RESEARCH ARTICLE

Frontiers of Biogeography
the scientific journal of
the International Biogeography Society

Macroecological correlates of richness, body size, and species range size in terrestrial vertebrates across the world

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Abstract

Species richness, body size, and range size are among key subjects in animal macroecology and biogeography. To date, the species richness–body size–range size nexus remains largely understudied at a global scale and for large taxonomic groups. Here we examine the relative role of species richness and body size in determining species range size among terrestrial vertebrates across spatial and taxonomic scales. We then test related hypotheses in the context of Rapoport's rule, latitude, and climate variation. To do this, we used simultaneous autoregressive analysis and structural equation modeling to test for statistical relationships among species richness, body size, and range size for all terrestrial vertebrates and for each continent. We then investigated the relative contributions of richness, body size, latitude, climate variation, and their combinations in the variations in species range sizes. We found that species richness consistently shows strong negative correlations with range size at global, regional, and within-region levels, and for all terrestrial vertebrates, and for each of the four classes (i.e., birds, mammals, amphibians, and reptiles). The strength of the relationships increased with richness and with spatial and taxonomic scales. Globally, species richness explained more variation in species range size than did latitude and climates. Body size contributed significantly to the range sizes of all four classes but especially reptiles and amphibians. However, the relative contributions of these factors varied substantially among the continents and terrestrial vertebrate classes. Comparison with the findings of a previous study shows that there were also significant differences in regional patterns between terrestrial vertebrates and plants and the relative contributions of diversity vs. latitude. Our findings show clear relationships among species richness, body size, and range size, but the strength of the relationships varies among regions and taxonomic groups. In general, species richness could predict species range size better than body size, latitude, and climate. These results have important theoretical and applied implications.

Highlights

- Species richness, body size, and range size were closely interrelated for global terrestrial vertebrates.
- Consistently negative richness–range size relationships were observed at global, regional, and within-region levels, and for each species group (class).
- The strength of the relationships increased with richness, and with spatial and taxonomic scales.
- The relative contributions of diversity *vs.* latitude varied substantially among biogeographic regions and terrestrial vertebrate classes.
- Species diversity of vertebrates predicts species range size better than latitude and climate.

Keywords: amphibians, Bergmann's rule, birds, climate, mammals, Rapoport's rule, reptiles, tetrapod

e-ISSN: 1948-6596 https://escholarship.org/uc/fb doi:10.21425/F5FBG61729

Introduction

Species richness, body size, and range size (distribution) are among the most studied key topics in macroecology, biogeography, and conservation biology (Brown 1995, Gaston 1998, Jetz et al. 2004). In the past, latitude has been frequently considered (sometimes clearly stated as a proxy of climate) in explaining species range size (i.e., Rapoport's rule; Stevens 1989, Lyons and Willig 1997). Later, species range size has most frequently been examined with climate factors (e.g., seasonal variability) and other abiotic factors to assess underlying mechanisms behind variations in species range size of constituent species at both regional and global scales and for various taxonomic groups (Orme et al. 2006, Boucher-Lalonde et al. 2014, Boucher-Lalonde et al. 2016, Li et al. 2016). However, few studies have directly examined the unique role of species richness and/or jointly with body size (animals only) in regulating species range sizes across both spatial and taxonomic scales.

Species richness, body size, and range sizes could be regulated by the same drivers, which makes it difficult to distinguish whether and how each variable directly and/or indirectly affects others. Earlier studies independently found that both richness and range size vary with latitude or elevation (e.g., as described in Rapoport's rule) but rarely link range size with richness (Stevens 1992). Also, past studies suggest that larger-bodied species seem to occupy larger geographical areas (range sizes) as they need more space and resources (Gaston and Blackburn 1996). It is possible that regional conditions promoting small ranges of component species allow for more species to accumulate, whereas factors (e.g., habitat heterogeneity or patchiness) that promote high species richness could limit the expansion of species ranges (Rosenzweig 1995). For example, narrower species ranges in the tropics indeed may facilitate more species to coexist at the regional scale. Higher diversity in the tropics suggests that most component species may not have large overall population sizes; thus, these species tend to have smaller ranges (and also presumably smaller body sizes) due to energy constraints (Wright 1983). This is because species distribution (range size) and abundance (overall population size) are usually positively related to each other (Brown 1984, Orme et al. 2006).

Research to date that links species range size with diversity and organism (or body) size is very rare, especially for larger taxonomic groups, such as all terrestrial vertebrates or all plants, and at the global scale. In addition, most related studies to date have mainly focused on relationships of species range size with latitude (Rapoport's rule) (e.g., Stevens 1989) and to a lesser extent in association with body size (Bergmann's rule – organisms in colder climates are usually larger than those in warmer climates; McNab 1971). Much less effort has been made to examine the relative importance of latitude (a proxy of climate), diversity, climate variation, and their various combinations to species range size. Recently, using plants around the world, Guo et al. (2022) found nearly universal negative relationships between plant species richness and the average range size of component species. Similar studies for animals remain lacking. Because life history and dispersal approaches differ substantially between plants and animals (BirdLife International 2021, IUCN 2022), whether the pattern observed for plants is consistent with that for animals needs to be tested.

