

Links between the Environment, Abundance and Diversity of Andean Moths

Jan Beck¹

Department of Environmental Sciences, Biogeography Section, University of Basel, St. Johannis-Vorstadt 10, 4056 Basel, Switzerland

Gunnar Brehm

Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, University of Jena, Erbertstraße 1, 07743 Jena, Germany

and

Konrad Fiedler

Department of Animal Biodiversity, University of Vienna, Rennweg 14, 1030 Vienna, Austria

ABSTRACT

Ideas on the spatial variation of biodiversity often imply a causal link between the abundance and species richness of organisms. We investigated this ‘more individuals hypothesis’ using light-trapping data of three unrelated groups of moths (Arctiidae, Geometridae and Pyraloidea) from the Ecuadorian Andes. We analyzed environmental correlates of specimen densities found in different habitats, finding effects of temperature, moonlight, forest succession, elevation and season. We corrected abundance data for light-trapping artefacts, and we measured species diversity with various metrics known to be unbiased by undersampling. We found significant positive correlations between abundance and species diversity for all three taxonomic groups. We discuss implications for a general evaluation of species-energy theory as well as for a better understanding of ecological processes in montane habitats of the Andes.

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

Key words: Ecuador; Lepidoptera; light trapping; species-energy theory; temperature.

A LARGE NUMBER OF HYPOTHESES attempt to explain the spatial distribution of biodiversity (*e.g.*, Rosenzweig 1995, Willig *et al.* 2003, Mittelbach *et al.* 2007), but testing or weighting these alternative explanations against each other remains a challenge (Gotelli 2008). Links between species richness and biologically available energy (often related to climatic variables) form an important set of hypotheses in this respect (species-energy theory), but the empirical evidence on species-energy links is heterogeneous with respect to strength and shape of the relationship (Mittelbach *et al.* 2001; Currie *et al.* 2004; Evans *et al.* 2005, 2006, 2008). This heterogeneity may be enhanced by differing interpretation of what ‘energy’ is and how to measure it (see Clarke & Gaston 2006 for review). For heterotrophic, mobile organisms relationships may be further complicated by the fact that rarely a whole community (*sensu* Fauth *et al.* 1996) is investigated, but rather particular taxonomic groups or ‘ensembles’ that have to share available energy with other, unstudied groups.

A crucial assumption of many species-energy ideas is a causal, positive link between total abundance (*i.e.*, sum of individuals of all species of a studied assemblage) and species richness. This *more individuals hypothesis* (Evans *et al.* 2005, Clarke & Gaston 2006) involves a chain of causalities that may be sketched as ‘higher productivity, more individuals, more species above minimum viable population size, fewer extinctions, more species that persist in the

system’. The more individuals hypothesis applies to many current ideas on species richness even where it is less explicitly stated—for example, the idea of ‘water-energy dynamics’ and other climatic explanations (Hawkins *et al.* 2003, Field *et al.* 2008). Testing for the existence of positive abundance–diversity relationships as a general rule, across regions, scales and taxonomic groups, should therefore help evaluating the plausibility of a whole set of mechanistic hypotheses on the distribution of biodiversity.

Far-reaching theoretical predictions on the interrelationships of total and per species abundance, species richness and area were already proposed by Preston (1962), but various obstacles complicate straightforward empirical analyses. Unbiased abundance data are difficult to gather, even if restricted to a density measure (rather than total abundance) relative to some other site. Methodological artefacts of sampling may distort measuring true abundances of mobile organisms, while in modular organisms (*i.e.*, plants) the link between productivity and individual number may be more diffuse than in organism of more similar, and finite, adult body size. Furthermore, species richness or other diversity measures may also be affected by individual numbers due to undersampling (particularly in species-rich systems)—with more individuals, it is more likely to sample even the rarer species (Preston 1962, Evans *et al.* 2005).

Light trapping of nocturnal insects, in particular Lepidoptera, has proven a highly effective method of inventorying insect biodiversity, sampling large numbers of individuals in identifiable condition with probably only little species-specific bias in abundance data (within families; Muirhead-Thomson 1991, Beck &

Received 5 February 2010; revision accepted 21 May 2010.

¹Corresponding author; e-mail: jan.beck@unibas.ch

© 2010 The Author(s)

Journal compilation © 2010 by The Association for Tropical Biology and Conservation

Linsenmair 2006) although catches are typically biased toward males (*e.g.*, Altermatt *et al.* 2009). More important here, it is long known that weather (in particular temperature) and moonlight affect catch size (*e.g.*, Bowden 1984, Yela & Holyoak 1997, Butler *et al.* 1999), whereas claims of effects of vegetation density (as an obstacle to visibility or flight) have not, to our knowledge, been substantiated by data. Links between individual numbers and species richness as well as unbiased diversity estimates in tropical moths have been reported (Beck & Chey 2008), but because of the above-mentioned sensitivity of light-trapping data to nightly weather and moonlight conditions these results have been difficult to interpret.

Apart from the putative link with diversity, the abundance of organisms is also a highly relevant feature related to their ecological functions and effects—in Lepidoptera, for example, their roles as pollinators (Petanidou *et al.* 2008), herbivores (Coley & Barone 1996) and as prey for birds, bats and invertebrates (van Emden & Rothschild 2004). Various environmental factors, apart from those related to light trapping (*i.e.*, moonlight and temperature, see above), were described or suspected to affect insect abundance in tropical ecosystems. Seasonal fluctuations of abundance have also been reported in tropical habitats (Janzen 1993, Intachat *et al.* 2001), and the succession state of vegetation may be related to available food quality and quantity for herbivores. Furthermore, temperature variation between sites is also likely to cause true abundance variation as it affects growth rates of plants (hence primary productivity; Brown *et al.* 2004, Ding *et al.* 2005).

In this paper, we analyze moth light-trapping data from the tropical Andes (along elevational and succession gradients) with regard to the following questions: (1) Which environmental variables correlate with individual densities (*i.e.*, number of individuals at light)? (2) Are (unbiased) density data related to (unbiased) diversity data (*i.e.*, is there support for the more individuals hypothesis at a local scale)?

We replicated analyses for three speciose groups of nocturnal Lepidoptera (Arctiidae, Geometridae and Pyraloidea) that represent different phylogenetic clades (Kristensen 1998) and differ substantially in their general biology, physiology and diversity patterns in the region (Fiedler *et al.* 2008).

METHODS

STUDY AREA AND FOCAL ORGANISMS.—Field work was conducted in southern Ecuador in the Reserva Biológica San Francisco (RBSF; 3°58' S, 79°05' W) and its surroundings. The area is naturally covered by species-rich montane forest. Its climate is characterized by high levels of precipitation and cloudiness (Beck *et al.* 2008). There is pronounced seasonality with regard to growth, leaf production, flowering and fruiting (Bendix *et al.* 2006, Cueva Ortiz *et al.* 2006). The study region has been identified as a global hotspot of moth biodiversity (Brehm *et al.* 2005) and its moth communities have been studied in some detail (summaries: Fiedler *et al.* 2008, Hilt & Fiedler 2008).

