

Conservation of Vascular Epiphyte Diversity in Shade Cacao Plantations in the Chocó Region of Ecuador

Xavier Haro-Carrión^{1,4}, Tannya Lozada², Hugo Navarrete¹, and G. H. J. de Koning³

¹ Herbario QCA, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Apartado 17-01-2184, Quito, Ecuador

² Agroecology, Georg-August-Universität Göttingen, Waldweg 26, D-37073 Göttingen, Germany

³ Institute of Soil Science and Forest Nutrition, Georg-August-Universität Göttingen, Buesgenweg 2, D-37770 Göttingen, Germany

ABSTRACT

To assess the contributions of rustic shade cacao plantations to vascular epiphyte conservation, we compared epiphyte species richness, abundance, composition, and vertical distributions on shade trees and in the understories of six plantations and adjacent natural forests. On three phorophytes and three 10 × 10 m understory plots in each of the agroforestry plantations and natural forests, 54 and 77 species were observed, respectively. Individual-based rarefaction curves revealed that epiphyte species richness was significantly higher on forest phorophytes than on cacao farm shade trees; detailed analyses showed that the differences were confined to the inner and outer crown zones of the phorophytes. No differences in epiphyte species richness were found in understories. Araceae, Piperaceae, and Pteridophyta were less species-rich in plantations than in forests, while there were no differences in Orchidaceae and Bromeliaceae. Regression analysis revealed that epiphyte species richness on trunks varied with canopy cover, while abundance was more closely related to soil pH, canopy cover, and phorophyte height. For crown epiphytes, phorophyte diameter at breast height (dbh) explained much of the variation in species richness and abundance. There were also pronounced downward shifts in the vertical distributions of epiphyte species in agroforests relative to natural forests. The results confirm that epiphyte diversity, composition, and vertical distributions are useful indicators of human disturbance and showed that while the studied plantations serve to preserve portions of epiphyte diversity in the landscape, their presence does not fully compensate for the loss of forests.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: agroforests; biodiversity; cacao culture; epiphytic plants; Johansson zones; land uses; phorophyte; shade tree.

SUBSTANTIAL AND CONTINUED HUMAN-INDUCED LOSSES of tropical forest cover promote calls to protect the remaining undisturbed forests and conserve biodiversity in human-affected ecosystems (Pimentel *et al.* 1992, Szaro & Johnston 1996). It is also thought that proper management of anthropogenic ecosystems can reduce pressure on pristine forests (Brown & Lugo 1990, Szaro & Johnston 1996, McNeely 1998). In any case, a better understanding of the ecology of these human-modified ecosystems is needed to support the implementation of landscape-level conservation measures (Brown & Lugo 1990, Putz *et al.* 2001).

Vascular epiphytes are important components of the biodiversity of tropical vegetation, and because they are reportedly susceptible to human activities, they have been proposed as indicators of levels of human disturbance and overall ecosystem health (Turner *et al.* 1994, Benzing 1998, Hietz 1999, Nadkarni 2002). With increasing anthropogenic disturbances, epiphyte species richness declines (Hietz 1999, Barthlott *et al.* 2001, Krömer & Gradstein 2003) and community composition changes (Flores-Palacios & García-Franco 2004, Werner *et al.* 2005). For example, in humid montane Andean forests, where the global maximum in vascular epiphyte diversity is observed (Gentry & Dodson 1987, Küper *et al.* 2004, Krömer *et al.* 2005), Barthlott *et al.* (2001) and Krömer and Gradstein (2003) found that epiphyte diversity in secondary vegetation was

only half that of undisturbed forest. Negative impacts of human activities on epiphyte diversity were also observed in lowland forests in Singapore and the Dominican Republic (Turner *et al.* 1994, Martin *et al.* 2004).

The differences between natural and managed ecosystems in species richness and composition of vascular epiphytes are often related to the intensity of human intervention (Hietz 1999, Barthlott *et al.* 2001, Hietz 2005, Wolf 2005). Most anthropogenic disturbances reduce the average size and diversity of host trees (phorophytes), which directly relate to declines in epiphyte diversity (Hietz-Seifert *et al.* 1996; Hietz 1999, 2005; Barthlott *et al.* 2001; Wolf 2005). The loss of particularly favorable phorophyte species and the drier and brighter conditions that result from human disturbance may also drive declines in epiphyte species diversity (Benzing 1990, 1998; Nieder *et al.* 2001; Nadkarni 2002; Acebey *et al.* 2003). In particular, species that require shade and high humidity, such as many Hymenophyllaceae ferns, decline in abundance or are locally extirpated when canopy cover is reduced (Barthlott *et al.* 2001, Krömer & Gradstein 2003, Flores-Palacios & García-Franco 2004, Hietz 2005, Werner *et al.* 2005, Wolf 2005). In contrast, drought-resistant species may benefit from anthropogenic disturbances and may be better represented in managed than in natural ecosystems. Examples of disturbance-favored vascular epiphytes include many ferns in the Polypodiaceae, hemiepiphytic aroids, and some species of bromeliads (Barthlott *et al.* 2001, Krömer & Gradstein 2003, Merwin *et al.* 2003, Martin *et al.* 2004, Werner *et al.* 2005, Hietz *et al.* 2006).

Received 3 October 2007; revision accepted 16 September 2008.

⁴Corresponding author; current address: Department of Biology, University of Florida, Bartram Hall 511, P.O. Box 118525, Gainesville, Florida 32611-8526, U.S.A.; e-mail: xavierhc@gmail.com

In multi-storied agroforestry systems (Schroth *et al.* 2004), epiphyte diversity is often substantial (Rice & Greenberg 2000, Hietz 2005, Solís-Montero *et al.* 2005). In shade coffee plantations, for example, similar numbers of vascular epiphyte species were found in plantations with old shade trees than in surrounding natural forests (Hietz 2005). Similarly, the nonvascular epiphyte community in shade cacao plantations may resemble that of tropical rain forest (Nöske 2004, Andersson & Gradstein 2005). Studies of animal communities in these agroforests have also reported notable preservation of various species of birds, bats, and insects (Reitsma *et al.* 2001; Waltert *et al.* 2003; Faria *et al.* 2006, 2007; Bos *et al.* 2007; Faria & Baumgarten 2007; Van Bael *et al.* 2007), but no comparable studies are apparently available for vascular epiphytes.

We compared species diversity, floristic composition, and vertical distributions of vascular epiphytes in natural forests and rustic shade cacao plantations. We also evaluated the main management-related factors that might influence vascular epiphyte diversity and composition. We carried out this study in a mosaic landscape with patches of forests, agroforests, and agricultural monocultures in the humid lowland tropical region of northwestern Ecuador.

