Beta-diversity of geometrid moths from northern Borneo: effects of habitat, time and space

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Summary

1. Spatial patterns of beta-diversity, an important property of species communities, are less well-studied than those of local species richness, particularly in insects from tropical rainforests.

2. We use geometrid moth samples from northern Borneo to quantify ensemble turnover across distances of > 700 km, consider habitat- and sampling-related impacts on their composition, and evaluate remaining spatial patterns in the data.

3. Geometrid moth ensembles from Borneo are shaped by environmental parameters such as elevation and habitat disturbance, by temporal factors acting at small (mediated by weather) and large scales (i.e. changes over decades), and by methodological differences of sampling (related to the nightly flight times of species).

4. These parameters explain a large portion of the spatial structure of ensemble composition, but residual variation still contains a pattern that is tentatively best explained by geographical distance, particularly at distances < 20 km.

5. Patterns of species turnover indicate no evidence for biotic homogenization due to human-caused degradation of habitats. Beta-diversity plays a crucial part in mediating the regional diversity of geometrids on Borneo.

Key-words: elevation, habitat disturbance, similarity decay, spatial autocorrelation, species turnover.

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Introduction

Beta-diversity, or spatial turnover, is a complex property of species communities (Koleff & Gaston 2002; Ricklefs 2004; Legendre, Borcard & Peres-Neto 2005) that is inherently connected to larger-scale measurements of species richness (i.e. gamma-diversity) through the species–area relationship found for almost all organisms investigated so far (e.g. Rosenzweig 1995; Tjørve 2003; Horner-Devine *et al*. 2004). Although the importance of beta-diversity is recognized and patterns are being investigated in a wide range of taxa and environments (e.g. Nekola & White 1999; Kerr, Southwood & Cilhar 2001; Condit *et al*. 2002; Green *et al*. 2004; MacNally *et al*. 2004; Titeux *et al*. 2004; Krasnov *et al*. 2006; Thompson & Townsend 2006), it is much less

understood than, for example, gradients in species richness or within-habitat (alpha-) diversity. There are only few data from tropical rainforest arthropods despite the importance of these high-diversity systems in research and conservation (e.g. Novotny & Weiblen 2005, references therein). Studies addressing tropical invertebrate beta-diversity typically either restricted themselves to report differences in assemblages as a result of particular habitat differences without addressing the impact of distance *per se* (for tropical Lepidoptera, e.g. Beck *et al*. 2002), or they did not find spatial effects within relatively small spatial scales of investigation (e.g. Hilt, Brehm & Fiedler 2006; but see Cleary *et al*. 2004; Cleary & Genner 2006).

Spatial autocorrelation (Legendre & Legendre 1998) describes the property of most geographical data to be more similar between nearby sites than between sites far distant from each other (see Diniz-Filho, Bini & Hawkins 2003 for analytical implications on diversity studies). The composition of species communities may be ruled by either local habitat conditions, or it might be

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influenced by historical, 'random' differences (Ricklefs 2004). Both mechanisms may lead to spatially autocorrelated assemblages, the former due to autocorrelated habitat parameters, the latter due to dispersal limitations of individuals or species (e.g. Bell 2001; Hubbell 2001).

In this paper, we aim to quantify the spatial turnover of moth ensembles across northern Borneo, consider habitat- and sampling-related consequences on ensemble composition, and evaluate remaining spatial patterns in the data. We use geometrid moth samples at distances between less than 50 m to almost 750 km from each other, stemming from different habitats (e.g. primary forests to open, degraded land; lowlands to 3750 m elevation) and times (different months, from the 1960s to 2003), to assess the importance of various parameters on the faunal similarity of sites.

Geometrids (Lepidoptera: family Geometridae) have often been used for biodiversity studies of herbivorous insects in tropical landscapes (e.g. Beck *et al.* 2002; Brehm, Süssenbach & Fiedler 2003; Axmacher *et al.* 2004). Their ensemble composition reacts sensitively to habitat change, they can be sampled in large numbers by light-trapping, and their high species richness makes them suitable for comprehensive statistical analyses of diversity patterns.

