Temporal Dynamics of Rich Moth Ensembles in the Montane Forest Zone in Southern Ecuador[1]

Nadine Hilt[2]

Department of Animal Ecology I, Universitätsstrasse 30, University of Bayreuth, 95440 Bayreuth, Germany

Gunnar Brehm

Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Erbertstrasse 1, 07743 Jena, Germany

and

Konrad Fiedler

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

ABSTRACT

We studied temporal dynamics of diverse moth ensembles (Arctiidae and Geometridae) in early and late succession stages of forest recovery in the montane zone of southern Ecuador. Moths were sampled using weak light sources (2 × 15 W tubes per trap) during three sampling periods (March–April 2002, wet season; October–November 2002, and August–October 2003, both "dry" seasons). Arctiid moth abundance hardly varied between sampling periods. Estimates of local diversity were lower in 2002 (wet and dry season) than in the dry season 2003, and ensemble composition was more strongly affected by sampling period rather than habitat differences. Geometridae ensembles revealed stronger temporal patterns. Geometrid abundance increased about twofold from the wet to the dry season, and temporal effects on species composition were far more pronounced that in arctiids. These differences might hint to variation in the dependence of geometrid versus arctiid larvae on ephemeral plant resources. Despite these significant temporal dynamics, in both families only a few of the more common species analyzed individually showed strong temporal changes in abundance. Almost all common species occurred as adults during all sampling periods. Therefore, even though temporal dynamics of moth ensembles are not negligible, both moth families are suitable "indicators" of community diversity and change along the succession gradient. Samples must be large enough, however, and preferably should be collated over various times of the year and in parallel, to allow for valid statements about moth diversity and species compositions in relation to habitat differences. These recommendations undermine the validity of the concept of "rapid biodiversity inventories" for speciose tropical insect communities.

RESUMEN

La dinámica temporal de dos familias de polillas muy rica en especies arctiid y geometrid, fue investigada en estadios sucesionales tempranos y tardíos de regeneración del bosque, en un área de la codillera Andina del sur de Ecuador. Las polillas fueron colectadas por atracción a una fuente de luz débil (2 × 15 W: luz negra y luz mezclada) durante tres etapas (marzo a abril 2002, estación lluviosa; octubre a noviembre 2002 y agosto a octubre 2003, ambas época seca). La cantidad de arctiid en el periodo de recolección apenas fluctúa. La estimación de la diversidad local fue baja en el año 2002 (estación lluviosa y periodo seco) que durante el periodo seco 2003, y la composición total fue más influenciada por el período de muestreo antes que por las diferencias en el hábitat. El conjunto de Geometrid reveló fuertes patrones temporales. La abundancia de geometrid se incrementó el doble desde el periodo húmedo al periodo seco. La dinámica temporal para Geometridae en general fue alta comparada con Arctidae y la diferencia de la composición de especies en los hábitats también es muy fuerte. Esto indica, que la mayoría de especies de Geometridae (en estado larvario) dependen más de recursos efímeros (como flores, yemas apicales juveniles de las plantas) que Arctiidae. Sin embargo esta significativa dinámica temporal, existió en ambas familias solo unas pocas de las especies más comunes analizadas individualmente mostraron fuertes cambios temporales en la abundancia. Casi todas las especies comunes ocurrieron como adultos durante todo el periodo de muestreo. Por lo tanto, aunque incluso la dinámica temporal de ambos conjuntos no son insignificantes, ambas familias de mariposas nocturnas son "indicadores" apropiados de la diversidad de la comunidad y cambios a lo largo de la gradiente sucesional. Sin embargo, las muestras deben ser lo suficientemente grandes, y preferentemente deberían ser colectados en paralelo en diferentes periodos del año, para permitir afirmaciones válidas acerca de la diversidad de mariposas y la composición de especies en relación a las diferencias del hábitat. Estas debilidades en la validación del concepto de "inventarios rápidos de biodiversidad" para comunidades de insectos tropicales ricos en especies.

MORE THAN HALF OF ALL DESCRIBED SPECIES ARE INSECTS (Groombridge 1992). They are thus of central importance for understanding patterns and processes of biological diversification (*e.g.*, DeVries *et al*. 1997). Moths of families such as the Arctiidae and Geometridae offer great potential to unravel mechanisms underlying patterns of tropical insect diversity. They are easily sampled and have a relatively well-advanced taxonomy (Brehm *et al*. 2005). As a consequence, arctiid and geometrid moths have frequently served as model targets in tropical insect ecology (*e.g.*, Holloway 1987, Intachat & Holloway 2000, Axmacher *et al*. 2004, Brehm *et al*. 2005).

Patterns in temporal variation of insect population abundances or community composition, and their underlying processes, are of major interest to ecologists. It has commonly been observed that insect abundance changes both in long-term (*e.g.* years) as well as