METHODS

STUDY SITES AND SAMPLING.—The study sites were in northwestern Ecuador near the coastal town of Cabo San Francisco (0°39'14" N, 80°02'59" W) in Esmeraldas Province at altitudes of about 200 m. The natural vegetation in this region is lowland tropical rain forest, with a mean annual rainfall of 3000 mm, no distinct dry season, and a mean annual temperature of approximately 25°C (Neill 1999). This area is part of the Chocó biogeographical region, one of the world's 25 biodiversity hotspots (Myers *et al.* 2000).

The study area is characterized by sloping terrain and a mosaic of relatively undisturbed natural forests (hereafter, referred to as 'FOREST'), shade cacao plantations (hereafter, referred to as 'CACAO'), and small pastures and arable crop fields. The forests experienced some selective logging, but the disturbances were relatively minor. The shade cacao plantations we studied fit the description of 'rustic cacao farms' of Rice & Greenberg (2000). These agroforests were minimally managed during the 15 years prior to this study, with no intensive weeding or pruning and no use of chemical herbicides. Only one of the 18 shade trees on which we inventoried epiphytes in the cacao farms was obviously planted, while the others, while not huge trees, were apparently forest relicts (See Table S1 for details).

The six CACAO plots in which we worked were all on small farms with similar management intensities; the FOREST plots were in natural forest adjacent to each CACAO plot. In each site, we established a 50 × 50 m plot in which we randomly selected three large trees from all of those that we judged safe to climb (*e.g.*, no obvious signs of branch rot). Each of these phorophytes was schematically divided into five height zones for sampling (modified after Johansson 1974): Johansson zone (JZ) 1 (JZ1) ranges from 0 to 1.5 m above ground; JZ2 from 1.5 m above ground to the first major ramification; JZ3 comprises the inner crown, JZ4 the middle

crown, and JZ5 the outer crown. Single-rope canopy techniques were used to access each tree crown (Perry 1978, Jepson 2003). Data on epiphyte species composition of the middle and upper canopy are based on a randomly chosen first-order main branch. When individual epiphytes were difficult to count or identify, the branch was removed and processed on the ground.

All vascular epiphytes (including hemiepiphytes as well as accidental and facultative epiphytes) were sampled and recorded by JZ. In the case of species that covered entire trunks or branches (mostly aroids or piperoids), we estimated the number of individuals by counting the number of green stems in the middle of the trunk or along the selected branch. In the case of clonal plants (mostly bromeliads), we counted each tank as an individual.

Because the epiphyte flora on shrubs and small trees in the forest understory is usually different from that on large canopy trees (Krömer *et al.* 2007), vascular epiphytes growing on the woody understory vegetation (including palms) were also sampled in 10 × 10 m plots around each phorophyte (modified after Gradstein *et al.* 2003). We defined 'understory' as woody vegetation reaching to no more than three quarters of the canopy height and plants 2–15 cm diameter at breast height (dbh), except palms, in which dbh was not taken into account. Voucher specimens were deposited in Herbarium QCA, with duplicates in QCNE, Quito, Ecuador.

Phorophytes were identified to species and their height, dbh, crown cover density, and surrounding soil pH were recorded (Table S1). Height was measured with a hypsometer (Vertex IV Hypsometer, Haglöf, Sweden). Canopy cover at 1.3 m from the ground was estimated with a canopy densiometer at two points 1.5–2.0 m from the trunk of each phorophyte. Because soil conditions are important, at least, for hemiepiphytes (Leimbeck & Balslev 2001), soil pH was measured in a 1:10 solution of fresh soil and distilled water (three soil samples taken 1–1.5 m of each phorophyte at 0–10 cm below the litter layer were bulked for each tree).

Because epiphytic bryophytes are known to provide suitable substrates for vascular epiphytes, and given that their removal changes the microclimate (Frahm & Gradstein 1991, Freiberg 2001, Nieder *et al.* 2001), bryophyte biomass (dry weight) was measured by taking 160-cm² samples in each JZ. Bryophyte trunk samples were taken from the middle of each trunk zone and at the base of each ramification in the crown.

Finally, the number of understory shrubs and small trees was recorded in the 10 × 10 m plots centered around each phorophyte. To characterize the abiotic environment in CACAO and FOREST plots, air temperature and relative humidity were measured continuously for 30 d at 10-min intervals using data loggers (HOBO Pro RH/Temp, Onset Pocasset, MA, USA) installed at the inner crown (JZ3) of phorophytes. We collected these data on one phorophyte in each of three and four pair of FOREST–CACAO plots.

DATA ANALYSIS.—Individual-based rarefaction curves computed with EstimateS software (V. 7.5) were used to compare patterns of epiphyte species richness between phorophytes, understory plots, and JZs in FOREST and CACAO. This approach corrects for differences in the numbers of individuals sampled in comparisons of species richness (Gotelli & Colwell 2001). We set individuals as

samples and then calculated the curves using the Mao Tao estimator (Colwell 2004). The significance of observed differences in species richness between land-use types (at $P < 0.05$) was evaluated by visually comparing rarefaction curves and their associated 95% confidence intervals (CIs). If the total observed richness (for a given community) fell outside the 95% CI, then we inferred that samples contained significantly different number of species.

We compared epiphyte abundance and the Simpson index (obtained in PAST version 1.31; Hammer *et al.* 2005) for total phorophyte, JZs, and understory) with *t*-tests. The same procedure was applied to compare phorophyte dbh, height, canopy cover, soil pH, and bryophyte cover as well as the densities of understory shrubs and small trees. Bryophyte biomasses in FOREST and CACAO were also compared by JZ. To compare temperatures and relative humidities between land-use types, instead of comparing the mean values, the differences between the highest and the lowest value (range) during each day were calculated and compared. We chose this approach because we believe that variation within days is more useful than the mean values in analyzing abiotic differences and their possible relationship with vascular epiphyte diversity. For reference, mean values are also provided. The differences between FOREST and CACAO in species richness and abundance of Araceae, Bromeliaceae, Orchidaceae, Piperaceae, and Pteridophyta were tested using the Mann–Whitney tests.

The effects of abiotic environmental variables and phorophyte characteristics on species diversity were assessed with general regression models (GRMs) with backward stepwise elimination. We used land use as a categorical independent variable, species richness and abundance per site as dependent variables, and phorophyte dbh, height, canopy cover, soil pH, and bryophyte biomass per site as continuous predictor variables. When there were significant correlations among individual variables, the best explanatory variable was used in the GRMs. Temperature and relative humidity data were excluded because simultaneous data was not available for all 12 sites.

