Elevational species richness gradients in a hyperdiverse insect taxon: a global meta-study on geometrid moths

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ABSTRACT

Aims: We aim to document elevational richness patterns of geometrid moths in a globally replicated, multi-gradient setting; and to test general hypotheses on environmental and spatial effects (i.e., productivity, temperature, precipitation, area, mid-domain effect, and human habitat disturbance) on these richness patterns.

Location: 26 elevational gradients worldwide (latitudes 28°S to 51°N)

Methods: We compiled field datasets on elevational gradients for geometrid moths, a family of the Lepidoptera. We documented richness patterns across each gradient while accounting for local richness undersampling. We incorporated data on habitat disturbance, together with other environmental and spatial predictor variables. We tested various climate-driven environmental hypotheses. Our analyses comprised two pathways: univariate correlations within gradients, and multivariate modelling on pooled data after correcting for overall richness variation among different gradients.

Results: The majority of gradients showed midpeak patterns of richness, irrespective of climate and geographic location. Excluding human-affected sampling plots did not change these patterns. Support for univariate main drivers of richness was generally low, although idiosyncratic support for particular predictors on single gradients occurred. Multivariate models, in agreement with univariate results, provided strongest support for an effect of area-integrated productivity, or alternatively for an elevational area effect. Temperature and the mid-domain effect received support as weaker, modulating covariates, while precipitation-related variables had no explanatory potential.

Main conclusions: Midpeak patterns predominate in geometrid moths along elevational gradients. Area-integrated net primary productivity, or area itself, were the strongest predictors of richness patterns, but further study of the landscape-wide effects of productivity is required in an elevational richness context. Multi-gradient studies like ours are essential to
assess the generality of hypothesized drivers of elevational richness patterns. Our findings contribute evidence on elevational richness patterns for a group of non-vertebrate organisms, which may facilitate future understanding of how trait variation explains diverse environment-richness relationships among different taxonomic groups.

Introduction

The pattern of species richness along elevational gradients may be viewed as a model system to investigate the environmental causes of larger-scale richness patterns, but it has proven challenging to understand variation in this pattern in its own right. Unimodal and decreasing richness patterns have most often been reported across many taxonomic and functional groups of organisms (e.g., Rahbek, 2005; McCain & Grytnes, 2010; Kessler et al., 2011). Uncertainty remains regarding the prime determinants of richness patterns within gradients and the causes of substantial variability observed between different mountain systems and different taxa.

Some broadly supported, climate-driven environmental effects on richness are applicable to elevational gradients, including variation in net primary productivity, temperature, and precipitation. High primary productivity (i.e., abundance of food resources for consumers) may lead to high consumer richness by sustaining large population sizes, hence decreasing extinction probabilities (Evans et al., 2005). In some vertebrate taxa (McCain, 2007a; 2009), highest richness in warm and wet habitats may indirectly support such a link. Direct tests of a positive effect of productivity on richness along many elevational gradients are hampered by a shortage of reliable field data on productivity. Temperature may also influence richness, independently of its impact on plant productivity, by its positive effect on metabolic rates, thereby shortening generation times and enhancing evolutionary processes such as
diversification (Allen et al., 2007). Alternatively or additionally, low temperatures may lead to foraging restrictions in ectotherms, reducing the food resources that they can utilize (Willmer, 1983). For example, temperature was found to be a strong predictor of elevational richness patterns in reptiles (McCain, 2010), and studies on hymenopteran insects highlighted the link between temperature and foraging activity along elevational gradients (Sanders et al., 2007; Classen et al., 2015). Both mechanisms (i.e., evolutionary speed, foraging limitation) predict a monotonic, positive effect of temperature on richness. However, due to the nearly universally monotonic decline of temperature with elevation, temperature alone cannot be the main driver of commonly reported midpeak richness patterns. Elevational effects of temperature in combination with water availability were supported in some multi-gradient studies (McCain, 2007a; 2009), but it remains unclear whether this interaction indicates direct effects of water and temperature limitation, or acts as a proxy for the distribution of plant productivity. Precipitation may also be directly linked to species occurrence and richness, particularly for organisms with specific moisture requirements like ferns (Kessler et al., 2011) or amphibians (Müller et al., 2013). Again, positive effects of water availability on richness would be expected. Spatial factors related to landscape topography could also be important drivers of elevational richness patterns, including an elevational species-area relationship (SAR) and the mid-domain effect (MDE). The SAR, monotonically increasing greater richness within a larger study area, is the best-supported empirical rule in biodiversity research (Dengler, 2009; and references therein). SARs may come about through a variety of mechanisms, among them increased habitat heterogeneity, community turnover, or larger population sizes and therefore lowered extinction risks in larger areas (Rosenzweig, 1995). However, larger areas also contain a greater total amount of resources (i.e., higher total productivity), which leads to an intricate interrelationship among area, productivity and richness (Wright, 1983; Storch et al., 2005). Elevational SARs, also called the indirect area effect (Romdal & Grytnes, 2007), are
based on the variability of the area among elevational bands in a mountainous landscape. Elevational SARs have been reported in various studies (e.g. Rahbek, 1997; Sanders, 2002; Beck & Kitching, 2009), although McCain (2007b) questioned the role of elevational area as a main driver of diversity, given that midpeak patterns dominate while area declines monotonically with elevation in the majority of mountain regions. Geometric constraints, i.e. distinct boundaries of a landscape or gradient, may lead to greater overlap of large-ranged species towards the centre of a gradient, resulting in a midpeak pattern of species richness even in the absence of any environmental variation (the MDE; Colwell & Hurtt, 1994). As MDE makes precise predictions for richness at each elevation, a monotonically increasing link of MDE and observed richness is expected. Although MDE is suggestive as an explanation of an elevational midpeak of richness and supportive data have been reported (e.g., Dunn et al., 2007), many authors have concluded that MDE is unlikely to be the sole driver of richness along elevation gradients. If unimodal at all, empirical patterns are often skewed, with their maximum richness located at elevations lower than the centre of the gradient (contrary to predictions based on a pure MDE; Dunn et al., 2007; McCain & Grytnes, 2010). However, MDE may well be acting as a modulator of other environmental effects (Wang & Fang, 2012; Colwell et al., re-submitted 2016). Other evolutionary or historical hypotheses for richness patterns exist, and some comprise mountain-specific mechanisms, including phylogenetic history (e.g., McCain, 2009), past climatic variation (Colwell et al., 2008; Colwell & Rangel, 2010), turnover at ecotones (McCain & Beck, 2016), and specific biotic interactions (e.g., Novotny et al., 2006; Dehling et al., 2014). Moreover, midpeaks could also be enhanced by more intense anthropogenic lowland disturbance (e.g., McCain & Grytnes, 2010).

