Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest

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Abstract. Turnover in species composition of the extremely species-rich family Geometridae (Lepidoptera) was investigated along an elevational gradient ranging from 1040 m to 2677 m above sea level. Moths were sampled using weak light traps (30 W) in three field periods in 1999 and 2000 in an Andean montane rainforest in the province of Zamora-Chinchipe in southern Ecuador. A total of 13 938 specimens representing 1010 species were analysed. Similarities of ensembles of all geometrid moths and of the subfamilies Ennominae and Larentiinae were calculated using the NESS index (with m_{max}). Ordinations performed using nonmetric multidimensional scaling (NMDS) and correspondence analysis depicted a gradual change of the ensembles along the altitudinal gradient. Extracted ordination scores significantly correlate with altitude ($-0.97 \leq r \leq -0.95$, $P < 0.001$) and with ambient air temperature ($0.93 \leq r \leq 0.97$, $P < 0.001$). Temperature is therefore assumed to be the most important abiotic determinant responsible for the species turnover among the moths. Matrix correlation tests were performed in order to compare faunal matrices with matrices derived from available environmental factors. Both tree diversity and vegetation structure significantly correlate with faunal data, but tree diversity explains considerably more of the data variability (range: Mantel $r = 0.81$–0.83, $P < 0.001$) than vegetation structure (range: Mantel $r = 0.35$, $P < 0.005$ to $r = 0.43$, $P < 0.001$). Tree diversity also changes gradually and scores of the first NMDS dimension are highly significantly correlated with altitude ($r = 0.98$, $P < 0.001$). A common underlying factor such as ambient temperature might also be responsible for such vegetation changes. Additionally, simulated model data was developed that assumed a constant turnover of moth species and equal elevational ranges of all species involved. Despite the simplicity of the models, they fit empirical data very well (Mantel $r > 0.80$ and $P < 0.001$ in all models).

Key words. Beta diversity, Ecuador, elevational gradient, Geometridae, Lepidoptera, rainforest, temperature, tree diversity, vegetation structure.

INTRODUCTION

Communities of organisms change along environmental gradients such as from dry to moist, cold to warm, and nutrient-poor to nutrient-rich. Whittaker (1972) named this phenomenon 'beta diversity' and defined it as the 'extent of differentiation of communities along habitat gradients'. One of the central aims of community ecology is to uncover the mechanisms responsible for such changes in community structure and diversity. Tropical communities are the most diverse but probably also among the least understood on Earth. For example, Gentry (1988) described patterns of diversity in plant communities and floristic composition along environmental and geographical gradients and concluded that plant diversity in the Neotropics correlates strongly with annual precipitation. Scale is an important issue in the analysis of diversity

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(Lawton, 1999; Whittaker *et al.*, 2001). Large-scale diversity patterns have been successfully analysed for a range of organisms in macro-ecology (Lawton, 1999; Gaston, 2000). While there is an increasing understanding of the mechanisms responsible for tropical phytodiversity at smaller scales (Hubbell, 2001), this cannot be said to be true for the majority of animal groups, including herbivorous insects. Few studies have analysed beta diversity and the possible underlying mechanisms responsible for changes in diversity in this guild across small spatial scales in tropical ecosystems (e.g. Schulze, 2000; Basset, 2001; Hill *et al.*, 2001).

Here, we attempt to identify determinants for the beta diversity of a very species-rich group of tropical herbivorous insects. We chose geometrid moths (Lepidoptera) as a model group and carried out investigations in a montane rainforest in southern Ecuador. Geometrid moths are well known in taxonomic terms (Scoble, 1999) and have served as model organisms for environmental changes in a range of studies, mainly in South-east Asia (e.g. Intachat *et al.*, 1997; Beck *et al.*, 2002). Geometrid moths in the study area are extremely diverse with local values of Fisher's alpha between 69 and 131 (Brehm *et al.*, 2003). Moreover, diversity is very high along the entire gradient investigated. The faunal composition changes gradually along the elevational gradient with an increasing proportion of the subfamily Larentiinae with rising altitude (Brehm & Fiedler, 2003).

This paper has the following aims:

- Description of the beta diversity of Geometridae and two of its major subfamilies (Ennominae and Larentiinae) along an extended altitudinal gradient;
- establishing correlations between faunal data and biotic as well as abiotic environmental factors;
- development of simulation models which reflect empirical patterns of geometrid beta diversity and assist in the interpretation of ordinations.

METHODS

Study area and sampling

The study area in southern Ecuador (Reserva Biológica San Francisco, 3°58′S, 79°5′W, and adjacent fractions of the Podocarpus National Park) is situated in the province of Zamora-Chinchipe within the East Cordillera of the Andes. It is covered with undisturbed or slightly disturbed montane rainforest (Madsen & Øllgaard, 1994). The vegetation of the study area was described by Bussmann (2001) and Paulsch (2002). Moths were sampled with weak light traps (2×15 W tubes) at 22 sites situated at 11 elevational levels between 1040 m and 2677 m above sea level. A detailed description of the sampling methods and sites was provided by Brehm (2002). We collected the specimens manually during three field periods (April to May 1999, October 1999 to January 2000, and October to December 2000) for three hours after dusk per sampling night. From each site between two and four catches were analysed. Specimens were first sorted to morphospecies and later determined at the Zoologische Staatssammlung, Munich and the Natural History Museum, London. More than 50% of a total of 1010 species and 60% of a total of 13 938 specimens could be determined to species level while most of the remainder could be assigned to genus level.

Ordination and similarity indices

Data on moth and tree ensembles of the sites was ordinated by nonmetric multidimensional scaling (NMDS) using the Statistica 5.5 software package (StatSoft, 1999). The NESS index (Grassle & Smith, 1976) with the sample size parameter m set to its maximum appears to be an appropriate abundance-based index for incompletely sampled, species-rich communities (e.g. Brehm, 2002) and was therefore chosen. It was calculated with a program provided by Meßner (1996). Results of the CNESS index introduced by Trueblood *et al.* (1994) lead to very similar ordinations and are not shown here. Further similarity indices such as the Morisita index or the binary Sørensen index were tested on the same data by Brehm (2002). He also applied correspondence analysis (CA) as another ordination method as well as single-linkage clustering. These analyses led to very similar results to those presented in this paper and are therefore not shown here. In addition to this Q-mode analysis, CA was applied to show an ordination of all geometrid species. Here, species are descriptors and sites are objects

(terminology: Legendre & Legendre, 1998). In CA as well as in Principal Component Analysis (PCA) the ordination of the objects (sites) might be regarded as the Q-mode, while the ordination of the descriptors (species) corresponds to the R-mode. Both ordinations are shown here because Holloway (1998) recommends analysing faunal data in both modes, R and Q.

