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General laws of biodiversity: Climatic niches predict plant range size and ecological dominance globally

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A longstanding question in ecology asks whether or not species that achieve large geographic ranges also have large climatic niche breadths. Using a dataset of ~250,000 terrestrial plant species spanning diverse clades (bryophytes, ferns, gymnosperms, and flowering plants), we demonstrate a consistent positive relationship between geographic range size and climatic niche breadth across latitudinal and elevational gradients. This relationship holds across major phylogenetic groups, suggesting a general biogeographical rule for range size variation. Our findings indicate that latitudinal and elevational gradients in range size arise from selective pressures and species sorting based on climatic tolerance. Additionally, we show that species with larger range sizes tend to be ecologically dominant, supporting a long-suspected connection between range size, niche breadth, and local and regional abundance. Our results suggest a spectrum of dominance, where species with extensive geographic ranges and broader climatic tolerances tend to be more abundant. We posit that the relationship between range size, niche breadth, and ecological dominance is an emergent macroecological pattern that can be used for understanding and predicting the impacts of climate change on species distributions.

latitudinal gradient | macroecology | niche breadth | species abundances | species distributions

Significance

Understanding the laws that determine species distributions is essential for predicting how plant species will respond to climate change. Here, we examine the macroecological relationship between geographic range size, climatic niche breadth, and variation in ecological dominance, three fundamental properties that shape biodiversity patterns. Climatic niche breadth represents the range of climatic conditions a species can tolerate, while geographic range size defines the spatial extent of its populations. Using a global dataset of major plant groups, we demonstrate that species that occupy larger geographic ranges tend to have broader climatic niches and are more likely to achieve high local abundances. These findings provide key insights into species' vulnerability to environmental change and the processes that structure biodiversity at global scales.

Why do a small fraction of species dominate vast geographic areas while most remain geographically rare and localized? How do these differences shape biodiversity and species coexistence? Darwin hypothesized* that natural selection promotes the evolution of traits that enhance competitive ability and environmental tolerance, allowing species to become more dominant and to expand both their niche breadth and geographic range (1). These linkages between species' climatic tolerances, distributions, and abundances lie at the heart of ecology, evolution, and biogeography (2–6) and remain critical for explaining biodiversity patterns, species rarity and commonness, ecological strategies, and responses to climate change and habitat loss (7).

Geographic range size and ecological dominance are key concepts in macroecology and biogeography (8–10). Range size refers to the spatial extent occupied by a species, with small-ranged species facing higher extinction risks than those with large ranges (10–13). Variation in range size is shaped by ecological and evolutionary processes, influencing species abundances, richness, and dispersal limitations (14). Studies of vertebrate species have demonstrated that climatic, geographic, and historical factors shape these patterns across latitudes (15–19). In contrast, ecological dominance refers to attributes of species that exert significant ecological influence, such as high abundance, biomass, or important functional roles (20–22). Dominant species disproportionately shape ecosystem structure and function, affecting energy flows, nutrient cycling, and habitat availability (23). In some cases, dominant species can be hyperdominant, where a smaller subset of species accounts for the majority of individuals and biomass (24) and carbon storage (25). While direct measurements of species' abundance data across geographic ranges remain scarce, global counts of species occurrence records can serve as proxies for relative global abundances, with species that have more occurrence records tending to be relatively more dominant

*In the *Origin of Species* Darwin notes that the process of evolution by natural selection can lead to a relationship between species range size, ecological dominance, and niche size or tolerance as reflected in increased variation in traits and varieties (implicitly niche size). On pages 53 and 54, Darwin reasons that "plants which have very wide ranges generally present varieties; and this might have been expected, as they become exposed to diverse physical conditions, and as they come into competition (which, as we shall hereafter see, is a far more important circumstance) with different sets of organic beings....the species which are most common, that is abound most in individuals, and the species which are most widely diffused within their own country (and this is a different consideration from wide range, and to a certain extent from commonness), often give rise to varieties sufficiently well-marked to have been recorded in botanical works. Hence it is the most flourishing, or, as they may be called, the dominant species - those which range widely over the world, are the most diffused in their own country, and are the most numerous in individuals—which oftenest produce well-marked varieties...".

Author contributions: G.M.M. and B.J.E designed research; G.M.M., C.M., B.M., B.B., and X.F. performed research; G.M.M. analyzed data; and G.M.M. and B.J.E. wrote the paper with assistance from all the coauthors.

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(26–28). Identifying the traits that confer dominance is essential for predicting ecological responses to environmental changes.

Darwin's hypothesis outlines a mechanistic link whereby natural selection favors traits that drive both ecological dominance and geographic expansion (*SI Appendix*, Fig. S1). Observations such as these have led to several interrelated macroecological hypotheses, formalized under the Breadth of Climatic Tolerance Hypothesis (BCTH) (9, 10), which proposes that species with broad climate tolerances achieve higher local abundances and occupy larger geographical ranges (6). The BCTH implies a positive correlation between range size and niche breadth (6). However, alternative explanations suggest that this relationship may be due to sampling bias (29) and/or geographic constraints, such as spatial autocorrelation in climatic variables (30, 31). Thus, testing whether observed relationships arise from biological processes or methodological artifacts is essential.

The BCTH encompasses three distinct but interrelated component macroecological hypotheses: the Latitudinal Range Size, the Elevational Range, and the Climatic Tolerance. These hypotheses express potentially different mechanisms underlying variation in range size, niche breadth, and ecological dominance (32). Despite their importance in ecology and evolution, the strength and generality of these relationships within and across major clades remain uncertain (6). These three hypotheses are not mutually exclusive and are likely to operate in interconnected ways across spatial and ecological contexts. For example, according to the Climatic Tolerance Hypothesis, broader climatic adaptations and ecological resilience may amplify the effects of climatic variability predicted by the Latitudinal Range Size Hypothesis and Elevational Hypothesis.

The Latitudinal Range Size Hypothesis posits that range size is larger in extratropical regions compared to tropical regions [also known as Rapoport's rule; (15)] given that species in extratropical regions have greater tolerance of varied climatic conditions. In contrast, species in tropical regions often have narrower ranges, limiting their abundances and potential for ecological dominance (14). This hypothesis predicts stronger relationships between range size and niche breadth at higher latitudes.

The Elevational Range Hypothesis extends the Latitudinal Range Size Hypothesis, suggesting that species in mountainous regions may have larger geographic ranges compared to lowland species (33, 34). This hypothesis is particularly relevant in tropical mountains, where exposure to diverse climatic conditions over short geographic distances selects for broader climatic tolerances. In contrast, lowland species, which inhabit flatter and more climatically uniform areas, are expected to have smaller geographic ranges and narrower niche breadths.

