



Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest

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Abstract

Aim The objective of this study was to describe and interpret the changes in faunal composition in the moth family Geometridae (Lepidoptera) along a small-scale elevational gradient in a tropical montane rain forest. This gradient was compared with a large-scale latitudinal gradient in Europe.

Location Investigations were carried out in the province Zamora-Chinchipe in southern Ecuador along a gradient ranging from 1040 to 2677 m above sea level at twenty-two sites.

Methods Moths were sampled with light-traps in three field periods in 1999 and 2000 and subsequently sorted and determined to species or morphospecies.

Results We analysed 13,938 specimens representing 1010 species of geometrid moths. The proportional contribution of subtaxa to the local geometrid fauna changes along the elevational gradient at all systematic levels considered. While proportions of species of the subfamilies Ennominae, Sterrhinae and Geometrinae significantly decrease, the proportion of Larentiinae increases with increasing altitude. Changes also occur within the subfamilies Ennominae and Larentiinae. The host-plant specialist ennomine tribes Cassymini, Macariini and Palyadini completely vanish, and the proportion of the tribe Boarmiini decreases at high altitudes. In contrast, the remaining tribes (mostly comprising polyphagous species) either do not show proportional changes (Azelinini, Nacophorini, Nephodiini, Ourapterygini) or even increase (Caberini, 'Cratoptera group'). Within Larentiinae, the species proportion of the genus *Eois* decreases, whereas concomitantly the proportion of *Eupithecia* increases. There is a remarkable similarity between the altitudinal patterns in Ecuador and those found along the latitudinal gradient in Europe.

Main conclusions Species of the subfamily Larentiinae seem to be particularly well-adapted to harsh environmental conditions, towards both high altitudes and latitudes. They might disproportionately profit from lower predation at higher altitudes. Many changes in the faunal composition can be explained by expected host-plant requirements of the species involved. Our results show that diversity estimates based on taxon ratios which are assumed to be constant must be regarded with caution because such ratios can change rapidly along environmental gradients.

Keywords

Geometridae, Larentiinae, Ennominae, elevational gradient, latitudinal gradient, taxon ratios, host-plant specialists, indicator taxa, biodiversity indicators.

Resumen

Objetivo La meta de este estudio era describir e interpretar los cambios y la composición faunística en la familia de mariposas Geometridae (Lepidoptera) a lo largo de un gradiente altitudinal de escala pequeña en un bosque de montaña en los trópicos. Este gradiente fue comparado con un gradiente latitudinal de escala grande en Europa.

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Localidad Las investigaciones fueron realizadas en la provincia Zamora-Chinchi en el sur del Ecuador a lo largo de un gradiente elevándose de 1.040 a 2.677 m.s.n.m. en veintidos sitios.

Métodos Las mariposas fueron colectadas con trampas de luz en tres periodos de campo en 1999 y 2000. Después fueron ordenadas y determinadas como especies o morfoespecies.

Resultados Se analizaron 13.938 espécimenes representando 1.010 especies de geometridos. La contribución proporcional de los subtaxa para la fauna local cambia a lo largo del gradiente altitudinal en todos los niveles sistematicos considerados. Mientras las proporciones de especies de las subfamilias Ennominae, Sterrhinae y Geometrinae disminuyen significativamente con la altura, la proporción de Larentiinae incrementa. También hay cambios dentro de las subfamilias Ennominae y Larentiinae. Las tribus ennominas Cassymini, Macariini y Palyadini, que son especialistas acerca de plantas huéspedes, desaparecen completamente y la proporción de la tribu Boarmiini disminuye en altitudes grandes. Por el contrario, las demás tribus (mayormente especies polífagas) no demuestran cambios proporcionales (Azelinini, Nacophorini, Nephodiini, Ourapterygini) o incluso incrementan (Caberini, grupo '*Cratoptera*'). Dentro de los Larentiinae la proporción de especies del genero *Eois* disminuye, mientras la de *Eupithecia* crece concomitantemente. Hay una similitud notable entre los resultados de Ecuador de un gradiente altitudinal y aquellos encontrados a lo largo de un gradiente latitudinal en Europa.

Conclusiones principales Las especies de la subfamilia Larentiinae parecen ser particularmente bien adaptadas a condiciones ambientales desfavorables, tanto hacia altitudes como latitudes grandes. Podrían beneficiarse desproporcionadamente de una depredación más baja en altitudes más grandes. Muchos cambios en la composición faunística pueden explicarse con demandas esperadas a plantas huéspedes de las especies involucradas. Nuestros resultados muestran que estimados de diversidad basados en relaciones entre los taxa supuestas constantes deben de considerarse con cuidado ya que tales relaciones pueden cambiar rápidamente a lo largo de gradientes ambientales.

INTRODUCTION

It is well known that animal species and higher taxa such as families are not evenly distributed throughout the Earth, and that their diversity often changes along environmental gradients. For example, most groups of insects such as ants, termites, butterflies and beetles are most species-rich at low latitudes. Relatively few insect groups, e.g. aphids, sawflies, syrphids, psyllids, ichneumonids, braconids and bees, reach their highest species numbers at higher latitudes (Gauld, 1987; Holloway, 1987; Gaston 2000 and references therein; but see Horstmann *et al.*, 1999). There is an intense debate about the possible underlying mechanisms of latitudinal patterns of species richness (Chown & Gaston, 2000). However, altitudinal gradients have often been neglected despite their potential as powerful natural experimental systems (Körner, 2000; Lomolino, 2001). Altitudinal gradients offer very different climates and habitat types in close proximity to each other. The role of historical factors such as long-lasting isolation is much less pronounced than in latitudinal gradients, and at least for

more mobile organisms, the regional species pool is virtually identical at all study sites. Hence, actual elevational distributions of species are influenced mainly by ecological factors. However, studies on insect diversity along altitudinal gradients are relatively scarce, in particular for tropical mountain areas (but see McCoy, 1990 with a review; Olson, 1994; Brühl *et al.*, 1999; Schulze, 2000; Holloway *et al.*, 2001).

