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Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica – species richness, community composition and ecology

Ingo Holz[1,*] and S. Robbert Gradstein[2]
[1]*Botanical Institute and Botanical Garden, University of Greifswald, Grimmer Str. 88, 17487 Greifswald, Germany;* [2]*Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany; *Author for correspondence (e-mail: ingo.holz@uni-greifswald.de)*

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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 presumed 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.

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 (Churchill et al. 1995a; Bruijnzeel and Hamilton 2000). Secondary forest communities are widely distributed and are increasingly becoming the most important repository of biodiversity in tropical uplands (Brown and Lugo 1990; Chazdon 1994; Holl and Kappelle 1999; Helmer 2000). Yet, only little is known about the biodiversity of these forests and the patterns and processes of recovery following clearing.

This paper deals with the biodiversity of cryptogamic epiphytes (mosses, hepatics, macrolichens) in primary and secondary montane forests. Tree diversity in these forests is low, while a high proportion of total species richness is achieved by the cryptogams (Wolf 1993a, 1993b; Churchill et al. 1995b; Gradstein 1995; Sipman 1995). Cryptogams play an important role in these forests, not only in terms of species diversity but also

in ecosystem functioning. Mats of cryptogams hold water, trap seeds, intercept and retain nutrients from fog, and provide anchorage for seedlings (Pócs 1982; Richards 1984; Nadkarni 1986, 1992; Veneklaas 1990; Hofstede et al. 1993; Wolf 1993b; Clark et al. 1998). They shelter an abundant and diverse fauna (e.g. Nadkarni and Matelson 1989; Ingram and 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, describing and analysing these communities is a research priority for conservation of biodiversity, and a prerequisite for a sustainable management of tropical montane forest (Chaverri and Hernández 1995; Hietz 1999; Gradstein et al. 2001a).

Studies on recovery of cryptogamic communities in secondary tropical forests are few and focus only on lowland, submontane or lower montane rain forests (e.g., Equihua and Gradstein 1995; Acebey et al. 2003), 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 and 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 and Kappelle 1999).

The present study for the first time compares cryptogamic (=non-vascular) epiphyte diversity and species composition in primary and secondary upper montane forests. The study focuses on bryophytes and macrolichens; ferns and microlichens are not included, the former as they are better studied with other vascular epiphytes, the latter because they are taxonomically poorly known. 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 (Figure 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 (Figure 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).