in short-term cycles (*e.g.*, weeks; for reviews see Wolda 1978, Cook & Graham 1996). While data on population size fluctuations and concomitant changes at community level are available for many temperate-zone ecosystems, much less is known about dynamics of Lepidoptera of the humid or seasonal tropics (Wolda 1978, Ehrlich 1984, DeVries *et al.* 1997, Schulze & Fiedler 2003). Climatic singularities such as strong El Niño Southern Oscillation (ENSO)-associated drought periods dramatically affect tropical butterfly populations and assemblages (Cleary 2003, Hill *et al.* 2003). But even in perhumid rain forests of Southeast Asia, where a true dry season does not occur regularly, pronounced fluctuations in the abundance of individual species or entire guilds are frequent, although consistent temporal trends are not always apparent (Schulze & Fiedler 2003, Fiedler & Schulze 2004). Despite pronounced temporal fluctuations in total catch size (*i.e.*, variation in the number of observed species and individuals), diversity of southeast Asian Pyraloidea (Schulze & Fiedler 2003) and Geometridae (Intachat & Holloway 2000) showed no clear cyclic trends (see also Barlow & Woiwod 1990). In more seasonal tropical climates, fluctuations in abundance and species richness have been documented in a number of insect groups (Wolda 1978, Smythe 1982, Wolda & Wong 1988). For example, DeVries *et al.* (1997) observed that both species richness and abundance of nymphalid butterflies in a lowland forest in Ecuador are depressed during the dry season and increase at the beginning of the rainy season. This seasonal pattern recurs in many other insect groups (such as Coleoptera, Hymenoptera, Homoptera, Lepidoptera, Orthoptera: *e.g.*, Janzen 1984, Wolda & Wong 1988, Brown 1991, Wolda 1992, Pinheiro *et al.* 2002). Yet, the magnitude of intra and interannual variation in species richness and abundance of tropical insects remains poorly known. Moreover, temporal dynamics of faunas might vary between more natural and anthropogenically altered habitats (but see Fiedler & Schulze 2004), or between taxonomic groups. These considerations also have practical consequences, *e.g.*, for conservation-oriented assessment of local faunas or for the purpose of "bioindication." If temporal dynamics lead to strong variation in diversity or species composition, the exact timing of sampling will be essential to warrant comparability and representativeness of samples in monitoring programs. Only if species diversity and composition of faunas remain largely stable over time, short-time sampling programs performed at different times will yield data that allow for further comparisons. This has frequently been assumed, but rarely tested, for those humid tropical habitats that are perceived as largely "aseasonal" (Schulze & Fiedler 2003, Fiedler & Schulze 2004).

We here analyze the temporal variation in diversity and species composition of species-rich ensembles of mobile herbivorous insects along a succession gradient in southern Ecuador. We chose two different moth families as model groups, namely the Arctiidae and the Geometridae. Species of both taxa are abundant and taxonomically well documented, and they can easily be sampled at artificial light sources. Yet, the two families differ prominently in important life history traits such as body size distributions, host-plant relationships, or the incidence of aposematism, mimicry, and sequestration of toxic plant compounds (Hilt, Brehm, and Fiedler, pers. obs., Kitching & Rawlins 1999, Minet & Scoble 1999).

We specifically address the following questions:

1. How variable are the communities over time (three sampling periods distributed over 18 mo, two periods in the drier and one in the very humid part of the year) with regard to overall abundance and local diversity?
2. Do the abundances of dominant species vary over time, and does this temporal variability differ between two different classes of succession habitats (early vs. late stages of forest recovery)?
3. How variable is species composition over time (temporal β-diversity)?
4. Do temporal dynamics of community composition differ along the succession gradient?

METHODS

STUDY AREA.—Moths were collected within the Eastern Cordillera of the Andes at the northern border of the Podocarpus National Park in southern Ecuador (3°58′S, 79°5′W) (Brehm *et al.* 2005, Hilt & Fiedler 2005). There are 10–11 humid months per year (Richter 2003) with a mean annual precipitation of *ca* 2000 mm and a mean annual air temperature of 15.5°C at 1950 m elevation. The rainfall maximum occurs between April and September (the wettest months are April, May, and June). A pronounced dry season is typically lacking in the eastern Andean slopes at altitudes between 1000 and 3600 m elevation (Fleischbein *et al.* 2005). The drier season, locally called "veranillo," is caused by the low-level jet stream, which reaches the eastern Andean slopes between October and March (Bendix & Lauer 1992). The mean monthly temperature and precipitation for the years 2002 and 2003 are shown in Figure 1.
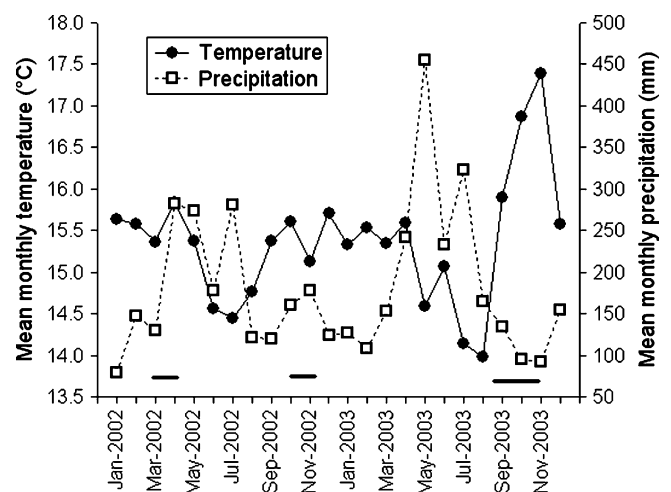

FIGURE 1.   Temperature and precipitation data for the study area (1960 m a. s. l.) in the years 2002 and 2003 (data from Richter, 2003 and updated; R. Rollenbeck, pers. comm.). Horizontal lines indicate the three sampling periods in these two years.

The potential natural vegetation is evergreen montane rain forests (Homeier 2004), but the forest has often anthropogenically been replaced by pastures, thickets of bracken (Hartig & Beck 2003), shrub encroachment, or regenerating forest (Paulsch 2002). We selected 15 sites representing different stages of vegetation succession (see Hilt & Fiedler 2005 for details about the vegetation at the sites and the distances between them). These sites (altitudinal range between 1800 m and 2005 m elevation) depict a gradient of forest recovery after a landslide as well as some of the most relevant types of disturbed habitats as a result of human land use practices. The sampling sites were grouped into two categories according to their successional stage (early [**E**] without woody vegetation: $N = 10$ sites, or $N = 8$ if the two pastures sites are excluded; late [**L**] with substantial coverage by woody shrubs or secondary forest aged *ca* 40 yr: $N = 5$). Early stage habitats included an almost bare landslide, grassy slopes, abandoned cattle pastures, and bracken thickets. Most habitat types were represented by two replicate sites. Sites were selected so that the vegetation in a radius of 50 m around the light "trap" (see below) was homogeneous. Moreover, at each site the "trap" was invisible (to humans at least) from the neighboring sites.

