

Habitat type modifies geometry of elevational diversity gradients in geometrid moths (Lepidoptera Geometridae) on Mt Kilimanjaro, Tanzania

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Changes in geometrid moth diversity are investigated at 61 plots representing various habitat types along an elevational gradient ranging from 1200 to 3700 m a.s.l. on the south-western slopes of Mt Kilimanjaro. Congruent with patterns commonly observed along elevational gradients, overall moth diversity decreases significantly with increasing altitude. A comparison between habitat types nevertheless reveals that this pattern is caused by significant decreases only in open and secondary forest habitats. Apparently in relation to less intensive agricultural management at higher elevations, diversity shows a slight increase with increasing elevation at agro-forestry plots. In mature forests, diversity increases significantly with increasing elevation. This unusual pattern may be explained by extremely wet microclimatic conditions at lower elevations and by boundary effects at higher elevations. Overall, the results demonstrate that generalizations of diversity gradients across heterogeneous habitat types are problematic and must be interpreted with great care.

KEY WORDS: agro-forest, elevation, habitat types, land-use, species diversity, rain forest, Geometridae, Mt Kilimanjaro.

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INTRODUCTION

Elevational gradients on tropical mountains are characterized by profound changes in a wide array of environmental factors, ranging from mean annual temperatures to radiation and precipitation. This renders them ideal to study the response of organisms to strong changes in these environmental parameters over small spatial scales. Prior biodiversity studies along elevational transects have demonstrated a great variation of diversity patterns in different taxa. Reviews by RAHBK (1995, 2005) revealed that the most commonly observed pattern is a hump-shaped distribution, but also a monotonic decrease has been observed. While the majority of studies of elevational gradients have focussed on plants and vertebrates, most studies investigating insects and other ectothermic invertebrates also revealed a hump-backed distribution of diversity (HOLLOWAY et al. 1990, MCCOY 1990, OLSON 1994, HOLLOWAY 1997, PYRCZ & WOJTUSIAK 2002, BREHM et al. 2007).

Forming one of the largest families of Lepidoptera, geometrid moths are generally well known to react sensitively to environmental change, which has rendered them a frequently used focal group to address a wide range of ecological questions (HOLLOWAY 1985; CHEY et al. 1997; INTACHAT et al. 1997, 1999; WILLOTT 1999; KITCHING et al. 2000; BECK et al. 2002; BREHM et al. 2003a; AXMACHER et al. 2004b). Patterns in alpha diversity of geometrid moths observed in tropical mountain rainforest habitats in the Ecuadorian Andes (BREHM et al. 2003b), in the Cordillera Central in Costa Rica (BREHM et al. 2007) and on Mt Kinabalu in Borneo (SCHULZE 2000) again generally followed a hump-shaped distribution. Remarkably, diversity levels for these moths remained widely constant at their maximum over a large elevational range, resulting in extensive diversity plateaus. On Mt Kilimanjaro, alpha diversity of geometrid moths within the montane forest belt also showed very little variation over a large elevational range (AXMACHER et al. 2004a), but this plateau was characterized by overall very low levels of species diversity.

Studies of elevational diversity patterns have so far mostly concentrated on investigations of single habitat types, hence widely neglecting the potential influences habitat types themselves may have on the diversity pattern. For example, different constraints in woody versus open vegetation might possibly cause divergent, or non-parallel, diversity patterns. This shortcoming will be addressed in the present study. Patterns in alpha diversity of geometrid assemblages with increasing elevation were analysed at open habitats, which are characterized by low shrubs and herbaceous vegetation. These results were then compared to patterns observed in closed-canopy secondary forest, mature forest, and agro-forestry plots. The results of this comparison enable the testing of the hypothesis that the geometry of elevational diversity gradients is consistent between different habitat types. This would be expected since changes in mesoclimatic conditions, which have been regarded as highly important in the explanation of species diversity patterns in ectothermic arthropods (e.g. AXMACHER et al. 2004b), follow similar gross directions in all habitats, even though local daily or seasonal amplitudes (e.g. of temperature or rainfall) may vary depending on vegetation.

