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ORIGINAL ARTICLE

Montane Andean rain forests are a global diversity hotspot of geometrid moths

Gunnar Brehm[1]*, Linda M. Pitkin[2], Nadine Hilt[1] and Konrad Fiedler[1,3]

[1]*Department of Animal Ecology I, University of Bayreuth, Bayreuth, Germany,* [2]*Department of Entomology, Natural History Museum, London, UK and* [3]*Department of Population Ecology, Faculty of Life Sciences, University of Vienna, Wien, Austria*

*Correspondence: Gunnar Brehm, Department of Animal Ecology I, University of Bayreuth, 95440 Bayreuth, Germany.
E-mail: gunnar_brehm@yahoo.com

ABSTRACT

Aim Andean forests are known to be a major diversity hotspot for vascular plants and vertebrates, but virtually nothing is known about the diversity of arthropods. We examined whether montane rain forests in southern Ecuador are also a diversity hotspot for arthropods, and chose geometrid moths as a model group.

Location The study area in southern Ecuador (Province Zamora-Chinchipe, 79° W, 04° S) covers *c.* 40 km^2, with 39 collecting sites within an elevational range of 1040–2677 m a.s.l. Thirty-five of the sites were situated in an area *c.* 2.5 km^2. Additional qualitative sampling was carried out in the same area and up to an elevation of 3100 m.

Methods Nocturnal moths were collected quantitatively and qualitatively using portable light towers consisting of two 15 W fluorescent tubes, and diurnal moths were collected qualitatively using an insect net. Insects were sampled in six fieldwork periods in the years 1999–2003. As diversity measures, Fisher's alpha of the log-series distribution as well as eight estimators of total species richness were applied.

Results A total of 1266 species were recorded, 63% of which were identified to named species, whereas the remainder are likely to include many undescribed species. Quantitative samples at light towers collected 35,238 specimens representing 1223 species. The extrapolated species number for these data is 1420 (incidence coverage estimator). Twenty-one additional nocturnal species and 22 exclusively diurnal species were sampled qualitatively at elevations between 1040 and 3100 m. The pooled value of Fisher's alpha for all quantitative samples is 246 ± 3.

Main conclusions The diversity of Geometridae documented here is much higher than anywhere else in the world, even without the inclusion of additional species from adjacent lowland rain forests. The number of recorded species in this small area corresponds to more than 6% of the known world fauna of geometrid moths. Our study emphasizes the importance of protecting the remaining montane Andean rain forests. For setting priorities in conservation, more studies on insect diversity are urgently required in other regions of the Andes, since montane forests are being destroyed at an alarming rate.

Keywords

Arthropods, cloud forest, conservation, Ecuador, gamma diversity, Geometridae, insects, landscape diversity, Lepidoptera, species richness.

INTRODUCTION

The tropical Andes have been recognized as one of the hotspots of diversity for vascular plants and vertebrates (6.7% and 5.7% endemic species, respectively; Myers *et al.*, 2000). Due to the very high diversity and endemism of plants, Brummitt & Lughadha (2003) ranked the tropical Andes as the top global hotspot. However, diversity of the

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most popular and conspicuous groups of organisms (vascular plants and vertebrates) is not necessarily concordant with diversity of the most speciose taxa: data for arthropods are much poorer, and quantitative studies on diversity of most groups are still completely lacking from the tropical Andean region. This is also true for most Lepidopteran taxa, except that butterflies have been found to have a diversity hotspot in the western Amazon basin (Robbins & Opler, 1997).

The moth family Geometridae is a major taxon of herbivorous insects with more than 21,000 valid described species, over 30% of which occur in the Neotropical region (Scoble, 1999). Although their impact on tropical ecosystems in food webs and as pollinators might be considerable due to the sheer number of species and individuals (see remarks on Lepidoptera by Scoble, 1992, p. 170), very little has been known until recently concerning the regional diversity of this group in the Neotropical region, and particularly in the Andean montane rain forests.

