

Diversity and ensemble composition of geometrid moths along a successional gradient in the Ecuadorian Andes

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Abstract: Little is known about the change of species-rich tropical insect communities along habitat gradients. Diversity and species richness of geometrid moths were investigated at 15 anthropogenically disturbed sites in a montane area in the Andes of southern Ecuador representing a successional gradient. These plots were compared with six closed-forest understorey sites. We collected a total of 23,720 individuals representing 868 morphospecies. Local diversity increased with forest recovery and decreased with increasing distance to the natural forest. 18.6% of all species were found as unique singletons. The mean proportions of local singletons differed significantly between three succession classes. Forest understorey showed a higher proportion of singletons than early and late successional stages. Ordination of the moth samples showed a clear separation of geometrid ensembles at successional sites vs. the forest understorey sites. Patterns of species turnover were influenced by the degree of habitat openness, and to a lesser extent by elevation. However, faunal differences were not related to geographical distances between the sampling sites. In conclusion, geometrid moth ensembles of regenerating Andean montane forest remain diverse, but change significantly in composition relative to adjacent natural forest, whereas the diversity and composition of the geometrid fauna are far more strongly affected in non-forested habitats and abandoned pastures.

Key Words: habitat disturbance, Geometridae, herbivorous insects, montane rain forest, species composition, species richness

INTRODUCTION

Andean highland ecosystems are among the best represented in protected areas due to the preponderance of highland parks in the eastern Andes (Armenteras *et al.* 2003). However, less than 4.5–6.4% of the original pre-Columbian extent of Andean and sub-Andean forests are currently protected (Armenteras *et al.* 2003). Annual deforestation rates continue to be high (0.94%; FAO 1997), especially outside protected areas. This will lead to the loss of many threatened species in the near future (Brooks *et al.* 2002). Fragmented habitats under human land-use regimes become increasingly important for the conservation of biodiversity. Even though the preservation of large areas of continuous, pristine habitat is crucial for the conservation of many species, human-dominated landscapes cover the majority

of land area in many parts of the world (Ricketts *et al.* 2001). A considerable number of studies have dealt with effects of logging on animal communities (Meijaard *et al.* 2005). However, less is known about changes of species-rich tropical insect communities along habitat gradients, representing different successional stages of forest recovery and land use after logging. While a substantial body of evidence has been collated for insects in South-East Asian forests (Beck *et al.* 2002, Chey *et al.* 1997, Fiedler & Schulze 2004, Holloway 1998, Intachat & Holloway 2000, Schulze 2000, Willott 1999), the far more species-rich Neotropical realm has received much less attention in that regard (Brehm & Fiedler 2005, Ricketts *et al.* 2001). Hence, it is still difficult to assess how much of the original biodiversity can be maintained in human-dominated tropical landscapes and how the structure and function of communities may change. Since more than half of global diversity in terms of numbers of described species is represented by insects, the way in which these organisms respond to changes in their habitat is an important concern (DeVries *et al.* 1997, Hamer & Hill 2000).

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The better-known groups of the Lepidoptera have often been advocated as useful indicators of environmental impact (Kitching *et al.* 2000). More than 90% of the known lepidopteran species are moths, the majority of which are nocturnal (Scoble 1995, Young 1997). The Macrolepidoptera are taxonomically relatively well known and usually attractable to light traps. Accordingly, the numbers of species as well as individuals that can be sampled in short periods of time give statistical power in site-to-site comparisons at high spatial and temporal resolution (Fiedler & Schulze 2004, Kitching *et al.* 2000). We chose geometrid moths as a model group. With more than 21,000 validly described species globally, of which some 6400 (30%) occur in the Neotropical region, Geometridae are one of the three most species-rich moth families (Scoble 1999).

Tropical geometrid moth ensembles (terminology: Fauth *et al.* 1996) were previously found to reflect ecological differences between habitats (Intachat *et al.* 1997, 1999) and to show high habitat fidelity (Chey *et al.* 1997, Holloway 1984). A number of recent studies dealt with geometrid diversity along altitudinal, habitat and successional gradients in tropical regions (altitudinal gradient: Axmacher *et al.* 2004a, Brehm 2002, Brehm & Fiedler 2003, Schulze 2000; habitat gradient: Brehm & Fiedler 2005, Chey *et al.* 1997, Holloway *et al.* 1992, Intachat *et al.* 1997, Ricketts *et al.* 2001, Willott 1999; successional gradient: Axmacher *et al.* 2004b, Beck *et al.* 2002, Holloway 1998, Kitching *et al.* 2000, Schulze 2000). All these studies indicate that geometrid moths respond sensitively to changes in habitat quality.

We compared 15 succession sites with six mature-forest understorey sites situated in the montane forest zone of the Ecuadorian Andes to test the following hypotheses:

- (1) Disturbed habitats have a significantly lower geometrid diversity than mature forest (Beck *et al.* 2002, Brehm & Fiedler 2005, Holloway *et al.* 1992, Kitching *et al.* 2000), because of the habitat specificity of geometrid moths (Brehm & Fiedler 2003).
- (2) The proportion of singletons (species represented by only one individual) is higher in early succession stages (Hilt & Fiedler 2005a) and in forest habitats (Brehm *et al.* 2003a, Novotný & Basset 2000, Ricketts *et al.* 2001, Willott 1999) compared with intermediate succession stages (Hilt & Fiedler 2005a), because in early succession stages many tourists or dispersers show up and mature tropical forest understorey is generally noted for a high proportion of singletons (Novotný & Basset 2000).
- (3) The dominance of a few species is higher in early succession stages than in mature forest understorey (Axmacher *et al.* 2004a, b; Fiedler & Schulze 2004). This assumption is based on the idea that after habitat disturbance, the developing pioneer community is

dominated by just a few species (Nummelin & Kaitala 2004).

