



Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect

Jan C. Axmacher*, Gabriele Holtmann*, Luis Scheuermann†, Gunnar Brehm†, Klaus Müller-Hohenstein* and Konrad Fiedler†

*Chair of Biogeography, University of Bayreuth, 95440 Bayreuth, Germany.
E-mail: jan.axmacher@web.de
†Chair of Animal Ecology I, University of Bayreuth, 95440 Bayreuth, Germany

ABSTRACT

Geometrid moths were investigated at 26 sites on 9 elevational levels along an elevational transect at Mt. Kilimanjaro (Tanzania), stretching from the fine-grained mosaic of small agroforest plots with combined cultivation of trees, shrubs and crops at 1650 m through mountain rainforest to heathland at 3300 m. We sampled moths manually at light between 19 : 00 and 22 : 00 in the rainy seasons of March to May and October to January in the years 2000, 2001 and 2002.

Along the transect, the composition of moth communities changed from a domination by Sterrhinae and Ennominae to a dominance of Larentiinae with increasing elevation. Overall, alpha diversity was very low compared to other tropical mountain regions. Fisher's alpha showed a maximum of 30 in the agroforest mosaic at 1650 m and decreased to values around 12 in the mountain rainforest. Communities of geometrid moths within the forest belt were significantly dissimilar from communities outside the forest. The diversity patterns on Mt. Kilimanjaro can be related to the young age, island-like position and history of the mountain. These factors have led to the formation of a homogeneous upper mountain rainforest habitat which in turn houses homogeneous moth communities with a low diversity compared to habitats at lower elevations. Here, a heterogeneous habitat mosaic allowing the intrusion of savannah species into this former forest habitat may account for an increased diversity. In the heath zone above the forest, climatic conditions are very harsh, permitting only few specialists to thrive in this ericaceous woodland. Edge effects were discernible at the forest–heathland boundary where some moth species from heathland invaded the closed forest. At the boundary between agroforest and a forest mosaic of exotic *Acacia* and *Eucalyptus* forest plantations and natural mountain forest, diversity values remained low as the dominant species *Chiasmia fuscataria* accounted for far higher proportions than other dominant species in any of the other habitats.

Keywords

Diversity, edge effect, elevation, Mt. Kilimanjaro.

Correspondence: Jan C. Axmacher, Chair of Biogeography, University of Bayreuth, Universitätsstr. 30, 95440 Bayreuth.
E-mail: jan.axmacher@web.de

INTRODUCTION

Many environmental factors such as mean annual temperature, levels of radiation or precipitation change along elevational gradients (Stevens, 1992; Kessler *et al.*, 2001; Lomolino, 2001). In elevational transects, geographical distances between different environments are small, thus allowing for a great potential of separating the influence of steep gradients of actual environmental factors on biodiversity from historical constraints (e.g. barriers to colonization).

Studies on different taxa along elevational transects reveal that there is large variation in diversity patterns. Even though diversity generally decreases at higher elevations in plants (Hamilton & Perrott, 1981; Kessler, 2001) and animals (Rahbeck, 1995; Gaston, 2000), various plant (Pócs, 1991; Kessler, 2001; Hemp, 2002) and animal taxa (Rahbeck, 1995, 1997; Heaney, 2001; Nor, 2001; McCain, 2004) exhibit a diversity maximum at mid-elevations, leading to a hump-backed diversity distribution.

For insects and other ectothermic invertebrates, most studies revealed a hump-backed distribution (Holloway *et al.*, 1990;

McCoy, 1990; Olson, 1994; Holloway, 1997; Pycz & Wojtusiak, 2002), whereas Wolda (1987) found a general decrease with increasing elevation. Brehm *et al.* (2003b) recorded an unusual pattern for geometrid moths in an Andean mountain rainforest. They discovered a broad maximum diversity plateau in the mountain rainforest between 1040 and 2670 m. Schulze (2000) likewise showed that high levels of diversity in geometrid moth communities occur over a broad elevational range in the tropical mountain rainforest of Mt. Kinabalu, Borneo.

To date, no comparable studies have been performed in the Afrotropical realm. The aim of our study is to investigate the diversity of geometrid moth communities along an elevational transect in Africa to validate if the incidence of broad plateaus of highly diverse communities is a general characteristic of geometrid moths in tropical mountain forests. Given the frequent use of geometrid moths as indicators for changes of environmental conditions (e.g. Intachat *et al.*, 1999b; Beck *et al.*, 2002; Thomas, 2002), it is particularly important to test how concordant results are across different habitats and regions.

Furthermore, we were interested in diversity changes that occur at habitat boundaries. It is commonly accepted that diversity increases at habitat boundaries due to a mixing of species from neighbouring habitats (Murcia, 1995; Risser, 1995; Didham, 1997). However, based on their investigation of amphipods, carabids and ants in an Afrotropical forest/grassland ecotone, Kotze & Samways (2001) stated that this effect might not be a general pattern. We therefore examined if the diversity of geometrid moth communities reaches maximum values at the two prominent landscape boundaries that occur along the elevational transect at Mt. Kilimanjaro, the borders between tropical mountain rainforest and either heathland or agroforest, respectively.

METHODS

Study area

Twenty-six sampling sites were selected along a transect ranging from 1650 m to 3300 m at the south-western slopes of Mt. Kilimanjaro, Tanzania. These sites were situated in the centre of plots with a homogeneous vegetation cover of more than 400 m², so that moth catches at weak light sources should largely reflect the local communities. The minimum distance between neighbouring sites was 50 m, with lamps not being visible from neighbouring sites.

Above the savannah plains on the foothills of Mt. Kilimanjaro, an agricultural belt stretches from about 1200 to 1900 m on the southern slopes. Higher elevations within this agricultural belt are characterized by a fine-grained mosaic of small agroforest plots, the traditional land-use patterns of the local Chagga tribe. Three sites were positioned within this mosaic in Machame village situated at an elevation of 1650 m. Three further sites were located in the transition zone between the agroforest mosaic and mountain rainforest near the Machame National Park Gate at 1850 m.

The mountain rainforest itself is highly disturbed at lower altitudes, but the intensity of logging and burning decreases with

increasing altitude. Inside the forest belt, three sites each were investigated at elevational levels of 2100 m inside heavily degraded secondary forest and at 2250 m, 2550 m, 2700 m and 2900 m, respectively, in the mature forest belt. All sites were situated near the Machame tourist route.