We investigated the diversity of geometrid moths in the Andes in southern Ecuador on the Amazonian slopes. We expected the tropical Andes to be a top global hotspot not only for vascular plants, but also for a very species-rich moth taxon. In addition to estimates of diversity of Geometridae and comparisons with other regions, we also indicate the proportion of species likely to be unknown to science, and we discuss the significance of these results for establishing conservation priorities. The complete species list is provided as Supplementary Material (Appendix S1).

MATERIALS AND METHODS

The study area is situated in southern Ecuador (province of Zamora-Chinchipe) in the Eastern Cordillera of the Andes (Fig. 1). It is located at the northern boundary of the Podocarpus National Park. We selected a total of 39 sites (22 in natural forest, 15 along a gradient of forest succession, and two in disturbed, deforested landscapes; Table 1). All 39 sites were situated at elevations between 1040 and 2677 m a.s.l., between 3°58 and 4°07′ S, and between 78°58 and 79°05′ W (exact positions and dates given by Brehm & Fiedler, 2003, 2005; Hilt & Fiedler, 2005). Additional qualitative sampling was carried out in the same elevational range and at 3100 m a.s.l. The area including the 39 sites where quantitative sampling was carried out was calculated as a polygon using the Gauss formula, and covers 39.9 km^2.

The vegetation consists of evergreen montane rain forests (Madsen & Øllgaard, 1994; Homeier *et al.*, 2002) and adjacent deforested landscapes. The mean monthly temperature ranges from 20–22 °C at 970 m to 10–12 °C at 2760 m, and precipitation in the area amounts to between *c.* 2000 and 4000 mm per year (Richter, 2003).

Moths were sampled manually using portable light 'towers' consisting of two 15 W tubes (Sylvania blacklight-blue, F 15 W/BLB-TB and Phillips TLD 15 W 05) within a white gauze cylinder (height 1.60 m, diameter 0.70 m). Sampling methods were described in detail and discussed by Brehm (2002) and Brehm & Fiedler (2003, 2005). Lights were run during the peak of moth activity after dusk between 18.30 and

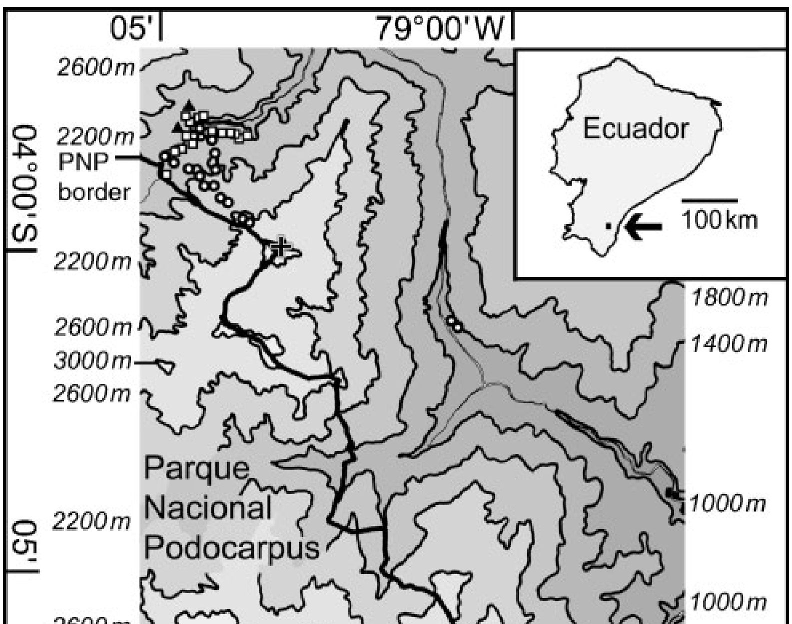

Figure 1 Geographical position of all sampling sites in southern Ecuador and in the vicinity of Podocarpus National Park/ Parque Nacional Podocarpus (PNP). Sampling was carried out quantitatively at 22 forest sites (open circles); at 15 sites along a gradient of succession (open rectangles); and at two disturbed sites (black triangles) in an elevational range between 1040 and 2677 m a.s.l. The core study area covers *c.* 2.5 km^2 (35 sites). The polygon that includes all 39 sites has an area of *c.* 40 km^2. Additional qualitative sampling was carried out at all forest sites and at a site at 3100 m a.s.l. (black cross). Map redrawn from Ecuadorian 1:50,000 topographical maps. It displays contour lines every 400 m elevation.

