

Effects of current climate, paleo-climate, and habitat heterogeneity in determining biogeographical patterns of evergreen broad-leaved woody plants in China

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Abstract: Understanding biogeographic patterns and the mechanisms underlying them has been a main issue in macroecology and biogeography, and has implications for biodiversity conservation and ecosystem sustainability. Evergreen broad-leaved woody plants (EBWPs) are important components of numerous biomes and are the main contributors to the flora south of 35°N in China. We calculated the grid cell values of species richness (SR) for a total of 6265 EBWP species in China, including its four growth-forms (i.e., tree, shrub, vine, and bamboo), and estimated their phylogenetic structure using the standardized phylogenetic diversity (SPD) and net relatedness index (NRI). Then we linked the three biogeographical patterns that were observed with each single environmental variable representing the current climate, the last glacial maximum (LGM)–present climate variability, and habitat heterogeneity, using ordinary least squares regression with a modified *t*-test to account for spatial autocorrelation. The partial regression method based on a general linear model was used to decompose the contributions of current and historical environmental factors to the biogeographical patterns observed. The results showed that most regions with high numbers of EBWP species and phylogenetic diversity were distributed in tropical and subtropical mountains with evergreen shrubs extending to Northeast China. Current mean annual precipitation was the best single predictor. Topographic variation and its effect on temperature variation was the best single predictor for SPD and NRI. Partial regression indicated that the current climate dominated the SR patterns of Chinese EBWPs. The effect of paleo-climate variation on SR patterns mostly overlapped with that of the current climate. In contrast, the phylogenetic structure represented by SPD and NRI was constrained by paleo-climate to much larger extents than diversity, which was reflected by the LGM–present climate variation and topog-

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raphy-derived habitat heterogeneity in China. Our study highlights the importance of embedding multiple dimensions of biodiversity into a temporally hierarchical framework for understanding the biogeographical patterns, and provides important baseline information for predicting shifts in plant diversity under climate change.

Keywords: evergreen broad-leaved woody plants; species richness; standardized phylogenetic diversity; net relatedness index; present climate; Quaternary climate variability; habitat heterogeneity

1 Introduction

The spatial patterns and causes of biodiversity are key questions in macroecology and biogeography (Rabosky *et al.*, 2015; Fung *et al.*, 2016; Tittensor *et al.*, 2016). Due to aggravated global climate change and habitat loss caused by human activities, the rate of species extinctions has been increasing (Cardinale *et al.*, 2012; Marchese, 2015). Understanding the spatial patterns and underlying mechanisms of biodiversity is important for identifying the origin, dispersal, and extinction of species, and provides a scientific basis for optimizing strategies for biodiversity conservation (Gaston, 2009).

Biodiversity is a complex concept with multiple dimensions (Dreiss *et al.*, 2015). In addition to the concept of taxonomic diversity, the metrics of phylogenetic diversity (PD) reveal direct information on the evolutionary history of taxa and provide novel insights on the mechanisms of biodiversity maintenance (Díaz *et al.*, 2016; Jarzyna and Jetz, 2016; Rosauer and Jetz, 2015). Thus, comparing taxonomic and phylogenetic diversity can provide additional insights for biodiversity conservation (Devictor *et al.*, 2010; Xu *et al.*, 2017; Brum *et al.*, 2017). For example, using comprehensive avian phylogenies and global distributional data for all extant birds, Voskamp *et al.* (2017) found significant geographical divergence between species richness (SR) and PD in high elevation areas, deserts, and islands. However, while the understanding of the mechanisms underlying biodiversity patterns has substantially increased over recent decades, the relative roles of the proposed mechanisms remain controversial (Currie *et al.*, 2004; Clarke and Gaston, 2006). Previous results were not consistent across the different taxonomic and ecological groups that have been investigated (Mao *et al.*, 2013; Kubota *et al.*, 2015). Furthermore, reports on the drivers of biodiversity patterns have also not been consistent regarding the spatial patterns of taxonomic, phylogenetic, and functional diversities (Devictor *et al.*, 2010; Feng *et al.*, 2014), demanding further tests to reach a consensus.

Among the influential factors considered, current climate, paleo-climate, and habitat heterogeneity are the most frequently cited explanations for the biodiversity patterns observed (Liu *et al.*, 2018). Whether diversity patterns are caused by the current climate or by historical factors has been discussed for a long time. For example, Francis and Currie (1998) emphasized the former, while Ricklefs *et al.* (1999) stressed the necessity of integrating history and ecology. Other results have emphasized the role of the interactions between contemporary environmental factors and evolutionary/historical processes (Ricklefs, 2004). Specifically, paleo-climate has received increasing attention as a significant driver for the current patterns of species diversity (Carnaval and Moritz, 2008; Kissling *et al.*, 2012a; Rakotoarinivo *et al.*, 2013). As an example, one global-scale study revealed that the endemism in birds, mammals, and amphibians seen today was significantly associated with the glacial–interglacial climate change velocity since the late Quaternary (Sandel *et al.*, 2011).

Mountains harbor exceptionally high levels of biodiversity (López-Pujol *et al.*, 2011; Qiu *et al.*, 2014) and are considered to be global or national diversity hotspots, especially in tropical and subtropical regions (e.g. Myers *et al.*, 2000). Benefitting from the heterogeneity of climates and soils regulated by topography (Tang *et al.*, 2006), mountains not only intensify intraspecific geographic isolation, leading to allopatric speciation, but also present multiple environmental gradients for adaptive diversification (Lei *et al.*, 2015; Liu *et al.*, 2016). Moreover, the velocity of climate change is lower in mountainous and higher in flat regions owing to topographic effects, resulting in distinct rates of extinction (Qiu *et al.*, 2014).

