























ORIGINAL RESEARCH

Diversity gradients of terrestrial vertebrates – substantial variations about a common theme

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Abstract

Environmental factors, such as temperature, precipitation, and elevation, explain most of the variation in species richness at the global scale. Nevertheless, richness patterns may have different drivers across taxa and regions. To date, a comprehensive global examination of how various factors such as climate or topography drive patterns of species richness across all terrestrial vertebrates, using the same methods and predictors, has been lacking. Recent advances in species-distribution data allowed us to model and examine the richness pattern of all terrestrial tetrapods comprehensively. We tested the relationship between environmental and biogeographical variables and richness of amphibians (5983 species), birds (9630), mammals (5004), reptiles (8939), and tetrapods as a whole, globally, and across biogeographical realms. We studied the effects of climatic, ecological, and

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biogeographic drivers using generalized additive models. Richness patterns and their environmental associations varied among taxa and realms. Overall precipitation was the predominant richness predictor. However, temperature was more important in realms where both cold and warm conditions exist. In the Indomalayan realm, elevational range was very important. Richness patterns of mammals, birds, and amphibians were strongly related to precipitation whereas reptile richness was mostly associated with temperature. Our results support the universal importance of precipitation but also suggest that future global-scaled research should incorporate other relevant variables other than climate, such as elevational range, to gain a better understanding of the richness–environment relationship. By doing so, we can further advance our knowledge of the complex relationships between biodiversity and the environment.

Introduction

The latitudinal diversity gradient, describing the increase in species richness from high to low latitudes, is one of the strongest and best-studied biogeographic patterns (Hillebrand, 2004; Lomolino *et al.*, 2017). It has been shown to prevail globally across taxa (e.g. plants – Kreft & Jetz, 2007; Scheiner & Rey-Benayas, 1994; invertebrates – Economo *et al.*, 2018, 2019; Pinkert *et al.*, 2022; vertebrates – Jetz & Fine, 2012; Wiens, 2007). Exceptions to the pattern are usually observed at lower spatial scales (i.e. locally, e.g. North America; Gaucherel *et al.*, 2018) and taxonomic scales (i.e. clades/taxa with relatively few species, e.g. pinnipeds; Cerezer *et al.*, 2022; Gaston, 1996).

Many hypotheses have been proposed to explain the latitudinal diversity gradient (Pontarp *et al.*, 2019). Hypotheses based on environmental drivers are usually strongly supported (Field *et al.*, 2009; Hawkins *et al.*, 2012; Hortal *et al.*, 2008). Climatic variables are thought to influence richness through various pathways (O'Brien, 1998, 2006; Storch *et al.*, 2012). According to the 'more-individuals hypothesis', resource availability, driven largely by temperature–water dynamics, limits the number of individuals and, consequently, the number of species (Srivastava & Lawton, 1998; Storch *et al.*, 2018; Wright, 1983). The 'evolutionary-rates hypothesis' proposes that diversification rates are faster in hot and humid places, resulting in greater species richness (Rohde, 1992). However, the relationship between diversification rates and current species richness is not always straightforward and, in some cases, faster diversification rates were found in temperate species-poor regions (e.g. Cerezer *et al.*, 2022; Rabosky, 2009; Rabosky *et al.*, 2018; Schluter, 2016). An additional hypothesis suggests that the long and relatively undisturbed evolutionary history of the tropics resulted in accumulation of more species than in temperate regions (Mittelbach *et al.*, 2007). Yet, past climates have been shown to explain less of the variation in current richness than current climates (Hawkins & Porter, 2003; Liang & Meiri, 2023). Environmental heterogeneity is also thought to substantially impact species richness (e.g. Hortal *et al.*, 2009; Stein *et al.*, 2014). A greater variety of habitats or topographic structures (usually represented by elevational range) is believed to result in numerous ecological niches which, in turn, fosters species specialization (Hortal *et al.*, 2013; MacArthur, 1964).

Insularity is postulated to have an impact on species richness as islands typically harbor fewer species per unit area than the mainland (e.g. Ding *et al.*, 2006; Field *et al.*, 2009; Whittaker & Fernández-Palacios, 2007). Islands are associated with higher rates of extinction due to their small size and isolation, and lower rates of immigration (Foufopoulos & Ives, 1999; MacArthur & Wilson, 1967).

Richness interacts differently with environmental and ecological predictors across regions (e.g. Bohdalková *et al.*, 2021; Qian, 2009). Productivity-related factors explained most of the global variation in vertebrate richness (e.g. mammals – Barreto *et al.*, 2019; birds – Davies *et al.*, 2007; Hawkins *et al.*, 2007; amphibians – Gouveia *et al.*, 2013, mammals, amphibians, and birds – Bohdalková *et al.*, 2021; all classes – Barreto *et al.*, 2021). Productivity and water mostly affect richness in warm regions (e.g. Bohdalková *et al.*, 2021; Hawkins, Porter, *et al.*, 2003). Temperature is often weakly, and sometimes negatively, correlated with richness in warm regions, but is strongly and positively correlated with richness in cold (mainly northern) areas (e.g. Hawkins, Field, *et al.*, 2003; Kalmar & Currie, 2006). Elevational range is often strongly correlated with species richness in less seasonal areas, such as the tropics (e.g. Lewin *et al.*, 2016; Rahbek & Graves, 2001; Tallowin *et al.*, 2017), whereas the correlation is weaker in more seasonal regions (e.g. Qian *et al.*, 2007; Rodríguez *et al.*, 2005; Terribile & Diniz-Filho, 2009).

Due to this non-stationarity, some studies compare richness–environment relationships between geographical regions (e.g. Alves *et al.*, 2018; Barreto *et al.*, 2019, 2021), such as biogeographical realms. Realms are often used to geographically divide richness–environment models (Qian, 2009; Roll *et al.*, 2015; Voskamp *et al.*, 2017), or as an explanatory variable (Buckley & Jetz, 2007; Hawkins, Porter, *et al.*, 2003). At a coarse geographic scale, realms represent distinct species pools generated by mostly independent evolutionary histories (Falaschi *et al.*, 2023; Ricklefs, 2004; Smith *et al.*, 2005). Differences in diversification and dispersal between realms can be viewed as largely independent events of biodiversity accumulation, making realms obvious units for biogeographic analyses.

