Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2017) **26,** 412–424

Global Ecology and Biogeography
A Journal of Macroecology

RESEARCH PAPER

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

Jan Beck[1]*, Christy M. McCain[1,2], Jan C. Axmacher[3], Louise A. Ashton[4,5], Florian Bärtschi[6], Gunnar Brehm[7], Sei-Woong Choi[8], Oldrich Cizek[9,10,11], Robert K. Colwell[1,12,13], Konrad Fiedler[14], Cristina L. Francois[15], Steven Highland[16], Jeremy D. Holloway[5], Jurie Intachat[17,18], Tomas Kadlec[10], Roger L. Kitching[4], Sarah C. Maunsell[4], Thomas Merckx[19], Akihiro Nakamura[4,20], Erica Odell[4], Weiguo Sang[21,22], Pagi S. Toko[23], Jaroslav Zamecnik[8,9,24,25], Yi Zou[3,26] and Vojtech Novotny[23,27]

[1]*University of Colorado, Museum of Natural History, Boulder, CO, USA,* [2]*Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA,* [3]*UCL Department of Geography, University College London, London, UK,* [4]*Griffith School of the Environment & Environmental Futures Research Institute, Griffith University, Nathan, Australia 4111,* [5]*Life Sciences Department, Natural History Museum, London, UK,* [6]*Umweltbüro Bärtschi, Basel, 4019, Switzerland,* [7]*Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Jena, Germany,* [8]*Department of Environmental Education, Mokpo National University, Muan, South Korea,* [9]*Hutur NGO, Hradec Kralove, Czech Republic,* [10]*Faculty of Environmental Sciences, University of Life Sciences, Prague, Czech Republic,* [11]*Biology Centre, Czech Academy of Science Institute of Entomology, České Budějovice, Czech Republic,* [12]*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA,* [13]*Departmento de Ecologia, Universidade Federal de Goiás, Goiânia, Brasil,* [14]*Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria,* [15]*Entomology and Insect Science, University of Arizona, Tucson, AZ, USA,* [16]*Bureau of Land Management, Mt Lewis Field Office, Battle Mountain, NV, USA,* [17]*Higher Education Department, Duchy College, Callington, Cornwall, UK,* [18]*Forest Research Institute Malaysia, Kepong, Malaysia,* [19]*Behavioural Ecology and Conservation Group, Biodiversity Research Centre, Earth and Life Institute, Université Catholique de Louvain (UCL), Louvain-la-Neuve, Belgium,* [20]*Key Laboratory of Tropical Forest Ecology, Chinese Academy of Sciences Menglun, Xishuangbanna Tropical Botanical Garden, Mengla, Yunnan, China,* [21]*Life and Environment College, Minzu University of China, Beijing, China,* [22]*Chinese Academy of Science, State Key Lay of Environment and Vegetation Change, Beijing, China,* [23]*New Guinea Binatang Research Center, Nagada Harbor, Madang, Papua New Guinea,* [24]*Museum of Eastern Bohemia, Hradec Kralove, Czech Republic,* [25]*Faculty of Arts, University Hradec Kralove Interdisciplinary Research Centre, Czech*

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 Twenty-six elevational gradients world-wide (latitudes 28° S to 51° N).

Methods We compiled field datasets on elevational gradients for geometrid moths, a lepidopteran family, and documented richness patterns across each gradient while accounting for local undersampling of richness. Environmental and spatial predictor variables as well as habitat disturbance were used to test various hypotheses. Our analyses comprised two pathways: univariate correlations within gradients, and multivariate modelling on pooled data after correcting for overall variation in richness among different gradients.

Results The majority of gradients showed midpeak patterns of richness, irrespective of climate and geographical location. The exclusion of human-affected sampling plots did not change these patterns. Support for univariate main drivers of richness was generally low, although there was idiosyncratic support for particular predictors on single gradients. Multivariate models, in agreement with univariate results, provided the 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 Despite the predicted decreasing diversity–temperature relationship in ectotherms, geometrid moths are similar to ants and salamanders as well as small mammals and ferns in having predominantly their highest diversity at mid-elevations. As in those comparative analyses, single or clear sets of drivers are elusive, but both productivity and area appear to be influential. More comparative elevational studies for various insect taxa are necessary for a more comprehensive understanding of elevational diversity and productivity.

