RESEARCH ARTICLE

Environmental filters shaping angiosperm tree assembly along climatic and geographic gradients

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Abstract

Question: Global-scale forest censuses provide an opportunity to understand diversification processes in woody plant communities. Based on the climatic or geographic filtering hypotheses associated with tropical niche conservatism and dispersal limitation, we analysed phylogenetic community structures across a wide range of biomes and evaluated to what extent region-specific processes have influenced large-scale diversity patterns of tree species communities across latitude or continent.

Location: Global.

Methods: We generated a data set of species abundances for 21,379 angiosperm woody plants in 843 plots worldwide. We calculated net relatedness index (NRI) for each plot, based on a single global species pool and regional species pools, and phylogenetic β-diversity (PBD) between plots. Then, we explored the correlations of NRI with climatic and geographic variables, and clarified phylogenetic dissimilarity along geographic and climatic differences. We also compared these patterns for South America, Africa, the Indo-Pacific, Australia, the Nearctic, Western Palearctic and Eastern Palearctic.

Results: NRI based on a global-scale species pool was negatively associated with precipitation and positively associated with Quaternary temperature change. PBD was positively associated with geographic distance and precipitation difference between plots across tropical and extratropical biomes. Moreover, phylogenetic dissimilarity was smaller in extratropical regions than in regions including the tropics, although temperate forests of the Eastern Palearctic showed a greater dissimilarity within extratropical regions.

Conclusions: Our findings support predictions of the climatic and geographic filtering hypotheses. Climatic filtering (climatic harshness and paleoclimatic change) relative to tropical niche conservatism played a role in sorting species from the global species pool and shaped the large-scale diversity patterns, such as the latitudinal gradient observed across continents. Geographic filtering associated with dispersal limitation substantially contributed to regional divergence of tropical/extratropical biomes among continents. Old, long-standing geographic barriers and recent climatic events differently influenced evolutionary diversification of angiosperm tree communities in tropical and extratropical biomes.

1 | INTRODUCTION

Understanding geographic differences in ecological diversification is fundamental to unravel the processes of species assembly along environmental gradients and between regions (Wiens & Donoghue, 2004). Prevailing hypotheses regarding global patterns of biodiversity include the centre-of-origin and vicariance hypotheses (Ricklefs, 2006). The former proposes that taxa originated from a localized area and dispersed to marginal regions in response to geographic/environmental constraints, whereas the latter asserts that regional diversity results from in situ diversification affected by geohistorical factors. In this context, environmental filtering associated with tropical niches restricts species dispersal from evolutionary centres (Wiens & Graham, 2005), predicting a high diversity in tropical regions (Romdal, Araújo, & Rahbek, 2013). Conversely, evolutionary radiations may be promoted by habitat stability through time (Stephens & Wiens, 2003) and by divergent selection or genetic drift through environmental heterogeneity or geographic isolation (Rundell & Price, 2009). These processes lead to a historical explanation for latitudinal patterns and regional differences in biodiversity (Mittelbach et al., 2007).

The global diversity patterns of woody angiosperm species are ideal for examining large-scale mechanisms related to tropical niche conservatism (or evolutionary radiation) and environmental filtering. In general, the latitudinal diversity gradient is relatively consistent between continents (Mutke & Bathlott, 2005). However, community diversity patterns differ substantially between neotropical and palaeotropical floras (Couvreur, 2014; Gentry, 1988), and between Nearctic and Palaearctic floras (Donoghue & Smith, 2004). Well-known examples are the lower diversity of Africa, called the 'odd man out' pattern in tropical rain forests (Richards, 1973), and the 'Asian bias' in species diversity of temperate floras (Qian & Ricklefs, 2000). These diversity anomalies of biomes between continents may be caused by geographic differences in radiations within disjunct families/genera in tropical or temperate forests (Donoghue & Smith, 2004; Gentry, 1988) or by selective extinctions related to past environmental changes in temperate forests (Eiserhardt, Borchsenius, Plum, Ordonez, & Svenning, 2015; Svenning, 2003). Climatic and geographic factors are important evolutionary constraints that have driven the large-scale patterns of woody plant diversity (Currie et al., 2004). Harsh climates can cause ecological bottlenecks that restrict particular families carrying an ancestral trait (e.g., intolerance to freezing) from dispersing into colder habitats (Hawkins, Rueda, Rangel, Field, & Diniz-Filho, 2014). Climate perturbations over geological time scales have affected species sorting through extinction and speciation, so historical climatic stability is also related to

environmental filtering (Graham, Moritz, & Williams, 2006). In addition, isolation by distance or elevation may result in species diversity through allopatric speciation related to dispersal limitations (Ohsawa & Ide, 2008). Therefore, evaluating the relative roles of climatic and geographic filtering can lead to a better understanding of the global and regional patterns of woody plant diversity (Kubota, Kusumoto, Shiono, Ulrich, & Jabot, 2016; Kubota, Shiono, & Kusumoto, 2015).

Community phylogenetic structures reflect significant signatures of large-scale dispersal, niche conservatism and/or niche divergence (Emerson & Gillespie, 2008). Therefore, a global-scale analysis of the phylogenetic structure of woody plant communities is a promising way to understand biogeographic histories of the latitudinal diversity pattern and regional diversity anomalies among continents (Pennington, Richardson, & Lavin, 2006). Phylogenetic clustering or overdispersion indicates that co-occurring species in a local community are more closely or less closely related than expected by chance, respectively (Webb, 2000). Moreover, phylogenetic dissimilarity (β-diversity) between local communities indicates spatial turnover of species in relation to environmental conditions or evolutionary divergence (Graham & Fine, 2008). These phylogenetic structures are expected to have been caused by species sorting associated with environmental filters (Verdu & Pausas, 2007), including dispersal limitation due to geographic constraints (Kubota, Hirao, Fujii, Shiono, & Kusumoto, 2014). Thus, community-level phylogenetic emergent properties can be an indicator of the importance of phylogenetic niche conservatism and other local historical factors in shaping biodiversity patterns (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Vamosi, Heard, Vamosi, & Webb, 2009). Nevertheless, intercontinental-scale studies on the community phylogenetics of plant assemblages have been scarce (Carlucci et al., 2017; Hardy, Couteron, Munoz, Ramesh, & Pélissier, 2012; Kissling et al., 2012). The lack of large-scale data sets on woody plant communities has restricted such analyses to mostly regional or continental scales (Hawkins et al., 2014; Kooyman, Rossetto, Cornwell, & Westoby, 2011).