Evergreen broad-leaved woody plants (EBWPs) have a global distribution and are dominant in many types of forest, shrub land and savanna in tropical and subtropical regions (DeFries *et al.*, 2000), supporting the persistence of other biodiversity components in great quantities. Most of the 35 global hotspots that have been defined are distributed in tropical and subtropical regions dominated by EBWPs (Mittermeier *et al.*, 2011), highlighting the critical role of EBWPs in biodiversity conservation. EBWPs are sensitive to environmental factors such as light, moisture, and temperature (Sakai, 1979; van Ommen Kloeke *et al.*, 2012; Kubota *et al.*, 2016), which make them suitable subjects for studying the effects of environmental variables on species diversity patterns and the underlying mechanisms. According to the floristic affinity system of Chinese flora (Wu, 1991), 49.8% of angiosperm woody species in China have an affinity for tropical regions (Wang *et al.*, 2010). The tropical affinity of EBWPs in China should be much higher than this value, as EBWPs mostly distribute in the tropical and subtropical regions. Along with climate warming in the last decades, the number and frequency of EBWPs have been repeatedly observed to increase in the temperate forests of Europe (Carraro *et al.*, 2001; Walther, 2002). This sensitivity of EBWPs to global warming has been noticed and suggested for its usefulness as indicators for climate change (Walther *et al.*, 2001). China has the largest and most diversified subtropical evergreen broad-leaved forests (Song, 2013); therefore, studying the distribution of EBWPs in China is critical for understanding their global distribution and for the conservation of the corresponding biomes.

In the present study, we associated Chinese EBWPs distribution data with three different environmental categories, i.e., current climate, climate shifts between the Last Glacial Maximum (21 ka, LGM) and the present, and habitat heterogeneity related to topography, to assess their relative roles in determining the multiple dimensions of species diversity of Chinese EBWPs. Whittaker and Field (2000) suggested that the current climate has the strongest influence on diversity, with history playing a secondary role. Similarly, here, we hypothesized that the effects of current climate, paleo-climate, and habitat heterogeneity on biogeographical patterns of the Chinese EBWPs, measured by three indices, would differ significantly and that current climate would be the main driver.

2 Materials and methods

2.1 Species distribution data

The species distribution data were mainly taken from the *Atlas of Woody Plants in China: Distribution and Climate* (Fang *et al.*, 2011), which is the most complete atlas of woody plants in China and contains county-level distribution maps for 11,405 native species. We es-

established a geographic distribution database for EBWPs in China with a spatial resolution of 50 km × 50 km (grid cell size), which was subsequently analyzed. We also supplemented and modified the species distribution data with field data from 1494 forest plots on 63 mountains across China (see Shen *et al.*, 2013 for detailed information). The botanical nomenclature of species in the database was standardized according to The Plant List (www.theplantlist.org). SR of total evergreen woody plants in each grid cell was taken as a count of EBWP species within that grid cell.

2.2 Phylogeny and phylogenetic indices

We used Phylomatic v3 (<http://phylodiversity.net/phylomatic/>) and the Angiosperm Phylogeny Group IV (Chase *et al.*, 2016) classification as a backbone to construct a phylogenetic supertree for the Chinese EBWPs. The branch lengths in the phylogenetic tree were adjusted using the BLADJ algorithm with the differentiation time for angiosperm plants (Wikström *et al.*, 2001). This approach has been used widely in analyses of large-scale spatial patterns of plant PD (Qian *et al.*, 2016; Tiede *et al.*, 2016).

We calculated PD following Faith (1992) as the length of all phylogenetic branches required to span a given set of species, which consistently increases with SR in an assemblage. To account for this association with SR, we applied a randomization-adjusted approach to calculate standardized PD (SPD). Specifically, for each grid cell, we calculated PD for a randomly-selected set of species in the grid cell and repeated this simulation 1,000 times to estimate a mean of the randomized PD values, and then SPD was calculated using the R package “picante” (Kembel *et al.*, 2010) with the following formula:

$$SPD = (PD_{\text{observed}} - \text{mean } PD_{\text{randomized}}) / sdPD_{\text{randomized}} \quad (1)$$

where, PD_{observed} refers to the PD value of observed species, $\text{mean } PD_{\text{randomized}}$ refers to the randomized mean PD, and $sdPD_{\text{randomized}}$ refers to the standard deviation of 1000 iterations of $PD_{\text{randomized}}$. We also calculated the net relatedness index (NRI) for each grid cell based on the mean pairwise phylogenetic distance (MPD) using the following formula (Webb *et al.*, 2002), provided in R package “picante”:

$$NRI = (MPD_{\text{randomized}} - MPD_{\text{observed}}) / (sdMPD_{\text{randomized}}) \quad (2)$$

where, MPD_{observed} refers to the observed MPD, $MPD_{\text{randomized}}$ refers to the expected MPD of the randomized assemblages ($n = 1000$), and $sdMPD_{\text{randomized}}$ refers to the standard deviation of 1000 iterations of $MPD_{\text{randomized}}$. A positive NRI value indicates that MPD is lower than would be expected by chance (i.e., species are more closely related than expected), and thus indicates phylogenetic clustering. Conversely, a negative NRI value indicates that the observed MPD is greater than would be expected by chance (i.e., species are more distantly related than expected by chance), and thus indicates phylogenetic evenness or overdispersion.

2.3 Environmental variables

Current (1950–2000) and LGM data were downloaded on January 20, 2018 from the WorldClim database (<http://www.worldclim.org>). For the LGM data, we employed the Community Climate System Model (CCSM) and the Model for Interdisciplinary Research On Climate (MIROC), both of which were developed based on the Paleoclimate Modelling Intercomparison Project Phase II (PMIP2).

Temperature and precipitation are two key climate factors in ecological and evolutionary theories on plant diversity and distribution (Qian *et al.*, 2016). Stressful and unstable climates also constrain species distributions (O'Brien, 2006; Wang *et al.*, 2010). Accordingly, we chose six variables to represent the current climate, i.e., MAT, mean annual temperature; MAP, mean annual precipitation; MTCM, minimum temperature of the coldest month; PDQ, precipitation of driest quarter; TSN, temperature seasonality; and PSN, precipitation seasonality. We represented paleo-climatic factors using the MAT anomaly (MATA, current MAT–LGM MAT), the MAP anomaly (MAPA, current MAP–LGM MAP), the spatial shift velocity of MAT (MATV, the ratio of temporal MAT gradient to the spatial MAT gradient), and the spatial shift velocity of MAP (MAPV, the ratio of the temporal MAP gradient to the spatial MAP gradient) (Loarie *et al.*, 2009; Sandel *et al.*, 2011).

