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Global Ecology and Biogeography | A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

Latitudinal Phylogenetic and Diversity Gradients Are Explained by a Tropical-Temperate Transitional Bioregion

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Received: 24 September 2025 | **Revised:** 28 July 2026 | **Accepted:** 29 August 2026

Handling Editor: Adam C. Algar

Keywords: biogeography | latitude diversity gradient | macroevolution | phylogenetics | phyloregionalization | trees

ABSTRACT

Aim: To investigate how large-scale ecological and evolutionary processes shape biodiversity patterns, with a focus on understanding the origins of latitudinal phylogenetic and diversity gradients. We emphasize the importance of accurately delineating bioregions to reveal the underlying evolutionary structure of biodiversity.

Location: Global, with emphasis on transitions between tropical and temperate bioregions.

Time Period: Contemporary distributions, analysed in the context of deep evolutionary histories.

Major Taxa Studied: Woody angiosperm tree species.

Methods: We compiled a comprehensive dataset of global tree species distributions and phylogenetic relationships. Using a data-driven clustering approach, we delineated phyloregions: bioregions based on shared evolutionary history. We further applied simulation models to test whether the presence of transitional regions influences the emergence of latitudinal gradients.

Results: We identified a previously unrecognized transitional zone between tropical and temperate bioregions, termed the "bridge" phyloregion. This phyloregion is characterized by a distinct evolutionary composition and a weaker association with climatic and environmental parameters compared with adjacent phyloregions. Simulation models demonstrate that the latitudinal diversity and phylogenetic gradients are much more likely to emerge when such a transitional phyloregion exists. This finding supports the interpretation of the bridge phyloregion as a stepping-stone facilitating colonization of species between contrasting climatic zones.

Main Conclusions: Our findings reveal that accurate delineation of evolutionary bioregions (phyloregions) uncovers previously hidden structures, including a bridge phyloregion with fundamental evolutionary roles. Recognizing these cryptic phyloregions provides new insights into the processes leading to large-scale patterning of biodiversity.

1 | Introduction

Biogeographic patterns emerge primarily out of the interaction between ecological and evolutionary forces (Latham and Ricklefs 1993; Huston 1999; Gaston 2000; Allen et al. 2006; Kreft and Jetz 2010). Efforts to map diversity patterns and to delineate and characterize the formation of bioregions have been ongoing for over a century (Clements 1916; Wallace 1876; Whittaker 1975), but the recent availability of global climatic data, large phylogenies, and detailed occurrence data now

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makes it possible to uncover and investigate biogeographical patterns in extensive detail (Gorel et al. 2022; Qian et al. 2013; Smith et al. 2018). One of the key axes along which biogeographic patterns emerge is latitude, with an important example being the diversity gradient (e.g., Chazot et al. 2021; Hawkins et al. 2007). However, the underlying ecological and evolutionary processes that have led to the emergence of many latitudinal gradients remains unclear.

Many types of latitudinal gradients have been identified, including gradients in body size (Blackburn et al. 1999), genetic diversity (Hughes and Hughes 2007; Yiming et al. 2021), and avian colourfulness (Cooney et al. 2022). While some latitudinal gradients have been well-characterized and attributed to environmental factors (e.g., larger body size in colder climates (Blackburn et al. 1999), higher primary productivity in the tropics due to higher solar radiation and rainfall (Gillman et al. 2015)), other gradients remain harder to explain. This is the case for two important latitudinal gradients: the latitudinal diversity gradient (Hillebrand 2004; Pontarp et al. 2019), where lower latitudes are characterized by higher species and genera diversities, and latitudinal phylogenetic gradients (Wiens and Graham 2005; Kerkhoff et al. 2014), measured by phylogenetic structure throughout bioregions, with some studies reporting lower latitudes characterized by higher phylogenetic clustering (Massante et al. 2019), whereas other studies report opposing associations (Kerkhoff et al. 2014; Qian et al. 2017). Because species compositions are affected by region-specific histories and between-region environmental filtering, explaining why diversity and phylogenetic structure vary with latitude requires identifying the processes that limit lineage movement, establishment, and diversification across bioregions.

A suggested explanation for these biogeographic patterns is climate niche conservatism, whereby closely related species tend to retain similar climatic tolerances throughout evolutionary time. Substantial bioregional differences in phylogenetic structure have been observed in many taxonomic groups (Hawkins et al. 2007; Kerkhoff et al. 2014; Rosser et al. 2012), and these are often interpreted through the 'Tropical Conservatism Hypothesis'. Here, lineages originating in warm, stable tropical environments are less likely to colonize extratropical climates when key climate tolerance is conserved (Donoghue and Edwards 2014; Hawkins et al. 2007; Segovia et al. 2020), resulting in a filtering effect for colonization outside the ancestral climate regime (Donoghue 2008; Crisp and Cook 2012), and contributing to latitudinal differences in phylogenetic structures of regional assemblages. Other suggested mechanisms that do not include niche retention have also been suggested, including bioregional-related evolutionary rates (Pigot and Etienne 2015; Crisp and Cook 2011; Cooper et al. 2010), species antagonism and competition (Wiens et al. 2011; Ricklefs 2010), or niche shifting (Cooper et al. 2010; Freckleton and Harvey 2006; see Crisp and Cook 2012 for a comprehensive review). Importantly, it has been suggested that the latitudinal diversity and phylogenetic gradients may have arised from shared ecological and evolutionary processes, including tropical niche conservatism (Kerkhoff et al. 2014; Chazot et al. 2021), because the long-term retention of ancestral lineages in the tropics may allow these regions to act as 'cradles' of species (i.e., higher speciation rates), and 'museums' (i.e., lower extinction or colonization of tropical species; Jablonski et al. 2006; Löwenberg-Neto et al. 2011; Ringelberg et al. 2020). In order to clarify the latitudinal phylogenetic gradient patterns, the underlying mechanism that generate them and their relationship to diversity gradients, it is important to consider how the interactions between different evolutionary forces may generate these global patterns (Crisp and Cook 2012; Wiens et al. 2010; Morinière et al. 2016) by integrating phylogenetic data into biogeographical studies.

Furthermore, whether transitions between biogeographical units occur as gradual changes or as spatial discontinuities can also strongly influence the spatial patterning observed. In most cases, at the boundary between bioregions, species turnover, lineage replacement, and phylogenetic structure change more abruptly than expected from latitude alone (Kreft and Jetz 2010; Daru et al. 2017; Holt et al. 2013). Bioregional shifts emerge because assemblages are shaped by multiple processes, including dispersal limitation, historical barriers, and environmental filtering (Vellend 2017; Graham and Fine 2008). However, the boundaries between distinct bioregions are not always sharp, and can take the form of biogeographical transition zones, where regional biotas overlap, or as a result of the partially maintained dispersal between bioregions through permeable boundaries or stepping-stone areas (Morrone 2024).

A major challenge, however, is that many studies rely on predefined geographic units, such as tropical versus temperate divisions (Kerkhoff et al. 2014), or predetermined bioregions (Chazot et al. 2021; Morinière et al. 2016). Such a priori delineations may obscure taxon-specific biogeographic boundaries and risk overlooking cryptic biotic areas. Additionally, species are not phylogenetically independent (Pennington et al. 2006; Vilhena and Antonelli 2015), and treating them as such may generate artefacts. Incorporating phylogenetic data into the bioregion delineation process is, therefore, critical for coherently describing latitudinal phylogenetic patterns. Moreover, accounting for these evolutionary relationships is important for interpreting the eco-evolutionary processes underlying spatial biodiversity patterns. Predictors such as dispersal barriers, historical connectivity, environmental tolerances, and environmental filters do not affect all lineages in the same way, because lineages differ in their evolutionary histories, traits, and constraints. Not accounting for these relationships can blur eco-evolutionary inference, whereby species turnover may be interpreted as a purely ecological or geographic pattern, even when it partly reflects shared ancestry, deeper evolutionary history, or lineage-specific constraints. Generating data-driven 'phyloregions' may, therefore, offer a way to account for phylogenetic structure while determining biologically meaningful regions (Daru et al. 2017; Segovia et al. 2020; Ruggiero and Morrone 2025).

A commonly used group for studying plant biogeographic patterns is trees (Kerkhoff et al. 2014; Gorel et al. 2022). Though not a monophyletic group, they are defined by a shared functional trait—woodiness—which has evolved independently across multiple lineages. In addition, tree distributions tend to align closely with biome boundaries (Lerner et al. 2023),

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partly because forest cover shapes and is shaped by the surrounding ecosystem (Torello-Raventos et al. 2013). Climate, soils, disturbance regimes, and other environmental factors influence where dense tree cover can establish, which can feedback by buffering local microclimate conditions, reinforcing forest stabilization (Torello-Raventos et al. 2013; Chapin III et al. 2011; Manning et al. 2006). Their broad global distribution and extensive taxonomic breadth, exceeding that of many monophyletic clades, also make them valuable for studying large-scale patterns such as latitudinal gradients. Owing to their long lifespans and slow dispersal rates, their distributions tend to reflect historical processes such as climatic shifts, glacial refugia, and dispersal corridors more faithfully than shorter-lived herbs, making them strong indicators of longer time biogeographic dynamics (Comes and Kadereit 1998; Svenning and Skov 2007). As such, understanding their biogeography is essential to determining biome partitions and distributions. In addition, because woodiness has evolved repeatedly across angiosperm lineages, trees provide multiple evolutionary replicates for examining macroecological and phylogenetic patterns. Although these replicates are not necessarily independent, this "study design" can strengthen inference about the ecological and evolutionary correlates of woodiness when phylogenetic structure is explicitly accounted for. Therefore, despite and because of the non-monophyly of trees, they have been a focus of multiple macroecological and evolutionary studies (Segovia et al. 2020; Gorel et al. 2022; Guo et al. 2023), similarly to the biogeographically well-studied non-monophyletic group of terrestrial birds (Voskamp et al. 2017).