Here, we use data on species richness, body size, and range size for all terrestrial vertebrate species across the globe to examine the relationships of species range size with species richness, body size, latitude, and climatic variables, and test whether the negative richness–range size relationship observed for plants (Guo et al. 2022) also exists for terrestrial vertebrates. Specifically, we test the following three main hypotheses: (1) species richness is negatively related to average species range size and body size but body size and range size are positively related; (2) different terrestrial vertebrate groups (classes) show negative richness–range size relationships but the strengths of these relationships also vary with spatial scales and taxonomic scales; and (3) the relative contributions of species richness, body size, latitude, and climate variation to species range size may vary among taxonomic groups and among continental regions (Fig. S1).

Materials & Methods

This study included all species in the four terrestrial vertebrate classes (i.e., birds, mammals, reptiles, and amphibians). We obtained the range maps of birds from BirdLife International (2021) and the other three vertebrate classes from IUCN (2022) and calculated the range size for each species. The body size (mass, g) data were obtained from Etard et al. (2020), Wilman et al. (2014), and Johnson et al. (2023). We divided the globe into 300 km × 300 km grid cells based on the Mollweide (equal-area) projection (Fig. 1). Grid cells that had less than 50% of their area on land or had no terrestrial vertebrate species were excluded from this study. We assigned each grid cell to one of the following six biogeographic ("continental") regions: Europe, Asia, Northern America, Africa, Australasia, and Southern America (Fig. S1), as in Guo et al. (2022). A total of 1469 grid cells were included in this study. For each grid cell, we determined the number of species and mean body size as well as the average of worldwide range sizes of the species in the grid cell. We did this for all species in the four terrestrial vertebrate classes combined and for each of the four classes.

We explored the relative strength of the relationship between average species range and species richness (SR) versus the relative strength of the relationship of average species range with latitude (LAT), mean annual temperature (MAT), temperature variability (temperature annual range; Tvar) as in Guo et al. (2022), and newly included body size (BS) in this study. Latitude per se has little biological meaning but it has been used to formalize some prominent patterns in ecology and evolution such as Rapoport's rule (Stevens 1989) and Bergmann's rule (McNab 1971), some of which are relevant to species range size (e.g., Rapoport's rule).

As a result, in addition to including relevant climatic variables in this study, we also included latitude as a separate variable for comparative purposes (with earlier studies). We acquired climate data (bio1 and bio7 for MAT and Tvar, respectively) at a resolution of 30-arc-seconds from the CHELSA climate database (https://chelsa-climate.org) (Karger et al. 2017). We calculated the averages of MAT and Tvar for each grid cell. We used partial linear regression models in variation partitioning analyses (Legendre and Legendre 2012) for the global and for each of the six regional terrestrial vertebrate assemblages. We then determined the unique contributions of SR, LAT, MAT, Tvar, and BS and joint contributions by SR+LAT, SR+MAT, SR+Tvar, or SR+BS. We used simultaneous autoregressive (SAR) error models, which account for spatial autocorrelation (Rangel et al. 2010), to estimate the coefficient of determination of each regression.

We tested for statistical correlations between species richness and average range size separately for the globe as a whole and for each of the six continental regions. We evaluated the strength of each statistical analysis by its effect size (e.g., correlation coefficient from correlation analysis, or coefficient of determination from regression analysis). Specifically, we considered a correlation (Spearman's rank correlation coefficient, r_s) to be strong for $|r_s| > 0.66$, moderate for $0.66 \geq |r_s| > 0.33$, or weak for $|r_s| \leq 0.33$ (Qian et al. 2019). We used SYSTAT (Wilkinson 1992) and Spatial Analysis in Macroecology (www.ecoevol.ufg.br/sam) (Rangel et al. 2010) to run the statistical analyses. Because the effects of richness and body size on species range size are expected to be mediated by latitude and associated climate variables with various levels of collinearity, we used structural equation modelling (SEM) to examine the effects of mean annual temperature, temperature seasonality, species richness, and body size on species range size, using the R package 'lavaan' (https://cran.r-project.org/web/packages/lavaan).

