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RESEARCH PAPERS

Phylogenetic age differences in tree assemblages across the Northern Hemisphere increase with long-term climate stability in unstable regions

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ABSTRACT

Aims: Long-term climate stability is hypothesized to drive the emergence of species assemblages with large species age differences due to the accumulation of relict species and relatively newly arisen species via reduced extinction and increased speciation. Few studies have addressed these predictions and so far no study has done so for plants across the Northern Hemisphere. Here, we linked Quaternary-scale climate variability to phylogenetic age differences between the oldest and youngest group of species in tree assemblages in 100 km × 100 km grid cells across the Northern Hemisphere to test these predictions.
Location: Northern Hemisphere.
Methods: Last Glacial Maximum (LGM)-to-present shifts in temperature and precipitation were used as proxies for Quaternary-scale glacial–interglacial climate variability. Simultaneous autoregressive (SAR) models were used to assess the relationships between phylogenetic age differences and Quaternary-scale climate variability.
Results: We found that phylogenetic age differences overall were largest in China and smallest in Europe, and they declined with increasing temperature instability as predicted, but only in Europe and North America. In China, the relatively mild Quaternary climate changes did not appear to have strongly affected phylogenetic age differences in tree assemblages.
Main conclusions: Our results show that phylogenetically diverse assemblages with large phylogenetic age differences among species are associated with relatively high long-term climate stability, with intra-regional links between long-term climate variability and phylogenetic composition especially strong in the more unstable regions. These findings point to future climate change as a key risk to the preservation of the phylogenetically diverse assemblages in regions characterized by relatively high paleoclimate stability, with China as a key example.

1 INTRODUCTION

The cause of the gradual decrease in species richness from the equator towards the poles is a central problem in biogeography and macroecology (Hillebrand, **2004**; Jansson & Davies, **2008**; Rolland, Condamine, Jiguet, & Morlon, **2014**; Willig, Kaufman, & Stevens, **2003**). Speciation, extinction and dispersal are the fundamental processes influencing species richness and are expected to vary along latitudes and among continents. Regions with long-term climate stability should have higher species diversity because of relatively high speciation rates and the preservation of ancient species from climate-driven extinctions (McKenna & Farrell, **2006**; Moreau & Bell, **2013**; Tzedakis, Lawson, Frogley, Hewitt, & Preece, **2002**). Hence, these regions with higher speciation and lower extinction rates are expected to include members of both basal and crown lineages of a phylogeny. Therefore, phylogenetic age differences between the basal and crown lineages are predicted to be larger in climatically stable areas than anywhere else (Pellissier et al., **2014**). Previous studies of this hypothesis have focused on animals such as leaf beetles, ants, fishes and marine bivalves (Jablonski, Roy, & Valentine, **2006**; Mckenna & Farrell, **2006**; Moreau & Bell, **2013**; Pellissier et al., **2014**). In contrast, few studies have assessed this hypothesis for plants across different continents (but see Hopper, **2009**, study about plant diversity on old, climatically buffered, infertile landscapes, namely OCBILs theory).

Although tree assemblages in China, North America and Europe have similarities in composition (notably shared genera and families) and structure, China has the highest species richness among the three regions (Fang et al., **2012**; Latham & Ricklefs, **1993**). The relatively stable climate during the Neogene and Quaternary glacial–interglacial cycles in East Asia has been suggested to be one important factor behind this discrepancy in diversity, notably in contrast to Europe (López-Pujol, Zhang, & Ge, **2006**; Qian & Ricklefs, **1999**). However, few studies have directly connected paleoclimatic stability with tree assemblage composition to examine its importance for the discrepancy in diversity among these regions. Northern Hemisphere regional tree floras were strongly affected by the late Neogene and Quaternary cooling and drying (Eiserhardt, Borchsenius, Plum, Ordonez, & Svenning, **2015**; Svenning, **2003**), with the former in particular leading to phylogenetically clustered survivorship via cooling filtering on phylogenetically conserved cold tolerance (Eiserhardt et al., **2015**). It is less clear to what extent speciation in Northern Hemisphere trees have been affected by the Quaternary climate, as most tree species in the region appear to be older (Kerkhoff, Moriarty, & Weiser, **2014**; López-Pujol et al., **2006**; Willis & Andel, **2004**); nevertheless, as similar dynamics have been going on since the Neogene (e.g., Willis, Kleczkowski, & Crowhurst, **1999**), there may be deeper time correlations to Quaternary patterns in climate stability.