Here, in order to understand how evolutionary forces shape biodiversity patterns in trees, we compiled and analysed an extensive dataset of tree species from across the globe. We applied a data-driven approach to delineate and characterize the main phyloregions of trees and use it to study the emergence of a latitudinal phylogenetic gradient. We identified an intermediate 'bridge' phyloregion between the ecologically well-defined tropical and temperate bioregions. To better understand the role of the 'bridge' phyloregion in the formation of diversity patterns, we modelled how macro-evolutionary forces give rise to the specific characteristics of the latitudinal gradients of tree phyloregions that we observed.

2 | Methods

2.1 | Data Set of Tree Species

This study was conducted by integrating the largest phylogeny to date of tree species (Sanchez-Martinez et al. 2020), resolved to the genus level, including 787 genera, with a large dataset of tree species distributions (Lerner et al. 2023), covering 3660 species from 1157 genera. The phylogeny of woody species was obtained from (Sanchez-Martinez et al. 2020), whereby a tree was constructed using sequences from the *rbc*L and *mat*K plastid genes. This finalized phylogenetic tree is a collaboration from multiple previous efforts (Segovia et al. 2020; Neves et al. 2020; Dexter and Chave 2016), and is resolved to the genus level to prevent the misidentification of species (Sanchez-Martinez et al. 2020; Gorel et al. 2022). The distribution of tree species was obtained from (Lerner et al. 2023), whereby polygons were generated from GBIF records, in order to represent the range of species. An integrated dataset, whereby each species was matched to its respective genus, generated a final phylogeny of 481 genera tips, including 2582 species of gymnosperms and angiosperms.

2.2 | Generation of Phyloregions

A complete map of phyloregions was generated by computing the pairwise phylogenetic turnover given the species found at each global individual grid unit using a phylogenetic β-diversity metric. We initially divided the world map into grid cells using the 'dggridR' package, which employs the ISEA Discrete Global Grid System for equal-sized grid projection on a 2-dimensional plane. Each grid cell was approximately 23,000 km^2.

Given the species composition within each grid, the pairwise phylogenetic turnover was calculated using Rao-H phylogenetic β-diversity (Rao 1982; Swenson 2014), a metric used to quantify the overall dissimilarity between two groups, in our case, grid cells, expressed as:

$$Rao's H = \sum_i \sum_j \delta_{ij} - \frac{\sum_i \overline{\delta_i} + \sum_j \overline{\delta_j}}{2}$$

where δ_{ij} is the most recent common ancestor (MRCA) between species in regions i and j. Species occurring in both communities have conspecific distances of zero, contributing to the mean pairwise turnover distance. We generated a 5722×5722 pairwise distance matrix. Due to the strong influence of species richness on diversity metrics (Swenson 2014), we excluded grid cells with fewer than five species to mitigate variance bias in species-poor regions such as deserts and high latitudes, obtaining a final matrix that includes 4835 global grid cells. We used Rao's H (derived from Rao's D), as this metric has been shown to be highly correlated with other equally common metrices that calculate the phylogenetic distance within and between regions (e.g., MPD; Swenson 2014).

Subsequently, we employed hierarchical clustering using the 'complete' method to minimize the maximum phylogenetic distance between each grid pair, thereby ensuring robust clustering based on phylogenetic similarities. To enhance the resolution of our clustering and reduce skewness in the data, we applied the natural log transformation to the outputs of Rao's H. This transformation moderated the extreme differences within the distance matrix, facilitating a more detailed and fine-scaled clustering of phyloregions.

Using the 'elbow' method, we identified $k = 9$ clusters in our hierarchical clustering analysis. This method involves plotting the total within-cluster sum of squares (WSS) against the number of clusters and identifying the point where the rate of decrease sharply shifts. This method allowed us to visually identify the most appropriate number of clusters, as it identifies the point at which adding more clusters does not significantly improve the variance explained by the model. The aim is to ensure that each phyloregion identified represents a distinct phylogenetic unit without over-fitting the model with

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an excessive number of clusters. In order to test for robustness, we reduced the choice of k clusters to 6, and observed very similar patterns (Figure S1), as further noted in the Results section.

This method is described in detail in (Daru et al. 2017).

All analyses were carried out in R (R Core Team 2021), using the libraries ape (Paradis and Schliep 2019), phytools (Revell 2024), and picante (Kembel et al. 2010).

2.3 | Community Ecology and Statistical Analyses

We included relative species abundance within each phyloregions in our analyses of phylogenetc α and β diversity. Relative abundance was measured by comparing the observed versus expected species occupancy in each phyloregion.

Phylogenetic β-diversity between phyloregions was calculated in a similar manner as it was calculated to generate phyloregions (between grid cells), by creating an $n \times n$ pairwise matrix, where n is the number of phyloregions (9 phyloregions). Taxonomic β-diversity was also calculated between the phyloregions using the Sørensen Index.

The relative species abundance within each phyloregions was included in our analyses of phylogenetic β diversity between phyloregions. Relative abundance was measured by calculating the relative presence of species occupancy in that phyloregion, given the number of grid cells within the phyloregion that the species occupies and the global presence of that species. Specifically, expected counts for each species within each phyloregion was estimated by dividing the observed species count in one phyloregion by the total counts of that species in all phyloregions, then multiplying the resulting proportion by the total species count in each phyloregion. A scaling factor was then applied by dividing each observed species count by the total count of that species, then multiplying the resulting proportion by the total species count in each phyloregion. This scaling factor was applied to ensure that the sum of expected counts matched the observed total counts for each phyloregion.

The $n \times n$ pairwise matrix distances for both β-diversity and phylo β-diversity were plotted on a 2-dimensional reduced representation using Principal Coordinates Analysis (PCoA). PCoA was chosen for phylogenetic analysis because it accommodates the actual distances calculated from the mean distance to the most recent common ancestor (MRCA) between phyloregions, which are critical for reflecting evolutionary relationships. To account for negative eigenvalues resulting from the non-Euclidean distance metric, a Lingoes correction was applied to the PCoA analysis.

To assess whether the sequential pattern observed from the PCoA 2D representations reflected the original multivariate dissimilarity structure, we examined nearest-neighbour relationships among phyloregions. For each phyloregion, we identified its nearest-neighbour as the phyloregion with the lowest pairwise dissimilarity value, and tested whether this neighbour corresponded to the expected latitudinal sequence from phyloregion 1 to 9. We then performed a permutation test by shuffling phyloregion labels ($n = 9999$ permutations) and comparing the observed proportion of sequential nearest-neighbour matches to the null distribution.

Phylogenetic α diversity was calculated using the mean phylogenetic distance (MPD) within phyloregions (Webb et al. 2002), in a similar way in which Rao's D is generated:

$$MPD = \frac{\sum_i \sum_j \delta_{ij}}{n}$$

where n is the number of species within a community. In order to allow for a comparative analysis between phyloregions, we standardized the effect size of MPD values (SES)–MPD for each phyloregion, whereby:

$$SES - MPD = \frac{observed_{\mathrm{MPD}} - \overline{null_{\mathrm{MPD}}}}{sd\left(null_{\mathrm{MPD}}\right)}$$

whereby $null_{\mathrm{MPD}}$ is generated using a null model by randomizing the names of the taxa on the tips of the phylogeny. We chose such a constrained permutation technique as it generates a random phylogeny with the same phylogenetic architecture (branch length and distribution) as the actual phylogeny, thus reducing the Type I error rate that would be generated under a less constrained randomization technique, for example, by simulating novel phylogenies or randomizing the distribution of species within phyloregions. The permutation was carried out 500 times, in order to obtain the mean $\overline{null_{\mathrm{MPD}}}$ and standard deviation $\mathrm{sd}\left(null_{\mathrm{MPD}}\right)$ used for the model. A positive SES-MPD value represents higher phylogenetic distances than expected by chance, indicating phyloregenetic over-dispersal. Alternatively, negative SES-MPD values suggest shorter phylogenetic distances between the species compared to the null model, thereby implying phylogenetic clustering.

Next, to assess the influence of environmental niches on the distribution of phyloregions, we employed a Random Forest model. The model was set up to estimate how different environmental variables could predict the extent of phyloregions. We extracted the average value of each environmental variable in all grid cells. To ensure a balanced and representative training dataset, we randomly selected 80% of the grid cells from each phyloregion. This stratified sampling approach ensured that each phyloregion was equally represented in the training set. The remaining 20% of the grid cells from each phyloregion constituted the testing set. The environmental variables included were: latitude, longitude, elevation, mean annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality, isothermality, and available phosphorous (Olsen P). All bioclimatic data was downloaded from WorlodClim Global Climate Data at a resolution of 5 arcminutes (Hijmans et al. 2005), extracted using the R package 'raster' (Hijmans 2024). Plant-available phosphorous was obtained from (McDowell et al. 2023). To validate the model and assess the reliability of its predictions, a bootstrap analysis was conducted. 100 bootstrap resampling of the original dataset were performed, with each sample drawn with replacement to match the size of the original dataset. For each bootstrap sample, the model was retrained, and its predictions

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were evaluated on a corresponding stratified test set, mimicking the original 80/20 split.