We here investigate the species-rich family Geometridae along an altitudinal gradient in a montane rain forest in southern Ecuador. Geometrids are a relatively habitat-specific group of herbivorous insects and thus very suitable for ecological studies (for tropical geometrids: Intachat *et al.*, 1997; Kitching *et al.*, 2000; Beck *et al.*, 2002). Changes of diversity along gradients can be documented in various complementary ways. Brehm *et al.* (in press) investigated the species diversity of geometrid moths in the Ecuadorian study area. In this paper, we compare community structures on a higher taxonomic level and assess the relative contributions of subfamilies, tribes and genera within the Geometridae. Geometrid moths occur in every biogeographical region

(Scoble *et al.*, 1995). World-wide the family contains *c.* 21,000 described species and is currently divided into nine subfamilies (Holloway *et al.*, 2001).

Fauna and flora can often be characterized by the relative proportions of their components (e.g. Gentry, 1988; Hayek & Buzas, 1997). Proportions (= ratios) of certain taxa compared with other taxa are frequently used for the estimation of species numbers (reviewed in Colwell & Coddington, 1994), but for this purpose the relevant ratios have to be approximately constant throughout the entities compared. The calculation does not require complete inventories and allows for comparison of samples taken from areas of different size. Thus, investigation of the composition of communities along environmental gradients can reveal important patterns which complement absolute measures of species diversity.

So far, the relative proportions of geometrid moth subfamilies have been investigated and quantified thoroughly only in the Indo-Pacific region (Holloway, 1987; Beck, 1998; Kitching *et al.*, 2000). Holloway showed that the subfamily Larentiinae increases in proportion with altitude and isolation of island habitats, whereas other subfamilies such as the species-rich Ennominae, as well as Geometrinae and Sterrhinae, decrease. In the Western Palaearctic region, Hausmann (2001) reported a strong proportional decline of Sterrhinae in southern Italy from 47% of geometrid species in lowland regions to 9% at higher elevations, while Larentiinae concomitantly increased to ratios of up to 61%. Notably, a similar increase of Larentiinae towards higher latitudes has been reported (e.g. Holloway, 1987), but has never been explicitly documented nor tested for significance.

It has been suggested to concentrate biodiversity inventories on certain well-known taxa and eventually extrapolate the diversity of related groups (e.g. Longino, 1994; Beccaloni & Gaston, 1995). However, such extrapolations must fail if proportions are changing from one place to

another. Therefore, the null-hypothesis assumes constant ratios of taxa within Geometridae along an elevational gradient on a small geographical scale. Moreover, we ask whether the patterns along the elevational gradient might parallel those seen in a latitudinal gradient. Unfortunately, no suitable data source of geometrid moths currently exists from the New World. However, the use of a recent checklist of geometrid moths of all European countries (Müller, 1996) offered an appropriate alternative because it contains reliable and detailed faunal information on a large continental scale.

MATERIALS AND METHODS

Study area

The study area in southern Ecuador is situated within the Eastern Cordillera of the Andes and politically belongs to the province of Zamora-Chinchipec (Fig. 1). It lies at the northern border of the Podocarpus National Park which comprises 146,280 ha of mostly undisturbed vegetation at elevations ranging from 1000 to 3600 m above sea level (Madsen & Øllgaard, 1994). A total of twenty-two sites were chosen at altitudes between 1040 and 2677 m, two replicate sites at each level of altitude. Eighteen plots lay within the area around the Estación Científica San Francisco (ECSF, 3°58' S, 79°5' W) and four were situated outside at lower elevations. Altitude and geographical coordinates were measured with the Global Positioning System (GPS) using a Garmin GPS III instrument (Appendix 1) (Garmin Instruments Inc., Olathe, KS, USA). Annual precipitation ranges between some 2000 mm at the lower elevations (Hagedorn, 2001) and reaches *c.* 5500 mm at the highest sites, depending on aspect and altitude (P. Emck, pers. comm.). The mean monthly temperature is 20–22°C at 970 m (Zamora) and 10–12°C at 2670 m (ECSF area)

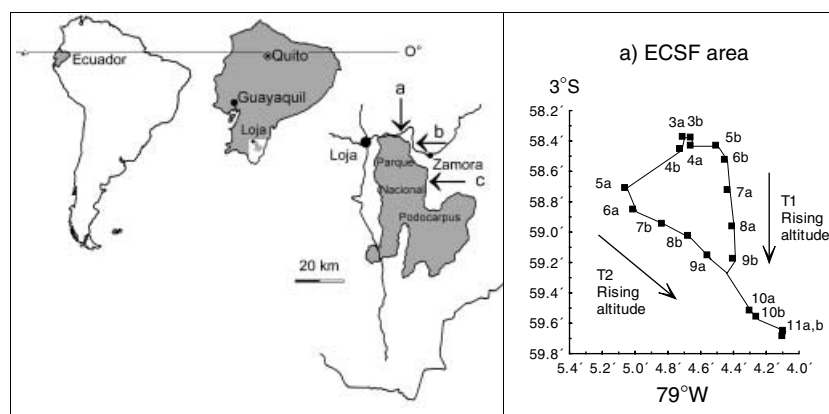


Figure 1 Geographical positions of the twenty-two sampling sites in South America and Ecuador at the northern border of the Podocarpus National Park, province Zamora-Chinchipec. Left: overview, right: sites in the area of the Estación Científica San Francisco (ECSF), covering *c.* 2.56×2.92 km² (7.46 km²). (a) Eighteen sites are situated within the area of the ECSF and range between 1800 m above sea level (sites 3a and 3b) and 2677 m (site 11b). (b) Two sites (2a and 2b) are situated close to the old road Loja-Zamora at 1400 m. (c) Two sites are situated south of Loja at Bombuscaro at 1040 m (1a and 1b). Appendix 1 provides a complete list of all altitudes and coordinates.

