

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

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50 ABSTRACT

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

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

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

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

71 **Main conclusions:** Midpeak patterns predominate in geometrid moths along elevational
72 gradients. Area-integrated net primary productivity, or area itself, were the strongest
73 predictors of richness patterns, but further study of the landscape-wide effects of productivity
74 is required in an elevational richness context. Multi-gradient studies like ours are essential to

75 assess the generality of hypothesized drivers of elevational richness patterns. Our findings
76 contribute evidence on elevational richness patterns for a group of non-vertebrate organisms,
77 which may facilitate future understanding of how trait variation explains diverse environment-
78 richness relationships among different taxonomic groups.

79

80

81 **Introduction**

82 The pattern of species richness along elevational gradients may be viewed as a model
83 system to investigate the environmental causes of larger-scale richness patterns, but it has
84 proven challenging to understand variation in this pattern in its own right. Unimodal and
85 decreasing richness patterns have most often been reported across many taxonomic and
86 functional groups of organisms (e.g., Rahbek, 2005; McCain & Grytnes, 2010; Kessler *et al.*,
87 2011). Uncertainty remains regarding the prime determinants of richness patterns within
88 gradients and the causes of substantial variability observed between different mountain
89 systems and different taxa.

90 Some broadly supported, climate-driven environmental effects on richness are applicable
91 to elevational gradients, including variation in net primary productivity, temperature, and
92 precipitation. High primary productivity (i.e., abundance of food resources for consumers)
93 may lead to high consumer richness by sustaining large population sizes, hence decreasing
94 extinction probabilities (Evans *et al.*, 2005). In some vertebrate taxa (McCain, 2007a; 2009),
95 highest richness in warm and wet habitats may indirectly support such a link. Direct tests of [a](#)
96 [positive effect of](#) productivity [on richness](#) along many elevational gradients are hampered by a
97 shortage of reliable field data on productivity. Temperature may also influence richness,
98 independently of its impact on plant productivity, by its positive effect on metabolic rates,
99 thereby shortening generation times and enhancing evolutionary processes such as

100 diversification (Allen *et al.*, 2007). Alternatively or additionally, low temperatures may lead to
101 foraging restrictions in ectotherms, reducing the food resources that they can utilize (Willmer,
102 1983). For example, temperature was found to be a strong predictor of elevational richness
103 patterns in reptiles (McCain, 2010), and studies on hymenopteran insects highlighted the link
104 between temperature and foraging activity along elevational gradients (Sanders *et al.*, 2007;
105 Classen *et al.*, 2015). Both mechanisms (i.e., evolutionary speed, foraging limitation) predict a
106 monotonic, positive effect of temperature on richness. However, due to the nearly universally
107 monotonic decline of temperature with elevation, temperature alone cannot be the main driver
108 of commonly reported midpeak richness patterns. Elevational effects of temperature in
109 combination with water availability were supported in some multi-gradient studies (McCain,
110 2007a; 2009), but it remains unclear whether this interaction indicates direct effects of water
111 and temperature limitation, or acts as a proxy for the distribution of plant productivity.
112 Precipitation may also be directly linked to species occurrence and richness, particularly for
113 organisms with specific moisture requirements like ferns (Kessler *et al.*, 2011) or amphibians
114 (Müller *et al.*, 2013). Again, positive effects of water availability on richness would be
115 expected.

116 Spatial factors related to landscape topography could also be important drivers of
117 elevational richness patterns, including an elevational species-area relationship (SAR) and the
118 mid-domain effect (MDE). The SAR, monotonically increasing ~~greater~~ richness within a larger
119 study area, is the best-supported empirical rule in biodiversity research (Dengler, 2009; and
120 references therein). SARs may come about through a variety of mechanisms, among them
121 increased habitat heterogeneity, community turnover, or larger population sizes and therefore
122 lowered extinction risks in larger areas (Rosenzweig, 1995). However, larger areas also
123 contain a greater total amount of resources (i.e., higher total productivity), which leads to an
124 intricate interrelationship among area, productivity and richness (Wright, 1983; Storch *et al.*,
125 2005). Elevational SARs, also called the indirect area effect (Romdal & Grytnes, 2007), are

