

## Research paper

# Geographic patterns of taxonomic and phylogenetic $\beta$ -diversity of angiosperm genera in regional floras across the world

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## ABSTRACT

Beta diversity ( $\beta$ -diversity) is the scalar between local ( $\alpha$ ) and regional ( $\gamma$ ) diversity. Understanding geographic patterns of  $\beta$ -diversity is central to ecology, biogeography, and conservation biology. A full understanding of the origin and maintenance of geographic patterns of  $\beta$ -diversity requires exploring both taxonomic and phylogenetic  $\beta$ -diversity, as well as their respective turnover and nestedness components, and exploring phylogenetic  $\beta$ -diversity at different evolutionary depths. In this study, we explore and map geographic patterns of  $\beta$ -diversity for angiosperm genera in regional floras across the world. We examine both taxonomic and phylogenetic  $\beta$ -diversity and their constituent components, and both tip-weighted and basal-weighted phylogenetic  $\beta$ -diversity, and relate them to latitude. On the one hand, our study found that the global distribution of  $\beta$ -diversity is highly heterogeneous. This is the case for both taxonomic and phylogenetic  $\beta$ -diversity, and for both tip-weighted and basal-weighted phylogenetic  $\beta$ -diversity. On the other hand, our study found that there are highly consistent geographic patterns among different metrics of  $\beta$ -diversity. In most cases, metrics of  $\beta$ -diversity are negatively associated with latitude, particularly in the Northern Hemisphere. Different metrics of taxonomic  $\beta$ -diversity are strongly and positively correlated with their counterparts of phylogenetic  $\beta$ -diversity.

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## 1. Introduction

Beta diversity, or  $\beta$ -diversity, quantifies the change in species composition across space or time. The proportion of species shared between two areas often decreases with increasing the distance separating them (Nekola and White, 1999). For a given geographic distance separating two areas,  $\beta$ -diversity can differ greatly between different regions (e.g., temperate versus tropical regions) (McFadden et al., 2019; Qian et al., 2020). Understanding geographic patterns of  $\beta$ -diversity is central to both conceptual questions of ecology and biogeography (such as the origin and distribution of biodiversity) and to applied issues of conservation biology (Whittaker, 1972; McKnight et al., 2007; Buckley and Jetz, 2008). Alpha diversity ( $\alpha$ -diversity), which describes species richness within single sites, and  $\beta$ -diversity together determine species richness at a regional extent such as a continent or biogeographic region (i.e., gamma diversity or  $\gamma$ -diversity) (Whittaker, 1972). For a given  $\alpha$ -diversity, greater  $\beta$ -diversity between areas within a region

would lead to greater  $\gamma$ -diversity in the region. It is thought that higher species diversity in tropical regions than in temperate regions is because  $\beta$ -diversity is higher in tropical regions, compared to temperate regions (Stevens, 1989).

Classical measures of  $\beta$ -diversity focus on species-centric metrics of  $\beta$ -diversity, i.e., taxonomic  $\beta$ -diversity (Koleff et al., 2003). Total  $\beta$ -diversity between areas can be quantified by dissimilarity indices such as the Sørensen dissimilarity index (Baselga, 2010). Total  $\beta$ -diversity measured by a dissimilarity index consists of two components: species turnover and species nestedness. Species turnover represents species replacement between areas whereas species nestedness represents the degree to which the species in the area with fewer species is a subset of the species in the area with more species (Baselga, 2010). A full understanding of the origin and maintenance of geographic patterns of  $\beta$ -diversity in a region requires investigating the relative importance of each of these two components to total  $\beta$ -diversity (Baselga, 2010; Qian et al., 2020).

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While metrics of taxonomic  $\beta$ -diversity are useful to measure the degrees of overlap and distinctness of species between areas, they do not account for evolutionary history, e.g., phylogenetic relatedness between species (Graham and Fine, 2008). Incorporating information regarding differences in evolutionary history between species in a study of  $\beta$ -diversity can help understand the ecological and evolutionary mechanisms structuring communities (Ives and Helmus, 2010). Phylogenetic  $\beta$ -diversity metrics, which are based on phylogenetic relatedness among species, can detect community similarity when two focal communities share no species. Examining taxonomic and phylogenetic  $\beta$ -diversity simultaneously can provide insights into both contemporary ecological and historical (evolutionary) mechanisms shaping variation in species diversity and composition among biological assemblages (Graham and Fine, 2008; Peixoto et al., 2017; Cássia-Silva et al., 2019; Qian et al., 2020). Analogous to taxonomic  $\beta$ -diversity, which measures change in species composition across space, phylogenetic  $\beta$ -diversity measures the extent to which assemblages differ in terms of the evolutionary relationships of its members (Graham and Fine, 2008).

Angiosperms (i.e., flowering plants) are major components of most terrestrial ecosystems across the world. A recent study (i.e., Xu et al., 2023) has investigated geographic patterns of  $\beta$ -diversity for angiosperm trees in the world. However, a large portion of the world's land was not included in their study. Furthermore, their study only included angiosperm tree species, which account for less than 20% of all angiosperm species in the world (Qian et al., 2019b, 2022). It is unknown how well the geographic patterns of angiosperm trees observed in their study can represent geographic patterns of overall angiosperm species. Several studies have investigated geographic patterns of  $\beta$ -diversity in angiosperm at regional scales (e.g., Qian et al., 2013, 2020, 2021), but such studies for overall angiosperms at a global scale remain lacking.

In this study, we explore and map geographic patterns of  $\beta$ -diversity for angiosperm genera in regional floras across the world. We examine both taxonomic and phylogenetic  $\beta$ -diversity and their constituent components, and both tip-weighted and basal-weighted phylogenetic  $\beta$ -diversity. Previous studies have shown that  $\beta$ -diversity decreases with increasing latitude within regions or continents (e.g., Qian et al., 2020, 2021). Accordingly, we test this hypothesis by examining the relationships of  $\beta$ -diversity and their constituent components with latitude at a global scale and for the Northern and Southern Hemispheres separately. This study fills a critical knowledge gap.

## 2. Materials and methods

### 2.1. Angiosperm assemblage data

Geographic units of this study were the 420 geographic standard units (Liu et al., 2023). Each geographic unit was, on average, 366,179 km<sup>2</sup>. Data of native angiosperm genera in each geographic unit were compiled based on the plant database of the Floristic Map of the World (FMW) available at <https://en.geodata.pku.edu.cn/index.php?c=content&a=list&catid=199>, which was used in Liu et al. (2023), and the database of the World Checklist of Vascular Plants (WCVP; accessible via Plants of World Online at <https://powo.science.kew.org/>; Brown et al., 2023). Specifically, we matched geographic units between the two data sources, used the package rWCV (Brown et al., 2023) to extract genus lists of native angiosperms from WCVP for each of the geographic units, used the genus lists derived from WCVP to filter out non-native genera in each geographic unit in the FMW data, and expanded and updated the FMW data with the WCVP data by adding those genera that are present as native in WCVP but absent from the FMW data for those geographic units that were perfectly matched between the two

data sources. As a result, a total of 13,814 genera of angiosperms were included in the 420 geographic units.