In this study, we compiled a novel data set of the species abundances across a global data set of forest plots and explored macroecological signals in the global diversity gradients and the regional diversity anomalies of angiosperm woody plant communities. Based on the concepts of tropical niche conservatism and geographic vicariance, we tested the predictions of the climatic (harshness and instability) filtering and geographic filtering hypotheses: (a) species are phylogenetically more clustered (or non-randomly sorted) in climatically harsh, historically unstable and isolated regions because of environmental constraints; and (b) phylogenetic dissimilarity between local communities is predominantly significant between continents

and increases as climatic difference or geographic distance increase because of abiotic filtering and dispersal limitations.

First, we compared the phylogenetic structures (phylogenetic relatedness) of communities in South America, Africa, the Indo-Pacific and Australia (including the tropics), and of communities in the Nearctic, Western Palearctic and Eastern Palearctic. Second, to understand the roles of climatic and geographic factors in shaping these woody plant communities, we examined the environmental variables to explain their phylogenetic clustering using a regression model. Third, we evaluated phylogenetic β-diversity between local communities and subsequently examined the responses of phylogenetic dissimilarity to environmental variables related to climatic and geographic factors. Finally, we discuss the importance of environmental filtering related to climatic harshness, climatic instability and geographic constraints, and how region-specific processes have influenced global-scale diversity patterns of woody plant communities.

2 | METHODS

2.1 | Data sets

To collect the data on forest plots, we searched the scientific literature on ISI Web of Science (Thomson-Reuters, New York, NY, USA) using the following string: 'relative abundance' OR 'species abundance' OR 'community' OR 'assemblage' OR 'composition' OR 'diversity or distribution'. We retrieved 92,678 publications and filtered them such that each included study was: (a) quantitative, counting tree individuals within a certain plot; and (b) contained tables of woody plant species composition. We excluded studies that investigated secondary (managed) forests or only dominant species and that summarized rare species as "other species", and removed studies with small size plots (<100 m^2) or that addressed oceanic islands. We also collected web-based information on forest plots. To complement the data for some regions, we compiled information from publications in non-indexed local journals using Google Scholar (http://scholar.google.com/). In total, data from 183 publications were used. From each study, we extracted plot area, minimum measured DBH and site description, such as geographic location (latitude–longitude). The final data set contained 843 plots (range = 100–520,000 m^2, mean area = 15,340 m^2) of old-growth forests with at least two angiosperm species from individual sources (references for these studies are provided in Supporting information: Appendix S1). A more detailed description (e.g., sampling size) of the plots is provided in Kubota et al. (2016). Species taxonomy was standardized using The Plant List (http://www.theplantlist.org/). The data set comprised 3,027,055 individual trees encompassing 21,379 woody angiosperm species in 231 families and 2,699 genera. Tropical studies often contained unnamed species and morphospecies identified only to genus; these accounted for 4.0% of all individual trees in the data set. In our analysis, each unidentified species was analysed as a unique species within its genus. Note that 141 gymnosperm (conifer) species were found in the data set but these species were removed from the analysis of angiosperm phylogenetic structure because gymnosperm evolutionary history differs from that of angiosperms. Most plots (67%) had no gymnosperm species. Therefore, removing gymnosperm species has little influence on interpreting assembly processes of angiosperm tree species.

2.2 | Environmental data

Six environmental variables related to climatic and geographic factors were compiled for the 843 plots. The geographic locations of the plots were classified into seven biogeographic regions: South America, Africa, the Indo-Pacific, Australia, the Nearctic, Western Palearctic and Eastern Palearctic. The plots in South America, Africa, the Indo-Pacific and Australia were mostly tropical (between 23°27′N and 23°27′S). Mean annual temperature (°C), mean annual precipitation (mm) and elevation (m) were extracted from WorldClim (http://www.worldclim.org) at a resolution of 30-arcsec (approx. 1 km × 1 km). For some studies (12% of plots) that did not provide detailed geographical coordinates or place names, we assigned environmental variables for each grid cell at 0.5° latitude × 0.5° longitude (approx. 50 km × 50 km) containing a plot. Mean annual temperature (°C) and mean annual precipitation (mm) during the last glacial maximum were also extracted from the Community Climate System Model (CCSM; http://www.worldclim.org). Historical climate stability was calculated as the differences in mean annual temperatures (°C) and annual total precipitation (mm) between the last glacial maximum and the present day, representing the degree of Quaternary climate changes.

2.3 | Community phylogenetic structure

We used the phylogeny of Smith, Beaulieu, Stamatakis, and Donoghue (2011), which included 3,350 species (16%) of the angiosperm woody plants in our data set, as the basis to construct a phylogenetic tree of the 21,248 species in our data set. In this tree, 19,450 species (92%) were resolved at the genus level. Unresolved genera were placed as basal polytomies within their families; similarly, species were placed as polytomies within genera. The branch lengths of the phylogenetic tree were adjusted using the family-level phylogeny (Qian & Zhang, 2014), and were then calculated by placing undated nodes evenly between dated nodes, as performed in the application Bladj in Phylocom (Webb, Ackerly, & Kembel, 2008). On the basis of this phylogenetic tree, we calculated three indices of abundance-weighted community phylogenetic structure (net relatedness index), together with a species diversity index (Fisher's α). We also calculated an index of phylogenetic β-diversity to examine phylogenetic dissimilarity between plots.

