
Moths at tropical forest margins – how mega-diverse insect assemblages respond to forest disturbance and recovery

Konrad Fiedler^{1*}, Nadine Hilt², Gunnar Brehm³, and Christian H. Schulze¹

¹ Department of Population Ecology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

² Chair of Animal Ecology I, University of Bayreuth, 95440 Bayreuth, Germany

³ Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, University of Jena, Erbertstrasse 1, 07745 Jena, Germany

*corresponding author: Konrad Fiedler, Email: konrad.fiedler@univie.ac.at

Summary

Tropical forest moth ensembles are often extraordinarily rich in species and complex in structure. There is an increasing number of quantitative studies from all major tropical realms which now allows for a more rigorous assessment of the ways how such ensembles change along habitat transects from the natural forest towards the edge of large conservation areas, or in the course of forest recovery at such margins. Such knowledge is also essential for deciding if moths can be used for monitoring the biotic effects of forest disturbance on mega-diverse insect faunas at all, and which moth groups are the most suitable targets for this purpose. Using very large data sets from low (Mt. Kinabalu National Park, Borneo) and high elevations (Podocarpus National Park, Ecuador), we investigate how species richness and species composition of moths change at small spatial scales along gradients of disturbance at the edge of natural forest reserves. Local species diversity did not always decline, and sometimes even increased, along the gradients. Ensembles of moths from the families Arctiidae or Sphingidae were as rich as in natural forest, or were even more diverse in habitats close to the forest margin. Geometridae and Pyraloidea ensembles, in contrast, tended to be impoverished. Correlations of alpha diversity measures between moth taxa were often poor and thus did not allow for using one group as a ‘biodiversity indicator’ of others. Estimates of local diversity also depended on the temporal scale of assessment. Species composition was remarkably sensitive to habitat alterations at forest edges even at very small spatial scales, despite the high dispersal potential of many

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moths. Patterns of beta diversity were highly concordant across unrelated moth taxa with very different life history syndromes. Geometridae ensembles responded more sensitively to changes in canopy openness than arctiid moths and yielded more robust results with regard to sampling effects. Therefore geometrids are particularly promising candidates for environmental monitoring in tropical landscapes. Much of the faunal differentiation between forest and margin habitats was due to shifts in abundance relationships, and not to the presence or absence of ‘indicator species’. Therefore, abundance-based monitoring appears more appropriate to detect effects of environmental change on mega-diverse moth ensembles. Our results suggest that patterns of beta (rather than alpha) diversity are generally more meaningful to assess the impact of processes at forest edges relevant to nature conservation and landscape planning.

Keywords: alpha diversity, Andes, Arctiidae, beta diversity, Borneo, community composition, disturbance gradient, Ecuador, forest recovery, Geometridae, herbivorous insects, moths, Mount Kinabalu, Pyraloidea, succession

1 Introduction

Tropical forests harbour the largest fraction of terrestrial biodiversity (Sayer et al. 2000, Wright 2005). Decline and deterioration of forests still progress at an alarming rate in most tropical countries (Wright 2005). Hence the reduction of tropical forests is one of the most pressing challenges to the preservation of global biodiversity. Apart from the loss of primary forest areas due to clear-cutting and conversion into agroforests, farmland or settlements, another suite of major threats is related to fragmentation issues (Laurance 1998, Laurance et al. 2002, Armenteras et al. 2003, Wright 2005). Most remaining tropical forests are islands embedded in a non-forested, anthropogenically transformed landscape matrix. Accordingly, principles of island biogeography and metapopulation dynamics (e.g. size and quality of forest remnants, or distances between fragments) determine the long-term fate of populations, species, and communities of organisms that thrive in these fragments. One special topic related to the island nature of today’s tropical forests are edge effects (Murcia 1995, Laurance 1998): forest edges are ecological boundaries characterized by very steep gradients from the forest interior to the surrounding open vegetation. Such gradients are well documented for abiotic factors (light, temperature, humidity, wind speed, rainfall; e.g. Camargo and Kapos 1995, Davies-Colley et al. 2000, Newmark 2001) and have manifold effects on the vegetation (Fox et al. 1997, Williams-Linera et al. 1998, Mesquita et al. 1999). Consequences for organisms at higher trophic levels are also evident. In phytophagous animals, such consequences may be mediated indirectly through the dependence on particular plant species whose presence or abundance changes as a consequence of altered abiotic conditions. Alternatively, abiotic conditions may

directly affect behaviour or impose physiological constraints (e.g. inability to tolerate intense solar radiation or low humidity outside the forest shade).

Edge effects are of special importance in small habitat fragments, where they may penetrate so far that the entire fragment must be rather viewed as an edge habitat (Fox et al. 1997). However, for large and rather well protected conservation areas understanding the processes at forest margins is also of paramount importance. These margins form the interface between forest and cultivated landscape, and they are usually characterized by a dynamic mosaic of succession habitats (villages, farmland, abandoned fields and pastures, shrub land, secondary forest). This habitat heterogeneity may even increase the species richness relative to forest areas of comparable size. On the other hand, disturbance regimes at forest margins may facilitate the establishment of invasive or weedy species in remaining natural habitats. Therefore, the study of tropical forest margins is an important issue in conservation biology.

