RESEARCH PAPER

Global Ecology and Biogeography | A Journal of Macroecology

WILEY

Environmental heterogeneity predicts global species richness patterns better than area

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[Correction added on 31 January 2021, after first online publication: Article type has been corrected.]

Abstract

Aim: It is widely accepted that biodiversity is influenced by both niche-related and spatial processes from local to global scales. Their relative importance, however, is still disputed, and empirical tests are surprisingly scarce at the global scale. Here, we compare the importance of area (as a proxy for pure spatial processes) and environmental heterogeneity (as a proxy for niche-related processes) for predicting native mammal species richness world-wide and within biogeographical regions.

Location: Global.

Time period: We analyse a spatial snapshot of richness data collated by the International Union for Conservation of Nature.

Major taxa studied: All terrestrial mammal species, including possibly extinct species and species with uncertain presence.

Methods: We applied a spreading dye algorithm to analyse how native mammal species richness changes with area and environmental heterogeneity. As measures for environmental heterogeneity, we used elevation ranges and precipitation ranges, which are well-known correlates of species richness.

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Results: We found that environmental heterogeneity explained species richness relationships better than did area, suggesting that niche-related processes are more prevalent than pure area effects at broad scales.

Main conclusions: Our results imply that niche-related processes are essential to understand broad-scale species–area relationships and that habitat diversity is more important than area alone for the protection of global biodiversity.

KEYWORDS

area, biodiversity, biogeographical region, environmental heterogeneity, global species richness, species–area relationship

1 | INTRODUCTION

Understanding biodiversity patterns is a core interest in ecology. One of the most pervasive of these patterns is the observation that the number of species contained in a spatial region increases with the area of that region. For example, a central observation in island biogeography is that islands with larger areas accommodate more individuals and, therefore, usually more species. Moreover, when sampling within any region, the number of species sampled usually increases with area. Such species–area curves are used as diagnostic macroecological tools to compare species–area relationships in different regions (Rosenzweig, 1995; Triantis et al., 2012).

When looking at explanations for this increase of species richness with area, a possible explanation would be that ecological communities are mainly structured by niche partitioning between species (e.g., Kadmon & Allouche, 2007; MacArthur & Wilson, 1967). Given that heterogeneous environments offer more niches, coexistence and species richness should increase with environmental heterogeneity (Ben-Hur & Kadmon, 2020; Potts et al., 2004; Whittaker, 1998). This mechanism, known as the environmental heterogeneity hypothesis (Palmer, 2007), is supported by several studies reporting that environmental heterogeneity is an important predictor of species richness for various taxonomic groups (Burnett et al., 1998; Kerr & Packer, 1997) and across spatial scales (Stein et al., 2014). Given that environmental heterogeneity typically increases with area, it offers one possible explanation for observed species–area relationships.

An alternative explanation for the increase of species richness with area are pure spatial processes (cf., e.g., Chase et al., 2019). By pure spatial processes, we mean any processes that affect the distribution of individuals in space and that are independent of niche-related processes. The simplest mechanism would be that individuals are distributed completely at random. Even under this assumption, a larger area will tend to sample more species on average. There are a large number of additional processes that could modify this relationship, without having to invoke niches. For example, MacArthur and Wilson's (1963, 1967) island biogeography theory predicts more coexisting species per fixed sampling area on larger islands owing to higher colonization rates and lower extinction rates compared with smaller islands. There are also mechanisms of disproportionate pure

area effects that act at the population level and particularly apply to islands. Specifically, larger areas accommodate larger populations, which are less likely to be affected negatively by demographic stochasticity or Allee effects (Hanski & Gyllenberg, 1993). Even sympatric speciation (Chase et al., 2019) and allopatric speciation (Rosenzweig, 1992) have been evoked to explain species–area relationships purely based on area.