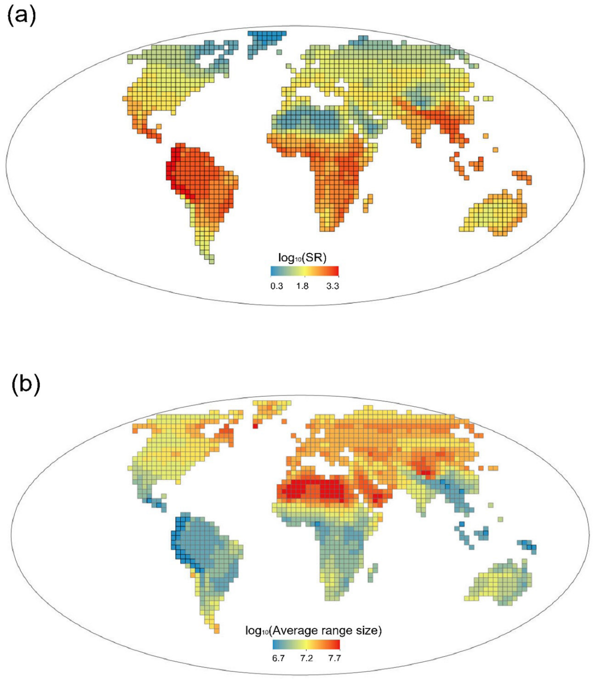

Fig. 1. Maps showing (**a**) species richness (SR) and (**b**) average range size (km^2) per species of all global terrestrial vertebrates in each grid cell (300 km × 300 km) based on the Mollweide (equal-area) projection.

Results

Taking all four terrestrial vertebrate groups together (i.e., when all species in the four groups were combined in analysis), we observed a strong negative relationship between species richness and species range size (Fig. 2a). Such negative richness–range size relationships were also observed within each of the six continental regions (Fig. 2b,c; see also Fig. S2).

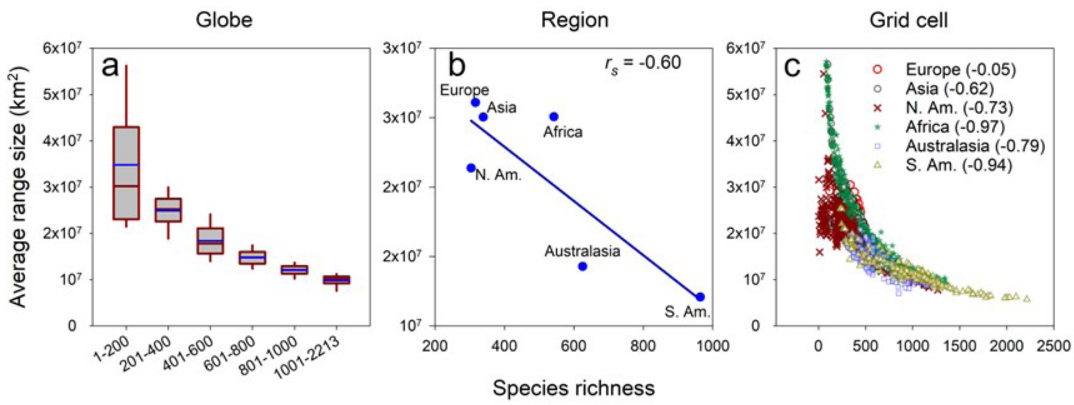

Fig. 2. (a) The relationships (r_s) between species richness and average range size (km^2) of all terrestrial vertebrate species across the globe. The box includes the lower 25th and higher 75th percentiles, the median (solid line in the box), and the mean (the blue line). The whiskers are the 95% confidence interval. (**b**) The relationships (r_s) between species richness and average range size for all terrestrial vertebrate species across the six continental regions (i.e., Europe, Asia, Northern America, Africa, Southern America, and Australasia; see also Fig. S1). **c.** The negative species richness–range size relationships (r_s) for all terrestrial vertebrates across grid cells in each of the six continental regions.

At the global scale, each of the four taxonomic groups of the world's terrestrial vertebrates also exhibited strong negative richness–range size relationships. The Spearman's rank correlation coefficient, r_s, increased as the species groups became larger in terms of species richness (Fig. 3a). The relationships between richness and body size in birds, mammals, and amphibians were also negative but positive for reptiles (Fig. 3b).

The average body sizes of the four terrestrial vertebrate groups were significantly different among the six regions (One-way ANOVA, $p < 0.001$). Contrary to spatial patterns that the average range size was smaller in species-rich regions (range size: South America < Australasia < Africa < Asia < Northern America < Europe while richness pattern was the opposite trend), at the class level, the average range size was larger in species-richer groups, i.e., across the globe, birds had the highest richness and largest average range sizes, followed by mammals, reptiles, and amphibians (Fig. S2).

At the global scale, species richness (SR) explained more variation in average species range size for the world's terrestrial vertebrates than latitude or temperature. Specifically, it explained 49.9%, 62.5%, 29.9%, and 58.9% of the variation in average species range size for birds, mammals, reptiles, and amphibians, respectively, which were higher than those explained by latitude (LAT), or mean annual temperature (MAT), or body size (BS), either separately or jointly. Particularly, the variation in range size uniquely explained by temperature variability (Tvar) was the smallest (< 1%) while SR and Tvar jointly explained 27.9% (Fig. 4). When MAT and Tvar were accounted for, LAT explained <2% of the variation in range size of the four classes of vertebrates (adjusted R^2 was 0.339 for the model with MAT and Tvar as explanatory variables and was 0.354 for the model with MAT, Tvar and LAT as explanatory variables).