Topographic heterogeneity promotes the co-existence of species by offering diversified niche space (Tews *et al.*, 2004) and promotes species persistence by providing shelters and refuges to resist climate change (Fjelds  *et al.*, 2012). To analyze the effect of topographic relief on diversity patterns of EBWPs, we used three indices to represent habitat heterogeneity. Elevation range (ELER) was calculated as the difference between the maximum and minimum elevations of a grid cell. Ranges of mean annual temperature (MATR) and mean annual precipitation (MAPR) were calculated as the differences between the maximum and minimum MAT and MAP in a grid cell, respectively. Elevation data were obtained from the Shuttle Radar Topography Mission (SRTM, <http://www.landcover.org/data/srtm/>) with a spatial resolution of 3', which is approximately 90 m at mid-latitudes according to the Beijing1954 Albers Equal Area Conic projection. The mean values of the 50 km × 50 km grid cell for each environmental variable were processed in ArcMap 10.1 (ESRI, Redlands, CA, USA).

2.4 Data analysis

Calculation of phylogenetic relatedness requires at least two species; therefore, grid cells with a land area smaller than 1250 km² or containing fewer than two EBWP species were excluded from the following statistical analyses. Firstly, we performed simple regressions to evaluate the explanatory power of each predictor for the spatial patterns of SR, SPD, and NRI. Since the grid cells were not spatially independent of each other, the degrees of freedom may be overestimated and inflate the chance of making a type I error (Legendre and Legendre, 1998). Therefore, we tested the statistical significance of the correlations using a modified *t*-test (Dutilleul *et al.*, 1993). We also used the Spearman's correlation to explore the collinearity between the predictive variables (Table 1). SR values are generally not normally distributed and are often over-dispersed (Shrestha *et al.*, 2017); therefore, we log-transformed SR to meet the assumptions of the general linear regression analysis. Moreover, we compared ordinary least squares (OLS) models and geographically weighted regression models for the geographical patterns of SR, SPD, and NRI, and quantified the spatial correlogram using Moran's I. It was revealed that significant positive spatial autocorrelation for all three biogeographical patterns existed at distances smaller than ~3–6 units (200 km, Moran's I >0.2, *p*<0.001), and negative autocorrelation only for SR at distances of ~9–19 units, and again positive autocorrelation at distances >21 units for SR and SPD (Supplementary Material Appendix, Figure A2). However, we focused on the explanatory power of the models (proportion of deviance explained) rather than on *p* values, and there was no spatial autocorrelation found in the residuals of all models. Therefore, we only used OLS models to estimate the explanatory power of the environmental

determinants. Moreover, we used a partial regression method proposed by Legendre and Legendre (1998) to partition the contributions of current climate, current–LGM climate variability, and habitat heterogeneity to the variation in the spatial patterns of SR, SPD, and NRI, respectively. All analyses were conducted using R 3.2.3.

Table 1 Matrix of Pearson’s correlation coefficients among the 13 environmental variables. The boldfaced value in each column indicates the most correlated variable within that column.

	MAT	TSN	MTCQ	MAP	PSN	PDQ	MATA	MAPA	MATV	MAPV	ELER	MATR	MAPR
MAT	1.000	−0.474	0.922	0.712	−0.548	0.662	−0.650	0.212	−0.171	0.208	−0.215	−0.244	0.279
TSN	−0.474	1.000	−0.718	−0.624	0.336	−0.417	0.800	−0.033	0.814	0.184	−0.427	−0.421	−0.439
MTCQ	0.922	−0.718	1.000	0.728	−0.599	0.682	−0.798	0.112	−0.420	0.057	0.011	−0.013	0.362
MAP	0.712	−0.624	0.728	1.000	−0.578	0.846	−0.514	0.306	−0.480	−0.019	0.068	0.037	0.530
PSN	−0.548	0.336	−0.599	−0.578	1.000	−0.734	0.493	−0.168	0.246	0.076	−0.031	0.007	−0.227
PDQ	0.662	−0.417	0.682	0.846	−0.734	1.000	−0.439	0.292	−0.291	0.050	−0.081	−0.112	0.334
MATA	−0.650	0.800	−0.798	−0.514	0.493	−0.439	1.000	−0.113	0.587	0.066	−0.214	−0.193	−0.240
MAPA	0.212	−0.033	0.112	0.306	−0.168	0.292	−0.113	1.000	−0.020	0.334	−0.165	−0.162	0.059
MATV	−0.171	0.814	−0.420	−0.480	0.246	−0.291	0.587	−0.020	1.000	0.407	−0.665	−0.661	−0.407
MAPV	0.208	0.184	0.057	−0.019	0.076	0.050	0.066	0.334	0.407	1.000	−0.512	−0.497	−0.242
ELER	−0.215	−0.427	0.011	0.068	−0.031	−0.081	−0.214	−0.165	−0.665	−0.512	1.000	0.989	0.481
MATR	−0.244	−0.421	−0.013	0.037	0.007	−0.112	−0.193	−0.162	−0.661	−0.497	0.989	1.000	0.444
MAPR	0.279	−0.439	0.362	0.530	−0.227	0.334	−0.240	0.059	−0.407	−0.242	0.481	0.444	1.000

3 Results

3.1 Basic statistics of the biodiversity of EBWPs in China

There were 6265 species of EBWPs native to China belonging to 123 families and 737 genera. The proportions of four different growth forms (trees, shrubs, vines, and bamboos) were 30.7%, 53.0%, 8.8%, and 7.5%, respectively. The most species-rich families were Ericaceae (790 species), Poaceae (470 species), and Lauraceae (445 species), and the most species-rich genera were *Rhododendron* (593 species), *Ilex* (210 species), *Lithocarpus* (131 species), *Camellia* (127 species), and *Ficus* (111 species). The SR, genus richness and family richness per grid cell for all EBWPs ranged from 1–1844, 1–474, and 1–109, respectively. The species distributed in areas north of 40°N were mainly frost-tolerant shrubs in *Rhododendron*, *Vaccinium*, *Ledum*, *Rosa*, and *Dryas*.