The Climatic Tolerance Hypothesis posits that species with broader climatic niches are more likely to achieve ecological dominance, resulting in greater local abundance across larger geographic extents and broader climatic conditions (6). This hypothesis predicts that dominant species will exhibit a stronger relationship between range size and niche breadth than nondominant species. While global datasets on species dominance remain limited, dominance has been better evaluated in tropical tree species (25). In this case dominant species tend to dominate local assemblages across all local sites within the geographic range. Thus, dominant species in tropical forests may provide insights into this pattern, as they are highly abundant in forest inventories across the Americas, Africa, and Asia.

While plants dominate terrestrial biomass and drive ecosystem functioning (35), previous theoretical and empirical assessments of the BCTH have primarily focused on animal taxa (15, 16, 19, 29). Plant range size variation has been previously studied (36–38). However, no global synthesis has evaluated the linkage between niche breadth, range size, and dominance across major plant clades. In this study, we test the BCTH and three related hypotheses using a global dataset of ~250,000 plant species spanning bryophytes, ferns and lycophytes, gymnosperms, and flowering plants. This large-scale analysis leverages data from the Botanical Information and Ecology Network [BIEN; (39)], which provides extensive global plant distribution data across phylogenetically and ecologically diverse groups. We test whether the positive relationship between niche breadth and range size is a global pattern and analyze how this relationship varies across biogeographic and climatic gradients, providing data-rich tests for the Latitudinal Range Size, Elevational Range, and Climatic Tolerance hypotheses. Given the accelerating impacts of climate change on biodiversity, understanding the mechanisms that structure species distributions and dominance is essential for predicting and mitigating shifts in global biodiversity patterns.

Results and Discussion

Macroecological Patterns. Using the BIEN dataset, we calculated range sizes for ~250,000 plant species (*SI Appendix*, *Supplementary Methods*) and found several interesting patterns among species' ranges. Range sizes were estimated to be 121 km^2 to 34,116,438 km^2, with larger range sizes in the higher latitudes of the northern hemisphere (Fig. 1*A*). This pattern was consistent across plant groups and longitudinal bands (Americas, Africa/Europe, and Asia/Oceania; *SI Appendix*, Fig. S2). The distribution of range size values peaks at 60° N but rapidly decreases in latitudes above that. Smaller ranges were found at 80° N (2.26 times smaller than at 60° N). Range sizes were larger in the northern hemisphere than at the equivalent latitudes in the southern hemisphere. At 55° S, range sizes were half the size of those at 55° N. At 60° N, mean range sizes were 1.18 times larger than at the Equator (0°). Among plant groups, bryophytes and gymnosperms exhibited the largest mean range sizes (1,208,174 km^2 and 578,193 km^2, respectively), whereas ferns and flowering plants had smaller ranges (572,426 km^2 and 553,277 km^2, respectively). Statistically significant differences in range size distributions were found only between bryophytes and ferns, as well as between bryophytes and flowering plants (*SI Appendix*, Fig. S3*A* and Table S1).

The calculations of the climatic niche breadth for each species enabled us to test various hypotheses. We began by measuring the climatic niche breadth, defined as the breadth of climatic conditions (climatic space) existing within each species' range (40) (*Materials and Methods*). Niche breadth ranged from 0 to 69 in relative measures in climatic space defined by a principal components analysis (PCA), which are unitless. The distribution of niche breadths was significantly different among plant groups (*SI Appendix*, Fig. S3*B* and Table S1). The distribution of niche breadth along the latitudinal gradient revealed larger niche breadths at 55° N in all three longitudinal bands and across all plant groups (*SI Appendix*, Fig. S4). On average, niche breadths at 55°N were 1.22 times larger than at the Equator (0°) and 3.17 times larger than at 55°S. Bryophytes and ferns exhibited broader niche breadths than gymnosperms and flowering plants (4.92 and 4.40, respectively, vs. 3.89 and 3.04).

Globally, niche breadths were highest at high latitudes in the Northern Hemisphere, in lowland tropical regions, and along mountain ranges (Fig. 1*B*). For bryophytes (*SI Appendix*, Fig. S5*A*), larger niche breadths were observed in regions of high elevation, such as Patagonia and the western and northeastern parts of China, as well as the southern Congo and Tanzania. For ferns (*SI Appendix*, Fig. S5*B*), larger niche breadths were observed across the Great Plains of North America, the South Andes, and

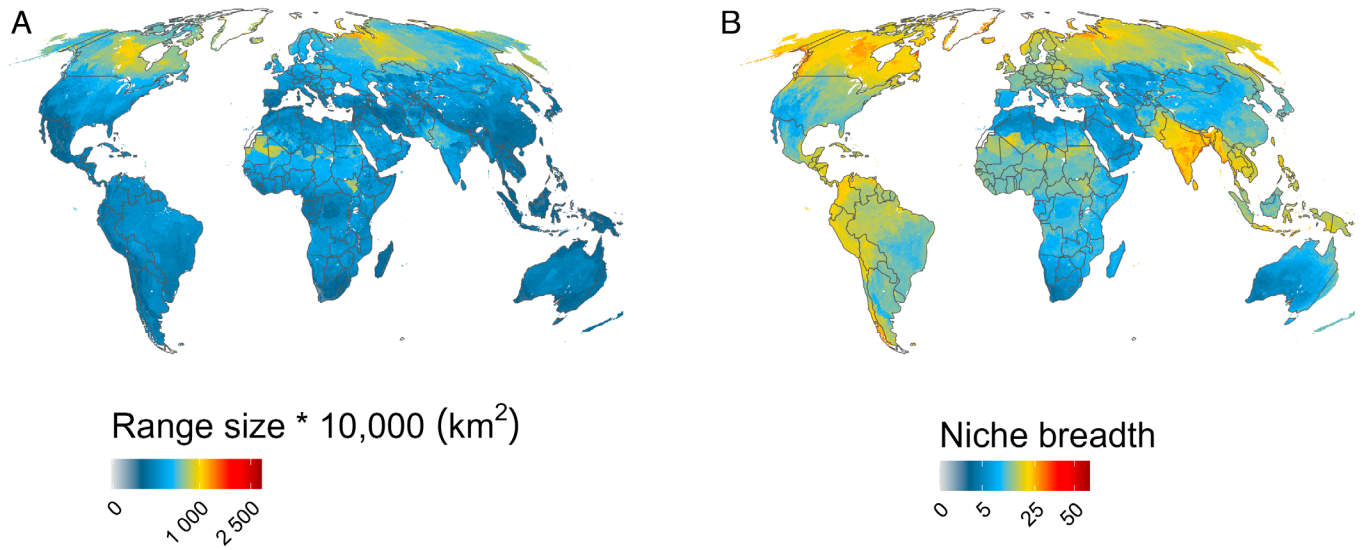

Fig. 1. Global map of species (*A*) geographic range size, and (*B*) niche breadth. Range size maps were made by overlaying species geographical ranges. Niche breadth maps for each species were made by assigning the corresponding values to their geographic ranges (one value for each species range) and then calculating the mean values for each 5 km grid cell. Niche breadth was calculated as the convex area around the occurrence points in the environmental space formed by the first and second PCA axis using climatic variables. The maps are under Mollweide equal-area projection.

