Received: 16 January 2018 | Revised: 11 January 2019 | Accepted: 20 January 2019

DOI: 10.1111/geb.12903

RESEARCH PAPER

WILEY Global Ecology and Biogeography A Journal of Macroecology

Elevational richness patterns of sphingid moths support area effects over climatic drivers in a near-global analysis

Florian Bärtschi[1,2] | Christy M. McCain[3,4] | Liliana Ballesteros-Mejia[5,6] | Ian J. Kitching[7] | Nicolas Beerli[1] | Jan Beck[1,3]

[1]Department of Environmental Sciences, University of Basel, Basel, Switzerland

[2]Umweltbüro Bärtschi, Basel, Switzerland

[3]Museum of Natural History, University of Colorado, Boulder, Colorado

[4]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado

[5]Museum national d'Histoire naturelle, Sorbonne Université, Institute de Systematique, Evolution, Biodiversité (ISYEB), UMR 7205 – CNRS, MNHN, UPCM, EPHE, Paris, France

[6]CESAB, Centre de Synthèse et d'Analyse sur la Biodiversité, Aix-en-Provence, France

[7]Department of Life Sciences, Natural History Museum, London, United Kingdom

Correspondence
Jan Beck, University of Colorado, Museum of Natural History, 265 UCB, Boulder, CO 80309.
Email: jan.beck@colorado.edu

Funding information
National Science Foundation, Grant/Award Number: 1542639; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 3100AO_119879

Editor: John-Arvid Grytnes

Abstract

Aim: We test hypotheses on the environmental control of elevational richness patterns of sphingid moths for their global applicability and generality. Specifically, we compare effects of area with climate-related drivers, such as primary productivity and temperature, while also considering direct effects of precipitation.

Major taxa: Sphingid moths (Lepidoptera).

Location: Eighty-six mountain ranges of the Old World and the Australia/Pacific region, from Scandinavia and Siberia through the African and Australasian tropics to South Africa and Southern Australia.

Methods: We used a large compilation of point locality records for 744 species, in addition to fine-grained range maps derived from species distribution modelling of these records, to characterize the elevational pattern of species richness in 86 custom-delineated mountain regions. For both types of data, we compared the effects of environmental drivers on richness by comparing standardized coefficients of multivariate models for pooled data after accounting for between-region variation in richness.

Results: We observed varying patterns of elevational richness across the research region, with a higher prevalence of midpeaks in arid regions. We found overwhelming support for area as a main determinant of richness, modulated by temperature and productivity, whereas we detected no effect of precipitation.

Main conclusions: Area, productivity and temperature are the main environmental predictors explaining a large proportion of variability in sphingid richness. This is consistent not only with other elevational studies, but also with empirical and theoretical biodiversity research in a non-elevational context (with the caveat of some unresolved issues in elevational area effects). However, distinct differences in elevational patterns remain even within the same mountain ranges when comparing with other Lepidoptera, that is, geometrid moths, which highlights the importance of understanding higher clade differentiation in ecological responses, within insects and in other groups.

KEYWORDS

altitude, diversity, Lepidoptera, precipitation, productivity, temperature

1 | INTRODUCTION

Understanding species richness patterns along elevational gradients as an effect of environmental variation has matured into a major field of biodiversity research during the last decades (Kessler, Kluge, Hemp, & Ohlemüller, 2011; McCain & Grytnes, 2010; Quintero & Jetz, 2018; Rahbek, 2005). Across taxa and biomes, most studies documented either unimodal patterns, with highest richness at mid-elevation ('midpeaks'), or declining richness with elevation, or a mix of those pattern types (McCain & Grytnes, 2010). These patterns proved difficult to explain from simple assumptions of environmental causes, such as the almost universal decline in temperature with elevation. Furthermore, the variation of patterns found across studies has only rarely been conceptualized into globally applicable hypotheses of general mechanisms (McCain, 2007a). A multitude of single-gradient studies makes it challenging to evaluate hypotheses for their generality, because methodological, taxonomic and regional differences contribute to idiosyncratic findings that are hard to reject in a rigorous testing framework. More informative, spatially replicated studies on the same taxonomic group exist for vertebrates (McCain, 2007a, 2009, 2010; McCain & Sanders, 2010; Quintero & Jetz, 2018), plants (Kessler et al., 2011) and a few insect taxa (ants: Sanders, 2002; Szewczyk & McCain, 2016; moths: Beck et al., 2017). Such replicated studies are based on compilations of individual datasets, selected for inclusion after quality vetting. Nevertheless, these data were usually sampled and processed by different researchers using different methods and protocols, often to address different research questions and without the intention of inclusion into a replicated meta-study.

Findings from these studies indicate that there is no strong support for a single environmental driver for the observed richness patterns. However, corresponding to theory and empirical findings on non-elevational, large-scale richness patterns, climatic factors, such as temperature and precipitation, were reported to shape elevational richness patterns of many different taxa (Field et al., 2009). Although there is theoretical underpinning of hypothesized direct temperature effects (Brown, Gillooly, Allen, Savage, & West, 2004; Rohde, 1992), precipitation effects presumably act rather indirectly via their effect on plant productivity (Evans, Warren, & Gaston, 2005). Furthermore, the variation of available area as a function of elevation in mountain ranges was considered to have a major effect on richness patterns [i.e., a species–area relationship (SAR); McCain, 2007b; Rahbek, 2005; Rosenzweig, 1995]. However, exactly like declining temperature, monotonically declining area with elevation alone cannot explain the existence of midpeak richness patterns. Productivity, on the contrary, does exhibit midpeak patterns in some mountain landscapes, owing to aridity at the base of mountains. Productivity has often been suggested as a possible cause of observed richness patterns, but the lack of fine-scale and reliable productivity data has prevented direct testing in many empirical studies (McCain, 2007a; Phillips, Hansen, & Flather, 2008).

Here, we used high-resolution estimates of primary productivity after assessing their utility at capturing patterns in mountain ecosystems. Furthermore, mechanistic details of the productivity–richness relationship are unclear, such as whether it acts via food and population sizes (the 'more-individuals hypothesis'; Rosenzweig, 1995; Classen et al., 2015; Storch, Bohdalkova, & Okie, 2018) or whether productivity per area, or summed productivity across the entire area of an ecological zone, is the relevant variable (Hurlbert & Stegen, 2014; Storch, Evans, & Gaston, 2005). Beck et al. (2017) recently presented data indicating strong effects of the latter, area-integrated productivity on geometrid moth richness in elevational richness patterns (see also Jetz & Fine, 2012). The mid-domain effect (MDE), caused by hard geometrical borders along a gradient, has also been proposed as an explanation for midpeak patterns of richness (Colwell & Hurtt, 1994). However, recent studies viewed MDE as a modulating effect on elevational richness pattern, rather than its primary driver (Beck et al., 2017; Colwell et al., 2016; Dunn, McCain, & Sanders, 2007).

Here, we present elevational richness patterns for sphingid moths replicated across a large number of mountain ranges of the Old World and the Australia–Pacific region. This study is unique not only because it provides new and comprehensive elevational richness data for an insect taxon across many tropical regions, but also because our data are based on the same methodological approaches for all mountain ranges, rather than being a compilation of local gradient studies, which reduces unwanted variability in analyses.