Above 3000 m, the natural forest has been widely replaced by ericaceous woodland as an effect of frequent large-scale fires (Salehe, 1997; Hemp & Beck, 2001). At 3100 m, we investigated two sites within a remnant mountain rainforest patch of several thousand square meters, with a third plot situated in the surrounding ericaceous woodland. Two more sites were located at an altitude of 3300 m in the heathland (Table 1). All heath plots had been affected by heavy fires in 1997 and were covered by dense re-growth of *Erica* species reaching a height of about 40 cm at the time of our study. The location of our sampling sites is illustrated in Fig. 1.

Sampling and identification of the moths

We selected geometrid moths as study group since they have often been used as models to investigate a range of ecological issues (Holloway, 1985; Chey *et al.*, 1997; Intachat *et al.*, 1997; Intachat *et al.*, 1999a; Willott, 1999; Kitching *et al.*, 2000; Beck *et al.*, 2002; Brehm *et al.*, 2003a). With about 21,000 known species (Scoble, 1999), this family is one of the largest in the Lepidoptera, yet taxonomic data on geometrids is comparatively good. Furthermore, geometrid moth individuals are encountered in large numbers also at high altitudes, rendering them an ideal group for studies along elevational transects.

Moths were attracted by a weak accumulator driven UV-emitting light source (Sylvania blacklight-blue, F 15 W/BLB-TB, Osram, Munich) placed within a white reflective gauze cylinder (diameter 0.8 m, height 1.7 m). Insects were sampled manually while they rested on the gauze. Standardized samples were taken during 82 catches between 19:00 and 22:00 local time. We restricted sampling to the rainy seasons from March to May and November to January in the years 2000, 2001 and 2002. At all sites, at least two nightly catches were performed (average: 3.2 ± 1.5 catches per site). Average temperature and relative humidity during sampling ranged from 17 °C and 84% at 1650 m to an average of 8 °C and 96% at 3300 m. We continued sampling until the pooled sample size exceeded 75 individuals per site. As the only exception, at site 2900 P3 we just obtained 52 geometrids during three nights. Catches were restricted to periods without strong moonlight (Yela & Holyoak, 1997), avoiding the time five days before to five days after full moon. All specimens were subsequently spread, sorted to morphospecies level and identified as far as possible at the Zoologische Staatssammlung, Munich.

Data analysis

To analyse the gross taxonomic composition of geometrid moth communities in relation to elevational changes, proportions of geometrid subfamilies were calculated for each site. The number of species sampled often yields a poor estimate of alpha diversity (Gotelli & Colwell, 2001). Especially for species-rich communities

Table 1 Number of geometrid moth species, individuals, and values for three alpha diversity measures at 29 sampling sites (leading figures in site labels indicate their elevation)

Site	Species	Individuals	Fisher's alpha	Chao 1	Rarefaction ($n = 50$)	habitat
1650 P1	37	77	28.0	63.4	28.6	agroforest
1650 P2	60	162	34.5	89.2	30.7	agroforest
1650 P3	39	84	28.3	62.2	28.4	agroforest
1850 P1	27	127	10.5	53.7	15.9	agroforest
1850 P2	28	117	11.7	50.0	15.6	agroforest
1850 P3	29	263	8.3	48.6	9.7	forest
2050 P1	32	131	17.7	67.0	19.9	forest
2050 P2	38	134	13.6	50.5	20.8	forest
2050 P3	23	150	7.6	28.8	14.1	forest
2250 P1	19	168	5.5	19.5	12.5	forest
2250 P2	22	149	7.1	29.6	12.9	forest
2250 P3	27	240	7.8	40.1	11.0	forest
2550 P1	33	177	11.9	44.6	20.2	forest
2550 P2	28	148	10.2	42.1	18.3	forest
2550 P3	31	107	14.6	42.3	21.5	forest
2700 P1	30	215	9.5	36.5	16.6	forest
2700 P2	31	215	9.9	42.6	17.4	forest
2700 P3	37	178	14.2	39.0	21.5	forest
2900 P1	32	147	12.6	36.5	19.7	forest
2900 P2	38	181	14.7	50.1	19.7	forest
2900 P3	21	52	13.1	40.9	20.5	forest
3100 P1	34	138	14.4	55.3	20.7	forest
3100 P2	26	196	8.1	27.9	14.9	forest
3100 P3	24	75	12.1	64.6	19.4	heath
3300 P1	21	157	6.5	26.3	14.7	heath
3300 P2	19	184	5.3	19.7	12.9	heath

of mobile organisms, complete inventories are virtually impossible to obtain. As a consequence, the observed number of species depends on sample size and sampling effort. We therefore used Fisher's alpha of the log series distribution as a measure of alpha diversity. Fisher's alpha is commonly employed in studies of insect diversity in the tropics (e.g. Wolda, 1983; Brehm *et al.*, 2003b; Schulze & Fiedler, 2003; Axmacher *et al.*, 2004).

Other approaches to assess alpha diversity are estimators for the total number of species which can be expected to occur at a site (Colwell & Coddington, 1994) and rarefaction of samples to a standardized sample size (Hurlbert, 1971). We employed the Chao 1 index and Hurlbert's rarefaction in our study. These three diversity indices were selected as they have proved to be widely independent of the sample size, and a comparison of the results yielded by the three mathematically completely different approaches allows conclusions about the robustness of the results gained.

For the analysis of beta diversity among communities of mobile organisms with many rare species, similar constraints resulting from sampling effects apply as for alpha diversity. We used nonlinear multidimensional scaling (NMDS) of the chord-normalized expected species shared (CNESS) index of dissimilarity (Trueblood *et al.*, 1994) for a small ($m = 1$), intermediate ($m = 35$) and large ($m = 70$) value of the sample size parameter m to analyse the similarity between communities of different sites and altitudes. For a low sample size parameter m , the similarity

between samples is strongly determined by dominant species, whereas for high values, the occurrence of rare species becomes increasingly important. Thus, by varying m , the similarity of samples can be investigated both with regard to dominant as well as rare species. Dissimilarity of moth communities within the forest belt to communities above and below the forest was investigated by an analysis of similarities (ANOSIM).

Fisher's alpha and Chao 1 were calculated using Estimates 6.0b1 (Colwell, 2000). The CNESS index was determined using COMPAH (Gallagher, 1998) and rarefaction and ANOSIM analyses were performed using PRIMER 5 (Clarke & Warwick, 2002). All other statistical analyses were performed using Statistica 6.0 (Statsoft, Tulsa, UK).

RESULTS

Subfamily proportions

We sampled a total of 3972 moths representing 188 morphospecies (Axmacher, 2003). Ninety-four (50%) of these morphospecies comprising 78% of all individuals were identified to species level, a further 86 (46%) morphospecies to genus level, and eight species (4%) could only be attributed to subfamily level.

