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Community dissimilarity of angiosperm trees reveals deep-time diversification across tropical and temperate forests

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Abstract

Question: To better understand the influence of deep-time diversification on extant plant communities, we assessed how community dissimilarity increases with spatial and climatic distances at multiple taxonomic ranks (species, genus, family, and order) in angiosperm trees. We tested the prediction that the dissimilarity–distance relationship should change across taxonomic ranks depending on the deep-time diversification in different biogeographical regions reflecting geohistories and geographical settings.

Location: Global.

Methods: Using a data set of plot-based surveys across the globe (861 plots), we compiled a community composition matrix comprising 21,455 species, 2,741 genera, 240 families, and 57 orders. We then calculated Sørensen's pairwise dissimilarity (β_{sor}), and its turnover (β_{sim}) and nestedness (β_{sne}) components, among plots within seven biogeographical regions. Finally, we modeled the relationships between the biotic dissimilarities and the spatial/climatic distances at each taxonomic rank, and compared them among regions.

Results: β_{sor} and β_{sim} increased with increasing spatial and climatic distance in all biogeographical regions: β_{sim} was dominant in all biogeographical regions in general, while β_{sne} showed relatively high contributions to total dissimilarity in the temperate regions with historically unstable climatic conditions. The β_{sim}-distance curve was more saturated at smaller spatial scales in the tropics than in the temperate regions. In general, the curves became flatter at higher taxonomic ranks (order or family), with the exception of Africa, North America, and Australia, pointing to region-specific geographical constraints.

Conclusions: Compositional dissimilarity was generally shaped through the abrupt turnover of species along spatial/climatic gradients. The relatively high importance of the nestedness component in the temperate regions suggests that historical dispersal filters related to extinction/colonization may play important roles. Region-specific

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changes in the turnover and nestedness components across taxonomic ranks suggest differential imprints of historical diversification over deep evolutionary time in shaping extant diversity patterns in each biogeographical region.

KEYWORDS

angiosperm trees, beta diversity, biogeographical regions, dispersal limitation, dissimilarity decomposition, distance decay, environmental filtering, taxonomic diversity

1 | INTRODUCTION

The similarity in species composition between local biological communities decreases with spatial/environmental distance. This pattern, known as distance decay of similarity or simply distance decay, is ubiquitous across organisms and biological systems (Nekola & White, 1999; Soininen et al., 2007). The decrease of similarity with distance is mechanistically driven by dispersal limitation (Hubbell, 2001) and niche constraints (Gilbert & Lechowicz, 2004), mediated through contemporary environmental gradients and evolutionary diversification. Indeed, there are a number of empirical studies that have applied a distance decay approach to answer different questions related to community assembly processes: niche partitioning along current environmental gradients (Bellier et al., 2014; Trujillo et al., 2019; Cacciatori et al., 2020), historical species sorting through dispersal of organisms (Qian, 2009; Saito et al., 2015), dispersal barriers related to geographical constraints (Stuart et al., 2012), differences in dispersal ability among taxa (Gómez-Rodríguez & Baselga, 2018; Gómez-Rodríguez et al., 2020) and historical habitat stability (Fitzpatrick et al., 2013). A common theme linking these studies is their use of the shape of distance decay curves as a measure to infer the role of historical and contemporary factors in generating diversity patterns under study (Morlon et al., 2008; Réjou-Méchain & Hardy, 2011; Gómez-Rodríguez & Baselga, 2018). Rooted in this approach, we here propose that assessing distance decay patterns at multiple taxonomic ranks (species, genus, family, and order) will allow inferring the influence of deep-time diversification on extant plant communities, and its contrasting relevance in tropical and temperate biogeographical regions.

Angiosperm tree floras in tropical and temperate regions are regarded as evolutionary source and sink, respectively. Many clades that now comprise the tropical flora have been hypothesized to have originated in western Gondwana, which was part of the supercontinent that contained South America and Africa (Fine & Ree, 2006; Christenhusz & Chase, 2012), and subsequently diversified, after crossing long-standing geographic barriers, among the continents through the Eocene, Oligocene, and Miocene (Hardy et al., 2012). In temperate areas, many extant lineages are thought to have originated from the Asian tropical flora (Wen, 1999; Donoghue, 2008) and afterward have regionally diversified in East Asia, Northern America, and Europe in response to the Plio–Pleistocene global cooling (Fine & Ree, 2006). Macroscale diversity patterns of angiosperm trees are characterized by evolutionary radiations within disjunct families/genera in tropical and temperate forests (Gentry, 1988; Donoghue & Smith, 2004) and taxon-specific selective dispersal/extinction related to paleoclimate changes in temperate regions (Svenning, 2003; Eiserhardt et al., 2015).

The afore-mentioned studies suggest that the study of taxonomic diversity across lower (species) to higher taxonomic ranks (genus, family, and order) could provide a fundamental basis for better understanding deep-time diversification related to geohistory including paleoclimates. Indeed, correlations of species richness within a higher taxonomic group (family or order) among continents have been shown to represent a consistent biogeographical pattern resulting from diversification at different evolutionary time scales and related to family-specific niche conservatism and global-scale dispersal (Chen et al., 2012; Munoz et al., 2012; Ricklefs & Renner, 2012). Therefore, we propose that assessing the distance decay curves of tree angiosperm communities at a range of taxonomic ranks, which provide a surrogate for a macroevolutionary hierarchy (Graham et al., 2018), should reveal any historical imprint on current spatial diversity patterns (Munoz et al., 2014; Yeh et al., 2019). Specifically, regional differences in deep-time diversification should be reflected in the geographical distribution of higher-rank taxa, such as genera, families or orders, through processes such as niche conservatism and dispersal limitation (Kerkhoff et al., 2014; Weiser et al., 2018).