Global species-richness patterns of amphibians, birds, and mammals are largely congruent (Grenyer *et al.*, 2006). However, there are some distinctions among taxa, mostly at

regional scales—and when reptiles are compared to other tetrapod taxa (e.g. Currie, 1991; Hawkins *et al.*, 2012; Powney *et al.*, 2010; Roll *et al.*, 2017). Consequently, richness–environment relationships vary across taxa (Barreto *et al.*, 2021; Currie, 1991). Most notably, reptile richness pattern is commonly found to be closely associated with temperature, whereas bird, mammal, and amphibian richness are consistently correlated with water-related factors or with primary productivity (e.g. Barreto *et al.*, 2021; Hawkins, Field, *et al.*, 2003; Qian, 2010; Rodríguez *et al.*, 2005).

Most studies that examined richness–environment relationship of terrestrial vertebrates were confined to one or two tetrapod classes (Allen *et al.*, 2002; Araújo *et al.*, 2008; Barreto *et al.*, 2019; Costa *et al.*, 2007; Evans *et al.*, 2005; Foody, 2004; Fritz *et al.*, 2016; Hawkins & Porter, 2003; Kerr & Packer, 1997; Qian *et al.*, 2007; Rahbek & Graves, 2001; Rodríguez *et al.*, 2005), or involve birds, mammals, and amphibians (Belmaker & Jetz, 2011; Bohdalková *et al.*, 2021; Buckley & Jetz, 2007; Davies *et al.*, 2007; Gouveia *et al.*, 2013; Grenyer *et al.*, 2006; Gudex-Cross *et al.*, 2022; Hawkins *et al.*, 2007, 2012; Hortal *et al.*, 2008; O'Malley *et al.*, 2023; Wu & Liang, 2018). Studies that incorporate all tetrapods (including reptiles) have usually been confined to one region (Currie, 1991; Lewin *et al.*, 2016; Powney *et al.*, 2010; Tallowin *et al.*, 2017; Whittaker *et al.*, 2007).

Until recently, data on the distribution of tetrapods, particularly that of reptiles, were limited and lacked comprehensive coverage of species (Roll *et al.*, 2017). Earlier work, thus, relied on incomplete species datasets (Jetz & Fine, 2012; Qian, 2009, 2010; Qian & Ricklefs, 2008). Although some recent studies use the now available comprehensive datasets, they tend to focus on limited sets of environmental factors, primarily productivity, precipitation, and temperature (Marin *et al.*, 2018 at the bioregion level; Barreto *et al.*, 2021 at the grid-cell level). Other factors, which are known to be linked to species richness, such as environmental heterogeneity and insularity, have so far only been evaluated at local scales or using incomplete tetrapod-richness datasets (e.g. Hortal *et al.*, 2009; Howard *et al.*, 2020; Stein *et al.*, 2014; Tallowin *et al.*, 2017). Although these factors are generally considered less important than climate (e.g. Barreto *et al.*, 2019; Belmaker & Jetz, 2011), incorporating them into a broad spatial and taxonomic analysis could offer new and intriguing insights.

We suggest that the comprehensive species-distribution data that have recently become available for all tetrapod taxa—most recently for reptiles (Caetano *et al.*, 2022; Roll *et al.*, 2017)—allow to accurately test their global and regional richness patterns and their correlations to various environmental parameters. We examined the global richness patterns of all amphibians, reptiles, birds, and mammals together and tested their relationships with environmental, topographic, insularity, and biogeographic variables. We further modeled reptile, amphibian, bird, and mammal richness separately, with common scales, model features, and explanatory variables, to enable meaningful comparisons between them. We compared the results within biogeographical realms presenting a comprehensive global analysis of the effects of varied environmental attributes on gamma diversity.

Materials and methods

We obtained distributional data for amphibians and mammals from the IUCN (2021), for birds from the BirdLife International data zone (BirdLife International & NatureServe, 2019), and for reptiles from an updated version of Roll *et al.* (2017) (GARD 1.7, Caetano *et al.*, 2022). Data were filtered to include only native distributions of species and their breeding ranges (where designated as such). We created species-richness maps at a 96×96 km resolution (using a Behrmann equal-area projection, roughly 1×1 degree at the equator). We excluded cells with land comprising $<90\%$ of the entire area of the cell (e.g. coastal cells), including most small islands (Fig. 1). This procedure retains 5983 amphibian, 5004 mammal, 9630 bird, and 8939 reptile species (Table S1). Cells with no species were retained in the analyses, but Antarctica was excluded. While ensuring model integrity by considering cells with similar sizes is important, we acknowledge that including only cells with $<90\%$ land area may have downplayed the importance of insularity (see below). Therefore, we conducted an additional analysis incorporating all cells and including log-transformed area as an additional predictor. Preliminary analyses which incorporated cells with $>30\%$ and $>10\%$ land area yielded similar results to those of the original analyses, which included cells with $>90\%$ land area (results not shown).

To assess the similarity of global richness patterns among the four tetrapod classes, we computed correlation coefficients between the richness values of each pair of tetrapod classes. We used Pearson's correlation adjusted for spatial autocorrelation, using the 'Spatialpack' package (Osorio *et al.*, 2016).

We modeled richness using: (1) mean annual temperature (hereafter 'temperature', °C, 30-s resolution; from Karger *et al.*, 2017); (2) log of mean annual precipitation (hereafter 'precipitation', mm, 30-s resolution; Karger *et al.*, 2017). Because similar linear differences in precipitations are more meaningful in areas with relatively low precipitation (e.g. in the desert edge) than in high ones (e.g. in a rainforest; Egozcue *et al.*, 2006), we used a multiplicative (log) scale; (3) elevational range representing habitat heterogeneity. We downloaded mean elevation data (in m, 30-s resolution, from WorldClim 2.1 initiative, Fick & Hijmans, 2017) and calculated the elevational range in each 1×1 degree cell (see richness-map creation above) by subtracting the minimum elevation from the maximum elevation. We standardized these three factors to provide comparable regression coefficients; (4) the number of ecoregions in each grid cell (Dinerstein *et al.*, 2017) a coarse proxy of habitat diversity; and (5) insularity was treated as a categorical factor distinguishing between mainland and islands (Field *et al.*, 2009). We classified each cell according to whether it is located on the mainland or on an island (see Fig. S1 for the classification; the largest island is Greenland— ~ 2 mil km² and the smallest mainland is Australia— ~ 7.7 mil km²). Cells comprising both mainland and island regions were considered mainland. We deleted the following predictors that have variance-inflation factors >5 (VIF; Rogerson, 2006), and concurrencies higher than 0.8 (i.e. the presence of covariates that are themselves well modeled as