(Hagedorn 2001). According to Sierra's (1999) vegetation classification system, the study sites are situated in three different types of forest (as translated from Spanish): evergreen forest of foothills (800–1300 m), evergreen lower montane forest (1300–1800 m) and montane cloud forest (1800–2800 m). Bussmann (2001) provided a more finely scaled approach for the ECSF area and split the latter category into montane broadleaved forest (1850–2100 m), upper montane forest (2100–2750 m), and subalpine elfin forest (from 2450 m upwards). Another approach has been pursued by Paulsch (2002), who classified the forest by structural characteristics of the vegetation.

Sampling and identification

Moths were sampled in an extraordinarily high diversity by attraction to weak artificial light sources. Light trap samples do not perfectly represent actual populations but rather reflect the activity of species attracted to light (Wolda, 1992; Butler *et al.*, 1999). However, for most nocturnal Lepidoptera this sampling method is unrivalled by any other in terms of specimen and species numbers that can be gathered (e.g. Brehm, 2002). Two 15-W tubes in a white gauze cylinder (height 1.6 m, diameter 0.6 m) were operated at ground level. Because of logistical problems, sampling had to be restricted to the peak time of activity during the evening hours between 6.30 and 9.30 p.m. local time. Although a certain proportion of 'late night species' might have been missed by this approach, this is not expected to influence the results on faunal composition in any significant manner. Specimens were collected manually during three field periods (April to May 1999, October 1999 to January 2000, and October to November 2000; Appendix 1). The sites at medium to high elevations were sampled during the first two periods, whereas the lowest and highest sites were sampled during the two last periods. Between two and four nightly catches were pooled and analysed from each site (Appendix 1). In the study area, there is no pronounced dry season and we found no evidence of marked seasonal changes of the moth communities (Brehm, 2002). Specimens were first sorted to morphospecies and later identified in the Zoologische Staatssammlung, Munich and the Natural History Museum, London. So far, a relatively high proportion of 52% of species and 67% of specimens could be assigned to species level, while most of the remainder was assigned to genera. Nomenclature follows Scoble (1999) and Pitkin (2002) and a detailed species list was provided by Brehm (2002).

Proportions of taxa

Proportions were calculated from species numbers as well as from specimen numbers. Within Geometridae, the four largest subfamilies (Ennominae, Larentiinae, Sterrhinae and Geometrinae) were compared. The remaining subfamilies Oenochrominae and Desmobaethrinae were ignored because of their minimal numbers (three and one species, respectively). The two largest subfamilies Ennominae and Larentiinae

had sufficiently high numbers of species to allow further analyses. Because of the availability of a modern revision of Neotropical genera (Pitkin, 2002), it was possible to analyse ennomines at tribal level. In Larentiinae, reliable allocation of all species to a tribe was not possible. However, analysis of the patterns of the three largest genera offered a suitable alternative, as the genera *Eois*, *Eupithecia* and *Psaliodes* account for more than 70% of the species and more than 60% of the specimens in combined samples from each site.

Data from the European latitudinal gradient were taken from Müller (1996). This checklist is not only ordered by countries, but also provides data for large islands such as Corsica and Sicily. Except for six of 915 species, we follow Müller's subfamilial classification. Hausmann (2001) transferred one species of the genus *Gypsochroa* from Larentiinae to Desmobaethrinae. Five species that were formerly assigned to the paraphyletic taxon 'Oenochrominae *sensu lato*' are now placed into Desmobaethrinae, Orthostixinae and Altophilinae (Hausmann, 2001). As these three taxa, as well as Archearinae, contain only three or fewer species, they were excluded from further analyses.

Latitudinal data (approximate centres of each country or island) were taken from the index of 'The new international atlas' (Rand McNally, 2001). Iceland and Malta were excluded from the analyses because of their very low total number of species, rendering proportional data imprecise. Data from Turkey were also discarded as only the European part of Turkey was considered in Müller's (1996) checklist. 'Eastern Europe' was excluded because of lacking a precise latitude. As this paper primarily focuses on Neotropical geometrid moths, analyses of European geometrids were restricted to the level of subfamilies.

Statistics

The Spearman rank correlation coefficient was used because this is recommended when proportions are measured and relationships cannot be expected to be linear (Fowler *et al.*, 1998). Analyses were performed with the program Statistica 5.5 (StatSoft, 1999). Multiple tests of significance on inter-related data sets were Bonferroni-corrected according to Hochberg (1988).

RESULTS

Proportions of subfamilies within Geometridae

Figure 2 shows the proportions of the subfamilies, based on the species number. Species of the subfamily Ennominae clearly dominate at low elevational levels. While proportions of Ennominae, Geometrinae and Sterrhinae steadily decrease, the proportion of Larentiinae increases towards high altitudes. Species proportions and altitude are all highly significantly correlated (Table 1). Very similar patterns occur when numbers of specimens are analysed (not shown in a figure, but see Table 1), although changes in the smaller subfamilies Geometrinae and Sterrhinae are of only modest significance, probably due to the result of stochastic effects.