However, across the six continental regions, the relative contributions of SR, LAT, MAT, Tvar, and BS and their combinations to variations in average range size of all global terrestrial vertebrates varied substantially, but in most cases, SR contributed the most, especially in species-rich regions such as Southern America, Africa, Australasia, and Asia (Table 1).

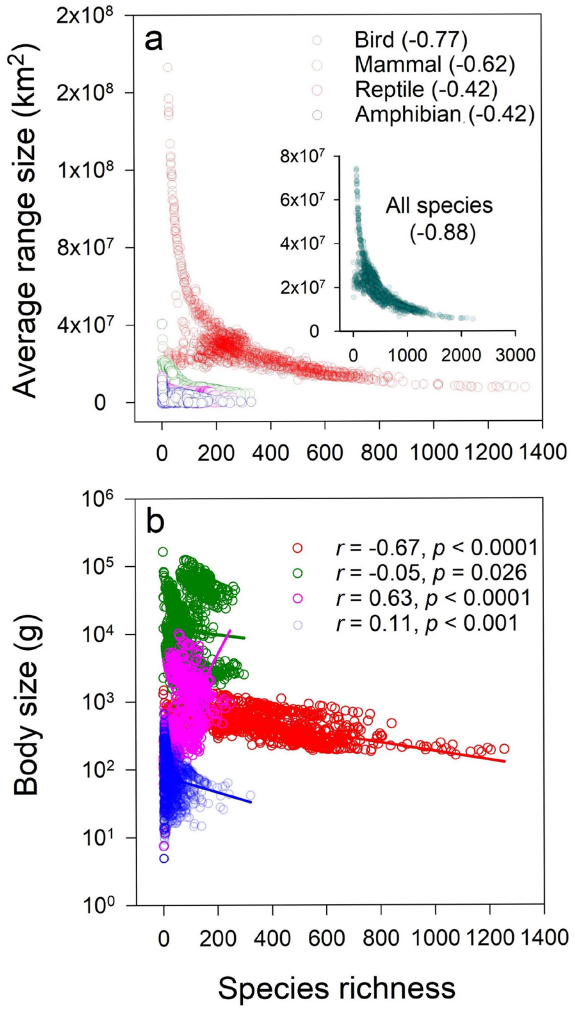

Fig. 3. a. The negative relationships (r_s) between species richness and average range size (km^2) for each of the four terrestrial vertebrate groups (classes) and for all terrestrial vertebrates (inserted panel) around the world (in all cases, $p < 0.001$). **b**. The relationships between species richness and average body size for each of the four groups and all species of world terrestrial vertebrates.

TABLE 1. Unique and relative contributions (%) of species richness (SR), latitude (LAT), mean annual temperature (MAT), temperature variability (Tvar), body size (BS) or jointly by SR+LAT, or SR+MAT, or SR+Tvar, or SR+BS to the variation in average range size (km^2) per species of global terrestrial vertebrates (birds, mammals, reptiles, and amphibians) for each of the six continental regions (i.e., Europe, Asia, Northern America, Africa, Australasia, and Southern America; Fig. S1). The highest values are marked in bold among the three factors in each case. SR is $\log_{10}$-transformed species richness. Darker cells indicate greater contributions.

Region	SR versus LAT			SR versus MAT			SR versus Tvar			SR versus BS		
	SR+LAT	SR	LAT	SR+MAT	SR	MAT	SR+Tvar	SR	Tvar	SR+BS	SR	BS
Europe	15.9	16	24.8	14.8	14.9	25.6	0.6	0.5	1.6	0.5	0.6	14.4
Asia	10.1	57	14.3	6.2	53.1	10	10.3	36.6	0.9	12.8	34.1	0
N. America	29.5	2.1	2.2	30.8	0.8	1.5	12.2	19.4	4.5	1.6	33.2	3.2
Africa	31.5	62.8	0.3	1.1	93.2	0.1	62.7	31.6	0.3	31.1	63.2	0.1
Australasia	25.9	30.9	0.3	0.1	56.7	0	45	11.8	0.5	9.9	46.9	2.2
S. America	43.1	47.2	1.4	25	65.3	1.2	37.2	53.1	3.3	61.4	28.9	< 0.1