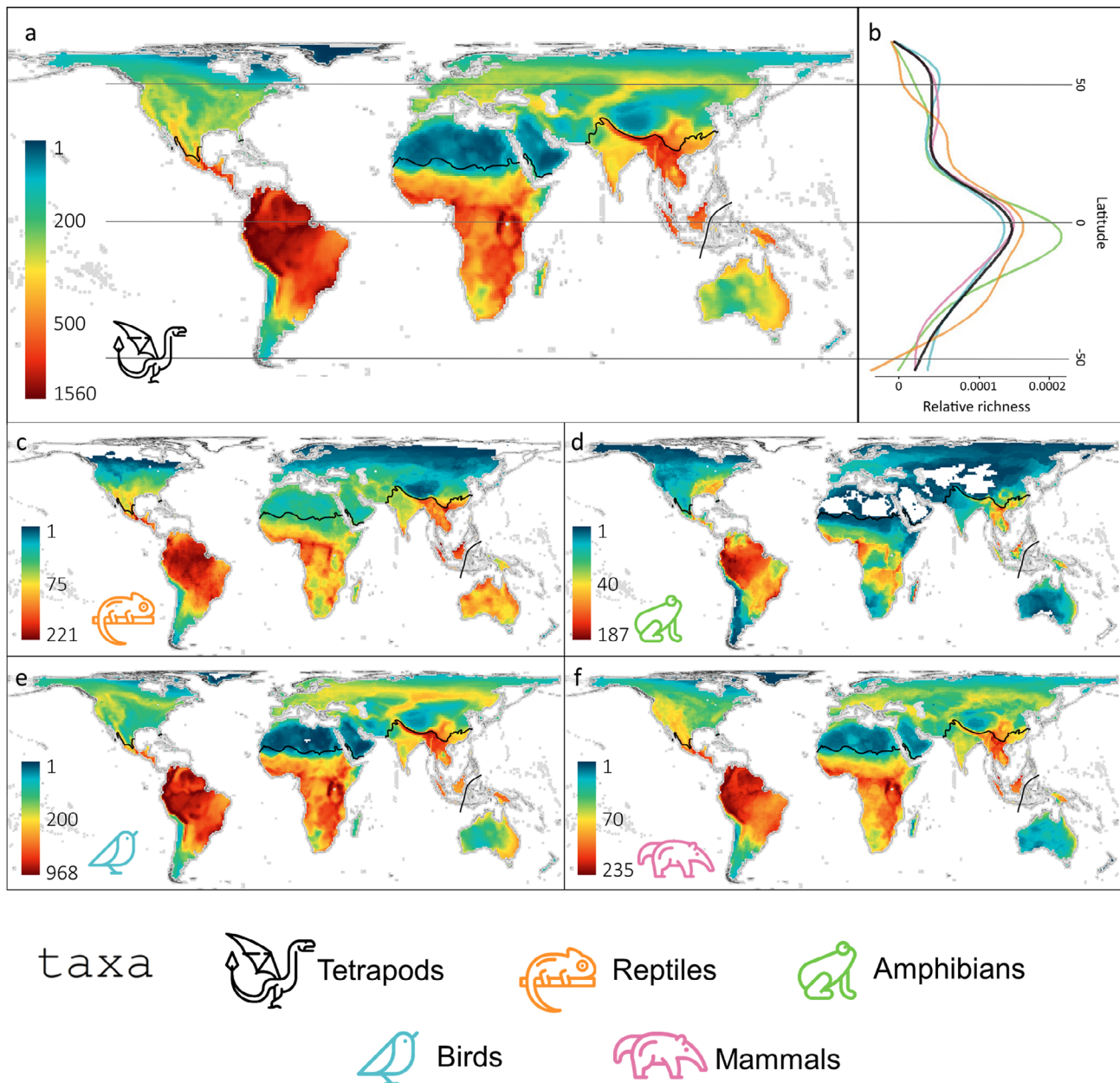


Figure 1 Species-richness patterns and latitudinal diversity gradient of terrestrial tetrapods. Richness of: (a) all tetrapods (amphibians, reptiles, birds, and mammals), (c) reptiles, (d) amphibians, (e) birds, (f) mammals. Light gray areas denote cells excluded from analyses because their land areas cover less than 90% of the cell's entire area. White land areas denote cells with richness values of zero. Dark blue colors denote regions with few species and red ones denote regions with many species (note that the scale differs between panels). Black lines denote borders between different realms. All maps are in an equal area Behrmann projection at a 96×96 km resolution. (b) Latitudinal diversity gradient depicted the change in global species richness along a latitudinal gradient. Regression lines of the relationship between latitude and richness were created using GAM with K parameter equals 10. For each group, the species-richness values were divided by their total number of species in order to depict relative species richness. Richness of all tetrapods together is depicted in black, reptiles in orange, amphibians in green, birds in blue, and mammals in pink.

smooth functions of other covariates in general additive models; Ito et al., 2005): (1) annual temperature range, (2) mean diurnal temperature range, (3) precipitation seasonality (all from Karger et al., 2017), (4) mean elevation, (5) habitat

homogeneity (based on NDVI; Tuanmu & Jetz, 2015), (6) net primary productivity (Imhoff & Bounoua, 2006), (7) interannual variation in mean temperature, (8) and total precipitation (both derived from Copernicus Climate Change Service

(C3S, 2017), (9) temperatures at the last glacial maximum (LGM), and (10) climate change velocity since the LGM (Karger *et al.*, 2017). We also excluded (11) geographical location (longitude and latitude interaction), which we aimed to use to account for spatial autocorrelation, due to high concurrency with mean annual temperature.

We conducted the analyses globally and within biogeographical realms (of Olson *et al.*, 2001), excluding Antarctica. In global models, we added biogeographical realms as a predictor. This measure of evolutionary/geological history is somewhat crude compared to other historical variables but represents distinctive lineage pools generated through historical interactions with biogeographical barriers (e.g. Ficetola *et al.*, 2017; Smith *et al.*, 2005).

To determine whether to use productivity or precipitation as predictors, we compared the AIC scores of models using either productivity or precipitation—and the other chosen predictors: temperature, elevational range, number of ecoregions, insularity, and realms for the global model. Models of precipitation had consistently lower AIC scores than models using productivity and we therefore used precipitation throughout.