While similarity indices are commonly used in distance decay studies (Nekola & White, 1999), compositional dissimilarity (i.e., 1 − similarity) metrics can describe the equivalent patterns and some of these metrics can be partitioned into turnover and nestedness-resultant components (Baselga, 2010; Legendre, 2014; Soininen et al., 2017). The turnover component represents taxonomic replacement that may be caused by species sorting associated with niche differentiation, evolutionary processes such as radiation and allopatric speciation, and/or dispersal limitation (Leibold et al., 2004; Leprieur et al., 2011). The nestedness component reflects changes in species richness caused by selective species loss or gain that may be associated with recent vicariance events, e.g., insular changes by sea-level rise (Rijsdijk et al., 2014), or a colonization lag after drastic environmental changes such as ice age disturbances (Hortal et al., 2011). Therefore, each component is expected to have an independent relationship with geographical and environmental distance (Antão et al., 2019; Bevilacqua & Terlizzi, 2020), and their relative

importance may change depending on historical habitat stability (Baselga et al., 2012). The turnover component can be expected to have a steep slope and an asymptotic relationship with spatial distance under strong dispersal limitation, while a flatter relationship would be observed when dispersal limitation is weak or absent (Gómez-Rodríguez et al., 2020). The nestedness component is expected to linearly decrease with increasing spatial/environmental distance under strong dispersal limitation, but to be independent of distance under no dispersal limitation (Gianuca et al., 2016; Antão et al., 2019).

Using a global dataset of forest plots (861 plots), we quantified pairwise compositional dissimilarity of angiosperm tree communities at different taxonomic ranks (species, genus, family, and order) in seven biogeographical regions (South American, African, Indo-Pacific, Australian, North American, West Eurasian, and East Eurasian). We compared the relationship between compositional dissimilarity and spatial/climatic distance (i.e., dissimilarity–distance relationship) between the biogeographical regions and between the taxonomic ranks in order to explore the effect of deep-time diversification on the spatial patterns of extant tree communities. Based on the afore-mentioned reasoning, we tested the following predictions: (a) taxonomic turnover will be the dominant component of dissimilarity in historically stable regions (Baselga et al., 2012), such as regions that contain tropical areas; (b) in contrast, the nestedness component will be predominant in historically unstable regions (e.g., temperate areas in higher latitudes) that have experienced extinction and colonization events in response to the expansion/retreat of ice sheets due to paleo-climate changes (Baselga et al., 2012; Soininen et al., 2017); (c) the relationship between the turnover component and spatial/climatic distance will be very steep at short distances, quickly saturating at maximum dissimilarity at the species level due to strong dispersal limitation, while the relationship will become flatter at higher taxonomic ranks. This flattening should be more marked in the regions containing tropical areas because of the older evolutionary age of tropical areas, which should have allowed higher-level taxa to spread across wider areas (i.e., lower dispersal limitation); (d) however, the steep relationship between the turnover component and spatial/climatic distances should remain asymptotic even at higher taxonomic ranks (Cowling et al., 2015) if climatic gradients and/or vicariance have been maintained over large time periods; and (e) the nestedness component should show a negative linear relationship with spatial/climatic distance at the species level in historically unstable regions, but be independent from the distances at higher taxonomic ranks due to less dispersal limitation.

2 | METHODS

2.1 | Angiosperm tree community data

Community composition data of angiosperm tree species were collated from a series of plot-based surveys across the globe (Ulrich et al., 2016; Kubota et al., 2018). The data were compiled from a literature census using various search engines, including Web-of-Science (Thomson-Reuters, New York, NY, USA) and Google Scholar (http://scholar.google.com/), and web-based forest plot databases (e.g., Gentry's data; www.wlbcenter.org/gentry_data.htm). Our dataset only includes plots where the absolute number of individuals was recorded for all tree species at a given census threshold in individual size (i.e., diameter at breast height). The taxonomic classification (species, genus, family, and order) was standardized following The Plant List (http://www.theplantlist.org/). Unnamed species and morphospecies identified only to genus were treated as individual species (we confirmed that excluding these species did not meaningfully affect the results of the dissimilarity–distance analyses). We excluded naturally/artificially disturbed plots and plots with less than two angiosperm tree species. We also excluded gymnosperms (163 species) from the data. The final dataset comprised 861 plots (range = 100–520,000 m^2; Figure 1). Using all plots, we created community composition matrices for four taxonomic ranks: species (21,455 species), genus (2,741 genera), family (240 families), and order (57 orders). We then subdivided each matrix into seven biogeographical regions. We defined the biogeographical regions using a modified version of Cox et al.'s floral Kingdoms (South American, African, Indo-Pacific, Australian, and Holarctic; Cox, 2001): we subdivided the Holarctic Kingdom into North American, West Eurasian and East Eurasian (Figure 1) because of differences in their geohistory and paleoclimatic conditions. The South American, African, Indo-Pacific, and Australian regions include tropical areas, while the North American, West Eurasian and East Eurasian are temperate areas. In this study, we avoided a more detailed regionalization (e.g., ecoregions) because of the limited number of plots and their spatially inhomogeneous distribution (Figure 1). More details of the data compilation process are provided in Ulrich et al. (2016) and Kubota et al. (2018).

Community undersampling is a potential problem in dissimilarity analyses (Beck et al., 2013), especially in cases such as ours where data are taken from multiple sources that have used different census schemes (e.g., plot area and the size criterion for measuring individuals). Therefore, the plots were screened based on sampling completeness: we estimated sample coverage (SC) based on relative species abundance, which is an unbiased estimate represented by the proportion of all detected individuals (Chao et al., 2020): SC values are in the range 0 to 1. We filtered the plots at SC ≥ 0.9 (n = 661; Figure 2) and also examined other criteria (≥0.7, ≥0.8, and ≥0.85) to test the potential influence of arbitrary choices of SC thresholds. SCs filtered out the incompletely sampled plots which cannot be distinguished by plot areas or census thresholds, allowing us to include the local communities which were equivalently well sampled (Appendix S1). Differences in plot areas and census thresholds are particularly likely to influence absolute abundance differences among the plots (Baselga, 2013). Therefore, we used presence/absence information in the dissimilarity analyses.