- (4) Between-habitat diversity (β -diversity) reflects the gradient of disturbance. Moth ensembles differ between habitats of different successional age due to their affiliation with plant resources the availability of which changes with progressing succession (Beck *et al.* 2002).

METHODS

Study area, sampling and identification

The study area in southern Ecuador (Reserva Biológica San Francisco, 3°58'S, 79°5'W) is situated within the Eastern Cordillera of the Andes at the northern border of the Podocarpus National Park (Brehm & Fiedler 2003, Brehm *et al.* 2005, Hilt & Fiedler 2005b). It is covered with undisturbed to slightly disturbed montane rain forest (Homeier *et al.* 2002, Paulsch 2002). At anthropogenically disturbed sites forest has been replaced by pastures, thickets of bracken (mainly *Pteridium arachnoideum* (Kaulf.) Maxon), shrub encroachment, or regenerating forest (Hartig & Beck 2003, Paulsch 2002).

Mean annual precipitation reaches around 2000 mm without a marked dry season, and the average monthly temperature was 15.6°C at an altitude of 1952 m asl (Richter 2003). We selected 15 sites (labelled A to I) representing seven different stages of vegetation succession and including two abandoned pastures (Hilt & Fiedler 2005a). For most of these stages two replicate sites were selected in close proximity (distance to natural forest between 22 and 445 m), but with minimum distances between the sites of 100 m. In addition, moth samples from six sites situated in the understorey of natural forest (labelled 3a to 5b) were analysed (two replicate sites at every 100 m elevation, Brehm & Fiedler 2003). At all sites, vegetation appeared to be homogeneous around the position of the light tower in a radius of at least 50 m. These 21 sites, situated in a narrow elevational band (1800–2000 m), represent a succession gradient of forest recovery. The earliest successional stage was represented by a landslide along a pathway. Landslides are the commonest form of forest disturbance on steep Andean slopes (Ohl & Bussmann 2004). Other early succession stages included grassy slopes, bracken thickets, and abandoned pastures (all without woody vegetation) and represented some of the most relevant types of habitats due to local land-use practices. Later succession stages were represented by secondary shrubs (about 5–10 y after clearing), secondary forest (about 40 y after clearing) and the transition zone between forest and a clearing; all these sites had extensive cover by woody vegetation. Altitude

and geographical coordinates of sampling sites were measured using a Garmin GPS III instrument (Garmin Instruments Inc., Olathe, KS, USA). Ambient temperature during moth sampling was measured every 30 min during each catch unit with an electronic thermometer (TFA, Dostmann, Wertheim, Germany) 1.60 m above ground (on top of the light tower). Temperature data were averaged over all catch nights for each site. Canopy cover was measured using one hemispherical photograph per site taken with a Nikon Coolpix 990 (3.34 megapixels, and an additional hemispheric lens [Nikon Fisheye F8-E8]). From these images, the 'visible sky' value as an estimate of habitat openness was calculated with the HemiView program, version 2.1 (Delta-T Devices, Burwell, Cambridge; see Brehm *et al.* 2003b). Depending on the type of analysis, the progress of succession was either scored on a rank scale (degree of succession) from 1 (young landslide with sparse vegetation) to 7 (mature forest), according to the proportion of woody plants (see Table 1 in Hilt & Fiedler 2005a). Alternatively, sampling sites were grouped into three categories according to their successional stage (early (E) without woody vegetation: N = 10 sites; late (L) with shrubs or young secondary forest: N = 5; understorey of closed-canopy forest (F): N = 6). For analysis of similarities (ANOSIM) the two abandoned pastures sites (P: N = 2) were separated from the earlier succession stages (E: N = 8 sites).

Moths were manually sampled using a portable light 'tower' (Fritz Weber, Stuttgart: height 1.60 m, diameter 0.60 m) with weak light sources (Sylvania blacklight-blue, F 15 W/BLB-TB and Phillips TLD 15 W 05). In contrast to automatic light traps, light towers have been demonstrated to catch a wider spectrum of geometrid moth species and a higher number of specimens per unit time (Axmacher & Fiedler 2004). We considered the use of these low-power light sources sufficient to minimize cross-attraction of moths between sampled habitats (Muirhead-Thomson 1991, Schulze & Fiedler 2003). We restricted sampling to the peak time of moth activity during the evening hours between 18h30 and 21h30 local time (closed-canopy forest) and 18h45 and 21h45 (succession habitats without closed canopy). Although 'late-night species' as well as strictly diurnal geometrids will have been missed by this approach, this is not expected to influence the comparisons between sites. Specimens were collected during five field periods. Between four and eight nightly catches from each site were pooled and analysed. Catches were restricted to periods without bright moonlight (McGeachie 1989, Yela & Holyoak 1997).

Specimens were first sorted to 'parataxonomic units' (*sensu* Krell 2004) and later taxonomically identified as far as possible using various reference collections (see Acknowledgements). Voucher specimens of all species are deposited in the State Museum of Natural History (SMNS), Stuttgart, Germany.

Statistical analyses

The choice of appropriate measures of alpha diversity for species-rich tropical moth ensembles was discussed by Brehm *et al.* (2003a). As a measure of local diversity we used Fisher's alpha (calculations with the program *Species diversity and richness*, Version 2.62, developed by P.A. Henderson and R.M.H. Seaby) and Hurlbert's rarefaction method for a standardized number of 350 specimens (URL for software: <http://www.zoology.ubc.ca/~krebs>, developed by A.J. Kenney and C.J. Krebs). Rarefaction is particularly useful if assemblages are sampled with different intensity or success (Gotelli & Colwell 2001), and for samples of different size (Hurlbert 1971, Schulze & Fiedler 2003).