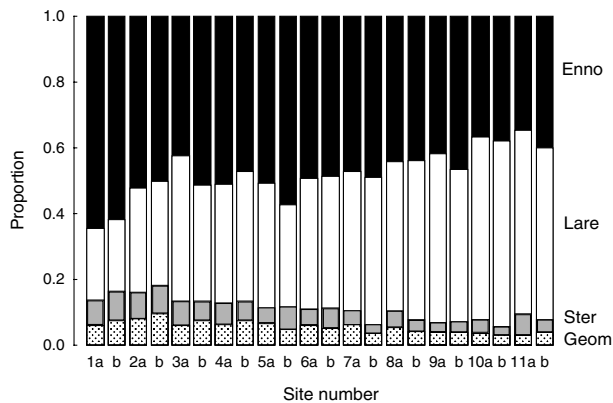


Figure 2 Proportions of subfamilies of the moth family Geometridae, based on species numbers, along an altitudinal gradient in a montane rain forest in Ecuador. See Table 1 for correlation coefficients. Sites are sorted by altitude. Geographical positions of all sites are provided in Appendix 1. Ennominae, Larentiinae, Sterrhinae, Geometrinae.

Table 1 Spearman rank correlation coefficients between proportions of four subfamilies within Geometridae and altitude ($n = 22$ sites)

	Ennominae	Larentiinae	Geometrinae	Sterrhinae
Species number	-0.84**	0.92**	-0.79**	-0.84**
Specimen number	-0.84**	0.89**	-0.45*	-0.52*

* $P < 0.05$, ** $P < 0.001$. All results remain significant after sequential Bonferroni correction.

Proportions of tribes within Ennominae

The picture of proportions within Ennominae is more complex because of the high number of analysed taxa (ten tribes and rest; Fig. 3). Three smaller tribes are restricted to a few lower sites (Cassymini) or vanish at the highest altitudes (Macariini and Palyadini). The remaining groups occur throughout the whole gradient. Only one of them, the Boarmiini, significantly decreases in species proportion. The other tribes all increase in their ratios, but this is significant only in the Caberini and the 'Cratoptera group'. The patterns of specimen proportions are similar in most tribes (Table 2), with two exceptions: Caberini (no significant relationship) and Nacophorini (a strong positive correlation between altitude and number of specimens).

Proportions of genera within Larentiinae

Clear patterns along the altitudinal gradient are also visible in this second large subfamily. Three large genera account for at least 70% of the species in this taxon (Fig. 4). The proportion of the genus *Eupithecia* increases significantly with altitude, whereas it decreases in the genus *Eois*. The genus *Psaliodes* shows no or only a modest correlation and

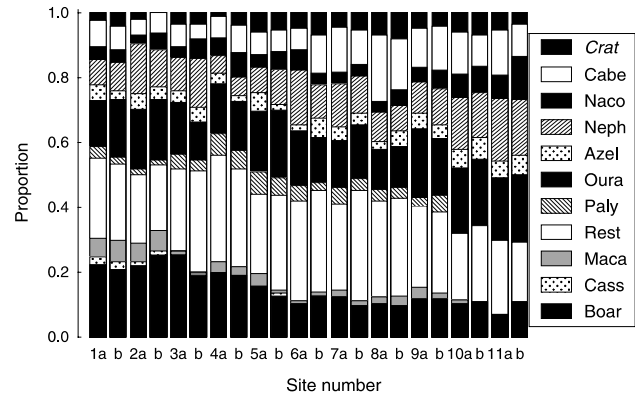


Figure 3 Geometrid moth faunas on an elevational gradient in Ecuador: proportional contribution, based on species numbers, of ten tribes and the remainder within Ennominae. Azelinini, Boarmiini, Caberini, Cassymini, 'Cratoptera group', Macariini, Nacophorini, Nephodiini, Ourapterygini, Palyadini, Rest: Ennominae not assigned to tribe. Sites are sorted by altitude. Geographical positions of all sites are provided in Appendix 1.

the remainder of species collectively shows a significant decrease only in specimen numbers (Table 3).

Proportions of subfamilies in the latitudinal gradient in Europe

The proportions of four large subfamilies and the remainder are shown in Fig. 5. Qualitatively the patterns largely resemble those found along the altitudinal gradient in Ecuador (Fig. 2). The large subfamilies follow the very same tendencies: all taxa significantly decline, except for Larentiinae which increases in proportion towards high latitudes (Table 4). Substantial differences exist in the overall relatively low proportion of Ennominae and the high proportion of Sterrhinae in Europe, compared with the study area in southern Ecuador.

DISCUSSION

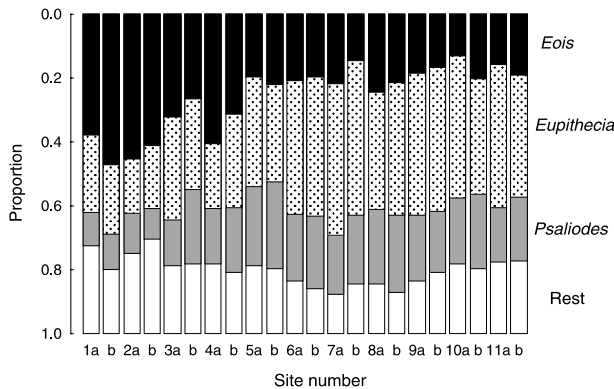
Ratio changes within Ennominae and Larentiinae

The patterns in Ennominae can partly be explained by the different host-plant preferences of the tribes. The available information on host-plant relationships of Neotropical geometrid moths has been reviewed by Brehm (2002). While tribes comprised of host-specialists tend to decline with altitude, the more polyphagous groups exhibit different patterns. Three small tribes vanish completely at higher altitudes and species in these tribes tend to be specialized towards Fabaceae (Cassymini, Macariini), or Myrsinaceae (Palyadini) (see also Scoble, 1995; Holloway, 1993; Holloway *et al.*, 2001). In Ecuador, Fabaceae are distributed mainly in lowland rain forests and decrease towards higher altitudes (Gentry, 1988; Jørgensen & León-Yáñez 1999; in the study area: J. Homeier, pers. comm.). The distribution of specialized herbivores depends on that of their host-plants.

