

Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest

Gunnar Brehm, Dirk Süssenbach and Konrad Fiedler

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Alpha-diversity of geometrid moths was investigated along an elevational gradient in a tropical montane rainforest in southern Ecuador. Diversity was measured using 1) species number, 2) extrapolated species number (Chao 1 estimator), 3) rarefied species number, and 4) Fisher's alpha. When applied to the empirical data set, 1 and 2 strongly depended on the sample size, whereas 3 and 4 were suitable and reliable measures of local diversity. At single sites, up to 292 species were observed, and extrapolation estimates range from 244 to 445 species. Values for Fisher's alpha are among the highest ever measured for this moth family, and range from 69 to 131 per site. In contrast to theoretical assumptions and empirical studies in other regions of the world, the diversity of geometrid moths remained consistently high along the entire gradient studied. Diversity measures correlated with neither altitude nor ambient temperature. The large subfamily Ennominae has previously been assumed to be a group that occurs mainly at low and medium elevations. However, no decline in diversity was found in the study area. The diversity of the other large subfamily, Larentiinae, even increased from the lowest elevations and was highest at elevations above 1800 m. The roles of a decreasing diversity of potential host-plants, decreasing structural complexity of the vegetation, increasingly unfavourable climatic conditions and possible physiological adaptations in determining herbivore species richness are discussed. A relatively low predation pressure might be an advantage of high-altitude habitats. The physiognomy of the Andes (folded mountains, large areas at high altitudes) might also have allowed speciation events and the development of a species-rich high-altitude fauna. There is evidence that the species-richness of other groups of herbivorous insects in the same area declines as altitude increases. This emphasises difficulties that are associated with biodiversity indicator groups, and calls for caution when making generalisations from case studies.

G. Brehm (gunnar_brehm@yahoo.com), D. Süssenbach and K. Fiedler, Dept of Animal Ecology I, Univ. of Bayreuth, D-95440 Bayreuth, Germany.

Biodiversity research in tropical regions has largely focussed on lowland rainforests, whereas montane rainforests have so far largely been neglected. This is particularly true with regard to studies on arthropods. For example, none of the 89 studies on canopy arthropods reviewed by Basset (2001) was conducted in a tropical montane habitat. The northern Andes have been recognised as a “hyper hotspot” on earth for vascular plants and vertebrates (Henderson et al. 1991, Myers et al. 2000). However, apart from a few exceptions, little is

known about patterns of insect diversity in Andean montane forest habitats.

The dominant environmental gradient in mountainous habitats is altitude, which is directly related to decreasing temperature and various other abiotic and biotic environmental factors. Significant changes in the vegetation along altitudinal gradients in the Andes were first documented by Alexander von Humboldt (von Humboldt and Bonpland 1807). Later studies yielded increasingly refined pictures (e.g. Grubb et al. 1963,

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Gentry 1988). Elevational changes in diversity have also been documented for a variety of animals in the Neotropical region (references in Brehm 2002). In a review on species richness patterns along elevational gradients, Rahbeck (1995) found that approximately half of the studies showed a continuous decline of species numbers with increasing altitude, whereas the other half detected a peak at medium elevations. Although some authors suggested that the occurrence of mid-elevational diversity peaks might be a sampling artefact (e.g. Wolda 1987), there is now substantial evidence for the existence of such peaks in a broad range of organisms (McCoy 1990, Grytnes and Vetaas 2002 with references therein). Among insects, several families of Lepidoptera in south east Asia have been reported to exhibit their greatest diversity at medium elevations, between 600 and 1000 m a.s.l. (Holloway 1987, Holloway and Nielsen 1999). However, only a few exceptions to an overall declining diversity at altitudes higher than 1000 m have been documented for arthropods. Examples include tropical larentiine moths (a subfamily of Geometridae), which are most species-rich at high altitudes, and also increase in relation to other subfamilies with latitude in temperate regions (Brehm and Fiedler 2003). Schulze (2000) reported that diversity of the moth families Geometridae and Arctiidae in Borneo attained richness maxima at altitudes between 1200 and 2000 m. Above this altitude, all available studies indicate that diversity of insect assemblages decreases. This suggests that environmental conditions within and above the cloud-forest zone of tropical mountains become so harsh that the number of ectothermic insect species that are able to cope with such circumstances decreases steadily above this level.

The moth family Geometridae is one of the three largest clades of Lepidoptera and currently includes > 21 000 described species (Scoble 1999), with some 6400 (30%) occurring in the Neotropical region. Compared to most arthropod taxa, the taxonomy of geometrid moths is relatively advanced, and they are a suitable group for biodiversity studies in tropical forests (Intachat and Woiwod 1999). However, prior to the present study, no detailed ecological studies of geometrids in the Neotropical region have ever been conducted.