We used generalized additive models (GAM) in order to incorporate nonlinear trends of the predictors and easily portray predictor–response relationships (Hastie & Tibshirani, 1990; Larsen, 2015). We analyzed GAM models of amphibians, birds, mammals, reptiles, and all tetrapods. We ran all analyses globally, and within each of the six major biogeographical realms (Neotropic, Nearctic, Palearctic, Afrotropic, Indomalaya, and Australasia), resulting in 35 GAM models. In all our models, the response variables were species richness per grid cell. We employed a log identity link function in all models, with a negative binomial error structure, which best fitted the data distribution and avoided overdispersion. For the continuous variables, precipitation, temperature, and elevational range, we examined the inclusion of interactions between predictors by trying all possible combinations. The K parameter value, which sets the upper limit on the degrees of freedom associated with the smooth function of the model, was also examined and incorporated with an automatic smoothness selection (Wood, 2017). We added insularity and the number of ecoregions as linear predictors. We evaluated model performance by R^2 and AIC values. We conducted all analyses using R 4.0 (R Core Team, 2021). We conducted GAM analyses, and concurrency testing, using the ‘mgcv’ package (Wood, 2017), and VIF analyses using the ‘car’ package (Fox & Weisberg, 2019).

To evaluate predictor importance, we checked the percentage decrease in R^2 between the model including all variables, and the model excluding each predictor. This decrease represents the additional variance in species richness explained by the predictor and its interactions that is not explained by the others. We produced partial-dependence plots that show the marginal effect each predictor has on model predictions (Hastie *et al.*, 2001).

Results

Global species-richness patterns

All tetrapod taxa show very similar global richness patterns (Fig. 1, Table 1) but with some notable exceptions. Tetrapod richness is highest near the Andes, especially along the Amazon basin, in northern Amazonia (Fig. 1). It is also high along southeastern South America, along the African Great Lakes, and through much of Southeast Asia. Richness is low at high latitudes and desert regions worldwide. Birds and mammals show very similar patterns to tetrapods combined (Table 1) except that mammals are species poor in Australia (Fig. 1). Amphibians are conspicuously absent from most of the world’s deserts but are relatively rich in southeastern United States and eastern Madagascar. Reptile richness is the least well correlated with tetrapods and the other taxa (Table 1). Reptile richness is relatively high in deserts globally and in Australia.

Latitudinal richness gradients

All taxa display strong latitudinal richness gradients. Richness peaks just south of the equator and decreases toward higher latitudes (Fig. 1b). Amphibians show the most marked tropical peak and the steepest latitudinal decline. Reptiles decline most slowly away from the tropics at mid-latitudes, especially in the southern hemisphere where richness is relatively high even at latitudes higher than 30°S. Other taxa (especially amphibians) decline more steeply. In the Northern Hemisphere, all taxa steeply decline away from the equator and reach a local minimum around the 25th parallel (roughly the southern Sahara but south of the Tibetan Plateau). Reptile richness, however, remains stable around the Tropic of Cancer where it is relatively higher than that of other taxa. At higher latitudes, reptile, and amphibian richness decreases, while endotherm richness actually increases slowly until around 40°N (mammals) and even 50°N (birds), then decreases toward the North Pole. Birds and

Table 1 Correlations of species richness among tetrapods using Pearson’s correlation corrected for spatial autocorrelation

	d.f.	Tetrapods	Reptiles	Amphibians	Birds	Mammals
R	Tetrapods		59.82	74.85	146.04	80.24
	Reptiles	0.86		59.74	68.22	66.31
	Amphibians	0.88	0.78		90.99	102.59
	Birds	0.98	0.76	0.82		90.99
	Mammals	0.96	0.78	0.83	0.93	

Correlation coefficients (R) in the bottom triangle. Degrees of freedom (d.f.) in the upper triangle. P -values are <0.0001 for all correlations.

mammals reach higher latitudes than reptiles and amphibians in the Northern, but not in the Southern Hemisphere (Antarctica excluded; Fig. 1).

Species-richness models

Chosen model parameters were consistent among all taxa and realms and set with temperature, precipitation, elevational range, and their interaction, with K parameter set at 150, and insularity and number of ecoregions as linear predictors. For global models, biogeographical realms were also set as a linear predictor. Environmental and biogeographical predictors explained 81% (amphibians), 82% (birds), 85% (mammals), 89% (all tetrapods), and 91% (reptiles) of the variation in global models (Table 2). For tetrapods and birds, all realm-specific models explained over 80% of the variation. For other taxa, models for the Afrotropical and Indomalayan realms were weaker ($R^2 = 58\text{--}74\%$). Models for Neotropical amphibians and Palearctic mammals had R^2 values of 73 and 76%, respectively. All other models had R^2 values exceeding 80%. Models of all taxa in the Nearctic were especially strong (R^2 values 94–96%), followed by models for the Australasian realm (88–92%, except for reptiles with 81%).

Predictor effects

Globally, precipitation was the most important predictor of richness patterns for all taxa except reptiles (Figs 2a and 4, Table S3), for which temperature was most important. The two predictors were positively associated with richness. Reptile richness peaked at maximum precipitation levels followed by amphibians that peaked at near maximum levels. However, the trend for reptile richness was weaker, with relatively high richness also seen at low precipitation levels. In contrast, the trend was very strong for amphibian richness, with extremely low richness at low precipitation levels. Endotherms showed an intermediate pattern (Fig. 2b). At low temperatures, ectotherms richness was lower compared to endotherms, while at the highest temperatures reptiles exhibited the highest richness among all taxa, resulting in the steepest trend. At the global scale, other predictors were less important. The richness of all taxa increased with the number of ecoregions and was lower on islands (Fig. 2c). Elevational range had a positive association with all groups at very low levels and a negative association at high levels (except for mammals). All groups' richness steeply increased up to ~750 m. Above that, mammal

richness slowly increased toward the highest elevational range levels. Reptile, tetrapod, and bird richness were fairly constant up to ~2500 m, above which reptile richness decreased toward the highest elevational ranges, while tetrapod and bird richness increased up to ~4500 m and then decreased. For amphibians, above ~750 m richness decreased up to ~2000 m then mildly increased toward ~5500 m, above which it declined.

Precipitation and temperature usually had the strongest (almost always positive) association with species richness across realms and taxa (Figs 3 and 4, Fig. S2, Table S3). Elevational range generally had a lower, more complex, association with richness, which varied across realms and taxa. However, its importance exceeded the one of precipitation or temperature in some cases (e.g. Indomalayan birds). Insularity (lower richness on islands than on continents in most realms and taxa) and the number of ecoregions (positively associated with richness) were usually the least important predictors (Fig. 3, Fig. S2).

Richness of different taxa was usually similarly related to the predictors within each realm, but differences exist (Figs 3 and 4, Fig. S2). Reptile richness was positively and strongly related to temperature, even within realms in which temperature had a weak or even a negative relationship with richness for the other taxa (most notably in the Australasian and Palearctic realms). Precipitation had a positive and strong association with amphibian richness in all realms, often stronger than for all other taxa (i.e. in the Nearctic, Afrotropic, and Palearctic realms; Figs 3 and 4, Fig. S2).