126 based on the variability of the area among elevational bands in a mountainous landscape.
127 Elevational SARs have been reported in various studies (e.g. Rahbek, 1997; Sanders, 2002;
128 Beck & Kitching, 2009), although McCain (2007b) questioned the role of elevational area as
129 a main driver of diversity, given that midpeak patterns dominate while area declines
130 monotonically with elevation in the majority of mountain regions. Geometric constraints, i.e.
131 distinct boundaries of a landscape or gradient, may lead to greater overlap of large-ranged
132 species towards the centre of a gradient, resulting in a midpeak pattern of species richness
133 even in the absence of any environmental variation (the MDE; Colwell & Hurtt, 1994). [As](#)
134 [MDE makes precise predictions for richness at each elevation, a monotonically increasing](#)
135 [link of MDE and observed richness is expected](#). Although MDE is suggestive as an
136 explanation of an elevational midpeak of richness and supportive data have been reported
137 (e.g., Dunn *et al.*, 2007), many authors have concluded that MDE is unlikely to be the sole
138 driver of richness along elevation gradients. If unimodal at all, empirical patterns are often
139 skewed, with their maximum richness located at elevations lower than the centre of the
140 gradient (contrary to predictions based on a pure MDE; Dunn *et al.*, 2007; McCain &
141 Grytnes, 2010). However, MDE may well be acting as a modulator of other environmental
142 effects (Wang & Fang, 2012; Colwell *et al.*, [re-submitted2016](#)). Other evolutionary or
143 historical hypotheses for richness patterns exist, and some comprise mountain-specific
144 mechanisms, including phylogenetic history (e.g., McCain, 2009), past climatic variation
145 (Colwell *et al.*, 2008; Colwell & Rangel, 2010), turnover at ecotones (McCain & Beck, 2016),
146 and specific biotic interactions (e.g., Novotny *et al.*, 2006; Dehling *et al.*, 2014). Moreover,
147 midpeaks could also be enhanced by more intense anthropogenic lowland disturbance (e.g.,
148 McCain & Grytnes, 2010).

149 There are a large number of single-gradient, elevational richness studies on a variety of
150 taxonomic groups, including many on various insect taxa (e.g., McCoy, 1990; Sanders, 2002;
151 Sanders *et al.*, 2007; Classen *et al.*, 2015; and references therein and in Appendix ES1).

152 However, with very few exceptions (e.g., Beck & Kitching, 2009; Kessler *et al.* 2011; Ashton
153 *et al.*, 2016; Szewczyk & McCain, [2016in press](#)), multi-gradient analyses for the same
154 taxonomic group, allowing comparisons of elevational richness patterns across
155 biogeographical realms and tests for general predictors, remain restricted to vertebrate taxa
156 (McCain & Grytnes, 2010; and references therein). For vertebrates, strong climatic drivers are
157 empirically supported, but conclusions vary by taxon. Consistent midpeaks shown in some
158 taxa are most difficult to link to single predictors and suggest a greater complexity of causal
159 agents. A framework conceptualizing the variability of richness patterns, and of links with the
160 environment across taxonomic groups, is still underdeveloped (e.g., via thermoregulatory
161 traits; Buckley *et al.*, 2012). Provision of multi-gradient data for invertebrate taxa, featuring
162 trait combinations not occurring in vertebrate groups (for Lepidoptera, e.g. herbivory with
163 specific host-plant links) may therefore offer an avenue for further crucial insights.