Materials and methods

THE DATA

Quantitative light-trapping samples of geometrid moths in Borneo were compiled from published sources (Holloway 1976; Abang & Karim 2003) and own sampling (see, e.g. Holloway, Kirk-Spriggs & Chey 1992; Chey 2000, 2002; Beck *et al.* 2002). All data were transformed to a unified nomenclature, following the relevant literature for Borneo (Holloway 1993, 1996, 1997). Each data set contained a number of unidentified 'morphospecies', most of which were damaged specimens that could not be precisely identified. As cross-referencing between collections was not feasible, we excluded these 213 specimens (*c*. 0·8% of total data) from all analyses. We also excluded all sampling locations with less than 50 individuals. This left a data set of almost 27 000 specimens, or 836 species, from 65 sites for analysis (Fig. 1).

Sites were classified as 'primary', old-grown forest, 'secondary' forest, or 'open, disturbed' landscape, the latter representing either small-scale agriculture of indigenous peoples, or soft-wood monocultures. Furthermore, elevation, forest stratum (understorey vs. canopy
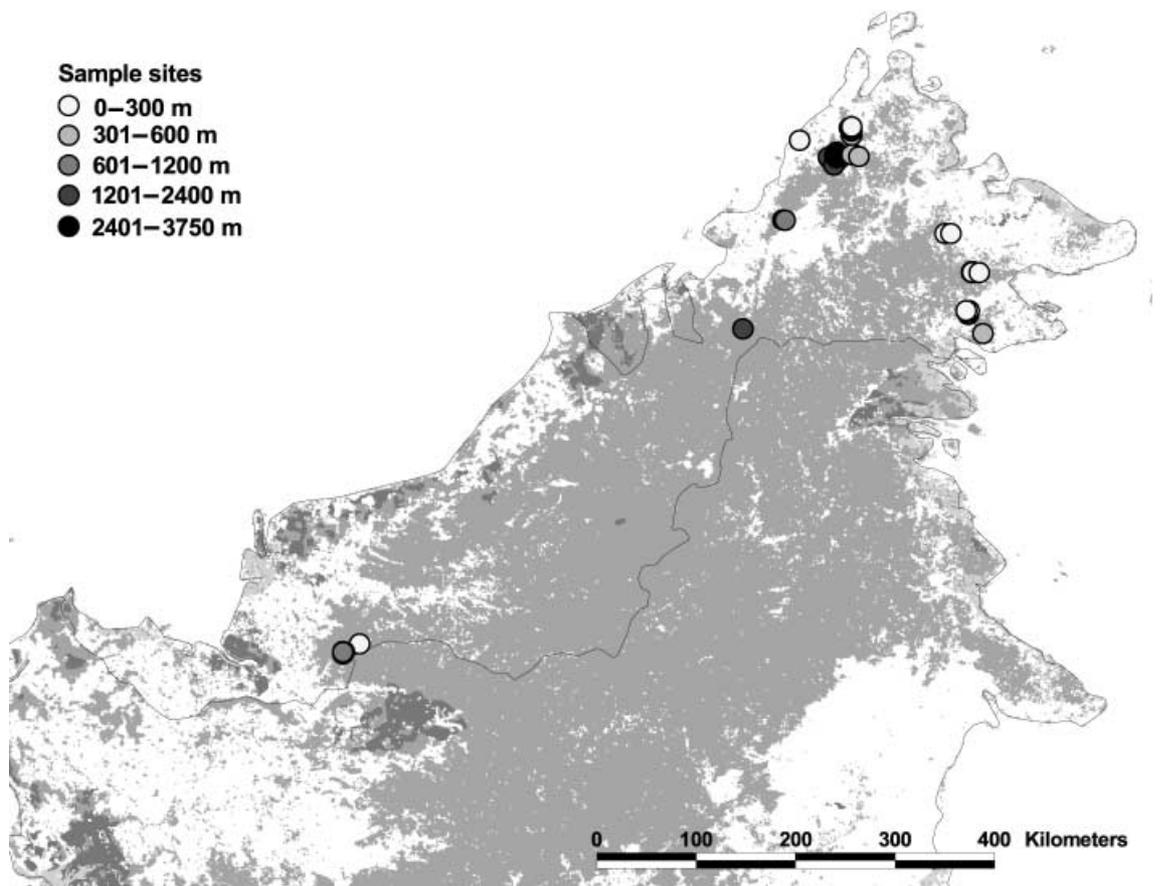
Fig. 1. Northern and central Borneo, showing location of sample sites and their elevation, as well as country borders of Malaysia, Indonesia and Brunei. Grey shades mark various types of closed forests, white areas indicate open, cultivated or mosaic landscapes that are disturbed by human activities (remote sensing data, simplified from Stibig, Beuchle & Janvier 2002). Note that sample sites in close proximity may appear as one point on the map.