We tested, specifically, the effect of elevational area variation against the two most likely climate-driven environmental effects on richness: net primary productivity (NPP) and mean annual temperature. Assessing the potential of these variables, fine-scaled NPP data in particular, is important for judging whether elevational richness patterns fall within the general mechanisms shaping biodiversity patterns on Earth, or whether they must continue to be considered an ecological phenomenon outside the norm. We also investigated direct effects of annual precipitation and those of area-integrated productivity (sum of NPP within an elevation band). After a first assessment of univariate correlations with richness (searching for a primary driver), we analysed effects with multivariate models after controlling for variation in richness between mountain ranges. Contrasting different types and qualities of richness data, we assure the robustness of our findings. We also compare sphingid elevational patterns with published data for geometrid moths (Beck et al., 2017) from the same mountain regions, which might elucidate the impact of phylogenetic histories and resulting trait variation on such patterns. We provide raw and processed data for future analyses.

2 | METHODS

2.1 | Sphingid moths

Sphingidae or hawkmoths are a family among the bombycoid Lepidoptera (Kitching & Cadiou, 2000; Regier et al., 2013). Their large body size, intermediate species richness (globally *c.* 1,987 species;

Kitching et al., 2018) and their attraction to artificial light sources, which provides a robust means of field collecting, have made them popular among amateur insect collectors and scientific entomologists for centuries. As a consequence, more information has accumulated about their life histories, distribution and phylogeny than for most other insect taxa. Over the last decade, they have emerged as a model taxon for investigations into insect macroecology and biogeography for otherwise data-deficient tropical regions in particular (Ballesteros-Mejia, Kitching, Jetz, & Beck, 2017). Many hawkmoth species have excellent flight capacity, and some cover huge areas within their geographical range, whereas others are geographically restricted endemics (Grünig, Beerli, Ballesteros-Mejia, Kitching, & Beck, 2017). Larvae feed on plant leaves with moderate to low host specificity (i.e., specialization below plant family level is uncommon), hence plant species distributions are unlikely to be linked tightly to those of hawkmoths (Beck, Kitching, & Linsenmair, 2006).

2.2 | Elevational range data

A total of 108 distinct mountain ranges were defined across our research region. These delineations represent an edited version of data published by Körner et al. (2017; for detailed methods and map, see Supporting Information Appendix S1).

We used two types of sphingid moth distribution data, point records of species from a multi-source compilation and comprehensive range maps based on species distribution models (SDMs) at high resolution (Ballesteros-Mejia et al., 2017). Subdividing point-record data further into a 'lenient' and a 'strict' selection of mountain ranges (see Section 2.3 for criteria), we had three datasets to repeat our analyses and compare consistency.

2.3 | Point locality data

We compiled georeferenced point locality records for all species of the Old World and Australia/Pacific from a multitude of sources, including databasing specimen label information in major natural history museums, private collections, our own field sampling, published literature and online sources (including the Global Biodiversity Information Facility, GBIF; www.gbif.org). During this *c*. 20-year endeavour, taxon and locality information was carefully checked and edited whenever sources seemed unreliable. This database is continuously expanded and updated (regarding new records and nomenclature); we used 2014 data here. Raw data for each species can be browsed and downloaded at Map of Life (www.mol.org). More details on data compilation and processing are provided by Ballesteros-Mejia et al. (2017). Given that many original records did not contain elevation information, we extracted this from a high-resolution digital elevation model [DEM; 30 arc s (*c*. 90 m); Robinson, Regetz, & Guralnick, 2014; see also Fattorini, 2014] based on latitude and longitude information. After excluding data with imprecise coordinates in addition to the GBIF records (which, in preliminary analyses, were too imprecisely georeferenced), we tested the reliability of extracting elevation data from a DEM using 26,190 points with original elevation data present, yielding $r^2 = .753$ in a correlation of original and extracted DEM elevation data. Acknowledging the trade-off between data quality and the amount of data available for analysis, in addition to replicate analyses based on range maps (see Section 2.4), we judged this acceptable and used *c*. 43,000 point records for 744 species located within the above-defined mountain ranges.

Point records are necessarily undersampled, because not all possible sites have been visited and thoroughly sampled, so we applied criteria to include only relatively well-sampled mountain ranges in analyses, resulting in the selection of a high-quality dataset ('strict') nested within a lower quality dataset ('lenient'). For the 'lenient' selection, we required a minimum elevation range of 1,500 m in a mountain range, 60% of the elevational gradient had to be sampled, lowest sampling had to be within 300 m of the mountain base, the mountain range as a whole had to contain a minimum of 10 species, and point-record data had to contain at least half of SDM-predicted richness. This resulted in 40 'lenient'-selected mountain ranges. For the 'strict' selection, we required a minimum elevation range of 2,000 m, 70% of the gradient had to be sampled, lowest sampling had to be within 200 m of the mountain base, the mountain range as a whole had to contain a minimum of 10 species, and point-record data had to contain ≥ 75% of SDM-predicted richness. This resulted in 19 'strict'-selected mountain ranges. See the Supporting Information (Appendix S1) for a map, data and method details.

2.4 | Range map data

Ballesteros-Mejia et al. (2017) provided range maps for all hawkmoth species in the region at 5 km × 5 km resolution. Ranges were estimated using SDMs informed from the point locality data compilation described above, in addition to 13 climate (e.g., annual temperature range, precipitation, etc.) and three vegetation variables (percentage of trees, herbs and bare ground). The SDM output was then expertly vetted and edited for dispersal limitation. Resulting data were also quality controlled for predictions on emergent phenomena, such as species richness (Ballesteros-Mejia et al., 2017; data at Map of Life, www.mol.org). Range estimates are considered comprehensive, and the entire available elevation gradient was included. However, for inclusion in this study we also demanded a minimum gradient length of 2,000 m and a minimum species richness of 10 across a mountain range. This resulted in 86 mountain ranges for analyses.

We acknowledge that both types of data, point records and range maps, suffer from potential yet complementary caveats (here and in any comparable studies). Point data are undersampled and require removal of a larger number of mountain ranges from analyses, whereas range maps are more complete but are estimates, thus not based on observed specimens confirmed to occur at all sites. We compensate for sampling deficiencies by comparing results from analyses of both types of data, focusing on the consistency of conclusions. Given that the results are highly concordant, we present in the main text mainly modelled data, whereas point data are in the Supporting Information where appropriate.

2.5 | Richness patterns

Each mountain range was binned into 100 m elevational bands, and we used interpolated species elevational ranges (i.e., assuming presence between the highest and lowest recorded specimen in each range) for both datasets, as is standard in elevational studies. Given that we used only elevational bands with sphingid presence recorded or modelled, there were no richness data with zero values in analysis.

Species richness across the 100 m elevational bands per mountain was visualized, and patterns were sorted into four different pattern types (decreasing, D; low plateau, LP; midpeak, MP; and low plateau with midpeak, LPMP) according to criteria outlined by McCain (2010) and McCain and Grytnes (2010). We classified mountain ranges as arid (including semi-arid) and humid according to the United Nations Environmental Program (UNEP) humidity index map (Deichmann & Eklundh, 1991) to search for consistent differences in moth richness patterns. We tested, in particular, the associations of midpeak patterns with arid mountain ranges (McCain, 2007a, 2009) using contingency table χ^2 tests.