Samples taken from tropical arthropod communities provide a methodological challenge for diversity measures. They are almost always incomplete and the numbers of specimens available for analysis often diverge considerably between sites (e.g. Schulze and Fiedler 2003). Moreover, tropical arthropod communities are characterised by a high proportion of rare species that cannot be excluded as artefact or a group of marginal importance (Price et al. 1995, Novotny and Basset 2000). From the plethora of available measures of alpha-diversity (e.g. Hayek and Buzas 1997, Southwood and Henderson 2000), four were selected and their

sample size dependence was tested. Suitable diversity measures should be able to discriminate between samples of different diversity, but at the same time be independent of sample size, in order to avoid misleading bias in the results.

In this first study of its kind in the Neotropical region, we aimed to investigate diversity patterns of Geometridae as model organisms of a "mega-diverse" group of herbivorous insects in a montane Andean rainforest. An analysis of changes of faunal composition and beta diversity of geometrid moths was provided by Brehm and Fiedler (2003) and Brehm et al. (2003). In this paper, we tested the expectation, derived from all comparable studies, that species diversity should decline in the upper part of the elevational gradient.

Methods

Study area, sampling, identification, temperature measurements

The study area in southern Ecuador is situated within the East Cordillera of the Andes and belongs to the province Zamora-Chinchi (Reserva Biológica San Francisco, 3°58'S, 79°5'W, and adjacent fractions of the Podocarpus National Park). It is covered with undisturbed to slightly disturbed montane rainforest. The vegetation in the upper part of the study area was described by Bussmann (2001) and Paulsch (2002). Moths were sampled manually using portable weak light-traps (2 × 15 W). Traps consisted of a white gauze cylinder (height 1.60 m, diameter 0.60 m) and were placed at the forest floor. We selected 22 sampling sites at 11 elevational levels between 1040 and 2677 m a.s.l. Sites were numbered from 1 to 11 (a + b) according to their elevational order. A detailed description of the sites and a discussion of the sampling methods was provided by Brehm (2002). Sampling occurred during three field periods (April–May 1999, October 1999–January 2000, and October–December 2000). Light-traps were run between 18:30 and 21:30 local time. Between two and four nightly catches from each site were pooled and analysed. Specimens were first sorted to morphospecies level and later determined in the Zoologische Staatssammlung, Munich and the Natural History Museum, London. Fifty-two percent of the taxa and 67% of the specimens were determined to species level (Brehm 2002). In parallel to the light trapping, the temperature during three to eleven nights per site was measured every 30 min from 18:30 to 21:30 using a Casio alti-thermo twin sensor at 1.60 m above ground level. Braun (2002) and Brehm (2002) showed that temperature in the study area declines linearly with increasing elevation. Thus, for each site the average of all available nightly measures taken at 20:00 was used as standard.

Alpha-diversity measures

The analysis was restricted to four selected measures and was performed separately for Geometridae and the two largest subfamilies Ennominae and Larentiinae. The remaining subfamilies (Desmobathrinae, Geometrinae, Oenochrominae, and Sterrhinae) were not analysed separately because of their low representation in the samples.

1) Species number

Measurement of species richness by complete census is only feasible for a few organisms. For most organisms, measurement means sampling (Colwell and Coddington 1994). However, species numbers are still widely used as a measure of diversity. Misleading results and biases must be expected with incomplete samples that differ in size (Gotelli and Colwell 2001).

2) Extrapolation

According to Colwell and Coddington (1994), if certain assumptions are not violated, the “true” number can be estimated using extrapolation methods. These authors recommended the use of non-parametric estimators, such as Chao 1, as promising quantitative techniques. Analyses were performed using the computer program EstimateS 6.0b1 (Colwell 2000), with the bias-corrected formula. Since all samples contained at least 380 specimens, the use of “Chao 1” appeared to be justified. However, a certain dependence on sample size was expected, because the recorded number of species is an integral part of the formula of the estimator.

3) Rarefaction

This method is particularly useful if assemblages are sampled with different intensity or success (Hurlbert 1971, Gotelli and Colwell 2001). The geometrid samples were rarefied to a shared number of specimens using a program developed by Kenney and Krebs (2000). The program also provided standard deviations. Rarefied expected species numbers were calculated at the level of 350 specimens for Geometridae, of 100 specimens for Ennominae, and of 50 specimens for Larentiinae. This measure is expected to be independent of sample size since samples are standardised to an equal level.