Table 2 Spearman rank correlation coefficients between proportions of species of ten tribes within Ennominae vs. altitude ($n = 22$ sites). Printed in *italics* are results that are not significant after sequential Bonferroni correction

	Azelinini	Boarmiini	Caberini	Cassymini	'Cratoptera group'	Macariini	Nacophorini	Nephodiini	Ourapterygini	Palyadini
Species number	0.45*	-0.86***	0.71***	-0.67***	0.61**	-0.61***	0.49*	0.41 <i>n.s.</i>	0.35 <i>n.s.</i>	-0.35 <i>n.s.</i>
Specimen number	0.38 <i>n.s.</i>	-0.79***	0.25 <i>n.s.</i>	-0.67***	0.81***	-0.67***	0.75***	0.44*	0.46*	-0.32 <i>n.s.</i>

n.s., not significant; * $P < 0.05$; ** $P < 0.005$; *** $P < 0.001$. Ennominae species not assigned to tribe $r = -0.16$, *n.s.*; Ennominae specimens not assigned to tribe: $r = 0.34$, *n.s.*

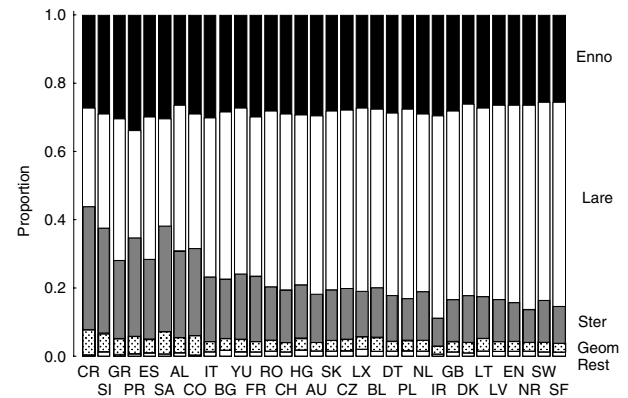
**Figure 4** Geometrid moth faunas on an elevational gradient in Ecuador: proportions of three large genera, based on species numbers, within the subfamily Larentiinae. Rest: Larentiinae not assigned to tribe. Sites are sorted by altitude. See Appendix 1 for geographical positions of all sites.**Table 3** Spearman rank correlation coefficients between proportions of three genera and rest within Larentiinae vs. altitude ($n = 22$ sites)

	<i>Eupithecia</i>	<i>Psaliodes</i>	<i>Eois</i>	Rest
Species number	0.77***	0.39 <i>n.s.</i>	-0.85***	-0.28 <i>n.s.</i>
Specimen number	0.78***	0.53*	-0.65**	-0.58**

n.s., not significant; * $P < 0.05$; ** $P < 0.005$; *** $P < 0.001$. All results remain significant after sequential Bonferroni correction.

In contrast, potential host-plants of Palyadini do occur at high-altitude habitats (Myrsinaceae: *Myrsine andina*) (Bussmann, 2001). Either there are physiological constraints that do not allow Palyadini to exceed altitudes of 2400 m or species such as *M. andina* are not suitable as hosts.

Polyphagous groups such as Nacophorini and Ourapterygini either do not change or even increase in ratio as altitude increases. On this higher taxonomical level, host-plants appear not to be a limiting factor, and the habitats seem to be structurally rich enough to support a high diversity of species. However, the same would be expected for all other tribes with mainly polyphagous larvae. Most species of the tribe Boarmiini are also expected to be rather polyphagous (Brehm, 2002), but Boarmiini decline in

**Figure 5** Proportions of subfamilies of European Geometridae. Data is from Müller (1996). Locations are sorted by their mean latitude (taken from Rand McNally, 2001). CR, Crete; SI, Sicily; GR, Greece; PR, Portugal; ES, Spain; SA, Sardinia; AL, Albania; CO, Corsica; IT, Italy; BG, Bulgaria; YU, (former) Yugoslavia; FR, France; RO, Romania; CH, Switzerland; HG, Hungary; AU, Austria; SK, Slovakia; CZ, Czech Republic; LX, Luxembourg; BL, Belgium; DT, Germany; PL, Poland; NL, the Netherlands; IR, Ireland; GB, Great Britain; DK, Denmark; LT, Lithuania; LV, Latvia; EN, Estonia; NR, Norway; SW, Sweden; SF, Finland. Iceland and Malta (small faunas), Turkey (incompletely covered fauna) and 'eastern Europe' (imprecise locality) were excluded from the analysis. Ennominae, Larentiinae, Sterrhinae, Geometrinae, Rest: Archiearinae, Desmobathrinae, Alsophilinae, Orthostixinae.

relation to all other Ennominae. Boarmiini species might possibly be less cold-adapted than species of the other tribes, but this hypothesis needs to be further tested.

The changes in species composition in Larentiinae are remarkable, but even more difficult to interpret than in Ennominae, as the host-plant relationships of Neotropical Larentiinae are particularly poorly documented (Brehm, 2002). In the genus *Eois* some preference for Piperaceae has been shown. *Eois* species dominate the Larentiinae ensembles at low altitudes where plant species of the family Piperaceae are more abundant than at higher altitudes (J. Homeier, pers. comm.). It is possible that the increase of the genus *Eupithecia* is related to the higher availability of potential hosts (e.g. inflorescences of Asteraceae: Brehm, 2002). Nothing is known about the larval hosts of the genus *Psaliodes*.

Table 4 Spearman rank correlation coefficients between proportions of species of eight subfamilies within European Geometridae and latitude of European countries and islands ($n = 32$). Species numbers of Alsophilinae (two species) and Desmobastrinae (three species) are not significantly correlated with latitude

Subfamily (species number)	Ennominae (298)	Larentiinae (389)	Geometrinae (30)	Sterrhinae (189)
r	-0.64*	0.97*	-0.74*	-0.95*

* $P < 0.001$. All results remain significant after sequential Bonferroni correction.