Predictors' association with richness varied between realms. Precipitation had an exceptionally strong positive association with Afrotropical taxa's richness whereas temperature had a weak association (Figs 3 and 4). In contrast, in the Nearctic, temperature had a very strong, generally positive association, whereas precipitation had a moderately negative relationship with tetrapod and endotherm richness, an extremely weak relationship with reptile richness, and a positive relationship with amphibian richness (Figs 3 and 4). In the Indomalayan realm, precipitation and elevational range were the most important predictors for the richness of all taxa (Fig. 4)—precipitation was positively associated with richness, whereas elevational range had a largely bimodal association. Richness peaked at ~2000 for all taxa, above which amphibian richness decreased while reptile and tetrapod richness peaked again and at ~5500 m and mammal and bird richness increased towards maximum elevational range levels (Fig. 3). In the Neotropics

Table 2 The adjusted R^2 of all the regression models explaining richness patterns across realms and for different taxa

Taxon/Realm	Neotropics	Afrotropics	Australasia	Indomalaya	Nearctic	Palearctic	Global
Amphibians	0.73	0.67	0.91	0.58	0.95	0.82	0.81
Birds	0.80	0.81	0.88	0.83	0.94	0.82	0.82
Mammals	0.87	0.74	0.92	0.66	0.95	0.76	0.85
Reptiles	0.91	0.67	0.81	0.71	0.96	0.85	0.91
Tetrapods	0.86	0.80	0.91	0.80	0.96	0.80	0.89

We built general additive models for each taxon, globally and within the different realms, resulting in 35 models. We modeled species richness as a function of environmental and biogeographical predictors.

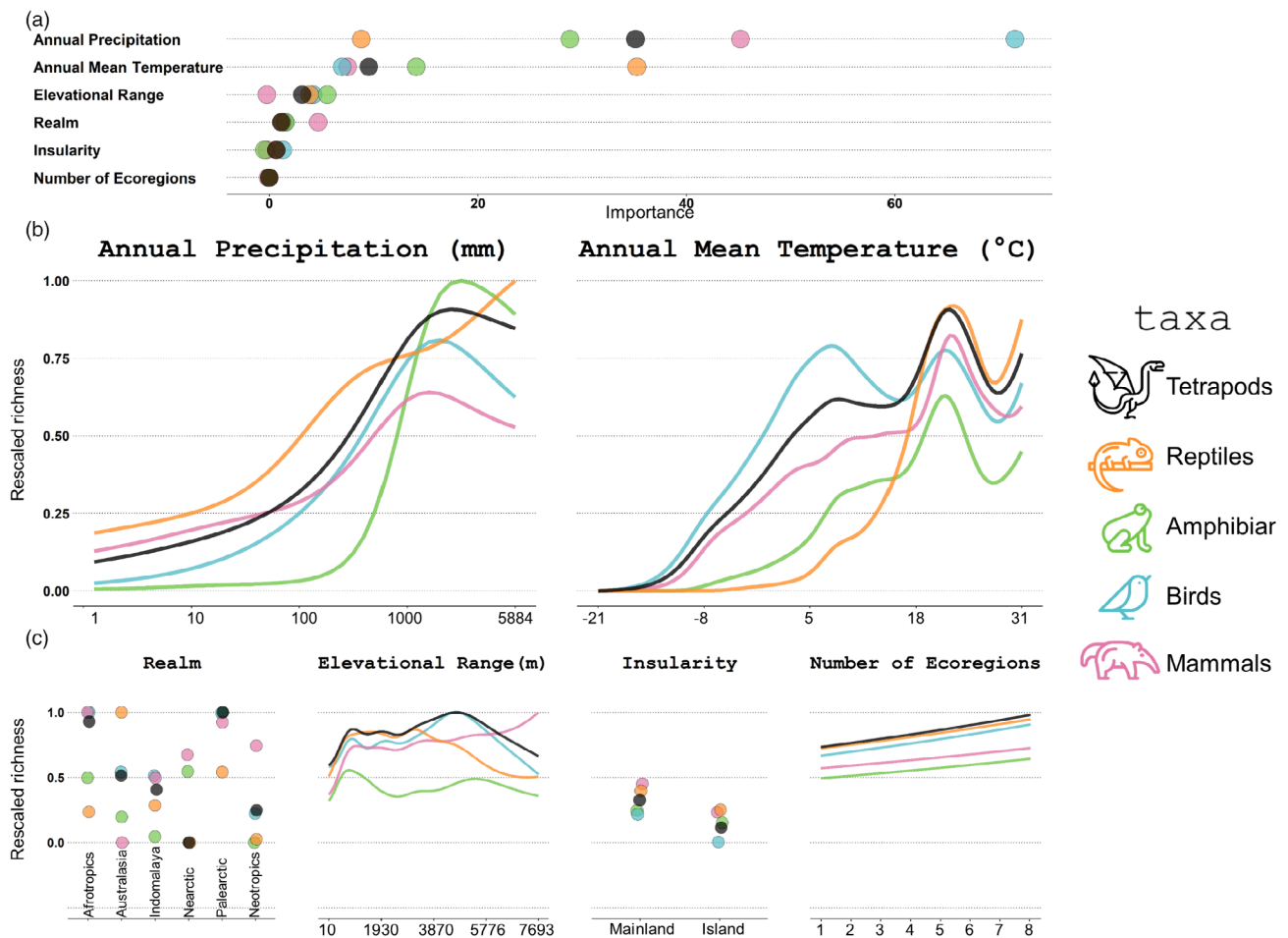


Figure 2 Global associations of environmental and biogeographical predictors with tetrapod richness. Species richness within each group was rescaled to range between 0 (lowest richness) and 1 (highest richness) using the formula: $z_i = \frac{x_i - \min(x)}{\max(x) - \min(x)}$ | $i = 1, 2, \dots, n$. Where x_i represents the original data and z_i the rescaled data. (a) Predictors' importance in explaining richness variation; rows denote the different predictors used in the model. A predictor importance (ranges from 0 to 72) is the percentage decrease in R^2 between the model including all variables and the model excluding the predictor. (b, c) Partial dependence plots representing the change in rescaled predicted global species richness along variable gradients: (b) the two most important predictors of species richness of all classes, (c) predictors with lower importance. Global models were fitted for each taxon separately (reptiles depicted in orange, amphibians in green, birds in blue, mammals in pink, and all tetrapods together in black). Annual precipitation is on a logarithmic scale, but raw values are presented.

and Australasia, precipitation had the strongest association with richness of all taxa except reptiles which were most strongly associated with temperature (Fig. 4). In the Palearctic realm, temperature and precipitation dominated all models, with elevational range third in importance for most taxa. Additionally, for amphibian richness, precipitation was much more important than temperature, whereas the reverse was true for reptiles (for which elevational range importance exceeded the one of precipitation).