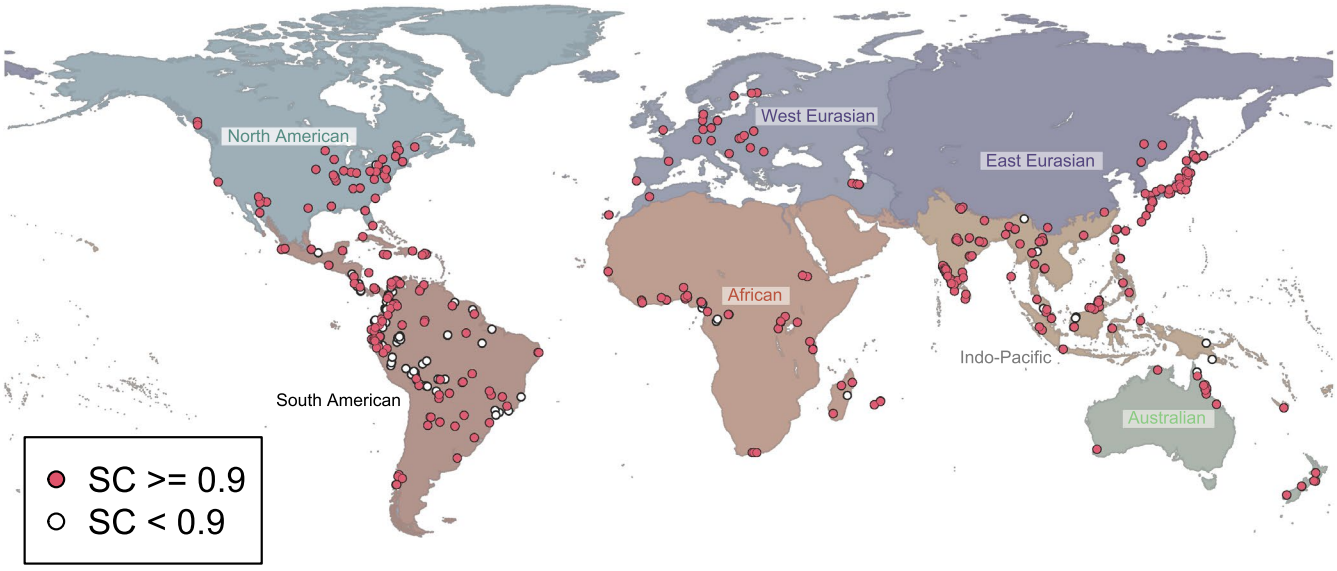

FIGURE 1 The global distribution of forest plots across seven biogeographical regions: South American, African, Indo-Pacific, Australian, North American, West Eurasian, and East Eurasian. Plots were colored by sample coverage (SC)

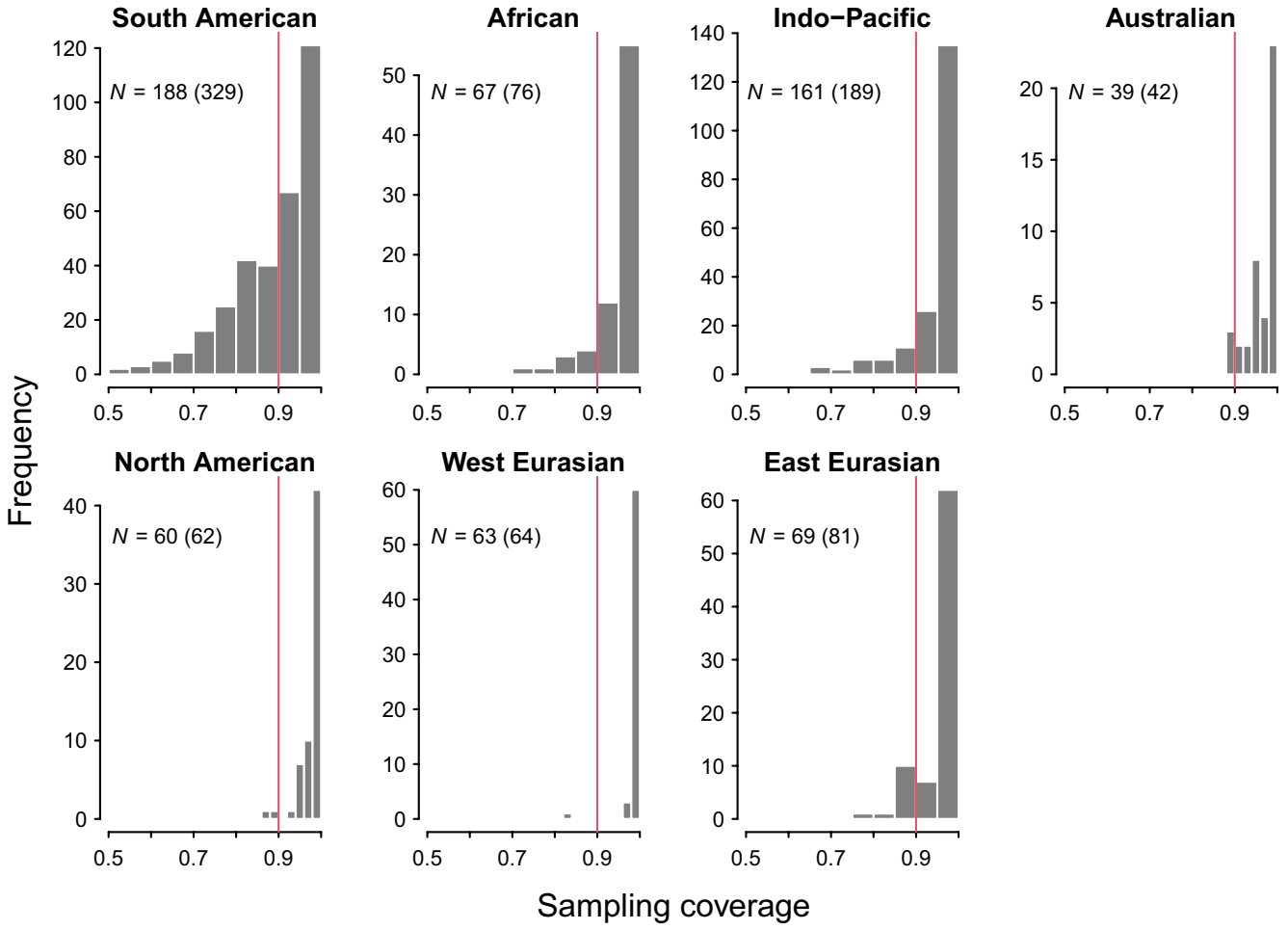

FIGURE 2 Histograms for sampling completeness evaluated as sample coverage (SC) per community in seven biogeographical regions (South American, African, Indo-Pacific, Australian, North American, West Eurasian, and East Eurasian). The equivalently well-sampled plots (SC ≥ 0.9) were used in the dissimilarity–distance analyses

2.2 | Dissimilarity calculation

Using the subset of equivalently well-sampled plots (SC ≥ 0.7, 0.8, 0.85, or 0.9), we calculated pairwise dissimilarity between plots within the same biogeographical region (Figure 1) for each taxonomic rank (species, genus, family, and order). We followed Baselga's (2010) beta diversity partitioning framework based on Sørensen dissimilarity (β_{sor}), which was decomposed into turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{sne}) components. The compositional dissimilarity of lower taxonomic ranks is inevitably influenced by the dissimilarity of higher taxonomic ranks due to the ranks being hierarchically structured: β_{sne} should be higher at higher taxonomic ranks, while β_{sim} should be higher at lower (e.g., species) taxonomic ranks. Before analyzing dissimilarity–distance relationships, we assessed whether the influence of deep-time diversification on beta diversity is region-specific or not by evaluating correlations between the dissimilarity matrices at different taxonomic ranks for each dissimilarity component ($\beta_{sor,}$ β_{sim}, and β_{sne}) in each biogeographical region.

