

## Disturbance effects on diversity of epiphytes and moths in a montane forest in Ecuador

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### Abstract

We sampled the diversity of epiphytes (lichens, bryophytes, vascular plants) and moths (Geometridae, Arctiidae) in mature and recovering forest and in open vegetation in the montane belt in Ecuador. No uniform pattern of change in species richness was detected among the different taxonomic groups with increasing disturbance. Species richness of epiphytic bryophytes and vascular plants declined significantly from mature forest towards open vegetation. In contrast, species richness of epiphytic lichens did not change with increasing forest alteration, while that of geometrid moths was significantly higher in recovering forest compared with mature forest and open habitats. Arctiidae were significantly more species-rich in recovering forest and open vegetation than mature forest. Hence, for some organisms, modified habitats may play an important role for biodiversity conservation in the Andes, whereas others suffer from habitat disturbance. However, trends of changes in species composition following deforestation were surprisingly concordant across most studied epiphyte and moth taxa.

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### Zusammenfassung

Wir untersuchten die Diversität von Epiphyten (Flechten, Moose, Gefäßpflanzen) und Nachtfaltern (Geometridae, Arctiidae) in ausgewachsenen und sich erholenden Wäldern sowie in offener Vegetation im montanen Bereich in Ecuador. Es wurde kein einheitliches Muster der Veränderung des Artenreichtums der verschiedenen taxonomischen Gruppen mit zunehmender Störung gefunden. Der Artenreichtum bei epiphytischen Moosen und Gefäßpflanzen nahm von ausgewachsenem Wald hin zu offener Vegetation signifikant ab. Im Gegensatz dazu änderte sich der Artenreichtum von Flechten mit zunehmender Umwandlung des Waldes nicht, während dieser bei Geometridae in sich erholendem Wald im Vergleich zu ausgewachsenem Wald und offenen Habitaten signifikant höher war. Arctiidae waren sowohl in sich erholendem Wald als auch in offener Vegetation signifikant artenreicher als in ausgewachsenem

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Wald. Demzufolge können abgewandelte Habitate für einige Organismen eine wichtige Rolle bei der Erhaltung der Biodiversität in den Anden spielen, wohingegen andere unter Störung des Habitats leiden. Im Gegensatz dazu stimmten die Trends der Veränderung der Artenzusammensetzung nach Entwaldung bei fast allen untersuchten Epiphyten- und Nachtfaltertaxa überraschend gut überein.

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**Keywords:** Andes; Anthropogenic disturbance; Non-vascular and vascular plants; Lepidoptera; Species richness; Species composition

## Introduction

The northern Andes are among the most species-rich regions on earth (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000) and therefore are considered a top-priority area for conservation (Brummitt & Lughadha, 2003). The high biodiversity in the region also applies to non-vascular and vascular plants (e.g. Gentry, 1995; Gradstein, Churchill, & Salazar-Allen, 2001; Sipman, 2002) and arthropods (Ødegaard, 2000; Brehm, Pitkin, Hilt, & Fiedler, 2005). However, very little is known about the effects of large-scale modifications of montane forest habitats on biodiversity. Previous studies have suggested that epiphytes and moths respond sensitively to changes in the environment. Epiphytes are strongly adapted to the microclimate of their habitat (Wolf, 1993; Krömer & Gradstein, 2004), while moths, due to their herbivorous way of life in the larval stages, show considerable fidelity to vegetation types (Thomas, 2002). Therefore, epiphytes and moths are useful model organisms to study habitat changes. Most studies on epiphytes in neotropical mountains reported impoverishment of the local flora following forest alteration (e.g., Acebey, Gradstein, & Krömer, 2003; Wolf, 2005). Other studies on epiphytes and arthropods, however, revealed an increase in species richness or at least similar species numbers in secondary forests in comparison with primary ones (Yanoviak, Kragh, & Nadkarni, 2003; Holz & Gradstein, 2005). Secondary habitats may thus act as a refuge for species diversity in the fragmented landscape (Chazdon, 1994).