Community composition was compared using the Chao–Jaccard–Raw abundance-based index (new Jaccard index) obtained

in EstimateS for each of the five JZs. Floristic similarity between communities in the two land-use types was analyzed, comparing each JZ in FOREST against all zones in CACAO to estimate differences in community similarity among zones. To describe community changes, the vertical distribution patterns of shared species and the location of exclusive species in FOREST and CACAO are provided as well. Shared species vertical distributions are represented by the species with the highest numbers of individuals present in both land-use types, and exclusive species vertical distributions are those restricted to one land-use type and with more than five individuals. The analyses were conducted in Statistica 6.0 (STATSOFT INC. 2003) unless specified otherwise.

RESULTS

EPIPHYTE DIVERSITY.—A total of 91 species and 2003 vascular epiphyte individuals were recorded on the 36 sampled trees and in their surrounding understories. Forty species were found in both land-use types, 37 exclusively in FOREST, and 14 exclusively in CACAO. The average number of epiphyte species in phorophytes was significantly higher in FOREST than in CACAO; Simpson’s index values for the epiphytes were also higher in FOREST ($P = 0.008$). The average number of epiphyte individuals, 138 (± 52 SD) and 101 (± 57 SD) in FOREST and CACAO, respectively, did not differ. Epiphyte species richness and densities were lower in the understory than on phorophyte trees but did not differ between the land-use types (Table 1; Fig. S1). Only 2 of the 14 species present only in CACAO and 13 of the 37 present only in FOREST were represented by more than 5 individuals, all of them in phorophytes and none in the understory (Fig. S2).

Comparisons among JZs revealed that the differences in epiphyte species diversity were concentrated in the crown zones. For FOREST, the highest numbers of species and individuals were in the inner crown (JZ3). In contrast, the highest densities of individuals in the cacao agroforests were on the upper phorophyte trunk (JZ2), while species richness was highest in JZ2 and JZ3. When comparing species richness in each of the zones between FOREST and CACAO, no differences were found in the phorophyte

TABLE 1. Mean (± 1 SD) vascular epiphyte species richness, abundance, and Simpson index in FOREST (F) and CACAO (C) for understory, total phorophyte, and each phorophyte Jobanson zone (JZ) independently (N = 6 sites). P values for species richness are based on the overlap of the 95% CIs around the rarefaction curves (significant differences in bold); *t*-tests were used to compare epiphyte abundance and Simpson index values.

	Species richness			Abundance			Simpson index		
	F	C	P	F	C	P	F	C	P
Understory	14 \pm 5	9 \pm 5	NS	59 \pm 22	36 \pm 19	0.079	0.8 \pm 0.04	0.7 \pm 0.19	0.179
Total phorophyte	29 \pm 13	15 \pm 4	< 0.05	138 \pm 52	101 \pm 57	0.276	0.9 \pm 0.04	0.8 \pm 0.06	0.008
JZ1	8 \pm 4	5 \pm 3	NS	19 \pm 11	16 \pm 12	0.759	0.7 \pm 0.15	0.6 \pm 0.15	0.192
JZ2	8 \pm 2	7 \pm 4	NS	30 \pm 8	44 \pm 33	0.319	0.7 \pm 0.15	0.7 \pm 0.08	0.937
JZ3	16 \pm 8	7 \pm 5	< 0.05	53 \pm 27	28 \pm 16	0.075	0.9 \pm 0.07	0.6 \pm 0.26	0.023
JZ4	7 \pm 5	3 \pm 2	NS	20 \pm 10	9 \pm 6	0.048	0.7 \pm 0.18	0.4 \pm 0.22	0.113
JZ5	5 \pm 5	1 \pm 1	< 0.05	16 \pm 20	4 \pm 7	0.088	–	–	–

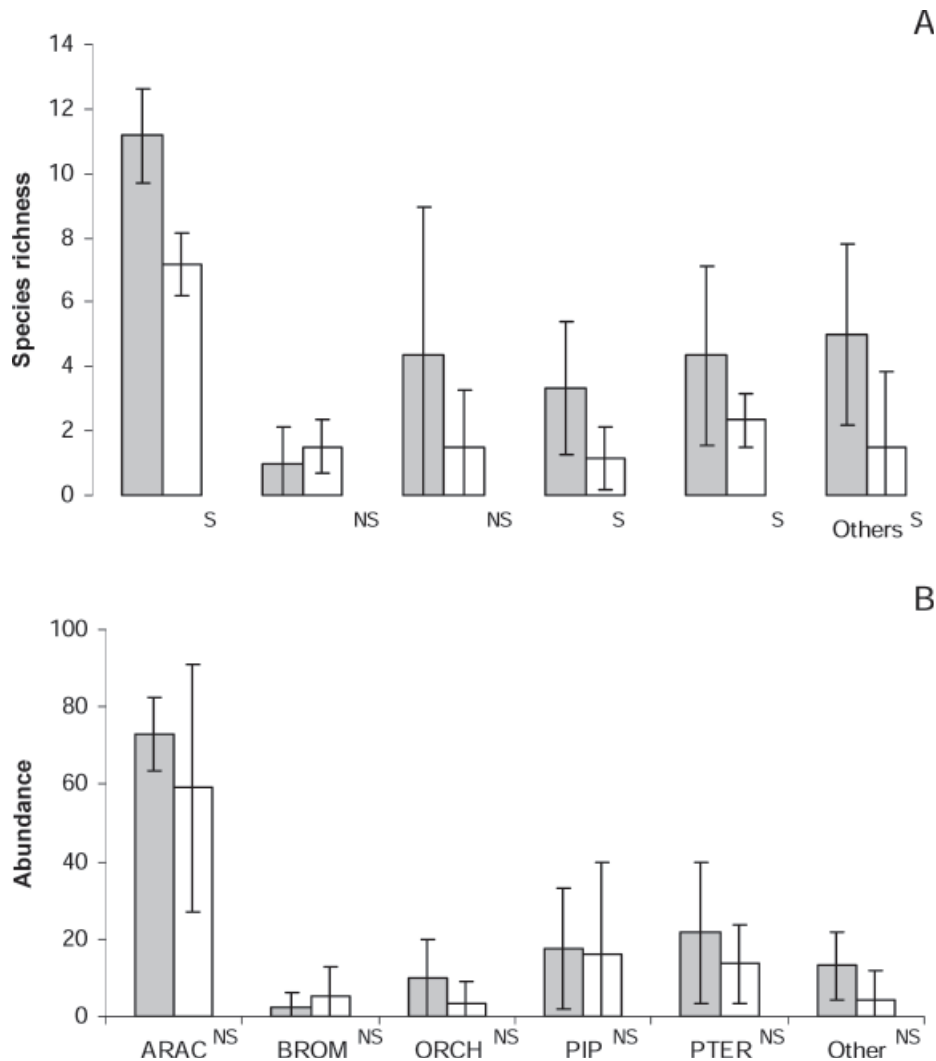


FIGURE 1. Mean (± 1 SD) of vascular epiphytes species richness (A) and abundance (B) of Araceae (ARAC), Bromeliaceae (BROM), Orchidaceae (ORCH), Piperaceae (PIP), Pteridophyta (PTER), and other families (Others) in FOREST (dark bars) and CACAO (white bars). S = significant differences, NS = no significant differences.