4) Fisher's alpha of the log-series

In contrast to other diversity indices, Fisher's alpha has been shown to be efficient in discriminating between sites, and is mainly influenced by the frequencies of species of medium abundance (Kempton and Taylor 1974). The fit of the log-series distribution was tested using a program developed by Henderson and Seaby (1998). Fisher's alpha and standard deviations (according to Fisher's original formula, Colwell pers. comm.) were calculated with the program EstimateS 6.0b1 (Colwell 2000). A minimum number of at least 100 speci-

mens is usually recommended for calculating Fisher's alpha (Hayek and Buzas 1997). This number was not reached in only one sample of the subfamily Larentiinae (site 1a: 65 specimens).

All diversity measures were tested for correlation with specimen numbers (i.e. sample size dependence), altitude, and temperature. Since relationships between data in this study are non-linear, the Spearman rank correlation coefficient was used. Multiple tests of significance were Bonferroni-corrected according to Hochberg (1988). All standard statistical analyses were performed using the software package Statistica 5.5 (Anon. 1999).

Results

A total of 14348 specimens were collected from 22 sites. Four hundred and ten specimens (2.9% of the total catch) could not be reliably sorted and had to be discarded. Figure 1A shows the fluctuating number of specimens per catch and site. Specimen numbers cannot be directly compared because of the variable number of nightly catches analysed. The minimum and maximum numbers of specimens per site are 384 and 1200, respectively. Figure 1B shows the total number of species per site, partitioned into the subfamilies. The number of observed species per site ranged from 134 (site 1a) to 292 (site 7a), but actual numbers were expected to be distinctly higher (see next section). Raw species counts showed no relationship with temperature or altitude for Geometridae and Ennominae, but strongly increased at higher elevations for Larentiinae.

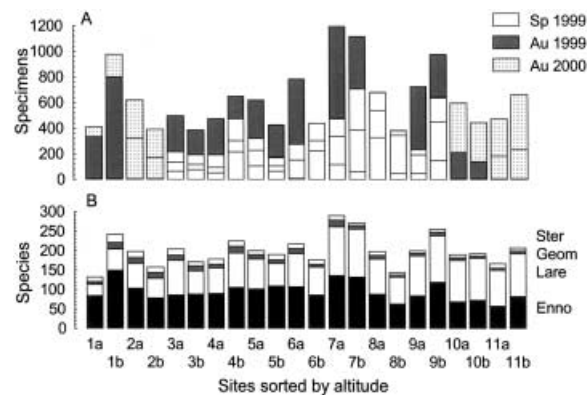


Fig. 1. A) Number of specimens collected at 22 sites. Sites are sorted by altitude and are partitioned according to the nightly catch and the sampling period. Sp 1999 – Spring 1999 (April–May), Au 1999 – Autumn 1999 (October 1999–January 2000), Au 2000 – Autumn 2000 (October–November 2000). B) Number of species at 22 sites (sorted by altitude and partitioned across subfamilies). Ster – Sterrhinae, Geom – Geometrinae, Lare – Larentiinae, Enno – Ennominae. Due to the chosen scale, Desmobathrinae and Oenochrominae are not visible. Desmobathrinae: one species at sites 1a and 1b. Oenochrominae: two species at sites 1b and 7b, one species at sites 1a, 2a, 5a, 7a, 7b, 8a, 10a, and 11b.

Table 1. Spearman rank correlations between four measures of alpha-diversity (species number, extrapolated species number (Chao 1), rarefied species number, and Fisher's alpha) and 1) specimen number, 2) altitude, and 3) mean ambient temperature (at 20:00 local time). ¹ Rarefied sample size for which the expected species number was calculated. Species numbers and extrapolated species numbers are highly significantly correlated with specimen numbers and are thus unreliable measures of local diversity. Only two (unreliable) measures in the subfamily Larentiinae are significantly correlated with altitude and temperature. ns not significant, ** $p < 0.01$, *** $p < 0.005$, **** $p < 0.001$. Printed in bold are results that remain significant after sequential Bonferroni correction according to Hochberg (1988).