In contrast to the effects of land-use practices such as selective logging (Meijaard et al. 2005), or the irreversible conversion of forest (establishment of agroforests and plantations, agriculture, settlement: Holloway et al. 1992), rather little is known as to how animal communities respond to the altered conditions at tropical forest margins. This is especially obvious when it comes to those organisms that account for the largest fraction of terrestrial species diversity, viz. the arthropods. Available studies often focus on single species or small sets of species. Here we review the response of very large insect ensembles to environmental changes at the margin of large tropical forest reserves. We selected moths as a model group for this approach. A growing number of studies in all tropical realms has been conducted in recent decades dealing with disturbance and/or edge effects on moth diversity (e.g. Holloway 1985, 1998, Holloway et al. 1992, Chey et al. 1997, Intachat et al. 1997, 1999, Willott 1999, Kitching et al. 2000, Basset et al. 2001, Lepš et al. 2001, Ricketts et al. 2001, Axmacher et al. 2004). We integrate our own findings with these studies to examine whether generalized trends can now be formulated.

Four reasons render moths suitable targets for this research approach.

1. Moths are very rich in species, thus allowing for the assessment of effects on 'megadiverse' ensembles (terminology: Fauth et al. 1996). At the same time, moths comprise many families that widely differ in ecological requirements (e.g. hostplant affiliations) and morphological traits (size, development of wings or mouthparts: Scoble 1995, Kristensen 1999, Holloway et al. 2001). Thus, cross-taxon comparisons are possible to test the generality of findings, but still within the boundaries of a common ground plan.
2. Moths are taxonomically far better known than any other insect group of comparable diversity (Scoble 1999, Holloway et al. 2001). Hence species identifications are possible for a large fraction of samples, with all the advantages precise identifications provide over mere parataxonomic sorting (Krell 2004).

3. Moths can be readily sampled in large numbers by attraction to light (Muirhead-Thomson 1991), resulting in samples amenable to thorough statistical evaluation with high power. In contrast to a commonly held misconception, weak artificial light sources have a small attraction radius (usually below 30 m: Beck and Linsenmair 2006, Wirooms 2005). Thus, samples are drawn from the local community around the trap site and allow for ecological characterization of moth ensembles at small spatial scales.
4. Adult moths and caterpillars differ widely in their resource requirements and dispersal capacities. Moth larvae are largely sedentary organisms, the majority being herbivores with often restricted host plant ranges. Adult moths, in contrast, are usually capable of flight (wing reductions occur in less than 1% species worldwide and are rare in tropical forests: Sattler 1991) and feed on nectar. Specialization to certain nectar sources is an exception, and many moths even do not feed at all ('capital breeders': Tammaru and Haukioja 1996). Moth communities are shaped by the balance between availability of resources (such as larval hostplants) and adult dispersal. If moth communities reflect habitat differences on small spatial scales (in the range some dozens to hundreds of meters distance between sites) it can be concluded that local resource availability is the major determinant of community composition. In contrast, if differences between communities largely depend on spatial distance, dispersal has to be regarded as the key to understand diversity patterns.

We use very large, quantitative samples of moths collated across habitat gradients at the margins of two large conservation areas (situated in Borneo and southern Ecuador) to address the following questions:

- How does moth diversity change along the gradient from the natural forest to the more disturbed habitats situated directly at forest margins? Are these changes uniform across regions or moth families with different life habits?
- How do species compositions change across forest margins? Is there an abrupt or continuous change? Are different moth taxa differentially sensitive? Is there a high species turnover, or do communities rather differ due to shifts in relative abundance of their component species?

To answer these questions we attracted moths to light-towers (gauze cylinders, height 1.6 m, diameter 0.6 m). These were placed at ground level and equipped with weak light sources (15 W blacklight tube in Borneo, 2 x 15 W tubes in Ecuador) to minimize attraction of moths from adjacent habitats. Sampling sites were selected to ensure that (a) in a radius of 50 m around the light source the vegetation was homogeneous and (b) that the light tower was not visible from the nearest other sampling site. All moth individuals of the selected target taxa which were attracted to the light source were sampled manually during the first 3 h after dusk. Manual sampling is more effective

than automatic traps in the case of Geometridae and the resulting specimens can be more easily identified due to their better condition (Axmacher and Fiedler 2004). All moth samples were subsequently set, sorted and identified using taxonomic literature and reference collections in large research museums (see acknowledgments). Further details on procedures for moth collecting and processing of samples can be found in Schulze (2000), Beck et al. (2002), and Fiedler and Schulze (2004) for the Bornean studies, and in Hilt and Fiedler (2005, 2006) and Hilt et al. (2006) for the sampling in Ecuador.