2.6 | Environmental predictors

Five predictor variables were tested for effects on elevational species richness, including the area of the 100 m elevational bands (*A*), mean annual temperature (*T*), annual precipitation (*P*), NPP, and the sum of NPP within an elevation band (SNPP; i.e., *A* × NPP). In preliminary analyses, we also considered the mean temperature of the months ≥ 0 °C (as a proxy of temperature of the growing season), but as the results were nearly identical to *T*, we do not present these data here.

For *A*, *T* and *P*, data were extracted from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at 30 arc s (*c*. 1 km) resolution using GIS tools. Global NPP was extracted from MODIS17 (Heinsch, 2003; Running et al., 2004) at 30 arc s resolution. Crucially, for our purposes, we edited NPP data by setting all 'no data' values to zero; 'no data' on land are caused by lack of vegetation reflectance (indicating vegetation-free regions, such as desert, bare rock or ice), hence there is zero NPP. For all variables, sea and larger inland waters were clipped out (based on a polygon map by National Imagery and Mapping Agency, 2009). The mean of each predictor variable was calculated across every 100 m band in all mountain ranges, except for *A*, where the sum was used (re-projected to a 1 km equal-area grid), and SNPP. We validated the NPP dataset (Turner et al., 2006) by plotting mean NPP for each elevational gradient and checked patterns for many regions that we knew personally (which convinced us of the appropriateness and overall quality of the dataset).

2.7 | Statistical analysis

Predictor and response variables were standardized to a mean of zero and unity standard deviation [*SD*; i.e., $(x - \bar{x})/SD$], which allowed direct comparison of model coefficients. Before that, some variables had to be transformed to reach normality; *P* was square root-transformed, whereas *A*, SNPP and species richness were $\log_{10}$-transformed. We subsequently fitted models expecting a Gaussian error distribution of the transformed data.

For a preliminary assessment of main effects in our data, we ran univariate correlations within each mountain range, plotting the frequency distribution of r^2 values across mountain ranges and using median r^2 values to compare which predictor was most strongly supported as a general, single driver of richness patterns. These data can be compared with earlier studies using this approach (e.g., Beck et al., 2017; McCain, 2009).

To identify environmental drivers more rigorously in a multivariate setting, we used generalized linear models (GLMs, Gaussian error) with pooled data (i.e., *n* = number of all 100 m bands across all mountain ranges). However, before that we controlled data for mountain range-specific variation in species richness by deducting the average richness of elevation bands within each mountain range (after transformation and standardization; (see Section 2.7)). We did this to limit regional effects of variation in richness (e.g., latitudinal) lending support to environmental drivers of local richness variation along elevation gradients (this is a variant of using a random intercept mixed model; for similar reasoning and application, see Beck et al., 2017). Trying various predictor comparisons, we evaluated models with the Akaike information criterion (AIC) and computed AIC-weighted averaged coefficients to compare effects. To avoid logical problems, we did not include the composite variable SNPP in models containing either NPP or *A*. We calculated pseudo-R^2 values of best models as linear correlations of predicted versus observed data. We also replicated multivariate analyses using non-transformed richness data in a GLM with Poisson-distributed error, which had been recommended by O'Hara and Kotze (2010).

3 | RESULTS

The majority of mountain regions featured a midpeak (MP) or low plateau–midpeak (LPMP) pattern of sphingid moth species richness (modelled data: 64%; point data, lenient selection: 75%; strict selection: 79%; Figure 1). With modelled data, 17 of 21 datasets (81%) with MP patterns were located in arid mountains, whereas only 16 of 65 (9%) non-MP patterns were in arid regions. The link of MP patterns and the aridity of landscapes is unlikely to be attributable to chance (contingency table analysis: $n = 86$, $\chi^2 = 19.0$, $p < .001$). For point locality data, the associations are somewhat weaker but still significantly supported (lenient: $n = 40$, $\chi^2 = 9.4$, $p = .002$; strict: $n = 19$, $\chi^2 = 4.4$, $p = .036$). The elevation of richness peaks was not affected by mountain-wide species richness (for data and implications, see Supporting Information Appendix S1). Supporting Information Appendix S2 shows plots of elevational richness for each region; the data are published as Supporting Information Appendix S3.

Preliminary univariate comparisons (Supporting Information Appendix S4) suggested area (*A*) as the strongest single predictor of elevational species richness. Temperature (*T*) and productivity variables (NPP and SNPP) were less strongly supported, whereas we found no support for precipitation (*P*) as a single, univariate driver of

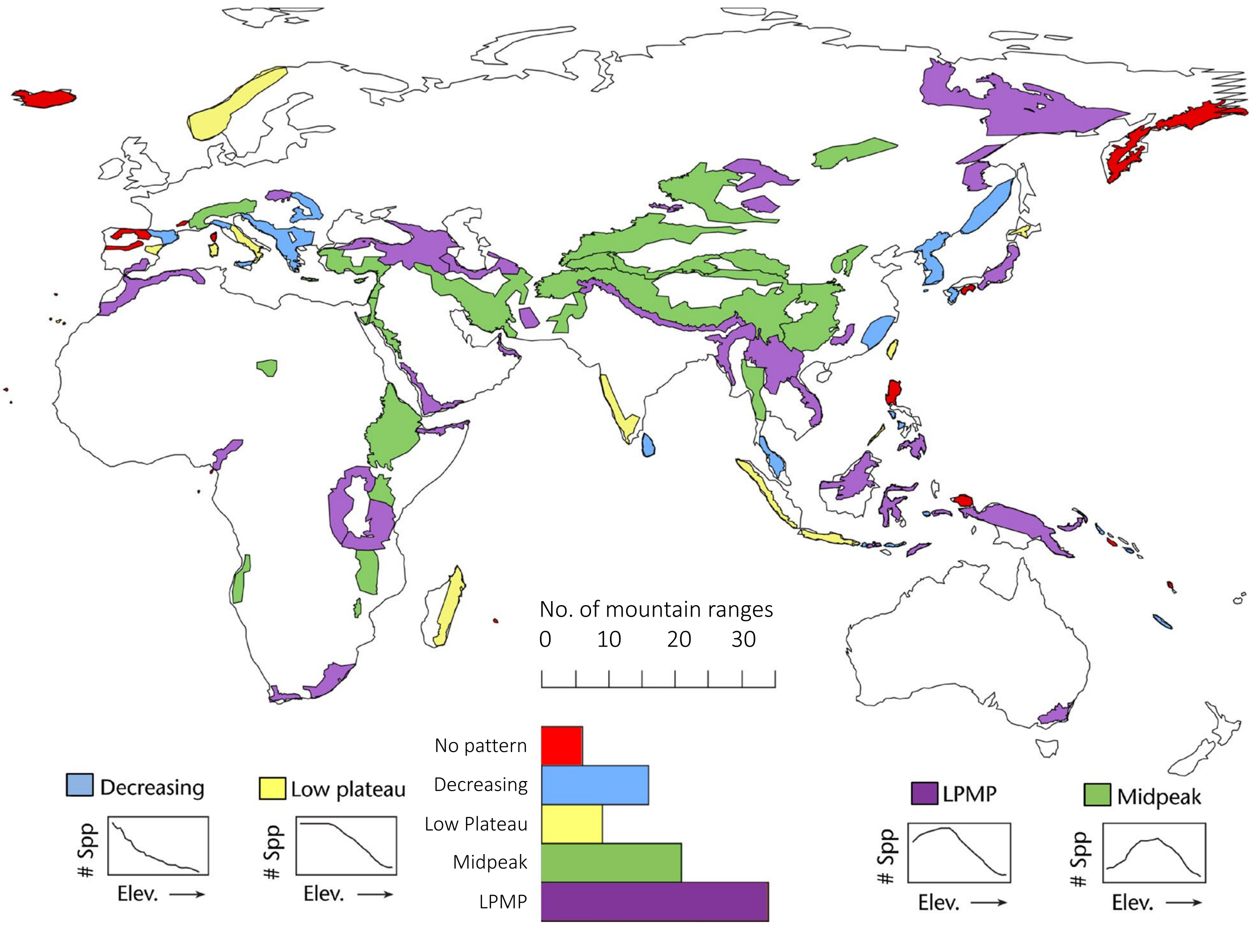

FIGURE 1 Mountain ranges and their prevailing richness pattern for sphingid moths (LPMP = low plateau–midpeak; pattern definitions and inset sketches are based on McCain & Grytnes, 2010). 'No pattern' identifies regions that did not fit any of these categories (for plots and data of all richness patterns, see Supporting Information Appendices S2 and S3) [Colour figure can be viewed at wileyonlinelibrary.com]

