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Research article

Global patterns in plant environmental breadths

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The latitudinal gradient in plant diversity is one of the most famous patterns in ecology. It is hypothesised that narrow niche breadths and restricted geographic ranges in the tropics allow more species to coexist with minimal overlap relative to high-latitude regions. Although a wealth of studies have investigated these questions across different regions and taxonomic groups, these have consistently yielded contradictory results, leading to the continued persistence of numerous ecological explanations. Here, using a global occurrence database containing over 100 000 plant species, we provide the first globally standardised investigation into the geographic relationships among latitudinal range, environmental breadth, and latitudinal median. We find limited evidence for a global latitudinal gradient in species' ranges and environmental breadths, with results varying between hemispheres and along latitude within each hemisphere. In agreement with previous observations, we show consistent support for a latitudinal gradient in environmental breadth and latitudinal range, but only for trees in the Northern Hemisphere and for tropical species. In the Southern Hemisphere, conversely, these trends are inverted for non-tropical species, with latitudinal range and environmental breadth decreasing with distance from the equator. Moreover, these relationships are even weaker with environmental breadth, even though there is a strong relationship between environmental breadth and latitudinal range. By applying standardised methods at the global scale, these results suggest that variation in species' ranges is largely a by-product of biogeographic patterns rather than niche processes. Collectively, this work illustrates that existing ecological 'rules' linking niche breadth to latitude predominantly reflect regional sampling biases and a historical focus on the Northern Hemisphere and certain taxonomic groups.

Keywords: biogeography, ecological niche, macroecology, range size, Rapoport's rule

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Introduction

The latitudinal gradient in species richness is one of the oldest and most studied patterns of biodiversity (Rosenzweig 1995, Hawkins 2001). A set of competing hypotheses have been proposed to explain this diversity pattern (Rohde 1992, Mittelbach et al. 2007, Pontarp et al. 2019), with 'Rapoport's rule' being a famous and controversial example, stating that species' latitudinal ranges increase from the tropics to the poles (Rapoport 1982, Stevens 1989). From a Hutchinsonian niche perspective (i.e. the 'fundamental niche' as a theoretical n-dimensional space and the 'realised niche' as the occupied part of this hypervolume), most of these suggested explanations are understood in terms of ecological carrying capacity, with equatorial regions providing a wider range of environmental conditions (and thus space) for species with different fundamental niches, or by allowing for species to occupy smaller realised niches (Hutchinson 1957, MacArthur and Levins 1967, MacArthur 1972). However, testing these hypotheses has proven to be particularly challenging (Hortal et al. 2015), due in part to the difficulty implementing manipulative experiments at the necessary scale (Willig et al. 2003), coupled with the lack of global ecological data with sufficient taxonomic, environmental, and spatial coverage (Pianka 1966, Fraser et al. 2013). A comprehensive understanding at the necessary global scale is currently lacking and needed to provide mechanistic insight into potential drivers underpinning the latitudinal species' richness gradient.

One of the initial arguments explaining the latitudinal species' richness gradient was purely spatial (i.e. 'areographic'; Rapoport 1982): if species in a region each occupy little space, then more species can coexist with minimal interference compared to regions where species have large spatial requirements. Moreover, the link between Rapoport's rule and species' richness may rely on the presumed relationship between their abiotic niche breadth (i.e. 'environmental breadth') and geographic range (Stevens 1989, Brown et al. 1996, Slatyer et al. 2013). Under this line of reasoning, Rapoport's rule emerges as a corollary to the hypothesised latitudinal gradient in abiotic niche breadth (MacArthur 1972), which in turn gives rise to the latitudinal gradient in species' richness.

Despite a long history of research on this topic, evidence for Rapoport's rule and the corresponding latitudinal gradient in niche breadth remains mixed. Rapoport's rule has been shown to apply to a variety of taxonomic groups, particularly in the Northern Hemisphere (Gaston et al. 1998, Ruggiero and Werenkraut 2007), but may not be general across all biogeographic regions. For instance, in the Southern Hemisphere, evidence for Rapoport's rule is sparse, with the few extant studies focusing on small latitudinal ranges and/or few species (Gaston et al. 1998, Ruggiero and Werenkraut 2007). The lack of a clear mechanistic basis underpinning Rapoport's rule, in tandem with idiosyncratic trends across hemispheres, has even led to questions about the relevance of this pattern in explaining biodiversity gradients (Gaston et al. 1998, Gaston and Chown 1999). Despite the broad historical interest in Rapoport's rule and similar hypotheses, the uncertainty over these questions persists largely because of a lack of global, standardised data and methods, which are necessary to disentangle how these patterns and processes shift across hemispheres, regions, and taxonomic groups.

Here, we model the distribution of 114 254 vascular plant species based on occurrence and environmental data to investigate the latitudinal gradient in both environmental breadth and latitudinal range, and quantify the relationship between species' environmental breadths and their latitudinal ranges. In contrast to previous studies, our approach is the first to test these hypotheses globally, at high resolution, using a standardised collection of datasets that encompasses a large, diverse, and broadly distributed taxonomic group of plant species. Using this collection, we investigate three questions: 1) Do species' latitudinal medians predict their latitudinal ranges? 2) Do species' environmental breadths predict their latitudinal ranges? and 3) Do species' latitudinal medians predict their environmental breadths? We explore these patterns across each hemisphere separately, as well as combined, and across both trees and non-tree plant species. In general, we posit a positive relationship between absolute median latitude and both latitudinal range (Stevens 1989) and environmental breadth (MacArthur 1972). Further, we hypothesise a positive relationship between latitudinal range and environmental breadth (Slatyer et al. 2013). Lastly, we anticipate more pronounced trends in trees than in non-tree species, as stronger relationships have been shown for suggested organisms (Hillebrand and Azovsky 2001).

