



Phylogenetic diversity of geometrid moths decreases with elevation in the tropical Andes

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Species diversity of geometrid moths (Lepidoptera, Geometridae) has previously been shown to be extremely and constantly high along a continuously forested elevational gradient in the Andes of southern Ecuador. We analysed samples taken from 32 sites between 1999 and 2011 in northern Podocarpus National Park and adjacent areas from 1020 to 2916 m a.s.l. We conjecture that high elevation habitats were historically mostly colonised by species from lower elevations, and that environmental filtering (e.g. through host plant specificity or temperature tolerance) constrained colonisation from lower elevations, which would yield a pattern of elevationally decreasing phylogenetic diversity. We analysed elevational phylogenetic patterns by means of: 1) the nearest-taxon index (NTI), 2) DNA barcode-based terminal branch lengths (TBLs) from maximum-likelihood phylogeny, 3) the subfamily composition of the local assemblages, and 4) the rarefied number of morphologically defined genera per site.

We counted a total of 1445 species. NTI values significantly increased with elevation, both in a conventional and a rarefaction approach. TBLs decreased significantly with elevation. Subfamily composition profoundly changed with elevation, particularly expressed as an increased proportion of the subfamily Larentiinae and decreased fractions of Sterrhinae and Geometrinae. The number of genera in equally rarefied species resamples significantly decreased with elevation. We conclude that environmental filtering indeed contributed to an altitudinal decrease in moth phylodiversity, but these constraints prevented only relatively few clades from colonising high elevation habitats.

One of the most prominent patterns in macroecology is the latitudinal gradient of species richness (Mittelbach et al. 2007). Latitudinal richness gradients are paralleled in mountains at smaller spatial scales by elevational gradients which are usually much better suited for ecological exploration (Sanders and Rahbek 2012). The interplay of these two environmental gradients is expressed by the coexistence of a great number of densely packed species in tropical mountain ecosystems. Particularly the eastern slopes of the tropical Andes, including the Andean foothills, are known as the globally ‘hottest hotspot’ of species diversity for a range of organisms, such as vascular plants, tetrapods, and many groups of arthropods (Brehm et al. 2008, Fjeldså and Irestedt 2009, Graham et al. 2009, Casner and Pycrz 2010, Rosser et al. 2012). Besides species diversity, functional (Mouchet et al. 2010) and phylogenetic diversity (Davies and Buckley 2011) are further dimensions of biodiversity that attract increasing attention. However, phylogenetic diversity or radiation patterns have scarcely been studied in tropical mountains so far, particularly in species-rich insect clades (Elias et al. 2009, Graham et al. 2009, Strutzenberger and Fiedler 2011).

With more than 21 000 described species (Parsons et al. 1999) geometrid moths are one of the largest clades within

the Lepidoptera, and diversity of the family in the tropical Andes is higher than anywhere else in the world. In an earlier study, 1266 morpho-species were counted in rain forests in a geographically small area in southern Ecuador (Brehm et al. 2005). Surprisingly, geometrid moth species richness is constantly high along a forested elevational gradient ranging from 1020 to 2677 m (Brehm et al. 2003b). Yet, these moth assemblages show a continuous elevational species turnover (Brehm et al. 2003a), and a concomitant change in gross taxonomic composition (i.e. contribution of subfamilies, tribes, and genera) along the gradient (Brehm and Fiedler 2003). Today, the phylogenetic relationships at subfamily and tribal level are fairly well resolved (Sihvonen et al. 2011), but the phylogenetic relationships of most Neotropical genera are still unknown.

