



On the relationship between species diversity and range size

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Abstract

Aim: What factors may affect species range sizes remains a central question in ecology and biogeography. Particularly, whether and how species richness may regulate average species range size remains largely elusive. Here, we explore the relationship between species diversity and species range size at a global extent and discuss its implications and significance for ecology and management.

Location: Worldwide.

Taxon: Plants and various groups of animals.

Methods: We used published data on plant richness and range size from around the world and synthesized related literature to assess the richness–range size relationships. We used paired t-tests and spatial autoregressive models in data analyses. We conducted a series of partial regressions to partition the variation in species ranges explained by paired independent variables (i.e. species richness versus latitude, species richness versus temperature or species richness versus temperature variability).

Results: A negative relationship between species diversity (richness) and species range size is nearly ubiquitous. In most cases, species diversity was a better predictor for species range size than latitude, temperature or temperature variability.

Main conclusions: The diversity predictor works well for different taxonomic groups, regions, continents, and for both terrestrial and marine biomes. High species diversity could imply stronger species interactions such as competition which limit the range sizes of constituent species. A nearly universal negative richness–range size relationship thus has significant implications for species invasion biology and conservation.

KEYWORDS

biodiversity, biotic interaction, climate change, conservation, distribution, Rapoport's rule

1 | INTRODUCTION

Numerous hypotheses have proposed mechanisms to explain the broad-scale patterns of biodiversity and species distributions (Gaston, 2000; Rosenzweig, 1995). An increasing number of studies has found that diversity (species richness) is somehow linked to the range sizes of the component species (Boucher-Lalonde et al., 2016; Eeley & Foley, 1999; Gaston, 1998), but the exact relationships between range sizes and species richness are still contentious (Weiser et al., 2007). A major challenge related to the diversity–range size

relationship is to separate causes from consequences as diversity and range size may simultaneously affect each other (Batt et al., 2017).

One of the dominant global diversity patterns is the decrease in diversity with latitude which is linked to the increase of range size of many taxa with increasing latitude. The latter phenomenon in large-scale biogeographical patterns, that is, ranges of plant and animal species usually increase with latitudes, is often described by 'Rapoport's rule' (Rapoport, 1982; Stevens, 1989). Despite their popularity in ecology and biogeography, the causes for both latitudinal patterns are still poorly understood (Stevens, 1989), particularly

because the interpretations for both are confounded by many other factors. For example, climate and climatic variability have been proposed as major factors that affect patterns of both species diversity and species ranges (Alahuhta et al., 2020; Eeley & Foley, 1999; Fernández & Vrba, 2005; Stevens, 1989). In comparisons between marine and terrestrial systems, Gaston (1998), among others, proposed that the larger ranges on average of marine than terrestrial species could be associated with a lower species richness in marine than in terrestrial systems. (For marine taxa, this negative correlation between richness and average range size holds, even though species diversity and range sizes often show opposite patterns to terrestrial environments, i.e. decreases in richness and range sizes with latitude in marine environments; Tomašových et al., 2016). He further speculated that such observations could be related to many other large-scale spatial patterns of biodiversity (e.g. along latitudinal, altitudinal and depth gradients).

A related and well-known eco-biogeographical pattern is the positive relationship between species' global population sizes and range sizes (Brown, 1984). If the negative richness–range size relationship and the positive range size–global population size abundance relationship are both ubiquitous, higher species diversity would mean smaller population size and range size. Previously, large-scale variation in species range sizes has been mostly examined latitudinally as the popular Rapoport's rule (Dyer et al., 2020; Rapoport, 1982; Stevens, 1989), not longitudinally across regions. Inferring mechanisms from such correlations remains challenging, since potential explanatory variables such as latitude, temperature and species richness also covary (Stevens, 1989). In this regard, latitude can only be treated as a surrogate of ecological gradients (e.g. temperature) that control population size and range size, and thus diversity. If so, the negative diversity–range size relationship could exist in other environmental gradients (i.e. not just latitude).