Material and methods

Our approach included four steps: 1) obtaining open-source occurrence data of vascular plants, 2) estimating observed latitudinal ranges and latitudinal medians for each species (based on locality data only), and 3) estimating the environmental breadth of each species by using a maximum entropy approach based on environmental correlates.

We perform the analyses in environmental space, rather than in geographic space, as climate is consistently the strongest factor explaining variation in global species' richness (Coelho et al. 2023). Moreover, projecting species distribution models in space at the scale of our investigation presents inherent challenges linked to each species' dispersal capability, and is likely to lead to overestimations with suitable conditions present in areas not accessible to individual species. We thus use statistical models to model the species' environmental breadths rather than project species' ranges. In addition, we focus on latitudinal ranges, rather than geographic area, in order to directly test the original formulation of 'Rapoport's rule' (Stevens 1989), which hypothesised a relationship between latitudinal range and the latitudinal gradient in species' richness.

The results were analysed using R v4.1.1 (www.r-project.org).

Data sources and filterings

We divided our analysis into trees and non-trees to reflect the fact that large woody species experience unique biophysical and physiological stressors due to their height, size, and longevity (Maynard et al. 2022). Tall, single-stem dendritic species with large crowns face an increased xylem cavitation and embolism risk in arid or cold environments, as well as elevated risk of mechanical failure in wind-prone regions (Read and Stokes 2006, Harja et al. 2012, Scheffer et al. 2014, Williams et al. 2019). Additionally, due to their long lifespans, trees invest in unique structures and life-history strategies for surviving disturbance, pests (e.g. wood- and bark-boring insects), and extreme weather events, including thick bark, dense wood, larger seeds, and delayed seed production (Scheffer et al. 2014, Pausas 2015, Lantschner and Corley 2023, Bialic-Murphy et al. 2024). Collectively, these factors lead to unique biogeographic constraints relative to ground-hugging plants, particularly in extreme arid, cold, and wind-prone regions (Götmark et al. 2016, Olson et al. 2018, Körner 2021), all of which affect their niche spaces, habitat preferences, and range limits (Morin and Chuine 2006, Morin and Lechowicz 2013, Aubin et al. 2016).

Cleaned tree species' occurrences were obtained from the literature (Paz et al. 2024). In brief, nine databases (Supporting information) were queried for tree occurrence data using the Botanic Gardens Conservation International GlobalTreeSearch list (Beech et al. 2017). Occurrences from all databases were merged (removing monocots and ferns) and then cleaned to identify environmental and geographic outliers using the 'occTest' package for R (www.r-project.org, Serra-Diaz 2022). Occurrence data of plants that were not classified as trees in the GlobalTreeSearch (Beech et al. 2017) were downloaded from seven sources (Supporting information) and taxonomically matched with the GBIF backbone taxonomy (published26 November 2021; GBIF Secretariat 2021). Only occurrences of vascular plants (Tracheophyta) were kept, and the taxonomy was aggregated to the species level. All observations were aggregated to a resolution of 0.09 degrees (corresponding to a resolution of ~ 10 × 10 km at the equator). Observations on pixels which were not present in the predictor layers were removed (e.g. small islands or observations that were very close to the coastline and were aggregated to a pixel of only water). For each species, the observations were thinned to 5 km (removing observations less than 5 km from each other) using the function *thin* of the R package 'spThin' ver. 0.2.0 (Aiello-Lammens et al. 2015). All species with more than 10 observations were kept (Hernandez et al. 2006).

A set of 24 environmental variables was chosen to estimate species' environmental breadths (Supporting information). Of these, 19 were climate variables obtained from CHELSA ver. 2.1 (Karger et al. 2017) with a resolution of 30 arc seconds. The remaining five were soil variables at a resolution of 250 m obtained from SoilGrids (Hengl et al. 2017). For modelling purposes, all variables were downscaled in Google Earth Engine (Gorelick et al. 2017) to a resolution of 0.09 degrees. These variables are fundamental in describing the growth rate of a plant individual and the distribution of a plant species at global scale at modelling resolution, as they represent key factors determining resource availability, metabolic rate, and/or disturbance constraints (Körner 2014, Lambers et al. 2019).

Latitudinal range estimation

We calculated latitudinal ranges and medians using the global dataset, and for each hemisphere independently. For this, we generated five separate datasets of species' occurrences, 1) a global dataset with all occurrences, 2) a Southern Hemisphere dataset containing all occurrences with negative latitude, 3) a dataset of species that only occur in the Southern Hemisphere, 4) a Northern Hemisphere dataset containing all occurrences with positive latitude, and 5) a dataset of species that only occur in the Northern Hemisphere. To estimate a species' latitudinal distribution centre, we calculated the median latitude of the species' observations globally, along with separate medians for each hemisphere. Thus, for example, if a species was on both hemispheres, it would have three values: a global median latitude, a median latitude for the Southern Hemisphere, and a median latitude for the Northern Hemisphere. As a measure of a species' latitudinal range, we computed the median absolute deviation (MAD) of the latitudinal values. This metric is the median of the absolute deviation of each observation from the specie's median, and is more resistant to the effect of outliers than the standard deviation. The MAD is multiplied with a scaling factor (typically 1.4826), to make it consistent with the standard deviation under a standard normal distribution:

$$\mathrm{MAD} = 1.4826 \times \mathrm{median}\left(\left|X_i - \mathrm{median}(X)\right|\right)$$

We computed the MAD of the latitude of species' occurrences globally and for both hemispheres separately. Lastly, because previous work has suggested that tropical species may exhibit unique latitudinal trends (Stevens 1989, Rohde 1996), we separated our analyses between tropical and other species. Specifically, because the observed 99th percentile of latitudinal range (MAD) was approximately 11 degrees across all species (Fig. 1B), we categorised species as tropical/non-tropical based on whether their median absolute latitude was less than or equal to 10 degrees, which ensured that the bulk of their range was fully contained within the tropical zone (± 23 degrees north/south latitude; Feeley and Stroud 2018). We built simple linear models at the global scale and for all combinations of hemispheres, plant groups, and for tropical and non-tropical regions, to estimate the slope of the relationships between 1) latitudinal median and latitudinal range, 2) latitudinal median and environmental breadth, and 3) latitudinal range and environmental breadth. Finally, we repeated the hemisphere-specific analyses using only those species found in that hemisphere (versus those that occur in both hemispheres).