In terms of EBWPs, China harbors 1925 species of trees, belonging to 77 families, and 305 genera; 3321 species of shrubs, belonging to 106 families, and 452 genera; 550 species of vines, belonging to 46 families, and 125 genera; and 470 species of evergreen bamboos, which belong to 33 genera of the single family Poaceae. The SR of evergreen broadleaved trees, shrubs, vines, and bamboos in each grid cell ranged from 0–689, 0–894, 0–226, and 0–68, respectively.

3.2 Biogeographical patterns of EBWPs

Among those four growth forms of EBWPs, trees were the most restricted while shrubs had

broadest distributions (Figure 1). The trees were mostly limited to the Qinling Mountain Range (ca. 33°), with a few scattered patches extending to the nearby mountains in the north. The shrubs, contrastingly, were distributed throughout China, with only a few empty patches, mostly in the central Qinghai–Tibet Plateau and the central Northeast China Plain. Evergreen vines had a geographical range similar to trees but extending farther north (ca. 40°) along the coast of eastern China. Bamboos also extended to the north, but mainly along the mountains of the eastern Qinghai–Tibet Plateau, Mt. Taihang, and Shandong Peninsula.

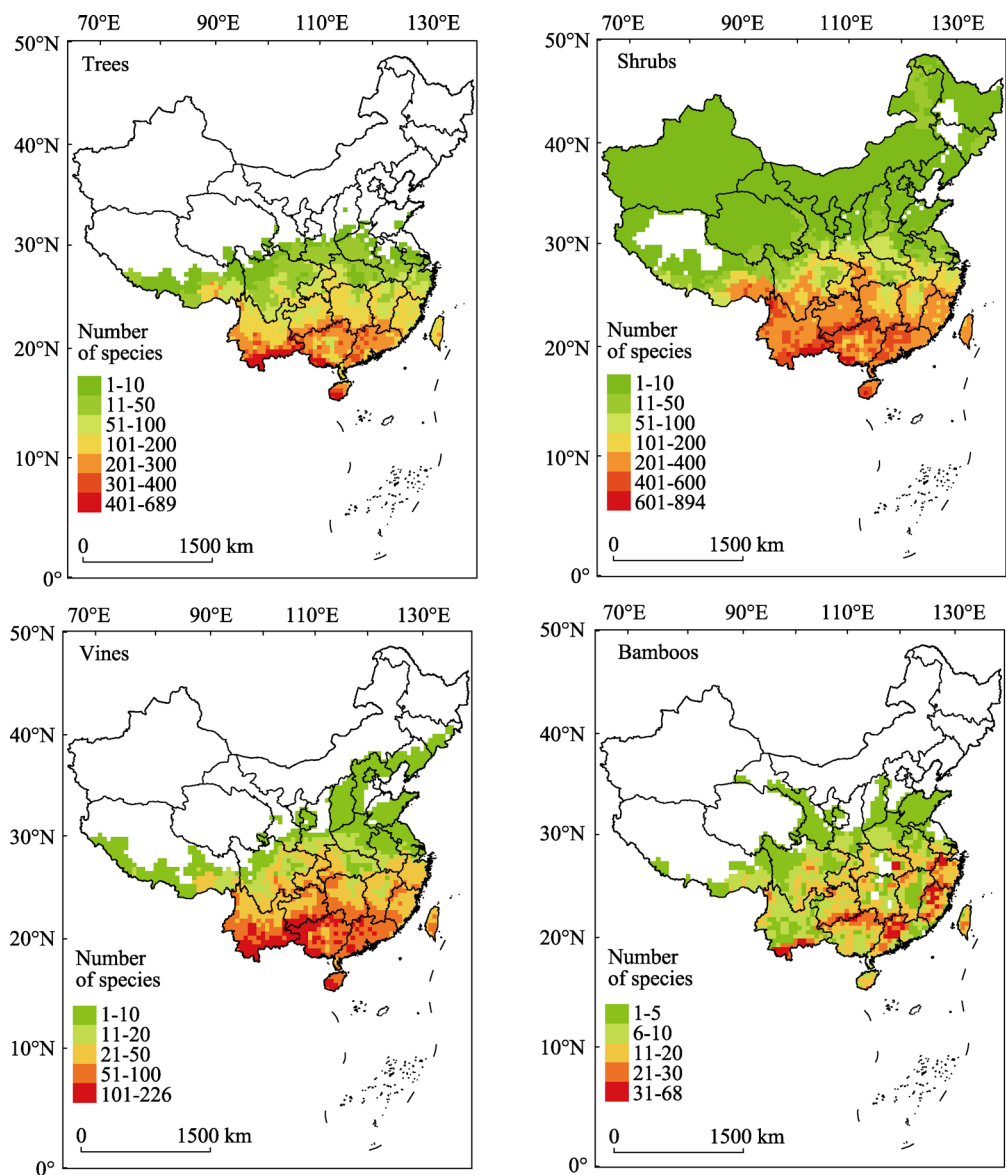


Figure 1 The spatial patterns of species richness of the four growth forms (i.e., tree, shrub, vine, and bamboo) of evergreen broad-leaved woody plants in China

With regard to the diversity centers of the four growth forms of EBWPs, Guangdong Province, Hainan Province, Guangxi Zhuang Autonomous Region, and southern Yunnan

Province were the main regions with high SR of trees, vines, and shrubs, but the SR of shrubs was also distinctly high in the subtropical regions. In contrast, regions of high SR of bamboos were found to be mostly scattered in the tropical and subtropical mountains, especially in southern and eastern China.

The richness of families, genera, and species of EBWPs exhibited similar distribution patterns, which decreased with increasing latitude (Figure 2). The regions with higher diversity were mainly distributed in tropical and subtropical mountainous area, such as the eastern Himalaya and Hengduan Mountains (EHHMs), the mountains at the junction of Yunnan, Guangxi, and Guizhou provinces, the Nanling Mountain Range, and the mountains on Hainan Island. Taiwan Island showed a much lower grid-cell SR of EBWPs than Hainan.