From analysis of species–area relationships alone, however, it is difficult to distinguish pure area effects from combined area and niche effects, because environmental heterogeneity tends to increase as area increases owing to the distance decay of environmental variables (Bell et al., 1993; Rosenzweig, 1995). Consequently, the species–area relationship is a fundamental prediction of both neutral theory (Hubbell, 2001) and niche theory (Chesson, 2000). These results produce pure area effects (Hubbell, 2001), but a pure area effect can be attributable to neutral or niche-related processes. Thus, important biodiversity patterns, including local species abundance patterns and species–area curves, can be produced by both neutral and niche-related processes (Báldi, 2008; Pyšek et al., 2002; Tews et al., 2004). The question is therefore not about whether species richness is correlated with area or environmental heterogeneity, respectively, but rather about the relative importance of the two in explaining species richness.

One major complication when conducting such a study is that it is not simple to measure the influence of environmental heterogeneity on species richness, because many potential environmental variables could be considered (Stein & Kreft, 2015). Commonly used environmental variables at broad geographical scales include elevation range and climatic descriptors, such as precipitation range and temperature range, or the spatial variation of vegetation indices (Rodríguez et al., 2005; Tuanmu & Jetz, 2015). Environmental variables combine multiple factors that promote mammal species richness, including ecological and evolutionary aspects (Field et al., 2009; Hawkins et al., 2003; Stein et al., 2015). Previous studies on the effect of environmental heterogeneity on diversity have often focused on only one of these variables (Báldi, 2008; Hawkins et al., 2003; Pyšek et al., 2002; Rodríguez et al., 2005; Tuanmu & Jetz, 2015). Apart from the question about the sufficient breadth of environmental effect, such univariate analyses bear the inherent

danger of confounding niche and neutral processes. To partition the effects of niche-related processes and pure area, one should therefore simultaneously investigate the influence of environmental heterogeneity and area on species richness (Chase et al., 2019; Legendre et al., 2005).

The relative importance of environmental heterogeneity and pure area for species richness can also depend on the region of focus (Sobéron, 2019) and the scale of observation (Palmer & White, 1994). Species–area relationships usually show steeper slopes at fine scales than at large scales (Fridley et al., 2005; Rosenzweig, 1995). However, there are exceptions to this rule. First, if the analysis accounts for sampling effects, this scale dependence vanishes, and the same species–area curve is applicable at the scale of individuals and at the scale of a province (Fridley et al., 2006). Second, at continental scales, the species–area relationship is steeper than at finer scales (Storch et al., 2012). Yet, broader scales up to the global scale are still rare among studies of species–area relationships (but see Storch et al., 2012; Stein et al., 2014, 2015). To our knowledge, no study has assessed the relative influence of environmental heterogeneity versus pure area on species richness at a global scale and within biogeographical regions. Biogeographical regions are distinct areas of the globe that are characterized by a unique biogeographical history and can be seen as evolutionary arenas where different clades diversify (Carstensen et al., 2013; Nürk et al., 2019). These regions have different climatic conditions and geomorphological characteristics that influence the current distributions of species and species richness patterns. Biogeographical regions have been used extensively in the macroecological literature (e.g., Hawkins et al., 2007; Kissling et al., 2009; Kreft & Jetz, 2007); they serve as a proxy for replicates to test whether species–area and species–heterogeneity relationships are globally consistent or affected by regional idiosyncrasies. Therefore, environmental heterogeneity in the different biogeographical regions of the globe might influence species richness relationships differently.

Here, we use global gradients in species richness of the terrestrial mammal fauna to investigate empirically the (relative) influence of area and environmental heterogeneity (elevation range and precipitation range) on species richness. The dataset contains data sourced from several empirical studies on environmental heterogeneity and species richness of mammals in terrestrial systems (outlined by Stein et al., 2015). We perform analyses at the global scale and for each biogeographical region to test whether environmental conditions in the different regions result in different species distributions. Biogeographical regions impose different phylogenetic constraints and different environmental requirements on the prevailing species, for example, regarding stress responses. Therefore, we expect that species richness can be explained better by pure area in some biogeographical regions and by niche-related processes in others. Simultaneous investigation of the influences of area and environmental heterogeneity on species richness relationships gives us an indication of the relative contributions of area and environmental heterogeneity to species richness patterns at global and biogeographical scales.