The net relatedness index (NRI) measures the degree of phylogenetic clustering or dispersion relative to a source-pool phylogeny (Webb, 2000). NRI weighted by species abundance was calculated as the negative standardized effect size: the observed mean phylogenetic distance (X_{obs}) minus the mean of the null distribution (X_{rand}) divided by the SD (sdX_{rand}) of the null distribution. X_{obs} was calculated from a phylogenetic distance matrix between species weighted by

local species relative abundances. We generated the null distributions for NRI$_{global}$ and NRI$_{region}$ by shuffling species positions among the tips of the phylogenetic tree in a single global species pool and regional species pools for each region, respectively (Kissling et al., 2012). Then, 1,000 values of X$_{rand}$ and the corresponding sdX$_{rand}$ weighted by species abundances were obtained. Positive values of NRI$_{global}$ or NRI$_{region}$ indicate phylogenetic clustering relative to the respective source pool NRI. Therefore, NRI$_{global}$ and NRI$_{region}$ can be used to infer ecological species sorting caused by environmental filtering.

The detection of phylogenetic signals is known to depend on the resolution of the phylogeny (Hardy & Senterre, 2007) and on the taxonomic breadth and reference species pool used in the studies (Cavender-Bares, Keen, & Miles, 2006). Taxonomic information of global plot data is partly uncertain (Webb & Donoghue, 2005): for example, some genera are poorly resolved (including a lot of polytomies in the genus) while others are well resolved up to species tip level. Therefore, the presence of polytomies within the genus (taxon-specific resolution of phylogeny) may bias measures of community phylogenetics (Davies, Kraft, Salamin, & Wolkovich, 2012; Swenson, 2009). To confirm this issue, we conducted additional analysis using the phylogeny degenerated, in which all species were fairly placed as polytomies within the genus or within the families. The NRI$_{global/region}$ values calculated by the genus/family-level phylogeny with polytomies of species were consistent with those by the original phylogeny ($r > 0.99$). Therefore, uneven uncertainty of phylogeny among genera or families had no influence on the behaviour of the measured NRI$_{global/region}$.

Phylogenetic β-diversity (PBD) was examined using the mean pair-wise phylogenetic distance between the plots. The mean pair-wise phylogenetic distance was calculated as the phylogenetic distance separating a pair of individuals that were drawn from each of two plots (Fine & Kembel, 2011). This measures the amount of phylogenetic dissimilarity.

2.4 | Statistical analyses

The statistical analyses comprised fourth parts. First, geographic pattern of forest plots was ordinated in global climatic space of mean annual temperature and mean annual precipitation, based on Whittaker's biome (Whittaker, 1975): tropical rain forest, tropical seasonal forest/savanna, temperate rain forest, subtropical desert, temperate deciduous forest, woodland/shrubland, taiga and tundra. Second, to understand the regional differences in phylogenetic community structure, we compared the Fisher's α, NRI$_{global}$ and NRI$_{region}$ between South America, Africa, the Indo-Pacific and Australia (regions including the tropics), and between the Nearctic, Western Palearctic and Eastern Palearctic and tested their regional differences using Tukey's all-pair comparisons. Third, to evaluate the importance of climatic and geographic factors in shaping species assembly patterns, we examined the correlations between community structure indices (Fisher's α, NRI$_{global/region}$ and PBD) and environmental variables by the multiple regression models.

In the multiple regression analysis, Fisher's α, NRI$_{global}$ and NRI$_{region}$ values in each plot were set as response variables, and temperature, precipitation, Quaternary temperature change, Quaternary precipitation change and elevation were set as explanatory variables. To remove the influence of differences in plot area and minimum measured DBH, we included these as covariates in the regression model. Precipitation, elevation and plot area were log-transformed. All the explanatory variables were standardized to have zero mean and unit variance before parameter estimation. The level of collinearity between these explanatory variables was tested by calculating the determinant of the correlation matrix (D), the condition index (CI) and the variance inflation factor (VIF): D was 0.21, the maximum CI value was 2.70 and the VIFs ranged from 1.10 to 2.10, indicating the absence of multicollinearity in the regression model. Moreover, to evaluate spatial autocorrelation in Fisher's α, NRI$_{global}$ and NRI$_{region}$ values, we calculated eigenvector-based spatial filters that were generated from a geographic distance matrix among the plots. The first eigenvector describes the spatial structure at a broad scale (see Supporting information: Appendix S2; Ulrich et al., 2016). To control for spatial autocorrelation (Diniz-Filho & Bini, 2005), therefore, we added the spatial filter as a predictor of the response variable. Then we calculated the relative importance of each explanatory variable in a regression model according to its partial coefficient of determination, and identified the predominant variables that accounted for >10% of the sum of partial determinations of the explanatory variables. The statistical significance of each variable was evaluated using F-tests with Bonferroni-corrected p-values. The spatial correlogram of the response variables (raw data) and the residuals of the regression model accounting for the first eigenvector were examined using Moran's I. In addition, we conducted the regression analysis excluding the spatial filter to confirm its influence on estimating the coefficients for the other explanatory variables.

The correlation between PBD values and the explanatory variables was tested with multiple regressions on distance matrices (MRMs; Graham et al., 2006). In MRM analysis, PBD was set as response variable, and geographic distances, biogeographic distinctions and differences in environmental variables between plots, i.e., distance matrices were set as explanatory variables. The matrix of biogeographic distinctions was defined as one categorical variable dividing the pair of plots; a value of 0 was given to the elements of two plots in the same region, and a value of 1 was given to the elements of two plots crossing different regions. To remove the influence of differences in plot area and minimum measured DBH, we included their distance matrices between plots as covariates in the MRM. The differences in precipitation, elevation, plot area and geographic distance between plots were log-transformed. Statistical significance of the parameter estimate for the multiple regression model on distance matrices was examined with the 1,000 permutations test.