Model performance was evaluated using a confusion matrix for each bootstrap iteration. The confusion matrix provides a detailed breakdown of the model's predictions, comparing predicted versus actual classifications. From the confusion matrices, we derived three key metrics: precision (the proportion of correct predicted identifications), recall (the proportion of positives that were correctly predicted, also known as sensitivity), and the F1-score (the harmonic mean of precision and recall). This process allowed the estimation of variability and confidence intervals.

We cross-validated the Random Forest classification using spatial blocking in order to account for spatial autocorrelation. Geographic cells were partitioned into spatial blocks of fixed size of 500 km. These blocks were then randomly assigned to five folds, such that all cells within a given block were assigned to the same fold. For each validation round, all cells belonging to one set of spatial blocks were withheld as the test data, while the remaining blocks were used for model training. Model performance was summarized across folds using macro-F1, which gives equal weight to each phyloregion class and is therefore less sensitive to differences in class representation.

2.4 | Simulating the Latitudinal Phylogenetic Gradient

2.4.1 | Model Design

We study two model versions, one with two discrete 'regions' representing a tropical and a temperate region, and one with an additional 'bridge' region. Genera can occupy one or more regions at any time step, and can also move between adjacent regions (representing a colonization event). The three-region model is structured in a sequential arrangement, by allowing species colonization between tropical and temperate regions only by passing through the bridge region (Figure 3a). In other words, colonization events in this model can only occur between the tropical and bridge regions, or between the temperate and bridge regions. Under this setup, we designed a spatially dependent non-zero sum extinction-speciation model, based on a previous study (Hurlbert and Stegen 2014). In our model, a genera originally occupies both the tropical and temperate regions. Speciation (λ), extinction (μ), and colonization (γ) are modelled as stochastic binomial processes, with region-dependent probability rates, whereby the chance of an event occurring is the per-lineage probability modelled at each time step, independent of the previous generation. In other words, at each time step each lineage has a fixed probability to speciate, a fixed probability to go extinct, and a fixed probability to colonize a different region. Therefore, regions with more genera will have a higher probability of speciation, extinction and outgoing colonization events (Hurlbert and Stegen 2014; Allen et al. 2006). We considered each time-step in the simulation as an interval of size 1, and randomly positioned each speciation event in this interval (uniformly at random); this avoids multiple simultaneous speciation events.

In the three region model that includes a bridge region, we modelled the reduced prediction of a defined niche space in the bridge region (Figure 2c) as a lack of region-dependent parameter rates. Therefore, the probabilities of λ and μ for genera occupying the bridge region were obtained from the region-dependent rates of the region from which the genera colonized the bridge.

2.4.2 | Simulation Output and Evaluation

We track the evolutionary history and geographic occurrence of all genera throughout the simulation. At the end of the simulation, we generate the phylogeny of the remaining genera using the tracked evolutionary history. We used the final distribution of genera to the different regions to compute SES-MPD values for each region. A null distribution was generated as described above in order to compute the standardized effect size (SES) of MPD by permuting the assignment of each tip of the phylogeny to one of the tree regions (500 permutations were used).

2.4.3 | Running Simulations

Simulations were ran for 5500 time steps. For model parameters, we selected γ, μ and λ values that generate a number of genera at the end of the simulation that is broadly comparable to the number of genera in our analysis of tree species (a few hundreds to 1–2 thousands; Figure S11). For speciation rates, we used three parameters: $\lambda = 1 \times 10^{-3}, 5 \times 10^{-4}$, and, 1×10^{-4}. For extinction rates, we used five parameters, defined as fractions of the speciation rates: $\mu = 0{,}0.15{,}0.3{,}0.45$ and 0.6; these values fall within the range of extinction rates relative to speciation rates previously reported for plant species (Magallón et al. 2018; Magallón and Castillo 2009). For colonization rates, we used four parameters: $\gamma = 1 \times 10^{-4}, 1 \times 10^{-3}, 1 \times 10^{-2}$ and 1×10^{-1}; these rates span several orders of magnitudes, ranging as low as the speciation rates we used and as high as 0.1 colonization events per genera per time step. The high colonization rate values align with rates previously reported for tree species between tropical and subtropical regions (Gorel et al. 2022). The parameter choice was done to ensure a wide span of the parameter space with plausible parameter values, rather than restrict the space to realistic parameter combinations, because our goal with the model simulations was to understand the effect of the bridge region and evolutionary parameters on the emergence of latitudinal gradients. Taking all combinations of these parameter values (two speciation parameters for the tropics and temperate regions, two extinction parameters for the tropics and temperate regions, and either four or two colonization parameters for the three- and two-region models), we have a parameter space of 57,600 parameter configurations for the three-region model and 3600 configurations for the two-region model.

We retained only simulations that produced phylogenetic trees between 20 and 2000 surviving genera (phylogenetic tips). For each parameter configuration, we generated 100 simulation replicates. We ran simulations until 100 successful simulations were obtained—defined as producing phylogenetic trees with 20–2000 surviving genera. Because of computational limitations, a maximum of 2000 simulations were allowed per

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parameter configuration, and if 100 "successful" simulations (with 20–2000 genera) were not achieved within this limit, this parameter configuration was excluded. As a result, we retained 97% of the parameter space for the two-region model and 87% for the three-region model.

3 | Results

3.1 | Global Phyloregions of Tree Species

In order to identify worldwide phyloregions for tree genera, we compiled an extensive dataset of geographic distributions of 2582 tree species (obtained from Lerner et al. (2023)), and integrated the data given matching genera with the tips of a temporally calibrated genus-level phylogeny (obtained from Sanchez-Martinez et al. (2020)). This resulted in a final dataset of 481 genera for which geographic and phylogentic data was available. We then used an unsupervised hierarchical clustering method aimed at minimizing phylogenetic β-diversity distances, based on the genera composition from independent geographical units. This method effectively delineates bioregions characterized by similar evolutionary histories and phylogenetic relationships, resulting in a map where each cluster represents a distinct phyloregion. To determine the number of phyloregions, we used the elbow criterion, which suggested $K = 9$ clusters. We observe that, although phyloregion assignment was made for each geographic location independently, the inferred phyloregions are composed of large continuous geographic areas, and that most phyloregions are present in different continents (Figure 1a). The tropics, especially in the New World, were represented by a single phyloregion (Cluster 9 in Figure 1a). By contrast, several higher latitude phyloregions (clusters 5, 7 and 8) appeared in both hemispheres, although a greater fraction was present in the northern than southern hemisphere. The same equator-centered pattern emerged when we reduced the clustering to $K = 6$ (Figure S1).

We characterized the phyloregions in terms of ecological features by comparing their geographical distribution with that of worldwide biomes (Figure 1b). Each phyloregion showed significant geographic overlap with at least one biome, allowing us to denote the ecological span of each phyloregion. Some clusters were associated with specific biomes: Cluster 9 was exclusively associated with tropical and subtropical biomes, Cluster 6 uniquely overlapped with the desert biome, Clusters 3–5 were primarily associated with the temperate biomes, and Clusters 1 and 2 were associated with boreal-tundra biomes. In contrast, clusters 7 and 8 were not associated with any specific biome type, but rather spanned across multiple biomes, including tropical, temperate, and desert. These two unique clusters, which we term 'bridge phyloregions', extend across grasslands, deserts, and montane bioregions (Figure 1b), spanning the Saharan, Arabian, Kalahari, central Asian, and Atakama deserts, as well as mountainous bioregions of the Himalayas, east African highlands, and the southern Andes. The presence of bridge phyloregions as a transition between the tropical (Cluster 9) and temperate (Clusters 4 and 5) phyloregions was most notably observed throughout the old world. Similarly, though to a lesser extent, a transitional bridge phyloregion was observed in the southern Neotropics and Australia. There are, however, specific areas where the tropical and temperate phyloregions are adjacent, such as in western Australia, southern-east Africa, south-east Asia, and across most of North America, with only a narrow bridge signal in Baja California. Thus, while bridge phyloregions are widespread, their presence and continuity vary by continent, and direct contact between tropical and temperate phyloregions occurs in certain areas.

This analysis was repeated with the inclusion of only geographic cells containing more than 30 genera (Figure S2), because small sample sizes may bias phylogenetic analyses Swenson (2014). The resulting phyloregion pattern is similar to the one obtained with the full dataset (Figure 1), with clear presence of bridge phyloregions (clusters 2 and 3 in this analysis) that span tropical, temperate and desert bioregions. Because most of the low sample size cells that were excluded are in boreal, tundra, or desert bioregions, we do not observe phyloregions that specifically represent these biomes.

Phylum-level composition differed across phyloregions (Figure S3), whereby all temperate and boreal/tundra phyloregions (with the exception of Cluster 5) were composed primarily of gymnosperms, in comparison to a higher proportion of angiosperms in the tropical, bridge, and desert phyloregions. This last result is expected because gymnosperms generally predominate at higher latitudes, and angiosperms predominate in tropical, subtropical, and lower-latitude bioregions (Darwin 1903; Bond 1989; Fragnière et al. 2015).