	Geometridae	Ennominae	Larentiinae
1) Correlation between specimen number and species number	0.91 ****	0.93 ****	0.94 ****
extrapolated species number (Chao 1)	0.58 ***	0.54 **	0.83 ****
rarefied species number	-0.07 ns	-0.09 ns	0.32 ns
Fisher's alpha	0.15 ns	0.29 ns	0.11 ns
2) Correlation between altitude and species number	0.13 ns	-0.39 ns	0.78 ****
extrapolated species number (Chao 1)	0.18 ns	-0.30 ns	0.65 ***
rarefied species number	0.01 ns	0.57 **	0.31 ns
Fisher's alpha	0.08 ns	0.11 ns	0.16 ns
(3) Correlation between temperature and species number	-0.08 ns	0.42 ns	-0.75 ****
extrapolated species number (Chao 1)	-0.14 ns	0.29 ns	-0.60 ***
rarefied species number	0.09 ns	-0.54 **	-0.29 ns
Fisher's alpha	0.11 ns	-0.07 ns	-0.17 ns
Rarefaction level ¹	350	100	50

Extrapolation

Extrapolated species numbers are on average 75% larger than the observed numbers in all three taxa. The estimate ranges from 29% (Larentiinae, site 11a) to 218% (Ennominae, site 8b) larger than the recorded species number. Figure 2A shows extrapolation results for Geometridae, Ennominae and Larentiinae for all 22 sites. For Geometridae, estimates range between 244 (site 2b) and 445 (site 7a) expected species per site. There is no relationship between the extrapolated number of species and either altitude or temperature for geometrid moths as a whole and Ennominae, while a distinct increase in species numbers for Larentiinae with altitude is notable (Table 1). However, these estimates have to be regarded with caution since the Chao 1 estimator is not a fully reliable measure of diversity in this particular data set because of its sample size dependence (see below).

Rarefaction

Figure 3 shows rarefaction curves of Geometridae for all 22 sites. All curves lie within a relatively narrow band and no clear altitudinal pattern is visible. Figure 2B shows the expected species numbers for geometrid samples rarefied to a standard size of 350 specimens plotted against altitude. While one site (1a at 1040 m) has a significantly lower rarefied species number (122) than all other sites, these sites again range in a continuous band between 135 and 168 expected species and show no tendency along the altitudinal and temperature gradient (Table 1).

Changes do occur at the subfamily level. Figure 2B shows rarefied species numbers for the subfamilies Ennominae and Larentiinae at rarefied sample sizes of 100 and 50 specimens, respectively. The patterns resemble each other. Surprisingly, rarefied species numbers of Ennominae even increase with altitude (Table 1), although this is not significant after sequential Bonferroni correction. A conspicuous difference between both subfamilies is visible at sites 3a, 3b, 4a, and 4b (at 1800–1875 m). While rarefied species numbers in Ennominae tended to be lower than in the neighbouring sites, those of Larentiinae tended to be higher.

Fisher's alpha of the log-series

A significant deviation from the log-series occurred in six ensembles of Geometridae, and in four ensembles of Ennominae, but not in Larentiinae (Table 2). However, after performing the sequential Bonferroni procedure suggested by Hochberg (1988), the log-series distribution was rejected only in Geometridae and Ennominae at the same single site (number 1b, Table 2). In all cases of deviation, the observed number of species in the first abundance class was larger than expected, i.e. there were "too many" rare species in the samples. Figure 2C shows Fisher's alpha values for Geometridae at all 22 sites. They range from 69.3 ± 5.4 to 130.6 ± 10.4 and are among the highest ever measured for local geometrid ensembles. There is no significant consistent change in Fisher's alpha along the altitudinal gradient. Alpha values for Ennominae range from 38.2 ± 3.4 to 66.7 ± 6.5 , and for Larentiinae from 20.1 ± 4.1 to 64.2 ± 6.2 . In both subfamilies, values of Fisher's alpha

