



# Determinants of diversity in afrotropical herbivorous insects (Lepidoptera: Geometridae): plant diversity, vegetation structure or abiotic factors?

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## ABSTRACT

**Aim** This study was conducted to investigate the potential of predicting alpha diversity and turnover rates of a highly diverse herbivorous insect family (Geometridae) based on vascular plant species richness and vegetation structure.

**Location** The study was carried out on the south-western slopes of Mount Kilimanjaro within a wide range of habitats between 1200 and 3150 m elevation.

**Methods** The floristic and structural composition of the vegetation was recorded at 48 plots of 400 m<sup>2</sup>. Geometrid moths were sampled manually at light sources located at the plot centres. Principal components analysis, redundancy analysis and multiple linear regression were used to explore how alpha diversity and species turnover of geometrid moths are related to vegetation structure and plant species richness.

**Results** Alpha diversity of geometrid moths was significantly correlated with species diversity patterns in the most common vascular plant families ( $R^2 = 0.49$ ) and with plant structural parameters ( $R^2 = 0.22$ ), but not with overall floristic diversity. Species turnover of geometrid moths was strongly linked to diversity changes in a range of plant families (40% explained variance), less strongly to changes in vegetation physiognomy (25%), and only weakly to overall floristic diversity (5%). Changes in elevation were a better predictor of both alpha diversity and species turnover of geometrid moths than any principal component extracted from the vegetation data.

**Main conclusions** Vegetation composition, diversity and structure all showed significant correlations with the diversity and species composition of geometrid moth assemblages. Nevertheless, in most cases relationships were indirect, via environmental parameters such as temperature and humidity, which influenced both vegetation and moth fauna. Possible direct links between geometrid diversity and potential food plants were much weaker. The lack of a significant correlation between overall plant species richness and geometrid diversity indicates that tropical geometrid moths may not be very selective in their food plant choice. Accordingly, a clear correlation between floral diversity and herbivore species richness must be regarded as overly simplistic, and the diversity of vascular plants cannot universally be used as a suitable biodiversity indicator for diverse insect taxa at higher trophic levels.

## Keywords

Diversity, elevation, floristic composition, Geometridae, herbivores, Lepidoptera, Mount Kilimanjaro, vegetation structure.

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## INTRODUCTION

Herbivorous insects account for a major fraction of global biodiversity (Novotny *et al.*, 2006; Lewinsohn & Roslin, 2008). In conjunction with their intermediate position in trophic cascades, this renders them ideal objects with which to study the effects of environmental gradients in habitat conditions on the diversity of faunal communities. Geometrid moths have a particularly high potential to serve as a model system in this respect. With more than 21,000 known species (Scoble, 1999), they are one of the three most species-rich families of Lepidoptera. Their potential as 'biodiversity indicators' has been extensively explored by studies in Southeast Asia (Holloway, 1985; Chey *et al.*, 1997; Intachat *et al.*, 1997, 1999a,b; Willott, 1999; Beck *et al.*, 2002), South and Central America (Brehm *et al.*, 2003b, 2007; Hilt *et al.*, 2006), Australia (Kitching *et al.*, 2000) and Africa (Axmacher *et al.*, 2004a,b).

Geometrid larvae feed predominantly on a wide variety of dicotyledonous plants and occasionally on gymnosperms, or very rarely on ferns and lichens (Robinson *et al.*, 2007). A substantial number of tropical geometrid caterpillars seem to prefer woody plants as a food source, and some have become infamous pest species in orchards and monoculture forest plantations (Swank *et al.*, 1981; Zanuncio *et al.*, 1998; Minet & Scoble, 1999; Guedes *et al.*, 2000). Nonetheless, current knowledge of food plant requirements for tropical geometrid caterpillars is very vague. Adult geometrid moths usually have a functioning proboscis, and it is likely that most tropical species rely on flower nectar as a food source, although, again, evidence is scarce. Given these functional links between geometrids and the vegetation, it can be hypothesized that the alpha diversity and species turnover of geometrid moth assemblages are closely linked to the composition and diversity of vascular plants. Alpha diversity in the context of this paper is understood to reflect a combination of the number of species per sampling site and the evenness of the respective species assemblages, whereas the terms 'species density' and 'species richness' both strictly relate to the number of species per site (Whittaker *et al.*, 2001).

The hypothesized link between geometrid moth and plant assemblages (Lewinsohn & Roslin, 2008) is corroborated by observations from Southeast Asia, where the alpha diversity of geometrid moths has been positively correlated with the overall species density of vascular plants, and particularly with the plant species richness in the forest understorey (Intachat *et al.*, 1997, 1999b; Beck *et al.*, 2002). By contrast, the alpha diversity of geometrid moths in an Andean rain forest was not strongly linked to plant species richness (Brehm *et al.*, 2003b), and a comparison of geometrid alpha diversity in clearings and secondary and mature rain forest in a small area of the mountain rain forest at Mount Kilimanjaro even revealed a strong negative correlation with plant species richness (Axmacher *et al.*, 2004a). These contrasting observations indicate that the relationship between the highly diverse, herbivorous members of the family Geometridae and the composition of

the vegetation in their habitats is complex and remains poorly understood.

The present study constitutes the first highly detailed analysis of these relationships, using the geometrid fauna of Mount Kilimanjaro as a model. We specifically set out to examine whether alpha diversity and species turnover of geometrid moths can best be predicted by structural features of the vegetation, overall plant species density, species richness of single plant families per plot, or by a combination of these characteristics.