Moths were sampled at 48 sites; 22 were situated in near-natural ridge forest forming an elevational transect (1020–2677 m asl), 17 in succession habitats in close proximity to the forest edge

(distance to forest < 500 m), and 9 sites in ravine forest in small side-valleys of the Rio San Francisco. For detailed site descriptions see Brehm (2002), Hilt (2005) and Günter *et al.* (2008). Geometridae (> 35,000 specimens collected), Arctiidae (> 13,000 specimens) and Pyraloidea (> 10,000 specimens) served as target organisms and were analyzed separately. However, geometrids and pyraloids were not collected and/or identified from all sites, leading to reduced numbers of sample sites for these groups.

FIELD METHODS.—Moths were attracted to weak, battery driven light sources (one 15 W blacklight plus one 15 W superactinic tube) that were placed in a gauze cylinder (1.70 m high, 70 cm diam, operated at ground level). All attracted arctiid, geometrid and pyraloid individuals were sampled and counted. We preferred manual over automatic sampling because of higher effectiveness (Brehm & Axmacher 2006). Mark-release-recapture studies (K. Fiedler, unpubl. data) have shown that the weak light sources used in our study have an attractive range of < 50 m, and often < 10 m (Wirrooks 2005, Beck & Linsenmair 2006). Moth sampling was limited to the first 3 h after dark (1830–2130 h local time in forested habitats, 1845–2145 h in open habitats). We avoided sampling from 5 d before until 3 d after full moon. Each site was sampled, in a random order, two to nine times. Samples were taken in the years 1999–2000 (near-natural forest), 2002–2003 (succession habitats) and 2005 (ravine forest).

During sampling we recorded ambient air temperature at the top of the light trap every 30 min. The mean of all temperature records per night and site served as a measure of local temperature per sampling unit. Canopy cover (as a proxy of vegetation density) was scored as proportion of visible sky from hemispherical photographs. At four sites where no such measures were available, canopy cover was interpolated from nearby sites. To account for effects of moonlight on the number of moths attracted to the light sources, we scored the background moonlight according to the lunar cycle on a relative scale between 0.00 (new moon) and 1.00 (full moon), in steps of $1/14 = 0.00715/d$ in the phase of waxing moon. During waning moon the effective illumination was set as 0.00, because at the latitude of the study area, and 4 d after full moon, the moon rises only later than 2130 h (*i.e.*, after each nightly sampling unit had been terminated). Season was coded as either 'dry' (samples taken between mid-September and very early January), or 'wet' (mid-February to mid-May). Succession was coded as 'near-natural forest understory', 'late succession habitats' (shrub vegetation or secondary forest) and 'early succession habitats' (without woody vegetation; see Hilt & Fiedler 2008 for classification of succession habitats).

DATA ANALYSIS.—Measured temperature may affect both 'true' abundance in the habitat as well as the number of individuals at light (*e.g.*, via temperature-dependent flight activity). We therefore needed to separate temperature means over ecologically relevant time spans from night-to-night weather variability. To achieve this, we used data from 21 Ecuadorian weather stations between 3 and 3058 m asl (mainland only; daily temperatures (mean of four measures) available from <http://www.ncdc.noaa.gov>). For each month

and year in which moth collecting was carried out we calculated an adiabatic regression (*i.e.*, a linear relationship between altitude and temperature). Regressions explained on average 95 percent of temperature variability in these monthly data. We used reduced major axis regressions (Bohonak & van der Linde 2004) to compute slope estimates for these regressions. Regression terms were utilized to estimate mean monthly temperatures for all sampling sites, for the month and year when sampling was carried out (called ‘estimated mean temperature’ in the following), and we tentatively interpret this measure to (potentially) affect abundance, *e.g.*, due to its effects on metabolism of moths and caterpillars, or on plant growth. Using temperature measures from field work (at the exact time of light trapping) we calculated deviations from estimated mean temperatures. We interpret these *temperature residuals* as night-to-night weather fluctuations that could affect moth flight activity, but not true abundance in the habitats.

We used $\log_{10}(\text{abundance}+1)$ transformations to avoid zero values yet reach normally distributed data. Model selection based on Akaike’s information criterion (AIC; Diniz-Filho *et al.* 2008, StatSoft 2008) was used to identify which environmental variables (Table 1) were relevant in explaining abundance variability (no interaction terms allowed). If model selection results were ambiguous with regard to what is the best model (*i.e.*, $\Delta\text{AIC} < 2$), we used a model averaging approach to calculate averages of parameters weighted by the relative likelihood for being the ‘best model’ among the (few) ‘good models’ (those with $\Delta\text{AIC} < 2$). We report both, slope parameters (which were used for further calculations, see below) and partial effect sizes. To allow direct comparison within and between families, we converted all partial *F*-values to a standardized effect size metric, Fisher’s *z*-transform (*z*_{*i*}; Rosenberg *et al.* 2000).

TABLE 1. Parameterized model terms of general linear models of log-transformed individual numbers, derived from model averaging of all ‘good models’ ($\Delta\text{AIC} < 2$). Dependent variables are $\log_{10}(\text{abundance}+1)$ of the respective moth families. Models consist of the sum of these terms (no interactions). Note that for categorical variable (succession, season) one category has the parameter zero by default (not reported). See main text on which variables were included in which of the single models. Presented values were rounded to three digits, but ten digits were used for calculations. Data structure for Pyraloidea did not allow assessing effects of habitat succession.

Variable	Arctiidae	Geometridae	Pyraloidea
Constant	− 5.079	1.849	2.843
Succession (forest)	− 0.190	− 0.084	
Succession (late)	0.238	0.184	
Season (dry)	0.133	0.147	0.064
Elevation (km)	0.907	0.279	− 0.680
Canopy openness	0.018	− 0.009	1.171
Estimated mean temperature (<i>K</i>)	0.302	0.002	− 0.005
Residual temperature (<i>K</i>)	0.067	0.055	0.021
Moon (arcsin-transf)	− 0.471	− 0.286	− 0.209

Using model selection avoids many, although not all, of the problems related to the spatial nonindependence of geographical data (Diniz-Filho *et al.* 2008). We report spatial autocorrelation for model residuals for transparency where this could potentially cause misinterpretations of model results. However, since such effects were small and confined to trivial situations (*i.e.*, re-sampling of identical sites; see ‘Results’), we decided against the further use of spatially explicit regression techniques (Bini *et al.* 2009). This is because we were exclusively concerned with regression coefficients and parameter estimates here, but not with significance assessments of individual effects which can be more strongly affected by autocorrelation. Whenever we were concerned with significance testing, spatial correlation techniques were used.

CORRECTING ABUNDANCE FOR LIGHT-TRAPPING ARTEFACTS.—We used model parameters of those variables tentatively associated with light-trapping yield to retrieve a (relative) estimate of the number of individuals (Ind_{corr}) that would have been collected under equal condition (*e.g.*, if temperature during collection would have been at the monthly mean, and there would have been no moonlight): $\log_{10}(\text{Ind}_{\text{corr}}+1) = \log_{10}(\text{Ind}_{\text{measured}}+1) - (\text{moonlight effect} + \text{residual temperature effect})$.