The coexistence of many geometrid species at all investigated elevations poses the question how this enormous diversity has originated and what has shaped the current elevational distribution of species and higher level phylogenetic lineages. There is evidence from various insect lineages that major radiations have occurred during the increased uplift of the Andes, i.e. in the Neogene (Elias et al. 2009, Casner and Pycrz 2010, Strutzenberger and Fiedler 2011,

Rosser et al. 2012, Matos-Maraví et al. 2013). When high elevation habitats in the Andes became established for the first time, likely between 10 and 15 Mya (Gregory-Wodzicki 2000), they must either have been colonised by South American lineages from lower elevations (i.e. 0–1000 m a.s.l.), by lineages from North America when land bridges existed either around 35 Mya ago or since 3 Mya (Wahlberg and Freitas 2007), or by wind drift from other continents (an example among small-sized geometrid moths is provided by the colonisation of remote oceanic islands such as Hawai'i by *Eupithecia*: Montgomery 1984). During the Pleistocene, strong climate oscillations triggered repeated cycles of forest retraction and expansion in the Andes (Hooghiemstra and Van der Hammen 2004, Brunschön and Behling 2010). The re-assembly of mountain forest biota at areas that had been devoid of forest during glacial maxima must have been fed through basically the same three colonisation routes. For the Neogene and Pleistocene period we expect a dominant role of the first route for forest insects with moderate mobility – the colonisation of high elevation forests by South American lineages from adjacent lower elevations.

Environmental filtering – through biotic interactions as well as the physiological and ecological characteristics of species (Webb et al. 2002, Graham et al. 2009) – probably has played a decisive role with regard to extant phylogenetic patterns of moth assemblages in the Andes. Successful high elevation colonisers must have had 1) the physiological ability to cope with the cooler conditions at high elevations, and 2) either an affiliation to larval host plants that were able to (re-)colonise high elevations or the ability to switch hosts. Frequently, most species within a clade retain their ancestral ecological traits and environmental distributions (niche conservatism: Wiens and Graham (2005)), such that filtering is expected to apply in a largely concordant manner across whole clades, allowing their component species to extend (or preventing them from entering) into novel habitats.

The high species diversity of geometrid moths along the elevational gradient in southern Ecuador (Brehm et al. 2003b) does not necessarily imply that all phylogenetic lineages were equally successful in the process of colonisation. On the contrary, one would expect that some lineages were subject to stronger environmental filtering and thus less successful than others, in particular if niche conservatism is as frequent as e.g. in butterflies (Hawkins 2010). Such conservatism among the Geometridae might be expected e.g. in the host plant specialist genera *Eois*, *Macaria*, and *Opisthoxia*.

To address elevational patterns of phylogenetic diversity we chose to apply four conceptually distinct methods: 1) the nearest-taxon index (NTI) enjoys a well-established framework as an indicator of phylogenetic filtering in assemblages (Webb et al. 2002). In contrast to other measures such as the net relatedness index (NRI), NTI is particularly suitable for phylogenetic trees with unresolved deeper nodes – as is the case in our dataset (Webb et al. 2002). 2) Assemblage-wide terminal branch lengths (TBLs), derived from molecular data (mitochondrial CO I gene), is an approximate measure of relative species age. TBLs provide meaningful results in fairly complete datasets, ideally including all species within a taxon. 3) Phylogenetic composition of local assemblages, expressed by proportions of four major subfamilies of the family Geometridae, is a straightforward measure of

assemblage composition. 4) The number of genera per site, corrected by rarefaction to control for the statistical dependence of the ratio of genera to species, documents the degree of phylogenetic heterogeneity at the generic level.

We expected the following patterns due to environmental filtering along the elevational gradient: 1) assemblages at higher elevations tend to be more phylogenetically structured than those at lower elevations; 2) the relative age of species in assemblages decreases; 3) the phylogenetic composition of the moth assemblages changes with elevation; 4) the number of genera decreases with elevation, for a given number of species.

