die Beschreibung epiphytischer Kryptogamengesellschaften (Moose und Makroflechten) in Primär- und Sekundärwäldern. Mit Hilfe einer aus dem Alpinismus abgeleiteten Klettertechnik wurden Bäume von der Stammbasis bis in die Zweige der äußeren Krone beprobt. Die Vegetationsaufnahmen repräsentieren die Variation der epiphytischen Vegetation. Prozentuale Deckungsgrade der rindenbewohnenden Moose und Makroflechten wurden geschätzt und mit Hilfe einer ‚Detrended Correspondence Analysis (DCA)' und nicht-metrischer ‚Multi-response Permutation Procedure (MRPP)' verglichen. Rindenproben der untersuchten Bäume wurden mit deionisiertem Wasser extrahiert und der pH-Wert bestimmt.

Kapitel 4 behandelt die epiphytischen Kryptogamengemeinschaften auf den dominierenden Baumarten (*Quercus copeyensis* und *Q. costaricensis*) primärer, hochmontaner Eichenwälder Costa Ricas.

Von den 153 in dieser Studie nachgewiesenen Arten sind 57 Flechten, 56 Lebermoose und 40 Laubmoose. Neben dem vertikalen Gradienten am Baum stellten sich in einer DCA die beiden Porophyten als der wichtigste für die Gesellschaftsdifferenzierung der epiphytischen Kryptogamen verantwortliche Faktor heraus. Viele der Arten bevorzugen oder sind ausschließlich auf entweder *Quercus copeyensis* oder *Quercus costaricensis* zufinden. Auch die nicht-metrische MRPP-Analyse bestätigt die signifikanten Unterschiede in der Artenzusammensetzung der einzelnen Höhenzonen auf den unterschiedlichen Porophyten. Außerdem geben der unterschiedliche pH-Wert, die Wasserkapazität und die Härte der Rinde der Porophyten eine gute Erklärung für die vorgefundenen Porophyt-Epiphyt-Beziehungen.

Zum ersten Mal wurde eine detaillierte Beschreibung der epiphytischen Kryptogamengemeinschaften auf Bäumen der oberen Baumschicht in primären, hochmontanen Eichenwäldern vorgelegt. Indikatorwerte der Arten wurden berechnet, ökologische Artengruppen beschrieben und die vertikale und horizontale Verbreitung der Arten beeinflussende Faktoren analysiert und diskutiert. Veränderungen des Artenreichtums, der Gesellschaftszusammensetzung und -struktur entlang des vertikalen Gradienten sind weitere Aspekte dieses Kapitels.

Kapitel 5 vergleicht Artenreichtum, Vergesellschaftung und Ökologie der epiphytischen Kryptogamen in primären und sekundären hochmontanen Eichenwäldern Costa Ricas. *Quercus copeyensis*-Bäume der oberen Baumschicht von Primär- und Sekundärwäldern wurden beprobt mit dem Ziel einen Einblick in Regenerationspotential, -muster und -prozesse der Epiphytensukzession nach anthropogener Störung zu erhalten.

Die Analyse der Moos- und Flechtendiversität ergab einen nahezu identischen Gesamtartenreichtum in Sekundär- und Primärwäldern, was zeigt, das Primärwälder nicht notwendigerweise diverser als Sekundärwälder sind. Die Ähnlichkeit der Artenzusammensetzung in Sekundärwäldern verglichen mit Primärwäldern nimmt mit dem Alter der Sekundärwälder zu, doch selbst nach 40 Jahren hatte ein Drittel (46 Arten) der Primärwaldarten den Sekundärwald nicht wiederbesiedelt. Als Indikatorarten und für den Naturschutz sind ausschließlich im Primärwald vorkomme Gattungen und Arten von besonderer Bedeutung. Auf der anderen Seite wurden 40 % (68 Arten) der in den Sekundärwäldern vorkommenden Arten nur in diesen gefunden, was die Bedeutung der Sekundärwälder für den Gesamtartenreichtum einer Region unterstreicht.

Für die Arten der Primär- und Sekundärwälder wurden Indikatorwerte berechnet, ökologische Artengruppen beschrieben und ökologische Faktoren, die die Verbreitung von Arten in den epiphytischen Mikrohabitaten bestimmen, diskutiert. Bei der Sukzession von epiphytischen Kryptogamengemeinschaften in Richtung naturnaher Sekundärwälder spielen Faktoren wie die erhöhte Diversität von Mikrostandorten durch den zunehmenden Baumwuchs wahrscheinlich eine größere Rolle als zwischenartliche Konkurrenz. Die hohe Zahl an Arten, die ausschließlich im Primärwald vorkommt, zeigt, dass die vollständige Wiederherstellung aller Mikrohabitate und die Re-invasion der an diese Nischen angepassten Arten eine lange Zeit brauchen wird.

Um eine möglichst hohe Diversität der Pufferzone des Biosphärenreservates La Amistad zu erhalten sollten Managementpraktiken angewandt werden, die zum Schutz der Diversität nicht-vaskulärer Epiphyten, alle gegenwärtig in dieser Waldlandschaft vorhandenen Sukzessionsstadien erhalten.

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Curriculum Vitae

Ingo Hubert Holz was born on 10th of July 1969 in Saarburg (Germany). After visiting the Elementary School „Grundschule Greimerath“, he went to Secondary Schools in Zerf and Saarburg and received the Abitur at the Staatliches Gymnasium Saarburg in 1988.