Available environmental data

At all 22 sites in the study area, altitude and geographical coordinates were measured with a Garmin GPS III (exact geographical positions provided by Brehm (2002)). Air temperature was measured during the catches (three to 11 nights, every 30 min during 18.30 and 21.30 local time) 1.6 m above ground with a Casio alti-thermo twin sensor. Although the type and quantity of these measurements did not fit regular meteorological standards, they appeared to be sufficient for the purpose of this study, and matched well with data from three weather stations in the study area (P. Emck, pers. comm.). Temperature measured at all seven times per night linearly decreased with altitude. Braun (2002) provided very similar data on temperature changes along the altitudinal gradient from the study area. Temperature declined at an average of 1.26 K ($\pm$ 0.36) between 19.00 and 21.00 (Brehm, 2002). Average temperatures of measures taken at 20.00 were subsequently used as standard.

In order to obtain an objective measure of canopy closure, hemispherical photographs were taken with a Nikon SLR 8 mm lens and a Nikon camera. From these, the 'visible sky' value was calculated with the HemiView program (Delta-T Devices, 1999). Five photographs were taken at each site: one in central position (i.e. exactly at the light trap's position) and four at a distance of 15 m each from the central point to the four points of the compass. Values of visible sky and their average for each site were calculated, and the latter used for further analysis. Due to technical problems, data are available for only 19 of the 22 sites (missing at three of the uppermost sites).

Data on vegetation structure as well as on tree diversity are restricted to the upper part of the study area (above 1800 m). For each of the sites where moths were sampled, we chose sites where vegetation structure had been documented in close proximity (Paulsch, 2002; further details in Brehm (2002)). 16 site pairs situated in the ridge forest were used for analyses. A perfect match between the sites could not always be achieved because light-trapping sites require some few square metres of fairly even ground and moderately open vegetation. The mean altitudinal distance between sites was 30 $\pm$ 29 m. However, in all cases forest structure was apparently similar between light-trapping sites and the plots where vegetation structure had been studied. Paulsch (2002) originally recorded a total of 144 structural parameters from a low and a high forest stratum (his strata 1 and 3) in plots of 400 m² in size. An intermediate stratum 2 occurred at only a few sites and was consequently discarded in the present analyses. Structural parameters included rank scale data of canopy shape, stem form, branch patterns, leaf size, leaf form, type of bark, occurrence of bryophytes, lichens, lianas, palms, bamboo, and ferns, as well as of epiphytic bromeliads and orchids. Variables with zero values at all 16 sites were ignored for subsequent analyses (stratum 1: 119 variables left, stratum 3: 123 variables left). Since an immediate effect on moth ensembles cannot be expected from all aspects of vegetation structure, a subset which included exclusively leaf parameters was selected and analysed separately. A high proportion of geometrid moths are known to be folivorous (Scoble, 1999; Holloway *et al.*, 2001; Brehm, 2002) and a consequent response of the moths to changes of leaf structures was therefore anticipated. Leaf parameters originally comprised 54 variables, of which 41 (stratum 1) and 47 (stratum 3) remained after discarding variables with only zero values. These parameters included leaf shape, consistency, colour, phenology, size (length, width), angle, presence of spines, hairiness as well as woodiness of the plants.

We recorded all tree individuals $\geq$ 5 cm diameter at breast height (d.b.h) in seven plots of 400 m² size in close proximity to light trapping sites within an elevational range between 1850 and 2450 m. The mean altitudinal distance between vegetation plots and light-trapping sites was 26 $\pm$ 26 m. Within these seven plots, we found a total of 531 tree individuals (excluding 15 tree fern individuals) belonging to 108 species. Seventy-three percent of the species as well as 73% of the individuals were assigned to species

level. The remainder was assigned to genus level and contains at least four new tree species (J. Homeier, unpubl. data).

Correlations with environmental data

Two principal methods were applied in order to relate moth faunal data to environmental parameters. Dimensional scores of moth samples extracted from two-dimensional NMDS ordinations were directly correlated with altitude, temperature and with the structural vegetation parameter 'visible sky'. Results derived from one-dimensional NMDS led to nearly identical results and are therefore not shown. For more complex (i.e. higher dimensional) data sets such as vegetation structure and tree diversity, Mantel tests for associations between matrices were performed with the program PC-Ord (McCune & Mefford, 1999). Matrices based on Euclidean distances were derived from data on vegetation structure, whereas a similarity matrix was derived from tree species data, based on the NESS index with $m_{max} = 19$. The matrices were subsequently tested for their association with faunal similarity matrices. In order to compare the performance of methods on the data sets, such matrices were also derived from ('one-dimensional') data on altitude and temperature. These procedures were all aimed at identifying those environmental factors which can be used to best explain patterns of faunal change.

Simulated model data

Simple simulation models of species distributions along an elevational gradient were developed (two examples in Fig. 5). Unlike empirical data sets, models contain no noise, and are intended to simplify complex real patterns. By creating models in this study, we wanted to learn more about the essential properties of the empirical moth data sets with regard to their beta diversity.

The simulation models are characterized by the following features and assumptions:

1. They are based on presence-absence information for simplicity.
2. All model species have the same span of altitudinal distribution, and each species occurs continuously within its complete range.
3. Sites which are situated at the same altitude are more similar to each other than to sites at a different altitude with regard to their species composition. In the models, this is reflected by a turnover of one species from one site to the next at the same level, and a turnover of two species to a site at the next higher (or lower) level.
4. Altitudinal change is modelled at elevational steps of 100 m. This reflects the empirical data set, where light-trapping sites were roughly spaced at steps of *c*. 100 m.
5. Due to difficulties of access in the lower part of the study area, the altitudinal steps between real sites were much larger there than in the upper part. In order to mimic this in the model, a step between the three lowest levels in the model data is reflected in a species turnover which is four times higher than in a 'normal' step.