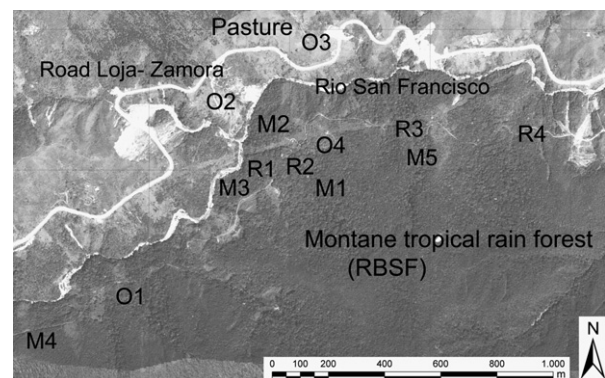
Most previous studies on the response of tropical biota to habitat alteration were restricted to single or closely related groups of organisms, while very few dealt simultaneously with unrelated groups (Cameroon: Lawton et al., 1998; Mt. Kilimanjaro: Axmacher et al., 2004; Indonesia: Schulze et al., 2004). Schulze et al. (2004) recorded a general decrease in species richness with increasing disturbance, which was significantly correlated between the studied plant and animal taxa. However, Lawton et al. (1998) observed very different patterns of change, with none of the investigated animal taxa suitable as an indicator for diversity changes in others. Axmacher et al. (2004) even reported diverging patterns of species richness of plants and moths during forest regeneration.

Our paper is a first cross-taxon comparison of a neotropical montane forest. We do this by synthesizing our data on the effects of anthropogenic disturbance on the diversity of different groups of organisms with greatly diverging traits (epiphytic bryophytes, lichens, vascular plants, geometrid and arctiid moths) in Ecuador (Brehm & Fiedler, 2005; Hilt, 2005; Hilt & Fiedler, 2005; Nöske, 2005; Werner, Homeier, & Gradstein, 2005; Hilt, Brehm, & Fiedler, 2006; Hilt & Fiedler, 2006).

## Material and methods

### Study area

Field work was carried out at an elevation of 1800–2000 m in the Reserva Biológica San Francisco and environs, situated in the San Francisco river valley between Loja and Zamora, southern Ecuador (79°04'W, 03°59'S; Fig. 1). Mean annual precipitation at this elevation is ca. 2200 mm and mean annual temperature ca. 16 °C; soils are acidic, nutrient poor inceptisols (Schrumpf, Guggenberger, Valarezo, & Zech, 2001;



**Fig. 1.** Composite aerial photograph of the area of the Reserva Biológica San Francisco (RBSF) and surrounding landscape, southern Ecuador. M1–5 = mature forest; R1–4 = recovering forest; O1–4 = open vegetation. Sampled habitats of (a) non-vascular epiphytes: M1–2, R1–2, O1–2; (b) vascular epiphytes: M1–3, M5, O2–3; (c) moths: M1–4, R2–4, O1–4.

Wilcke, Yasin, Valarezo, & Zech, 2001). The southern slopes of the valley are covered by mature evergreen montane tropical rain forest with small patches of ca. 50-year-old recovering forest and open vegetation (Bussmann, 2001; Paulsch, 2002). On the northern slopes the forest is almost entirely converted to currently grazed or abandoned pastures. Brehm, Homeier, Fiedler, Kottke, Illig et al. (in press) highlight the remarkable species richness of non-vascular and vascular plants and moths in this small reserve.

## Data collection

### Non-vascular epiphytes

Epiphytic lichen and bryophyte diversity was investigated in mature forest (M), 50-year-old disturbed forest (R) and on isolated trees on former pastureland (O) during 2001 and 2002 (Fig. 1). The inventory followed the method proposed by Gradstein, Nadkarni, Krömer, Holz & Nöske (2003). In each habitat type, two 0.5 ha plots were established. In each plot, five canopy trees were randomly selected (see Nöske, 2005 for details on phorophytes) and sampled in five zones: tree base, trunk, inner, middle and outer canopy (Johansson, 1974). Trees were climbed using the single rope technique (Perry, 1978). Abundance of species was determined in each zone by the presence/absence and estimation of percent cover of species in 600 cm<sup>2</sup> subplots (Braun-Blanquet, 1964). In each zone at least four subplots were taken in every cardinal direction (N, E, S, W). Vouchers are deposited at the Botanical Museum, Free University of Berlin (B), University of Göttingen (GOET), Universidad Nacional de Loja (LOJA) and Pontificia Universidad Católica del Ecuador, Quito (QCA).