eastern Europe. Flowering plants exhibited broad niche breadths along the Andes and in higher latitudes of Canada and southern Argentina (*SI Appendix*, Fig. S5*C*). In contrast, gymnosperms showed broad niche breadths along the west coast of North America, Europe, Southeast Asia, and Papua New Guinea (*SI Appendix*, Fig. S5*D*). Many of these regions, characterized by large niche breadths, overlap with global hotspots of plant species richness and phylogenetic diversity (41).

The broad range of plant sizes and niches in the high latitudes of the Northern Hemisphere resembles patterns found in mammals and birds (18). This finding supports the idea that the greater land area available in the Northern Hemisphere allows species to achieve larger ranges compared to similar latitudes in the Southern Hemisphere, where land area is more restricted (36). Indeed, the distribution of geographic centroids of species range areas along the latitudinal gradient indicates a bimodal shape, with larger range sizes being found in larger land areas in both high and low latitudes (*SI Appendix*, Fig. S6). Latitudes above 50°N represent a distinct distributional boundary for many plant species (42), contributing to high species turnover and a decrease in species richness beyond these latitudes. Extratropical regions have been subjected to higher climatic instability during the Pleistocene and have also been more affected by short-term seasonal variations than tropical regions (43). As a result, plant species that tolerate greater climatic variation tend to exhibit larger range sizes and broader niche breadths in these regions. In contrast, the more stable climatic conditions of the tropics still allow some species to achieve large range sizes and niche breadths. Broad niche breadths are most common in regions where seasonal climatic variation is high (below 50°N), whereas above 60°N, only species with narrow climatic tolerances and specific adaptations persist (14).

Range Sizes and Niche Breadth Along the Latitudinal Gradient. To test the Latitudinal Range Size Hypothesis, we classified all ~250,000 plant species based on whether their ranges were confined to tropical or extratropical regions (above 23° in either hemisphere) or spanned both regions. Species occupying both tropical and extratropical regions (i.e. latitudinal generalists) exhibited significantly larger niche breadths (Fig. 2*A*) and range sizes (Fig. 2*B*) than species confined to either region alone. This trend was consistent across all plant groups. When comparing only tropical and extratropical regions, bryophytes, flowering plants, and gymnosperms tend to have larger niche breadths (*SI Appendix*, Fig. S7 *A–C*) and range sizes (*SI Appendix*, Fig. S7 *D–F*) in extratropical regions than in the tropical regions. The climatic differences along latitudinal regions have led many ecologists to speculate that species from higher latitudes would have larger range sizes (i.e., Rapoport's rule). Indeed, this was the case when examining latitudinal bins but not necessarily when considering the latitudinal region affiliation of each species' geographic range (*SI Appendix*, Fig. S2). Our findings suggest that while Rapoport's rule holds in some cases, climatic variability plays a more critical role in shaping biodiversity gradients, with both tropical and extratropical species exhibiting broader tolerances in response to seasonal and environmental heterogeneity.

As predicted, the range size-niche breadth relationship was positive for all plant groups (Fig. 1*C*). The coefficients of this relationship (intercept and slope) were significantly different among latitudinal regions (*SI Appendix*, Table S2). We found that the range size-niche breadth relationship was stronger for bryophytes and flowering plants with geographic ranges encompassing extratropical regions than for those in other latitudinal regions (Fig. 3 *A* and *C* and *SI Appendix*, Table S3). For ferns and gymnosperms, the range size-niche breadth relationship was significantly stronger for tropical species (Fig. 3 *B* and *D* and *SI Appendix*, Table S3) than for extratropical species. Previous studies have demonstrated a similar positive relationship in other taxa, such as mammals, birds, and trees, within specific geographic regions, like the Americas (18), or through multitaxa meta-analyses (38). Our global-scale results confirm a strong connection between range size and niche breadth, demonstrating that species with larger range sizes tend to be those exposed to more heterogeneous climatic conditions (14, 36).

Elevation as a Driver of Niche Breadth–Range Size Relationships. In testing the Elevational Range Hypothesis, we found that the range size (Fig. 4*A*) and niche breadth values (Fig. 4*B*) of all ~250,000 plant species decrease with increasing elevation. With this finding, we suggest that elevation is not a critical factor in determining range sizes, underscoring the unique role of