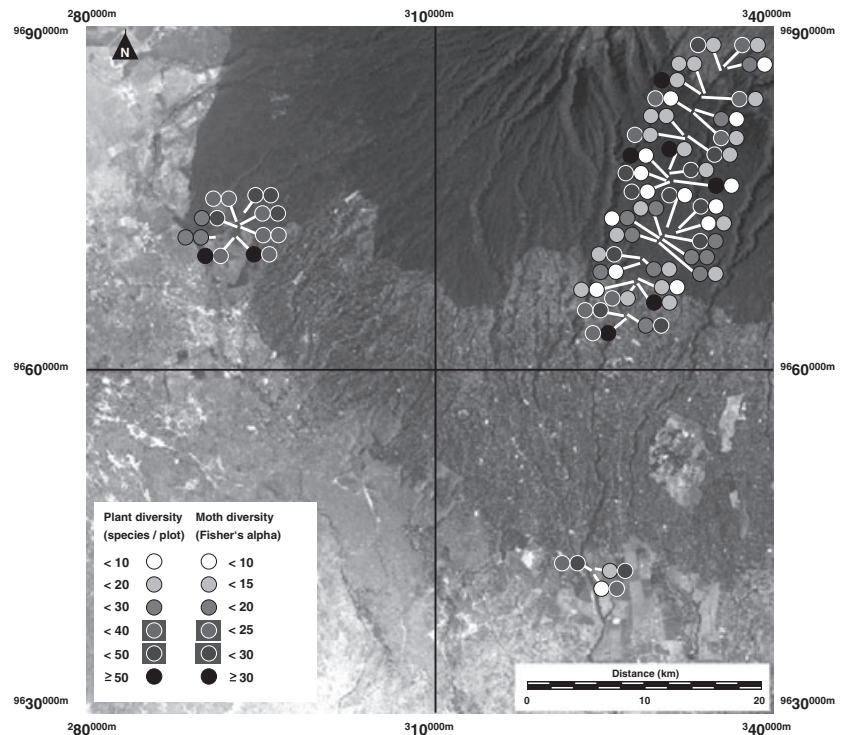
## MATERIALS AND METHODS

### Study area and site selection

The study area was located on the south-western slopes of Mount Kilimanjaro, Africa's highest mountain (Fig. 1). On these slopes, the vegetation changes from large-scale agricultural farmland and savanna vegetation below 1300 m to a mosaic of small agro-forestry plots extending to elevations of 1800 m. Above this zone, secondary and mature forest covers the slopes between 1800 and 3000 m, with heathland replacing the forests above this elevation. Detailed descriptions of these vegetation types are given in Hemp (2001, 2006a,b). Forty-eight plots of 20 × 20 m<sup>2</sup> each were established in clusters at elevations ranging from 1200 to 3150 m at intervals of *c.* 200 m. These clusters represent the respective ranges of typical habitats occurring at the various elevations (Table 1). Plots representing different habitats were interspersed in the clusters. The highest numbers of plots were located at important ecotones in order to effectively cover the large variety of habitats in these zones. Large clusters were thus established at the lower boundary of the forest belt at 1400 m on the western slopes and at 1850 m on the southern slopes of the mountain, and at the boundary between secondary and mature forest at *c.* 2200 m (Fig. 1). In plot selection, it was ensured that the vegetation was homogeneous at each of the plots. In two cases, the extent of homogeneous vegetation was slightly smaller than 400 m<sup>2</sup>, so plot sizes had to be adjusted. In both cases, plant species numbers were within the range observed at neighbouring plots representing the same habitats. Plots were established at a minimum distance of 35 m from each other, and the weak light sources used in this study were invisible from neighbouring plots in order to ensure that moth samples were independent.

### Recording of vegetation and geometrid moths

At each plot, all species of vascular plants were recorded separately for the herb, shrub and tree layer, as well as all vascular epiphytes growing below a height of 2 m. Furthermore, data on vegetation structure, including information on stratification, cover, leaf morphology, and branching patterns (for a complete list of parameters see Table 2), were obtained from each plot. The percentage cover of the various strata were estimated, and the other parameters were recorded separately



**Figure 1** Map of the study area showing the locations of the study plots (white lines) and the respective diversity recorded at the sites (paired circles representing plant diversity (species/plot) on the left and geometrid diversity (Fisher's alpha) on the right; underlying satellite image: Landsat 7 TM+, 21/02/2000, channels 1,2,3, UTM -37 S, 280,000–340,000, 9,630,000–9,690,000). Dark grey shades show dense vegetation cover.

for each individual tree, with percentage values representing the proportion of trees possessing the respective structural characteristic at each plot.

Geometrid moths were sampled manually from the surface of white reflective gauze cylinders (diameter 0.8 m, height 1.7 m) illuminated by a weak UV light source (Sylvania blacklight-blue, F 15 W/BLB-TB) (Axmacher & Fiedler, 2004). These 'light towers' were placed at the centre of each plot and were operated during the assumed peak activity of moths from 19:00 to 22:00 h. No sampling occurred in the period 5 days before to 4 days after the full moon, as light trapping is much less effective during these periods (McGeachie, 1989; Yela & Holyoak, 1997). In total, 164 samples were collected between October and May in the years 2000, 2001 and 2002. On two plots, sampling was stopped after the first samples, as they contained more than 200 individuals. All other plots were visited between two and eight times to ensure a minimum sample size of at least 50 individuals. In 40 cases, the overall sampling size exceeded 100 individuals. Moths were later classified at the Zoologische Staatssammlung in Munich (Germany). Most geometrids were identified to species level, with the remainder identified to genus level and sorted to morpho-species. The resulting data took the form of a species  $\times$  site matrix with abundance data for each of the 279 moth species (Axmacher, 2003).

### Data analysis

Multicollinearity within data sets potentially distorts the results of regression models such as multiple linear regression (MLR) and redundancy analysis (RDA). To avoid such distortions and

to account for the large number of environmental parameters investigated, the vegetation data sets were condensed by means of principal components analysis (PCA). A first PCA was based on the overall number of vascular plant species on each plot as well as on the number of species in each vegetation layer per plot. In a second analysis, the number of species for each of the 40 most common families of vascular plants was taken as the basis of a PCA. Similarly, the data on vegetation structure were also subjected to a PCA. The statistically independent principal components gained during these transformations were then used as predictor variables for geometrid moth diversity in both an MLR and an RDA.

The numbers of mobile insects sampled in light traps depend on a variety of factors, including sampling effort, background illumination, general visibility and weather conditions. These factors often render the observed number of species a poor measure of alpha diversity (Gotelli & Colwell, 2001). Various methods have therefore been developed to allow the interpretation of differences in the numbers of species and specimens between light-trap samples from different habitats and sampling events (Hayek & Buzas, 1997; Southwood & Henderson, 2000). In this study, Fisher's alpha (Fisher *et al.*, 1943), a parametric index based on the assumption of a logarithmic series distribution of specimens per species, was calculated as a measure of alpha diversity of geometrid moths using the computer program Species Diversity and Richness (Henderson & Seaby, 2002). Fisher's alpha has been widely used and has proved to be a robust measure with which to assess tropical arthropod diversity (Brehm *et al.*, 2003b; Schulze & Fiedler, 2003; Axmacher *et al.*, 2004a). Estimated values of Fisher's alpha were highly correlated with

**Table 1** Habitat type, elevation and alpha diversity [including standard deviation (SD) for Fisher's alpha] of geometrid moths and vascular plants at the various plots.