Patterns along altitudinal and latitudinal gradients

Altitudinal and latitudinal gradients are similar in many ways (e.g. declining temperature), but differ fundamentally in others (e.g. increase of seasonality at high latitudes and much greater distances among sampling sites). Chown & Gaston (2000) stressed the importance of latitudinal gradients in the understanding of macroecological patterns, whereas Körner (2000) emphasized the advantages of investigating altitudinal gradients. Our study shows that despite these differences moth faunal structures exhibit striking parallelism.

Ennomines are overall much less prevalent in Europe and have a very different tribal composition than in South America. Differences in their total ratio are thus difficult to interpret. The occurrence of many Sterrhinae species (particularly *Idaea*) in dry habitats can be explained by their ability to use leaf litter and detritus as food (Hausmann, 2001). Sterrhinae are therefore important in the Mediterranean, but strongly decline towards higher latitudes in Europe. As strong wet-dry gradients exist in the Andes, it would be very interesting to test whether the occurrence of Sterrhinae also might reflect such gradients there.

Both the more local analysis along the altitudinal gradient in Ecuador and the large-scale comparison along the latitudinal gradient in Europe reveal that the proportions of Larentiinae increase significantly towards cooler environmental conditions. This pattern strongly suggests a common underlying mechanism. Holloway (1987) already emphasized the montane characteristics of Larentiinae. However, it remains thus far unknown which physiological properties confer the unusual resistance of Larentiinae moths to unfavourable conditions. Although some larentiines have evolved a remarkable physiology that allows for flight activity at temperatures close to 0°C (*Operophtera* species: Heinrich & Mommsen, 1985), this winter moth habit is by no means exclusive to that subfamily. At any rate, in Ecuador, larentiines are able to develop and fly in large numbers of species and specimens under the cool and humid climatic conditions such as prevail at the upper end of the investigated elevational gradient. The annual precipitation is more than 5500 mm, and the average monthly temperature ranges between 10 and 12°C (P. Emck, pers. comm.). Similarly unfavourable conditions are also found at high latitudes, e.g. in Iceland, where 16 of 17 geometrid moth species are larentiines (Müller, 1996). Typically, larentiine

species are much more delicate in body design as compared with the often more robust ennomines, and thus appear to be relatively weak nocturnal flyers. Hence, larentiines might profit disproportionately from a nearly enemy-free space with regard to insectivorous bats. In the Andes, bats, as well as predators such as insectivorous birds, strongly decline in diversity and abundance with rising altitude (Rahbeck, 1997; Matt, 2001). The species richness of bats also declines with rising latitude (e.g. Kaufmann & Willig, 1998). At high latitudes in Europe, where only very few insectivorous bats occur, moth communities have been shown to be shaped by this relaxation of predation pressure (Rydell & Lancaster, 2000). An additional explanation for the relative increase of Larentiinae is offered by subfamilial differences in host-plant use. Larentiinae larvae predominantly feed on herbaceous plants (e.g. Skou, 1986), whereas most Ennominae caterpillars feed on woody plants. As diversity of trees or shrubs declines disproportionately at high latitudes in Europe (> 60° N), this could contribute to the proportional reduction of Ennominae (Neuvonen & Niemelä, 1983).

Generally, it has to be considered that faunal proportions do not necessarily reflect species diversity patterns. For example, the proportions of Larentiinae significantly decline in both gradients analysed (see above). However, species richness patterns differ between the gradients: diversity of larentiines along the elevational gradient is relatively low at low elevations of the Ecuadorian study area (1040 m) and reaches almost constant high levels from 1800 to 2677 m (Brehm, 2002). In contrast, absolute species numbers of Larentiinae steadily decline along the latitudinal gradient in Europe. When countries of similar area size such as Italy (301,225 km²) and Norway (323,878 km²) are compared, many more larentiine species occur in Italy (263 compared with 166 in Norway: Müller, 1996). The analysis of the latitudinal gradient is further complicated by the occurrence of elevational gradients nested within latitudinal gradients. For example, many larentiine species in Italy occur at higher elevations (Hausmann, 2001). However, the conclusion that Larentiinae with *c.* 5700 described species world-wide (Scoble *et al.*, 1995) are a remarkable insect group with regard to their geographical distribution remains unaffected by these qualifications. In any case, the latitudinal gradient of geometrid moth diversity and faunal composition in Europe deserves a more profound analysis in the future. For such macroecological investigations on European Lepidoptera, the checklist provided by Karsholt & Razowski (1996) offers an excellent opportunity.

Are taxon ratios useful for diversity estimations?

Assuming constant ratios, it might be sufficient to restrict sampling to certain 'indicator' taxa. Some authors have therefore suggested that the diversity of entire groups can be estimated by sampling of much less diverse indicators or 'focal taxa' (Colwell & Coddington, 1994; Longino, 1994; Beccaloni & Gaston, 1995). However, the approximate constancy of such ratios is often not based on empirical evidence but rather used as postulate (Gaston, 1992; Prendergast *et al.*,

1993; Colwell & Coddington, 1994). This study shows that taxon ratios can change rapidly along environmental gradients. Hence, before ratios can be utilized as a basis for extrapolation, it is essential to assess at the outset of each case study the influence of environmental gradients in an area. Once a reliable pattern has been identified, the study of indicator taxa might indeed be sufficient for certain purposes. If, for example, only the subfamily Larentiinae could have been sampled at a certain altitude in the study area in Ecuador, the diversity of Ennominae could be predicted quite accurately. However, if local changes in species composition are not taken into consideration, extrapolations can be highly misleading. In a hypothetical new study at another Andean locality, a new calibration of ratios would be required because altitudinal shifts in composition might vary geographically. Variation between small and large mountains may result from the Massenerhebungseffekt (Tanner, 1977; Holloway, 1984; Flenley, 1995). Similar problems would arise for species extrapolation on the much larger geographical scale in the latitudinal gradient in Europe. This undermines the practicability of extrapolation by ratios. Hence, in order to achieve a better understanding of global biodiversity, case studies of large groups of organisms at multiples scales, from local to continental, are required. Geometrid moths, with their good taxonomic coverage (Scoble, 1999) and versatility as environmental indicators (Intachat *et al.*, 1997; Beck *et al.*, 2002) lend themselves as models for further study.