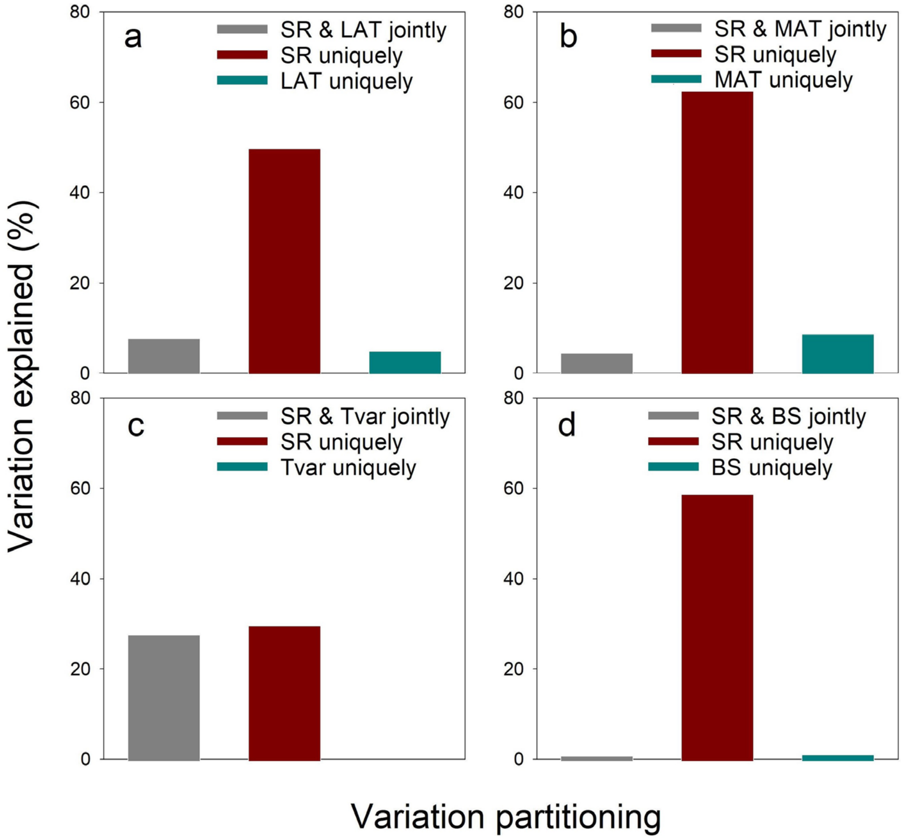

Fig. 4. Variation in average range size (km^2) per terrestrial vertebrate species uniquely explained only by species richness (SR), only by either latitude (LAT) or mean annual temperature (MAT) or temperature variability (Tvar) or body size (BS), or jointly by SR+LAT or SR+MAT or SR+Tvar or SR+BS for all terrestrial vertebrates across the globe. Terrestrial vertebrates included all species of birds, mammals, reptiles, and amphibians. SR is $\log_{10}$-transformed species richness. All models were significant ($p < 0.05$).

When contributions from SR and LAT to range size variation were considered either separately or jointly, LAT made a significant contribution only in Europe and Asia, and SR and LAT jointly contributed the most in Northern America and second to SR in Africa, Australasia, and Southern America. When SR and MAT were considered either separately or jointly, SR's contribution was much higher in Asia, Africa, Australasia, and Southern America, and MAT was only important in Europe and Asia. However, when SR and Tvar were analyzed either separately or jointly, SR was most important in Asia, Northern America, and Southern America while SR and Tvar jointly contributed the most in Africa and Australasia, and Tvar contributed much less in all the six regions. When SR and BS were jointly or separately considered, SR also made the largest contribution except in South America where the joint contribution from SR and BS was the largest (Table 1).

Across taxonomic groups and at the global scale, the relative contributions of SR, LAT, MAT, Tvar, BS, and various paired combinations to variations in average range size were not consistent. Specifically, the contributions of these factors and their various combinations varied substantially among the six continental regions and among the four vertebrate classes (Table S1).

The SEM that related species range size simultaneously to species richness, body size, mean annual temperature, and temperature seasonality explained 94%, 24%, 27%, and 26% of the total variations in range size for birds, mammals, reptiles, and amphibians, respectively (Fig. 5). Across the globe and in each group, species richness was consistently and negatively related to range size, and species range size generally increased with body size (Fig. 5). We also found complex and inconsistent correlations among other contributing variables such as MAT and Tvar. For example, MAT was positively correlated with the range size of birds and reptiles but negatively correlated with the range size of mammals and amphibians. In contrast, Tvar was positively correlated with the range size of birds and mammals but negatively correlated with the range size of reptiles and amphibians. The SEM analyses showed that of the four explanatory variables of species range size in each SEM, the effect of species richness on species range size was greater than any other variables for birds and reptiles, but body size was the most dominant contributor to range size of amphibians and the second dominant factors to range size of reptiles (Fig. 5).