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

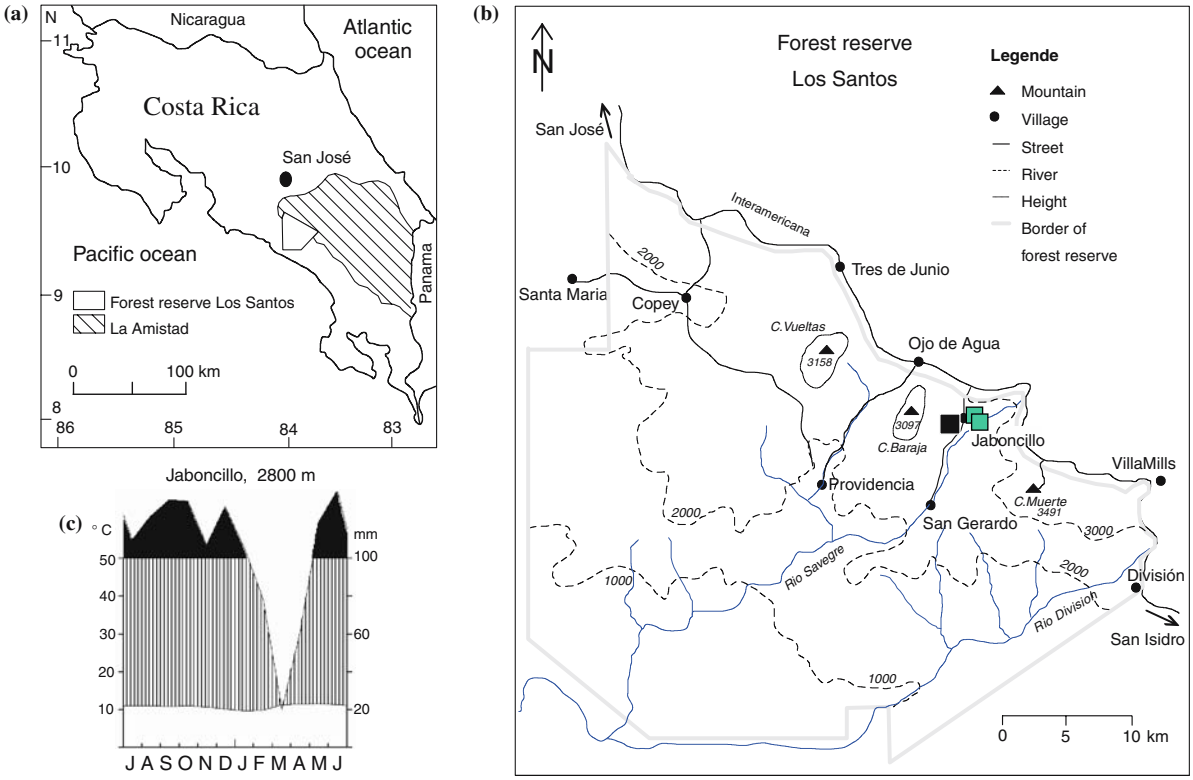

Figure 1. Study area. (a) Map of Costa Rica, showing La Amistad Biosphere Reserve and Los Santos Forest Reserve on the Pacific-facing slope of the Cordillera de Talamanca. (b) Map of Los Santos Forest Reserve, showing Río Savegre valley and study sites; black square = primary forest, grey squares = secondary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

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 area-consuming orchards are now accompanied by a secondary forest succession on the cleared land (Kappelle 1995, 1996; Helmer 2000).

Methods

Study sites

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 (Figure 1b). The vascular plant vegetation of the three sites has been described by Kappelle et al. (1995); characteristics are provided in Table 1. In spite of their different ages and forest structure, all three sites showed clear vertical profiles of humidity (Figure 2) and air temperature (Köhler 2002).

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).

Table 1. Description of study sites.

	Primary forest	Early secondary forest	Late secondary forest
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 > 3 cm)	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*

Data on leaf area index and biomass from 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)

A 12–14 m tall, closed stand, of about 40 years in age is dominated by *Quercus costaricensis* and *Q. copeyensis*. Accompanying species with high cover are the trees *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 dark and cover of the shrub layer is less than 30%.

Sampling and data analysis

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 for 2 h and measured with a standard pH electrode (Sensolyt SE, WTW). 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 and Cornelissen 1988). In total, 437 plots were inventoried on 15 trees (177 plots in PF, 76 in ESF and 184 in LSF). Several plots were taken on each tree and in each height zone of the tree (Johansson 1974, modified). In PF 29 plots 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 plots on upper twigs. Plot size was 600 cm^2 (20 cm × 30 cm, on smaller branches 15 cm × 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 plot, 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 plot 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 sample 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 plot were collected and identified to species level. Voucher specimens were deposited at INB with duplicates in GOET, MO (some) and NY (some). Nomenclature follows