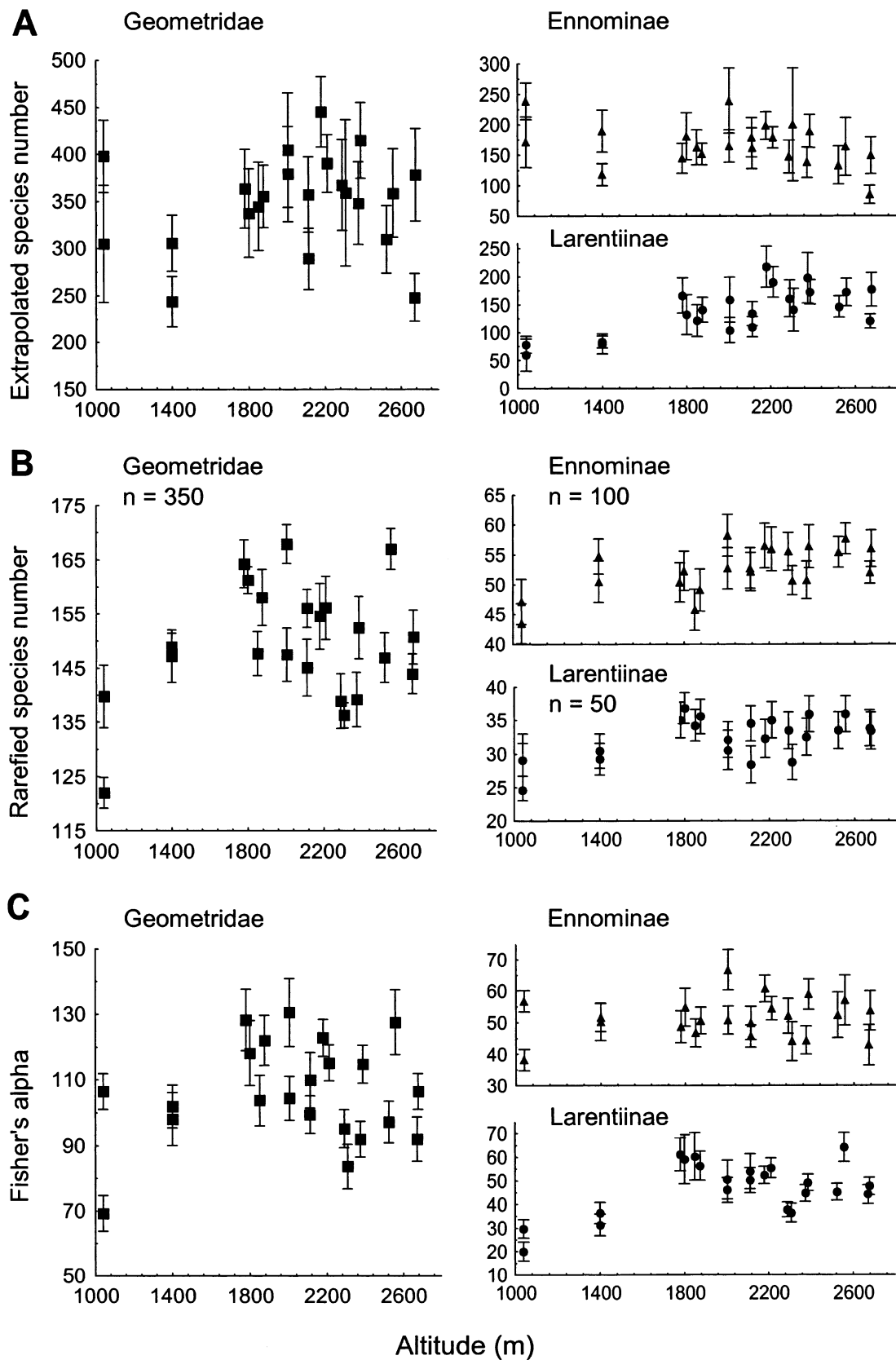


Fig. 2.

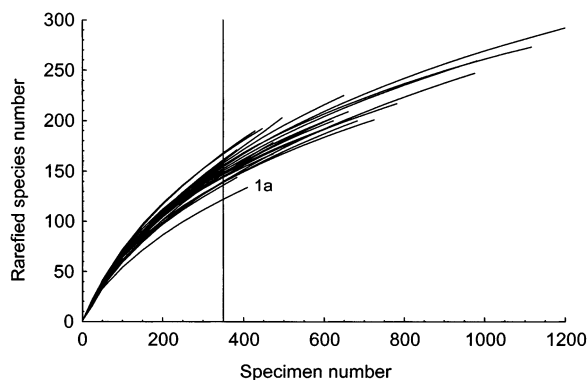


Fig. 3. Rarefaction curves for Geometridae at all 22 sites. For clarity, standard deviation curves are omitted. The vertical line indicates the standardised sample size (350 specimens), see Fig. 2B. The lowest rarefied species number was calculated for site 1a (1040 m).

are neither correlated with altitude nor with temperature (Table 1). However, in Larentiinae, Fisher's alpha is lowest at the lowest elevations (Fig. 2C).

Sample size dependence of diversity measures and concordance

Table 1 shows correlations between specimen numbers and different measures of alpha-diversity for Geometridae, Ennominae, and Larentiinae across the 22 study sites. In all three taxa, the recorded species number is strongly correlated with the number of specimens collected. Extrapolated species numbers also show significant correlations in all taxa, although the relationship is less pronounced than with recorded specimen numbers. In contrast, values of rarefied species numbers and

Table 2. Nominally significant deviations of samples from the log-series distribution. Provided are p-values from χ^2 -tests after arranging species-abundances in octaves (between 3 and 4 degrees of freedom) (Henderson and Seaby 1998). Printed in bold: significant after sequential Bonferroni correction (Hochberg 1988). Samples from all other sites (levels 2, and 5–11) and all Larentiinae samples did not deviate from the log-series. A complete list of sampling sites and their geographical coordinates was provided by Brehm (2002) and Brehm and Fiedler (2003).