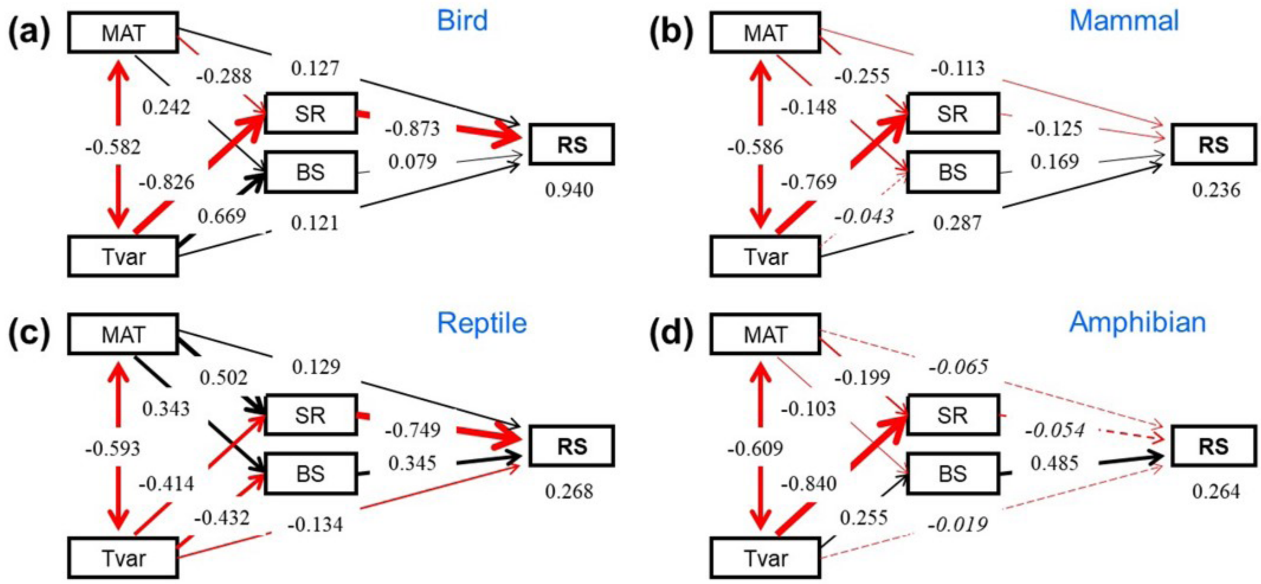

Fig. 5. Structural equation models (SEMs) showing relationships among mean annual temperature (MAT), temperature seasonality (Tvar), species richness (SR), mean body size (BS) in explaining the variation in mean species range size (RS) of terrestrial vertebrates in grid cells across the world. Numbers on arrow lines are standardized path coefficients; numbers on lines with double arrows are covariance, numbers below boxes for mean species range are R^2 values ($p < 0.05$ in all cases). Numbers or dashed lines in italic type are not significant ($p > 0.05$). Black line = positive correlations and red lines = negative correlations. All data were $\log_{10}$-transformed to meet the requirements of normal distribution for modeling.

Discussion

When all terrestrial vertebrate species are considered together at the global scale, the negative richness–range size relationships observed here confirm those seen in earlier studies on individual animal groups (classes), such as birds and mammals, at regional scales (e.g., Lyons and Willig 1997, Agosta et al. 2013). The observed negative diversity–range size relationships for terrestrial vertebrate species at global and regional scales are also consistent with those observed for plant species at both global and regional scales (Guo et al. 2022). However, the strength of the relationship (as reflected by r_s) appears to be correlated with overall species richness in each terrestrial vertebrate group (Fig. 4).

Possible underlying causes

Some explanations for similar negative richness–range size relationships for global plants may be applied to animals, such as terrestrial vertebrates, as well. Resources, such as energy and space availability, can pose a major constraint on the success of many animal species (Wright 1983, Currie and Fritz 1993, Kelt and Van Vuren 1999, Hurlbert 2004). Although lower latitudes receive more energy (e.g., heat, light), the available energy cannot match the amount of energy needed if species at lower latitudes have the same body size, abundance, and range size as those at higher latitudes. High species richness can lead to stronger biotic interactions (competition, predation) at lower latitudes (than at higher latitudes), and could thus limit species range size and range expansion (Paquette and Hargreaves 2021, Matysioková and Remeš 2022). Also, areas across the tropics usually have higher environmental heterogeneity than higher latitudes, thus across a given extent of area (i.e., same spatial scale), more habitat types (and species) will be found, and the size of each habitat type would be smaller (Guo et al. 2023a). Consequently, the ranges of many component species would be smaller as well. However, habitat dispersal may be particularly important for species with more specialized resource and environmental requirements (e.g., specialists with narrow niches). For species with broad niches, heterogeneity becomes less important and it will interact with other factors such as species' dispersal power in regulating species' range sizes (e.g. Liu et al. 2014).

Global patterns and regional differences

Terrestrial vertebrates show strong negative richness–range size relationships across the globe. The strength of the relationships varies among continental regions. The regional differences in contributions from the five factors (SR, LAT, MAT, Tvar, and BS) and their various combinations to the overall diversity–range size relationship for all terrestrial vertebrates (four classes) could be explained by the overall diversity and differences in ecological and biogeographical features (e.g., the location, context, latitudinal extent, climate) among the six continental regions. For example, in species-rich regions such as Southern America, Africa, and Australasia, SR is likely to contribute the most.

The joint SR+LAT and SR+Tvar contributions are important in equatorial regions (i.e., Africa, Southern America, and Australasia). However, it remains unclear why LAT and MAT appear more important in regions with higher latitudes but lower terrestrial vertebrate richness (i.e., Europe, Northern America, and Asia, all in the Northern Hemisphere; Fig. S1). One possible cause could be that abiotic forces might be more important at higher latitudes while biotic interactions are more important at lower latitudes (Paquette and Hargreaves 2021, Matysioková and Remeš 2022).