### Vascular epiphytes

Vascular epiphyte diversity was sampled in mature forest (M) and on isolated remnant trees in currently grazed pastures (O) during 2000 and 2001 (Fig. 1). Six trees in mature forest and 15 on pastures were selected at random and climbed by the single-rope technique (see Werner et al., 2005 for details). Trees were sampled in the five zones after Johansson (1974) as described above. Abundance of species was determined in each zone by counting the number of stands of each species. According to Sanford (1968), a stand is a group of stems or plants spatially separated from another group of the same species by an area on the tree devoid of epiphytes or occupied by another species. Vouchers are deposited at the University of Aarhus (AAU), Estación Científica San Francisco (ECSF), Missouri Botanical Garden (MO), QCA, Herbario Nacional del Ecuador, Quito (QCNE) and Marie Selby Botanical Garden (SEL).

### Moths

The diversity of geometrid and arctiid moths was studied in mature forest (M) in 1999 and 2000, and in late successional habitats (R) and abandoned pastures (O) in 2002 and 2003 (Fig. 1). In mature forest and pastures six sites each and in late succession habitats five sites were selected (see Hilt & Fiedler, 2005; Hilt et al., 2006 for details on sites). Catches were replicated 4–9 times at each site to improve coverage and representativeness, and were collated in one sample for analysis, since the moth ensembles in the study area show no evidence of seasonal changes across years (Süßenbach, 2003; Hilt & Fiedler, 2006).

Moths were manually sampled at portable weak light sources (2 × 15 W tubes: Sylvania black light blue, F15W/T8/BLB and Philips TLB 15 W 05) operated in a white gauze cylinder (height 1.6 m, diameter 0.6 m) at ground level (Brehm & Axmacher, 2006). Nightly trapping occurred from 18:30 to 21:30 (mature forest) and 18:45 to 21:45 h (sites without closed canopy; Brehm, 2002; Süßenbach, 2003). Nights with strong moonlight were avoided (McGeachie, 1989). Vouchers are deposited at the State Museum of Natural History in Stuttgart (SMNS).

## Data analysis

Species richness estimations according to first-order jackknife (Colwell, 2005) indicate that sampling for lichens and bryophytes (coverage of at least 83% of estimated flora) was representative (Table 1). Hence, the number of observed species of non-vascular epiphytes was a sufficient measure of species richness. In contrast, despite intensive sampling, coverage of the species-rich vascular epiphytes (ca. 65%) and geometrid and arctiid moths was far from complete (at most 84%, Table 1), so that observed species numbers may poorly reflect true species diversity (Gotelli & Colwell, 2001). For moths, therefore, Fisher's alpha of the log series distribution was used, which is less sensitive to sampling size and effort (Magurran, 2004; computed with the software developed by Henderson & Seaby, 1998). In the vascular epiphytes the number of observed species in the studied habitat types was clearly different and the main pattern, i.e., a much-reduced diversity in open vegetation compared with mature forest, would not have changed with increased sampling effort. Therefore, we used the number of observed species as a measure of species richness of vascular epiphytes.

Variance in species richness among the different taxonomic groups across habitat types was compared for normally distributed data using one-way ANOVA (non-vascular epiphytes, moths), followed by a Scheffé test; otherwise Kruskal–Wallis–ANOVA (vascular epiphytes) was used. Similarity of epiphyte assemblages was quantified by the incidence-based Sørensen index. For moth ensembles, the abundance-based CNESS