Table 1 Sampling sites, habitat types, collection periods (month and year), and individuals and species analysed

Source	Elevation (m)	Sites (n)	Habitat	Collection period	Individuals	Species
Quantitative data						
Brehm (2002) updated; sites and dates: Brehm & Fiedler (2003)	1040–2677	22	Forests	IV–VI 1999, X 1999–I 2000, X–XII 2001	13,939	1013
Brehm & Fiedler (2005) updated	1950–2005	2	Disturbed sites	X–XI 2001	629	197
N.H. (unpubl. data), sites: Hilt & Fiedler (2005)	1822–1973	15	Gradient of succession	III–IV 2002, X–XI 2002, VIII–X 2003	20,670	775
Sum: 2.5 km^2 core polygon	1800–2677	35	Various		32,845	1075
Sum: 40 km^2 complete polygon	1040–2677	39	Various		35,238	1223
Qualitative data						
G.B. (unpubl. data)	1040–2677	–	Forests, secondary forests		–	18 nocturnal, 22 diurnal
G.B. (unpubl. data)	3100	–	Subparamo		–	3 nocturnal
Sum	1040–3100	–	Various		–	43 (21 nocturnal, 22 diurnal)

21.45 local time, with all moths being collected within these 3 h.

The 22 forest sites were sampled between two and four times, since limited resources did not allow analysis of a larger number of samples. Based on these samples, Brehm (2002) provided a preliminary species list with 13,938 specimens belonging to 1010 species. The data base for this list has been constantly refined by G.B. during the past 3 years as identification progressed, with addition or removal of species names involving *c.* 100 species. Many further identifications have now been made to species level. Fourteen specimens that could not be assigned previously have been identified as belonging to other families. Despite these amendments, the current species total of the forest sites (1013) is almost the same as it was in 2002. The changes to the data base have had no significant impact on the results of analyses of alpha- and beta-diversity and of faunal composition (Brehm & Fiedler, 2003; Brehm *et al.*, 2003a,b). In addition to the forest sites, 15 sites along a gradient of succession and two disturbed sites are included in the analyses for the present study. Table 1 provides an overview of the data sources, elevations, habitat types, and numbers of individuals and species collected. Further specimens were sampled qualitatively at the 22 forest sites, using the same methods (Table 1). A few specimens were also collected at 3100 m a.s.l. around the summit of the mountain range of the main study area. Additionally, diurnal geometrids were sampled qualitatively by collection with a net during field visits in 1999 and 2000.

The moths were identified by comparison with type specimens and other reliably identified material in the collections of the Natural History Museum in London, UK; the National Museum of Natural History in Washington, DC, USA; the American Museum of Natural History in New York, USA; the Senckenberg Museum in Frankfurt, Germany; and the Zoologische Staatssammlung München, Germany, including the Herbulot collection. Taxonomy follows Pitkin (2002) for the subfamily Ennominae, and Scoble (1999) for all remaining species. Identification was carried out using wing pattern and other external characters (including the relevant type material). Genitalia slides were made in this study to aid in the most problematic cases for identification (*c.* 100 species). However, study of species identities and taxonomy is an ongoing process, and the species list provided in Appendix S1 will be updated in the future as new information becomes available.

Of the 1266 species recorded, 795 (63%) were identified to species level. The remaining 469 species could not be formally identified, but in most cases were assigned to genera. Of these unidentified species, 182 are considered to be near, but not identical with, a described species.

Brose & Martinez (2004) provided a decision framework for choosing the most accurate estimators of species richness. Following this, we first calculated regional species richness using eight different estimators (abundance coverage estimator, incidence coverage estimator, Bootstrap, Chao1 and 2, Jackknife 1 and 2, Michaelis–Menten means: 50 randomizations) provided in the EstimateS software (Colwell, 2004). Pooled samples of each of the 39 sites were used as samples of local diversity. In a second step we calculated the sample coverage of each estimator (the ratio of recorded to estimated species number) and chose the most appropriate estimator.