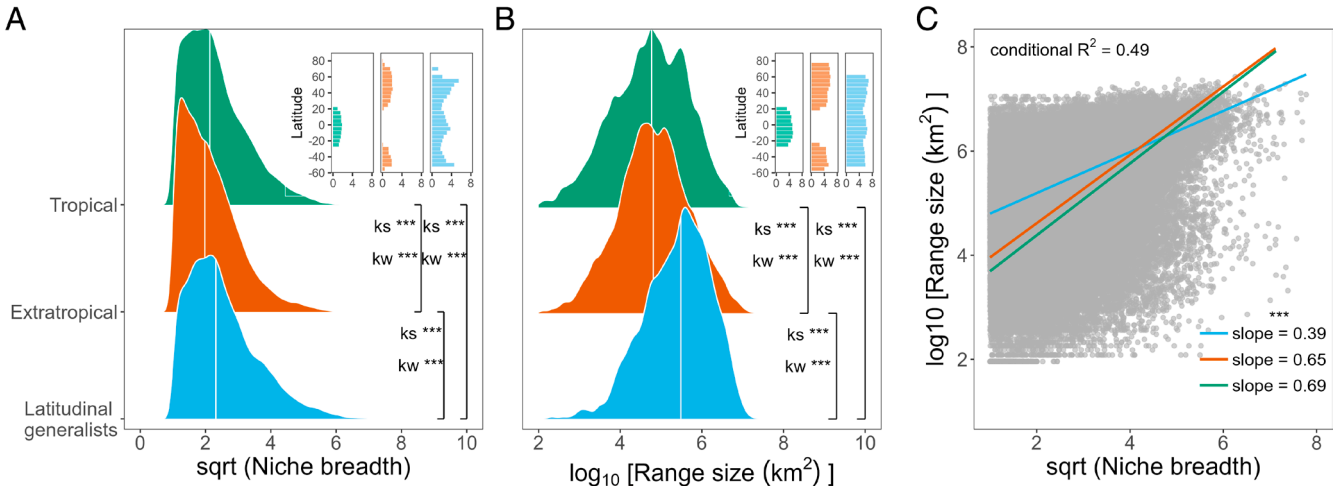

Fig. 2. Testing the Latitudinal Range Size Hypothesis. Do species exhibit larger geographic ranges and niche breadth in the different latitudinal regions? (*A*) Niche breadth and (*B*) range size distributions across latitudinal regions for ~250,000 plant species show large values for species with range areas encompassing both tropical and extratropical regions (i.e., Latitudinal generalists). The test of the range size-niche breadth relationship across latitudinal regions (*C*) reveals a positive relationship across all latitudinal regions. Each plant species corresponds to a gray-dot. Tukey test was applied to compare the regression slopes for the different latitudinal regions indicating that slopes differ from each other. The differences between distributions were evaluated using the Kolmogorov–Smirnov (KS) test, which compares the shapes of both distributions, and the Kruskal–Wallis (KW) test, which compares the medians of both distributions. *Inset* panels show the median values of niche breadth and range size per latitudinal region along the latitudinal gradient, as aggregated every 5°. Asterisks indicate statistical significance: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, and "n.s." for nonsignificant results.

mountains in promoting larger niches due to sharp temperature and precipitation gradients from lowlands to high elevations (26, 44). However, contrary to the predictions of the Elevational Range Hypothesis, which predicts that range sizes and niche breadths should increase as elevation increases, our results show that lowland species have larger range sizes and niche breadths relative to their mountain counterparts.

Climatic variation at broad spatial scales interacts with topographic relief to create steep environmental gradients, particularly in tropical mountainous regions (45). These gradients can provide diverse habitats within relatively small geographic areas, fostering climatic heterogeneity and increasing the niche breadth that can be achieved over small areas. However, we did not find that mountain species have larger range sizes or niche breadth (Fig. 4). The Elevational Range Hypothesis is attributed to the observation that climatic conditions, primarily temperature, increase monotonically with elevation, as supported by specific study systems (46). A global assessment like ours may not capture the elevation effect as expected due to the high environmental complexity of mountain systems worldwide.

Previous studies have applied arbitrary thresholds to classify elevation gradients into lowlands and mountains. One of these classifications defines lowlands as regions <1,000 m.a.s.l. and mountains as regions >1,000 m.a.s.l (34). Even when applying this classification, our results consistently show that neither range size nor niche breadth is larger in mountain species (*SI Appendix*, Figs. S8 and S9). Moreover, when considering elevation, the range size-niche breadth relationship was not clearly distinct across plant groups and latitudinal regions. For bryophytes, elevation differences in the niche breadth-range size relationship were found for species occurring in both tropical and extratropical and for those exclusive in extratropical regions (*SI Appendix*, Fig. S10 *A–C* and Table S4); for ferns, in both tropical and extratropical and in species exclusive of tropical regions (Fig. S11 *D–F* and Table S4); for flowering plants, in all latitudinal regions (*SI Appendix*, Fig. S10 *G–I* and Table S4); and for gymnosperm, no differences were found (*SI Appendix*, Fig. S10 *J–L* and Table S4). We therefore focus next on the role of topographic complexity in promoting niche expansion (33, 34).

Range Size, Niche Breadth, and Ecological Dominance. To test the Climatic Tolerance Hypothesis, we first assigned the dominance status (25) of tropical tree species to the BIEN species list. We then compared the range size and niche breadth values, as well as their relationship with hyperdominant and other nondominant species. We found that hyperdominant species have consistently larger ranges and niche breadths compared to nondominant species (Fig. 5 *A* and *C*). This pattern was consistent across all tropical regions (the Americas, Africa, and Asia) where hyperdominance was observed (*SI Appendix*, Fig. S11). Ecologically dominant species, particularly in tropical forests, are able to achieve widespread geographic distribution with increasing climatic tolerances. Our regression models showed that the positive relationship between range size and niche breadth was steeper for hyper- than for nondominant species in the tropical regions (*SI Appendix*, Fig. S12 and Table S5).

Our results highlight that species dominance is underpinned by the ability to occupy broader climatic niches and geographic extents (24). This result, however, does not imply habitat generalism and high abundance throughout the range of hyperdominant species, and no available data exist to evaluate this assumption. We emphasize that our analysis does not attempt to infer the mechanisms underlying local dominance (e.g., habitat specialization or dispersal limitation) but instead focuses on the empirical correlation between observed dominance (using hyperdominance classification and occurrence frequency) and both geographic range size and climatic niche breadth. It is important to remember that our use of abundance of hyperdominant species is the sum of abundances across all local sites within the range.

In addition to assessing dominance as a species trait, such as the hyperdominance of trees in tropical forests, we also investigated whether the number of species occurrences, another known measure of dominance (26, 28), is positively correlated with niche breadth and range size values. Indeed, this proxy for dominance was highly correlated with niche breadth and range size (Fig. 5 *C* and *D*). This pattern was consistent across all tropical regions (*SI Appendix*, Fig. S13). Thus, our findings confirm the generality of the relationship between range size, niche breadth, and ecological dominance,