**Table 1.** Sampling effort, species richness and abundance along the disturbance gradient.

	Sampled trees <sup>a,b</sup> /sites <sup>c</sup>	Subplots <sup>a</sup> /Nights <sup>c</sup>	Observed species (Fisher's alpha <sup>c</sup> )	Estimated species Jackknife 1 (coverage in %)	Mean observed species number per tree <sup>a,b</sup> /site <sup>c</sup>	Presence <sup>a</sup> /stands <sup>b</sup> /individuals <sup>c</sup>
<i>Mature forest</i>						
Lichens	10	348	92	93 (99)	54	3582
Bryophytes	10	348	72	82 (88)	30	2601
Vascular plants	6	–	225	348 (65)	59	4974
Geometridae	6	24	503 (119)	664 (76)	196	3050
Arctiidae	6	46	178 (31)	248 (72)	65	1494
<i>Recovering forest</i>						
Lichens	10	342	101	109 (93)	59	4093
Bryophytes	10	342	65	78 (83)	27	2553
Vascular plants	–	–	–	–	–	–
Geometridae	5	31	656 (149)	779 (84)	383	9031
Arctiidae	5	31	217 (47)	264 (82)	125	3383
<i>Open vegetation</i>						
Lichens	10	349	102	107 (95)	62	5089
Bryophytes	10	349	49	57 (86)	21	1709
Vascular plants	15	–	67	104 (64)	11	1534
Geometridae	6	39	562 (111)	762 (74)	255	6215
Arctiidae	6	39	194 (43)	247 (79)	94	2488

<sup>a</sup>Non-vascular epiphytes.<sup>b</sup>Vascular epiphytes.<sup>c</sup>Moths.

index was used as a measure of faunal distances, which takes sampling effects into account more efficiently (Legendre & Gallagher, 2001). The CNESS index can be adjusted with regard to an optimal sample size parameter  $m$  (Trueblood, Gallagher, & Gould, 1994). We used medium values to account for both the rare and the common species in a balanced manner (Arctiidae:  $m = 50$ , Geometridae:  $m = 170$ ). CNESS values were calculated with COMPAH96 (Gallagher, 1999). To assess whether the change in species composition with habitat disturbance was correlated between the studied taxa, we performed pair-wise matrix correlation tests (999 permutations) based on Spearman's rank correlation (Clarke & Gorley, 2001). In this test we included only non-vascular epiphytes and moths, which were sampled in all three habitat classes (M, R and O). To homogenize dimensionality to a common set of 17 sampling units, we randomly removed epiphyte sampling trees, reducing the data set to  $n = 6$  for M,  $n = 7$  for R and  $n = 4$  for O habitats. Statistical analysis was performed with Statistica 6.1 (StatSoft 2003).