In the same year, he began to study Applied Physical Geography at the University of Trier with majors in Geobotany and Soil Science. In September 1996 he finished his diploma thesis entitled “Moosflora und -vegetation der Liassandsteinfelsen und -blöcke des Ferschweiler Plateaus”, which was funded by the grant “Arten- und Biotopschutz” from the Ministry for the Environment and Forests of the Land Rhineland-Palatinate.

From the end of 1996 to early 1999 he worked as a scientific assistant in the Department of Botany at the Staatliches Museum für Naturkunde in Stuttgart. Apart from treating various taxa for the Moss Flora of Baden-Württemberg, performing floristic and vegetation mapping, herbarium work and the organisation of the Annual Meeting of the BLAM, he was also involved for several months in the project „Environmental registration in forest-biological diversity“ of the Norwegian Forest Research Institute (NISK) in Sigdal, Central Norway.

In February 1999, he went to the Albrecht-von-Haller-Institute for Plant Sciences at the Georg-August University of Göttingen. As a research assistant in the Department of Systematic Botany he worked in the DFG funded project “Diversität und Ökologie kryptogamischer Epiphytenvegetation im Kronenraum tropischer Bergregenwälder entlang einer Gradienten anthropogener Zerstörung (Changes in the diversity and ecology of cryptogamic epiphytes in tropical cloud forest canopies along gradients of human-induced disturbance)”, which expired in July 2003. In the frame of this study, he performed field work in the Cordillera de Talamanca, Costa Rica, from March 1999 to July 2000. During this period he performed other field trips to Costa Rica, French Guiana, Argentina, Chile and Ecuador.

Since December of 2002, he is a research assistant in the Working Group General and Special Botany at the Botanical Institute and Botanical Garden of the University of Greifswald. Apart from establishing a Molecular Laboratory for systematic and population ecological studies as well as light microscopy and SEM based methods, he is strongly involved in teaching activities at the institute.

Present dissertation gives full account on the scientific results of the studies on the diversity and ecology of bryophytes and macrolichens in primary and secondary montane oak forests in the Cordillera de Talamanca (Costa Rica).

Curriculum Vitae

Ingo Hubert Holz wurde am 10. Juli 1969 in Saarburg geboren. Nach dem Besuch der Grundschule Greimerath ging er 1979 an die Grund- und Hauptschule Zerf über, wo er 1984 den Hauptschulabschluss ablegte. An der Hauptschule Saarburg besuchte er das freiwillige 10. Schuljahr der Hauptschule zum Erwerb des qualifizierten Sekundarabschlusses I. Im Juni 1988 legte er das Abitur am Staatlichen Gymnasium Saarburg ab, das er seit der 11. Klasse besuchte.

Im selben Jahr begann er sein Studium der Angewandten Physischen Geographie, mit den Nebenfächern Geobotanik und Bodenkunde, an der Universität Trier. Im September 1996 legte er das Diplom als Geograph, mit einer Diplomarbeit zum Thema ‚Moosflora und -vegetation der Liassandsteinfelsen und -blöcke des Ferschweiler Plateaus' die durch das Stipendium „Arten- und Biotopschutz" des Ministeriums für Umwelt und Forsten des Landes Rheinland-Pfalz gefördert wurde, ab.

Von Ende 1996 bis Anfang 1999 arbeitete er als wissenschaftlicher Volontär in der Abteilung Botanik des Staatlichen Museums für Naturkunde Stuttgart. Neben der Bearbeitung von verschiedenen Taxa für das Grundlagenwerk „Die Moose Baden-Württembergs", floristischer und vegetationskundlicher Kartierungen, Herbariumsarbeiten und der Organisation der BLAM-Jubiläumstagung 1998 am Museum war er in dieser Zeit für mehrere Monate im Projekt „Environmental registration in forest-biological diversity" des Norwegian Forest Research Institute (NISK) in Sigdal, Norwegen tätig.

Im Februar 1999 begann er als wissenschaftlicher Mitarbeiter in der Abt. Systematische Botanik am Albrecht-von-Haller-Institut für Pflanzenwissenschaften der Georg-August-Universität Göttingen, wo er bis Juli 2003 in einem von der Deutschen Forschungsgemeinschaft geförderten Projekt zum Thema "Diversität und Ökologie kryptogamischer Epiphytenvegetation im Kronenraum tropischer Bergregenwälder entlang eines Gradienten anthropogener Zerstörung" arbeitete. Hierzu führte er von März 1999 bis Juli 2000 Feldarbeiten in der Cordillera de Talamanca (Costa Rica) durch. Im Rahmen zahlreicher Forschungsreisen führte er in dieser Zeit auch Feldarbeiten in Costa Rica, Französisch Guyana, Argentinien, Chile und Ecuador durch.

Seit Dezember 2002 ist er wissenschaftlicher Mitarbeiter in der AG Allgemeine und Spezielle Botanik des Botanischen Institutes und Botanischen Gartens der Universität Greifswald. Neben dem Aufbau eines molekularen Labors zur Durchführung systematischer und populationsökologischer Untersuchungen, sowie der Etablierung Licht- und Elektronenmikroskopischer Untersuchungsmethoden nimmt er hier zahlreiche Aufgaben in der Lehre des Institutes wahr.

Die vorliegende Dissertation fasst seine Untersuchungsergebnisse zur Diversität und Ökologie von Moosen und Makroflechten in primären und sekundären Eichenwäldern der montanen Stufe der Cordillera de Talamanca (Costa Rica) zusammen.