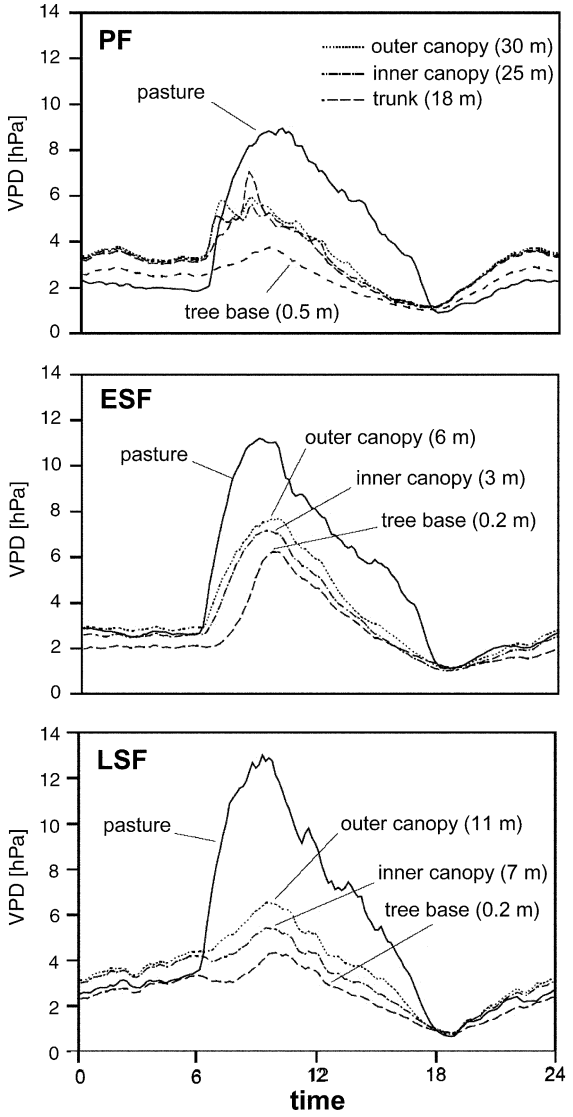

Figure 2. Mean daily course of vapour pressure deficit (VPD) during the dry season (1999/2000) in different tree height zones of the investigated oak forests. PF = primary forest (mean of 49 days), ESF = early secondary forest (mean of 45 days), LSF = late secondary forest (mean of 34 days). Figure modified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

Allen (1994, 2002), Buck (1998), and Sharp et al. (1994) for mosses, and Uribe and Gradstein (1998) for hepatics.

All statistical analyses were performed using the program package PC-ORD for Windows – Version 4.17 (McCune and Mefford 1999). Measurements of alpha and beta diversity follow McCune et al. (2000). The main data matrix (species cover) used consisted of 437 rows (plots) and 168 columns (species). There were 73416 cells in this matrix and 93.6% of these cells were zero. The second data matrix consisted of 437 rows (plots) 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 plot in the tree, relative height of plot 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 plots defined by height zone and/or host tree species, forest type and host tree number were compared with non-metric MRPP (Multiresponse Permutation Procedures, Mielke 1984). 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 plots × 132 species, following removal of species with less than three occurrences, was subject to *Detrended correspondence analysis* (DCA, Hill and Gauch 1980) and *non-metric multidimensional scaling* (NMS, Kruskal 1964; Clarke 1993), 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 favourability 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 plot based on associating species that were present as well in that plot. 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 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 and 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 and Legendre 1997). Species indicator values were tested for statistical significance using a Monte Carlo procedure with 1000 replicates (Dufrene and Legendre 1997).

Results

Species diversity

In total, 168 species (60 of macrolichen, 67 of hepatic, 41 of moss) were found in 437 plots taken on 15 trees in PF, ESF and LSF (Table 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 2.

In total, 100 species were found in PF, 87 in ESF and 106 in LSF. In all the three forest types hepatics were the most specious group followed by lichens and mosses. Figure 3 shows species-accumulation curves of randomly pooled plots 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 (Table 3).

In terms of numbers of families, PF (36 families) is the most diverse of the forest types, followed by LSF (34) and ESF (30). Distribution of species over families is very similar in all forest types (Figure 4). *Lejeuneaceae* (hepatics), *Parmeliaceae* (lichens), *Plagiochilaceae* (hepatics), *Lobariaceae* (lichens), *Physciaceae* (lichens), *Jubulaceae* (hepatics) and *Orthotrichaceae* (mosses) are the species-richest families. *Collemataceae* (lichens) replace Jubulaceae in the ESF in terms of species richness. In the primary forest, *Parmeliaceae* (with the speciose genus *Hypotrachyna*) is the most speciose family, *Lejeuneaceae* in the secondary forest. The species-richest family of mosses in all forest types are the *Orthotrichaceae* (incl. *Macromitriaceae*).

Species richness per plot was variable (Table 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 plot is highest in ESF and lowest in PF. Hepatics are the richest group in all zones and in all forest types (Figure 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 (Figures 5 and 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 plot and total number of species. Tree base in PF had the lowest number of species per plot.

In ESF, the tree trunks are richest in species, both in total number and number per plot. 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 plot 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 plot in the inner canopy. Tree base in LSF are poorest both with regard to total number of species and number per plot.

It thus appears that diversity in terms of total number of species and number of species per plot is lowest on trunk in the ESF and highest in the

Table 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.