In this paper, we study tree assemblages in China, North America and Europe to test the hypothesis that long-term climate stability drives the emergence of species assemblages with large phylogenetic age differences due to the accumulation of both relict species and newly arisen species via reduced extinction and increased speciation. In terms of climate stability, we focus on Quaternary climate, given the massive impact of the Pleistocene glaciations on Northern Hemisphere tree floras (Davis, **1983**; Svenning, **2003**), using the Last Glacial Maximum (LGM)-to-present shift to represent the general pattern of glacial–interglacial climate shifts across the period (Jansson, **2003**). We address the following predictions: (a) comparing the three regions, overall assemblage phylogenetic age differences should be greatest in the most stable region (China) and smallest in the least stable region (Europe) (López-Pujol et al., **2006**; Qian & Ricklefs, **1999**); and (b) within regions, phylogenetic age differences of tree assemblages should be negatively correlated with LGM-to-present climate change, with the weakest relationship in the region most mildly affected by Quaternary climate change (i.e., China).

2 MATERIALS AND METHODS

2.1 Tree distribution data

In this study, we focused on tree species with a maximal canopy height ≥ 10 m because of data availability. Gymnosperms were not included in the study because they could unduly influence the results because of their phylogenetically isolated position relative to the rest of the tree species in the study regions. Hence, only angiosperm trees were included. The study covered three regions: China, North America and Europe. Tree distribution data for China came from the Chinese Vascular Plant Distribution Database, which is mainly compiled from *Flora Republicae Popularis Sinicae* (Editorial Committee of Flora Reipublicae Popularis Sinicae, **1959**–2004), provincial and regional floras. Tree distribution data for North America were compiled from the *Atlas of United States Trees* (Little, **1971**–1978), digitized and available at the U.S. Geological Survey Geosciences and Environmental Change Science Center. Tree distribution data for Europe were compiled from the *Atlas Florae Europapeae* (AFE; Jalas & Suominen, **1994–1999**), combined with the range maps used by Montoya, Rodríguez, Zavala, and Hawkins (**2007**) and supplemented with expert information on the distribution of *Acer sempervirens* and *Malus trilobata* (A. Strid, personal communication, 30 June 2010). All the distribution maps where converted to the Lambert azimuthal equal-area projection and rasterized to a 100 km × 100 km resolution. For our analyses, we only used grid cells with > 50% of land area. The study covered 2,154 tree species in China, 159 in Europe and 367 in North America.

2.2 Phylogeny

To estimate the age of tree species, we used a time-calibrated species-level phylogeny covering 31,749 plant species (Qian & Jin, **2015**; Zanne, Tank, & Cornwell, **2014**). This phylogeny was generated based on seven gene regions and includes 98.6% of families and 51.6% of genera of all extant seed plants in the world (Zanne et al., **2014**). Givven that species age derived from terminal branch length could be sensitive to the algorithum of adding species to the base tree, we randomly (100 times) added the species not included in the phylogeny within their relevant genera and families, producing 100 estimated phylogenies.

2.3 Environmental variables

Contemporary climate was characterized by mean annual temperature (MAT) and mean annual precipitation (MAP), which were downloaded from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, **2005**). Elevation range per grid cell was computed based on a digital elevation model available in the same source. Temperature and precipitation during the LGM were extracted from the Community Climate System Model version 3 (CCSM3; Hijmans et al., **2005**; Otto-Bliesner et al., **2006**) and the Model for Interdisciplinary Research on Climate version 3.2 (MIROC3.2; Hasumi & Emori, **2004**). LGM temperature and precipitation were then summarized as the mean of the two models. LGM-to-present anomalies (contemporary climate minus LGM climate) in MAT and MAP and LGM-to-present velocities in MAT and MAP were used to represent paleoclimate change directly. Velocity describes the speed of movement of climate across the time period evaluated, estimated by relating the rate of temporal climate change to the local spatial gradient in climate (Loarie et al., **2009**). All environmental variables were processed in ArcMap 10.1. (Environmental Systems Research Institute, Redlands, CA).

