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RESEARCH PAPER

The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient

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ABSTRACT

Aim The biodiversity of geometrid moths (Lepidoptera) along a complete tropical elevational gradient was studied for the first time. The patterns are described, and the role of geometric constraints and environmental factors is explored.

Location The study was carried out along the Barva Transect (10° N, 84° W), a complete elevational gradient ranging from 40 to 2730 m a.s.l. in Braulio Carrillo National Park, Costa Rica, and adjacent areas.

Methods Moths were sampled manually in 2003 and 2004 at 12 rain forest sites using light 'towers', each with two 15 W ultraviolet fluorescent tubes. We used abundance-based rarefaction, statistical estimation of true richness (Chao 1), geographically interpolated observed richness and Fisher's alpha as measures of local diversity.

Results A total of 13,765 specimens representing 739 species were analysed. All four measures showed a hump-shaped pattern with maxima between 500 and 2100 m elevation. The two subfamilies showed richness and diversity maxima at either lower (Ennominae) or higher (Larentiinae) elevation than Geometridae as a whole. Among the four environmental factors tested, relative humidity yielded the highest correlation over the transect with the rarefaction-based richness estimates as well as with estimated true species richness of Geometridae as a whole and of Larentiinae, while rainfall explained the greatest variation of Ennominae richness. The elevational pattern of moth richness was discordant with both temperature and with tree species richness. A combination of all environmental factors in a stepwise multiple regression produced high values of r^2 in Geometridae. The potential effects of geometric constraints (mid-domain effect, MDE) were investigated by comparing them with observed, interpolated richness. Overall, models fitted very well for Geometridae as a whole and for Ennominae, but less well for Larentiinae. Small-ranged species showed stronger deviations from model predictions than large-ranged species, and differed strikingly between the two subfamilies, suggesting that environmental factors play a more pronounced role for small-ranged species. We hypothesize that small-ranged species (at least of the Ennominae) may tend to be host specialists, whereas large-ranged species tend to be polyphagous. Based on interpolated ranges, mean elevational range for these moths was larger with increasing elevation, in accordance with Rapoport's elevational rule, although sampling effects may have exaggerated this pattern. The underlying mechanism remains unknown because Rapoport's 'rescue' hypothesis could not explain the observed pattern.

Conclusions The results clearly show that moth diversity shows a hump-shaped pattern. However, remarkable variation exists with regard to taxon and range size. Both environmental and geometric factors are likely to contribute to the observed patterns.

Keywords

Barva Transect, Costa Rica, diversity, Geometridae, La Selva, Lepidoptera, MDE, rain forest, Rapoport's rule.

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INTRODUCTION

It is well known that the diversity of organisms on Earth is not uniformly distributed along latitudinal and altitudinal gradients. Species richness in most groups of organisms peaks at low latitudes and decreases towards the poles (e.g. Gaston, 2000; Willig *et al.*, 2003). Along elevational gradients, hump-shaped and monotonically decreasing patterns are most frequently observed (Rahbek, 2005). However, the underlying mechanisms are still poorly explored. Many factors (biotic, abiotic and historical) have been discussed that may be responsible for elevational patterns of species richness (for reviews see McCoy, 1990; Rahbek, 1995, 2005). In recent years, geometric constraints have played an increasing role in their interpretation (Colwell & Hurtt, 1994; Willig & Lyons, 1998; Colwell & Lees, 2000; Colwell *et al.*, 2004). The random placement of species geographical ranges within a bounded geographical domain produces a hump-shaped pattern of species richness. The effect has been termed the mid-domain effect (MDE), and the concept has been critically discussed by various authors (e.g. Hawkins & Diniz-Filho, 2002; Zapata *et al.*, 2003, 2005; Colwell *et al.*, 2004, 2005; Hawkins *et al.*, 2005). Although the MDE cannot provide biological explanations for the causes of the distribution of individual taxa, it shows that hump-shaped patterns (rather than uniform distributions) of species richness within geographical domains are appropriate null models.

Although many studies of species richness and diversity along elevational gradients have been published, they show a strong bias towards plants and the temperate zones. However, the global majority of terrestrial organisms are tropical arthropods, and knowledge of their richness patterns along altitudinal gradients is still very poor. The reasons for this bias are: (1) accessible, complete elevational gradients in intact habitats are scarce and (2) arthropods present a methodological challenge because of their often extreme richness in tropical regions and associated difficulties in sorting and identification (Novotny & Basset, 2000; Longino *et al.*, 2002). In this paper we analyse a unique data set that covers, at the species level, a complete tropical gradient (from near sea level to near the top of a mountain) of a very species-rich group of insects.

Geometrid moths have been used as a model group in a number of recent ecological studies along habitat gradients in various regions in the world (e.g. Beck *et al.*, 2002; Brehm *et al.*, 2003a,b, 2005; Holloway & Intachat, 2003; Axmacher *et al.*, 2004). Previous studies found diversity maxima at medium elevations (Indo-Australia: Holloway, 1987) or a diversity plateau along a broad elevational range (Ecuador: Brehm *et al.*, 2003b). Although rich in species, provisional identification of geometrids is usually possible and leads to reliable estimations of species richness (Brehm *et al.*, 2005). Until this study, no complete elevational gradient in mature tropical forest habitats from sea level to a mountaintop had been explored for this or any other group of moths. The Barva Transect, which lies between near sea level and 2900 m a.s.l. on the Atlantic slope of the Cordillera Central in Costa Rica, is the last remaining continuous gradient of mature forest in Central America to cover such a wide elevational range (Lieberman *et al.*, 1996; Blake & Loiselle, 2000). Several studies on the diversity of plants and animals have been conducted along this gradient that allow a comparison of available data, and in selected cases are adequate for regression analysis (see Materials and Methods).

First, we investigated the pattern of geometrid species richness along the Barva Transect. Secondly, we examined the explanatory potential for elevational patterns of moth diversity of four environmental factors for which data are available: humidity, rainfall, temperature and tree diversity. In addition to such ecological factors, stochastic MDE models were used to assess the explanatory potential of geometric constraints on range location. To date, elevational MDE models for arthropods have been explored only for ants (Sanders, 2002) and butterflies (Lees *et al.*, 1999), but not previously for a species-rich group of moths. Thirdly, we investigated 'Rapoport's elevational rule', i.e. whether the average range size of species increases with elevation as suggested by Stevens (1992). So far, only two studies have examined evidence for the rule along elevational gradients in insects (Fleishman *et al.*, 1998; Sanders, 2002), but no study has ever investigated a complete elevational gradient. Our analyses were carried out for all geometrid species recorded in this study, and, in addition, for the subsets of species belonging to the two largest subfamilies: Ennominae and Larentiinae. The focus of this paper is large-scale richness patterns and their potential determinants. Analyses of beta diversity, landscape diversity and seasonal patterns will be published elsewhere (Brehm, in press; G. Brehm, unpublished data).