Moths belonging to the five subfamilies Larentiinae, Ennominae, Sterrhinae, Geometrinae and Desmobathrinae were encountered

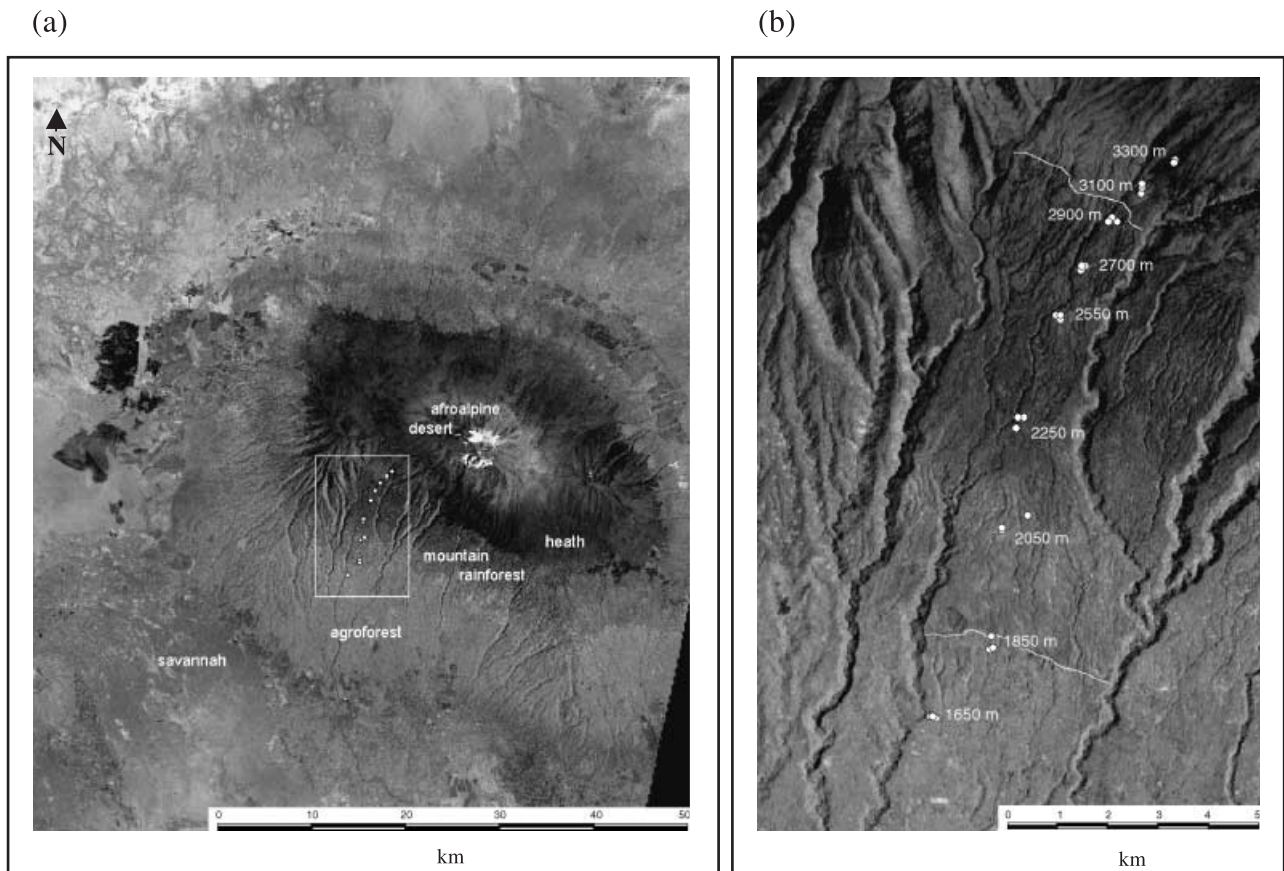


Figure 1 Satellite image of Mt. Kilimanjaro (Landsat 7 TM +, channel 8 (multispectral), resolution $15\text{ m} \times 15\text{ m}$, 21.02. 2000, UTM 270000–340000, 9620000–9700000 (a); 300000–310000, 9645000–9660000 (b)). White dots indicate the locations of study plots, white lines show the lower and upper boundary of the closed mountain rainforest in the study area.

in the study area. The proportions of subfamilies based on morphospecies found at each plot are presented in Fig. 2(a). Members of Sterrhinae accounted for high proportions only at the lowest elevations and strongly decreased with elevation (Spearman rank correlation: $r_s = -0.80$, $P < 0.001$, $n = 26$). No Sterrhinae moths were encountered above 2600 m. For Ennominae, highest proportions in the catches were also recorded at low elevations, this subfamily also decreased with increasing elevation ($r_s = -0.59$, $P < 0.01$). However, proportions close to 40% were still recorded at single sites situated around 2900 m. The proportion of Larentiinae, on the opposite, increased with increasing elevation ($r_s = 0.44$, $P < 0.05$), with species of this subfamily becoming dominant at all sites above 2000 m. Geometrinae did not show a consistent trend along the transect, while members of the subfamily Desmobaethrinae were generally rare.

When considering proportions of individuals of the different subfamilies in the catches (Fig. 2b), the resulting picture slightly changes. Again, Sterrhinae were most numerous at low elevations ($r_s = -0.83$, $P < 0.001$). Ennominae clearly dominated at the boundary of agricultural land and forest with decreasing abundances above this boundary ($r_s = -0.66$, $P < 0.001$). Geometrinae showed a bimodal pattern, accounting for large proportions at high elevations especially in heath vegetation as well as in

the agroforest region around 1650 m. This bimodal pattern was caused by the mass occurrence (251 individuals) of one single species (*Comostolopsis simplex*) in heathland and near the upper tree line. Other Geometrinae in the study area were restricted to the mature forest and agroforest zone. The proportion of Larentiinae increased with elevation ($r_s = 0.38$, $P = 0.06$) and representatives of this subfamily accounted for more than 50% of the individuals at all sites above 2000 m. This subfamily was generally very numerous in the study area with the exception of the agroforest–forest boundary.

Alpha- and gamma-diversity of geometrid ensembles

Fisher's alpha at individual sites ranged from 34.5 in the agroforestry zone at 1650 m to 5.3 at 3300 m in the ericaceous woodland (Table 1). Estimated total species richness and rarefied species numbers were both highly correlated with values of Fisher's alpha (Pearson correlation: $r_p > 0.83$, $P < 0.001$, $n = 26$). Thus, we hereafter only discuss results for the latter. Figure 3 illustrates the changes in mean values of Fisher's alpha (for groups of three replicate sites per elevational level) along the elevational transect as well as the values for a combination of all catches at each elevational level.