Methods

Sampling

Ca 40 000 moths were collected by light-trapping from 32 sites in the years 1999–2011 along a continuously forested elevation gradient spanning from 1020 to 2916 m a.s.l. (3°58'S, 78°58'W to 4.07°S, 79°10'W, Supplementary material Appendix 1, Table A1; methods: Brehm (2002), Brehm et al. (2005)). For an introduction into the ecosystems and vegetation units of the study region, see Beck et al. (2008) and Homeier et al. (2008). Sampling sites were situated in the northern area of the Podocarpus National Park and the adjacent Reserva Biológica San Francisco in the provinces of Zamora Chinchipe and Loja, southern Ecuador (Brehm et al. 2003b, 2005). The maximum distance between any of the sampling sites was ca 23 km. Most moths (96.5%) were assigned to genera and the remainder to subfamilies. Identification at species level is provisional because the number of undescribed species has been shown to be unexpectedly high in the area (e.g. 87% in the genus *Eois*, Brehm et al. 2011).

DNA was extracted and the 658 bp long barcode region of the mitochondrial Cytochrome Oxidase Subunit I (COI) gene amplified using standard protocols for single legs (small species) or tarsi (large species) of 4119 specimens (Ivanova et al. 2006, Strutzenberger et al. 2011). Samples were either analysed in the laboratories of the Univ. of Vienna (442 samples) or submitted to the Canadian Centre for DNA Barcoding in Guelph/Canada (3677 samples). All sequences shorter than 651 bp were excluded, resulting in a dataset of 3382 sequences for analyses. Successfully sequenced samples were not biased with regard to sampled taxa. See Supplementary material Appendix 1, Table A3 for a list of all 3382 taxa including GenBank accession numbers for all sequence records.

Data analysis

The elevational range of each species was determined using the distribution data of all 3382 specimens (Supplementary material Appendix 1, Table A1, A3). We assumed spatially continuous distributions of all species and interpolated elevational ranges where gaps occurred. Fifty meters of elevational range were added to the upper and lower observed elevational distribution of each species in order to counterbalance undersampling (Brehm et al. 2007).

Still, interpolated/extrapolated species numbers per site are likely to underestimate true species richness due to incomplete sampling coverage even after years of collecting, a typical feature of tropical arthropod communities (Coddington et al. 2009).

Our complete sequence dataset (3382 sequences) was first analysed using the Kimura 2-parameter model. A neighbour-joining (NJ) tree was calculated with the online platform Boldsystems 2.5 (Ratnasingham and Hebert 2007). We applied a 2% threshold for species delimitation as proposed for geometrids by Hausmann et al. (2011) and Strutzenberger et al. (2011). As a result, 1445 provisional geometrid moth species were identified from the dataset. See Supplementary material Appendix 1, Fig. A1 for a NJ tree of all 3382 specimens. In all cases where a species was represented by more than one sequence (53% of the species) we selected the sequence with the shortest distance to its nearest interspecific neighbour for inclusion in further analyses. A maximum likelihood tree was calculated from the 1445 sequence dataset with the MPI version of RAxML 7.0.4 (Stamatakis 2006). The six geometrid subfamilies were constrained to be monophyletic, and interrelationships on subfamily level were fixed to the topology recovered by Sihvonen et al. (2011). The best-known likelihood tree was estimated with 200 replicates under the GTRMIX model. See Supplementary material Appendix 1, Fig. A2 for the best-known ML tree.

Terminal branch lengths (TBLs) were then extracted from this tree for each of the assemblages at the 32 sampling sites, including interpolated and extrapolated elevational range data. TBLs are defined as the distance between terminal nodes (taxa) and the following node for the assemblage-level phylogenetic trees.

NTI values were calculated with the software package Phylocom (Webb et al. 2008). We applied the `comstruct` command using the best-known likelihood tree along with a taxon partitioning scheme corresponding to the 32 sampling sites. Runs were performed with 10 000 replicates and null model no. 2 as described in the Phylocom manual. This particular null model retains species richness for each sample while the content of each sample is randomised. Samples are drawn without replacement from the entire phylogeny for the null models. To control for the effects of varying sampling effort among collection sites we additionally employed a rarefaction approach to obtain sample-size-corrected NTI values. All collection sites were rarefied to a level of 61 species, corresponding to the least species-rich sampling site. We generated 1000 rarefied Phylocom partitioning files for each site with the statistical package 'R', which were then used to calculate NTI values with the `comstruct` command as described above. The mean of these 1000 NTI values obtained per site was calculated and used for further analysis. NTI values for collection sites with identical species inventories were calculated once and used for all identical sites.