MATERIALS AND METHODS

Study area and elevational gradients

The study area is situated on the Atlantic slopes of Volcán Barva within the Cordillera Central of Costa Rica. The Barva Transect ranges from lowland tropical rain forests at *c.* 30 m to montane rain forests near the summit of the dormant Volcán Barva at 2906 m a.s.l. Old growth forests dominate the vegetation, but old secondary forests occur within the study area (Blake & Loiselle, 2000). The gradient spans over *c.* 35 km (Fig. 1). The 12 sampling sites were situated at elevations between 40 and 2730 m a.s.l. in Parque Nacional Braulio Carrillo (PNBC) or in adjacent areas, including La Selva Biological Station (Fig. 1; elevations Table 1). Virtually every environmental factor changes along an elevational gradient as extensive as the one analysed in this study. Unfortunately, quantitative data are available for only a few environmental variables along the Barva Transect, and regression analysis was restricted to those factors that might be expected to have an influence on insect species richness or distributions. The four factors analysed were: humidity, rainfall, temperature and tree species diversity. Humidity and rainfall were expected to have mainly indirect effects on moth richness via the vegetation, but both factors are likely to play a significant role for moth flight behaviour. Temperature was generally expected to be positively correlated with moth species richness, because higher temperatures usually allow faster larval development. As many geometrid species feed on woody plants (Scoble, 1999; Brehm, 2002), a positive

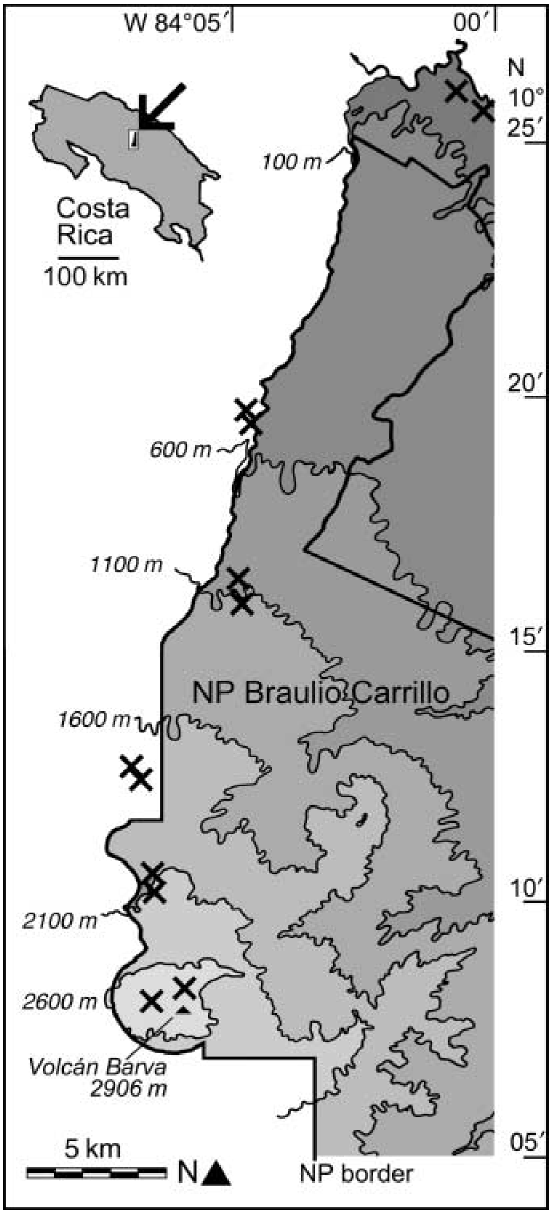

Figure 1 The Barva Transect study area in Costa Rica (Heredia province). The 12 study sites at six elevational levels are situated at elevations between 40 and 2730 m a.s.l. NP = National Park.

correlation between tree and moth richness could reasonably be expected. Original environmental data were extracted from Kluge *et al.* (2006) and tree data from Lieberman *et al.* (1996).

Vegetation

In their botanical study along the Barva Transect, Lieberman *et al.* (1996) found that woody species density (≥ 10 cm d.b.h.) peaked at 300 m a.s.l. with 149 species ha^{-1} and decreased to 29 species ha^{-1} at 2600 m a.s.l. Rarefied to 400 stems to correct for variation in stem density (Gotelli & Colwell, 2001), tree species richness peaked at about 130 species at 300–500 m a.s.l., decreasing to 25 species at 2600 m a.s.l. (Cardelús *et al.*, 2006). To estimate values at the elevations of the moth sampling sites, these rarefied data for tree species richness were interpolated between adjacent pairs of sites studied by Lieberman *et al.* (1996) (by fitting a polynomial function to their data over the complete transect).

Tree height ranged between 38 and 47 m at 300 m a.s.l. and 22 and 28 m at 2600 m a.s.l. Among all plants investigated, dicot trees dominated in all plots. Palms and lianas were relatively common and species-rich at the lower sites but became rare or absent at higher elevations (Chazdon, 1987), whereas tree ferns and hemi-epiphytes mostly occurred at medium elevations. Lieberman *et al.* (1996) found no discontinuities or evidence for discrete vegetation zones along the gradient. Further quantitative studies on particular plant taxa or life forms along the gradient are still scarce, and would be required for the analysis for specific moth taxa, e.g. the host plant relationship between moths of the genus *Eois* and plants of the genus *Piper*. Studies on ferns (not known to be used by neotropical geometrids) and epiphytic plants have recently been carried out (Cardelús *et al.*, 2006; Kluge *et al.*, 2006; Watkins *et al.*, 2006) but botanical data from these recent studies were not included in the analyses in this paper.

Climate

Mean annual rainfall at La Selva is *c.* 4000 mm (Sanford *et al.*, 1994). Rainfall increases orographically towards medium elevations and might reach as much as 8000 mm year^{-1} at 700 m a.s.l. (Lieberman *et al.*, 1996). It decreases at higher elevations to *c.* 3300 mm year^{-1} in the summit area (Sacramento; Hartshorn & Peralta, 1988). Precipitation might be underestimated at high elevations because of cloud-driven precipitation (McCain, 2004), but it is evident that rainfall, per se, shows a peak at medium elevations. Figure 2(b) shows the rainfall values that were used for our regression analyses, which were compiled from the Instituto Meteorológico Nacional (IMN) in San José, Costa Rica (Kluge *et al.*, 2006) and from Heaney & Proctor (1990) (2260 m a.s.l.).

Relative air humidity and temperatures were measured by Kluge *et al.* (2006) at four points along the Barva Transect (40, 650, 1800 and 2800 m a.s.l.) from July 2002 to November 2003 using 27 Microdaq data loggers HoboPro RH/Temp. Data were measured, whenever possible, in different vegetation types (zonal forest, ravine forest, ridge forest) at each recording elevation. Data loggers were positioned near tree trunks in order to avoid direct sunlight. Data were recorded at intervals of 10 min at heights of 50 cm, 200 cm and as high as possible (10–15 m) in the inner canopy. Data were subsequently averaged to 1-h intervals. By taking data from such a wide range of forest types and tree heights, we sought to minimize possible biases in the humidity data due to small-scale microclimatic differences. We chose daily minimum values of humidity because maximum values were always > 99%, and minimum humidity appeared to be more likely to constrain moth flight physiology.

