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

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## 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 to 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, as well as 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 richness variation.

**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 sphingid richness variability. 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, i.e.  geometrid moths, which highlights the importance of understanding higher-clade differentiation in ecological responses, within insects as well as in other groups.

## 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 (Rahbek, 2005; McCain & Grytnes, 2010; Kessler *et al.*, 2011; Quintero & Jetz, 2018). 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 as 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 with 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). While there is theoretical underpinning of hypothesized direct temperature effects (Rhode, 1992; Brown *et al*., 2004), precipitation effects presumably act rather indirectly via their effect on plant productivity (Evans *et al.*, 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; Rosenzweig, 1995; Rahbek, 2005; McCain, 2007b). However, just 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, due 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 *et al*., 2008). Here we utilized 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; e.g., whether it acts via food and population sizes (the 'more individuals-hypothesis'; Rosenzweig, 1995; Classen *et al.*, 2015; Storch *et al*., 2018), or whether productivity per area, or summed productivity across the entire area of an ecological zone, is the relevant variable (Storch *et al*., 2005; Hurlbert & Stegen, 2014). 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 geometric 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 (Dunn *et al.*, 2007; Colwell *et al.*, 2016; Beck *et al.*, 2017).

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 annual mean 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 analyzed effects with multivariate models after controlling for richness variation 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 may elucidate the impact of phylogenetic histories and resulting trait variation on such patterns. We provide raw and processed data for future analyses.

## Methods

### 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 ca. 1987 species; Kitching *et al.*, 2018), and their attraction to artificial light sources, which provides a robust means of field collecting, has 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 recent 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 *et al.*, 2017). Many hawkmoth species have excellent flight capacity and some cover huge areas within their geographic range, whereas others are geographically restricted endemics (Grünig *et al.*, 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 tightly linked to those of hawkmoths (Beck *et al.*, 2006).

## 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; see Appendix S1for detailed methods and map).

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 below for criteria), we had three datasets to repeat our analyses and compare consistency.

## 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 ca. 20-year endeavor, taxon and locality information was carefully checked and edited whenever sources seem 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 found in Ballesteros-Mejia *et al.* (2017). As many original records did not contain elevation information, we extracted these from a high-resolution digital elevation model (DEM; 30 arcsec ≈ 90 m; Robinson *et al.*, 2014; see also Fattorini, 2014) based on latitude and longitude information. After excluding data with imprecise coordinates as well as 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 $r^2 = 0.753$ in a correlation of original and extracted DEM elevation data. Acknowledging the trade-off between data quality and amount of data available for analysis, as well as replicate analyses based on range maps (see below), we judged this acceptable and utilized ca. 43,000 point records for 744 species located within the above-defined mountain ranges.

Point records are necessarily undersampled, as 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 1500 m in a mountain range, 60 percent 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-model predicted richness. This resulted in 40 'lenient'-selected mountain ranges. For the 'strict' selection we required a minimum elevation range of 2000 m, 70 percent 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 at least 75 percent of SDM-model predicted richness. This resulted in 19 'strict'-selected mountain ranges. See S1 for map, data and method details.

### Range map data

Ballesteros-Mejia *et al.* (2017) provided range maps for all hawkmoth species in the region at 5 x 5 km resolution. Ranges were estimated using species distribution models (SDMs) informed from the point locality data compilation described above, as well as 13 climate (e.g., annual temperature range, precipitation, etc.) and 3 vegetation variables (percentage of trees, herbs and bare ground). SDM output was then expert-vetted and edited for dispersal limitation. Resulting data was 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 2000 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 removing a larger number of mountain ranges from analyses, whereas range maps are more complete but are estimates, so 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 consistency of conclusions. As the results are highly concordant, we present in the main text mainly modelled data, whereas point data are in appendices where appropriate.

## 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. As 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; low plateau with midpeak – LPMP) according to criteria outlined in McCain (2010) and McCain & Grytnes (2010). We classified mountain ranges as arid (incl. semi-arid) and humid according to the UNEP humidity index map (Deichmann & Eklundh, 1992) to compare for consistent differences in moth richness patterns. We tested, in particular, for associations of midpeak patterns with arid mountain ranges (McCain, 2007a; 2009) using contingency table $\chi^2$ tests.

## Environmental predictors

Five predictor variables were tested for effects on elevational species richness, including area of the 100 m elevational bands (A), mean annual temperature (T), annual precipitation (P), net primary productivity (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 $\geq 0$ °C (as a proxy of temperature of the growing season) but since 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 *et al.*, 2005) at 30 arcsec (~1 km) resolution using GIS tools. Global NPP was extracted from MODIS17 (Heinsch *et al.*, 2003, Running *et al.*, 2004) in 30 arcsec 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 (reprojected 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).

## 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. Prior to 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 to 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 to earlier studies using this approach (e.g., McCain, 2009; Beck *et al.*, 2017).