Ecologists and land managers would like to know whether species range size is always negatively related to species diversity (species richness). The perceived richness–range size relationship could offer important clues regarding the causes of large-scale species invasions. For example, if species diversity constrains the range sizes of all component species in the region, the ranges of invading non-native species might be similarly limited (Beaury et al., 2019). For species conservation, if species-rich regions contain more rare species with small ranges (thus low overall abundance), the negative richness–range size relationship implies that diversity hotspots should be given priority when resources for conservation are limited (Eeley & Foley, 1999).

While most of the perceived negative richness–range correlations have been inferred from the latitudinal or altitudinal patterns related to Rapoport's rule, there is an urgent need to know whether such negative correlations exist in other settings as well without considering the role of latitude or altitude. And if so, what would such correlations mean in species conservation and biotic invasions? If the negative richness–range size is universal (i.e. richness does play an important role), invasive species should also have smaller ranges in species-rich regions than in species-poor regions.

SIGNIFICANCE STATEMENT

The relationship between diversity and range size is critical to macroecology and biogeography. Previous research was limited to certain taxonomic groups or regions. Using global plant data, we show consistent negative richness–range size relationships at both global and regional levels. Our findings have practical implications for species invasions and conservation

Previous studies on species range sizes have mostly focused on physical constraints (e.g. temperature, precipitation, climatic variability). Increasing efforts are being made to examine and predict species range size using life-history and genetic traits, but species richness is rarely used as a specific predictor. If strong associations between richness and range size indeed exist, this major information gap could at least partly be filled. For this reason and also to answer the above questions, in this study, we investigate the role of species diversity in regulating the average range size of component species (Batt et al., 2017; Boucher-Lalonde et al., 2016). We hypothesize that the average species range size in a species assemblage is negatively associated with the species richness of the assemblage.

2 | MATERIALS AND METHODS

To examine how species richness is related to average range size of component species, we examined global and continental plant data based on several published datasets (see also Supporting Information). We obtained the distributions and range size data of native plants primarily from World Plants (WP; <https://www.worldplants.de>) and Plants of the World online (POWO; <http://www.plantsoftheworldonline.org>). Both of these databases provide information on the presence–absence of each species within geographical units defined by the Taxonomic Databases Working Group (TDWG), commonly called TDWG units (Brummitt, 2001). We extracted plant occurrence records for TDWG level 3 units for most countries and for level 4 units for several countries with large geographical extents (e.g. China). For Russia, its geographical units located in Europe are political regions shown in Map 5 of the TDWG geographic system (Brummitt, 2001), and geographical units located in Siberia and Russian Far East are those defined in Zhang et al. (2018), as shown in Figure S1. Maps showing TDWG level 3 and 4 units are available in Brummitt (2001). Geographical units representing small oceanic islands were not included in this study. Because plant distributions in Western Sahara and Morocco were commonly not distinguished in botanical data sources, we treated these regions as a single geographical unit. As a result, we used 392 geographical in this study, which we grouped into six biogeographical ('continental') regions (i.e. Europe, Asia, Northern America, Africa, Australasia and Southern America; Figure S1). We supplemented the occurrences of each species in the geographical units derived from WP and POWO by



additional data sources, which included: global fern occurrences in GBIF reported in Suissa et al. (2021), Australian Plant Census ([www.anbg.gov.au/chah/apc](http://anbg.gov.au/chah/apc)), Brazilian Flora (<http://floradobrasil.jbrj.gov.br>), plants in southern South America (<http://www2.darwin.edu.ar/Proyectos/FloraArgentina/Especies.asp?Letra>), Flora of China online (http://www.efloras.org/flora_page.aspx?flora_id=2), the PLANTS Database (<https://plants.usda.gov/home>), Plants of southern Africa (<https://www.sanbi.org/link/plants-of-southern-africa>), Checklist of the native vascular plants of Mexico (Villaseñor, 2016) and Russian regional floras and plant checklists (<http://herba.msu.ru/shipunov/school/sch-ru.htm>). We standardized the botanical nomenclature according to WP (<https://www.worldplants.de>), and combined infraspecific taxa with their respective species. Non-native species distributions in each geographical unit were excluded. We calculated the total geographical range of each species as the total area of the geographical units in which the species was found.