2 Moths at the margin of Mount Kinabalu National Park (Sabah, North East Borneo)

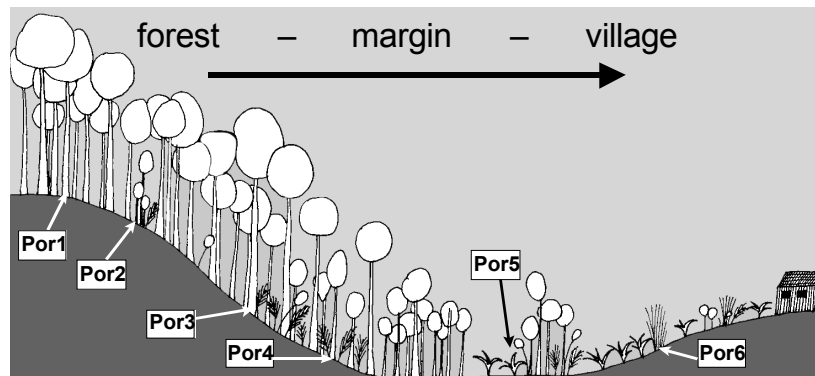


Fig. 1. Schematic illustration of the sampled transect from natural forest to the forest margin at Poring (Mt. Kinabalu National Park, Borneo) showing the locations of light trapping sites (modified from Fiedler and Schulze 2004, see Beck et al. 2002 for more information about sampling sites). Por1: primary forest without signs of recent anthropogenic disturbance; Por2: disturbed primary forest; canopy layer opened due to a large old tree fall gap promoting dense understory vegetation with pioneer plants; Por3: old secondary forest with large gaps caused by selective logging; Por4: young secondary forest approx. 20m high with dense upper canopy layer and understory vegetation; Por5: secondary forest fragment situated in cultivated area adjacent to a banana plantation; Por6: cultivated area with banana plantation and dense bamboo thicket. Distance between Por1 and Por6 was less than 2 km.

Mount Kinabalu National Park is one of the last remaining large forest areas in NE Borneo (Wong and Phillipps 1996). We sampled moth ensembles along two habitat gradients from primary forest to farmland, one situated at the north eastern (Serinsim village) and the other at the south eastern margin (Poring village; Figure 1) of the park (Schulze 2000, Beck et al. 2002, Fiedler

and Schulze 2004). Sampling sites were situated at low elevations (170-630 m a.s.l.) and represented forest margin ecotones in the lowland to hill forest zone. In one large family, the Geometridae (500 observed species, 4585 individuals), species diversity decreased along both gradients, but not in a uniform manner. Species diversity (measured as Fisher's alpha to alleviate the strong sample size dependence of recorded species numbers: Rosenzweig 1995) at disturbed forest sites towards the margin was as high, or partially even higher, than in natural forest (Beck et al. 2002). Maximum local diversity was not observed

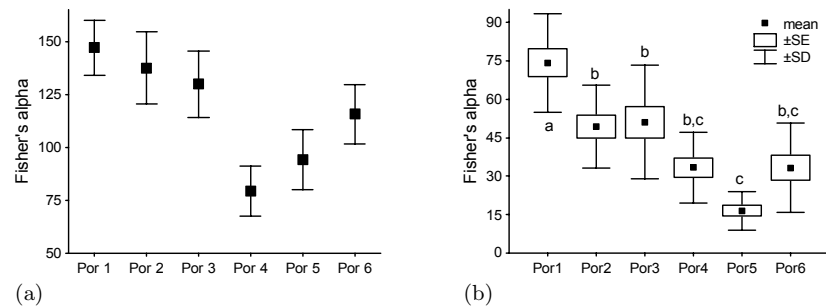


Fig. 2. Local diversity of Pyraloidea moth ensembles along the transect depicted in Figure 1, analysed at two temporal scales. (a) Fisher's alpha \pm 95% confidence intervals of 13 aggregated nightly samples per site. (b) Fisher's alpha (filled squares: means, boxes: \pm 1SE, whiskers: \pm 1SD) for the same data set, based on averages of diversity estimates per sampling night. Means marked with different letters differ significantly (Scheffé test, $P < 0.05$, following ANOVA: $F_{5;72} = 18.47$, $P < 0.0001$). The 13 nightly samples were taken in two collecting periods in the year 1997 (see Fiedler and Schulze 2004).

in natural forest, but in secondary forest sites at both forest margins. Margin habitats without closed canopy held an impoverished geometrid fauna, even though the natural forest was only a few hundred meters away. In another very large ensemble, the superfamily Pyraloidea (680 species observed, 7724 individuals), the pattern was somewhat different. Forest sites with old-grown trees were characterized by exceptionally high species diversity. Margin habitats where no old-grown trees were left, in contrast, had a far less diverse (but still rich) pyraloid fauna (Figure 2a). Interestingly, a slightly different pattern emerged when viewed at higher temporal resolution (Figure 2b). Pyraloids are the single most abundant moth group in SE Asia to be attracted to artificial light sources. Therefore, even samples taken during single nights are large enough for the calculation of meaningful diversity measures. We resampled pyraloid ensembles at 6 sites near Poring 13 times within one year (Fiedler and Schulze 2004). At this small temporal scale primary forest indeed ranked as the most diverse habitat. Weakly disturbed forest sites held significantly

lower pyraloid diversity, and the latter decreased further towards the forest margin. However, losses of diversity towards the forest margin of Mt. Kinabalu National Park were not observed in all moths. Tiger moth diversity (Arctiidae, 29 observed species, 420 individuals) was practically constant from forest to farmland; this applied to the subfamilies Arctiinae and Syntominiinae (Schulze 2000) as well as to combined samples (K. Fiedler and C.H. Schulze, unpublished data). Hawkmoth ensembles also turned out to be rather insensitive (Schulze and Fiedler 2003). Only with large samples from multiple sites a subtle disturbance effect on hawkmoth diversity could be detected (Beck et al. 2006).