A number of models were eventually developed, in which the (equal) altitudinal range of the species was varied from 300 m to 1600 m (maximum range of the gradient). This simultaneously changed the number of species involved in the models. Figure 5 shows graphically two such models with all species' altitudinal ranges being set to 700 m and 900 m, respectively. From the simulated data sets, matrices of similarity between sites were calculated with the Sørensen index which is the most appropriate for presence-absence data (Wolda, 1981). These matrices were subsequently compared with matrices derived from the empirical data set by using Mantel tests. The overall best-fitting model (species distributional range: 700 m) was chosen to perform ordinations. In this way it was possible to compare NMDS ordinations derived from simulated data with those derived from empirical data.

RESULTS

Ordinations and correlations with environmental data

Figure 1 shows NMDS ordinations for Geometridae (Q-mode), the two large subfamilies Ennominae and Larentiinae, and model data. All ordinations of moth samples very clearly reflect the relative altitudinal positions of sites from level 1 (1040 m) to level 11 (2677 m). They have
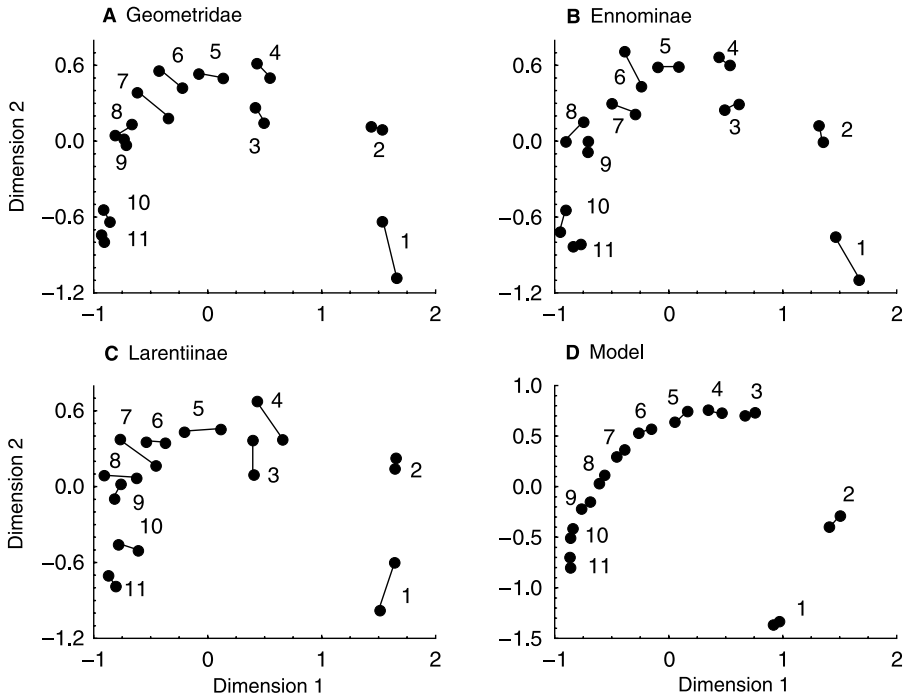
Fig. I Nonmetric multidimensional scaling plots (two dimensions) of samples of **A** Geometridae (stress 0.04), **B** Ennominae (stress 0.07), **C** Larentiinae (stress 0.07) and **D** model data (stress 0.04). Ordinations are based on matrices calculated with the NESS similarity index with m_{max} (A, B, C) or the Sørensen index (D). The NESS values of the empircial data are provided in Appendix 1. Numbers from 1 to 11 correspond to rising altitudinal levels from low (1040 m) to high elevations (2677 m). The low stress values indicate a high goodness-of-fit of the ordinations.

a U-shaped arrangement of sites in common. The ordination based on simplified model data looks very similar to those based on empirical data. The original similarity matrices based on the NESS (m_{max}) index of the empirical data are provided in Appendix 1. Figure 2 shows a correspondence analysis of all 1010 geometrid species ('R-mode'). The species are arranged in the same U-shape as in Fig. 1, although many species are scattered within the arch.

Table 1 shows correlations between environmental data (altitude, temperature and visible sky) and scores extracted from the first dimension of NMDS. Across the three taxa (Geometridae, Ennominae, Larentiinae) there are extremely high correlations between altitude as well as temperature and scores of the first dimension of the ordinations ($-0.97 \leq r \leq -0.95$ and $0.93 \leq r \leq 0.96$, respectively, all $P < 0.001$). As an example, Fig. 3

shows graphically the correlation of temperature and extracted scores of the first NMDS dimension of Geometridae. In contrast, visible sky is not significantly correlated with the first ordination axis ($-0.39 \leq r \leq -0.34$).

The significant correlations of altitude and temperature with moth data are confirmed by Mantel tests for associations between entire matrices (Table 2). Correlations are weaker but still highly significant (all $r > 0.85$, $P < 0.001$). Matrices of vegetation structure are also significantly correlated with faunal matrices, but correlations are substantially weaker ($0.35 \leq r \leq 0.45$, $P < 0.005$). There are only small differences between the two forest strata as well as between the full data set and the selected leaf parameters, but correlations tend to be weaker in stratum 1 of the full data set. In contrast to matrices derived from vegetation structure, those derived
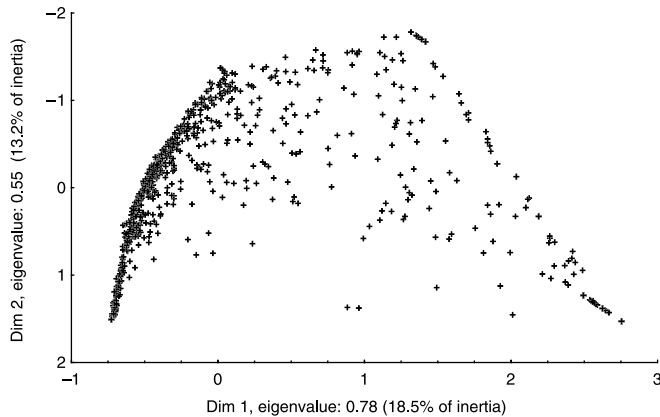
Fig. 2 Correspondence analysis (CA) of all 1010 species of geometrid moths of the study area. Note that many species have almost the same scores and therefore overlap.