Taxon	Acronym	*N*	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
			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. and 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. and Gottsche) Slageren and 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 and 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 and 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
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

Table 2. Continued

Taxon	Acronym	*N*	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
			177	29	48	48	52	76	5	21	25	25	184	25	76	30	53		IV	*p*
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. and 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. and 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. and 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. and Redon	Hete.lut	11	100	0	0	0	100	0	0	0	0	0	0	0	0	0	0	PF	6.2	0.001**
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 and 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
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 and 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 and 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. and 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. and 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 and 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

Table 2. Continued

Taxon	Acronym	*N*	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
			177	29	48	48	52	76	5	21	25	25	184	25	76	30	53		IV	*p*
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*
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. and 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 and 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 and 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*
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 and 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 and 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
Sematophyllum swartzii (Schwägr.) W.H.Welch and 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 and 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			

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.

Table 3. Species diversity overall and broken down by taxonomic groups and forest types.

Group (sample size)	Average species richness per plot (SD)	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

Beta diversity was measured as the total number of species divided by the average number of species. SD = standard deviation.

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 3). Overall beta diversity of cryptogamic epiphytes is very high (15.7), reflecting the wide range of habitats sampled.

Although total number of species in PF is relatively low compared to the two secondary forest types (Figures 3 and 5), PF has the highest number of species exclusive to one forest type (46% of all species in PF; 27% of all species found; Table 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.

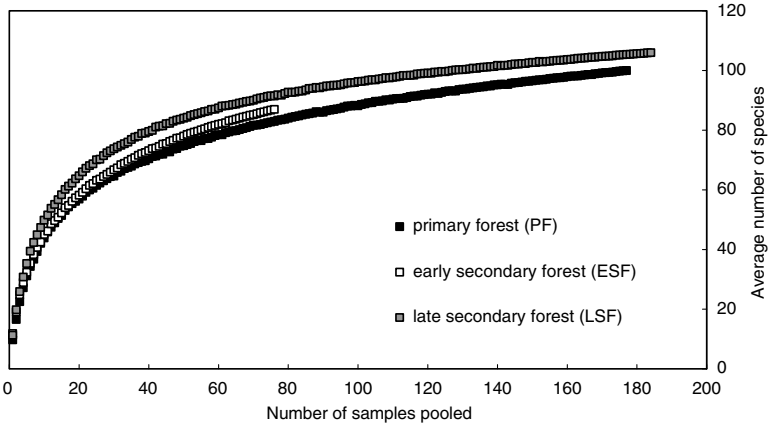

Figure 3. Species-accumulation curves (rarefaction) of cryptogamic epiphyte plots in primary forest (PF), early secondary forest (ESF) and late secondary forest (LSF).

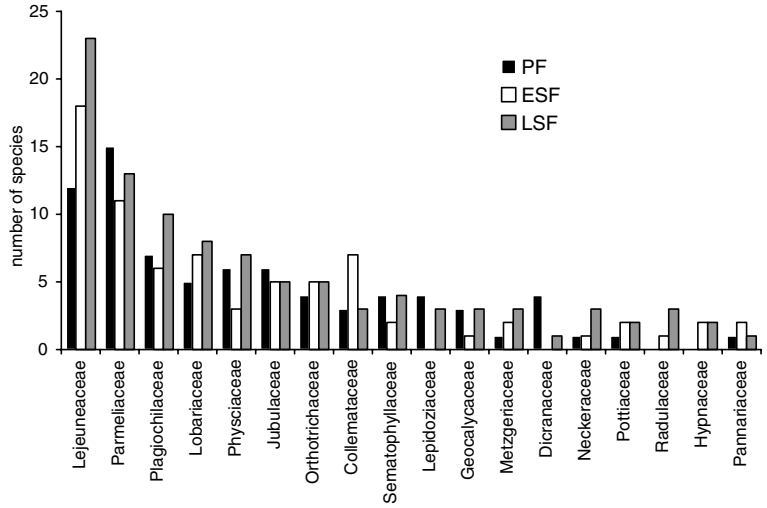

Figure 4. Number of species in lichen, hepatic and moss families within the studied forest types.

