

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

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

Running head: Regional patterns of community dissimilarity

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46

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-to-distance relationship should change across taxonomic ranks depending on the deep-time diversification in different biogeographic regions reflecting geohistories and geographical settings.

Location: Global

Methods: Using a dataset 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 modelled 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 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 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; biogeographical regions; beta diversity; dissimilarity decomposition; dispersal limitation; distance decay; environmental filtering; taxonomic diversity

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 biogeographic 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 aforementioned 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 (Ricklefs & Renner 2012; Munoz et al. 2012; Chen et al. 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. 2016), 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 vicariant 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-to-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 aforementioned reasoning, we tested the following predictions: i) taxonomic turnover will be the dominant component of dissimilarity in historically stable regions (Baselga et al. 2012), such as regions that contain tropical areas; ii) 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); iii) 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); iv) 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 v) 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.

Materials and Methods

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-to-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 m²; Fig. 1). Using all plots, we created community composition matrices for four taxonomic ranks: species (21,455 species), genus (2741 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 et al. 2001): we subdivided the Holarctic Kingdom into North American, West Eurasian and East Eurasian (Fig. 1) because of their differences in geohistory and paleoclimatic conditions. South American, African, Indo-Pacific, Australian regions include tropical areas, while 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 (Fig. 1). More details of the data compilation process are provided in Ulrich et al. (2016) and Kubota et al. (2018).

Community under-sampling 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 $SC \geq 0.9$ ($n = 661$; Fig. 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 (Fig. S1 in 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.

Dissimilarity calculation

Using the subset of equivalently well-sampled plots ($SC \geq 0.7$, 0.8 , 0.85 , or 0.9), we calculated pairwise dissimilarity between plots within the same biogeographic region (Fig. 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 rank, although β_{sim} is predominant at lower (e.g. species) taxonomic rank. Before analyzing dissimilarity-to-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 (β_{sor} , β_{sim} , and β_{sne}) in each biogeographical region.

Spatial and climatic distances

The 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 and 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).

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 $1 - (\text{model deviance}/\text{null deviance})$ (McFadden 1973). The two functions provided similar fits to the data according to Akaike's Information Criterion (Table S1 in Appendix S1), and thus we only present results for the negative exponential model in the main text (see Fig. S2 in Appendix S1 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 ($SC = 0.7\sim 0.9$) 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.

Results

The parameters (especially slopes) of the negative exponential models at lower SC thresholds (0.7–0.85) differed from those estimated using $SC \geq 0.9$, particularly for the

climatic distance model (Fig. S3 in Appendix S1). 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 criteria ($SC \geq 0.9$) 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 its degree between the regions (Table S2 in Appendix S1), indicating the influence of region-specific deep-time diversification on shaping turnover/nestedness-resultant beta diversity.

Total dissimilarity and spatial distance

β_{sor} increased with increasing spatial distance between sites, and this finding was consistent within all biogeographical regions (Fig. 3). The negative exponential model provided a relatively good fit to the dissimilarity-distance pattern at the species level ($r^2 = 0.34\text{--}0.74$), but the amount of explained variance generally decreased along taxonomic ranks from genus to order (Fig. 4; $r^2 = 0.08\text{--}0.66$ for genera; $r^2 = 0.01\text{--}0.55$ for families; $r^2 = <0.01\text{--}0.43$ for orders). The intercept and slope of the negative exponential model became smaller at higher taxonomic ranks (Fig. S4 and S5 in Appendix S1).

Relationships between turnover and nestedness-resultant components and spatial distance

The spatial patterns of β_{sim} were well characterized by the negative exponential model,

311 especially at the species level (Fig. 3a), and exhibited an asymptotic increase with spatial
312 distance (Fig. 4). β_{sim} was the predominant component of β_{sor} in all geographical regions
313 except for sites near to each other in the West Eurasian region (Fig. 5), but the relative
314 importance of β_{sim} decreased along the taxonomic ranks from genus to order. The intercept
315 and slope of the β_{sim} -distance curve were smaller in the temperate regions (North
316 American, West Eurasian, and East Eurasian) where the β_{sim} at species level slowly
317 saturated over the entire geographical extent at the species level (Fig. S4 and S5). In
318 contrast, the intercept and/or slope of the β_{sim} -distance curve was larger in the regions
319 containing tropical areas (South American, African, and Indo-Pacific) where the β_{sim} at
320 species level saturated at a smaller geographical extent (Fig. 4). The β_{sim} values became
321 lower, and the shape of the curve became flatter, at higher taxonomic ranks in the South
322 American and Indo-Pacific regions (Fig. 4). In contrast, the slope of the curve was
323 relatively steep even at the family and order levels in the African, Australian, and North
324 American regions (Fig. 4 and S5).

325
326 β_{sne} was poorly explained by the negative exponential model (Fig. 3a); the relationship
327 between β_{sne} and spatial distance was mostly flat, while a negative linear relationship was
328 found at the species level in the Holarctic regions, especially in West Eurasian (Fig. 4 and
329 S5). At the species level, β_{sne} accounted for a major proportion of β_{sor} only within sites
330 near to each other in the Holarctic regions (Fig. 5). However, the relative importance of
331 β_{sne} increased at higher taxonomic ranks even in the regions containing tropical areas,
332 especially in South American (Fig. S4).

333
334 *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 (Fig. S6-S8 in Appendix S1). 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 (Fig. 3). β_{sor} and β_{sim} exhibited steep slopes and quick asymptotic saturation in all regions 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) (Fig. S6). 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 (Fig. S6 and S8). The relative importance of β_{sim} to β_{sor} increased with the climatic distance, especially in the West Eurasian at the species level, while the pattern was less clear at the family and order levels (Fig. 5).