Table 1 Pearson correlation coefficients between 1) altitude, 2) mean temperature during moth sampling at 20.00. 3) the parameter 'visible sky' (canopy closure) and the extracted scores of the first dimension of NMDS ordinations in three taxa (Geometridae, Ennominae and Larentiinae). Ordinations are based on the NESS index with its sample size parameter m set to its maximum

	Altitude		Temperature		Visible sky	
	r	P	r	P	r	P
Geometridae						
NESS $m_{max} = 192$	−0.97	***	0.96	***	−0.39	ns
Ennominae						
NESS $m_{max} = 62$	−0.97	***	0.96	***	−0.38	ns
Larentiinae						
NESS $m_{max} = 32$	−0.95	***	0.93	***	−0.34	ns

ns: not significant, *** $P < 0.001$. All nominally significant results remain so after sequential Bonferroni correction (Hochberg, 1988).

from tree species similarity (based on NESS m_{max}) are highly significantly correlated with faunal matrices ($r \geq 0.81$, $P < 0.001$). Hence, beta diversity of trees is strongly associated with the beta diversity of moths. The NMDS ordination of tree species samples in Fig. 4 very clearly depicts a gradual change in tree species composition along the first dimension. Very similar to the results for the fauna, extracted scores of the first dimension highly significantly correlate with altitude ($r = 0.98$, $P < 0.001$).

The average pairwise similarity values for all sites ($n = 231$ pairwise comparisons) are presented in Table 3, together with average values of 11 site pairs that are situated at the same level of altitude (< 35 m of altitudinal difference). NESS m_{max} yields the highest similarity values, whereas values of the NESS indices $m = 50$ and $m = 1$, and values of Sørensen's index were considerably smaller. All three NESS indices show high similarities for sites that are situated at the same altitudinal level (average values c. 0.9), i.e. they indicate that the ensembles from which the samples had been drawn are nearly identical. In contrast, Sørensen values are noticeably lower (mean 0.56) due to chance sampling effects.

Table 2 Mantel correlations of similarity matrices of three moth taxa (Geometridae, Ennominae and Larentiinae) vs. distance matrices of different environmental factors. Faunal similarity matrices are based on data from 22 sites from a montane rainforest in southern Ecuador (1040–2677 m). These matrices were derived from the NESS index (m_{max}). Not all environmental data sets were available from all the 22 sites where moths were sampled: full sets include altitude and temperature. Data on tree diversity were available from seven sites between 1850 and 2450 m. The tree diversity matrix was derived from the NESS index (m_{max}). Data on vegetation structure was available from 16 plots in the upper part of the study area (above 1850 m, Euclidean distance matrices) from two forest strata (stratum 1 and stratum 3 according to Paulsch (2002))

	Altitude		Temperature		Tree diversity		Vegetation structure all parameters				Vegetation structure leaf parameters			
							Stratum 1		Stratum 3		Stratum 1		Stratum 3	
Sites distances	22 Euclidean		22 Euclidean		7 NESS m_{max}		16 Euclidean				16 Euclidean			
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Geometridae	0.90	***	0.88	***	0.83	***	0.36	*	0.43	***	0.43	***	0.41	***
Ennominae	0.87	***	0.85	***	0.81	***	0.35	**	0.41	***	0.41	***	0.37	**
Larentiinae	0.88	***	0.85	***	0.82	***	0.37	*	0.40	***	0.45	***	0.42	***

The full set of structural parameters as well as a selected subset of leaf parameters was tested. * $P < 0.01$, ** $P < 0.005$, *** $P < 0.001$; all results are significant after sequential Bonferroni correction (Hochberg, 1988).
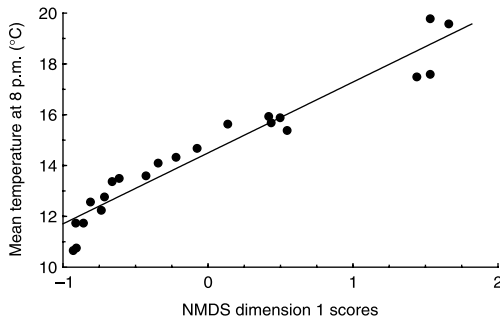
Fig. 3 Correlation of ambient temperature (measured at 20.00), and scores of light-trapping sites according to the first dimension of nonmetric multidimensional scaling (Geometridae, NESS index with m_{max} = 192). $r = 0.96$, $P < 0.001$.
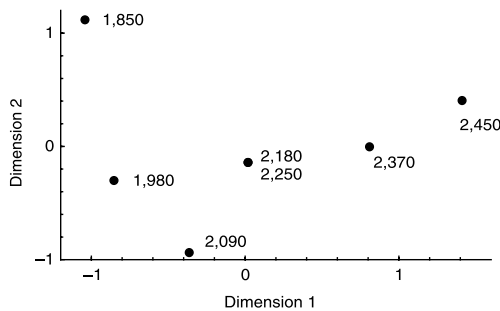
Fig. 4 Nonmetric multidimensional scaling plot (two dimensions) of samples of tree species at seven sites in the study area (stress 0.00). The elevation above sea level of each site is indicated in metres. Scores of the first dimension significantly correlate with altitude ($r = 0.98$, $P < 0.001$).