DOI: 10.1111/geb.12548

Republic, [26]Department of Environmental Science, Xi'an Jiaotong-Liverpool University, Suzhou, China, [27]Biology Centre, Czech Academy of Sciences and Zoology Department, University of South Bohemia, Ceske Budejovice, Czech Republic

*Correspondence: Jan Beck, University of Colorado, Museum of Natural History, 265 UCB, Boulder, CO 80309, USA.
E-mail: jan.beck@colorado.edu

Keywords

Altitude, diversity, Lepidoptera, productivity, species-area relationship, temperature, tropical mountains.

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 proved challenging to understand variation in this pattern in its own right. Unimodal and decreasing patterns of richness 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 the 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. an 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, such as 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 richness with 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 quantity 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 the MDE makes precise predictions for richness at each elevation, a monotonically increasing link between MDE predictions and observed richness is expected. Although the MDE is promising as an explanation for an elevational midpeak of richness and supportive data have been reported (e.g. Dunn *et al.*, 2007), many authors have concluded that the MDE is unlikely to be the sole driver of richness along elevational gradients. If they are at all unimodal, 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, the MDE may well be acting as a modulator of other environmental effects (Wang & Fang, 2012; Colwell *et al.*, 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; see also Appendix S1 in the Supporting Information). However, with very few exceptions (e.g. 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, for example, herbivory with specific host-plant links) may therefore offer an avenue for further crucial insights.

Geometrid moths (having caterpillars known as loopers or inchworms) are a family of Lepidoptera that represents a truly hyperdiverse insect taxon with *c.* 23,000 described and over 40,000 estimated species (Miller *et al.*, 2016). Geometrids rank among the most abundant lepidopteran 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 host-plant 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 Appendix S1). The adult moths can be robustly sampled using artificial light sources (Beck & Linsenmair, 2006), and many comparable studies exist (e.g. Table S1.1 in Appendix S1). Here, we present a unique compilation of all available geometrid richness data known to us, from elevational gradients across the world, based on the literature and our own sampling. We compare elevational richness patterns and their global variability. We test the effects of key environmental (productivity, temperature, precipitation) and spatial predictors (area, the MDE). 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 that 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 fewer then 20 sampled individual moths 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; see Fig. 1; details in Table S1.1 in Appendix S1). Abundances and species composition from light trapping are influenced by many factors, including the 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 S1.1. 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 collection and specimen identifications in our datasets were conducted by lepidopterists specializing in 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