To evaluate evolutionary relationships among phyloregions, we quantified community-level taxonomic and phylogenetic dissimilarities (Figures 2c and S4). Phylogenetic dissimilarity showed a strong latitudinal structure, whereby low-latitude tropical phyloregions were positioned at one end of the main axis, whereas high-latitude boreal/tundra phyloregions occupied the opposite end. This structure was primarily captured by the first PCoA axis, which explained 61.2% of the variation, compared with 9.5% explained by the second axis (Figure 2c). This visual pattern was further supported by a nearest-neighbour permutation test based on the original phylogenetic dissimilarity matrix, indicating that phyloregions were more often most similar to their expected adjacent phyloregions along the latitudinal sequence than expected by chance (observed proportion of adjacent nearest-neighbour matches = 0.78; null expected proportion = 0.2; 97.5% null interval: 0 – 0.55; permutation $p < 0.01$). Thus, phylogenetic dissimilarity among phyloregions is consistent with the expected latitudinally ordered sequence. However, taxonomic dissimilarity showed a more complex pattern. Although the ordination also separated low and high latitude phyloregions, variation was distributed more evenly across the first two PCoA axes (with axis 1 explaining 46.5% and axis 2 explaining 33.9% of the variation; Figure S4). Consistent with this more multidimensional structure, the nearest-neighbour permutation test did not support a strict sequential arrangement of taxonomic dissimilarities (observed proportion = 0.11; null proportion = 0.2; $p = 0.86$). Thus, while taxonomic composition shows broad spatial differentiation among phyloregions, the sequential latitudinal pattern is stronger and more clearly supported for phylogenetic beta diversity than for taxonomic beta diversity.

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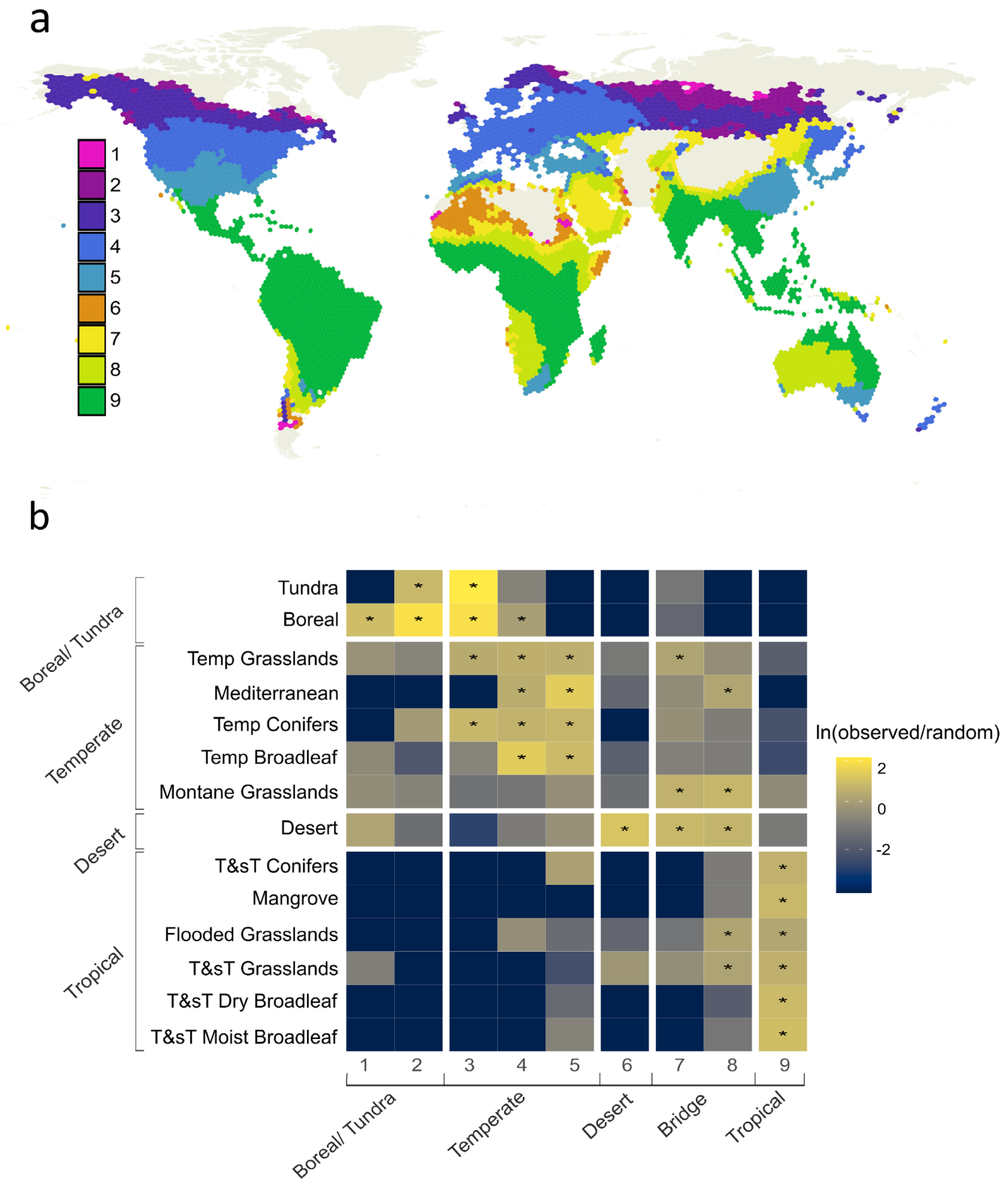


FIGURE 1 | Phyloregion delineation of tree species. (a) Nine inferred phyloregions of tree species. The phyloregions are inferred using a clustering analysis of 5851 geographical locations, taking into account the genera compositions and phylogenetic distances. (b) Proportion of overlap between each ecological biome and the nine phyloregions, compared to a randomized phyloregion bootstrap. The heat map shows the natural logarithm of the ratio between the actual overlap and the bootstrap overlap, with yellower colours signifying higher-than-random overlap. Statistical significance of high overlap is marked with an asterisk ($p < 0.01$). Based on the overlap with biomes, we assigned the nine clusters to five phyloregion types, denoted below the heatmap.

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3.2 | The Latitudinal Diversity and Phylogenetic Gradients in Relation to Tropical Niche Conservatism

We quantified diversity of the main phyloregion groupings (tropic, desert, temperate, and boreal/tundra phyloregion groups) by genera counts and phylogenetic clustering by taking the standardized effect size of the pairwise mean phylogenetic distance (SES-MPD) among the genera assigned to each cluster. We observed both a latitudinal gradient in phylogenetic structure (Figure 2a) and the latitudinal diversity gradient (Figure 2b). Genera diversity decreased with increasing latitude, but there was no substantial difference in the number of genera between temperate and bridge phyloregions, and the desert phyloregion showed less diversity than expected from its latitude. For phylogenetic structure, SES-MPD revealed a latitudinal gradient, with significant phylogenetic clustering in tropical phyloregions and a transition toward phylogenetic overdispersion in boreal/tundra phyloregions (Figure 2a). This pattern was also observed when SES-MPD was analysed at the biome level (Figure S5).

We tested to see if the strong differential latitudinal patterning of angiosperms vs. gymnosperms—specifically the higher presence of gymnosperms at higher latitudes (Figure S3b) —affected the emergence of the latitudinal phylogenetic gradient. When excluding gymnosperms and including all cells (Figure S6c), the general pattern changed to that of significant clustering at higher latitudes and non-significant clustering of the desert phyloregion (Figure S6a); however, when excluding gymnosperms but restricting the analysis to well-sampled cells (> 30 genera) the pattern was similar to the one when all genera are included (Figure S6b). In addition, we repeated the SES-MPD analysis after rarefying each retained cell to 30 genera, in order to assess whether the inferred pattern was sensitive to differences in genera richness within cells, performed for both the full dataset and the angiosperm-only dataset (Figure S7). The recovery of a similar latitudinal SES-MPD pattern in both analyses indicates that, although gymnosperm inclusion and low-richness cells influence the SES-MPD gradient, the broad latitudinal phylogenetic gradient is not an artefact of either gymnosperm presence or poorly sampled cells.

We next evaluated how accurately environmental variables predicted phyloregion identity. High predictive accuracy would indicate that phyloregions occupy distinct environmental conditions, whereas low accuracy would indicate that phyloregions are not characterized by specific environmental conditions. Because phyloregions inherently account for lineage evolutionary history, their association to environmental variables is suggestive of niche conservatism, given its contribution to the maintenance of phylogenetically structured assemblages. However, this alone does not directly test for phylogenetic niche conservatism as ancestral niche retention.

To quantify the extent to which environment explains distributions, we conducted a random-forest classification analysis using present-day environmental factors (e.g., climate, elevation, soil-available phosphorous), aimed at predicting genera compositions for geographic locations from environmental data. In general, we found that environmental factors are strongly predictive of phyloregion assignment for geographic locations (accuracy of model = 91%). However, prediction accuracy varied substantially for different phyloregions, with the model accurately predicting the distribution for the tropical, temperate and boreal phyloregions, but less so for the bridge and desert phyloregions (Figure 2d). A similar random classifier model, treating all phyloregions as independent clusters, as opposed to the main phyloregion groupings (boreal/tundra, temperate, desert, bridge and tropical), produced similar results for all except for phyloregion 1 (Figure S8b). This low predictive accuracy of phyloregion 1 could suggest that this phyloregion, although primarily composed of boreal bioregions, also includes bioregions that were not successfully classified into any other phyloregion (Figure 1a), mainly within deserts. Miss-classification of areas that do not fit into any other category is a common limitation of hierarchical clustering techniques (Everitt et al. 2011). Because spatial autocorrelation can inflate predictive performance, we evaluated model robustness using two complementary approaches. We first repeated model validation using spatial blocking, in order to account for spatial autocorrelation. In addition, we compared models with and without geographic coordinates as predictors. The similar performance across these analyses further confirms the strong environmental differentiation among phyloregions (Figure S8c).