richness (median $r^2 < .01$). Notably, despite these clear assessments of variable importance across all mountain ranges, all variables featured the entire range of r^2 values within single mountain ranges (i.e., from $r^2 < .1$ to $r^2 > .9$). These first assessments were supported by model-based and point locality data (Supporting Information Appendix S4).

Multivariate models containing *A*, *T*, *P* and NPP as predictors were always best with a wide margin [according to AIC; modelled data: (pseudo-)$R^2 = .689$; points-lenient: $R^2 = .715$; points-strict: $R^2 = .795$], whereas models containing SNPP were weaker. They were highly concordant in their AIC-based assessment among the three data sources (Supporting Information Appendix S5). Averaged coefficients (Figure 2) clearly point to the paramount importance of *A* in predicting richness in all three datasets, followed by *T*, NPP and SNPP, whereas *P* was always a non-significant predictor. Alternative analyses (using untransformed richness and Poisson-error models) confirmed most of the above effects but were ambiguous on whether there is an effect of *P* or not (Supporting Information Appendix S6; see there also for discussion on the necessity and reliability of this approach for our data).

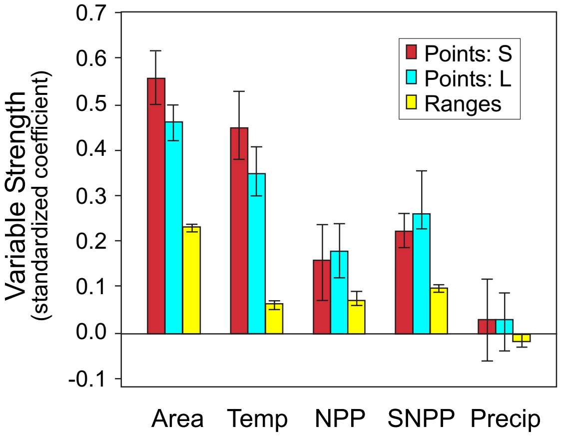

FIGURE 2 Averaged standardized coefficients (bars; Akaike information criterion weighted) and 95% confidence intervals (whiskers) from multivariate linear models (for model details, see Supporting Information Appendix S5; L = lenient selection; NPP = net primary productivity; S = strict selection; SNPP = sum of NPP within an elevation band). Positive associations were expected for all predictors (Supporting Information Appendix S4) [Colour figure can be viewed at wileyonlinelibrary.com]

Repeating univariate correlation analyses separately for humid and arid mountains, we found slightly higher fits of richness with temperature in humid mountains but lower, rather than higher, fits in NPP in arid mountains, contrary to predictions (Supporting Information Appendix S7). Both arid and humid mountain data individually supported the same conclusions drawn for the combined dataset.

Sphingid and geometrid moth elevational richness along 15 elevational gradients did not correspond strongly, with geometrids featuring midpeak (or LPMP) patterns more often than sphingids. This might indicate that taxon-specific effects contribute to shape these patterns (for methods and details, see Supporting Information Appendix S8).

4 | DISCUSSION

Our study provides the most comprehensive analysis of elevational gradients for any insect taxon, covering 86 mountain ranges from the northern-temperate, tropical to the southern-temperate regions (Figure 1; Supporting Information Appendix S1). This allowed us to compare the variation in species richness patterns across ecologically diverse zones with different biogeographical histories and to test hypotheses on environmental drivers of richness for their global generality. Consistent for different data types (modelled range maps and point locality records) and analytical approaches (multivariate and univariate), we found that the area of elevational bands (i.e., the topography of mountains) had the strongest impact on measured richness. Multivariate modelling (Figure 2) indicated that this area-shaped pattern is further modulated by temperature and primary productivity (NPP), but not by precipitation per se. We did not find strong support for the area-integrated metric of productivity (SNPP).

4.1 | Mountain topography and its effect on species richness

Our finding of strong elevational area effects is consistent with earlier regional studies on other taxa, such as vertebrates (McCain, 2007b; Rahbek, 1997) and plants (Karger et al., 2011). It is also consistent with non-elevational SARs (Preston, 1962; Rosenzweig, 1995), 'ecology's most general pattern' (Lomolino, 2000). The same mechanisms that shape non-elevational SARs, among them more comprehensive sampling and higher habitat heterogeneity in larger areas, could affect regional-scale richness in mountains (i.e., richness of elevational bands), which could then 'echo' down to a (weakened) area effect on the species richness in local samples (Romdal & Grytnes, 2007; Rosenzweig & Ziv, 1999). Consistent with this idea, many elevational studies based on local samples of richness also reported correlations with area (e.g., Beck et al., 2017). Furthermore, Karger et al. (2011) showed that an area-correction of regional richness yields higher correspondence of regional and local richness patterns than uncorrected data, supporting the causal link of area to regional-to-local richness. However, we see at least three issues that cast some doubt on this apparent consensus of (largely non-elevational) SAR theory and empirical studies on mountain biodiversity.

First, although area effects seem best supported even in our univariate analyses (with very high median r^2 values; Supporting Information Appendix S4), area alone cannot account for the highly prevalent richness midpeaks (or similar curvilinear patterns; Figure 1). Area usually declines, often monotonically, with elevation, except in landlocked landscapes (where lowest elevations can occur in valleys or ravines; McCain, 2007b), as long as the surrounding lowlands are included (our selection included lowlands contained approximately within 50 km pixels; see Methods). Thus, there must be additional, modulating effects on richness patterns (McCain, 2007b). Among the candidates for such modulation, climate and productivity patterns (see Section 4.2) could lead to a variation in richness patterns in different parts of the world (as observed; Figure 1; McCain, 2007a, 2007b), whereas the MDE (not addressed here; Colwell & Hurtt, 1994; Colwell et al., 2016) would lead to symmetrical midpeaks uniformly among all mountain ranges (not observed).