Discussion

Our results reveal substantial differences in patterns of variation in local angiosperm tree communities across different biogeographic 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 Australian region showed intermediate trends (Fig. 4, S5, S6, and S8).

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 South American region (Fig. 4), providing a 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 South American region than in the other regions (Fig. 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 in regard to the turnover component (Fig. S5), 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, 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 (Figs. 3, S4 and S5). 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 (Fig. 3, 4, and S6), 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 at the species level (Fig. 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 (Fig. 4-5, S4-S5) 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 $\geq 90\%$). Loosening of the SC threshold down to 70% did not alter the general dissimilarity trends (Fig. S3), 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.

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; Kasel et al. 2017; Chun & Lee 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 though it is potentially informative to understand the imprints of deep-time diversification in 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-to-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 extratropics. However, and third, we also found relatively steep turnover patterns with spatial/climatic distances in 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 is available from Zenodo (doi: 10.5281/zenodo.4572404).

References

Antão, L.H., Brian, M., Magurran, A.E., Soares, A., & Dornelas, M. 2019. β -diversity scaling patterns are consistent across metrics and taxa. *Ecography*, 42, 1012–1023. doi: 10.1111/ecog.04117

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19, 134–143. doi: 10.1111/j.1466-8238.2009.00490.x

Baselga, A. 2013. Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*, 4, 552–557. doi: 10.1111/2041-210X.12029

Baselga, A., Gómez-Rodríguez, C., & Lobo, J.M. 2012. Historical legacies in world amphibian diversity revealed by the turnover and nestedness components of beta diversity. *PLoS ONE*, 7, e32341. doi: 10.1371/journal.pone.0032341

Baselga, A., & Orme, C. D. L. 2012. betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812. doi: 10.1111/j.2041-210X.2012.00224.x

521 Beck, J., Holloway, J.D., & Schwanghart, W. 2013. Undersampling and the
522 measurement of beta diversity. *Methods in Ecology and Evolution*, 4, 370–382.
523 doi: 10.1111/2041-210x.12023

524 Bellier, E., Grøtan, V., Engen, S., Schartau, A., Herfindal, I., & Finstad, A.G. 2014.
525 Distance decay of similarity, effects of environmental noise and ecological
526 heterogeneity among species in the spatio-temporal dynamics of a dispersal-limited
527 community. *Ecography*, 37, 172–182. doi: 10.1111/j.1600-0587.2013.00175.x

528 Bevilacqua, S., & Terlizzi, A. 2020. Nestedness and turnover unveil inverse spatial
529 patterns of compositional and functional β -diversity at varying depth in marine
530 benthos. *Diversity and Distributions*, 26, 743–757. doi: 10.1111/ddi.13025

531 Byrne, M. 2008. Evidence for multiple refugia at different time scales during
532 Pleistocene climatic oscillations in southern Australia inferred from
533 phylogeography. *Quaternary Science Reviews*, 27, 2576–2585. doi:
534 10.1016/j.quascirev.2008.08.032

535 Cacciatori, C., Tordoni, E., Petruzzellis, F., Sérgio, C., Garcia, C., Chiarucci, A., &
536 Bacaro, G. 2020. Drivers of distance-decay in bryophyte assemblages at multiple
537 spatial scales: Dispersal limitations or environmental control? *Journal of*
538 *Vegetation Science*, 31, 293–306. doi: 10.1111/jvs.12790

539 Chao, A., Kubota, Y., Zelený, D., Chiu, C.-H., Li, C.-F., Kusumoto, B., Yasuhara, M. et
 540 al. 2020. Quantifying sample completeness of a biological survey and comparing
 541 diversities among assemblages based on incomplete surveys. *Ecological Research*,
 542 35, 292–314. doi: 10.1111/1440-1703.12102

543 Chen, A., Wang, S., & Pacala, S.W. 2012. Comment on “Global Correlations in
 544 Tropical Tree Species Richness and Abundance Reject Neutrality”. *Science* 29:
 545 1639. doi: 10.1126/science.1222534

546 Christenhusz, M.J.M., & Chase, M.W. 2012. Biogeographical patterns of plants in the
 547 Neotropics - dispersal rather than plate tectonics is most explanatory. *Botanical*
 548 *Journal of the Linnean Society*, 171, 277–286. doi: 10.1111/j.1095-
 549 8339.2012.01301.x

550 Chun, J.-H., & Lee, C.-B. 2017. Disentangling the local-scale drivers of taxonomic,
 551 phylogenetic and functional diversity in woody plant assemblages along
 552 elevational gradients in South Korea. *PLoS ONE*, 12, e0185763. doi:
 553 10.1371/journal.pone.0185763

554 Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Núñez, P. et
 555 al. 2002. Beta-diversity in tropical forest trees. *Science*, 295, 666–669. doi:
 556 10.1126/science.1066854

557 Cowling, R.M., Potts, A.J., Bradshaw, P.L., Colville, J., Arianoutsou, M., Ferrier, S.,
558 Forest, F. et al. 2015. Variation in plant diversity in mediterranean-climate
559 ecosystems: the role of climatic and topographical stability. *Journal of*
560 *Biogeography*, 42, 552–564. doi: 10.1111/jbi.12429

561 Cox, B. 2001. The biogeographic regions reconsidered. *Journal of Biogeography*, 28,
562 511–523. doi: 10.1046/j.1365-2699.2001.00566.x

563 Donoghue, M.J. 2008. A phylogenetic perspective on the distribution of plant diversity.
564 *Proceedings of the National Academy of Sciences*, 105, 11549–11555. doi:
565 10.1073/pnas.0801962105