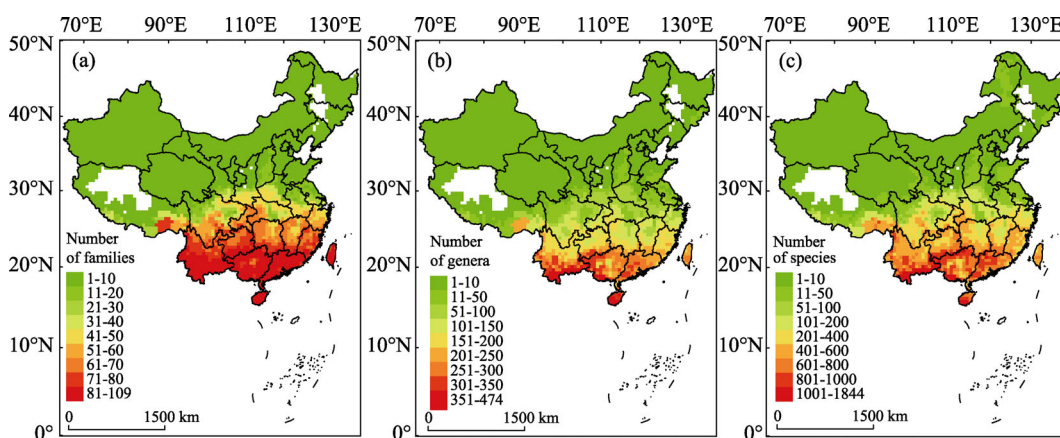


Figure 2 Distribution patterns for richness of (a) families, (b) genera, and (c) species (SR) for evergreen broad-leaved woody plants (EBWPs) in China. Empty areas indicate the absence of EBWPs.

In contrast, the SPD of EBWPs revealed a distinct pattern with high values (>1.0) mostly occurring in the tropical regions (Figure 3a). Across the broad subtropical zone of $\sim 22.5\text{--}32.5^\circ\text{N}$, SPD in the west was generally lower than in eastern China. Interestingly, SPD in the temperate regions was generally higher than that in the subtropical regions, except in the northwestern and northeastern parts. SPD values of <-3.0 occurred in the EHHMs of Southwest China, and the Greater Hing'an Mountains in Northeast China. Similarly, a clear trend appeared to be lacking in the NRI values with increasing latitude (Figure 3b), whereas NRI was generally higher in western than eastern China. Moreover, there were two areas with especially high NRI values, the EHHMs, and the Greater Hing'an Mountains, indicating a more clustered phylogenetic structure than that predicted by chance. However, the EBWP taxa showed significant random or over-dispersed phylogenetic structuring in the eastern part of the tropical, subtropical, and temperate regions of China.

A significant negative correlation was revealed between latitude and $\log(\text{SR})$ ($r = -0.830$, $p < 0.001$), and latitude and SPD ($r = -0.166$, $p < 0.05$), but no correlation was found between latitude and NRI ($r = 0.065$, $p > 0.05$). Among the three biogeographical indices of biodiversity, geographical patterns were statistically independent of each other (Figure A1).

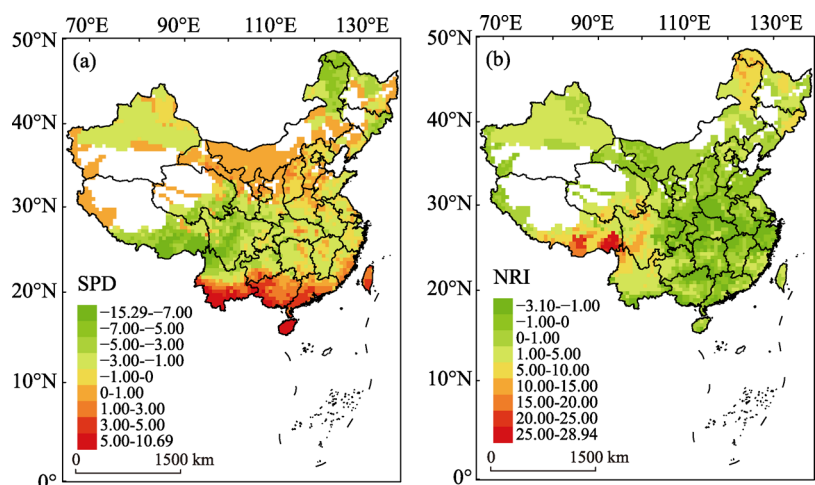


Figure 3 Spatial variation in (a) standardized phylogenetic diversity (SPD) and (b) net relatedness index (NRI). Empty areas are those with less than two species of EBWP recorded in one grid cell.

3.3 The determinants of the biogeographical patterns of EBWPs

Of the 13 environmental variables, those of the current climate were the significant predictors of SR, except PSN, but only MAT had a significant positive correlation with SPD (Table 1). No significant correlation was revealed between current climate and NRI. In contrast, no significant correlation was revealed between Quaternary climate variables, although the relationships were mainly negative. The variables of habitat heterogeneity were all significant predictors of NRI, and MAPR was significantly positively correlated with SR. Habitat heterogeneity was associated with SPD in a generally negative form, but the relationship was only significant in terms of ELER and MATR.

Table 1 The r^2 of univariate OLS regression models with p values of modified t -test of the biogeographical indices against environmental variables, all with spatial autocorrelation. The minus in braces indicate negative relationship, the statistical significant p values are boldfaced.

Environmental factors	Predictors	SR		SPD		NRI	
		r^2	p	r^2	p	r^2	p
Current climate	MAT	0.469	0.038	0.151	0.014	(-)0.135	0.078
	MAP	0.733	0.006	(-)0.005	0.672	(-)0.003	0.779
	MTCM	0.692	0.013	0.073	0.084	(-)0.051	0.295
	PDQ	0.463	0.048	0.025	0.344	(-)0.018	0.541
	TSN	(-)0.561	0.033	(-)0.013	0.537	(-)0.078	0.277
	PSN	(-)0.297	0.088	0.038	0.336	(-)0.084	0.247
Paleo-climate	MATA	(-)0.405	0.098	(-)0.061	0.130	0.067	0.260
	MAPA	0.029	0.537	<0.001	0.938	(-)0.023	0.388
	MATV	(-)0.392	0.052	0.029	0.258	(-)0.032	0.380
	MAPV	(-)0.025	0.464	0.032	0.137	(-)0.040	0.167
Habitat heterogeneity	ELER	0.067	0.251	(-)0.112	0.004	0.140	0.003
	MATR	0.053	0.310	(-)0.111	0.006	0.149	0.003
	MAPR	0.219	0.005	(-)0.015	0.191	0.059	0.019

The environmental variables considered here account for 85.8%, 33.0%, and 39.1% of the variation in geographical patterns of SR, SPD, and NRI, respectively. The results of variation partitioning indicated that current climate played a primary role compared to paleo-climatic variability and habitat heterogeneity in determining the species richness pattern of EBWPs across China (Figure 4a). However, the effect of current climate on SPD or NRI was much weaker than on SR. Correspondingly, both the paleo-climatic variability and habitat heterogeneity played larger roles in the variation of SPD and NRI than on that of SR (Figures 4b and 4c). Moreover, the effect of paleo-climatic variation on SR patterns was mostly nested within the effect of the current climate, leaving only 1.1% independent effect, whereas for the patterns of SPD and NRI, the paleo-climate had much larger percentages of independent effect. The percentages of variation explained independently by habitat heterogeneity also increased from SR to SPD and NRI.