There are a large number of single-gradient, elevational richness studies on a variety of taxonomic groups, including many on various insect taxa (e.g., McCoy, 1990; Sanders, 2002; Sanders et al., 2007; Classen et al., 2015; and references therein and in Appendix ES1).
However, with very few exceptions (e.g., Beck & Kitching, 2009; Kessler et al. 2011; Ashton et al., 2016; Szewczyk & McCain, 2016), multi-gradient analyses for the same taxonomic group, allowing comparisons of elevational richness patterns across biogeographical realms and tests for general predictors, remain restricted to vertebrate taxa (McCain & Grytnes, 2010; and references therein). For vertebrates, strong climatic drivers are empirically supported, but conclusions vary by taxon. Consistent midpeaks shown in some taxa are most difficult to link to single predictors and suggest a greater complexity of causal agents. A framework conceptualizing the variability of richness patterns, and of links with the environment across taxonomic groups, is still underdeveloped (e.g., via thermoregulatory traits; Buckley et al., 2012). Provision of multi-gradient data for invertebrate taxa, featuring trait combinations not occurring in vertebrate groups (for Lepidoptera, e.g. herbivory with specific host-plant links) may therefore offer an avenue for further crucial insights.

Geometrid moths (with caterpillars known as loopers or inchworms) are a family of Lepidoptera that represents a truly hyperdiverse insect taxon with ca. 23,000 described and over 40,000 estimated species (Miller et al., 2016). Geometrids rank among the most abundant Lepidoptera families in many tropical and temperate habitats. They are mostly nocturnal, characterized by small body size and a short generation time. At least in many temperate species, caterpillars feed on a single hostplant family or genus (e.g. Ward & Spalding, 1993; see also Novotny et al., 2004; Bodner et al., 2012). Geometrids are assumed to be tightly linked to local environmental conditions. They have been frequently utilized as ‘indicator taxa’ of human environmental impacts (e.g., industrial melanism, habitat disturbance, climate change; see ES1). The adult moths can be robustly sampled using artificial light sources (Beck & Linsenmair, 2006), and many comparable studies exist (e.g., Table ES1.1). Here, we present a unique compilation of all available geometrid richness data known to us, from elevation gradients across the world, based on literature and our own sampling. We compare elevational richness patterns and their global variability. We test
effects of key environmental (productivity, temperature, precipitation) and spatial predictors (area, mid-domain effect). We compare conclusions from two different analytical frameworks—univariate comparisons on individual gradients and multivariate analysis on globally pooled data—to identify support among the hypothesized drivers of elevational richness patterns.

