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Latitudinal gradients in phylogenetic relatedness of angiosperm trees in North America

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ABSTRACT

Aim To test two predictions of the phylogenetic niche conservatism hypothesis for the latitudinal diversity gradient: (1) species in colder regions tend to be more phylogenetically related to each other (i.e. greater phylogenetic clustering) than those in warmer regions, and (2) clades are younger in colder regions.

Location North America.

Methods Correlation analysis was used to relate richness, mean clade age and phylogenetic relatedness (measured as phylogenetic species variability and net relatedness index) of angiosperm trees in 1175 regional assemblages (each with 12100 km²) to latitude and minimum temperature. The analysis was conducted for North America north of Mexico as a whole as well as for each of the three longitudinal bands (eastern, central and western) of North America.

Results Species richness and mean clade age are negatively correlated with latitude and positively correlated with minimum temperature. Tree species in regional assemblages tend to be more phylogenetically related (clustered) in regions at higher latitudes with lower temperatures.

Main conclusions The results of this study support two of the major predictions of the phylogenetic niche conservatism hypothesis for the latitudinal diversity gradient: species tend to be more phylogenetically clustered and ages of clades tend to be younger in colder regions, compared with those in warmer regions.

Keywords

Angiosperm trees, cold tolerance, community assembly, habitat filtering, latitudinal diversity gradient, phylogenetic community ecology, phylogenetic niche conservatism, tropical conservatism hypothesis.

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INTRODUCTION

The number of species per unit area generally decreases from the equator to the poles (Willig *et al.*, 2003). This latitudinal diversity gradient is the most conspicuous species diversity pattern on the earth (Rosenzweig, 1995). It has been over two centuries since the latitudinal diversity gradient was first described (Humboldt & Bonpland, 1807) but its causes remain poorly resolved (Mittelbach *et al.*, 2007). Strong correlations between environmental variables and species diversity have been found for many taxa at all spatial scales across the globe, and, on this basis, environmental variables have been considered as primary drivers of global diversity patterns by some authors (e.g. O'Brien *et al.*, 2000; Francis & Currie, 2003). However, environmental

variables per se do not produce species (Wiens & Donoghue, 2004; Stevens, 2006). Because speciation, extinction and dispersal directly change species richness patterns (Wiens, 2007), studying these processes can help understand the origin and maintenance of species diversity patterns.

One hypothesis that integrates both evolutionary and ecological factors to explain global diversity patterns is the 'phylogenetic conservatism of ecological niche' hypothesis, or simply called 'phylogenetic niche conservatism' hypothesis, which is defined as retention of ecological traits over evolutionary time among related clades or species (e.g. Wiens *et al.*, 2010). Under this hypothesis, the causes of origin and maintenance of the latitudinal diversity gradient may be explained as follows. Most of the clades of current species originated during the time when