164 Geometrid moths (with caterpillars known as loopers or inchworms) are a family of
165 Lepidoptera that represents a truly hyperdiverse insect taxon with ca. 23,000 described and
166 over 40,000 estimated species (Miller *et al.*, 2016). Geometrids rank among the most
167 abundant Lepidoptera families in many tropical and temperate habitats. They are mostly
168 nocturnal, characterized by small body size and a short generation time. At least in many
169 temperate species, caterpillars feed on a single hostplant family or genus (e.g. Ward &
170 Spalding, 1993; see also Novotny *et al.*, 2004; Bodner *et al.*, 2012). Geometrids are assumed
171 to be tightly linked to local environmental conditions. They have been frequently utilized as
172 ‘indicator taxa’ of human environmental impacts (e.g., industrial melanism, habitat
173 disturbance, climate change; see ES1). The adult moths can be robustly sampled using
174 artificial light sources ([Beck & Linsenmair, 2006](#)), and many comparable studies exist ([e.g.,](#)
175 [Table ES1.1](#)). Here, we present a unique compilation of all available geometrid richness data
176 known to us, from elevation gradients across the world, based on literature and our own
177 sampling. We compare elevational richness patterns and their global variability. We test

178 effects of key environmental (productivity, temperature, precipitation) and spatial predictors
179 (area, mid-domain effect). We compare conclusions from two different analytical frameworks
180 —univariate comparisons on individual gradients and multivariate analysis on globally pooled
181 data—to identify support among the hypothesized drivers of elevational richness patterns.

182

183 **Methods**

184 Geometrid moth datasets

185 We compiled data from all suitable elevational gradient studies of geometrid moths we
186 could trace from the literature, and from our own, unpublished field data. Of these datasets we
187 excluded those with minimal sampling effort (i.e., removing sites with <20 sampled moth
188 individuals unless we could confirm that sampling effort was substantial despite low
189 specimen numbers), sampling based on only one section of a gradient, and those with unclear
190 taxonomic resolution. All data consisted of local, quantitative light trapping samples at
191 consecutive elevations within defined mountainous regions (26 gradients, Fig. 1; details in
192 Table ES1.1). Abundances and species composition from light trapping are influenced by
193 many factors, including type of light source and natural variation due to weather, moonlight
194 and season, as well as nightly sampling schedule and collecting effort (Brehm & Axmacher,
195 2006; Jonason *et al.*, 2014). Details and references for each dataset appear in Table ES1.1.
196 While variation in field methods obviously influences abundance and diversity in a moth
197 inventory, field methods in the evaluated studies were mostly standardized within each
198 gradient, thus allowing a robust relative assessment of the elevational richness patterns.

199 Field collecting and specimen identifications in our datasets were conducted by
200 lepidopterists specializing in the local moth faunas. However, due to high species richness,
201 taxonomic accuracy can still occasionally be a challenge, particularly for diverse tropical
202 regions. Geometrid faunas from some regions of the world lack comprehensive taxonomic

203 treatments, making it necessary to rely on approximate, parataxonomic morphospecies sorting
204 (groupings based on morphological differences within a dataset; Basset *et al.*, 2004).
205 Furthermore, tropical faunas may contain multiple cryptic species that are recognizable only
206 with molecular methods (e.g., DNA barcoding). However, Brehm *et al.* (2016) have shown, in
207 an extensive molecular re-assessment of identifications in the Ecuadorian dataset, that
208 including a very large number of previously unrecognized, cryptic species did not change the
209 elevational richness pattern.

210 Gradients varied in elevational scope, number of sampling sites, and survey effort
211 (Table ES1.1), but based on sampling descriptions in publications and information from data
212 collectors, we detected no strong elevational biases in sampling effort (see also Fig. ES1.32).
213 To address the geographic variation in sampling among the 26 gradients for elevational
214 diversity comparisons, we classified 19 gradients as ‘analysis-grade’ data and, nested within
215 those, 7 gradients as ‘best subset’ data (Table ES1.1). Our analysis-grade criteria required
216 sampling sites within 400 m elevation of the mountain base and sampling at least 50% of the
217 elevational range of the mountain region (elevational domain). For the ‘best subset’ we
218 additionally required sampling across at least 70% of an elevational domain for mountains of
219 800 m or greater height. We focused analyses on the analysis-grade subset, but we repeated
220 core analyses for the ‘best subset’ as well as all gradients to examine the consistency of
221 results. We classified all local plots as ‘near-natural’ or ‘human-disturbed’ habitat based on
222 descriptions provided by the data collectors, thus identifying analyses without disturbance, or
223 with minimally disturbed sites. We aggregated all diversity data into 100 m elevational bands
224 to improve scale comparability among gradients (e.g., Colwell, 2009; McCain, 2005; 2010).