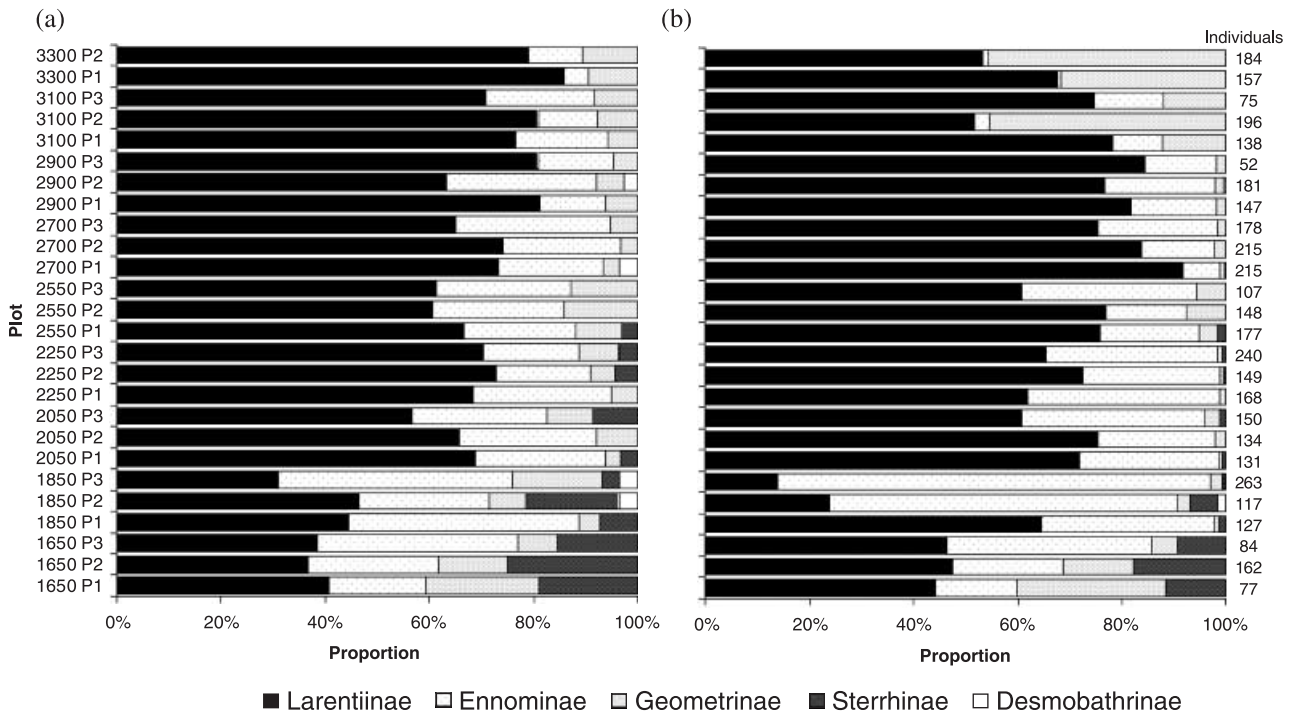


Figure 2 Proportion of subfamilies at the study sites, sorted by altitude. (a): species number (b): number of individuals, the figure on the right shows the sample size.

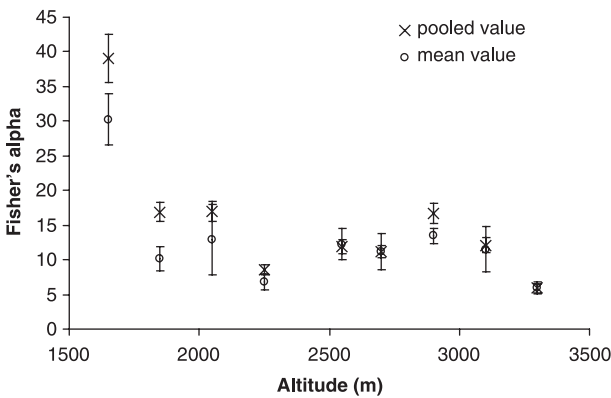


Figure 3 Fisher's alpha at different elevational levels along the transect: × Fisher's alpha of all catches pooled at one elevational level; ○ mean value of Fisher's alpha of the three samples at each elevational level; bars indicate standard deviations.

Within the agricultural belt, the diversity of geometrid moth communities reaches a mean value of 30.5 at 1650 m. It then strongly declines at the agroforest-mountain rainforest transition zone to values around 10. With the exception of the most humid region within the mountain rainforest at 2250 m where the diversity of geometrid moths is exceptionally low (Axmacher *et al.*, 2004), mean values vary only marginally ($\alpha = 11.2\text{--}12.9$) in the forest belt between 2100 and 3100 m. Geometrid moth communities occurring in the ericaceous woodland at 3300 m have a very low diversity with alpha values ranging between 5.5 and 6.5.

Values of Fisher's alpha for samples pooled within elevational levels strongly correlate with mean values of Fisher's alpha per elevational level along the transect (Pearson correlation coefficient: $r_p = 0.97$, $P < 0.001$, $n = 9$). Diversity measures for pooled samples are generally slightly higher than means of individual samples. They decrease from 39.1 at 1650 m to values between 11.2 and 17.0 in the forest and 5.9 above the tree line. The moth community in closed forest at 2250 m again showed a very low diversity ($\alpha = 8.6$). Fisher's alpha for the combination of all samples along the elevational transect (i.e. as a measure of gamma diversity) reaches a value of 41.0, which is not significantly higher than the value of geometrid moth communities at 1650 m in the agroforestry zone. The extrapolated number of species along the whole transect is 245. The 188 species caught would hence represent 77% of all species expected to occur along the transect.

Beta diversity along the elevational gradient

For all three different values of the sample-size parameter m , non-metric multidimensional scaling (NMDS) of the chord-normalized expected species shared (CNESS) index of dissimilarity (Fig. 5) yields similar ordinations of the moth ensembles in a horse-shoe pattern. Samples are ordered along the first extracted dimension according to the altitude of their sampling sites (Pearson correlation between scores of first dimension and altitude: $r_p > 0.68$, $P < 0.001$, $n = 26$). The only exception from this regular pattern are samples from sites within the rainforest situated at 2550 m and 2700 m, which change positions in the ordination for $m = 1$.