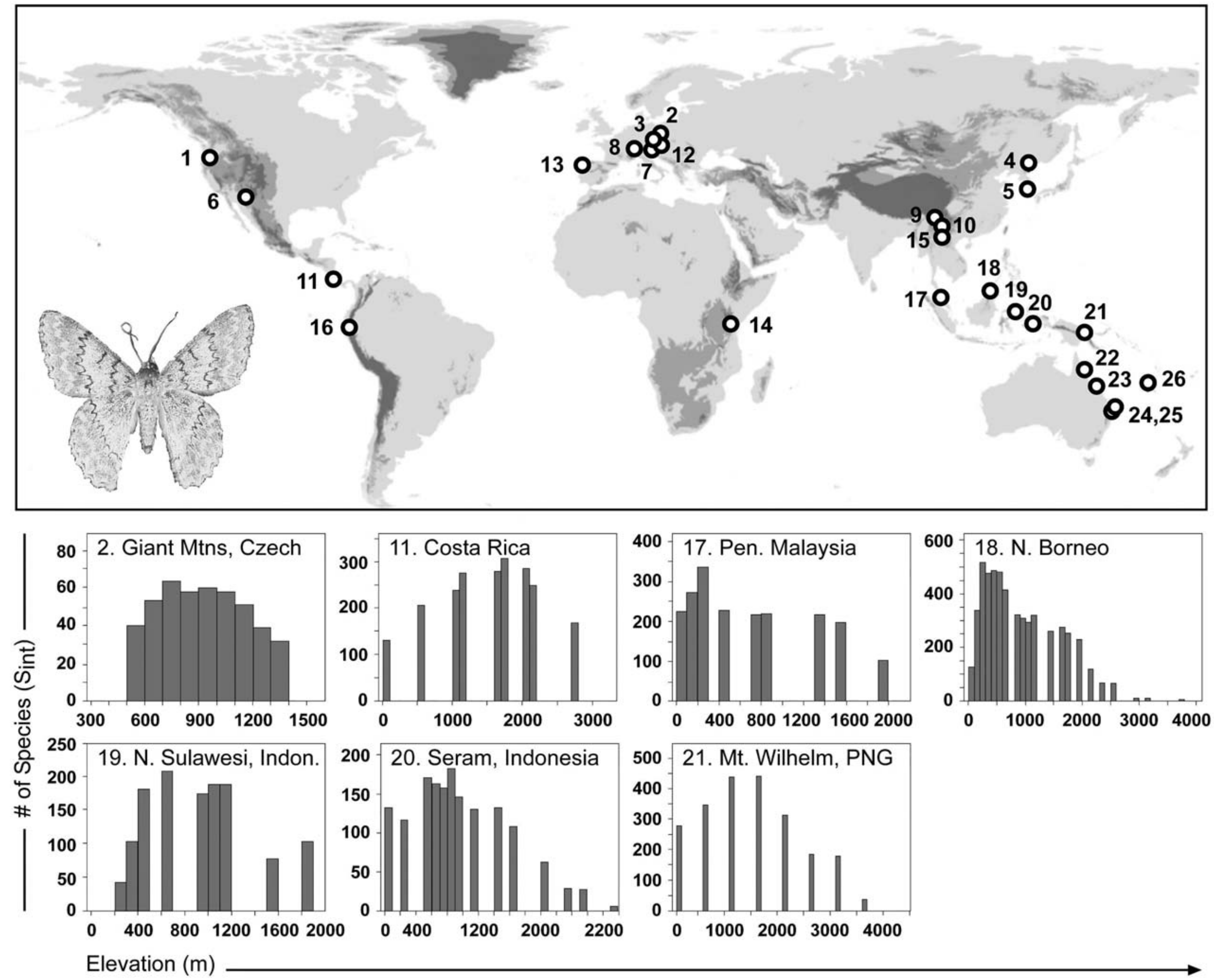

Figure 1 Map with locations of the 26 elevational gradients included in this study. The graphs in the lower part of the figure show the species richness pattern for the seven 'best subset' gradients. Each bar represents the richness in a 100-m elevational band. The length of the *x*-axis represents the full elevational gradient available in each landscape. For data on all gradients see Fig. S1.1 in Appendix S1. The specimen pictured is *Pingasa chlora*, a common geometrid at low to mid-elevations in the Oriental region. PNG, Papua New Guinea.

(e.g. DNA barcoding). However, Brehm *et al.* (2016) have shown, in an extensive molecular re-assessment of identifications in the Ecuadorian dataset, that the inclusion of a very large number of previously unrecognized, cryptic species did not change the elevational richness pattern.