Models including all cells (as opposed to cells >90% land) had nearly consistently lower R^2 values (Table S2). However, insularity became an important negative predictor of richness in the Neotropics for tetrapods, birds, and mammals, and in Australasia for reptiles and amphibians (Table S4).

Discussion

Our study provides a comprehensive account of key environmental and biogeographical factors that underlie the richness patterns of all terrestrial vertebrates. We support previous findings (e.g. Barreto *et al.*, 2021; Qian, 2010) that precipitation is most strongly (and positively) related to tetrapod species richness (except reptiles), globally and largely in all realms except for the Nearctic (Figs 2–4). We show that associations between species richness and elevational range differ between taxa, globally and regionally, especially between endotherms and ectotherms (Figs 2 and 3). Moreover, we show that elevational range is a very strong predictor of species richness in Indomalaya while insularity has minor importance in explaining

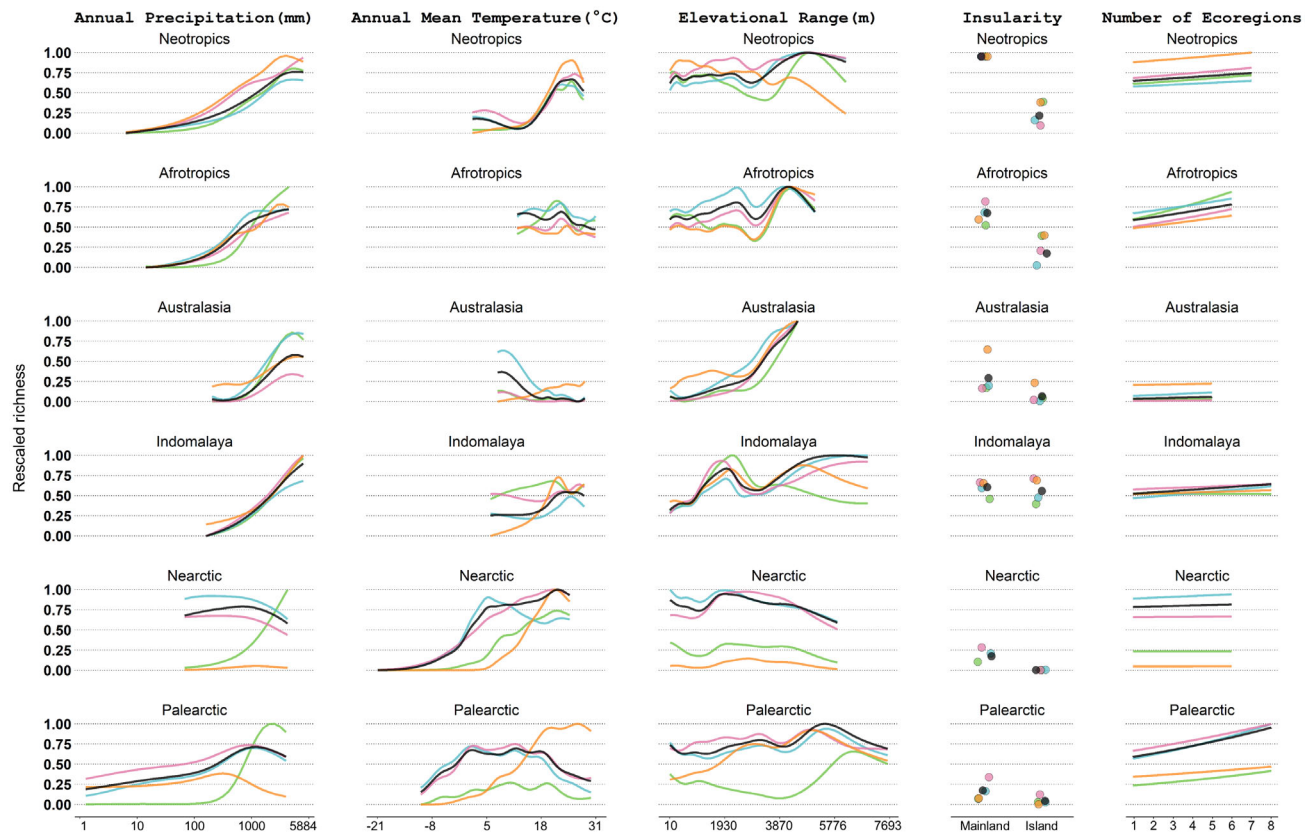


Figure 3 The associations of environmental and biogeographical predictors with tetrapod richness within the different realms. Predictor (= column) relationship with rescaled richness, showing marginal effects on predicted species richness in each of the six biogeographical realms (rows). The marginal effect of each predictor is represented by a partial dependence plot. Models were fitted for each taxon separately (reptiles: orange, amphibians: green, birds: blue, mammals: pink, all tetrapods: black). Species richness of each group (y-axis) was scaled to range between 0 (lowest richness) and 1 (highest richness). Annual precipitation is on a logarithmic scale, but the raw values are presented.

variation in species richness (Fig. 4). Within realms, we find great variability in environment–richness relationships (consistent with Qian, 2010).

Taxonomic variation in richness–environment relationships

The overall tetrapod-richness pattern is very similar to that of birds and mammals (Table 1). This is probably because bird species have the largest ranges (Li et al., 2016) and amphibians and reptiles the smallest, thus, since large-ranged species influence more cells, endotherms more strongly influence tetrapod richness patterns (compare scales in Fig. 1; Jetz & Rahbek, 2002; Lennon et al., 2004; White et al., 2023). Consequently, the richness of birds, mammals, and tetrapods was similarly correlated with the environmental predictors, whereas amphibians and reptiles, often displayed different relationships (Figs 2–4; e.g. Barreto et al., 2021; Belmaker & Jetz, 2011; Buckley & Jetz, 2007; Jetz & Fine, 2012).