Subfamily composition was measured as the proportion of species at each site belonging to one of the four major subfamilies. This measure is largely independent of sample size and area but requires representative sampling of all subordinate taxa (Holloway 1987, Brehm and Fiedler 2003), a prerequisite fulfilled by our study design.

A simple and meaningful, though coarse approach to detect phylogenetic changes of assemblages, is the count of genera. Although the delimitation of genera can be arbitrary and not all genera may represent natural clades, the comparison of their numbers at different locations represents a proxy of deeper-level diversity. Because the number of genera is a non-linear function of the number of species in an assemblage, for any random sample (Gotelli and Colwell 2001), it is necessary to rarefy all samples to a common number of species. Usually, rarefaction is applied as a species richness measure that thins out larger samples to a common number of specimens (Hurlbert 1971). In the present study, we rarefied the number of species instead of specimens. The lowest species number at any of the 32 sites was 61 species belonging to 41 genera. All other sites were statistically rarefied to a common level of 61 species, and the average number of expected genera was calculated using 1000 permutations with the programme Ecological Methodology by Kenney and Krebs (2000).

Results

A total of 1445 species were delimited by the 2% sequence divergence criterion, belonging to the subfamilies Ennominae (659 spp., 45.6%), Larentiinae (573 spp., 39.7%), Sterrhinae (106 spp., 7.3%), Geometrinae (97 spp., 6.7%) and the small (probably paraphyletic) assemblage Oenochrominae-Desmobathrinae (10 spp., 0.1%).

NTI values per site increased significantly with elevation (Fig. 1A, Table 1). This relationship was largely the same after application of a rarefaction approach to control for uneven sampling coverage. TBL values significantly decreased with elevation in a nearly linear manner (Fig. 1B, Table 1). These measures agree in showing that assemblages at higher elevations were less phylogenetically diverse than assemblages at lower elevations, taking assemblage richness into account.

Subfamily composition of local geometrid assemblages also changed significantly along the elevational gradient (Fig. 1C, Table 1). Sites at 1000 m a.s.l. were characterised by a high proportion of Ennominae species, but also relatively high proportions of Sterrhinae and Geometrinae. The proportion of Larentiinae significantly increased with elevation, whereas the proportions of the other subfamilies decreased, particularly in the Sterrhinae from ca 15% down to < 3% at the highest sites. Finally, the number of rarefied genera significantly decreased with elevation (Fig. 1D, Table 1), but with larger scatter than TBL and NTI.

Discussion

Elevational patterns of phylogenetic diversity

Despite substantial methodological differences of the four approaches chosen, all measures of phylogenetic structure in local moth assemblages show highly significant and concordant patterns along the elevational gradient.

As we conjectured, NTI values significantly decreased with elevation. Sites between 1000 and 1800 m a.s.l. had values around 0 or negative values, indicating no