Additionally, to correcting for partial effects of moonlight and temperature residuals (*corr1*), we also carried out an alternative correction that included effects of canopy openness (assuming that this is related to horizontal vegetation density; *corr2*). This reflects uncertainty about whether canopy openness affects abundance because of habitat conditions (*e.g.*, higher productivity of fresh leaves in re-growing vegetation, hence affecting ‘true’ abundance), or because habitat openness may increase the effective light-trapping radius (representing a light-trapping artefact). We used raw abundance as well as both versions of corrected values for correlations with site diversity. Ignoring model constants does not pose any problem as we are only interested in a relative correction between sample sites.

AN UNBIASED MEASURE OF DIVERSITY.—Positive relationships between the number of individuals and the number of species in assemblages are trivial when not all species present in the habitat have been collected (*cf.* Preston 1962), and undersampling is an expected data feature in tropical entomology (Coddington *et al.* 2009). What is needed, therefore, is a metric of diversity that is unbiased by undersampling. We carried out analyses for a range of metrics that were proposed as such, *i.e.*, (1) Fisher’s α , (2) the exponent of bias-corrected Shannon entropy (e^{Hbc}), (3) rarefied species richness at the maximum possible number of individuals for each taxon per site (*i.e.*, 54 for Arctiidae, 265 for Geometridae, 77 for Pyraloidea) and (4) the Chao1-estimate of ‘true’ species richness (Southwood & Henderson 2000, Chao & Shen 2003, Beck & Schwanghart 2010; software BiodivToolbox [Matlab], EcoSim). This variety seemed necessary to assure that results were not due to the properties of a chosen metric. In particular, there is room for argument as to whether metrics that explicitly refer to the species-abundance distribution of samples (*e.g.*, Fisher’s α) introduce circularity into

analyses. We do not think so, but data corroborated that results were largely independent of the metric used.

To test for correlations between abundance and diversity, we regressed individuals per trap-night (*i.e.*, average individuals per night at a site) against the aforementioned range of measures of local moth species diversity (per site, *e.g.*, for data pooled over all sampling nights, thus avoiding too imprecise diversity measures resulting from very small sample size). We used spatial correlation (adjusted degrees of freedom, Dutilleul's method implemented in software by Rangel *et al.* 2006) to account for spatial nonindependence of data when making significance assessments. We repeated this procedure for 'raw' (*i.e.*, measured) number of individuals as well as corrected estimates (Ind_{corr} , see above). With the same procedure of spatial correlations we assessed relationships between moth abundance (corr1) or diversity and estimated mean temperature per site.

RESULTS

ARCTIIDAE.—The two models with lowest AIC contained all variables except canopy openness (best model) or all variables (second best model; $\Delta\text{AIC} = 1.83$). All other models were clearly worse ($\Delta\text{AIC} > 7.8$). For further calculations we used the averaged model ($R_{\text{adj}}^2 \approx 0.45$). Residuals were close to normality, and we investigated spatial autocorrelation effects in residuals. There was a significant positive effect ($P < 0.01$, based on 500 randomizations) only for the smallest lag-distance class (0–50 m; Moran's $I = 0.346$) which essentially indicates that nightly replicates at identical sites were not spatially independent (all other $I < 0.1$, $P = \text{ns}$).

Model parameters (Tables 1 and 2) indicate mostly expected effects, *e.g.*, both temperature measures as well as canopy openness are positively related to moth abundance, whereas moonlight is negatively affecting the number of individuals at the trap. More moths were captured during the dry season, and late succession forest had more individuals than both primary forest and early succession vegetation. Interestingly, there is a positive relationship between elevation and the number of individuals (when temperature and habitat effects are factored out). This may be biologically meaningful (*i.e.*, indicating another relevant environmental parameter that is related to elevation), but the highly collinear nature of

estimated mean temperature and elevation may also lead to modeling artefacts (Graham 2003). Model effects and general results were, however, largely unaffected when elevation was not included in the model (data not shown).

All abundance–diversity relationships were positive and highly significant, when using raw or both versions of corrected numbers of individuals, irrespective of the diversity measure being used (Table 3; Fig. 1).

GEOMETRIDAE.—Three models with low AIC contained all variables except canopy openness ($\Delta\text{AIC} = 1.90$), estimated mean temperature ($\Delta\text{AIC} = 1.95$), or both (best model). All other models were considerably weaker ($\Delta\text{AIC} > 2.6$). For further calculations we used the averaged model ($R_{\text{adj}}^2 \approx 0.45$). Residuals were close to normality, those of the best model were free of spatial autocorrelation at all lag distances (all $|I| < 0.1$, $P > 0.08$; 500 randomizations).

Direction of effects are similar to those in Arctiidae, but the weak effect of canopy openness points toward more, rather than less moths under closed canopies. Notably, however, while temperature residuals were important in all groups, the effects of estimated mean temperature was very weak in geometrids (and pyraloids; see below and Table 2), while it was strong in arctiids.

Abundance–diversity regressions were only significant if corrected abundance figures were used (Table 3; Fig. 1). Regressions with diversity based on rarefied species richness were positive but not significant ($P < 0.10$). Otherwise, abundance–diversity relationships were highly concordant across diversity measures.

PYRALOIDEA.—Low variability (due to reduced sample size) did not allow incorporating 'succession' in the model selection routine for Pyraloidea. Model selection among remaining variables identified three good models—a model with all variables except estimated mean temperature (best model), all variables except both temperature metrics ($\Delta\text{AIC} = 0.27$) and the full model ($\Delta\text{AIC} = 1.85$). For further calculations we used the averaged model ($R_{\text{adj}}^2 \approx 0.55$). Residuals were close to normality; however, there was weak ($I = 0.13$) yet significant ($P = 0.02$, 500 randomizations) spatial autocorrelation in residuals at a lag distance up to 100 m. Unusual features in the pyraloid data were a weak effect of estimated mean temperature (present only in the model with third-lowest AIC), a strong positive effect of canopy openness, a negative partial effect of elevation, and a generally higher variability in parameter values among the three 'good models' (data not shown).

Abundance–diversity regressions were positive and significant except if rarefied species richness data were used ($P < 0.10$; Table 3). Abundance data were not normally distributed (Fig. 1), but residuals from regression analyses fulfilled normality assumptions. Correcting abundance for canopy openness (which had a large effect on pyraloid data, but not on geometrids or arctiids) lead to significant effects, but this is most likely due to the fact that habitat succession could not be included in the multivariate model, so that canopy openness accounted for habitat effects. Therefore, we do not think that for pyraloids this correction is valid as accounting for light-trapping artefacts only.

TABLE 2. Environmental effects in general linear models of log-transformed individuals numbers ($|z_r|$, based on partial F-values), derived from model averaging of all 'good models' ($\Delta\text{AIC} < 2$; see Table 1 for details and parameters).