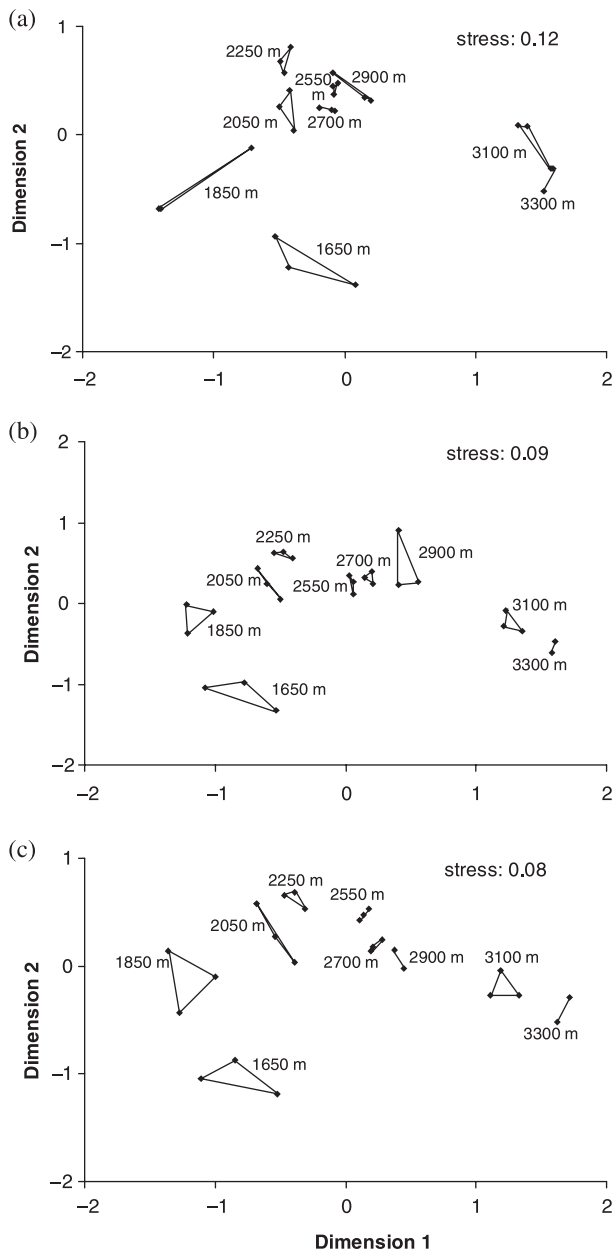


Figure 4 Nonlinear two-dimensional scaling (MDS) of the CNESS dissimilarity matrix for sample-size parameters $m = 1$ (a), $m = 35$ (b), and $m = 70$ (c). Samples from sites located at identical altitude are connected by lines.

Furthermore, the ordinations reveal that moth communities in the finely grained agroforestry mosaic at 1650 m and in the agroforest-forest transition zone at 1850 m appear to be more dissimilar from each other than communities at most other elevational levels. Moth samples from 2900 m elevation provide the only exception displaying a greater dissimilarity, especially for $m = 35$. The analysis of similarity (ANOSIM, 999 permutations) shows that moth communities from sites below ($r > 0.86$, $P < 0.001$) and above ($r = 0.93$, $P < 0.002$) the forest belt are significantly dissimilar from ensembles within this belt.

DISCUSSION

Subfamily composition and diversity patterns along the elevational gradient

Changes in subfamily composition of geometrid moths along elevational transects in the tropics have been studied in the Ecuadorian Andes (Brehm & Fiedler, 2003). The results of our study strongly resemble the changes observed in Ecuador, with Sterrhinae and Ennominae accounting for highest proportions at low elevations, while Larentiinae dominate at higher elevations. This also parallels patterns of geometrid moths along latitudinal gradients, where Larentiinae become increasingly dominant in temperate and boreal zones as compared to the tropics (Brehm & Fiedler, 2003).

Local diversity of geometrid ensembles on Mt. Kilimanjaro decreases with increasing elevation at the lowest portions of our transect, reaching but very low values in the montane rainforest above 2000 m. This stands in stark contrast to the findings of Brehm *et al.* (2003b) in Ecuador, who recorded a diversity plateau within the mountain rainforest up to 2670 m with extremely high levels of diversity (Fisher's alpha ranging from 69 to 131). Accordingly, geometrid diversity in the mountain rainforest of Mt. Kilimanjaro is nearly 10 times lower than in the tropical Andes. Values as observed on Mt. Kilimanjaro even rank at the lower margin of the range found in temperate-zone geometrid moth communities (Mörtter, 1988; Thomas, 2002). Diversity patterns were concordant using various quantitative measures (Fisher's alpha, extrapolated or rarefied species richness, averaged individual vs. pooled samples from elevational levels), underpinning the robustness of our results.

Similar to the findings in Ecuador, alpha diversity of geometrid moths remains remarkably stable with changing altitude across the entire rainforest belt. Furthermore, the species composition within the forest belt is more homogeneous than outside this habitat type, as revealed by the ordination and ANOSIM analyses. Thus within the whole forest belt covering an elevational range of more than 1000 m, the species pool changes more slowly than outside the forest. The moth ensembles of forest sites are positioned according to their elevation in the ordinations. It can therefore be concluded that these gradual faunal changes are mainly related to gradual changes in the environment with altitude, again resembling the situation in the Ecuadorian Andes (Brehm *et al.*, 2003a).

Catches from the lowest mature forest sites at 2250 m and those at 2900 m have more than a quarter of their species in common, whereas sites at 1850 m share only 17.5% and sites at 1650 m only 11.8% of their species with the forest sites at 2250 m. This indicates the prominent species turnover below the mountain forest zone.

Low moth diversity on Mt. Kilimanjaro

Overall, the African continent harbours only half the species number of geometrid moths than South America and 25% less species than SE Asia (Scoble *et al.*, 1995). Hence, already on this large (continental) scale biogeographical constraints partly account

for the low moth diversity recorded on Mt. Kilimanjaro as compared to the Ecuadorian Andes or Borneo. On a more restricted regional scale, 1173 geometrid species (Chao 1 estimator) are expected to occur (and 1010 have been observed: Brehm, 2002) in an Andean transect of 1630 m elevational extension, even though the study covered only tropical mountain rainforest. This contrasts strongly with 245 expected and 188 recorded species in the Tanzanian transect of 1650 m elevational extension, which also included agroforest and heath habitats. Diversity differences are therefore so pronounced that other factors also have to be taken into consideration.

