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Impact of management intensity on non-vascular epiphyte diversity in cacao plantations in western Ecuador

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Abstract. A first study on the biodiversity of non-vascular epiphytes in cacao (*Theobroma cacao* L.) plantations in western Ecuador yielded 112 species (51 bryophytes, 61 lichens). Epiphyte assemblages of cacao plantations resembled those of tropical rain forests but species richness was usually lower and individual species were found at lower heights on the trunks. The vast majority of the species are widespread neotropical or pantropical species; one species, *Spruceanthus theobromae* (Spruce) Gradst., is endemic to cacao plantations of western Ecuador. Differences in management intensity, by manual removal of epiphytes from tree trunks ('*limpia*'), had a significant impact on epiphyte species diversity. Total species richness was significantly reduced in plantations with high management intensity, due mainly to the decreased diversity of lichens and liverworts; moss diversity was not affected by management regime. Total percentage cover of bryophytes was highest in plantations with low management intensity, while lichen cover was greatest in plantations with high management intensity. Crustose lichens and smooth mats growing closely appressed to the substrate were little affected by the *limpia* and their growth may have been promoted when larger-sized species were removed, by reducing competition. Cacao plantations with low and moderate management intensity serve as an important substitute habitat for ecological specialists (sun epiphytes, shade epiphytes) of the rain forest and are of considerable significance for their conservation.

Introduction

Cacao is an important crop in western Ecuador, which covers a total area of about 360,000 ha (17% of total agricultural land). It is cultivated mainly along the foothills of the Andes, from sea level to 500 m, and is traditionally grown under shade trees. Shade-management systems provide a suitable substitute habitat for various groups of tropical rain forest biota and may play an important role in species conservation (Greenberg 1998). High biodiversity in cacao plantations has been recorded for ants, lizards, birds, and mammals (Leston 1970; Room 1971, 1975; Robbins et al. 1992; Estrada et al. 1993a, b, 1994, 1997; Parrish et al. 1998; Power and Flecker 1998; Reitsma et al. 2001). They are also believed to be rich in epiphytes, especially bryophytes and lichens, but quantitative data on epiphyte diversity in these systems are lacking. Gradstein (1999) listed 30 species of liverworts occurring in cacao plantations in tropical America. Most of these are

Figure 1. Trunks of cacao trees in low (left; without *limpia*) and high management plantation (right; shortly after *limpia*).

common and widespread species. One, *Spruceanthus theobromae* (Spruce) Gradst., is endemic to western Ecuador where it occurs exclusively in cacao plantations subjected to low management intensities (Kautz and Gradstein 2001).

Cacao is cultivated mainly by small-scale farmers (Young 1994; Rice and Greenberg 2000). Plantations vary between 1 and 5 ha and use a low-input management type, without application of fertilizers or chemicals (Suárez 1993). A common management method in Ecuador is the so-called *limpia* (literally 'cleaning'), which involves the manual removal of epiphytic bryophytes and lichens from trunks and branches of the cacao trees (Figure 1). This practice is based on the assumption that the epiphyte layer negatively affects flower development and thus reduces cacao yield. The impact of epiphytes on cacao production has never been investigated, however, and it may well be less severe than is believed by the local farmers. On the other hand, it may be assumed that the diversity of the epiphytes is being decreased by their frequent removal (Kautz and Gradstein 2001).

The exclusive occurrence of the rare *S. theobromae* and the lack of data on epiphyte diversity in cacao plantations in general prompted us to undertake a study of the diversity of non-vascular epiphytes (bryophytes and lichens) in these systems. A first paper focused on the status of *S. theobromae* (Kautz and Gradstein 2001). In this second paper we present an analysis of the biodiversity of epiphytic bryophytes and lichens in cacao plantations and the impact of different management intensities (*limpia*).

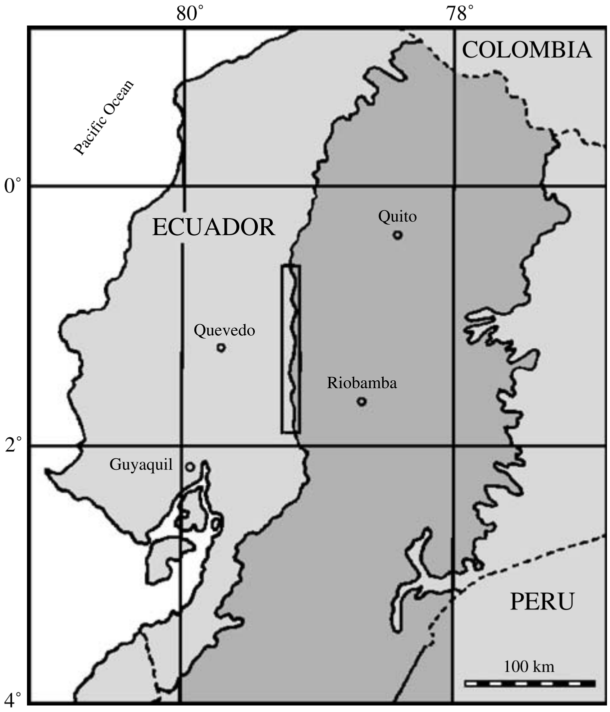

Figure 2. Geographical position of the investigation area (rectangle).