Figure 2(a) and (c) show the estimated mean daily minimum values of air humidity and average mean temperature (linearly interpolated between pairs of measurement sites). Kluge *et al.* (2006) estimated the temperature lapse rate on the gradient to be

Table 1 Elevation of 12 sampling sites, number of individuals collected, recorded species numbers, and Fisher's alpha of Geometridae and the subfamilies Ennominae and Larentiinae

	Geometridae			Ennominae			Larentiinae		
Elevation (m)	Individuals	Observed species	Fisher's alpha ± SD	Individuals	Observed species	Fisher's alpha ± SD	Individuals	Observed species	Fisher's alpha ± SD
40	424	88	33.8 ± 2.7	210	41	15.2 ± 1.7	21	13	14.6 ± 6.0
45	400	90	36.1 ± 2.9	195	45	18.3 ± 2.1	7	5	7.8 ± 6.2
525	397	147	84.4 ± 6.8	210	73	39.7 ± 4.4	41	24	24.3 ± 6.9
550	528	149	69.1 ± 4.8	243	62	26.9 ± 2.7	48	25	21.0 ± 5.2
1070	1224	212	74.0 ± 3.5	656	105	35.3 ± 2.3	408	70	24.3 ± 2.0
1115	1409	239	82.6 ± 3.7	793	121	39.8 ± 2.4	445	72	24.3 ± 1.9
1690	1372	230	79.0 ± 3.6	736	105	33.5 ± 2.1	563	98	34.3 ± 2.4
1710	1471	261	92.2 ± 4.0	888	122	38.3 ± 2.2	514	107	41.1 ± 2.9
2090	1647	247	80.6 ± 3.4	913	96	27.1 ± 1.6	635	117	42.1 ± 2.7
2140	1700	225	69.5 ± 2.9	1034	94	25.1 ± 1.5	588	108	38.8 ± 2.6
2725	1286	132	36.9 ± 1.9	613	53	13.9 ± 1.1	602	67	19.3 ± 1.4
2730	1907	133	32.5 ± 1.5	820	54	13.0 ± 0.9	1032	70	17.0 ± 1.1
	13,765	739	167.1 ± 3.1	7311	325	69.7 ± 1.9	4904	248	55.1 ± 1.7

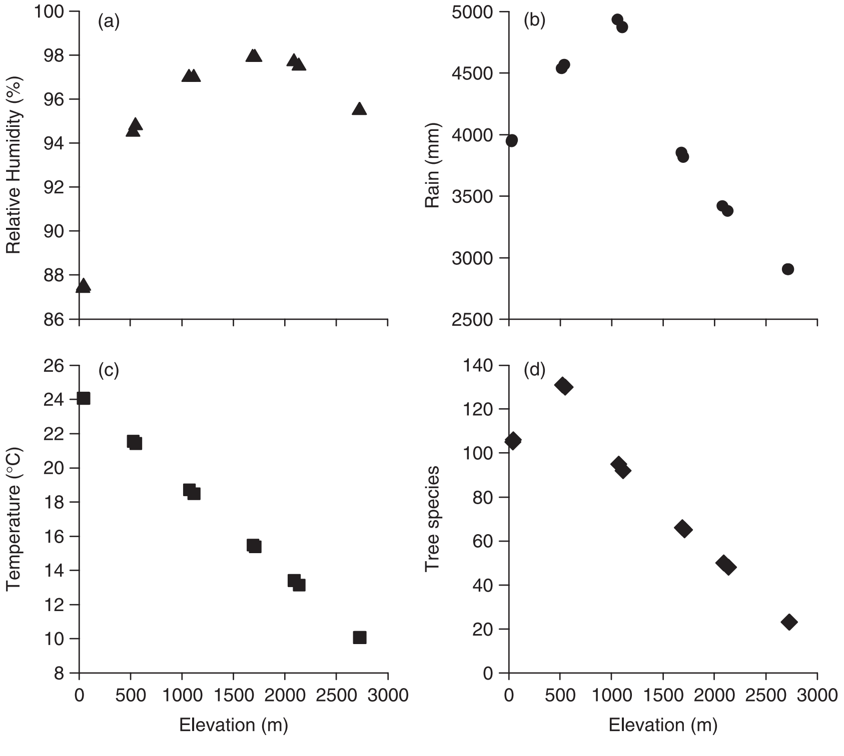

Figure 2 Environmental factors used for regression analysis. Original data for (a) humidity, (b) rainfall and (c) temperature were extracted from Kluge *et al.* (2006). Tree species data (d) were compiled from Lieberman *et al.* (1996), and rarefied to equalize the number of individual stems sampled for richness. Data were interpolated to estimate values at the elevations of the moth sampling sites.

5.5 K per 1000 m. Data from Lieberman *et al.* (1996) as well as temperature measurements during moth collection (G. Brehm, unpublished data) correspond well with these data.

Other environmental factors

A number of other environmental factors change along the elevational gradient. Quantitative data are available only for a few, and not every factor is appropriate to explain insect diversity patterns. For example, soil parameters such as total nitrogen and total carbon increase with altitude in the gradient investigated (Lieberman *et al.*, 1996), but they are not expected to have a direct impact on the species richness of moths. Although desirable, the incorporation of available leaf nitrogen in the analysis was hampered by the unavailability of such data along the Barva transect as well as by current ignorance of the larval food requirements of the vast majority of geometrid species. Ecosystem productivity has often been discussed as a determinant of species richness (species–energy theory; Rosenzweig, 1995; Whittaker *et al*., 2001) but forest productivity estimates are not available for the Barva Transect.

Moth sampling and identification

Moths were sampled manually using light traps (Fritz Weber, Stuttgart, Germany) with two 15 W UVA tubes (Sylvania, blacklight blue, F15W/T8/BLB and Sylvania blacklight F15W/BL350) located in their centres (Brehm & Axmacher, 2006). The diameter of the trap was *c.* 0.70 m and its height was *c.* 1.70 m. Sampling was carried out from 18:30 to 21:30, to coincide with peak activity of moths. Nights with bright moonlight were avoided (Brehm & Axmacher, 2006). Twelve sites at six elevational levels were selected (Fig. 1) and sampled at least twice in the period April–June 2003, and at least twice in the period February–March 2004.

Much greater numbers of moths per night were collected at higher elevations than at lower sites (see Appendix S1 in Supplementary Material), possibly due to reduced predation pressure by ants, bats and birds. As a consequence, collecting the same number of samples at each site would have produced highly unequal numbers of individuals at each site, thereby biasing observed richness (Gotelli & Colwell, 2001) as well as observed elevational ranges (Colwell & Hurtt, 1994). In an effort to reduce the disparity among sites in numbers of individuals collected, additional sampling was carried out at the three lowest elevational levels, resulting in a total of between four and eight samples from each site. These samples yielded a minimum number of 397 specimens (site 3) and a maximum number of 1907 (site 12; Table 1). In other words, despite double sampling effort at the lowest sites, numbers of individuals at these sites were still less than half the numbers at high-elevation sites.

Numbers of individuals and species collected per sampling night may vary, for example depending on the weather and moon conditions (e.g. Yela & Holyoak, 1997; Brehm & Axmacher, 2006). However, the applied sampling scheme very likely provides reliable data, given the replication at each elevational level and the subsequent careful statistical analysis of the results.

Appendix S1 in Supplementary Material provides a detailed list of all sampling dates and the numbers of moths sampled on each date. The moths were identified by the first author by comparison with original type specimens or other reliably identified material in several museums (see Acknowledgements). The nomenclature follows Pitkin (2002) for the largest subfamily, Ennominae, and otherwise follows Scoble's (1999) catalogue. A full species list is provided in Appendix S2 in Supplementary Material.

