

Spatial variation in direct and indirect effects of climate and productivity on species richness of terrestrial tetrapods

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Abstract

Aim: We aimed to dissect the spatial variation of the direct and indirect effects of climate and productivity on global species richness of terrestrial tetrapods.

Location: Global.

Time period: Present.

Major taxa studied: Terrestrial tetrapods.

Methods: We used a geographically weighted path analysis to estimate and map the direct and indirect effects of temperature, precipitation and primary productivity on species richness of terrestrial tetrapods across the globe.

Results: We found that all relationships shift in magnitude, and even in direction, among taxonomic groups, geographical regions and connecting paths. Direct effects of temperature and precipitation are generally stronger than both indirect effects mediated by productivity and direct effects of productivity.

Main conclusions: Richness gradients seem to be driven primarily by effects of climate on organismal physiological limits and metabolic rates rather than by the amount of productive energy. Reptiles have the most distinct relationships across tetrapods, with a clear latitudinal pattern in the importance of temperature versus water.

KEYWORDS

biodiversity gradients, climate, geographically weighted regression, metabolic theory, non-stationarity, path analysis, productivity, species–energy relationship, structural equation modelling, water–energy hypothesis

1 | INTRODUCTION

For centuries, ecologists have been trying to uncover the processes underlying geographical gradients of biodiversity, such as the striking increase in richness from the poles to the tropics. Diversity gradients are known to result from multiple factors operating non-independently and at different scales (Belmaker & Jetz, 2015; Mittelbach et al., 2007; Rangel et al., 2018). Current environmental factors, especially those related to climate (temperature and

precipitation) and primary productivity, are among the strongest predictors of richness for terrestrial and aquatic organisms across multiple regions and spatial scales (Field et al., 2009; Hawkins et al., 2003). However, studies rarely consider how climate and productivity are interrelated and that their relative importance to diversity patterns potentially varies across geographical space (Gouveia et al., 2013; Hawkins et al., 2003). Here, we use a geographically weighted path analysis to revisit hypotheses on how climate and productivity relate to species richness of terrestrial tetrapods

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globally by allowing direct and indirect effects to vary geographically. We assess these relationships for the four terrestrial tetrapod groups (amphibians, birds, mammals and reptiles), which are likely to differ in their environment–richness relationships because of their differences in physiology (ecto- and endotherms), rate of niche evolution, and dispersal ability (Buckley et al., 2012; Qian, 2010; Rolland et al., 2018; Stevens et al., 2014).

Several hypotheses have been proposed to explain why species richness tends to be greater in more productive, warmer and wetter environments (Clarke & Gaston, 2006; Currie et al., 2004; Field et al., 2009). The “more individuals hypothesis” proposes that species richness increases with productivity because more individuals can be supported if there is a greater amount of energy present in a food web, thus increasing the number of viable populations and reducing extinction rates (Brown, 1981; Hutchinson, 1959; Storch et al., 2018; Wright, 1983). Increasing productive energy is also proposed to increase richness by providing greater diversity of niches, thus facilitating the coexistence of more species in this increased niche space (i.e., “niche diversity hypothesis”; Chase & Leibold, 2002; Evans, Warren, et al., 2005; Hurlbert & Jetz, 2010). Climate variables such as temperature and precipitation are expected to influence species richness through the thermal tolerances and physiological requirements of organisms (i.e., “physiological tolerance hypothesis”; Currie et al., 2004). In particular, ectotherms are more dependent on climate than endotherms, given their need for external sources of heat to regulate body temperature and, in the case of amphibians, water to maintain metabolism and reproduction (Buckley et al., 2012). Another group of theories, known as the “metabolic theory” and the “evolutionary speed hypothesis”, propose that a positive temperature–richness relationship arises for all groups because higher thermal and kinetic energy is linked to faster metabolic, mutation and speciation rates (Allen et al., 2006; Brown et al., 2004; Rohde, 1992).

Disentangling the different mechanisms behind the species–climate and species–productivity relationships is difficult because they do not act in isolation and are therefore not mutually exclusive (Clarke & Gaston, 2006; Currie et al., 2004; Evans, Warren, et al., 2005), because productivity is strongly dependent on climate (Šímová & Storch, 2017). Given that productive energy does not increase monotonically with temperature and precipitation (Šímová & Storch, 2017), positive climate–richness relationships might not be observed when indirect effects of climate, through productivity, are considered. Although these two pathways (Figure 1) are usually acknowledged, indirect paths are generally ignored in statistical analysis (Allen et al., 2012; Hawkins et al., 2003). Thus, it is unclear to what extent the effects of precipitation and temperature on richness act directly via physiological controls and constraints of organisms and metabolic rates and to what extent they act indirectly, mediated by productivity (i.e., mediation effect; Grace, 2006).