SAMPLING AND IDENTIFICATION.—Moths were sampled manually by attraction to weak light sources (2 × 15 W tubes; Sylvania blacklight-blue, F 15 W/BLB-TB and Philips FLD 15 W 05; in a white gauze cylinder, F. Weber, Stuttgart; height 1.6 m; diameter 0.6 m). Low-power light sources are sufficient to minimize cross-attraction of moths between sampled habitats (Schulze & Fiedler 2003, Beck & Linsenmair 2006). The effective "radius of attraction" for moths has been estimated to be only between 10 and 30 m (Muirhead-Thomson 1991, Beck & Linsenmair 2006), but may vary with habitat structure (*e.g.*, density of vegetation). However, in our dataset, the mean number of Geometridae specimens attracted per night was significantly higher at later rather than early succession sites, and no differences were seen in Arctiidae (Hilt & Fiedler 2005, Hilt *et al.* 2006, and Fig. 2). Thus, we have no indication that sampling was more effective in the open early succession vegetation (also Schulze & Fiedler 2003). We restricted sampling to the peak time of moth activity during the evening hours between 1845 and 2145 h. Moths were collected during three periods in the years 2002 (wet season: March to April [**P1**], dry season: October to November [**P2**]), and 2003 (dry season: August to October [**P3**]). These three periods showed the climatic characters typical for the region (Fig. 1). Rainfall was very high in P1, distinctly lower in veranillo P2, and even lower in veranillo P3. Temperature was unusually high in the very dry veranillo P3 and otherwise rather constant. At each site and within each period, two to four nightly catches were pooled to provide the data basis for the subsequent analyses. Catches were restricted to phases between 4 d after full moon until 6 d before full moon, because the moon phase has an important impact on the efficiency of light traps (McGeachie 1989, Yela & Holyoak 1997).

Specimens were sorted to morphospecies and later taxonomically identified as far as possible using published literature and reference collections (see Acknowledgments; species lists can be found in Brehm *et al.* 2005 and Hilt 2005).
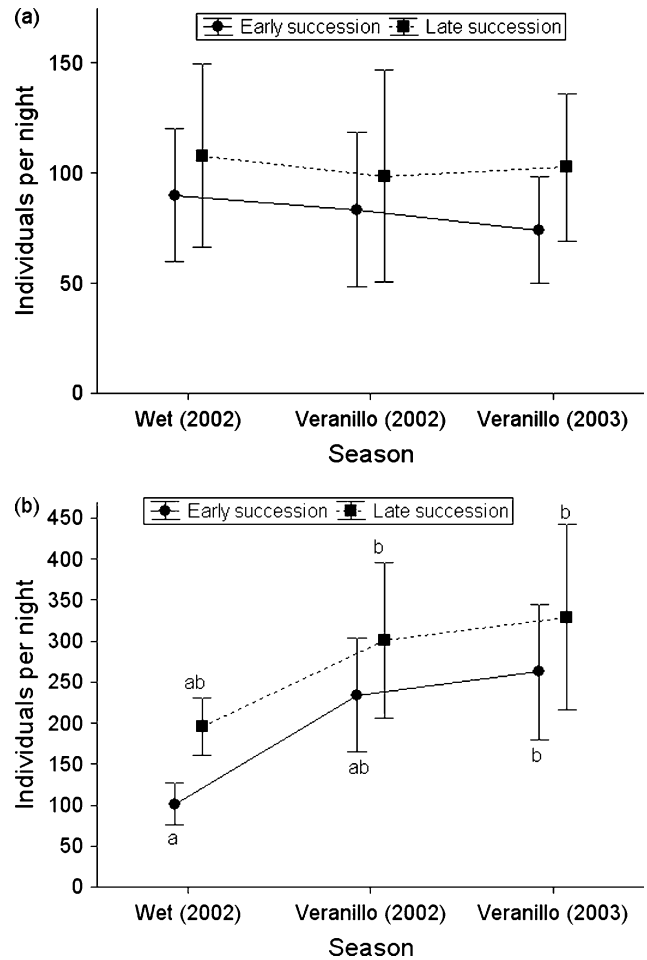

FIGURE 2.   Mean numbers ± 95 percent confidence intervals of (a) arctiid and (b) geometrid individuals attracted per night in the two different succession habitat classes and the three sampling periods. Wet season: March–April 2002; veranillo (drier season): October–November 2002; and August–October 2003. Symbols accompanied by different letter codes are significantly different (Scheffé post hoc test, $P < 0.05$, following two-way repeated measures ANOVA). See text for statistical results.

QUANTITATIVE ANALYSIS.—We calculated Fisher's alpha as a measure of local diversity using a program developed by Henderson and Seaby (1998). Numbers of arctiid and geometrid individuals and diversity estimates were compared between pooled samples of each of the three sampling periods. Fisher's alpha values were statistically compared using Solow's (1993) test, implemented in Henderson and Seaby's program. Additionally, numbers of species and individuals, and values of Fisher's alpha for every site in the three different periods were compared using a repeated measurements ANOVA approach. The extent of temporal abundance variation of individual species was tested in the commonest species only, that is, species where the total catch (summed over all sites and seasons) was $N > 100$ for Arctiidae (20 species) and $N > 150$ for Geometridae (17 species). For rarer species, sampling effects are expected to be so pronounced that they undermine credibility of detailed species-level

analyses. In these common species, numbers of moths were converted to relative abundances (setting the total catch per each site and sampling period as 1), since light-trap data do not provide sound measures of absolute abundance, but yield useful data of relative abundances for those species that are attracted to light (Fiedler & Schulze 2004). Relative abundances were then analyzed by two-way ANOVA with habitat type and collecting period as effects. Where necessary to homogenize variances, data were log- or square-root transformed. If these transformations failed to homogenize variances, a rank transformation (Conover & Iman 1981) was applied.