2 | MATERIALS AND METHODS

Our global terrestrial mammal data comprised 4,954 native species derived from extent-of-occurrence distribution maps provided by the International Union for Conservation of Nature (IUCN, 2013), from which species richness across an equal-area grid with cells of 12,364 km^2 (*c.* 111 km × 111 km at the equator) was aggregated by Stein et al. (2015) (Figure 1; see Supporting Information Appendix S1, Table S1.5). Strictly speaking, these maps show potential species richness, but at the coarse grain size that we use here, actual and potential species richness become the same (Hurlbert & Jetz, 2007). This dataset was split into eight biogeographical regions (Kreft & Jetz, 2010; Olson et al., 2001). We excluded introduced species, vagrant species, bats and species for which no specific localities were known. We removed grid cells with no indigenous terrestrial mammals present (which excluded the biogeographical regions of Antarctica and Oceania) and grid cells containing only water (oceans and large lakes).

We analysed two measures of environmental heterogeneity across the same 12,364 km^2 grid cells in all biogeographical regions of the globe (except for Antarctica and Oceania): elevation range and precipitation range (Figure 1). These two measures of environmental heterogeneity are known to be strong predictors of terrestrial mammal species richness at broad scales and are uncorrelated at this scale, whereas temperature and elevation are highly correlated (see Supporting Information Appendix S1, Table S1.1 and Figure S1.4; Rahbek, 2005; Rodríguez et al., 2005; Tuanmu & Jetz, 2015). Data for mean annual precipitation (in millimetres per year; for the time period 1950–2000) and elevation (in metres above sea level) were taken from the WorldClim dataset (Hijmans et al., 2005) at an original resolution of 30 arc-sec (corresponding to *c.* 1 km at the equator). The elevation and precipitation ranges were then derived by calculating the absolute differences between the maximum and minimum values across our global equal-area grid at 111 km × 111 km (following the aggregation procedure as described by Stein et al., 2015).