Table 3 Average values of the Sørensen index, and three NESS indices ($m = 1$, $m = 50$ and m_{max} = 192) of ensembles of Geometridae for all 231 comparisons between the 22 sites, and for 11 pairs of sites situated at the same elevational level. Printed in bold are indices with the highest values

	All 231 pairs ± SD	11 pairs ± SD
Sørensen	0.31 ± 0.15	0.56 ± 0.06
NESS $m = 1$	0.28 ± 0.27	0.88 ± 0.08
NESS $m = 50$	0.37 ± 0.26	0.89 ± 0.08
NESS $m = 193$	**0.44** ± 0.25	**0.92** ± 0.07

Models

The two models shown in Fig. 5 correspond well with the empirical data set of Geometridae, based on the NESS index of similarity (m_{max} = 192). The correlations between the matrices are very strong ($r = 0.95$ and $r = 0.94$ for models A and B, respectively, $P < 0.001$). They have the same magnitude as the correlations of faunal data have with temperature and altitude (correlation of ordination scores: $r = -0.96$ and -0.97, respectively; matrix correlation $r = 0.88$ and $r = 0.90$, respectively, all $P < 0.001$).

Other models (not shown graphically) also fit well with matrices derived from empirical data. Figure 6 shows the matrix correlation coefficients of model data which differ in the (equal) altitudinal distribution of species in a range from 300 m to 1600 m. For all three taxa considered, the best matches are obtained at elevational ranges of individual species that span between 600 and 800 m. The match rapidly decreases as altitudinal ranges become smaller whereas models with larger ranges still fit empirical data quite well.

DISCUSSION

Interpretation of the ordinations

NMDS ordinations clearly indicate the dominant altitudinal gradient and reveal arch-like forms in two-dimensional plots. The interpretation of such arches is a controversial issue. Hill & Gauch (1980) described arches as mathematical artefacts with no real corresponding structure in the data. Wartenberg *et al.* (1987) stated that, on the contrary, arches are an accurate representation of the data and the curvature is a result of the partially overlapping distribution of each species along a one-dimensional environmental gradient. In this study, the ordination of simulated data argues in favour of Wartenberg's interpretation. Arches result from changes along one single gradient (coenocline) in the simulated data. These coenocline patterns are very similar to those obtained from the empirical data. It can therefore be concluded that the empirical data also reflects a coenocline. Accordingly, the scores of only the first dimension can be extracted for the purpose of correlation with environmental factors, whereas this is not appropriate
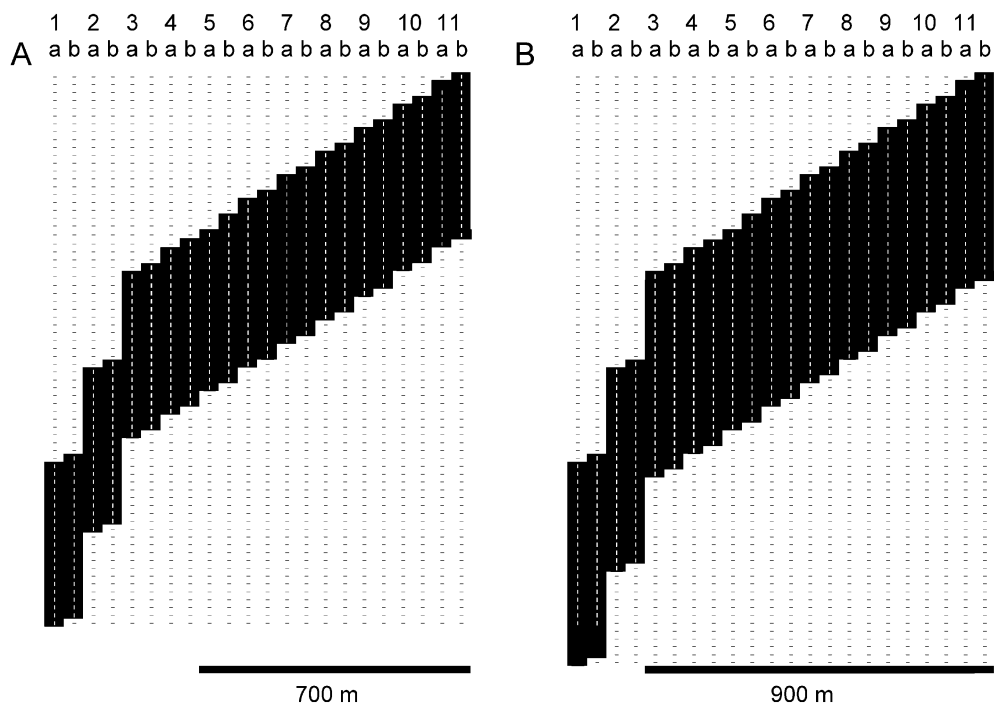
Fig. 5 Two models of simulated species distributions along an altitudinal gradient of 1600 m. First row: altitudinal levels 1–11, separated by 400 m (1–3), and 100 m (3–11). Second row (ab): replicate sites at the same altitudinal level. Remaining rows: species distributions with species present (black rectangles), and species absent (–). Sørensen similarity matrices were calculated and tested from the models for associations with a matrix derived from empirical data (Geometridae, NESS m_{max} = 192). Model A (70 species, range of each species: 700 m): Mantel r = 0.95, P < 0.001. Model B (75 species, range of each species: 900 m): Mantel r = 0.94, P < 0.001.

with scores of the second dimension or higher dimensions.

The NMDS ordinations show a gradual change of geometrid ensembles along the elevational gradient. Very similar patterns appear in the two large subfamilies Ennominae and Larentiinae. Some sites show small divergences from a perfectly smooth change as shown in the model. The larger gaps between elevational levels 1, 2 and 3 are due to the larger elevational separation of these sites and correspond well to the model. Sites at level 3 show a deviation particularly along the *y*-axis that could be caused by the close proximity of disturbed area and the role of some 'tourist species' that slightly changed community composition (Brehm, 2002). The gap between site levels (10 + 11) and level 9 again reflects a larger elevational step between the sites (minimum 137 m

between levels 10 and 9 compared to a minimum of 67 m between levels 9 and 8).

However, these results give no hint as to the occurrence of distinct categories of communities, such as 'lower montane forest geometrid ensembles' or 'cloud forest geometrid ensembles'. Rather, a smooth gradual transition occurs and species are successively replaced by others. This is underpinned by the ordination of species in Fig. 2. There is no clumping of species into discrete categories. At least for the Andean gradient investigated, the ordinations cannot confirm the discontinuities between montane and lowland faunal zones found, e.g. by Holloway *et al*. (1990) in the fauna of Sulawesi.