One reason for the low levels of moth diversity at Mt. Kilimanjaro can be seen in the history of this volcanic complex. Eruptions in the region which is now covered by the mountain started only about 1 Myr ago (Downie & Wilkinson, 1972), leaving limited time available for immigration to the mountain and for evolutionary processes to generate endemic species. This is also reflected in low levels of endemism and low species richness of Mt. Kilimanjaro with regard to butterflies (deJong & Congdon, 1993) or reptiles (Spawls *et al.*, 2002) as compared to other East African mountains, especially the prominent diversity hotspot in the mountains of the neighbouring Eastern African Arc (Lovett & Wasser, 1993).

While these continental and regional factors account for the overall low moth diversity at Mt. Kilimanjaro, there remains the question: why geometrid richness is so particularly low in mountain rainforest, while in other tropical mountain rainforest regions geometrid diversity remains exceptionally high even at altitudes well above 2000 m.

Again, history and biogeography of Mt. Kilimanjaro may at least partly explain this phenomenon. First of all, the mountain forest belt remained isolated from other mountain or lowland rainforests throughout its entire young history (Lovett, 1993). Furthermore, a series of fossil horizons in the soils at all forest sites of our transect (M. Schrupf, pers. comm.) indicate that the forest was regularly affected by volcanism, most probably leading to substantial reductions in the area of intact mountain rainforest during peaks of volcanic activity. These factors further constrain the formation of a species-rich montane forest moth community.

In the agroforestry zone, the situation is quite different. This zone was originally also covered with forests. Remaining isolates of these forests show that their floristic composition differed from the rainforests encountered above 1850 m, characterized by a higher diversity of dicotyledonous plants as a whole and of tree species in particular (Hemp, 2001, 2002). Current rainfall patterns also imply that these forests were markedly dryer.

Two thousand years ago, settlers widely cleared these lower mountain forests, with human settlements extending along the slopes of the mountain up to elevations of 1700 m (Schmidt, 1989). The natural forest was widely replaced by an agroforestry system. At present, a finely grained habitat mosaic occurs at the upper edge of the agroforestry zone. This consists of small agroforestry plots (with sizes of only a few ha) where a mixture of crops (e.g. coffee, corn, peas, beans, lettuce, lemon grass) are grown under the canopy of some native, but mainly exotic, shade

trees like *Eucalyptus* spp. (Myrtaceae), *Grevillea robusta* (Proteaceae) or *Mangifera indica* (Anacardiaceae), intermingled with patches of meadow, fallow land and remnants of the natural forest in deep gorges and at sacred sites.

Moth species formerly occurring within the natural forest at this altitude may therefore still find refuges either in natural forest remnants or at the agroforestry plots in parts where components of the original herbaceous vegetation still persist. Furthermore, moth species formerly restricted to the huge savannah plains surrounding the mountain also find suitable habitat conditions especially on meadows and fallow land in the agroforestry zone. Therefore, the higher habitat heterogeneity in the agroforestry zone favours a higher diversity of geometrid moths.

The extremely low diversity in the heath can be explained by the harsh environmental conditions, with frost regularly occurring (own observations) and fires frequently destroying large areas of ericaceous woodland (Salehe, 1997; Hemp & Beck, 2001). Under these conditions, only few specialized species still flourish. Nevertheless, we found at least three different *Eupithecia* species (Larentiinae) at altitudes just below 4000 m, which indicates that the highest sites included in our transect are still far below the upper elevational limit for the occurrence of geometrid moths on Mt. Kilimanjaro.

Homogeneity of moth communities in the forest belt

Why does the local geometrid diversity remain so constant across the entire montane forest belt? One major point is related to the history of these forests already discussed above. Young age, isolation and catastrophic disturbances due to volcanic activities account for a comparatively low diversity of dicots and tree species in the mountain rainforest. Only two tree species, *Ocotea usambarensis* and *Podocarpus latifolius*, dominate the canopy of the mature rainforest sites.

Furthermore, the whole forest is characterized by very humid conditions. Maximum precipitation exceeding 3000 mm was recorded at about 2100 m, with 70% of this maximum still occurring at 2700 m (Hemp, 2001). As the cloud cover increases and temperature and hence evapotranspiration decreases at higher altitudes, we consider the whole forest as a very humid habitat. This is underlined by the mass occurrence of Hymenophyllaceae ferns and huge moss layers within the forest. This habitat homogeneity is mirrored by the homogeneity of the moth communities.

A further example underlining this homogeneity is given by the fact that *Mimoclystia corticearia* (Larentiinae) is among the three most dominant species in catches from all plots within the closed forest belt. Here, the 613 individuals of this species account for more than a quarter of all individuals caught. *M. corticearia* is the single most dominant species on 12 of 15 plots investigated within this belt, explaining the high similarity of the forest plots especially for a low sample size parameter *m*.

Edge effects at forest boundaries

With increasing proximity to settlements, human influence on the mountain rainforest is ever increasing. Directly above the

uppermost agroforest plots, the natural forest is highly degraded, and large parts are replaced by homogenous plantations of Australian *Eucalyptus* spp. (Myrtaceae) and *Acacia mearnsii* (Mimosaceae). In this boundary region, diversity of geometrid moth ensembles is distinctly lower than in the agroforest zone itself, hence opposing the general idea of enhanced diversity at habitat boundaries. A closer look at communities within this interface between the agroforest and the natural forest-plantation forest mosaic reveals a possible reason for this phenomenon. One species, *Chiasmia fuscataria* (Ennominae), becomes extremely dominant in this region, even though individuals of the species are encountered in a much wider elevational range (1650–2900 m). Many *Chiasmia* spp. are known for their preference for legumes as host plants (Robinson *et al.*, 2003). It seems therefore very likely that *Chiasmia fuscataria* uses *Acacia mearnsii* in the plantations as food resource. As this *Acacia* species grows in high density along the forest boundary, this might explain why these moths also occur in extremely high abundance along the lower forest margin. Here, *C. fuscataria* accounts for up to 75% of all individuals caught per site, the highest dominance of any species along the transect. Hence the lack of a diversity maximum in the transition zone can be attributed to the over-dominance of *Chiasmia fuscataria*.

At the forest–heathland boundary, a slight increase in alpha diversity can be observed just below the margin of the closed forest at 2900 m. The enhanced diversity of moth communities at these highest sites within the closed forest can be related to an intrusion of species typically occurring in the heath and forest remnants, as the plots at 2900 and 3100 m share 45.4% of their species, and plots at 2900 and 3300 m still have a common share of 36.9% of their species. This indicates that an edge effect occurs at this habitat boundary.