Fisher's alpha was also calculated using EstimateS. This alpha-diversity index is influenced mainly by the frequency of species of medium abundance, and has been proven to be a reliable measure of diversity (Hayek & Buzas, 1997). The fit of the log-series distribution was confirmed using the program Species Diversity and Richness (Henderson & Seaby, 1998).

RESULTS

Quantitative samples from 39 sites consisted of 35,238 specimens representing 1223 species (Table 1). Additional

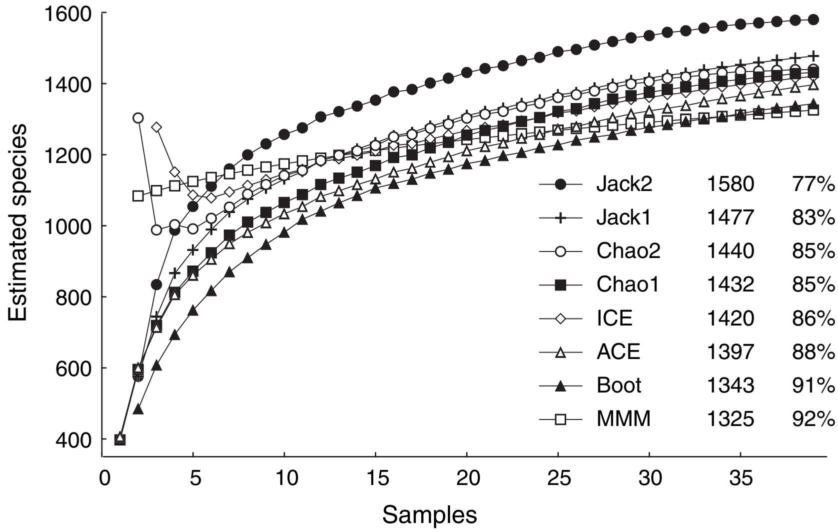

Figure 2 Estimated species number of geometrid moths in an area of montane rain forest, adjacent sites along a gradient of succession and disturbed sites in southern Ecuador (1040–2677 m a.s.l.). Data is from quantitative samples from 39 sites of 35238 specimens representing 1233 species. The inserted table provides the estimated species numbers and the estimated coverage (in %) for all 39 sites. Abbreviations: ACE = abundance coverage estimator, Boot = Bootstrap, ICE = incidence coverage estimator, Jack = Jacknife, MMM = Michaelis-Menten Means.

qualitative samples added 43 further species to the list (Table 1). Hence Appendix S1 records a total of 1266 species from the whole Ecuadorian study area. Of the 1266 species recorded, the majority belong to the subfamily Ennominae (622 species), followed by Larentiinae (485), Sterrhinae (88), Geometrinae (67), Oenochrominae (3) and Desmobathrinae (1).

Among the quantitative samples (1223 species from 39 sites), 221 species (18%) were found with only one specimen (singletons), and 117 species (10%) with only two individuals (doubletons). The three most abundant species in the study were *Pantherodes conglomerata* (Ennominae, 2613 specimens); *Sabulodes thermidora* (Ennominae, 1058 specimens); and *Idaea recrinita* (Sterrhinae, 525 specimens).

Figure 2 shows curves of the eight estimators. For all 39 sites, the estimators indicate a species richness between 1325 (Michaelis–Menten means) and 1580 (Jackknife 2). The coverage ranges between 77% and 92% (mean 87%). For a sample coverage between 86% and 96%, Brose & Martinez (2004) recommended the incidence coverage estimator, which gives an estimate of 1420 species. The value of Fisher's alpha for all quantitative samples pooled is 246 ± 3.