566 Donoghue, M.J., & Smith, S.A. 2004. Patterns in the assembly of temperate forests
567 around the Northern Hemisphere. *Philosophical Transactions of the Royal Society*
568 *of London. Series B: Biological Sciences*, 359, 1633–1644. doi:
569 10.1098/rstb.2004.1538

570 Eiserhardt, W.L., Borchsenius, F., Plum, C.M., Ordonez, A., & Svenning, J. 2015.
571 Climate-driven extinctions shape the phylogenetic structure of temperate tree
572 floras. *Ecology Letters*, 18, 263–272. doi: 10.1111/ele.12409

573 Fick, S.E. and Hijmans, R.J. 2017. WorldClim 2: new 1km spatial resolution climate
574 surfaces for global land areas. *International Journal of Climatology*, 37, 4302–

575 4315. doi: 10.1002/joc.5086

576 Fine, P.V.A., & Ree, R.H. 2006. Evidence for a time-integrated species-area effect on
577 the latitudinal gradient in tree diversity. *The American Naturalist*, 168, 796–804.
578 doi: 10.1086/508635

579 Fitzpatrick, M.C., Sanders, N.J., Normand, S., Svenning, J.-C., Ferrier, S., Gove, A.D.,
580 & Dunn, R.R. 2013. Environmental and historical imprints on beta diversity:
581 insights from variation in rates of species turnover along gradients. *Proceedings of*
582 *the Royal Society B: Biological Sciences*, 280, 20131201. doi:
583 10.1098/rspb.2013.1201

584 Gentry, A.H. 1988. Changes in plant community diversity and floristic composition on
585 environmental and geographical gradients. *Annals of the Missouri Botanical*
586 *Garden*, 75, 1–34. doi: 10.2307/2399464

587 Gianuca, A.T., Declerck, S., Lemmens, P., & Meester, L. 2016. Effects of dispersal and
588 environmental heterogeneity on the replacement and nestedness components of β -
589 diversity. *Ecology*, 98, 525–533. doi: 10.1002/ecy.1666

590 Gilbert, B., & Lechowicz, M.J. 2004. Neutrality, niches, and dispersal in a temperate
591 forest understory. *Proceedings of the National Academy of Sciences*, 101, 7651–
592 7656. doi: 10.1073/pnas.0400814101

593 Gómez-Rodríguez, C., & Baselga, A. 2018. Variation among European beetle taxa in
594 patterns of distance decay of similarity suggests a major role of dispersal
595 processes. *Ecography*, 41, 1825–1834. doi: 10.1111/ecog.03693

596 Gómez-Rodríguez, C., Miller, K.E., Castillejo, J., Iglesias- Piñeiro, J., & Baselga, A.
597 2020. Disparate dispersal limitation in Geomalacus slugs unveiled by the shape
598 and slope of the genetic–spatial distance relationship. *Ecography* 43: 1229–1240.
599 doi: 10.1111/ecog.05142

600 Graham, C. H., Storch, D., & Machac, A. 2018. Phylogenetic scale in ecology and
601 evolution. *Global Ecology and Biogeography*, 27, 175-187. doi:
602 10.1111/geb.12686

603 Graves, S., Piepho, H.-P., & Selzer, L. 2019. multcompView: Visualizations of Paired
604 Comparisons. R package version 0.1-8. Available at [https://cran.r-](https://cran.r-project.org/web/packages/multcompView/index.html)
605 [project.org/web/packages/multcompView/index.html](https://cran.r-project.org/web/packages/multcompView/index.html) [Acceced 8 September 2020]

606 Hardy, O.J., Couteron, P., Munoz, F., Ramesh, B.R., & Pélissier, R. 2012. Phylogenetic
607 turnover in tropical tree communities: impact of environmental filtering,
608 biogeography and mesoclimatic niche conservatism. *Global Ecology and*
609 *Biogeography*, 21, 1007–1016. doi: 10.1111/j.1466-8238.2011.00742.x

610 Hijmans, R.J. 2019. geosphere: Spherical Trigonometry. R package version 1.5-10.

611 Available at <https://cran.r-project.org/web/packages/geosphere/index.html>
612 [Accessed 8 September 2020]

613 Hortal, J., José, D., Bini, L.M., Rodríguez, M.Á., Baselga, A., David, N., Rangel, T.F. et
614 al. 2011. Ice age climate, evolutionary constraints and diversity patterns of
615 European dung beetles. *Ecology Letters*, 14, 741–748. doi: 10.1111/j.1461-
616 0248.2011.01634.x

617 Hsieh, T.C., Ma, K.H., & Chao, A. 2016. iNEXT: an R package for rarefaction and
618 extrapolation of species diversity (Hill numbers). *Methods in Ecology and*
619 *Evolution*, 7, 1451–1456. doi: 10.1111/2041-210X.12613

620 Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*.
621 Princeton, U.S., Princeton University Press.