### 2.2. Phylogenetic tree

We generated a genus-level phylogenetic tree for angiosperms using the functions `build.nodes.1` and Scenario 3 of the package U.PhyloMaker (Jin and Qian, 2023) and the megatree GBOTB.extended.WCVP.tre (Jin and Qian, 2022, 2023), which was an updated version of the megatree GBOTB.tre generated by Smith and Brown (2018), as a backbone phylogeny. We pruned to resulting phylogenetic tree to retain one tip per genus. For a genus with multiple species, a tip of the most inclusive cluster of the genus was used to represent the genus. Phylogenetic trees generated by U.PhyloMaker or its sister packages (Qian and Jin, 2016; Jin and Qian, 2019, 2022) have been commonly used in studies on phylogenetic diversity and structure in regional and global floras (e.g., Qian and Jin, 2021; Yue and Li, 2021; Zhang et al., 2021; Huang et al., 2023; Qian, 2023; Zhou et al., 2023).

### 2.3. Metrics of taxonomic and phylogenetic $\beta$ -diversity

We used the Sørensen dissimilarity index ( $\beta_{sor}$ ) to measure both taxonomic and phylogenetic  $\beta$ -diversity. We partitioned  $\beta_{sor}$  into two components: turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{nes}$ ).  $\beta_{sim}$  is the Simpson dissimilarity index; it quantifies  $\beta$ -diversity due to turnover (or replacement) of species between geographic units; thus it quantifies true turnover of species without the influence of difference in species richness between geographic units.  $\beta_{nes}$  quantifies  $\beta$ -diversity resulting from nestedness of species between geographic units.  $\beta_{sor}$  and its two components are defined as follows (Baselga, 2010):  $\beta_{sor} = (b + c)/(2a + b + c)$ ,  $\beta_{sim} = \min(b, c)/(a + \min(b, c))$ , and  $\beta_{nes} = \beta_{sor} - \beta_{sim}$ , where, when taxonomic  $\beta$ -diversity is concerned,  $a$  is the number of species shared by the two localities,  $b$  is the number of species unique to one locality and  $c$  is the number of species unique to the other locality (Baselga, 2010); when phylogenetic  $\beta$ -diversity is considered, shared and unique species are replaced with shared and unique branch lengths, respectively (Leprieur et al., 2012). We denoted  $\beta$ -diversity and its two components as  $\beta_{sor,tax}$ ,  $\beta_{sim,tax}$  and  $\beta_{nes,tax}$  for taxonomic  $\beta$ -diversity, and as  $\beta_{sor,phy}$ ,  $\beta_{sim,phy}$  and  $\beta_{nes,phy}$  for phylogenetic  $\beta$ -diversity. Both  $\beta_{sor,tax}$  and  $\beta_{sor,phy}$  vary from 0 (all species or branch lengths shared by the two sites) to 1 (no species or branch lengths shared by the two sites).

The ratio of  $\beta_{nes}$  to  $\beta_{sor}$  (i.e.,  $\beta_{ratio} = \beta_{nes}/\beta_{sor}$ ) represents the relative influence of turnover and nestedness on total  $\beta$ -diversity (Dobrovolski et al., 2012; Peixoto et al., 2017). We calculated  $\beta_{ratio}$  for both taxonomic and phylogenetic  $\beta$ -diversity (Dobrovolski et al., 2012; see also Peixoto et al., 2017; Pinto-Ledezma et al., 2018; Qian et al., 2020). A value of  $\beta_{ratio}$  smaller than 0.5 indicates that  $\beta$ -diversity is determined mainly by turnover whereas a value of  $\beta_{ratio}$  greater than 0.5 indicates that nestedness is the more important component than turnover in driving  $\beta$ -diversity (Dobrovolski et al., 2012).  $\beta_{ratio}$  for taxonomic and phylogenetic  $\beta$ -diversity was denoted as  $\beta_{ratio,tax}$  and  $\beta_{ratio,phy}$ , respectively.

Phylogenetic  $\beta$ -diversity deviation ( $\beta_{dev}$ ) from taxonomic  $\beta$ -diversity was calculated as:  $\beta_{dev} = (\beta_{sor,tax} - \beta_{sor,phy})/\beta_{sor,tax}$  (Qian et al., 2020).  $\beta_{dev}$  measures the extent to which the dissimilarity in the species composition between two communities mirrors differences at deeper phylogenetic levels.  $\beta_{dev}$  reflects the degree of lineage exchanges between localities over time (Peixoto et al., 2017; Pinto-Ledezma et al., 2018). When values of  $\beta_{dev}$  are compared across a geographic region,  $\beta_{dev}$  identifies places where turnover of phylogenetic lineages is high or low with respect to turnover of species.

$\beta_{sor,phy}$  is a tip-weighted metric of phylogenetic  $\beta$ -diversity and is more sensitive to turnover near the tips of the phylogeny (i.e.,

more recently diverged clades) (Swenson, 2011). In contrast,  $\beta_{\text{mpd}}$  (also called  $D_{\text{pw}}$  in the literature; e.g., Swenson, 2011; McFadden et al., 2019; Qian et al., 2021) measures the mean pairwise phylogenetic distance between all species pairs in two assemblages (Webb et al., 2008; Swenson, 2011). Thus,  $\beta_{\text{mpd}}$  measures turnover of deeper nodes of the phylogeny, compared with  $\beta_{\text{sor.phy}}$ .  $\beta_{\text{mpd}}$  is a basal-weighted metric of phylogenetic  $\beta$ -diversity (Swenson, 2011; McFadden et al., 2019). In addition to exploring geographic patterns of tip-weighted phylogenetic  $\beta$ -diversity (i.e.,  $\beta_{\text{sor.phy}}$ ) reflecting shallow evolutionary history, we also explored geographic patterns of basal-weighted phylogenetic  $\beta$ -diversity (i.e.,  $\beta_{\text{mpd}}$ ) reflecting deep evolutionary history. We used the formula for  $D_{\text{pw}}$  in Swenson (2011) to calculate  $\beta_{\text{mpd}}$ .

We used the following R packages in computing  $\beta$ -diversity metrics: betapart (Baselga and Orme, 2012), vegan (Dixon, 2003), picante (Kembel et al., 2010), and PhyloMeasures (Tsirogianis and Sandel, 2016).

#### 2.4. Data analysis

We used a neighborhood approach (also called moving window approach) to determine  $\beta$ -diversity for each of the 420 geographic units. Specifically, we calculated the average  $\beta$ -diversity between a focal geographic unit and each of its six closest neighboring geographic units. This approach, or a similar one, has been commonly used in  $\beta$ -diversity studies (e.g., McFadden et al., 2019; Qian et al., 2020, 2021). In our preliminary analyses, we also calculated the average  $\beta$ -diversity between a focal

geographic unit and each of its four closest neighboring geographic units, and found that the average values of  $\beta$ -diversity metrics based on the four closest neighboring geographic units were highly correlated with those based on the six closest neighboring geographic units (e.g., correlation coefficient is 0.967 for  $\beta_{\text{sor.tax}}$ ), indicating that the approach of using the six closest neighboring geographic units in our study would be sufficiently robust. We did not use a larger number of the closest neighboring geographic units to avoid or minimize the inclusion of neighboring geographic units that were far away from the focal geographic unit. In this study, on average, the distance between the centroid of each geographic unit and the centroids of its six closest neighboring geographic units was 718 km.