Apart from this, ordinations reveal that moth communities at 3100 m in both forest remnants and heath vegetation are still strikingly dissimilar from the communities within the closed forest below, even though the forest remnants show an alpha diversity of the same magnitude as moth communities in the closed mature forest. This pattern is most pronounced for small values of the sample size parameter m and hence caused by dominant species, whereas for larger m -values, the dissimilarity becomes smaller. It can be concluded that although there are patches of mountain rainforest even at high altitudes, the community of geometrid moths within these patches is altered from the composition at the intact forest belt especially with regard to dominant species, and more strongly resembles the community of the surrounding heath vegetation. For example, the species *Parortholitha nictitaria*, *P. arenaria* and *Xanthorhoe sublesta* (Larentiinae) which are otherwise common elements in the heathland geometrid faunas, are abundantly represented in forest remnants surrounded by heath vegetation.

CONCLUSION

Overall, geometrid moth communities in the mountain forest zone of Mt. Kilimanjaro show typical changes in faunal composition with regard to subfamilies also observed in tropical mountain

regions elsewhere. However, alpha diversity is much lower and diversity patterns along the elevational gradient are quite different as compared to other tropical mountain rainforests. Most likely, these differences reflect the unique biogeographical history of Mt. Kilimanjaro. Furthermore, species diversity may not always increase at prominent habitat boundaries. Rather, edge effects also depend on the type and characteristics of such boundaries and human influences upon them. Hence, caution is required for generalizations from any case studies, as geometrid moths on Mt. Kilimanjaro tell a slightly different story than their taxonomic relatives do in other tropical mountain regions.

ACKNOWLEDGEMENTS

We want to thank the following institutions for their kind support: German Research Foundation (Mu 364/14), our Tanzanian Counterparts from the Botany Department, University of Dar es Salaam, the Forestry and Beekeeping Division, Kilimanjaro National Park, Tanzania National Parks, the Tanzanian Commission for Science and Technology and the CITES office. Our Tanzanian and German field assistants were of great help with sampling and sorting of geometrid moths in the field. M. Schrupf kindly provided information about soil conditions in the study area. We are greatly indebted to A. Hausmann (Zoologische Staatssammlung, Munich) for assistance with identification of geometrid moths. Constructive comments by three reviewers and David Richardson considerably improved this paper.

REFERENCES

- Axmacher, J.C. (2003) *Diversität von Geometriden (Lepidoptera) und Gefäßpflanzen entlang von Habitatgradienten am Südwest-Kilimanjaro*. PhD Dissertation, University of Bayreuth, Bayreuth, Germany, <http://opus.ub.uni-bayreuth.de/volltexte/2003/35/index.html>. 15.05.04.
- Axmacher, J.C., Tünte, H., Schrupf, M., Müller-Hohenstein, K., Lyaruu, H.V.M. & Fiedler, K. (2004) Diverging diversity patterns of vascular plants and geometrid moths during forest regeneration on Mt Kilimanjaro, Tanzania. *Journal of Biogeography*, **31**, 895–904.
- Beck, J., Schulze, C.H., Linsenmair, K.E. & Fiedler, K. (2002) From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. *Journal of Tropical Ecology*, **17**, 33–51.
- Brehm, G. (2002) *Diversity of geometrid moths in a montane rainforest in Ecuador*. Dissertation, University of Bayreuth, Bayreuth, Germany.
- Brehm, G. & Fiedler, K. (2003) Faunal composition of geometrid moths changes with altitude in an Andean montane rainforest. *Journal of Biogeography*, **30**, 431–440.
- Brehm, G., Homeier, J. & Fiedler, K. (2003a) Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions*, **9**, 351–366.
- Brehm, G., Süßenbach, D. & Fiedler, K. (2003b) Unique elevational patterns of geometrid moths in an Andean montane rainforest. *Ecography*, **26**, 456–466.