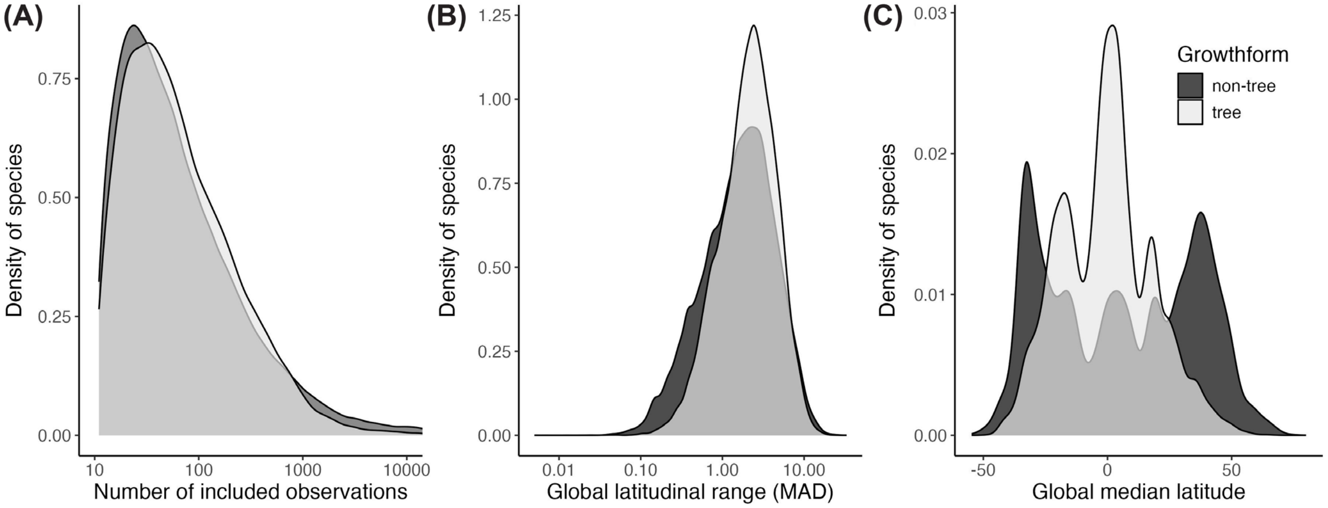

Figure 1. Overview of the included data. (A) Distribution of the number of included observations per species and growth form. A clear peak in the number of observations can be seen between 0 and 100 included observations. (B) Global absolute latitudinal range of the included species. Most included species have a narrow latitudinal range. (C) Distribution of the included species along latitude. Tree species are mostly tropical while non-tree plant species are mostly temperate. (MAD = median absolute deviation).

Environmental breadth estimation

Whereas latitudinal ranges and medians were estimated using raw occurrence data, species' environmental breadths were estimated using MaxEnt (Phillips et al. 2017, Phillips 2021). The basic approach involved fitting MaxEnt models for each species, extracting the environmental tolerances from these models, and using multivariate environmental similarity surfaces (Elith et al. 2010) to weight these values to account for differences in geographic range sizes.

MaxEnt is a presence–background method that operates on the principle of maximum entropy to model species' ranges by estimating the distribution that is most spread out (or has maximum entropy), subject to the constraints provided by the presence data and environmental covariates (for a detailed explanation, see Elith et al. 2011). This method is robust to collinearity in predictor variables and internally accounts for redundancy, thus allowing for the inclusion of all 24 predictors (Feng et al. 2019). For species with fewer than 1000 observations, the background was selected from a buffer of 4 degrees around each observation. For species with more than 1000 observations, a minimum convex polygon with a 4 degree buffer was built around the points. MaxEnt models were implemented in the 'maxnet' package ver. 0.1.4 in R (www.r-project.org). We randomly sampled 10 000 background points from the background using the function *penvs_bgSample* of the R package 'Wallace' ver. 2.0 (Kass et al. 2018). If the background area was smaller than 10 000 pixels, all possible background points were selected.

For model training and cross validation, the occurrence and background data were partitioned using a spatial partitioning method in which the environmental grids – i.e. layers of environmental variables – are aggregated into a checkerboard-like grid creating 2 bins, and then further partitioned into two more creating 4 groups for each species as implemented with the *checkerboard2* function (Muscarella et al. 2014).