We related  $\beta$ -diversity to latitude (the centroid of each geographic unit). We considered a correlation (Spearman's rank correlation coefficient,  $r_s$ ) to be strong for  $|r_s| > 0.66$ , moderate for  $0.66 \geq |r_s| > 0.33$ , and weak for  $|r_s| \leq 0.33$  (Qian et al., 2019a). We used SYSTAT v.7 (Wilkinson et al., 1992) for statistical analyses.

### 3. Results

#### 3.1. Total $\beta$ -diversity

Total taxonomic  $\beta$ -diversity ( $\beta_{\text{sor.tax}}$ ) was strongly correlated to total phylogenetic  $\beta$ -diversity ( $\beta_{\text{sor.phy}}$ ) ( $r_s = 0.994$ ,  $P < 0.001$ ). As a result, geographic patterns of taxonomic  $\beta$ -diversity are very similar to those of phylogenetic  $\beta$ -diversity (Fig. 1). Regions with high total  $\beta$ -diversity were located in a belt including northern

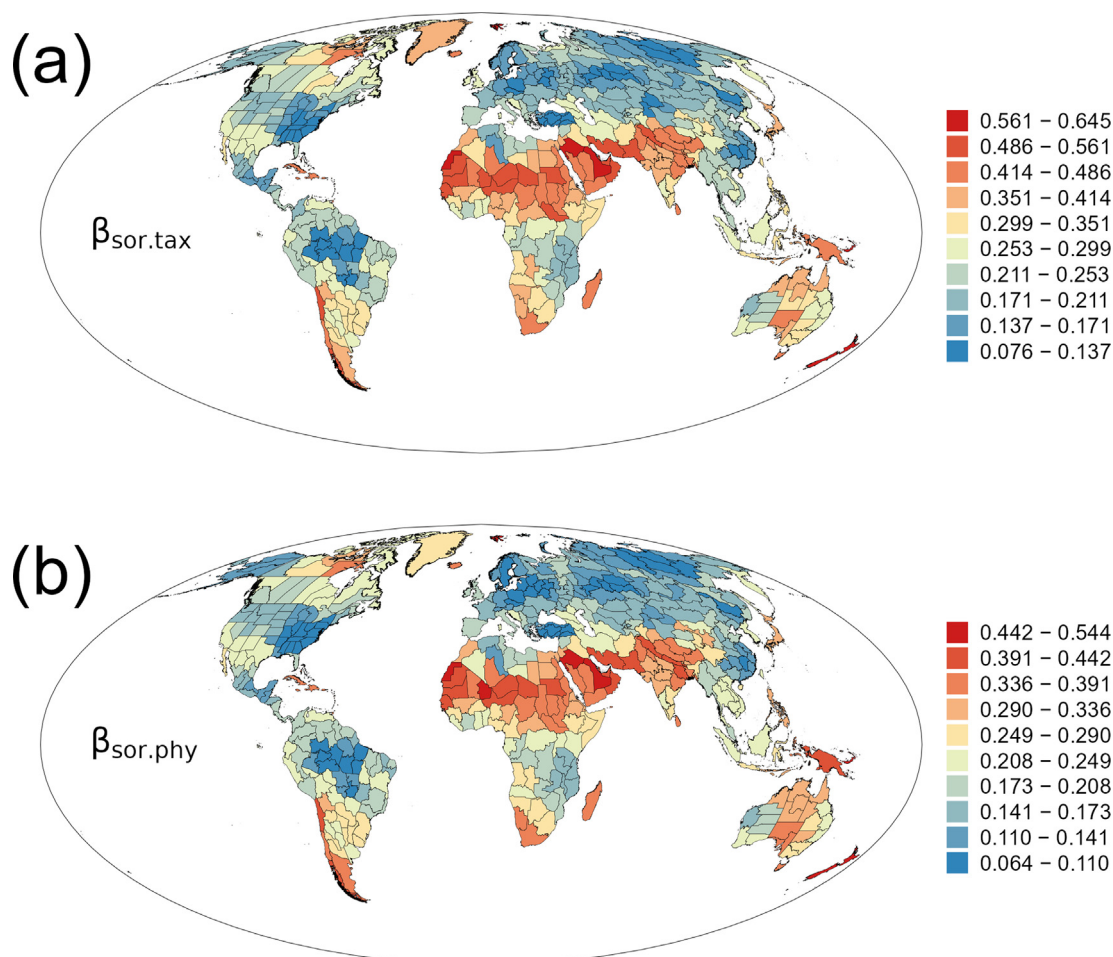


Fig. 1. Geographic patterns of total taxonomic and phylogenetic  $\beta$ -diversity ( $\beta_{\text{sor.tax}}$  and  $\beta_{\text{sor.phy}}$ ) for angiosperm genera in regional floras in the world.



Africa, Arabian Peninsula, eastward to India and eastern Himalaya, which were followed by northeastern North America, southern South America, southern Africa, Madagascar, and several regions in Oceania (Fig. 1). Regions with low total  $\beta$ -diversity were located in Brazil, southeastern North America, northern Eurasia, and southeastern China (Fig. 1).

### 3.2. Turnover component of $\beta$ -diversity

The turnover component of taxonomic  $\beta$ -diversity ( $\beta_{\text{sim,tax}}$ ) was also strongly correlated with that of phylogenetic  $\beta$ -diversity ( $\beta_{\text{sim,phy}}$ ) ( $r_s = 0.977$ ,  $P < 0.001$ ). Geographic patterns of the turnover component of taxonomic  $\beta$ -diversity ( $\beta_{\text{sim,tax}}$ ) were similar to those of phylogenetic  $\beta$ -diversity ( $\beta_{\text{sim,phy}}$ ) (Fig. 2). They were, to a large degree, similar to those of total  $\beta$ -diversity (compare Fig. 2 with Fig. 1). Correlation coefficient was 0.774 ( $P < 0.001$ ) between  $\beta_{\text{sim,tax}}$  and  $\beta_{\text{sor,tax}}$ , and was 0.728 ( $P < 0.001$ ) between  $\beta_{\text{sim,phy}}$  and  $\beta_{\text{sor,phy}}$ .

### 3.3. Nestedness component of $\beta$ -diversity

The nestedness component of taxonomic  $\beta$ -diversity ( $\beta_{\text{nes,tax}}$ ) was strongly correlated to that of phylogenetic  $\beta$ -diversity ( $\beta_{\text{nes,phy}}$ ) ( $r = 0.978$ ,  $P < 0.001$ ). Geographic patterns of the nestedness component of taxonomic  $\beta$ -diversity ( $\beta_{\text{nes,tax}}$ ) were similar to those of phylogenetic  $\beta$ -diversity ( $\beta_{\text{nes,phy}}$ ) (Fig. 3). They were, to some

degree, similar to those of total  $\beta$ -diversity (compare Fig. 3 with Fig. 1) and those of the turnover component of  $\beta$ -diversity (compare Fig. 3 with Fig. 2). Coefficients of correlation of  $\beta_{\text{nes,tax}}$  with  $\beta_{\text{sor,tax}}$  and  $\beta_{\text{sim,tax}}$  were 0.740 and 0.220, respectively, and coefficients of correlation of  $\beta_{\text{nes,phy}}$  with  $\beta_{\text{sor,phy}}$  and  $\beta_{\text{sim,phy}}$  were 0.792 and 0.224, respectively ( $P < 0.05$  in all cases).