Methods

Geometrid moth datasets

We compiled data from all suitable elevational gradient studies of geometrid moths we could trace from the literature, and from our own, unpublished field data. Of these datasets we excluded those with minimal sampling effort (i.e., removing sites with <20 sampled moth individuals unless we could confirm that sampling effort was substantial despite low specimen numbers), sampling based on only one section of a gradient, and those with unclear taxonomic resolution. All data consisted of local, quantitative light trapping samples at consecutive elevations within defined mountainous regions (26 gradients, Fig. 1; details in Table ES1.1). Abundances and species composition from light trapping are influenced by many factors, including type of light source and natural variation due to weather, moonlight and season, as well as nightly sampling schedule and collecting effort (Brehm & Axmacher, 2006; Jonason et al., 2014). Details and references for each dataset appear in Table ES1.1. While variation in field methods obviously influences abundance and diversity in a moth inventory, field methods in the evaluated studies were mostly standardized within each gradient, thus allowing a robust relative assessment of the elevational richness patterns.

Field collecting and specimen identifications in our datasets were conducted by lepidopterists specializing in the local moth faunas. However, due to high species richness, taxonomic accuracy can still occasionally be a challenge, particularly for diverse tropical regions. Geometrid faunas from some regions of the world lack comprehensive taxonomic
treatments, making it necessary to rely on approximate, parataxonomic morphospecies sorting (groupings based on morphological differences within a dataset; Basset et al., 2004). Furthermore, tropical faunas may contain multiple cryptic species that are recognizable only with molecular methods (e.g., DNA barcoding). However, Brehm et al. (2016) have shown, in an extensive molecular re-assessment of identifications in the Ecuadorian dataset, that including a very large number of previously unrecognized, cryptic species did not change the elevational richness pattern.

Gradients varied in elevational scope, number of sampling sites, and survey effort (Table ES1.1), but based on sampling descriptions in publications and information from data collectors, we detected no strong elevational biases in sampling effort (see also Fig. ES1.32).

To address the geographic variation in sampling among the 26 gradients for elevational diversity comparisons, we classified 19 gradients as ‘analysis-grade’ data and, nested within those, 7 gradients as ‘best subset’ data (Table ES1.1). Our analysis-grade criteria required sampling sites within 400 m elevation of the mountain base and sampling at least 50% of the elevational range of the mountain region (elevational domain). For the ‘best subset’ we additionally required sampling across at least 70% of an elevational domain for mountains of 800 m or greater height. We focused analyses on the analysis-grade subset, but we repeated core analyses for the ‘best subset’ as well as all gradients to examine the consistency of results. We classified all local plots as ‘near-natural’ or ‘human-disturbed’ habitat based on descriptions provided by the data collectors, thus identifying analyses without disturbance, or with minimally disturbed sites. We aggregated all diversity data into 100 m elevational bands to improve scale comparability among gradients (e.g., Colwell, 2009; McCain, 2005; 2010).

Measuring diversity
Quantitative samples of species-rich invertebrates are mostly incomplete, and observed species richness will therefore be an underestimate. We used various approaches to account for richness underestimation, including interpolated species richness and two richness estimators: \textit{(Chao}1 and Fisher’s $\alpha$) and rarefied richness. Interpolated species richness ($S_{\text{int}}$) assumes that a species is found at all elevations between its lowest and highest recorded occurrence. $S_{\text{int}}$ accounts for false absences at intermediate elevations, but not at the edge of a species’ elevational range (Gryntes & Vetaas, 2002). Although $S_{\text{int}}$ provides estimates for all 100 m bands within study boundaries, we utilized only data for 212 bands that have actually been sampled (i.e., contain at least one field plot). \textit{Chao}1 ($S_{\text{Chao1}}$) is a nonparametric minimum estimator of true richness, based on observed richness and the number of singletons and doubletons within each local sample. Calculations were conducted with EstimateS; classic or biased-corrected equations were chosen as advised (Colwell, 2013). For the Fisher’s $\alpha$ richness estimate, we first estimated $\alpha$ (a parameter of the log-series species-abundance distribution model; \textit{Fisher} \textit{et al.}, 1943)) for each local site. Second, we estimated species richness as $S_{\alpha} = \alpha*\ln(1+N/\alpha)$ ($N =$ sum of individuals in the sample; Colwell & Coddington, 1994). For the best subset of gradients, we also calculated rarefied richness expected at a fixed common sample size (detailed methods and results: see Appendix ES4). To aggregate diversity into 100 m bands (separately for $S_{\text{Chao1}}$ and $S_{\alpha}$), we calculated the average of local richness estimates within each band to reduce the influence of outliers. While other valuable diversity estimators are available, we lack specific data (i.e., quantitative data for replicated samples) needed for their calculation.