The regression coefficients using global-scale data are sensitive to the range of variables. Therefore, we conducted the analyses at two different scales: the regression analyses were applied to the
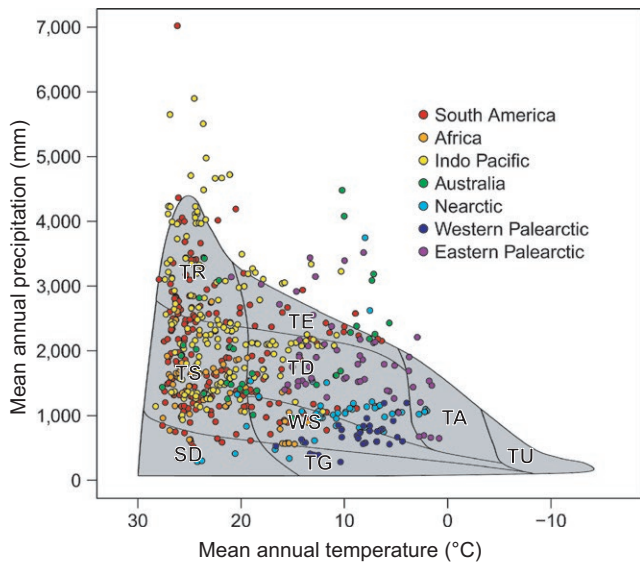
FIGURE 1 Location of forest plots in global climatic space; the relationship between mean annual temperature and mean annual precipitation based on Whittaker's biome:(TR) tropical rain forest; (TS) tropical seasonal forest/savanna; (TE) temperate rain forest; (SD) subtropical desert; (TD) temperate deciduous forest; (WS) woodland/shrubland; (TG) temperate grassland/desert; (TA) taiga; (TU) tundra

global data set along the whole gradient and also separately to the regional data sets. In this way, we examined global-scale and region-specific environmental drivers of Fisher's α, $NRI_{global/region}$ and PBD.

Finally, to illustrate historical diversification of forest communities that would be related to environmental factors including geography, we ordinated patterns of forest plots using NMDS based on the values of phylogenetic β-diversity. We also tested the differences in phylogenetic distance between pairs of the regions using permutational multivariate ANOVA (PERMANOVA) with 999 permutations and examined their geographic separation.

All the analyses were performed and the graphics were constructed using the R Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, Austria): 'picante' (Kembel et al., 2010) for editing the phylogenetic trees and calculating phylogenetic metrics; 'geosphere' for calculating the distance between the plots; 'vegan' for standardizing the environmental variables, NMDS and PERMANOVA; 'ncf' for analysing the spatial correlogram; 'multcomp' for multiple comparisons; 'raster' for editing raster data; and 'ecodist' (Goslee & Urban, 2007) for MRM analysis.

3 | RESULTS

Forest plots were ordinated along the gradients of mean annual temperature and mean annual precipitation (Figure 1): the data set contained tropical rain forest, tropical seasonal forest, woodland/shrubland, temperate rain forest, temperate deciduous forest and taiga. The phylogenetic structure indices substantially showed non-random geographic patterns (Figure 2). In South America,

Africa, the Indo-Pacific and Australia including the tropics, Fisher's α differed along longitudinal gradient between regions; e.g., South America had higher diversity (Figure 3). NRI_{global} was significantly larger in the Nearctic, Western Palearctic, Eastern Palearctic and Africa; and NRI_{region} showed no significant differences between the regions.

At the global scale, Fisher's α was positively associated with temperature and precipitation, and was negatively associated with Quaternary precipitation change (Table 1). NRI_{global} and NRI_{region} were negatively associated with precipitation, and NRI_{global} was positively associated with Quaternary temperature change. Note that plot area or minimum measured DBH were generally not associated with the phylogenetic structure indices (Table 1). Although Fisher's α, NRI_{global} and NRI_{region} of the plots were autocorrelated (Supporting information: Appendix S3), the estimation of regression coefficients and their significance levels were not substantially biased by spatial autocorrelation; the presence or absence of the spatial filter had little effect on estimating the coefficients for the other explanatory variables (Table 1, Supporting information: Appendix S4).

The predictor variables of regional Fisher's α values and phylogenetic structure partly differed between biogeographic regions (Supporting information: Appendix S5). Fisher's α was positively associated with temperature in South America, the Indo-Pacific region and Australia, was positively associated with precipitation in South America and Africa, and was negatively associated with Quaternary precipitation change in South America and the Indo-Pacific region. A negative correlation of NRI_{global} or NRI_{region} with precipitation was observed in South America and the Eastern Palearctic.