### 3.4. Ratio of nestedness to total $\beta$ -diversity

Geographic patterns of  $\beta_{\text{ratio}}$ , which quantifies how much the nestedness components contribute to total  $\beta$ -diversity, were highly congruent between taxonomic and phylogenetic  $\beta$ -diversity ( $r = 0.961$ ,  $P < 0.001$ ). The ratio was, in general, high in regions in northern North America, at mid latitudes in Eurasia, western China, and tropical Africa (Fig. 4). The vast majority of these regions had values of  $\beta_{\text{ratio,tax}}$  and  $\beta_{\text{ratio,phy}}$  larger than 0.5.

### 3.5. Deviation between phylogenetic and taxonomic $\beta$ -diversity

Deviation between phylogenetic and taxonomic  $\beta$ -diversity (i.e.,  $\beta_{\text{dev}}$ ) was positive in all regions across the world (Fig. 5). Regions with high values of  $\beta_{\text{dev}}$  was primarily located in North America, northern Eurasia, northeastern Africa, and Brazil (Fig. 5), whereas regions with low values of  $\beta_{\text{dev}}$  was primarily located in mid latitudes of Asia and Indo-China, northern and southern South America, northwestern and central Africa, and eastern Australia (Fig. 5).

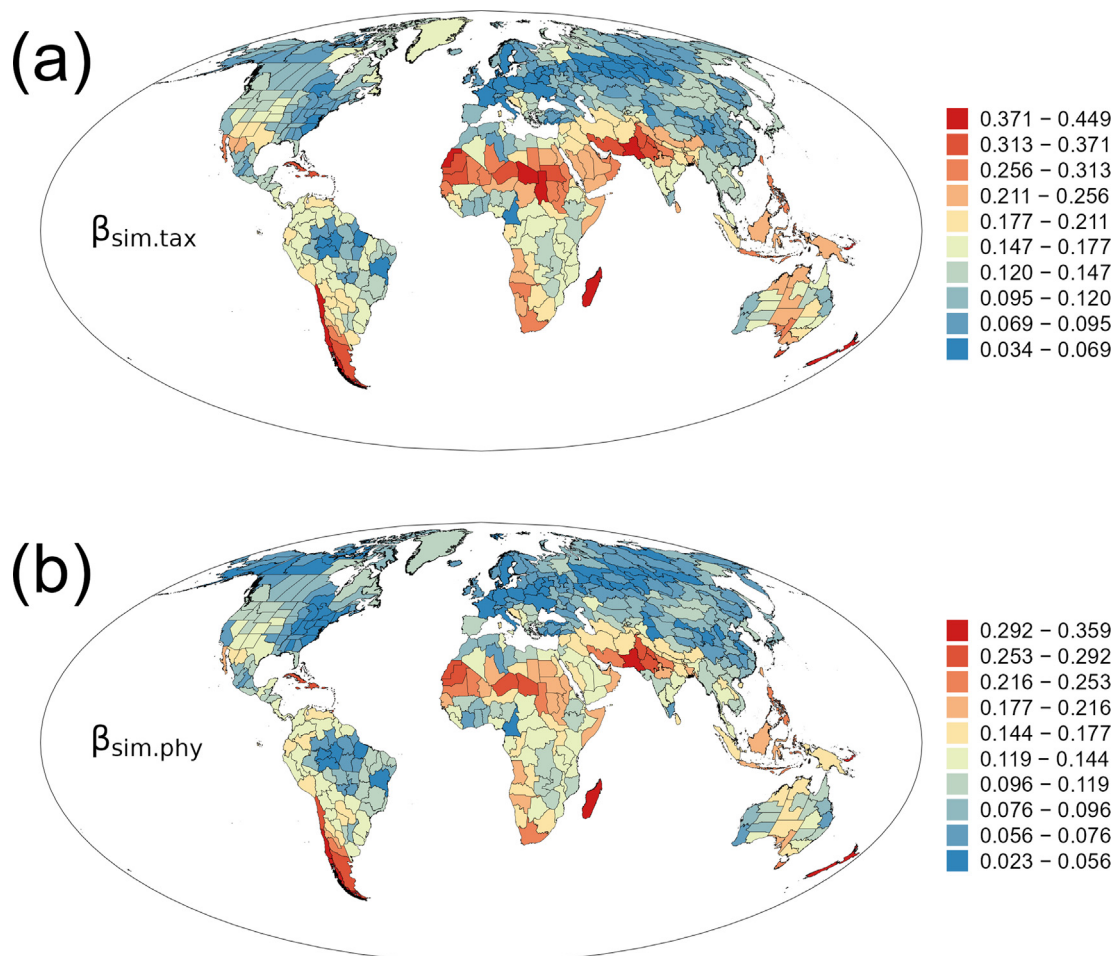


Fig. 2. Geographic patterns of the turnover components of taxonomic and phylogenetic  $\beta$ -diversity ( $\beta_{\text{sim,tax}}$  and  $\beta_{\text{sim,phy}}$ ) for angiosperm genera in regional floras in the world.

### 3.6. $\beta$ -diversity at deep evolutionary history

Geographic patterns of high versus low values of basal-weighted phylogenetic  $\beta$ -diversity ( $\beta_{\text{mpd}}$ ) were conspicuous (Fig. 6). In the New World, most of the regions in South America and eastern North America had high  $\beta_{\text{mpd}}$ , and regions with low  $\beta_{\text{mpd}}$  were located in southwestern North America and southernmost South America (Fig. 6). In the Old World, regions with low  $\beta_{\text{mpd}}$  were located in the combination of the mega-region from central Asia westward to northern Africa and northwestward to northern Europe; and most of the remainder regions, which were from eastern and southwestern China southward to Australia and New Zealand, had high  $\beta_{\text{mpd}}$  (Fig. 6).

### 3.7. Relationships between $\beta$ -diversity and latitude

When all the 420 geographic units worldwide were considered together, taxonomic and phylogenetic  $\beta$ -diversity (i.e.,  $\beta_{\text{sor.tax}}$  and  $\beta_{\text{sor.phy}}$ ) and their turnover and nestedness components (i.e.,  $\beta_{\text{sim.tax}}$ ,  $\beta_{\text{nes.tax}}$ ,  $\beta_{\text{sim.phy}}$  and  $\beta_{\text{nes.phy}}$ ), were negatively correlated with latitude (Table 1). Basal-weighted phylogenetic  $\beta$ -diversity (i.e.,  $\beta_{\text{mpd}}$ ) was also negatively correlated with latitude. However, the ratio of nestedness to total  $\beta$ -diversity (i.e.,  $\beta_{\text{ratio.tax}}$  and  $\beta_{\text{ratio.phy}}$ ) and the deviation between phylogenetic and taxonomic  $\beta$ -diversity (i.e.,  $\beta_{\text{dev}}$ ) were all positively correlated with latitude (Table 1). When geographic units in the Northern and Southern Hemispheres were analyzed separately, each metric of taxonomic

and phylogenetic  $\beta$ -diversity (i.e.,  $\beta_{\text{sor.tax}}$  and  $\beta_{\text{sor.phy}}$ ) and their turnover and nestedness components (i.e.,  $\beta_{\text{sim.tax}}$ ,  $\beta_{\text{nes.tax}}$ ,  $\beta_{\text{sim.phy}}$  and  $\beta_{\text{nes.phy}}$ ) was also negatively correlated with latitude in the Northern Hemisphere (Fig. 7), consistent with the pattern at the global scale, but was positively correlated with latitude in the Southern Hemisphere (Fig. 7). Basal-weighted phylogenetic  $\beta$ -diversity (i.e.,  $\beta_{\text{mpd}}$ ) was negatively correlated with latitude in both Northern and Southern Hemispheres (Fig. 8).