For each gradient and richness metric we counted elevational richness patterns by the categories suggested in McCain & Grytnes (2010): decreasing, low-plateau, low-plateau with a midpeak (LPMP), midpeak, and increasing. Our metrics differ in scale; $S_{\text{int}}$ is a gamma diversity estimate whereas $S_{\text{Chao1}}$ and $S_{\alpha}$ are alpha diversity estimates. However, data for the three metrics are highly correlated (for analysis-grade data: $S_{\text{int}}$ and $S_{\text{Chao1}}$: $r^2 = 0.78$; $S_{\text{int}}$ and
S_α: r^2 = 0.75; S_α and S_{Chao1}: r^2 = 0.89; Fig. ES1.3). We present \( S_{int} \)-based analyses in the main text because it allows direct comparison with previously published multi-gradient analyses. Results based on \( S_{Chao1} \) and \( S_α \), presented in ES3, are not qualitatively different.

Diversity predictors

The distribution of anthropogenic disturbance along the gradients, particularly lowland disturbance, has been proposed to lead to mid-elevational peaks in species richness on elevational gradients (McCain & Grytnes, 2010; and references therein). We examined this potential trend by removing plots in human-disturbed habitat from the assessments of elevational richness, then comparing richness patterns for these reduced datasets to patterns across all plots. The predicted pattern after removal of lowland disturbance impacts would be decreasing or low-plateau richness patterns, compared to richness midpeaks for the full datasets, including both disturbed and natural sites.

As no field measures of environmental variables were collected on most of our gradients, environmental data from GIS sources were used, for all gradients. These included area of elevational bands [A]; mean annual temperature [T]; non-freezing temperatures [VegT]; precipitation [Prec]; humidity [Hmd]; average productivity [NPP]; and summed productivity [SNPP], all available at 30” resolution (acronyms are used in all graphs and tables). Climate and elevation data were taken from Worldclim (www.worldclim.org) and projected to Mollweide World equal area projection (1x1 km cells). Area within each 100 m elevation band was calculated within a 200 km radius around the maximum elevation of each gradient (GIS software: ArcGIS 10.3). For other environmental variables, average annual values for 100 m bands for each region were calculated for polygons defined to contain zones of similar climate around sampled gradients (i.e., not crossing sharp climatic changes along some mountain ridges; shape files are available on request). VegT was calculated as a coarse
proxy for temperature during the growing season: the annual average temperatures for those months with average monthly temperatures ≥0°C. Sub-freezing temperatures may be of little relevance to ectotherm metabolism if individuals spend unsuitable seasons in physiologically inactive life stages (dormancy). Absolute precipitation may be associated with very different water availability in a landscape depending on evapotranspiration and edaphic factors. Therefore, we calculated an index of humidity [Hmd] as Prec/PET, where PET is potential evapotranspiration for the mountainous region (Willmott & Kenji, 2001). Since PET data exist only at coarse resolution (0.5° grain), Hmd is primarily suitable for comparisons between gradients but is still proportional to Prec among elevational bands within a gradient.

For NPP, we used fine-grained estimates of annual net primary productivity (NPP) from Running et al. (2004). This dataset is based on remotely-sensed, normalized differential vegetation index (NDVI) measurements (MODIS, 30” grain), while coarser-scaled precipitation data was factored in via data interpolation to account for effects of stomata closure during dry spells in some regions of the world. Raw NDVI or other proxies of NPP, such as growing season length, would ignore such effects. To our knowledge, this is the only NPP dataset available at a spatial resolution that makes elevational analyses feasible. Pixels without measurable vegetation were labelled ‘No Data’ in the dataset; for the purposes of our analyses we set such pixels to zero unless they were sea or large lakes, because no vegetation equals zero plant productivity (e.g., deserts and high-altitude rock). We calculated average NPP across elevational bands; as a quality control we visually checked elevational NPP patterns for a large number of mountain ranges across the globe, including many that we knew from personal visits and field work. We found patterns to match expectations (e.g., maximum NPP at mid-elevations on mountains with arid bases). As an alternative capture of productivity (SNPP), we calculated productivity integrated over available area of 100 m elevational bands (rather than averaged; i.e., SNPP = A x NPP). We discuss, transparently,
differences between area and SNPP (a “composite” variable that combines area and NPP), and their implications for inference regarding the drivers of richness patterns.