Materials and methods

Study area

The study area is located in western Ecuador in the main cacao producing zone, along the 200 m contour line of the Andes (79°17′ W, 0°35′ S) (Vera Barahona 1993) (Figure 2). At elevations between 150 and 250 m, 15 cacao plantations of different management types were selected (Table 1). The age of plantations ranged from 20 to 50 years. The region has a warm-tropical, semi-humid climate with average monthly temperatures of 23–25 °C, a rainy season between December and June and a pronounced dry season from July to November (Lauer and Erlenbach 1987; Vera Barahona 1993). Annual precipitation is about 2500 mm with peak values during the rainy season. Monthly rainfall in the dry season usually does not exceed 50 mm (Canadas and Estrada 1978). The climate differs from that elsewhere in the lowlands of western Ecuador by its higher annual rainfall and by the more frequent incidence of fog during morning hours. These fogs generate high relative humidity, averaging over 80% even in the dry season (Fowler et al. 1956). The natural vegetation in this region, consisting mainly of semi-deciduous tropical lowland rain forest (Canadas and Estrada 1978; Harling 1979), is nowadays almost completely

Table 1. Characteristics of 15 cacao plantations in western Ecuador.

Municipality	Geographical position	Altitude [m.a.s.l]	Management intensity[a]	Plot number	S_{obs}[b]	±1 SD[c]	S_{exp}[d]	S_{rare}[e]
San Luis	79°19′ W, 0°35′ S	260	1	18	31	6.443	33	29
Patricia Pilar 1	79°19′ W, 0°36′ S	220	1	18	40	4.116	47	31
Yatubí	79°19′ W, 0°36′ S	200	1	18	42	5.646	70	31
Pital 1	79°19′ W, 1°38′ S	200	1	18	43	6.045	63	31
Temistocles	79°20′ W, 1°25′ S	180	1	18	42	7.700	56	37
La Indústria	79°18′ W, 1°33′ S	250	2	18	40	5.534	65	36
Las Naves	79°19′ W, 1°17′ S	110	2	18	59	9.742	75	50
Tigre Alto	79°19′ W, 0°37′ S	240	2	17	40	4.583	47	36
Barranco	79°19′ W, 1°32′ S	140	2	18	33	3.048	35	28
Pital 2	79°19′ W, 1°37′ S	190	2	17	51	9.675	57	43
Pital 3	79°19′ W, 1°38′ S	250	3	20	27	3.200	35	20
El Pasaje	79°18′ W, 1°21′ S	180	3	18	41	8.367	46	33
Calope	79°17′ W, 1°02′ S	200	3	13	32	6.237	39	30
Asunción	79°20′ W, 1°35′ S	200	3	14	26	5.503	28	25
Patricia Pilar 2	79°20′ W, 0°35′ S	200	3	18	30	5.233	35	25

[a] 1 – low, 2 – moderate, 3 – high; [b] S_{obs}: observed species number; [c] SD: standard deviation; [d] S_{exp}: Chao2 estimate of species richness; [e] S_{rare}: rarefied species richness (standardized for 12 plots per plantation).

converted into cultivated land, such as citrus (*Citrus* sp.), cacao, oil palm (*Elaeis guineensis* Jacq.) and banana (*Musa* sp.) plantations, cassava (*Manihot esculenta* Crantz) fields and pastures.

Data sampling

Fieldwork was carried out between October and December, 1999. In each of the 15 plantations, six to eight cacao trees and one to four shade trees (coffee, citrus, avocado (*Persea americana* Miller), laurel (*Cordia alliodora* (Ruiz & Pav.) Oken)) were selected at random and sampled (Table 1). A total of 116 cacao trees and 29 shade trees were inventoried. On each cacao tree, two 30 cm × 40 cm plots were sampled for presence/absence of epiphytic bryophyte and lichen species: one plot at trunk base (height zone 1: 0–30 cm) and one plot higher up the trunk (height zone 2: 30–150 cm). Total percentage cover of bryophytes and lichens in each plot was estimated. Plots were positioned on the side of the trunk most densely covered with bryophytes. On shade trees one plot in height zone 2 was sampled.

Management regime of plantations was determined based on field observations and information from local farmers. Plantations were classified into three management types:

1. *Management intensity low*: removal of epiphytes, infected fruits and branches very incomplete and infrequent.
2. *Management intensity moderate*: removal partial and occasional (less than four times a year).
3. *Management intensity high*: removal complete and frequent (more than four times a year).