We confirmed the presence of a latitudinal phylogenetic gradient (Figure 2a), with suggestive evidence that niche conservatism contributes to this pattern, especially for the tropic, temperate and boreal/tundra phyloregions but not for the desert and bridge phyloregions (Figure 2d). In addition, we observed that the bridge phyloregion is positioned between temperate and tropical zones (Figure 2c), spans across several ecological biomes, and is less constrained by environmental conditions than the other phyloregions (Figure 2d). These features challenge our understanding of how the latitudinal phylogenetic gradient is formed.

3.2.1 | The Role of the Bridge Phyloregion in the Emergence of Latitudinal Gradients

To better understand how the attributes of the transitional bridge phyloregion impact the macro-evolutionary processes driving the latitudinal phylogenetic and diversity gradients, we designed a modelling framework that incorporated key macro-evolutionary forces—speciation, extinction, and colonization. We model three regions, representing the tropics, the temperate and the bridge phyloregions, where speciation and extinction occur at given rates in each region, but colonization can occur only between the bridge regions and the other two regions. For comparison, we also modelled the same scenario without the bridge region, with only two regions representing the tropics and the temperate between which colonization can occur. We simulated a birth-death speciation-extinction process with colonization, and noted the SES-MPD values for each region at the end of each simulation, defined as the time for which a total of at least 500 extant species was reached.

Because climate strongly influences diversification rates (Soberón 2007; Hua and Wiens 2013; Weir and Schluter 2007), we assigned speciation and extinction rates to the tropical and

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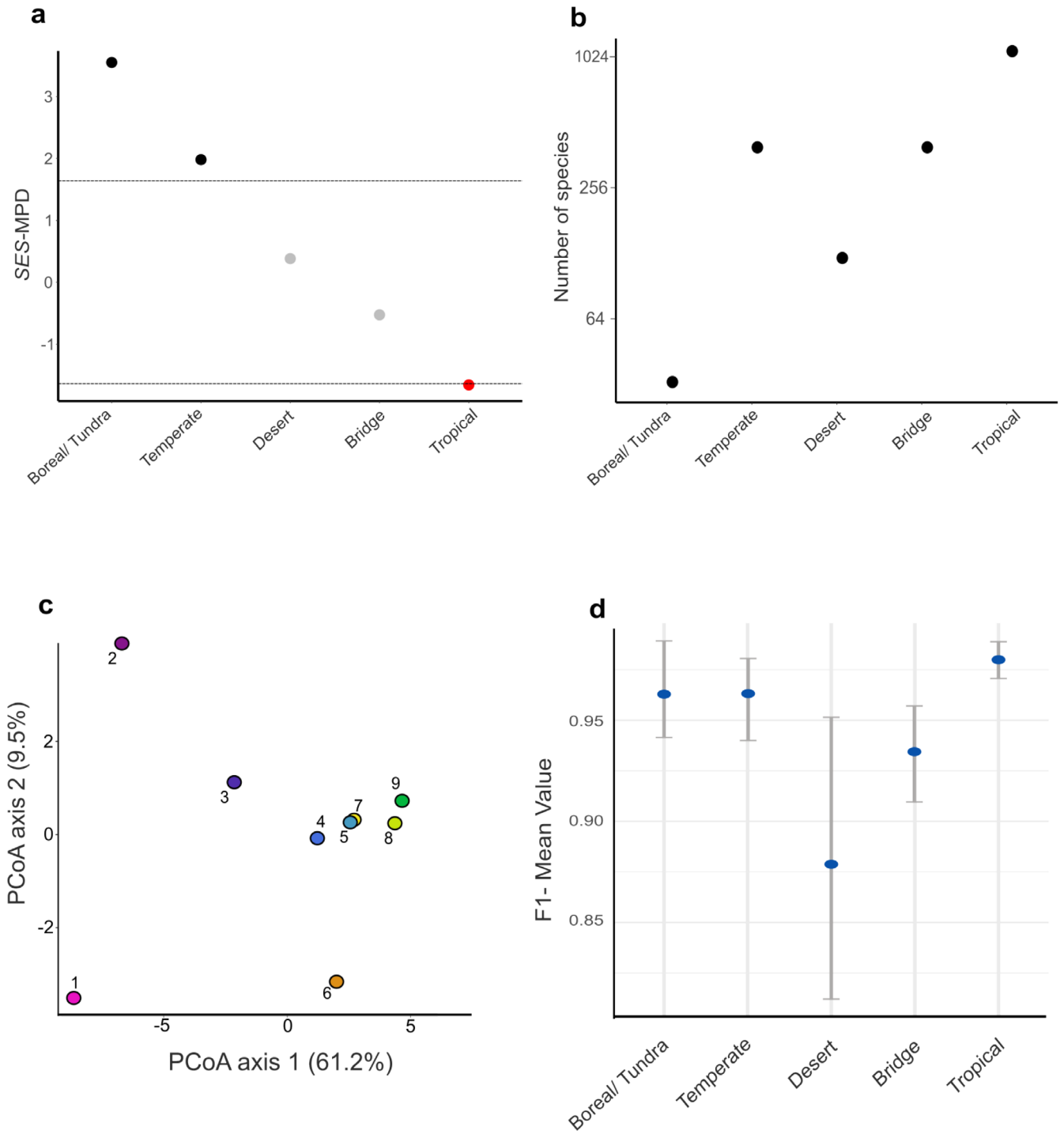


FIGURE 2 | Evolutionary and ecological characteristics of tree phylogerions. (a) Phylogenetic divergence throughout the different phyloregion types, measured as SES-MPD Z-scores, for the five main phyloregion types identified. Phyloregions with SES-MPD z-scores < -1.96 are denoted with red dots, and represent significant phylogenetic clustering of tree species in these phyloregions. Phyloregions with SES-MPD z-scores > 1.96 are denoted with black dots, and represent significant phylogenetic over-dispersal of tree species. The values shown are the average value for the SES-MPD of all phyloregions assigned to a phyloregion type. (b) Genera diversity of phyloregions, measured as the average number of genera in each of the phyloregions types. (c) Evolutionary relationship among phyloregions in terms of Phylogenetic β diversity. Shown is a PCoA ordination plot of the phylogenetic distances between phyloregions, measured using Rao's D index. (d) Relationship between environmental factors and phyloregions. A random-forest model trained with environmental variables was used to predict phyloregion type assignment, to determine the extent that phyloregions are associated with environmental conditions. Show are the means and 95% confidence intervals of the fraction of correctly identified phyloregion-type (F1-score), representing the ability of environmental data to predict phyloregion assignment.

temperate regions while the bridge region was not assigned a unique rate, in order to reflect its weak association with environmental variables (Figure 2d). Instead, genera dispersing to the bridge region kept the rates from their ancestral region. We then simulated lineages to test how adding a transitional bridge region affected phylogenetic and diversity gradients (Figure 3a).

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Specifically, we looked for parameter sets that recreate (i) a latitudinal diversity gradient, given highest genus richness in the tropical region and lowest in the temperate region (denoted as 'Condition 1'); (ii) a latitudinal phylogenetic gradient, defined by a large SES-MPD difference between tropical and temperate regions (denoted as 'Condition 2'). This condition was defined to be satisfied when the SES-MPD in the tropical region was in the bottom 20% out of all SES-MPD values attained in our simulations, and the temperate SES-MPD was in the top 20% of SES-MPD values; we also evaluated a more stringent of this condition, denoted as 'Condition 2*', where SES-MPD values in the temperate and tropics were required to be in the extreme top or bottom 10% of values, respectively. For simulations that included the bridge region, we also required that $SES\text{-}MPD^{trop} < SES\text{-}MPD^{bridge} < SES\text{-}MPD^{temp}$ to ensure a gradient in phylogenetic structure, with stronger phylogenetic clustering in tropical assemblages and higher phylogenetic overdispersion in temperate assemblages (Figure 3a). We compared the frequency