the planet (including polar regions) was predominately under tropical environments (Behrensmeyer *et al.*, 1992; Graham, 1999). For example, over 90% of angiosperm families originated during the time period from the beginning of the Cretaceous (~146 Ma) to the end of Eocene (~35.5 Ma) (Davies *et al.*, 2004). During the global cooling process initiated in the early Eocene (~50 Ma; Condamine *et al.*, 2012), because temperature decreased more quickly at higher latitudes, the gradient of temperature from the equator to the poles became steeper when time approached to the Last Maximum Glaciation (~18 ka). The climate cooling process forced tropical species at higher latitudes to migrate into lower (warmer) latitudes, to evolve into species that could tolerate colder temperatures or to go extinct. Because ecological traits (e.g. cold tolerance) are phylogenetically conserved (Donoghue, 2008) and because an evolutionary event can rarely produce a clade that is able to survive and reproduce in novel climatic conditions such as freezing temperature (Latham & Ricklefs, 1993; Wiens & Donoghue, 2004; Ricklefs, 2006), fewer clades have crossed ecophysiological barriers to harsher (e.g. colder) environments (Ricklefs, 2006). Accordingly, relatively few clades in tropical regions can spread into temperate regions, fewer clades in tropical regions can spread into boreal regions, and fewest clades in tropical regions can spread into polar regions. Consequently, the process results in a decreasing gradient of species richness from the tropics to the poles (i.e. latitudinal diversity gradient). Furthermore, because extratropical environments have evolved only since the global cooling (~35.5 Ma) and thus are much younger than tropical environments (e.g. boreal environments are only 10–4 million years old; Graham, 1999; Willis & McElwain, 2002; Fine & Ree, 2006), clades in a colder region are generally a subset of the clades in a warmer region that spread into the colder region, and there has been too little time for species of them to accumulate (through *in situ* speciation) to the same level seen in tropical regions (Willis, 1922; Stebbins, 1974; Stephens & Wiens, 2003). Overall, the phylogenetic niche conservatism hypothesis predicts that species richness is high in regions characterized by warm temperatures and abundant rainfall because these conditions characterized the ancestral niches of many clades, that species in a colder or dryer region tend to be phylogenetically more related to each other (i.e. phylogenetic clustering) than expected by chance and that clades are younger in colder or dryer regions.

A critical but rarely tested component of the phylogenetic niche conservatism hypothesis is that phylogenetic niche conservatism maintains the disparity in species richness between tropical and extratropical regions over long evolutionary timescales (Wiens & Donoghue, 2004). It has been hypothesized that most tropical clades fail to disperse into extratropical regions because they lack the necessary ecological and physiological adaptations to survive cold winter temperatures (Ricklefs & Schluter, 1993; Futuyma, 1998). This is an essential aspect of the phylogenetic niche conservatism hypothesis because it potentially explains why so many clades that arose in the tropics have not spread into extratropical regions and because it links the evolutionary and biogeographic processes (i.e. speciation and

dispersal) that directly change species numbers with the climatic variables that are strongly correlated with species richness in many ecological studies of the latitudinal gradient (Wiens *et al.*, 2006). This part of the phylogenetic niche conservatism hypothesis predicts that clades in regions with lower temperatures (and at higher latitudes) are more phylogenetically related (clustered) due to phylogenetic niche conservatism. However, few studies (e.g. Algar *et al.*, 2009) have rigorously tested this prediction.

The objective of the present study is to utilize a comprehensive data set including all angiosperm tree species in North America north of Mexico to test two predictions of the phylogenetic niche conservatism hypothesis: (1) tree species in regional assemblages are more phylogenetically clustered in regions with colder minimum temperature, and (2) the mean clade age of trees in regional assemblages tends to decrease with decreasing minimum temperature (and thus with increasing latitude). Trees are an ideal group of organisms for testing these hypotheses because trees are phylogenetically dispersed rather than monophyletic (Fine & Ree, 2006). North America offers an excellent setting for testing hypotheses about large-scale species richness patterns because it includes many major vegetation zones including tropical to boreal forests (Barbour & Billings, 1999) and because of its geographic setting (see Methods).

METHODS

Study area and data

Our study area is North America north of Mexico (simply North America hereafter). We used the Lambert azimuthal equal-area projection to divide North America into equal area quadrats of 12100 km² (110 km × 110 km or approximately equivalent to a 1° × 1° latitude-longitude square near the equator). This spatial scale has been commonly used in studies examining species diversity patterns at a broad scale (e.g. Hawkins *et al.*, 2007; Buckley *et al.*, 2010). We excluded those quadrats that contain land < 75% of a full-sized quadrat. We determined the presence or absence of each species in each quadrat by superimposing species distribution maps on the grid system and generated species lists for each quadrat. Species distribution maps of angiosperm trees in North America were obtained from <http://esp.cr.usgs.gov/data/atlas/little/>. This database or its original data source (Little, 1971–78) was used in previous studies (e.g. Currie & Paquin, 1987). Details about the original data are available in Little (1971–78). There are a total of 1340 quadrats in North America that each have ≥ 75% of terrestrial area (90% of these quadrats each have > 95% of area on land) and at least one angiosperm tree species.