## Results

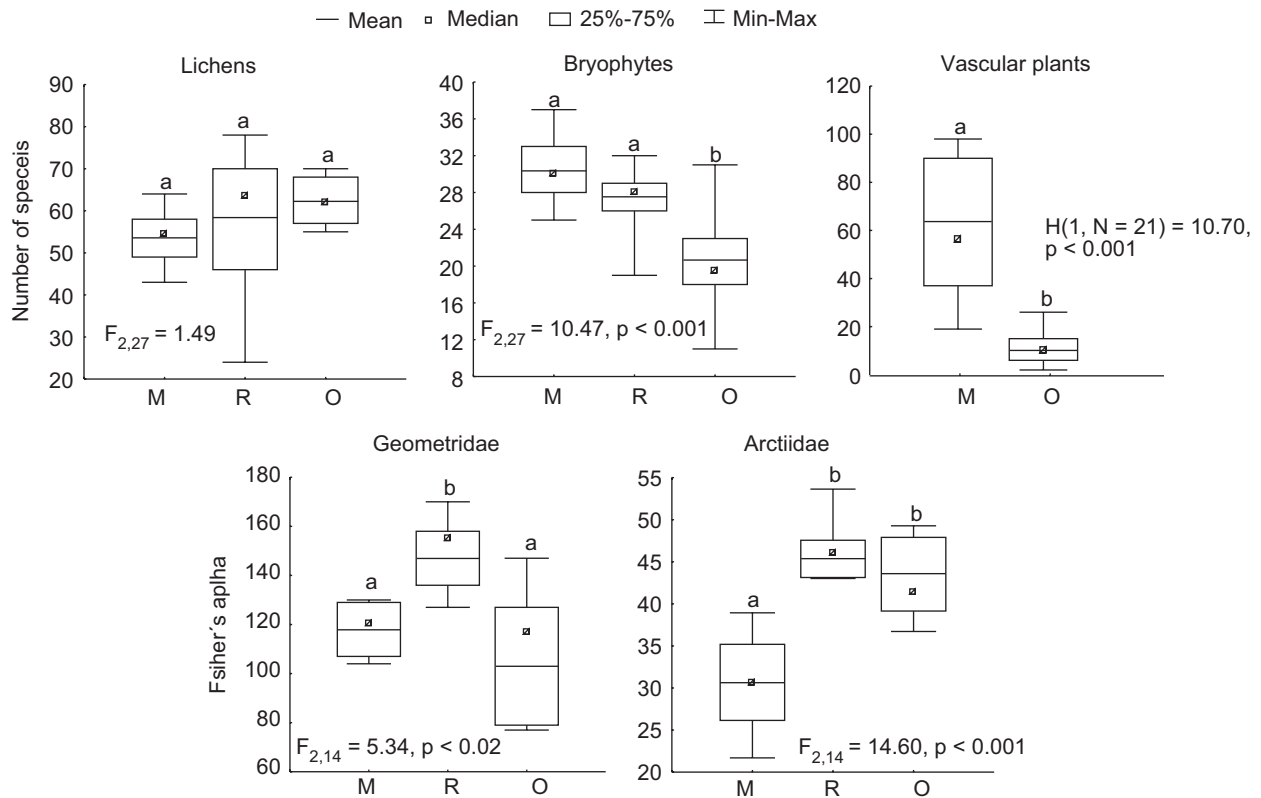
### Species richness

In total, 92 species of bryophytes, 115 species of lichens, 253 species of vascular plants, 282 species of

arctiid moths and 829 species of geometrid moths were recorded from the three habitat types along the gradient of disturbance. Patterns of species richness and abundance of the five taxonomic groups varied considerably from mature forest towards open vegetation (Table 1). ANOVA revealed that species richness of lichens did not change along the disturbance gradient (Fig. 2). In contrast, species richness of bryophytes and vascular plants was significantly reduced in open habitats (Fig. 2). However, species richness of Geometridae and Arctiidae was significantly promoted in habitats with recovering woody vegetation and of Arctiidae also in open habitats. In contrast, species richness of Geometridae showed no difference between mature forest and open vegetation (Fig. 2).

### Species composition

Rank correlations between the distance matrices of the different taxonomic groups were predominantly significant and always positive in sign (Table 2). Shifts in species composition along the disturbance gradient were most strongly correlated between the two non-vascular epiphyte groups, and between the two moth families, respectively. Changes in species composition were also correlated between bryophytes and moths, though to a lesser extent. Correlations between distance matrices of



**Fig. 2.** Species richness of epiphytes and moths in the different habitat types. M = mature forest, R = recovering forest, O = open vegetation. Non-vascular plants and moths: one way ANOVA followed by a Scheffé test. Vascular plants: Kruskal–Wallis ANOVA; Boxes labelled with same letters are not significantly different at  $P < 0.05$ .

**Table 2.** Multiple matrix correlations, based on Spearman's rank correlation with 999 permutations, between non-vascular epiphytes and moths sampled in all three habitat classes ( $n = 17$  light-trapping sites or trees, respectively)

	Lichens	Bryophytes	Geometridae
Bryophytes	0.838***	–	–
Geometridae	–	0.566*	–
Arctiidae	–	0.558*	0.955***

Correlations printed in bold are significant after controlling for a table-wide false discovery rate at  $P < 0.05$  (Benjamini & Hochberg, 1995); significance: \*\*\*  $P < 0.001$ , \*  $P < 0.05$ .

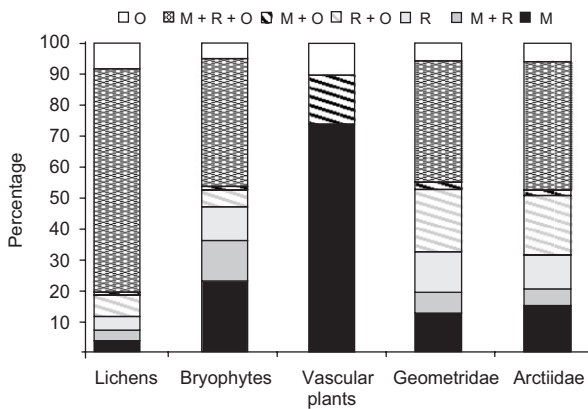
moths and lichens, however, were less pronounced and just not significant ( $P < 0.065$  for both moth families).