To alleviate sampling effects in comparisons of the species composition of rich, but incompletely sampled moth ensembles, we used the chord-normalized expected species shared index (Gallagher's CNESS index: Trueblood *et al.* 1994) as a measure of dissimilarity between samples. This index is widely independent of sample size and diversity, and includes the effect of rare species. We calculated CNESS distances using the program COMPAH96 (available from E. Gallagher, University of Massachusetts, Boston, URL: http://alpha.es.umb.edu/faculty/edg/files/edgwebp.htm). CNESS distance values between individual samples depend on a sample size parameter m, which can range from $m = 1$ to the largest common sample size $m = m_{max}$. At low m values the CNESS distance is more strongly affected by common species, whereas with increasing m values the rare species receive successively larger emphasis. We graphically present ordinations only for $m = 1$, whereas for Analysis of Similarities (ANOSIM) calculations we selected three to four different m values for each taxon: $m = 1$, $m =$ intermediate, and $m =$ maximum. This approach allows to assess how robust, or sensitive, analyses of β-diversity are with respect to the commonness or rarity of species, and thus to concomitant sampling effects. Species composition of local moth ensembles was visualized using nonmetric multidimensional scaling (NMDS: Clarke 1993, Brehm & Fiedler 2004). Ordinations were performed with Statistica 6.1 (StatSoft 2004). The significance of faunal differences between predefined groups of sites was assessed by ANOSIM (Clarke & Gorley 2001) with 1000 random permutations. The R statistic of ANOSIM was used as a measure of effect size. Exclusion of all rare species of Arctiidae (*i.e.*, those represented with overall 15 or fewer individuals) from our analyses yielded the same results as with all species included (data not shown). Hence, we used all species in our analyses. In these common species, numbers of moths were converted to relative abundances (setting the total catch per each site ensemble-wide comparisons irrespective of their commonness or rarity. 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

Temporal variation in overall moth abundance and diversity.—The samples on which the subsequent analyses are based were very large (Arctiidae: 7717 individuals, 250 species, Fisher's alpha with 95% ci: 49.5 ± 2.1; Geometridae: 20,670 individuals, 775 species, Fisher's alpha: 159.1 ± 11.9). The temporal pattern in the mean number of moths caught per night differed between the two families. Arctiid abundance (Fig. 2a) did not significantly differ between seasons, and was only slightly and non-significantly higher in late succession habitats (two-way ANOVA with repeated measurements: habitat: $F_{1,24} = 1.75$, $P > 0.19$; season: $F_{2,48} = 0.21$, $P > 0.80$; interaction term: $F_{2,48} = 0.09$, $P > 0.91$; Levene test all $P > 0.1$). On the contrary, mean numbers of geometrid individuals caught per night (Fig. 2b) almost doubled from the wet season to the veranillo and were also, but less strongly so, influenced by the habitat (two-way ANOVA with repeated measurements: habitat: $F_{1,24} = 6.00$, $P < 0.05$; season: $F_{2,48} = 9.04$, $P < 0.001$; interaction term: $F_{2,48} = 0.10$, $P > 0.90$, Levene test all $P > 0.1$).

In the Geometridae, diversity estimates (Fisher's alpha) were significantly lower for the dry season P2 than for the two other seasons. This result was only obtained when combining all samples from each sampling period (Table 1), but was far less so distinct when comparing individual sites (Fig. 3b). There was a clear habitat effect and a weaker temporal effect (two-way ANOVA with repeated measurements: habitat: $F_{1,11} = 18.06$, $P < 0.005$; season: $F_{2,22} = 3.85$, $P < 0.05$; interaction term: $F_{2,22} = 0.02$, $P > 0.98$). In the Arctiidae, diversity was also lowest in period P2. This temporal difference was significant when comparing means of individual sites (two-way ANOVA with repeated measurements: habitat: $F_{1,11} = 4.56$, $P < 0.06$; season: $F_{2,22} = 13.57$, $P < 0.001$; interaction term: $F_{2,22} = 0.72$, $P > 0.49$), but was only weakly expressed when analyzing cumulated samples (Table 1, Fig. 3a). Habitat (early vs.

TABLE 1. *Numbers of arctiid and geometrid individuals (*N*), observed species (*S*), and estimates of Fisher's alpha with 95% confidence interval. Catches at the 15 sites were pooled for each of the three sampling periods (P1–P3) over all sites and sampling nights. Different superscript letters indicate significant results of Solow tests (pairwise comparisons within families) at* $P < 0.05$.

|	March–April 2002 (P1)			October–November 2002 (P2)			August–October 2003 (P3)		
	Individuals (*N*)	Species (*S*)	Fisher's alpha	*N*	*S*	Fisher's alpha	*N*	*S*	Fisher's alpha
Arctiidae	2693	191	$47.0^{ab} \pm 3.5$	2257	168	$42.0^b \pm 3.3$	2767	204	$50.9^a \pm 3.9$
		13 sites/27 sampling nights			15 sites /34 sampling nights			15 sites/33 sampling nights	
Geometridae	3629	519	$165.7^a \pm 26.4$	7772	586	$147.2^b \pm 11.6$	9269	653	$160.4^a \pm 11.9$
		13 sites/27 sampling nights			15 sites/33 sampling nights			15 sites/35 sampling nights	
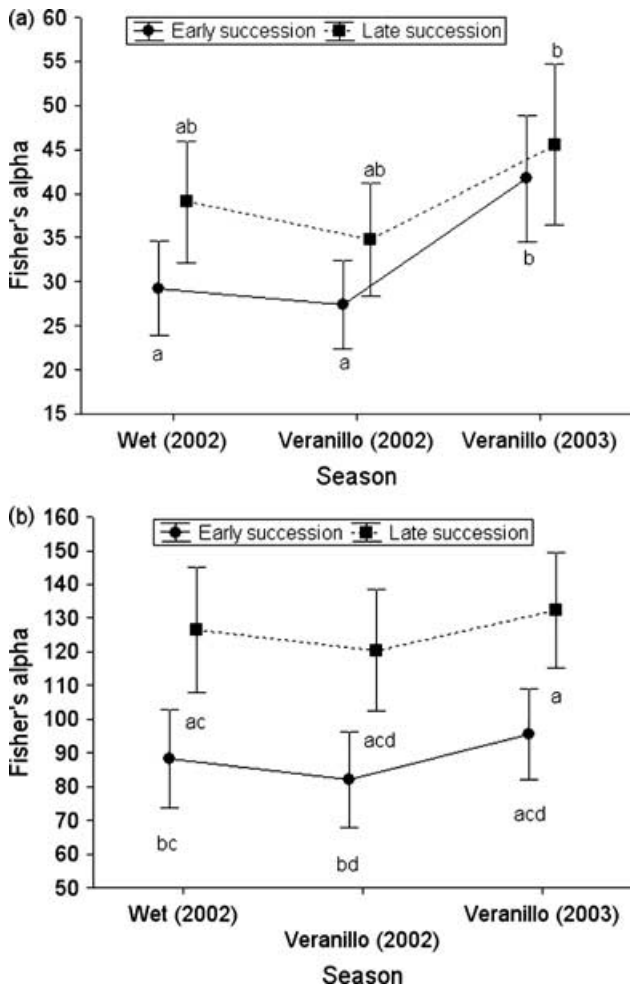
FIGURE 3. Diversity (expressed as mean values of Fisher's alpha ± 95 percent confidence intervals, averaged over the pooled samples per site and season for early vs. late succession stages) of (a) Arctiidae and (b) Geometridae moths across the three sampling periods. Symbols accompanied by different letter codes are significantly different (Scheffé's post hoc test). Further statistical details see text.