Bryophyte species were identified using Gradstein et al. (2001a) for liverworts and Sharp et al. (1994), Churchill and Linares (1995), and Buck (1998) for mosses. Lichens were determined to genus level and where possible to species level using Sipman (2001) and Hawksworth et al. (1995). Voucher specimens were deposited in the herbaria of the Catholic University of Quito, Ecuador (PUCE), the National Herbarium of Quito, Ecuador (QCA) and the University of Göttingen (GOET). Species were classified into life-form types following Richards (1984) and Bates (1998). Life-forms of bryophytes in the study area included turfs, mats, wefts, feathers, or pendants. Those of lichens were foliose, filamentose and squamulose macrolichens, and crustose microlichens. Geographical ranges of species were determined from taxonomic treatments and monographs. Four range types were distinguished: (1) *endemic*: restricted to Ecuador; (2) *neotropical*: widespread in tropical America but not occurring elsewhere; (3) *neotropical-montane*: occurring above 500 m in the mountains of tropical America; or (4) *pantropical*: widespread in the Tropics (America, Africa, Asia). By their ecological distribution in natural forest, species were classified into shade epiphytes, sun epiphytes and generalists following Acebey et al. (2003), Cornelissen and ter Steege (1989), Gradstein (1992), Gradstein et al. (2001b), Montfoort and Ek (1990), and Richards

(1954). Shade epiphytes are restricted to the forest understorey in dense, natural forest, sun epiphytes are restricted to the forest canopy, and generalists occur in the canopy as well as in the understorey.

Data processing

All data except moss data were normally distributed (Shapiro–Wilk, NS) with homogeneous variances (Levene-Test, NS). Count data (species richness) were submitted to parametric tests, ordinal data (bryophyte and lichen percentage cover) and moss count data were submitted to non-parametric tests.

Sampling completeness was calculated using the incidence-based Chao2-estimate (Chao 1987; Southwood and Henderson 2000):

$$S_{\mathrm{exp}} = S_{\mathrm{obs}} + \frac{a^2}{2b}$$

where S_{exp} = estimated species number, S_{obs} = observed number of species present in one site, a = species number recorded once (i.e., number of species only present on one cacao tree of a site/plantation), and b = number of species recorded twice. Individual cacao trees were treated as independent samples. Rarefaction was applied to standardize sampling effort for the different management intensities, using Coleman's method (Coleman 1981; Brewer and Williamson 1994). Species diversity among plantations was compared using 1-way ANOVA and *post hoc* Tukey test for normally distributed data (liverworts and lichens), and Kruskal–Wallis Test for moss data. The χ^2-test was applied to analyze life-forms, geographical ranges and ecological distributions as a function of management, the paired *t*-test was performed to analyze species richness as a function of vertical distribution. Non-parametric tests were used to compare the medians of bryophyte and lichen percentage coverage (Greig-Smith 1964; Fowler et al. 1998; all tests two-tailed with α set at 0.05). All statistical calculations were performed with SPSS 10.0 (SPSS 2000). Accumulation and rarefaction curves were computed with *EstimateS*, running 100 randomizations (Colwell 2000).

Results

Species diversity. 112 species of epiphytic bryophytes and lichens, in 30 families and 64 genera, were recorded from the 15 cacao plantations (261 plots) (Table 2). The pooled estimate of expected species diversity predicted that fewer than 40 additional species remain to be found (Chao2 = 154.67). Observed (S_{obs}) and expected (S_{exp}) species numbers for each of the plantations are given in Table 1. Accumulation curves indicate that sampling was representative for mosses and liverworts, but incomplete for lichens (Figure 3). The latter were the most diverse group, with 61 species in 17 families, followed by 38 species in four families of liverwort, and 13 species in nine families of moss. The most important family in terms of species number were the Lejeuneaceae (liverworts) with 32 species (about

Table 2. List of epiphytic bryophyte and macrolichen* species identified on 116 cacao trees and 29 shade trees in 15 cacao plantations in western Ecuador.

Species	Frequency[a]	Host trees[b]	Management[c]			Height zone[d]	Life-form[e]	Geographical distribution[f]	Ecological distribution[g]
			1	2	3				
Musci									
Crossomitrium patrisiae (Brid.) Müll. Hal.	I	C, A	×	–	×	1, 2	f	n	G
Cyrto-hypnum involvens (Hedw.) Buck	II	C, A	×	×	×	1, 2	w	n	Sh
Fissidens minutus Thwaits & Mitt.	II	C	×	×	×	1, 2	t	p	Sh
Henicodium geniculatum (Mitt.) Buck	I	C, A	–	×	×	1, 2	n.a.	p	S
Lepidopilum sp.	I	C	×	–	–	2	m	n.a.	Sh
Neckeropsis undulata (Hedw.) Reich.	IV	C, A	×	×	×	1, 2	f	n	G
Octoblepharum albidum Hedw.	I	A	×	×	–	1, 2	t	p	G
Pilotrichum evanescens (Müll. Hal.) Crosby	II	C, A	×	×	×	1, 2	n.a.	n	S
Pireella cymbifolia (Sull.) Card.	II	C, A	×	×	×	1, 2	n.a.	n	Sh
Pterogonidium pulchellum (Hook.) Müll. Hal.	I	C, A	×	×	×	1, 2	n.a.	n	S
Sematophyllum subpinnatum (Brid.) E. Britt.	I	A	–	–	×	1, 2	m	p	G
Syrrhopodon incompletus Schwaegr. var. *incompletus*	III	C, A	×	×	×	1, 2	t	p	Sh
Zelometeorium patulum (Hedw.) Manuel	II	C, A	×	×	×	1, 2	p	p	G
Hepaticae									
Aphanolejeunea camillii (Lehm.) Schust.	II	C, A	×	×	×	1, 2	m	p	G
Aphanolejeunea truncatifolia Horik.	I	C, A	×	×	×	1, 2	m	p	G
Archilejeunea auberiana (Mont.) Evans	II	C, A	×	×	×	1, 2	m	p	S
Archilejeunea parviflora (Nees) Schiffn.	I	C	–	×	×	1	m	p	Sh
Bryopteris filicina (Sw.) Nees	III	C, A	×	×	×	1, 2	f	nm	Sh
Ceratolejeunea cornuta (Lindenb.) Steph.	II	C, A	×	×	×	1, 2	m	n	G
Ceratolejeunea cubensis (Mont.) Schiffn.	III	C, A	×	×	×	1, 2	m	n	G
Ceratolejeunea filaria (Taylor ex Lehm.) Steph.	I	C	–	×	–	2	m	n	G