and 'pseudo-canopy', i.e. cliffs with canopy outlook), sampling schedule (full night vs. part of the night), and year of sampling were used to characterize samples. Geometrid ensembles are influenced by the precipitation of months prior to sampling (Intachat, Holloway & Staines 2001). We had no precise weather data for sampling locations and times, but classified months as relatively 'wet' or 'dry' according to weather data from Brunei (Cranbrook & Edwards 1994) and eastern Sabah (Danum Valley Field Centre, unpublished; monthly means from 18 years). We used this classification of the month of sampling, as well as 2 months prior, as additional parameters. The locations of many sampling sites were provided by GPS data, whereas we located others on maps or by visiting the vicinities of sites and taking our own GPS measurements. We estimate that these approximations do not cause location errors > 1 km. Software by Jenness (2005) was used to calculate pair-wise distances of all sites from each other, using UTM projections of latitude and longitude data.

ANALYSIS

The dissimilarity of samples was measured by the CNESS index (*chord-transformed normalized expected shared species*; Trueblood, Gallagher & Gould 1994; software by Gallagher 1998). This index considers not only the presence or absence of species in samples, but also their abundances. Furthermore, as the original, nontransformed NESS index (Grassle & Smith 1976) it is not biased by incomplete sample coverage. High values of the index parameter m lead to higher weightings of rare species in dissimilarity assessments. We present here analyses based on $CNESS_{m=50}$ (the highest possible value in our samples, following advice by Brehm & Fiedler 2003). We repeated all analyses with $m = 10$, $m = 20$ and with Bray–Curtis indices, but did not find qualitatively different results.

Univariate tests of a relation between habitat parameters and the similarity of geometrid samples were performed with a nonparametric permutation test (Anosim, 20 000 runs; primer v.5, 2002). Continuous elevation data were grouped in octaves (0–300 m, 301–600 m, 600–1200 m, etc.) and years in half-decades. Selected parameters were also tested in two-way cross-designs. For a multivariate assessment of the impact of habitat parameters on the moth sample similarities, we used a Generalized Linear Model (GLM; StatSoft

2005) that allows combinations of interval-scaled and categorical predictor variables. To provide dependent variables from the similarity matrix, we first rescaled CNESS-values (which take values between 0 and √2) to a dissimilarity measurement between 0 and 1. We then applied multidimensional scaling (MDS; StatSoft 2005) to ordinate sites according to their faunal similarity, extracting three dimensions without losing too much of the original data variability (stress = 0·138). Dimension scores were used as dependent variables in the GLM. A GLM predicting values for three MDS dimensions from all available sample parameters was in danger of over-fitting (StatSoft 2005). Based on univariate effects (Table 1) and preliminary trials (not shown) we chose elevation and year as continuous predictors, whereas only disturbance, precipitation (in the month of sampling) and sampling schedule were included as categorical predictors. Furthermore, no higher-level parameter interactions could be allowed in the model. Spatial autocorrelation of dependent and independent variables as well as GLM residuals were measured by correlograms of Moran's I (Moran 1950; software by Sawada 1999), using 5-km steps up to lag-distances of 100 km.

To test for a relation between distance and faunal similarity we used a Mantel-type permutation test (10 000 runs, software by Bohonak 2002). Preliminary analyses suggested that log-transformed distances, regressed on raw CNESS index values, produced highest r^2 values (i.e. best linear fit of data). A linear relation between log-distances and species data was also predicted in neutral models (Hubbell 2001), but previous studies have found different combinations of log-transformed distances or beta-diversity measurements useful (e.g. Nekola & White 1999; Condit *et al*. 2002). We applied reduced major axis (RMA) regressions to compare the slopes of similarity decay with distance; jackknifing over sites was used for a rigorous estimate of 95% confidence intervals of regression slopes. We re-tested matrix correlations with a nonparametric technique that does not make any assumption on the linearity of the relationships (Relate, 10 000 runs; primer v.5, 2002), but report results only where they deviate from linear matrix correlations.