Insect assemblages in tropical rain forests usually contain large numbers of rare species (singletons). Novotný & Basset (2000) distinguished between 'local singletons', i.e. species found as a single individual in component communities, and 'unique singletons', viz. species found as a single individual in a combined data set. We calculated the proportion of both types of singletons for every sampling site. To compare the proportion of singletons from succession sites vs. mature forest we randomly rarefied the larger cumulative sample (geometrids of all succession habitats, 20,670 individuals) to the level of the smaller sample from natural forest (3050 individuals). We then compared the proportion of observed singletons in natural forest to the 95% confidence interval for singletons in succession habitats calculated after 10 randomisation runs. Comparisons of the numbers of individuals and species observed per night were performed with ANOVA across the three habitat categories. Dominance of the commonest species was expressed through the Berger-Parker index (Southwood & Henderson 2000). We restricted quantitative comparisons of relative abundances to the 10 overall most abundant species (i.e. those recorded with > 235 individuals in total).

We ordinated moth samples by non-metric multidimensional scaling (NMDS; Clarke 1993) to study species composition of local geometrid ensembles using the full abundance information for all species. To alleviate sampling effects (which are especially prevalent if sampling is not complete, samples contain many rare species, and are of different size and diversity; Brehm & Fiedler 2004) we used the chord-normalized expected species shared index (Gallagher's CNESS index; Trueblood *et al.* 1994) as a measure of dissimilarity between samples. The CNESS index can be adjusted by choice of the sample size parameter, m . At its minimum of $m = 1$, CNESS emphasizes the role of dominant species. At the other extreme, CNESS dissimilarities for maximum m values stress the contribution of rare species to faunal differences. We also used an intermediate value ($m = 170$). We calculated CNESS distances using

the program COMPAH96 (available from E. Gallagher, University of Massachusetts at Boston, via website, URL: <http://alpha.es.umb.edu/faculty/edg/files/edgwebp.htm>). Ordinations were performed with an updated version of Statistica 6 (StatSoft Tulsa, UK). The significance of faunal differences between predefined groups of sites was assessed by ANOSIM (Clarke & Warwick 2001) with 1000 random permutations. We investigated the association between distance matrices using a rank test based on Spearman coefficients, as implemented in PRIMER v5 (Clarke & Warwick 2001) with 1000 random permutations. All other statistical analyses were performed using an updated version of Statistica 6. Where necessary, multiple tests of significance were corrected for a table-wide false discovery rate (FDR) of $P < 0.05$ according to the step-up procedure by Benjamini & Hochberg (1995).

RESULTS

Alpha diversity of geometrid moths

We sampled a total of 23,720 individuals representing 868 species during 120 sample nights (Table 1). A detailed species list will be provided elsewhere (N. Hilt, unpublished data; see also Brehm *et al.* 2005). Five hundred and sixty-four (65%) of these morphospecies comprising 78.1% of all individuals could be taxonomically identified at species level, of which 366 species (42.2%) were restric-

ted to the succession sites, 92 (10.6%) to the mature forest understorey and 410 (47.2%) were shared between both types of habitats. The minimum and maximum numbers of collected individuals per site were 384 (site 3b) and 2079 (site G1), respectively. Numbers of observed species per site ranged from 171 (site 3b) to 423 (site I). The average number of individuals caught per night varied significantly across all three different habitat categories (one-way ANOVA: $F_{2,117} = 12.1$; $P < 0.001$; Levene-test for homogeneous variances, $P > 0.09$). Nightly catches in later successional stages (mean value \pm 1 SD: 291 ± 126 with $N = 31$; sites G to I) were significantly higher than at earlier successional stages (mean value: 176 ± 146 with $N = 65$) and forest understorey (mean value: 127 ± 84 with $N = 24$), respectively. Only the difference between late-successional habitats and the two other habitat classes (early, forest understorey) was significant (Scheffé test $P < 0.001$). The mean number of observed species per night (ANOVA: $F_{2,18} = 7.75$, $P < 0.005$; Levene-test for homogeneous variances $P > 0.05$) was significantly higher in later successional stages (mean \pm SD: 62 ± 6) than in earlier ones (43 ± 11) (Scheffé test, $P < 0.005$), but the difference in comparison with mature forest understorey (49 ± 5) was not large enough to reach statistical significance (Scheffé test, $P > 0.07$).

Values of Fisher's alpha were strongly correlated with rarefied species richness ($r_p = 0.91$, $P < 0.001$) and showed therefore the same pattern along the succession gradient (see Table 1). Thus we subsequently restricted our analyses to the rarefied species numbers. Figure 1a

Table 1. Numbers of collected species and individuals, sampling nights, two measures of species richness and diversity, the number of singletons, and the habitat category for all 21 study sites. Habitat categories: E = early succession, L = Late succession, F = Forest, P = Abandoned pasture.