Plot	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12
Elevation (m)	2090	2135	2140	2155	2090	2165	2260	2265	2265	2250	2320	2320
Habitat type*	1	1	1	2	2	2	3	3	3	3	3	3
Geometrid moths												
Species	38	38	46	49	32	46	14	27	22	19	36	31
Individuals	134	174	226	242	131	207	200	240	149	168	230	138
Fisher's alpha	17.7	15.0	17.5	18.0	13.6	18.3	3.4	7.8	7.1	5.5	12.0	12.4
Fisher's alpha SD	4.7	3.6	3.7	3.6	3.7	4.0	1.0	1.8	1.9	1.5	2.6	3.3
Vascular plants												
Total	13	6	13	29	26	42	40	53	48	53	50	48
Epiphytes	2	0	0	11	8	20	20	30	33	25	31	20
Herb layer	2	1	1	14	20	32	27	31	33	36	35	23
Shrub layer	9	5	12	9	9	13	18	18	20	21	19	13
Tree layer	0	0	0	3	5	4	5	3	5	6	8	8

Plot	P13	P14	P15	P16	P17	P18	P19	P20	P21	P22	P23	P24
Elevation (m)	1875	1880	1870	2580	2575	2580	2710	2710	2700	2900	2894	2900
Habitat type*	2	2	1	3	3	1	3	3	1	3	3	1
Geometrid moths												
Species	25	31	42	28	33	31	31	37	30	38	32	21
Individuals	124	111	126	148	177	107	215	178	215	181	147	52
Fisher's alpha	9.4	14.3	22.1	10.2	11.9	14.6	9.9	14.2	9.5	14.7	12.6	13.1
Fisher's alpha SD	2.7	4.2	6.1	2.7	2.9	4.4	2.3	3.4	2.2	3.4	3.3	5.8
Vascular plants												
Total	25	28	19	37	44	19	39	39	27	30	52	17
Epiphytes	7	8	0	17	20	0	13	15	0	4	7	0
Herb layer	11	11	19	15	21	19	18	23	27	17	40	16
Shrub layer	12	13	0	8	11	0	7	9	0	5	12	2
Tree layer	6	3	0	7	6	0	8	3	0	5	4	0

Plot	P25	P26	P27	P28	P29	P30	P31	P32	P33	P34	P35	P36
Elevation (m)	3080	3090	3085	2075	2120	2120	1810	1820	1850	1860	1650	1650
Habitat type*	3	3	1	1	3	3	1	4	2	2	4	4
Geometrid moths												
Species	34	24	26	28	23	20	27	28	26	29	60	37
Individuals	138	75	196	145	150	110	127	117	148	263	162	77
Fisher's alpha	14.4	12.1	8.1	10.3	7.6	7.2	10.5	11.7	9.1	8.3	34.5	28.0
Fisher's alpha SD	3.8	4.3	2.0	2.7	2.0	2.2	2.9	3.4	2.4	1.8	8.5	10.5
Vascular plants												
Total	40	35	21	5	47	49	39	51	19	12	39	36
Epiphytes	4	4	0	0	20	29	0	3	5	0	15	12
Herb layer	28	22	18	1	31	33	39	37	11	11	21	23
Shrub layer	14	13	4	4	17	16	0	9	9	4	5	2
Tree layer	5	4	0	0	7	7	0	3	4	0	1	1

Plot	P37	P38	P39	P40	P41	P42	P43	P44	P45	P46	P47	P48
Elevation (m)	1660	1220	1220	1220	1450	1450	1420	1420	1420	1450	1360	1360
Habitat type*	1	4	1	4	1	2	2	2	1	4	5	1
Geometrid moths												
Species	39	46	40	41	39	35	43	47	42	51	44	27
Individuals	84	122	99	122	105	93	118	130	93	173	108	72
Fisher's alpha	28.3	26.9	25.0	21.7	22.5	20.4	24.4	26.4	29.5	24.4	27.7	15.7
Fisher's alpha SD	10.1	7.6	7.9	6.1	6.9	6.6	7.0	7.3	9.9	5.8	8.5	5.8
Vascular plants												
Total	27	15	31	6	53	53	39	39	23	30	47	28

**Table 1** Continued

Plot	P37	P38	P39	P40	P41	P42	P43	P44	P45	P46	P47	P48
Epiphytes	0	0	0	1	0	7	2	4	0	0	0	0
Herb layer	27	13	31	3	21	23	20	21	22	29	12	27
Shrub layer	0	2	0	1	41	30	18	11	1	1	29	1
Tree layer	0	0	0	1	0	13	8	10	0	1	19	0

\*Habitat types: 1, opening or gap; 2, secondary forest; 3, mature forest; 4, agro-forest; 5, gallery forest.

**Table 2** Loading of the structural vegetation parameters recorded in each of the study plots on the eight resulting principal components (unrotated structural principal components, SPCs). Only PCs with eigenvalues > 1 are considered.

Structural parameters	Factor 1 (SPC1)	Factor 2 (SPC2)	Factor 3 (SPC3)	Factor 4 (SPC4)	Factor 5 (SPC5)	Factor 6 (SPC6)	Factor 7 (SPC7)	Factor 8 (SPC8)
Vegetation cover < 50 cm	0.380	0.361	0.571	-0.288	-0.131	0.258	-0.193	-0.103
Vegetation cover – 2 m	-0.019	-0.806	-0.052	0.037	-0.084	-0.246	0.102	-0.032
Vegetation cover – 5 m	0.115	-0.223	-0.464	0.104	0.204	0.405	-0.367	-0.378
Vegetation cover – 10 m	0.304	-0.087	-0.082	0.091	0.129	-0.694	-0.022	-0.067
Vegetation cover > 10 m	0.808	0.181	-0.018	-0.092	0.033	-0.073	0.257	-0.160
Tree crown diameter < 50 cm	-0.625	0.371	0.335	0.074	0.269	0.163	0.276	0.205
Tree crown diameter – 1 m	-0.194	-0.112	0.109	0.067	-0.755	0.012	0.067	0.109
Tree crown diameter – 2 m	-0.098	-0.678	0.166	0.061	0.090	0.234	0.021	0.194
Tree crown diameter – 5 m	0.095	0.080	0.163	0.049	0.086	-0.192	-0.852	0.122
Tree crown diameter – 10 m	0.191	0.143	-0.010	0.036	0.017	-0.072	0.212	-0.813
Leaves sub-leptophyll	0.064	0.160	0.111	0.024	-0.815	0.127	0.025	-0.022
Leaves leptophyll	-0.440	0.121	0.244	0.041	0.284	0.105	0.342	0.089
Leaves microphyll	-0.231	0.395	0.292	0.142	0.368	0.253	0.216	0.379
Leaves macrophyll	0.109	0.039	-0.018	-0.958	0.033	0.013	0.046	-0.059
Leaves megaphyll	-0.279	-0.083	0.035	-0.008	0.049	-0.717	-0.398	0.021
Leaves compound	0.107	0.027	0.014	-0.970	0.032	0.044	-0.007	-0.026
Leaves pinnate	-0.048	0.161	-0.896	0.127	0.106	0.041	-0.025	0.076
Percentage malacophyllous trees	-0.684	-0.127	0.232	0.132	0.151	-0.139	0.160	0.313
Percentage semi-sclerophyllous trees	0.163	0.156	-0.785	-0.373	0.098	-0.096	0.202	0.020
No branching top 20 cm	-0.672	0.330	0.042	0.122	0.255	0.325	0.070	0.188
Intermediate branching top 20 cm	0.323	-0.623	0.398	0.036	0.146	-0.140	-0.297	0.096
Epiphyte cover lower 1 m	0.842	-0.104	0.086	-0.082	0.093	0.151	-0.120	-0.069
Percentage cover vascular epiphytes	0.430	0.046	0.255	-0.218	0.115	0.056	-0.112	-0.713
Maximum vegetation height	0.917	0.087	0.008	-0.114	0.096	-0.104	0.012	-0.004
Maximum diameter at breast height	0.796	-0.046	0.208	0.076	0.231	-0.001	-0.071	-0.165
Eigenvalue	6.1	2.9	2.7	1.9	1.8	1.5	1.2	1.2
Explained variance (%)	24.5	11.7	10.7	7.7	7.2	5.8	5.0	4.7
Cumulative explained variance (%)	24.5	36.2	46.9	54.6	61.8	67.6	72.6	77.3