Endotherms are more tolerant of cold temperatures than ectotherms, and many birds avoid harsh seasonal environments through migration (Buckley et al., 2012; Hurlbert &

Haskell, 2003). However, endotherms require high and continuous food supply (Buckley et al., 2012; Pough, 1980; Shine, 2005). Thus, their richness is presumably less limited by solar energy than by resource availability. Accordingly, precipitation, which has considerable impacts on productivity (Liu et al., 2020), was overall the most important predictor of bird and mammal richness (Fig. 4). While consistent with most prior research (e.g. Hawkins, Field, et al., 2003; Rodríguez et al., 2005), Qian and Ricklefs (2008; at the country level, for all tetrapods) and Belmaker and Jetz (2011; for mammal assemblages) found that temperature indices were more important than water indices in predicting global species richness. It is worth noting that this could be due to the limited desert-region samples (refer to Fig. 1 in both papers), pivotal in global precipitation patterns. Moreover, data accessibility may have favored samples from Nearctic and Western European regions, known for their wide temperature ranges (Fig. S3; Bohdalková et al., 2021). Howard et al. (2020, Fig. S9) found that temperature seasonality was more important than precipitation for tetrapod, mammal, and bird species richness. However, it is worth considering that the inclusion of highly correlated factors, such as temperature seasonality and temperature, may

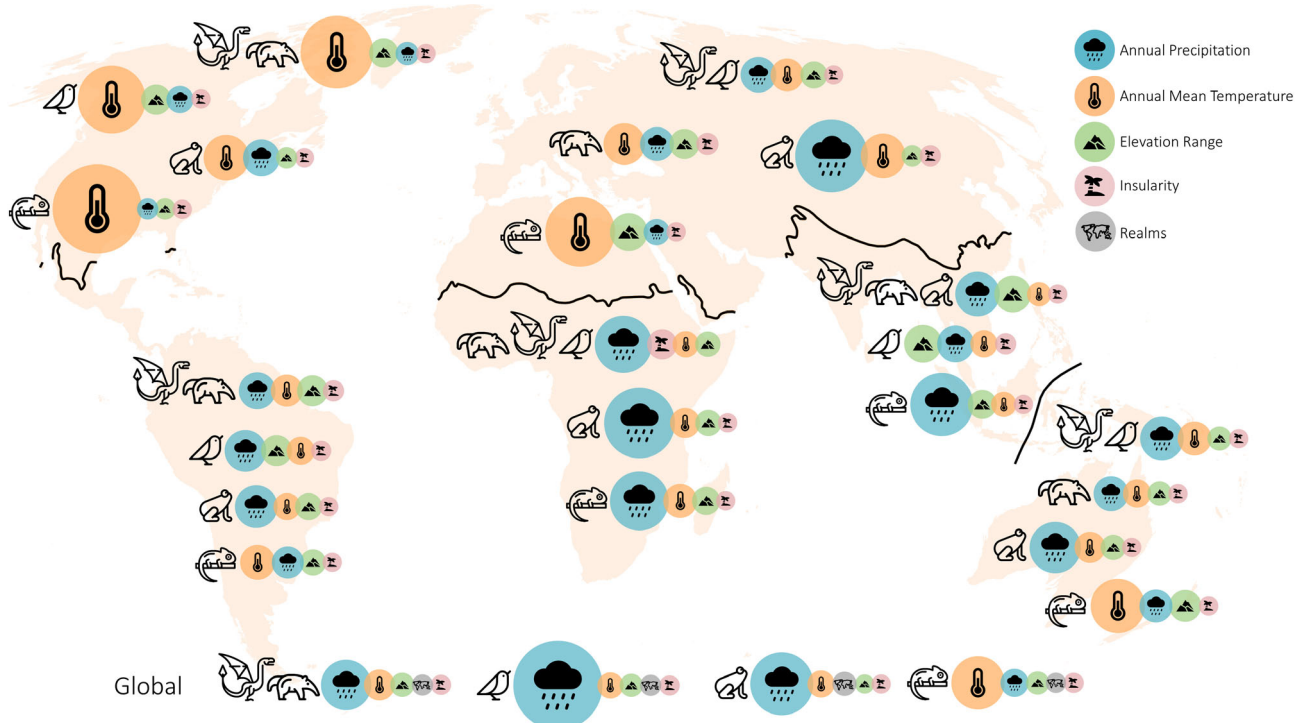


Figure 4 Spatial variance in the importance of environmental predictors on tetrapod species richness. The size of a circle is in accordance with its importance value calculated as the percentage decrease in R^2 between the model including all variables and the model excluding the predictor. The predictor importance is depicted for each realm, and the global model is presented at the bottom. The number of ecoregions is excluded due to its small impact on species richness in our models. Grouping of different taxa (e.g. mammals, birds, and tetrapods in the Afrotropics) occurs when the predictor importance is very similar between the different taxa. In such a case, the circle size corresponds to the mean of the importance values. The colored icons depict the environmental and biogeographical predictors used in the models (annual precipitation in blue, temperature in orange, elevation range in green, insularity in pink, and realms in gray).

have influenced their conclusions. Reptiles, which display a strong and positive relationship with temperature (Figs 2–4; in accordance with e.g. Barreto *et al.*, 2021; Qian & Ricklefs, 2008; Qian *et al.*, 2007), are highly dependent on ambient temperatures, but can cope with dry conditions (Buckley *et al.*, 2012; Schall & Pianka, 1978; e.g. see the high richness in the deserts of Australia in Fig. 1c). Amphibians, for which precipitation had the strongest positive correlation (Figs 3 and 4, Fig. S2; in accordance with, e.g. Buckley & Jetz, 2007), require readily available water or humid conditions for key physiological processes and activities (Feder & Burggren, 1992; Tracy, 1976).

Our research revealed that elevational range often exhibits distinct associations with the different taxa, often varying between endothermic and ectothermic species richness (Figs 2c and 3). Elevational range is thought to represent habitat heterogeneity and usually has a positive impact on species richness (e.g. Field *et al.*, 2009; Kerr & Packer, 1997; Stein *et al.*, 2014). For example, the peak in species richness around elevational range of ~4000 m in the Indomalayan and Palearctic realm (and to some extent in the global model; Figs 2c and 3) corresponds to the high habitat heterogeneity induced by the biogeographical barrier between the Indomalayan and the

Palearctic realm. However, elevational range is also correlated with mean elevation (global Pearson correlation coefficient 0.48). In very high elevations the assumption that greater elevational ranges include more available habitats is often not met due to harsher conditions (Hortal *et al.*, 2013). Thus, wide elevational ranges can negatively impact richness (e.g. Barreto *et al.*, 2019; Hortal *et al.*, 2013; Qian *et al.*, 2007). Accordingly, we found that for most regions and taxa, there is a decline in species richness at high values of elevational range (Figs 2c and 3). Moreover, ectotherms show in some regions (Global, Indomalaya, and Neotropical) a steeper or earlier (from lower elevational ranges) decline in species richness than endotherms (Fig. 3). It is possible that endotherms better cope with the cold conditions at high elevations (Buckley *et al.*, 2012).