late succession) showed a weak effect on local species diversity ($P < 0.06$).

CONTRIBUTION OF INDIVIDUAL SPECIES TO TEMPORAL ENSEMBLE DYNAMICS.—Arctiidae and Geometridae showed a strikingly similar pattern of the distribution of species across three sampling periods (Table 2). In both families, 52 percent of the species, which represented approximately 92 percent of all sampled moth individuals, were observed in all three sampling periods (P1–P3). Twenty-one to twenty-three percent of the species occurred in two periods, and 24.9 percent of geometrid species and 26.8 percent of arctiid species were sampled in only one period, respectively. However, these latter species accounted for but a small fraction (1.4–1.9%) of the total catch.

Relative proportions of the commonest species were tested to assess whether certain species show preferred flight periods. Overall,

23 of 37 common moth species (9 of 17 Geometridae, 14 of 20 Arctiidae) showed no significant temporal abundance fluctuations (Tables 3 and 4). A few species in both families showed different relative abundances along the succession gradient independent of collecting period or season. The arctiids *Agkonia pega*, *Areva albogrisea*, and *Metalobosia holophaea* as well as the geometrids *Eois paraviolascens*, *Microxydia ruficomma*, *Perizoma emmelesiata*, *Perizoma zenobia*, and *Sabulodes thermidora* differed in their relative abundance between early and later succession stages. Very few species showed pronounced temporal abundance fluctuations irrespective of the habitat. *Agylla nivea*, *Agylla seperata*, *Cosmosoma meridense* (all Arctiidae) and *Chloropteryx opalaria*, *Lomographa tributaria*, *Physocleora* sp. (all Geometridae) were numerous in the wet season, whereas *Epectaptera* sp. and *Pantherodes conglomerata* occurred frequently in the veranillo, but were rare in the wet season. Others exhibited a significant habitat × season interaction with regard to their relative abundance (*e.g.*, Arctiidae: *Napata* sp.; Geometridae: *Lissochlora latuta*). For example, the arctiid *Macroptila laniata* was common in early succession sites and in the wet season, whereas the geometrids *Oxydia trychiata* and *Perissopteryx nigricomata* were often found in the later succession stages and in the veranillo. In *O. trychiata* and *P. nigricomata*, habitat had a stronger effect on relative abundances, whereas season had a stronger effect in *Pantherodes colubraria* and *M. laniata*.

TEMPORAL DYNAMICS OF ENSEMBLE COMPOSITION.—Two-dimensional ordinations based on CNESS values with $m = 1$ (*i.e.*, emphasizing dominant species: Fig. 4a) and concomitant ANOSIM calculations for the 15 succession sites revealed a distinct segregation of arctiid faunas between early and late succession stages, and a slightly weaker segregation according to the three sampling periods (Table 5). When emphasizing the moderately abundant ($m = 10$) or the rare species ($m_{max} = 25$), the effect of sampling period remained unaffected, whereas habitat effects became diluted and nonsignificant (Table 5). The geometrid fauna showed a similar picture as the arctiid ensembles (Fig. 4b). For $m = 1$, there also occurred a distinct segregation between early and late succession stages, as well as between the three sampling periods (Table 5).

Significant pairwise differences only emerged between the wet season (P1) and the two drier seasons (P2 and P3), respectively, but not between the drier seasons of successive years. With increasing m values, samples taken in these two drier seasons became significantly segregated from each other. For all m values, the influence of collecting period was slightly stronger than the habitat effect. Moreover, in all tests except for the comparison between the periods P1 and P2 at $m = 1$, Geometridae faunas showed far stronger spatial and temporal differentiation than Arctiidae ensembles, as evidenced by the much higher R values.

DISCUSSION

TEMPORAL DYNAMICS OF MOTH ABUNDANCE AND DIVERSITY.— Seasonality of tropical insect populations and communities has almost universally been detected wherever well-defined wet and dry seasons alternate regularly (*e.g.*, Wolda 1978, 1980, 1992; DeVries

TABLE 2. *Distribution of arctiid and geometrid species and their relative proportions (in %, in parentheses) among three sampling periods (P1– P3) for the 15 succession sites.*

	Arctiidae		Geometridae	
	Number of species (total $N = 250$)	Represented number of individuals (total $N = 7717$)	Number of species (total $N = 775$)	Represented number of individuals (total $N = 20,670$)
All periods	130 (52.0)	7240 (93.8)	402/(51.9)	19,126/(92.6)
Two periods	53 (21.2)	329/(4.3)	180/(23.2)	1246/(6.0)
One period only	67 (26.8)	148/(1.9)	193/(24.9)	298/(1.4)
P1 only	25 (10.0)	53/(0.7)	44/(5.7)	63/(0.3)
P2 only	13 (5.2)	15/(0.2)	60/(7.7)	86/(0.4)
P3 only	29 (11.6)	80/(1.0)	89/(11.5)	149/(0.7)

et al. 1997, 1999; Novotny & Basset 1998; Kitching *et al.* 2000). Even in perhumid tropical ecosystems with weakly pronounced climatic seasonality, a great variety of temporal patterns in the abundance of light-trapped insects was found (*e.g.*, Kato *et al.* 1995).