For direct comparison of the impact of habitat vs. distance we performed a principal components analysis (PCA; StatSoft 2005) of sample parameters, calculated Euclidian distances between factor values and used the

Table 1. Results of univariate Anosim (20 000 runs) of habitat parameters and sample dissimilarity ($CNESS_{m=50}$)

Parameter	Spearman's ρ	*P*	Pairwise tests significant for:
Disturbance	0·064	0·128	
Elevation	0·487	< 0·0001	All except (300 m, 600 m)
Stratum	0·045	0·265	
Sampling schedule	−0·01	0·499	
Precipitation	0·271	< 0·0001	(wet, dry) (wet, all year)
Precipitation (−2 months)	0·371	< 0·0001	All
Year	0·497	< 0·0001	All

resulting distance matrix, together with geographical distances, as predictors of faunal dissimilarity in a partial, Mantel-type permutation test (10 000 runs, software by Bohonak 2002).

Legendre *et al.* (2005) pointed out that analyses based on raw data, rather than dissimilarity indices, may be statistically more powerful to analyse environmental and spatial effects on beta-diversity. However, light-trapping data carries a number of biases that make raw data comparisons between sites not feasible (e.g. Beck & Linsenmair 2006, references therein). Furthermore, our samples are incomplete in their coverage of the 'true' species richness of sites (as are almost all samples of tropical invertebrates), which favours the use of a dissimilarity index that corrects for such biases.

Results

HABITAT AND SAMPLING PARAMETERS

Table 1 summarizes univariate tests of a relation between habitat parameters and ensemble similarity. Significant relationships were discovered for elevation, the year of sampling and the precipitation of the months of sampling, and 2 months prior to sampling. Univariate effects could neither be found for forest stratum and habitat disturbance, nor between sites sampled all night long or just in the first half (or less) of the night. However, habitat disturbance (unlike the other parameters, data not shown) has a highly significant effect if controlled for elevation in a two-way cross design (elevation: $\rho = 0.67$, disturbance: $\rho = 0.46$, both $P < 0.0001$), with significant differences between all three disturbance classes. Furthermore, a two-way cross-design confirms effects of elevation and year, so they are not artefacts of parameter collinearity.

The GLM makes significant predictions for all three MDS dimensions that explain relatively large proportions of data variance ($n = 65$ sites; dimension 1: $R^2_{corr} = 0.89$, $F_{7,57} = 78.1$; dimension 2: $R^2_{corr} = 0.53$, $F_{7,57} = 11.5$; dimension 3: $R^2_{corr} = 0.42$, $F_{7,57} = 7.7$; all $P < 0.0001$). All five included sample parameters make a significant contribution to the model (Table 2).

SIMILARITY DECAY OF ENSEMBLES

Pooled data of all 65 sites are weakly, but significantly, related to distance between sites when tested in the

semilogarithmic design (Fig. 2; $r^2 = 0.14$, $P < 0.0001$), but not in a nonparametric test (RELATE; Spearman's $\rho = 0.05$, $P = 0.17$). Restrictions to lowland (≤ 600 m) understorey sites within the three disturbance classes gives the impression that correlations are stronger in disturbed habitats (Fig. 2; primary: 20 sites, $r^2 = 0.37$, $P < 0.0001$; secondary: nine sites, $r^2 = 0.51$, $P < 0.002$; disturbed: 11 sites, $r^2 = 0.51$, $P = 0.0001$). Furthermore, linear RMA regressions of sample dissimilarity and log-transformed distances (in m) indicate steeper slopes in open, disturbed habitats than in forests. However, differences in slope (or intercept, not shown) are not statistically significant (primary: slope$_{(95\%CI: min., max.)} = 0.15_{(0.11, 0.19)}$; secondary: slope = $0.13_{(-0.03, 0.29)}$; disturbed: slope = $0.20_{(0.06, 0.34)}$). The slope of pooled data is intermediate ($0.18_{(0.15, 0.21)}$), whereas montane sites (1200–3750 m) have a weaker relationship with distance (12 sites, $r^2 = 0.11$, $P < 0.006$) and a considerably, but not significantly, steeper slope than any other habitat category ($0.40_{(-1.43, 1.32)}$).