Second, given the ubiquitous pattern of declining temperature on almost all mountain ranges of the world (Barry, 1992), combined with theoretically sound and empirically well-documented effects of temperature on richness, it is unwise a priori to 'correct' richness for area via residuals from the Arrhenius function (as is commonly done; e.g., Karger et al., 2011; Rahbek, 1997; Sanders, 2002). Such an a priori area correction is likely to capture variation of other potential, collinear predictors, such as temperature, which leads to biased estimates of effects (i.e., overestimating area effects, underestimating collinear effects; Freckleton, 2002). Furthermore, parameter estimates of area effects are often uncertain owing to small sample sizes (i.e., number of elevation bands on a mountain). Empirically measured SAR slopes ('z-values') are highly variable in non-elevational empirical studies (Dengler, 2009) despite the elegant theoretical deduction of $z = .27$ in idealized landscapes (Preston, 1962). In an elevational context, there is not even any certainty of what to expect theoretically. Instead, area effects should be accounted for as partial coefficients in a multivariate setting (Freckleton, 2002). However, for illustration, we carried out an a priori correction for area effects (Supporting Information Appendix S9), the results of which highlighted the problems listed above.

Third, area effects on richness, even when strongly supported as a single driver in elevational studies (Supporting Information Appendix S4), imply effects of environmental variation along mountain slopes on the level of individual species. Without elevational habitat or climatic specificity for individual species that lead to range limits there could be no elevational SAR; such elevational zones (or bands) would be identical, continuous habitat. Elevational range limits can be caused only by environmental variables (abiotic or biotic), because the proximity of elevational bands in a mountain range makes dispersal limitation an implausible mechanism. Most organisms covered in elevational biodiversity studies can be assumed to be sufficiently mobile to be able to disperse to suitable available habitat within the studied mountain slope, which often covers only few kilometres in travel distance. This is in contrast to non-elevational SARs, where dispersal limitation could theoretically cause distinct geographical ranges even in a 'neutral' world (Preston, 1962). Thus, elevational area effects require the assumption of environmentally determined elevational range limits of species to explain a non-environmental, area-driven effect on the emergent level of species richness. This is not a contradiction to elevational SARs, but spelling out its inherent assumptions draws strong parallels to the MDE, where the same assumption of a priori set, species-specific elevational ranges, had sparked a very controversial discourse (e.g., Hawkins, Diniz-Filho, & Weis, 2005).

4.2 | Temperature and productivity, but not precipitation

Our multivariate analyses indicated independent, partial effects of temperature and productivity (Figure 2); temperature is also supported as a single 'main driver' of richness (Supporting Information Appendix S4), whereas NPP is not. Both effects are consistent with a very large number of studies on the environmental control of biodiversity, yet both assume mechanistic underpinnings that are controversial and not yet well substantiated. Temperature or kinetic energy, as a direct driver of richness variation, has been hypothesized to affect generation times, speciation rates and the speed of evolution (Rohde, 1992), for example through its effect on chemical reaction speeds and metabolism (e.g., the 'metabolic theory of ecology'; Allen, Gillooly, & Brown, 2007; Brown et al., 2004). Empirical evidence for the precise predictions on temperature effects on richness is mixed (Brown et al., 2004; Hawkins et al., 2007).

Primary productivity is clearly affected by climatic factors, such as temperature and precipitation, in addition to evaporation rates, but its effect on richness, empirically shown here and in many other studies (Ballesteros-Mejia et al., 2017; Mittelbach et al., 2001) must not be confused with direct effects of these variables. Potential energy supplied into a system by photosynthesis could affect richness through various hypothetical mechanisms (Allen et al., 2007; Evans et al., 2005; Mittelbach et al., 2001; Storch et al., 2005), but the most commonly assumed causal pathway is via increased food resources and thus population sizes, which would reduce extinction rates in a system (the 'more-individuals hypothesis'; Evans et al., 2005). Surprisingly, given its relevance for the understanding of biodiversity patterns, there are very few rigorous, comprehensive tests of all four aspects of this idea (productivity, food resources, population sizes and diversity), yielding mixed results (Classen et al., 2015; McCain, King, Szewczyk, Gardner, & Beck, 2018), and tests for two or three variables are also equivocal. Given that overall productivity may not necessarily be linked tightly to the fraction of productivity available to a given taxon (e.g., owing to feeding specialization or competition from other taxa), analyses of NPP may underestimate the relevance of available food resources on richness (but see McCain et al., 2018).

One potential mechanism for how area and productivity could affect richness might be the combined influence of both; for example, the area-integration of productivity. The reasoning behind this is that the total, regional amount of potential energy, not its local average, affects population sizes, hence extinction rates (Evans et al., 2005; Hurlbert & Stegen, 2014; Jetz & Fine, 2012; Storch et al., 2005). Although Beck et al. (2017) presented supporting data for such a mechanism in an elevational context for geometrid moths, these data did not indicate superior effects of SNPP over area alone (but instead, weaker ones) for sphingid moths. Nevertheless, SNPP was a stronger single 'main' driver of richness than NPP alone (Supporting Information Appendix S4). Further evaluations of SNPP by exploring landscapes with uncorrelated or even opposite area and NPP gradients might thus be informative.

Our analyses reject any direct effect of precipitation on richness (but see Supporting Information Appendix S6, and discussion therein). However, we found a higher prevalence of midpeak patterns in arid regions, which points towards a precipitation-influenced midpeak of productivity. In arid regions, water availability is usually the limiting factor for plant growth (hence productivity), and arid mountains typically feature higher precipitation at mid-elevation compared with the base of the mountains (because precipitation increases with elevation across the mountains; Barry, 1992; McCain & Colwell, 2011). Thus, we suggest that earlier reports of precipitation effects on richness might, in part, have been indirect, owing to its effect on primary productivity, data for which were not readily available in many past studies. In arid mountains, for example, (actual) evaporation and productivity typically peak at mid-elevations, where both precipitation (increasing with elevation) and temperature (declining with elevation) are not too low. However, neither temperature nor precipitation necessarily has a direct effect on richness in such situations, despite detected empirical correlations. Exceptions may be taxonomic groups whose life history is tightly bound to water (e.g., ferns, amphibians). A caveat to this assessment, however, is the unreliability of WorldClim interpolated precipitation data from tropical regions with few weather stations (Soria-Auza et al., 2010). This might have hidden precipitation effects. Nonetheless, when restricting analysis to 15 European mountain ranges (where raw climate data used for interpolation were presumably more comprehensively sampled), we also found no evidence for positive precipitation effects on richness (i.e., for model data, univariate analysis: median $r^2 = 0$; all but one mountain range featured negative coefficients). Our published data (Supporting Information Appendix S3) will allow future retesting with alternative or future improved climate data.

Our study does not exclude the possibility of further modulation of richness patterns by variables not included in our analysis, among them the MDE (Colwell et al., 2016), past climatic change (Colwell, Brehm, Cardelus, Gilman, & Longino, 2008), biotic interactions, geology and locally idiosyncratic evolutionary histories. Furthermore, human landscape modification has the potential to affect richness patterns. Diversity-eroding habitat modifications, agriculture in particular, are most prevalent in lowlands, and it has been suggested that human impacts could therefore shift naturally declining richness patterns towards midpeaks (McCain & Grytnes, 2010). If this were true, we would find midpeaks predominantly in regions of high, long-lasting human disturbance. We could not address this hypothesis rigorously here owing to uncertainties of the timing of human disturbance in relationship to point record data sampling in our sphingid data. However, preliminarily, Figure 1 does not lend support to low-elevation disturbance and midpeaks. For example, although the Alps, as a region of heavy human impact for many centuries, exhibit a midpeak (consistent with the hypothesis), the neighbouring and equally disturbed Dinarids and Pyrenees show a decreasing pattern, as do heavily disturbed regions in eastern Asia. Furthermore, some regions with the world's least and most recent human disturbance, such as Borneo, New Guinea, Central Asia and Siberia, also feature (low-plateau) midpeaks. Beck et al. (2017) drew the same conclusion for geometrid moth data across the globe.