Additional complexity is added to the study of climate– and productivity–richness relationships because they vary among taxonomic groups and geographical regions (Hawkins et al., 2003; Qian, 2010; Whittaker et al., 2007). In the warm tropics, where temperature is not usually a physiological limitation, water availability

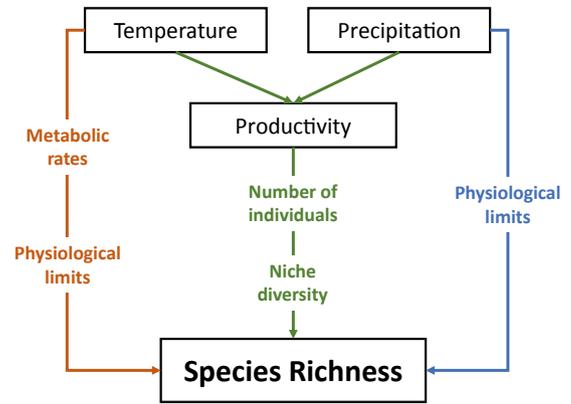


FIGURE 1 Path model depicting the analysed directional relationships and the underlying hypotheses linking different energy measures to species richness [Colour figure can be viewed at wileyonlinelibrary.com]

should be a stronger limiting factor of species richness. In contrast, the lower input of thermal energy in temperate to arctic regions should lead to temperature and productivity being the primary limiting factors of species richness. This latitudinal variation in the relative importance of water versus energy on species richness is termed the “water–energy hypothesis” (Hawkins et al., 2003). The spatial variation in the relative importance of predictors might explain, in part, why support for hypotheses varies across studies and regions (Cassemiro et al., 2007).

Here, we tackle the spatial non-stationarity of direct and indirect pathways connecting climate and productivity with global species richness using a geographically weighted path analysis. We use a distance-weighted moving window (Fotheringham et al., 2002) to calibrate the regression models locally and estimate path coefficients (i.e., standardized partial slope coefficient of a multiple regression) along continuous global gradients, removing the need to split the data arbitrarily into geographical subregions or latitudinal bands. This approach allows us to test hypotheses on environmental richness relationships comprehensively at broad spatial scales and to map the relative strength of the effect of each environmental condition on diversity across the globe, potentially identifying new patterns that could be revealed only because of the exploratory nature of the analysis.

We expect to find the well-known positive direct effects of all predictors on species richness (Currie et al., 2004; Qian, 2010; Whittaker et al., 2007), with the strength of the relationships following a spatial pattern inverse to that of the predictor itself (e.g., species–temperature relationships becoming stronger with decreasing temperatures). Given the strong limiting effect imposed by climate on organismal physiological tolerances and metabolic rates, we hypothesize that direct effects will generally be stronger than the indirect ones, but indirect ones should also influence species richness patterns. The strong physiological dependence of ectotherms on climatic conditions (Buckley et al., 2012) should lead to reptiles being influenced more strongly by the direct effect of temperature (Coops et al., 2018; Powney et al., 2010; Whittaker

et al., 2007) and amphibians by the direct effect of precipitation (Buckley & Jetz, 2007) across most of the globe. In contrast, endotherms are hypothesized to be constrained mostly by the amount of productive energy (Buckley et al., 2012; Pough, 1980; Qian, 2010). Overall, across the four taxonomic groups, when considering direct and indirect pathways to diversity, we expect stronger effects of precipitation on richness in the tropics and temperature in regions poleward of the tropics, as proposed by the water–energy hypothesis (Hawkins et al., 2003). This latitudinal pattern is expected to be stronger for amphibians and reptiles (ectotherms) than for mammals and birds (endotherms) (Qian, 2010; Whittaker et al., 2007).

2 | METHODS

2.1 | Datasets

We used range maps of the global distribution of each of the four terrestrial tetrapod groups from publicly available databases (BirdLife International & NatureServe, 2015; IUCN, 2017; Roll et al., 2017), totalling 10,425 species of birds, 5,408 mammals, 6,515 amphibians and 10,066 reptiles after the exclusion of introduced species. We overlaid range maps with a grid composed of squared cells of 110 km × 110 km at the Equator using the Behrman equal-area projection and calculated the number of species whose range overlapped with each cell to derive richness maps for each taxonomic group.

We selected mean annual precipitation as a measure of water availability, mean annual temperature as a measure of thermal energy, and mean annual net primary production (NPP) and fraction of photosynthetically active radiation (fPAR) as measures of productive energy. We obtained data on temperature and precipitation from CHELSA (Karger et al., 2017) at 0.008° × 0.008° resolution and aggregated it at 1° × 1° resolution. The NPP estimates the amount of biomass produced per unit area and time, whereas the fPAR measures the fraction of the incident photosynthetically active radiation (PAR) that is absorbed by plants (Šímová & Storch, 2017). At large spatial scales, NPP can be estimated using different approaches that yield fairly similar results (Šímová & Storch, 2017). We summarized mean annual NPP and fPAR over the years of 2003 to 2015 obtained from remotely sensed imagery of the MODIS sensor onboard the NASA TERRA satellite (MOD17A2 product). We gathered fPAR data from the Dynamic Habitat Indices (Hobi et al., 2017) and divided the annual cumulative fPAR over the 46 measures taken within each year. We computed the mean annual value of each environmental variable for each cell in our grid using the “raster” package (Hijmans, 2016) in the R statistical environment.