2.3 | Spatial and climatic distances

Spatial distance was defined by the great-circular distance between each pair of plots. We downloaded climatic (Bio-1–19) and elevation data at 30-arc-second resolution from the WorldClim ver. 2.1 database (Fick & Hijmans, 2017; http://www.worldclim.org), overlapped them with the plot coordinates, and assigned the information to each plot. To analyze the effect of climatic distance, we calculated the Euclidean distance in the 20-dimensional space between plots using the variables after standardization (i.e., mean = 0 and variance = 1).

2.4 | Statistical analysis

We modeled the relationship between pairwise compositional dissimilarity (β_{sor}, β_{sim}, and β_{sne}) and spatial/climatic distance (i.e., the dissimilarity–distance curve) in each region and for each taxonomic rank using both negative exponential and power-law functions (Nekola & McGill, 2014); these functions were fitted using a generalized linear modelling approach with a Gaussian distribution and a log-link function (Millar et al., 2011). Model fit was evaluated using pseudo-r^2 defined as 1 − (model deviance/null deviance; McFadden, 1973). The two functions provided similar fits to the data according to Akaike's Information Criterion (Appendix S2), and thus, we only present results for the negative exponential model in the main text (see Appendix S3 for the results using the power-law model). In the negative exponential model, the intercept and slope can be interpreted as the initial dissimilarity (inherent compositional variation among the closest local communities) and the speed of compositional change (or rate of decay), respectively. We tested for differences in the intercepts and slopes of the negative exponential model between biogeographical regions by bootstrapping (multiple comparisons among each pair of regions): we computed 1,000 bootstrap samples for each parameter, calculated the difference in parameter values between two regions, calculated the proportion of positive and negative differences respectively, and used the smaller of these (i.e., upper or lower tails) proportions as a *P*-value. We also assessed the influence of SC thresholds (SC = 0.7 ~ 0.9) on the parameter estimation by evaluating the inter-regional rank correlations for the effect size of parameters between the different SC thresholds. In addition, we fitted a locally estimated scatterplot smoothing curve to visualize changes in the relative importance of the turnover component to overall dissimilarity (β_{sim}/β_{sor}) along the spatial/climatic distance gradients.

All statistical analyses and graphical works were undertaken using R ver. 3.6.1 (R Core Team, 2019) and the following packages: *betapart* (Baselga & Orme, 2012) to calculate and decompose pairwise compositional dissimilarity, *geosphere* (Hijmans, 2019) to calculate spatial distance, *iNEXT* (Hsieh et al., 2016) for calculating the sampling completeness of each plot, and *multcompView* (Graves et al., 2019) for multiple comparisons.

3 | RESULTS

The parameters (especially slopes) of the negative exponential models at lower SC thresholds (0.7–0.85) differed from those estimated using SC ≥ 0.9, particularly for the climatic distance model (Appendix S4). The inter-regional ranking of effect size was consistent for the spatial distance models (i.e., Spearman's rank correlation $\rho = 1$), whereas change in the order was observed in the climatic distance model ($\rho = 0.75 \sim 1.00$). Therefore, we only show the results using the most strict criterion (SC ≥ 0.9) for all subsequent analyses.

Total dissimilarity (β_{sor}), the turnover component (β_{sim}), and the nestedness component (β_{sne}) showed strong correlations between the taxonomic ranks, but with substantial variation in degree between the regions (Appendix S5), indicating the influence of region-specific deep-time diversification on shaping turnover/nestedness-resultant beta diversity.

3.1 | Total dissimilarity and spatial distance

Between sites, β_{sor} increased with increasing spatial distance and this finding was consistent within all biogeographical regions (Figure 3). The negative exponential model provided a relatively good fit to the dissimilarity–distance pattern at the species level (r^2 = 0.34 − 0.74), but the amount of explained variance generally decreased along taxonomic ranks from genus to order (Figure 4; r^2 = 0.08–0.66 for genera; r^2 = 0.01–0.55 for families; $r^2 \leq$ 0.01–0.43 for orders). The intercept and slope of the negative exponential model became smaller at higher taxonomic ranks (Appendices S6 and S7).