trunks (JZ1 and JZ2). In the phorophyte middle (JZ3) and outer crown (JZ5), species richness was significantly higher in FOREST than in CACAO. In the middle crown zone (JZ4), we observed no differences in species richness, at least partially, because of the high variances (Table 1; Fig. S1). Simpson's index was significantly higher in total FOREST phorophyte and JZ3 specifically, but could not be calculated for JZ5 because of the complete absence of epiphytes in this zone in four of six CACAO sites. Epiphyte densities in FOREST and CACAO differed only in JZ4 (Table 1). Those species restricted to only one land-use type were concentrated in the crowns. The trunks of CACAO had no exclusive species, and the trunks of FOREST contained just one species restricted to JZ1 (*Trichomanes collariatum* Bosch); the remaining exclusive species were more widely distributed around the phorophytes (Fig. S2).

Among the analyzed groups of epiphytes, Araceae, Piperaceae, and Pteridophyta were more species-rich in FOREST than in

CACAO, while Bromeliaceae and Orchidaceae were similarly rich in both land-use types. Epiphyte densities did not differ in any group (Fig. 1).

ECOLOGICAL FACTORS AFFECTING EPIPHYTE SPECIES DIVERSITY.—Phorophyte dbh, height, canopy cover, and densities of understory shrubs and small trees were all higher in FOREST than in CACAO, while soil pH and total bryophyte biomass did not differ between the two land-use types. Bryophyte biomass on phorophytes was higher in FOREST in the middle and upper canopy (JZ4 and JZ5), but otherwise did not differ. The mean temperatures were 23.1°C (± 0.6 SD) in FOREST and 23°C (± 0.3 SD) in CACAO, and relative humidities were 95% (± 1.3 SD) and 94% (± 3.1 SD), respectively. The ranges of these parameters differed more than the means but were also not significant (Table 2).

TABLE 2. Mean (± 1 SD) of phorophyte characteristics and environmental variables in FOREST (F) and CACAO (C) (N = 6 sites). P values indicate significance (significant differences in bold).

	F	C	P
Phorophyte dbh (m)	0.658 \pm 0.16	0.478 \pm 0.026	0.023
Phorophyte height (m)	25.48 \pm 4.07	20.69 \pm 3.24	0.048
Canopy cover (%)	82.03 \pm 4.86	73.54 \pm 6.89	0.033
Soil pH	6.14 \pm 0.14	6.26 \pm 0.18	0.231
Shrubs and small trees in the understory	9.05 \pm 2.16	5.55 \pm 2.54	0.029
Temperature ranges ($^{\circ}$ C)	3.17 \pm 0.42	3.85 \pm 0.71	0.232
Relative humidity ranges (%)	14.26 \pm 1.01	18.22 \pm 2.33	0.054
Total bryophyte cover biomass (g)	4.11 \pm 1.53	2.11 \pm 2.16	0.095
JZ1 bryophyte cover biomass (g)	0.28 \pm 0.31	0	0.056
JZ2 bryophyte cover biomass (g)	0.2 \pm 0.17	0.03 \pm 0.07	0.052
JZ3 bryophyte cover biomass (g)	1.64 \pm 0.89	1.39 \pm 1.4	0.715
JZ4 bryophyte cover biomass (g)	1.4 \pm 0.67	0.5 \pm 0.61	0.037
JZ5 bryophyte cover biomass (g)	0.73 \pm 0.37	0.13 \pm 0.19	0.005

Because land use mainly affected epiphyte species diversity in the tree crowns, we applied the GRM for trunk epiphytes and crown epiphytes separately. Soil pH was excluded as a predictor variable for crown epiphytes, and just one value of bryophyte biomass for trunks (the mean of JZ1 and JZ2) and crowns (the mean of JZ3, JZ4, and JZ5) was used. For epiphytes on tree trunks, canopy cover explained a significant proportion of the variance in epiphyte species richness ($F = 6.62$, $P = 0.001$, adjusted $R^2 = 0.6$), and canopy cover, soil pH, and phorophyte height helped explain abundance patterns ($F = 13.9$, $P = 0.001$, adjusted $R^2 = 0.8$). For tree crowns, phorophyte dbh explained both species richness and abundance of epiphytes (species richness: $F = 9.97$, $P = 0.01$, adjusted $R^2 = 0.45$; density: $F = 1263$, $P = 0.01$, adjusted $R^2 = 0.39$). These results suggest that different factors affect epiphyte diversity on tree trunks and crowns (Table 3).

COMMUNITY COMPOSITION.—Comparisons of epiphyte community composition between FOREST and CACAO JZs showed different patterns for phorophyte trunks and crowns. If the vertical distributions of species were similar, we would expect the highest similarity values between the same zones for FOREST and CACAO. This similarity was observed only for the trunk zones (JZ1 and JZ2; Fig. 2). In contrast, epiphyte community composition for the inner crown zone in FOREST (JZ3) was most similar to that of the upper trunk zone in CACAO (JZ2). Similarly, FOREST JZ4 was most similar to CACAO JZ3, and FOREST JZ5 was most similar to CACAO JZ3, although the lack of epiphytes in JZ5 in four of the six CACAO sites precluded this analysis. These results indicate that crown epiphyte communities in FOREST phorophytes were most similar to those in lower zones in CACAO (Fig. 2).

TABLE 3. Variables used in the GRM equations to explain species richness and abundance variation in the trunks and crowns of the phorophytes (N = 6 sites). P values indicate significance (only variables with significant differences used in the model are shown).