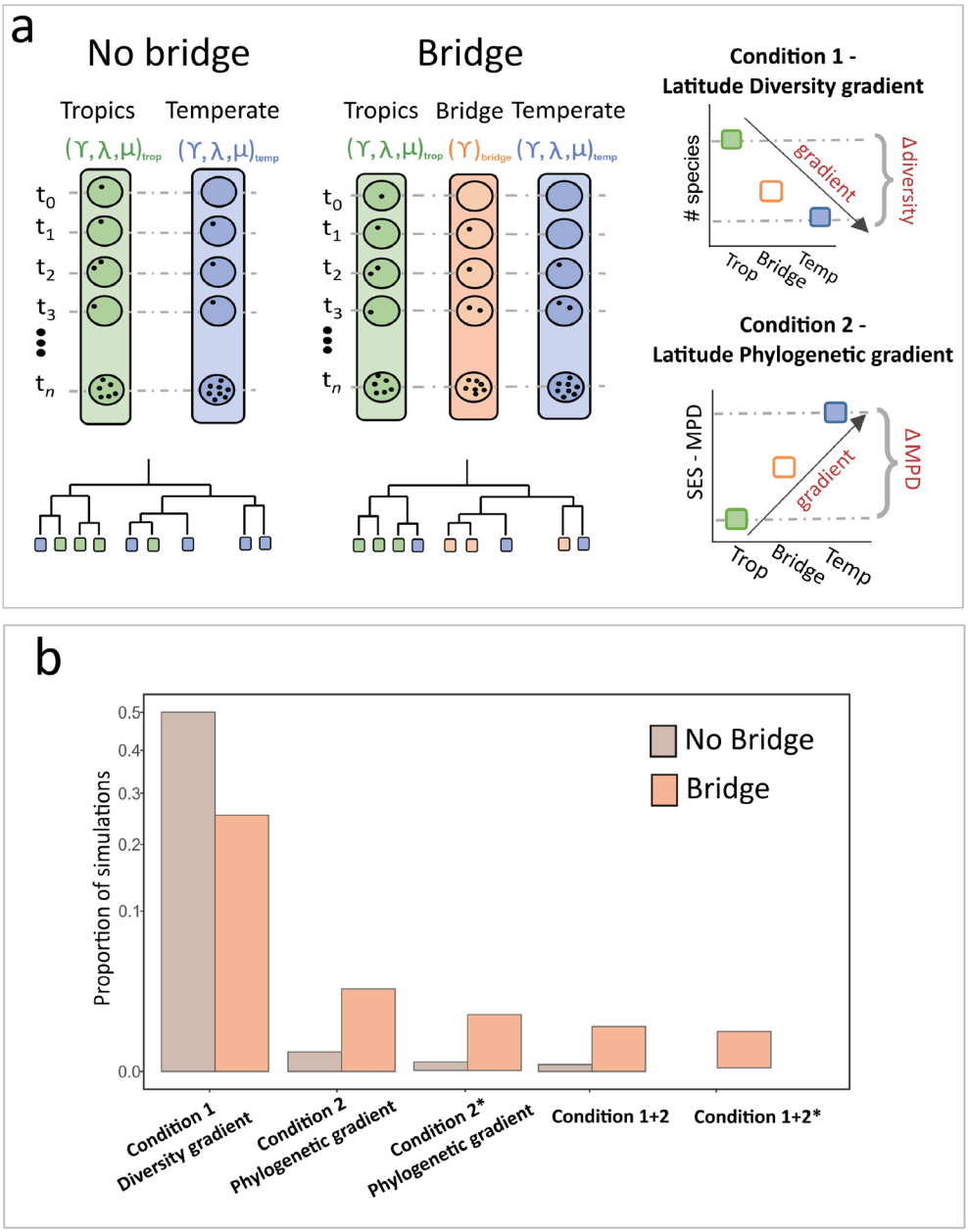


FIGURE 3 | The role of the bridge phyloregion in a simulation model. (a) A schematic representation of our modelling framework for studying the role of the bridge phyloregion in generating latitudinal gradients. We model 2–3 regions, representing the tropical (green), temperate (blue), and bridge (orange) regions. In one set of simulations we include the bridge region, and in the other exclude it. For a set of parameters (speciation, extinction for each regions, and dispersal rates between regions) we track the phylogeny, and compute the standardized effect size mean phylogenetic distances (SES-MPD) of the regions, as well as genera diversity. We consider the outcomes of a (i) a latitudinal diversity gradient (Condition 1), (ii) a latitudinal phylogenetic gradient (Condition 2) and (iii) a combination of phylogenetic and diversity gradient (Condition 1 and 2). (b) The proportion of the simulations for which the latitudinal diversity gradient, phylogenetic gradient, and the combination of both emerged in the simulation including and excluding the bridge regions. Two versions of Condition 2 were evaluated, where 2* is more stringent than Condition 2. *y*-axis is scaled using a square root transformation to allow visualization of cases with a small proportion of simulations.

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of these two conditions in simulations run with and without the bridge region.

Although the model without a bridge region had a higher fraction of simulations that met Condition 1 alone (only diversity gradient), the inclusion of the bridge region substantially increased the proportion of simulations that satisfied both conditions 1 and 2 (Figures 3b and S9), with a 30-fold increase compared to the model without the bridge region. Under the more stringent Condition 2*, none of the simulations that did not include the bridge region resulted in both conditions being met. This result highlights the role that the bridge region plays in generating phylogenetic patterns, and may indicate that patterns such as those presented in Figure 2a,b are unlikely without such a transitional region between tropical and temperate regions.

3.2.2 | Evolutionary Dynamics Leading to the Latitudinal Phylogenetic and Diversity Gradients

To further characterize the scenarios in which the latitudinal gradients emerge, we partitioned the parameter space into categories based on the colonization dynamics each configuration represents. For simulations including the bridge region, we define five colonization classes: (i) 'equal colonization', where all colonization rates are the same, (ii) 'out-of-the-tropics', where net colonization is from the tropics outwards, (iii) 'into-the-tropics', where net colonization is from the temperate region outwards, (iv) 'out-of-the-bridge', where colonization tends to occur from the bridge outwards toward the tropics and temperate regions, and (v) 'into-the-bridge', where colonization tends to occur from the tropics and temperate regions into the bridge (Figure 4a shows the exact conditions used to partition the parameter space into the five categories). For the simulations that excluded the bridge region, we used only three categories: 'equal colonization', 'out-of-the-tropics', and 'into-the-tropics'. We then compared the proportion of simulations for which each latitudinal gradient, diversity or phylogenetic, emerges, as well as the proportion of simulations in which both emerge.

Under four of the five colonization categories we observed simulations that met both latitudinal gradient conditions, whereas for the 'into-the-bridge' scenario no simulation resulted in both gradients (Figure 4b). This result was robust to varying thresholds of extreme SES-MPD values, obtained by comparing the highest and lowest proportions of SES-MPD values between tropical and temperate regions (Figure S9). Although 'into the tropics' scenario had the highest proportion of simulations producing a latitudinal diversity gradient, the 'equal colonization' scenario appeared as the scenario with the highest proportion of simulations that met both conditions. In contrast, the other three scenarios ('out-of-the-tropics', 'into-the-tropics', and 'out-of-the-bridge') showed consistent differences in the proportion of simulations that resulted in both conditions (Figures 4b and S9). These results indicate that both latitudinal gradients emerge when the bridge region serves to connect the tropical and temperate regions, by acting either as a stepping-stone ('equal colonization', 'out-of-the-tropics', and 'into-the-tropics') or as a source ('out-of-the-bridge') for species—but not as a sink ('into-the-bridge').

When looking at the combination of parameters that result in both the latitudinal diversity and phylogenetic gradients, we observed that there were higher proportion of simulations generating them for higher tropical than temperate speciation rates and higher colonization rates from tropical regions ($\gamma_{trop\rightarrow bridge}$) than for temperate regions ($\gamma_{temp\rightarrow bridge}$), but no specific enrichment of extinction rate differences between tropical and temperate regions (Figures 4c and S10). An asymmetry in colonization rates was observed across all four colonization scenarios that generated both gradients, with greater tropical than temperate colonization ($\gamma_{trop\rightarrow bridge} > \gamma_{temp\rightarrow bridge}$; Figure 4c). Surprisingly, this pattern emerged even under the 'into-the-tropics' scenario that was limited to higher temperate colonization rates ($\gamma_{temp\rightarrow bridge} > \gamma_{trop\rightarrow bridge}$). This last result can occur when colonizations rates between tropical and bridge region (both $\gamma_{trop\rightarrow bridge}$ and $\gamma_{bridge\rightarrow trop}$) are higher than those between bridge and temperate regions (both $\gamma_{temp\rightarrow bridge}$ and $\gamma_{bridge\rightarrow temp}$; Figure 4a). Overall, our findings suggest that the emergence of both the latitudinal phylogenetic and diversity gradients is more likely to occur in the presence of a transitional niche-unconstrained bridge region, with higher tropical than temperate speciation and colonization rates.

4 | Discussion

Using a data-driven approach, we detected major phyloregions broadly corresponding to well-known bioregions, and a transitional ('bridge') phyloregion between tropical and temperate domains (Figure 1). This phyloregion spans tropical and temperate bioregions and is strongly represented in deserts and grasslands. It is characterized by intermediate phylogenetic structure, falling between the phylogenetically clustered tropical phyloregion and the more overdispersed temperate phyloregion, with weaker association to climatic and environmental parameters. The identification of the bridge phyloregion was made possible when evolutionary relationships among lineages were incorporated into regional delineation, highlighting the importance of phylogenetic distances for detecting structure that may be obscured by species composition or environmental similarity alone. We therefore term this the 'bridge phyloregion', since it seems to be a transition zone between two main bioregions, rather than a clearly defined niche.

Our simulations showed the latitudinal diversity and phylogenetic gradients were far more likely to arise when an intermediate bridge phyloregion is present than when it is not, mediating exchange between tropical and temperate phyloregions. Because the simulations explored a broad parameter space, this suggests that the presence of a bridge phyloregion is sufficient for the joint emergence of both latitudinal gradients, at least under a large set of parameter combinations, although this does not imply that this mechanism uniquely explains the empirical pattern.