Gradients varied in elevational scope, the number of sampling sites and survey effort (Table S1.1), but based on sampling descriptions in publications and information from data collectors, we detected no strong elevational biases in sampling effort (see also Fig. S1.2 in Appendix S1). To address the geographical variation in sampling among the 26 gradients for comparisons of elevational diversity, we classified 19 gradients as 'analysis-grade' data and, nested within those, seven gradients as 'best subset' data (Table S1.1). 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 higher. 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 from minimally disturbed sites. We aggregated all diversity data into 100-m elevational bands to improve scale comparability among gradients (e.g. 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 underestimation of richness, including interpolated species richness, two richness estimators (Chao1 and Fisher's α) and rarefied richness. Interpolated species richness (S_{int}) assumes that a species is found at all elevations between its lowest and highest recorded occurrence. S_{int} accounts for false absences at intermediate elevations but not at the edge of a species' elevational range (Grytnes & Vetaas, 2002). Although S_{int} provides estimates for all 100-m bands within the study boundaries, we only utilized data for 212 bands that have actually been sampled (i.e. contain at least one field plot). Chao1 (S_{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 α richness estimate, we first estimated α (a parameter of the log-series species–abundance distribution model; Fisher *et al.*, 1943) for each local site. Second, we estimated species richness as $S_{\alpha} = \alpha \ln(1 + N/\alpha)$, where N is the sum of individuals in the sample (Colwell & Coddington, 1994). For the best subset of gradients, we also calculated rarefied richness (S_{rar}) expected at a fixed common sample size (for detailed methods and results see Appendix S4). To aggregate diversity into 100-m bands (separately for S_{Chao1} and S_{α}), 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 the 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_{int} is a gamma-diversity estimate whereas S_{Chao1}, S_{α} and S_{rar} are alpha-diversity estimates. However, data for all metrics are highly correlated (for analysis-grade data: S_{int} and S_{Chao1}, $r^2 = 0.78$; S_{int} and S_{α}, $r^2 = 0.75$; S_{α} and S_{Chao1}, $r^2 = 0.89$; Fig. S1.3 in Appendix S1; see Appendix S4 for S_{rar}). 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}, S_{α} and S_{rar}, presented in Appendices S3 & S4, 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). 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 with patterns across all plots. The predicted pattern after removal of impacts of lowland disturbance would be decreasing or low-plateau richness patterns, compared with 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/symbols are used in all graphs and tables). Climate and elevation data were taken from WorldClim (http://www.worldclim.org) and projected to the Mollweide world equal area projection (1 km × 1 km cells). The 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 were factored in via data interpolation to account for the effects of stomatal 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 that patterns matched 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 × 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 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 the assumptions of the MDE refer to the geometric constraints of the entire landscape. As many of our gradients were not completely sampled (Table S1.1), 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 the 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 (Appendix S5); 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, $(x - \text{mean})/\text{SD}$, 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 the strength of the relationship in multivariate models. We drew inferences on landscape geometry (A, MDE) and environmental effects (all other variables) 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 the Akaike information criterion with correction for small sample sizes (AICc; Burnham & Anderson, 2002). We included 44 candidate models with different predictor combinations. These models never contained variables that were highly collinear or conceptually unfeasible (i.e. never both T and VegT; Prec and Hmd; SNPP and A and/or NPP). For the 'best' models and closely related models, we calculated pseudo-R^2 as Pearson's r^2 of the correlation between the model prediction and observed value. We plotted model residuals against elevation to assess any 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 × 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 the data variability (not shown). This approach is conceptually similar to a random-intercept mixed model, but ensures that remaining 'fixed effects' are due only to elevational variation and not to any other geographical variability. Richness predictions for MDE were adjusted in the same manner. We judged this approach to be 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 R software (v. 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 as 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 S1.1). Almost a third of the (morpho-)species were found at only a 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 seven of the 'best subset' datasets showed diversity midpeaks (Fig. 1). With richness estimated as S_{Chao1} and S_{α}, midpeaks were still strongly dominant, although there was a broader spread of other patterns, including decreasing, LP, LPMP and increasing patterns (Fig. S1.4). The 'best subset' contained one dataset that was decreasing with both S_{Chao1} and S_{α}, 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 (average $r = 0.99$; Fig. S2.1 in Appendix S2). Unless otherwise specified, results presented in the main text therefore refer to 19 analysis-grade datasets including all samples with S_{int} as the response variable.

In the univariate analyses, correlations between richness and individual environmental or spatial predictors indicated only weak associations (all median r^2 values ≤ 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 of 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 are given in Table S3.1 in Appendix 3). The 'best' model (lowest AICc) included SNPP, MDE and VegT, with a pseudo-$R^2 = 0.40$. The second best model (ΔAICc = 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 (ΔAICc = 0.02). Pooled input data presented a LP 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-analysing different data groupings ('best subset', all gradients) and different richness estimates (S_{Chao1}, S_{α}, S_{rar}) led to the same conclusions (detailed results are given in Appendices S3 & S4). 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' datasets. Notably, for the 'best subset' gradients, r^2 were 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 with using the empirical RSFD (which was not reliably available for other gradients; Fig. S3.3.2 in Appendix S3).

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. S1.4). 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. S2.1). 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