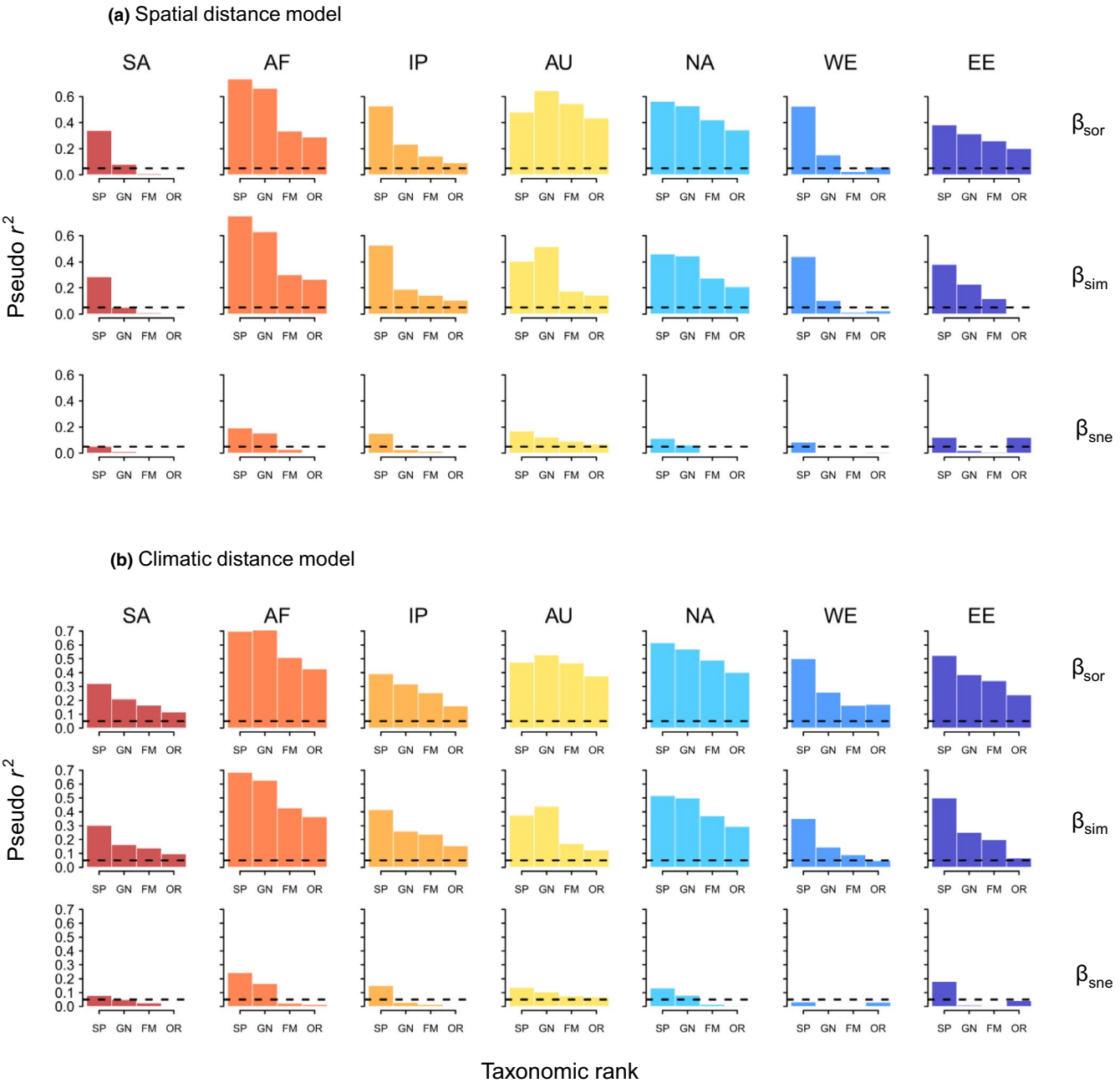

FIGURE 3 Pseudo-r^2 of negative exponential models for the relationships between taxonomic dissimilarity and (a) geographical and (b) climatic distance per taxonomic rank [species (SP), genus (GN), family (FM) and order (OR)] in each biogeographical region: South American (SA), African (AF), Indo-Pacific (IP), Australian (AU), North American (NA), West Eurasian (WE) and East Eurasian (EE). Total dissimilarity matrices (β_{sor}) were decomposed into turnover (β_{sim}) and nestedness (β_{sne}) components. Dashed line represents 5% for a visual guide

3.2 | Relationships between turnover and nestedness-resultant components and spatial distance

The spatial patterns of β_{sim} were well characterized by the negative exponential model, especially at the species level (Figure 3a), and exhibited an asymptotic increase with spatial distance (Figure 4). In all geographical regions except for sites near to each other in the West Eurasian region, β_{sim} was the predominant component of β_{sor} (Figure 5), but the relative importance of β_{sim} decreased along the taxonomic ranks from genus to order. The intercept and slope of the β_{sim}–distance curve were smaller in the temperate regions (North American, West Eurasian, and East Eurasian) where the β_{sim} slowly saturated over the entire geographical extent at the species level (Appendices S6 and S7). In contrast, the intercept and/or slope of the β_{sim}–distance curve was larger in the regions containing tropical areas (South American, African,