2.2 | Analysis

Path analysis is useful for exploring the complex web that connects environmental drivers and biodiversity by partitioning the total association between predictors and response variables (i.e.,

total effects) into direct and indirect effects. We designed a path model based on the proposed hypotheses of how different measures of energy might be related directly and indirectly with species richness (Figure 1). Given that it is unrealistic to assume that these relationships are the same across the geographical space (Gouveia et al., 2013; Hawkins et al., 2003), we relaxed the assumption of spatial stationarity by using a geographically weighted path analysis (GWPath; code available in Supporting Information Appendix S1). Under the GWPath framework, path coefficients can vary regionally because of a distance-based Gaussian weighting function that assigns greater weights to nearby cells, similar to a geographically weighted regression (GWR; Fotheringham et al., 2002). We implemented GWPath using the “gwr” function of the “spgwr” R Package (Bivand & Yu, 2017).

Deciding on the radius of the spatial kernel function (bandwidth) for GWPath is non-trivial, and the radius should be chosen based on biological and statistical reasons (Farber & Páez, 2007). Previous global-scale studies suggest that radii of c. 1,000 km capture patterns in coefficient variation of environmental drivers of biodiversity (Davies et al., 2011; Ficetola et al., 2017). Therefore, we used this value as a guide to explore visually a series of radii ranging from 700 to 2,000 km at 100 km intervals. If a radius is too large, the analysis converges back to the spatial stationarity assumption, and if it is too narrow, the model overfits residual variations (Fotheringham et al., 2002). Overfitting leads to large shifts in the coefficients among nearby cells, causing the formation of coefficient islands (Fotheringham et al., 2002). Consistent with previous work, we found that a bandwidth of 1,000 km best captured large-scale patterns in coefficient variation, because it yielded results similar to those from coarser bandwidths while avoiding overfitting.

Our path model is composed of two multiple regressions with species richness and productivity as endogenous/response variables: (1) species richness ~ productivity + precipitation + temperature and (2) productivity ~ precipitation + temperature (Figure 1). To compare coefficients among taxonomic groups, geographical regions and connecting paths, we fitted the same path model to each vertebrate group across the entire geographical space using standardized response and predictor variables (z-scores). We ran all analyses twice, once using NPP as the measure of productive energy and once using fPAR. Given that the results were qualitatively and quantitatively similar (see Supporting Information Figures S1–S20), we chose to display and discuss the results from the model with NPP in the main text. We ln-transformed all variables because of the potential non-linearity of species–energy relationships, which led to an increase in the coefficient of determination (R^2) in most focal cells for all taxonomic groups apart from mammals (Supporting Information Figure S1). We assessed multicollinearity among predictors by calculating variance inflation factors (VIFs) and condition numbers (CNs) for each focal cell. Both measures indicated that multicollinearity was not a problem in our analysis, because VIF scores were lower than eight (mean ± SD: 1.56 ± 1.06; Supporting Information Figure S2) and CNs were < 40 (mean ± SD: 10.80 ± 7.87; Supporting Information Figure S3) (Dormann et al., 2013).

3 | RESULTS

3.1 | Direct effects

As predicted, the geographically weighted path analysis revealed that direct effects of productivity, temperature and precipitation were mainly positive, but it also uncovered unexpected exceptions (Figures 2 and 3). For all taxonomic groups, our analysis revealed a latitudinal gradient in the strength of the relationship between productivity and species richness, with stronger coefficients at higher latitudes (Figure 3a–d). Global or near global positive productivity–richness relationships were confirmed for birds, mammals and amphibians (Figure 3a–c), whereas productivity was negatively related to richness of reptiles, mainly poleward of the Tropic of Cancer (Figure 3d).

Temperature was directly associated with increases in species richness of reptiles globally, with stronger coefficients outside the tropics (Figure 3h). However, temperature was negatively associated with richness of birds, mammals and amphibians in much of the tropics, especially in Africa and Asia (Figures 3e–g; Supporting Information Figures S4–S6), and in South America and Australia for birds (Supporting Information Figure S4). Precipitation showed a positive relationship everywhere only for amphibian richness (Figure 3k). In contrast, we found negative effects of precipitation on species richness of birds and mammals in North America (Figure 3i,j) and of reptiles at high latitudes and in parts of Australia (Figure 3l; Supporting Information Figures S4, S5 and S7).

3.2 | Indirect effects

Temperature and precipitation were also related to species richness indirectly via productivity; however, indirect effects were often weaker than direct ones (maps in Figure 3 cf. maps in Figure 4; Supporting Information Figure S8). Indirectly, the effect of temperature on richness was weakly positive above the Tropic of Cancer and negative or zero beneath it for all groups (Figure 4a–d and Supporting Information Figures S4–S7). In general, a negative

temperature–richness relationship was more common in the indirect (via productivity) than direct paths (Figure 3e–h cf. Figure 4a–d).