Table 2. (*continued*)

Species	Frequency[a]	Host trees[b]	Management[c]			Height zone[d]	Life-form[e]	Geographical distribution[f]	Ecological distribution[g]
			1	2	3				
Ceratolejeunea laetefusca (Aust.) Schiffn.	II	C, A	×	×	×	1, 2	m	n	G
Cheilolejeunea adnata (Kunze) Grolle	II	C, A	×	×	×	1, 2	m	n	G
Cheilolejeunea rigidula (Nees ex Mont.) Schust.	II	C, A	×	×	×	1, 2	m	p	G
Cheilolejeunea trifaria (Reinw., Blume & Nees) Mizut.	I	C	×	–	–	1, 2	m	p	G
Drepanolejeunea fragilis Bischl.	I	C, A	×	×	–	1	m	n	G
Frullania riojaneirensis (Raddi) Aongstr.	I	C, A	×	–	×	1, 2	m	nm	S
Harpalejeunea oxyphylla (Nees & Mont.) Schiffn.	I	C	–	×	–	1	m	n	Sh
Lejeunea caespitosa Lindenb.	I	C, A	×	×	–	1, 2	m	n	G
Lejeunea cancellata Nees & Mont.	II	C	×	×	×	1, 2	m	n	G
Lejeunea phyllobola Nees & Mont.	II	C, A	×	×	×	1, 2	m	n	G
Lejeunea controversa Gott. & Rabenh.	I	C, A	×	–	–	2	m	n	Sh
Lejeunea filipes Spruce	II	C, A	×	×	×	1, 2	m	n	G
Lejeunea laetevirens Nees & Mont.	III	C, A	×	×	×	1, 2	m	n	S
Lejeunea tapajosensis Lindenb.	II	C, A	×	×	×	1, 2	m	n	G
Lopholejeunea subfusca (Nees) Schiffn.	II	C, A	×	×	×	1, 2	m	p	S
Marchesinia brachiata (Sw.) Schiffn.	IV	C, A	×	×	×	1, 2	m	p	G
Mastigolejeunea auriculata (Wils.) Schiffn.	I	A	–	×	–	1, 2	m	p	S
Microlejeunea sp.	I	C, A	×	–	–	1, 2	m	n.a.	n.a.
Odontolejeunea lunulata (Web.) Schiffn.	I	C, A	×	–	–	1, 2	m	p	G
Plagiochila diffusa Steph.	I	C	×	×	×	1, 2	m	nm	Sh
Plagiochila montagnei Nees	V	C, A	×	×	×	1, 2	f	nm	G
Plagiochila subplana Lindenb.	I	C	–	×	×	1, 2	f	n	G
Prionolejeunea muricato-serrulata (Spruce) Steph.	I	C	×	–	–	2	p	n	Sh

Table 2. (*continued*)

Species	Frequency[a]	Host trees[b]	Management[c]			Height zone[d]	Life-form[e]	Geographical distribution[f]	Ecological distribution[g]
			1	2	3				
Radula javanica Gott.	II	C	×	×	×	1, 2	m	p	G
Radula quadrata Gott. et al.	I	C, A	×	×	–	1, 2	m	n	G
Spruceanthus theobromae (Spruce) Gradst.	II	C, A	×	×	–	1, 2	m	e	n.a.
Stictolejeunea squamata (Willd. ex Weber) Schiffn.	I	C	×	×	×	1, 2	f	n	Sh
Symbiezidium barbiflorum (Lindenb. & Gott.) Trev.	III	C, A	×	×	×	1, 2	m	p	G
Taxilejeunea pterigonia (Lehm. & Lindenb.) Schiffn.	I	C	×	×	×	1, 2	p	nm	G
Taxilejeunea obtusangula (Spruce) Evans	II	C, A	×	×	–	1, 2	m	n	G
Macrolichens									
Agonimia papillata (Eriksson) Died. & Aptroot	III	C, A	×	×	×	1, 2	s	p	
Coenogonium linkii Ehrenb.	IV	C, A	×	×	×	1, 2	fi	p	
Heterodermia obscurata (Nyl.) Trev.	II	C, A	×	×	×	1, 2	fo	n.a.	
Leptogium azureum (Ach.) Mont.	II	C, A	×	×	×	1, 2	fo	n.a.	
Leptogium cyanescens (Rabenh.) Körber	IV	C, A	×	×	×	1, 2	fo	n.a.	
Leptogium marginellum (Sw.) Gray	II	C, A	×	×	×	1, 2	fo	p	
Leptogium reticulatum Mont.	II	C	×	×	–	1, 2	fo	n.a.	
Parmotrema endosulphureum (Hillm.) Hale	I	C, A	–	×	×	1, 2	fo	p	
Parmotrema sp.	I	C	–	×	–	2	fo	n.a.	
Phyllopsora cf. *parvifoliella* (Nyl.) Müll. Arg.	III	C, A	×	×	×	1, 2	s	n.a.	
Phyllopsora sp.	I	C	×	–	–	2	s	n.a.	
Physcia atrostriata Moberg	I	C, A	×	×	×	1, 2	fo	p	