Site number	Altitude (m)	Geometridae	Ennominae
1a	1040	0.038	–
1b	1040	< 0.001	0.003
3a	1800	0.027	0.048
3b	1800	0.015	–
4a	1850	0.010	0.006
4b	1875	0.015	0.035

Fig. 2. Diversity of Geometridae (left), and the largest subfamilies Ennominae and Larentiinae (right) along an altitudinal gradient ranging from 1040 to 2677 m in a montane rainforest in southern Ecuador. Diversity measured A) by extrapolation with the estimator Chao 1, B) by rarefaction (the level of specimens to which samples have been rarefied is indicated), and C) with Fisher's alpha. Error bars indicate ± 1 SD.

Fisher's alpha are all independent of sample size. Despite their differences with regard to sample size dependence, all four measures are highly associated (Kendall's coefficient of concordance: Geometridae $r_K = 0.95$, Ennominae $r_K = 0.91$, Larentiinae $r_K = 0.98$, all $p < 0.001$).

Discussion

Diversity within a world context

Values of Fisher's alpha of up to 131 per site for the species-rich family Geometridae are among the highest ever measured in the world. While most geometrid ensembles in temperate regions reach values between 10 and 35 (Barlow and Woiwod 1989, Thomas and Thomas 1994, Thomas 2002), the highest values to date have been found in rainforests of Peninsular Malaysia and Borneo at elevations between 200 and 700 m, with alpha scores of 127 and 128, respectively (Barlow and Woiwod 1989, Beck et al. 2002). An all-year-round sampling would probably lead to even higher values of Fisher's alpha because the sites in Ecuador were only sampled between two and four times. Since species numbers at single sites have been shown to be highly dependent on sample size, and samples are incomplete, raw species counts cannot be compared directly with other data. However, the total number of 1010 nocturnal geometrid moth species collected in the study area is the highest ever counted in a small geographic area (Brehm 2002).

Altitudinal patterns of different geometrid taxa

All diversity measures reveal similar results along the altitudinal gradient (all Kendall's $r_K > 0.9$). In all three taxa considered here (Geometridae, subfamilies Ennominae and Larentiinae) diversity either remained more or less constantly high or increased over an elevational range from 1040 to 2677 m. The patterns are very remarkable, because a decline of insect diversity towards higher altitudes was expected (Wolda 1987, a review by McCoy 1990, Hanski and Niemelä 1990, Brühl et al. 1999). Insect diversity often does not decrease steadily along elevational gradients, but peaks at medium elevations (Janzen et al. 1976, Holloway 1987, Olson 1994, Chey 2000). Our study is the first that revealed such an extended elevational diversity maximum of a very species-rich insect group at very high altitudes. So far, a similar pattern has only been observed in the geometrid subfamily Larentiinae in south

east Asia (Holloway et al. 1990, Schulze 2000). However, above 2000 m, even in Larentiinae only declining diversity has been detected so far. The high diversity of the subfamily Ennominae at high elevations was unexpected because this taxon was previously thought to be most diverse at lower montane zones (Holloway et al. 1990). We assume that the diversity of geometrid moths in the Andes declines only at very high altitudes in the transition zone between montane cloud rain-forest and the páramo vegetation. Indeed, sporadic sampling in the summit region of the study area (ca 3100 m) revealed minimal numbers of geometrid moths. However, effects of isolation and small habitat area might have been responsible for this (see below). Further studies with an extended elevational coverage in neighbouring or other areas could reveal more detailed patterns.

Diversity patterns and environmental factors

The exceptional, unique distributions of geometrid moths including their two largest subfamilies Ennominae and Larentiinae, call for explanations. Lawton et al. (1987) listed four hypotheses for declining diversity of herbivorous insects at higher altitudes: 1) reduction of habitat area, 2) reduction of resource diversity, 3) reduction of primary productivity, 4) increasingly unfavourable environments. Despite these constraints, diversity of geometrids remained constant or was even lower at low altitudes. How can this be explained? The points listed by Lawton et al. seem to be either not applicable in the study area (1 and 2), or might be compensated for by other factors (3 and 4).