Sample site	Altitude (m)	Species number	Number of individuals	Sample nights	Mean collected number per night	Fisher's alpha	Rarefied species number (350 individuals)	Number of local singletons	Habitat category
A	1913	329	1588	6	265	126	134	170	E
B1	1872	287	1337	6	223	112	140	128	E
B2	1925	246	970	6	162	106	145	109	E
C	1830	277	1529	8	191	98	130	114	E
D1	1894	194	879	7	126	77	112	106	E or P
D2	1908	186	746	7	107	79	118	104	E or P
E1	1832	225	624	7	89	126	161	121	E
E2	1863	292	1485	6	248	108	132	135	E
F1	1917	269	928	6	155	127	161	120	E
F2	1921	361	1553	6	259	147	164	165	E
G1	1886	414	2079	7	297	155	175	156	L
G2	1912	376	2016	6	336	136	169	127	L
H1	1900	334	1629	6	272	127	147	136	L
H2	1920	366	1444	6	241	158	180	138	L
I	1973	423	1863	6	311	170	186	158	L
3a	1800	204	497	4	124	129	164	119	F
3b	1800	171	384	4	96	118	161	107	F
4a	1850	181	473	4	118	107	149	112	F
4b	1875	226	649	4	162	123	158	118	F
5a	2005	202	618	4	155	104	147	107	F
5b	2005	190	429	4	107	130	167	114	F

Table 2. Relative abundances of the 10 commonest geometrid species. Included are results of Kruskal–Wallis ANOVAs for each species and the mean relative abundance \pm SD. P values marked with # are not significant after step-up FDR correction of $P < 0.05$.

Species name and author	Number of individuals	Species rank	H(2, N = 21) statistic	P value	Early succession (N = 10)	Late succession (N = 5)	Forest understorey (N = 6)
<i>Pantherodes conglomerata</i> Warren 1894	2597	1	15.1	0.0005	17.4 \pm 11.0	6.0 \pm 2.6	0.4 \pm 0.4
<i>Sabulodes thermidora</i> Thierry–Mieg 1894	1006	2	7.9	0.019	6.4 \pm 4.8	1.5 \pm 1.1	3.4 \pm 4.2
<i>Argyrotope prospectata</i> Snellen 1874	432	3	3.7	0.159	2.5 \pm 2.2	1.0 \pm 0.9	1.6 \pm 2.3
<i>Chloropteryx opalaria</i> Guenée 1857	334	4	8.5	0.014	1.1 \pm 0.9	1.3 \pm 0.9	2.8 \pm 1.3
<i>Physocleora pulverata</i> Warren 1907	327	5	12.7	0.0018	0.4 \pm 0.3	0.4 \pm 0.1	7.9 \pm 6.8
<i>Eois paraviolascens</i> Dognin 1900	321	6	6.7	0.036#	0.5 \pm 0.6	2.8 \pm 4.0	0.3 \pm 0.3
<i>Oxydia trychiata</i> Guenée 1858	297	7	5.1	0.078	0.8 \pm 0.4	1.8 \pm 0.8	1.7 \pm 1.2
<i>Physocleora</i> sp.	288	8	12.7	0.002	1.2 \pm 0.9	1.7 \pm 0.4	0.1 \pm 0.2
<i>Perissopteryx</i> sp. nr. <i>nigricomata</i> Warren 1901	249	9	12.8	0.002	0.8 \pm 0.6	1.8 \pm 1.2	0.1 \pm 0.1
<i>Perizoma zenobia</i> Thierry–Mieg 1893	242	10	10.9	0.004	1.6 \pm 1.1	0.2 \pm 0.1	1.0 \pm 0.8

shows the rarefied species richness at a standard sample size of 350 individuals. Diversity was significantly higher in the later succession stages than in earlier stages. However, the difference in moth diversity between the later succession stages and the mature forest understorey was not significant. Only the early succession stages had distinctly lower diversity values. Correlations between abiotic factors, e.g. altitude, mean temperature, canopy openness and distance of the sites from the mature forest vs. values of Fisher's alpha and rarefaction were not significant with one exception. Irrespective of the measure used, diversity decreased with increasing distance to the natural forest (distance vs. Fisher's alpha: $r_p = -0.59$, $P < 0.005$ and vs. rarefied species numbers: $r_p = -0.65$, $P < 0.005$).

A total of 161 species (18.6%) was found as unique singletons, i.e. only with one specimen, and 91 species (10.5%) were doubletons. Rarefaction analysis (i.e. 3050 individuals, see Methods) was used to compare the proportions of unique singletons between succession and forest sites. The observed proportion of singletons at the forest understorey sites (59.8%) was almost twice as high as at the succession sites (expected proportion of singletons \pm SD: 32.2% \pm 1.1%). The ratio of singletons at individual sites (local singletons) varied between 33.8% and 62.6% of the species (Table 1). The mean proportions of local singletons (Figure 1b) differed significantly between the three succession classes (ANOVA: $F_{2,18} = 28.2$, $P < 0.001$). The highest proportion was found in the forest understorey, followed by the earlier succession stages, while the lowest values were found in succession stages after the onset of recovery of woody vegetation.

The Berger–Parker index varied between 0.03 (site G1) and 0.32 (sites A and E2). Mean dominance values (Figure 1c) differed among the three habitat categories (Kruskal–Wallis ANOVA: $H(2, N = 21) = 7.50$, $P < 0.05$), but the difference was only significant

between the early and the late-successional stages (post hoc test, $P < 0.05$). The highest values were found in the early stages, followed by the mature forest understorey and the later successional stages. The ten overall commonest species are listed in Table 2. The relative abundance of *Pantherodes conglomerata* decreased significantly along the succession gradient from early stages to mature-forest understorey (Kruskal–Wallis ANOVA: $H(2, N = 21) = 15.1$, $P < 0.001$). Some species were equally common in all three habitat categories (*Argyrotope prospectata*, and *Oxydia trychiata*, ranks 3, and 7), whereas some species showed a clear preference for succession sites (*Pantherodes conglomerata*, *Sabulodes thermidora*, *Physocleora* sp., *Perissopteryx* sp. near *nigricomata*, ranks 1, 2, 8, and 9) or forest understorey (*Chloropteryx opalaria*, *Physocleora pulverata*, ranks 4 and 5). In most cases the relative abundances of these 10 commonest species differed significantly between the habitat categories (Table 2).