622 Ibanez, T., Keppel, G., Baider, C., Birkinshaw, C., Culmsee, H., Cordell, S., Florens et
623 al. 2018. Regional forcing explains local species diversity and turnover on tropical
624 islands. *Global Ecology and Biogeography*, 27, 474–486. doi: 10.1111/geb.12712

625 Kasel, S., Bennett, L.T., Aponte, C., Fedrigo, M., & Nitschke, C.R. 2017.
626 Environmental heterogeneity promotes floristic turnover in temperate forests of
627 south-eastern Australia more than dispersal limitation and disturbance. *Landscape*
628 *Ecology*, 32, 1613–1629. doi: 10.1007/s10980-017-0526-7

629 Keil, P., Schweiger, O., Kühn, I., Kunin, W.E., Kuussaari, M., Settele, J., Henle, K. et
 630 al. 2012. Patterns of beta diversity in Europe: the role of climate, land cover and
 631 distance across scales. *Global Ecology and Biogeography*, 21, 1473–1486. doi:
 632 10.1111/j.1466-8238.2011.00733.x

633 König, C., Weigelt, P., & Kreft, H. 2017. Dissecting global turnover in vascular plants.
 634 *Global Ecology and Biogeography*, 26, 228–242. doi: 10.1111/geb.12536

635 Kubota, Y., Hirao, T., Fujii, S. J., Shiono, T., & Kusumoto, B. 2014. Beta diversity of
 636 woody plants in the Japanese archipelago: the roles of geohistorical and ecological
 637 processes. *Journal of Biogeography*, 41, 1267–1276. doi: 10.1111/jbi.12290

638 Kubota, Y., Kusumoto, B., Shiono, T., & Ulrich, W. 2018. Environmental filters
 639 shaping angiosperm tree assembly along climatic and geographic gradients.
 640 *Journal of Vegetation Science* 29: 607–618. doi: 10.1111/jvs.12648

641 Laffan, S.W. 2018. Phylogeny-Based Measurements at Global and Regional Scales. In
 642 *Phylogenetic Diversity*, pp. 111–129. Cham, Springer International Publishing.

643 Legendre, P. 2014. Interpreting the replacement and richness difference components of
 644 beta diversity. *Global Ecology and Biogeography*, 23, 1324–1334. doi:
 645 10.1111/geb.12207

646 Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes,

647 M.F., Holt, R.D. et al. 2004. The metacommunity concept: a framework for multi-
 648 scale community ecology. *Ecology Letters*, 7, 601–613. doi: 10.1111/j.1461-
 649 0248.2004.00608.x

650 Lenoir, J., Virtanen, R., Oksanen, J., Oksanen, L., Luoto, M., Grytnes, J., & Svenning,
 651 J. 2012. Dispersal ability links to cross-scale species diversity patterns across the
 652 Eurasian Arctic tundra. *Global Ecology and Biogeography*, 21, 851–860. doi:
 653 10.1111/j.1466-8238.2011.00733.x

654 Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S., &
 655 Oberdorff, T. 2011. Partitioning global patterns of freshwater fish beta diversity
 656 reveals contrasting signatures of past climate changes. *Ecology Letters*, 14, 325–
 657 334. doi: 10.1111/j.1461-0248.2011.01589.x

658 McFadden, D. 1973. Conditional logit analysis of qualitative choice behavior. In:
 659 Zarembka, P. (Ed.). *Frontiers in Econometrics*. Academic Press, pp. 105-142.

660 Middleton, D. J., K. Armstrong, Y. Baba, H. Balslev, K. Chayamarit, R. C. K. Chung,
 661 B. J. Conn et al. 2019. Progress on Southeast Asia’s Flora projects. Gardens’
 662 Bulletin Singapore, 71, 267–319. doi: 10.26492/gbs71(2).2019-02

663 Millar, R. B., Anderson, M. J., & Tolimieri, N. 2011. Much ado about nothings: using
 664 zero similarity points in distance-decay curves. *Ecology*, 92, 1717–1722.

doi.org/10.1890/11-0029.1

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. et al. 2008. A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters* 11: 904–917. doi: 10.1111/j.1461-0248.2008.01202.x

Munoz, F., Couteron, P., & Hubbell, S.P. 2012. Comment on “Global Correlations in Tropical Tree Species Richness and Abundance Reject Neutrality”. *Science* 29: 1639. doi: 10.1126/science.1222718

Munoz, F., Ramesh, B.R., & Couteron, P. 2014. How do habitat filtering and niche conservatism affect community composition at different taxonomic resolutions? *Ecology*, 95, 2179–2191. doi: 10.1890/13-0064.1

Myers, J.A., Chase, J.M., Jiménez, I., Jørgensen, P.M., Araujo-Murakami, A., Paniagua-Zambrana, N., & Seidel, R. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology letters*, 16, 151–157. doi: 10.1111/ele.12021

Nekola, J.C., & White, P.S. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, 26, 867–878. doi: 10.1046/j.1365-2699.1999.00305.x

683 Nekola, J. C., & McGill, B. J. 2014. Scale dependency in the functional form of the
684 distance decay relationship. *Ecography*, 37, 309-320. doi: 10.1111/j.1600-
685 0587.2013.00407.x

686 Olivier, P.I., & van Aarde, R.J. 2014. Multi-scale sampling boosts inferences from beta
687 diversity patterns in coastal forests of South Africa. *Journal of Biogeography*, 41,
688 1428–1439. doi: 10.1111/jbi.12303

689 Pennington, R.T., Lavin, M., & Oliveira-Filho, A. 2009. Woody plant diversity,
690 evolution, and ecology in the tropics: perspectives from seasonally dry tropical
691 forests. *Annual Review of Ecology, Evolution, and Systematics*, 40, 437–457. doi:
692 10.1146/annurev.ecolsys.110308.120327

693 Prinzing, A., Durka, W., Klotz, S., & Brandl, R. 2001. The niche of higher plants:
694 evidence for phylogenetic conservatism. *Proceedings of the Royal Society B:*
695 *Biological Sciences*, 268, 2383–2389. doi: 10.1098/rspb.2001.1801

696 Qian, H. 2009. Beta diversity in relation to dispersal ability for vascular plants in North
697 America. *Global Ecology and Biogeography*, 18, 327–332. doi: 10.1111/j.1466-
698 8238.2009.00450.x

699 Qian, H., & Ricklefs, R.E. 2016. Out of the tropical lowlands: latitude versus elevation.
700 31: 738–741. *Trends in Ecology and Evolution*, 31, 738-741. doi:

701 10.1016/j.tree.2016.07.012

702 R Core Team. 2019. R: A language and environment for statistical computing.

703 Available at: <https://www.R-project.org/> [Accessed 8 September 2020]

704 Réjou-Méchain, M., & Hardy, O.J. 2011. Properties of similarity indices under niche-

705 based and dispersal-based processes in communities. *The American Naturalist*,

706 177, 589–604. doi: 10.1086/659627

707 Ricklefs, R.E., & Renner SS. 2012. Global correlations in tropical tree species richness

708 and abundance reject neutrality. *Science* 335: 464–467. doi:

709 10.1126/science.1215182

710 Rijdsdijk, K. F., Hengl, T., Norder, S. J., Otto, R., Emerson, B. C., Ávila, S. P., van

711 Loon, E.E. et al. 2014. Quantifying surface-area changes of volcanic islands driven

712 by Pleistocene sea-level cycles: biogeographical implications for the Macaronesian

713 archipelagos. *Journal of Biogeography*, 41, 1242–1254. doi: 10.1111/jbi.12336

714 Saito, V.S., Soininen, J., Fonseca-Gessner, A.A., & Siqueira, T. 2015. Dispersal traits

715 drive the phylogenetic distance decay of similarity in Neotropical stream

716 metacommunities. *Journal of Biogeography*, 42, 2101–2111. doi:

717 10.1111/jbi.12577

718 Shiono, T., Kusumoto, B., Yasuhara, M., & Kubota, Y. 2018. Roles of climate niche

719 conservatism and range dynamics in woody plant diversity patterns through the
720 Cenozoic. *Global Ecology and Biogeography*, 27, 865–874. doi:
721 10.1111/geb.12755

722 Soininen, J., Heino, J., & Wang, J. 2017. A meta-analysis of nestedness and turnover
723 components of beta diversity across organisms and ecosystems. *Global Ecology*
724 *and Biogeography*, 27, 96–109. doi: 10.1111/geb.12660

725 Soininen, J., McDonald, R., & Hillebrand, H. 2007. The distance decay of similarity in
726 ecological communities. *Ecography*, 30, 3–12. doi: 10.1111/j.0906-
727 7590.2007.04817.x

728 Stuart, Y.E., Losos, J.B., & Algar, A.C. 2012. The island–mainland species turnover
729 relationship. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4071–
730 4077. doi: 10.1098/rspb.2012.0816

731 Svenning, J. 2003. Deterministic Plio-Pleistocene extinctions in the European cool-
732 temperate tree flora. *Ecology Letters*, 6, 646–653. doi: 10.1046/j.1461-
733 0248.2003.00477.x

734 Tiffney, B.H., & Manchester, S.R. 2001. The use of geological and paleontological
735 evidence in evaluating plant phylogeographic hypotheses in the Northern
736 Hemisphere Tertiary. *International Journal of Plant Sciences*, 162, S3–S17. doi:

737 10.1086/323880

738 Tolley, K.A., Tilbury, C.R., Measey, J.G., Menegon, M., Branch, W.R., & Matthee,
739 C.A. 2011. Ancient forest fragmentation or recent radiation? Testing refugial
740 speciation models in chameleons within an African biodiversity hotspot. *Journal of*
741 *Biogeography*, 38, 1748–1760. doi: 10.1111/j.1365-2699.2011.02529.x

742 Trujillo, L.N., Cerda, Í.G. la, Pardo, I., Macía, M.J., Cala, V., & Arellano, G. 2019.
743 Niche-based processes outperform neutral processes when predicting distance
744 decay in co-dominance along the Amazon – Andes rainforest gradient. *Journal of*
745 *Vegetation Science*, 30, 644–653. doi: 10.1111/jvs.12761

746 Tuomisto, H., Ruokolainen, K., & Markku, Y.-H. 2003. Dispersal, environment, and
747 floristic variation of western Amazonian forests. *Science*, 299, 241–244. doi:
748 10.1126/science.1078037

749 Ulrich, W., Kusumoto, B., Shiono, T., & Kubota, Y. 2016. Climatic and geographic
750 correlates of global forest tree species-abundance distributions and community
751 evenness. *Journal of Vegetation Science*, 27, 295–305. doi: 10.1111/jvs.12346

752 Wang, X., Wiegand, T., Anderson-Teixeira, K.J., Bourg, N.A., Hao, Z., Howe, R., Jin,
753 G. et al. 2018. Ecological drivers of spatial community dissimilarity, species
754 replacement and species nestedness across temperate forests. *Global Ecology and*

Biogeography, 27, 581–592. doi: 10.1111/geb.12719

Wang, X., Wiegand, T., Wolf, A., Howe, R., Davies, S.J., & Hao, Z. 2011. Spatial patterns of tree species richness in two temperate forests: Detecting underlying mechanisms controlling species-area relationships. *Journal of Ecology*, 99, 1382–1393. doi: 10.1111/j.1365-2745.2011.01857.x

Wen, J. 1999. Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. *Annual Review of Ecology and Systematics*, 30, 421–455. doi: 10.1146/annurev.ecolsys.30.1.421

Xiang, Q.-Y. (J.), Zhang, W.H., Ricklefs, R.E., Qian, H., Chen, Z.D., Wen, J., & Li, J.H. 2004. Regional differences in rates of plant speciation and molecular evolution: a comparison between eastern Asia and eastern North America. *Evolution*, 58, 2175. doi: 10.1554/03-712

Yeh, C. F., Soininen, J., Teittinen, A., & Wang, J. 2019. Elevational patterns and hierarchical determinants of biodiversity across microbial taxonomic scales. *Molecular Ecology*, 28, 86-99, doi: 10.1111/mec.14935

Supporting information

Appendix S1. Supplementary tables and figures

Figure legends

Fig. 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 sampling completeness (SC).