Table 1. Spearman rank correlations (r_S and P values, 1000 permutations for matrix correlations, Clarke and Gorley 2001) of alpha and beta diversity in three moth groups at the margin of Mt. Kinabalu National Park (Borneo). Alpha diversity was measured as Fisher's alpha at six sites near Poring (Beck et al. 2002, Fiedler and Schulze 2004). Matrix correlations are based on pairwise NESS similarities between samples (sample size parameter set as $m=10$). Note that correlation coefficients are high and positive in sign. Due to the low number of sites ($n=6$) and hence small statistical power, none of the reported relationships is significant if controlled for a table-wide false discovery rate ($P<0.05$) according to the method of Benjamini and Hochberg (1995).

		Pyraloidea	Arctiidae
alpha diversity	Geometridae	$r_S=0.77$ $P=0.07$	$r_S=0.83$ $P=0.04$
	Pyraloidea		$r_S=0.60$ $P=0.21$
beta diversity	Geometridae	$r_S=0.52$ $P=0.05$	$r_S=0.42$ $P=0.07$
	Pyraloidea		$r_S=0.84$ $P=0.02$

Changes in species composition across the forest margin were pronounced in all studied moth taxa. Ordinations of geometrid samples (using non-metric multidimensional scaling based on NESS or CNESS indices; Brehm and Fiedler 2004) depicted the gradient from the forest interior to the margin habitats, yet with slight differences between the two study areas (Beck et al. 2002). In Pyraloidea, a major break was observed between three sites with and three sites without old-grown trees (Fiedler and Schulze 2004). A similar pattern recurred within the Arctiidae. Matrix rank correlation tests reflect the conclusions drawn from ordination analyses (Table 1): the pattern of faunal change was more concordant between Arctiidae and Pyraloidea than both families were to the Geometridae. Within Pyraloidea, temporal dynamics and between-site differences affected ensemble composition almost

equally (two-way crossed ANOSIM, 1000 permutations, statistics based on Spearman's rank correlation as implemented in Clarke and Gorley 2001; site differences: $r_S = 0.436$, sampling time: $r_S = 0.485$, both $P < 0.001$). Overall, dynamics of pyraloid ensembles were concordant across the forest margin and were not more pronounced at the more open sites than in the forest interior (Fiedler and Schulze 2004).

3 Moths at the margin of Podocarpus National Park (Andes, southern Ecuador)

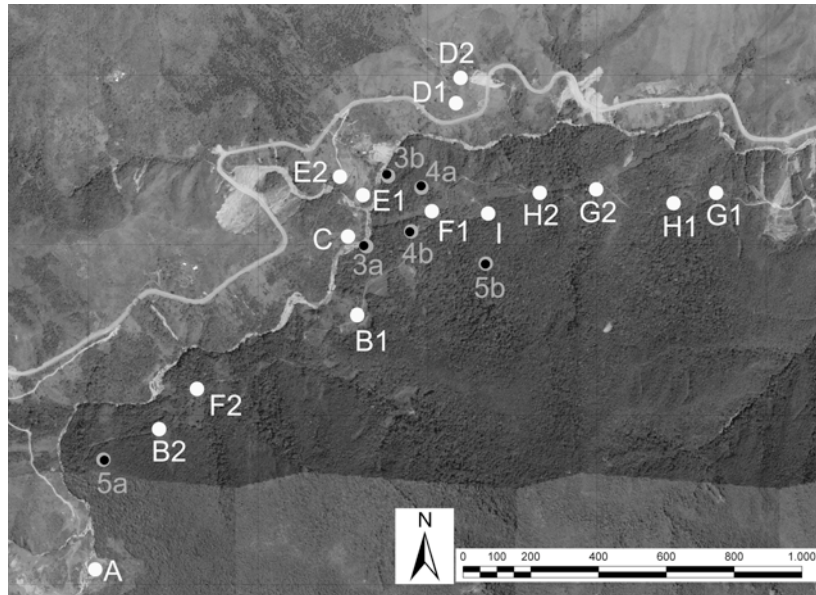


Fig. 3. Composite aerial photograph of the study area at the margin of Podocarpus National Park, southern Ecuador (after Hilt and Fiedler 2005). Moth ensembles were monitored at 21 sites representing a succession gradient, with 4-9 samples taken per site (Hilt and Fiedler 2005, Hilt et al. 2006). Sites A, B, C and E are early succession sites (without woody vegetation) situated near the margin of closed natural forest; sites D are two abandoned cattle pastures; sites G, H and I are late succession habitats (with shrub or tree cover); and sites 3a to 5b are located inside natural forest. Note the small spatial scale of the study. Photograph courtesy of E. Jordan.

Podocarpus National Park is one of the last remaining large blocks of continuous montane forest in southern Ecuador (Madsen and Øllgaard 1994).

We sampled moth ensembles (Geometridae, Arctiidae) at 21 sites situated in various types of succession habitats and in natural forest along the boundary of this conservation area (Figure 3; see Hilt and Fiedler 2005, 2006 for further details about sites). All sites were situated in a narrow altitudinal belt (1800-2000 m a.s.l.) where montane forest is the potential natural vegetation (Paulsch 2002, Homeier 2004). Light-trapping sites were close to the margin of continuous natural forest, with a maximum distance of 445 m (Hilt and Fiedler 2005). The study area is part of a global biodiversity hotspot (e.g. Myers et al. 2000, Brooks et al. 2002), and this is also true for moths (Brehm et al. 2005).