Variable	Arctiidae	Geometridae	Pyraloidea
Succession	1.64	1.69	
Season	2.15	2.56	1.64
Elevation	2.14	1.74	2.71
Canopy openness	0.22	0.15	2.95
Estimated mean temperature	2.51	0.11	0.16
Residual temperature	1.86	1.82	0.99
Moon	2.69	2.37	1.92

TABLE 3. Abundance–diversity relationships from spatial correlations, using adjusted degrees of freedom, df_{adj} (ordinary least square [OLS] regressions [not shown] indicated effects of equal or greater magnitude). For each taxon, regressions with raw abundance (raw), corrected abundance regarding moonlight and temperature residuals (corr1) and corrected abundance regarding moonlight, temperature residuals and canopy openness (corr2) are shown. Analyses were carried out on per site basis, i.e., averaging abundances of nightly catches from the same sites in comparison with total diversity measured at each site. Putatively unbiased diversity metrics were used (FA, Fisher's α ; raref., rarefied species richness; e^{Hb} , exponent of bias-corrected Shannon entropy; Chao1, estimate of true species richness; see "Methods"). We also calculated regressions for observed species richness, which were all significant at $P < 0.005$ (however, they may be due to undersampling effects). Significant effects are printed in bold.

	Raw abundance				Corr1—abundance				Corr2—abundance			
	FA	Raref.	e^{Hb}	Chao1	FA	Raref.	e^{Hb}	Chao1	FA	Raref.	e^{Hb}	Chao1
Arctiidae ($N = 48$)												
r	0.603	0.417	0.574	0.615	0.617	0.483	0.621	0.633	0.617	0.483	0.620	0.628
$F_{adj.}$	22.51	8.74	19.61	24.93	21.77	11.17	21.78	25.62	22.09	11.29	22.12	25.25
$df_{adj.}$	39.47	41.51	39.96	40.95	35.47	36.65	34.76	38.42	35.98	37.15	35.40	38.76
$P_{adj.}$	< 0.001	0.005	< 0.001	< 0.001	< 0.001	0.002	< 0.001	< 0.001	< 0.001	0.002	< 0.001	< 0.001
Geometridae ($N = 37$)												
r	0.259	0.154	0.251	0.354	0.407	0.272	0.367	0.471	0.408	0.270	0.364	0.475
$F_{adj.}$	2.54	0.83	2.37	4.53	7.25	3.07	5.90	8.11	7.29	3.03	5.83	8.27
$df_{adj.}$	35.42	34.38	35.27	31.61	36.42	38.35	37.97	28.46	36.49	38.52	38.11	28.40
$P_{adj.}$	0.120	0.367	0.133	0.041	0.011	0.088	0.020	0.008	0.010	0.090	0.021	0.008
Pyraloidea ($N = 22$)												
r	0.596	0.449	0.583	0.582	0.626	0.467	0.625	0.602	0.811	0.683	0.823	0.769
$F_{adj.}$	6.31	3.34	6.07	5.77	7.19	3.60	7.32	6.24	18.29	9.61	20.60	13.54
$df_{adj.}$	11.43	13.21	11.80	11.25	11.14	12.91	11.45	10.95	9.50	10.97	9.79	9.33
$P_{adj.}$	0.028	0.090	0.03	0.035	0.021	0.080	0.020	0.030	0.002	0.010	0.001	0.005

TEMPERATURE, ABUNDANCE AND SPECIES DIVERSITY.—We tested for univariate relationships between sites' mean expected temperature (which was highly correlated to elevation) with both abundance (corr1 *sensu* Table 3) and diversity. Results differed between families (Table 4), with no temperature-links of abundance or diversity in Geometridae, yet strong positive effects in most correlations involving Arctiidae and Pyraloidea.

DISCUSSION

ENVIRONMENTAL EFFECTS ON ABUNDANCE DATA.—Various environmental variables were clearly related to the number of specimens found at light traps (Tables 1 and 2). Some of these effects were quite consistent across all three moth clades, *i.e.*, residual local temperature and moonlight (corroborating collectors' experience and published quantitative data on light-trapping artefacts), but also season and forest succession (the latter was missing for pyraloid models). Other variables were less consistent in their effects, such as estimated mean temperature (discussed below) and elevation, which may be an erroneous effect due to variable collinearity. Canopy openness, as a proxy for vegetation density, did not have strong effects on moth abundance (in contrast to earlier suggestions, see Wirooms 2005), apart from a (probably) spurious effect in pyraloids ('taking over' effects of succession in the multivariate model).

Effects of monthly (estimated) mean temperature in multivariate models differed strongly between moth groups—they were

strong in Arctiidae, but weaker in the other taxa, particularly in geometrids. However, nightly flight activities reacted similarly to residual temperature between taxa (Table 2). Many Geometridae are known to share a peculiar flight physiology, as they can fly at thorax temperatures just marginally above ambient temperatures (Utrio 1995, Rydell & Lancaster 2000). Geometrids also do not have to engage in energetically costly shivering behavior before take-off, in contrast to many other moths (Heinrich 1993). Hence, possibly the ability, or cost, of flight are causal to the variation in observed temperature effects—not as individual behavior but by giving some clades an advantage to occupy certain habitats through pre-adaptation for flight in the cold. Similar effects in this context of climatic niche conservatism have been suggested from various taxa and systems (Wiens & Graham 2005, Beck & Chey 2008 for tropical moths).

There was a clear activity peak in the drier period of the year in our Andean study area. This was strongest in Geometridae (Tables 1 and 2) and weaker in Arctiidae and particularly Pyraloidea. Many Geometridae are bound to feed on young foliage or inflorescences of trees and shrubs (Bodner *et al.* in press). In our study area, many trees produce leaf-flushes or flowers in the period from August to December (Bendix *et al.* 2006). Hostplant data of pyraloids (from Costa Rica) also indicate that larvae of many species depend on such seasonal resources (Janzen & Hallwachs 2009). In contrast, many Arctiidae larvae feed on resources that show less variation in seasonal availability, including lichens, grasses or herbs (Janzen &

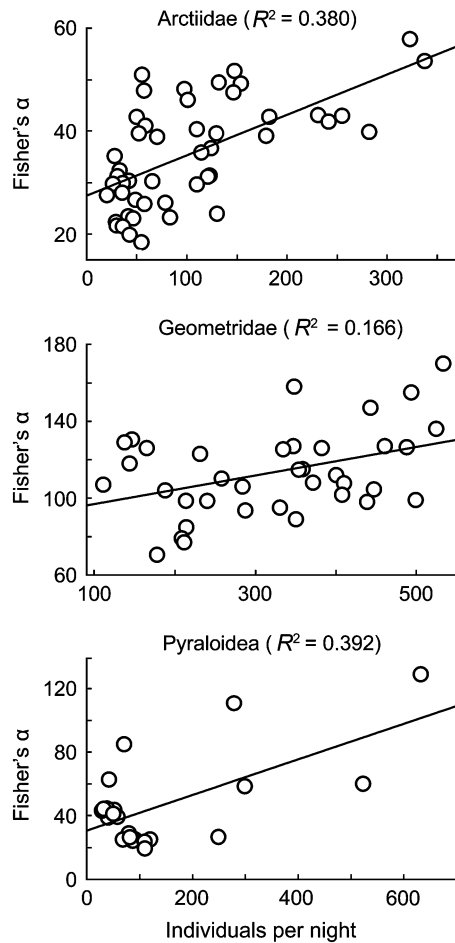


FIGURE 1. Plots of moth abundance at a site (average number of individuals per night, corrected for moonlight and temperature residuals; Corr1 *sensu* Table 3) and diversity of the site (Fisher's α is shown exemplarily). See Table 3 for significance assessments and data for other diversity metrics.