	Species richness parameter	F	P	R^2	Abundance of individuals parameter	F	P	R^2
<i>Trunk epiphytes</i>								
	Intercept	108.0	7.38	0.01				
	Phorophyte height				1.15	6.90	0.02	
	Canopy cover	-0.423	17.5	0.001	0.616	17.5	0.001	
	Soil pH				27.2	10.9	0.007	
	Model		6.62	0.01	0.6	15.9	0.001	0.8
<i>Crown epiphytes</i>								
	Phorophyte dbh	0.547	4.53	0.04	2.08	4.53	0.04	
	Model		9.97	0.01	0.45	1263	0.01	0.39

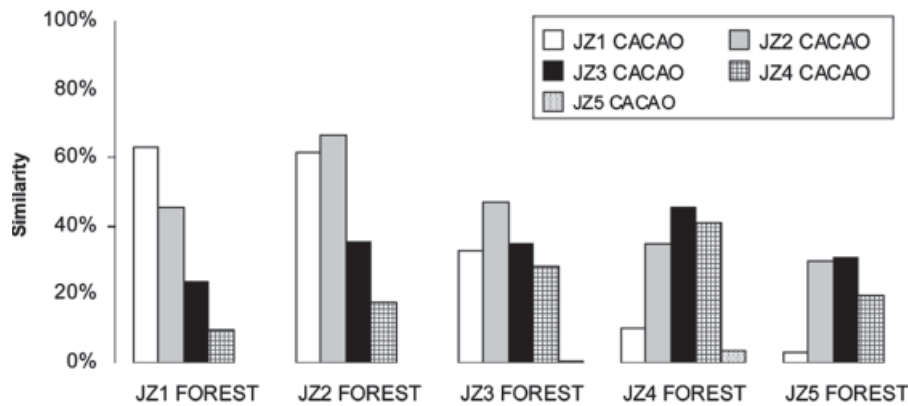


FIGURE 2. Similarity of epiphyte communities based on the Chao-Jaccard-Raw abundance-based index. In natural communities, the highest similarity value would be expected between the same JZs, as occurred in JZ1 and JZ2 (phorophyte trunks). A downward shift in CACAO, however, is clear for JZ3-JZ5 communities, though the relationships of JZ5 might be underestimated because of the absence of individuals in four of the six cacao sites.

A downward shift in the epiphyte distribution was also demonstrated by the differences in the vertical distributions of shared species. Among the 18 species with sufficient numbers of individuals, only three (all aroids) showed the same vertical distribution in both land-use types. In contrast, all the remaining aroids present in FOREST showed downward shifts in CACAO. The same tendency was observed in the remaining epiphytes, mostly crown holopiphytes, which either occurred lower or showed a more restricted vertical distribution in CACAO. Two exceptions were the fern *Polypodium bombycinum* Maxon and the bromeliad *Guzmania monostachia* (L.) Rusby ex Mez, whose vertical distributions in the phorophytes were clearly expanded in CACAO (Fig. 3).

DISCUSSION

SHADE CACAO PLANTATIONS AND SPECIES DIVERSITY.—Shade cacao plantations are usually considered among the most biologically rich managed systems and are assumed to be an important alternative habitat for various species (Rice & Greenberg 2000; Reitsma *et al.* 2001; Waltert *et al.* 2003; Schroth *et al.* 2004; Andersson & Gradstein 2005; Faria *et al.* 2006, 2007; Bos *et al.* 2007; Faria & Baumgarten 2007; Van Bael *et al.* 2007). In this study, epiphyte diversity was found to be lower in CACAO than in FOREST. With 57 species of vascular epiphytes in the cacao agroforests, these managed ecosystems obviously contribute to epiphyte conservation, as reported for other agroforests (Hietz 2005). Nevertheless, the substantial reduction in total species richness in CACAO indicates that epiphytes are collectively vulnerable to anthropogenic disturbances, as observed elsewhere (Turner *et al.* 1994; Hietz-Seifert *et al.* 1996; Benzing 1998; Hietz 1999, 2005; Barthlott *et al.* 2001; Nadkarni 2002; Krömer & Gradstein 2003; Flores-Palacios & García-Franco 2004; Werner *et al.* 2005; Wolf 2005).

No differences in epiphyte species diversity or floristic composition were found between the two land-use types in the understory. This finding was unexpected, given that the understory is typically

severely affected in this type of managed habitat (Rice & Greenberg 2000), and the number of understory shrubs and small trees was lower in CACAO than in FOREST. A possible reason for this lack of differences is that, in contrast to patterns observed in montane forests (Krömer *et al.* 2007), most epiphytes observed in the understories of both land-use types were juveniles of trunk epiphytes, especially the very disturbance-tolerant aroids.

Consideration of which families of epiphytes differed in abundance and species richness in CACAO and FOREST reveals some explainable patterns. The differences in species richness among certain families of epiphytes verify their susceptibility to human disturbance, in agreement with other studies that suggest that they are useful ecosystem health indicators (Turner *et al.* 1994, Barthlott *et al.* 2001, Krömer & Gradstein 2003). Araceae, Piperaceae, and Pteridophyta were found to be less species-rich in CACAO than in FOREST. The only families that did not differ in species richness were Bromeliaceae and Orchidaceae. Many bromeliads are known to be tolerant of disturbance (Krömer & Gradstein 2003, Merwin *et al.* 2003, Flores-Palacios & García-Franco 2004, Werner *et al.* 2005). Similarly, although orchids constitute a broad and diverse group with many species that are sensitive to ecosystem change, others flourish in disturbed habitats (Solís-Montero *et al.* 2005, Werner *et al.* 2005, Hietz *et al.* 2006). Unfortunately, the spatially heterogeneous distribution of orchids in this study makes it difficult to decipher their species-specific responses to different land uses. In contrast to the overall negative effect of habitat transformation on epiphyte species richness, the observed proliferation of some species in CACAO indicates that a focus on overall abundance of epiphytes may conceal the real impacts of management on epiphyte communities.

Epiphytes that grow in tree crowns responded strongly to the differences between CACAO and FOREST. In particular, the smaller phorophytes with less dense crowns in CACAO are apparently not favorable to many epiphytes, as reported for other managed ecosystems (Hietz 2005, Solís-Montero *et al.* 2005). The observed decrease in crown density of CACAO phorophytes most likely