Fig. 2 Histograms for sampling completeness evaluated as sampling 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 ($SC \geq 0.9$) were used in the dissimilarity-distance analyses.

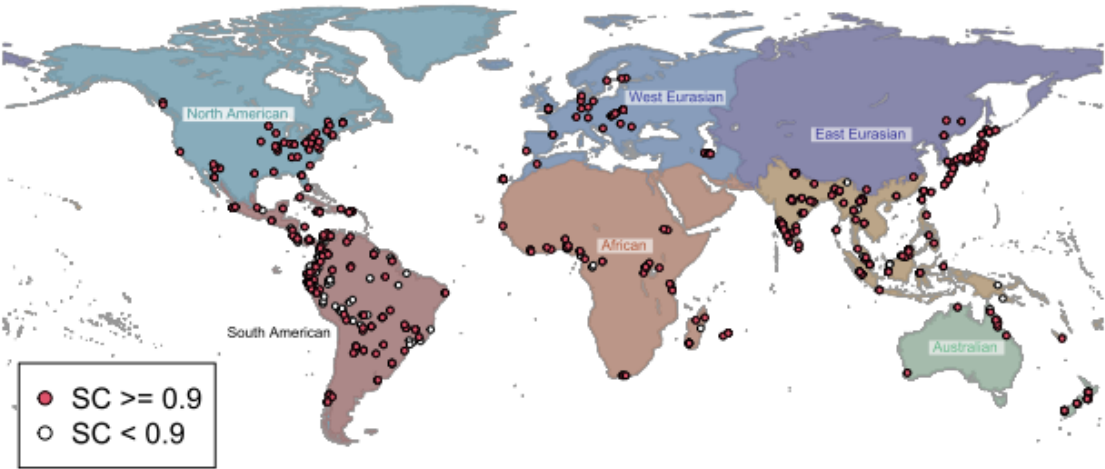
Fig. 3 Pseudo r^2 of negative exponential models for the relationships between taxonomic dissimilarity and (a) geographical and (b) climatic distance per taxonomic rank [species (SP), genus (GN), family (FM) and order (OR)] in each biogeographical region: South American (SA), African (AF), Indo-Pacific (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.

Fig. 4 The relationship between pairwise dissimilarity and spatial distance (dissimilarity-to-distance relationship) as fitted by a negative exponential model from 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.

Fig. 5 Changes in the relative importance of the turnover component to total dissimilarity ($\beta_{\text{sim}}/\beta_{\text{sor}}$) 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.