Table 2. (*continued*)

Species	Frequency[a]	Host trees[b]	Management[c]			Height zone[d]	Life-form[e]	Geographical distribution[f]	Ecological distribution[g]
			1	2	3				
Physcia sorediosa (Vain.) Lynge	I	C	–	×	–	1, 2	fo	n.a.	
Physcia Typ 1 + 2	I	C	×	×	–	2	fo	n.a.	
Pyxine sp.	I	A	–	×	–	2	fo	n.a.	
Sticta sp.	I	C	–	×	–	2	fo	n.a.	

*In most cases microlichens could be identified only to generic level; they include: *Arthonia* sp., *Bacidia* Typ 1–3, *Clathroporina* sp., *Cresponea* sp., *Cryptothecia* Typ 1–3, *Cryptothecia rubrocincta* (Ehrenb.) Thor, *Cyclographina* Typ 1–3, *Dichosporidium nigrocinctum* (Ehrenb.) Thor, *Dimerella* sp., *Graphina confluens* (Fée) Müll. Arg., *Graphina virginea* (Eschw.) Müll. Arg., *Graphina* Typ 1–2, *Graphis caesiella* Vain. s.l., *Graphis* Typ 1–2, *Letrouitia domingensis* (Pers.) Haf. & Bellem., *Letrouitia vulpina* (Tuck.) Haf. & Bellem., *Malcolmiella* Typ 1–7, *Myeloconis* sp., *Opegrapha* sp., *Pertusaria* sp., *Polymeridium* sp., *Porina mastoidea* (Ach.) Müll. Arg., *Porina nucula* Ach., *Porina* Typ 1–3, *Pyrenula* Typ 1–2, *Schistophoron tenue* Stirton, *Trypethelium* sp.

[a] Frequency (percentage of samples in which a species has been found): I – 0–5%, II – 6–20%, III – 21–40%, IV – 41–60%, V – 61–80%, VI – ≥81%.

[b] C – cacao trees, A – accompanying trees.

[c] 1 – low, 2 – moderate, 3 – high.

[d] 1 – tree base, 2 – 1.5 m height.

[e] f – feather, fi – filamentose, fo – foliose, m – mat, p – pendant, s – squamulose, t – turf, w – weft.

[f] e – endemic, n – neotropical, nm – neotropical–montane, p – pantropical.

[g] G – generalist, S – sun epiphyte, Sh – shade epiphyte, n.a. – no information available.

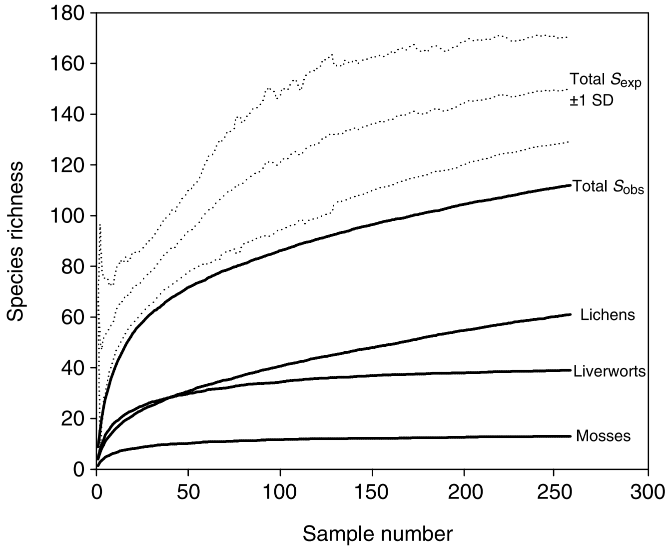

Figure 3. Species richness curves of the pooled replicates of moss, liverwort, and lichen diversity for a given number of randomly sampled plots. Solid lines indicate the observed species richness. Dotted lines represent the expected total species richness (Chao2 ± 1 SD).

30% of all epiphytic bryophytes and lichens, and over 80% of all bryophytes). The most common species were the bryophytes *Ceratolejeunea cubensis*, *Marchesinia brachiata*, *Neckeropsis undulata*, and *Plagiochila montagnei*, and the lichens *Dichosporidium nigrocinctum* and *Leptogium cyanescens*. They occurred in more than 30% of the plots, had highest percentage cover and determined the visual appearance of the epiphytic vegetation.