METHODS

Sixty-one sampling sites were established at the south-western slopes of Mt Kilimanjaro (Tanzania) along an elevational transect ranging from the base of the mountain at 1220 to 3700 m. These sites comprised 22 plots in open habitats at elevations between 1220 and 3700 m, seven agro-forestry plots between 1220 and 1820 m, three semi-natural gallery forest plots at about 1350 m, 14 secondary forest plots between 1415 and 2165 m, and 15 mature montane forest plots at elevations ranging from 2250 to 3090 m. Secondary and mature forests were distinguished by the presence or absence of pioneer tree species such as *Macaranga kilimandscharica* Pax 1895 or *Hagenia abyssinica* J.F. Gmelin 1791 and late successional tree species such as *Ocotea usambarensis* Engl. 1894 and *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb. 1825. Plots representing open habitats were generally characterized by a complete lack of a canopy formed by woody plants. On most of the plots representing this habitat type, grass species formed the dominant vegetation components, while some forest gaps especially at lower elevations were also dominated by bracken (*Pteridium aquilinum* (L.) Kuhn 1879) and bramble (*Rubus* spp.). The minimum distances between neighbouring plots was 50 m, and sampling devices were not visible between neighbouring plots.

Moths were sampled using light towers consisting of one weak (15 w) battery-driven blacklight tube (Sylvania blacklight-blue, F 15W/BLB-TB, Osram, Munich) to ensure that moths were only attracted from the direct vicinity of the light towers. The tubes were placed inside a white reflective gauze cylinder (diameter 0.8 m, height 1.7 m, AXMACHER & FIEDLER 2004). All geometrids arriving at the gauze cylinder between 18:30 and 21:30 were sampled to cover their main activity peak (J. AXMACHER personal observation). The period 5 days before to 5 days after the full moon was avoided to minimize the effect of backlight illumination (YELA & HOLYOAK 1997). An overall total of 210 catches was obtained between October and May in the years 2000-2002. All specimens were subsequently spread, sorted to morpho-species level and identified by J. Axmacher as far as possible at the Zoologische Staatssammlung, Munich.

Numbers of moths caught on Mt Kilimanjaro strongly varied with weather conditions, habitat and elevation. Hence, differences in sample size rendered the number of species sampled from each location a highly inaccurate measure of diversity. To overcome these limitations, alpha diversity was expressed as Fisher's alpha, a robust index widely employed in investigations of tropical moth communities (e.g. SCHULZE & FIEDLER 2003; AXMACHER et al. 2004a, 2004b) which is also relatively insensitive to under-sampling (MAGURRAN 2004). Fisher's alpha was calculated using the software Species Diversity and Richness 3 (HENDERSON & SEABY 2001), while all other statistical analysis was performed using Statistica 6.0 (Statsoft, Tulsa, USA). For the calculation of Pearson's r^2 at the overall transect and the open habitats, the elevation data was log-transformed.

RESULTS

In total, 8408 specimens representing 302 species of geometrid moths were sampled along the altitudinal transect (species lists are accessible online in AXMACHER 2003). A comparison of Fisher's alpha values including all habitats along the complete transect (Fig. 1) shows that overall, diversity decreases highly significantly with increasing elevation from the base of the mountain to 3700 m (Pearson's r^2 (log-transformed) = 0.53, $P < 0.0001$).