Although our phyloregionalization analysis revealed some direct contact between tropical and temperate phyloregions (e.g., in south-east Africa, Figure 1a), the phylogenetic dissimilarity analysis (Figure 2c) suggests that lineage turnover is structured more strongly along a sequential tropical-to-bridge-to-temperate arrangement than along a direct tropical-to-temperate

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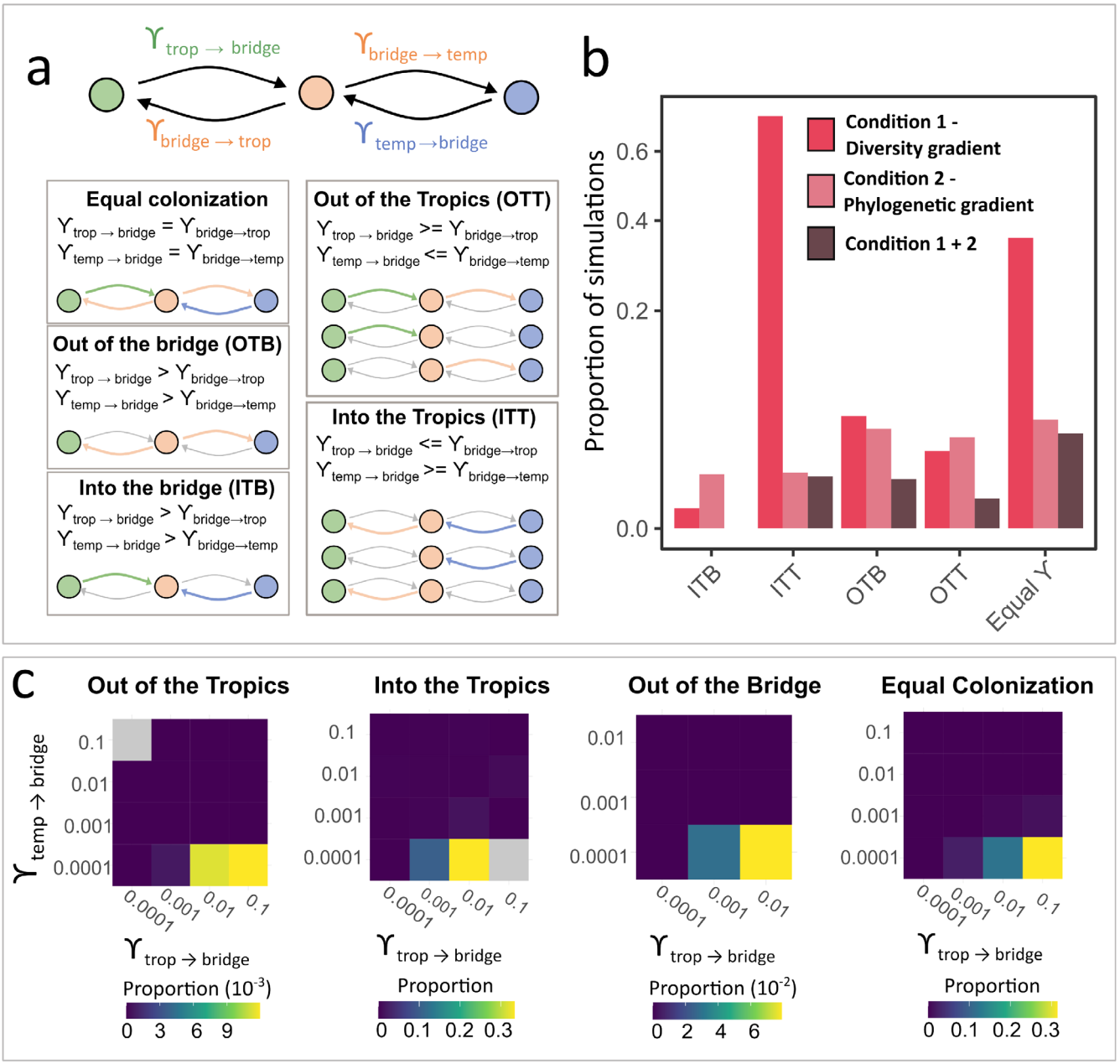


FIGURE 4 | Scenarios in which latitudinal gradients emerge. (a) The parameter space for our simulations was partitioned into five categories based on colonization pattern configurations when the bridge region was included, and three categories ('out-of-the-tropics', 'equal colonization rates', 'into-the-tropics') when the bridge region was excluded. (b) The proportion of the simulations for which the latitudinal diversity gradient, the latitudinal phylogenetic gradient and a combination of both emerged, for each colonization category. *y*-axis is scaled using a square root transformation. (c) Analysis of the proportion of colonization configurations that generate both latitudinal gradients. Parameters $\gamma_{trop \to bridge}$ and $\gamma_{temp \to bridge}$ represent the colonization rates described in (a). The grey quadrants represent combinations that do not exist for this configuration of parameters under this colonization scenario.

transition, further supported by a significant nearest-neighbour sequentiality permutation test. In contrast, taxonomic turnover did not strongly reflect a genera-level turnover following the same simple sequential structure. The stronger sequentiality in phylogenetic than taxonomic turnover suggests that the bridge phyloregion captures a deeper historical signal of lineage movement and replacement across the tropical-temperate gradient, while present-day species composition may be shaped by additional ecological and regional processes, including local filtering, recent dispersal, extinction, and endemism, which can obscure this broader evolutionary structure. In addition, our simulations support this idea of step-wise colonization by showing that only when the bridge phyloregion is included do we consistently observe both the latitudinal diversity and phylogenetic gradients. This implies that the bridge serves as a stepping-stone, or even a net source (rather than a sink), for lineages dispersing between tropical and temperate bioregions. However, there are exceptions to this, for example in North America where the bridge phyloregion is largely absent except for a narrow enclave in Baja California.

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Transition zones at the intersection of distinct bioregions have long been recognized as important components of the biogeographical landscape (Ferro and Morrone 2014; Laffan et al. 2016; Morrone 2024). Here, we interpret the bridge phyloregion as a biologically meaningful transition zone for three main reasons. First, its spatial distribution (Figure 1a) strongly corresponds with the major global transition zone previously identified (Morrone and Ebach 2022). Second, the bridge phyloregion is characterized as an independent bioregion that acts as a stepping-stone for species from distinct evolutionary histories and bioregions (Ruggiero and Morrone 2025). Finally, its functional role in shaping evolutionary processes, both within the region and at the global scale, closely matches the description of transition zones as areas where biogeographic patterns can be linked to ecological and evolutionary processes (Riddle and Hafner 2010; Morrone 2024). In this study, we interpret the geographically disconnected areas represented by the bridge phyloregion as a unified functioning transition zone. However, these areas may differ in their regional histories, environmental settings, and biome composition, and future studies could examine whether different bridge areas vary in their specific underlying processes. Our study, therefore, contributes to the literature on transition zones from both ecological and evolutionary perspectives (Morrone 2024) by characterizing the bridge phyloregion as a bioregion that harbours lineages with distinct biotic histories and by showing that its presence and functional role can influence key global ecological and evolutionary patterns.

Previous studies have pointed to grasslands as stepping-stones in the colonization and further diversification of species between distinct climatic zones (Galley et al. 2007; Daru et al. 2016). Similarly, the expansion of grasslands in the late Miocine and early Pleiocene transitional eras led to the increased colonization rates of tropical species (Howard et al. 2023; Couvreur et al. 2021). The interspace between tropical and temperate bioregions was shown to harbour more colonization events to other bioregions than either the temperate or tropical bioregions themselves (Kerkhoff et al. 2014). These studies support our results that the bridge phyloregion acts as a transitional hub, where lineage overlap, environmental filtering, and dispersal across climatic boundaries may jointly promote turnover and colonization. This interpretation is also compatible with the concept of "bridge species" (Jablonski et al. 2013), namely those species that can successfully overcome the tropical niche conservatism barrier, and thus, facilitate evolutionary transitions between climatic zones. Indeed, such species may be dominant in the lineage pool of the bridge phyloregion, and may help explain the elevated turnover and colonization rates we detected.

The 'into-the-bridge' scenario was the only colonization dynamic that failed to produce both diversity and phylogenetic gradients (Figure 4), suggesting that the bridge phyloregion functions primarily as migration corridors for species moving between the tropical and temperate phyloregions, rather than acting as sink habitats that retain colonizing species. Although the mechanisms by which bridge phyloregions facilitate the colonization of both tropical and temperate species remain unclear, we suggest that the low-competition environments of grasslands and deserts and broad latitudinal spans of these bioregions allow the bridge phyloregion to act as a permeable evolutionary transition zone between adjacent bioregions.

4.1 | The Tension Between the 'Tropical Niche Conservatism' and 'Out of the Tropics' Hypotheses

The direction of the latitudinal phylogenetic gradient we observed is in accordance with some studies (Massante et al. 2019), but differs from others (Qian et al. 2013; Kerkhoff et al. 2014; Kubota et al. 2018). We suggest that these differences likely reflect variation in phylogenetic metrics, spatial scale and taxonomic scope considered in each case, rather than contrasting underlying processes. For example, metrics such as PD_z (Kerkhoff et al. 2014), which quantify overall evolutionary history rather than average phylogenetic distances (as measured by SES-MPD), are less sensitive to divergence among distantly related species clusters (Swenson 2014), and therefore yield different phylogenetic clustering patterns (Duchêne and Cardillo 2015). Likewise, studies using small spatial units to analyse latitudinal phylogenetic patterns (Qian et al. 2013, 2017; Kubota et al. 2018) could overlook multiple independent lineage transitions (Cardillo et al. 2017) that may become apparent when assemblages are integrated across broader biogeographical scales, as in our phyloregion framework. This could lead to an underestimation of phylogenetic overdispersion at high latitudes (Swenson 2014). Notably, whereas stronger tropical than temperate clustering in woody species has previously been attributed largely to the inclusion of gymnosperms (Massante et al. 2019), the persistence of phylogenetic gradient signal after excluding gymnosperms in our study (Figure S6) suggests that this pattern is not driven solely by the deep angiosperm-gymnosperm split. The distinct latitudinal phylogenetic gradient signals observed between studies, therefore, possibly highlight the sensitivity of inferred phylogenetic clustering patterns to the methodology used.