For our final predictor, the mid-domain effect [MDE], expected richness values are usually derived by randomizing empirically measured elevational range sizes of species within the sampling domain. This procedure preserves the empirical range size frequency distribution (RSFD). However, this approach is problematic if the sampled gradient length is only a fraction of the true gradient available in a landscape, because assumptions of the MDE refer to the geometric constraints of the entire landscape. As many of our gradients were not completely sampled (Table ES1.1), we resorted to MDE predictions from a binomial RSFD (Willig & Lyons, 1998; Model 2 in Colwell & Hurtt, 1994), using the elevational domain of each gradient as geometric boundaries. For the ‘best subset’ of gradients (>70% of gradient sampled) we additionally computed predictions for the randomized, observed RSFD (software Mid-Domain Null; McCain, 2004) to assess potential differences between the two approaches.

Lastly, there is potentially a long list of additional important variables for elevational species richness of nocturnal moths with herbivorous larvae (plant diversity, mutualistic and antagonistic interactions, habitat complexity, etc.) but standardized data for these variables do not currently exist at the appropriate scale across all datasets. All richness and predictor variables are available (ES4ES5); as new data become accessible in the future, further analyses will become possible.

Statistical analyses

For standardization, we log-transformed all richness data and predictor variables, and z-transformed ([x-mean]/standard deviation) the pooled data that combined all gradients. Log-transformation was necessary for some variables to fulfil normality assumptions, and for some relationships we had a priori expectations of power law relationships (which are linearized by
log-transformations; e.g., area, Dengler, 2009; temperature, Allen et al., 2007). Standardized data allowed a direct comparison of model coefficients as a measure of relationship strength in multivariate models. We drew inferences on landscape geometry (A, MDE) and environmental effects (all others) on richness from two conceptually different analyses: comparisons among univariate analyses per gradient and multivariate models of pooled data for all gradients.

Univariate correlations of predictor variables with richness were calculated within each gradient and Pearson’s $r^2$ values were used as a measure of hypothesis support. As all hypotheses predicted a positive relationship with richness, we set $r^2$ values with negative coefficients to zero. We used the frequency distribution and medians of $r^2$ values across all gradients to assess the overall support of each variable as a main predictor of richness. This method has been used in various earlier analyses of elevational richness (e.g., McCain, 2005, 2007a). We also considered single gradient multivariate models, but sample sizes (number of 100 m bands) were too low for meaningful model fitting.

In the multivariate analyses, we combined standardized richness and predictor data for all gradients. We used Generalized Linear Models (linear link, Gaussian error distribution) within a model selection framework based on Akaike’s information criterion with small-sample correction (AICc; Burnham & Anderson, 2002). We included 44 candidate models with different predictor combinations. These models never contained variables that were highly collinear or conceptually infeasible (i.e., never both T & VegT; Prec & Hmd; SNPP & A and/or NPP). For ‘best’ models and closely related models, we calculated pseudo-$R^2$ as Pearson’s $r^2$ of the correlation between model prediction and observed value. We plotted model residuals against elevation to assess remaining, unexplained elevational variation. We used AICc-weighted model averaging to extract averaged standardized coefficients (and their 95% confidence intervals, CI). Because SNPP is a composite of two variables (A x NPP), we
also calculated a ‘corrected’ AICc with one additional parameter to evaluate ‘best’ model conclusions drawn from model selection.

Our multivariate approach enforces one coefficient per effect (e.g., the slope of richness with temperature is constant across all gradients), unlike univariate coefficients that may vary among gradients (as long as they are positive). This is a more rigorous test of general, global effects, but it necessitates correcting data for non-elevational differences between gradients before pooling data, as richness varies among gradients, e.g. latitudinally. Before model fitting, we controlled for such variation by subtracting the mean of (standardized, log-transformed) richness of each gradient from its respective 100 m band values, resulting in relative richness values. This procedure accounted for almost 50% of data variability (not shown). This approach is conceptually similar to a random-intercept mixed model, but assures that remaining ‘fixed effects’ are due only to elevational variation, and not to any other geographic variability. Richness predictions for MDE were adjusted in the same manner. We judged this approach superior over other options, but acknowledge potential bias arising from varying mountain height. However, the congruence of conclusions from univariate per-gradient and pooled multivariate analyses pragmatically indicates that this procedure did not greatly affect results. Statistical modelling was carried out in software R 3.2 (package AICcmodavg).