Mean overall similarity of epiphyte assemblages on individual host-trees was highest among lichens with ca. 70%, followed by bryophytes with 55%, and vascular epiphytes with only 29% (as calculated from the Sørensen index). Mean similarity of moth ensembles between pairs of sites was 42% among Arctiidae, and just 33% among Geometridae (as scaled to square root 2, which is the maximum possible value of CNESS).

A high percentage of species occurred in all three habitat types along the disturbance gradient, especially among lichens (Fig. 3). The percentages of species restricted to only one of the three habitat types were rather similar for bryophytes (39%), Geometridae (31%) and Arctiidae (32%), and lower (16%) in lichens (data on vascular plants lacking for all three habitat types).

## Discussion

Our results show that different taxonomic groups respond idiosyncratically to forest disturbance in montane habitats in southern Ecuador with regard to species richness. These findings are consistent with Lawton et al. (1998) and Axmacher et al. (2004), who both documented a multitude of responses of different taxa to local habitat changes. Schulze et al. (2004), however, showed that a uniform diversity pattern across a wide range of animal and plant groups following tropical forest alteration may also occur. Schulze et al. (2004) assume that the correlated decrease in species richness in their study taxa was partially caused by the



**Fig. 3.** Percentages of species restricted to mature (M), recovering forest (R), and open vegetation (O) or occurring in more than one habitat type. For vascular epiphytes, R was not sampled.

high degree of fragmentation of habitats under survey, whereas Axmacher et al. (2004) point out that diverging patterns in their study were related to biogeographical factors and the availability of microhabitats in the study area. Besides peculiarities of the investigated areas, the selection of focal taxa likely influences the outcome of species richness studies. Lawton et al. (1998), for example, included organisms which are highly specific to soil or upper canopy microhabitats. Divergent diversity patterns should be expected for organisms that are habitat specialists with highly different habitat requirements. In our study, the dissimilar species richness patterns of epiphytes and moths can also be related to their dissimilar habitat requirements. Decrease in epiphyte diversity with increasing disturbance has previously been shown from neotropical montane areas (e.g., Acebey et al., 2003; Wolf, 2005). Epiphytes are most negatively affected by conversion of forest into pastures due to immediate loss of their host-trees (Hietz-Seifert, Hietz, & Guevara, 1995). Bryophyte and vascular epiphytes are subjected to elevated drought stress after forest alteration, whereas the occurrence of lichens is favored through reduction of excessive humidity and shade (Nöske, 2005; Werner et al., 2005). Accordingly, lichens preferably grow in the canopy of primary forest and can survive in disturbed habitats (Rhoades, 1995). However, Holz and Gradstein (2005) found that diversity of bryophytes in upper montane forest in Costa Rica increased with increasing disturbance, whereas that of lichens decreased. The higher species richness in the secondary forest in this latter study was explained by the dense canopy of this forest, resulting in permanently high humidity, which promoted bryophyte growth but was less favourable for lichens. In our Ecuadorian study area, on other hand, the canopy was more open in disturbed habitats, causing

a decrease in relative air humidity with increasing disturbance (Nöske, 2005). In addition to microclimate, establishment of epiphytes depends on host-tree characteristics, particularly roughness and chemical composition of the bark (Gradstein et al., 2003). Distance to source populations may also play an important role (Hietz-Seifert et al., 1995; Wolf, 2005) as does bryophyte cover, which serves as a substrate and as a source of nutrients and water for vascular epiphytes (Krömer & Gradstein, 2004; Werner et al., 2005).

Species richness of moths in tropical lowland forests may achieve peak values in old secondary forest habitats (Schulze, 2000; Beck, Schulze, Linsenmair, & Fiedler, 2002) or after moderate selective logging (Holloway, 1998; Willott, 1999). This also applies to geometrid and arctiid moths in our montane study area (see Hilt & Fiedler, 2005, 2006; Hilt et al., 2006). Local niche heterogeneity is increased in recovering habitats, and species from open vegetation and forest may co-occur in such situations. Highest diversity of geometrid moths was also detected for old secondary forest on Mt. Kilimanjaro (Axmacher et al., 2004), although, overall diversity of Geometridae was conspicuously low in this area when compared with Ecuadorian sites (Brehm et al., 2005).