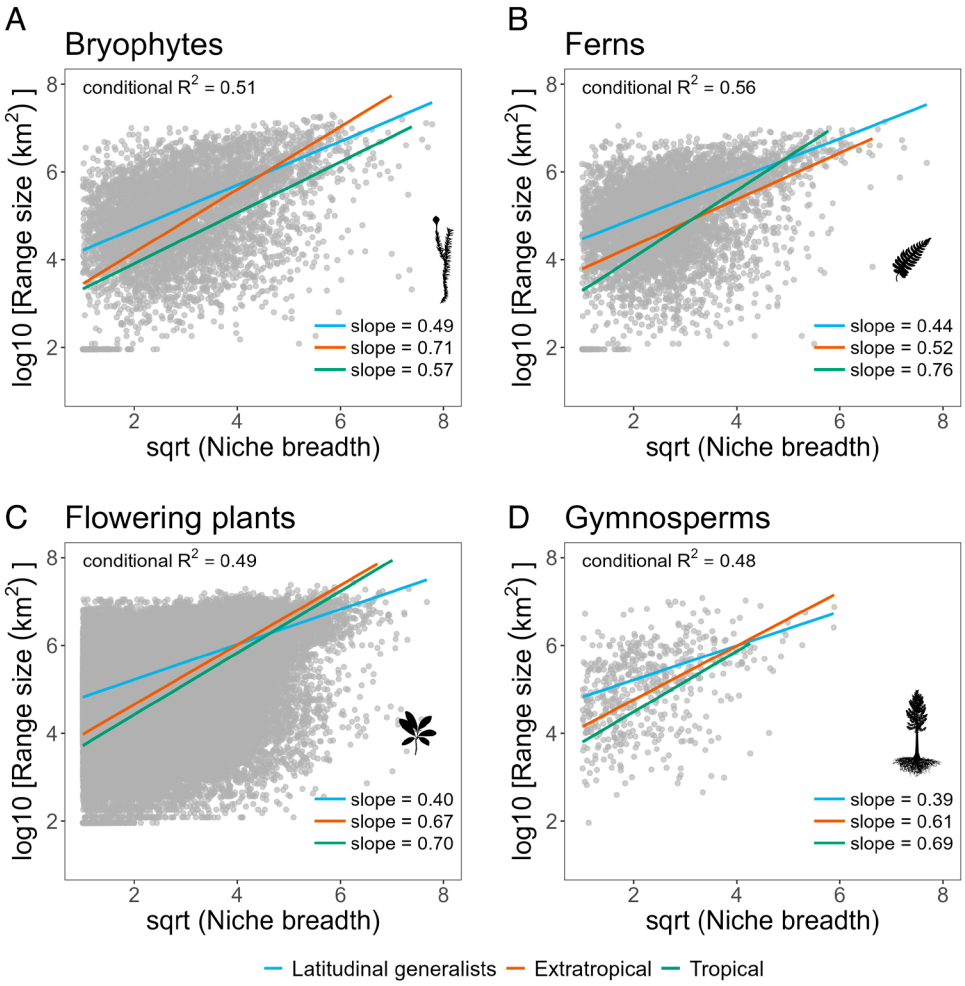

Fig. 3. Testing of the range size-niche breadth relationship across latitudinal regions and plant groups. That relationship differs in Latitudinal generalists, tropical and extratropical regions for (*A*) bryophytes, (*B*) ferns, and (*C*) flowering plants, but not for (*D*) gymnosperms. Species with extratropical ranges tend to have larger range sizes for a given niche breadth. Each plant species corresponds to a gray-dot. Statistical results comparing the fitted slopes are in *SI Appendix*, Table S3.

suggesting it as an ecological rule. This generality is consistent with evolutionary dynamics in species' geographic distribution and degree of generalization as implied by the Taxon cycle (47, 48), reflecting niche expansion, competitive exclusion, and broader ecological resilience, which underlie tolerance and dominance (4, 20).

Niche Breadth and Range Sizes Are Biologically Structured. We compared the observed regression slope of the range size-niche breadth relationship with slopes from the same relationship calculated using 50 randomized climatic layers (which served as the null model for each species). Broad climatic niches and large geographic ranges can appear correlated due to spatial autocorrelation, geometric constraints, sampling effects, or random species placement (18, 31). For example, some widespread Amazonian species span climatically uniform lowland rainforest, resulting in large ranges without broad climate tolerance (49). In contrast, montane species confined to narrow elevational bands may experience steep climatic gradients, resulting in broad climatic niches despite their small geographic ranges (50). These contrasts underscore the need to test whether observed relationships differ from those expected under spatially explicit null models that lack ecological or evolutionary mechanisms (30, 51).

Recent studies show that null models can be constructed by randomizing climatic layers while preserving their spatial structure (31, 52). By maintaining the geographic range shapes, orientations, and locations of species while randomizing the climatic layers, we recalculated niche breadths under these conditions, enabling us to determine whether observed relationships have a biological basis. If the regression slope of the observed range size-niche breadth relationship did not differ from those of the null models, the niche breadths calculated from the randomized climatic variables would be as relevant as the observed niche breadth in predicting range sizes (30). We found that the observed slope was significantly larger than that calculated using the null models (*SI Appendix*, Fig. S14). We also found that all slopes were significantly different from the null expectation for other plant groups across continents longitudinal regions, except species whose geographic distribution is in Oceania/Asia, where the coefficients were not significantly different (*SI Appendix*, Fig. S15).

Steeper-than-expected slopes in the size-niche breadth relationship indicate that other ecological processes are involved in determining this relationship beyond the inherent spatial autocorrelation of climatic conditions in geographical space. This result is similar to the findings of Dallas and Ten Caten (53), who used a different null model than ours. Yet, when comparing the two models, we found a consistent result (*SI Appendix*, Fig. S16) suggesting that the observed relationship is not merely an artifact of spatial autocorrelation among climate variables but rather a general pattern that reflects underlying ecological and evolutionary processes shaping species' climate breadths and tolerances. While spatial