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. Considering that the same species might occur in several geographical units this could lead to spatial autocorrelation between neighbouring geographical units. Since autocorrelation could inflate tests of statistical significance, we followed previous authors (e.g. Fritz & Rahbek, 2012; Hawkins et al., 2011) and opted not to report *p*-values for statistical analyses. Instead, 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 to be strong for $|r| > 0.66$, moderate for $0.66 \geq |r| > 0.33$ or weak for $|r| \leq 0.33$ (Qian et al., 2019).

In addition to the species richness–range size correlations, we explored the relationships of range size with latitude, mean annual temperature and temperature variability (temperature annual range). We obtained mean annual temperature and temperature variability data at a resolution of 30-arc-seconds from the CHELSA climate database (bio1 and bio7, respectively; <https://chelsa-climate.org/bioclim>; Karger et al., 2017), and then calculated the average mean annual temperature for each geographical unit. We conducted a series of variation partitioning analyses (i.e. partial linear regression models; Legendre & Legendre, 2012) for the entire world and for each of the six continental regions. We determined the variation in average range size that was explained uniquely by species richness, explained uniquely by latitude or temperature (either mean annual temperature or temperature variability), and explained jointly by species richness and latitude or jointly by species richness and temperature. To assess whether variation in area among geographical regions would affect the results of this study, in addition to conducting correlation and regression analyses without accounting for variation in area among geographical regions, we conducted another set of analyses in which variation in area among geographical regions was statistically accounted for. Specifically, we regressed average species range on log-transformed area; residuals of the regression were average species ranges after accounting for variation in area among geographical regions, which were used in

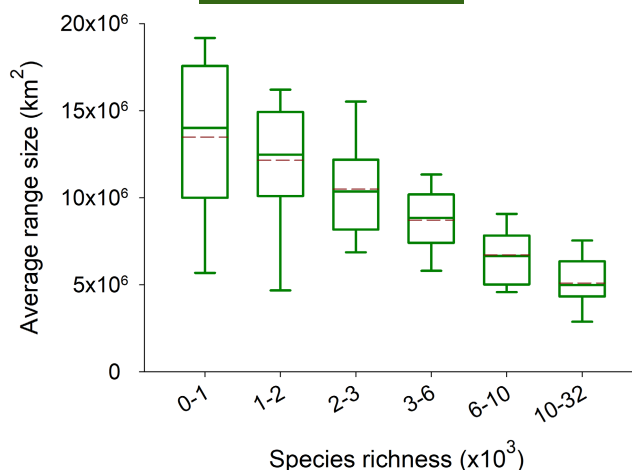


FIGURE 1 The negative relationship between plant richness and range size (km²) based on global plant data. The box represents the lower 25th and higher 75th percentiles. The solid line in the box is the median, the dashed line is mean and the whiskers are error bars (the 95% confidence interval). Both richness and range size data were log₁₀-transformed.

further correlation and regression analyses. This approach has been commonly used to account for the effect of a covariate in a statistical analysis (e.g. Hawkins & DeVries, 2009; Hu et al., 2021). We standardized the resulting average species ranges to vary from 0 to 1, using the formula $(x - \text{minimum}) / (\text{maximum} - \text{minimum})$. We applied spatial autoregressive model (Kissling & Carl, 2008) for all regression analyses. We used SYSTAT (Wilkinson, 1992) and Spatial Analysis in Macroecology (www.ecoevol.ufg.br/sam/; Rangel et al., 2010) to run our statistical analyses.