North America has two south-north-oriented mountain systems (i.e. the Appalachian Mountains in the east and the American Cordillera in the west) and a relatively lowland zone between them. Because history, geography and major ecosystems differ substantially across North America longitudinally (e.g. moist forests in eastern North America, prairies and grasslands in central North America, dry lands in south-western North America and unglaciated areas and biological refugia

during the Last Ice Age in north-western North America) and because these differences among regions may influence the phylogenetic structure of species in regional floras, we divided North America into three longitudinal bands (eastern, central and western; see Fig. S1 in Supporting Information). The eastern and western bands each include a major south-north-orientated mountain system (the Appalachian Mountains and the American Cordillera, respectively), and central band generally is low in elevation from the south to the north. This geographical setting has favoured organism dispersal in the south-north direction during climate oscillations, particularly during the Pleistocene, which had many glacial-interglacial cycles (Paillard, 1998). Therefore, within each longitudinal band, geographic barriers to species dispersal between southern and northern latitudes have been minimized, and the degree to which distributions of plants along a latitudinal gradient reflect their tolerance to low temperature would be presumably maximized.

Mean clade age for a quadrat was measured as the mean age of families within the quadrat. We calculated the mean family age (MFA) for each quadrat in two ways. First, we generated a family list for each quadrat, in which a family appeared no more than once in a given quadrat, and then calculated MFA as the sum of family ages of all families in the quadrat divided by the number of families in the quadrat, as did in Hawkins *et al.* (2011). Second, for each species in each quadrat, we assigned it the age of the family to which the species belongs, and calculated species-weighted MFA (MFAW) as the sum of family ages of all species in the quadrat divided by the number of species in the quadrat. The family ages used in this study were obtained from a dated version of megatree of Davies *et al.* (2004).

Minimum temperature (MINT) was measured as mean coldest month (January) temperature, which is related to frost and freezing tolerance. MINT data, which were obtained from New *et al.* (1999), were documented at a resolution of 0.5° in latitude and longitude. We assigned each 0.5° pixel to a quadrat according to the latitude and longitude of each pixel's midpoint, and calculated the average of MINT for each quadrat, using all 0.5° pixels within the quadrat.

Phylogenetic supertree and phylogenetic relatedness index

North America comprises 554 angiosperm tree species. We standardized the generic nomenclature of the species according to Kartesz (1999), and assigned each species to a family of Angiosperm Phylogeny Group (2009). We used the phylomatic function of Phylocom 4.2 (Webb *et al.*, 2008) and a maximally resolved supertree of angiosperms (available at <http://www.phylodiversity.net>) to assemble the species list into a phylogeny for the angiosperm tree flora of North America (i.e. the continental species pool phylogeny). Branch lengths were estimated with the BLADJ algorithm based on family ages in a dated version of megatree of Davies *et al.* (2004) implemented in phylomatic. We treated genera as polytomies within

families and species as polytomies within genera (e.g. Hardy *et al.*, 2012).

We used two metrics to quantify the degree of phylogenetic relatedness among species for each quadrat: phylogenetic species variability (PSV; Helmus *et al.*, 2007) and net relatedness index (NRI; Webb, 2000). Both metrics measure overall relatedness among species within an assemblage, and have been successfully used in previous studies as a measure of phylogenetic relatedness (e.g. Algar *et al.*, 2009; Savage & Cavender-Bares, 2012). We followed Hortal *et al.* (2011) to exclude quadrats ($n = 165$) with five or fewer species to avoid the spurious effects of low sample size. PSV is defined as (Helmus *et al.*, 2007):