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REFERENCES

Beccaloni, G.W. & Gaston, K.J. (1995) Predicting the species richness of Neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. *Biological Conservation*, **71**, 77–86.

Beck, J. (1998) *Zur Diversität von Spannern (Lepidoptera: Geometridae) in verschiedenen gestörten Habitattypen auf Borneo*. Diploma Thesis, University of Würzburg, Würzburg.

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.

Brehm, G., Süßenbach, D. & Fiedler, K. (in press) Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. *Ecography*.

Brühl, C.A., Mohamed, M. & Linsenmair, K.E. (1999) Altitudinal distribution of leaf litter ants along a transect in primary forest on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology*, **15**, 265–277.

Bussmann, R.W. (2001) The montane forests of Reserva Biológica San Francisco (Zamora-Chinchipe, Ecuador). *Die Erde*, **132**, 9–25.

Butler, L., Kondo, V., Barrows, E.M. & Townsend, E.C. (1999) Effects of weather conditions and trap types on sampling for richness and abundance in forest Macrolepidoptera. *Environmental Entomology*, **28**, 795–811.

Chown, S.L. & Gaston, K.J. (2000) Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology and Evolution*, **15**, 311–315.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society London B*, **345**, 101–118.

Flenley, J.R. (1995) Cloud forest, the Massenerhebung effect, and ultraviolet insolation. *Tropical montane cloud forests* (eds L.S. Hamilton, J.O. Juvik and F.N. Scatena), pp. 150–155. Springer, Heidelberg, New York.

Fowler, J., Cohen, L. & Jarvis, P. (1998) *Practical statistics for field biology*. Wiley, New York.

Gaston, K.J. (1992) Regional numbers of insect and plant species. *Functional Ecology*, **6**, 243–247.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–226.

Gauld, I.D. (1987) Some factors affecting the composition of tropical ichneumonid faunas. *Biological Journal of the Linnean Society*, **30**, 299–312.

Gentry, A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, **75**, 1–34.

Hagedorn, A. (2001) Extent and significance of soil erosion in southern Ecuador. *Die Erde* **132**, 75–92.

Hausmann, A. (2001) *The geometrid moths of Europe* Vol. 1. Apollo Books, Stenstrup.

Hayek, L.-A. & Buzas, M.A. (1997) *Surveying natural populations*. Columbia University Press, New York.

Heinrich, B. & Mommsen, T.P. (1985) Flight of winter moths near 0°C. *Science*, **228**, 177–179.

Hochberg, Y. (1988) A sharper Bonferroni procedure for multiple tests of significance. *Biometrika*, **75**, 800–802.

Holloway, J.D. (1984) The larger moths of the Gunung Mulu national park: a preliminary assessment of their distribution, ecology, and potential as environmental indicators. *The Sarawak Museum Journal*, **30**, 149–190.

Holloway, J.D. (1987) Macrolepidoptera diversity in the Indo-Australian tropics, geographic, biotopic and taxonomic variations. *Biological Journal of the Linnean Society*, **30**, 325–341.

- Holloway, J.D. (1993) The moths of Borneo: family Geometridae, subfamily Ennominae. *Malayan Nature Journal*, **47**, 1–309.
- Holloway, J.D., Kibby, G. & Pegg, D. (2001) *The families of Malesian moths and butterflies*. Brill, Leiden.
- Horstmann, K., Floren, A. & Linsenmair, E.K. (1999) High species richness of Ichneumonidae (Hymenoptera) from the canopy of a Malaysian rain forest. *Ecotropica*, **5**, 1–12.
- 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.
- Jørgensen, P.M. & León-Yáñez, S. (eds) (1999) *Catalogue of the vascular plants of Ecuador*. Missouri Botanical Garden Press, St Louis, Missouri.
- Karsholt, O. & Razowski, J. (eds) (1996) *The Lepidoptera of Europe*. Apollo Books, Stenstrup.
- Kaufmann, D.M. & Willig, M.R. (1998) Latitudinal patterns of mammalian species richness in the new world: the effects of sampling method and faunal group. *Journal of Biogeography*, **25**, 795–805.
- 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.
- Körner, C. (2000) Why are there global gradients in species richness? Mountains might hold the answer. *Trends in Ecology and Evolution*, **15**, 513–514.
- Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, **10**, 3–13.
- Longino, J.T. (1994) How to measure arthropod diversity in a tropical rainforest. *Biology International*, **28**, 3–13.
- Madsen, J.E. & Øllgaard, B. (1994) Floristic composition, structure, and dynamics of an upper montane rain forest in southern Ecuador. *Nordic Journal of Botany*, **14**, 403–423.
- Matt, F. (2001) *Pflanzenbesuchende Fledermäuse im tropischen Bergregenwald: Diversität, Einnischung und Gildenstruktur – Eine Untersuchung der Fledermausgemeinschaften in drei Höhenstufen der Andenostabdachung des Podocarpus Nationalparks in Südecuador*. Dissertation, University of Erlangen-Nürnberg, Erlangen.
- McCoy, E.D. (1990) The distribution of insects along elevational gradients. *Oikos*, **58**, 313–322.
- Müller, B. (1996) Check-list of Geometridae. *The Lepidoptera of Europe* (eds O. Karsholt and J. Razowski), pp. 218–249. Apollo Books, Stenstrup.
- Neuvonen, S. & Niemelä, P. (1983) Species richness and faunal similarity of arboreal insect herbivores. *Oikos*, **40**, 452–459.
- Olson, D.M. (1994) The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. *Journal of Tropical Ecology*, **10**, 129–150.
- Paulsch, A. (2002) *Development and application of a classification system for undisturbed and disturbed tropical montane forests based on vegetation structure*. Dissertation, University of Bayreuth, Bayreuth.
- Pitkin, L.M. (2002) Neotropical ennomine moths: a review of the genera (Lepidoptera: Geometridae). *Zoological Journal of the Linnean Society*, **135**, 121–401.
- Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, **365**, 335–337.
- Rahbeck, C. (1997) The relationship among area, elevation, and regional species richness in Neotropical birds. *The American Naturalist*, **149**, 875–902.
- Rand McNally (2001) *The new international atlas*, Chicago.
- Rydell, J. & Lancaster, W.C. (2000) Flight and thermoregulation in moths were shaped by predation from bats. *Oikos*, **88**, 13–18.
- Schulze, C.H. (2000) *Auswirkungen anthropogener Störungen auf die Diversität von Herbivoren – Analyse von Nachtfalterzönosen entlang von Habitatgradienten in Ost-Malaysia*. Dissertation, University of Bayreuth, Bayreuth.
- Scoble, M.J. (1995) A review of the moth tribe Palyadini with the description of a new genus (Geometridae: Ennominae). *Systematic Entomology*, **20**, 35–58.
- Scoble, M.J. (ed.) (1999) *Geometrid moths of the world – a catalogue (Lepidoptera: Geometridae)*. CSIRO Publishing, Collingwood.
- 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.
- Sierra, R. (ed.) (1999) *Propuesta preliminar de un sistema de clasificación de vegetación para el Ecuador continental*. Proyecto INEFAN/GEF-BIRF y EcoCiencia, Quito, Ecuador.
- Skou, P. (1986) *The geometroid moths of North Europe*. *Entomonograph*, Vol. 6. Brill, Leiden.
- StatSoft (1999) *Statistica for Windows*, Version 5.5. StatSoft Inc., Tulsa.
- Tanner, E.V.J. (1977) Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of interrelations. *Journal of Ecology*, **65**, 883–918.
- Wolda, H. (1992) Trends in abundance of tropical forest insects. *Oecologia*, **89**, 47–52.