To compare our results with previous publications, we conducted a non-exhaustive literature search using Google Scholar with the keywords 'diversity OR species richness AND range size'. Although the search returned a very large number of publications, only a small subset of studies examined both richness and range size (identified by reference titles with both terms: diversity/richness and range size). Of this subset, we further selected studies that directly examined the richness–range size relationships or that indirectly examined latitudinal trends in both richness and range size. This selection criterion provided fewer than 100 studies for comparative analyses. Many of these studies only examined a specific taxon such as certain groups of organisms (e.g. snakes and lizards) or were highly restricted in their spatial extent.

3 | RESULTS

Our observations based on published data show strong negative relationships between species diversity and range size, and thus support our primary hypothesis. Such negative relationships are indeed very common (almost no exceptions unless a very small taxonomic grouping was used) in any setting and across any gradient (i.e. latitude, longitude, altitude) or continents/habitats.

We observed a negative, moderate species richness–range size relationship using global plant data (boxplot regression of medians:

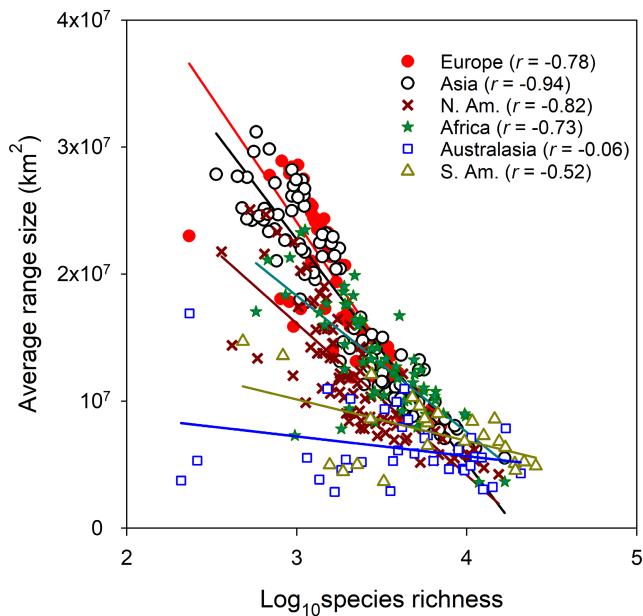


FIGURE 2 The negative relationship between $\log_{10}$ -transformed species richness and range size (km^2) based on plant data in each of the six continental regions (i.e. Europe, Asia, Northern America, Africa, Australasia and Southern America). Note that corresponding back-transformed values from the $\log_{10}$ -transformed species richness values on the x-axis are: 2 = 100, 3 = 1000, 4 = 10,000 and 5 = 100,000, respectively. The lines are linear least-squares best fits; we used them to show linear trends, not for statistical tests. Correlation coefficient (r) values were derived from spatial autoregressive (SAR) models. The relationship for Australasia was weak possibly due to its unique geographical setting and landmass composition and lack of climatic variability, relative to those of others (Figure S1; Smith et al., 1994).

$r = -0.57$, $p < 0.001$; Figure 1). Similarly, we observed negative relationships for each of the six continental regions (Figure 2). When all the 392 geographical units were analysed together, the variation in species range sizes that was uniquely explained by species richness was more than twice as great as the variation uniquely explained by latitude, temperature or temperature variability (Figure 3). When the geographical units of each of the six biogeographical regions were analysed separately, the variation in species range sizes uniquely explained by species richness was greater than the variation uniquely explained by latitude in five of the six biogeographical regions (Figure 4); the variation in species ranges uniquely explained by species richness was also greater than the variation uniquely explained by temperature or by temperature variability in four or five of the six biogeographical regions, respectively (Figure 4). When variation in area among the geographical units were accounted for, the results derived from the analyses with variation in area among the geographical units being accounted for were, in general, similar to those without accounting for variation in area among the geographical units (compare Figures S2–S4 with Figures 2–4).