We applied PCA to the five significant 'habitat parameters' from the GLM and extracted three factors (eigenvalues > 1) that cover 87% of the original data variance. A Euclidian distance matrix of these data has stronger independent effects on the geometrid dissimilarity of all sites (partial correlation: $r^2 = 0.30$) than log-transformed geographical distances (partial correlation: $r^2 = 0.12$; both $P < 0.0001$).
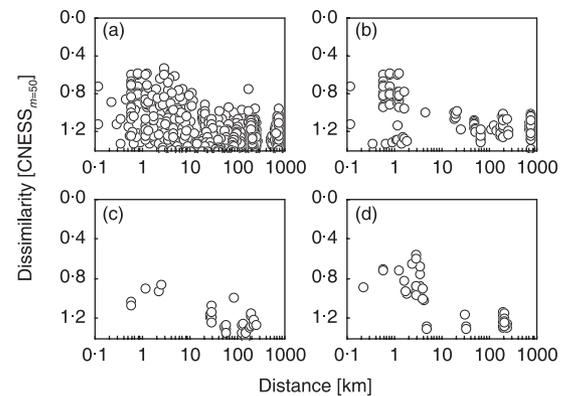
Fig. 2. Similarity decay of geometrid sample similarity (*x*-axis, note inversed scale of dissimilarity measure CNESS) and log-transformed distance for (a) all data, (b) lowland primary forests (only understorey samples), (c) lowland secondary forests (only understorey) and (d) lowland disturbed habitats. See text for statistical analysis and regression fitting.

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230–237

Table 2. Contributions of sample parameters to GLM (1-Wilks' λ is equivalent to r^2-values in models with multiple dependent variables; StatSoft 2005) and univariate effects on MDS dimensions. Significance of univariate effects on dimensions is indicated as *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Parameter	1-Wilks' λ	F	d.f.	P	F_{dim1}	F_{dim2}	F_{dim3}
Disturbance	0.724	3.21	6	0.006	0.31	0.10	9.87***
Sampling schedule	0.514	17.35	3	< 0.0001	1.05	45.41***	1.34
Precipitation	0.557	6.22	6	< 0.0001	3.21*	10.32***	5.37**
Elevation	0.362	32.26	3	< 0.0001	63.07***	28.48***	2.95
Year	0.422	25.14	3	< 0.0001	16.94***	33.33***	12.01**

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SPATIAL AUTOCORRELATION OF ENSEMBLES, SAMPLE PARAMETERS, AND RESIDUALS

Figure 3 shows correlograms of Moran's I of MDS dimension values, selected sample parameters, and residuals of the GLM. Dimension values and sample parameters are positively autocorrelated at distances from 5 km to up to over 40 km. The similarity of pattern in sampling year and elevation is probably caused by the focus of one of our data sources (Holloway 1976) on montane samples from Borneo's highest mountain, Mt Kinabalu. Furthermore, autocorrelations of elevation (particularly in high montane habitats) are enforced by the physical geography of Borneo, with sites from Mt Kinabalu being up to almost 2000 m higher than any other sampled habitat. Precipitation classes and sampling schedules are not spatially autocorrelated (data not shown).

GLM residuals are almost void of spatial autocorrelation, indicating that spatial patterns of ensemble similarity can be largely attributed to the spatial patterns of sample parameters. An exception is the persistent similarity of dimension 3 residuals at distances up to 15 km. Low numbers of neighbouring sites (< 10) occur at lag-distances between 40 and 70 km due to the irregular positioning of sites. This decreases the power of statistical tests and lead to Moran's I calculations based on only few site comparisons. We will therefore not seek ecological explanations for erratic patterns at these distances.

As alternative analysis we applied a simultaneous autoregressive model (SAR; Rangel, Diniz-Filho & Bini 2006), which confirmed that effects of elevation, disturbance and year on geometrid ensembles (as represented by MDS dimension values) are significant even if distances between sites are explicitly considered

(data not shown; precipitation and sampling schedule have no significant spatial structure in our data and were not included in this analysis). A comparison of the SAR model to a spatially nonexplicit *ordinary least square* regression of the same data (based on Akaike's information criterion; Johnson & Omland 2004) indicates that accounting for the spatial component (i.e. SAR) provides a better explanation for values of dimension 3 ($P = 0.004$), but not for dimension 1 ($P = 0.262$) or dimension 2 ($P = 0.051$).