225

226 Measuring diversity

227 Quantitative samples of species-rich invertebrates are mostly incomplete, and
228 observed species richness will therefore be an underestimate. We used various approaches to
229 account for richness underestimation, including interpolated species richness and two richness
230 estimators: (*Chao1* and Fisher's α) and rarefied richness. Interpolated species richness (S_{int})
231 assumes that a species is found at all elevations between its lowest and highest recorded
232 occurrence. S_{int} accounts for false absences at intermediate elevations, but not at the edge of a
233 species' elevational range (Gryntes & Vetaas, 2002). Although S_{int} provides estimates for all
234 100 m bands within study boundaries, we utilized only data for 212 bands that have actually
235 been sampled (i.e., contain at least one field plot). *Chao1* (S_{Chao1}) is a nonparametric minimum
236 estimator of true richness, based on observed richness and the number of singletons and
237 doubletons within each local sample. Calculations were conducted with EstimateS; classic or
238 biased-corrected equations were chosen as advised (Colwell, 2013). For the Fisher's α
239 richness estimate, we first estimated α (a parameter of the log-series species-abundance
240 distribution model; Fisher et al., 1943) for each local site. Second, we estimated species
241 richness as $S_{\alpha} = \alpha * \ln(1 + N/\alpha)$ (N = sum of individuals in the sample; Colwell & Coddington,
242 1994). For the best subset of gradients, we also calculated rarefied richness expected at a fixed
243 common sample size (detailed methods and results: see Appendix ES4). To aggregate
244 diversity into 100 m bands (separately for S_{Chao1} and S_{α}), we calculated the average of local
245 richness estimates within each band to reduce the influence of outliers. While other valuable
246 diversity estimators are available, we lack specific data (i.e., quantitative data for replicated
247 samples) needed for their calculation.

248 For each gradient and richness metric we counted elevational richness patterns by the
249 categories suggested in McCain & Grytnes (2010): decreasing, low-plateau, low-plateau with
250 a midpeak (LPMP), midpeak, and increasing. Our metrics differ in scale; S_{int} is a gamma
251 diversity estimate whereas S_{Chao1} and S_{α} are alpha diversity estimates. However, data for the
252 three metrics are highly correlated (for analysis-grade data: S_{int} and S_{Chao1} : $r^2 = 0.78$; S_{int} and

253 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
254 text because it allows direct comparison with previously published multi-gradient analyses.
255 Results based on S_{Chao1} and S_{α} , presented in ES3, are not qualitatively different.

256

257 Diversity predictors

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

266 As no field measures of environmental variables were collected on most of our
267 gradients, environmental data from GIS sources were used, for all gradients. These included
268 area of elevational bands [A]; mean annual temperature [T]; non-freezing temperatures
269 [VegT]; precipitation [Prec]; humidity [Hmd]; average productivity [NPP]; and summed
270 productivity [SNPP], all available at 30" resolution (acronyms are used in all graphs and
271 tables). Climate and elevation data were taken from Worldclim (www.worldclim.org) and
272 projected to Mollweide World equal area projection (1x1 km cells). Area within each 100 m
273 elevation band was calculated within a 200 km radius around the maximum elevation of each
274 gradient (GIS software: ArcGIS 10.3). For other environmental variables, average annual
275 values for 100 m bands for each region were calculated for polygons defined to contain zones
276 of similar climate around sampled gradients (i.e., not crossing sharp climatic changes along
277 some mountain ridges; shape files are available on request). VegT was calculated as a coarse