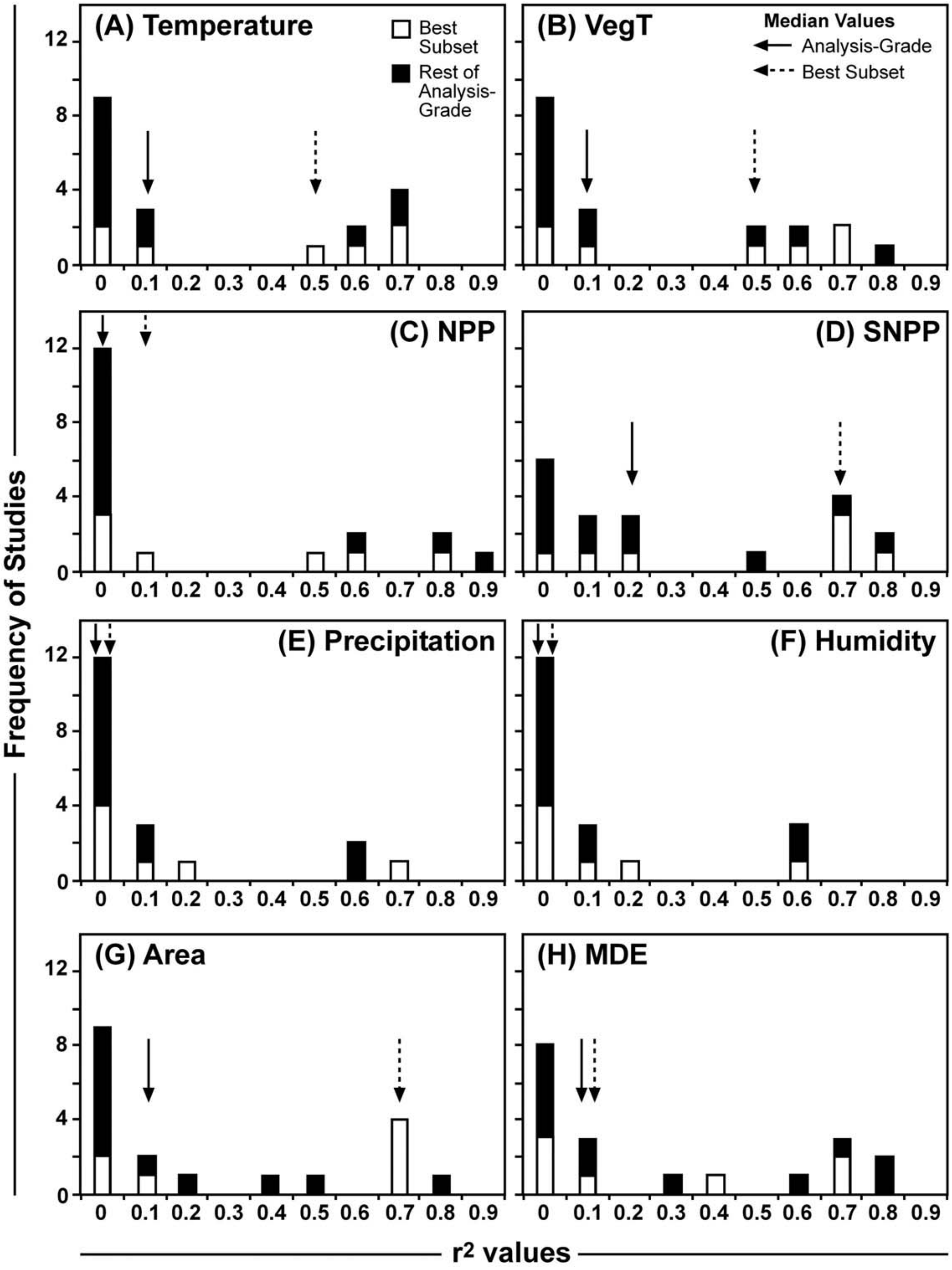

Figure 2 Frequency distributions of Pearson's r^2 values for univariate correlations of environmental and spatial predictors with richness (S_{int}) within gradients. Data for 19 analysis-grade gradients are shown as bars. Arrows indicate the median r^2. Note that r^2 for negative correlations was set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

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

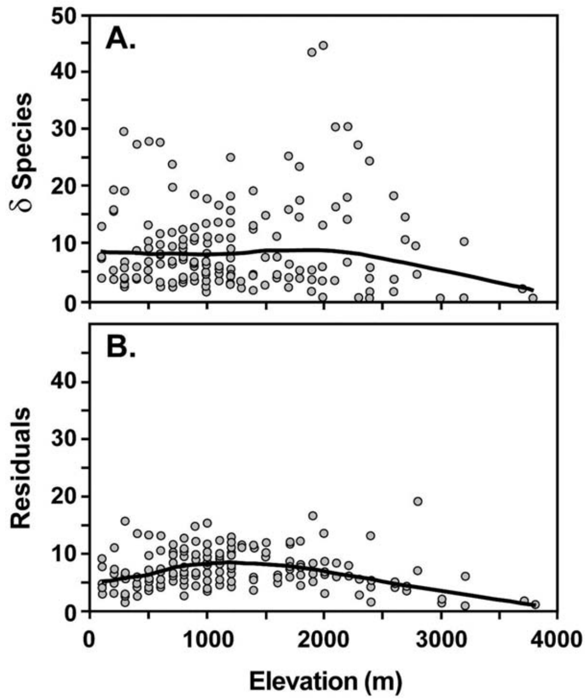

Figure 3 (a) Elevational pattern of species richness (S_{int}, all analysis-grade gradients pooled and adjusted to the same average richness; δ Species). Note that both *y*-axes have linear scaling, while log-transformed and standardized data were used for modelling. (b) Elevational pattern of residuals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

exceptions (Mounts Lemmon and 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). Ants are also predominantly mid-elevational, although not as consistently (Szewczyk & McCain, 2016). These 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 variation in geometrid elevational richness (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.