Concurrent with elevational studies on various taxa (Beck et al., 2017; Kessler et al., 2011; McCain, 2007a, 2007b; McCain & Beck, 2016), we observed high idiosyncrasies of results from individual mountain ranges despite finding clear, interpretable results from pooled data. This implies that single-gradient studies can lead to spuriously different results on the drivers of diversity. Our study also highlights how range maps based on fine-grained SDMs can be used in combination with point locality records to balance each other's weaknesses and uncertainties.

Raw richness differed clearly between point records and model data in many mountain ranges (Supporting Information Appendix S2). Most point data indicate overall lower richness than model data (probably owing to undersampling in point records), but a similar richness trend with elevation. Furthermore, some mountain richness patterns differ because point records often show a faster decline of richness towards high elevations compared with model data. Possibly, high elevations are particularly undersampled, probably owing to difficulties of access. Alternatively, model data might overestimate ranges at high elevations in particular. Species distribution models were fitted to point records including data from lowland regions (not analysed in the present study). If a species occurred widely across lowlands of a given climate, it might also be predicted on a mountain of similar climate even if mountain-specific environmental circumstances might cause its absence. Given that mountains overall have a small area compared with lowlands, their impact on SDM fitting and evaluation might be too small to avoid such effects. Furthermore, the grain size of SDMs (5 km) might cause error at high elevations, where environmental gradients are often very steep (i.e., 5 km may encompass a large elevational variation in mountain-top regions). However, we do not have the relevant data to address these speculations empirically. Other pattern variability occurred, in particular, where undersampling seemed an issue (i.e., large difference in absolute numbers between point records and model data) or on small mountains with few elevational bands (Supporting Information Appendix S2), both pointing towards random effects. To reiterate, both point records and modelled data led to very similar conclusions with respect to the environmental drivers of richness.

The present study is another step towards summarizing and conceptualizing the wealth of Lepidoptera data on elevation gradients. Comparing pattern variation and underlying differences in adaptations among this hugely diverse order might help to formulate and test new hypotheses on evolutionary impacts on the environment–richness relationship. Data on geometrid moths (i.e., inchworms) from Beck et al. (2017; see Supporting Information Appendix S8) show predominantly midpeak richness patterns irrespective of the geographical position of gradients, whereas we have shown here strong variation in patterns for sphingids, particularly between arid and humid mountains (Figure 1). The likely causes for the incongruent patterns between geometrid and sphingid moths are currently far too complex for speculation, because geometrids and sphingids differ in many aspects of their ecology, among which are body size, mobility and larval host-plant specificity (for further discussion, see Supporting Information Appendix S8). Future, comprehensive multi-gradient assessments for other major moth taxa [such as arctiine erebids (Brehm, 2009); pyraloids (Fiedler, Brehm, Hilt, Süssenbach, & Häuser, 2008)] might help to pinpoint more clearly how ecological differences co-vary with richness patterns. Owing to their high diversity, the potential for experimental studies, and more detailed descriptive analyses that include variables that are more difficult to measure (such as local productivity, taxon-specific food resources and species abundances), we see potential in insects and other understudied taxonomic groups for testing macro-scale predictions on biodiversity effects in relation to major life-history traits, as has been attempted already in vertebrates (Buckley, Hurlbert, & Jetz, 2012). For birds, arguably the best-studied taxon in macroecology, Quintero and Jetz (2018) have recently gone one step further by studying phylogenetic patterns along elevational gradients (i.e., diversification rates). With the proliferation of phylogenetic information in other clades, increasingly so within insects, future research will also involve cross-taxon comparisons of such patterns. By publishing our data, both raw and condensed for elevational analysis, we help to make sphingid moths a part of such comparative endeavours, possibly as the only insect representative so far.

4.3 | Outlook

Our results on global-scale elevational richness pattern variability and on the main drivers of richness patterns are consistent with patterns found in other taxonomic groups and with main environmental correlates of richness found in non-elevational settings, in sphingid moths (Ballesteros-Mejia et al., 2017) and other taxa (e.g., Davies et al., 2007; Fritz et al., 2016; Kreft & Jetz, 2007). Rather than viewing this as a lack of novelty, we find it highly reassuring. Elevational gradients have been proposed as model systems to study larger-scale richness patterns, but the repeated observation of midpeak patterns of richness variation in many mountains had cast doubt on this. It seemed as if something fundamentally different goes on in shaping mountain biodiversity. Our study tentatively suggests that this is not the case for sphingids; it simply requires the inclusion of fine-grained primary productivity data as a driver of richness to explain not only such seemingly strange patterns, but also where they occur and where they do not (McCain, 2007a). Pseudo-R^2 values between .7 and .8 from our relatively simplistic, one-fits-all global multivariate models indicate a very good fit, given the inevitable error and uncertainty in predictor and response data, which are estimates themselves. This suggests that although clade-specific adaptations and their effects urgently require better understanding, the principal mechanisms shaping biodiversity patterns can be reconciled among elevational and non-elevational studies. Elevational richness gradients, however, will continue to play a central role in biodiversity research owing to their natural replication, exclusion of unwanted dispersal limitation effects, and breadth of environmental gradients within small study regions, among other advantages.

ACKNOWLEDGMENTS

We thank Jens Paulsen and Christian Körner for sharing their GIS data with us ahead of publication and for helpful discussion on mountain delineations. We are grateful to the huge number of institutions and private collectors who shared their sphingid moth point records with us. The data compilation was, in part, supported by the Swiss National Science Foundation (SNF grant 3100AO_119879 to J.B.). C.M.M. was funded, in part, through NSF 1542639.

AUTHOR CONTRIBUTIONS

F.B. and J.B. designed the study and analysed data, supported by N.B. and C.M.M.; J.B., L.B.-M. and I.J.K. provided sphingid moth data; J.B., F.B. and C.M.M. wrote the manuscript, with input from all authors.

DATA ACCESSIBILITY

Richness data per 100 m elevation band are available in spreadsheet format (Supporting Information Appendix S3).

Model-based range maps for all non-American sphingid species can be browsed and downloaded in GIS-compatible format at Map of Life (www.mol.org).

Point locality records can be browsed at www.mol.org, including maps of point records for each species and species lists for localities (i.e., 50 km radius around user-defined points, various Map of Life-defined polygons of interest). Owing to its continued updating and use in ongoing projects, this dataset is not yet publicly available for download. Please inquire with the corresponding author for options of using these data.

ORCID

Jan Beck https://orcid.org/0000-0003-1170-4751

REFERENCES

Allen, A. P., Gillooly, J. F., & Brown, J. H. (2007). Recasting the species–energy hypothesis: The different roles of kinetic and potential energy in regulating biodiversity. In D. Storch (Ed.), *Scaling biodiversity* (pp. 1–29). Cambridge, UK: Cambridge University Press.

Ballesteros-Mejia, L., Kitching, I. J., Jetz, W., & Beck, J. (2017). Putting insects on the map: Near-global variation in sphingid moth richness along spatial and environmental gradients. *Ecography*, *40*, 698–708. https://doi.org/10.1111/ecog.02438

Barry, R. G. (1992). *Mountain weather and climate*. London, UK: Routledge.