The total species number recorded in all moderately managed plantations was 86, as compared to a total of 78 and 65 species in plantations with low and high management intensity, respectively. Estimated species richness was 115, 118 and 84 for plantations with low, moderate and high management intensity. Significantly more species were found in moderately managed plantations than in plantations with high management intensity (ANOVA: $F_{2,12} = 5.058$, $P < 0.05$; standardized for sampling effort (rarefaction); Table 1, Figure 4). High species richness in low and moderately managed plantations was mainly due to lichens, while liverwort and moss diversity were nearly identical. The species richness of liverworts and lichens but not of mosses was significantly less in highly managed plantations (ANOVA: $F_{2,12} = 3.954$, $P < 0.05$ (liverworts), $F_{2,12} = 4.024$, $P < 0.05$ (lichens); Kruskal–Wallis: $H_2 = 1.032$ (mosses, NS)).

The frequency of many species was much reduced (more than 50%) in plantations with high management intensity. Many macrolichens, shade epiphytes (e.g., *Harpalejeunea oxiphylla*, *Lejeunea controversa*, *Lepidopilum* sp., *Prionolejeunea muricato-serratula*), and the endemic *S. theobromae* were absent. Other species appeared to be less sensitive to management intensity and were found with more or

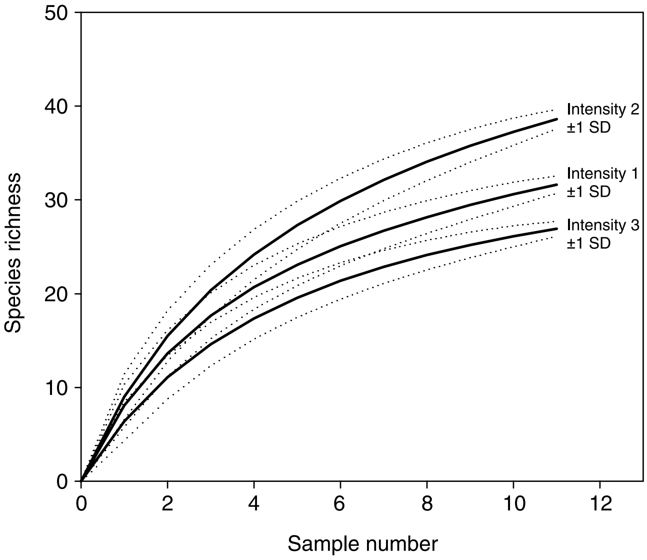

Figure 4. Rarefaction curves of the average species richness in cacao plantations with low, moderate and high management intensity (ANOVA: $F_{2,12} = 5.058$, $P < 0.05$; standardized for 12 plots per plantation). Dotted lines: ±1 SD. 1 – low, 2 – moderate, 3 – high management intensity.

less the same frequency in each of the three types of plantations (e.g., bryophytes *Aphanolejeunea camillii*, *Cheilolejeunea adnata*, *C. rigidula*, *Pireella cymbifolia*, *Pterogonidium pulchellum*, *P. montagnei*, *Symbiezidium barbiflorum*, *Zelometeorium patulum*, and lichens *Dimerella* sp., *Phyllopsora* cf. *parvifoliella*, and *Porina* sp.). A few species were found more frequently in plantations with high management intensities, for example, several crustose lichens and the bryophytes *Lopholejeunea subfusca* and *Henicodium geniculatum*. In the natural forest these species are typical drought-tolerant sun epiphytes.

Life-forms and percentage cover. 67% of the 51 bryophytes were mats, the majority of them Lejeuneaceae, followed by 18% feathers and pendants, and 8% turfs and wefts. Among the lichens 72% were crustose, 20% foliose, and 5% squamulose or filamentose. Species number of mats was more than 25% lower in plantations with high management intensity, as compared with moderate or low management intensity. Species numbers of other life-forms were not significantly reduced (χ^2-test, $\chi^2_6 = 1.730$ (NS)). The percentage cover of bryophytes was significantly less in plantations with high management intensity (Kruskal–Wallis: $H_2 = 13.786$, $P < 0.01$). Lichens had higher cover values in high management intensity plantations than in low or moderate, but the differences were not significant (Kruskal–Wallis: $H_2 = 1.945$ (NS)). Visual observation indicated that larger-sized life-forms such as large mats, feathers, pendants and macrolichens were negatively affected by *limpia*, by reducing their size and vigor.

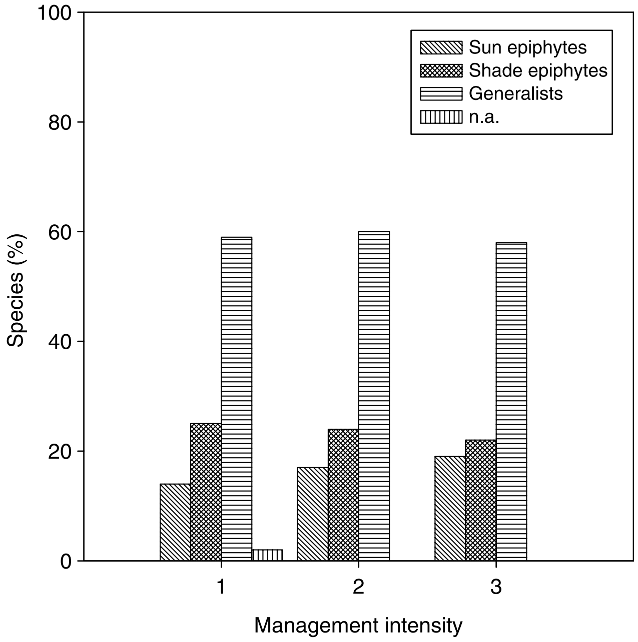

Figure 5. Ecological distribution of bryophyte species in plantations with low, moderate and high management intensities (n.a. = no classification available due to a lack of information for these species).