As the focal region or taxonomic group becomes smaller, divergent patterns emerge. The group size (number of species), dispersal capacity, evolutionary age, and the features of each region jointly affect the observed patterns. The potential effects of these factors could also be reflected by the differences in the strength of the diversity–range size relationship and the amount of variation explained by diversity, latitude, climate, and their combinations for each group and in each continental region (Table S1).

Differences among terrestrial vertebrate groups

The results reported in Figure 4 showed that the relationships between body size and latitude are more similar (at least in the same direction) among birds, mammals, and amphibians, compared to that of reptiles. One may wonder if this pattern reflects the constraint of phylogeny and evolutionary history. A widely accepted hypothesis of the phylogenetic relationship among the four classes of terrestrial vertebrates is as follows: (amphibians,(mammals,(reptiles,birds))) (Hedges et al. 2015), indicating that birds are more closely related to reptiles than to either mammals or amphibians. Because the relationship between body size and latitude for birds differs more from that for reptiles than that for either mammals or amphibians (Fig. 4), it is unlikely that the differences among the four classes in the relationship between body size and latitude observed in this study are constrained by phylogeny and evolutionary history. Furthermore, the differences among the four classes in the relationship between body size and latitude, as well as other relationships, observed in this study resulted from differences in species richness among the four classes, because the distribution of species richness of birds is closer to that of reptiles than that of either mammals or amphibians.

In general, using a large category, ectothermic reptiles, and amphibians have lower diversity and smaller range sizes than endothermic birds and mammals (Fig. S2). However, the explanations for the major differences in the richness–range size relationships among the four classes cannot be convincingly given based simply on such thermal category (i.e., warm- vs. cold-blooded). Rather, the similarities and differences among the four groups of terrestrial vertebrate species may mainly be due to the intrinsic features of each group (e.g., lifespan, basal metabolic rate). For example, dispersal capacity (birds > mammals > reptiles ≈ amphibians) could to a large extent control the overall range size (Agosta et al. 2013). This may explain why our SEM for birds accounted for a much higher portion (94%) of the variation in range size of birds, compared to the other three groups of vertebrates (i.e., birds have stronger dispersal capacity and thus are expected to have reached a higher level of climatic equilibrium, compared to any one of the other three vertebrate groups). Böhm et al. (2017) recently found that the post-glacial expansion of ranges is weaker for snakes than for more mobile birds and mammals. In addition, the differences in range sizes of the same vertebrate species group among continental regions are also most likely due to the latitudinal range and geographic features in each region (Fernández and Vrba 2005). In addition to the internal biotic factors (species traits such as body size), it is possible that a more pronounced lack of habitat availability for reptiles and amphibians (e.g., snakes, turtles, and lizards) at higher latitudes could be partly responsible (Böhm et al., 2017).

To some extent, a similar logic to that explaining the negative richness–range size relationship could be applied to the negative richness–body size relationship. This is because it is less likely that, in a species-rich habitat or region, many species can have large sizes due to limitations in resources and space. However, the exceptional positive richness–body size relationship for reptiles (Fig. 3b) is puzzling, as all other groups show negative relationships as expected. This is especially the case in the Southern Hemisphere: unlike the other three groups, reptiles in Southern America, Africa, and Australasia all have much higher richness and larger body sizes than in other regions (One-Way ANOVA, $p < 0.001$). More work is needed in this regard to examine the causes behind such macroecological and biogeographical "outliers".

Comparisons between vertebrates and plants

Although negative diversity–range size relationships were observed for both terrestrial vertebrates (this study) and plants (Guo et al. 2022) and at both global and regional scales, we found some significant differences between plants and vertebrates. First, for plants, species-richer regions such as Southern America, Australasia, and Africa have weaker diversity–range size relationships (Fig. 2 in Guo et al. 2022), whereas terrestrial vertebrates exhibit exactly the opposite pattern (Fig. 2c in this study). Second, SR makes a much greater contribution to the patterns found in terrestrial vertebrates, while SR and LAT jointly make the most contribution to patterns in plants (see Fig. 3 in Guo et al 2022 vs. Fig. 4 in this study). The species richness–latitude correlation is tighter for vertebrates than for plants, but no significant difference is found in regression slopes between the two taxa ($p > 0.05$). This could in part be because animals can track climate change better than plants due to their higher mobility and some species can make more rapid range shifts across latitudes in response to glacier retreat in the past and recent climate warming than others). It is also possible that habitat availability is more limited for certain groups than for others at higher latitudes or higher elevations. However, the causes for the differences in diversity–range size relationships between plants and vertebrates at the regional scale require more extensive studies in the future.