The review of published studies shows near-universal negative richness–range size relationships or correlations (Table 1). For example, a recent intercontinental comparative study shows that the aquatic plant richness and mean range size were negatively correlated in both Europe ($r = -0.59$, $p < 0.001$) and North America ($r = -0.61$, $p < 0.001$; Alahuhta et al., 2020). Studies that specifically examined the Rapoport phenomenon across latitude or altitude mostly showed negative richness–range size correlations since richness and range size exhibited strong opposite correlations with latitude or altitude (e.g. Stevens, 1989, 1992; Table 1). However, the studies which did not find evidence of the typical Rapoport phenomenon generally examined very narrow clades (e.g. conifers, willows, Australian skinks) rather than broad taxonomic groups.

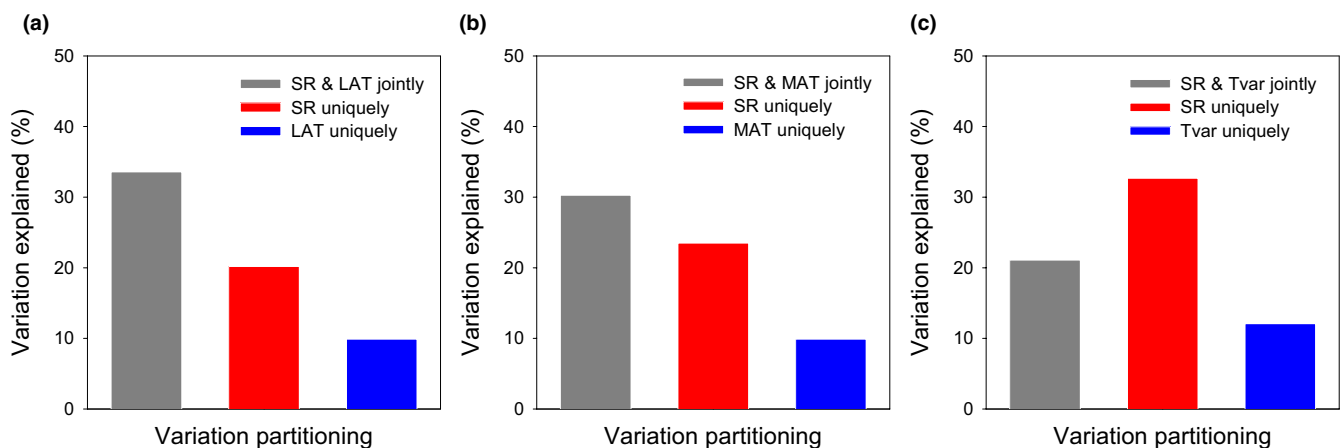


FIGURE 3 Variation in average range size (km^2) per plant species explained only by species richness (SR), only by either latitude (LAT) or mean annual temperature (MAT) or temperature variability (Tvar), or jointly by either SR and LAT or SR and MAT or SR and Tvar for the globe. SR is $\log_{10}$ -transformed species richness. All models were significant ($p < 0.05$).