## 4. Discussion

Here we have leveraged a large dataset of distributions and evolutionary relationships to map taxonomic and phylogenetic  $\beta$ -diversity of angiosperm genera in regional floras across the world. Previous studies on  $\beta$ -diversity of angiosperms either did not simultaneously investigate both taxonomic and phylogenetic  $\beta$ -diversity or investigated both taxonomic and phylogenetic  $\beta$ -diversity but included assemblages in only one or two continents (e.g., North America, Qian et al., 2013; Pinto-Ledezma et al., 2018; Americas, McFadden et al., 2019; China, Qian et al., 2020). To the best of our knowledge, the present study is the first to explore taxonomic and phylogenetic  $\beta$ -diversity of angiosperms at a global scale. Thus, the finding of this study fills a critical knowledge gap.

Our study found that taxonomic and phylogenetic  $\beta$ -diversity is highly heterogeneous across the world. At the global scale, we found that both taxonomic and phylogenetic  $\beta$ -diversity is negatively, albeit not strongly, correlated with latitude. This finding is

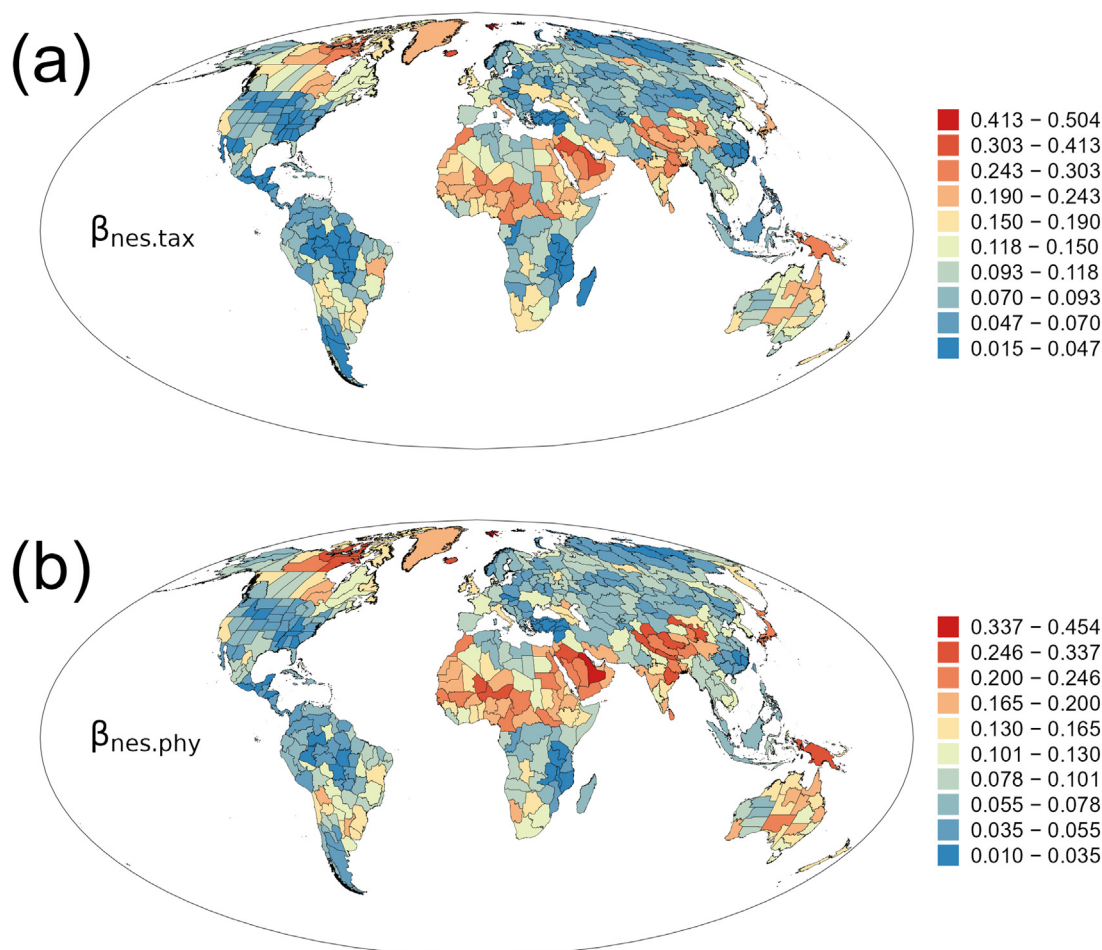


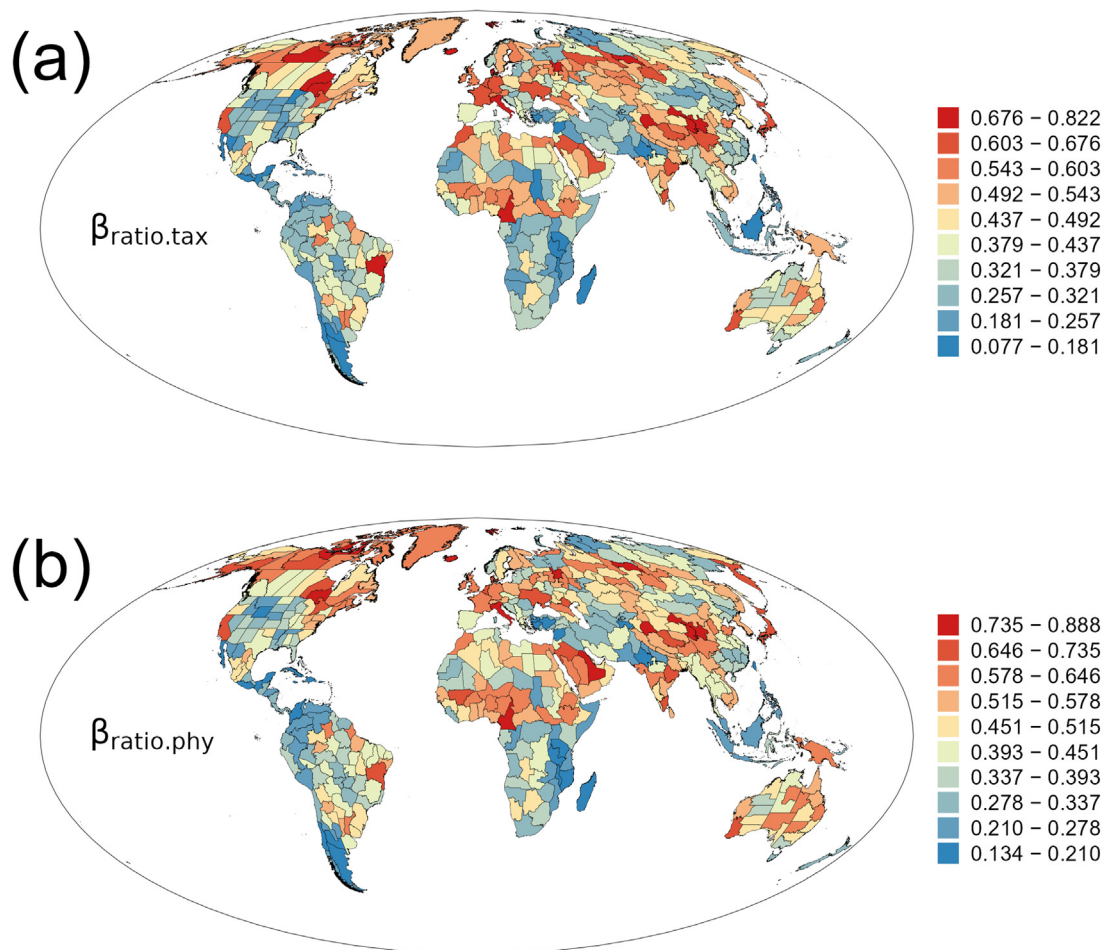
Fig. 3. Geographic patterns of the nestedness components of taxonomic and phylogenetic  $\beta$ -diversity ( $\beta_{\text{nes.tax}}$  and  $\beta_{\text{nes.phy}}$ ) for angiosperm genera in regional floras in the world.