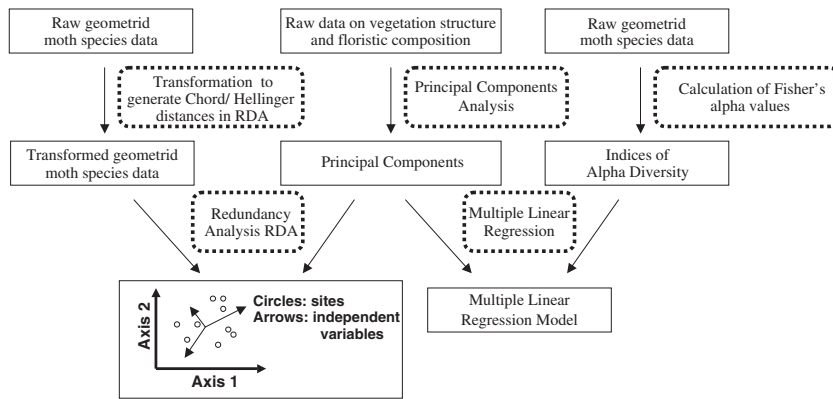
other measures of alpha diversity, for example with rarefied species numbers at 50 individuals per sample ( $R^2 = 0.89$ ) and with the species richness estimator Chao 1 ( $R^2 = 0.59$ ; J. Axmacher, unpublished data). Hence, the results presented can be safely considered to be robust measures of geometrid diversity.

A series of multiple linear regressions was then performed to investigate how alpha diversity of geometrid moths as the dependent variable was related to the vegetation in their habitats, using the principal components (PCs) derived from PCA for floristic and structural data. The stepwise forward MLR was stopped when new PCs did not contribute significantly ( $P = 0.05$ ) to the overall model. Redundancy analysis was used as a constrained ordination technique to analyse how

geometrid species composition, as a matrix of dependent variables, relates to changes in floristic composition and structure of their habitats, again using PCs as independent predictor variables. Moth species data were transformed to allow calculations based on Chord and Hellinger distances rather than on Euclidean distances in order to avoid problems associated with the large number of zero-values in the data set (Legendre & Gallagher, 2001). The overall pathway of analysis is shown in Fig. 2.

## RESULTS

A total of 7074 geometrid moths representing 279 species, and 115 vascular plant families with 319 genera and 447 species



**Figure 2** Structure of the statistical analyses undertaken in this study.

(species lists are published in Axmacher, 2003) were recorded in the study area. Fisher’s alpha values for geometrid moth assemblages varied between 3.4 and 34.5, with a mean value of 15.8 and a standard deviation of 7.5. The diversity of vascular plants varied between five and 53 species per plot. A test for a simple correlation between Fisher’s alpha of geometrid moths and the total number of vascular plants per plot showed no significant result (Pearson’s  $R^2 = 0.017$ ,  $P = 0.37$ ,  $n = 48$  plots).

**Principal components analysis of vegetation data**

The PCA based on the overall plant species density of plots and vegetation layers yielded only two PCs (phytodiversity principal components: PDPCs) with eigenvalues > 1 (Table 3). These PDPCs explained 80.8% of the overall variance. The first PDPC accounted for 59.3% and was closely linked to overall plant species density, species numbers in the tree and shrub layers, and the number of vascular epiphytes. The second PDPC, explaining 21.5% of the variance, was strongly linked to the species richness in the herb layer.

The PCA of the floristic data based on the 40 most common plant families (Table 4) resulted in nine floristic principal components (FPCs) with eigenvalues > 1. These FPCs jointly explained 78.5% of the total variance. The first FPC accounted for 30.1% of the variance, and a number of fern families as well

as the Rubiaceae had high loadings on this FPC. The second FPC, explaining 13.2%, represented mainly the occurrence of the two families Rosaceae and Grammitaceae and was furthermore the only FPC significantly correlated with elevation ( $R^2 = 0.57$ ,  $P < 0.001$ ). FPCs 3 and 4 explained 9.0% and 7.8% of the variance, respectively, with Euphorbiaceae and Rutaceae having high loadings on FPC3, and Commelinaceae on PC4. All other FPCs explained < 5% of the variance.

The PCA of the structural data set (Table 2) resulted in eight PCs (structural principal components, SPCs) with eigenvalues > 1. These SPCs jointly explained 77.3% of the total variance. The height of the vegetation, diameter at breast height, cover of the tree layer and epiphyte cover all had high loadings on the first SPC, which explained 24.5% of the total variance. The cover of the vegetation < 2 m had high loadings on the second SPC, and the leaf characteristics pinnate and semi-sclerophyllous on the third SPC, with these components explaining 11.7% and 10.7% of the total variance, respectively. SPCs 4 and 5 explained 7.7% and 7.2% of the total variance, with divided leaves and macrophyllous plants (SPC 4) as well as sub-leptophyllous plants and trees with crown diameters < 1 m (SPC 5) having high loadings. Finally, SPCs 6, 7 and 8 explained 5.8%, 5.0% and 4.7% of the overall variance, respectively, and were strongly related to plants with mega-phyllous leaves (SPC 6), to tree crowns with diameters < 5 m (SPC 7), and to tree crown diameters < 10 m as well as to richness of vascular epiphytes (SPC 8).

**Table 3** Loading of species richness of vascular plants at various vegetation layers on the two principal components extracted by principal components analysis (unrotated phytodiversity principal components, PDPCs).