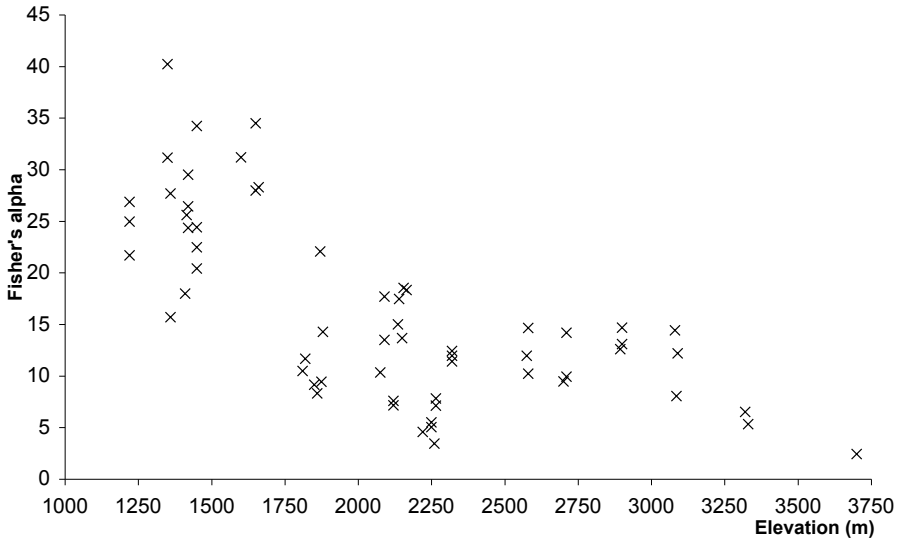


Fig. 1. — Overall change in species diversity (measured as Fisher's alpha) of geometrid moth ensembles along the altitudinal transect on Mt Kilimanjaro, Tanzania.

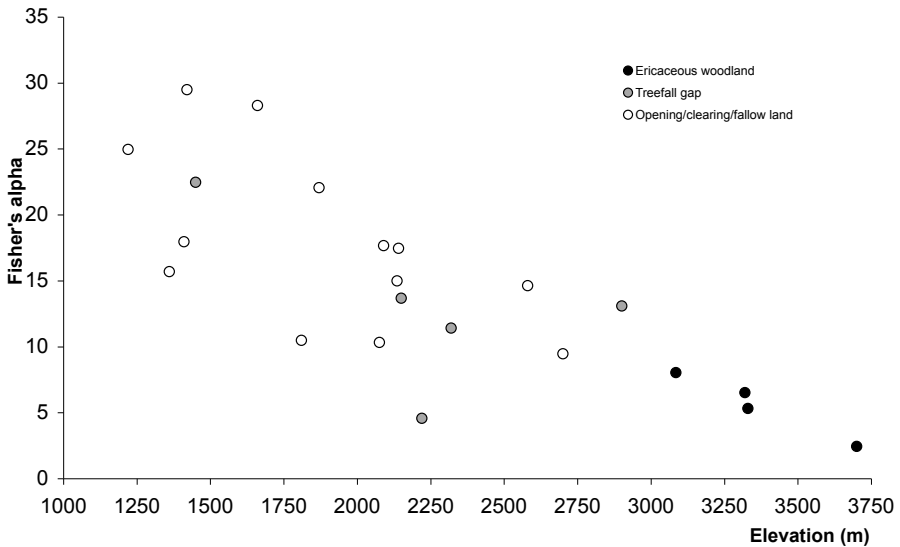


Fig. 2. — Alpha diversity (Fisher's alpha) of geometrid moth ensembles in relation to elevation at open habitats, including fallow land, large openings and clearings, tree-fall gaps and recently burned ericaceous woodland.

However, over a sizeable proportion of the gradient between 1800 and 3100 m, alpha diversity shows no correlation with elevation (Pearson's r^2 (log-transformed) = 0.0001, $P = 0.94$). When only considering moth diversity at sites in open habitat (Fig. 2), the negative correlation between Fisher's alpha and elevation becomes more pronounced (Pearson's r^2 (log-transformed) = 0.62, $P < 0.0001$), and can well be approximated also by a simple linear decrease (Pearson's $r^2 = 0.61$, $P < 0.0001$), with an average decrease in Fisher's alpha of 8 units per 1000 m increase in elevation.