The correlation of PBD values with the differences in environmental variables between plots was relatively weak (Table 2). Nonetheless, PBD was significantly positively associated with geographic distance and precipitation difference between plots (Table 2). In addition, differences in minimum measured DBH were not significantly associated with PBD, although differences in plot area were substantially correlated with PBD (Table 2). Precipitation difference showed the strongest relationship with PBD, as indicated by the relatively large partial determination coefficients (Table 2). At the regional scale, PBD was mainly positively correlated with geographic distance and precipitation or temperature difference (Supporting information: Appendix S6), although PBD of the Indo-Pacific and Australia was primarily driven by geographic distance. The NMDS divided plots in two dimensions (Figure 4); the first and second axes largely reflected biogeographic regions. The regional differences were statistically significant for all of the pairs (PERMANOVA, $p < 0.05$). The explanatory power (r^2) of the variance among plots differed between the pairs (Figure 4). The intra-regional phylogenetic dissimilarity was relatively small in the Nearctic, Eastern Palearctic and Western Palearctic in comparison with those in South America, Africa, the Indo-Pacific and Australia, as shown by larger r^2 values (Figure 4) and the scores of both NMDS axes (Figure 5). In addition, plots for the Eastern Palearctic showed a relatively similar pattern to those in the Indo-Pacific, especially on the first axes of the NMDS (Figure 5).
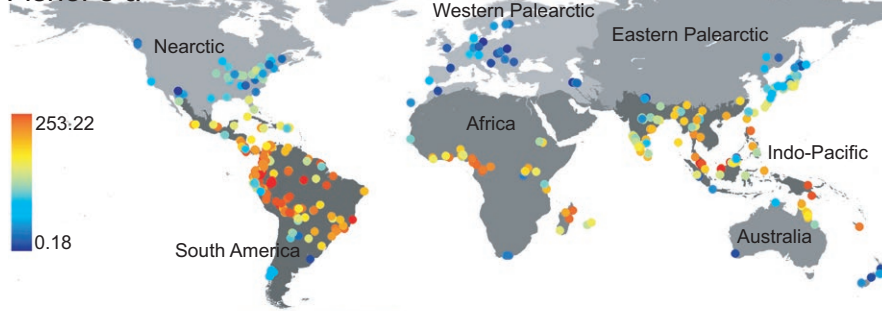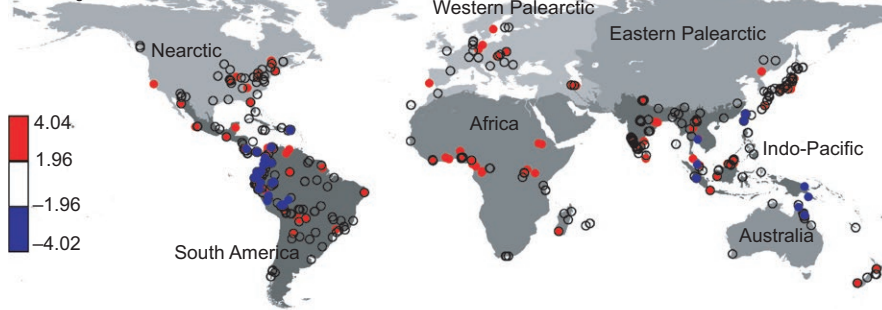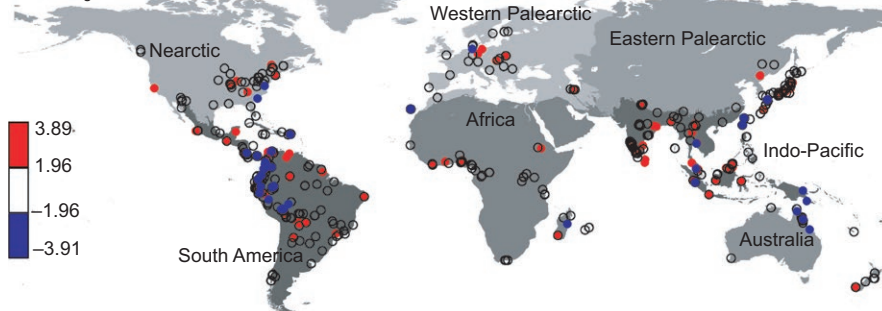
FIGURE 2 Geographic patterns of Fisher's diversity index (Fisher's α), net relatedness index to global species pool (NRI$_{global}$) and net relatedness index to regional species pools (NRI$_{region}$) for woody angiosperm communities. Red and blue colours indicate phylogenetic clustering and overdispersion relative to the respective source pool NRI, respectively. White colour indicates values of NRI within |±1.97| that mean no significant deviation from random expectation: 76.4% and 78.2% plots for NRI$_{global}$ and NRI$_{region}$ were within the range of random expectation
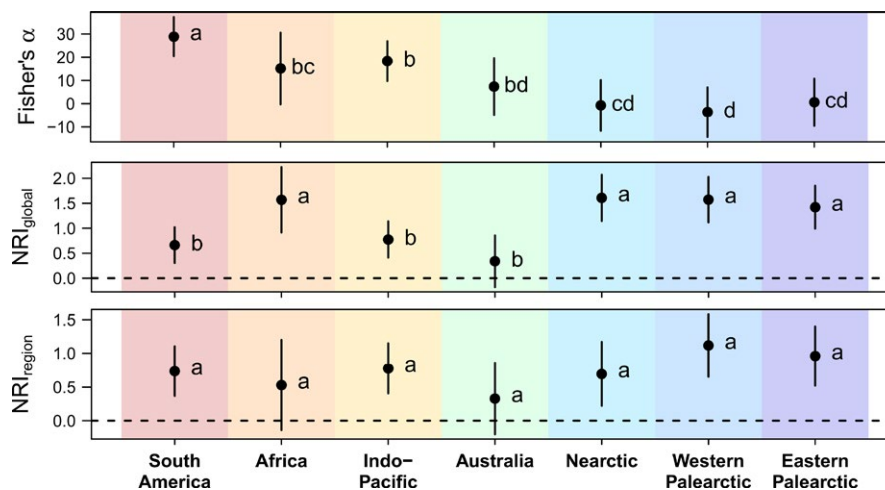
FIGURE 3 Regional differences in species diversity and phylogenetic structure for woody angiosperm communities between the seven regions. Plot area and minimum measured DBH were included in the model as covariates to remove the effects of sampling effects between plots. Fisher's α, Fisher's diversity index; NRI$_{global}$, net relatedness index based on global species pool; NRI$_{region}$, net relatedness index based on regional species pools for each region. Dots indicate mean values for the indices in each region, and bars represent the 95% confidence intervals. The statistical significance of differences between the regions was tested with Tukey's all-pair comparison. Dot-bars with different letters indicate values that are significantly different ($p < 0.05$) from each other

TABLE 1 Standardized regression coefficients and coefficients of partial determination (%) in regression models explaining the global-scale patterns of species diversity and net relatedness index for woody angiosperm communities