Geographical ranges. About half of the bryophytes (49%) were widespread neotropical species, 18 (35%) had a pantropical range, and five (10%) were neotropical-montane. One, *S. theobromae*, was endemic to western Ecuador. Range size did not differ among plantations with different management intensity (χ^2-test, $\chi^2_4 = 0.988$ (NS)). However, species with wide, pantropical distributions were more common in plantations with high management intensity. Species with narrow ranges were more scarce. *Spruceanthus theobromae*, the single endemic species of the western Ecuadorian cacao plantations, was only found in plantations with low and moderate *limpia* and did not occur in plantations with high management intensity. This is presumably due to its large size and frequent projecting growth.

Ecological distribution. Almost 60% of the bryophytes were generalists, 24% (12 species) were shade epiphytes, and 16% (eight species) sun epiphytes. Plantations with different management intensities did not differ with respect to the ecological distribution of species (χ^2-test, $\chi^2_4 = 0.410$ (NS)). However, the percentage of sun epiphytes increased in plantations with high management intensity whereas diversity of shade epiphytes diminished with increasing management intensity (Figure 5).

Vertical distribution. Species richness in all plantations was significantly higher in the middle region (zone 2) than in the basal region of the trunk (zone 1) (paired *t*-test:

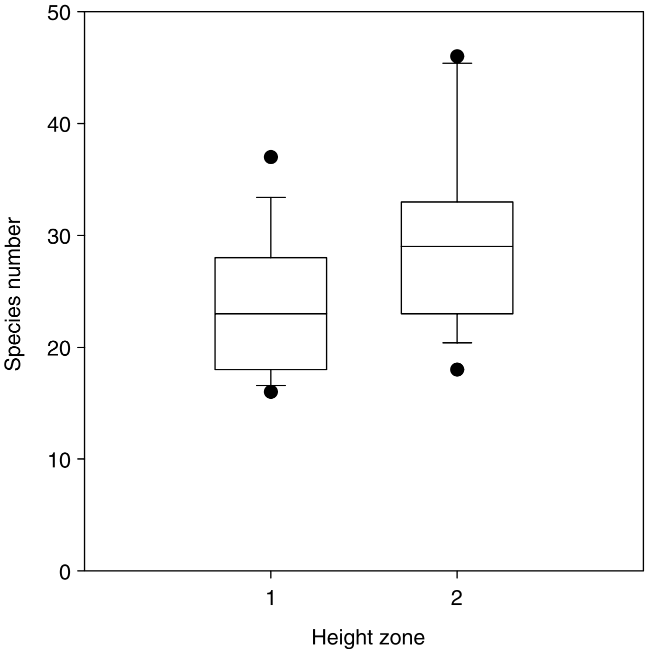

Figure 6. Species richness of bryophytes and lichens in height zones 1 and 2 (GLM: $F = 10.083$, $P < 0.01$). In the box plot, the middle line stands for the median. The ends of the boxes ('hinges') represent the lower and upper quartile (25th to 75th percentile). The two vertical lines ('whiskers') outside the box extend to the minimum and maximum values within 1.5 the interquartile range. Outliers are displayed as separate points (●).

$t_{14} = -6.244$, $P < 0.01$) (Figure 6). The observed differences were mainly caused by the higher diversity of lichens in the middle region (47 species) as compared to the basal region (31 species); the species richness of bryophytes was nearly identical in the two zones. Similarly, percentage cover of lichens was significantly greater in the middle region than in the basal region, while bryophyte coverage showed no differences (Wilcoxon Signed-Ranks: $Z = -3.181$, $P < 0.01$ and $Z = -0.534$ (NS), respectively). All sun epiphytes except *P. pulchellum* occurred with higher frequency in the middle region than in the basal region of the trunk. On the other hand, shade epiphytes such as *Archilejeunea parviflora*, *Fissidens minutus*, and *Cyrto-hypnum involvens*, showed clear preferences for the basal region.

Discussion

Species diversity. Cacao plantations are generally considered to be one of the most biologically rich agricultural systems and are assumed to be an important substitute habitat for various biota (Rice and Greenberg 2000). This paper is the first study of non-vascular epiphyte diversity in cacao plantations. The number of species found (61 of lichen, 38 of liverwort, and 13 of moss) is about half to two thirds the number recorded from selected trees in lowland rainforests in the Guianas and a submontane rainforest at 600 m in Bolivia (Cornelissen and ter Steege 1989; Montfoort and Ek 1990; Acebey et al. 2003), about the same as recorded from four trees in a submontane rainforest at 1000 m in Colombia (Wolf 1993), 1.3 times higher than in 1.5 ha of Amazonian rainforest along the Rio Surumoni in Venezuela (Gradstein, unpublished), and 2.5 times higher than in two coffee plantations at 1700 m in Colombia (van Dunné and Wolf 2001; 45 mostly unidentified species recorded).