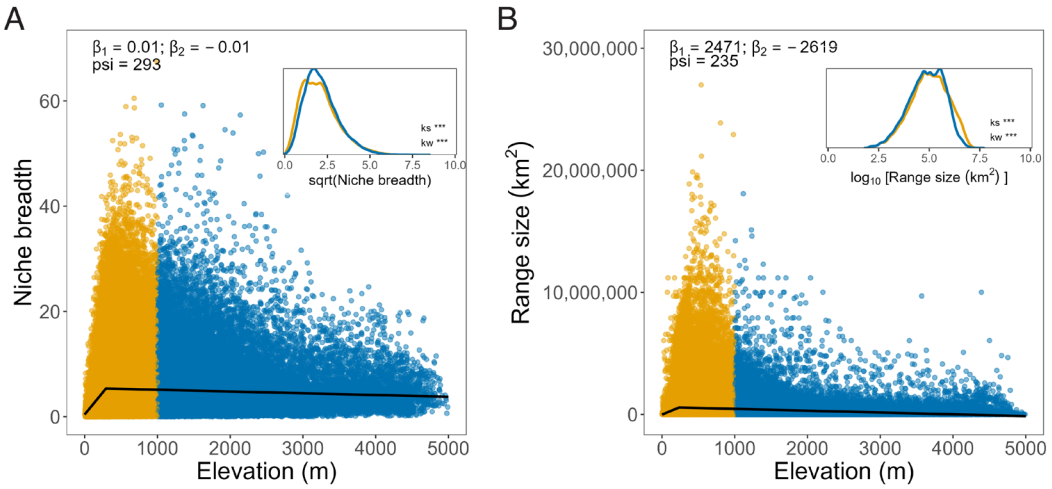

Fig. 4. Testing the Elevational Range Hypothesis. Do species in mountainous regions exhibit larger geographic ranges compared to lowland species? Niche breadth (*A*) and range size (*B*) values for ~250,000 plant species decrease with increasing elevation. Regression lines were adjusted with piecewise regression with a single breakpoint (psi). β1 and β2 are the slope values of each segment. In general, in contrast to the elevational range hypothesis, for plant species with ranges extending above ~300 m, β2 are negative, indicating species at higher elevations have smaller ranges and niche breadths. Colors separate species according to the elevation limit (1,000 m.a.s.l) that separates low- and highlands. Inset plots show the distribution of range size and niche breadth values for species with ranges encompassing low elevations (<1,000 m.a.s.l., in yellow) or mountains (>1,000 m.a.s.l., in blue). The differences between distributions were evaluated with the KS test, which compares the shapes of both distributions, and the KW test, which compares the medians of both distributions. Asterisks indicate statistical significance: **P* < 0.05, ***P* < 0.01, ****P* < 0.001, and n.s. for nonsignificant results.

autocorrelation influences ecological patterns, our results are consistent with the roles of other factors (the evolution of dispersal capabilities, climate tolerances, and historical biogeography) playing critical roles in shaping range size, niche breadth, and ecological dominance. Species' distributions are thus shaped by evolution: the appropriate mutations to adapt to environmental extremes and confer climatic tolerances (54).

Caveats. A common criticism of studies supporting BCTH arises when niche breadth is quantified based on realized climatic tolerance or habitat specificity (43, 55). This approach may fail to capture the full range of climatic conditions a species could potentially occupy, leading to an underestimation of its ecological niche (climatic or Grinnellian) (56, 57). For example, tropical lowland species may have broader fundamental niche breadths than their realized niche breadths simply because there are no hotter environments available under the current climate, or because dispersal barriers prevent them from expanding into suitable regions (58, 59). As climatic conditions change rapidly, further research is needed to understand how species' climatic limits might shift and whether or not there is available habitat for the species with the necessary environmental conditions to allow range shifts (60).

Testing the biological determinants of range size using realized climate niches rests on the assumption that realized climatic niches closely approximate species' physiological tolerances [i.e., their fundamental niches, (61)]. However, this assumption is frequently challenged, as niche estimates may be incomplete representations of climate (57). The climatic tolerance of species, as determined by their realized niche, can be described as the conditions that support nonnegative population growth rates (62). Nevertheless, if a species occupies a broad range of environmental conditions and maintains viable populations across these environments, it should, in theory, exhibit a larger geographic range (6), regardless of the difference between realized and fundamental climatic niches.

Macroecological analysis often faces the challenge of nonindependence of the data. In our case, both range size and niche breadth were calculated from the same dataset. Because both geographic range size and climatic niche breadth are estimated from species occurrence data, they may appear correlated due to shared data structure (63). To evaluate whether the observed relationship is stronger than expected by chance, we implemented a spatially constrained null model that maintains the observed number of occurrences per species and the spatial clustering of observations but randomizes the identity of the species occupying each location (31). This approach breaks any species-specific ecological associations while preserving the spatial sampling structure, allowing us to test whether the observed correlation exceeds a realistic null expectation. Finally, one of our measures of ecological dominance, the number of species occurrences, is derived from the BIEN dataset, which was also used in modeling species range areas, potentially leading to nonindependence between the two measures. Although completely removing independence is in this case not possible, the raw frequency of occurrence data was spatially filtered (*Materials and Methods*) prior to calculating range sizes, thus reducing the inherent dependence between the number of occurrences and dominance.

Implications and Final Remarks. This study demonstrates that species with broader climatic tolerances tend to have larger geographic ranges and greater ecological dominance. These findings contribute to understanding and forecasting species' responses to climate change. Predicting species' range responses based on traits has been challenging due to the complex and context-dependent relationships between species traits and range shifts (60, 64). This study strengthens the evidence that niche breadth is a strong predictor of species' ability to persist and expand under changing climatic conditions (54), offering a valuable baseline for assessing biodiversity risks and ecological resilience.

Our results are particularly critical for conservation planning, as they enable the identification of species with limited niche breadths that are most vulnerable to climate-driven habitat changes. This knowledge can guide targeted efforts to mitigate biodiversity loss, prioritize areas for protection, and develop strategies for maintaining ecosystem functionality. Although the