Irrespective of this lack of a distinct zonation, ensembles found at different altitudes have 'typical' properties, such as a certain composition
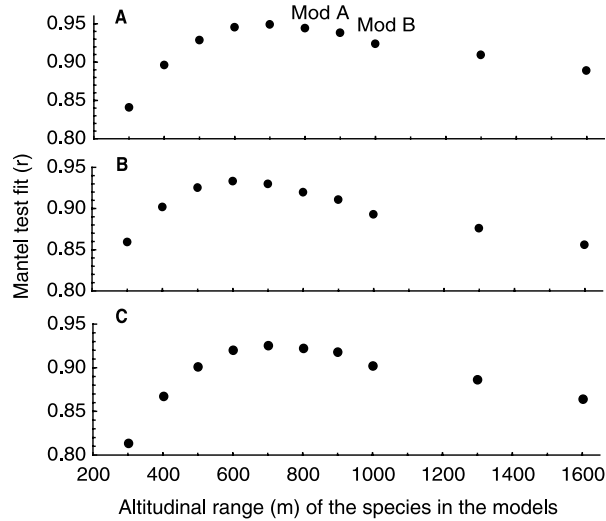
Fig. 6 Mantel test associations of model data matrices with empirical data matrices (**A** Geometridae, **B** Ennominae, **C** Larentiinae). Mod A, Mod B: corresponding to the models presented in Fig. 5. The empirical data matrices are based on the NESS index of similarity (m_{max}: Geometridae: 192, Ennominae: 62, Larentiinae: 32). Model matrices (Sørensen index values) were derived from simulated data of species distributions (see text and Fig. 5). Models differ in the altitudinal range of species (*x*-axis). Irrespective of the considerable differences in the altitudinal range of species in the models, all model data matrices fit the empirical data well (all $r > 0.80$, all $P < 0.001$).

of higher taxa. For example, cloud forest is characterized by a high proportion of larentiine moths, whereas ennomine moths dominate in lower montane forests. However, the ratios of these subfamilies also do not alter abruptly within the gradient but change gradually (Brehm & Fiedler, 2003).

Although data from only seven plots on tree diversity were available for the analysis presented here, a very similar pattern as in the faunal ordinations occurs. This confirms the results of Lieberman *et al*. (1996) who found gradual rather than zonal changes in the vegetation across a large elevational gradient in rainforests in Costa Rica.

Interpretation of model data

The discovery that moth ensembles change gradually rather than abruptly is underpinned by the extremely good fit between simulated data and empirical data. All models assume a monotonic, continuous turnover of species rather than distinct communities which partially overlap. It must be emphasized that the models are not aimed at reflecting all properties of the communities, such as alpha diversity. In fact, they are a gross abstraction with regard to the number of species and their abundance. The two illustrated models (Fig. 4) comprise only 70 and 75 species, respectively, compared with empirical numbers of between 390 and 1010 species per taxon observed (Brehm, 2002). In contrast to the uniform occurrence of species in the models, the species sampled in the field also differ significantly in abundance: at most sites, species-abundance relationships followed log-series distributions well. Insect samples from tropical rainforests usually contain high numbers of rare species (Novotný & Basset, 2000); this is also the case here. We decided not to vary the models further, to include a higher (and more 'realistic') number of species or to allow for variable altitudinal ranges of species (1) in order to sustain the most simplistic assumptions, and (2) because even the coarse models already exhibited an excellent fit with the empirical data set.

The role of environmental factors: methodological constraints

The search for the mechanisms responsible for diversity and its changes in natural ecosystems is methodologically constrained. Arguments often rely on plausibility rather than on rigorous evidence because of the immense number of variables which are beyond control. There are approaches towards the experimental manipulation of relatively simple ecosystems (e.g. grasslands (Tilman, 1999)), but this is impractical in highly diverse systems such as tropical rainforests (Moon *et al.*, 1999). Therefore, precise descriptive analysis along existing gradients is probably the only method of obtaining an understanding of diversity patterns in species-rich real ecosystems. We were searching for correlations by using two different approaches. Generally, the fact that variables are correlated does not necessarily mean that one causes the other. However, correlative studies are the appropriate first step in searching for causal relationships and in the building of hypotheses before field experiments can be carried out (e.g. Sollins, 1998).

Unfortunately, altitudinal gradients comprise a large number of intercorrelated variables that potentially could (or could not) affect organismic diversity. Abiotic factors change, as do the diversity and functional roles of organisms. For example, as elevation decreases, temperature decreases almost linearly (Braun, 2002; Brehm, 2002), precipitation increases (P. Emck pers. comm.), and nitrogen availability and primary productivity decrease (Waide *et al.*, 1998; Schrumpf *et al.*, 2001). The local diversity of many groups of organisms decreases at least from medium altitudes onwards as elevation increases. In the study area (above 1800 m) this is true for trees > 5 cm diameter at chest height (Homeier *et al.*, 2002), lianas (S. Matezki pers. comm.), birds (Rahbeck, 1997), bats (Matt, 2001), bushcrickets (Braun, 2002), and arctiid and pyralid moths (Süßenbach, 2003). Beta diversity in all these groups will show a certain degree of similarity in the way that species are replaced by others as elevation rises. Very strong correlations between groups of organisms might indicate a causal relationship, but they might also hint at a common underlying environmental factor. As a consequence, the underlying mechanisms which drive the beta diversity of a certain group, such as geometrid moths, can possibly never be fully understood in highly complex ecosystems such as tropical rainforests.

Interpretation of environmental factors

Despite these constraints on their interpretation the available data give some clear indications about dominant factors. Altitude, ambient temperature and tree diversity match the observed beta diversity patterns very well. While altitude per se is not meaningful in a biological sense, ambient temperature and tree diversity are. Climatic influences were, e.g. detected as the most important factors for population changes in British butterflies (Roy *et al.*, 2001). The excellent fit of temperature profiles to species turnover argues in favour of different ecophysiological (i.e. thermal) constraints on geometrid species. This hypothesis could be tested with experiments to explore the performance of different species at different temperatures (e.g. in terms of larval growth, survival, pupal weight or flight physiology). Such experiments could also reveal whether the ecophysiological range of species (i.e. their fundamental niches) corresponds well with the patterns found in the field (i.e. their actual niches).