consistent with the finding of a recent study (Qian et al., 2023) that taxonomic and phylogenetic  $\alpha$ -diversity of angiosperms in regional floras across the world is negatively correlated with latitude. However, there exist conspicuous discrepancies in geographic patterns between  $\alpha$ -diversity and  $\beta$ -diversity for angiosperms in some continental regions. For example, regions with the highest taxonomic and tip-weighted phylogenetic  $\beta$ -diversity of angiosperms are located in the Sahara and the Arabian Peninsula (Fig. 1), but these regions have, in general, low taxonomic and phylogenetic  $\alpha$ -diversity of angiosperms, as shown in fig. 1 of Qian et al. (2023). Within the New World, regions at high latitudes have higher taxonomic and tip-weighted phylogenetic  $\beta$ -diversity of angiosperms than those at low latitudes (Fig. 1), but the opposite pattern is observed for taxonomic and phylogenetic  $\alpha$ -diversity of angiosperms (Qian et al., 2023). Furthermore, regions within a large land mass located in the combination of southern China and Indo-China, which is located in warm and humid subtropical or tropical climates, have high taxonomic and phylogenetic  $\alpha$ -diversity of angiosperms (Qian et al., 2023), but these regions have low taxonomic and tip-weighted phylogenetic  $\beta$ -diversity of angiosperms, as shown in this study. Because these two studies focused on different taxonomic ranks (i.e., the genus rank in this study, the species rank in Qian et al., 2023), part of the discrepancies between these two studies may result from the use of composition data at different taxonomic ranks. It is also possible that at a given taxonomic rank,

geographic patterns of  $\beta$ -diversity do not match those of  $\alpha$ -diversity at a global scale, although consistency in geographic patterns of  $\alpha$ - and  $\beta$ -diversity has been found in studies at regional and continental scales (e.g., Qian et al., 2019a, 2020).

Interestingly, when geographic units in the Northern and Southern Hemispheres were analyzed separately, each metric of taxonomic and phylogenetic  $\beta$ -diversity and their turnover and nestedness components (i.e.,  $\beta_{\text{sor,tax}}$ ,  $\beta_{\text{sim,tax}}$ ,  $\beta_{\text{nes,tax}}$ ,  $\beta_{\text{sor,phy}}$ ,  $\beta_{\text{sim,phy}}$  and  $\beta_{\text{nes,phy}}$ ) was negatively correlated with latitude in the Northern Hemisphere, but was positively correlated with latitude in the Southern Hemisphere (Fig. 7). Why the two hemispheres show the opposite relationships between the phylogenetic metrics and latitude remains not clear.

We found that taxonomic and tip-weighted phylogenetic  $\beta$ -diversity (i.e.,  $\beta_{\text{sor,tax}}$  and  $\beta_{\text{sor,phy}}$ , respectively) is highly correlated across the world (Fig. 1). This is true also for their turnover and nestedness components (i.e.,  $\beta_{\text{sim,tax}}$  versus  $\beta_{\text{sim,phy}}$ ;  $\beta_{\text{nes,tax}}$  versus  $\beta_{\text{nes,phy}}$ ). Similar findings have been reported in studies for regional assemblages of angiosperm in China and North America (Qian et al., 2013, 2020). Our study found that taxonomic  $\beta$ -diversity is higher than tip-weighted phylogenetic  $\beta$ -diversity for each angiosperm assemblage across the world ( $\beta_{\text{dev}} > 0$ ), which is expected as phylogenetic  $\beta$ -diversity captures deeper evolutionary similarity in biological community composition. Our finding suggests that  $\beta$ -diversity patterns predominantly consist in the exchange of



**Fig. 4.** Geographic patterns of the relative importance of the nestedness component of  $\beta$ -diversity ( $\beta_{\text{ratio,tax}}$  for taxonomic  $\beta$ -diversity;  $\beta_{\text{ratio,phy}}$  for phylogenetic  $\beta$ -diversity) for angiosperm genera in regional floras in the world.



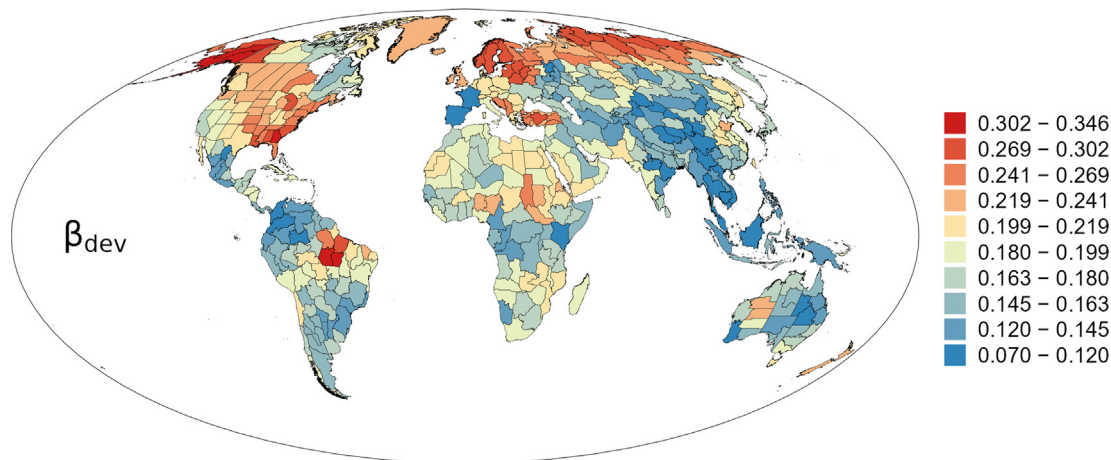


Fig. 5. Geographic patterns of the deviation of phylogenetic  $\beta$ -diversity with respect to taxonomic  $\beta$ -diversity ( $\beta_{dev}$ ) for angiosperm genera in regional floras in the world.