Results

Sampling along the 26 elevational gradients encompassed 315,220 specimens from 796 individual sampling plots. Total species richness was estimated between 2848 (counting only moths that were identified to a named species) and 7165 (accepting each morphospecies as a unique species), but is realistically closer to the upper estimate due to the faunal uniqueness of the morphospecies localities (i.e., due to their spatial distance it seems unlikely)
that many unnamed species are shared between regions; Table ES1.1). Almost a third of the
species were found only at one single plot (average per gradient = 27%; range = 4.3% –
48%). Elevational richness patterns ($S_{int}$) were dominated by midpeaks (16 of 19 gradients,
plus one each showing a low-plateau (LP), a low-plateau with a midpeak (LPMP), and an
increasing pattern). All 7 of the ‘best subset’ datasets showed diversity midpeaks (Fig. 1).
With richness estimated as $S_{\text{Chao1}}$ and $S_{\alpha}$, midpeaks still dominated strongly, although there
was a broader spread of other patterns, including decreasing, LP, LPMP, and increasing
patterns (Fig. ES1.4). The ‘best subset’ contained one dataset that was decreasing with both
$S_{\text{Chao1}}$ and $S_{\alpha}$, whereas all others retained midpeaks. There were no associations between the
elevation of maximum diversity along a gradient and the absolute latitude or elevational
domain of the gradient. Elevational richness patterns were not strongly influenced by
excluding or including human-disturbed sites. Patterns based on near-natural sites alone were
nearly identical to those including all sites (avg. $r = 0.99$; Fig. ES2.1). Unless otherwise
specified, results presented in the main text therefore refer to 19 analysis-grade datasets
including all samples with $S_{int}$ as response variable.

In the univariate analyses, correlations between richness and individual environmental
or spatial predictors indicated only weak associations (all median $r^2$ values $\leq 0.21$ for analysis-
grade data; Fig. 2). The median $r^2$ values of the two purely spatial predictors, A and MDE,
were on the higher end of the distribution, with $r^2$ values at 0.13 and 0.18, respectively. The
median $r^2$ values of the environmental predictors showed greater variations. Precipitation and
humidity effects were weakest (both 0.01), temperature (T, VegT) and NPP were intermediate
(0.10, 0.11, and 0.02, respectively), while area-integrated productivity (SNPP) displayed the
highest support (0.21). No single predictor showed a clear, consistent association with
elevational species richness of geometrid moths. The distribution of $r^2$ values, however,
indicated that individual predictors can be very strongly correlated with richness on particular
gradients.
Multivariate models of pooled data (after adjusting for differences in average richness between gradients) led to similar conclusions (details for all 44 models: Table ES3.1). The ‘best’ model (lowest AICc) included SNPP, MDE, and VegT, with a pseudo-$R^2 = 0.40$. The second-best model ($\Delta$AICc = 2.14) contained NPP and A instead of SNPP, and had an identical pseudo-$R^2$. Penalizing models containing SNPP for its hidden (additional) parameter rendered the ‘best’ and second-best model AICc almost identical ($\Delta$AICc = 0.02). Pooled input data presented a low-plateau pattern (with wide scatter, Fig. 3A; linear and quadratic fits of elevation and richness, both $r^2 < 0.02$, p = n.s), while residuals from the ‘best’ model exhibited a unimodal elevational pattern (Fig. 3B; linear fit, $r^2 < 0.02$, p = n.s.; quadratic fit, $r^2 = 0.13$, p < 0.001). We used averaged standardized coefficients across all 44 candidate models, weighted by their AICc, to compare the strengths of partial effects of predictors (Fig. 4). The spatial predictors, A and MDE, as well as SNPP were the most supported, whereas T, VegT, and NPP received intermediate support. Again, water-related effects had consistently the lowest support, with their confidence limits including zero.

Re-analyzing different data groupings (‘best subset’, all gradients) and different richness estimates ($S_{Chao1}$, $S_{\alpha}$, rarefied richness) led to the same conclusions (detailed results in ES3 and ES4). In particular, ‘best’ models and the ranking of averaged standardized effects were independent of the choice of richness estimate, although pseudo-$R^2$ was generally slightly lower for numerical richness estimates. Results based on all 26 gradients were similar to those restricted to ‘analysis-grade’ data sets. Notably, for the ‘best subset’ gradients, $r^2$ was distinctly higher than for analysis-grade datasets. In univariate analyses, both A and SNPP increased dramatically when restricted to analysis-grade datasets, but T and Veg T also increased, whereas MDE and precipitation measurements (Prec, Hmd, NPP) remained relatively low (Fig. 2). Similarly, the ‘best’ multivariate models exhibited a stronger pseudo-$R^2$ of 0.64, and average coefficients were substantially higher, although the order of predictor support was the same as for analysis-grade datasets (Fig. 4). For the ‘best subset’, the use of a
theoretical RSFD for MDE predictions did not greatly affect results, compared to using the empirical RSFD (which was not reliably available for other gradients; Fig. ES3.3.2).