2.4 Statistical analyses

Tree species in each grid cell were sorted according their ages and then divided into three equally sized age groups. The difference in median age between the oldest and youngest group was then used to represent the age differences, to use a metric that should be relatively robust to the coarse resolution of the available phylogeny. For each estimated phylogeny, we obtained a phylogenetic age difference in each grid cell. We then used the mean of the phylogenetic difference estimated based on each of the 100 estimated phylogenies as the final phylogenetic age difference for a given grid cell. Environmental variables that were not normally distributed were log10-transformed. Finally, all variables were standardized to allow the estimation of standardized regression coefficients.

Multiple comparisons of phylogenetic age differences among the three regions were computed using Tukey's honestly significant difference (HSD) test. Relationships between phylogenetic age differences and the environmental predictors were estimated by simultaneous autoregressive (SAR) models to account for spatial autocorrelation. To find the best combination of variables associated with phylogenetic age differences, we performed multiple linear regressions. Given that climate change velocity is highly correlated with anomaly in climate and elevation range, we divided the models into the following two groups: group 1 includes MAT, MAP, velocity in MAT and velocity in MAP; and group 2 includes MAT, MAP, anomaly in MAT, anomaly in MAP and elevation range. In each group, SAR models for all possible combinations of variables were run, and Akaike's information criterion (AIC) was used to choose the best combination of predictors for each group. All analyses were done in R (version 3.1.1; R Core Team, **2014**).