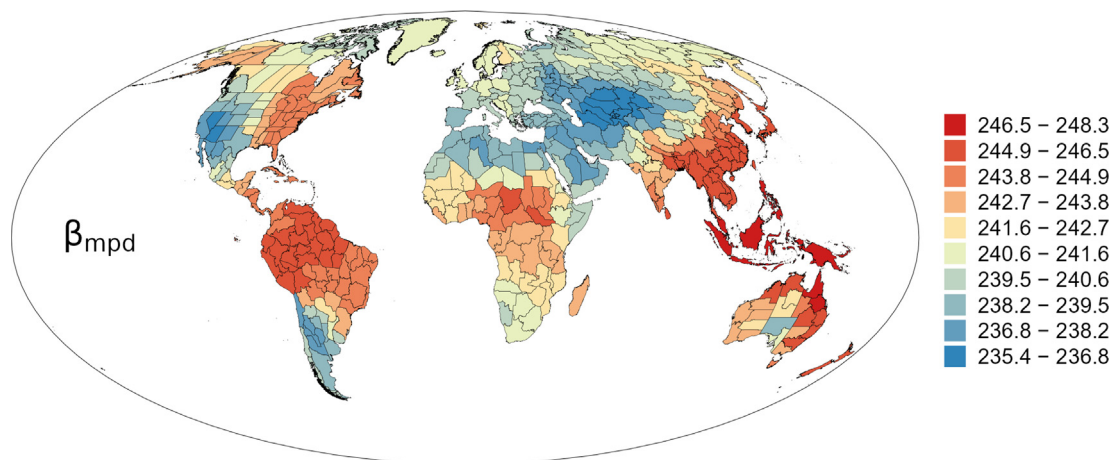


Fig. 6. Geographic patterns of basal-weighted phylogenetic  $\beta$ -diversity ( $\beta_{mpd}$ ) for angiosperm genera in regional floras in the world.

phylogenetically close species across space (i.e., species belonging to the same lineage) rather than distant ones (i.e., species belonging to different lineages). Lower tip-weighted phylogenetic  $\beta$ -diversity than taxonomic  $\beta$ -diversity has been also found in previous regional or continental studies on  $\beta$ -diversity for angiosperms (e.g., Qian et al., 2020). Interestingly, in their study on  $\beta$ -diversity in mammals across the world, Peixoto et al. (2017) found that some regions have negative values of  $\beta_{dev}$ , which is not expected.

Our study found that turnover and nestedness components of  $\beta$ -diversity are positively correlated with each other, regardless of whether taxonomic  $\beta$ -diversity or phylogenetic  $\beta$ -diversity is considered. This finding is inconsistent with that of Qian et al. (2020), who found that patterns of variation in the turnover and nestedness components tend to be opposite for both taxonomic and phylogenetic  $\beta$ -diversity of angiosperm species in China. This discrepancy may result from differences in spatial extent (i.e., global versus regional) and at taxonomic rank (i.e., the genus rank in our study versus the species rank in their study).

Of the ten metric of  $\beta$ -diversity examined in this study, the metric of basal-weighted phylogenetic  $\beta$ -diversity (i.e.,  $\beta_{mpd}$ ) showed the strongest geographic pattern, and was correlated most strongly with latitude ( $r_s = -0.508$ ; Table 1). Global geographic patterns of  $\beta_{mpd}$  are highly consistent with those of phylogenetic  $\alpha$ -diversity reported in Qian et al. (2023). For example, regions in

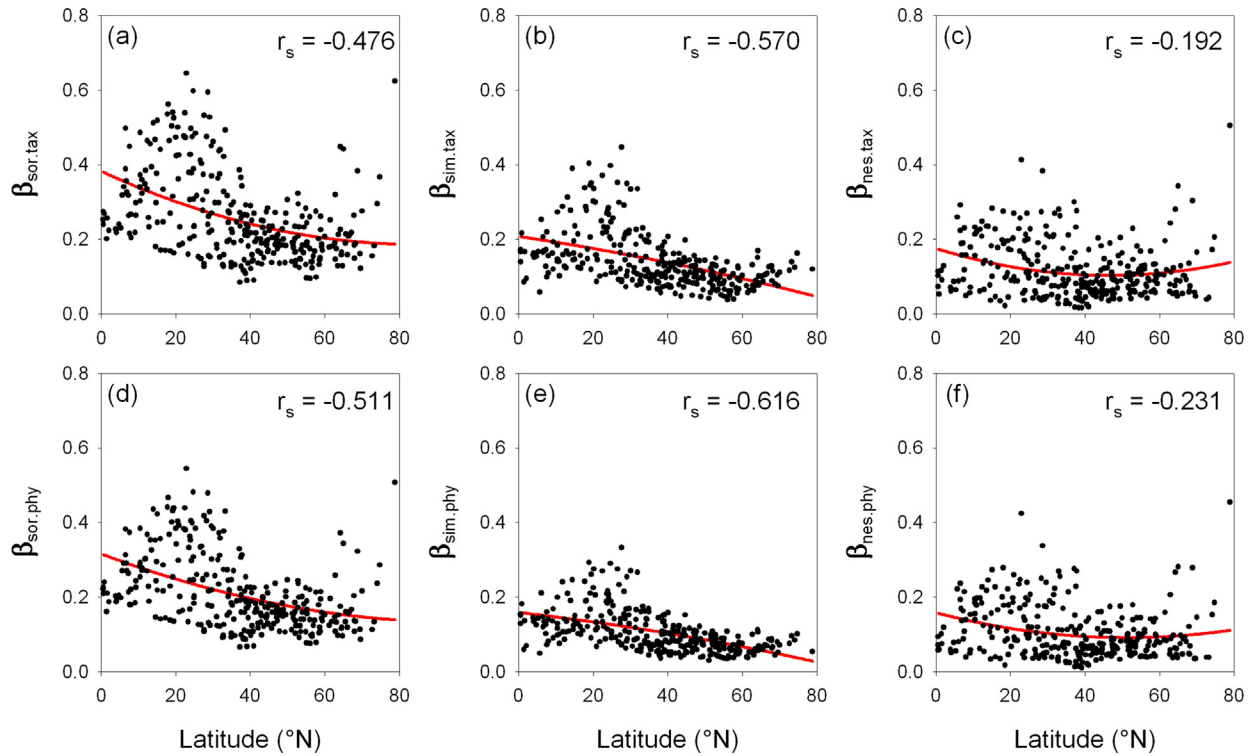
humid tropical climates in Africa, Asia, and South America have high values of both  $\beta_{mpd}$  and Faith's (1992) phylogenetic diversity (compare Fig. 6 with fig. 1b of Qian et al., 2023). Our study showed that the hotspot of the basal-weighted phylogenetic  $\beta$ -diversity is located on islands in Southeast Asia, from where it decreases northwestwards until reaching central Asia, which is to the cold-spot of the basal-weighted phylogenetic  $\beta$ -diversity. This finding is generally consistent with the finding of Qian et al. (2021), who found that within China, basal-weighted phylogenetic  $\beta$ -diversity