Species richness and diversity measures

As discussed above, sample size (number of individual moths collected) varied considerably among sites (Table 1) in spite of efforts to equalize it. The number of species observed in incompletely sampled communities increases nonlinearly with sample size and is thus an unreliable measure of the true, local species richness (Gotelli & Colwell, 2001). We used four distinct approaches to cope with this problem. The first approach relied on individual-based (classic) rarefaction (Gotelli & Colwell, 2001) to compare sites at comparable numbers of individuals (which reduces the number of species to below the observed richness for sites with more individuals in samples). We refer to these estimates as *rarefied richness*. The second approach was to use non-parametric statistical estimators of true local species richness to reduce the bias of incomplete sampling (Chao, 2005). We call these values *estimated richness.* The third approach was based directly on the recorded species × site incidence data. On the working assumption that each species' range is continuous along the transect, we indicated a species as being present at all sampling sites between (and including) its lowest and highest recorded presence, whether or not it was actually recorded at intermediate sites. The resulting richness values for each elevation are referred to here as *interpolated richness*. For the fourth approach, to allow comparison with other studies that use it, we computed Fisher's alpha, a widely used index of diversity that is relatively insensitive to undersampling (Magurran, 2004). Rarefied richness values were calculated using a program developed by Kenney & Krebs (2000), at the level of 397 individuals in Geometridae, 195 individuals in Ennominae and 41 individuals in Larentiinae. Fisher's alpha and estimated richness (Chao 1) were calculated using ESTIMATES 7.50 (Colwell, 2005a), and interpolated richness was computed from interpolated species ranges using RANGEMODEL 4 (Colwell, 2005b).

Geometric constraints

We used RANGEMODEL 4 (Colwell, 2005b) to estimate predicted richness under the assumption of random placement of interpolated moth elevational ranges. Incomplete sampling routinely underestimates range size (Colwell & Hurtt, 1994), with the most extreme case being species recorded from only a single elevation (including many species in our study) which thus have an observed elevational range of 0 m. Following the strategy of Cardelús *et al.* (2006), we adjusted for range underestimation by adding 293 m to each end of each recorded range (for all ranges), half the maximum elevational distance between any two adjacent sampling elevations. For each species recorded at the lowest sites (40 and 45 m a.s.l.), however, we added only 40 or 45 m to the downhill end of the range (and 293 m to the uphill end). Likewise, for each species recorded at the highest sites (2725 and 2730 m), we added only 171 or 176 m to the uphill end of the range, because the top of the mountain lies at 2906 m a.s.l. Range augmentation also adds realism in another way: without it, single-site species would otherwise have been 'lost' between sampling elevations during the randomization of the midpoints and would thus have failed to contribute to expected patterns. Because none of the augmented ranges extends to an adjacent sampling elevation (considering the paired sampling sites in Table 1 each as a single elevation, e.g. 525 m and 550 m), augmentation has no effect on the pattern of interpolated richness. All species ranges and midpoints are provided in Appendix S2 in Supplementary Material.

RANGEMODEL 4 systematically reassigns the location of each of the interpolated, augmented ranges within the domain (0–2906 m) at random (sampling without replacement) and then records the predicted richness at each of the 12 field sampling points. After a specified number of randomizations (we specified 1000), RANGEMODEL reports the mean richness and its 95% confidence interval (CI) for each sampling point (inspired by McCain, 2003).

Range interpolation assumes that a species observed at two different elevational levels is present or at least potentially present everywhere between these levels, i.e. it assumes continuous species distributions, as commonly done in macroecology. As a consequence, interpolated species richness is somewhat greater than recorded species richness, particularly in the middle of the gradient where interpolated species ranges are more likely to overlap (Grytnes & Vetaas, 2002). To assess whether this effect of interpolation might have produced artefactual results, we regressed mean predicted species richness (generated by RANGEMODEL) against: (1) rarefied species numbers, (2) extrapolated species richness (Chao 1), as well as against (3) interpolated species richness. To explore the effect of range size on MDE predictions (Colwell *et al.*, 2004), we split each of the three taxa (Geometridae, Ennominae and Larentiinae) into two classes, the 50% of species with the largest elevational ranges and the 50% of species with the smallest elevational ranges (Lees *et al.*, 1999; Jetz & Rahbek, 2002), and repeated the same analyses that we conducted on the full geometrid data set.

To explore the potential of individual factors (humidity, rainfall, temperature, tree species and geometric constraints) to explain elevational patterns of species richness, we performed simple ordinary least squares (OLS) regressions of species richness (rarefied, estimated or interpolated) for each taxon and range-size moiety against each of these factors. We report r^2 for each regression. Because geographical data such as these are generally spatially autocorrelated, data values for nearby points are not statistically independent, so that degrees of freedom are inflated and ordinary P-values for r^2 are underestimated. To correct for spatial autocorrelation in regression residuals, we calculated for each regression the effective number of degrees of freedom according to Dutilleul's method (Dutilleul, 1993; Legendre *et al.*, 2002), and we report adjusted P-values (P_{adj} for r^2) based on the effective degrees of freedom.

We also computed multiple linear regressions to explore multivariate explanations for elevational patterns of moth species richness. We selected the best model from among all possible combinations of simple variables, guided by Akaike information criterion (AIC) statistics (Burnham & Anderson, 1998). For comparison with the best model, we also computed an *environmental model* that included all four environmental factors, as well as a *geometric constraints model* that included only MDE predictions. Regression residuals were examined for spatial autocorrelation based on Moran's I for distance-classes. However, because of the limited sample size (12 sites, spatially arranged in six pairs), it did not prove feasible to apply spatial autoregressive analyses with five explanatory variables. Thus no P-values are reported for the multiple regressions. All regression analyses were performed using SAM (Rangel *et al.*, 2006), freely available at www.ecoevol.ufg.br/sam.

Rapoport's rule

We used RANGEMODEL software (Colwell, 2005b) to compute mean elevational range size among the species of Geometridae, Ennominae and Larentiinae occurring at each of the 60 elevations for interpolated range data (following the method of Stevens, 1992).

RESULTS

Species richness and diversity along the elevational gradient

A total of 13,765 geometrid moths were sampled at 12 sites along the elevational gradient (Table 1). They were sorted to 739 morphospecies of which 388 (53%) were identified to named species. A large proportion of the remaining taxa are likely to be new to science and need to be described taxonomically in the future. A full list is provided in Appendix S1 in Supplementary Material. Of the specimens sampled, 7311 (325 species) were assigned to the subfamily Ennominae, 4904 (248 species) to the subfamily Larentiinae, and the remainder to four other subfamilies (Desmobathrinae, Geometrinae, Oenochrominae, Sterrhinae). Geometrid moth richness and diversity clearly showed a hump-shaped pattern along the elevational gradient. While recorded species richness, estimated species richness and interpolated species richness show a broad peak of richness between *c.* 1100 and 2100 m a.s.l. (Table 1 and Fig. 3a,b), rarefied richness and Fisher's alpha indicate a broader hump of similar richness and diversity between *c.* 500 and 2100 m (Table 1 and Fig. 3a). All measures clearly show that richness and diversity of geometrid moths decreases towards both ends of the elevational gradient.

The subfamily Ennominae (325 species) largely reflects the pattern of the whole family. However, diversity of ennomine moths tends to peak at lower elevations compared with the geometrids as a whole (between *c.* 500 and 1700 m a.s.l., depending on the measure). In contrast, species richness and Fisher's alpha for the Larentiinae (248 species) peak at very high elevations between *c.* 1700 and 2100 m a.s.l. (Table 1 and Fig. 3) but decline in the summit area of Volcán Barva as well as at lower elevations (1100 m and below).