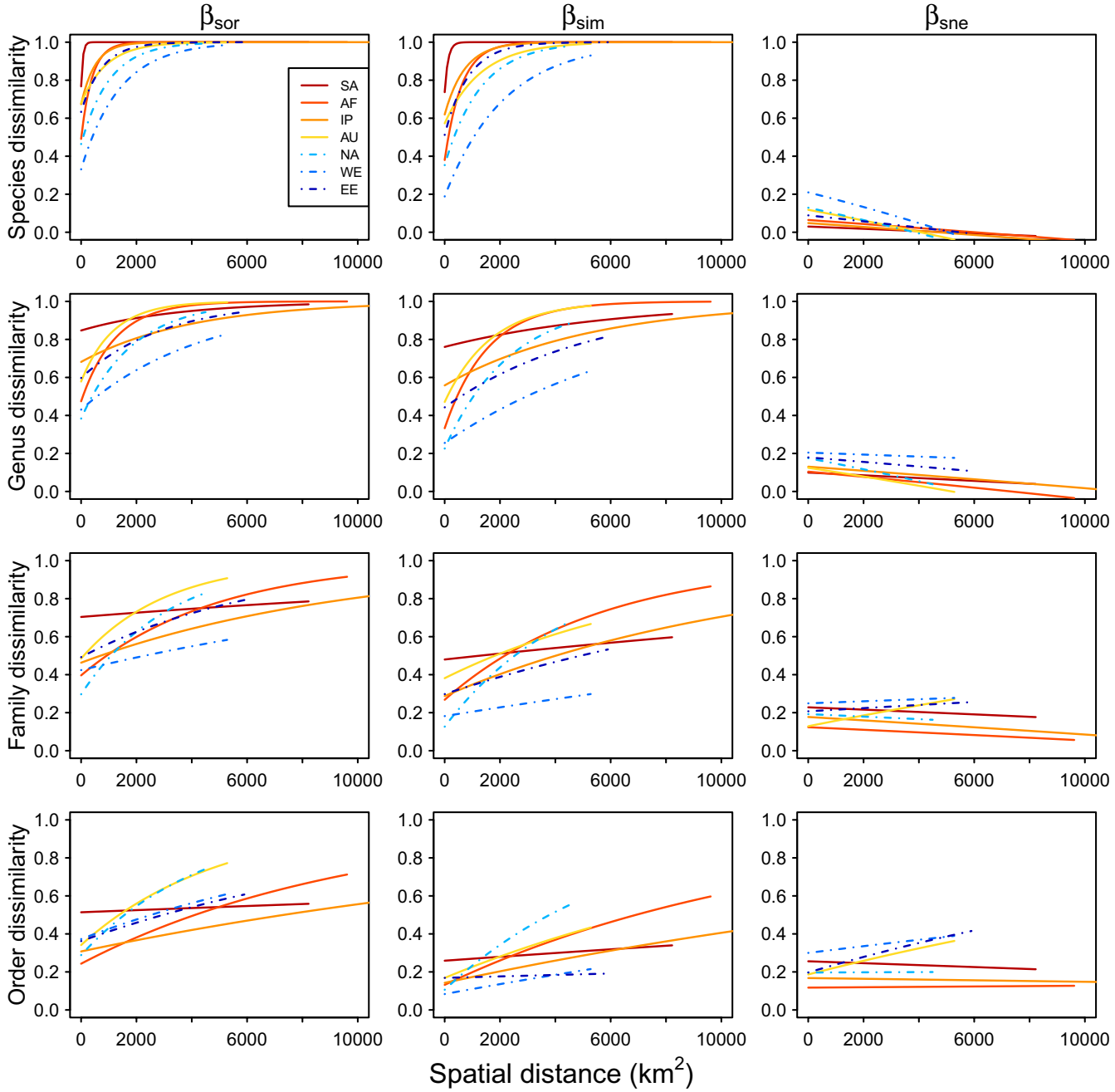

FIGURE 4 The relationship between pairwise dissimilarity and spatial distance (dissimilarity–distance relationship) as fitted by a negative exponential model using presence/absence composition data at the species, genus, family and order levels, in each biogeographical region: South American (SA), African (AF), Indo-Pacific (IP), Australian (AU), North American (NA), West Eurasian (WE) and East Eurasian (EE). Total dissimilarity matrices (β_{sor}) were decomposed into the turnover (β_{sim}) and nestedness-resultant (β_{sne}) components

and Indo-Pacific) where the β_{sim} at species level saturated at a smaller geographical extent (Figure 4). The β_{sim} values became lower, and the shape of the curve became flatter, at higher taxonomic ranks in the South American and Indo-Pacific regions (Figure 4). In contrast, the slope of the curve was relatively steep even at the family and order levels in the African, Australian, and North American regions (Figure 4 and Appendix S7).

The negative exponential model poorly explained β_{sne} (Figure 3a); the relationship between β_{sne} and spatial distance was mostly flat, while a negative linear relationship was found at the species level in the Holarctic regions, especially in West Eurasian (Figure 4 and Appendix S7). At the species level, β_{sne} accounted for a major proportion of β_{sor} only within sites near to each other in the Holarctic regions (Figure 5). However, the relative importance of β_{sne} increased

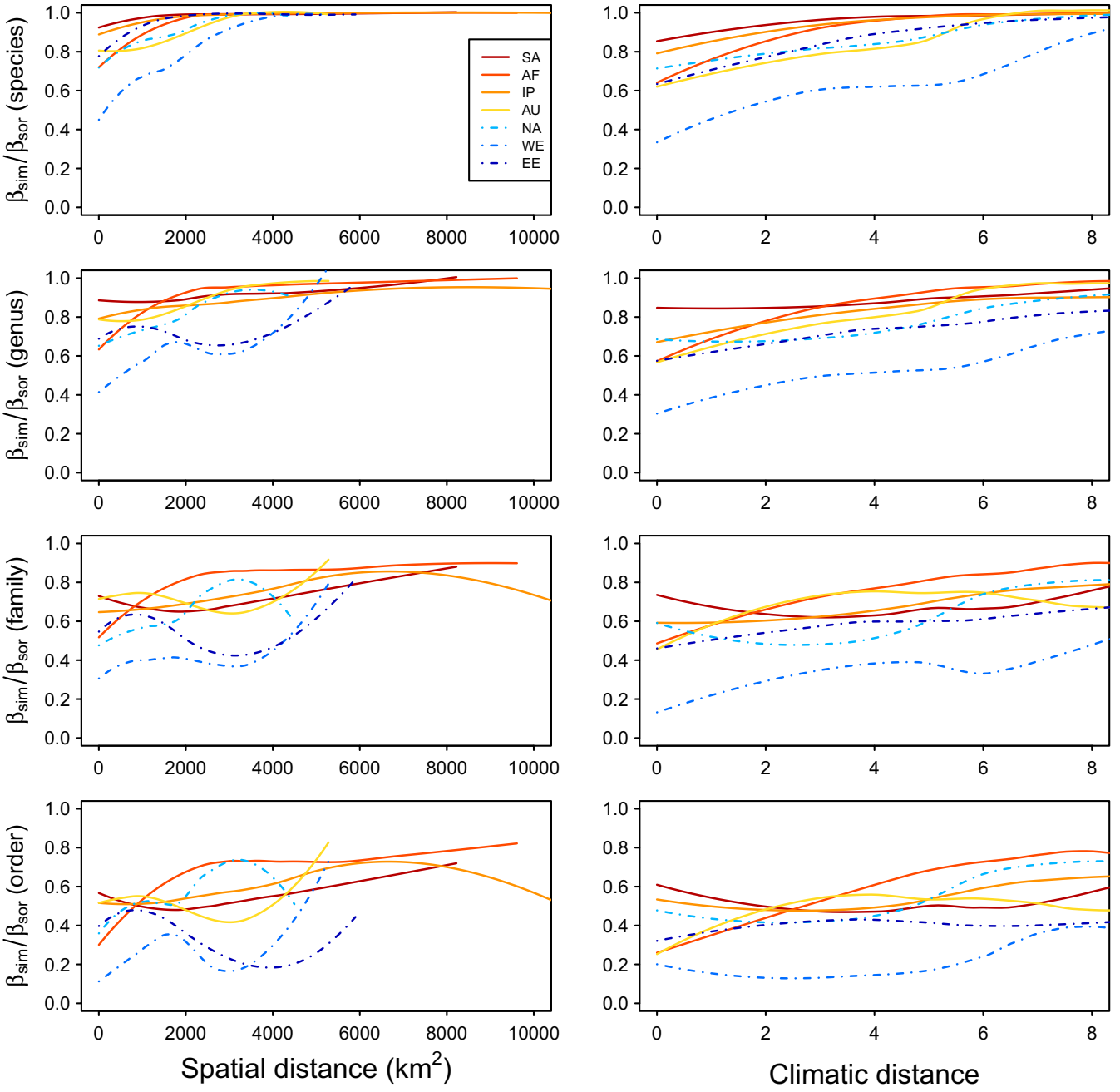

FIGURE 5 Changes in the relative importance of the turnover component to total dissimilarity (β_{sim}/β_{sor}) along geographical (left) and climatic (right) distance per taxonomic rank [species (SP), genus (GN), family (FM) and order (OR)] in each biogeographical region: South American (SA), African (AF), Indo-Pacific (IP), Australian (AU), North American (NA), West Eurasian (WE) and East Eurasian (EE). Climatic distance is calculated as the Euclidian distance between sites based on 19 bioclim variables and elevation. Locally estimated scatterplot smoothing curves (LOESS) are shown

at higher taxonomic ranks even in the regions containing tropical areas, especially in the South American region (Appendix S6).