Spatial variation in richness–environment relationships

Previous studies found that the relationship between environmental predictors and tetrapod richness differs across space (e.g. Alves *et al.*, 2018; Barreto *et al.*, 2021; Davies *et al.*, 2007). Bohdalková *et al.* (2021) suggested that the relationship between richness and temperature is only strong in

regions with a wide temperature range. In contrast, the relationship between richness and productivity appears to be more universal. Unlike temperature, our analysis suggests that high variation in elevational range does not necessarily lead to a strong correlation with richness (Fig. S3). Such a strong correlation is apparent in Indomalaya, but not in the Neotropics or Australasia, despite elevational range having a higher variation than precipitation and temperature in these regions. The large area of relatively homogeneous environment of the wet and warm Amazon, may harbor many large-ranged species and high range overlap, leading to higher richness (James & Shine, 2000), which is unrelated to the variation in elevational range (similarly, the hot and arid zone in Australia may induce a lower species richness for most taxa).

We found a negative relationship between temperature and richness in Australasia for amphibians, birds, and mammals and a humped-shape relationship in the Palearctic for these taxa (Fig. 3). Barreto *et al.* (2021) also found mixed trends in most realms, but for Nearctic birds, we found a richness peak at medium temperatures ($\sim 5^{\circ}\text{C}$) while Barreto *et al.* (2021) found a positive association. Our focus solely on breeding ranges, as opposed to their inclusion of non-breeding grounds in warmer regions, likely accounts for the temperature-dependent difference in species richness.

The latitudinal diversity gradient

The decrease in richness away from the equator is not symmetrical in any taxon (Fig. 1b). Species richness in the southern hemisphere is usually higher than in equivalent latitudes in the northern hemisphere in many taxa (e.g. Blackburn & Gaston, 1996; Burns, 2007; Dunn *et al.*, 2009). This might be explained by the higher temperatures in southern latitudes, which result from an extensive area of oceans in comparison with the more continental northern hemisphere (Chown *et al.*, 2004; Gaston & Chown, 1999).

Arid areas are much more extensive in the northern hemisphere than in the southern one. The Sahara Desert alone accounts for 45% of the world's hyperarid zones (FAO, 2019). This great desert (together with the Tibetan Plateau) potentially causes the steeper decline in richness from the equator toward high latitudes in the northern, versus the southern, hemisphere (Fig. 1b). North of these drylands, precipitation levels increase while temperatures decrease (Fig. S4), creating suitable conditions for many endotherm species, but less so for amphibians and reptiles (Fig. 1). The rise in tetrapod, bird, and mammal richness from 25° to 45° latitude contradicts the usual trend of diversity decreasing with latitude (Gaucherel *et al.*, 2018). Instead, it corresponds with higher levels of precipitation and productivity.

Caveats

Species-richness data are essential for understanding the history, ecology, and conservation priorities (Jenkins *et al.*, 2013). However, they suffer from data shortfalls. Most notably, there is a great spatial sampling bias, as diversity in deserts, high mountains, and geopolitically less stable, or poorer countries,

are less studied than, e.g. the USA, Canada, Australia, and Europe (e.g. Hickisch *et al.*, 2019; Marshall & Strine, 2019; Meyer *et al.*, 2015). Such biases reflect both the dearth of samples and often the lack of the necessary taxonomic expertise to properly identify the faunas of these regions. These Linnean and Wallacean shortfalls might cause inaccuracies in species-richness maps, which rely on global knowledge of species distributions (Hughes *et al.*, 2021; Yang *et al.*, 2013). However, as undersampling is probably strongest in the tropics, which have the highest richness values despite this bias, and our models had high explanatory power (Table 1), we think the main richness–environment patterns we found are generally robust. Nonetheless, spatial variation in biodiversity knowledge is significant even within the tropics (e.g. the Neotropics vs. Afrotropics and Indomalaya; Martin *et al.*, 2012; Wallace, 1859) which might more strongly impact our results. Additionally, many terrestrial vertebrates, particularly amphibians and reptiles, are still undescribed and are assumed to exist mainly in the tropics (e.g. Giam *et al.*, 2011; Melville *et al.*, 2021; Moura & Jetz, 2021). However, newly described species most likely have small range sizes (Giam *et al.*, 2011; Meiri, 2016), and thus their impact on large-scale species-richness patterns is probably small.

Conclusions

We have built upon recent advances in the availability of species-distribution data (Caetano *et al.*, 2022; IUCN, 2021; Roll *et al.*, 2017) and conducted thorough analyses of richness–environment relationships for terrestrial vertebrates, both collectively and separately for birds, mammals, amphibians, and reptiles at both global and biogeographical realms levels. While numerous studies have examined many of the patterns we present in this study, individually or partially, conducting them within a single study, while providing detailed richness–environment associations, allows us to make solid comparisons among variables, taxa, and regions. We support some earlier observations that precipitation is generally the most important factor to predict tetrapod species richness. Nevertheless, we also highlight two main exceptions: (1) reptile richness is strongly associated with temperature—as can be expected given reptiles' physiological and ecological needs, and (2) in the Nearctic, and to some extent the Palearctic, temperature is often the strongest predictor of richness—probably due to the high variance in temperatures across these realms. We further show that while elevational range is usually less important than climate, it is highly influential in the Indomalaya, and its relationship with species richness differs among taxa, especially between endotherms and ectotherms. Recent studies on species richness extensively investigated high-resolution richness–environment relationships and provided interesting insights (Barreto *et al.*, 2021; Bohdalková *et al.*, 2021). However, their focus has been limited to climatic variables. We suggest that future studies consider incorporating other relevant variables such as elevational range into their analyses. Such investigations may yield further novel insights and advance our understanding of the complex relationships between biodiversity and the environment.

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Author contributions

TR, SM, and UR conceived the ideas and designed the study; All authors collected the data; TR and UR analyzed the data; TR led the writing of the paper; All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

The distributional data used in this study to create the species richness maps can be obtained from the mentioned sources in the text.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. The insularity predictor used in the models.

Figure S2. Predictors' importance for all regional models.

Figure S3. Spatial variation in the variance of environmental predictors and their importance on tetrapod species richness.

Figure S4. The continuous predictors used in the models.

Table S1. Species included in the creation of the species richness maps.

Table S2. The adjusted R^2 of all the regression models.

Table S3. Predictors' importance for all the models.

Table S4. Predictors' importance for all the models including all cells.