For each species, we individually tuned the models, testing different parameter combinations using ENMeval2 (Kass et al. 2021) within the R package 'Wallace' ver. 2.0 (www.r-project.org). Our approach employed a leave-one-out cross-validation method, utilising the *model_maxent* function of 'Wallace' ver. 2.0. In each iteration, one of the four groups was reserved for testing. To prevent overfitting, we chose linear and quadratic features, aligning with ecological theories that suggest species' responses to environmental variables are typically unimodal (Austin 2007, Merow et al. 2013). We also tested a range of regularisation multipliers, from 1 to 4 in 0.5 steps, to penalise over-complexity and limit the number of variables in each model. For every species, we evaluated 14 combinations of feature classes and regularisation multipliers. The selection of the best-fit model was based on average validation statistics across partitions, prioritising the lowest omission rate (Leroy et al. 2018) and then the highest area under the curve (AUC). Therefore, the model predictions omitting the least amount of known occurrences and with the highest discrimination in prediction accuracy were selected. After model selection, we excluded models with an omission rate (using a 10th percentile threshold) outside the 5–30% range, or with an AUC value below 0.55. For model evaluation we also computed the continuous Boyce index (CBI) averaged across partitions (Hirzel et al. 2006). In total, we modelled 128 238 species, of which we retained 114 254 after filtering (26 540 tree and 87 714 non-tree species; Supporting information).

To estimate the environmental breadth, for each continuous model, we computed Levins' B2 values (Levins 1968):

$$\mathrm{B2} = \frac{1}{\sum p_i^2}$$

where p_i represents the proportion of the ith environmental variable used by the species and the summation ($\sum$) is over all environmental variables. This results in a value between 0 and 1, with a high B2 value (e.g. 0.9) indicating that the species utilises a large part of the environmental breadth. Conversely, a lower B2 value (e.g. 0.1) indicates that the species utilises only a small part of the available environmental breadth. We computed B2 using a modified version of the *env.breadth* function of the R package 'ENMTools' ver. 1.0.6 that included the possibility of using cloglog outputs (Warren et al. 2021). To analyse the main driving factors of individual species' distributions and environmental breadth we extracted the variables used by the model from each species' distribution model and tallied the number of times each variable was used for each of the two datasets (trees, non-trees), noting whether it was linear or quadratic.

For each species, we generated three layers – one global layer, one layer for the Northern Hemisphere, and one layer for the Southern Hemisphere – of multivariate environmental similarity surface (MESS) values (Elith et al. 2010) using the function *mess* of the R package 'dismo' ver. 1.3-9 (Hijmans et al. 2022). The resulting layers include positive and negative values, with positive values indicating that the environmental conditions of that pixel are included in the range of environmental values of the training area. In contrast, negative values indicate a dissimilar environment compared to the one included in the training area. Finally, we calculated the proportion of positive pixels in the map. This ratio indicates how representative the selected background of a species is for the range of environmental conditions of the respective layer, thus how representative the computed environmental breadth of the species is in a global context, within the Northern Hemisphere or within the Southern Hemisphere. The computed environmental breadths differ in the size of the range used for modelling (dependent on the range of the available observations) as well as in the range of environmental conditions present within the range. To make the values comparable, we multiplied the environmental breadth by the ratio of positive pixels in the MESS analysis, resulting in the global fraction of environmental conditions in which a species would be able to persist. We then normalised the values through the fourth-root transformation.

Results

In our dataset, trees and non-trees have a similar distribution of the number of observations per species (Fig. 1A) and in their latitudinal ranges (Fig. 1B). Most tree species had a median latitude around 0 degrees with smaller peaks at mid-latitudes north and south, whereas most non-tree species had a median latitude at mid-latitudes with a smaller peak at 0 median-latitude (Fig. 1C). Species excluded from the analyses due to small sample size had no particular geographic bias (i.e. tropical species were not penalised more than boreal species, Supporting information). The species' distribution models of the included species displayed a median AUC value of 0.89 (standard deviation: 0.08, Supporting information), a median 10% omission rate of 0.14 (standard deviation: 0.05%, Supporting information), and a median CBI value of 0.78 (standard deviation: 0.21, Supporting information). The dataset of the modelled species had a large latitudinal range on both hemispheres, with tree species displaying the highest number of species in the tropics and decreasing towards higher latitudes (Supporting information). In contrast, non-tree species are more uniform across latitudes, with an abrupt decrease at approximately −45 and +50 degrees latitude (Supporting information). For both trees and non-trees, linear predictor variables demonstrated a higher frequency of inclusion, each being present in approximately 35% of the models on average, whereas quadratic predictor variables were comparatively less utilised, each being used in only approximately 20% of the models on average (Supporting information). The five soil variables were consistently selected as linear terms across models, with each one retained in at least 50% of all models (Supporting information). Among climate variables, precipitation seasonality and precipitation of the warmest quarter were the most commonly retained linear variables (40–50% of models), whereas temperature seasonality was the most frequent quadratic term (~ 30% of models). In general, we observed almost identical variable selection patterns between trees and non-trees, indicative of the overall similar variation in environmental spaces and study backgrounds across the world.

Relationship between latitudinal median and latitudinal range (Rapoport's rule)

When considering the global relationships between latitudinal median and latitudinal range (Fig. 2A, D), we found distinct trends for both tree and non-tree species. In the tropical region of the Northern Hemisphere, we found a positive relationship (slope $\beta > 0$) between median latitude and the latitudinal range for trees ($\beta = 0.170$, 95% CI [0.157, 0.184]; Fig. 2B), and for non-tree species ($\beta = 0.176$, 95% CI [0.164, 0.188]; Fig. 2E), lending some support to Rapoport's theory. However, this relationship's strength varied across the latitudinal gradient. Among trees, the slope flattens markedly from the tropics to the temperate region (an 8-fold decrease to $\beta = 0.020$, 95% CI [0.013, 0.026]; Fig. 2B), and for non-trees, it even turned negative ($\beta = -0.005$, 95% CI [−0.007, −0.003]; Fig. 2E). In the tropical region of the Southern Hemisphere, both trees ($\beta = 0.482$, 95% CI [0.465, 0.498]; Fig. 2C) and non-trees ($\beta = 0.470$, 95% CI [0.453, 0.488]; Fig. 2F) again displayed a strong positive relationship between median latitude and latitudinal range. In contrast, for southern non-tropical regions, the relationship was inverse, with both trees ($\beta = -0.079$, 95% CI [−0.085, −0.073]; Fig. 2C) and non-trees ($\beta = -0.089$, 95% CI [−0.092, −0.085]; Fig. 2F) showing increasingly smaller ranges at higher