Hallwachs 2009, Wagner 2009; F. Bodner & K. Fiedler, unpubl. data)—hence, the strong seasonality effect on numbers of individuals was less expected from arctiid larval resource affiliations.

One might have expected that moth density generally increases with regeneration from very disturbed open habitats to near-natural forest. However, in arctiids as well as geometrids, the highest moth densities by far were recorded in late succession habitats close to near-natural forest. In Neotropical forests there is a distinct and rich Lepidoptera canopy fauna which we did not cover by our sampling regime (*e.g.*, arctiids in Costa Rica lowland rain forest; Brehm 2007). Hence, the entire forest arctiid community is likely to be more numerous. The high arctiid densities in late succession habitats can largely be attributed to a few species that are extremely common there (especially lichen moths of the genera *Agylla* and *Macroptila*). Similarly, a few Geometridae such as certain *Eois* and *Isochromodes* species benefit from the habitat conditions prevailing at such sites.

Our empirical analyses and interpretations depend on the assumption that flight activity, after correcting for the most evident

TABLE 4. Univariate spatial correlations between sites' mean expected temperature (average across sampling nights) and the abundance (corr1), as well as diversity (see Table 3 for acronyms) of the three moth taxa (significant correlations printed bold).

	r	F_{adj}	df_{adj}	P
Arctiidae ($N = 48$)				
Abundance	0.459	11.5	42.9	0.002
Fisher's α	0.429	8.2	36.2	0.007
Rarefaction	0.508	12.1	34.7	0.001
e^{Hbc}	0.491	11.1	34.9	0.002
Chao1	0.135	0.7	36.9	0.414
Geometridae ($N = 37$)				
Abundance	-0.069	0.2	34.3	> 0.50
Fisher's α	0.115	0.4	31.5	> 0.50
Rarefaction	-0.129	0.7	41.8	> 0.40
e^{Hbc}	-0.128	0.7	39.4	> 0.40
Chao1	0.240	1.8	29.7	0.188
Pyraloidea ($N = 22$)				
Abundance	0.636	7.9	11.7	0.016
Fisher's α	0.856	26.8	9.8	< 0.001
Rarefaction	0.777	15.4	10.1	0.003
e^{Hbc}	0.776	15.5	10.2	0.003
Chao1	0.902	42.5	9.7	< 0.001

light-trapping artefacts, is a sufficient proxy for true abundance (*i.e.*, that there are no systematic differences in the proportion of individuals that would be on the wing during sampling). It is reasonable to assume that nocturnal, winged moths will fly at some time, even if they will prefer flying during the warmer nights of their adult life (and such nightly weather variation has been accounted for separately). There is no indication that tropical montane forest moths in the Andes would generally reduce nightly flight activity (and therefore forbid any inference on true abundance from light trapping; however, we concede that there is little natural history knowledge on behavioral strategies of moths in the region). Rather, taxa in cooler habitats would probably concentrate flight activity during early evening (the warmest part of the nights, when sampling was carried out). Indeed, flight activity of moths in the area peaked between 1900 and 2000 h and decreased afterwards, particularly at high elevations (Brehm 2002, Süssenbach 2003). In warmer tropical lowland habitats on the contrary, moths may spread their temporal flight niches across the night (Beck & Linsenmair 2006). This would lead to the opposite effect of what has been observed (positive temperature-abundance link, Table 1), indicating that such an artefact must be of rather minor magnitude.

DO INDIVIDUAL NUMBERS DETERMINE DIVERSITY?—We found significant correlations of individual density and species diversity, supporting the 'more individuals hypothesis' (Clarke & Gaston 2006). It is particularly noteworthy that this result was clearly found in three rather distinct phylogenetic lineages (Table 3) that differ, among many ecological properties, in the biodiversity patterns

found in the study region (Fiedler *et al.* 2008). This lends plausibility to all those ideas on species richness that assume mechanisms operating through population dynamics and their effect on extinction rate (whatever environmental factor may be limiting total individual numbers; Currie *et al.* 2004, Evans *et al.* 2005), although it is not sufficient proof for any such theories.

Temperature, which has been used in many studies as a vague proxy for ‘energy’ (but see Clarke & Gaston 2006) has also been proposed as a determinant of diversity *via* an alternative chain of causalities involving metabolic rates and the speed of evolution and speciation (Rohde 1992, Brown *et al.* 2004, Hawkins *et al.* 2007, Stegen *et al.* 2009). Our data indicated both temperature–abundance relationships as well as temperature–diversity relationships (Table 4), but effects were inconsistent across taxa as to whether temperature was more closely related to diversity or to abundance. The competing theories (productivity vs. temperature) differ in their predictions of which correlation should be stronger. These inconsistencies point out that underlying mechanisms could be heavily modulated by taxon-specific, idiosyncratic ecological patterns (*e.g.*, by flight physiology in geometrids, where no univariate ‘mean temperature’ – effects were observed). Random error in data (due to sampling and estimation) may also have introduced unwanted variability that could have obscured relevant patterns.

Future and more rigorous testing of the more individuals hypothesis would benefit from an explicit formulation of the expected shape of links between (total) abundance in a habitat, its manifestation as density in local samples, and regional and local species richness (*cf.* Preston 1962; note that most diversity metrics used should scale approximately linearly with [true] species richness). Expectations of a functional abundance–diversity theory will be dependent on the actual size of ‘minimum viable populations’, which may not only differ between species, but which is simply unknown for most organisms. Also, the size of the habitat (*cf.* Storch *et al.* 2005 for species–area–energy relationships, Beck & Kitching 2009 for altitudinal area effects) and the mobility of taxa may be relevant aspects (apart from local density) to get abundance estimates suitable to address a causal link hypothesis. In our data (*e.g.*, Fig. 1) scatter was too high and the scale of variability too low to draw conclusions on the detailed shape of the relationship.

Our results may be encouraging to propose larger-scale light-trapping programs of Lepidoptera to address these issues. Most studies on these topics used data on vertebrates (in particular, birds), whereas some invertebrate studies also documented similar patterns (Kaspari *et al.* 2000, Mittelbach *et al.* 2001, Kumschick *et al.* 2010). Providing such information on a broad taxonomic base is important to not only avoid an obvious phylogeny (and hence life history) bias, but also to be able to recognize possible differences between types of field and data collection methods, each of which may have their respective strengths and weaknesses.

THE ALTITUDINAL PATTERN OF ABUNDANCE AND ITS FUNCTIONAL SIGNIFICANCE.—Abundance and biomass of herbivorous insects are expected to decrease with altitude, particularly at elevations above 2000 m (McCoy 1990). Our data generally support this assessment for pyraloids (Fig. 2), but the distribution of corrected abundance is

very even across altitudes in arctiids and slightly unimodal in geometrids. Arctiidae were expected to show an elevational decline in numbers because of their sensitivity of flight for temperature, although some habitat specialists (notably lichen moths: Fiedler *et al.* 2008) may reach substantial densities in upper montane forest. For surprisingly many Geometridae species (*e.g.*, the very diverse genera *Eupithecia* and *Psaliodes*) and at least for some habitat specialists among the Pyraloidea (*e.g.*, Scopariinae) the extremely humid and cool upper montane forest provides ideal habitat allowing these moths to reach high abundances there.