Response variable	Temp	Prec	Q.tc	Q.pc	Elev	Area	Size	spPC1	r^2
Fisher's α	0.24 (11%)*	0.50 (53%)*	0.03 (0%)	−0.21 (13%)*	−0.05 (1%)	0.01 (0%)	−0.12 (5%)*	0.24 (17%)*	0.34
NRI_{global}	0.15 (7%)*	−0.39 (56%)*	0.17 (10%)*	−0.04 (1%)	−0.01 (0%)	−0.01 (0%)	0.09 (5%)*	−0.21 (21%)*	0.18
NRI_{region}	0.17 (12%)*	−0.34 (60%)*	0.08 (3%)	−0.01 (0%)	0.02 (0%)	−0.04 (1%)	0.09 (6%)	−0.17 (17%)*	0.1

Notes. Regression analyses were applied to the global data set of woody angiosperm communities ($n = 843$). Fisher's α, Fisher's diversity index; NRI_{global}, net relatedness index based on the global species pool; NRI_{region}, net relatedness index based on regional species pools for each region; Temp, mean annual temperature; Prec, log-scaled annual precipitation; Q.tc, Quaternary temperature change; Q.pc, Quaternary precipitation change; Elev, log-scaled elevation; Area, log-scaled plot area; Size, minimum measured DBH; spPC1, the first eigenvector of a geographic distance matrix among the plots. r^2 indicates the coefficient of determination for a multiple regression model with a full set of explanatory variables. The values in parentheses are the proportion of the explanatory variable in the sum of partial determinations. Statistical significance of the parameter estimate for the partial regression model was tested with the F-test with the Bonferroni correction: *$p < 0.05/8$. Result of regional-scale patterns is shown in Supporting information: Appendix S5.

4 | DISCUSSION

4.1 | Global-scale predictors of phylogenetic structure

Plot data set compiled in this study shows global-scale effort of vegetation research including forest census across a wide range of biomes (Figure 1). Plot data are characterized by arbitrary research protocols (e.g., sampling size or measurement criteria), and in addition the sample size of plots that are distributed unevenly within each region may not be sufficient. Despite these drawbacks (or limitations), global-scale plot data sets provide an ideal opportunity to test diversification processes in plant communities by accounting for the influence of plot area and minimum measured DBH on the patterns of phylogenetic structure (Kooyman et al., 2011). Our results suggest that even with fine-grained plot data, their phylogenetic assembly patterns allow us to interpret macroecological signals in angiosperm tree assemblages (Hardy et al., 2012; Hawkins et al., 2014).
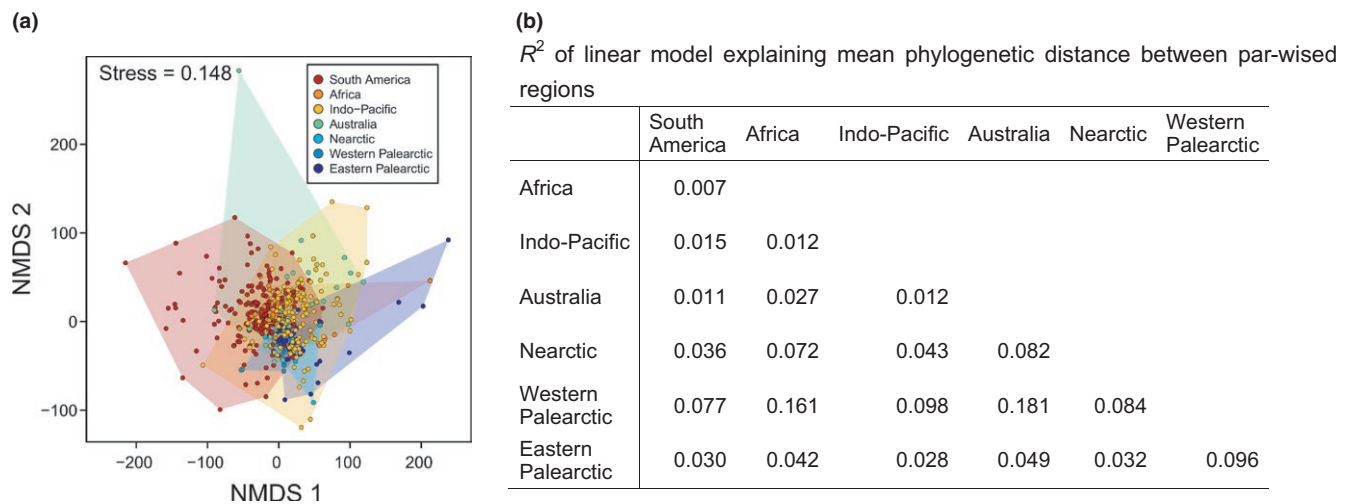
Large-scale processes that determine the global diversity patterns of tree species have been proposed on the basis of regional differences in species richness (Latham & Ricklefs, 1993). Recent studies have focused on phylogenetic patterns in woody plant communities within a region (Hawkins et al., 2014; Kooyman et al., 2011; Kubota, Kusumoto, Shiono, & Tanaka, 2017). These demonstrated phylogenetic clustering of species assembly in sub-tropical or temperate regions and thus suggested that harsh environments might act as a filter to exclude tropical taxa and to favour particular clades adapted to a cold climate. In this study, we revisited these findings from the viewpoint of global-scale predictors of phylogenetic structure (net relatedness and phylogenetic β-diversity) and discovered regional differences associated with climatic and geographic factors. Niche traits relevant to phylogeny (e.g., physiological cold tolerance; Hawkins et al., 2014) were not included in our analyses, and thus correlative analyses of the phylogenetic metrics and environmental factors do not demonstrate causation between variables. The explanatory power of the climate variables in the variance of the phylogenetic structure was relatively low, probably because of the influence of local environmental factors on species assembly.