A relationship between the beta diversity of trees and that of geometrid moths appears to be readily interpretable because most geometrid moths are arboreal defoliators (Scoble, 1999). At much lower elevations in Borneo, understorey vegetation diversity emerged as the single most important predictor of geometrid moth diversity (Beck *et al.*, 2002). Only rather few geometrid moth species in our study area such as the ennomine tribe Macariini appear to be host plant specialists. For these, any change in vegetation composition will result in a pronounced turnover of moth species whenever host plants drop out completely. The majority of Neotropical geometrid species, however, is not expected to be specialized but rather polyphagous (Brehm, 2002). Host plant specialization in tropical forests generally appears to be much lower than previously thought (Novotny *et al.*, 2002). It is unlikely that the turnover in potential host plants plays an important role for polyphagous herbivorous species since these can easily switch to alternative hosts. For most tropical herbivores, food supply is likely to be a function of the availability of young foliage (Basset, 1992). Therefore, we assume that a common

underlying gradient regulating both trees and moths (such as ambient temperature) actually plays a greater role than the functional relationship between trees and moths. This hypothesis should be tested with future investigations. Paulsch (2002) found that forest structure differs considerably between stands on ridges (where moth sampling was performed) and in ravines. The same applies for tree diversity and species composition (Homeier *et al.*, 2002). A systematic comparison of sites which are situated at the same altitude but differ with regard to aspect could reveal whether temperature or vegetation characters are the more important environmental factor responsible for the beta diversity of geometrid moths at this small spatial scale.

In contrast to temperature and tree diversity, the available data on vegetation structure fit the beta diversity patterns of geometrid moths worse. Even the reduction of the original data set to 'promising' factors of vegetation structure such as leaf parameters did not substantially improve the strength of correlations. The results presented by Paulsch (2002) suggest that vegetation structure shows a less gradual change along the elevational gradient than trees and moths do. Vegetation structure might also be more heterogeneous at small scales because differences in aspect, steepness, nutrient availability and successional age of sites will have a considerable effect on structural characteristics even if plant species composition remains essentially the same. On the contrary, insect diversity will be less affected because many tropical successional mosaics may represent a relatively permanent and predictable habitat for them (Lepš *et al.*, 2001). Furthermore, most insects are mobile, and vegetation mosaics on *very* small scales cannot be reflected by the insect communities present. The relatively weak correlations between vegetation structure and the beta diversity of geometrid moths indicate that forest structure is not a decisive determinant for these ectophagous herbivorous insects. However, habitat structures have to fulfil a number of criteria in order to be appropriate to geometrids. These include the provision of a suitable microclimate, as well as larval host plants and feeding sources for the adults. Since tropical geometrid moths are known as a group of mainly forest-dwelling insects, they respond sensitively to habitat alterations (e.g. Kitching *et al.*, 2000; Beck *et al.*, 2002).

The suggestion that temperature might be the dominant driving force behind species turnover rates, rather than vegetation factors, is further supported by the remarkably high similarity of beta diversity patterns among different moth taxa. For example, similarity matrices derived from the two subfamilies Ennominae and Larentiinae correlate with $r = 0.95$ ($P < 0.001$). Relationships to environmental data are also almost identical between both groups. However, the subfamilies show contrasting elevational patterns of alpha diversity (Brehm *et al.*, 2003), and also substantially differ with regard to host plant relationships (Brehm, 2002). There is also a high similarity of matrices derived from the geometrid data set and a data set of pyralid moths collected in the same study area, despite the profound differences with regard to the ecology and the contrasting patterns of local diversity of the groups (Süßenbach, 2003).

This study adds information on beta diversity patterns of a very species-rich insect group in tropical rainforests over a large elevational range. It shows that descriptive approaches are a necessary first step towards a better understanding of the underlying factors of tropical diversity. Now that first hypotheses could be generated, based on an extensive data set, further experimental research should test the hypothesis that ambient temperature is the main factor actually responsible for herbivore species turnover along tropical elevational gradients.

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Appendix I Original similarity matrices of **A** Geometridae, **B** Ennominae, and **C** Larentiinae based on the NESS index with m_{max}. m_{max} $_{Geometridae}$ = 192, $m_{max\ Ennominae}$ = 62, $m_{max\ Larentiinae}$ = 32. Numbers 1–11 correspond to elevational levels from low (1a at 1040 m) to high (11b at 2677 m). Elevations of all 22 sites as well as coordinates were provided by Brehm (2002) and Brehm & Fiedler (2003).

A	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	7a	7b	8a	8b	9a	9b	10a	10b	11a
1b	0.87																				
2a	0.35	0.53																			
2b	0.41	0.54	0.96																		
3a	0.25	0.31	0.46	0.48																	
3b	0.23	0.28	0.40	0.39	1.04																
4a	0.20	0.36	0.49	0.46	0.75	0.75															
4b	0.13	0.28	0.46	0.41	0.81	0.75	0.89														
5a	0.15	0.25	0.32	0.33	0.68	0.71	0.76	0.74													
5b	0.14	0.22	0.29	0.28	0.57	0.61	0.70	0.64	0.91												
6a	0.12	0.20	0.24	0.23	0.51	0.61	0.60	0.52	0.76	0.89											
6b	0.10	0.17	0.19	0.20	0.43	0.51	0.47	0.49	0.60	0.80	0.82										
7a	0.13	0.20	0.25	0.22	0.51	0.56	0.50	0.51	0.69	0.77	0.84	0.85									
7b	0.07	0.15	0.19	0.16	0.41	0.44	0.42	0.44	0.59	0.67	0.81	0.77	0.83								
8a	0.12	0.14	0.17	0.14	0.36	0.42	0.38	0.42	0.54	0.58	0.65	0.70	0.83	0.75							
8b	0.08	0.12	0.12	0.11	0.34	0.41	0.31	0.35	0.46	0.49	0.64	0.63	0.76	0.86	0.88						
9a	0.09	0.14	0.16	0.12	0.38	0.37	0.35	0.37	0.47	0.51	0.61	0.64	0.78	0.76	0.87	0.89					
9b	0.08	0.13	0.16	0.12	0.40	0.40	0.32	0.38	0.48	0.54	0.61	0.62	0.79	0.76	0.92	0.96	0.96				
10a	0.06	0.09	0.13	0.09	0.30	0.27	0.24	0.26	0.31	0.32	0.36	0.39	0.51	0.49	0.58	0.63	0.69	0.67			
10b	0.08	0.12	0.15	0.13	0.30	0.27	0.22	0.24	0.30	0.33	0.34	0.34	0.47	0.41	0.53	0.60	0.66	0.65	0.97		
11a	0.07	0.09	0.14	0.10	0.28	0.24	0.20	0.19	0.23	0.27	0.32	0.31	0.41	0.37	0.48	0.58	0.54	0.59	0.87	0.91	
11b	0.06	0.10	0.12	0.11	0.27	0.26	0.20	0.20	0.26	0.29	0.34	0.32	0.43	0.39	0.48	0.58	0.56	0.59	0.88	0.94	0.97
B																					
1b	0.87																				
2a	0.26	0.41																			
2b	0.38	0.52	0.96																		
3a	0.21	0.28	0.40	0.46																	
3b	0.19	0.21	0.32	0.36	1.04																
4a	0.10	0.26	0.48	0.50	0.78	0.67															
4b	0.07	0.17	0.41	0.40	0.80	0.71	0.84														
5a	0.08	0.18	0.29	0.30	0.59	0.60	0.69	0.65													