Our findings have implications on possible ecosystem functions of moths in Andean montane forest. The generally high moth abundance observed in upper montane forest (Fig. 2) does not support the idea that cool and perhumid climatic conditions would *per se* translate into constraints in terms of pollinator or prey availability at high elevations in the tropics. The herbivory pressure exerted by lepidopterans on the vegetation should, as a whole, also not be relaxed in upper montane forest in our study area as compared with lower elevations. Rather, it is tempting to speculate that upper montane tropical forest moths enjoy a kind of ‘enemy-free space’, because at least two major groups of predators (ants preying on caterpillars; bats hunting moths) are very rare in these habitats (Patterson *et al.* 1998, Brühl *et al.* 1999).

High-altitude pyraloid samples contained large numbers of Scopariinae (Fiedler *et al.* 2008), whose larvae usually feed on mosses. These moths are known to become more prevalent at high altitudes in the tropics (Nuss 1999). Numbers of pyraloids in light-trap samples from the upper montane forest (where mosses abound: Gradstein *et al.* 2007) may be related to this unusual feeding habit for herbivorous insects.

Taxon-specific differences in the patterns and effects reported can only be understood by studying in more depth the variation in relevant functional traits, such as thermal and feeding ecology of adults, host-plant affiliations of caterpillars or susceptibility to

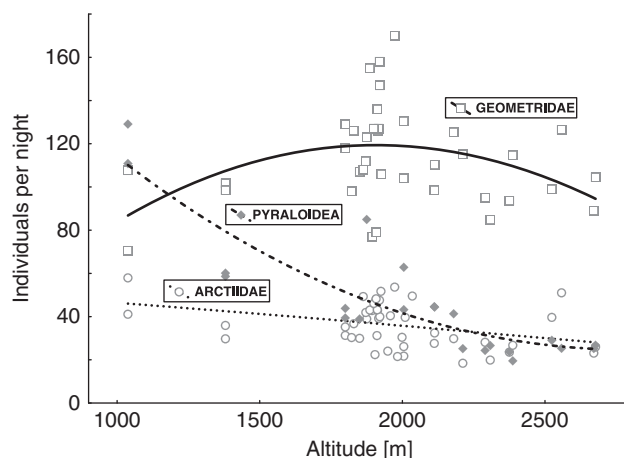


FIGURE 2. Altitudinal patterns of the average number of moth individuals per night (corrected for moonlight and residual temperature effects [corr1]). Negative exponential weighted least square regressions were fitted to display major patterns.

predation. A better knowledge of the organisms and their specific requirements emerges as a key prerequisite for understanding patterns and processes at the community or ecosystem level. Fusing such natural history knowledge with a priori hypotheses of effects and testing them in a comparative, quantitative framework appears as a way forward from the current standard of describing environment–diversity relationships without being specific on hypothetical causalities (McGill *et al.* 2006, Gotelli 2008).

ACKNOWLEDGMENTS

N. Hilt, D. Süßenbach, M. Zimmermann and a number of student helpers carried out large portions of sampling, processing and identifying moths. C. H. Schulze and an anonymous reviewer kindly provided comments on an earlier manuscript version, L. Ballesteros wrote the Spanish abstract. The foundation Nature & Culture International gave access to the study sites and logistic support. The Ministerio del Medio Ambiente (Quito and Loja) issued research permits. Supported by the Deutsche Forschungsgemeinschaft (grants # Fi 547/6 to 547/10, FOR 402, FOR 816).