The lower species diversity of both moth taxa in mature forest in comparison to recovering forest may be biased by restricting the sampling to the understorey. Previous studies however, found no evidence of a true geometrid canopy fauna (Intachat & Holloway, 2000; Beck et al., 2002; Brehm, 2007), whereas tropical arctiid moths are significantly more abundant and diverse in the canopy than in the understorey (Schulze, Linsenmair, & Fiedler, 2001; Brehm, 2007). Thus, diversity of arctiid moths in tall-grown natural forest in Ecuador may have been underestimated by our sampling strategy. This underscores the necessity of using diversity measures, which account for sampling (Fisher's alpha, CNESS index), in the analyses of moth catches.

While no uniform pattern in species richness was detected along the disturbance gradient in Ecuador, matrix rank correlations revealed similar trends of changes in species composition of almost all taxa following deforestation. As expected, changes in species composition along the disturbance gradient were highly significantly correlated within the non-vascular epiphytes on the one hand, and within the moths on the other hand. Habitat requirements and life-history traits are, despite all specific differences, more similar within non-vascular epiphytes and within moths, respectively. Moreover, in these within-group comparisons data had been collected at exactly the same sites and at the same time. Nevertheless, shifts in species composition were also correlated between bryophytes and the two moth families, in spite of differences between sampling procedures.

These similarities do not reflect trophic relationships between bryophytes and moths, since hardly any representatives of Arctiidae and Geometridae are known to feed on bryophytes (Powell, Mitter, & Farrell, 1999). Correlations between the two moth taxa and lichens were just not significant. Lichen-feeding is somewhat more common in moths, including a few species in the Geometridae as well as in quite a number of Arctiidae (Powell et al., 1999; Jacobson & Weller, 2002). We suppose that similar trends in changes of species composition of bryophytes, geometrids and arctiid moths, as evidenced by the similar proportions of species occurring in one, two, or all three habitat types, is because of common responses to environmental changes. Epiphyte species restricted to mature forest are typically shade epiphytes, which are adapted to growth in the dark and humid understorey of the forest, while species restricted to disturbed habitats are able to tolerate a high light intensity and low air humidity (Gradstein et al., 2001; Acebey et al., 2003; Krömer & Gradstein 2004; Nöske, 2005). Moreover, proportion of ‘exclusive’ species or species with a wider distribution across habitats also reflects the dispersal and establishment abilities of the organisms under study (e.g., Ricketts, Daily, Ehrlich, & Fay, 2001; Cascante Marín, Wolf, Oostermeijer, Nijs, Sanahuja et al., 2006).

The degree of changes in species composition varied between the studied taxonomic groups. Other studies comparing beta-diversity between different habitat types have also demonstrated a lower beta-diversity in lichens than in bryophytes and vascular plants (Wolf, 1993; Pharo, Beattie, & Binns, 1999). The high beta-diversity of vascular epiphytes in our study area is consistent with a survey in montane rain forest in Bolivia (Krömer & Gradstein, 2004). The somewhat higher similarity among Arctiidae ensembles reflects their overall larger size and robustness as opposed to the Geometridae with many delicate species which are also more bound to intact forest (Hilt & Fiedler, 2006; Hilt et al., 2006). Hence, the presumed larger range of activity in arctiids is more likely to alleviate sampling effects. It is nevertheless remarkable that, despite their good flight potential, all these moth taxa showed clear faunal segregation between habitat types at the small spatial scale of our study.

In conclusion, our observations on species richness suggest that the dynamics of organisms along disturbance gradients do not follow a uniform pattern. They rather may be taxon-specific and also depend on the study area. Responses of organisms to disturbance are shaped by the availability of niches and their ecological flexibility, and they may also considerably differ across regions. This severely undermines the concept of “biodiversity indication”, e.g. as a tool in conservation ecology. The correlation of diversity patterns, or the lack of such relationships, may more often reflect the

choice of target groups than the ecological gradient under study. However, anthropogenic disturbance in the Ecuadorian study area resulted in similar trends of changes in species composition across the different taxonomic and functional groups of organisms. Our findings agree with those of Lawton et al. (1998) that local species richness may not be an appropriate measure to assess and predict changes induced by anthropogenic habitat alteration. Especially, generalizations from one group to another may often be unjustified. Instead, focussing on species composition may be a more powerful approach (Legendre, Borcard, & Peres-Neto, 2005).

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