	Factor 1 (PDPC 1)	Factor 2 (PDPC 2)
Vascular plants		
All species	-0.954	-0.165
Epiphytes	-0.746	-0.182
Herb layer	-0.650	-0.702
Shrub layer	-0.751	0.492
Tree layer	-0.716	0.530
Eigenvalue	3.0	1.1
Explained variance (%)	59.3	21.5
Cumulative explained variance (%)	59.3	80.8

**Multiple linear regression: predicting alpha diversity of geometrid moths from vegetation parameters**

In the MLRs, Fisher’s alpha of the geometrid moth assemblages was taken as the dependent variable. For the first MLR, the two PDPCs were combined with elevation to give three independent variables, after ensuring that no significant correlation between these factors occurred (Pearson’s  $R^2 < 0.025$  in all cases). The results (Table 5) show that neither of the two PDPCs explains a significant amount of variability within the data set, whereas elevation ( $\beta = -0.61$ ,  $P < 0.001$ ) is included in the model (adjusted  $R^2 = 0.38$ ,  $F_{1,46} = 29.6$ ,  $P < 0.001$ ).

The MLR model based on the FPCs as independent variables (Table 5) resulted in an adjusted  $R^2$  of 0.49 ( $F_{5,42} = 9.9$ ,

**Table 4** Loading of the species richness of the 40 most common plant families on nine principal components extracted by principal components analysis (unrotated floristic principal components, FPCs). Only PCs with eigenvalues > 1 are shown.

Plant family	Factor 1 (FPC1)	Factor 2 (FPC2)	Factor 3 (FPC3)	Factor 4 (FPC4)	Factor 5 (FPC5)	Factor 6 (FPC6)	Factor 7 (FPC7)	Factor 8 (FPC8)	Factor 9 (FPC9)
Aspleniaceae	0.694	0.396	0.215	0.094	0.072	0.316	0.025	0.131	0.267
Rubiaceae	0.848	-0.171	-0.166	0.119	-0.034	0.018	0.050	0.185	0.025
Asteraceae	-0.359	0.148	-0.095	-0.584	-0.183	-0.062	0.193	-0.081	-0.342
Poaceae	-0.272	-0.249	-0.241	-0.274	-0.660	-0.070	0.041	0.003	-0.304
Lomariopsidaceae	0.846	0.290	0.170	0.069	0.124	0.061	-0.078	0.196	0.122
Cyperaceae	0.023	0.478	0.302	0.192	-0.595	-0.060	0.106	0.244	0.179
Polypodiaceae	0.231	0.110	0.017	-0.077	0.022	0.871	0.082	0.105	-0.005
Hymenophyllaceae	0.867	0.174	0.170	0.048	0.051	0.077	-0.102	0.121	0.202
Euphorbiaceae	-0.193	-0.101	-0.902	-0.046	-0.076	0.133	-0.097	-0.058	0.007
Acanthaceae	0.443	-0.101	-0.451	-0.436	0.045	-0.203	0.128	-0.095	0.385
Rosaceae	0.021	0.782	0.198	0.167	0.032	0.040	0.134	-0.151	0.014
Balsaminaceae	0.776	0.370	0.173	0.011	-0.012	0.142	0.244	-0.075	0.067
Leguminosae	-0.256	-0.276	-0.674	-0.149	-0.444	-0.047	-0.048	0.107	0.000
Dennstaedtiaceae	0.162	0.325	0.353	0.431	-0.155	0.044	0.390	0.204	0.157
Myrsinaceae	0.610	0.432	0.149	0.227	0.203	-0.024	-0.108	0.129	-0.115
Piperaceae	0.651	-0.127	0.226	0.239	0.120	0.329	0.204	0.061	0.101
Urticaceae	0.150	0.330	-0.135	-0.021	0.034	-0.006	0.078	-0.071	0.773
Dryopteridaceae	0.507	0.656	0.212	0.086	0.004	0.113	0.125	0.037	0.135
Lamiaceae	0.325	0.057	-0.019	-0.181	-0.078	-0.006	0.782	-0.042	0.114
Cucurbitaceae	0.416	0.400	-0.027	-0.200	0.045	-0.016	0.257	-0.384	-0.067
Araliaceae	0.499	0.190	-0.158	0.274	0.245	0.026	0.113	0.488	0.218
Orchidaceae	0.234	0.205	-0.124	-0.090	-0.163	0.636	-0.239	-0.249	0.172
Begoniaceae	0.673	-0.205	0.121	0.343	0.314	-0.019	0.120	-0.090	-0.321
Commelinaceae	-0.277	-0.332	-0.127	-0.704	0.055	0.273	-0.057	-0.310	-0.001
Lauraceae	0.670	-0.103	-0.220	0.283	0.241	0.105	0.022	0.462	-0.069
Amaranthaceae	-0.168	-0.218	-0.444	-0.563	0.141	-0.260	0.050	-0.013	0.122
Apiaceae	-0.090	-0.056	-0.020	0.019	-0.827	0.101	0.025	-0.129	-0.059
Ericaceae	-0.275	0.535	0.124	0.121	-0.091	-0.008	-0.094	0.534	-0.026
Ranunculaceae	-0.179	0.603	0.070	0.059	0.031	0.088	0.474	0.022	-0.012
Rhamnaceae	-0.220	-0.210	-0.503	0.106	0.254	-0.114	0.086	-0.417	0.330
Podocarpaceae	0.564	0.474	0.192	-0.041	0.008	0.024	-0.213	0.186	0.291
Rutaceae	-0.064	-0.121	-0.914	-0.002	0.079	-0.070	0.055	0.033	0.173
Aquifoliaceae	0.870	0.000	0.150	0.050	0.027	0.014	0.011	0.024	0.152
Dracaenaceae	0.879	-0.083	0.050	-0.042	-0.050	0.167	0.125	-0.206	-0.142
Vitaceae	0.037	-0.315	-0.192	0.651	0.357	0.034	-0.063	-0.209	-0.148
Cyatheaceae	0.818	-0.075	0.086	0.074	-0.015	-0.057	0.047	-0.248	-0.112
Gesneriaceae	0.855	-0.036	0.033	0.027	0.039	-0.046	0.094	-0.161	-0.157
Grammitaceae	-0.024	0.841	0.113	-0.031	0.054	0.128	-0.093	0.135	0.221
Menispermaceae	-0.165	0.076	-0.474	0.078	0.096	0.142	0.086	0.114	0.697
Oxalidaceae	-0.176	-0.308	0.028	-0.643	0.030	0.352	0.170	-0.044	-0.143
Eigenvalue	12.05	5.28	3.58	3.12	1.96	1.71	1.40	1.17	1.09
Explained variance (%)	30.14	13.21	8.95	7.80	4.91	4.28	3.50	2.93	2.73
Cumulative explained variance (%)	30.14	43.35	52.30	60.10	65.01	69.29	72.79	75.73	78.46

$P < 0.0001$ ). This model included FPC 1 ( $\beta = -0.42$ ,  $P < 0.001$ ), FPC 4 ( $\beta = -0.34$ ,  $P = 0.001$ ), FPC 2 ( $\beta = -0.33$ ,  $P = 0.002$ ), FPC 3 ( $\beta = -0.28$ ,  $P = 0.007$ ) and FPC 6 ( $\beta = 0.24$ ,  $P = 0.021$ ), contributing 0.18, 0.12, 0.11, 0.08 and 0.06 to the adjusted  $R^2$ , respectively.