Regression on environmental factors

The upper portion of Table 2 shows r^2 values and associated P-values (based on degrees of freedom adjusted for spatial autocorrelation) for simple linear regressions between three measures of species richness as a function of four environmental factors plus geometric constraints (MDE model predictions) for the three taxa considered (Geometridae and its subfamilies Ennominae and Larentiinae). The lower portion of Table 2 reports the results of model selection for multiple regressions of richness measures

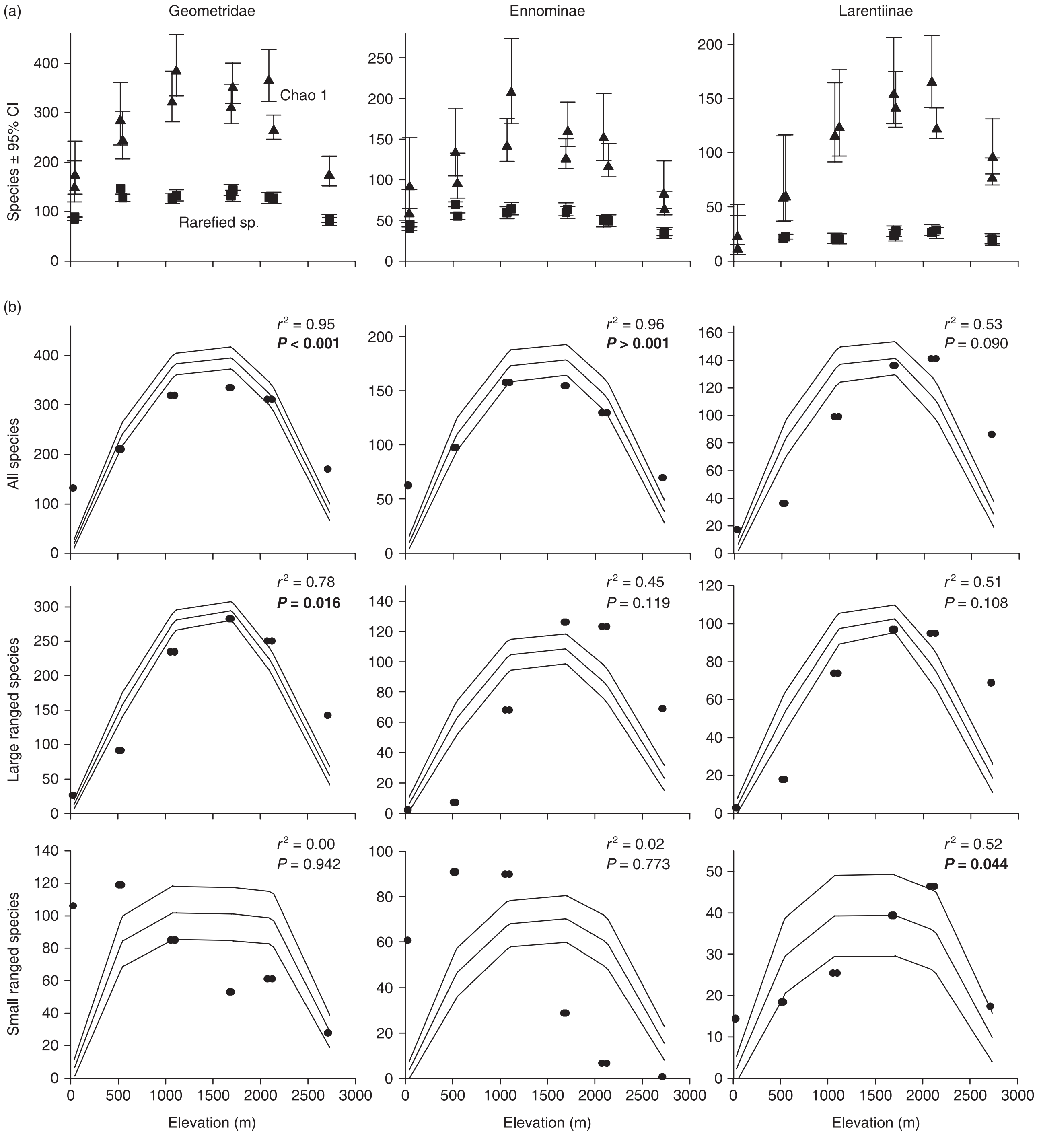

Figure 3 (a) Estimated species richness (Chao 1, triangles) and rarefied species numbers (squares) of Geometridae and the subfamilies Ennominae and Larentiinae along an elevational gradient in Costa Rica. (b) Predicted species richness under the assumption of random range placement (MDE) (central line and upper and lower 95% CI limits) and interpolated, observed species richness (circles) of Geometridae and two subfamilies along an elevational gradient in Costa Rica. The first row shows richness for all species, the second row shows richness for the 50% of species with the largest ranges, and the third row shows richness calculated for the 50% of species with the smallest ranges. See Table 2 for a regression analysis comparing interpolated richness and predicted richness. Note that no rarefied species numbers were calculated for the two lowest sites for Larentiinae because the number of individuals was very low (7 and 21). r^2 values indicate the variance in interpolated, observed species richness that is explained by predicted species richness. P_{adj} indicates the P-value for r^2, based on degrees of freedom adjusted to account for spatial autocorrelation using Dutilleul's (1993) method.

Table 2 Simple OLS and multiple regression analysis of (a) rarefied species richness, (b) estimated species richness (Chao 1), (c) interpolated species richness (all species, 50% of species with largest ranges, 50% of species with smallest ranges) vs. four environmental factors and geometric constraints (MDE model predictions) for three geometrid taxa. P_{adj} *(in italics)* is the *P*-value for r^2, based on degrees of freedom adjusted to account for spatial autocorrelation using Dutilleul's (1993) method. Model selection (*best model*) for multiple regressions (which do not account for spatial autocorrelation) was based on minimizing AIC, with consideration of all possible models. For comparison with the best model, r^2 and AIC are also shown for a model incorporating geometric constraints only (*geometric constraints model*) and a model with all environmental factors included and geometric constraints excluded (*environmental model*). *Beta* is the standardized regression slope for each factor in the best model. Numbers of specimens were rarefied to 397 in Geometridae, to 195 in Ennominae and to 41 in Larentiinae (see Fig. 2). Negative relationships are indicated by (–). Bold faced entries indicate significant r^2 (P_{adj}) ≤ 0.05 for individual tests