As with temperature, the direct and indirect (via productivity) effects of precipitation on species richness showed differing spatial patterns for different groups of tetrapods. Indirect effects of precipitation on richness were consistently positive for all groups except for reptiles, where the relationship was mostly negative at high latitudes and nearly zero elsewhere (Figure 4e–h; Supporting Information Figures S4–S7). In general, the direct and indirect effects of precipitation on reptile richness were weaker than in the other groups (Figure 3i–l cf. Figure 4e–h). The consistent indirect positive effects of precipitation on the richness of birds, mammals and amphibians arise from the mainly positive effect of precipitation on productivity, which in turn, is associated with an increase in species richness of these taxonomic groups (Supporting Information Figures S1–S6).

3.3 | Relative importance of climate and productivity

The relative strength of the effects of productivity, temperature and precipitation on species richness was not constant across the globe and differed among the four taxonomic groups (Figures 2–4; Supporting Information Figure S9). As expected, when comparing the total effects (i.e., sum of direct and indirect paths) of the three environmental conditions across taxonomic groups, precipitation was a stronger predictor of amphibian richness (shades of pink in Figure 5c) and temperature of reptile richness (shades of yellow in Figure 5d). For reptiles, we found a clearer latitudinal pattern of precipitation being more important in much of the tropics, whereas temperature was important outside of the tropics (Figure 5d), a pattern that emerged only when the indirect effects were considered (Supporting Information Figure S9). For mammals and birds, our model showed that temperature and productivity were relatively more predictive above the Tropic of Cancer, whereas temperature and precipitation were more predictive below the Tropic of Cancer (Figures 5a,b; Supporting Information Figures S4 and S5).

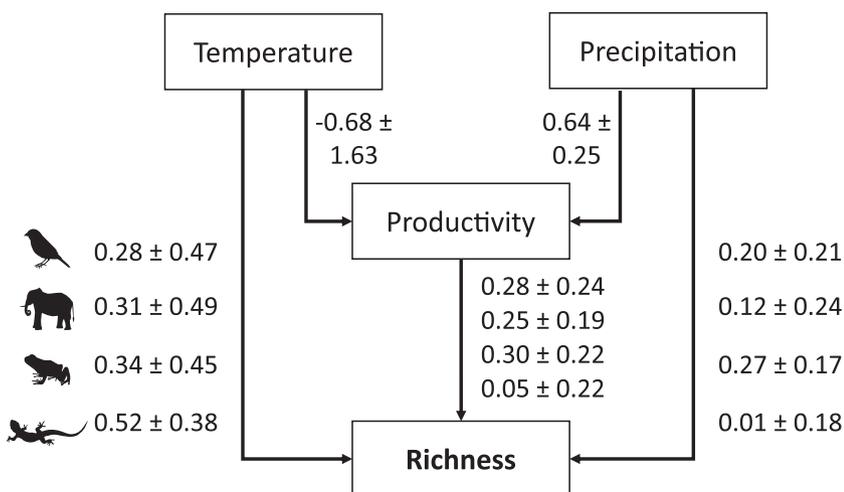


FIGURE 2 Path model depicting the mean \pm SD of the path coefficients (i.e., standardized beta coefficients) over the globe. The direct effects of temperature, productivity and precipitation on the species richness of each of the terrestrial tetrapod groups are ordered as represented by their silhouettes: birds, mammals, amphibians and reptiles. Silhouette images were taken from www.freepik.com