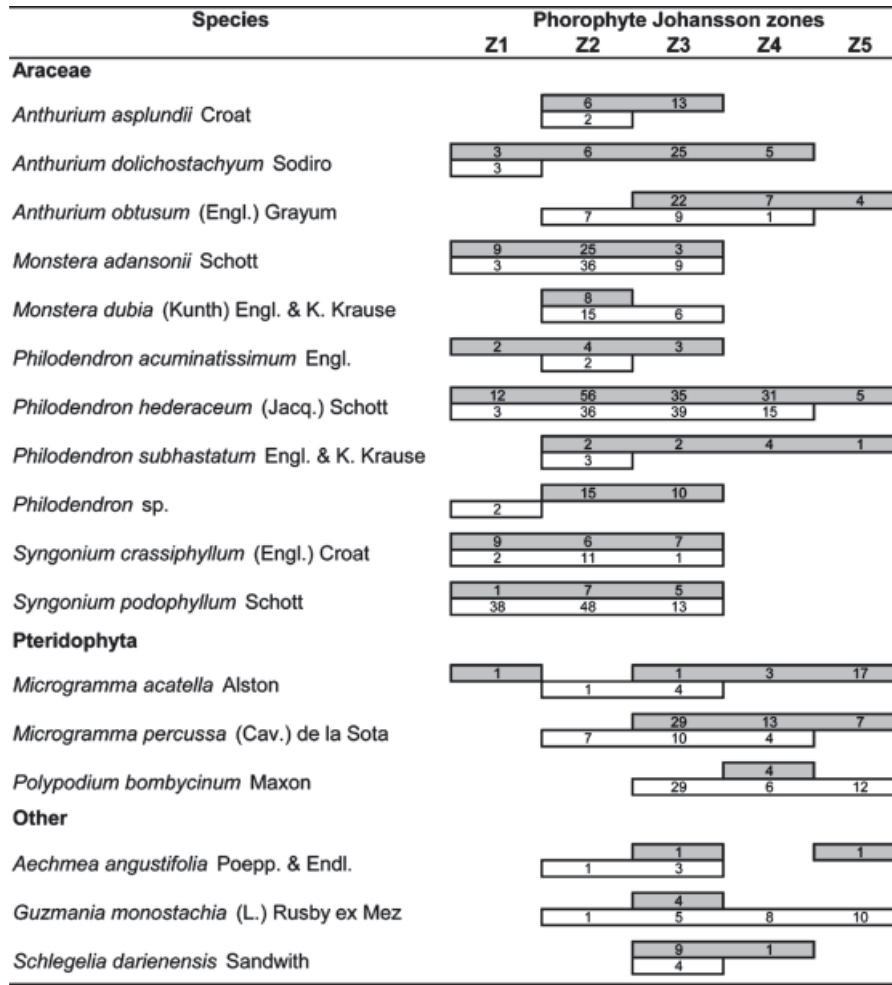


FIGURE 3. Vertical distribution of representative shared species in FOREST (gray) and CACAO (white). Numbers inside the boxes indicate the number of individuals.

results in increased temperatures, vapor pressure deficits, and insulation, all being conditions that are hostile for many crown epiphytes. In support of this argument, bryophyte biomass was lower in the middle and outer canopy in CACAO and was positively correlated with canopy cover (60%). Bryophyte cover reportedly benefits epiphyte seed germination and establishment (Nadkarni 1984, Freiberg 1997, Nieder *et al.* 2000, Zotz & Vollrath 2003), and direct relationships between vascular epiphyte species richness and bryophyte cover were reported for other habitats (Werner *et al.* 2005). Relative humidity ranges recorded in the middle crown are also potentially higher near the edge of the canopy because of stronger sun exposure, indicating changes in the microclimatic conditions within the canopy that may affect epiphyte growth (Ter Steege & Cornelissen 1989, Freiberg 1997).

The observed similarities in epiphyte species richness and abundance on phorophyte trunks in FOREST and CACAO were mostly due to the presence of drought-resistant hemiepiphytes, mainly Araceae, a group often observed to be well represented in

managed ecosystems (Hietz-Seifert *et al.* 1996, Krömer & Gradstein 2003). The high diversity of Araceae and the fact that they occur mostly on trunks as hemiepiphytes in the humid Chocó (Jácome *et al.* 2004) can explain the lack of differences in the trunks. Hemiepiphytes are reportedly more resistant than holoepiphytes to habitat changes because they are rooted in the soil for, at least, a major portion of their lives (Benzing 1990, Hietz-Seifert *et al.* 1996, Barthlott *et al.* 2001, Nieder & Barthlott 2001, Nieder *et al.* 2001, Krömer & Gradstein 2003). We confirmed this relationship in our regression models that contained the variable canopy cover (significantly lower in CACAO), which explained much variation in species richness, and the variables phorophyte height, soil pH, and canopy cover, which explained abundance variation. The majority of trunk epiphytes seemed to benefit from, or at least tolerate, higher light intensities, and larger trees are obviously able to offer more space for more individuals. The overall reduction of Araceae species richness in CACAO was due to holoepiphytic and shade-adapted species, such as *Philodendron tenuipes* (Engl.), which were not in the farms.

COMMUNITY DISTRIBUTION PATTERNS.—We observed downward shifts in the vertical distributions of vascular epiphytes in shade cacao plantations relative to natural forest, a trend previously reported for nonvascular epiphytes (Acebey *et al.* 2003, Andersson & Gradstein 2005). Crown communities of CACAO resembled those of lower FOREST communities, probably as a result of changes in their microenvironments. *G. monostachia* (L.) Rusby ex Mez (Bromeliaceae) and *P. bombycium* Maxon (Polypodiaceae) could expand their vertical distributions in CACAO presumably because they are tolerant to drought and high light intensities (Merwin *et al.* 2003); the same case probably holds for other species of Bromeliaceae as well as for some species of Polypodiaceae (Krömer & Gradstein 2003, Flores-Palacios & García-Franco 2004, Werner *et al.* 2005). The changes in the vertical distributions of epiphyte species and communities thus represent good indicators of modifications of environmental conditions caused by human activities.

CONCLUSIONS.—The adoption of agroforestry practices may help preserve Chocó biodiversity. Our results indicate that, at least, for vascular epiphytes, shade cacao plantations preserve a portion of the diversity but do not fully compensate for the loss of forest.

Our results suggest some management practices that might improve vascular epiphytic conservation in cacao agroforests. The retention or development of forest-like phorophytes would help conserve a higher proportion of epiphyte diversity, particularly crown holoepiphytes. The maintenance of large shade trees could also help preserve understory and canopy vascular epiphyte diversity even in intensely managed plantations. Trunk epiphytes and hemiepiphytes, which are typically tolerant of habitat transformation, are also likely to benefit from the retention of large forest trees for shade in agroforestry plantations.

The future prospects for epiphyte conservation in shade cacao plantations remain difficult to predict because of the lack of long-term studies on the maintenance of diversity. Some vascular epiphyte species are able to survive and reproduce in shade-grown coffee plantations (Solis-Montero *et al.* 2005), and a similar pattern is expected in shade cacao plantations. In contrast, other species may depend on the continued proximity of natural forest as propagule sources. The consequences of the natural mortality of shade trees, and whether new shade trees are planted, may also have important implications for the diversity of vascular epiphytes in shade cacao plantations. Studies on the identity of epiphyte-favoring phorophytes in managed ecosystems would also be informative. Finally, studies on epiphyte conservation in a wider range of managed ecosystems would help reveal how epiphytes react to human-induced changes and how they can be preserved.