	Geometridae					Ennominae					Larentiinae				
			Interpolated					Interpolated					Interpolated		
	Rarefied	Chao 1	All	Large ranges	Small ranges	Rarefied	Chao 1	All	Large ranges	Small ranges	Rarefied	Chao 1	All	Large ranges	Small ranges
Simple OLS regression															
Humidity (r^2)	0.38	0.52	0.69	**0.80**	0.28 (–)	0.17	0.35	0.57	0.63	0.08 (–)	0.44	**0.80**	**0.73**	**0.76**	0.47
P_{adj}	*0.107*	*0.070*	*0.058*	***0.036***	*0.291*	*0.218*	*0.104*	*0.063*	*0.099*	*0.532*	*0.051*	***0.036***	***0.041***	***0.040***	*0.142*
Rainfall (r^2)	0.30	0.20	0.07	0.00 (–)	**0.58**	**0.55**	0.26	0.18	0.15 (–)	**0.91**	0.03 (–)	0.01 (–)	0.08 (–)	0.10 (–)	0.03 (–)
P_{adj}	*0.077*	*0.206*	*0.442*	*0.910*	***0.019***	***0.021***	*0.121*	*0.218*	*0.306*	***0.002***	*0.739*	*0.746*	*0.418*	*0.280*	*0592*
Temperature (r^2)	0.01	0.01 (–)	0.10 (–)	0.35 (–)	**0.89**	0.11	0.0 (–)	0.03 (–)	0.55 (–)	**0.68**	0.01 (–)	0.401 (–)	0.53 (–)	0.62 (–)	0.21 (–)
P_{adj}	*0.799*	*0.783*	*0.511*	*0.254*	***0.003***	*0.303*	*0.957*	*0.697*	*0.136*	***0.020***	*0.847*	*0.216*	*0.153*	*0.107*	*0.349*
Tree species (r^2)	0.12	0.01	0.03 (–)	0.22 (–)	**0.95**	0.31	0.01	0.00 (–)	0.46 (–)	**0.78**	0.01 (–)	0.25 (–)	0.41 (–)	0.49 (–)	0.13 (–)
P_{adj}	*0.319*	*0.868*	*0.724*	*0.316*	< ***0.001***	*0.114*	*0.768*	*0.959*	*0.109*	***0.005***	*0.869*	*0.268*	*0.148*	*0.107*	*0.372*
Geometric constraints (r^2)	**0.76**	**0.87**	**0.95**	**0.78**	0.00	**0.59**	**0.69**	**0.96**	0.45	0.02	0.26	**0.69**	0.53	0.51	**0.52**
P_{adj}	***0.003***	***0.001***	< ***0.001***	***0.016***	*0.942*	***0.012***	***0.009***	< ***0.001***	*0.119*	*0.773*	*0.212*	***0.027***	*0.090*	*0.108*	***0.044***
Multiple regression															
Geometric constraints model	0.76	0.87	0.95	0.78	0.00	0.58	0.69	0.96	0.45	0.02	0.26	0.69	0.53	0.51	0.52
(r^2, AIC)	*68.48*	*90.50*	*78.96*	*100.29*	*92.69*	*57.71*	*85.39*	*59.46*	*96.33*	*96.21*	*31.19*	*89.07*	*93.04*	*87.67*	*60.71*
Environmental model	0.94	0.84	0.99	0.99	0.94	0.88	0.73	0.99	0.99	> 0.99	0.86	0.93	0.99	0.99	0.94
(r^2, AIC)	*70.89*	*112.87*	*78.34*	*85.28*	*76.64*	*62.95*	*103.56*	*65.04*	*68.88*	*38.85*	*44.61*	*90.72*	*64.48*	*57.52*	*54.47*
Best model (r^2, AIC)	0.94	0.87	0.99	0.97	0.93	0.88	0.69	0.96	0.99	> 0.99	0.44	0.83	0.99	> 0.99	0.99
	62.14	*90.50*	(*)*78.3*	*62.85*	*60.60*	*47.27*	*85.39*	*59.46*	*52.66*	*38.85*	*28.42*	*86.28*	*61.04*	*31.61*	*32.57*
Humidity (beta)	1.88		2.28						–0.455	–0.769	0.662	0.660	–0.276		–0.215
Rainfall (beta)	–0.74		–0.616	–0.131					–0.626	1.239			–0.410	–0.169	–0.787
Temperature (beta)	1.90		3.25							–1.277					–0.854
Tree species (beta)			–1.97	–0.353	0.965	0.542			–0.361	0.741			–0.445	–0.559	
Geometric constraints (beta)		0.933	(*)	0.935		0.760	0.831	0.978	1.29			0.290	1.132	0.776	2.681

(*) An alternative model with only slightly higher AIC (78.96), includes only Geometric constraints (beta = 0.975) on the environmental variables and MDE predictions. In each case, the model with the lowest AIC is reported (*best model*), as well as a model with all four environmental factors (*environmental model*) and a model with MDE predictions only (*geometric constraints model*). The results in Table 2 should be considered exploratory, rather than definitive, for four reasons: (1) despite the massive effort invested in the field work for this study, the sample size for these regressions is nonetheless quite small ($n = 12$ sites), especially for multiple regression with five explanatory variables; (2) spatial non-independence (autocorrelation) between sites has been accounted for in the simple regressions, but not in the multiple regressions; (3) unmeasured environmental variables may be important; and (4) there is evidence of substantial collinearity among explanatory variables [e.g. temperature and rain with tree species richness ($r^2 = 0.86$, $r^2 = 0.71$, respectively)] that cannot be confidently resolved (Graham, 2003) with such a small sample size.

With these caveats, the results for simple regressions (upper section of Table 2) show that the strength of the relationships depended upon: (1) the environmental factor (or geometric constraints), but also on (2) the taxon investigated, (3) the particular measure of species richness used, and (4) the size of the species ranges. For the Ennominae (and for the Geometridae as a whole), as predicted by the MDE theory (Colwell & Lees, 2000; Colwell *et al.*, 2004), environmental factors tended to be more important in explaining the richness patterns of small-ranged species, whereas geometric constraints (MDE) were more explanatory for large-ranged species. For small ranges in the Ennominae, rainfall, temperature and tree species richness all showed evidence of a positive relationship with richness. In contrast, for small-ranged Larentiinae, the environmental factors considered were relatively less important, whereas humidity showed a positive relationship with richness of large-ranged species (a positive relationship with humidity was also evident for the large-ranged Geometridae as a whole). Large-ranged species showed results similar to those for all species (within a taxon), to which they contribute disproportionately because they occur at many sites (Jetz & Rahbek, 2002; Colwell *et al.*, 2004). The strength of the relationships differed considerably depending upon the measure of species richness, but generally showed the same tendencies.

The multivariate results (lower section of Table 2) were generally supportive of these patterns. As often happens with multivariate regressions when multicollinearity is present, certain factors tended to 'capture' much of the variance shared with other factors, making rigorous causal interpretations difficult. Examination of Moran's I for distance-class residuals from the multiple regressions for the models selected using the AIC revealed substantial spatial autocorrelation in some of the models, calling for additional caution in interpreting these results.

Regression with MDE model data

Figure 3(b) shows MDE model predictions generated with interpolated ranges (augmented as detailed in the Materials and Methods) and randomized range placement. Predicted species richness approximated interpolated richness quite closely for Geometridae and Ennominae (all species; $0.95 \le r^2 \le 0.96$, $P_{adj} < 0.001$), but considerably less well for Larentiinae (all species; $r^2 = 0.53$, $P_{adj} = 0.090$). Even though r^2 values are very high, overall, interpolated species richness does not fall within the 95% confidence limits at most individual sites. Interpolated richness in Geometridae and Ennominae is always higher than predicted richness at the ends of the gradient, and tends to be lower in the middle of the gradient (Fig. 3b). In Larentiinae, the interpolated richness curve is shifted towards higher elevations compared with the predicted richness curve. The pattern of all species is mirrored by the large-ranged species in Geometridae, which dominate the information in the pattern for all species (Fig. 3b). However, a remarkable shift of the curves occurs in Ennominae and Larentiinae. Large-ranged species of both families are clearly underrepresented at the lower elevations, compared to MDE expectations, whereas interpolated species richness is disproportionately high at high elevations. On the contrary, small-ranged ennomines are very species rich at low elevations and strongly decline at high elevations. As a consequence, the correlation between interpolated species richness and the MDE model predictions drops to only $r^2 = 0.02$ ($P_{adj} = 0.733$) for small-ranged Ennominae, contributing to a similar pattern in small-ranged Geometridae as a whole (Fig. 3b). Interpolated richness of small-ranged Larentiinae still peaks at 1700 m, but shows higher values at the lowest sites than large-ranged species.

Rapoport's elevational rule

Figure 4(a) shows that average geometrid species range sizes increase with increasing elevation ($r^2 = 0.69$). The relationship is almost linear in the Ennominae (Fig. 4b, $r^2 = 0.82$). However, the curve of the Larentiinae is asymptotic, reflected by a lower value of r^2 (Fig. 4c, $r^2 = 0.39$). We report no P-values for these results because the data points in Stevens plots are not independent (Rohde *et al.*, 1993).