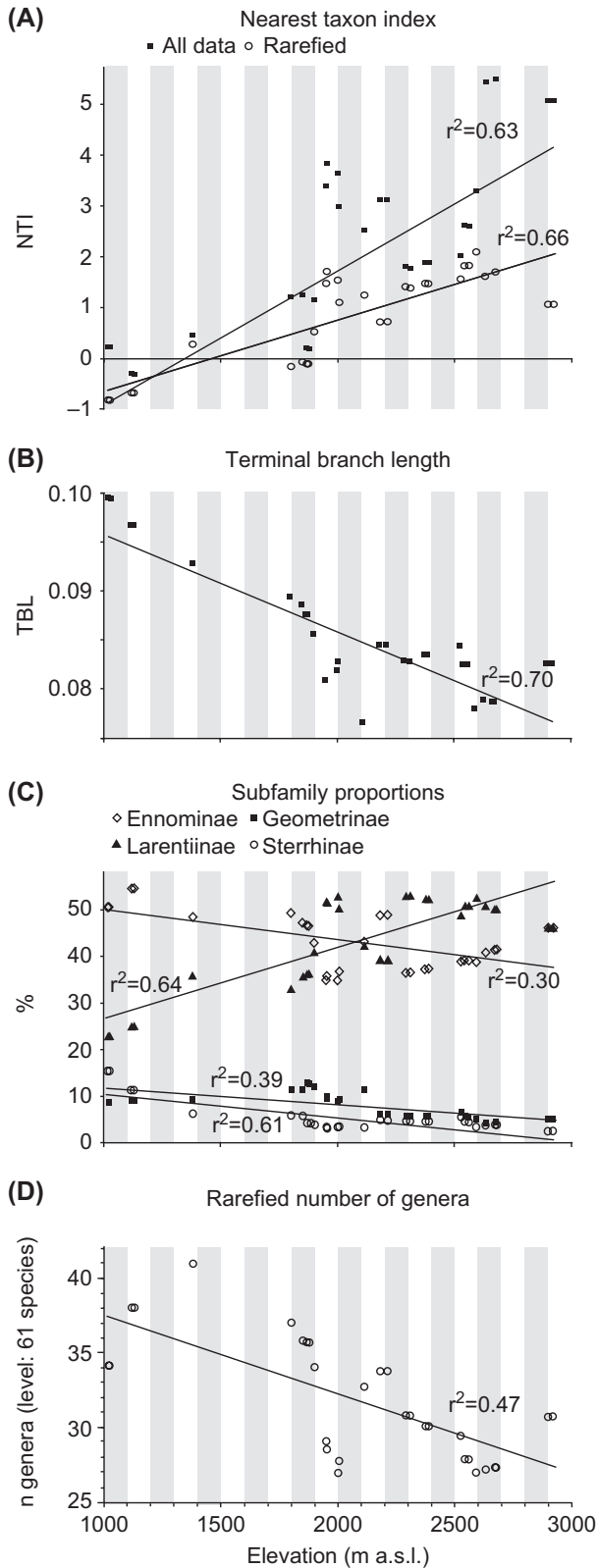


Figure 1. Trends of phylogenetic structure of geometrid moth assemblages along a forested elevational gradient in southern Ecuador ($n = 32$ sites). (A) Nearest taxon index (all data/rarefied), (B) terminal branch lengths, (C) subfamily proportions, (D) rarefied number of genera (level: 61 species per local assemblage). Included are regression lines plus their corresponding coefficients of determination r^2 .

Table 1. Statistical properties (r^2 and p values) of four measures of phylogenetic structure along an elevational gradient in southern Ecuador ($n = 32$ sites).

Measure	r^2	p
Nearest taxon index	0.63	< 0.001
Nearest taxon index, rarefied	0.66	< 0.001
Terminal branch length	0.70	< 0.001
Number of genera, rarefied	0.47	< 0.001
Subfamilies		
Ennominae	0.30	< 0.001
Larentiinae	0.64	< 0.001
Geometrinae	0.39	< 0.001
Sterrhinae	0.61	< 0.001