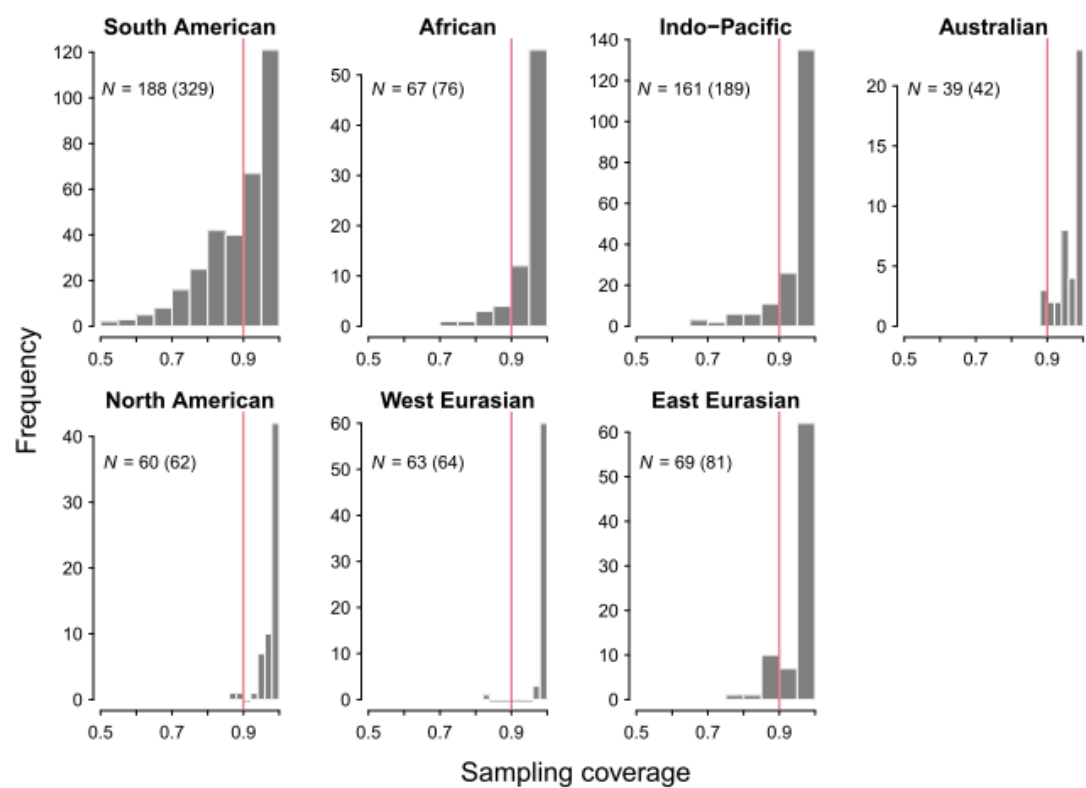
811 **Fig. 1**



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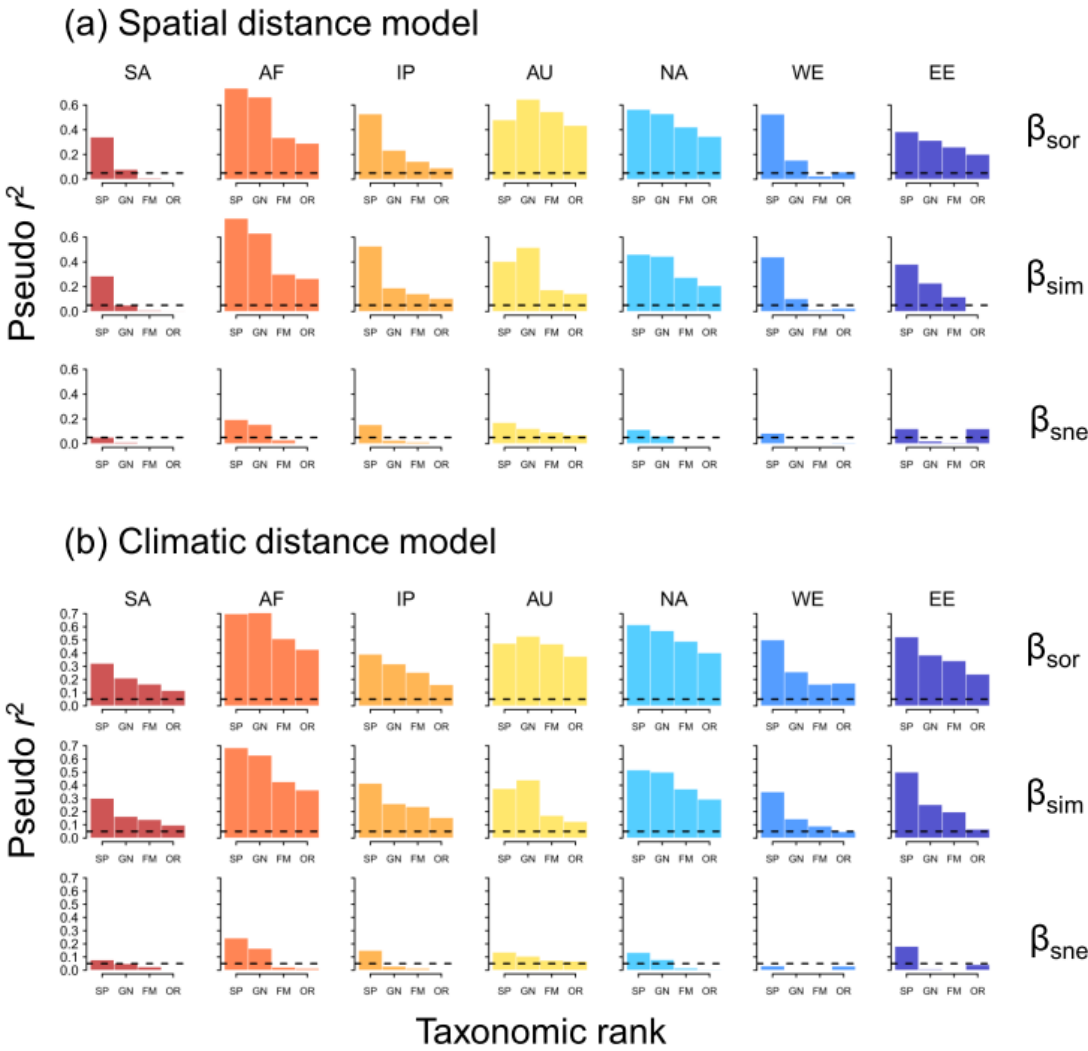
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814 **Fig. 2**