We analysed species richness as a function of area, elevation range and precipitation range for the globe and the six remaining biogeographical regions at scales ranging from one to 50 grid cells. We removed extreme values from the datasets for the globe and all biogeographical regions by cutting off the top 1% for each environmental heterogeneity variable. This was done because we were interested in typical species richness patterns rather than responses of species richness to extreme values. Grid cells were selected using a spreading dye algorithm that randomly selected neighbouring cells from an initial grid cell [see Supporting Information Appendix S1; run in R 3.3.0 (R Core Team, 2016)]. Starting from an initial ("focal") cell, the second cell was selected randomly within the eight-cell neighbourhood. The next cell was chosen from the eight-cell neighbourhoods of the previously selected cells, excluding cells already selected. The algorithm stopped when a cell group had no not-yet-selected neighbouring cells or when the maximum of 50 cells was reached. Each cell served 50 times as the focal cell (i.e., 50 iterations per focal cell). For further technical detail,
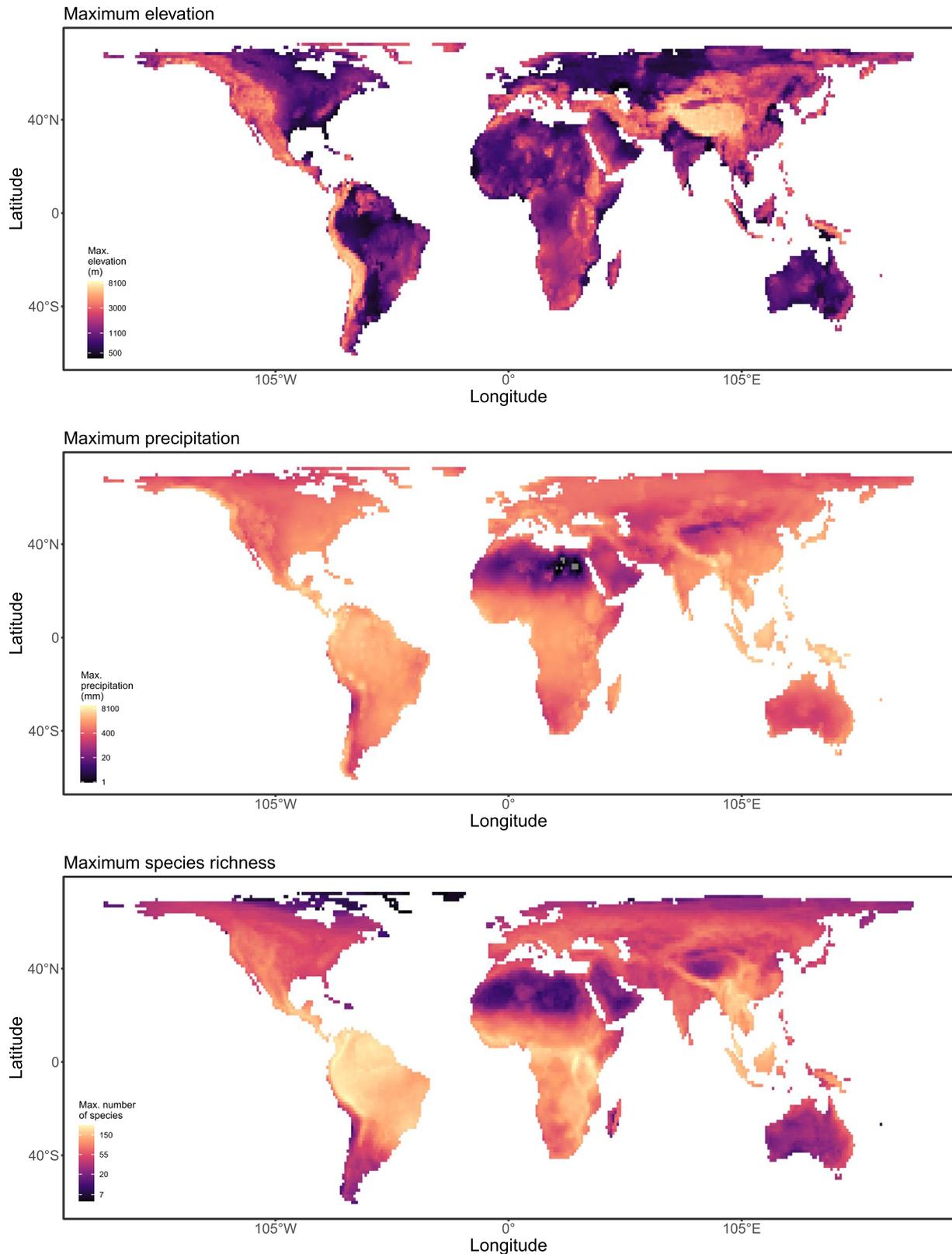
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FIGURE 1 Maxima of elevation (in metres), precipitation (in millimetres) and number of mammalian species per grid cell across the globe. The colour scale is logarithmic, meaning that smaller values are more finely resolved than larger values within a single map [Colour figure can be viewed at wileyonlinelibrary.com]

see the Supporting Information (Appendix S1, Figures S1.1 and S1.2). In comparison to rectangular or circular sampling procedures, this spreading dye algorithm is able to adapt to any given

spatial configuration of cells through a flexible neighbour selection, is random through randomized selection of neighbours, and has a dynamic sampling window that allows observations of all

possible realizations of a given spatial dataset that include edge or peripheral grid cells, such as coastlines. We applied a rectangular sampling procedure, the spreading square algorithm, and one other algorithm to our dataset for comparison and found qualitatively the same results as with the spreading dye algorithm (see Supporting Information Appendix S2 and see also animations of different sampling algorithms in Supporting Information Figure S3.1). Notable differences in absolute values between the algorithms were found only in island-rich regions, which exhibit long coastlines and are thus particularly amenable to the spreading dye algorithm. We note that values calculated at different scales are autocorrelated because values at larger spatial scales depend, in part, on those at smaller spatial scales, similar to strictly nested quadrat construction algorithms (see Scheiner, 2003; Storch et al., 2012). We applied the spreading dye algorithm to create sets of nested areas for seven datasets: the global dataset with 10,704 grid cells, Nearctic with 1,731 grid cells, Palaearctic with 4,257 grid cells, Indo-Malay with 690 grid cells, Neotropics with 1,553, Afrotropics with 1,771 and Australasia with 702 grid cells. The ranges of absolute values of variables per grid cell were as follows: species richness, 5-463; elevation, 10–8,235 m a.s.l.; and precipitation, 0–11,210 mm.