When PCs based on vegetation structure (SPCs) were used as independent variables, the resulting model (Table 5) had an adjusted  $R^2$  of 0.22 ( $F_{3,46} = 5.3$ ,  $P = 0.003$ ). SPC 3 ( $\beta = -0.33$ ,

$P = 0.014$ ), SPC 1 ( $\beta = -0.29$ ,  $P = 0.029$ ) and SPC 8 ( $\beta = 0.27$ ,  $P = 0.04$ ) contributed significantly, by 0.09, 0.07 and 0.06, to the adjusted  $R^2$ . A comparison of the three MLR models using the Akaike information criterion (AIC) showed that the model including the FPCs (AIC = 300.5) performed only slightly better than the model using elevation as the single criterion (AIC = 302.9), but both were superior to the model based on the structural vegetation data (AIC = 322.6).

**Table 5** Results of the three stepwise forward multiple linear regression models, using Fisher's alpha of geometrid moth assemblages as the dependent variable. The phytodiversity principal components combined with elevation (Model 1), the floristic principal components (Model 2), and the structural principal components (Model 3) served as independent variables.

Model and independent variables	Multiple			Adjusted		
	<i>R</i>	<i>F</i>	<i>R</i> <sup>2</sup>	<i>R</i> <sup>2</sup>	<i>P</i>	d.f.
1. Diversity of vegetation layers and elevation	0.625	29.561	0.391	0.378	< 0.0001	1.46
2. Diversity of dominant plant families	0.736	9.934	0.542	0.487	< 0.0001	5.42
3. Vegetation structure	0.517	5.339	0.267	0.217	0.0032	3.44

Model	Variable	$\beta$	Standard error of $\beta$	<i>B</i>	<i>P</i>	<i>t</i>
1. Diversity of vegetation layers and elevation	Intercept	–	–	33.071	< 0.0001	9.85
	elevation	–0.607	0.114	–0.008	≤ 0.0001	–5.31
2. Diversity of dominant plant families	Intercept	–	–	15.819	< 0.0001	21.45
	FPC1	–0.421	0.100	–3.143	0.0001	–4.22
	FPC4	–0.344	0.100	–2.563	0.0014	–3.44
	FPC2	–0.329	0.100	–2.452	0.0021	–3.29
	FPC3	–0.283	0.100	–2.113	0.0072	–2.84
	FPC6	0.241	0.100	1.796	0.0208	2.41
3. Vegetation structure	Intercept	–	–	15.819	< 0.0001	16.72
	SPC3	–0.329	0.128	–2.454	0.0139	–2.57
	SPC1	–0.290	0.128	–2.163	0.0289	–2.26
	SPC8	0.273	0.128	2.037	0.0390	2.13

$\beta$  represents the standardized and *B* the non-standardized regression coefficient; *t* represents the *t*-test value.

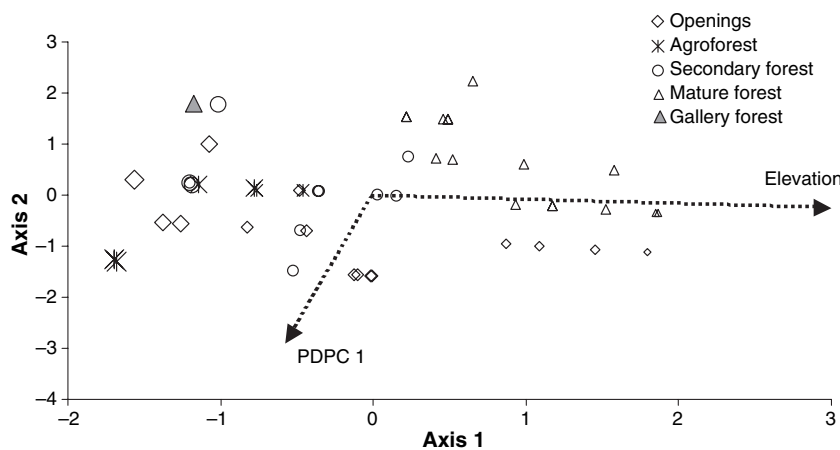
**Redundancy analysis: geometrid moth species composition and vegetation**

The analysis of changes in the composition of geometrid moth assemblages in relation to vegetation structure and floristic composition resulted in similar outcomes for Chord- and Hellinger-distance-transformed geometrid moth data. Therefore, only results obtained after Chord-distance transformation will be presented here.

A first RDA model (Fig. 3) was calculated combining the two PDPCs and elevation as independent variables. Elevation alone accounted for 19.6% of the variability in the data set (*F* = 11.5, *P* = 0.002, related to the first axis in reduced ordination space: Pearson's *R*<sup>2</sup> = 0.99, *P* < 0.001), and the PDPC 1 also contrib-

uted significantly to the explained variance (5.0%, *F* = 2.5, *P* = 0.028, related to the second ordination axis).

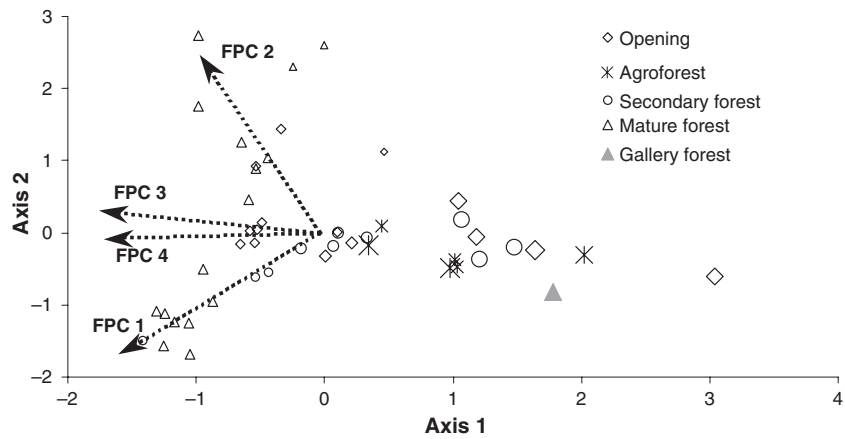
With regard to the dominant plant families, the first four FPCs all explained similarly significant proportions of the variation in the geometrid moth distribution. FPC 1, FPC 4, FPC 3 and FPC2 explained 11% (*F* = 5.7, *P* = 0.002), 10% (*F* = 5.1, *P* = 0.002), 10% (*F* = 5.1, *P* = 0.002) and 9% (*F* = 4.5, *P* = 0.006) of the variance in the data set, respectively. Overall, 40% of the variation in the geometrid moth assemblages could be related to these four FPCs. In the ordination (Fig. 4), FPCs 1 and 2 were located at an angle of roughly 90° to each other. FPCs 3 and 4 took intermediate positions between them and ran parallel to the first ordination axis. The distribution of geometrid moth assemblages along