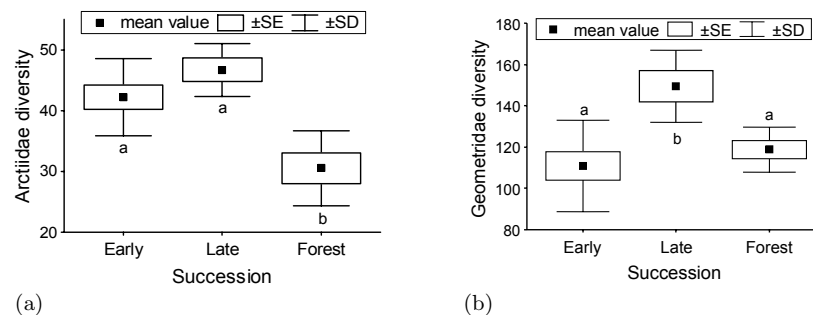


Fig. 4. Local diversity of Arctiidae (a) and Geometridae (b) at the margin of Podocarpus National Park, measured using Fisher's alpha for aggregated samples from each site. Sites were grouped into three categories: natural forest understorey ($N=6$), late succession sites ($N=5$), and early succession sites plus abandoned cattle pastures (i.e. margin habitats without woody vegetation, $N=10$). Filled squares: means, boxes: $\pm 1SE$, whiskers: $\pm 1SD$. Means marked with different letters differ significantly (Scheffé test, $P < 0.05$, following ANOVA: $F_{2,18} > 7.30$, $P < 0.005$).

Diversity patterns varied at the local scale between the studied moth families. Local arctiid diversity, measured again as Fisher's alpha (recorded totals: 287 species, 9211 individuals), was significantly higher in late and early succession habitats close to the forest edge than in natural forest understorey (Figure 4a). Geometrid diversity (recorded totals: 868 species, 23720 individuals) was clearly highest in late successional habitats again, but was markedly low in open early succession habitats (Figure 4b; see Brehm and Fiedler 2005, Hilt et al. 2006). The differences between the two moth families in their response to habitat differences became even more obvious when examining the covariance of local diversity measures (Table 2). Correlations were never significant, and sometimes even negative in sign, in all comparisons between arctiids and geometrids. Correlations were significantly positive within Geometridae and also mostly within Arctiidae (Hilt and Fiedler 2006). In the latter family, only the subfamily Lithosiinae (whose larvae are suspected to feed frequently

Table 2. Concordance between local diversity of moth ensembles from the margin of Podocarpus National Park (Ecuador) across different taxonomic levels. Given are Pearson's correlation coefficients r between alpha diversity of Archidae, Geometridae and various subordinated taxa (measured as Fisher's alpha of the log-series distribution). A: Archidae, G: Geometridae, Ennominae and Larentiinae are subfamilies of Geometridae; Phaegopterini and Ctenuchini (here viewed as including Eucheromini; see Jacobson and Weller 2002) are clades in the Archidae-Archinae; Lithosiinae are another subfamily of Archidae. * $P < 0.01$, ** $P < 0.005$, *** $P < 0.001$, n.s. not significant ($P > 0.05$). Bold figures: results significant after controlling for a table-wide false discovery rate ($P < 0.05$) according to the method of Benjamini and Hochberg (1995).

	Archidae total	Ennominae (G)	Larentiinae (G)	Phaegopterini (A)	Ctenuchini/ Eucheromini (A)	Lithosiinae (A)
Geometridae total	0.18, n.s.	0.94***	0.73***	-0.24, n.s.	-0.14, n.s.	0.12, n.s.
Archidae total		0.10, n.s.	-0.01, n.s.	0.63**	0.65**	0.74***
Ennominae (G)			0.55*	-0.27, n.s.	-0.19, n.s.	-0.002, n.s.
Larentiinae (G)				-0.26, n.s.	-0.25, n.s.	0.02, n.s.
Phaegopterini (A)					0.68***	0.15, n.s.
Ctenuchini/ Eucheromini (A)						0.21, n.s.

on lichens instead of vascular plants: Weller et al. 1999, Kitching and Rawlins 1999) revealed no concordance with other arctiid clades.

The poor concordance of diversity patterns across more distantly related moth clades indicates that differences in the habitat requirements of these insects are so strong that they lead to differential success in colonizing microhabitats in the heterogeneous mosaic at the forest margin. In addition, this finding undermines the potential to use one such moth group to predict diversity of others ('biodiversity indication': Lawton et al. 1998, Brehm and Fiedler 2003, Schulze et al. 2004). Even at the small spatial scale of the sampling design adopted here, idiosyncrasies of clades prevented the emergence of common ecological trends in local species diversity. Some moth groups, like Arctiidae, obviously do better in margin habitats than others do, such as the Geometridae. This finding is in line with earlier observations in SE Asia and Australia that arctiid ensembles tend to be less sensitive to anthropogenic habitat disturbance and may even benefit from opening of the forest canopy (Holloway 1985, 1998, Kitching et al. 2000, Schulze 2000).