- Chey, V.K. & Holloway, J.D. & Speight, M.R. (1997) Diversity of moths in forest plantations and natural forests in Sabah. *Bulletin of Entomological Research*, **87**, 371–385.
- Clarke, K.R. & Warwick, R.M. (2002) PRIMER 5 for Windows, Version 5.2.9. Primer-E Ltd.
- Colwell, R.K. (2000) *Estimates: statistical estimation of species richness and shared species from samples*. Altura Software.
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London, Series B*, **345**, 101–118.
- deJong, R. & Congdon, T.C.E. (1993) The montane butterflies of the eastern Afrotropics. *Biogeography and ecology of the rain forests of Eastern Africa* (ed. by J.C. Lovett and S.K. Wasser), pp. 133–172. Cambridge University Press, Cambridge.
- Didham, R.K. (1997) An overview of invertebrate responses to forest fragmentation. *Forests and insects* (ed. by A.D. Watt, N.E. Stork and M.D. Hunter), pp. 303–320. Chapman & Hall, London.
- Downie, C. & Wilkinson, P. (1972) *The Geology of Kilimanjaro*. The Department of Geology, University of Sheffield, Sheffield.
- Gallagher, E.D. (1998) Compah96, <http://www.es.umb.edu/faculty/edg/files/pub/COMPAH.EXE> (15.05.2004).
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gotelli, N. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- Hamilton, A.C. & Perrott, R.A. (1981) A study of the altitudinal zonation in the montane forest belt of Mt. Elgon, Kenya/Uganda. *Vegetatio*, **45**, 107–125.
- Heaney, L.R. (2001) Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology and Biogeography*, **10**, 15–39.
- Hemp, A. (2001) Ecology of the Pteridophytes on the southern slopes of Mt. Kilimanjaro. Part II: Habitat selection. *Plant Biology*, **3**, 493–523.
- Hemp, A. (2002) Ecology of the Pteridophytes on the southern slopes of Mt. Kilimanjaro. I Altitudinal distribution. *Plant Ecology*, **159**, 211–239.
- Hemp, A. & Beck, E. (2001) *Erica excelsa* as a fire-tolerating component of Mt. Kilimanjaro's forests. *Phytocoenologia*, **31**, 449–475.
- Holloway, J.D. (1985) Moths as indicator organisms for categorizing rain forest and monitoring changes and regeneration processes. *Tropical rain forests: the Leeds symposium* (ed. by A.C. Chadwick and S.L. Sutton), pp. 235–242. Leeds Philosophical and Literary Society, Leeds.
- Holloway, J.D. (1997) The moths of Borneo: Family Geometridae, subfamilies Sterrhinae and Larentiinae. *Malayan Nature Journal*, **51**, 1–242.
- Holloway, J.D., Robinson, G.S. & Tuck, K.R. (1990) Zonation of the Lepidoptera of northern Sulawesi. *Insects and rain forests of south-east Asia (Wallacea)* (ed. by W.J. Knight and J.D. Holloway), pp. 153–166. The Royal Entomological Society, London.
- Hurlbert, S.H. (1971) The non-concept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–586.
- Intachat, J., Chey, V.K., Holloway, J.D. & Speight, M.R. (1999a) The impact of forest plantation development on the population and diversity of geometrid moths (Lepidoptera: Geometridae) in Malaysia. *Journal of Tropical Forest Science*, **2**, 329–336.
- Intachat, J., Holloway, J.D. & Speight, M.R. (1997) The effects of different forest management practices on geometroid moth populations and their diversity in Peninsular Malaysia. *Journal of Tropical Forest Science*, **9**, 411–430.
- Intachat, J., Holloway, J.D. & Speight, M.R. (1999b) The impact of logging on geometroid moth populations and their diversity in lowland forests of Peninsular Malaysia. *Journal of Tropical Forest Science*, **11**, 61–78.
- Kessler, M. (2001) Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. *Biodiversity and Conservation*, **10**, 1897–1921.
- Kessler, M., Herzog, S.K. & Fjeldsa, J. (2001) Species richness and endemism of plant and bird communities along two gradients of elevation, humidity and land use in the Bolivian Andes. *Diversity and Distributions*, **7**, 61–77.
- Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. & Graham, A.W. (2000) Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology*, **37**, 284–297.
- Kotze, D.J. & Samways, M.J. (2001) No general edge effect for invertebrates at Afromontane forest-grassland ecotones. *Biodiversity and Conservation*, **10**, 443–466.
- Lomolino, M.V. (2001) Elevation gradients of species density: historical and prospective views. *Global Ecology and Biogeography*, **10**, 3–13.
- Lovett, J.C. (1993) Climatic history and forest distribution in eastern Africa. *Biogeography and ecology of the rain forests of Eastern Africa* (ed. by J.C. Lovett and S.K. Wasser), pp. 23–28. Cambridge University Press, Cambridge.
- Lovett, J.C. & Wasser, S.K. (1993) *Biogeography and ecology of the rain forests of Eastern Africa*. Cambridge University Press, Cambridge.
- McCain, C.M. (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography*, **31**, 19–31.
- McCoy, E.D. (1990) The distribution of insects along elevational gradients. *Oikos*, **58**, 313–322.
- Mörtter, R. (1988) Vergleichende Untersuchungen zur Faunistik und Ökologie der Lepidopteren in unterschiedlich strukturierten Waldflächen im Kottenforst bei Bonn. *Neue Entomologische Nachrichten*, **21**, 1–182.
- Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, **10**, 58–62.
- Nor, S.M.D. (2001) Elevational diversity patterns of small mammals on Mt. Kinabalu, Sabah, Malaysia. *Global Ecology and Biogeography*, **10**, 41–62.
- Olson, D.M. (1994) The distribution of leaf litter invertebrates along a neotropical altitudinal gradient. *Journal of Tropical Ecology*, **10**, 129–150.
- Pócs, T. (1991) The significance of lower plants in the conservation of Mt. Kilimanjaro. *The conservation of Mount Kilimanjaro* (ed. by W.D. Newmark), pp. 21–33. IUCN, Nairobi.

- Pyrz, T.W. & Wojtusiak, J. (2002) The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along an elevational transect in Monte Zerpa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. *Global Ecology and Biogeography*, **11**, 211–221.
- Rahbeck, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **18**, 200–205.
- Rahbeck, C. (1997) The relationship between area, elevation, and regional species richness in Neotropical birds. *American Naturalist*, **149**, 875–902.
- Risser, P.G. (1995) The status of the science investigating ecotones. *Bioscience*, **45**, 318–325.
- Robinson, G.S., Ackery, P.R., Beccaloni, G.W., Kitching, I.J. & Hernandez, L.M. (2003) HOSTS — The Natural History Museum's database of the hostplants of the moth and butterfly caterpillars of the world. <http://flood.nhm.ac.uk/cgi-bin/perth/hosts>. (15.05.04).
- Salehe, J. (1997) *Preliminary assessment of the Mount Kilimanjaro forest fires of February and Marine 1997*. IUCN, Nairobi.
- Schmidt, P.R. (1989) Early exploitation and settlements in the Usambara Mountains. *Forest conservation in the East Usambara mountains, Tanzania* (ed. by A.C. Hamilton and R. Bensted-Smith), pp. 75–78. IUCN, Nairobi.
- Schulze, C.H. (2000) *Auswirkungen anthropogener Störungen auf die Diversität von Herbivoren — Analyse von Nachtfalterzönosen entlang von Habitatgradienten in Ost-Malaysia*. PhD Dissertation, University of Bayreuth, Bayreuth, Germany.
- Schulze, C.H. & Fiedler, K. (2003) Vertical and temporal diversity of a species-rich moth taxon in Borneo. *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy* (ed. by Y. Basset, V. Novotny, S. Miller and R.L. Kitching), pp. 69–85. Cambridge University Press, Cambridge.
- Scoble, M.J. (1999) *Geometrid moths of the world: a catalogue (Lepidoptera, Geometridae)*. The Natural History Museum, CSIRO, London.
- Scoble, M.J., Gaston, K.J. & Crook, A. (1995) Using taxonomic data to estimate species richness in Geometridae. *Journal of the Lepidopterists' Society*, **49**, 136–147.
- Spawls, S., Howell, K.M., Drewes, R.C. & Ashe, J. (2002) *A field guide to the reptiles of East Africa*. Academic Press, London.
- Stevens, G.C. (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *American Naturalist*, **140**, 893–911.
- Thomas, A.W. (2002) Moth diversity in a north-eastern North American, red spruce forest. II. *The effect of silvicultural practices on geometrid diversity (Lepidoptera: Geometridae)*. Canadian Forest Service, Natural Resources Canada, New Brunswick.
- Trueblood, D.D., Gallagher, E.D. & Gould, D.M. (1994) The three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbour. *Limnology and Oceanography*, **39**, 1440–1454.
- Willott, S.J. (1999) The effects of selective logging on the distribution of moths in a Bornean rainforest. *Philosophical Transactions of the Royal Society of London, Series B*, **354**, 1783–1790.
- Wolda, H. (1983) Diversity, diversity indices and tropical cockroaches. *Oecologia*, **58**, 290–298.
- Wolda, H. (1987) Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society*, **30**, 313–323.
- Yela, J.L. & Holyoak, M. (1997) Effects of moonlight and meteorological factors on light and bait trap catches of noctuid moths (Lepidoptera: Noctuidae). *Population Ecology*, **26**, 1283–1290.