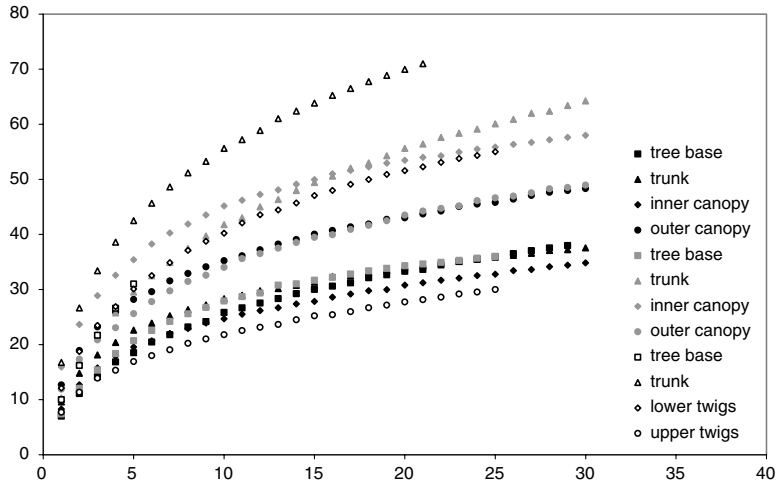

Figure 5. Species-accumulation curves (rarefaction) of plots taken in different height zones in the primary forest (PF: black symbols), early secondary forest (ESF: white symbols) and late secondary forest (LSF: grey symbols).

Community composition of epiphytes

Multi-response permutation procedure analysis (MRPP) revealed no significant difference between the plots from each of the five *Quercus copeyensis* trees in PF, in ESF or in LSF (Table 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 (Table 5). 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 ($A > 0.10$; Table 6).

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

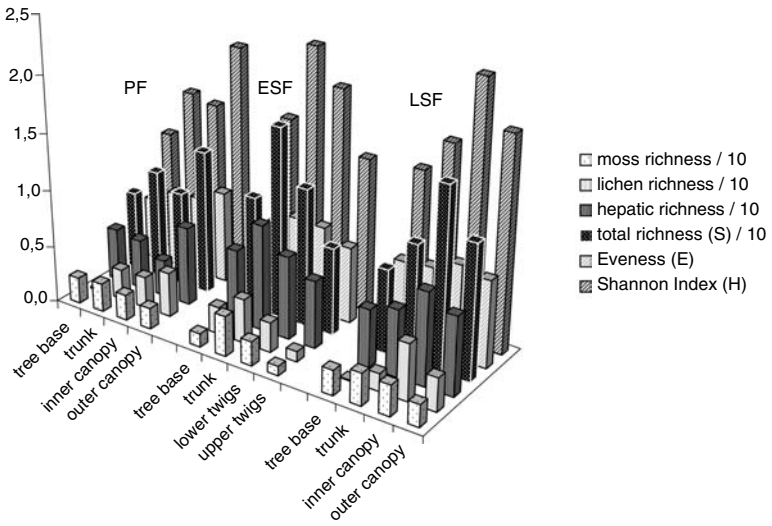

Figure 6. Mean species richness, evenness and Shannon diversity Index per plot within different height zones in the primary forest (PF), early secondary forest (ESF) and late secondary forest (LSF).

canopy plots of PF, inner and outer canopy plots of LSF and twig plots 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 (Figure 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 plot 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 plots 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 plot in the tree.

Table 4. Habitat preferences of non-vascular 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

Table 5. Comparison of differences in epiphyte community composition using non-metric MRPP, based on Sørensen distances.

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	$< 10^{-8}$

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.

Table 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

In NMS ordination of raw cover data (Figure 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 plot in the tree.

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 and 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 or 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):