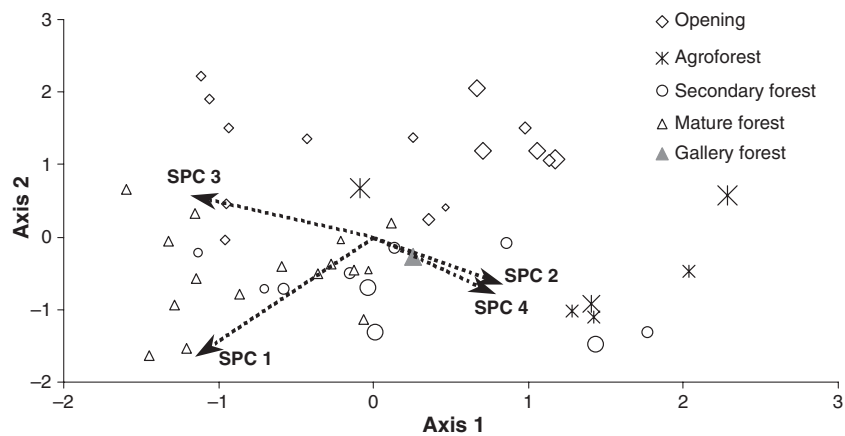
**Figure 3** Ordination plot for the redundancy analysis combining the Chord-distance-transformed geometrid distribution as the dependent variable and the phytodiversity principal components (PDPCs) combined with elevation as independent parameters (elevation: *F* = 11.5, *P* = 0.002, explained variance = 20%; PDPC1: *F* = 2.4, *P* = 0.028, explained variance = 5%). Symbol size decreases with increasing elevation of the plots.



**Figure 4** Ordination plot for the redundancy analysis combining the Chord-distance-transformed geometrid distribution as the dependent and the floristic principal components (FPCs) as independent parameters (FPC1:  $F = 5.7$ ,  $P = 0.002$ , explained variance = 11%; FPC3:  $F = 5.1$ ,  $P = 0.002$ , explained variance = 10%; FPC4:  $F = 5.1$ ,  $P = 0.002$ , explained variance = 10%; FPC2:  $F = 4.5$ ,  $P = 0.006$ , explained variance = 9%). Symbol size decreases with increasing elevation of the plots.



**Figure 5** Ordination plot for the redundancy analysis combining the Chord-distance-transformed geometrid distribution as the dependent variable and the structural principal components (SPCs) as independent parameters (SPC1:  $F = 3.9$ ,  $P = 0.002$ , explained variance = 8%; SPC3:  $F = 3.9$ ,  $P = 0.006$ , explained variance = 8%; SPC4:  $F = 2.2$ ,  $P = 0.036$ , explained variance = 5%; SPC2:  $F = 2.1$ ,  $P = 0.042$ , explained variance = 4%). Symbol size decreases with increasing elevation of the plots.



the first axis was significantly correlated with the altitude of their habitats (Pearson's  $R^2 = 0.45$ ,  $P < 0.001$ ). Geometrid moth assemblages from habitats with similar vegetation types did not group together.

In relation to vegetation structure, the first four SPCs in the RDA (Fig. 5) again explained a significant proportion of the variance in the geometrid species composition at the various plots. Nevertheless, with 8% (SPC 1,  $F = 3.9$ ,  $P = 0.002$ ), 8% (SPC 3,  $F = 3.9$ ,  $P = 0.006$ ), 5% (SPC 4,  $F = 2.2$ ,  $P = 0.036$ ) and 4% (SPC 2,  $F = 2.1$ ,  $P = 0.042$ ), the combined explained variance in the geometrid moth data set attributable to these four SPCs amounted to only 25%. Similar to the RDA based on plant families, the first axis in this ordination again represented the altitudinal gradient, although the correlation between altitude and plot scores on the first axis was slightly weaker (Pearson's  $R^2 = 0.36$ ,  $P < 0.001$ ). SPCs 2 and 4, and SPC 3, pointing in the opposite direction, mainly stretched along the first axis, whereas SPC 1 reached high scores on both the first and second axis. In the diagram, assemblages originating from habitats with similar vegetation types were mostly grouped together, with mature forest assemblages in the lower left section, assemblages from openings and gaps in the upper section, and agroforestry assemblages mostly in the lower right section.

## DISCUSSION

The most important outcome of this study is that the alpha diversity of geometrid moths in the study area is not directly linked to the species richness of vascular plants in a given plot. This stands in contrast to the central hypothesis that had motivated the study, namely that the species richness of plants as primary producers determines the alpha diversity of consumers at the next higher trophic layer (Siemann, 1998; Lewinsohn & Roslin, 2008). In contrast, the alpha diversity of geometrid moths seems to be very strongly related to the suite of environmental factors associated with changes in elevation, which as a single factor explains 38% of the variation in Fisher's alpha.

In contrast to mere plant species richness, the composition of the vegetation (i.e. changes in the contribution of the 40 most dominant families of vascular plants) proved to explain nearly half of the variation in geometrid moth alpha diversity. Does this result suggest a direct functional link between these plant families and geometrid moths? A closer inspection of the PCs representing the diversity of the various vascular plant families reveals that this inference can only partly be justified. The first FPC, which explained 18% of the variation in geometrid alpha diversity, is strongly related to a number of

vascular plant groups, such as pteridophytes, Balsaminaceae and Piperaceae. However, these groups are, to our current, limited, knowledge, of little importance as geometrid caterpillar food plants. Furthermore, the standardized regression coefficient obtained in the MLR model is negative, whereas the aforementioned plant taxa have positive loadings on this principal component. Hence, an increase in the species richness of these plant groups leads to a significant decrease in geometrid moth diversity. As species richness, especially of ferns, is closely linked to extremely humid conditions, the pattern discovered here is likely to reveal a negative correlation between geometrid moths on Mount Kilimanjaro and the extremely humid conditions prevailing in the central parts of the mountain rain forest, as was observed in an earlier study (Axmacher *et al.*, 2004a).