Discussion

DETERMINISTIC FACTORS OF ENSEMBLE COMPOSITION

Our analyses have confirmed on a large, spatially extensive data set that geometrid samples from northern Borneo change with elevation, human-caused habitat conversion and the precipitation at (and prior to) sampling. All this has already been anticipated in more localized studies (see references above). However, our data also showed that ensembles changed with time from the 1960s to 2003 (independently of habitat; Table 2), an effect that has also been noted in tropical sphingid moths (Beck, Kitching & Linsenmair 2006). We also observed differences in ensembles depending on the sampling schedule (full night vs. part of the night), which is not surprising yet of methodological significance. Beck & Linsenmair (2006), for example, have shown temporal 'niches' in the activity of tropical sphingid moths. Our data did not show a consistent difference between understorey and canopy samples, although such differences were found in a number of local comparisons (e.g. Beck *et al.* 2002; Schulze & Fiedler 2003). Possibly our classification of sites with
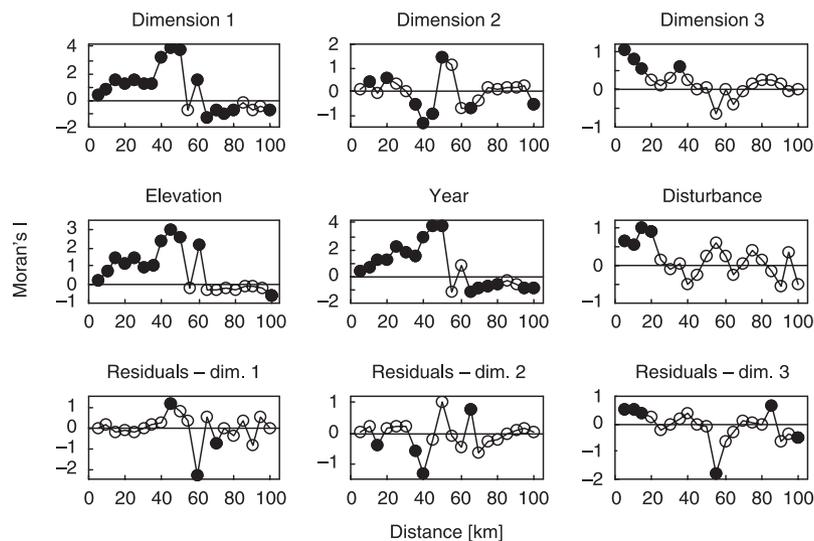

Fig. 3. Correlograms of Moran's I of the three MDS dimensions representing the similarity of geometrid ensembles (upper row), selected sample parameters with impact on these dimensions (middle), and residuals of a GLM with five predictive sample parameters (bottom row; see Table 2). Moran's I measures spatial autocorrelation similarly to Pearson's r^2 at different lag-distances, significant correlations ($P < 0.05$) are indicated by filled dots (significance level adjusted for multiple tests). Note the different scales of *y*-axes. No autocorrelations were found at larger distance classes (data not shown).

canopy 'outlook' (i.e. cliffs, steep slopes) weakens these comparisons, as such sites may actually sample a mixed community.

SPATIAL PATTERN OF SIMILARITY

Our analyses suggest that the spatial pattern of ensemble similarity can be attributed to a large degree to spatial autocorrelations in deterministic habitat parameters, particularly elevation and, to a lesser degree, disturbance (the spatial pattern of sampling year is a peculiarity of our data set, but may not generally be expected). This finding agrees with other lines of argument on herbivore insects in tropical forests (Novotny & Weiblen 2005; references therein). However, residuals from our model retain positive spatial autocorrelation at small distances (5–15 km) on the MDS dimension that is associated with habitat disturbance (and which has lowest R^2-values of all dimensions in the GLM), and spatial effects were found at an even smaller scale in a cluster of nine sites in homogeneous lowland forest (Beck, Mandel & Peer, in press). This finding is consistent with two competing explanations: a further deterministic factor with a spatial pattern at these scales may have been overlooked (e.g. Diniz-Filho *et al.* 2003), or dispersal limitation caused differences in communities even in an ecologically neutral habitat matrix (e.g. Hubbell 2001). A system like the one studied here holds an almost infinitive number of additional, hypothetical habitat parameters that deny falsification of the first explanation. To name just those few for which there are indication from local studies, leaf and flower phenology can change geometrid ensembles (Intachat *et al.* 2001), habitat parameters related to disturbance can explain ensemble changes at a much finer resolution than used here (e.g. understorey plant diversity; Beck *et al.* 2002), or differences in vegetation mediated by soil type (e.g. alluvial, swamp, limestone) or dispersal limitation of host plants (Condit *et al.* 2002) may favour some species over others (Holloway 1993, 1996, 1997). The spatial pattern at 5–15 km also seems at a scale that could reasonably be related to dispersal effects of geometrid moths, which are presumably relatively weak dispersers (but we are not aware of any empirical data on dispersal distances in this group).