3.3 | Relationships between taxonomic dissimilarity and climatic distance

In general, the increase in pairwise taxonomic dissimilarity (β_{sor}, β_{sim}, and β_{sne}) with climatic distance was similar to that observed with spatial distance (Appendices S8–S10). The negative exponential models fitted using climatic distance had slightly better explanatory power than the models fitted using spatial distance for most regions and ranks, but provided worse fits at the species and genus levels in the Indo-Pacific, African, West Eurasian, and Australian regions (Figure 3). In all regions, β_{sor} and β_{sim} exhibited steep slopes and quick asymptotic saturation at the species level, while the saturation was relatively slower in Australian and the temperate regions compared to the South American, African

and Indo-Pacific regions (all containing tropical areas; Appendix S8). The slope of the β_{sim}–distance curve was smaller at higher taxonomic ranks, but it remained relatively high even at the family and order levels in the African and North American regions (Appendices S8 and S10). The relative importance of β_{sim} to β_{sor} increased with the climatic distance, especially in the West Eurasian region at the species level, while the pattern was less clear at the family and order levels (Figure 5).

4 | DISCUSSION

Our results reveal substantial differences in patterns of variation in local angiosperm tree communities across different biogeographical regions, with contrasting effects of deep-time processes of diversification between the biogeographical regions with and without tropical areas. The overall dissimilarity of angiosperm communities between forest plots was found to increase with spatial and climatic distance (a distance decay pattern) in all biogeographical regions, and was mainly driven by the turnover component at lower taxonomic ranks (species and genus), although its relative contribution decreased at higher taxonomic ranks (family and order). However, these patterns showed region-specific variations. The regions containing tropical areas (South American, African, and Indo-Pacific) showed steeper increases in total dissimilarity and the turnover component with spatial/climatic distances compared with the temperate regions (North American, West Eurasian, and East Eurasian), while the Australian region showed intermediate trends (Figure 4, Appendices S7, S8, and S10).

The fast increase in dissimilarity in regions with tropical areas was mostly associated with the turnover component, indicating a fast compositional replacement along spatial and climatic distance gradients, especially at the species level. This is in line with previous studies of tropical forests (Condit et al., 2002; Tuomisto et al., 2003; Pennington et al., 2009; Trujillo et al., 2019) that found an important role of environmental filtering and dispersal limitation in generating species turnover. The decreasing compositional dissimilarity with increasing taxonomic rank (from species, genus, family to order) and the flattening of the dissimilarity–distance curves may reflect the deeper evolutionary history of tropical forests (Munoz et al., 2014). Specifically, orders and families of angiosperm trees probably radiated globally across phylogenetic niche space (Hubbell, 2001) under warmer climates through the Cretaceous to the Paleogene, and then subsequently species and genera within those regions diversified in response to different drivers, including geographical isolation and tropical-specific historical habitat stability through the Cenozoic (Fine & Ree, 2006). Indeed, our results showed the highest species turnover rates in the South American region (Figure 4), providing support for the view of the region as an evolutionary "engine" of plant diversity (Antonelli et al., 2015). Moreover, the turnover–distance relationships were flatter at the higher taxonomic ranks, suggesting that the persistence or accumulation (dispersal) of old lineages (Coronado et al., 2015) plays a role in generating the high degrees of overall dissimilarity across the taxonomic ranks (Pennington et al., 2009). This interpretation is also supported by the higher contribution of the nestedness component at the family and order levels in the South American region than in the other regions (Figures 4 and 5). Meanwhile, some regions (e.g., African, Australian, and North American regions), regardless of whether they include tropical areas, exhibited a persistent steep dissimilarity–distance curve regarding the turnover component (Appendix S7), at both the family and order levels. This suggests taxonomic diversification at deeper time scales (Prinzing et al., 2001) and/or the persistence of different and older lineages in isolated sites (Tiffney & Manchester, 2001; Tolley et al., 2011) as a result of geohistorically related biogeographical constraints, e.g., elevational gradients in the tropics (Qian & Ricklefs, 2016) or climatic refugia (Tiffney & Manchester, 2001; Byrne, 2008; Tolley et al., 2011).

In contrast, the North American and both West and East Eurasian regions, comprising temperate floras, showed a slower saturation in total dissimilarity and the turnover component with spatial and climatic distances, and a relatively higher contribution of the nestedness component in shaping the dissimilarity patterns of angiosperm tree communities than in the remaining regions, all of them containing tropical areas (Figure 3, Appendices S6 and S7). In addition, the nestedness component was less dependent on either spatial or climatic distance in these regions. These findings are consistent with the findings of previous studies of the temperate biota (Keil et al., 2012; Lenoir et al., 2012; Fitzpatrick et al., 2013; Soininen et al., 2017; Antão et al., 2019), which suggest that the nestedness component reflects the signal of historical processes that become more evident under unstable and harsh environmental conditions in higher latitudes (Baselga et al., 2012). Indeed, temperate angiosperm tree assemblages have been shown to have experienced genus level local extinction in response to Quaternary glaciations and/or global cooling in the Holarctic regions (Svenning, 2003; Eiserhardt et al., 2015; Shiono et al., 2018), supporting the role of historical dispersal filters in shaping the nestedness-resultant dissimilarity of angiosperm tree communities in temperate forests.