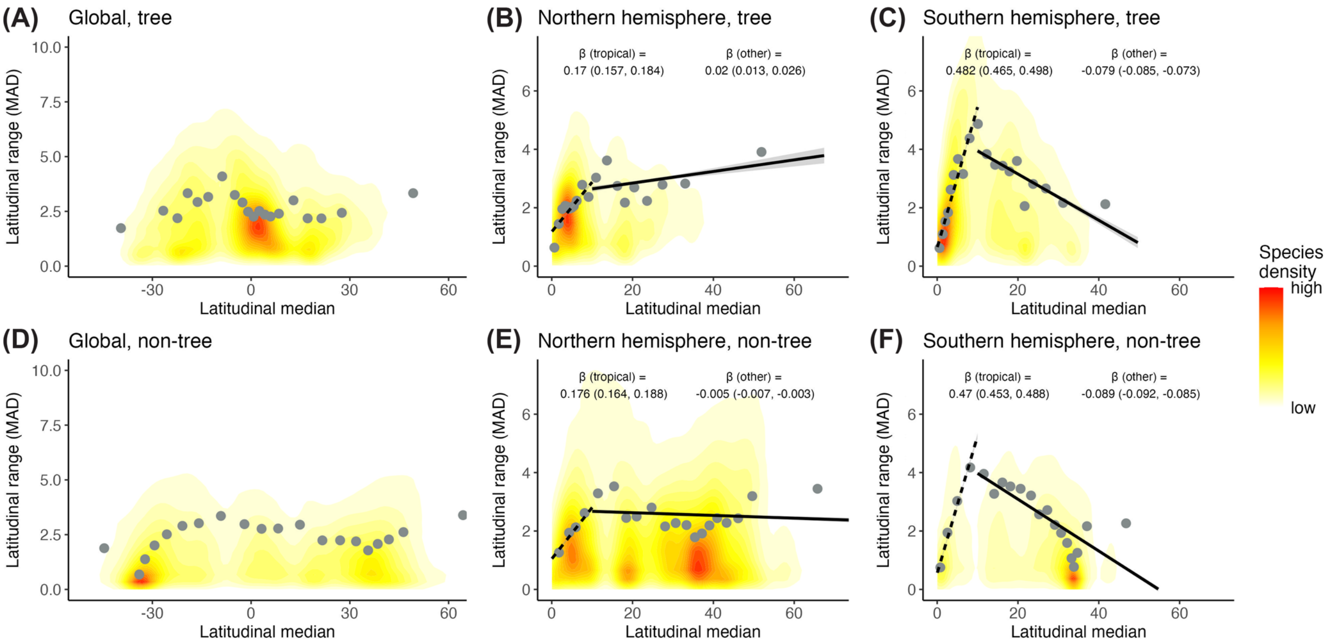

Figure 2. Latitudinal gradient of latitudinal range. (A) All tree species globally, (B) tree species within the Northern Hemisphere, (C) tree species within the Southern Hemisphere, (D) non-tree species globally, (E) non-tree species within the Northern Hemisphere, and (F) non-tree species within the Southern Hemisphere. Species' occurrence data have been filtered by hemisphere. Colours represent species' density, with areas in red displaying the highest density of species and areas in white the lowest. Latitudinal range denotes the median absolute deviation (Methods). The grey points represent the mean for each 5% quantile of observations. Regression lines are generated from the full set of data and not from the grey mean points. Dashed regression lines represent tropical species (median absolute latitude below 10 degrees) while solid lines represent non-tropical species. The slopes are presented with a 95% confidence interval, which has been derived using a 1000-fold bootstrapping approach. (MAD = median absolute deviation).

latitudes. This relationship showed a markedly higher degree of variation in range size for trees near the equator (Fig. 2A, Supporting information) compared to a more constant degree of variation along latitude for non-trees (Fig. 2B, Supporting information). When removing species present on both hemispheres, the observed directions of the relationships were unchanged but the magnitude decreased for the Southern Hemisphere for both plant groups (Supporting information). In contrast, in the Northern Hemisphere, the removal of species markedly decreased the strength of the relationship in the tropics and accentuated the relationship at higher latitudes.

Relationship between environmental breadth and latitudinal range

For both trees and non-trees, and irrespective of the global or hemisphere-specific calculations, we found a strong positive relationship between environmental breadth and latitudinal range (Fig. 3). Most of the species are concentrated at the lower end of environmental breadth (and higher end of model performance, Supporting information) and latitudinal ranges. In fact, almost 90% of the species have a global environmental breadth of < 0.50 and almost 74% of the species have a median absolute deviation in latitudinal range of < 5 globally, with increasing variance in latitudinal range at large environmental breadths (Fig. 3A, D). The slope of the relationship between environmental breadth and latitudinal range is smaller for tropical species (Fig. 3B, C, E, F), with this difference being stronger for trees than for non-trees. When comparing the relationship between latitudinal range and environmental breadth for the subset of species endemic to only one hemisphere, the same trends emerge, although the slopes are generally flatter for both groups and hemispheres (Supporting information). When considering the MESS analysis using a single hemisphere, this relationship is even weaker for both plant groups and in both hemispheres, and for tropical species in the Southern Hemisphere this relationship almost disappears and even changes direction (Supporting information).