Discussion

Elevational richness patterns

We detected a global predominance of mid-elevational richness peaks in geometrid moths (Fig. 1), which was generally consistent for all three richness estimators (Fig. ES1.4). The absolute elevation of maximum diversity within a gradient was unrelated to the latitude or elevational scope of the gradient. Anthropogenic disturbance in the lowlands did not explain midpeak patterns, as the same trends were detected using data exclusively from near-natural sites (Fig. ES2.1). This result does not, however, exclude more subtle disturbance effects on elevational richness patterns, such as species attrition at near-natural sites due to surrounding wide-scale disturbance, or sampling effects arising from limited availability of near-natural sites in strongly human-affected lowlands.

The predominance of midpeaks in our data is surprising for two reasons. Geometrids are relatively small organisms with few physiological or behavioural options for thermoregulation. Consequently, a preference for warmer habitats, and hence overall decreasing elevational richness patterns, might have been expected. Although we did find a partial effect of temperature in the multivariate analyses, it was relatively weak (Fig. 4). Furthermore, explanations of midpeak patterns in some vertebrate groups pointed towards effects of water limitation at the base of mountains (McCain, 2007a; 2009). Low temperatures towards the high elevations, and drought at the mountain bases, were hypothesized as a cause for diversity peaks at mid-elevations. However, with few exceptions (Mt. Lemmon, Kilimanjaro), most of our gradients are not in arid landscapes, and many are very wet indeed – but they displayed midpeak patterns nevertheless. Only a few other taxa have shown
similarly consistent mid-elevational peaks in species richness, including non-volant small mammals (McCain, 2005), salamanders (McCain & Sanders, 2010), and ferns (Kessler et al., 2011). These four groups share few ecological traits; they include ectotherms and endotherms, only some have strong ecological links to water, and they occupy various trophic levels — primary producers, herbivores, and predators.

Environmental and spatial predictors of richness patterns

Similar to analyses of other taxa with predominantly midpeak patterns (e.g., McCain, 2007b), there was little support for any single univariate driver in explaining geometrid elevational richness variation (Fig. 2). We examined the correlation between richness and environmental and spatial factors for each gradient. Across individual gradients, predictor variables demonstrated poor fits, although among the best subset, both area-integrated productivity (SNPP) and area were more strongly supported. Similar conclusions were apparent in the multivariate analyses of pooled data (Fig. 4; ES3). Like other taxa with predominantly midpeak patterns, richness appears to be driven by a complex interplay of variables.

The strong support for SNPP in both univariate and multivariate analyses, closely followed by area, is in line with theoretical conjectures on productivity effects on species richness that act via population sizes (“more individuals hypothesis”; Evans et al., 2005; Hurlbert & Stegen, 2014). According to this view, what matters for population size maintenance is the total amount of available energy (i.e., food resources) in a habitat, not necessarily its density or local concentration. Total productivity is closely related to area (cf. Wright, 1983; Storch et al., 2005), because a larger habitat, all else being equal, offers more resources than a small area. This scaling effect with area is captured by our area-integrated productivity measure (SNPP). We are not aware of other tests of this idea on elevational data,
but conceptually similar approaches were followed in coarse-grained global species richness analyses (Jetz & Fine, 2012). Strong effects of area-integrated productivity, compared to area effects alone, in independent datasets (regarding region and taxon) could provide further evidence in favour of our finding. Ideally, geographic settings that allow a decoupling of elevational area sizes and productivity (e.g., inverse gradients of the two variables) could be utilized.

We also found support for models that contained area alone, instead of SNPP, or area and average productivity as separate variables, to a similar degree as models containing SNPP (Fig. 4, Table ES3.1; ΔAICc <3 (<2 when penalizing SNPP-models for an extra parameter)).

Earlier studies (see above) found evidence for an area effect on elevational richness patterns without attempting to account for productivity, based on traditional SAR arguments. Thus, further tests are required to investigate the hypothesis that the elevational SAR is mediated by total productivity variation, rather than area per se.

Despite relatively strong fits of the ‘best’ multivariate models (pseudo-$R^2$ = 0.40, 0.40, 0.64; all data, analysis-grade, ‘best subset’, respectively), the residuals demonstrate a mid-elevational maximum trend for geometrid moth diversity (Fig. 3). Hence, the combination and strength of the included predictor variables is insufficient to fully explain the midpeak richness patterns. Because area, SNPP and temperature all decline monotonically with increasing elevation, they alone cannot drive a mid-elevational peak in richness. Although MDE was supported in multivariate analyses as a moderating factor (but not as a main driver), its inclusion also failed to fully explain the trend towards lowered richness in the lowlands compared with mid-elevations. We can only speculate on possible reasons. Historical effects, for instance past climatic variation (Colwell & Rangel, 2010) or phylogenetic effects (Brehm et al., 2013), are feasible conceptually but difficult to integrate into multi-gradient tests due to lack of complete, species-level, time calibrated phylogenies or climatic reconstructions. There
are other ecological effects, such as predation pressure, host-plant diversity \citep{Lin2015,Novotny2006}, and habitat heterogeneity, that could be critically important to moth elevational diversity, but we lack data to test them across all gradients.