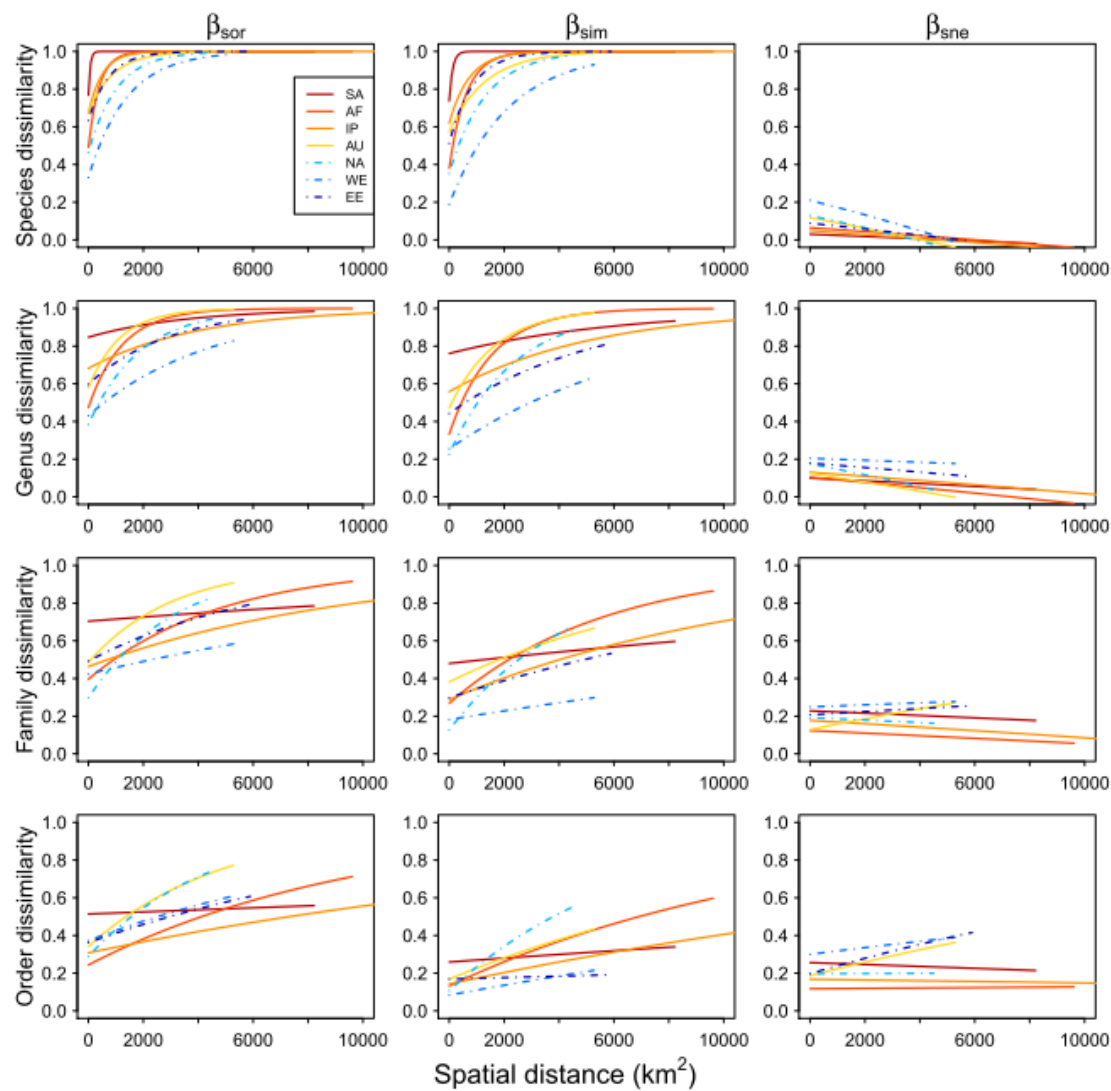


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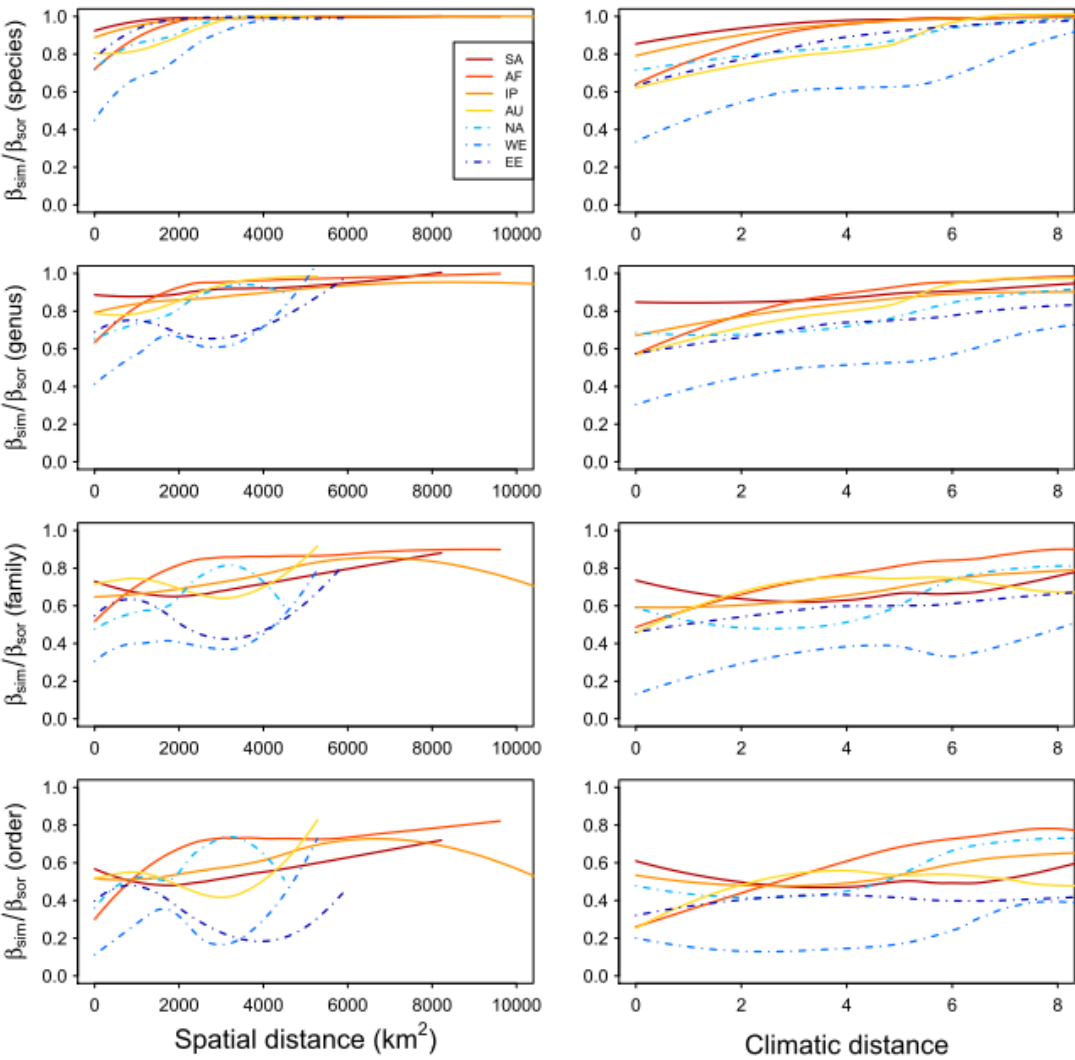


820 **Fig. 4**



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