Relationship between latitudinal median and environmental breadth

Overall, the relationship between species' latitudinal median and environmental breadth is weaker than expected for both trees and non-trees (Fig. 4A, D). In the Northern Hemisphere, for both tropical and non-tropical tree species, the relationship between latitudinal median and environmental breadth is slightly positive ($\beta = 0.005$, 95% CI [0.004, 0.006], and $\beta = 0.004$, 95% CI [0.004, 0.004], respectively; Fig. 4B). For the non-tree species, the relationship is positive only for the tropical species and flat for the others ($\beta = 0.007$, 95% CI [0.006, 0.008], and $\beta = 0$, respectively; Fig. 4E). In the Southern Hemisphere, however, for both groups the

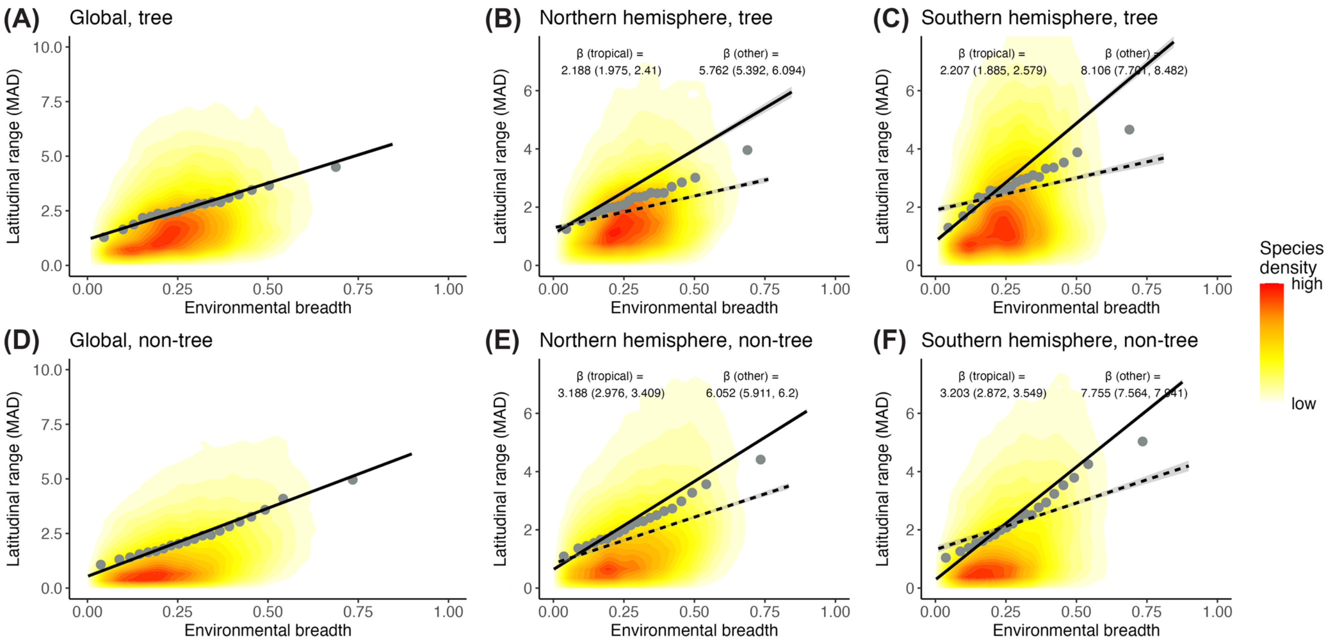

Figure 3. Relationship between environmental breadth and latitudinal range for (A) tree species globally, (B) tree species within the Northern Hemisphere, (C) tree species within the Southern Hemisphere, (D) non-tree species globally, (E) non-tree species within the Northern Hemisphere and (F) non-tree species within the Southern Hemisphere. Species occurrence data have been filtered by hemisphere. Colours represent species density, with areas in red displaying the highest density of species and areas in white the lowest. The grey points represent the mean of an equally large subset of species. Regression lines are generated from the full set of data and not from the grey mean points. Dashed regression lines represent tropical species (median absolute latitude below 10 degrees) while solid lines represent non-tropical species. The slopes are presented with a 95% confidence interval, which has been derived using a 1000-fold bootstrapping approach. (MAD = median absolute deviation).

relationship between latitudinal median and environmental breadth is only positive for the tropical species (trees: $\beta = 0.003$, 95% CI [0.002, 0.004]; non-trees: $\beta = 0.003$, 95% CI [0.002, 0.004]; Fig. 4C, F) and becomes slightly negative for the non-tropical species (trees: $\beta = 0$, 95% CI [−0.001, 0]; non-trees: $\beta = -0.003$, 95% CI [−0.004, −0.003]; Fig. 4C, F). When exploring the latitudinal gradients with the subset of species endemic to only one hemisphere, the direction of the relationships was the same, although slopes were flatter for both groups and hemispheres (Supporting information). This relationship is slightly weaker and the variance is higher for both plant groups in both hemispheres if the MESS analysis is performed on one hemisphere only (Supporting information). Furthermore, with this approach, the direction of the relationship changes for tropical, Southern Hemisphere species of both plant groups.