DISCUSSION

Our study supports the ranking of the tropical Andes as the top global diversity hotspot (Brummitt & Lughadha, 2003) for a very species-rich insect group. The number of recorded

Table 2 Regional diversity (observed species richness and Fisher's alpha) of geometrid moths in selected areas of the world

Location	Area (km^2)	Elevational range	Observed species (individuals)	Fisher's alpha	Source
Southern Ecuador	2.5	1800–2677	1075* (32,845)	213 ± 3	This study
Southern Ecuador	40	1040–2677	1223† (35,238)	246 ± 3	This study
Malaysia: Borneo: Poring Hot Springs	2	460–630	302 (1832)	103	C.H. Schulze (pers. comm.)
Malaysia: Borneo: vicinity of Mt Kinabalu	*c.* 500	20–630	500 (4585)	143	Beck *et al.* (2002); area, J. Beck (pers. comm.)
Malaysia: Borneo: Gunung Mulu National Park	85	50–2630	632 (6989)	169	Holloway (1984)
Malaysia: Malaysian Peninsula, Pasoh	0.5	100	413 (19,077)	74.8	Holloway & Intachat (2003)
Malaysia: Malaysian Peninsula	6000‡	0–2000	587 (5200)	170	Intachat *et al.* (2005)§; J. Intachat (pers. comm.)
Tanzania: south-west slopes of Mt Kilimanjaro	300	1000–3500	305 (9178)	60	Axmacher (2003)
Germany: Kottenforst/Bonn	40	170	172 (21,728)	25.5	Mörtter (1988)
Canada: Acadia Research Forest, New Brunswick	0.5	80–100	169 (11,445)	27.9	Thomas (2002)

*Plus 43 species from qualitative samples up to an elevation of 3100 m a.s.l.
†Plus 23 species from qualitative samples.
‡Forested area of Peninsular Malaysia.
§More diversity data at local level are provided.

Geometridae species, 1266, is the highest ever counted for such a small geographical area. The vast majority of recorded species in the core study area (1098; Table 2) were collected in an area of only 2.5 km^2 (Table 1). The total area, including also the four sites at the lowest elevations, does not exceed 40 km^2. The estimator we regard as most appropriate (incidence coverage estimator) calculates a number of 1420 expected species based on the quantitative data set. The 22 exclusively diurnal species that occur in the area are additional to this number, and more diurnal geometrids can be expected since sampling of these was restricted to elevations below 2200 m. Hence the minimum true number of species is estimated to be > 1450, which would be equivalent to *c.* 7% of the world's described fauna of geometrid moths. This is more than has ever been found in any other region of comparable size in the world. For example, the total number of Geometridae in the whole of the Western Palaearctic is *c.* 920 species (Hausmann, 2001), and even on the very species-rich, large island of Borneo, it is estimated to be no more than 1079 species (Holloway, 1997). Table 2 provides an overview of regional geometrid diversity in other selected regions of the world. Species richness on a landscape level in Southeast Asia, as measured with Fisher's alpha, reaches values of up to 169 depending on the area size. Regional diversity in eastern Africa, however, is low by comparison (Kilimanjaro: Axmacher, 2003; Axmacher *et al.*, 2004), but no data are available from other African sites. The value of Fisher's alpha (246) from the study area in southern Ecuador is unrivalled by any previous study, and such a high level of regional diversity has never been documented before for geometrid moths.

The regional diversity of Geometridae is probably still underestimated. First, if the elevational gradient had included the Amazonian foothill region as well as higher altitudes, the number of observed species would have increased. Second, an unknown (but probably small) proportion of geometrid species in the Neotropical region are neither attracted to artificial light sources nor active at daytime. This proportion is unknown, but data from other regions indicate that *c.* 90% of geometrid moth species are attracted to light (northern Europe: Skou, 1986). Third, some species (probably not many: G.B., pers. obs.) might have been missed because of their peak of activity late at night. If these species could be included and sampling were to be carried out for longer periods, the species number might reach an even higher proportion of the world's known geometrid fauna than has already been recorded along this single elevational gradient.

The study on diversity of Geometridae parallels earlier records of diversity for trees (Gentry & Smith, 1988), arboreal ants (Wilson, 1987), and butterflies (Robbins *et al.*, 1996) in Peruvian lowland rain forests. Our study shows that Andean rain forests at high elevations might contribute as important a biodiversity hotspot for certain arthropod taxa as the western Amazonian lowland rain forests. The study area is also a hotspot for another speciose moth family: 442 species of Arctiidae were observed there, with an estimated total of 562 species (Süßenbach, 2003; N.H. & K.F., unpubl. data). This is equivalent to 5% of the global arctiid fauna (11,000 known species: Scoble, 1992). The diversity of other arthropod taxa still needs to be investigated, and more studies on the Amazonian and Pacific slopes of the Andes need to be carried out to give a better understanding of complementarity and regional diversity patterns of geometrid moths. Other regions, from Colombia to Peru and Bolivia, are also likely to be very diverse, but no quantitative data exist so far.