2.1 | Statistical analyses

Our overall approach to the statistical analyses of samples was: (a) to create subsamples to correct for variance differences between realms, (b) to run linear regressions of bootstrapped subsamples, and (c) to carry out variance partitioning. The reason for the first step of creating subsamples was to avoid spurious effects attributable to differences in the overall variance of species richness in different biogeographical regions. Models were fitted using a random subsample of focal cells for each biogeographical region, instead of using all available cells as focal cells in that region (for sample sizes per region, see Supporting Information Appendix S1, Table S1.6). The sample sizes for the respective biogeographical regions were chosen such that all samples had the same sample precision with respect to species richness. Sample precision was half the width of the confidence interval of mean species richness in focal cells. We used a sample precision of $\pm$ 4 species. This reduction of focal cells simultaneously reduced spatial autocorrelation in the samples.

In the second step, model selection was done using linear regressions with linear and quadratic effects for all three variables (area, elevation range and precipitation range, all untransformed) for every dataset (global, Nearctic, Palaearctic, Indo-Malay, Neotropics, Afrotropics and Australasia), with mammal species richness as the response variable. The full model had the form lm(species.richness to be explained by area + area_squared + elevation.range + elevation.range_squared + precipitation.range + precipitation.range_squared). To test whether the model overfitted, we removed the quadratic

terms in a stepwise manner, in all possible combinations, from the full model for every dataset (for all tested model structures, see Supporting Information Appendix S1, Table S1.3), but the full model with all polynomial terms always received the highest Akaike information criterion support (Supporting Information Appendix S1, Tables S1.2–S1.4).

We bootstrapped the input data for the regressions 500 times for each focal cell to obtain a robust estimate of the uncertainty of the estimated relationships (see also fine black lines in Figure 3 in the Results section). Predictions for species richness were calculated from these models; these were limited to a minimum of zero for all variables because it is biologically impossible to have a negative number of species.

To calculate which variable (area, elevation range or precipitation range) had the largest influence on species richness relationships, in the third step we partitioned the variance using polynomial models with all three predictors (full model). Variance partitioning was calculated using the varPart function from the ᴍᴏᴅEvA package (Barbosa et al., 2016), which is based on R^2 values. This was done by regressing species richness on the environmental and area variables simultaneously and separately and feeding the results (see code snippet in Supporting Information Appendix S1, Table S1.7) into the varPart function. We used an R^2-based method instead of an Akaike information criterion-based method because we were interested in explained variability instead of prediction-oriented model performance.

3 | RESULTS

Both environmental heterogeneity variables showed saturating relationships with area, whereby an increase in area corresponded to an increase in the range of each variable (Supporting Information Appendix S1, Figure S1.3). The results from variance partitioning (Figure 2) indicated, for the globe and all assessed biogeographical regions, that environmental heterogeneity variables (elevation range and precipitation range) explain more of the species richness than does area alone. The variance accounted for by area alone was always smaller in comparison to the variance accounted for by our environmental heterogeneity variables.

The nature of the relationship between species richness and environmental heterogeneity was, however, not as simple as that between species richness and area (Figure 3). Increasing area resulted in an increase in species richness, except in the Indo-Malaya region, whereas the response to elevation range and precipitation range was more diverse. The pattern with respect to elevation range was a general increase, with flat, positive and negatively curved responses, except for the Neotropics, where the pattern with species richness was negative. Species richness in response to an increase in precipitation range also generally increased up to medium precipitation ranges, except for the Palaearctic, which displayed a hump-shaped relationship. At very large precipitation ranges, species richness slightly decreased again in the