Methodological aspects

Very strong, idiosyncratic univariate environmental correlates of richness occasionally appeared in our analyses, for some gradients (high $r^2$; Fig. 2), but these were not generally supported across gradients. This discordance could be due to genuine differences among the ecological settings, or it could be due to statistical artefacts common in non-replicated studies \citep{Ioannidis2005}. Whatever the cause, this finding highlights the need for multi-gradient studies if the aim is testing hypotheses for their generality. We found trends towards clearer results when analyses were scaled on data quality. For example, we detected both stronger $r^2$ and stronger standardized coefficients when using the ‘best subset’ data, compared with the less-demanding, analysis-grade datasets, or all gradients (Figs. 2, 4). Thus, insufficient sampling potentially obscured some ecological patterns. Data quality reduction can arise from incomplete sampling at each sampling elevation (hence the necessity to work with estimated rather than observed richness), and/or incomplete overall sampling of gradients. More coordinated and standardized sampling programs, including targeted sampling of a wider taxonomic base along multiple gradients, would be beneficial to overcome the need for multi-source compilations of data that were originally sampled for other purposes. Nonetheless, the general conclusions and relative strength of support among predictor variables was identical among all three nested datasets, regardless of perceived sample quality.

Conclusions
Geometrid moths typically show midpeak patterns of species richness along elevational gradients across the globe, irrespective of the geographic or climatic settings of gradients. We identified area-integrated net primary productivity of elevational bands, or the area of these bands itself, as strongest predictor of geometrid richness in univariate and multivariate analyses. Because effects of these two variables cannot be unambiguously statistically separated with our data, further study is needed of the landscape-scale effects of productivity on species richness within elevational gradients. We also found support for the mid-domain effect and temperature as weaker covariates that modify richness patterns. These findings are in line with theories on major climate-based drivers of biodiversity, both within elevational and other contexts, but they fail to account fully for midpeak patterns in species richness. Our data indicate that multi-gradient studies are paramount for testing candidate drivers of elevational richness patterns for generality. These findings contribute evidence on multi-gradient elevational richness patterns and their potential drivers for a group of organisms other than vertebrates. Our results should facilitate a future understanding of how trait variation explains distinct environment-richness relationships common among taxonomic and functional groups along elevational gradients.

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Appendix: Electronic Supplements

ES1: Data details
ES2: Patterns with and without human-disturbed sites
ES3: Detailed modelling results
ES4: Methods and results of rarefaction analyses
Biosketch: All authors are interested in the distribution of biodiversity along environmental gradients and the mechanisms that shape it.

References


FIGURE LEGENDS

Figure 1 Map with locations of the 26 elevational gradients included in this study. The graphs in the lower part of the figure show the species richness pattern for the seven ‘best subset’ gradients. Each bar represents the richness in a 100 m elevational band. The length of the x-axis represents the full elevational gradient available in each landscape. For data on all gradients see Fig. ES1.1. The pictured specimen is *Pingasa chlora*, a common geometrid at lowland to mid-elevations in the Oriental region.

Figure 2 Frequency distributions of Pearson’s $r^2$ values for univariate correlations of environmental and spatial predictors with richness ($S_{int}$) within gradients. Data for 19 analysis-grade gradients are shown as bars. Arrows indicate the median $r^2$. Note that $r^2$ for negative correlations was set to zero, because only positive correlations were expected by our hypotheses. Acronyms: VegT = mean annual temperature in non-freezing months, NPP = average net primary productivity, SNPP = summed net primary productivity across elevational band, MDE = mid-domain effect.

Figure 3 (A) Elevational pattern of species richness ($S_{int}$, all analysis-grade gradients pooled and adjusted to the same average richness; $\delta$Species). Note that both y-axes are in linear scaling, while log-transformed and standardized data were used for modelling. (B) Elevational pattern of residuals from the ‘best’ model (lowest AICc, pseudo-$R^2 = 0.40$). LOESS fits (black lines) are shown to visualize overall patterns in data. See main text for linear and quadratic fits. Similar patterns were recovered when using the ‘best subset’ data alone (not shown).

Figure 4 Averaged, AICc-weighted standardized coefficients with 95% confidence intervals across 44 candidate multivariate models allow comparison of the strengths of the predictors’ partial effects.