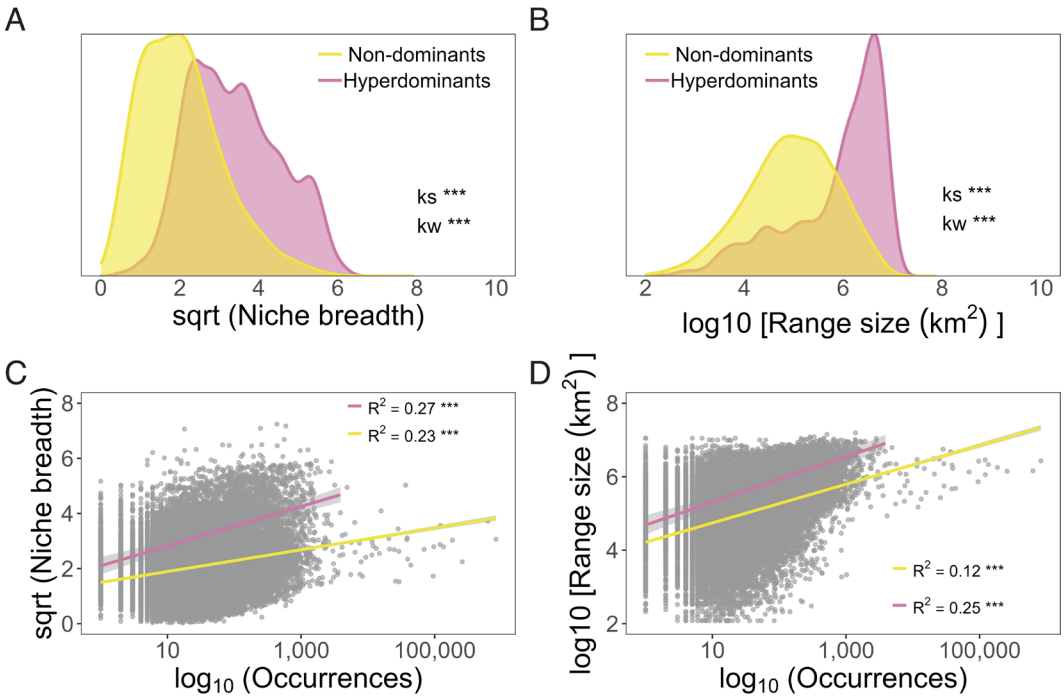

Fig. 5. Testing the Climatic Tolerance Hypothesis. Do species with high dominance exhibit large range sizes and niche breadths? The distribution of niche breadth (*A*) and range size (*B*) values shows that hyperdominant plant species (in pink) have larger range sizes and niche breadths than the nondominant species (in yellow). (*C*) The relationship between niche breadth and (*D*) range size, as well as the number of occurrence records (a proxy for dominance), shows a positive correlation, with a steeper slope for the hyperdominant species. The differences between distributions were evaluated with the KS test, which compares the shapes of both distributions, and the KW test, which compares the medians of both distributions. Asterisks indicate statistical significance: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, and n.s. for nonsignificant results. All results were highly significant.

macroecological patterns are robust, the spatial distribution patterns of range sizes need to be interpreted with care in data-scarce regions (such as India and parts of central Asia). In this case, by leveraging detailed, standardized distributional data across a megadiverse group of organisms using the BIEN datasets (65), this study establishes a foundation for exploring the ecological and evolutionary drivers of diversity and their intersection with the impacts of climate change on biodiversity at large spatial scales.

Materials and Methods

Plant Species Occurrence Data and Geographic Range Construction. We used the BIEN workflow (39, 66) to obtain species occurrence points and construct geographic ranges for ~250,000 plant species. In brief, we employed species distribution models to infer the geographic distributions of species based on occurrences from the BIEN database (version 4.2.8; https://bien.nceas.ucsb.edu/bien/about/) along with climate and soil characteristics. BIEN occurrence records are compiled through a linked workflow that standardizes, integrates, corrects, and validates data from disparate data sources and data formats, including herbarium collections, ecological plots and surveys, and trait observations from various sources (*SI Appendix*).

Extensive data cleaning was performed to ensure the reliability and harmonization of records compiled from different data contributors to the BIEN database. Taxon names associated with BIEN occurrence records were corrected and standardized using the Taxonomic Name Resolution Service (TNRS) (67). When available in the original data, family information was included along with the species name submitted to the TNRS. This information enables the TNRS to detect homonyms (identical names referring to different taxa) in other families. The declared political division names of occurrences were standardized using the Geographic Name Resolution Service (GNRS; https://bien.nceas.ucsb.edu/bien/tools/gnrs/), which corrects spelling errors and standardizes names, codes, and abbreviations. Occurrence records that fall outside of a species' native range were identified using the Native Species Resolver (NSR; https://bien.nceas.ucsb.edu/bien/tools/nsr/), which uses published checklists and endemism data to determine whether the observed species is native in a given location. Observations of potentially cultivated plants are flagged and removed from the observation data.

Additional steps were undertaken to prepare the cleaned data for species distribution modeling. To reduce spatial autocorrelation, only one record was retained if multiple records were found in a 5-km grid cell. Such thinning is recommended when modeling the occurrence density (in contrast to the density of individuals, in which retaining each record is critical) (68). The occurrences were further filtered to ensure that all retained records were at least 10 km apart, using the default thinning algorithm of spthin (v.0.2.0) (69).

The geographic distributions of plant species were modeled using 12 climate and eight soil variables (correlation coefficients < 0.7) at a 5 km resolution. The 12 bioclimatic variables were obtained from CHELSA (70), including BIO1 (Annual Mean Temperature), BIO12 (Annual Precipitation), BIO14 (Precipitation of the Driest Month), BIO15 (Precipitation Seasonality-Coefficient of Variation), BIO18 (Precipitation of the Warmest Quarter), BIO19 (Precipitation of the Coldest Quarter), BIO2 (Mean Diurnal Range), BIO8 (Mean Temperature of the Wettest Quarter), Frost Change Frequency, Growing Season Length, Growing Season Temperature, and Snow Water Equivalent. The eight SoilGrids variables (71) were Cation Exchange Capacity, Coarse Fragments Volume, clay content in the soil, total nitrogen content, Organic Carbon Stock, pH in water, the percentage of silt content in the soil, and Soil Organic Carbon.

Three modeling techniques were employed based on the number of species occurrences. For plant species with at least 15 spatially unique records ($n = 45,318$), we used Poisson point process models (a generalized version of MaxEnt) fit with the R package glmnet (v.4.0-2) (72). For species with 3 to 14 spatially unique records ($n = 94,011$), we used a range-bagging algorithm (73), which uses an ensemble of statistically generated convex hulls in environmental space. For any species with 1 to 3 spatially unique records ($n = 115,385$), we considered the cells in which records were found (at 5 km resolution) to be its range. The selection of algorithms is based on the philosophy of using a more conservative approach when there are few data for model training. Details of each modeling technique can be found in *SI Appendix, Supplementary Methods*.

Range Size, Centroid, and Elevation Calculations. Species' range sizes were calculated as the geographic range extension in km^2 from rasters projected in Mollweide equal area (5 km resolution). The geographic centroid of each range was determined by using the mid-latitude and longitude. These calculations were performed individually for each species using the function centroids of the R package terra (74) with the argument "inside=FALSE," allowing centroids to fall outside polygons whenever they are of "bean shaped" or fragmented into multiple pieces. According to the species' geographic range limits (longitude and latitude minima and maxima), each species was classified as tropical, extratropical (i.e., occurring in subtropical, temperate, or polar zones), or both (those species with geographic ranges encompassing both tropical and extratropical zones). We defined the tropics as the landmass between 23° North and South (75). We also classified species according to their position in each of the three global longitudinal bands: the Americas, Africa/Europe, and Asia/Oceania, as described in ref. 76. Longitudinal bands were used as three "replicates" to test the relationship between niche breadth and range sizes, as previous studies have indicated variation in plant diversity between these bands (76). Finally, we calculated species mean elevation values (m.a.s.l.) by extracting species elevation values per grid cell from the Shuttle Radar Topographic Mission (SRTM) digital elevation model at 0.05° resolution. A single elevation value per species makes it possible to test whether the relationship between niche breadth and range sizes is influenced by elevational variation. We classify species as occurring in lowlands (mean range elevation < 1,000 m.a.s.l.) or in mountains (mean range elevation > 1,000 m.a.s.l.) (34).