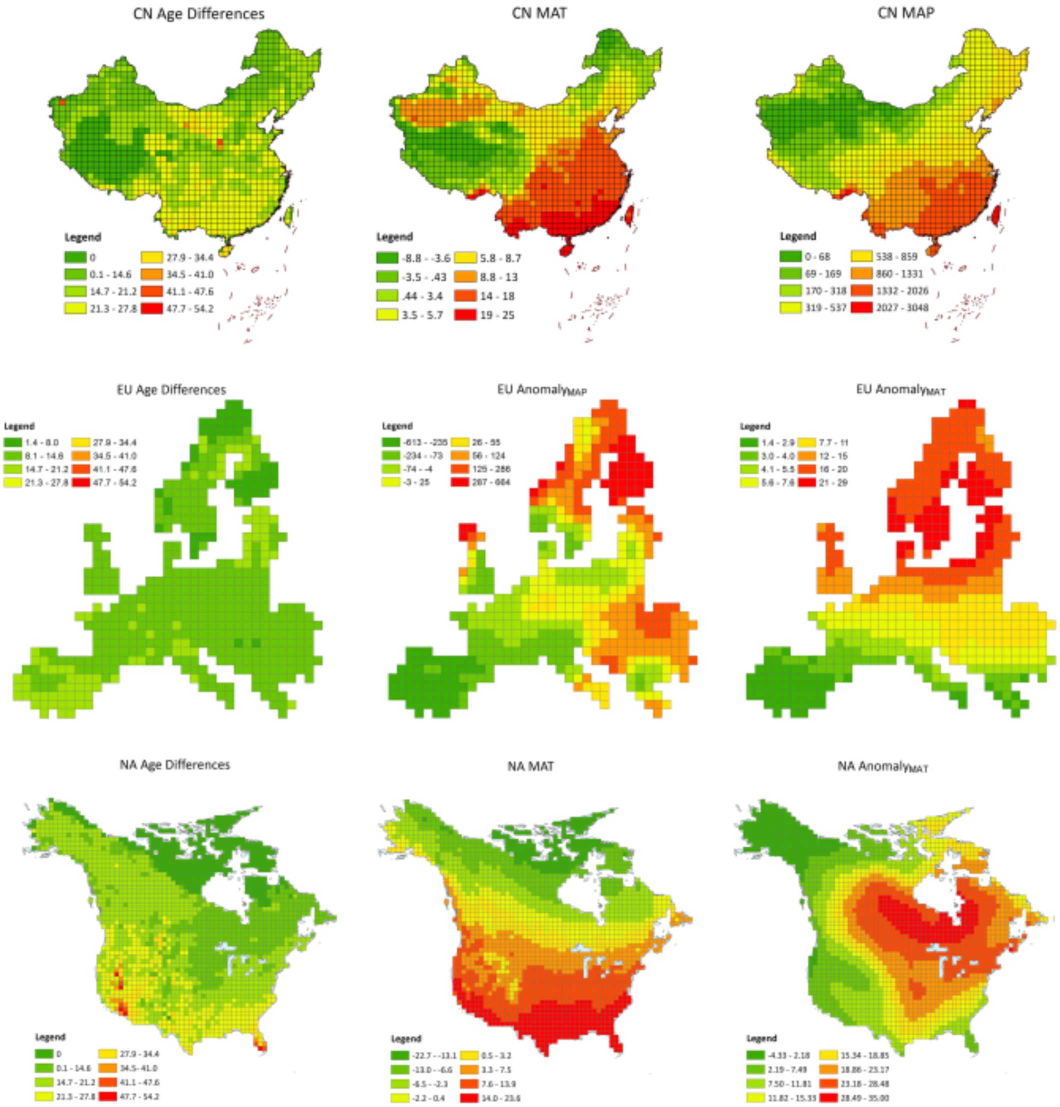

Figure 1. Maps of phylogenetic age differences in median value between the oldest and youngest group in each 100 km × 100 km grid cell and its two most related variables in China (820 grid cells), Europe (502 grid cells) and North America (1,609 grid cells), which are MAT and MAP in China, LGM-to-present anomaly of mean annual precipitation and temperature (AnomalyMAP/MAT) in Europe, and MAT and AnomalyMAT in North America. CN = China; EU = Europe; LGM = Last Glacial Maximum; MAP = mean annual precipitation; MAT = mean annual temperature; NA = North America

3 RESULTS

Tukey's HSD test showed that phylogenetic age differences in tree assemblages in Europe were smaller than in North America, which again were smaller than in China (Figure 1; $p < .01$). Single-variable SAR models showed that the LGM-to-present anomaly in temperature was one of the two variables most associated with phylogenetic age differences in both Europe and North America (Figures 1 and 2; Supporting Information Table S1; $p < .05$ in Europe and $p < .01$ in North America). In contrast, the two variables most associated with phylogenetic age differences in China were the two contemporary climate variables (Figures 1 and 2; Supporting Information Table S1; $p < .01$ for mean annual temperature). Ignoring significance levels, all associations with paleoclimate instability tended to be negative, whereas all associations with contemporary temperature and precipitation tended to be positive. This indicates that phylogenetic age differences tend to be larger in areas with a more stable paleoclimate in Europe and North America and in regions with higher contemporary temperature and more precipitation in China (Figure 2; Supporting Information Table S1).