FIGURE 2 Variance partitioning diagrams for the globe and each biogeographical region were calculated from quadratic (second-order) polynomial models. The colours of the circles correspond to each variable. Bold values indicate the highest explained variance, and red values indicate unexplained variance [Colour figure can be viewed at wileyonlinelibrary.com]
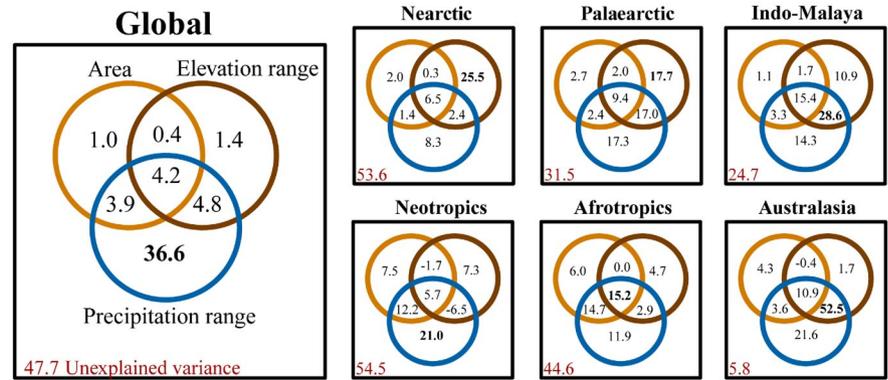
Nearctic, Indo-Malayan, Neotropical and Afrotropical regions. Given that predictions for all variables were calculated from multiple regression models, where all variables were present, the strength of the relationships between species richness and each variable is indicated by the deviation of the blue lines from a constant; that is, the flatter the line, the smaller the influence, whereas considerable variability in the line represents important contributions. This is also reflected in the results from variance partitioning as, for example, species richness for the globe was explained better by precipitation range (explained variation = 36.6%) than by area (explained variation = 1.0%).

4 | DISCUSSION

In this study, we tested for the explanatory power of area, precipitation range and elevation range on species richness. The two environmental heterogeneity variables explained a larger share of the species richness relationships than area, supporting the idea that diversity is structured by niches at broad spatial scales (Figure 2). These results were consistent at the global scale and at the level of the biogeographical regions. Our study provides strong evidence of a consistently larger relative importance of environmental heterogeneity than of pure area for species richness at biogeographical and global scales.

4.1 | Predictors of species richness

For global species richness patterns, precipitation range was the strongest predictor. This finding is supported by Field et al. (2009) and Hawkins et al. (2003), which reinforces our more general finding that climate variables are the strongest drivers of species richness at broad scales. A possible explanation is that climate varies more strongly than other heterogeneity variables over large geographical areas (Field et al., 2009; Hawkins et al., 2003). Precipitation range was also the strongest explanatory variable for the Neotropical biogeographical region, most probably owing to a strong gradient from desert and temperate to tropical zones within this single biogeographical region (Figure 1; Hawkins et al., 2003). Interestingly, maximum species richness was reached in the Neotropics at precipitation ranges slightly below the maximum

ranges (Figure 3). This might be attributable to the inclusion of species-poor dry areas in the samples showing very high precipitation ranges.

Elevation range had the strongest influence on species richness patterns in the Nearctic and Palaearctic biogeographical regions, presumably because these regions include large mountain ranges (Figure 1). This pattern agrees with findings from Kerr and Packer (1997) and Davies et al. (2007), who also found that elevation range is an important predictor of mammal richness in the Palaearctic and in parts of the Nearctic biogeographical regions. In the Palaearctic, the influence of elevation range on species richness patterns was only slightly stronger than that of precipitation range (Figures 2 and 3) and of the two combined (Figure 2). The reason could be the strong covariance between precipitation and elevation in this region, with regions of high elevation also having higher precipitation (Figure 1). The large proportion of mountainous areas in the Nearctic and Palaearctic biogeographical regions could drive the pattern of species richness increasing with elevation range (Figure 1). Topographical isolation through elevational heterogeneity that led to evolutionary species diversification (Hughes & Eastwood, 2006; Kay et al., 2005) could also explain why elevation range has a large influence on species richness in mountainous biogeographical regions. But species diversification through topographical isolation occurs at regional scales and, although important, probably does not have a large influence at the broader scales we investigated (Kisel et al., 2011).