This pattern completely changes when only agro-forest sites are considered. Samples from the highest sites were completely dominated by *Chiasmia fuscataria* Möschler 1887, a geometrid feeding on legumes and presumably invading the site from surrounding *Acacia* plantations, accounting for 58% of the individuals caught. Due to this unusual situation caused by a single species apparently alien to the habitat, the plot was excluded from further analysis. Diversity of the remaining agro-forest plots showed a clear tendency to increase with increasing elevation (Pearson's $r^2 = 0.55$), although this increase did not reach statistical significance at a 95% confidence level ($P = 0.087$).

Forest habitats were further subdivided into secondary forests, represented by the disturbed gallery forests at the very base of the transect and closed secondary forests at elevations below 2200 m, and mature forests at elevations above 2200 m (Fig. 3). Both secondary and mature forests showed significant, but diverging changes in alpha diversity with elevation. While in secondary forests, moth diversity significantly decreased with increasing ele-

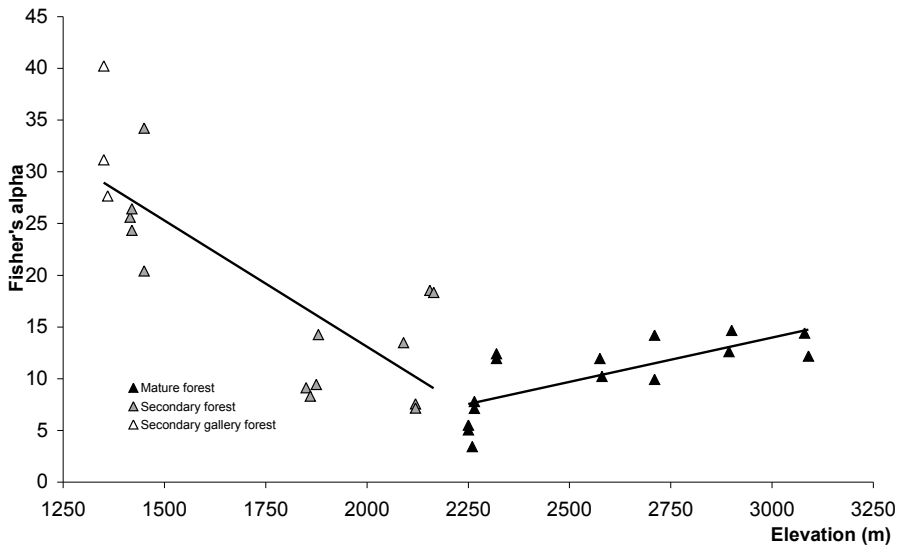


Fig. 3. — Alpha diversity (Fisher's alpha) of geometrid moth ensembles in relation to elevation at forest sites, with gallery forests at the lowest elevations, secondary forest below, and mature forest above 2200 m. The lines result from separate linear regression analyses for the secondary forest and mature forest plots, respectively (see text for details).

vation (Pearson's $r^2 = 0.63$, $P = 0.0001$) and at a much stronger rate than in open habitats with 24 units/1000 m, values of Fisher's alpha showed a positive correlation with elevation in mature forest sites (Pearson's $r^2 = 0.55$, $P = 0.002$), with an increase of diversity of 8 units per 1000 m increase in elevation, hence somehow mirroring the decrease in open habitats.

DISCUSSION

Our results clearly indicate that patterns in the species diversity of geometrid moths along the extensive elevational transect at Mt Kilimanjaro are habitat-specific. This somehow contrasts earlier findings (AXMACHER et al. 2004b), which indicated that elevation and related changes in climatic conditions was the dominating factor relating to both local diversity and species turnover of these insects. Nonetheless, along the extensive gradient investigated here, which stretched over a range of about 2500 m, local habitat conditions do seem to strongly modify the overall negative relationship between elevation and diversity. Reasons for these deviations from the common theme of decreasing diversity at higher elevations with their cooler climate must be inherent in the specific local conditions of the different habitats.