We consider that the proportion of taxa identified as named species (63%) to those not formally identified (37%) reflects the current state of taxonomy of geometrid moths in the Neotropical Region. It is likely that about one-third of all species sampled are new to science. Indeed, six species on the list have recently been described as new (Brehm, 2004, 2005; Pitkin, 2005). Compared with well known groups such as birds or vascular plants, several hundred new species sampled in the course of a single study is very high. However, the proportion of undescribed species from tropical samples of other groups of organisms, such as most small and inconspicuous arthropods, is frequently much higher. For example, Hansson (2002) and Noyes (2004) found 84% and 93% new species, respectively, in their studies of Costa Rican Chalcidoidea (Hymenoptera). From this viewpoint, geometrid moths are a good group to serve as environmental indicators because identification at species level is possible for a large majority (Holloway & Intachat, 2003). However, the use of indicators in variable environments is generally hampered by rapidly changing taxon ratios along habitat gradients (Brehm & Fiedler, 2003). The percentage of individuals from the quantitative data that could be assigned to species level is 76%, that is, commoner species are better known to science. Well documented species lists with corresponding voucher specimens, as in this study, are verifiable and available for new investigations and subsequent amendment, in contrast to abstract numbers or lists of morpho-species (Krell, 2004).

Conservation of tropical Andean forests is obviously an urgent task. Hamilton *et al.* (1995) pointed out that habitat loss of tropical cloud forests exceeds that of tropical lowland rain forest, and that the area covered by montane forests is small on a global scale. For example, > 90% of the cloud forests in the northern Andes have already been destroyed (Hamilton *et al.*, 1995), and only an area of *c.* 5% of the pre-Columbian extent of all Andean and sub-Andean forests is currently protected (Armenteras *et al.*, 2003). Despite the invention of a large system of national parks and reserves in Ecuador in the early 1980s, they are not totally effective (Ridgely & Greenfield, 2001) and, particularly in southern Ecuador, habitats and endemic plant species are not sufficiently protected (Borchsenius, 1997). The Podocarpus National Park mostly covers high elevations above 2000 m a.s.l. (Fig. 1), whereas much of the surrounding area of lower montane forest is threatened by the extension of agriculture and settlements, fire and logging (Paulsch *et al.*, 2001). Areas between the foothill region and the higher montane forests appear to be particularly threatened, despite the fact that the diversity of many groups of organisms peaks at medium elevations (Rahbek, 2005). However, our knowledge of most components of biological diversity in the Andes is very limited. If no specific effort is made towards the large-scale conservation of Andean rain forests, with representative areas in all regions, much of their extremely high, unique and still unexplored biodiversity might disappear within the next few decades.

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SUPPLEMENTARY MATERIAL

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Appendix S1 Geometridae species list.

BIOSKETCHES

Gunnar Brehm is a biologist focusing on biodiversity research in diverse moth communities. He is currently studying environmental gradients in tropical rain forests in Ecuador and Costa Rica, and is also interested in body-size patterns, host–plant relationships, chemical ecology of moths and butterflies associated with pyrrolizidine alkaloids, and conservation issues. He has a strong interest in insect systematics and taxonomy, in particular of Neotropical Geometridae and Arctiidae.

Linda M. Pitkin is an entomologist focusing on the taxonomy of moths of the family Geometridae, particularly in the Neotropics. The main emphasis of her research has been in broad-scope revisions.

Nadine Hilt is an ecologist studying biodiversity of species-rich moth communities along succession gradients in tropical montane rain forests, mainly with Arctiidae and Geometridae. She is also interested in the morphology of the Arctiidae.

Konrad Fiedler is an evolutionary biologist and ecologist. In addition to the functional and evolutionary ecology of interspecific interactions (such as herbivory and mutualism), his research interests are concentrated on diversity patterns of rich arthropod communities along habitat gradients, and the processes and mechanisms that generate them.

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