ACKNOWLEDGMENTS

We thank the landowners of Cabo San Francisco who allowed us to work on their lands. N. Castaño and M. Arboleda assisted with fieldwork. J. Putz, T. Krömer, and S. R. Gradstein provided assistance and advice. Z. Pearson, M. Knowles, M. López, M. J. Endara, E. Carrión, G. Haro, D. Alvarado, and B. Pico provided useful help.

Species identifications were provided by T. B. Croat, R. Moran, J. M. Manzanares, N. Williams and his research group, and L. Jost. G. Onore provided field equipment. This project is part of the BioTEAM research program sponsored by the Federal Ministry of Education and Research (BMBF), Germany.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. CACAO and FOREST phorophytes.

FIGURE S1. Individual-based species rarefaction curves for FOREST (F) and CACAO (C) vascular epiphytes in total phorophytes (A), understories (B), Johansson zone 1 (JZ1) (C), JZ2 (D), JZ3 (E), JZ4 (F), and JZ5 (G).

FIGURE S2. Vertical distribution of exclusive species in FOREST (gray) and CACAO (white).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

LITERATURE CITED

- ACEBEY, A., S. R. GRADSTEIN, AND T. KRÖMER. 2003. Species richness and habitat diversification of corticolous bryophytes in submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* 19: 9–18.
- ANDERSSON, M. S., AND S. R. GRADSTEIN. 2005. Impact of management intensity on non-vascular epiphyte diversity in cacao plantations in western Ecuador. *Biodivers. Conserv.* 14: 1101–1120.
- BARTHLOTT, W., V. SCHMIT-NEUERBURG, J. NIEDER, AND S. ENGWALD. 2001. Diversity and abundance of vascular epiphytes: A comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. *Plant Ecol.* 152: 145–156.
- BENZING, D. H. 1990. *Vascular epiphytes. General biology and related biota.* Cambridge University Press, New York, NY.
- BENZING, D. H. 1998. Vulnerabilities of tropical forests to climate change: The significance of resident epiphytes. *Clim. Change* 39: 519–540.
- BOS, M. M., P. HÖHN, S. SALEH, B. BÜCHE, D. BUCHORI, I. STEFFAN-DEWENTER, AND T. TSCHARNTKE. 2007. Insect diversity responses to forest conversion and agroforestry management. *In* T. Tscharntke, C. Leuschner, M. Zeller, E. Guhardja, and A. Bidin (Eds.). *Stability of tropical rain forest margins, linking ecological, economic and social constraints of land use and conservation*, pp. 279–296. Springer, Berlin, Germany.
- BROWN, S., AND A. E. LUGO. 1990. Tropical secondary forests. *J. Trop. Ecol.* 5: 131–150.
- COLWELL, R. K. 2004. *EstimateS: Statistical estimation of species richness and shared species from samples. User's guide and application. Version 7.51.* University of Connecticut, Storrs, Connecticut. Available from <http://viceroy.eeb.uconn.edu/estimates> (accessed December, 2005).
- FARIA, D., AND J. BAUMGARTEN. 2007. Shade cacao plantations (*Theobroma cacao*) and bat conservation in southern Bahia, Brazil. *Biodivers. Conserv.* 16: 291–312.
- FARIA, D., R. R. LAPS, J. BAUMGARTEN, AND M. CETRA. 2006. Bat and bird assemblages from forest and shade cacao plantations in two contrasting landscapes in the Atlantic forest of southern Bahia, Brazil. *Biodivers. Conserv.* 15: 587–612.