Table 1

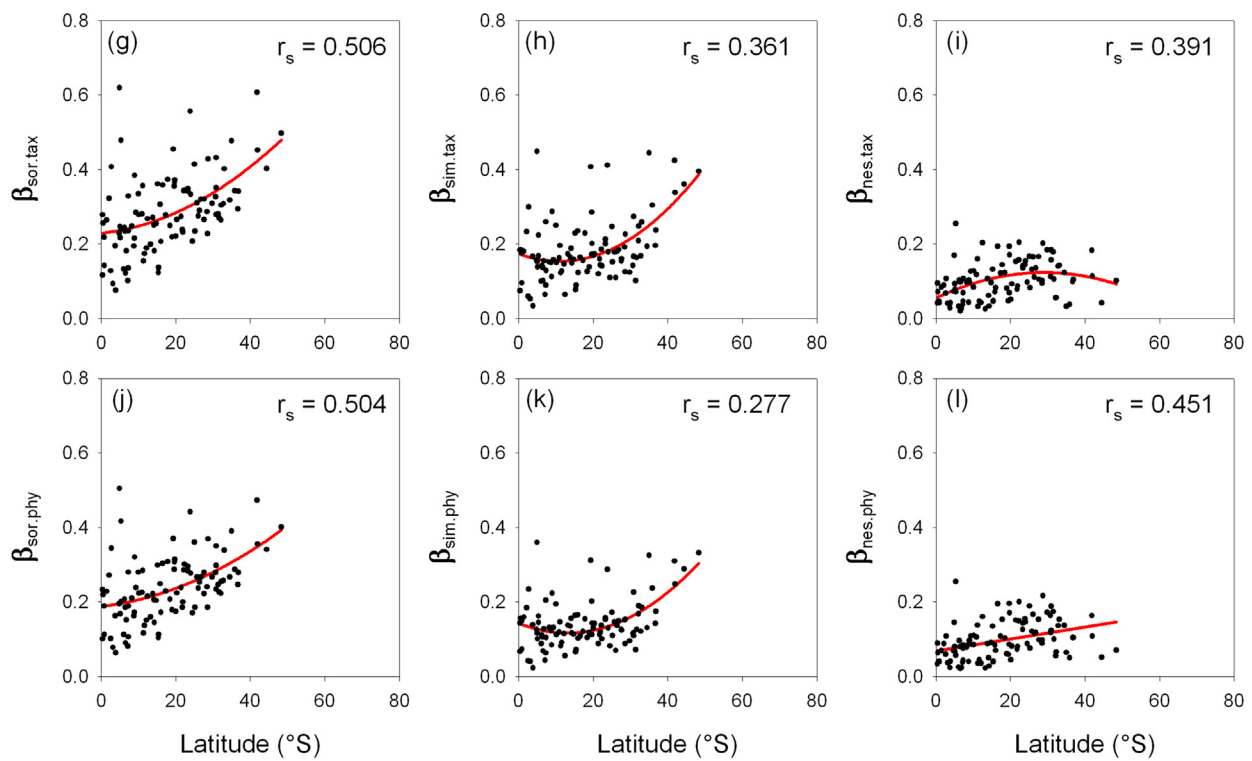
Spearman's rank correlation coefficient for the relationship between each metric of  $\beta$ -diversity and absolute latitude for angiosperm genera in regional floras in the world.

Metric	$r_s$	$P$ -value
$\beta_{sor.tax}$	-0.354	< 0.001
$\beta_{sor.phy}$	-0.384	< 0.001
$\beta_{sim.tax}$	-0.477	< 0.001
$\beta_{sim.phy}$	-0.521	< 0.001
$\beta_{nes.tax}$	-0.084	0.084
$\beta_{nes.phy}$	-0.125	0.010
$\beta_{ratio.tax}$	0.239	< 0.001
$\beta_{ratio.phy}$	0.222	< 0.001
$\beta_{dev}$	0.349	< 0.001
$\beta_{mpd}$	-0.508	< 0.001

(1) Northern Hemisphere

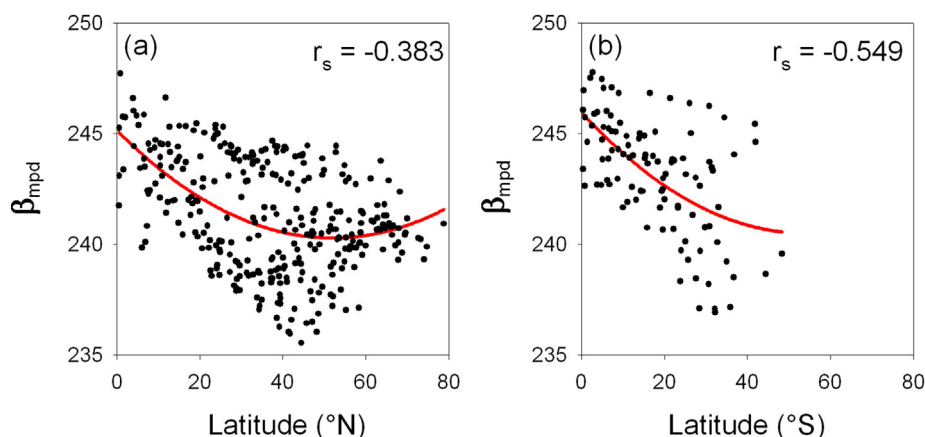


(2) Southern Hemisphere



**Fig. 7.** Relationships (Spearman's rank correlation coefficient,  $r_s$ ) between each metric of taxonomic and phylogenetic  $\beta$ -diversity and latitude for angiosperm genera in regional floras in (1) the Northern Hemisphere and (2) the Southern Hemisphere. Lines are the least squares fitting with the second-degree polynomial.





**Fig. 8.** Relationships (Spearman's rank correlation coefficient,  $r_s$ ) between basal-weighted phylogenetic  $\beta$ -diversity ( $\beta_{\text{mpd}}$ ) and latitude for angiosperm genera in regional floras in (a) the Northern Hemisphere and (b) the Southern Hemisphere. Lines are the least squares fitting with the second-degree polynomial.

decreases from the southeast towards the northwest. [McFadden et al. \(2019\)](#) investigated geographic patterns of basal-weighted phylogenetic  $\beta$ -diversity across Americas. The geographic patterns reported in their study are generally opposite to the geographic patterns of basal-weighted phylogenetic  $\beta$ -diversity observed in our study for Americas. For example, they found that regions with high values of basal-weighted phylogenetic  $\beta$ -diversity are located in southwestern North America and southern South America, as shown in their fig. 4c, but these regions had low values of basal-weighted phylogenetic  $\beta$ -diversity in our study ([Fig. 6](#)). It is not clear whether the use of taxa at different taxonomic ranks might have resulted in the discrepancy between the two studies.

In conclusion, we have explored geographic patterns of various aspects of taxonomic and phylogenetic  $\beta$ -diversity for angiosperm genera in regional floras across the world. Our study found that taxonomic and phylogenetic  $\beta$ -diversity is highly heterogeneous across the world on the one hand, and there are highly consistent geographic patterns among different metrics of phylogenetic  $\beta$ -diversity on the other hand. In most cases, metrics of  $\beta$ -diversity are negatively associated with latitude, particularly in the Northern Hemisphere. Different metrics of taxonomic  $\beta$ -diversity are strongly and positively correlated with their counterparts of phylogenetic  $\beta$ -diversity.

#### Author contributions

H.Q. designed research, analyzed data, and wrote the paper; S.Q. compiled and analyzed data; both authors participated in revising the paper.

#### Data availability statement

The data used in this study have been published and cited.

#### Declaration of competing interest

The authors have no competing interest to declare.

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