However, in perhumid regions of SE Asia all moth ensembles studied thus far revealed little evidence for cyclic seasonal dynamics (*e.g.*, Barlow & Woiwod 1990, Orr & Häuser 1996, Intachat & Holloway 2000, Schulze & Fiedler 2003), even though leaf flushing, flowering, or fruit set of many plants that serve as larval host plants display seasonal peaks (Sakai *et al.* 1999, Wich & van Schaik 2000, Hamann 2004). It must, however, be stressed that our survey of

TABLE 3. *Results of two-way analyses of variance (ANOVA) on relative abundances of 20 common arctiid moth species with total catch N > 100 for the 15 sites, according to habitat categories (early vs. late succession) and sampling period (March–April 2002, October–November 2002, August–October 2003). Species were sorted in descending order according to their total absolute abundance. Bold figures indicate significant differences below the < 0.05 level that persist after FDR correction. *P < 0.05, **P < 0.01, ***P < 0.005, ****P < 0.001, NS: not significant.*

Species name	F (Habitat) (df = 1;37)	F (Period) (df = 2;37)	F (Interaction) (df = 2;37)
Macroptila laniata	**6.97***	**12.0*****	NS
Cosmosoma sp.15	NS	NS	NS
Agylla zucarina	NS	NS	NS
Agylla hampsoni	NS	NS	NS
Metalobosia holophaea	**7.48****	NS	NS
Holophaea endoleuca	NS	NS	NS
Agylla sp.14	NS	NS	NS
Agylla flavitincta	NS	NS	NS
Agylla seperata	NS	**5.87****	NS
Cosmosoma meridense	NS	**3.70***	NS
Areva albogrisea	**13.52*****	NS	NS
Agylla sp.19	4.30*	NS	NS
Agkonia pega	**8.89****	NS	NS
Napata sp.3	NS	**3.61***	**3.60***
Eucereon zizana	NS	NS	NS
Agylla nitridalis	NS	NS	NS
Ischnocampa mamona	NS	NS	NS
Agylla nivea	NS	**5.61****	NS
Epectaptera sp.1	NS	**4.14***	NS
Agylla sp.25	NS	NS	NS

TABLE 4. *Results of two-way analysis of variance (ANOVA) on relative abundances of 17 common geometrid moth species with total catch N >150 for the 15 sites, according to habitat categories (early vs. late succession) and sampling period (March–April 2002, October–November 2002, August–October 2003). Species were sorted in descending order according to their absolute total abundance. Bold figures indicate significant effects at the < 0.05 level that persist after FDR correction. * P < 0.05, **P < 0.01, ***P < 0.005, ****P < 0.001, NS: not significant.*

| Species name	F (Habitat) (df = 1;37)	F (Period) (df = 2;37)	F (Interaction) (df = 2;37)
Pantherodes conglomerata	NS	**14.97*****	NS
Sabulodes thermidora	**22.75*****	NS	NS
Argyrotome prospectata	4.61*	NS	NS
Eois paraviolascens	**11.00****	NS	NS
Physocleora sp.	NS	**8.62*****	NS
Chloropteryx opalaria	NS	**8.82****	NS
Oxydia trychiata	**15.89*****	**9.19*****	NS
Perissopteryx nigricomata	**26.78*****	**10.70*****	NS
Perizoma zenobia	**52.39*****	NS	NS
Lomographa tributaria	NS	**8.42*****	NS
Nemoria nigrisquama	NS	NS	NS
Eois chrysocraspedata	NS	NS	NS
Microxydia ruficomma	**6.10***	NS	NS
Pantherodes colubraria	**6.62***	**11.97*****	NS
Lissochlora latuta	**17.82*****	NS	**5.30****
Perizoma emmelesiata	**13.10*****	NS	NS
Melinodes saeta	NS	NS	NS
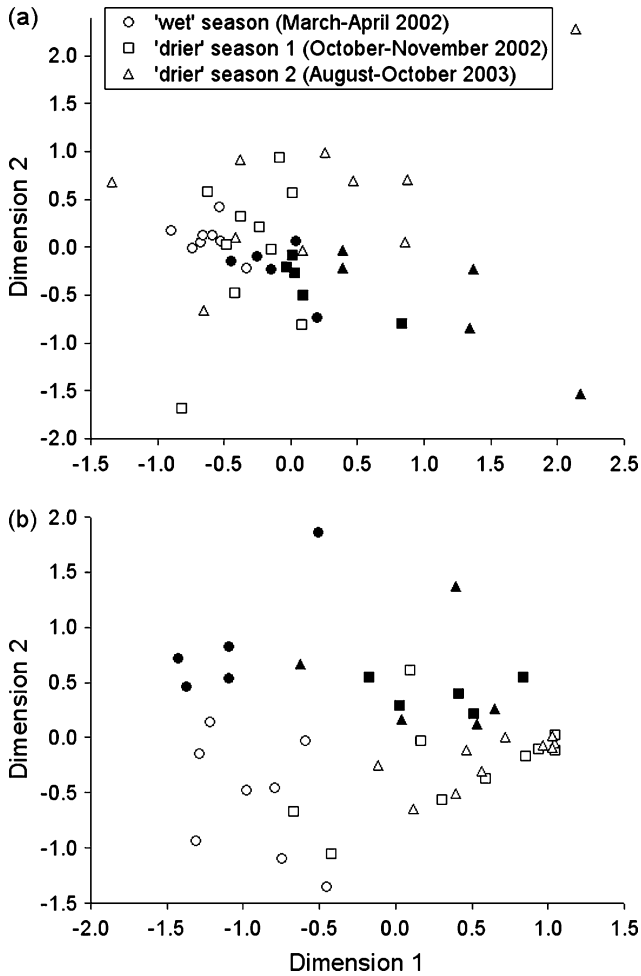
FIGURE 4.   Nonlinear two-dimensional scaling plots for the arctiid samples (a; stress: 0.185) and geometrid samples (b; stress: 0.147) of the 15 succession sites, segregated according to the three sampling periods. Ordinations are based on CNESS distance values with $m = 1$. Open symbols: early succession stages; filled symbols: later succession stages.