Species turnover along the successional gradient

For all three different values of the sample size parameter m (Figures 2a–c), non-metric two-dimensional scaling of the CNESS index yielded similar ordinations of the moth ensembles. In all three cases the successional sites were significantly separated from the mature forest understorey (ANOSIM with step-up FDR correction; E vs. F: $0.76 < R < 0.82$, $P < 0.005$; L vs. F: $0.34 < R < 0.74$, $P < 0.05$). Geometrid moth samples from the natural forest understorey formed a distinct group which clearly reflected the altitudinal gradient from the lower sites (3a, 3b) to the higher ones (5a, 5b). A separation between the earlier and later successional sites was only found when the common or moderately abundant species were emphasized, i.e. with $m = 1$ and $m = 170$ (E vs. L: $0.37 < R < 0.40$, $P < 0.05$). No difference between these

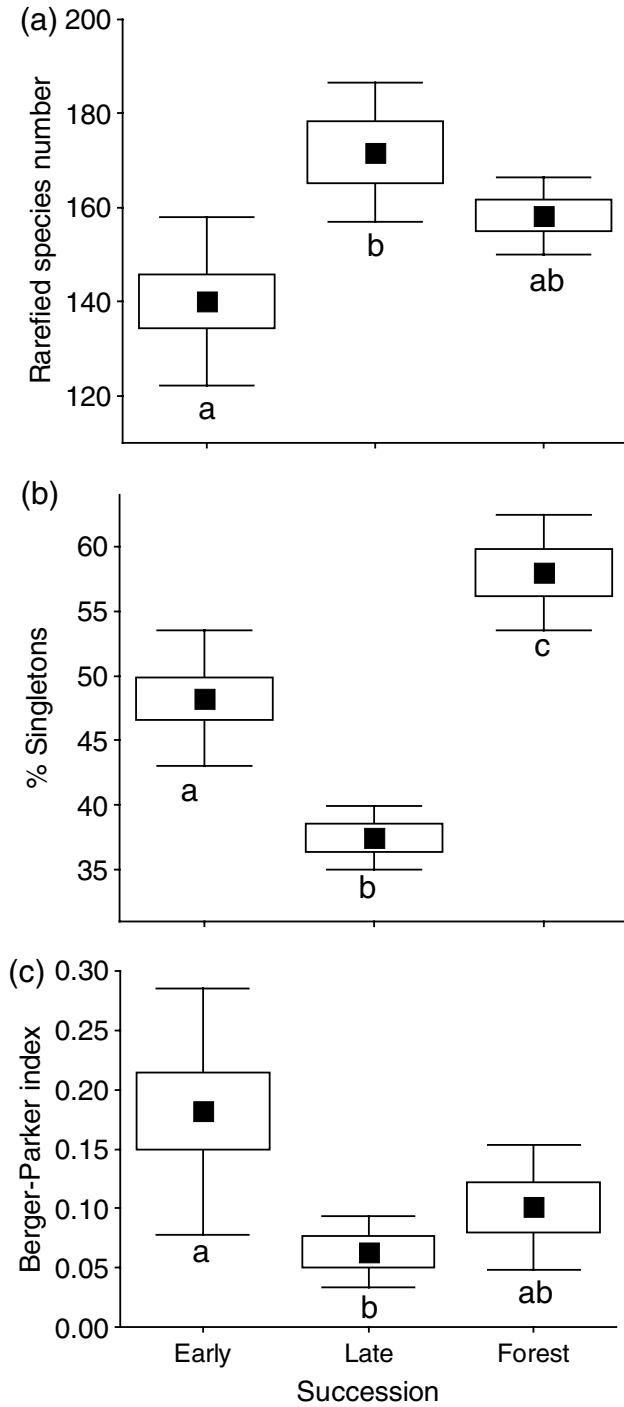


Figure 1. (a) Diversity expressed as rarefied species number (350 individuals; ANOVA: $F_{2,18} = 7.82$, $P < 0.005$; Levene test $P > 0.2$), (b) proportion of local singletons (in per cent of species), and (c) Berger–Parker index for geometrid moths in the three different habitat classes. Boxes labelled with different letters differ significantly at $P < 0.05$ (one-way ANOVA followed by Scheffé test). Symbols = means, boxes = ± 1 SE, rules = ± 1 SD.

different successional classes could be found, when the rare species were emphasized at $m = 384$ (E vs. L: $R = 0.24$, $P > 0.05$). However with increasing m , the