Methodological implications of our findings are that studies analysing beta-diversity must not ignore spatial effects. In particular, sampling along transect gradients at critical lag-distances, where difference in habitat increase with spatial distance (e.g. in Beck *et al.* 2002) carries a risk of confusing effects of habitat with those of location. Studies should be designed to control for spatial effects (i.e. sample sites should be either approximately equidistant at minimum distances, or so far distant from each other that spatial autocorrelation plays no role), or analysis has to address potential spatial effects, e.g. by data filtering or the application of spatially explicit tests (Rangel *et al.* 2006, references therein).

Direct analyses of similarity decay (Fig. 2) show many similarities with data of butterfly ensembles (coincidentally also from Borneo, but different regions; Cleary *et al.* 2004; Cleary & Genner 2006) – they are also approximately linear on log-distance vs. similarity plots, and high similarities occur at sites ≤ 10 km from each other. In apparent contradiction to analyses of spatial autocorrelation discussed above, a partial correlation of geographical distances (controlled for habitat parameters) is not much weaker than a univariate correlation. This difference in conclusion may be caused by the loss of different information in the two lines of analysis (in PCA, MDS), the different magnitude of analysed distances (100 km vs. > 700 km), or the unjustified assumption of a linear relation in semilogarithmic plots (considering overall low r^2, discrepancy between linear correlation and nonparametric RELATE). Consistently with the latter, a restriction of plots to distances > 15 km does not suggest any relationship at visual inspection.

HABITAT HOMOGENIZATION AND THE SLOPE OF SIMILARITY DECAY

Destruction of tropical rainforest and their conversion into cultivated or otherwise 'unnatural' habitats is a major threat to biodiversity (e.g. Sodhi *et al.* 2004 for South-east Asia). Among the feared consequences of such conversion is not only a reduction in alpha-diversity (which has been shown in many organisms including Borneo geometrids, e.g. Beck *et al.* 2002), but a reduction in habitat heterogeneity that may reduce beta-diversity (MacKinney & Lockwood 1999). However, focusing on lowland (≤ 600 m) understorey samples, we did not find supporting evidence of this effect at the spatial scale of our data. Neither was average ensemble dissimilarity lower in disturbed habitats (median $CNESS_{m=50} = 1·17$) than in primary forests (median $CNESS_{m=50} = 1·12$), nor did we observe a flatter slope of similarity decay across disturbed sites than across primary sites (see Results).

LOCAL AND REGIONAL DIVERSITY

Novotny & Weiblen (2005) recently suggested that the high regional diversity of herbivorous insects in tropical lowland rainforests may be mainly caused by high local diversity, but not by an exceedingly high species turnover between sites. Owing to the heterogeneity of beta-diversity measures in published data, as well as effects of the spatial scale and grain size of beta-diversity analyses (Hui, McGeoch & Warren 2006, and references therein), it is difficult to assess this claim on a larger taxonomic and geographical scale. For Borneo, the described regional species richness of geometrid moths amounts to *c.* 1100 species, but a complete inventory may be considerably higher (Holloway 1997). We applied the *Chao1* species richness estimator (Colwell 2005) to sample data, which suggest that our

raw data cover a mean$_{(\pm 95\% \text{ CI})}$ of $57_{(\pm 4)}\%$ of the 'true' species richness of sites. A mean of only $147_{(\pm 18)}$ and a maximum of 291 species are estimated to occur locally. These data suggest that beta-diversity plays a substantial role in maintaining the regional species diversity of Bornean geometrids. Only nine (of 836) species occur at $> 50\%$ of sites, the species with the highest occupancy (*Hypochrosis bineaxata* Walker) occurs at 54 of 65 (83%) of sites. Even of the 60 species with samples sizes of > 100 specimens (i.e. disregarding all 'rare' species), 51 occur at $< 50\%$, and 25 occur at $< 20\%$ of sites.

Conclusions

Geometrid moth ensembles from Borneo are shaped by environmental parameters such as elevation and habitat disturbance, and by temporal factors acting at small (mediated by weather) and large scales (i.e. changes over three decades). Samples are also influenced by methodological differences of sampling related to the nightly flight times of species. These parameters explain a large portion of the spatial structure of ensemble composition, but residual variation still contains a pattern that is tentatively best explained by geographical distance, particularly at distances < 20 km. Beta-diversity plays a crucial role in mediating the regional diversity of geometrids on Borneo.

Acknowledgements

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