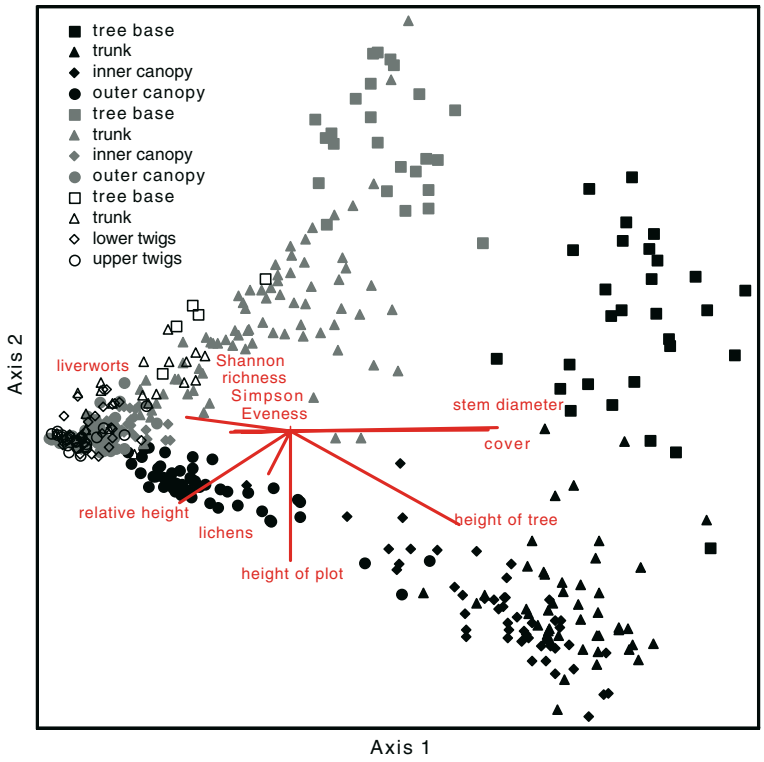

Figure 7. Ordination of plots in epiphyte species space using DCA after Beals smoothing. Symbols indicate height zones in the different forest types where plots were taken. Primary forest (PF): black symbols, Early secondary forest (ESF): white symbols, Late secondary forest (LSF): grey symbols.

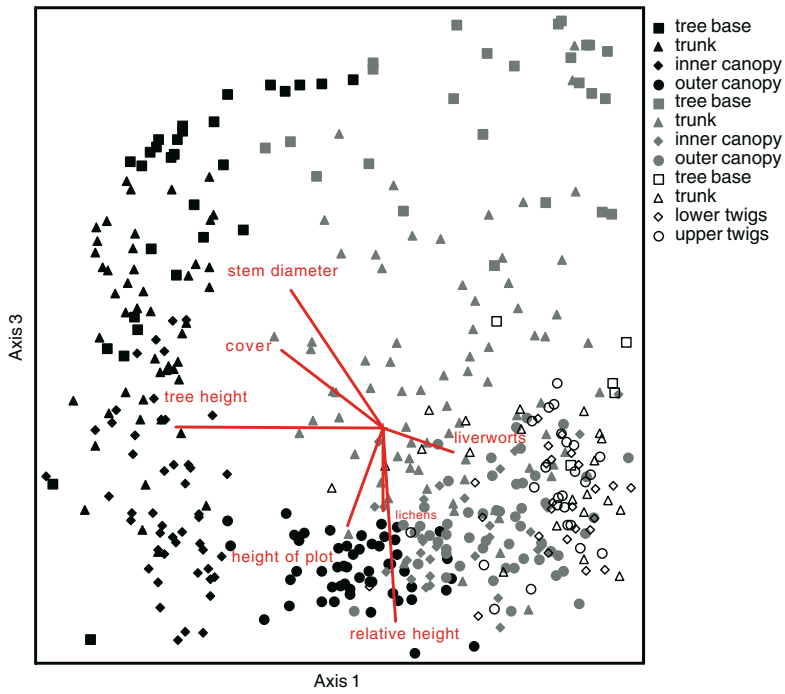

Figure 8. Ordination of plots in epiphyte species space (raw cover data) using NMS. Symbols indicate height zones in the different forest types where plots were taken. Primary forest (PF): black symbols, Early secondary forest (ESF): white symbols, Late secondary forest (LSF): grey symbols.

(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.

(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 (Table 7) and is paralleled by decreasing pH values with height in the tree in PF (Holz and Gradstein, submitted).