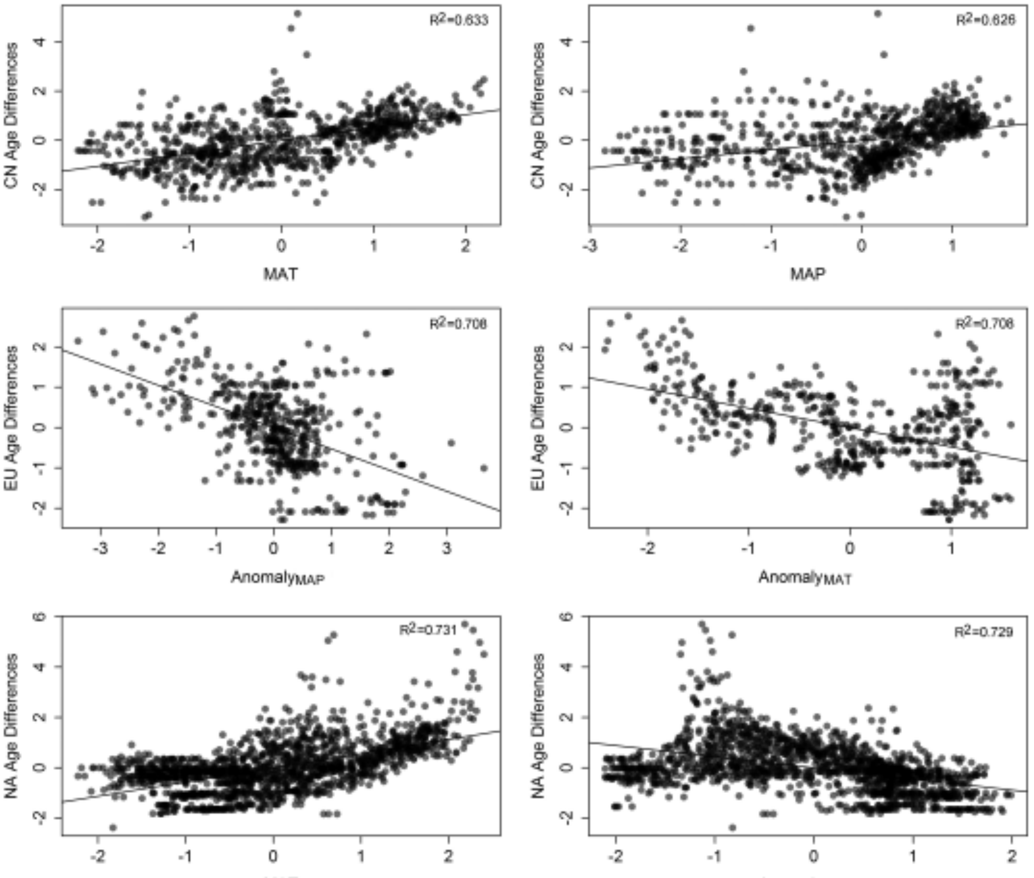

Figure 2. Scatter plots of phylogenetic age differences in median value between the oldest and youngest group in each 100 km × 100 km grid cell against their two most associated variables in China (820 grid cells), Europe (502 grid cells) and North America (1,609 grid cells), which are MAT and MAP in China, LGM-to-present anomaly of mean annual precipitation and temperature (AnomalyMAP/MAT) in Europe, and MAT and AnomalyMAT in North America. MAP in China and AnomalyMAT in Europe are log10-transformed. The points are semi-transparent to display the density of the point clouds. Linear regression fits and pseudo-*R*2 are given. CN = China; EU = Europe; LGM = Last Glacial Maximum; MAP = mean annual precipitation; MAT = mean

annual temperature; NA = North America

The multiple regressions provided similar results, indicating the important role of paleoclimate in North America and Europe (although the standardized coefficients in Europe were not significant) and the important role of contemporary climate in China in shaping the phylogenetic age differences (Table 1). Notably, the best combination of variables includes both contemporary climate and paleoclimate in North America, emphasizing the complementary effect of these two sets of variables (Table 1).

	China		**Europe**		**North America**	
	Coefficient	**w**	**Coefficient**	**w**	**Coefficient**	**w**
Group 1						
MAT	0.31***	1		0.413	0.60***	1
MAP	0.19**	0.792	−0.052	0.547	−0.15***	0.997
VelocityMAT		0.293		0.368	−0.31***	1
VelocityMAP		0.451		0.358		0.298
*R*2	.635		.707		.737	
AIC	1,509.3		815.8		2,425.5	
Group 2						
MAT	0.31***	1		0.321	0.52***	1
MAP	0.19**	0.854		0.407	−0.08**	0.775
ALT		0.298		0.327	0.08**	0.853
AnomalyMAT		0.472	−0.24*	0.609	−0.35***	1
AnomalyMAP		0.278	−0.14*	0.646		0.275
*R*2	.635		.709		.736	
AIC	1,509.3		813.4		2,434.1	

Note. Standardized coefficients for the model with the lowest Akaike information criterion for a given variable group (see below) are given, as well as the Akaike weight (w) for each variable based on the full model sets per group. Model sets involved all possible combinations of associated variables, for the following two groups of variables: group 1, MAT/MAP and LGM-to-present MAT/MAP velocity; and group 2, MAT, MAP, elevation range (ALT) and LGM-to-present MAT/MAP anomaly. ALT = elevation range; LGM = Last Glacial Maximum; MAP = mean annual precipitation; MAT = mean annual temperature; w = Akaike weight. *$p < .1$. **$p < .05$. ***$p < .01$.