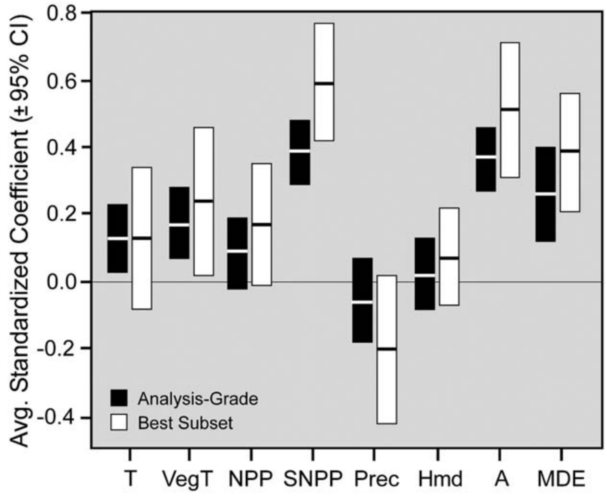

Figure 4 Averaged, AICc-weighted standardized coefficients with 95% confidence intervals across 44 candidate multivariate models allow comparison of the strengths of the predictors' partial effects.

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 (the 'more individuals hypothesis'; Evans *et al.*, 2005; Hurlbert & Stegen, 2014). According to this view, what matters for the maintenance of population size 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 a coarse-grained global species richness analyses (Jetz & Fine, 2012).

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 S3.1; ΔAICc < 3 (or <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 elevational SAR is mediated by total productivity variation rather than by area per se. Strong effects of area-integrated productivity, compared with area effects alone, in independent datasets (regarding region and taxon) could provide further evidence in favour of our finding. Ideally, geographical settings that allow a decoupling of elevational area sizes and productivity (e.g. inverse gradients of the two variables) could be utilized.

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 (Novotny *et al.*, 2006; Lin *et al.*, 2015; but see Axmacher *et al.*, 2009; Jetz *et al.*, 2009) and habitat heterogeneity, that could be critically important for 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 (Ioannidis, 2005). Whatever the cause, this finding highlights the need for multi-gradient studies if the aim is to test 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. A reduction in data quality can arise from incomplete sampling at each sampling elevation (hence the need to work with estimated rather than observed richness) and/or incomplete overall sampling of gradients. More coordinated and standardized sampling programmes, 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 geographical or climatic settings of gradients. We identified area-integrated NPP 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 MDE and temperature as weaker covariates that modify richness patterns. These findings are in line with theories on major climate-based drivers of biodiversity, within both 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.

ACKNOWLEDGEMENTS

This study was initiated during a workshop organized by V. Novotny *et al.* in 2013 (University of South Bohemia). We thank the following colleagues for help with data collection, specimen identifications or other support: F. Altermatt, F. Bodner, V. K. Chey, M. Corley, M. Forister, R. Hagmann, J. Sumpich, S. Lang, R. Leuschner, E. M. Marabuto, H. M. Pereira, C. H. Schulze, D. Süßenbach. C. M. McCain funding was in part through NSF 1542639 (to J. C. Lendemer *et al.*). For details of financial support for individual sampling programmes please refer to the references in Appendix S1.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1 Data details.
Appendix S2 Patterns with and without human-disturbed sites.
Appendix S3 Detailed modelling results.
Appendix S4 Methods and results of rarefaction analyses.
Appendix S5 Richness data (csv-format) per site and per 100-m band.

BIOSKETCHES

All authors are interested in the distribution of biodiversity along environmental gradients and the mechanisms that shape it.

Editor: John-Arvid Grytnes

DATA SOURCES

Ashton, L. A., Odell, E. H., Burwell, C. J., Maunsell, S. C., Nakamura, A., McDonald, W. J. F. & Kitching, R. L. (2015) Altitudinal patterns of moth diversity in tropical and subtropical rainforest. *Austral Ecology*, **41**, 197–208.

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