deviation from the null model or possibly a moderate degree of phylogenetic overdispersion. In contrast, sites at higher elevations had positive NTI values, indicating significant phylogenetic clustering. In accordance with this result, TBL values decreased with elevation, indicating a higher average age of taxa in assemblages at lower elevations compared to higher elevations. Both patterns partly reflect the decreasing proportion of the smaller subfamilies Geometrinae and Sterrhinae in local assemblages. These two subfamilies are characterised by relatively larger TBLs than Ennominae and Larentiinae (data not shown). The observed gross phylogenetic pattern of decreasing proportions of Ennominae, Sterrhinae and Geometrinae vs increasing proportions of the Larentiinae in the study area was already observed by Brehm and Fiedler (2003) as well as in several previous studies in other mountain regions of the world (Beck and Chey 2008) and along the latitudinal gradient in Europe (Brehm and Fiedler 2003). The underlying mechanism is still unknown, but it is assumed that Larentiine moths are in some way better adapted to cool environments than species of other subfamilies, in particular Sterrhinae and Geometrinae. In detail, some smaller deviations occurred between the present study and the one by Brehm and Fiedler (2003). These can be explained as follows: 1) the selection of sampling sites differed from those reported by Brehm and Fiedler (2003), e.g. new sites at higher elevations and within different forest types were included. 2) The barcoding approach allowed discrimination of previously unrecognised cryptic species. For example, a substantially higher number of minute *Idaea* species were counted at the lowermost sites in the present study.

As conjectured, the rarefied number of genera decreased from lower to high elevations, reflecting a ca 25–30% generic impoverishment of the assemblages at high elevations.

Unexpectedly, the two uppermost sites (around 2900 m a.s.l.) showed a reversed trend, reflected in all measures, when compared to sites situated around 2700 m a.s.l. This deviation from the general pattern is probably due to different forest types (valley bottom forests vs ridge forests): at these uppermost sites, forests are characterised by taller trees and a more species-rich vegetation than the ridge forests investigated between ca 2200 and 2700 m a.s.l. Future sampling efforts should take such small-scale differences in local forest vegetation between ridges, slopes and ravines (Homeier et al. 2010) systematically into account by parallel sampling.

Moderate environmental filtering

Patterns of increasing NTI values and decreasing phylogenetic distances in animal assemblages along elevational gradients have been found in a few other cases, so far, e.g. in Bolivian ovenbirds (Fjeldså and Irestedt 2009) and Ecuadorian hummingbirds (Graham et al. 2009), as well as in ants along elevational gradients in North America and Europe (Machac et al. 2011), but not in Neotropical salamanders (Wiens et al. 2007). However, in contrast with the richness pattern for geometrid moths, species richness of all above mentioned groups also declines substantially with elevation.

Environmental filtering may have prevented the colonisation of high elevation habitats in different groups through different constraints: not all hummingbird lineages may be able to sustain their energy-expensive means of locomotion at cool, high elevations (Graham et al. 2009), and in ants, only a few lineages are able to physiologically persist in such habitats (Machac et al. 2011). In contrast, most lineages in the Geometridae are present at high elevations. Some of these clades have apparently even been able to 'counterbalance' the moderate phylogenetic impoverishment at high elevations by increased speciation rates (or alternatively: lower extinction rates) compared with lower elevation lineages. For example, large genera (> 45 spp. in the study area) such as *Eois*, *Eupithecia*, *Psaliodes*, *Nephodia* and *Isochromodes* are characterised by equally high levels of alpha diversity at all or nearly all investigated elevations.

Both abiotic and biotic constraints, such as the availability of host plants, can act as environmental filters (Graham et al. 2009) for those lineages of the Geometridae that are not present at high elevations. While little is known regarding climatic barriers acting in these moths (except that such barriers do not seem to exist for the large majority of clades), constraints imposed through larval host plant affiliations could be important in specialist lineages. However, this type of biotic constraint is unlikely to play a role in polyphagous species or in specialist lineages whose hosts are widely distributed along the elevational gradient.