Discussion

Using a large standardised database representing ~ 60% and ~ 44% of the known tree and non-tree species (Govaerts et al. 2021, Cazzolla Gatti et al. 2022), respectively, we conducted the first global analysis to explore three previously hypothesised global relationships for a large and diverse taxonomic group: 1) the increase in latitudinal range from the tropics to the poles (Rapoport's rule), 2) the relationship between environmental breadth and latitudinal range, and 3) the presence of a latitudinal gradient in environmental breadth. Our results suggest limited support for Rapoport's rule, with these patterns being hemisphere- and region-specific. Although the average size of the latitudinal range weakly increased for trees in the Northern Hemisphere, we also observed an inverse relationship outside of tropical systems in the Southern Hemisphere. We observe a strong correlation between environmental breadth and latitudinal range, albeit with substantial variation, leading to a weak relationship between latitudinal median and environmental breadth. Collectively, by using a standardised collection of datasets and considering patterns across hemispheres and regions, our results provide consistent answers to the question of how plant species' ranges relate to latitude, suggesting that relationships among latitudinal range, environmental breadth, and latitudinal median predominantly reflect geography and evolutionary histories, rather than mechanistic constraints on niche size.

Overall, we find limited evidence for a global latitudinal gradient in latitudinal range or environmental breadth (Fig. 2, 4). Trends were stronger for latitudinal ranges compared to environmental breadth, with results similar to Weiser et al. (2007) showing the largest latitudinal ranges at approximately −15 degrees of latitude. Northern Hemisphere trees are the only group in line with both original theories (MacArthur 1972, Stevens 1989), albeit weakly, confirming previous findings for Northern Hemisphere trees and Southern and

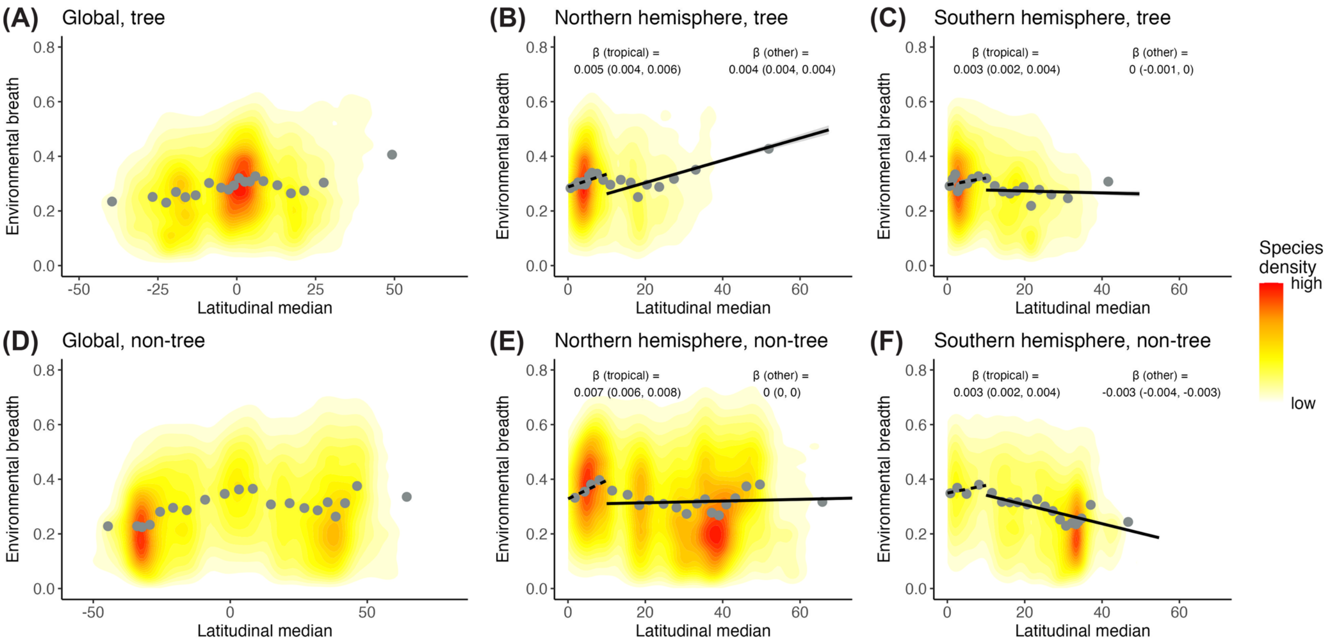

Figure 4. Latitudinal gradients of environmental breadth of (A) tree species globally, (B) tree species within the Northern Hemisphere, (C) tree species within the Southern Hemisphere, (D) non-tree species globally, (E) non-tree species within the Northern Hemisphere and (F) non-tree species within the Southern Hemisphere. Species occurrence data have been filtered by hemisphere. Colours represent species' density, with areas in red displaying the highest density of species and areas in white the lowest. The grey points represent the mean of an equally large subset of species. Regression lines are generated from the full set of data and not from the grey mean points. Dashed regression lines represent tropical species (median absolute latitude below 10 degrees) while solid lines represent non-tropical species. The slopes are presented with a 95% confidence interval, which has been derived using a 1000-fold bootstrapping approach.

Northern Hemisphere cacti (Mourelle and Ezcurra 1997, Morin and Chuine 2006, Lane 2007). Notably, strong support for the original theories only emerged in tropical latitudes, a region often overlooked in tests of Rapoport's rule, particularly in studies of plants (Weiser et al. 2007). However, non-tropical Southern Hemisphere species display a markedly reverse trend to Rapoport's rule, as their latitudinal ranges decrease with increasing latitude. This observed reverse trend can be partially explained given that non-tropical species are limited in their latitudinal range by geometric constraints (Colwell and Hurtt 1994). This is also consistent with the hypothesis that smaller domains in the Southern Hemisphere should lead to range truncation in the species from those latitudes (Šizling et al. 2009). Indeed, the 'mid-domain effect' has long served as a possible explanation for geographic patterns in species' ranges (Zapata et al. 2005), positing that species' distributions, and hence ranges, should be maximal towards the interior of large bodies of land. Our findings lend some support to this hypothesis; yet, the relationship between terrestrial land area and latitudinal range is weak overall (Supporting information), and appears to be valid only for species with exceedingly little terrestrial land available (< 20 000 km^2). Collectively, these results indicate that Rapoport's rule may be a relatively local phenomenon restricted to trees in the Northern Hemisphere (Rohde 1996, Ruggiero and Werenkraut 2007) and to tropical species, especially in the Southern Hemisphere. When removing species that occur in both hemispheres, the patterns weaken slightly but remain consistent (Supporting information), providing some support for the 'equatorial effect' hypothesis – especially in the Northern Hemisphere – which posits that truncating hemispheres will amplify the latitudinal gradient in range size (Šizling et al. 2009).