With regard to beta diversity the picture changes remarkably. Matrix rank correlations between CNESS distance matrices of Geometridae and Arctiidae were all highly significant, irrespective of the weight given to rare or abundant species ($0.576 < r_s < 0.902$, all $P \ll 0.001$: Hilt 2005). Also within the Arctiidae, matrix rank correlations were significant for most comparisons between subfamilies and tribes (Hilt and Fiedler 2006). Hence, while various moth taxa obviously respond quite discordantly with regard to their potential to form diverse or poor ensembles in different microhabitats along the forest margin, the pattern of species turnover turned out to be unexpectedly concordant. It should be noted at this point that site-to-site variation of moth ensembles within natural forest does of course exist. However, species composition was remarkably similar between natural forest sites at comparable altitude in the Ecuadorean study area (Brehm et al. 2003, Süßenbach 2003), and this also extends to forest sites after moderate experimental manipulation (K. Fiedler and M. Zimmermann, unpublished results).

4 Moth ensembles in environmental gradients: do taxa differ in sensitivity?

The above results already indicate that not only individual species, but even entire moth taxa differ in their overall sensitivity to environmental change. This is an important issue for practical conservation measures: the selection of target groups that are to be included in biodiversity assessment or monitoring programmes should be based on solid evidence as to the suitability of the chosen 'indicators'. From what has been shown above, and in line with the pertinent literature, it would appear that Arctiidae comprise a greater fraction of 'weedy' species (Holloway 1985, 1998, Kitching et al. 2000), i.e. species whose polyphagous larvae thrive on cultivated plants and especially on pioneer

vegetation. In contrast, Old World tropical Geometridae ensembles respond very sensitively to the loss or reduction in canopy cover of forest habitats (Intachat et al. 1997, 1999, Beck et al. 2002, but see Axmacher et al. 2004). We here apply two analytical approaches to our very large New World (i.e. Ecuadorian) data set to test this hypothesis.

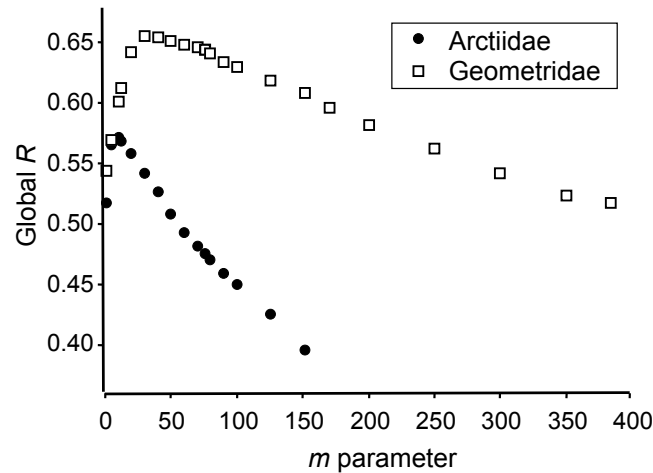


Fig. 5. Discriminatory power of Analyses of Similarities (expressed as values of the global R statistics, one-way ANOSIM, 1000 permutations) as a function of the sample size parameter m (of CNESS indexes as a measure of faunal distances) for two moth families. Basis for the analyses were the samples from 21 sites at the margin of Podocarpus National Park, Ecuador, separated into four habitat categories (natural forest understorey, late succession habitats with woody vegetation, early succession habitats without woody vegetation, abandoned pastures). Highest resolution is obtained at $m=10$ for the Arctiidae and $m=30$ for the Geometridae. Resolution decays more strongly with increasing emphasis on rare species (= high m values) in the Arctiidae. Due to lower samples sizes, no values were available in Arctiidae beyond $m=152$.

As a first approach, we explored how well faunal distance matrices for Arctiidae and Geometridae reflect habitat groupings according to their vegetation and successional status. The 21 sites at the margin of Podocarpus National Park were *a priori* grouped into abandoned cattle pastures, early and late succession habitats, and mature forest understorey. We then used the R statistics of ANOSIM (Clarke 1993, Legendre and Legendre 1998) as a measure of the sensitivity of a given moth group to reflect habitat differences. For this purpose, we calculated all possible pairwise distances between moth samples from the 21 sites. Since samples from mega-diverse tropical moth

communities are never ‘complete’ and prone to sampling effects (Brehm and Fiedler 2004), the NESS index or its metric analogue CNESS (Trueblood et al. 1994) are the most suitable measures of faunal distances in such cases. In this comparison, Geometridae clearly emerged as the environmentally more sensitive moth group with higher R values throughout (Figure 5). Since this difference was observed at all values of the sample size parameter m , the higher resolution of analyses based on Geometridae samples cannot be regarded as merely an effect of the larger catch sizes that were achieved with the more abundant and more speciose geometrids. Arctiidae achieved relatively good discriminatory power only in a small range of values of the sample size parameter m , while ecological resolution was heavily reduced when emphasizing dominant ($m=1$) or rare species (high m values). Geometridae were superior in that regard since high segregation between samples was obtained over a wide range of m values. In practice this means that in a monitoring study robust results can be expected with Geometridae as target groups.