The majority of geometrid species are probably not severely constrained by host-plant affiliations, as many of the larger Ennominae clades are polyphagous and/or feed on algae and lichens (e.g. *Isochromodes*, *Oxydia*, *Nephodia*, *Pero*: Bodner et al. 2010). The relatively well studied genus *Eois* appears to have undergone parallel radiation together with its main host plant genus *Piper* (Strutzenberger et al. 2010), although host plant species richness peaks at slightly lower elevations than moth species richness, resulting in a denser packing of host plant specialists on fewer hosts (Rodríguez-Castañeda et al. 2010). Fifty-one out of 160 *Eois* species (32%) in our study have been observed exclusively at elevations ≥ 2590 m a.s.l. It is possible that some of these species have managed to shift to other hosts, because few *Piper* species exist at such high elevations (Jørgensen and León-Yáñez 1999). Clearly, elevationally restricted host plant specialists represent a minority within Neotropical Geometridae (Brehm 2002), as for example the genus *Macaria*. These moths are probably constrained to lower elevations by the distribution of their respective Fabaceae host plants (Brehm 2002). Among the 11 *Macaria* species found in our study area, none has been recorded above 2200 m.

However, geometrid moths may not be fully representative within the Lepidoptera with regard to environmental filtering at high elevations, since other moth clades appear to be far more strongly affected by environmental filtering. For example, species richness and activity density of the Erebidae-Arctiinae and the Pyraloidea decline with elevation (Fiedler et al. 2008, Beck et al. 2011). Richness of 'hot-blooded' (i.e. temporarily thermoregulating) Lepidoptera lineages such as sphingid and saturniid moths very strongly decreases with elevation in the study area (Brehm and Fiedler unpubl.), possibly constrained by prevailing cool temperatures. Like *Macaria* geometrid moths, host plant specialists such as Heliconiinae and Ithomiinae butterflies (Elias et al. 2009, Rosser et al. 2012) are absent from high elevation habitats in our study area, probably because their hosts are largely lacking (Heliconiinae: *Passiflora*; Ithomiinae: Solanaceae) (Jørgensen and León-Yáñez 1999).

Certain lineages of geometrid moths are presently restricted to elevations above ca 1500 m a.s.l. in the tropical Andes, for example the genera *Callipia*, *Cnephora* and the *Acrotomodes clota* group (Brehm 2005). Such groups may have colonised the tropical Andes from lower elevations at higher latitudes, and environmental filtering possibly prevented them from colonising low elevations in the tropics. Host-plant restrictions as well as limited heat tolerance (Deutsch et al. 2008) might have acted as barriers for these few taxa. A moderate phylogenetic overdispersion at lower elevations was observed, as described for plants (Cavender-Bares et al. 2004), mammals (Cooper et al. 2008) and hummingbirds (Graham et al. 2009). The mechanism responsible for overdispersion remains uncertain. Density-dependent forces, or ecological speciation are possibly responsible for overdispersion (Silva and Batalha 2009), whereas competition has rarely been demonstrated in herbivorous insects, whose communities are shaped far more through bottom-up (plant quality) and top-down processes (predation) (Denno and Kaplan 2006, Kalka et al. 2008).

Conclusions

Geometrid moths are exceptionally species-rich at all sites between 1000 and 3000 m a.s.l. in montane forests in southern Ecuador. The expected phylogenetic impoverishment at high elevations was clearly discernible, but relatively weak possibly due to moderate environmental filtering, perhaps because only forested habitats were compared. Forests at lower elevations have on average phylogenetically more diverse moth assemblages, and phylodiversity gradually diminishes when passing upslope through the montane forest zones. The most likely explanation for this modest reduction in phylodiversity is that many geometrid clades are not severely constrained by larval host-plant availability, i.e. they encounter acceptable host-plants at most sites within mountain and elfin forest. Indeed, broad host-plant ranges appear to generally facilitate colonisation of high-elevation habitats by herbivorous insects (Pellissier et al. 2012). At the same time, geometrid moths appear to be less strongly affected by thermal constraints in comparison to other nocturnal moths (Beck et al. 2011). Hence, this balance of moderate constraints through larval host-plant affiliations plus tolerance

to cooler temperatures may be responsible for the unusual elevational diversity patterns observed in this species-rich moth clade in the Andes.

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Supplementary material (Appendix ECOG-00030 at <www.oikosoffice.lu.se/appendix>). Appendix 1.