FPC 2 explains 11% of the variation in geometrid moth alpha diversity and is highly correlated with elevation. Again, the regression coefficient is negative, whereas all plant families associated with this FPC have a positive loading. Hence, the decrease in geometrid alpha diversity associated with this FPC can again be related to adverse changes in environmental conditions with increasing elevation, rather than directly to potential food plant diversity. The floristic principal components FPC 4 and 6, which collectively explain a further 18% of the variation in Fisher's alpha, are linked to Commelinaceae, Oxalidaceae, Polypodiaceae, Orchidaceae and Vitaceae, with the first four families positively related to geometrid diversity. However, very few records of geometrid caterpillars feeding on members of any of these plant families exist. This renders a direct relationship via food resources again unlikely. It cannot be ruled out, however, that some geometrids on Mount Kilimanjaro do feed on such plants, as food plant data records are extremely sketchy. Finally, the regression coefficient for FPC 3 is negative, and two plant taxa known to be important food plant for African geometrids – Euphorbiaceae and legumes – have high negative loadings on this principal component. Hence, there is a strong possibility that the 8% explained variance in Fisher's alpha by this principal component is indeed related to food plant associations.

Vegetation structure overall explains only 22% of the variation in geometrid alpha diversity. The results underline the trends observed above with regard to floristic composition.  $\beta$  for SPC 3, which explains 9% of the variability, is negative, and the leaf form 'pinnate' has a high negative loading on this principal component. This leaf form is common among legumes, one of the most important food plant groups for African geometrid moths. The increase in geometrid alpha diversity associated with a significant increase in the leaf form typical for legumes might hence be interpreted as a direct link. The other two SPCs significantly influencing Fisher's alpha and jointly explaining 12% of the variation represent structural characteristics typical for closed, mature forest, namely thick stems, a large maximum height of trees and large crowns, leading to a dense cover of the tree layer and a high cover of stems by vascular epiphytes. All these factors are negatively associated with alpha diversity of

geometrid moths, as is expected given the low species numbers of geometrid moths in Mount Kilimanjaro's closed mountain rain forests.

These results are somewhat contradictory to the findings of Beck *et al.* (2002) and of Intachat *et al.* (1997, 1999b), who recorded a significant positive correlation between geometrid moth diversity and plant diversity, particularly in the undergrowth in Malaya and Borneo. However, Brehm *et al.* (2003b) did not find significant correlations between the alpha diversity of geometrids and plant species richness in the Ecuadorian Andes. Studies on butterflies present a similarly inconclusive picture, with Schulze *et al.* (2004) recording significant positive correlations between the diversity of butterflies, beetles and plants from Sulawesi, but Kremen (1992) finding no such correlations – either for plant diversity or for parameters of vegetation structure. Finally, Hawkins & Porter (2003) argue that, even though they recorded a significant correlation between the diversity of butterflies and plants, this linkage is widely indirect via the similar responses of the two groups to the same environmental parameters. This is in line with our analyses, in that correlations between the alpha diversity of geometrids and the species richness of the most common vascular plant families are also widely indirect and can be attributed to the abiotic conditions encountered at the respective habitats, whereas direct links are much weaker. In this regard, it is worth emphasizing that the inclusion of phytodiversity parameters did not improve model quality (as measured by the AIC) when predicting geometrid moth diversity, while a regression model encompassing vegetation structure performed even less well in that regard.

A number of studies show strong positive correlations between the diversity of plants and that of herbivorous insects (Knops *et al.*, 1999; Haddad *et al.*, 2001; Asteraki *et al.*, 2004; Procheş & Cowling, 2006; Lewinsohn & Roslin, 2008), whereas other studies are much less conclusive (Southwood *et al.*, 1979; Prendergast *et al.*, 1993; Burel *et al.*, 1998; Siemann, 1998; Kruess & Tschardtke, 2002). These discrepancies emphasize the importance of abiotic factors, rather than of plant diversity alone, as key to explaining differences in insect diversity. This is especially evident for species-rich insect ensembles, which probably contain a significant fraction of polyphagous herbivores and in which component species have very different specific affiliations with regard to the types and numbers of plant species eaten. Both of these properties apply to the Geometridae, but also to many other clades of herbivorous insects. The more polyphagous species an insect clade or guild contains, the weaker the relationship between plant and insect diversity should be. Under such conditions, it would be optimal to restrict plant diversity measures to those fractions of plants that can be eaten by the groups in question. Unfortunately, data on host plant affiliations of African Geometridae are still too sparse to allow a more rigorous analysis of this kind.

With regard to the species turnover of geometrid moth assemblages, our results are very similar to the patterns

observed by Brehm *et al.* (2003a). On Mount Kilimanjaro, habitat altitude again emerged as the single most important factor governing turnover rates, explaining almost 20% of the beta diversity. Similarly, and in contrast to the lack of correlation between altitude and species richness of plants, Hemp (2006a) also identified altitude, followed by temperature, as the main determinant for changes in plant species composition.

Ordination plots for all three RDA models reveal that geometrid moth samples are primarily ordered according to habitat elevation along the first axis. The species richness of vascular plants, the contribution of major plant families, as well as parameters of vegetation structure all contributed, to different degrees, to explaining significant, but smaller, proportions of the spatial dynamics of geometrid moth species composition. As with the analysis of alpha diversity, it has to be remembered that, for the interpretation of the second RDA model, FPC 1 represents a gradient of humidity, whereas FPC 2 represents the altitudinal gradient. Therefore, even though significant, the direct biotic contribution of plant species composition to explaining the variance in species composition of geometrid moths is again much smaller than are the abiotic effects of temperature and humidity. In contrast to the first two ordinations, the third ordination based on vegetation structure led to a distribution of plots into groups representing different habitat types.

## CONCLUSIONS

We conclude that, although the composition, species richness and structure of vegetation are all significantly correlated with the alpha diversity and species turnover of herbivorous geometrid moth assemblages in some way, these relationships are often indirect, via abiotic parameters that concomitantly affect both the vegetation and the moth fauna. Elevation was identified as the single best predictor of geometrid moth alpha diversity and change in species composition. A second important parameter is humidity, which is also closely linked to vegetation structure. Compared with these abiotic conditions, direct links between geometrid alpha diversity and potential food plants are much weaker predictors on the community level. Such links may become more pronounced at the level of a particular species or guild associated with subsets of the local flora. The lack of very strong links may be taken as evidence that few geometrid moths on Mount Kilimanjaro are so narrowly specialized with regard to their host plants that any change in the vegetation translates directly into faunal turnover. For example, Novotny *et al.* (2005) demonstrated for caterpillar assemblages on *Ficus* trees along an elevational gradient that host plant affiliations give sufficient leverage to enable shifts between related plant species. Accordingly, the assumption of a clear correlation between floral species richness and herbivore diversity must be rejected as overly simplistic. As a corollary, this means that the species richness of vascular plants cannot universally be used as a suitable biodiversity indicator, for example for the mega-diverse insect

taxa at the next higher trophic level. The strong focus on plant diversity inventories commonly applied for the identification of biodiversity hotspot areas, combined with a disregard of invertebrate diversity patterns, therefore seems highly problematic.

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## BIOSKETCH

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