Perspectives

The negative species richness–range size relationship seems to persist regardless of whether Bergmann's rule or Rapoport's rule is supported by data and whether the general latitudinal diversity patterns are closely followed for the taxonomic group (class) and/or in a particular region (McNab 1971, Meiri and Dayan 2003, Alahuhta et al. 2020). This can be evidenced by the cases where latitude is less important in explaining species range sizes (e.g., Fig. 4). First, when Bergmann's rule is followed for whatever reason(s) (e.g., new taxa may not have enough time to spread), species with larger body size at higher latitudes are expected to use more space, home range, and energy, and thus are expected to have larger ranges than smaller sized species (Brown 1995, Diniz-Filho et al. 2005, Böhm et al. 2017). However, when Bergmann's rule is not followed in some cases, such as for certain plants (e.g., Drezner 2003) or for certain reptiles (e.g., Pincheira-Donoso et al. 2008), our findings still show clear negative richness–range size relationships. Second, the deviation in species range size from Rapoport's rule (i.e., species range size increases with latitude) could be because in certain situations species richness does not follow the latitudinal pattern either (e.g., some marine organisms). Similar to the role of evolutionary age (Willis et al. 1922, Rohde 1998), the size of the taxonomic group is another important factor, i.e., the larger the group, the greater the chance of following pervasive biological (ecological) rules.

At present, using climate alone to predict species range sizes has several limitations. Particularly, many (if not most) species are not occupying their full ranges that climate conditions allow (e.g., projected by niche models). Some species, especially invading species, may not have enough time to reach their full potential ranges as projected by climate niche models, mainly because of dispersal limitations. This can be evidenced by successful intercontinental species invasions and human-assisted relocations of many species around the world (Vittand et al. 2009). Second, climate niche modeling to date still cannot fully take species interactions into account, especially in places where many species coexist. Therefore, using climate conditions to predict species range size may not reach the idealized accuracy. In contrast, our findings seem to show that species richness could better predict species range size than latitude and/or climate variation. However, while climate niche modeling could predict the potential location of a focal species, one of the two main components of species distribution, species richness, could help to predict the range size that a species may occupy (the other main component of species distribution).

Using body size to predict range size works well for birds, mammals, and amphibians but not for reptiles. Also, such predictions can only be used within classes, not among classes. For example, mammals have larger mean body sizes than birds (Brown 1995) but birds still have much larger range sizes on average (Fig. S2).

Finally, because marine and terrestrial assemblages often show different (sometimes opposite) biodiversity patterns, future studies comparing the richness–range size relationships between the two realms are critically needed (Gaston 1998, Dawson 2012, Tomašových et al. 2016, Lenoir et al. 2020).

The possible role of species richness, particularly the negative richness-range size relationships observed for native species, in biotic invasions, has been discussed by Guo et al. (2022). Indeed, even exotic species may be successful in invading species-rich habitats such as those in the tropics, following the negative richness–range size relationship, the likelihood for the exotic invaders to have large ranges (and high abundance) may be relatively small due to diversity resistance. This has gained increasing support from more recent studies (e.g., Beaury et al. 2020, Guo et al. 2023b).

Conclusions

Our results using global terrestrial vertebrates confirm previous findings based on global plant data with consistent negative relationships between diversity and range size (Guo et al. 2022). Although the negative richness–range size relationships seem ubiquitous, the strength of the relationships increases with the region's richness level and taxon size. It also increases from regions to the globe for all terrestrial vertebrates and for each class, possibly because of the increase in the extent of underlying environmental gradients (Guo et al. 2023a). Cross-region and taxonomic group comparisons thus appear to be indispensable for better understanding biodiversity patterns and underlying causes. Future work could concentrate on the underlying mechanisms and utilities of the negative richness–range size relationships in other fields of ecology and evolution. Particularly, the differences in forming and explaining the richness–range size relationships among the six continental regions and among the taxonomic groups (Table S1) deserve further investigation. We hope our work will stimulate more efforts to improve our understanding of how climate change and land use may simultaneously affect both species richness and species range size, and their spatial-temporal relationships.

Acknowledgements

We thank Michael Dawson and Jon Knott for their helpful comments. We are also grateful for the constructive comments provided by the editors (Robert J. Whittaker and Frank A. La Sorte) and anonymous reviewers. This work is supported by the Innovation Program of Shanghai Municipal Education Commission (2023ZKZD36) to J.Z. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Data Availability Statement

All data used in this study have been published. Sources and links of the data were provided in the manuscript: i.e., https://www.iucnredlist.org, http://datazone.birdlife.org/home, https://doi.org/10.6084/m9.figshare.10075421, https://doi.org/10.6084/m9.figshare.c.3306933.v1, www.amphibianbiodiversity.org.

Supplementary Material

This material is available as part of the online article from https://escholarship.org/uc/fb

Figure S1. Maps showing the six geographic regions represented by six different colors were considered as six continental regions in this study.

Figure S2. (a) Species richness and average range size of the four terrestrial vertebrate groups around the world. (b) The amount of variation in species richness and range size of all terrestrial vertebrate species within each region.

Table S1. Variation in average range size (km^2) per species of four terrestrial vertebrate groups (classes) uniquely and jointly explained by species richness, latitude, and selected climate variables.

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Submitted: 13 August 2023
First decision: 19 September 2023
Accepted: 25 October 2023

Edited by Frank La Sorte and Robert J. Whittaker