DISCUSSION

Richness patterns and environment

It was long believed that species richness in insects shows a monotonic decline along elevational gradients. Peaks at mid-elevations have sometimes been regarded as sampling artefacts (Wolda, 1987; McCoy, 1990). However, the paradigm has changed, and peaks at medium elevations are generally accepted as being the rule rather than the exception (for a review see Rahbek, 2005). Such peaks often occur at relatively low elevations and have sometimes been overlooked when sampling was restricted to higher elevations (Rahbek, 1995; Lomolino, 2001; Kluge *et al.*, 2006). Examples include groups such as butterflies and ants, which show a maximum diversity in tropical regions far below 1000 m a.s.l. (DeVries, 1994; Brühl *et al.*, 1999; Fisher, 2002). However, evidence is still scarce because only a very few insect studies have investigated complete elevational gradients.

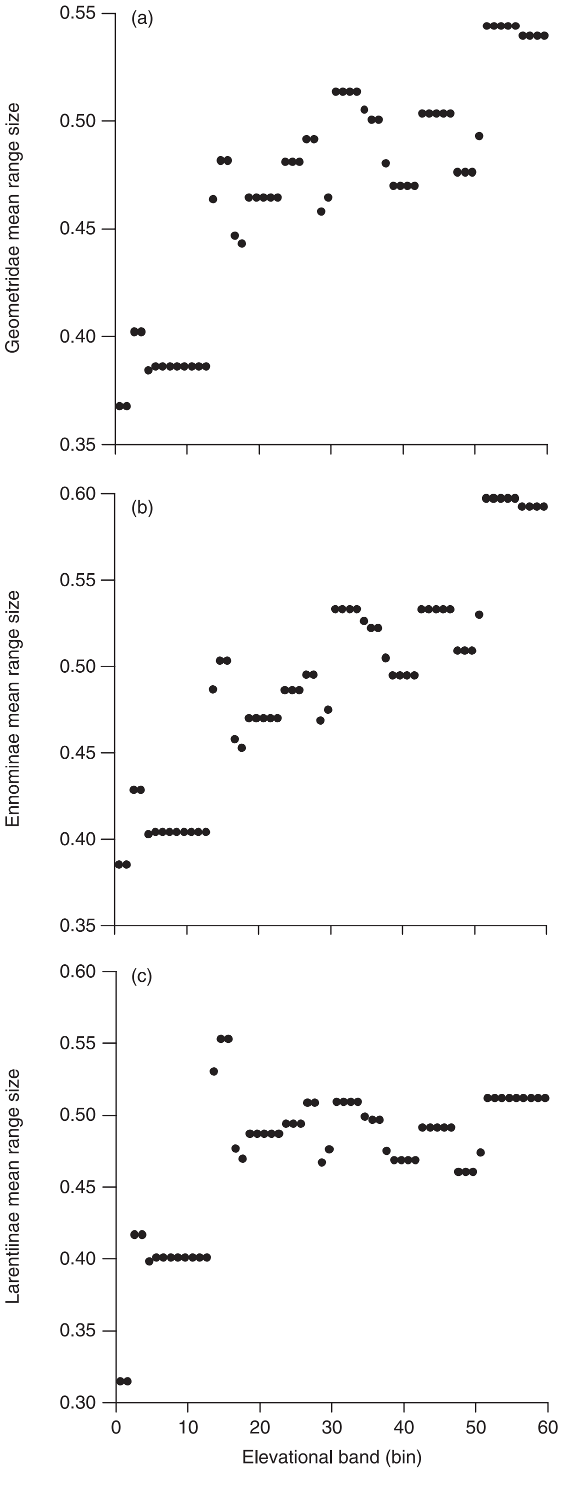

Figure 4 Stevens plots (mean moth range size for 60 elevational bands) along an elevational gradient in Costa Rica: (a) Geometridae, (b) Ennominae, (c) Larentiinae. Rapoport's elevational rule is supported because the mean range size increases with increasing elevation, although the pattern of variation in the number of individuals sampled may exaggerate this effect.

So far, only a few exceptions to an overall declining diversity of insects at elevations higher than 1000 m have been documented. Examples include arctiid and geometrid moths in Borneo (Holloway, 1997; Schulze, 2000) and Ecuador (Brehm *et al.*, 2003b). Diversity patterns of these taxa have not previously been investigated along a tropical elevational gradient ranging from sea level to a mountain top. The present study confirms that geometrid moths have a predominantly montane distribution with exceptionally high species richness at elevations up to 2100 m a.s.l. Richness at the lowest elevations is markedly lower, and also decreases towards higher elevations at the mountain summit.

Regression analyses of selected environmental factors as carried out in this study are generally hampered by the fact that whereas moth richness may be explained statistically by certain environmental factors there may well be no causal relationship. Moreover, because some environmental factors are correlated with each other, it is difficult to interpret positive correlations with richness. Finally, the set of available environmental factors is limited, especially in poorly investigated tropical regions (such as the Barva Transect, which is rugged and difficult to access) where suitable data (e.g. host plant relationships, host plant richness, leaf nitrogen, etc.) do not yet exist. The available data appeared nevertheless to be an appropriate first set of factors for an exploratory analysis.

The results suggest, not surprisingly, that a combination of environmental factors may affect the richness patterns of geometrid moths, rather than a single factor. Humidity is strongly correlated with richness of large-ranged Geometridae and Larentiinae, whereas rainfall and temperature are strongly correlated with small-ranged ennomine richness. Humidity and rainfall can have direct or indirect effects, via the vegetation, on herbivorous insects. It remains to be shown whether or not ambient humidity levels could act as a physiological constraint to certain moth species.

Geometrid moths have frequently been regarded as predominantly being feeders of trees and shrubs (e.g. Scoble, 1999; Brehm, 2002). Moth species richness in this study is positively correlated with tree species diversity for small-ranged Geometridae and Ennominae, but not for large-ranged species in these taxa, nor for Larentiinae. These positive correlations are obscured when species of all range sizes are considered together. In a montane forest in Ecuador, Brehm *et al.* (2003b) found that tree species richness declined along an elevational gradient spanning *c.* 1600 m, but total diversity of geometrid moths remained at a constantly high level up to elevations of *c.* 2700 m a.s.l. Hence, in both areas, total species richness in this herbivorous taxon remains high despite the declining availability of potential host plants at higher elevations. Given the results of this study, it is tempting to suggest that small-ranged species (at least of Ennominae and Geometridae as a whole) may be host specialists, whereas large-ranged species may tend to be polyphagous. However, this conclusion remains speculative as long as no further host plant data are available for Neotropical geometrids.

Temperature is obviously an important environmental factor, especially for ectothermic organisms like insects. Brehm *et al.*

(2003b) and Brehm & Fiedler (2003) discussed possible physiological adaptations of geometrid moths (particularly Larentiinae) to low flight temperatures. Geometrids clearly demonstrate that not all insects prefer the warmest climates, although richness of small-ranged Ennominae and Geometridae as whole showed a significantly positive correlation with temperature. The decline of richness around 2700 m a.s.l. in Costa Rica could be an effect of reduced habitat area rather than a negative effect of environmental factors such as temperature (Fig. 1 gives an impression how limited this elevational belt is in total area). Brehm *et al.* (2003b, 2005) showed that diversity of geometrids at the same elevation in Ecuador was still as high as it was at lower elevations. Richness declined only at the highest elevations in the summit area (3100 m a.s.l.) of the mountain range studied.