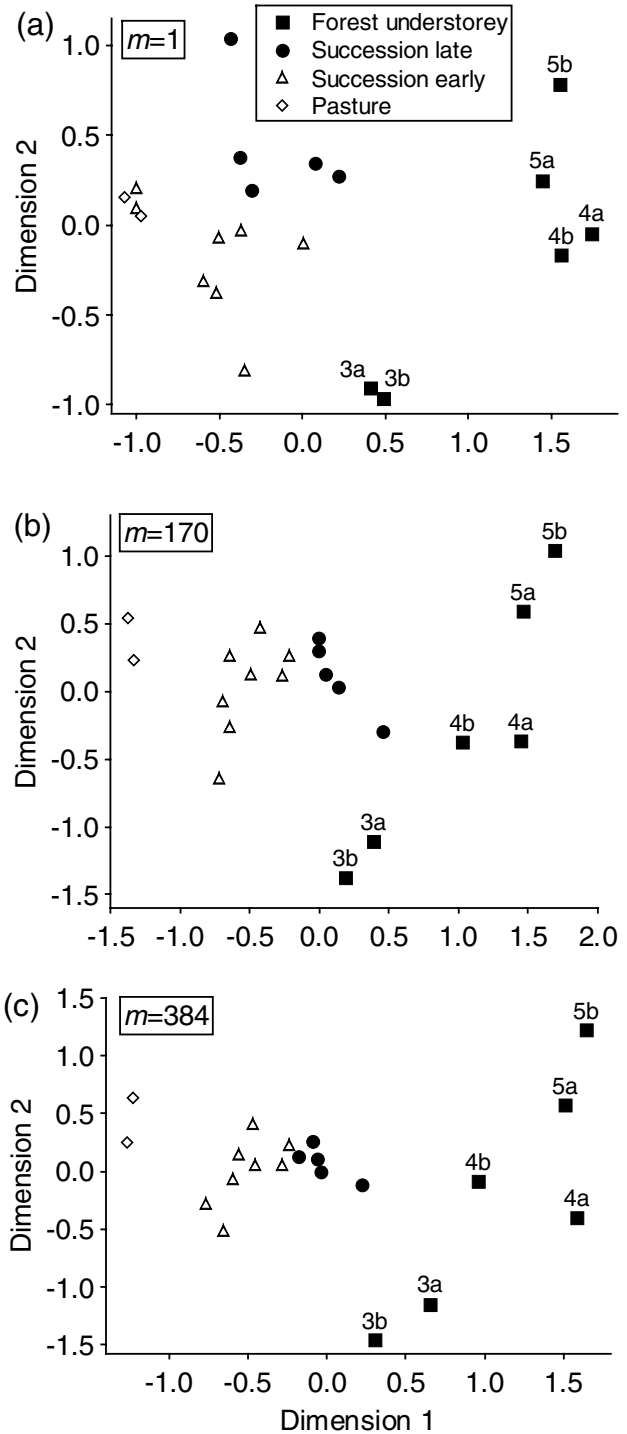


Figure 2. Non-linear two-dimensional scaling plots of moth samples from 21 sites based on CNESS distances with different values of the sample size parameter m : (a) $m = 1$, stress 0.10; (b) $m = 170$, stress 0.12, and (c) $m = 384$, stress 0.11.

earlier successional stages were more clearly separated from the two abandoned pasture sites ($m = 170$ and 384 ; E vs. P: $0.77 < R < 0.90$, $P < 0.05$).

Table 3. Pearson correlation coefficients between the axis scores of geometrid samples extracted from two-dimensional NMDS ordinations and different environmental factors (altitude, 'visible sky', distance of the sites from forest, and temperature) as well as Spearman rank correlation coefficients for the degree of succession. m – Sample size parameter of the CNESS index. All nominally significant results remain so after correction for a FDR of $P < 0.05$. n.s.: not significant. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Altitude	'Visible sky'	Degree of succession	Distance from forest	Temperature
$m = 1$					
Axis 1	0.14 n.s.	−0.88***	0.83***	−0.70***	0.50*
Axis 2	0.69***	0.07 n.s.	0.17 n.s.	0.05 n.s.	−0.16 n.s.
$m = 170$					
Axis 1	0.29 n.s.	−0.89***	0.90***	−0.81***	0.55**
Axis 2	−0.85***	−0.30 n.s.	0.14 n.s.	−0.22 n.s.	0.41 n.s.
$m = 384$					
Axis 1	−0.23 n.s.	0.92***	−0.90***	0.79***	−0.60**
Axis 2	0.85***	0.22 n.s.	−0.14 n.s.	0.22 n.s.	−0.35 n.s.

Table 4. Results of matrix rank correlations (based on Spearman coefficients, 1000 random permutations) between faunal dissimilarity (CNESS distances) and distance matrices for elevation, geographic position, temperature and 'visible sky'. For environmental variables, Euclidean distances between sites were used. All figures are significant after a step-up FDR correction of $P < 0.05$. n.s.: not significant. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

m value	Elevation	Geographic distance	'Visible sky'	Temperature
1	0.26**	−0.05 n.s.	0.73**	0.18 n.s.
170	0.34**	−0.07 n.s.	0.75**	0.20*
384	0.36**	−0.11 n.s.	0.72**	0.21*

Extracted scores of the moth samples along the first NMDS dimension correlated with the following environmental factors (ordered according to strength of the correlation) (Table 3): 'visible sky', degree of succession, distance of the sites from the natural forest, and temperature during sampling. Samples were ordered along the second dimension according to the elevation of the sites (correlation between the extracted scores of the second dimension and altitude: $r_p > 0.68$, $P < 0.001$). Rank-based matrix correlation tests revealed significant relationships between faunal dissimilarity and the degree of habitat openness ('visible sky') as well as elevation and temperature during sampling (Table 4). However, temperature effects were significant only with higher m values. Faunal dissimilarity was not at all related to the geographical distance between sampling sites ($P > 0.64$). Thus, 'visible sky' emerged as the strongest predictor of faunal change, but altitude of sampling sites also significantly influenced faunal similarity.

DISCUSSION

High moth diversity in advanced successional stages

With 868 observed geometrid species along a gradient of succession, the study area is very species rich at a small spatial scale (c. 2 km²). Overall, gamma-diversity across the succession gradient (expressed as Fisher's

alpha of all samples combined \pm SD) reached a value of 177 ± 2.8 . Compared with studies from Africa (188 species, Axmacher *et al.* 2004a), South-East Asia (500 species, Beck *et al.* 2002) and Australia (wet season: 122 species and dry season: 94 species, Kitching *et al.* 2000) at comparably small scales our data underscore the outstanding species richness of Andean montane habitats (Brehm *et al.* 2005).