TABLE 5.   *Influence of habitat and sampling period on β-diversity of arctiid and geometrid samples at 15 succession sites. Given are ANOSIM results for two-way crossed analyses (Global* R *and* P*), as well as pairwise comparisons among the three sampling periods. Results are reported for CNESS faunal distances at different levels of the sample size parameter* m. *P1: March–April 2002; P2: October–November 2002; P3: August–October 2003. Figures in italics indicate no significant effects at the* P *< 0.05 level after FDR correction.*

		Arctiidae			Geometridae	
m		R	P	m	R	P
1	**Habitat**	0.27	0.003	1	0.31	0.001
	Season	0.19	0.002		0.41	0.001
	P1 vs. P2	*0.14*	*0.02*		0.60	0.001
	P1 vs. P3	0.33	0.002		0.78	0.001
	P2 vs. P3	0.16	0.002		0.01	0.36
10	**Habitat**	*0.16*	*0.043*	50	0.42	0.001
	Season	0.19	0.001		0.45	0.001
	P1 vs. P2	*0.11*	*0.036*		0.55	0.001
	P1 vs. P3	0.32	0.001		0.61	0.001
	P2 vs. P3	0.16	0.002		0.27	0.001
25	**Habitat**	0.06	0.22	100	0.32	0.001
	Season	0.17	0.001		0.40	0.001
	P1 vs. P2	0.08	0.094		0.48	0.001
	P1 vs. P3	0.30	0.001		0.52	0.001
	P2 vs. P3	0.15	0.002		0.28	0.001
	Habitat			132	0.26	0.002
	Season				0.37	0.001
	P1 vs. P2				0.43	0.001
	P1 vs. P3				0.48	0.001
	P2 vs. P3				0.26	0.001

Ecuadorian moths did not allow for detecting seasonal phenomena in a strict sense. Our data cover only three sampling periods distributed over 18 mo. We have sampled only two veranillos and lack a replicate wet season for the succession habitats covered in the present study. However, sampling in two more years (1999 and 2000) in natural forest in the same area revealed many parallels to the 2002 and 2003 data. For example, Geometridae abundances were generally higher in the veranillos of these 2 yr than in the wet period, while Arctiidae showed less pronounced fluctuations (Brehm 2002, Süßenbach 2003). Therefore, even though further monitoring will be required to better understand temporal changes in these diverse moth faunas we feel that our data are sufficiently robust to warrant interpretation.

In our study area in the Eastern Andes of southern Ecuador, the montane rain forests receive substantial rainfall throughout the year. However, a period occurs between September and January when precipitation rates drop to 75 to 150 mm per month, while excessive rainfall occurs between April and July (Fig. 1; Richter 2003, Bendix *et al.* 2006). These climatic cycles are also reflected by patterns in plant phenology in the southern Ecuadorian Andean forest. For example, Homeier (2004) discriminated two groups of trees regarding to their main flowering phase. Most tree species, such as *Heliocarpus americanus* and *Clethra revoluta*, had their main flowering phase in the wettest months (March–June), whereas other species (*Tabebuia chrysantha, Purdiaea nutans*) flowered in the drier period (August–December). However, the proportion of flowering and fruiting tree individuals shows strong annual variation. Dziedzioch (2001) investigated the phenology of ornithophilous plant species in the same study area. She showed that most species flowered during March and September, peaking in the wettest month (April). Hence, at least for herbivores that rely on young foliage or reproductive plant organs the availability of resources varies strongly over times.

Most previous studies conducted in seasonal tropical areas showed an increase in insect abundance in the wet season, suggesting

that a seasonal correlation with rainfall is typical of tropical insect communities (overview in Janzen 1973, DeVries & Walla 2001, Intachat *et al.* 2001, Pinheiro *et al.* 2002). The onset of rainfall triggers budbreak and flowering in many plants and thus makes available resources for lepidopteran larvae (fresh plant biomass) as well as adults (flower nectar). Accordingly, the more severe the dry season is, the stronger the association between rainfall and moth ensembles is to be expected. Only few studies found decreasing insect abundance in the wet season (*e.g.*, Boinski & Scott 1988). This can be expected if strong rainfall negatively affects flight performance or insect behavior. As a consequence, differences in the tightness of the link between insect dynamics and temporal patterns in climate should be attributable to variation between regions and with regard to the direct and indirect constraints imposed by climate onto different taxonomic groups.

In our extensive data set, geometrid moths showed a clear increase in abundance for all habitat categories from the wet season to the drier season. However, mean local geometrid diversity was equal across the two seasons (wet (P1) vs. veranillo (P2/3); mean Fisher's alpha: 102.9 vs. 103.2). Thus, higher Geometridae abundance in the dry seasons did not translate into higher diversities of resulting samples. In contrast, abundance of arctiid moths did not vary significantly across three sampling periods. Arctiid diversity showed some minor seasonal differences: the two successive dry seasons differed in their diversity when cumulated samples were compared, and also on a site-to-site basis (means of Fisher's alpha of early vs. late succession sites). But there was only a significant difference between Fisher's alpha values of the early succession sites in the two seasons of the year 2002 versus the veranillo 2003. Mean values of Fisher's alpha of the later succession stages did not vary with the season. Together with the much higher faunal differentiation as revealed by ANOSIM this indicates that Andean geometrid moths respond more sensitively than arctiid moths to variation in weather and its effects on vegetation, and also on forest disturbance. In line with this hypothesis, mainly geometrid abundance and to a lesser extent diversity, were lower in the samples from veranillo P2, which was characterized by distinctly lower temperatures and higher precipitation, than the veranillo P3 of the subsequent year (Fig. 1).