Table 1. Simultaneous autoregressive models of phylogenetic age differences in median value between the oldest and youngest group in each 100 km × 100 km grid cell against combinations of environmental variables in China (820 grid cells), Europe (502 grid cells) and North America (1,609 grid cells)

4 DISCUSSION

Long-term climate stability is hypothesized to drive the emergence of species assemblages with large species age differences due to the accumulation of both relict species and newly arisen species via reduced extinction and increased speciation (Dynesius & Jansson, **2000**; Fjeldså & Lovett, **1997**). Our results provide overall support for this idea. Notably, we found that phylogenetic age differences have the following characteristics: (a) they are smaller in Europe than in the other regions, consistent with stronger climate-driven extinction in this more climatically unstable region; (b) they are negatively correlated with LGM-to-present climate change in Europe and North America; and (c) they are not correlated with LGM-to-present climate change but are linked with contemporary climate in China. These links to climate instability in Europe and North America are consistent with the hypothesis that phylogenetic age differences are larger in areas with stable climate because of the co-occurrence of both ancient and new species, preserved from climate-driven extinction and promoted by recent speciation, respectively. The weak link to climate instability in China is consistent with the relatively minor effect of glacial–interglacial climate change on the Chinese flora. We acknowledge that there is limited evidence for tree speciation during the Quaternary, so the geographical variability in phylogenetic age differences must primarily reflect differential extinction rates (with the extinctions causing phylogenetic filtering, cf. Eiserhardt et al., **2015**). Nonetheless, relative recent (but probably for the most part pre-Quaternary) speciation may also play a role if areas that were stable during the Quaternary were also relatively stable on longer time scales. In addition, newly formed species with small ranges would have been more susceptible to climate-driven extinction during the Quaternary, which may also contribute to the pattern.

4.1 Climate change and trees in Europe

Using 10 m in maximal canopy height as a cut-off, Europe has only 159 tree species, much less than North America (367 species) and China (2,154 species). A key factor in this diversity anomaly is a much greater extinction rate among trees in Europe during the late Neogene and Quaternary because of a stronger cooling and drying trend in this region (Davis, **1983**; Eiserhardt et al., **2015**; Qian & Ricklefs, **1999**). Phylogenetic structure of the temperate tree flora in Europe is more clustered than in North America and China, because of the stronger phylogenetically selective extinction in Europe (Eiserhardt et al., **2015**).

Previous studies have shown strong evidence that glacial cooling has led to large range contractions in surviving tree species in Europe, albeit a subset of the more hardy species remained relatively widespread (Svenning, Normand, & Kageyama, **2008**; Willis & Andel, **2004**). Although less severe, many tree species have also exhibited range contractions during glacial maxima in North America (Bell, Bradford, & Lauenroth, **2014**; Ordonez & Williams, **2013**) and East Asia (Ni, Cao, Jeltsch, & Herzschuh, **2014**; Zhao et al., **2016**). These dynamics still shape diversity patterns within the regions, affecting endemism (Feng, Mao, Sandel, Swenson, & Svenning, **2016**; Svenning & Skov, **2007**), phylogenetic structure (Ma, Sandel, & Svenning, **2016**) and even functional diversity (Ordonez & Svenning, **2015, 2016**).

Extending these findings, our results here show that phylogenetic age differences in Europe are relatively smaller than in North America and China (Figure 1), in line with the stronger impact of Quaternary climate change on tree diversity in Europe because of the selective loss of phylogenetic clades (Eiserhardt et al., **2015**). Furthermore, the two variables most associated with phylogenetic age differences in Europe were the LGM-to-present anomaly in temperature and precipitation (Figures 1 and 2), again emphasizing the role of Quaternary climate change in shaping the diversity patterns in this region.