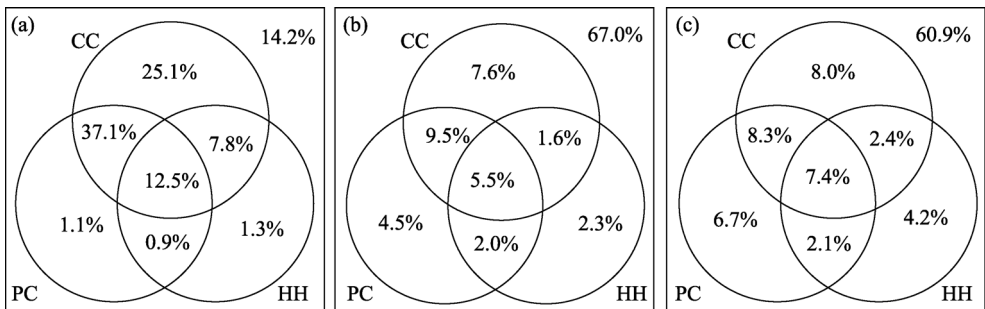


Figure 4 The partitioning of the variance (R^2 , %) in (a) log(SR), (b) SPD, and (c) NRI accounted for by each of the three environmental factors using partial regression methods. See Legendre and Legendre (1998) for details of the method. CC = current climate; PC = paleo-climate; HH = habitat heterogeneity.

4 Discussion

4.1 Distribution patterns of EBWPs in China

EBWPs are unevenly distributed across China. The richness of families, genera, and species of EBWPs showed similar distribution patterns decreasing with increasing latitude. The areas with high taxonomic diversity and PD of EBWPs corresponded with the tropical and subtropical mountains in China, as suggested in previous studies (Ying, 2001; Wang *et al.*, 2010; López-Pujol *et al.*, 2011; Qiu *et al.*, 2014). It has been demonstrated that mountainous regions of China act as both species refugia and speciation centers, maintaining high biodiversity through geological history (Myers *et al.*, 2000; Tang *et al.*, 2006; Xu *et al.*, 2017). As an exception to this rule, high EBWP SR in the EHHMs was coupled with low SPD values and high NRI values. This combination of biogeographic indices consistently indicated that the rich EBWPs in this region comprised young clades and had high phylogenetic relatedness. This implied an active diversification (or speciation) center of evergreen woody plants. In other words, the EHHMs are a cradle of EBWPs in China, as also being demonstrated for other clades (Favre *et al.*, 2015; Lei *et al.*, 2015; Yan *et al.*, 2015). Moreover, Xing and Ree (2017) showed that, about 8.0 Ma, the rate of *in situ* diversification of angiosperms in-

creased significantly in the Hengduan Mountains, which is temporally congruent with independent estimates of orogeny. Another diversification center for EBWPs was shown in the Greater Hing'an Mountains in Northeast China, which is also a diversity center of cold-tolerant dwarf evergreen shrubs of *Vaccinium*. However, the combination of high SR and SPD and low NRI values consistently imply that the tropical mountains in the southern provinces, including Yunnan, Guangxi, Guangdong, Hainan, and Taiwan, are also the main museums of EBWPs in China. Moreover, similar levels of biodiversity were observed in scattered patches of mountains in the Chinese subtropical region, mainly in the eastern part. These patches probably acted as refugia for EBWPs in the Quaternary glaciation events, as also indicated by other evidence (Tang *et al.*, 2018; Chen *et al.*, 2018).

4.2 Relative roles of environmental factors

Our research has demonstrated that current climate variables dominated the spatial variation of SR of EBWPs in China, showing an explanatory power much higher than that of paleo-climate variation at LGM and topography-derived environmental variation that took effect on longer time scales (with independent contributions of 25.1% versus 1.1% and 1.3%, respectively, Figure 4a). Similarly, Hawkins and Porter (2003) found that current climate explained two to seven times more variance in SR patterns of mammals and birds in deglaciated North America than paleo-environmental factors. Furthermore, the high explanatory power of current climate for biodiversity patterns has been repeatedly demonstrated for numerous assemblages of plants and animals (Hawkins *et al.*, 2003; Buckley and Jetz, 2007; Wang *et al.*, 2010). The high percentage of joint effects between current climate and paleo-climate variables might indicate climate stability in the major distribution areas of EBWPs since the LGM.

While the total explanatory power of the environmental factors for SPD (indicating assemblage age) and NRI patterns were much lower than that for SR patterns, paleo-climate and habitat heterogeneity appeared to play relatively large independent roles in the SPD and NRI patterns (Figures 4b and 4c). These differences indicate that age and phylogenetic composition were more resistant than the SR of EBWPs to climate changes in the short term. They also reveal a clear imprint of the uplift of the Qinghai-Tibet Plateau, a critical geological event of longer duration than the glacial-interglacial cycling, for the diversification of Chinese EBWPs. Specifically, the negative correlations between SPD and MATA, TSN indicated that older taxonomic groups occur in areas less affected by LGM-present climate instability, that is, in areas with more stable climate; whereas, the negative correlation between SPD and indices of habitat heterogeneity (ELER, MATR, and MAPR) indicate that phylogenetically younger groups of EBWPs tend to occupy mountainous areas (Figure 3a). Long-term environmental changes have been found to be well correlated with phylogenetic structural pattern at large geographic scales (Ma *et al.*, 2016). For example, Kissling *et al.* (2012b) found that global patterns in phylogenetic structure for palm assemblages are strongly linked to Cenozoic climate change. Hortal *et al.* (2011) found a strong increase in phylogenetic clustering with increasing LGM-present MAT anomaly for scarab beetles in Europe. Feng *et al.* (2014) also suggested that the LGM-present anomaly in temperature was the strongest explanatory factor for PD in forests of China with modern climate also important. The importance of climatically stable areas for China's rich diversity of EBWPs suggests a

strong need to focus on protecting these areas from fragmentation and deforestation to maintain or enhance their ability to buffer against future climate change.