LITERATURE CITED

- ALTERMATT, F., A. BAUMEYER, AND D. EBERT. 2009. Experimental evidence for male biased flight-to-light behavior in two moth species. *Ent. Exp. Appl.* 130: 259–265.
- BECK, E., J. BENDIX, I. KOTTKE, F. MAKESCHIN, AND R. MOSANDL. 2008. Gradients in a tropical mountain ecosystem of Ecuador. Springer, Berlin, Germany.
- BECK, J., AND V. K. CHEY. 2008. Explaining the elevational diversity pattern of geometrid moths from Borneo: A test of five hypotheses. *J. Biogeogr.* 35: 1452–1464.
- BECK, J., AND I. J. KITCHING. 2009. Drivers of moth species richness on tropical altitudinal gradients: A cross-regional comparison. *Global Ecol. Biogeogr.* 18: 361–371.
- BECK, J., AND K. E. LINSÉNMAIR. 2006. Feasibility of light-trapping in community research of moths: Attraction radius of light, completeness of samples, nightly flight times and seasonality of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae). *J. Res. Lepid.* 39: 18–36.
- BECK, J., AND W. SCHWANGHART. 2010. Comparing measures of species diversity from incomplete inventories: An update. *Methods Ecol. Evol.* 1: 38–44.
- BENDIX, J., J. HOMEIER, E. CUEVA, M. C. ORTIZ, P. EMCK, S. W. BRECKLE, M. RICHTER, AND E. BECK. 2006. Seasonality of weather and tree phenology in a tropical evergreen mountain rain forest. *Int. J. Biometeorol.* 50: 370–384.
- BINI, L. M., J. A. F. DINIZ-FILHO, T. F. L. V. B. RANGEL, F. S. ALBUQUERQUE, M. B. ARAÚJO, A. BASELGA, J. BECK, M. I. BELLOCQ, K. BÖHNING-GAESE, P. A. V. BORGES, F. J. CABRERO-SAÑUDO, I. CASTRO-PARGA, V. K. CHEY, P. DE MARCO, D. FERRER-CASTÁN, R. FIELD, J. FILLOY, E. FLEISHMAN, J. F. GÓMEZ, M. GREVE, N. GUIL, J. HORTAL, J. B. IVERSON, J. T. KERR, D. KISSLING, I. J. KITCHING, J. L. LEÓN-CORTÉS, C. LEVI, J. M. LOBO, T. OBERDORFF, M. Á. OLALLA-TÁRRAGA, J. G. PAUSAS, H. QIAN, C. RAHBEK, M. Á. RODRÍGUEZ, A. RUGGIERO, P. SACKMAN, N. J. SANDERS, P. WILLIAMS, AND B. A. HAWKINS. 2009. Coefficient shifts in geographical ecology: An empirical evaluation of spatial and non-spatial regression. *Ecography* 32: 193–204.
- BODNER, F., G. BREHM, J. HOMEIER, P. STRUTZENBERGER, AND K. FIEDLER. In press. Caterpillars and host plant records for 59 species of Geometridae (Lepidoptera) from a montane rainforest in southern Ecuador. *J. Insect Sci.* Available at <http://insectscience.org/10.67>.
- BOHONAK, A. J., AND K. VAN DER LINDE. 2004. RMA: Software for Reduced Major Axis regression for Java. Available at <http://www.bio.sdsu.edu/pub/andy/rma.html> (accessed January 2010).
- BOWDEN, J. 1984. Latitudinal and seasonal changes of nocturnal illumination with a hypothesis about their effect on catches of insects in light-traps. *Bull. Entomol. Res.* 74: 279–298.
- BREHM, G. 2002. Diversity of geometrid moths in a montane rainforest in Ecuador. PhD dissertation, University of Bayreuth, Bayreuth, Germany. Available at <http://opus.lib.uni-bayreuth.de/volltexte/2003/20>.
- BREHM, G. 2007. Contrasting patterns of vertical stratification in two moth families in a Costa Rican lowland rain forest. *Basic Appl. Ecol.* 8: 44–54.
- BREHM, G., AND J. C. AXMACHER. 2006. A comparison of manual and automatic moth sampling methods (Lepidoptera: Arctiidae, Geometridae) in a rain forest in Costa Rica. *Environ. Ent.* 35: 757–764.
- BREHM, G., L. M. PTKIN, N. HILT, AND K. FIEDLER. 2005. Montane Andean rain forests are a global diversity hotspot of geometrid moths. *J. Biogeogr.* 32: 1621–1627.
- BROWN, J. H., J. F. GILLOOLY, A. P. ALLEN, V. M. SAVAGE, AND G. B. WEST. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.
- BRÜHL, C. A., M. MOHAMED, AND K. E. LINSÉNMAIR. 1999. Altitudinal distribution of leaf-litter ants along a transect in a primary forest on Mount Kinabalu, Sabah, Malaysia. *J. Trop. Ecol.* 15: 265–267.
- BUTLER, L., V. KONDO, E. M. BARROWS, AND E. C. TOWNSEND. 1999. Effects of weather conditions and trap types on sampling for richness and abundance in forest Macrolepidoptera. *Environ. Ent.* 28: 795–811.
- CHAO, A., AND T.-J. SHEN. 2003. Nonparametric estimation of Shannon's index of diversity when there are unseen species in sample. *Environ. Ecol. Stat.* 10: 429–443.
- CLARKE, A., AND K. J. GASTON. 2006. Climate, energy and diversity. *Proc. R. Soc. Lond. B* 273: 2257–2266.
- CODDINGTON, J. A., I. AGNARSSON, J. A. MILLER, M. KUNTNER, AND G. HORMIGA. 2009. Undersampling bias: The null hypothesis for singleton species in tropical arthropod surveys. *J. Anim. Ecol.* 78: 573–584.
- COLEY, P. D., AND J. A. BARONE. 1996. Herbivory and plant defences in tropical forests. *Annu. Rev. Ecol. Evol. Syst.* 27: 305–335.
- CUEVA ORTIZ, E., J. HOMEIER, S.-W. BRECKLE, J. BENDIX, P. EMCK, M. RICHTER, AND E. BECK. 2006. Seasonality in an evergreen tropical mountain rainforest in southern Ecuador. *Ecotropica* 12: 69–85.
- CURRIE, D. J., G. G. MITTELBACH, H. V. CORNELL, R. FIELD, J.-F. GUÉGAN, B. A. HAWKINS, D. M. KAUFMAN, J. T. KERR, T. OBERDORFF, E. O'BRIEN, AND J. R. G. TURNER. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett.* 7: 1121–1134.
- DING, T.-S., H.-W. YUAN, S. GENG, Y.-S. LIN, AND P.-F. LEE. 2005. Energy flux, body size and density in relation to bird species richness along an elevational gradient in Taiwan. *Global Ecol. Biogeogr.* 14: 299–306.
- DINIZ-FILHO, J. A. F., T. F. L. V. B. RANGEL, AND L. M. BINI. 2008. Model selection and information theory in geographical ecology. *Global Ecol. Biogeogr.* 17: 479–488.
- EVANS, K. L., N. A. JAMES, AND K. J. GASTON. 2006. Abundance, species richness and energy availability in the north American avifauna. *Global Ecol. Biogeogr.* 15: 372–385.
- EVANS, K. L., S. E. NEWSON, D. STORCH, J. J. D. GREENWOOD, AND K. J. GASTON. 2008. Spatial scale, abundance and the species-energy relationship in British birds. *J. Anim. Ecol.* 77: 395–405.
- EVANS, K. L., P. H. WARREN, AND K. J. GASTON. 2005. Species–energy relationships at the macroecological scale: A review of the mechanisms. *Biol. Rev.* 80: 1–25.
- FAUTH, J. E., J. BERNARDO, M. CAMARA, W. J. RESETARITS, J. VAN BUSKIRK, AND S. A. MCCOLLUM. 1996. Simplifying the jargon of community ecology. *Am. Nat.* 147: 282–286.