In the Indo-Malayan and Australasian biogeographical regions, combinations of explanatory variables influenced species richness patterns more than individual variables. Elevation range and precipitation range together had the largest effect on richness in these regions (Figure 2). In the Indo-Malayan region, species richness increased with increasing elevation range and precipitation range up to a maximum before dropping slightly at very large ranges (Figure 3). This could be attributable to high spatial heterogeneity in elevation and precipitation and because high values of the ranges of both variables often overlapped (Supporting Information Appendix S1, Figure S1.4). In Australasia, areas of high elevation range and high precipitation range supported the highest species richness (Figure 3). This makes sense, because the east coast of Australia has the highest elevation range on the continent owing to the presence of mountains and higher levels of precipitation, which correspond to higher species richness.
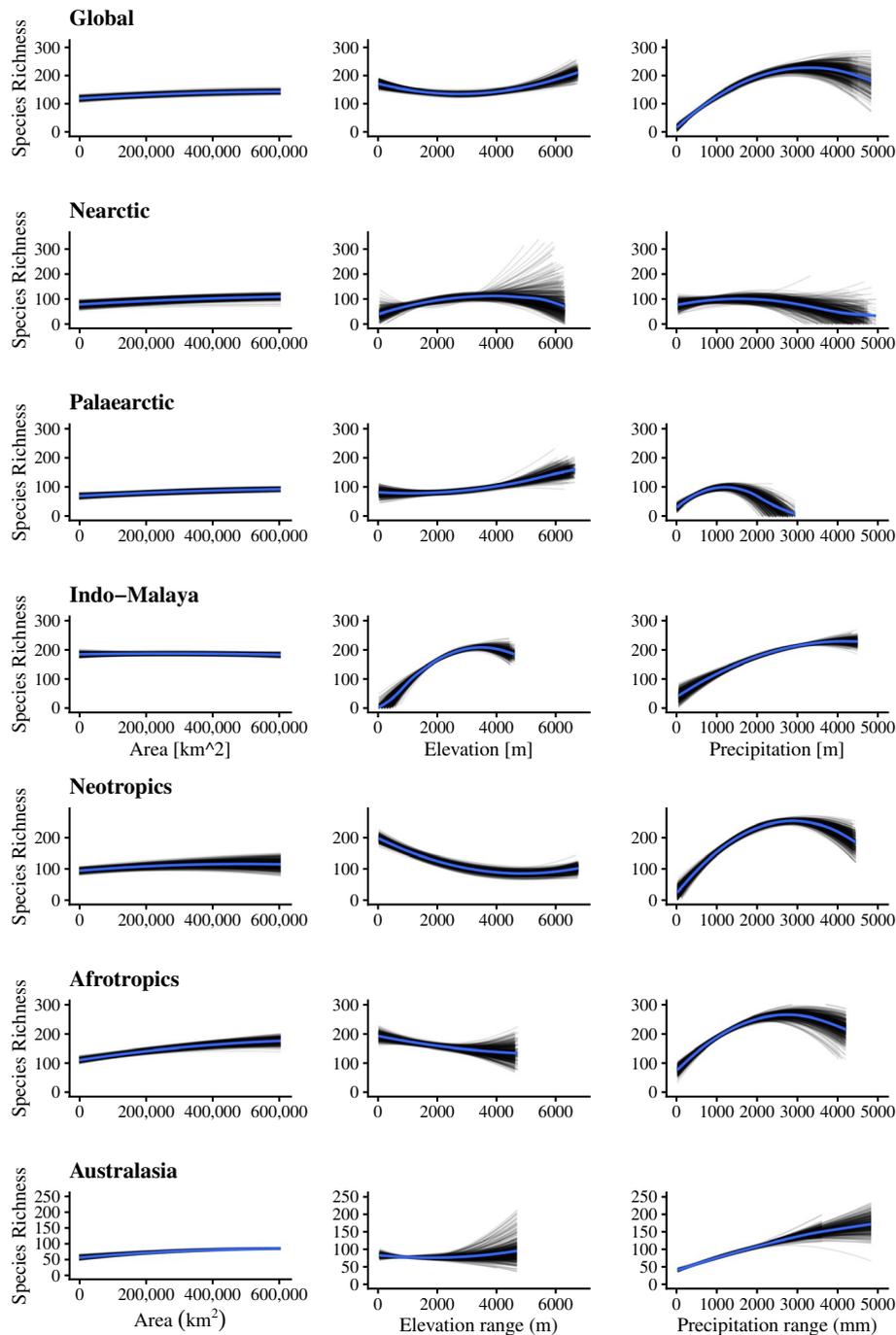
FIGURE 3 Species richness relationships dependent on area and ranges of elevation and precipitation, based on predictions calculated from multiple polynomial regression models where all variables were present, for the globe and biogeographical regions. These are marginal effects plots based on regression models where all but the focal predictor variable were kept constant at their mean value. Blue lines represent the mean of 500 bootstraps of the input data of the regressions, and each black line represents one of these bootstrap iterations [Colour figure can be viewed at wileyonlinelibrary.com]