Nonetheless, the results were generally in agreement with the predictions of the climatic and geographic filtering hypotheses in terms of phylogenetic niche conservatism and vicariance. Specifically, tree species were more phylogenetically clustered in climatically harsh and/or historically unstable areas. Although the patterns of phylogenetic metrics are sensitive to the taxonomic breadth of the reference species pools used in these studies, our global-scale analysis supported the previously reported phylogenetic patterns (Hawkins et al., 2014; Kooyman et al., 2011). In addition, phylogenetic clustering in arid regions indicated the importance of precipitation for phylogenetic structure. Notably, we detected a marked correlation of precipitation or temperature differences, Quaternary climate changes and geographic distance with phylogenetic dissimilarity among local communities: the predominant effects of climatic gradients on phylogenetic dissimilarity indicated the importance of climatic filtering (Kubota et al., 2014), as well as geographic filtering

TABLE 2 Standardized regression coefficients and coefficients of partial determination (%) in the multiple regression models explaining global-scale phylogenetic β-diversity for woody angiosperm communities

RegionM	DistM	TempM	PrecM	Q.tcM	Q.pcM	ElevM	AreaM	SizeM	r^2
−0.03	0.16	0.09	0.18	−0.16	0.08	0.07	−0.11	0.01	0.13
(1%)	(14%)*	(8%)*	(27%) *	(26%)*	(8%)*	(6%)*	(12%)*	(0%)	

Notes. Phylogenetic β-diversity was calculated using the mean pair-wise phylogenetic distance between the plots. PBD, phylogenetic β-diversity; RegionM, differences between biogeographic regions; DistM, log-scaled geographic distance; TempM, differences in mean annual temperature; PrecM, differences in log-scaled annual precipitation; Q.tcM, differences in Quaternary temperature change; Q.pcM, differences in Quaternary precipitation change; ElevM, differences in log-scaled elevation; AreaM, differences in log-scaled plot area; SizeM, differences in minimum measured DBH. r^2 indicates the coefficient of determination for a multiple regression model with a full set of the explanatory variables. Statistical significance of the parameter estimate for the multiple regression model on distance matrices was examined with the 1000 permutations test: *$P < 0.05$. The result of the regional-scale phylogenetic β-diversity is shown in Supporting information: Appendix S6.

(a)

(b)

R^2 of linear model explaining mean phylogenetic distance between par-wised regions

	South America	Africa	Indo-Pacific	Australia	Nearctic	Western Palearctic
Africa	0.007					
Indo-Pacific	0.015	0.012				
Australia	0.011	0.027	0.012			
Nearctic	0.036	0.072	0.043	0.082		
Western Palearctic	0.077	0.161	0.098	0.181	0.084	
Eastern Palearctic	0.030	0.042	0.028	0.049	0.032	0.096

FIGURE 4 NMDS of the 843 plots across the seven regions, based on the mean pair-wise phylogenetic distance (phylogenetic dissimilarity) between the plots. Phylogenetic dissimilarity between pairs of the regions was tested using PERMANOVA with 999 permutations. The regional differences were statistically significant (PERMANOVA, *p* < 0.05) for all of the pairs, and their explanatory power (r^2) differed between the pairs. A relatively larger r^2 value found in the pairs between the Nearctic, Eastern Palearctic and Western Palearctic resulted from a smaller degree of phylogenetic dissimilarity between plots, in comparison with those in South America, Africa, the Indo-Pacific and Australia

that prevented dispersal across different continents (Graham & Fine, 2008). These findings suggested that multiple environmental filters related to climatic harshness, climatic stability and geographic constraints together contribute to shaping the global diversity patterns of woody angiosperm species.

4.2 | Regional differences in phylogenetic structures

Our study showed regional differences in species diversity (Fisher's α) along a longitudinal gradient from South America, Africa and the Indo-Pacific to Australia including tropical biomes (Figure 3). The pattern of taxonomic (genus) composition across the Neotropics, tropical Asia and Australia could be linked to long-distance dispersal driven by plate tectonic history (Gentry, 1988), suggesting continental divergences of tropical forests originated from global species pool, especially in South America, throughout the Cenozoic (see review of Hughes, Pennington, & Antonelli, 2013). Therefore, non-significant differences in regional-scale phylogenetic relatedness

(NRI$_{region}$) between biogeographic regions (Figure 2) suggest that species assemblies in local communities were sorted through filtering or dispersal from a single global species pool across different continents, rather than regional species pools (Kissling et al., 2012). The higher level of phylogenetic dissimilarity across South America, Africa, the Indo-Pacific and Australia (Figures 4, 5) may reflect in situ diversification across a tropical biome origin to marginal regions (Christenhusz & Chase, 2013; Hardy et al., 2012). Moreover, the correlations of global-scale phylogenetic relatedness (NRI$_{global}$) or phylogenetic dissimilarity between local communities with environmental factors (Tables 1, 2) suggest the influence of climatic filtering and geographic isolation on shaping large-scale diversity patterns of tropical communities across different continents (Hardy et al., 2012). Additionally, regional patterns of phylogenetic assembly (Supporting information: Appendix S6), such as South American communities driven by current climate and Quaternary climate changes, or the Indo-Pacific and Australian communities primarily driven by geographic constraints such as insularity, may be ascribable to diverse
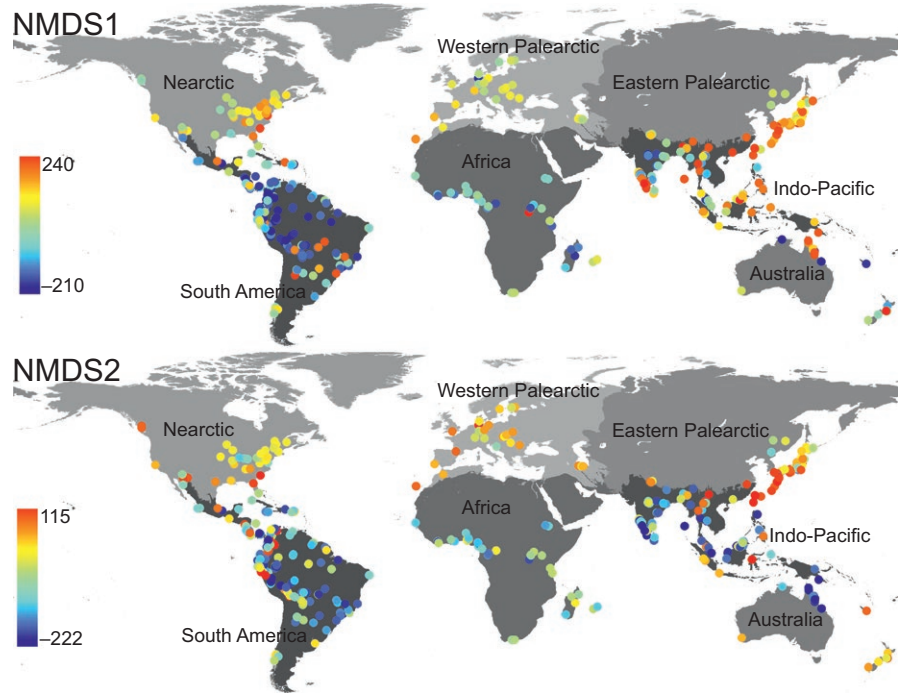
FIGURE 5 Geographic pattern of phylogenetic dissimilarity of angiosperm tree communities. Each plot is coloured according to the scores of the first and second axes of the NMDS illustrated in Figure 4. Phylogenetic dissimilarity between plots was smaller in extratropical regions than those of the regions including the tropics. Plots for the Eastern Palearctic showed a relatively similar pattern to those in the Indo-Pacific, especially on the first axis of the NMDS