Appendix 1 *continued.*

A	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	7a	7b	8a	8b	9a	9b	10a	10b	11a
5b	0.08	0.16	0.28	0.27	0.46	0.52	0.64	0.56	0.85												
6a	0.06	0.16	0.24	0.21	0.41	0.49	0.52	0.40	0.73	0.84											
6b	0.06	0.11	0.18	0.16	0.38	0.40	0.48	0.43	0.58	0.78	0.81										
7a	0.06	0.16	0.26	0.23	0.45	0.44	0.48	0.44	0.69	0.78	0.86	0.84									
7b	0.04	0.13	0.19	0.16	0.35	0.40	0.40	0.38	0.58	0.66	0.80	0.69	0.84								
8a	0.07	0.06	0.12	0.10	0.28	0.33	0.31	0.33	0.48	0.53	0.60	0.58	0.77	0.79							
8b	0.03	0.07	0.10	0.10	0.23	0.26	0.22	0.23	0.36	0.34	0.56	0.46	0.61	0.84	0.90						
9a	0.05	0.14	0.19	0.15	0.23	0.23	0.32	0.26	0.39	0.48	0.55	0.50	0.68	0.73	0.84	0.80					
9b	0.04	0.09	0.14	0.13	0.35	0.33	0.29	0.32	0.48	0.51	0.59	0.54	0.75	0.78	0.91	0.93	1.00				
10a	0.02	0.09	0.13	0.10	0.17	0.19	0.16	0.24	0.20	0.27	0.33	0.30	0.43	0.46	0.57	0.60	0.72	0.66			
10b	0.02	0.07	0.10	0.10	0.19	0.19	0.13	0.17	0.20	0.23	0.26	0.25	0.36	0.35	0.45	0.53	0.60	0.59	1.00		
11a	0.03	0.06	0.15	0.14	0.16	0.19	0.16	0.15	0.19	0.27	0.28	0.25	0.38	0.31	0.37	0.52	0.47	0.48	0.79	0.89	
11b	0.02	0.08	0.12	0.10	0.21	0.27	0.18	0.21	0.22	0.22	0.29	0.18	0.34	0.33	0.39	0.53	0.49	0.53	0.86	0.95	0.95
C																					
1b	0.89																				
2a	0.37	0.51																			
2b	0.35	0.45	1.00																		
3a	0.18	0.21	0.36	0.33																	
3b	0.14	0.24	0.27	0.26	1.01																
4a	0.23	0.37	0.46	0.40	0.60	0.61															
4b	0.10	0.25	0.38	0.33	0.71	0.64	0.91														
5a	0.18	0.18	0.22	0.25	0.63	0.59	0.65	0.62													
5b	0.15	0.15	0.18	0.18	0.46	0.43	0.52	0.53	0.87												
6a	0.11	0.11	0.12	0.13	0.52	0.56	0.52	0.46	0.62	0.77											
6b	0.10	0.11	0.12	0.18	0.35	0.41	0.37	0.42	0.52	0.77	0.83										
7a	0.15	0.11	0.12	0.13	0.43	0.45	0.39	0.41	0.53	0.64	0.79	0.90									
7b	0.03	0.06	0.08	0.09	0.38	0.33	0.30	0.36	0.45	0.57	0.75	0.84	0.73								
8a	0.12	0.11	0.10	0.09	0.33	0.32	0.33	0.34	0.48	0.60	0.70	0.80	0.89	0.67							
8b	0.07	0.06	0.03	0.03	0.29	0.32	0.20	0.27	0.35	0.49	0.62	0.70	0.73	0.82	0.74						
9a	0.05	0.05	0.05	0.05	0.39	0.34	0.28	0.32	0.46	0.53	0.65	0.75	0.82	0.77	0.86	0.83					
9b	0.04	0.04	0.05	0.03	0.36	0.29	0.25	0.29	0.37	0.52	0.62	0.68	0.77	0.74	0.89	0.91	0.94				
10a	0.08	0.04	0.06	0.06	0.33	0.24	0.25	0.23	0.37	0.44	0.45	0.46	0.50	0.50	0.56	0.57	0.66	0.69			
10b	0.12	0.09	0.12	0.12	0.37	0.29	0.27	0.24	0.38	0.47	0.45	0.42	0.50	0.46	0.55	0.57	0.67	0.69	0.98		
11a	0.08	0.07	0.09	0.07	0.31	0.23	0.18	0.15	0.21	0.24	0.32	0.33	0.36	0.38	0.45	0.50	0.51	0.59	0.84	0.85	
11b	0.09	0.05	0.07	0.07	0.28	0.19	0.16	0.15	0.23	0.30	0.36	0.41	0.41	0.39	0.47	0.51	0.56	0.61	0.88	0.92	0.93