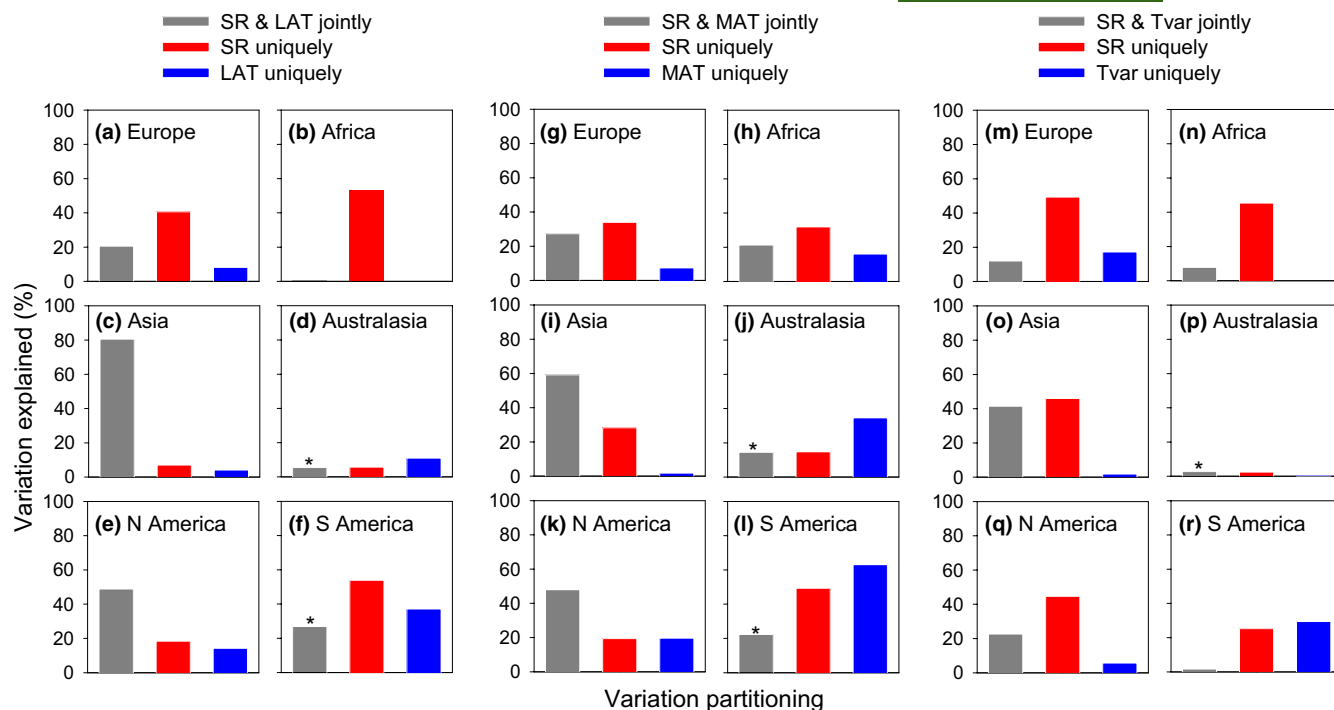


FIGURE 4 Variation in range size (km^2) per plant species explained uniquely by species richness (SR), uniquely by either latitude (LAT) or mean annual temperature (MAT) or temperature variability (Tvar), or jointly by either SR and LAT or SR and MAT or SR and Tvar for each of the six continental regions (i.e. Europe, Asia, Northern America, Africa, Australasia and Southern America). SR is $\log_{10}$ -transformed species richness. All models were significant ($p < 0.05$) except for the models with LAT and Tvar for Australasia (see also Figure 2). An asterisk represents a negative value resulting from the variation partition (see Legendre & Legendre, 2012 for statistical interpretation of a negative value).

4 | DISCUSSION

An increasing number of studies have reported negative diversity–range size relationships (Batt et al., 2017; Soberón & Ceballos, 2011). But surprisingly, most relevant studies did not elaborate and discuss the possible mechanisms and implications of the negative diversity–range size relationship. In the past, the negative diversity–range size relationship was mostly derived from studies that examined Rapoport's rule, across either latitude or altitude. In such cases, Rapoport's rule may simply be treated as a surrogate for the correlates of both diversity and range size with latitude. However, when this negative diversity–range size relationship is also frequently observed across other ecological gradients, it cannot be treated as a simple result of both diversity (negatively) and range size (positively) being correlated with latitude or altitude, that is, when the Rapoport phenomenon does not occur or is very weak (Orme et al., 2006; Stevens, 1992).

Strong species interactions such as competition and predation may force species to specialize in a way that limits population growth rates ('negative density dependence'; LaManna et al., 2017) and reduces the range size of coexisting species. If competition or predation is important, species range size and total population size of each component species could be constrained by strong species interactions (Beckage & Clark, 2005; Roslin et al., 2017).