278 proxy for temperature during the growing season: the annual average temperatures for those
279 months with average monthly temperatures $\geq 0^{\circ}\text{C}$. Sub-freezing temperatures may be of little
280 relevance to ectotherm metabolism if individuals spend unsuitable seasons in physiologically
281 inactive life stages (dormancy). Absolute precipitation may be associated with very different
282 water availability in a landscape depending on evapotranspiration and edaphic factors.
283 Therefore, we calculated an index of humidity [Hmd] as Prec/PET , where PET is potential
284 evapotranspiration for the mountainous region (Willmott & Kenji, 2001). Since PET data
285 exist only at coarse resolution (0.5° grain), Hmd is primarily suitable for comparisons
286 between gradients but is still proportional to Prec among elevational bands within a gradient.

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

303 differences between area and SNPP (a “composite” variable that combines area and NPP), and
304 their implications for inference regarding the drivers of richness patterns.

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

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

322

323 Statistical analyses

324 [For standardization, we](#) log-transformed all richness data and predictor variables, and z-
325 transformed ([\[x-mean\]/standard deviation](#)) the pooled data that combined all gradients. Log-
326 transformation was necessary for some variables to fulfil normality assumptions, and for some
327 relationships we had *a priori* expectations of power law relationships (which are linearized by

328 log-transformations; e.g., area, Dengler, 2009; temperature, Allen *et al.*, 2007). Standardized
329 data allowed a direct comparison of model coefficients as a measure of relationship strength
330 in multivariate models. We drew inferences on landscape geometry (A, MDE) and
331 environmental effects (all others) on richness from two conceptually different analyses:
332 comparisons among univariate analyses per gradient and multivariate models of pooled data
333 for all gradients.

334 Univariate correlations of predictor variables with richness were calculated within each
335 gradient and Pearson's r^2 values were used as a measure of hypothesis support. As all
336 hypotheses predicted a positive relationship with richness, we set r^2 values with negative
337 coefficients to zero. We used the frequency distribution and medians of r^2 values across all
338 gradients to assess the overall support of each variable as a main predictor of richness. This
339 method has been used in various earlier analyses of elevational richness (e.g., McCain, 2005,
340 2007a). We also considered single gradient multivariate models, but sample sizes (number of
341 100 m bands) were too low for meaningful model fitting.

342 In the multivariate analyses, we combined standardized richness and predictor data for all
343 gradients. We used Generalized Linear Models (linear link, Gaussian error distribution) within
344 a model selection framework based on Akaike's information criterion with small-sample
345 correction (AICc; Burnham & Anderson, 2002). We included 44 candidate models with
346 different predictor combinations. These models never contained variables that were highly
347 collinear or conceptually infeasible (i.e., never both T & VegT; Prec & Hmd; SNPP & A
348 and/or NPP). For 'best' models and closely related models, we calculated pseudo- R^2 as
349 Pearson's r^2 of the correlation between model prediction and observed value. We plotted
350 model residuals against elevation to assess remaining, unexplained elevational variation. We
351 used AICc-weighted model averaging to extract averaged standardized coefficients (and their
352 95% confidence intervals, CI). Because SNPP is a composite of two variables (A x NPP), we

353 also calculated a ‘corrected’ AICc with one additional parameter to evaluate ‘best’ model
354 conclusions drawn from model selection.

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

371

372 **Results**

373 Sampling along the 26 elevational gradients encompassed 315,220 specimens from
374 796 individual sampling plots. Total species richness was estimated between 2848 (counting
375 only moths that were identified to a named species) and 7165 (accepting each morphospecies
376 as a unique species), but is realistically closer to the upper estimate due to the faunal
377 uniqueness of the morphospecies localities ([i.e., due to their spatial distance it seems unlikely](#)