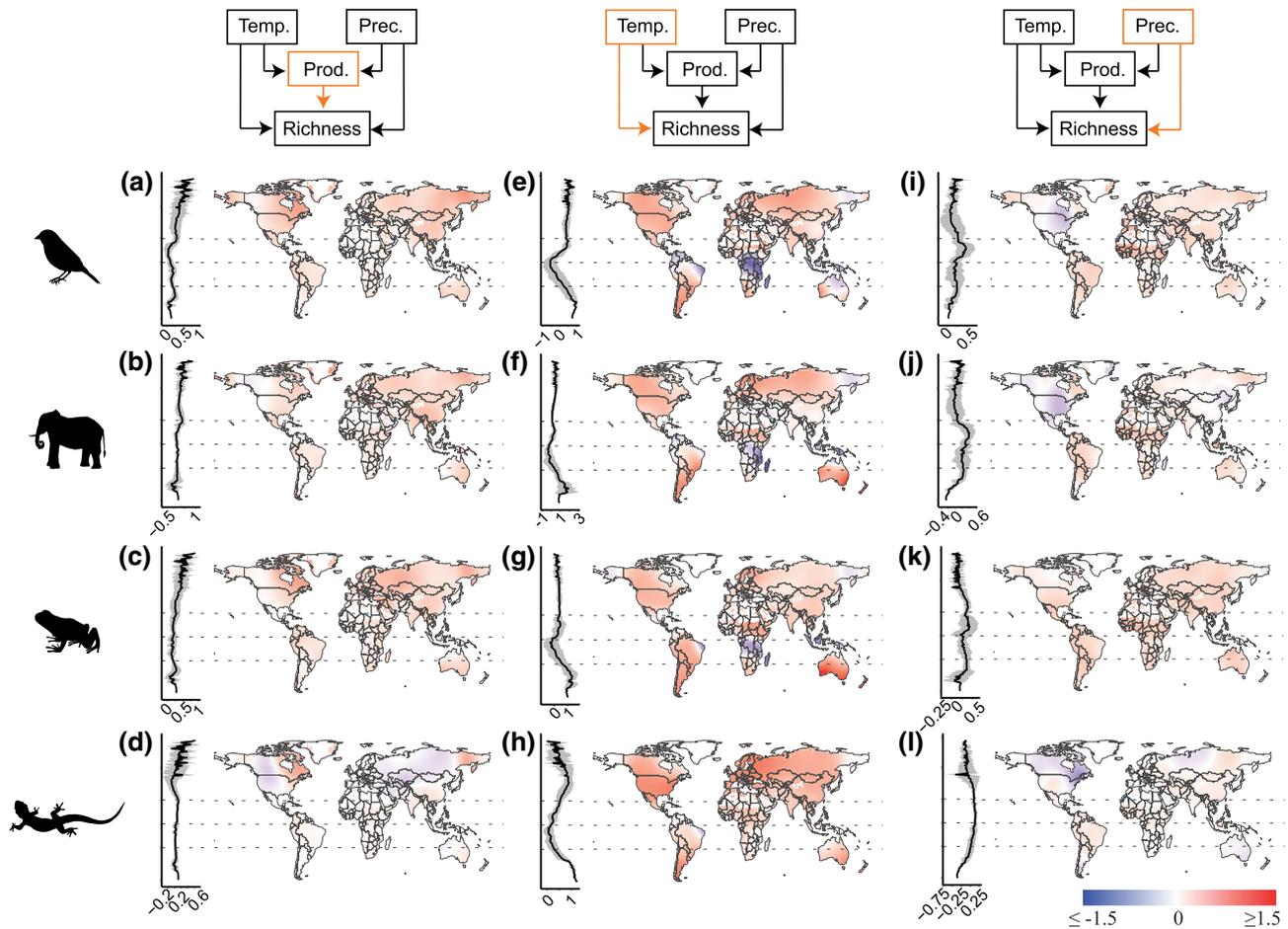


FIGURE 3 Direct coefficient strengths between species richness of terrestrial tetrapods and productivity (Prod.; a–d), temperature (Temp.; e–h) and precipitation (Prec.; i–l), according to the geographically weighted path model. Path coefficients are standardized and are mapped using the same colour scale, allowing direct comparison of their magnitudes. Silhouettes indicate the organism group for which the result is mapped. The full set of coefficient maps for all four taxonomic groups is available in the Supporting Information (Figures S4–S7). The line plot next to each map summarizes the path coefficient across latitude, plotted with the mean (black line) and the standard deviation (grey area). Dotted lines indicate the Tropic of Cancer, the Equator and the Tropic of Capricorn, respectively, from top to bottom. Silhouette images were taken from www.freepik.com [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

The relationship between climate and species richness is one of the most ubiquitous in ecology (Evans, Warren, et al., 2005; Field et al., 2009), yet it remains uncertain how much of the climatic effects on diversity act directly or indirectly via productivity and the extent to which these relationships are spatially stationary. Using a new approach, we mapped a path analysis that explicitly evaluates the importance of temperature, precipitation and productivity for explaining species richness of terrestrial tetrapods. Overall, climate and productivity–richness relationships varied considerably in magnitude, and sometimes even in direction, across the globe, depending on the variable and the pathways connecting it to richness (i.e., direct and indirect) and taxonomic group. We found that nearly everywhere climate was a stronger driver of richness than productivity (Figure 5). In addition, direct effects of climate were often stronger than their indirect effects, suggesting that the influence of temperature and precipitation on species richness is attributable mostly to

metabolic and physiological processes rather than to niche diversity and the number of individuals supported by the environment. Also, we detected a clear latitudinal gradient in the relative importance of water only versus temperature, in support of the water–energy hypothesis, among reptiles and only when we considered both direct and indirect pathways. Taken together, our results suggest that when dissecting the environment–diversity relationships, the global pattern of constraints on biodiversity is much more complex than previously anticipated.