Habitat area

Habitat area is not expected to be a limiting factor in this study, because the highest site is situated ca 500 m below the mountain summit and large areas of similar forested habitat exist next to the study area. However, area might also come into play as a limiting factor at higher altitudes in the Andes. Rahbeck (1997) and Körner (2000) emphasised the importance of decreasing area at high altitudes, and Holloway (1987) discussed a higher diversity of moths in montane Papua New Guinea compared to Borneo, as a consequence of greater land area situated above 2000 m. The Andes are folded mountains and provide a habitat area at high altitudes that is by far larger than on relatively isolated mountains such as Mount Kinabalu in Borneo, where the high altitude fauna is less species-rich. Furthermore, the biogeographical conditions in the Andes support the isolation of local populations (e.g. during glacial periods), subsequent speciation events, and a later co-existence of species. These fea-

tures might explain a considerable part of the exceptional diversity of geometrid moths in Ecuador.

Resource diversity

The possible reduction of resource diversity, including spatial niches, is difficult to assess because of widely lacking information describing which resources are actually used by Neotropical geometrid moths. However, some conclusions can be drawn from available information on host-plant use (Brehm 2002), and from vegetation data covering the study area. The structural complexity of the forest clearly declines along the altitudinal gradient (Paulsch 2002). Upper montane forests in the study area provide a far poorer offer of structural niches, e.g. because of the lower height and the absence of lianas. As a consequence, structural niches do not seem to be a limiting factor in the diversity of geometrids. The level of floristic diversity is more difficult to interpret, but there is evidence that the diversity of potential host-plants of geometrid moths generally decreases along altitudinal gradients in the Neotropical region (e.g. Gentry 1988, Lieberman et al. 1996). In a few cases there are indications of specialism towards certain host plant groups, and these geometrid groups indeed decline towards high altitudes (Brehm 2002). For example, the ennomine tribes Cassymini and Macariini are specialised Fabaceae feeders and are not present at the highest sites in the study area. Only very few Fabaceae species have been found in the study area (Homeier pers. comm.). Lianas also decrease along the altitudinal gradient in the study area, whereas in herbaceous vines this trend is less pronounced (Matezki pers. comm.). The number of tree species (> 5 cm diameter at breast height, 400 m² plots) in ridge forests in the study area decreases from ca 30 species at 1850 m to ca 20 species at 2450 m (Homeier et al. 2002). In contrast, the diversity of shrubs might be constant or even increase with increasing altitude. This latter resource (e.g. shrub-like Asteraceae) might play an important role for the very species-rich larentiine genus *Eupithecia*. There are also indications of a constant and high diversity of epiphytic plants (Werner 2002), which is generally known to be very high in Neotropical montane forests (Gentry and Dodson 1987, Nieder et al. 2001). However, most epiphytic vascular plants are monocotyledons and ferns (Rauer and Rudolph 2001). Both these plant groups are hardly exploited by Neotropical Geometridae (Brehm 2002). Overall, the total diversity of hosts that are actually used can be expected to decrease with altitude, but the extent of this decrease remains unknown. Irrespective of these uncertainties, the diversity of geometrids does not appear to be limited by a reduction of potential resource diversity.

Primary productivity

Primary productivity usually decreases along altitudinal gradients (Brujinzeel and Veneklaas 1998, Waide et al. 1998, but see Singh et al. 1994). According to Tanner et al. (1998), nutrient limitation is widespread in montane soils and foliar nitrogen decreases with increasing altitude. Significant changes in soil properties have also been documented along the elevational gradient in the study area (Schumpf et al. 2001). They reported decreasing pH values and nitrogen availability with rising altitude. Given these constraints, diversity of herbivorous geometrid moths remained unaffected.

Climate and physiology

Obviously, the moths are able to resist the cool and humid climate at high altitudes. The monthly average temperature decreases linearly by ca 10 K along the gradient, and precipitation more than doubles from ca 2000 mm to ca 5500 mm per annum (Hagedorn 2001, Emck pers. comm.). Geometrid moths appear to be physiologically predisposed towards such cool conditions. Heinrich (1993) and Rydell and Lancaster (2000) reported that many geometrid moth species were able to fly with lower thoracic temperatures than most other Lepidoptera species do. This could be a major energetic advantage and might allow geometrid moths to colonise habitats that are unsuitable for most other insects. However, the knowledge about the flight physiology of the vast majority of species is still unknown. Further investigations could test this hypothesis. We expect that members of the subfamily Larentiinae are particularly cold-adapted because of their dominance at high altitudes and latitudes.

Are high-altitude habitats an enemy-free space?