4.2 Climate change and trees in North America

Although the similarities in flora between North America and China have been widely reported in the past decades, plant species richness in China is much higher than in North America (Fang et al., **2012**; Milne, **2006**; Wen, **1999**). One of the drivers for this pattern is the more extensive continental ice sheet during the Quaternary in North America, albeit southern parts of North America functioned as glacial refugia for many plant species (Eiserhardt et al., **2015**; Milne, **2006**). Several studies have found that current tree diversity patterns in North America still partly reflect this dynamic. For example, the accessibility to recolonization from glacial refugia and current climate co-determine the functional diversity pattern of broad-leaved trees across North America (Ordonez & Svenning, **2016**). Furthermore, there is a more clustered phylogenetic structure of temperate trees in western North America than in eastern North America, linked to the more severe climate-driven extinctions in the former region (Eiserhardt et al., **2015**). Nonetheless, glacial refugia in north-west North America along the coast have high local plant diversity and several endemic species, compared with inland glacial regions (Gavin, **2009**). In addition, phylogenetic diversity of North American angiosperms is also correlated with current climate (i.e., minimal temperature), with more clustered phylogenetic structure in colder regions (Qian, Zhang, Zhang, & Wang, **2013**).

In line with these studies, the best combination of variables for phylogenetic age differences in North America includes both paleoclimate and contemporary climate (Table 1). Notably, the two variables most associated with phylogenetic age differences here are mean annual temperature and the LGM-to-present anomaly in temperature (Figures 1 and 2). In addition, the significantly negative associations between phylogenetic age differences and LGM-to-present climate change strongly support the hypothesis of the effect of long-term climate stability on phylogenetic structure of tree assemblages in North America.

4.3 Climate change and trees in China

Compared with Europe and North America, China was relatively mildly affected by the LGM (López-Pujol et al., **2006**; Qian & Ricklefs, **1999**), consistent with our finding that the phylogenetic age differences in China are most associated with two contemporary climate variables, namely MAT and MAP (Figures 1 and 2). Species richness of trees in China is also well linked to contemporary climate, especially temperature-related variables (Wang, Brown, Tang, & Fang, **2009**).

As in other regions, there is evidence for the impact of Quaternary glacial–interglacial climate change on tree assemblage composition and structure in China, with effects on, for example, endemism in woody plants, phylogenetic structure of forest tree communities and spatiotemporal biome shifts (Feng et al., **2016, 2014**; Ni et al., **2014**). However, it is also clear that there were widely distributed glacial refugia for forests and trees not only in southern China, but also in northern and north-western China (Ma, Zhang, & Sanderson, **2012**; Tian et al., **2009**), probably providing a key explanation for the survival of many tree genera that went extinct in North America and Europe during the late Cenozoic and Quaternary (e.g., Eiserhardt et al., **2015**). These dynamics are consistent with the weak negative relationship between phylogenetic age differences in China and LGM-to-present climate change variables found in the present study.

5 CONCLUSIONS

Our study extends the results from studies on the effects of long-term climate stability on phylogenetic structure for other organism groups and regions (Jablonski et al., **2006**; McKenna & Farrell, **2006**; Moreau & Bell, **2013**; Pellissier et al., **2014**) to show its applicability to the Northern Hemisphere tree floras. Notably, our results show that phylogenetically diverse assemblages with large phylogenetic age differences among species are associated with relatively high long-term climate stability, with intra-regional links between long-term climate variability and phylogenetic composition being especially strong in the more unstable regions. These findings point to future climate change as a key risk to the preservation of the phylogenetically diverse assemblages in regions characterized by relatively high paleoclimate stability, with China as a key example.

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BIOSKETCHES

Gang Feng is interested in combing community ecology with macroecology and biogeography to assess the relative roles of local, regional and historical factors in shaping diversity patterns.

Lingfeng Mao is interested in understanding the mechanisms of plant extinction, spatial patterns of plant diversity and key functional traits.

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