The direct effects of temperature, precipitation and productivity on species richness were mainly positive, in agreement with the metabolic theory and the physiological tolerance, the more individuals and the niche diversity hypotheses (Currie et al., 2004; Evans, Warren, et al., 2005). Nevertheless, by allowing relationships to vary geographically, without splitting data arbitrarily into geographical subregions, our analysis revealed spatially structured exceptions to the well-known positive relationships, consistent with a previous finding for tetrapods in Australia (Powney et al., 2010) and for

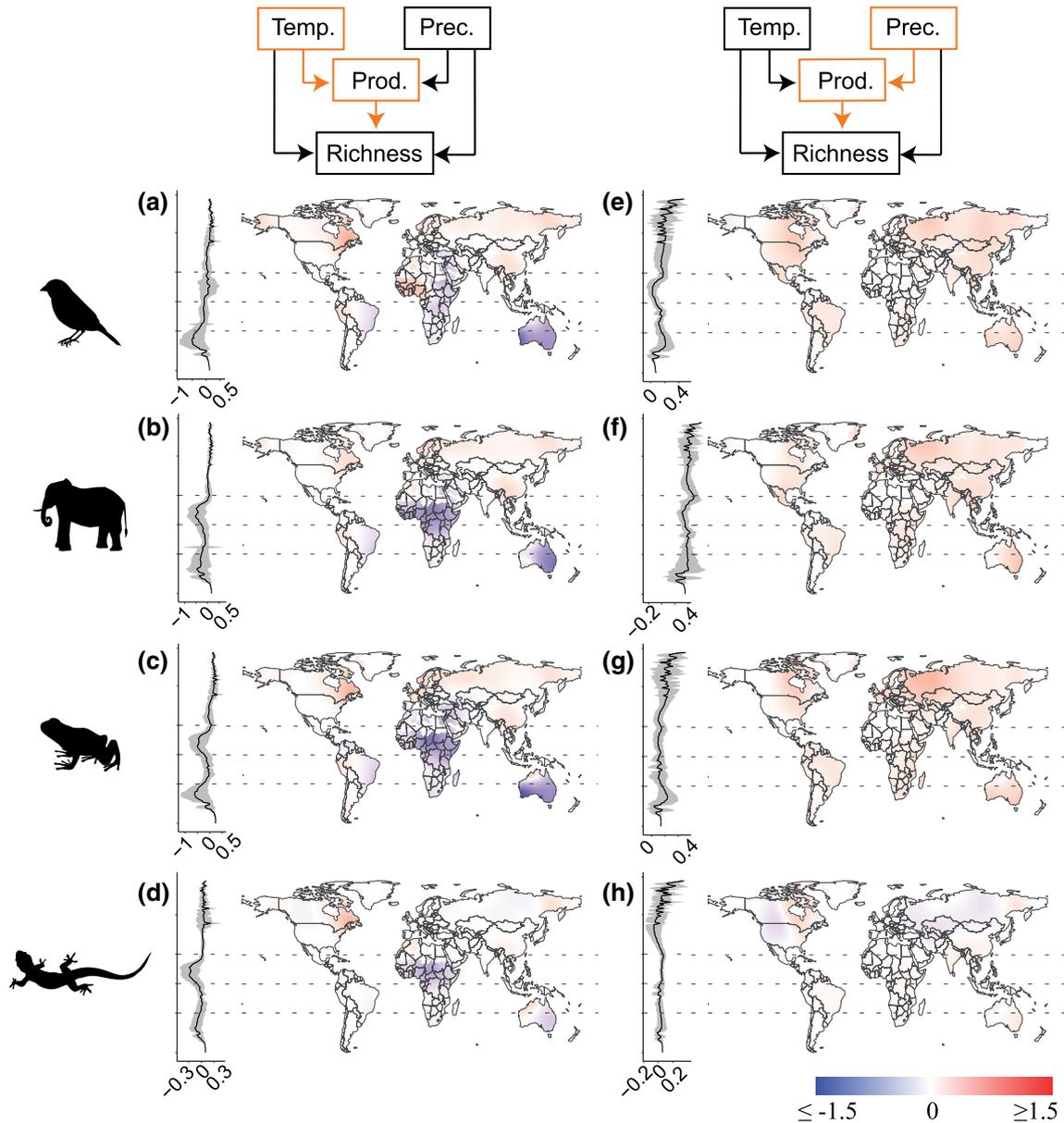


FIGURE 4 Indirect coefficient strengths between species richness of terrestrial tetrapods and temperature (Temp.; a–d) and precipitation (Prec.; e–h), according to the geographically weighted path model. Path coefficients are standardized and are mapped using the same colour scale, allowing direct comparison of their magnitudes. Silhouettes indicate the organism group for which the result is mapped. The full set of coefficient maps for all four taxonomic groups is available in the Supporting Information (Figures S4–S7). The line plot next to each map summarizes the path coefficient across latitude, plotted with the mean (black line) and the standard deviation (grey area). Dotted lines indicate the Tropic of Cancer, the Equator and the Tropic of Capricorn, respectively, from top to bottom. Silhouette images were taken from www.freepik.com [Colour figure can be viewed at wileyonlinelibrary.com]

mammals globally (Barreto et al., 2019; Davies et al., 2011). A negative productivity–richness relationship was found only for reptiles around the Tropic of Cancer, offering insights into the lower richness of this group relative to other tetrapods in this region (Roll et al., 2017). In the light of the more individuals hypothesis, this negative relationship could be explained by the evidence that reptile abundance also scales negatively with productivity (Santini et al., 2018), thus leading to increased extinction rates (Wright, 1983), and consequently, lower species richness with increasing productivity. Additionally, the negative relationship between productivity–richness and

productivity–abundance in reptiles might be related to their competition with endothermic groups, which would have an advantage in more climatically challenging environments (Grady et al., 2019). Our results provide insight into the potential causes of the reported idiosyncratic productivity–richness relationship among lizard clades; areas where we uncovered positive relationships (red areas in Figure 3d) are occupied mostly by lizard clades whose richness is known to respond positively to productivity (Skeels et al., 2019).