4.3 Temperature versus precipitation

The results of the present study showed that MAP under current climate conditions is the best predictor of spatial variance in SR. This agrees with the finding that water is more important than energy at mid-latitudes in the Northern Hemisphere (Hawkins *et al.*, 2003; Wang *et al.*, 2010; Chen *et al.*, 2011). Xu *et al.* (2016) demonstrated that the impact of energy on global oak species diversity strongly depends on the availability of water. Li *et al.* (2016) suggested that precipitation significantly affects the relationship between the percentage of untoothed species and the temperature of woody plants in China. However, using the same data source, Wang *et al.* (2010) studied the SR patterns of all woody angiosperm species in China and found that frost filtering was the primary determinant for the patterns observed. Moreover, Qian (2013) provided another study of the spatial patterns of woody plant species at a coarser geographical scale (provincial level) and suggested that temperature seasonality was the dominant factor. Most of the climate in China is deeply influenced by the Asian monsoon, which dominantly affects the seasonal synchronicity of both temperature and precipitation, especially in the areas occupied by EBWPs (Song, 2013). Therefore, a persistent unresolved issue is to determine the independent effects of energy and moisture on biodiversity patterns. Here, our data suggested that EBWPs may be more sensitive to limits of precipitation than low temperatures.

In contrast, spatial patterns of SPD were more strongly tied to Quaternary climate change in terms of temperature rather than precipitation (Table 1). This differs from previous studies from Africa, which demonstrated a more likely explanation for the LGM–present precipitation anomaly of palm SR across Madagascar compared to the LGM–present temperature anomaly (Rakotoarinivo *et al.*, 2013). However, Feng *et al.* (2015) found that endemism patterns of plant species in Chinese forests were more strongly tied to MATA than to MAPA, which was consistent with the results of our study. The world has been becoming warmer and more humid over approximately the same time periods (Wolfe, 1975). Furthermore, some previous studies of paleo-climate in China also suggested that the LGM climate was much drier than the present in some areas, especially in southern China (Wang *et al.*, 2012). Hence, the effects of historical precipitation change may be underestimated in the present study. It is suggested that simulations of LGM precipitation are more uncertain than those for temperature, and that there is wider variation among different models (Waltari *et al.*, 2007). Besides, the millennial-scale variability in monsoon strength and precipitation in China is likely not well represented by the LGM–present MAP anomaly used to represent past changes in precipitation herein (Feng *et al.*, 2015).

4.4 The impacts of habitat heterogeneity

Habitat heterogeneity, represented by topographical heterogeneity, spatial climatic or edaphic variation, and land cover diversity in different studies, has long been considered to be a critical, sometimes dominant factor in the formation of biodiversity patterns (Kerr *et al.*, 2001; Kreft and Jetz, 2007; O'Brien *et al.*, 2000). Higher levels of habitat heterogeneity can

lead to higher niche diversity for species co-existence (Rahbek and Graves, 2001; Jetz and Rahbek, 2002), but also provide a higher chance of spatial isolation leading to increased speciation (Graham and Fine, 2008).

For Chinese EBWPs, habitat heterogeneity has a remarkable (22.5%) contribution to SR patterns, but its independent contribution of 1.3% was minor. Specifically, it was only the topography-related precipitation variability that showed a significant effect on SR patterns. However, the three indices of habitat heterogeneity, namely ELER, MATR, and MAPR, had prominent effects on the family age and phylogenetic structuring of EBWPs (Table 1). This indicates that habitat heterogeneity plays a larger role as an environmental filter affecting community assembly than it does for determining the overall SR.

Qian *et al.* (2016) found significant correlations between NRI and temperature indices for angiosperm trees in 57 forest plots sampled across a latitudinal transect in China. For the geographical distribution of Chinese EBWPs, however, significant correlations were found between NRI and habitat heterogeneity, rather than the climate variables. This is probably because the two-dimensional biogeographical patterns are far more complex than the one-dimensional patterns sampled in forest plots along a primary environmental gradient. Significant topographical heterogeneity and the prominent longitudinal moisture gradient, intensified by the Asian monsoon, substantively complicated the biogeographical patterns in China, as demonstrated in previous studies (Chen *et al.*, 2011; Chen *et al.*, 2018; Qiu *et al.*, 2014).

The biogeographical patterns of taxonomic diversity, phylogenetic diversity and structure of EBWPs in China showed highly divergent associations with the potential driving factors. In short, SR was most strongly constrained by current climate conditions, while phylogenetic structure was affected more by the deep-time environmental context, as indicated by the LGM-present climate variation and the topographic variation formed at even longer time scales. Hence, our results indicate the necessity of adopting a hierarchical framework of multiple spatial and temporal scales, for better understanding the roles of various mechanisms for the origins of biodiversity patterns (Wiens and Donoghue, 2004; Swenson, 2011).

5 Conclusions

As a major component of plant diversity, assemblages of EBWPs are optimal for testing the environmental constraints on biogeographical patterns. For the first time, this study explored the geographical patterns of 6,265 species of EBWP in China. With the partial regression methods, the spatial variations of SR, SPD and NRI were able to be accounted for by 85.8%, 33.0% and 39.1%, respectively. Our results highlighted the importance of tropical and subtropical mountains for maintaining the species diversity of EBWPs in China, and provided support for the hypothesis that current climate was the main driver of taxonomic diversity. Meanwhile, LGM-present climate variability and topography-related habitat heterogeneity played a more important role in shaping the spatial patterns of phylogenetic structure and diversity. The results of this study demonstrated the complementary importance of current climate and paleo-environmental factors in shaping plant biodiversity patterns at the macroscale. The generality of this result, regarding the relative importance between contemporary and historical factors, however, may be further tested by examining more paleo-climatic proxies from a range of archives and linking them to extant diversity patterns.