378 | [that many unnamed species are shared between regions](#); Table ES1.1). Almost a third of the
379 species were found only at one single plot (average per gradient = 27%; range = 4.3% –
380 48%). Elevational richness patterns (S_{int}) were dominated by midpeaks (16 of 19 gradients,
381 plus one each showing a low-plateau (LP), a low-plateau with a midpeak (LPMP), and an
382 increasing pattern). All 7 of the ‘best subset’ datasets showed diversity midpeaks (Fig. 1).
383 With richness estimated as S_{Chao1} and S_{α} , midpeaks still dominated strongly, although there
384 was a broader spread of other patterns, including decreasing, LP, LPMP, and increasing
385 patterns (Fig. ES1.4). The ‘best subset’ contained one dataset that was decreasing with both
386 S_{Chao1} and S_{α} , whereas all others retained midpeaks. There were no associations between the
387 elevation of maximum diversity along a gradient and the absolute latitude or elevational
388 domain of the gradient. Elevational richness patterns were not strongly influenced by
389 excluding or including human-disturbed sites. Patterns based on near-natural sites alone were
390 nearly identical to those including all sites (avg. $r = 0.99$; Fig. ES2.1). Unless otherwise
391 specified, results presented in the main text therefore refer to 19 analysis-grade datasets
392 including all samples with S_{int} as response variable.

393 In the univariate analyses, correlations between richness and individual environmental
394 or spatial predictors indicated only weak associations (all median r^2 values ≤ 0.21 for analysis-
395 grade data; Fig. 2). The median r^2 values of the two purely spatial predictors, A and MDE,
396 were on the higher end of the distribution, with r^2 values at 0.13 and 0.18, respectively. The
397 median r^2 values of the environmental predictors showed greater variations. Precipitation and
398 humidity effects were weakest (both 0.01), temperature (T, VegT) and NPP were intermediate
399 (0.10, 0.11, and 0.02, respectively), while area-integrated productivity (SNPP) displayed the
400 highest support (0.21). No single predictor showed a clear, consistent association with
401 elevational species richness of geometrid moths. The distribution of r^2 values, however,
402 indicated that individual predictors can be very strongly correlated with richness on particular
403 gradients.

404 Multivariate models of pooled data (after adjusting for differences in average richness
405 between gradients) led to similar conclusions (details for all 44 models: Table ES3.1). The
406 ‘best’ model (lowest AICc) included SNPP, MDE, and VegT, with a pseudo- $R^2 = 0.40$. The
407 second-best model ($\Delta AICc = 2.14$) contained NPP and A instead of SNPP, and had an
408 identical pseudo- R^2 . Penalizing models containing SNPP for its hidden (additional) parameter
409 rendered the ‘best’ and second-best model AICc almost identical ($\Delta AICc = 0.02$). Pooled
410 input data presented a low-plateau pattern (with wide scatter, Fig. 3A; linear and quadratic fits
411 of elevation and richness, both $r^2 < 0.02$, $p = n.s.$), while residuals from the ‘best’ model
412 exhibited a unimodal elevational pattern (Fig. 3B; linear fit, $r^2 < 0.02$, $p = n.s.$; quadratic fit, r^2
413 $= 0.13$, $p < 0.001$). We used averaged standardized coefficients across all 44 candidate models,
414 weighted by their AICc, to compare the strengths of partial effects of predictors (Fig. 4). The
415 spatial predictors, A and MDE, as well as SNPP were the most supported, whereas T, VegT,
416 and NPP received intermediate support. Again, water-related effects had consistently the
417 lowest support, with their confidence limits including zero.