To identify environmental drivers more rigorously in a multivariate setting, we used generalized linear models (GLM, Gaussian error) with pooled data (i.e., N = number of all 100 m bands across all mountain ranges). However, prior to 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 above). We did this to limit regional effects of richness variation (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; see Beck *et al.*, 2017 for similar reasoning and application). 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 vs. 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 & Kotze (2010).

## 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%; Fig. 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 due to chance (contingency table analysis: N = 86, $\chi^2 = 19.0$, $p < 0.001$). For point locality data the associations are somewhat weaker but still significantly supported (lenient: N = 40, $\chi^2 = 9.4$, $p = 0.002$; strict: N = 19, $\chi^2 = 4.4$, $p = 0.036$). The elevation of richness peaks was not affected by mountain-wide species richness (see

Appendix S1 for data and implications). Appendix S2 shows plots of elevational richness for each region; the data are published as Appendix S3.

Preliminary univariate comparisons (Appendix S4) suggested area (A) as the strongest single predictor of elevational species richness. Temperature (T) and productivity variables (NPP, SNPP) were less strongly supported, whereas we found no support for precipitation (P) as a single, univariate driver of richness (median $r^2 < 0.01$). 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 $r^2 < 0.1$ to $r^2 > 0.9$). These first assessments were supported by model-based as well as point locality data (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-)$R^2 = 0.689$; points-lenient: $R^2 = 0.715$; points-strict: $R^2 = 0.795$), whereas models containing SNPP are weaker. They are highly concordant in their AIC-based assessment among the three data sources (Appendix S5). Averaged coefficients (Fig. 2) clearly point to the paramount importance of A in predicting richness in all three datasets, followed by T, NPP and SNPP, while P was always a non-significant predictor. Alternative analyses (using untransformed richness and Poisson- error models) confirmed most above effects but were ambiguous on whether there is an effect of P or not (Appendix S6; see there also for discussion on the necessity and reliability of this approach for our data).

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 (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 strongly correspond, with geometrids featuring mid-peak (or LPMP) patterns more often than sphingids. This may indicate that taxon-specific effects contribute to shape these patterns (see Appendix S8 methods and details).

## 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 (Figs. 1, Appendix S1). This allowed us to compare the variation in species richness patterns across ecologically diverse zones with different biogeographic histories, and test hypotheses on environmental drives of richness for their global generality. Consistent for different data types (modelled range maps, 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 (Fig. 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).

### 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 (Rahbek, 1995; McCain 2007b) and plants (Karger *et al*., 2011). It is also consistent with non-elevational species-area relationships (SAR; 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 (Rosenzweig & Ziv, 1999; Romdal & Grytnes, 2007). Consistent with this idea, many elevational studies based on local samples of richness also reported correlations with area (e.g., Kessler *et al*., 2009; 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; Appendix S4), area alone cannot account for the highly prevalent richness midpeaks (or similar curvilinear patterns; Fig. 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 below) could lead to a variation in richness patterns in different parts of the world (as observed; Fig. 1; McCain, 2007a, b), whereas the mid-domain effect (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 temperature effects on richness, it is unwise *a priori* to ‘correct’ richness for area via residuals from the Arrhenius-function (as is commonly done; e.g., Rahbek, 1995; Sanders, 2002; Karger *et al*., 2011). 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 due 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 $z = 0.27$ 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 (Appendix S9), results of which highlighted the problems listed above.

Third, area effects on richness, even when strongly supported as a single driver in elevational studies (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 only be caused 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 kilometers 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 mid-domain effect, where the same assumption of *a priori*-set, species-specific elevational ranges had sparked a very controversial discourse (e.g., Hawkins *et al*., 2005).

## Temperature and productivity, but not precipitation

Our multivariate analyses indicated independent, partial effects of temperature as well as productivity (Fig. 2); temperature is also supported as a single 'main driver' of richness (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 (Rhode, 1992), for example through its effect on chemical reaction speeds and metabolism (e.g., the 'metabolic theory of ecology'; Brown *et al*., 2004; Allen *et al*., 2007). 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 as well as evaporation rates, but its effect on richness, empirically shown here and in many other studies (Mittelbach *et al*., 2001; Ballesteros-Mejia *et al*., 2017) 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 (Mittelbach *et al*., 2001; Evans et al. 2005; Storch *et al*., 2005; Allen *et al*., 2007), 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-diversity), yielding mixed results (Classen *et al*., 2016; McCain *et al*., 2018) and tests for two or three variables are also equivocal. Because overall productivity may not necessarily be tightly linked to the fraction of productivity available to a given taxon (e.g., due 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 as well as productivity could affect richness may be their 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; Storch *et al.*, 2005; Jetz & Fine, 2012; Hurlbert & Stegen, 2014). 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 rather weaker ones) for sphingid moths. Nevertheless SNPP was a stronger single 'main' driver of richness than NPP alone (Appendix S4). Further evaluations of SNPP by exploring landscapes with uncorrelated or even opposite area and NPP gradients, may thus be informative.