Richness patterns and geometric constraints

Considered alone, MDE models explained rarefied richness, estimated richness and interpolated richness of all geometrid moth species (all range sizes considered together) better than any of the available single environmental factors (Table 2). Overall, the models fitted the interpolated richness pattern very well for Geometridae and Ennominae. However, the models consistently predicted lower species richness at the ends of the gradient, and often higher species richness at medium elevations than observed in nature. A qualitatively similar pattern of underestimation of richness by the model at the ends of the domain was found by Kluge *et al.* (2006) and Watkins *et al.* (2006) for ferns, and by Cardelús *et al.* (2006) for epiphytes along the same elevational gradient. An explanation for the underestimation of species richness at the limits of the domain could be the one-dimensionality of such models and the conservative assumptions of the randomization algorithm, which requires each randomly placed range to fit entirely within the domain without the dynamic adjustment permitted in related, two-dimensional models (Jetz & Rahbek, 2002). In reality, species richness at the domain limits will probably never be zero (Grytnes & Vetaas, 2002; Connolly, 2005).

As for the higher predicted richness than interpolated richness in the middle of the domain, the absolute magnitude of predicted richness is influenced by the magnitude of range size augmentations (see Materials and Methods); the greater the augmentation, the higher the peak richness, because larger ranges tend to be sampled at more sites. We assessed the sensitivity of results to this effect by reducing the range size augmentation to about half (150 m on each end) the values specified in the Materials and Methods section. With this change, mid-domain richness peaks were actually lower than interpolated richness, but the relative magnitude (the 'shape' of the curves) was virtually unchanged, and the r^2 for fit was identical. Only a higher density of elevational sampling sites and long-term sampling could reduce the uncertainty regarding the appropriate degree of range augmentation (which is necessitated by species that occur in only one site) in future studies.

The separate analysis of the large subfamilies Ennominae and Larentiinae shows that a good fit of the model for the whole group is not necessarily reflected by all subordinate taxa. Richness of larentiine moths is correlated more weakly with the model richness predictions because the larentiine curve is 'shifted' towards higher elevations. Hence, richness of larentiines is likely to be strongly driven by other than stochastic factors. Possible causes for the richness of Larentiinae moths in high montane habitats were discussed by Brehm & Fiedler (2003). Larentiines such as winter moths could be particularly well adapted to cool temperatures, allowing the colonization of montane forests. Despite their potentially unfavourable climatic conditions, these habitats could be advantageous in terms of reduced predation pressure from ants, and insectivorous bats and birds.

Jetz & Rahbek (2002) and Colwell *et al.* (2004) argued that large-ranged species were more likely to be constrained by geometry, whereas small-ranged species were more likely to show the effects of underlying environmental or historical drivers. Our data strongly support this concept statistically for the Geometridae as a whole and for the Ennominae, for which interpolated richness of large-ranged species is much more strongly correlated ($r^2 \geq 0.95$) with MDE model predictions than interpolated richness of small-ranged species, which is virtually uncorrelated with MDE predictions ($0.00 \leq r^2 \leq 0.02$) (Fig. 3b). In fact, the strong correlation between humidity and the richness of large-ranged (but not small-ranged) Geometridae and Larentiinae (Ennominae was nearly significant, at $P_{adj} = 0.063$) may actually reflect the strong collinearity between humidity and MDE predictions for large-ranged species, rather than an effect of humidity itself on species richness.

In contrast, the strength of the correlation for Larentiinae was largely independent of range size, though significant only for small-ranged species and for estimated richness of all Larentiinae.

The patterns of deviation of interpolated richness curves from model predictions, however, provide some of the most interesting results. Both large-ranged ennomine and large-ranged larentiine species showed a modest shift towards higher elevations compared with MDE model predictions (Fig. 3b), whereas the pattern of richness for small-ranged species in the two subfamilies revealed a striking contrast between the two subfamilies: small-ranged ennomine richness was strongly focused at lower elevations whereas small-ranged larentiine richness was concentrated at higher elevations. These contrasting patterns for large-ranged vs. small-ranged species suggest that richness patterns for these two rich groups are likely to have been driven by completely different factors, depending upon range size, and that the two subfamilies might have different biogeographical origins — the ennomines at low to medium elevations and the larentiines at high elevations.

Rapoport's elevational rule

Rapoport's rule (Stevens, 1989) states that species ranges become larger with increasing latitude. Stevens (1992) extended the rule to elevation as an explanation for monotonic decreases in species richness with increasing elevation. So far, existing studies suggest that the rule has no general applicability (Gaston *et al.*, 1998), but very little evidence exists for insects. The present study finds a Rapoport effect in all three analysed taxa, based on interpolated ranges (Fig. 4). When species richness varies among sites, and equal numbers of individuals are sampled but the inventory is incomplete at all sites, ranges tend to be underestimated at richer sites, producing a spurious Rapoport effect (Colwell & Hurtt, 1994). Although, in our study, local richness was not correlated with range size, the number of individuals collected (Table 2) was rather strongly correlated with mean range size (Fig. 4) among elevations. For this reason, the observed Rapoport effect is probably exaggerated, and could even be entirely artefactual. The same effect may shift curves for observed, large-ranged species richness (Fig. 3b) to somewhat higher elevations than equal sampling would produce. Individual-based rarefaction of the species × elevations matrix to produce equal numbers of individuals at each elevation might resolve these uncertainties, but is beyond the scope of this paper.

As for the effect of area at different elevations, on a regional scale, lowland areas dominate the Caribbean slopes of Costa Rica as well as the study area, and area sharply declines with increasing elevation (Kluge *et al*., 2006). Thus, the observed hump-shaped richness pattern obviously cannot be positively correlated with area.

To the degree that our Rapoport results are genuine, this study confirms the findings of the only two existing insect studies on Rapoport's elevational rule that were carried out in North America on butterflies (Fleishman *et al*., 1998) and ants (Sanders, 2002). Both found the same combination of a mid-elevational richness peak and Rapoport's elevational rule, although no complete gradients were investigated. The mechanism behind the rule is still unknown, and different factors might be involved in different groups of organisms. For example, the Rapoport 'rescue' hypothesis (Stevens, 1992) suggests that low-elevation populations are relatively intolerant of environmental stochasticity because short-term climatic variability is positively correlated with elevation. Hence, species that inhabit higher elevations must have larger climatic tolerances and thus can be found along a greater elevational range. Stevens (1992) used this hypothesis to explain monotonically decreasing species richness patterns. However, because species richness of geometrid moths is hump-shaped, the Rapoport 'rescue' hypothesis must be rejected.

Our results suggest that both stochastic and environmental factors are likely to be responsible for the observed richness peaks of geometrid moths at medium elevations. No single key factor could be found to explain all patterns because marked differences occurred between different taxa and between species with different range sizes. An improved knowledge of the life histories of species-rich tropical invertebrates as well as more environmental data will be required in the future for a better understanding of their richness patterns.

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BIOSKETCHES

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SUPPLEMENTARY MATERIAL

The following material is available for this article:

Appendix S1 Sampling dates and numbers of individuals collected on each date at 12 sampling sites. Total numbers sampled are provided in Table 1.

Appendix S2 Complete list of 739 geometrid species recorded at 12 rain forest sites along a complete elevational gradient in Costa Rica (Barva transect).

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-822x.2006.00281.x

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