Contrary to our expectations, the highest geometrid diversity along the succession gradient was found in the later succession stages and not in the mature forest understorey. Thus, geometrid ensembles of advanced succession sites in the Ecuadorian Andes are particularly rich in species and occasionally even slightly surpass those of mature natural forest. High geometrid moth diversity in advanced regenerating forest was also found by Beck *et al.* (2002) along a habitat gradient ranging from cultivated areas to primary rain forest on Borneo. In the montane forest zone on Mt. Kilimanjaro geometrid diversity was likewise not maximal in mature forest, but in disturbed habitats close to intact forest (Axmacher *et al.* 2004b). However, other studies did not find significant differences in moth diversity between disturbed sites and natural forest (SE Asia: Chey *et al.* 1997, Willott 1999). Apart from minor variations between moth taxa and between regions, all these studies show that moth faunas in tropical secondary forests or in regenerating succession habitats may retain considerable diversity, as long as natural forests as source areas for recolonization remain in the vicinity (see also Schulze 2000).

Possible reasons for the lower species richness in the natural forest as compared to later successional stages in Ecuador could be: (1) Sampling effort differed between habitat types (see above). However, rarefaction analyses should have eliminated sampling bias. (2) Sampling was restricted to the understorey at the forest sites, and did not include the canopy layer. For example, Willott (1999) found that moth diversity was 26% lower in understorey samples compared to the understorey and canopy combined. On the contrary, Beck *et al.* (2002) showed that in the Geometridae diversity estimates for

combined understorey plus canopy samples did not significantly exceed the scores for understorey ensembles alone (see also Schulze 2000). A similar pattern was observed in a Costa Rican lowland rain forest (GB, unpublished data), indicating that understorey sampling is likely to be sufficient in areas with steep slopes and small trees (15–20 m in the study area in Ecuador; Homeier 2004). (3) The effective attraction radius of the light trap may depend on habitat structure, e.g. the density of the vegetation. As a consequence, moths might be attracted from a larger distance in open habitats such as early successional stages. However, the highest numbers of individuals caught per night and the highest local diversities were found in the later successional stages, which have also denser vegetation than the earlier stages.

The reasons for higher numbers of species and individuals in the later successional stages are possibly (1) secondary-forest fauna contains species, which are otherwise more abundant in, or even restricted to, the canopy (Willott 1999), (2) these habitats contain a mixture of species from open habitats such as early successional stages as well as from mature forest. Disturbance creates opportunities for species not found in undisturbed forest, and the habitat mosaic resulting from regeneration after patchy disturbance further increases the number of niches available.

We found no evidence that generally larger numbers of geometrid moth species and individuals would be attracted at open sites than within closed-forest understorey. Mean numbers of observed species per night were only different between the early and later succession stages, but not in comparison with the forest understorey. Brehm & Fiedler (2003) also observed similar average numbers of geometrid individuals during 3-h catch units (which even exceeded 200 individuals per night) at the forest sites. Moreover, as detailed above, a growing number of studies has revealed that diversity of tropical moth ensembles is usually not lower, and sometimes even higher, in habitats under moderate anthropogenic disturbance as compared to closed forest. Collectively, the available pieces of evidence underline that this diversity pattern cannot be disregarded as a sampling artefact of light-trapping. The influence of disturbance on moth diversity also depends on the spatial scale considered (Hill & Hamer 2004, see also Rahbek 2005). The extent of such scale dependence needs to be explored in tropical montane forests in the future.

The much lower diversity of geometrid moths in the earlier successional stages can be explained with the preference of many geometrids (especially in the subfamily Ennominae) for woody plants as larval hosts (Scoble 1999). Furthermore, specialized geometrid species such as the genus *Eois* frequently depend on larval food plants that only occur in mature forests or later stages of succession (Brehm & Fiedler 2005). Geometrids

have also been regarded as a group with limited mobility and relatively high habitat fidelity (Holloway 1984, Intachat & Holloway 2000, Thomas 2002). Although geometrid moths may only rarely disperse across larger distances following disturbance to their natural habitats (Summerville & Crist 2004), 'tourist' species from natural forest are likely to occur in all investigated habitats because of their close proximity to each other (Brehm & Fiedler 2005). The high proportion of singletons in our samples underscores the fact that such dispersing individuals are common in open habitats (Figure 1b). Thus, species diversity of these early succession habitats may be overestimated.

Rare and abundant species in tropical moth communities

Insect communities in tropical rain forests mostly contain large numbers of rare species. Singletons often comprise more than half of the species total (Novotný & Basset 2000). In samples from tropical moth ensembles usually c. 30–60% of all species occurs as singletons (Brehm *et al.* 2003a, Ricketts *et al.* 2001, Schulze & Fiedler 2003, Willott 1999). All these data suggest that these moth samples were drawn from very large species pools. Our results from a successional gradient in the Ecuadorian Andes fit well into this range of observations. As expected, the proportion of unique singletons was much lower (18.6%) than local singletons.

Singletons were far more prevalent in the mature forest than in disturbed habitats. This applied to the comparison of rarefied samples (59.8% vs. 32.2%) as well as when comparing mean local singleton ratios (Figure 1b). This indicates that the contribution of rare species to moth ensembles is reduced as a consequence of habitat disturbance. In our study, the ratio of local singletons was not only high in the mature forest, but also in the earlier succession stages. Many singletons in these open, disturbed habitats must probably be regarded as colonists, which were sampled during dispersal flights from the nearby forest. However, even early successional stages support the existence of geometrid species with caterpillars that feed on 'pioneer' plants, e.g. certain members of the genus *Eupithecia* and other species (Brehm & Fiedler 2005; see also Intachat & Holloway 2000, Lepš *et al.* 2001).