If diversity promotes speciation (Boucher-Lalonde et al., 2016; Emerson & Kolm, 2005), negative richness–range size relationships could arise during speciation since many species may not have had enough time to expand their ranges. Over time, rare or transient species continue to expand their ranges, leading to higher regional species richness (Batt et al., 2017; Eeley & Foley, 1999). In this sense, species range size affects species richness (Boucher-Lalonde et al., 2016). However, when richness and the abundance/range size of component species reach a certain level, competition could become stronger and thus constrain species range size and abundance (Huston, 2014). When this happens, species richness controls species range size. Across various stages of community development, transient balances between colonization and extirpation (or speciation and extinction) could be reached before the next major disturbance or catastrophic event occurs (Batt et al., 2017; Huston, 2014).

In attempts to explain the Rapoport's rule along latitude, Stevens (1989) suggested that the greater variation in climatic conditions has favoured high-latitude species. Over the same spatial scale, habitats at higher latitudes tend to be more homogeneous (i.e. similar conditions exist over larger areas) than lower latitudes, but seasonal climate is more variable (Stevens, 1989). The possible role of climatic variation has also been discussed in explaining changes in range sizes across elevation gradients (e.g. Qian et al., 2017; Stevens, 1992), where average range size is often negatively correlated with species richness. Our study showed that species range

TABLE 1 Examples of case studies showing negative species richness–range size relationships

Taxon or habitat	Context, region or reference variable	Evidence or related statement	Main drivers	Source
Birds	Global	Regional differences caused by different mechanisms	Speciation, extinction, dispersal, 'mass effect'	Orme et al. (2006)
Marine fishes and invertebrates	Temporal; Nine open marine regions around North America	Species richness was negatively correlated with mean range size	Time, transient species, climate change, fishing	Batt et al. (2017)
Freshwater plants	Europe, North America	Similar patterns found in both continents	Mutual effects of current climates on both richness and range size	Alahuhta et al. (2020)
Terrestrial mammals	Global	All patterns are different from those generated by null models	Geography, history, dispersal capacity	Soberón and Ceballos (2011)
Trees, mammals, breeding birds, etc.	Latitude (global)	All taxa supporting the Rapoport's rule show negative richness–range size correlations as richness and range size exhibit opposite trends with latitude	Heterogeneity, climatic variability, 'rescue effect', 'mass effect'	Stevens (1989)
Trees	Altitude (selected mountains)	Alaska, $r^2 = 0.93$, $p < 0.01$; Tennessee, $r^2 = 0.93$, $p < 0.01$; Costa Rica, $r^2 = 0.24$, $p < 0.05$	Immigration, 'Rapoport-rescue hypothesis'	Stevens (1992)
Birds and mammals	The Americas	Not clear how climate (temperature and precipitation) may directly or indirectly affect the richness–range size relationship	Contemporary top-down effects	Boucher-Lalonde et al. (2016)
Terrestrial vs marine	Global	Marine species have larger ranges than terrestrial may be due to their lower species richness	Speciation, extinction, and transformation	Gaston (1998)
Woody plants	New World	The negative richness–range size correlation formed across latitude. Using portions of the entire gradient may produce incorrect conclusions	Similar mechanisms for Rapoport's rule and dispersal barriers	Weiser et al. (2007)
African anthropoid primates (catarrhines)	Africa	The relationship between richness and range size remained even after latitude and longitude were removed	Climatic variability, heterogeneity	Eeley and Foley (1999)
Terrestrial birds and marine bivalves	Global and regional (New World)	Terrestrial and marine taxa should opposite patterns across latitudes (in both richness and range size)	Dispersal ability, environmental tolerance, species diversification	Tomašových et al. (2016)



size is more strongly associated with species diversity than with climatic variation (i.e. temperature variability in our study). Mean annual temperature and temperature variability (seasonality) that were examined in this study are among the six climatic variables that have been considered the most important climatic variables influencing plant distributions (Qian et al., 2022). We did not consider the other four climatic variables (i.e. annual precipitation, minimum temperature of the coldest month, precipitation during the driest month, precipitation seasonality) because their correlations with the mean range size of species were weaker than mean annual temperature and temperature variability (e.g. $r = -0.394$ and 0.340 for mean annual temperature and temperature variability, respectively, and $|r|$ ranges from 0.137 to 0.318 for the other four climatic variables at the global extent). Although there are many deviations in the latitudinal and altitudinal diversity gradients (e.g. Sahara, Europe) and patterns that do not follow Rapoport's rule (Alahuhta et al., 2020), the negative species richness–range size relationship seems to hold true.