Beck, J., Kitching, I. J., & Linsenmair, K. E. (2006). Diet breadth and host plant relationships of Southeast-Asian sphingid caterpillars. *Ecotropica*, *12*, 1–13.

Beck, J., McCain, C. M., Axmacher, J., Ashton, L. A., Bärtschi, F., Brehm, G., … Novotny, V. (2017). Elevational species richness gradients in a hyperdiverse insect taxon: A global meta-study on geometrid moths. *Global Ecology and Biogeography*, *26*, 412–424. https://doi.org/10.1111/geb.12548

Brehm, G. (2009). Patterns of arctiid diversity. In W. E. Conner (Ed.), *Tiger moths and woolly bears: Behavior, ecology, and evolution of the Arctiidae* (pp. 223–232). Oxford, UK: Oxford University Press.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789. https://doi.org/10.1890/03-9000

Buckley, L. B., Hurlbert, A. H., & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, *21*, 873–885. https://doi.org/10.1111/j.1466-8238.2011.00737.x

Classen, A., Peters, M. K., Kindeketa, W. J., Appelhans, T., Eardley, C. D., Gikungu, M. W., … Steffan-Dewenter, I. (2015). Temperature versus resource constraints: Which factors determine bee diversity on Mount Kilimanjaro, Tanzania? *Global Ecology and Biogeography*, *24*, 642–652.

Colwell, R. K., & Hurtt, G. C. (1994). Nonbiological gradients in species richness and a spurious Rapoport effect. *The American Naturalist*, *144*, 570–595. https://doi.org/10.1086/285695

Colwell, R. K., Brehm, G., Cardelus, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, *322*, 258–261. https://doi.org/10.1126/science.1162547

Colwell, R. K., Gotelli, N. J., Ashton, L. A., Beck, J., Brehm, G., Fayle, T. M., … Novotny, V. (2016). Midpoint attractors and species richness: Modeling the interaction between environmental drivers and geometric constraints. *Ecology Letters*, *19*, 1007–1185.

Davies, R. G., Orme, C. D. L., Storch, D., Olson, V. A., Thomas, G. H., Ross, S. G., … Gaston, K. J. (2007). Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 1189–1197. https://doi.org/10.1098/rspb.2006.0061

Deichmann, U., & Eklundh, L. (1991) Global digital data sets for land degradation studies: A GIS approach. In *GRID case study series, No. 4*. (pp. 29–32). Nairobi, Kenya: UNEP/GEMS and GRID.

Dengler, J. (2009). Which function describes the species–area relationship best? A review and empirical evaluation. *Journal of Biogeography*, *36*, 728–744. https://doi.org/10.1111/j.1365-2699.2008.02038.x

Dunn, R. R., McCain, C. M., & Sanders, N. J. (2007). When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. *Global Ecology and Biogeography*, *16*, 305–312. https://doi.org/10.1111/j.1466-8238.2006.00284.x

Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species-energy relationships at the macroecological scale: A review of the mechanisms. *Biological Reviews*, *80*, 1–25. https://doi.org/10.1017/S1464793104006517

Fattorini, S. (2014). Disentangling the effects of available area, mid-domain constraints, and species environmental tolerance on the altitudinal distribution of tenebrionid beetles in a Mediterranean area. *Biodiversity and Conservation*, *16*, 2531–2538.

Fiedler, K., Brehm, G., Hilt, N., Süssenbach, D., & Häuser, C. L. (2008). Variation of diversity patterns across moth families along a tropical elevational gradient. *Ecological Studies*, *198*, 167–179.

Field, R., Hawkins, B. A., Cornell, H. V., Currie, D. J., Diniz-Filho, J. A. F., Guegan, J.-F., ... Turner, J. R. G. (2009). Spatial species-richness gradients across scales: A meta-analysis. *Journal of Biogeography*, *36*, 132–147. https://doi.org/10.1111/j.1365-2699.2008.01963.x

Freckleton, R. P. (2002). On the misuse of residuals in ecology: Regression of residuals vs. multiple regression. *Journal of Animal Ecology*, *71*, 542–545. https://doi.org/10.1046/j.1365-2656.2002.00618.x

Fritz, S. A., Eronen, J. T., Schnitzler, J., Hof, C., Janis, C. M., Mulch, A., ... Graham, C. A. (2016). Twenty-million-year relationship between mammalian diversity and primary productivity. *Proceedings of the National Academy of Sciences USA*, *113*, 10908–10913. https://doi.org/10.1073/pnas.1602145113

Grünig, M., Beerli, N., Ballesteros-Mejia, L., Kitching, I. J., & Beck, J. (2017). How climatic variability is linked to the spatial distribution of range sizes: Seasonality versus climate change velocity in sphingid moths. *Journal of Biogeography*, *44*, 2441–2450. https://doi.org/10.1111/jbi.13051

Hawkins, B. A., Albuquerque, F. S., Araújo, M. B., Beck, J., Bini, L. M., Cabrero-Sañudo, F. J., ... Williams, P. (2007). A global evaluation of metabolic theory as an explanation of terrestrial species richness gradients. *Ecology*, *88*, 1877–1888.

Hawkins, B. A., Diniz-Filho, J. A. F., & Weis, A. E. (2005). The mid-domain effect and diversity gradients: Is there anything to learn? *The American Naturalist*, *166*, E140–E143.

Heinsch, F. A., Reeves, M., Votava, P., Kang, S., Milesi, C., Zhao, M., ... Running, S. W. (2003). GPP and NPP (MOD17A2/A3) products NASA MODIS land algorithm. *MOD17 User's Guide*, 1–57. Retrieved from https://s3.amazonaws.com/academia.edu.documents/36531869/MOD17UsersGuide.pdf?AWSAccessKeyId=AKIAIWOWYYGZ2Y53UL3A&Expires=1550571541&Signature=1evsSoh84VgZ89y2GKHKrXRWNBA%3D&response-content-disposition=inline%3B%20filename%3DUsers_Guide_GPP_and_NPP_MOD17A2_A3_Produ.pdf

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. https://doi.org/10.1002/joc.1276

Hurlbert, A. H., & Stegen, J. C. (2014). When should species richness be energy limited, and how would we know? *Ecology Letters*, *17*, 401–413.

Jetz, W., & Fine, P. V. A. (2012). Global gradients in vertebrate diversity predicted by historical area–productivity dynamics and contemporary environment. *PLoS Biology*, *10*, e1001292. https://doi.org/10.1371/journal.pbio.1001292

Karger, D. N., Kluge, J., Krömer, T., Hemp, A., Lehnert, M., & Kessler, M. (2011). The effect of area on local and regional elevational patterns of species richness: Local biodiversity, regional biodiversity and area. *Journal of Biogeography*, *38*, 1177–1185. https://doi.org/10.1111/j.1365-2699.2010.02468.x

Kessler, M., Kluge, J., Hemp, A., & Ohlemüller, R. (2011). A global comparative analysis of elevational species richness patterns of ferns. *Global Ecology and Biogeography*, *20*, 868–880. https://doi.org/10.1111/j.1466-8238.2011.00653.x

Kitching, I. J., & Cadiou, J. M. (2000) *Hawkmoths of the world: an annotated and illustrated revisionary checklist (Lepidoptera: Sphingidae)*. London, UK: The Natural History Museum; New York, NY: Cornell University Press.