BIOSKETCHES

Gunnar Brehm is an ecologist focusing on biodiversity research of 'mega-diverse' arthropod communities such as moths and butterflies in tropical rain forests. He is also interested in host-plant relationships, in chemical ecology of Lepidoptera associated with pyrrolizidine alkaloids, and in conservation issues. He has a strong interest in insect systematics and taxonomy, in particular of Neotropical Geometridae.

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Appendix I List of sampling sites (sorted by altitude), geographical positions and dates of collection. Coordinates were measured using the Global Positioning System; Localities: B, Bombuscaro; S, Road between Loja and Zamora; T1, T2, transect paths in the area of the ECSF. Each site was sampled between two and four times. Further data on the sites were provided by Brehm (2002)

Site	Locality	Latitude (S)	Longitude (W)	Altitude (m)	Dates of collection
1a	B	4 °06 '870	78 °58 '031	1040	5 December 1999, 27 October 2000
1b	B	4 °06 '985	78 °58 '089	1040	5 December 1999, 27 October 2000
2a	S	4 °01 '109	79 °00 '948	1380	30 October 2000, 22 November 2000
2b	S	4 °01 '109	79 °00 '948	1380	30 October 2000, 22 November 2000
3a	T1	3 °58 '454	79 °04 '726	1800	13 April 1999, 6 May 1999, 23 May 1999, 26 December 1999
3b	T2	3 °58 '375	79 °04 '710	1800	19 April 1999, 7 May 1999, 17 May 1999, 26 December 1999
4a	T2	3 °58 '379	79 °04 '661	1850	12 April 1999, 26 April 1999, 16 May 1999, 28 December 1999
4b	T1	3 °58 '431	79 °04 '661	1875	11 April 1999, 25 April 1999, 11 May 1999, 28 December 1999
5a	T1	3 °58 '710	79 °05 '063	2005	20 April 1999, 11 May 1999, 18 May 1999, 30 December 1999
5b	T2	3 °58 '429	79 °04 '507	2005	21 April 1999, 3 May 1999, 13 May 1999, 30 December 1999
6a	T1	3 °58 '853	79 °05 '011	2112	24 April 1999, 10 May 1999, 18 May 1999
6b	T2	3 °58 '522	79 °04 '455	2113	16 April 1999, 3 May 1999, 13 May 1999
7a	T2	3 °58 '724	79 °04 '435	2180	14 April 1999, 5 May 1999, 12 May 1999, 29 December 1999
7b	T1	3 °58 '944	79 °04 '837	2212	27 April 1999, 7 May 1999, 17 May 1999, 2 January 2000
8a	T2	3 °58 '962	79 °04 '409	2290	17 April 1999, 5 May 1999, 12 May 1999
8b	T1	3 °59 '025	79 °04 '679	2308	25 April 1999, 9 May 1999, 21 May 1999, 3 January 2000
9a	T1	3 °59 '153	79 °04 '560	2375	26 April 1999, 9 May 1999, 21 May 1999, 3 January 2000
9b	T2	3 °59 '173	79 °04 '403	2387	21 April 1999, 6 May 1999, 10 May 1999, 1 January 2000
10a	T1	3 °59 '516	79 °04 '300	2524	16 December 1999, 18 October 2000
10b	T1	3 °59 '558	79 °04 '262	2558	16 December 1999, 18 October 2000
11a	T1	3 °59 '648	79 °04 '096	2671	21 October 2000, 20 November 2000
11b	T1	3 °59 '684	79 °04 '103	2677	21 October 2000, 20 November 2000