Across our global dataset, the relationship between environmental breadth and latitudinal range was positive (Fig. 3), as is expected under the climatic variability hypothesis (Slatyer et al. 2013). However, the observations had very high variance, especially at higher values of both latitudinal range and environmental breadth. Thus, the positive relationship between environmental breadth and latitudinal range (Fig. 3) translates only weakly into a latitudinal gradient of environmental breadth (Fig. 4), with a negative relationship for non-tropical species of non-tree plants in the Southern Hemisphere. This consistently negative relationship in the Southern Hemisphere has been observed previously, and might arise from a disconnect between environmental breadth and geographic extent due to the reduced area available (Šizling et al. 2009). Indeed, even if there is a relationship between environmental heterogeneity and range size this does not necessarily imply that this variation would be latitudinal (Pintor et al. 2015), as there is substantial global environmental heterogeneity longitudinally, with marked differences in the Northern and Southern Hemispheres, with the latter harbouring the majority of endemism hotspots due to its fragmented geography (Tietje et al. 2023). Attempts to identify the mechanism underpinning these patterns are further complicated by the uneven distribution of clades within and across environmental gradients, which can lead to marked variation in range limits due to interactions between evolutionary history and abiotic conditions (Wiens 2004, Ricklefs 2006), and subsequently lead to the clustering of clades (and hence range limits) within specific regions irrespective of the environment. Regardless of the exact underlying mechanisms, our results further support the importance of regional geography, suggesting the observed gradient in species' richness is unlikely to emerge from variation in species' abiotic range tolerances alone (Liang et al. 2022).

A key challenge when demarcating species' abiotic tolerances is that observed ranges typically underestimate true ranges due to dispersal barriers (Janzen 1967) or evolutionary time constraints (Paul et al. 2009), which can prevent species from reaching their geographic equilibrium. By assuming that species' current ranges reflect their global potential, our results lend support to this hypothesis: tropical species generally exhibited a steeper relationship between their latitudinal median and range, along with a weaker relationship between environmental breadth and latitudinal range – both of which support the inference of non-equilibrium distributions for tropical species (Arita and Vázquez-Domínguez 2008). Such geographical limitation should also lead to an underestimation of tropical species' environmental breadths, which would only further exacerbate the trends seen here and flatten the latitudinal relationships. Whether such patterns are a byproduct of biotic processes or geographic and evolutionary constraints is an important outstanding research question (Sexton et al. 2009), which in part will depend on increasing representation of tropical regions to better demarcate the ranges of rare species. Answering such questions is critically important for understanding how species' ranges will respond to changing environmental conditions over the coming century.

There are several important considerations when interpreting these results. In conducting a comprehensive global analysis, we tried to includeas many species and ranges as possible, including narrow-ranged species. Despite these efforts, species with restricted geographical distributions might still be underrepresented, especially those situated in tropical regions. This under-representation may be attributable to sampling biases and the presence of species not yet described in the scientific literature (Freeman and Pennell 2021, Cazzolla Gatti et al. 2022). We aimed to minimise this effect by compiling one of the most comprehensive plant occurrence databases to date, with a particular focus on bolstering the representation of tropical species by incorporating regional datasets of tropical plants (e.g. RainBio and NeoTropTree, see Supporting information). We further maximized the inclusion of rare species by considering species with as few as ten observations. An additional consideration is that the resolution of our analysis was constrained by computational resources, which could exclude species with extremely narrow distributions (ca 30 × 30 km). An analysis with a higher resolution could also be impeded by the relatively coarse resolution of available global environmental layers. This aspect is particularly critical in mountainous areas, where environmental gradients can vary over relatively small spatial extents (Janzen 1967).

We found limited evidence that plant environmental breadth increases linearly with latitude, which suggests that other biotic (Pillet et al. 2018), evolutionary (Mittelbach et al. 2007), or geographical processes (Janzen 1967, Šizling et al. 2009) predominantly shape the latitudinal gradient in species' richness. By investigating this pattern across thousands of plant species, we show that the complexity of the latitudinal species' richness gradient extends beyond variation in latitudinal range and environmental breadth, and might be more pronounced in larger organisms, in line with previous research (Gaston et al. 1998, Hillebrand and Azovsky 2001, Vázquez and Stevens 2004, Granot and Belmaker 2020). Our results indicate that single-hemisphere studies tend to overemphasise or underestimate the complexity of these gradients. The historical support for Rapoport's rule in the Northern Hemisphere, for instance, could be attributed to historical sampling biases. Our findings highlight a notable gap between the inherent complexity of tropical and southern ecosystems and the historical scope of academic research, suggesting that any residual evidence for Rapoport's rule predominantly reflects biogeography, combined with sampling- and taxonomic biases, rather than ecological niche processes. Such findings might help inform and refine global strategies that aim to enhance the study and conservation of these ecosystems, characterised by their ecological complexity and narrow ranges.

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Author contributions

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Data availability statement

Data and code are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0vt4b8h8k (Barandun et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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