The balance between temperature and water appears to result in negative relationships in parts of the globe for some taxonomic

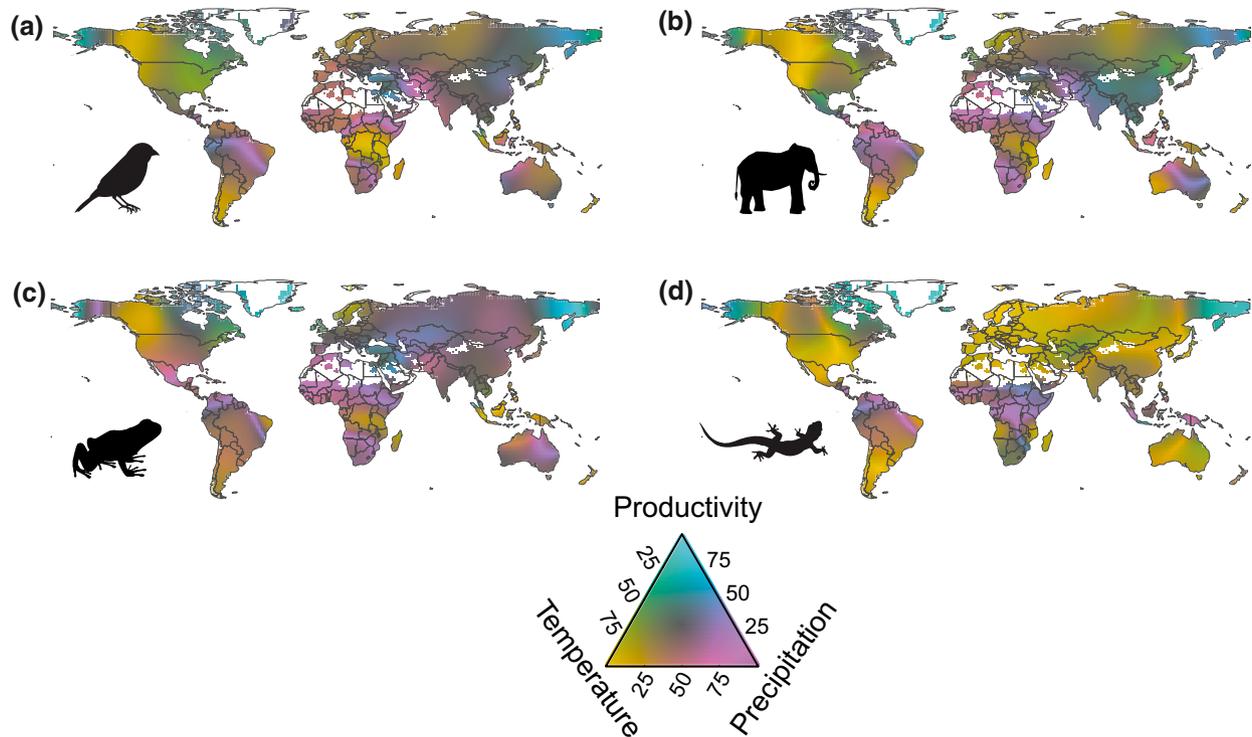


FIGURE 5 Relative importance of productivity, temperature and precipitation to the species richness of terrestrial tetrapods when considering both direct and indirect effects of temperature and precipitation through productivity. Colours indicate how much, as a percentage, a measure of energy is important to explain species richness based on the magnitude of the summed, standardized path coefficients. Shades of green indicate productivity, yellow temperature and pink precipitation as relatively more important. The black silhouette indicates the organismal group to which the result belongs. Silhouette images were taken from www.freepik.com [Colour figure can be viewed at wileyonlinelibrary.com]

groups. For instance, the direct effect of temperature on the richness of birds, mammals and amphibians was negative in parts of the tropical region, where temperatures are highest, suggesting that the tropics might be too warm for these groups. In these regions, temperature and precipitation might interact in their effect on diversity, such that with increasing temperatures, species richness increases only if there is sufficient moisture available (Francis & Currie, 2003; Hawkins et al., 2003; O'Brien, 1998). This is also likely to hold true for the negative relationship between precipitation and the richness of reptiles, birds and mammals in temperate regions, especially in North America. Precipitation does not promote an increase in species richness in these areas if it is not warm enough; a similar pattern has been found for angiosperms (Francis & Currie, 2003).