418 Re-analyzing different data groupings (‘best subset’, all gradients) and different
419 richness estimates (S_{Chao1} , S_{α} , rarefied richness) led to the same conclusions (detailed results
420 in ES3 and ES4). In particular, ‘best’ models and the ranking of averaged standardized effects
421 were independent of the choice of richness estimate, although pseudo- R^2 was generally
422 slightly lower for numerical richness estimates. Results based on all 26 gradients were similar
423 to those restricted to ‘analysis-grade’ data sets. Notably, for the ‘best subset’ gradients, r^2 was
424 distinctly higher than for analysis-grade datasets. In univariate analyses, both A and SNPP
425 increased dramatically when restricted to analysis-grade datasets, but T and Veg T also
426 increased, whereas MDE and precipitation measurements (Prec, Hmd, NPP) remained
427 relatively low (Fig. 2). Similarly, the ‘best’ multivariate models exhibited a stronger pseudo-
428 R^2 of 0.64, and average coefficients were substantially higher, although the order of predictor
429 support was the same as for analysis-grade datasets (Fig. 4). For the ‘best subset’, the use of a

430 theoretical RSFD for MDE predictions did not greatly affect results, compared to using the
431 empirical RSFD (which was not reliably available for other gradients; Fig. ES3.3.2).

432

433 **Discussion**

434 Elevational richness patterns

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

444 The predominance of midpeaks in our data is surprising for two reasons. Geometrids
445 are relatively small organisms with few physiological or behavioural options for
446 thermoregulation. Consequently, a preference for warmer habitats, and hence overall
447 decreasing elevational richness patterns, might have been expected. Although we did find a
448 partial effect of temperature in the multivariate analyses, it was relatively weak (Fig. 4).
449 Furthermore, explanations of midpeak patterns in some vertebrate groups pointed towards
450 effects of water limitation at the base of mountains (McCain, 2007a; 2009). Low temperatures
451 towards the high elevations, and drought at the mountain bases, were hypothesized as a cause
452 for diversity peaks at mid-elevations. However, with few exceptions (Mt. Lemmon,
453 Kilimanjaro), most of our gradients are not in arid landscapes, and many are very wet indeed
454 – but they displayed midpeak patterns nevertheless. Only a few other taxa have shown

455 similarly consistent mid-elevational peaks in species richness, including non-volant small
456 mammals (McCain, 2005), salamanders (McCain & Sanders, 2010), and ferns (Kessler *et al.*,
457 2011). These four groups share few ecological traits; they include ectotherms and endotherms,
458 only some have strong ecological links to water, and they occupy various trophic levels —
459 primary producers, herbivores, and predators.

460

461 Environmental and spatial predictors of richness patterns

462 Similar to analyses of other taxa with predominantly midpeak patterns (e.g., McCain,
463 2007b), there was little support for any single univariate driver in explaining geometrid
464 elevational richness variation (Fig. 2). We examined the correlation between richness and
465 environmental and spatial factors for each gradient. Across individual gradients, predictor
466 variables demonstrated poor fits, although among the best subset, both area-integrated
467 productivity (SNPP) and area were more strongly supported. Similar conclusions were
468 apparent in the multivariate analyses of pooled data (Fig. 4; ES3). Like other taxa with
469 predominantly midpeak patterns, richness appears to be driven by a complex interplay of
470 variables.

471 The strong support for SNPP in both univariate and multivariate analyses, closely
472 followed by area, is in line with theoretical conjectures on productivity effects on species
473 richness that act via population sizes (“more individuals hypothesis”; Evans *et al.*, 2005;
474 Hurlbert & Stegen, 2014). According to this view, what matters for population size
475 maintenance is the total amount of available energy (i.e., food resources) in a habitat, not
476 necessarily its density or local concentration. Total productivity is closely related to area (cf.
477 Wright, 1983; Storch *et al.*, 2005), because a larger habitat, all else being equal, offers more
478 resources than a small area. This scaling effect with area is captured by our area-integrated
479 productivity measure (SNPP). We are not aware of other tests of this idea on elevational data,

480 but conceptually similar approaches were followed in coarse-grained global species richness
481 analyses (Jetz & Fine, 2012). Strong effects of area-integrated productivity, compared to area
482 effects alone, in independent datasets (regarding region and taxon) could provide further
483 evidence in favour of our finding. Ideally, geographic settings that allow a decoupling of
484 elevational area sizes and productivity (e.g., inverse gradients of the two variables) could be
485 utilized.