In the agro-forests, human influence on the vegetation composition as the major resource of geometrid moths with their herbivorous larval stages can be regarded as a main cause for the slight increase in diversity with increasing elevation observed in this study. The southern slopes of Mt Kilimanjaro between 1000 and 1800 m are the traditional settlement area for the Chagga tribe (O'KTING'ATI & KESSY 1991), who have developed and maintained the agro-forestry system of their home-gardens for many centuries (FERNANDES et al. 1984). Traditional home-gardens still cover most of the central and higher elevations of the agricultural belt at the mountain, which stretches from the base to elevations of 1800 m on its southern side. During and after the colonial period, more intensive farming systems have nevertheless widely replaced the traditional systems on the base of the mountain. The resulting large-scale coffee plantations dominating at low elevations are characterized by a much less complex vegetation structure compared to the Chagga home-gardens. Hence, although diversity maxima were observed both for forests and fallow land at low elevations, the modern large-scale farms located here harbour a significantly less diverse geometrid moth fauna than the traditional agro-forestry systems at higher elevations. The conclusion that more complex vegetation also translates into more diverse moth faunas is corroborated by the observation that, where banana and coffee plants are jointly cultivated in the shrub layer, geometrid moth ensembles are also particularly rich in species. The low diversity of the highest agroforestry plot as putatively related to the dominance of the geometrid *C. fuscataria* has already been discussed.

The contrasting patterns observed in closed-canopy secondary and mature forest can also be related to the different conditions in these two habitat types. Geometrid ensembles in secondary forest widely follow the negative correlation observed as an overall trend in the ectothermic insects

along the transect. The steep diversity decrease in secondary forests may be attributed to climatic factors like decreasing temperatures at higher elevations in the open secondary forests with a generally poorly developed shrub layer, in connection with a decrease in host plant diversity, particularly in legumes which form an important food resource for geometrid moths (AXMACHER 2003, ROBINSON et al. 2007, AXMACHER et al. 2008). The opposing pattern of slightly increasing diversity in mature forest from mid- to high elevations is ascribed first of all to the extremely perhumid conditions prevailing in the mature forests at mid-elevations, coinciding with extremely low values for Fisher's alpha which are only paralleled by geometrid moth ensembles in open sub-alpine heathland at elevations more than 1000 m higher. This low moth diversity is particularly remarkable since the diversity of vascular plants in the respective mature forests is relatively high, especially when compared to forest gaps and the secondary forest plots at slightly lower elevations (AXMACHER et al. 2004a). Another factor potentially contributing to the diversity minimum encountered in the mature forests at mid-elevation could be boundary effects at the upper forest margin enhancing diversity in mature forest sites at high elevations, where geometrid moth species associated with ericaceous woodlands mix with forest species (AXMACHER et al. 2006).

Finally, the monotonic decrease in diversity of geometrids in open habitats, similar to the decrease observed in secondary forest, can be both related to a decrease in foodplant diversity as well as to increasingly harsh environmental conditions at upper portions of the transect. As there is no tree cover at these open sites to dampen oscillations in temperature and humidity, both daily and seasonal fluctuations in ambient conditions are much more pronounced as compared to forest. This is particularly true for elevations above 3000 m, where sub-zero temperatures regularly occur at night in the ericaceous woodland, and main flight activity of a number of geometrid moth species shifts to periods shortly before sun-set (J. AXMACHER unpublished data).

In conclusion, elevational gradients in the diversity of geometrid moths cannot *prima facie* be generalized across different habitat or land-use types. On the contrary, even within one type of plant formation, the tropical mountain rainforest, different patterns were observed in secondary forest at lower elevations and in the mature natural forest above. Hence, considerable caution is needed in any generalizations of diversity patterns along elevational gradients particularly if they comprise of a wide range of habitats, or when results have been gained in just one habitat type. In this study, the distinct habitat-specific idiosyncrasies became completely swamped in an overall analysis lumping all sites from all habitat types and elevations. These finer scale local patterns that hint to distinct, habitat-specific responses of geometrid moth ensembles, became visible only after partitioning the data set.

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