Phytosociologically, the epiphytic bryophyte vegetation of the western Ecuadorian cacao plantations belongs to the *N. undulata–Bryopteris filicina* association (Kürschner et al. 1999), a community of primary lowland and submontane rainforests. The occurrence of this community in cacao plantations supports the notion that these plantations are similar to tropical rainforests in terms of their epiphyte assemblages, although they harbor less species diversity.

As expected, the exposed, relatively dry middle parts of the trunks of the cacao trees (zone 2) were mainly inhabited by sun epiphytes and generalists, including macrolichens. Shade epiphytes occurred primarily on the moister trunk bases (zone 1). Vertical distribution of species was markedly lowered as compared with natural forest. Thus, canopy specialists of the forest occurred at relatively low height on the trunks of the cacao trees. This vertical shift is usually explained by the higher light intensities and drier microclimate in the plantations as compared with dense forest (Sipman and Harris 1989; Gradstein 1992; Acebey et al. 2003). About 60% of the bryophyte species were ecological generalists, followed by 24% shade epiphytes and 16% sun epiphytes. These percentages are very different from rainforests, which harbor many more specialists than generalists (Cornelissen and Gradstein 1990; Gradstein et al. 1990). Strikingly, one out of every four bryophytes in cacao plantations was a shade specialist (Table 2). Shade epiphytes, characteristic of the understorey of dense primary forest, are considered to be less drought resistant than sun epiphytes and generalists, and therefore more susceptible to deforestation than other species (Gradstein 1992; Acebey et al. 2003). Their establishment and survival in secondary woody habitats is usually impeded by the drier and warmer conditions in these vegetations, caused by the more open and lower canopy as compared with the primary forest. Shade epiphytes are therefore considered threatened organisms (Gradstein et al. 2001a). The frequent presence of shade epiphytes in the investigated cacao plantations is of significant importance to their conservation and lends strong support to the notion that these plantations may act as refugia for threatened rainforest organisms (Greenberg 1998).

Management intensity. Differences in management regime had a significant impact on the diversity of non-vascular epiphytes. Total species richness of lichens and liverworts was significantly reduced in plantations with high management intensity. This effect could not be explained by smaller sample size (verified by rarefaction) and thus was not due to chance effects. Species richness of mosses, however, was not affected by the management regime. Total percentage cover of lichens increased with higher management intensity, that of bryophytes decreased. *Limpia* furthermore impacted the size and vigor (but not the total species number) of the larger-sized plants such as feathers, large mats, pendants, and macrolichens (personal observation). The lack of the endemic *S. theobromae* in plantations with high management intensity should also be due to its large plant size. Plants growing closely appressed to the substrate such as smooth mats and crustose lichens were less affected by *limpia*. Their growth might even be promoted due to reduced competition when large species are removed. This finding is reflected in the increased frequencies of crustose microlichens and sun epiphytes (mats) in intensively managed plantations.

The peak of species richness at the moderate management intensity level might be interpreted as a confirmation of the intermediate disturbance hypothesis (IDH) (Connell 1978; Petraitis et al. 1989; Huston 1994), which assumes that 'the highest diversity is maintained at intermediate scales of disturbance'. Recently, this hypothesis has been intensively discussed (e.g., Collins et al. 1995; Chesson and Huntly 1997; Wootton 1998; Beckage and Stout 2000; Buckling et al. 2000; Mackey and Currie 2000, 2001; Kondoh 2001; Ikeda 2003). It has been argued that disturbance is difficult to measure or quantify, and that the diversity-disturbance model of Connell is difficult to apply in practice (Reynolds et al. 1993; Underwood 1999; Glitzenstein et al. 2003). On the other hand, the usefulness of the IDH in conservation management has become widely accepted. In view of the importance of the hypothesis, we consider that our findings lend additional support to the IDH proposed by Connell.

Conclusions

Cacao plantations are an important substitute habitat for non-vascular rainforest epiphytes (bryophytes and lichens) in spite of their somewhat reduced species diversity. Plantations with low and moderate management intensity serve as a refuge for ecological specialists (sun epiphytes, shade epiphytes) and are of importance for their conservation. Depending on its frequency, the traditional *limpia* of western Ecuadorian cacao plantations may severely impact epiphyte diversity by diminishing species diversity (but not of crustose lichens), particularly of shade epiphytes and the endemic *S. theobromae*.

Cacao plantations in Ecuador are considered low-input agroecosystems because agrochemicals are not used. The possible conversion of the traditional shade systems into low-diversity shade or even full-sun systems, a tendency observed in recent years in cacao production in Peru and Colombia (Rice and Greenberg 2000), is probably a more severe threat to epiphyte diversity than current management practices. With world cacao prices decreasing, farmers in western Ecuador may be forced to intensify management or change to more profitable crops such as banana or oil palm (Food and Agriculture Organization 2001). At the same time, the remnant rainforests of western Ecuador are highly endangered by the pressure of the growing human population, and many of its native endemic species may be on the brink of extinction (Dodson and Gentry 1991; but see also Valencia et al. 2000). In the part of western Ecuador where this study has been undertaken, patches of undisturbed forest remain in only three small reserves (100–300 ha each). Thus, rainforest species in western Ecuador are clearly threatened. The continued existence in the region of cacao plantations with low and moderate management intensities is therefore of significant importance for the conservation of the local bryophyte and lichen diversity.

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