The balance between thermal energy and water availability seems to be less ubiquitous for ectotherms, because almost everywhere reptile and amphibian species richness was related positively to temperature and precipitation, respectively. The positive relationship between reptile richness and temperature, even when statistically holding precipitation constant, is consistent with the strong dependence of this group on external thermal energy for metabolic maintenance and reproduction (Adolph & Porter, 1993; Coops et al., 2018; Powney et al., 2010). Also, reptiles have strongly conserved thermal niches, which are likely to constrain the number of species capable of surviving and diversifying in colder environments

(Pie et al., 2017; Rolland et al., 2018). In contrast, amphibians are more strongly constrained by water availability because of their high vulnerability to desiccation and, for many species, dependence on water for reproduction (Buckley & Jetz, 2007; Gouveia & Correia, 2016).

Our geographically weighted path analysis confirmed that temperature and precipitation influence species richness not only directly (Brown et al., 2004; Currie et al., 2004), but also indirectly, mediated by the effect of climate on productivity (Hawkins et al., 2003). Spatial patterns of indirect effects are complex, because productivity results from an interaction among multiple climatic factors and does not increase monotonically with temperature and precipitation, especially not in the tropics (Clark et al., 2001; Šímová & Storch, 2017). Across large spatial scales, temperature and precipitation are often found to be stronger drivers than productivity of richness patterns (Šímová & Storch, 2017 and references therein). The importance of climate could emerge because of both its direct and indirect influences on species richness. However, we found this not to be the case, because direct effects of climate alone were often stronger than the direct effect of productivity, especially among ectotherms, and stronger than their indirect effects via productivity. These results suggest that species richness is driven more strongly by the physiological tolerance of organisms to climatic conditions and to climatic factors influencing metabolic rates and, ultimately, speciation rates (Brown et al., 2004; Currie et al., 2004)

than by the diversity of niches and/or the amount of energy flowing through the food webs (Evans, Warren, et al., 2005; Wright, 1983).

The need to consider the two pathways of effects and their complex spatial patterns explain the lack of consensus among tests for the relative importance of climate versus productive energy for explaining species richness (i.e., the water–energy hypothesis; Hawkins et al., 2003). Previous tests of this hypothesis were often conducted in different regions of the world by using predefined spatial unities (e.g., latitudinal band, biogeographical realms) and accounting for only direct effects (Davies et al., 2011; Qian, 2010; Whittaker et al., 2007). We found that only reptiles have a clear latitudinal pattern of water–richness relationships, with greater importance of water in the tropics and thermal energy elsewhere; a pattern that emerges only once the productivity-mediated indirect effects are considered. This finding contrasts with previous assessments, which did not uncover a latitudinal trend for reptiles (Hawkins et al., 2003; Whittaker et al., 2007) or found reptiles to be the group of tetrapods with the weakest sign of a latitudinal gradient (Qian, 2010). Regarding the other tetrapod groups, we found amphibians to be constrained by water across most of the globe, especially in the Palaearctic region, whereas birds and mammals were more constrained by temperature and productivity above the Tropic of Cancer; below it, temperature and precipitation became more important for these groups.

Variation in the strength and direction of species–energy relationships across the globe (i.e., spatial non-stationarity) might be associated with several factors other than the spatial variance of the energy variable itself. For example, non-stationarity could be associated with historical factors of each region (Davies et al., 2011; Ficetola et al., 2017; Gouveia et al., 2013; Hortal et al., 2011) or with the proportion of ecological groups within a region, because different groups might respond differently to energy conditions, such as specialists versus generalists (Evans, Greenwood, et al., 2005) or thermoregulators versus thermoconformers (Buckley et al., 2015; Sunday et al., 2014). Spatial variation in species–energy relationships can also emerge if different processes prevail in different regions (Davies et al., 2011). For instance, at high latitudes the effect of temperature might be related more strongly to thermal tolerances and to overcoming tropical niche conservatism (Smith et al., 2012), whereas at mid latitudes it may be associated more strongly with diversification rates (Machac & Graham, 2017). Expanding our spatial path model to incorporate other variables, such as diversification rates, abundance and elevation (Belmaker & Jetz, 2015; Chu et al., 2019; Marin et al., 2018), is a promising way forward to explore the spatial variations of different underlying processes in future studies.

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AUTHOR CONTRIBUTIONS

All authors contributed to design of the study. E.B. led the analysis, with input from M.T.P.C., T.F.R. and C.H.G. E.B. wrote the first draft, and all authors contributed to the final version of the manuscript.

DATA AVAILABILITY STATEMENT

All data used in this work are publicly available in the databases mentioned in the main text. The R code to perform geographically weighted path analysis and a spatial file containing the variables and results of this study are available in Appendix S1 in the Supporting Information.

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BIOSKETCH

Elisa Barreto has a PhD in Ecology and Evolution and is interested in understanding what drives the spatial patterns of multiple dimensions of biodiversity in different regions of the globe.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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