Furthermore, the Australasian biogeographical region includes Papua New Guinea, which also has linked patterns of elevation and precipitation, because precipitation is lowest in the mountains (Figure 1). Papua New Guinea therefore has a large heterogeneity of both elevation and precipitation from the lowlands towards the island centre. In the Afrotropical biogeographical region, all three variables combined (area, elevation and precipitation) explained species richness patterns the best (Figures 2 and 3). This could be attributable to low environmental

heterogeneity throughout large regions of Africa and weak gradients of elevation and precipitation (Figure 1).

4.2 | Niche versus pure area effects

The observed increase of species richness with area could be produced by both pure area effects and niche-related processes. Our analysis

suggests that, of the two, environmental heterogeneity (i.e., niche-related processes) is more important for explaining the species–area relationship at broad scales (cf. Field et al., 2009; Rosenzweig, 1995). In a univariate analysis, however, area is still an excellent predictor of species richness, because it is correlated strongly with environmental heterogeneity (Allouche et al., 2012; Rosenzweig, 1995).

Identification of ranges of elevation or precipitation where the change in species richness is highest offers a fresh perspective on the factors shaping species richness in different regions. For instance, elevation is known to be a strong predictor of species richness globally, with particularly high richness at mid-elevation along elevation gradients (McCain & Grytnes, 2010). The patterns of change in species richness with heterogeneity in elevation and precipitation are more complex than species–area curves, but they do improve our understanding and predictions of how species richness patterns are structured in different areas of the globe. This approach might be particularly useful in light of large-scale homogenization of Earth's environments and species, attributable either to vast homogeneous landscapes or to the mobilization of species across the globe (Davies et al., 2008).

These results should be viewed with caution because we did not account for the size of the underlying species pool in the different biogeographical regions or the influence of regional geographical influences, such as isolation, fragmentation history and human influence. There might also be other important environmental predictors of species richness that we did not test. However, we still find a strong influence of our predictors, and the addition of more predictors would only increase the explained variance of species richness patterns.

4.3 | Conclusion

Our findings indicate that the increase of species richness with area at the global scale is primarily attributable to the increase of environmental heterogeneity with area, and only secondarily to area effects alone. This suggests that niche-related processes have a stronger influence than pure area effects on species richness patterns at broad scales. Our findings also demonstrate that there is still a limited understanding of the processes that underlie species–area relationships across scales. Analyses like ours could help to identify broad sets of predictors, thus increasing our understanding of species richness relationships specifically and biodiversity in general, and improving our ability to protect global biodiversity under global change.

AUTHOR CONTRIBUTIONS
All authors designed the study. M.F. and C.K. created the spreading dye algorithm. S.H. implemented the two alternative algorithms, and K.U. analysed the output data. All authors contributed to manuscript writing, and K.M. and K.U. led the revisions with contributions from all authors. [Correction added on 29 January 2021, after first online publication: Author Contributions section has been modified.]

DATA AVAILABILITY STATEMENT
All data and R code supporting the results are archived in a Dryad digital repository available at: https://doi.org/10.5061/dryad.1rn8p k0qs

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[Corrections added on 29 January 2021, after first online publication: ORCID section has been updated.]

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BIOSKETCH

The authors were part of a workshop of the Research Training Group "Scaling Problems in Statistics". The authors come from different scientific backgrounds but share an interest in macroecology and investigating species richness patterns using statistics.

SUPPORTING INFORMATION

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