486 We also found support for models that contained area alone, instead of SNPP, or area
487 and average productivity as separate variables, to a similar degree as models containing SNPP
488 (Fig. 4, Table ES3.1; $\Delta AICc < 3$ (< 2 when penalizing SNPP-models for an extra parameter)).
489 Earlier studies (see above) found evidence for an area effect on elevational richness patterns
490 without attempting to account for productivity, based on traditional SAR arguments. Thus,
491 further tests are required to investigate the hypothesis that the elevational SAR is mediated by
492 total productivity variation, rather than area *per se*.

493 Despite relatively strong fits of the ‘best’ multivariate models (pseudo- $R^2 = 0.40, 0.40,$
494 0.64 ; all data, analysis-grade, ‘best subset’, respectively), the residuals demonstrate a mid-
495 elevational maximum trend for geometrid moth diversity (Fig. 3). Hence, the combination and
496 strength of the included predictor variables is insufficient to fully explain the midpeak
497 richness patterns. Because area, SNPP and temperature all decline monotonically with
498 increasing elevation, they alone cannot drive a mid-elevational peak in richness. Although
499 MDE was supported in multivariate analyses as a moderating factor (but not as a main driver),
500 its inclusion also failed to fully explain the trend towards lowered richness in the lowlands
501 compared with mid-elevations. We can only speculate on possible reasons. Historical effects,
502 for instance past climatic variation (Colwell & Rangel, 2010) or phylogenetic effects (Brehm
503 *et al.*, 2013), are feasible conceptually but difficult to integrate into multi-gradient tests due to
504 lack of complete, species-level, time calibrated phylogenies or climatic reconstructions. There

505 | are other ecological effects, such as predation pressure, host-plant diversity ([Lin et al., 2015](#),
506 | [Novotny et al., 2006](#), but see [Jetz et al., 2009](#)) and habitat heterogeneity, that could be
507 | critically important to moth elevational diversity, but we lack data to test them across all
508 | gradients.

509

510 | Methodological aspects

511 | Very strong, idiosyncratic univariate environmental correlates of richness occasionally
512 | appeared in our analyses, for some gradients (high r^2 ; Fig. 2), but these were not generally
513 | supported across gradients. This discordance could be due to genuine differences among the
514 | ecological settings, or it could be due to statistical artefacts common in non-replicated studies
515 | (Ioannidis, 2005). Whatever the cause, this finding highlights the need for multi-gradient
516 | studies if the aim is testing hypotheses for their generality. We found trends towards clearer
517 | results when analyses were scaled on data quality. For example, we detected both stronger r^2
518 | and stronger standardized coefficients when using the ‘best subset’ data, compared with the
519 | less-demanding, analysis-grade datasets, or all gradients (Figs. 2, 4). Thus, insufficient
520 | sampling potentially obscured some ecological patterns. Data quality reduction can arise from
521 | incomplete sampling at each sampling elevation (hence the necessity to work with estimated
522 | rather than observed richness), and/or incomplete overall sampling of gradients. More
523 | coordinated and standardized sampling programs, including targeted sampling of a wider
524 | taxonomic base along multiple gradients, would be beneficial to overcome the need for multi-
525 | source compilations of data that were originally sampled for other purposes. Nonetheless, the
526 | general conclusions and relative strength of support among predictor variables was identical
527 | among all three nested datasets, regardless of perceived sample quality.

528

529 | Conclusions

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

546

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553

554 **Appendix: Electronic Supplements**

555 ES1: Data details

556 ES2: Patterns with and without human-disturbed sites

557 ES3: Detailed modelling results

558 | [ES4: Methods and results of rarefaction analyses](#)

559 | ES5: Data [per site \(5a\)](#) and [per 100m band \(5b\)](#), as used in analyses ([csv-format](#))

560

561 **Biosketch:** All authors are interested in the distribution of biodiversity along environmental gradients
562 and the mechanisms that shape it.

563

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706

707 **FIGURE LEGENDS**

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

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

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

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

730

731