The general positive global population size–range size relationship (Brown, 1984) also has implications for the richness–range size relationship and has consequences for other ecological and biogeographical patterns (i.e. community assembly rules). When species diversity (richness) is high, it is impossible for many constituent species to have large ranges and thus high overall abundance. In other words, high diversity is usually associated with low mean abundance for each component species (i.e. due to resource and space limitations there is no way for every species to be abundant if diversity is high). When many species prefer tropical conditions, each species will have to have a relatively low abundance to coexist with other species (i.e. higher evenness or lower dominance). As range size and population size are positively related, on average, the range of each species is inevitably correspondingly smaller.

Previous research has also examined the effects of genetic and life-history traits such as ploidy level, seed size and body size (or plant height) on species range sizes (Guo et al., 2000; Murray et al., 2005; Nunez-Mir et al., 2019; Sporbert et al., 2021). Others have examined the role of life-form (Koide et al., 2021; Ricklefs et al., 2008) and macrophysiology (Agosta et al., 2013) in species distribution and range sizes. Here, using species richness as a powerful indicator, we could confidently estimate the size of the ranges of the component species.

In short, our study adds more and strong support to the nearly ubiquitous negative richness–range size relationship. However, evidence to date seems to show a circular causal relationship between richness and range size for which the causes and effects could not be clearly separated (Alahuhta et al., 2020). This is mostly because both richness and range size mutually affect each other and are simultaneously affected by the same set of environmental and historical factors. But the importance and implications of such diversity–range size relationship in predicting one from the other cannot be overemphasized.

5 | IMPLICATIONS

Many previous studies show a positive relationship between the total number of individuals in a community and species diversity (Storch et al., 2018), suggesting that in places with higher diversity the average abundance of each species is lower (and thus average range size is smaller) due to resource and space constraints. This, plus the commonly observed positive population size–range size relationship (e.g. Brown, 1984), suggests implications for explaining present, and predicting future species invasions. Species-rich regions could better resist the establishment of invading species and/or reduce the likelihood for invading species to become abundant or colonize a wide geographical range, although some species-rich areas could still be invaded by extremely invasive species after disturbances.

The main difference in latitudinal patterns or the richness–range size relationships between native and exotics could mainly be attributed to the time factor (many exotic species have not had enough time to spread within their potential ranges) and the initial locations of introduction (Dyer et al., 2020). Under climate change and habitat homogenization, some species will naturally expand their ranges and those of others will shrink partly due to competition. Floristic homogenization is by far the most important driver for plant extinctions in the Anthropocene (it mostly increases the abundance of common species but reduces the abundance of rare or transient species; Lockwood & McKinney, 2001). Poleward shifting species, especially the common ones, are pushing out species at higher latitudes/altitudes and could cause some of these species to go extinct (Koide et al., 2021).

In sum, high diversity seems to constrain the average range size of component species due to increased species interactions such as competition and predation (Legault et al., 2020). Although high diversity is usually associated with high resource availability (tropics vs. polar regions), each species' share of resources would be smaller in habitats with higher diversity. The possible universal negative diversity–range size relationship across any gradient regardless of latitude, longitude and/or elevation could have highly significant applications and implications for basic ecology and management.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in github at <https://doi.org/10.5281/zenodo.7055680>.

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BIOSKETCHES

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Author contributions: QG initiated the research, JZ and HQ provided the plant data. HQ and QG analysed the data, and all authors contributed to developing and writing of the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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