ANOSIM, like unconstrained ordination techniques such as non-metric multidimensional scaling (Clarke 1993), draws exclusively on faunal data and does not include environmental variables *a priori*. We therefore also applied a constrained ordination technique (Økland 1996) to our data, namely Redundancy Analysis (RDA; Legendre and Legendre 1998), to explore differential sensitivity of Arctiidae and Geometridae. As environmental variables we used canopy openness (measured from hemispherical photographs) as a proxy of integrity of the forest, and altitude as a proxy of overall habitat temperature regimes. Studies in natural forest in Podocarpus National Park revealed how sensitive moth ensembles respond to even minor altitudinal differences in species composition (Brehm et al. 2003). Geometridae responded very sensitively to canopy openness (Figure 6a). Altitude had a measurable effect as well, which was almost independent of canopy openness. In the Arctiidae, in contrast, the effects of these two environmental variables were less pronounced, and more difficult to separate from each other (Figure 6b). Therefore, also according to the RDA, geometrid moths were more indicative of environmental gradients than arctiids. Notably, arctiids appeared not to be as suitable for indication purposes as has been found for these moths in Nearctic forests (Summerville et al. 2004). Our analyses underscore how different the responses of moth ensembles at the community level are. They also support the view that Geometridae make up excellent targets for environmental monitoring of insect faunas of tropical forests, even at small spatial scales, where the flight capacity of all species should be large enough to allow them to reach any site when dispersing from the remaining natural forest.

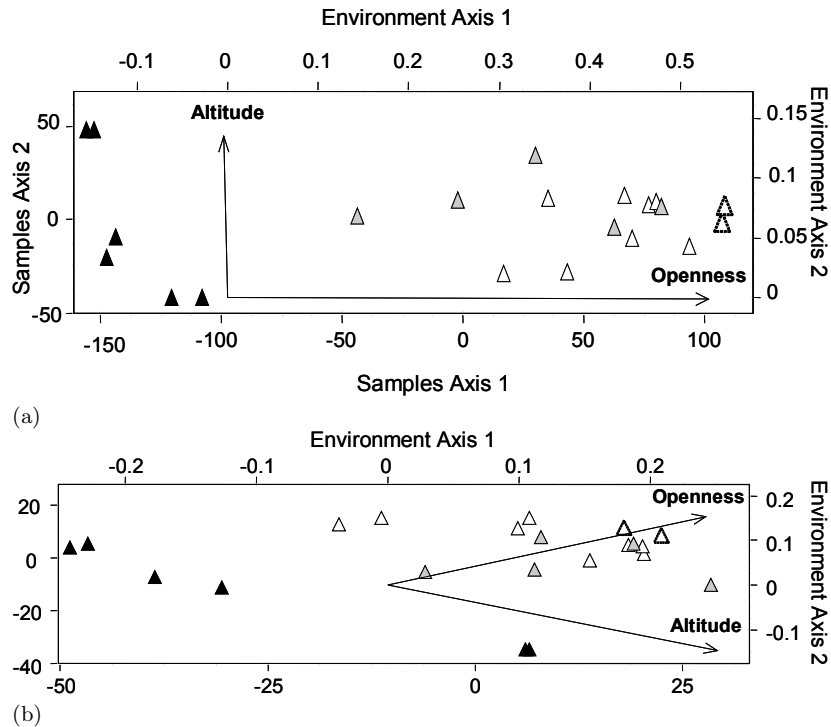


Fig. 6. Explanatory power of two environmental variables (canopy openness, measured from hemispherical photographs; and altitude) for variation in ensemble composition of moths at the margin of Podocarpus National Park (Ecuador). Graphs are ordination plots of samples with vectors of predictor variables overlaid according to a Redundancy Analysis (RDA). Arrows: environmental vectors, symbols: 21 sites at the forest margin. Filled symbols: natural forest understory, shaded symbols: late woody succession vegetation, open symbols: early succession stages, dotted triangles: abandoned pastures. (a) Geometridae. Canonical axis 1 explains 28.2%, axis 2 explains 1.9% of data variance (total: 30.1%). Correlations with altitude are -0.004 (axis 1) and 0.136 (axis 2), and those with canopy openness are 0.531 (axis 1) and -0.002 (axis 2). (b) Arctiidae. Canonical axis 1 explains 12.2%, axis 2 explains 4.4% of data variance (total: 16.8%). Correlations with altitude are 0.251 (axis 1) and -0.147 (axis 2), and those with canopy openness are 0.242 (axis 1) and 0.152 (axis 2). Environmental variables explain differences between Geometridae ensembles far better than those in Arctiidae ensembles. Moreover, the two environmental variables have almost independent effects in Geometridae, but are less well separable in their influence on Arctiidae.

5 Moth ensembles in margin habitats: how different from forest?

This leads to the issue as to how different moth ensembles are across the habitats of a forest margin. For species that can thrive equally well inside and outside the forest this distinction is obviously irrelevant. Very few, if any, of the moth species covered by our studies in Borneo and Ecuador appear to have such generalist habitat requirements. One might rather expect that different species live in either the forest or the surrounding landscape matrix. If so, there should be a sharp boundary and little overlap between ensembles inside and outside the forest. Alternatively, habitats outside the natural forest might be so poor in quality for practically all moth species (for example due to frequent human intervention) that they are just sinks which rely on frequent immigration of dispersers from nearby forest. If this were the case, the further away from the source forest, the more depauperate the moth ensembles should be. Moreover, such ensembles from margin habitats should consist of impoverished subsets of the forest fauna, which can hierarchically be nested in the forest fauna with increasing distance from the source area.