Kitching, I. J., Rougerie, R., Zwick, A., Hamilton, C. A., St. Laurent, R. A., Naumann, S., ... Kawahara, A. Y. (2018). A global checklist of the Bombycoidea (Insecta: Lepidoptera). *Biodiversity Data Journal*, *6*, e22236. https://doi.org/10.3897/BDJ.6.e22236

Körner, C., Jetz, W., Paulsen, J., Payne, D., Rudmann-Maurer, K., & Spehn, E. M. (2017). A global inventory of mountains for bio-geographical applications. *Alpine Botany*, *127*, 1–15. https://doi.org/10.1007/s00035-016-0182-6

Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences USA*, *104*, 5925–5930. https://doi.org/10.1073/pnas.0608361104

Lomolino, M. V. (2000). Ecology's most general, yet protean pattern: The species–area relationship. *Journal of Biogeography*, *27*, 17–26.

McCain, C. M. (2007a). Could temperature and water availability drive elevational species richness? A global case study for bats. *Global Ecology and Biogeography*, *16*, 1–13.

McCain, C. M. (2007b). Area and mammalian elevational diversity. *Ecology*, *88*, 76–86.

McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, *18*, 346–360. https://doi.org/10.1111/j.1466-8238.2008.00443.x

McCain, C. M. (2010). Global analysis of reptile elevational diversity. *Global Ecology and Biogeography*, *19*, 541–553. https://doi.org/10.1111/j.1466-8238.2010.00528.x

McCain, C. M., & Beck, J. (2016). Species turnover in vertebrate communities along elevational gradients is idiosyncratic and unrelated to species richness. *Global Ecology and Biogeography*, *25*, 299–310. https://doi.org/10.1111/geb.12410

McCain, C. M., & Colwell, R. K. (2011). Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecology Letters*, *14*, 1236–1245. https://doi.org/10.1111/j.1461-0248.2011.01695.x

McCain, C. M., & Grytnes, J. A. (2010). Elevational gradients in species richness. *Encyclopedia of life sciences*. Chichester, UK: Wiley. https://doi.org/10.1002/9780470015902.a0022548

McCain, C. M., & Sanders, N. J. (2010). Metabolic theory and elevational diversity of vertebrate ectotherms. *Ecology*, *91*, 601–609. https://doi.org/10.1890/09-0704.1

McCain, C. M., King, S., Szewczyk, T., Gardner, H., & Beck, J. (2018). Direct effects, not indirect effects, drive the productivity-diversity relationship. *Journal of Biogeography*, *45*, 2533–2545.

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., ... Gough, L. (2001). What is the observed relationship between species richness and productivity? *Ecology*, *82*, 2381–2396.

National Imagery & Mapping Agency. (2009). *Vector map level 0 (digital chart of the world), ed. 5*. Alexandria, VA: National Imagery and Mapping Agency, United States Geological Service & American Geoscience Institute. Retrieved from http://www.agiweb.org/pubs/globalgis/

O'Hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, *1*, 118–122.

Phillips, L. B., Hansen, A. J., & Flather, C. H. (2008). Evaluating the species energy relationship with the newest measures of ecosystem energy: NDVI versus MODIS primary production. *Remote Sensing of Environment*, *112*, 3538–3549. https://doi.org/10.1016/j.rse.2008.04.012

Preston, F. W. (1962). The canonical distribution of commonness and rarity: Part I. *Ecology*, *43*, 187–215. https://doi.org/10.2307/1931976

Quintero, I., & Jetz, W. (2018). Global elevational diversity and diversification of birds. *Nature*, *555*, 246–250. https://doi.org/10.1038/nature25794

Rahbek, C. (1997). The relationship among area, elevation, and regional species richness in Neotropical birds. *American Naturalist*, *149*, 875–902.

Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns: Scale and species-richness patterns. *Ecology Letters*, *8*, 224–239. https://doi.org/10.1111/j.1461-0248.2004.00701.x

Regier, J. C., Mitter, C., Zwick, A., Bazinet, A. L., Cummings, M. P., Kawahara, A. Y., ... Mitter, K. T. (2013). A large-scale, higher-level, molecular phylogenetic study of the insect order Lepidoptera (moths and butterflies). *PLoS ONE*, *8*, e58568. https://doi.org/10.1371/journal.pone.0058568

Robinson, N., Regetz, J., & Guralnick, R. P. (2014). EarthEnv-DEM90: A nearly-global, void-free, multi-scale smoothed, 90m digital elevation model from fused ASTER and SRTM data. *ISPRS Journal of Photogrammetry and Remote Sensing*, *87*, 57–67. https://doi.org/10.1016/j.isprsjprs.2013.11.002

Rohde, K. (1992). Latitudinal gradients in species diversity: The search for the primary cause. *Oikos*, *65*, 514–527. https://doi.org/10.2307/3545569

Romdal, T. S., & Grytnes, J.-A. (2007). An indirect area effect on elevational species richness patterns. *Ecography*, *30*, 440–448. https://doi.org/10.1111/j.0906-7590.2007.04954.x

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge, UK: Cambridge University Press.

Rosenzweig, M. L., & Ziv, Y. (1999). The echo pattern of species diversity: Pattern and processes. *Ecography*, *22*, 614–628. https://doi.org/10.1111/j.1600-0587.1999.tb00510.x

Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., & Hashimoto, H. (2004). A continuous satellite-derived measure of global terrestrial primary production. *BioScience*, *54*, 547–560. https://doi.org/10.1641/0006-3568(2004)054[0547:ACSMOG]2.0.CO;2

Sanders, N. J. (2002). Elevational gradients in ant species richness: Area, geometry, and Rapoport's rule. *Ecography*, *25*, 25–32. https://doi.org/10.1034/j.1600-0587.2002.250104.x

Soria-Auza, R. W., Kessler, M., Bach, K., Barajas-Barbosa, P. M., Lehnert, M., Herzog, S. K., & Böhner, J. (2010). Impact of the quality of climate models for modeling species occurrence in countries with poor climatic documentation: A case study from Bolivia. *Ecological Modelling*, *221*, 1221–1229.

Storch, D., Bohdalková, E., & Okie, S. (2018). The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecology Letters*, *21*, 920–937. https://doi.org/10.1111/ele.12941

Storch, D., Evans, K. L., & Gaston, K. J. (2005). The species–area–energy relationship. *Ecology Letters*, *8*, 487–492. https://doi.org/10.1111/j.1461-0248.2005.00740.x

Szewczyk, T., & McCain, C. M. (2016). A systematic review of global drivers of ant elevational diversity. *PLoS ONE*, *11*, e0155404. https://doi.org/10.1371/journal.pone.0155404

Turner, D. P., Ritts, W. D., Cohen, W. B., Gower, S. T., Running, S. W., Zhao, M., … Ahl, D. E. (2006). Evaluation of MODIS NPP and GPP products across multiple biomes. *Remote Sensing of Environment*, *102*, 282–292. https://doi.org/10.1016/j.rse.2006.02.017

BIOSKETCH

Florian Bärtschi completed his MSc in the research team of J.B., which focused on insect macroecology and the environmental impacts on biodiversity.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Bärtschi F, McCain CM, Ballesteros-Mejia L, Kitching IJ, Beerli N, Beck J. Elevational richness patterns of sphingid moths support area effects over climatic drivers in a near-global analysis. *Global Ecol Biogeogr*. 2019;28:917–927. https://doi.org/10.1111/geb.12903