In general, the negative exponential models fitted using spatial and climatic distance had comparable explanatory power and were similar in terms of the shape of the dissimilarity–distance curves (Figures 3 and 4, and Appendix S8), suggesting that environmental filtering and/or dispersal limitation have important roles in driving compositional turnover (Trujillo et al., 2019). However, a relatively lower explanatory power for the climatic distance model (i.e., it explained 11% less variance than the spatial distance model) was observed in the Indo-Pacific region at the species level (Figure 3). This suggests that taxonomic turnover in this region is likely to be driven by dispersal limitation and/or other geographical factors, such as the spatial separation between islands and continental landmasses, and variation in island sizes (Ibanez et al., 2018). Moreover, the Indo-Pacific tropical forests are phylogenetically similar to the East Eurasian temperate forests (Kubota et al., 2018), suggesting the regional divergence of the temperate flora originating from the Asian tropics (out-of-Asia hypothesis; Donoghue, 2008). Therefore, in the East Eurasian region, the highest contribution

of the turnover component compared with the other Holarctic regions (Figures 4 and 5, Appendices S6 and S7) may also be promoted by in situ diversification of angiosperm trees through geographical vicariance related to high insularity and highly dissected topography (Xiang et al., 2004; Kubota et al., 2014).

One potential caveat of analyzing assemblage dissimilarity between local plots is that species occurrence data obtained in vegetation plots might potentially suffer from sampling incompleteness (Beck et al., 2013). To deal with sampling bias, we computed sampling completeness using species relative abundance in individual plots (Chao et al., 2020) and assessed the spatial patterns of taxonomic dissimilarity by only analyzing nearly completely sampled plots (sampling completeness ≥ 90%). Loosening of the SC threshold down to 70% did not alter the general dissimilarity trends (Appendix S4), but it did cause a slight reduction in the slope of the dissimilarity–spatial distance curve in some regions. This suggests that including incomplete plots in which common species are likely to be well sampled but rare species are likely to be missed may overestimate similarity among local communities. Another potential bias is related to the shortfall of taxonomic knowledge, especially at higher taxonomic levels (family or order). Indeed, the taxonomic resolution of lineages differs among clades and regions, and in particular, is poorly resolved for the tropics (Laffan, 2018). For example, in Malesia, it is estimated that only 29% (of approximately 45,000) vascular plant species have been comprehensively treated taxonomically in the Flora Malesiana, and while there are additional taxonomic publications and treatments for this region, these are fragmented and overall the flora very much remains incompletely known and described (Middleton et al., 2019). From the viewpoint of filling gaps in our knowledge of plant biodiversity, further taxonomic and systematic studies are needed to better understand the relative role of evolutionary events at different time scales in shaping the taxonomic dissimilarity of woody angiosperms globally.

5 | CONCLUDING REMARKS

As with many macroecological patterns, the increase in dissimilarity with distance can be studied at multiple spatial scales (Nekola & White, 1999; Wang et al., 2011; Fitzpatrick et al., 2013; Olivier & van Aarde, 2014; Chun & Lee, 2017; Kasel et al., 2017; Trujillo et al., 2019). There have been many studies focused on the dissimilarity–distance pattern of vegetation that measure beta diversity at different spatial extents, from local scales (Morlon et al., 2008; Wang et al., 2011; Wang et al., 2018) through to regional (Condit et al., 2002; Tuomisto et al., 2003) and global scales (Fitzpatrick et al., 2013; König et al., 2017). Despite these previous studies of beta diversity at local, regional and global scales, there are few examples of studies that use local community data to analyze large-scale dissimilarity patterns (but see Myers et al., 2013; Kubota et al., 2018). In addition, beta diversity patterns at multiple taxonomic scales were unexplored, even though it is potentially informative to understand the imprints of deep-time diversification on extant diversity patterns. The present study contributes to filling this knowledge gap by showing how pairwise taxonomic dissimilarity and its components (calculated within biogeographical regions) at different taxonomic ranks change across biogeographical regions through the analysis of local tree communities across the globe. Our findings of taxonomic dissimilarity among angiosperm tree communities, which showed region-specific variations in the dissimilarity–distance relationships across taxonomic ranks, reveal the geographical pattern of diversification that is mechanistically driven by niche assembly at higher taxonomic ranks (Ricklefs & Renner, 2012), and global/regional-scale dispersal limitation (Hubbell, 2001).

To conclude, our results generally supported our five predictions. First, taxonomic turnover increased faster with spatial/climatic distance in those biogeographical regions encompassing the tropics, i.e., in those areas where climatic conditions have been more stable historically, compared to the temperate regions. Second, in general, the turnover component decreased and its relationship with spatial/climatic distance became flatter at higher taxonomic ranks (order or family); this may reflect the evolutionary histories of angiosperm trees associated with region-specific geohistories in the tropics and outside the tropics. However, and third, we also found relatively steep turnover patterns with spatial/climatic distances in the African, North American, and Australian regions at family and/or order levels, which may be related to region-specific geographical constraints. Fourth, the nestedness component was generally smaller than the turnover component and almost independent from spatial/climatic distance in the regions containing tropical areas at the species level. However, and fifth, the nestedness component comprised a relatively larger proportion of overall dissimilarity in the Holarctic regions, which are often more historically unstable regions. In sum, the relationship between pairwise dissimilarity and distance for angiosperm tree communities at species, genus, family, and order levels illustrates the importance of geographical filters associated with historical and contemporary factors, in shaping regional beta diversity patterns of angiosperm trees.

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DATA AVAILABILITY STATEMENT

The relevant data used in this study are available from Zenodo (https://doi.org/10.5281/zenodo.4572404).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Relationship between sampling coverage and plot-size and tree diameter threshold of individuals

Appendix S2. Difference in Akaike Information Criteria between negative exponential and power-law models

Appendix S3. The relationship between pairwise dissimilarity and spatial distance analyzed by a power-law model

Appendix S4. Comparison of intercept and slope in the negative exponential models with different thresholds of sampling coverage

Appendix S5. Pearson's correlation of compositional dissimilarity matrices between taxonomic ranks

Appendix S6. Comparison of the intercept of the negative exponential model of dissimilarity-spatial distance

Appendix S7. Comparison of the slopes of the negative exponential model of dissimilarity-spatial distance at four taxonomic ranks

Appendix S8. The relationship between taxonomic dissimilarity and climatic distance analyzed by a negative exponential model

Appendix S9. Comparison of the intercept of the negative exponential model of dissimilarity-climatic distance at four taxonomic ranks

Appendix S10. Comparison of the slopes of the negative exponential model of dissimilarity-climatic distance at four taxonomic ranks

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