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Appendix

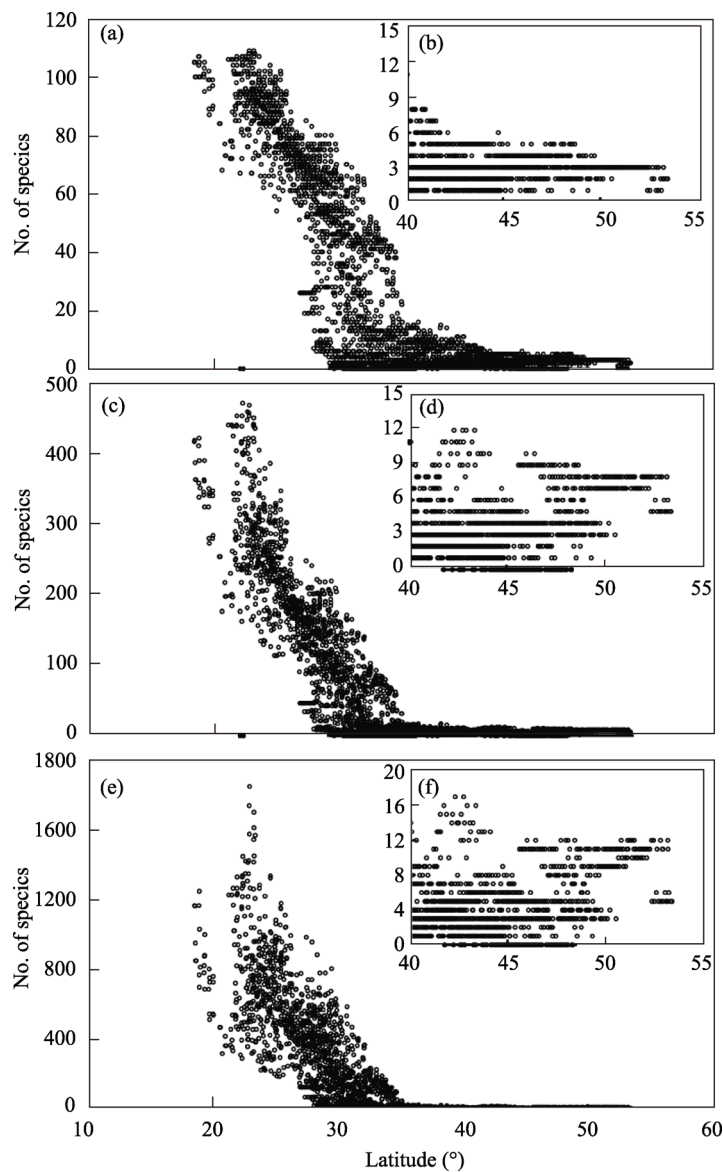


Figure A1 Latitude gradients of (a) families richness, (c) genera richness and (e) species richness of EBWPs in 50 km×50 km grid cells across China. (b), (d) and (f) reflect the detailed information of the latitude gradients of families richness, genera richness and species richness of EBWPs distributed north of 40°N in China.

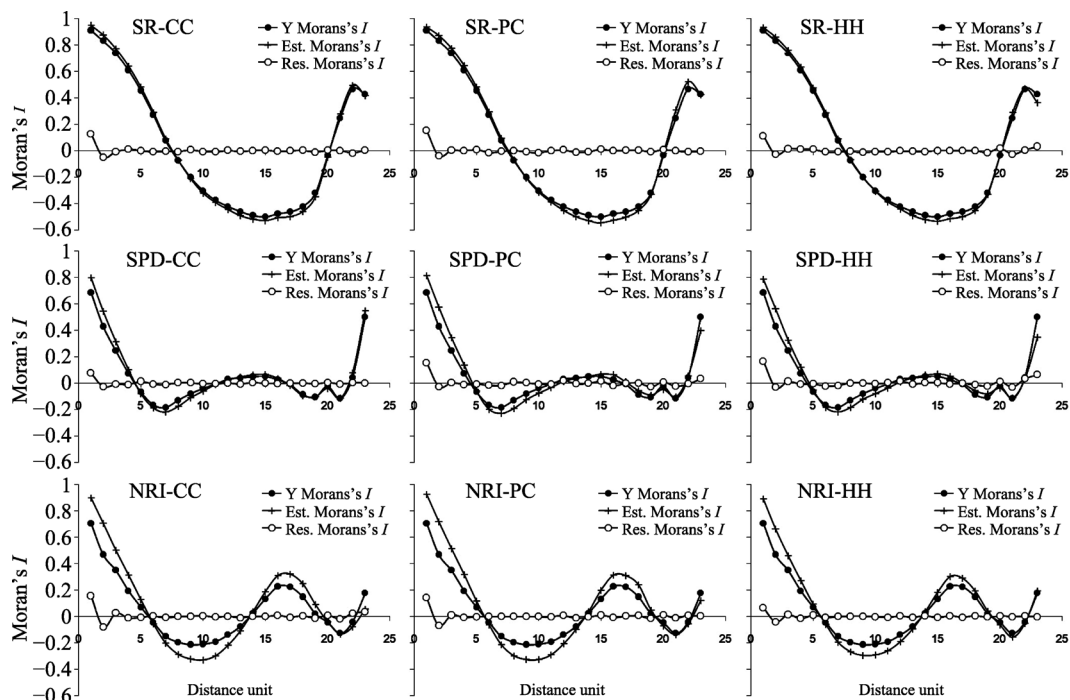


Figure A2 Spatial correlograms for the geographic patterns in species richness (SR), standardized phylogenetic diversity (SPD) and net relatedness index (NRI) of the EBWPs in China, and the estimates and residuals of the combined models. Spatial correlograms are estimated by Moran's I coefficients. In the figures, solid dots represent Moran's I for raw data (Y), while crosses and solid dots represent Moran's I for the estimates and residuals of the explanatory models of current climate (CC), the paleo-climate variation (PC) and that of habitat heterogeneity (HH).