- FARIA, D., M. L. BARRADASPACIENCIA, M. DIXO, R. R. LAPDS, AND J. BAUMGARTEN. 2007. Ferns, frogs, lizards, birds and bats in forest fragments and shade cacao plantations in two contrasting landscapes in the Atlantic forest, Brazil. *Biodivers. Conserv.* 16: 2335–2357.
- FLORES-PALACIOS, A., AND J. G. GARCÍA-FRANCO. 2004. Effect of isolation on the structure and nutrient content of oak epiphyte communities. *Plant Ecol.* 173: 259–269.
- FRAHM, J. P., AND S. R. GRADSTEIN. 1991. An altitudinal zonation of tropical rain forests using bryophytes. *J. Biogeogr.* 18: 669–678.
- FREIBERG, M. 1997. Spatial and temporal pattern of temperature and humidity of a tropical premontane rain forest tree in Costa Rica. *Selbyana* 18: 77–84.
- FREIBERG, M. 2001. The influence of epiphyte cover on branch temperature in a tropical tree. *Plant Ecol.* 153: 241–250.
- GENTRY, A. H., AND C. H. DODSON. 1987. Diversity and biogeography of Neotropical vascular epiphytes. *Ann. Missouri Bot. Gard.* 74: 205–233.
- GOTELLI, H. J., AND R. K. COLWELL. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4: 379–391.
- GRADSTEIN, S. R., N. M. NADKARNI, T. KRÖMER, I. HOLZ, AND N. NÖSKE. 2003. A Protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. *Selbyana* 24: 105–111.
- HAMMER, Ø., D. A. T. HARPER, AND P. D. RYAN. 2005. PAST: Palaeontological statistics software package for education and data analysis. Version 1.31. Available from: http://palaeo-electronica.org/2001_1/past/issue1_01.htm (accessed November, 2005)
- HIETZ, P. 1999. Diversity and conservation of epiphytes in a changing environment. *Pure Appl. Chem.* 70: 2114 Available from <http://uiupac.org/symposia/proceedings/phuket97/hietz.html> (accessed February, 2006).
- HIETZ, P. 2005. Conservation of vascular epiphyte diversity in Mexican coffee plantations. *Conserv. Biol.* 19: 391–399.
- HIETZ, P., G. BUCHBERGER, AND M. WINKLER. 2006. Effect of forest disturbance on abundance and distribution of epiphytic bromeliads and orchids. *Ecotropica* 12: 103–112.
- HIETZ-SEIFERT, U., P. HIETZ, AND S. GUEVARA. 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. *Biol. Conserv.* 75: 103–111.
- JÁCOME, J., G. GALEANO, M. AMAYA, AND M. MORA. 2004. Vertical distribution of epiphytic and hemiepiphytic Araceae in tropical rain forest in Chocó, Colombia. *Selbyana* 25: 118–125.
- JEPSON, J. 2003. The tree climber's companion. A reference and training manual for professional tree climbers, 2nd edition. pp. 1–104. Beaver Tree Publishing, Longville, Maine.
- JOHANSSON, D. 1974. Ecology of epiphytic orchids in West African rain forest. *Acta Phytogeogr. Suecica* 59: 1–136.
- KRÖMER, T., AND S. R. GRADSTEIN. 2003. Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. *Selbyana* 24: 190–195.
- KRÖMER, T., M. KESSLER., S. R. GRADSTEIN, AND A. ACEBEY. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *J. Biogeogr.* 32: 1799–1809.
- KRÖMER, T., M. KESSLER, AND S. R. GRADSTEIN. 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: The importance of the understory. *Plant Ecol.* 189: 261–278.
- KÜPER, W., H. KREFT, J. NIEDER, N. KÖSTER, AND W. BARTHLOTT. 2004. Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. *J. Biogeogr.* 31: 1477–1487.
- LEIMBECK, R. M., AND H. BALSLEV. 2001. Species richness and abundance of epiphytic Araceae on adjacent floodplain and upland forest in Amazonian Ecuador. *Biodivers. Conserv.* 10: 1579–1593.
- MARTIN, P. H., R. E. SHERMAN, AND T. J. FAHEY. 2004. Forty years of tropical forest recovery from agriculture: Structure and floristics of secondary and old-growth riparian forests in the Dominican Republic. *Biotropica* 36: 297–317.
- MCNEELY, J. E. 1998. The science of the canopy: Who needs the information and how they can use it. *Selbyana* 19: 135–140.
- MERWIN, M. C., S. A. RENTMEESTER, AND N. M. NADKARNI. 2003. The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations, La Selva, Costa Rica. *Biotropica* 35: 37–47.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DA FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- NADKARNI, N. M. 1984. Epiphyte biomass and nutrient capital of a Neotropical elfin forest. *Biotropica* 16: 249–256.
- NADKARNI, N. M. 2002. Potential effect of climate change on canopy communities in a tropical cloud forest: An experimental approach. *Oecologia* 131: 580–586.
- NEILL, D. 1999. Vegetation. Vegetation types. In P. M. Jørgensen and S. León-Yáñez (Eds.). *Catalogue of the vascular plants of Ecuador*, pp. 13–25. Missouri Botanical Garden Press, St. Louis, Missouri.
- NIEDER, J., AND W. BARTHLOTT. 2001. Epiphytes and their role in the tropical forest canopy. In J. Nieder and W. Barthlott (Eds.). *Epiphytes and canopy fauna of the Otonga Rain Forest (Ecuador)*, vol. 2, pp. 23–86. Results of the Bonn-Quito epiphyte project funded by the Volkswagen Foundation, Bonn, Germany.
- NIEDER, J., S. ENGWALD, M. KLAUN, AND W. BARTHLOTT. 2000. spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland Amazonian rain forest (Surumoni crane plot) of southern Venezuela. *Biotropica* 32: 385–396.
- NIEDER, J., J. PROSPERÍ, AND G. MICHALOUD. 2001. Epiphytes and their contribution to canopy diversity. *Plant Ecol.* 153: 51–63.
- NÖSKE, N. 2004. Effekte anthropogener Störung auf die Diversität kryptogamischer Epiphyten (Flechten, Moose) in einem Bergregenwald in Südecuador. PhD dissertation, Georg-August University, Göttingen, Germany.
- PERRY, D. R. 1978. A method of access into the crowns of emergent and canopy trees. *Biotropica* 10: 155–177.
- PIMENTEL, D. D., U. STASHOW, D. A. TAKACS, H. W. BRUBAKER, A. R. DUMAS, J. J. MEANEY, J. A. S. O'NEIL, D. E. ONSI, AND D. B. CORZILIUS. 1992. Conserving biological diversity in agricultural/forestry systems. *Bioscience* 42: 354–362.
- PUTZ, F., G. M. BLATE, K. H. REDFORD, R. FIMBEL, AND J. ROBINSON. 2001. Tropical forest management and conservation of biodiversity: An overview. *Conserv. Biol.* 15: 7–20.
- REITSMA, R., J. D. PARRISH, AND W. MCLARNEY. 2001. The role of cacao plantations in maintaining forest avian diversity in southeastern Costa Rica. *Agrofor. Syst.* 53: 185–193.
- RICE, R. A., AND R. GREENBERG. 2000. Cacao cultivation and the conservation of biological diversity. *Ambio* 29: 167–173.
- SCHROTH, G., G. A. B. DA FONSECA, C. A. HARVEY, C. GASCON, H. L. VASCONCELOS, A. M. N. IZAC, A. ANGELSEN, B. FINEGAN, D. KAIMOWITZ, U. KRAUSS, S. G. LAURANCE, W. F. LAURANCE, R. NASI, L. NAUGHTON-TREVES, E. NIESTEN, D. M. RICHARDSON, E. SOMARRIBA, N. I. J. TUCKER, G. VICENT, AND D. S. WILKIE. 2004. *Agroforestry and biodiversity conservation in tropical landscapes—a synthesis*. Island Press, Washington, DC.
- SOLÍS-MONTERO, L., A. FLORES-PALACIOS, AND A. CRUZ-ANGÓN. 2005. Shade-coffee plantations as refuges for tropical wild orchids in central Veracruz, Mexico. *Conserv. Biol.* 19: 908–916.
- STATSOFT INC. 2003. *Statistica 6.0*. Statsoft Inc., Tulsa, Oklahoma.
- SZARO, R. C., AND D. W. JOHNSTON. 1996. *Biodiversity in managed landscapes*. Oxford Press, New York, New York.
- TER STEEGE, H., AND J. H. C. CORNELISSEN. 1989. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. *Biotropica* 21: 331–339.

- TURNER, I. M., H. T. W. TAN, Y. C. WEE, A. B. IBRAHIM, P. T. CHEW, AND R. T. CORLETT. 1994. A study of plant species extinction in Singapore: Lessons for the conservation of tropical biodiversity. *Conserv. Biol.* 8: 705–712.
- VAN BAELE, S. A., P. BICHIER, I. OCHOA, AND R. GREENBERG. 2007. Bird diversity in cacao farms and forest fragments of western Panama. *Biodivers. Conserv.* 16: 2245–2256.
- WALTERT, M., A. MARDIASTUTI, AND M. MÜHLENBERG. 2003. Effect of land use on bird species richness in Sulawesi, Indonesia. *Conserv. Biol.* 18: 1339–1346.
- WERNER, F. A., J. HOMEIER, AND S. R. GRADSTEIN. 2005. Diversity of vascular epiphytes on isolated remnant trees in the montane forest belt of southern Ecuador. *Ecotropica* 11: 21–40.
- WOLF, J. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. *Forest Ecol. Manage.* 212: 376–393.
- ZOTZ, G., AND B. VOLLRATH. 2003. The epiphyte vegetation of the palm *Socratea exorrhiza*—correlations with tree size, tree age, and bryophyte cover. *J. Trop. Ecol.* 19: 81.