climates (Hughes et al., 2013), historical habitat stability for wet tropics (Kooyman et al., 2011) or dispersal limitation by geological conditions (Slik et al., 2011). The environmental filters involving long-standing geographic barriers and region-specific environmental constraints promoted evolutionary diversification of tropical angiosperm tree communities between or within regions.

In contrast, the origins of temperate and boreal biomes were relatively recent, 4–10 million years ago (Fine & Ree, 2006). Interestingly, phylogenetic dissimilarity of angiosperm tree communities was smaller in extratropical regions than those of the regions including the tropics (Figures 4, 5). This indicates that recent geohistorical or paleoclimatic events played a critical role in the formation of temperate forests, which might provide support for the out-of-Asia hypothesis (Donoghue, 2008) to explain the regional divergence of temperate flora between the Nearctic, Eastern Palearctic and Western Palearctic. Notably, angiosperm tree communities of the Eastern Palearctic showed a larger dissimilarity in extratropical regions but a relatively similar pattern to tropical forests in the Indo-Pacific (Figures 4, 5). East Asian temperate flora across a broad latitudinal range was historically developed by dispersal permeability between tropical and temperate climates (Milne & Abbott, 2002) and was diversified in relation to topographic heterogeneity caused by orogeny and insularity from Quaternary sea level changes (Harrison, Yu, Takahara, & Prentice, 2001; Kubota et al., 2017; Qian & Ricklefs, 2000). These biogeographic processes are a clear contrast to Nearctic or Western Palearctic flora, which was influenced by regional-scale selective extinction and incomplete recolonization in response to Plio-Pleistocene environmental changes (Eiserhardt et al., 2015; Svenning, 2003; Svenning & Skov, 2007). Moreover, we discovered a significant role of Quaternary climatic change in shaping phylogenetic clustering in Nearctic and Western Palearctic. Our findings suggest the imprint of region-specific filtering or dispersal limitation related to tropical niche conservatism, geography and paleoclimatic change in extratropical biomes.

5 | CONCLUSIONS

The overall patterns of phylogenetic clustering and dissimilarity along environmental gradients showed that environmental filters are important to explain diversity patterns of angiosperm tree species. Climatic filtering (climatic harshness and paleoclimatic change) related to tropical niche conservatism played a significant role in species sorting from the global species pool and shaped the large-scale diversity patterns, such as the latitudinal gradient observed across continents. Geographic filtering (relative to dispersal limitation) substantially contributed to regional divergence within tropical/extratropical biomes among continents. This study demonstrates a future possibility of vegetation science as big data synthesis (Wiser, 2016): global-scale vegetation/plot data sets including angiosperm non-woody plants and gymnosperms. In this respect, the limitation of phylogenies including all vascular plants might hinder an analysis of community phylogenetics (Davies et al., 2012; Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015), because herbs and conifers are characterized by different evolutionary histories and functional traits, and thus their diversity patterns differs from that of angiosperm woody plants (Engemann et al., 2016). The present study demonstrates the importance of environmental filtering, which was associated with historical dispersal limitation, in diversification of angiosperm tree communities in tropical and extratropical biomes. Further explorations using a more detailed species-level phylogeny of all vascular plants, e.g.,

β-diversity studies that disentangle turnover and nestedness components related to richness differences (König, Weigelt, & Kreft, 2017), will illuminate the respective roles of multiple assembly processes in biome development.

AUTHOR CONTRIBUTIONS

YK, BK and TS created the database of forest plots and analysed the data; WU contributed to interpreting results and revising the manuscript; all authors contributed to the final version.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Source references of plot data used in this study

Appendix S2 Spatial trends in the first eigenvector generated from a geographic distance matrix between the plots

Appendix S3 Spatial correlogram of the response variables (raw data) and of the residuals of the regression model accounting for the first eigenvector of a geographic distance matrix between the plots

Appendix S4 Standardized regression coefficients and coefficients of partial determination (%) in regression models without the spatial filter. The regression models, which explain the global-scale patterns of species diversity and net relatedness index for woody angiosperm communities, share the same response and explanatory variables with the regression models in Table 1

Appendix S5 Standardized regression coefficients and coefficients of partial determination (%) in the regression models explaining the regional-scale patterns of phylogenetic structure and species diversity for woody angiosperm communities

Appendix S6 Standardized regression coefficients in the multiple regression models explaining the regional-scale phylogenetic β-diversity for woody angiosperm communities