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

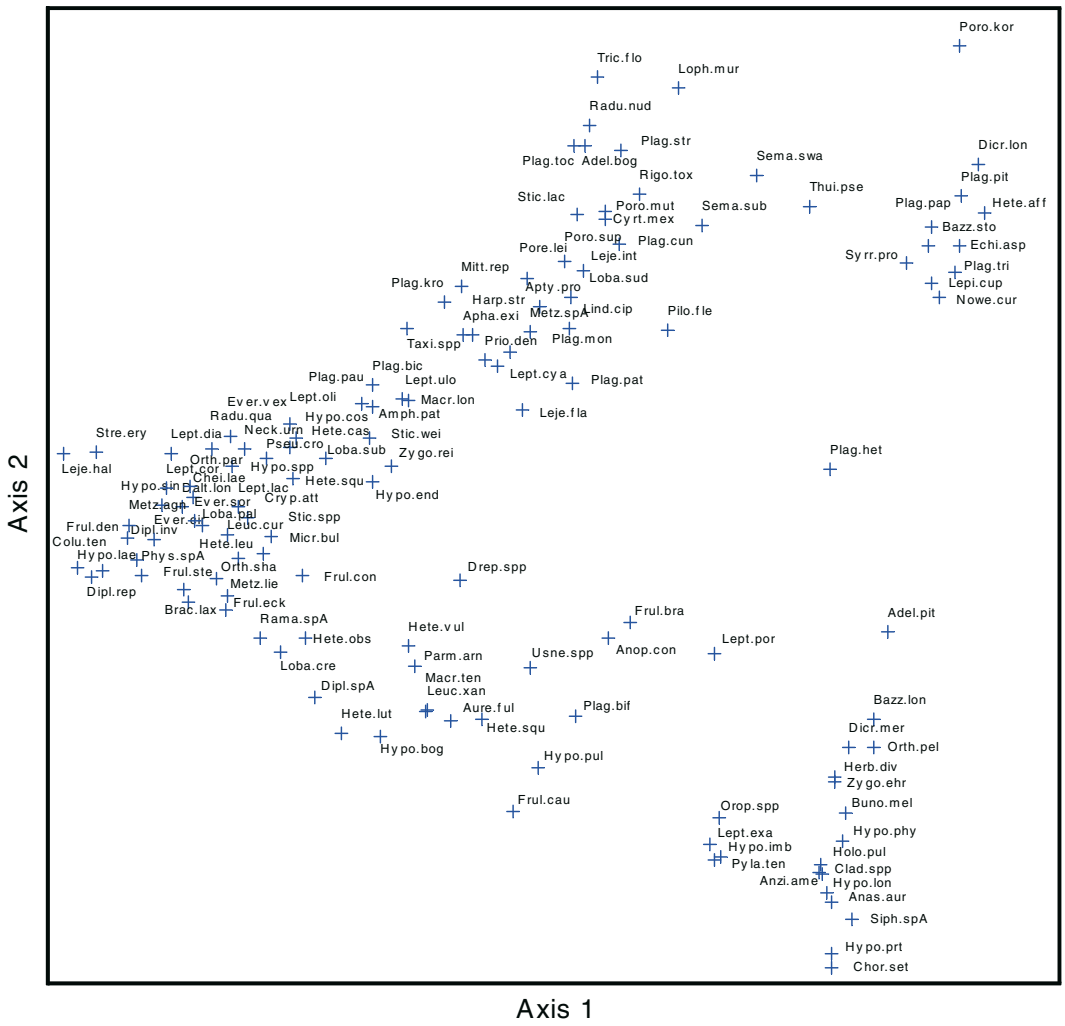

Figure 9. Ordination of species in the epiphyte species space using DCA after Beals smoothing. For acronyms of species see Table 2.

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, Figure 3), in spite of the large differences in tree height and forest structure between the three forest types (Table 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 and Holz, in press).

Table 7. pH of bark plots of *Quercus copeyensis* from about 2 m above ground.

$N = 5 \times 2 = 10$	PF	ESF	LSF
Average	4.1	5.1	4.5
SD	0.1	0.15	0.1

SD = standard deviation.

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 (Figure 6). In fact, the canopy of LSF was denser and the understorey more shaded than that of PF (Table 1, Figure 2). 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 (Table 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.

Although in general alpha diversity increases with three height (Figure 7), it reaches its highest values in the 'light transition zone' (McCune et al. 1997). This corresponds well with the fact, that alpha diversity is highest on trunks and lower branches in the ESF; but in the more dense LSF and PF the outer canopy is the zone showing the highest diversity (Figure 6). In contrast, 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 plot (Table 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 and 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. Cryptogamic epiphytes 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 (light, humidity, air temperature) and substrate (bark roughness, bark pH) conditions of their microhabitats. These conditions covary in different primary and secondary forest stands and along the vertical gradient within each forest stand (Pócs 1982; Richards 1984; Gradstein 1992; Holz et al. 2002; Köhler 2002).

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 cryptogamic epiphytes, 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 (Table 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 and 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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