- FIEDLER, K., G. BREHM, N. HILT, D. SÜSSENBACH, AND C. L. HÄUSER. 2008. Variation of diversity patterns across moth families along a tropical elevational gradient. *Ecol. Stud.* 198: 167–179.
- FIELD, R., B. A. HAWKINS, H. V. CORNELL, D. J. CURRIE, J. A. F. DINIZ-FILHO, J.-F. GUÉGAN, D. M. KAUFMAN, J. T. KERR, G. G. MITTELBACH, T. OBERDORFF, E. M. O'BRIEN, AND J. R. G. TURNER. 2008. Spatial species-richness gradients across scales: A meta-analysis. *J. Biogeogr.* 36: 132–147.
- GOTELLI, N. J. 2008. Hypothesis testing, curve fitting, and data mining in macroecology. *IBS Newsl.* 6: 3–7, Available at <http://biogeography.org/pdfs/2008Vol6Iss4.pdf> (accessed September 2009).
- GRADSTEIN, S. R., C. BOCK, N. MANDL, AND N. M. NÖSKE. 2007. Bryophyta: Hepaticae. Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, S. Ecuador). *Ecotrop. Monogr.* 4: 69–87.
- GRAHAM, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84: 2809–2815.
- GÜNTER, S., O. CABRERA, M. WEBER, B. STIMM, M. ZIMMERMANN, K. FIEDLER, J. KNUTH, J. BOY, W. WILCKE, S. IOST, F. MAKESCHIN, F. WERNER, S. R. GRADSTEIN, AND R. MOSANDL. 2008. Natural forest management in Neotropical mountain rain forests—an ecological experiment. *Ecol. Stud.* 198: 363–375.
- HAWKINS, B. A., F. S. ALBUQUERQUE, M. B. ARAÚJO, J. BECK, L. M. BINI, F. J. CABRERO-SANUDO, I. CASTRO-PARGA, J. A. F. DINIZ-FILHO, D. FERRER-CASTÁN, R. FIELD, J. F. GÓMEZ, J. HORTAL, J. T. KERR, I. J. KITCHING, J. L. LEÓN-CORTÉS, J. M. LOBO, D. MONTOYA, J. C. MORENO, M. Á. OLALLA-TÁRRAGA, J. G. PAUSAS, H. QIAN, C. RAHBEK, M. Á. RODRÍGUEZ, N. J. SANDERS, AND P. WILLIAMS. 2007. A global evolution of metabolic theory as an explanation of terrestrial species richness gradients. *Ecology* 88: 1877–1888.
- HAWKINS, B. A., R. FIELD, H. V. CORNELL, D. J. CURRIE, J. F. GUÉGAN, D. M. KAUFMAN, J. T. KERR, G. G. MITTELBACH, T. OBERDORFF, E. M. O'BRIEN, E. E. PORTER, AND J. R. G. TURNER. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84: 3105–3117.
- HEINRICH, B. 1993. The hot-blooded insects. Strategies and mechanisms of thermoregulation. Harvard University Press, Boston, Massachusetts.
- HILT, N. 2005. Diversity and species composition of two different moth families (Lepidoptera: Arctiidae vs. Geometridae) along a successional gradient in the Ecuadorian Andes. PhD dissertation. University of Bayreuth, Bayreuth, Germany. Available at <http://opus.ub.uni-bayreuth.de/volltexte/2006/201> (accessed September 2009).
- HILT, N., AND K. FIEDLER. 2008. Succession stages of faunal regeneration—a case study on megadiverse moths. *Ecol. Stud.* 198: 343–349.
- INTACHAT, J., J. D. HOLLOWAY, AND H. STAINES. 2001. Effects of climate and phenology on the abundance and diversity of geometroid moths within a Malaysian natural tropical rainforest environment. *J. Trop. Ecol.* 17: 411–429.
- JANZEN, D., AND W. HALLWACHS. 2009. Philosophy, navigation and use of a dynamic database (ACG Caterpillars SRNP) for an inventory of the macrocaterpillar fauna, and its foodplants and parasitoids, of the Area de Conservación Guanacaste (ACG), north-western Costa Rica. Available at <http://janzen.sas.upenn.edu> (accessed March 2009).
- JANZEN, D. H. 1993. Caterpillar seasonality in a Costa Rican dry forest. *In* N. E. Stamp and T. M. Casey (Eds.). *Caterpillars—ecological and evolutionary constraints on foraging*, pp. 448–477. Chapman and Hall, London, UK.
- KASPARI, M., S. O'DONNELL, AND J. R. KERCHER. 2000. Energy, density, and constraints to species richness: Ant assemblages along a productivity gradient. *Am. Nat.* 155: 280–293.
- KRISTENSEN, N. P. (ed.). 1998. *Lepidoptera. Butterflies and moths. Vol. 1: Evolution, systematics, and biogeography. Handbook of Zoology, Vol. IV, part 35.* W. de Gruyter, Berlin, Germany.
- KUMSCHICK, S., M. H. SCHMIDT-ENTLING, T. HICKLER, X. ESPADALER, AND W. NENTWIG. 2010. Determinants of local ant (Hymenoptera: Formicidae) species richness and activity density across Europe. *Ecol. Entomol.* 34: 748–754.
- MCCOY, E. D. 1990. The distribution of insects along elevational gradients. *Oikos* 58: 313–322.
- MCGILL, B. J., B. J. ENQUIST, E. WEIHER, AND M. WESTOBY. 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21: 178–185.
- MITTELBACH, G. G., D. W. SCHEMSKE, H. V. CORNELL, A. P. ALLEN, J. M. BROWN, M. B. BUSH, S. P. HARRISON, A. H. HURLBERT, N. KNOWLTON, H. A. LESSIOS, C. M. MCCAIN, A. R. MCCUNE, L. A. MCDADE, M. A. MCPEEK, T. J. NEAR, T. D. PRICE, R. E. RICKLEFS, K. ROY, D. F. SAX, D. SCHLUTER, J. M. SOBEL, AND M. TURELLI. 2007. Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecol. Lett.* 10: 315–331.
- MITTELBACH, G. G., C. F. STEINER, S. M. SCHEINER, K. L. GROSS, H. L. REYNOLDS, R. B. WAIDE, M. R. WILLIG, S. I. DODSON, AND L. GOUGH. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.
- MUIRHEAD-THOMSON, R. C. 1991. *Trap responses of flying insects.* Academic Press, London, UK.
- NUSS, M. 1999. Revision der Gattungen der Scopariinae (Lepidoptera, Pyraloidea, Crambidae). *Nova Suppl. Entomol.* 13: 1–151.
- PATTERSON, B. D., D. STOTZ, S. SOLARI, J. FITZPATRICK, AND V. PACHECO. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *J. Biogeogr.* 25: 593–607.
- PETANIDOU, T., A. S. KALLIMANIS, J. TZANOPOULOS, S. P. SGARDELIS, AND J. D. PANTIS. 2008. Long-term observation of a pollination network: Fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecol. Lett.* 11: 564–575.
- PRESTON, F. W. 1962. The canonical distribution of commonness and rarity: Part I. *Ecology* 43: 185–215.
- RANGEL, T. F. L. V. B., J. A. F. DINIZ-FILHO, AND L. M. BINI. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecol. Biogeogr.* 15: 321–327.
- ROHDE, K. 1992. Latitudinal gradients in species diversity: The search for the primary cause. *Oikos* 65: 514–527.
- ROSENBERG, M. S., D. C. ADAMS, AND J. GUREVITCH. 2000. *MetaWin, Version 2. Statistical software for meta-analysis.* Sinauer Associates Inc., Sunderland, Massachusetts.
- ROSENZWEIG, M. L. 1995. *Species diversity in space and time.* Cambridge University Press, Cambridge, UK.
- RYDELL, J., AND W. C. LANCASTER. 2000. Flight and thermoregulation in moths were shaped by predation from bats. *Oikos* 88: 13–18.
- SOUTHWOOD, T. R. E., AND P. A. HENDERSON. 2000. *Ecological methods* (3rd Edition). Blackwell Science Ltd., Oxford, UK.
- STATSOFT. 2008. *Statistica for Windows, Version 8 (software and user guide).* StatSoft Inc., Tulsa, Oklahoma. Available at <http://www.statsoft.com> (accessed September 2009).
- STEGEN, J. C., B. J. ENQUIST, AND R. FERRIERE. 2009. Advancing the metabolic theory of biodiversity. *Ecol. Lett.* 12: 1001–1015.
- STORCH, D., K. L. EVANS, AND K. J. GASTON. 2005. The species-area-energy relationship. *Ecol. Lett.* 8: 487–492.
- SÜSSENBACH, D. 2003. *Diversität von Nachtfaltergemeinschaften entlang eines Höhengradienten in Südecuador (Lepidoptera: Pyraloidea, Arctiidae).* PhD dissertation, University of Bayreuth, Bayreuth, Germany. Available at <http://opus.ub.uni-bayreuth.de/volltexte/2003/33/> (accessed September 2009).
- UTRIO, P. 1995. On flight temperatures and foraging strategies of nocturnal moths. *Baptria* 20: 113–121.
- VAN EMDEN, H., AND M. ROTHSCCHILD (Eds.). 2004. *Insect and bird interactions.* Intercept, Andover, UK.
- WAGNER, D. L. 2009. The immature stages: Structure, function, behavior and ecology. *In* W. E. Conner (Ed.). *Tiger moths and woolly bears—*

- behavior, ecology and evolution of the Arctiidae, pp. 31–53. Oxford University Press, Oxford, UK.
- WIENS, J. J., AND C. H. GRAHAM. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* 36: 519–539.
- WILLIG, M. R., D. M. KAUFMAN, AND R. D. STEVENS. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* 34: 273–309.
- WIROOKS, L. 2005. Die ökologische Aussagekraft des Lichtfangs—eine Studie zur Habitatbindung und kleinräumigen Verteilung von Nachtfaltern und ihren Raupen. Verlag Wolf & Kreuels, Havixbeck-Hohenholte, Germany.
- YELA, J. L., AND M. HOLYOAK. 1997. Effects of moonlight and meteorological factors on light and bait trap catches of noctuid moths (Lepidoptera: Noctuidae). *Environ. Ent.* 26: 1283–1290.