Niche Breadth Calculation. To define the dimensions to be used in calculating each species' climatic niches, we selected 10 of the 17 available Worldclim v.2 bioclimatic variables (77) that describe mean and seasonal temperatures and water availability, as suggested by Coelho et al. (40). These variables include annual temperature (BIO1), mean diurnal air range temperature (BIO2), isothermality (BIO3), temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum air temperature of the coldest month (BIO6), annual precipitation amount (BIO12), precipitation of the wettest month (BIO13), precipitation of the driest month (BIO14), and precipitation seasonality (BIO15). We then computed the principal components on the correlation matrix of these climatic layers. By doing this, we overcame the issue of several correlated bioclimatic variables (61) and reduced the number of dimensions used in the niche breadth calculation, substantially reducing variance inflation and computational time. Principal components were calculated using the globally projected climatic information at 0.05° resolution. Before the PCA calculation, climatic variables were centered and scaled. The PCA values were reprojected back to the geographic space using the function *predict* of the R package terra, and the predicted PCA layers were reprojected to the Mollweide equal area to match species range projections. Because the first two principal components explained more than 75% of the climatic variation (*SI Appendix*, Fig. S17), only these two were selected as dimensions for the niche breadth calculations, as suggested by Coelho et al. (40).

To calculate the climatic niche breadth of each species, we first selected species coordinates from the raster cells in which they occurred. Species with fewer than three occurrences, i.e., occurring in fewer than three grid cells, were not included in the niche calculation due to the impossibility of calculating a convex hull polygon area with fewer than three occurrence points. For all remaining species, occurrence points were used to extract climatic data values from the PCA projected layers. A species' niche breadth was defined as the minimum convex hull polygon area that enclosed that species' geographic coordinates in the climatic space formed by the first two PCs. The minimum convex hull approach requires no parameterization compared to similar methods, such as alphahull (78). Moreover, sensitivity analyses done by Dallas and Kramer (18) showed no significant differences between the two approaches. We calculated the species' minimum convex hull area using the function convhulln from the R package geometry (79).

Spatial Autocorrelation Null Model. Null models were constructed (31) to test whether the relationship between geographic range size and climatic niche breadth was an artifact of spatial autocorrelation in the climatic variables. We used the code available in the supplementary material of ref. 31. The simulations involved randomly rearranging the raster cells of the climatic layers, where the resampled gradient was constrained to have a similar spatial structure to the real observed gradients, thereby returning realistic climatic conditions in comparison to full randomization (80). To generate the simulated layers, we first calculated the mean, variance, and spatial correlation of the 10 bioclimatic layers with the use of a continuous Gaussian field defined by a fixed effect (intercept equal to the mean value of the climate data across the dataset) and a Matérn correlation function describing how the correlation in climate between cells decreases with the distance between them (equation 1 in ref. 31).

We then estimated the parameters of the models using integrated nested Laplace approximation implemented in the R-INLA package (81). Once the models were fitted, we used the parameters to generate 50 simulations of each environmental layer. We calculated the principal components for each of the 50 randomized sets and extracted the first two PCs, similar to the procedure with the observed climatic layers. Then, we superimposed the observed plant ranges (254,714 on each set of randomized climatic variables to recalculate each species' climatic niche breadth; species * 50 simulations = 12,735,700 niches recalculated).

It is essential to note that the proposed null model does not aim to eliminate the spatial autocorrelation of the climatic space but instead establishes a spatially structured baseline against which we can rigorously assess whether this ecological signal is consistent in the relationship between range size and niche breadth. Spatial autocorrelation of climatic variables can result in a positive relationship between range size and niche breadth, because the probability of sampling more variable climatic conditions increases with the size of the sampled area (i.e., range size) without the need to invoke any ecological process (31). The key test we make, then, is whether the observed slope differs from this null expectation. Finally, we also tested a sample of our observed slope against a second null model used by Dallas and Ten Caten (53), which simulated "virtual species" by sampling geographic space, buffering these points, and recalculating niche breadth and range size.

Data Analyses. The distributions of geographic range size and climatic niche breadth values for all species were compared for differences in their shapes using a two-sample KS test, allowing for a two-sided hypothesis test; and for differences in their medians using the nonparametric KW test. To test the relationship between elevation and range size and niche breadth, we fitted piecewise regressions to the relationship between range size and niche breadth using species mean elevation values, allowing for a single breakpoint with the R package segmented (82).

We performed generalized linear mixed models (GLMM) to evaluate the range size–niche breadth relationship across plant groups, latitudinal regions, elevational classes, and dominance status. For the Latitudinal Range Size Hypothesis, the model evaluated the range size–niche breadth relationship across latitudinal regions (obtained from species classification in tropical, extratropical, or both). For the Elevational Range Size Hypothesis, the model evaluated the range size–niche breadth relationship across two elevation classes (lowland and mountains) and latitudinal regions. For the Climatic Tolerance Hypothesis, the model assessed the range size–niche breadth relationship for species with different dominance statuses (measured as total summed abundance or frequency across sites) and the longitudinal bands of America, Africa, and Asia, as they represent independent classifications in the original hyperdominance dataset (25).

All models were set to allow grouping factors for random intercepts and slopes. We compared the slopes of each model across the grouping variable using a Tukey test, available in the function emtrends of the R package *emmeans* (83). Before modeling, range size was log-transformed, and niche breadth was square-root transformed to linearize this relationship without losing the original scale information of the variables (84). The model's goodness of fit was obtained with pseudo-R squared, the conditional coefficient of determination for GLMM, which is available in the R package MuMIn (85). We performed GLMM using the R package lme4 (86). We also tested for variation in the coefficients of the range size–niche breadth relationship (intercept and slope) across latitudinal regions by fitting bivariate lines using the sma function of the R package smart (87).

To test whether the observed range size–niche breadth relationship differed from a null expectation, we performed a simple linear regression with the transformed variables. We evaluated whether the slope coefficient of the relationship between range size and niche breadth for the observed data fell within the 95% CI of the slope distributions (either tail) for the same relationship using simulated layers (i.e., our spatial autocorrelation null model). Finding that the slope from the observed data differs from the slopes of the regressions with the simulated

layers would be interpreted as evidence that the range size–niche breadth relationship has biological meaning rather than being just determined by the climatic autocorrelation

All data analysis was done with the software R (R Core Team, 2024). Maps were produced using functions of the R packages terra (74) and tidyterra (88).

Data, Materials, and Software Availability. We provide the species information in BIEN (https://www.biendata.org/)(89), and all necessary information for the users in the README file of our repository in Zenodo (https://doi.org/10.5281/zenodo.17467476) (90), which follows code archiving recommendations for ecological data.

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