Dominance in tropical moth assemblages is usually low (Wolda 1992). The most common species typically attains 5–10% of all individuals in a light-trap sample (Brehm 2002, Schulze 2000, Willott 1999), as opposed to 8–29% in moth ensembles from temperate regions (Germany: undisturbed sites < 8% vs. disturbed sites > 8%; Israel: undisturbed sites c. 17% vs. disturbed sites 25–29%; A. Hausmann, pers. comm.). Dominance in tropical assemblages may increase as a response to habitat disturbance

(Fiedler & Schulze 2004, Nummelin & Kaitala 2004). For example, Fiedler & Schulze (2004) found that dominance of a few species was more pronounced in Bornean pyraloid ensembles from more heavily disturbed sites. We observed similar changes in ensemble structure in Andean geometrids. The Berger–Parker index was highest in the earlier succession stages (mean \pm SD: $18.2 \pm 10.4\%$), but only 10.1 ± 5.3 in mature forest. Interestingly, dominance was lowest in late-successional habitats, and not in natural forest. This indicates that geometrid samples in advanced secondary habitats have a particularly even rank-abundance distribution. The reasons for this may be found in the mosaic nature of these late-successional habitats, where many different species are able to thrive but do not reach full dominance. A few species benefit disproportionately from habitat disturbance, probably because their resources are boosted temporarily.

Nummelin & Kaitala (2004), however, gave a short review of dominance in different data sets (e.g. beetles, butterflies, plants) in logged vs. unlogged forest sites and concluded that dominance indices are not universally suitable indicators of rain forest disturbance.

The most prominent beneficiary among Andean geometrids in our samples was *Pantherodes conglomerata*. Eighteen per cent of all individuals caught in early successional habitats belonged to this single species. At individual sites, *P. conglomerata* made up 5–32% of the geometrid samples. Thus, this species can be regarded as a typical inhabitant of disturbed habitats. Recorded host plants are species of *Boehmeria* (Urticaceae) and *Vernonia* (Asteraceae) (URL: <http://www.caterpillars.org>). *Boehmeria* sp. is only common in disturbed habitats in the study area (J. Homeier, pers. comm.). Only for a few additional common species are host-plant data available: *Physocleora* sp. (Euphorbiaceae: *Alchornea* sp.), *Sabulodes thermidora* (Asteraceae: *Baccharis latifolia*), and *Oxydia trychiata* (Cupressaceae: *Cupressus* sp. and Pinaceae: *Pinus* sp.; Phytolaccaceae: (URL: <http://www.nhm.ac.uk/entomology/hostplants/>; <http://www.caterpillars.org>; Brehm 2003). All these host plants are characteristic of succession habitats (*Baccharis*, *Alchornea*) or are exotic tree species (*Pinus*, *Cupressus*). Thus, the commonness of the aforementioned geometrid moths in habitats under anthropogenic influence may well reflect increased resource availability.

Changes in species composition

As discussed above, the proportion of rare species and the contribution of dominant species changed markedly with forest regeneration. Also, taking the entire ensembles into account, there was a distinct change in species composition during succession. However, this

was by no means a radical species turnover. Almost half of the species observed were shared between the successional sites and the forest understorey. Ordination analyses revealed a clear segregation of these two habitat categories. However, the more heavily the rare species were weighted (i.e. using intermediate and high values of the sample size parameter m for the CNESS distance measure), the more clearly did the ordinations of moth samples mirror the progress of succession. However, the highest resolution was achieved with an intermediate m parameter value. This means that neither the most common nor the rarest species have highest indicator potential in the Geometridae. Abundances of some of the commonest species varied erratically which partially obscured differentiation (e.g. between abandoned pastures and early succession habitats). The rare species were for the most part (>60%) identical in the different succession stages (results not shown), while there was a prominent turnover of these rare geometrids to the forest understorey. Geometrid ensembles in habitats dominated by grassland vegetation (abandoned pastures D1, D2 as well as sites E1, E2) turned out to be different from those at the remaining successional sites. This pattern is largely due to the extreme dominance of *Pantherodes conglomerata* at such sites (see above).

The ordination diagrams yielded two axes that reflected two important environmental gradients. The first NMDS dimension was essentially a disturbance axis and reflected variables such as the degree of openness ('visible sky'), the degree of habitat disturbance, the distance of the sites to the natural forest and air temperature. Ambient temperature drops more quickly in open habitats (Basset *et al.* 2001, Murcia 1995, Toral *et al.* 2002). The second axis reflected the altitude of the sites. These ecological interpretations of ordination axes were equally well supported by matrix rank correlation tests and explorations of axis scores extracted by ordination.

Despite the short distances between habitats studied, local ecological processes were strong enough to allow for a differentiation between moth ensembles from mature forest and anthropogenically disturbed sites.

In conclusion, despite the small spatial scale at which this investigation was conducted we found clear patterns of alpha and beta diversity along the succession gradient from early succession stages to the mature forest understorey. Alpha diversity was very high and increased with forest recovery. The analysis of between-habitat diversity revealed clear responses to anthropogenic (disturbance) and natural habitat gradients (altitude) in geometrid moths. This underscores the usefulness of geometrid moths as sensitive indicators for environmental change. Even though many moths are relatively mobile organisms (Daily 1996), Ricketts *et al.* (2001) and Summerville & Crist (2004) showed that their diversity often declines strongly in disturbed and secondary

habitats, if the connection to source habitats is lost. It is to be expected that similar effects will occur in the moth fauna we have studied here, which is the richest thus far known globally (Brehm *et al.* 2005). Hence, further studies should explore the role of spatial scale (> 1 km from the natural forest) as well as geographical proximity of sites for recolonization and diversity of disturbed habitats in the Andes.

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