The 'Out of the Tropics' hypothesis (Jablonski et al. 2006), which postulates that the tropics act as cradles for both tropical and temperate species, might seem mutually exclusive with the long-standing 'tropical niche conservatism' theory (Wiens and Donoghue 2004), which states that species that originate in the tropics tend to remain within (Wiens and Graham 2005; Kerkhoff et al. 2014). The two theories, therefore, can be viewed as assuming either high ('out of the tropics') or low ('tropical niche conservatism') colonization capabilities for tropical species, suggesting an apparent conflict. Our results reflect the tension between the two theories because we show strong support for a latitudinal phylogenetic gradient on the one hand (Figure 2b), but our simulations show that colonization that is higher from tropical than from temperate species plays a key role in maintaining both the latitudinal phylogenetic and diversity gradients (Figures 3, 4 and S10). Our analysis does not directly test niche conservatism, which would require explicitly linking climatic tolerances to phylogeny, for example through ancestral-state reconstruction.

One perspective in which the tension between the tropical niche conservatism and out of the tropics theories can be resolved is by highlighting the following question—is phylogenetic niche conservatism a process or a pattern? In other words, is the retention of species within a specific niche the underlying evolutionary force leading to phylogenetic niche conservatism, or is it a phylogenetic signature that is the consequence of the interaction between other evolutionary forces (Wiens et al. 2010; Crisp and Cook 2012; Graham and Fine 2008; Cavender-Bares et al. 2004).

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Ultimately, phylogenetic clustering is a tool for quantifying trait and niche similarity between closely related species (Webb et al. 2002; Losos 2008). Our results show that a latitudinal phylogenetic gradient can coexist with high colonization (emigration) of tropical species. This apparent paradox can be reconciled by considering phylogenetic niche conservatism not as a causal mechanism, but as an emergent pattern arising from an underlying evolutionary process. Indeed, previous studies (Pigot and Etienne 2015; Mazel et al. 2016; Rangel et al. 2018) have noted that phylogenetic signals leading to phylogenetic niche conservatism occur under evolutionary scenarios not unique to reduced colonization rates, such as increased extinction rates in the tropics (Pigot and Etienne 2015; Cooper et al. 2010). Our findings thus support the idea that bioregions dominated by high emigrating species can still exhibit a phylogenetic clustering signature. Specifically, our model results suggest that high clustering observed in the tropics does not require strong niche conservatism; rather, it can result from high colonization and adaptive capabilities of tropical lineages dispersing into other bioregions.

4.2 | Diversification Rates in Relation to the Phylogenetic and Diversity Latitudinal Gradient

Previous studies have emphasized the significance of tropical niche conservatism and lower extinction rates in the tropics compared to temperate bioregions as the leading causes of the latitudinal diversity gradient (Pontarp et al. 2019; Wiens and Graham 2005; Weir and Schluter 2007). However, a growing body of research is challenging the tropical niche conservatism hypothesis (Pigot and Etienne 2015) and is highlighting a lack of consensus regarding lower tropical extinction as the primary driver of the latitudinal diversity gradient (Tietje et al. 2022; Igea and Tanentzap 2020; Quintero and Jetz 2018). We observed that the latitudinal phylogenetic and diversity gradients more often emerge under a combination of higher speciation rates in the tropics compared to temperate bioregions and directional colonization from tropical to temperate bioregions (Figures 4 and S10). Therefore, our findings are in line with increasing evidence suggesting that the relationship between both speciation and extinction rates and latitudinal diversity gradients may be more complex than previously thought (Tietje et al. 2022; Weir and Schluter 2007).

Studying woody species, a keystone ecological group in terrestrial ecosystems, is challenging due to the several transitions between woody and herbaceous forms that have occurred over time (Judd et al. 1994; Smith et al. 2018; Klimeš et al. 2022). These evolutionary reversals from woody to herbaceous forms may be misinterpreted as missing tips in the phylogeny, akin to extinction events. For example, the higher rate of these transitions at lower latitudes, although tested uniquely on insular woodiness (Zizka et al. 2022), could reflect a potential bias in evolutionary rates in tropical bioregions (Smith et al. 2018). However, the frequent occurrence of bidirectional evolutionary transitions between herbaceous and woody states across different taxonomic groups (Klimeš et al. 2022), assuming they occur ubiquitously throughout the landscape, might counter this potential bias.

Notably, our simulations managed to reproduce the latitudinal phylogenetic and diversity gradients even without explicitly incorporating the historical dynamics of gymnosperm clade displacement by angiosperms at low latitudes (Figure 3). Despite the fact that we did not include complex mechanisms of clade turnover in our model, like sudden bursts of extinction, we managed to reproduce the patterns of latitudinal phylogenetic gradient. Nevertheless, we do observe that clade displacement plays a role in the observed latitudinal phylogenetic gradient (Figure 2a vs. Figure S6a,b). Interestingly, the evolutionary dynamics in the model that generate the latitudinal gradients we studied, higher tropical than temperate speciation coupled with tropical to temperate colonization, coincide with dynamics of the clade displacement of gymnosperms, whereby gymnosperms were excluded from the tropics by rapid tropical speciation of angiosperms and increased extinction of gymnosperms. Importantly, our modelling results suggest that the latitudinal phylogenetic gradient can emerge even in simplified models that do not account for the detailed evolutionary histories of whole clade speciation and extinction events.

Author Contributions

D.L. conceived the project. D.L. and G.G. designed the simulation methodology with strong contribution from J.T.W., D.L. conducted the analysis. D.L., G.G. and J.T.W. interpreted the results. D.L. wrote the first draft of the manuscript. All authors contributed to the manuscript revision and approved the final version.

Funding

This study was supported by the JNF Climate Scholarship and the Minerva Center for the Study of Population Fragmentation. TK was supported by the Henri Gutwirth research award. JTW was supported by an NSERC Discovery Grant (RGPIN-2022-04817).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and scripts used in this study are publicly available via Zenodo: https://doi.org/10.5281/zenodo.16919580.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Phyloregion of tree species, with $k = 6$ clusters. **Figure S2:** Generating phyloregions under a conserved filtering constrain. Generating phyloregion patterns of tree species, when accounting only for cells containing more than 30 species. (a) Phyloregion map distribution with $k = 5$ clusters (b) Proportion of overlap between each ecological biome and phyloregions, compared to a randomized phyloregion bootstrap. The heatmap shows the natural logarithm of the ratio between the actual overlap and the bootstrap overlap, with yellower colours signifying higher than random overlap. Statistical significance of high overlap is marked with an asterisk ($p < 0.01$). (c) Phylogenetic diversity of each of the phyloregions, measured as SES-MPD Z-scores. **Figure S3:** Phyloregion taxonomic composition. (a) Phylogenetic tree of woody-species genera used to compute phyloregions, subdivided between gymosperms and angiosperms. Outer layers represent the presence or absence of each genus (phylogenetic tip) within each of the phyloregions. (b) Difference between observed and expected presence of the taxonomic groups in each of the phyloregions, as a function of the total occupancy of genus/phyloregion. **Figure S4:** Community relationship among phyloregions. PCoA plot of the distance matrix between phyloregions measured using Sørensen's β-diversity index. **Figure S5:** Phylogenetic diversity measured as SES−MPD along the biomes. Corresponding mean phylogenetic distance (SES-MPD, *Z*-score). Phyloregions with SES-MPD *Z*-scores < -1.96 (red dots) have a significant phylogenetic clustering of tree species, phyloregions with SES-MPD *Z*-score > 1.96 (black dots) have significant phylogenetic over-dispersal of tree species. **Figure S6:** Phylogenetic diversity measured as SES−MPD when accounting only the distribution of angiosperms (excluding gymnosperms). (a) Corresponding mean phylogenetic distance (SES-MPD, *Z*-score). Phyloregions with SES-MPD *Z*-scores < -1.96 (red dots) have a significant phylogenetic clustering of tree species, phyloregions with SES-MPD *Z*-score > 1.96 (black dots) have significant phylogenetic over-dispersal of tree species. (b) Phylogenetic diversity of the phyloregions accounting only for angiosperms. Phylogeneric diversity is missing forphyloregion 3 given that this phyloregion had no cell that overcome the minimal threshold of 30 genera per cell (c) Distribution of genera richness per cell across major phyloregion groups for the full dataset and the angiosperm-only dataset when accounting for $n > 5$ filter and $n > 30$ filter. The text above each boxplot reports the number of cells retained under the corresponding richness threshold for the full and the angiosperm-only datasets. **Figure S7:** Distribution of SES-MPD values across 100 rarefied permutations of the full genera dataset and the dataset selecting only angiosperms, in which 30 genera were randomly sampled from each retained cell before calculating SESMPD. Points show the mean SES-MPD for each phyloregion across permutations, and error bars represent one standard deviation. **Figure S8:** Phylogenetic and climatic niche conservatism F-1, Precision and Recall rates for (a) each cluster of phyloregions and (b) for each phyloregion

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from a random forest model. (c) F1 performance under a spatial blocking for a global model (including environmental predictors and geographic coordinates—latitude and longitude) and for the environmental model (excluding geographic coordinates). The third panel shows macro-F1 values across the spatial-block validation folds, representing the average F1 score across phyloregion classes. Error bars indicate standard deviation across validation folds. **Figure S9:** Scenarios in which latitudinal gradients emerge. The proportion of the simulations for which the latitudinal diversity gradient (Condition 1), the latitudinal phylogenetic gradient (Condition 2) and a combination of both emerged for each type of colonization dynamic under varying threshholds of MPD values, where the highest X% of tropical MPD values and the lowest X% of temperate MPD values were selected. **Figure S10:** Proportion of simulations where a range of parameters enable the expected output for the latitudinal phylogenetic and diversity gradients to occur. The extinction rates (μ) shown are the proportions of speciation rates (λ). **Figure S11:** Histograms showing the sizes of the phylogenetic trees generated from the models with and without a bridge phyloregion.

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