Our studies in Borneo and Ecuador reveal that neither of these extremes is the case. While some moth species turned out to be ‘true’ forest dwellers, and others exclusively occur in the landscape matrix around closed forest, most species were found on both sides of the forest margin, but at different abundances. Generally, the segregation of moth ensembles was more robust when abundances (i.e. CNESS or NESS index measures) rather than incidences (e.g. the Soerensen index or CNESS with very high m values) were used to express faunal similarities. This indicates that shifts in the local abundance relations, rather than the mere presence or absence of species, generate the gradients in beta diversity across forest margins. On the other hand, our data also allow to refute a strict source-sink concept. If moth ensembles from a habitat in the surrounding landscape matrix were really just impoverished subsets of forest ensembles (e.g. would contain only the more dispersive species, but in roughly the same abundance relationships as they have in the forest), then CNESS distances would become negligible at least at high m values. This is because at high m values the differences caused by ‘sampling effects’ (here: viewing the ensemble outside the forest as a small sub-sample from the source community) should vanish. This was, however, never the case (e.g. Hilt and Fiedler 2005, 2006, Hilt et al. 2006).

We therefore conclude that moth ensembles at forest margins are governed by a balance of both of these processes. There is considerable dispersal of mobile moths (described by Ricketts et al. 2001 as ‘halos’ of forest moths around natural forest remnants), and certainly not all of these stray individuals will find suitable resources at all sites to successfully reproduce. In line with that conclusion we observed high proportions of singletons among arctiid and geometrid samples from early succession habitats and especially on abandoned pastures (Hilt and Fiedler 2005, Hilt et al. 2006). Such habitats are likely

to represent sinks for the majority of arctiid and geometrid moth species in Ecuador since most potential larval host plants are not available. However, at the same time there are abundance shifts of species that are a permanent component of communities inside as well as outside the forests. These shifts, caused by the matching of habitat requirements and local resource availability for each individual species, allow some moths to be more abundant in the margin habitats (e.g. species that otherwise live in tree-fall gaps, landslide areas or forest canopies; see also Schulze et al. 2001), whereas others are more abundant in closed forest, without being ‘exclusive’ species of any of these habitat types.

6 Conclusions and Outlook

Very species rich moth ensembles at the margins of tropical conservation areas revealed a high sensitivity towards environmental change at surprisingly small spatial scales. Hence, despite the substantial dispersal potential of most moths, these organisms are perfectly suitable to monitor effects of environment on the diversity and dynamics of mega-diverse herbivore communities. A common pattern emerging from our studies is that local alpha diversity of different taxonomic groups shows quite discordant idiosyncratic responses. For example, Geometridae ensembles are distinctly impoverished just a few dozen meters away from the natural forest, while this is never the case in Arctiidae moths. Moreover, it is a matter of scale whether ensembles from disturbed habitats appear as more, or less, diverse than the respective ensembles in ‘undisturbed’ natural forest. Such a scale dependency is not only restricted to the spatial dimension (Hill and Hamer 2000, 2004, Rahbek 2005), but may also extend to the temporal dimension, as shown by our results on Pyraloidea from Borneo. In contrast to these less predictable patterns of alpha diversity, the patterns of species turnover (beta diversity) were surprisingly invariant across taxonomic groups with widely diverging life history syndromes. They were also rather stable with regard to reductions in sample size (i.e. when comparing smaller samples of subordinated clades with each other or the entire moth family: Brehm et al. 2003, Hilt and Fiedler 2006). We therefore suggest that for the assessment of environmental effects on rich insect communities the monitoring and analysis on the community level is a much more promising and powerful approach than the selection of a few ‘indicator’ species, the choice of which is by necessity arbitrary.

Our analyses also underline that in mobile organisms the differentiation between local communities is a matter of shifts in relative abundance composition rather than species composition. Hence, analyses using abundance information are far more sensitive than those relying on presence-absence data. This problem is particularly obvious in speciose tropical communities, where sampling effects (tourists, singletons, under-recording of many rare species in finite samples: Novotny and Basset 2000, Gotelli and Colwell 2001, Brehm

and Fiedler 2004) pose great challenges to the modes of data collection and analysis.

Finally, our results show that margin faunas are different from those seen in the 'natural' forest as well as in the open landscape matrix dominated by human interference. The analysis of ensemble structures suggests that margin communities are neither simple subsets of the forest fauna, nor comprised predominantly of 'weedy' non-forest species. Such ensembles are rather a unique blend of species, reflecting local habitat conditions (e.g. resource availability and microclimate) in the habitat mosaic of the forest margin. Further research, especially on larger temporal scales, will be needed to assess how unique and stable such margin ensembles really are, and how they depend on the varying influx from source populations inside and outside the forest. For tropical insects, such a deeper mechanistic understanding will only become feasible once more is known about the habitat requirements and life histories of the component species. Given the poor knowledge of even most basic traits such as host plant affiliations and adult food requirements of insects in tropical realms, this is a long way to go – and one which needs to be pursued immediately in the light of ongoing losses of tropical near-natural habitats and their unique biodiversity.

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