More than 50 percent of the moth species, which represented >90 percent of all individuals, were caught in all three periods. This pattern was strikingly similar between the two studied moth families. Moreover, among the common moth species, few showed clear abundance peaks at certain times of the year. For example, the geometrid species *P. colubraria* and *P. conglomerata* had strong abundance peaks during the veranillos, whereas *Physocleora* sp. and *C. opalaria* as well as the arctiid *M. laniata* occurred in highest numbers in the wet season. Yet all of them do occur as adults also during other months of the year. Along an elevational gradient in natural forest in the same region in southern Ecuador, Süßenbach (2003) found that only a few abundant arctiid and pyraloid moth species showed strong temporal abundance variation. These abundant species were largely responsible for the differences he observed between wet season and veranillo ensembles, but most of them were also found in both seasons.

Our observations that most moth species are on the wing during the whole year confirm observations made by Hebert (1980) in humid tropical forests in Papua New Guinea. Stork and Brendell (1990) observed similar patterns for beetles in Sulawesi, and Novotny and Basset (1998) for adult stages of sap-sucking hemipterans in New Guinea. More prominent seasonal abundance fluctuations were, in contrast, reported from regions in South and Central America with a pronounced dry season (Brazil: Pinheiro *et al.* 2002; Costa Rica: Janzen 1973, Boinski & Fowler 1989; Eastern Ecuador: DeVries *et al.* 1997, DeVries & Walla 2001; Panama: Wolda 1992).

TEMPORAL DYNAMICS ON THE ENSEMBLE LEVEL.—Multivariate analyses on ensemble level (NMDS ordinations, ANOSIM) revealed that arctiid and geometrid samples all changed over time with regard to species composition. As with the abundance, these temporal effects were far more pronounced in the Geometridae. Temporal effects were consistently larger than habitat effects in this family and did hardly vary depending on how strongly, or weakly, the rare or abundant species were weighted (using different levels of the sample size parameter m in the CNESS index). In contrast, temporal effects were overall smaller (as indicated by lower R values in ANOSIM comparisons) in the family Arctiidae. Pyraloid moth ensembles in natural forest also showed higher temporal variation as compared to the Arctiidae (Süßenbach 2003). The higher temporal dynamics of Andean geometrid and pyraloid moths relative to the Arctiidae may be linked to the dependence of many geometrid or pyraloid caterpillars on young foliage, inflorescences, or fruits. For example, the larvae of large geometrid clades such as the Eupitheciini and Geometrinae predominantly feed on inflorescences and seeds (McGuffin 1958, Holloway 1997, Brehm 2003); sources which change temporally in our study area (Homeier 2004, see above). In contrast, larvae of Arctiidae are not known as specialist flower feeders, and may be less affected by the phenology of the surrounding vegetation. However, available host plant data are currently too scarce for a more thorough evaluation of the factors underlying pronounced abundance fluctuations, and their variation across moth taxa. Moreover, long-term studies would be urgently needed to assess which of the temporal patterns documented here are really related to cyclic, "seasonal" patterns in climate and plant phenology.

TEMPORAL DYNAMICS AND THE ESTIMATION OF COMMUNITY PARAMETERS.—Our observations show that highly speciose Andean moth ensembles (Arctiidae and Geometridae) have a substantial β-diversity both with regard to sampling time and habitat. In remnants of upland rain forest in Australia, Kitching *et al.* (2000) also found a segregation of moth assemblages according to season (wet vs. dry) and forest type. DeVries *et al.* (1997) reported a high β-diversity of fruit-feeding butterflies in a lowland Ecuadorian rain forest in vertical, horizontal, and temporal dimensions. Such findings may have imminent consequences for topics in applied ecology, such as assessing and monitoring insect faunas for conservation purposes. If diversity or species composition change profoundly with time (*e.g.*, between seasons), then only sampling and monitoring programs performed during exactly the same time periods will yield

meaningful data for comparisons between habitats or for assessing management effects.

In Borneo, Schulze and Fiedler (2003) as well as Fiedler and Schulze (2004) observed that α-diversity and dynamics of speciose pyraloid moth assemblages largely reflected habitat differences, even though species composition did change over time. During a 3-yr study on SE Asian hawkmoths, species richness and species composition were also strongly indicative of habitat differences between sites, and hardly differed between seasons and years (Beck 2005, Beck & Linsenmair 2006). Under such circumstances, samples taken at almost any time will yield reliable information about species richness and composition, provided that the samples are large enough and thus representative and amenable to statistical analysis. In our samples, the Arctiidae comprise such a case. Here, diversity and species composition turned out to be only marginally affected by temporal patterns, especially if rare species (whose records are particularly susceptible to sampling effects) are not weighted too high. Geometridae, in contrast, revealed higher temporal variation, and therefore sufficient care must be taken when comparisons are made across samples that were collated at different times. However, arctiid as well as geometrid moth ensembles in southern Ecuador closely reflected anthropogenic habitat disturbance and forest recovery (Brehm & Fiedler 2005, Hilt & Fiedler 2005, Hilt *et al.*, 2006), thus corroborating the potential of tropical moth ensembles to be used as environmental indicators (Kitching *et al.* 2000, Holloway & Intachat 2003, Summerville *et al.* 2004).

In conclusion, samples from species rich tropical moth communities can reliably be used for statements about the diversity and species composition, for example along environmental gradients. However, it should always be explicitly assessed how variable community patterns are over time. Preferably, even in humid tropical regions without a real dry season, sampling should be spread as evenly as resources permit over the annual cycle. Quantitative measures of community patterns (*i.e.*, α- and β-diversity) remained largely unaffected and still mirrored habitat differences in both moth families tested here irrespective of the sampling period. Moreover, as evidenced by diverse moth ensembles in our study area, the highest insect abundances and diversities are not universally found in the more humid parts of the year.

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