Predation can have impacts on the diversity of herbivorous insects. For example, Williams et al. (2001) pointed out that resources may often be less important than natural enemies in determining the distribution of herbivores. On the one hand, predators might regulate prey populations and prevent the dominance of single species. On the other hand, low predation pressure might allow an unconstrained radiation of herbivorous insects in nearly enemy-free space. Since predation pressure probably strongly declines with increasing altitude (see below), we find little support for the first hypothesis because neither diversity nor dominance values significantly change along the elevational gradient (Brehm 2002). The diversity of insectivorous species of bats, birds and ants in the Andes markedly decreases with altitude. Up to 38 species of insectivo-

rous bat species co-occur in lowland rainforests in Panama (Kalko 1997), whereas only eight occur above 1800 m and four above 2800 m in the study area in Ecuador (Matt 2001). Mixed species flocks of birds that forage in rainforests are expected to have a large impact on leaf-chewing insects (Braun 2002) and occur more prominently in lowland rather than montane forests (Rahbeck 1997, Thiollay 1999). Ants are the most prevalent invertebrate predators in many tropical forests (Hölldobler and Wilson 1990). However, they strongly decrease in diversity as altitude increases (Stork and Brendell 1990, Brühl et al. 1999). At higher altitudes in the Ecuadorian study area (above ca 2000 m), only very few ant species occur (unpubl.). Therefore, habitats are indeed a nearly enemy-free space with regard to this otherwise very important group of potential predators (Novotny et al. 1999, Floren et al. 2002). The knowledge on parasitoids and their role for Neotropical geometrid moths is still extremely scarce. However, parasitoids appear not to be a dominant factor since Brehm (2003) found only a low percentage of parasitised larvae in the study area.

Are the results representative of other groups?

This study has demonstrated exceptional altitudinal patterns of one major group of herbivorous insects. Further sampling would be required to confirm whether the results of this study are also applicable for other groups. According to Holloway (1987) the relative contribution of geometrids to local moth assemblages increases with altitude, suggesting that diversity patterns should be discordant even among moths as a guild. Indeed moth taxa in the Ecuadorian study area such as Pyraloidea and Arctiidae exhibit completely different altitudinal diversity patterns (Süßenbach 2003). Beccaloni and Gaston (1995) found a relatively constant ratio of species of the nymphalid subfamily Ithomiinae among all butterflies, and Longino (1994) reported a number of tropical invertebrate "focal taxa" that might represent suitable "survey taxa". The transfer of results from one group to others is part of the controversial debate about the usefulness of biodiversity indicators. Although several studies have established parallels between diversity patterns of different groups of organisms (Wolda 1996, Kerr et al. 2000), others found that there were none (Lawton et al. 1998, Ricketts et al. 2002). Simberloff (1998) criticised the concept of biodiversity indicators because of a lacking consensus as to what indicators should indicate and which organisms are the most versatile. If various taxa exhibit fundamentally different diversity patterns even among the herbivorous Lepidoptera, there is no reason to assume that patterns of, for example, detritivorous or predatory insects are better reflected.

Choice of measurement and sample size dependence

Our results confirm that unless it is possible to achieve complete inventories, the recorded species number is an unreliable measure of diversity because of its extreme dependence on the number of specimens collected (correlation coefficients all > 0.9 , $p < 0.001$). As expected, it has to be rejected as a meaningful measure of diversity for the purpose of discriminating between samples that are incompletely sampled (Gotelli and Colwell 2001). The estimator Chao 1 has also been shown to be significantly sample size dependent, though not to the same extent as species number. It is very probable that the true local richness is still substantially underestimated at most sites. This is illustrated by the very high ratios of singletons at single sites, i.e. species that were collected only once (41–60% of the species). A very high ratio of rare species is typical for samples of tropical arthropods. For example, Novotny and Basset (2000) found very similar singleton rates of 45% in samples of herbivorous insects in New Guinea. Underestimation occurs if samples are too sparse (Colwell and Coddington 1994). This study shows that even samples of at least 134 species and 384 individuals can be “too sparse” for extrapolation in extremely rich moth ensembles. According to Colwell and Coddington (1994), estimators correlate with sample size until about half the total fauna is observed and thereafter become gradually independent of sample size. Obviously, this level has not been reached at many sites because they could not be sampled more than two to four times.

Rarefied species numbers were independent of sample size. The measure can overestimate diversity if species have clumped distributions (Achtziger et al. 1992), but this is of relatively little importance in large samples and does not affect the results presented in this study. Fisher's alpha values did not correlate with specimen numbers and were thus independent of sample size. However, it is possible that values of Fisher's alpha would further increase with an increasing number of samples (Wolda 1987, Intachat and Holloway 2000, Schulze and Fiedler 2003). Since goodness-of-fit of the log-series model was not always satisfactory, it does not seem to be appropriate to rely solely on this measure. The use of several different measures can be recommended since they complement each other in different aspects of diversity as well as in the mathematical assumptions underlying their usage.

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