Our analyses reject any direct effect of precipitation on richness (but see 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 to the base of the mountains (as precipitation increases with elevation across the mountains; Barry, 1992; McCain & Colwell, 2011). Thus, we suggest that earlier reports of precipitation effects on richness may in parts have been indirect due 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 may 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 (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 mid-domain effect (Colwell *et al*., 2016), past climatic change (Colwell *et al.,* 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, is 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 region of high, long-lasting human disturbance. We could not rigorously address this hypothesis here due to uncertainties of the timing of human disturbance in relation to point record data sampling in our sphingid data. However, preliminarily, Fig. 1 does not lend support to low-elevation disturbance and midpeaks. For example, whereas the Alps, as a region of heavy human impact for many centuries, exhibit a midpeak (consistent with the hypothesis), the neighboring 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) concluded the same for geometrid moth data across the globe.

Concurrent with elevational studies on various taxa (McCain, 2007a,b; Kessler *et al*., 2011; McCain & Beck, 2016; Beck *et al*., 2017) 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 (Appendix S2). Most point data indicate overall lower richness than model data (probably due to undersampling in point records), but a similar richness trend with elevation. Furthermore, some mountains richness patterns differ because point records often show a faster decline of richness towards high elevations compared to model data. Possibly high elevations are particularly undersampled, likely due to difficulties of access. Alternatively, model data may overestimate ranges at high elevations in particular. SDMs were fitted to point records including data from lowland regions (not analyzed in this study). If a species occurred widely across lowlands of a given climate, it may also be predicted on a mountain of similar climate even if mountain-specific environmental circumstances may cause its absence. Because mountains overall have a small area compared to lowlands, their impact on SDM fitting and evaluation may be too small to avoid such effects. Furthermore, the grain size of SDMs (5 km) may 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 (Appendix S2), both pointing towards random effects. To reiterate, both point records and modelled data led to very similar conclusions with regard to the environmental drivers of richness.

This 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 may help to formulate and test novel hypotheses on evolutionary impacts on the environment-richness relationship. Data on geometrid moths (i.e., inchworms) from Beck *et al*. (2017; see Appendix S8) show predominantly midpeak richness patterns irrespective of the geographic position of gradients, whereas we have shown here strong variation in patterns for sphingids particularly between arid and humid mountains (Fig. 1). The likely causes for the incongruent patterns between geometrid and sphingid moths is currently far too complex for speculation, as geometrids and sphingids differ in many aspects of their ecology − among which are body size, mobility and larval host plant specificity (see Appendix S8 for further discussion). Future, comprehensive multi-gradient assessments for other major moth taxa (such as arctiine erebids; Brehm, 2009; pyraloids; Fiedler *et al.*, 2008) may help to pinpoint more clearly how ecological differences co-vary with richness patterns. Due to their high diversity, potential for experimental studies, and more detailed descriptive analyses that include more difficult-to-measure variables (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 *et al*., 2012). For birds, the arguably best-studied taxon in macroecology, Quintero & 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, raw as well as condensed for elevational analysis, we help make sphingid moths a part of such comparative endeavors, possibly as the presently only insect representative.

## Outlook

Our results on global-scale elevational richness pattern variability as well as 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; Kreft & Jetz, 2007; Fritz *et al*., 2017). 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 pattern, 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 just 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 not (McCain, 2007a). Pseudo-$R^2$ values between 0.7 and 0.8 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 while 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 due to their natural replication, exclusion of unwanted dispersal limitation effects, and breadth of environmental gradients within small study regions, among other advantages.

## Supporting Information

**Appendix S1** Mountain ranges used for analyses

**Appendix S2** Plots of elevational species richness for all mountain ranges

**Appendix S3** Richness data per 100m elevation band for all mountain ranges (csv file)

**Appendix S4** Univariate correlations

**Appendix S5** AIC-based model comparisons

**Appendix S6** Alternative modelling

**Appendix S7** Humid vs. arid mountains

**Appendix S8** Comparison of geometrid and sphingid elevational patterns

**Appendix S9** *A priori* correction for area

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## Biosketch

Florian Bärtschi completed his MSc in the research team of JB, which focussed on insect macroecology and the environmental impacts on biodiversity. *Author contributions*: FB and JB designed the study and analysed data, supported by NB and CMM; JB, LB-M and IJK provided sphingid moth data; JB, FB and CMM wrote the manuscript, with input from all authors.

## Data availability statement

Raw distribution records can be viewed, model-based range maps for all non-American sphingid species can be viewed and downloaded* at www.mol.org.

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

*) will be made accessible upon publication

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FIGURE CAPTIONS

**Fig. 1** Mountain ranges and their prevailing richness pattern for sphingid moths (LPMP = low plateau-midpeak; pattern definitions and inset sketches based on McCain & Grytnes 2010). "No pattern" identifies regions that did not fit any of these categories (see Appendices S2 & S3 for plots and data of all richness patterns).

**Fig. 2** Averaged standardized coefficients (bars; AIC weighted) and 95% confidence intervals (whiskers) from multivariate linear models (see Appendix S5 for model details; S = strict selection, L = lenient selection). Positive associations were expected for all predictors (Appendix S4).