Elevational species richness gradients in a hyperdiverse insect taxon: a 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, 2016~~in 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 ≥0°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., SNPP = A x 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 (ΔAICc = 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 (ΔAICc = 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; ΔAICc <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

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

Appendix: Electronic Supplements

ES1: Data details

ES2: Patterns with and without human-disturbed sites

ES3: Detailed modelling results

ES4: Methods and results of rarefaction analyses

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

564 **References**

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706

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

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

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

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