$$\text{PSV} = (\text{tr}C - \Sigma C) / n(n-1)$$

where n is the number of species, C is a covariance matrix that summarizes the correlation structure of the community phylogeny, $\text{tr}C$ is the trace (sum of the diagonal elements) of C , ΣC is the sum of all elements in C . PSV is standardized to vary from zero, indicating perfect relatedness (clustering), to one, indicating that species in the assemblage are unrelated (evenness or overdispersion), i.e. all species are from disparate parts of the phylogenetic tree (Algar *et al.*, 2009). Thus, values of PSV from a set of different biological assemblages within a region represent different degrees of phylogenetic clustering (smaller PSV values) to phylogenetic evenness (larger PSV values) with respect to the regional species pool. This metric is independent of species richness (Helmus *et al.*, 2007; Savage & Cavender-Bares, 2012). Time-calibrated branch lengths were incorporated into the calculation of PSV.

NRI measures the standardized effect size of mean phylogenetic distance (MPD), which estimates the average phylogenetic relatedness between all possible pairs of taxa in an assemblage. NRI is defined as (Webb, 2000):

$$\text{NRI} = -1 \times (\text{MPD}_{\text{observed}} - \text{MPD}_{\text{randomized}}) / (\text{sdMPD}_{\text{randomized}})$$

where $\text{MPD}_{\text{observed}}$ is the observed MPD, $\text{MPD}_{\text{randomized}}$ is the expected MPD of the randomized assemblages ($n = 1000$), and $\text{sdMPD}_{\text{randomized}}$ is the standard deviation of the MPD for the randomized assemblages. Time-calibrated branch lengths were incorporated into NRI. A positive NRI value indicates that MPD is lower than expected by chance (i.e. species more closely related than expected) and that phylogenetic clustering of species is occurring. Conversely, a negative NRI value results when the observed MPD is greater than expected by chance (i.e. species more distantly related than expected by chance) and thus indicates phylogenetic evenness or overdispersion.

The significance of each phylogenetic metric for a given quadrat was assessed by comparing its observed value to a null distribution of the metric measured based null assemblages. The null model shuffled the names of taxa across the tips of the phylogeny 999 times. We followed previous authors (e.g. Kembel, 2009; Vamasi *et al.*, 2009; Santos *et al.*, 2010) to calculate a P -value for each quadrat by dividing the number of runs in which the expected mean was smaller or greater than the observed mean by the total numbers of runs (i.e. 1000 in our

case). For $\alpha = 0.05$ (one-tail *t*-test), a value of phylogenetic metric was considered significant if its *P*-value is < 0.025 or > 0.975 (Cardillo, 2011).

We conducted correlation analyses to assess the relationship between different variables. We consider a correlation being weak, moderate or strong if its Pearson's correlation coefficient is < 0.50 , $0.50\text{--}0.75$ or > 0.75 , respectively. Because quadrats are not spatially independent of each other, the number of degrees of freedom calculated based on traditional statistical approach may be overestimated and thus may inflate the rate of type I error (Diniz-Filho *et al.*, 2003). Because there is no consensus among ecologists on how spatial autocorrelation may influence a significance test and what method is best to account for spatial autocorrelation, we used two methods to account for spatial autocorrelation. First, because testing the significance of the correlation of two variables is equivalent to testing the significance of a simple regression of one variable against the other, we applied the commonly used spatial autoregressive model (e.g. Dormann, 2007; Qian, 2010) to determine the significance of the relationship between paired variables after accounting for spatial autocorrelation. Second, for each of the four data sets (i.e. entire, eastern, central and western North America), in addition to conducting correlation analyses including all samples and using the above-mentioned method to account for spatial autocorrelation, we used only 5% of samples randomly drawn from the original data set in a correlation analysis. We generated 1000 randomized data sets with only 5% of samples of each original data set for each correlation, calculated the averages of correlation coefficients and *P*-values from the 1000 randomized data sets and determined the significance of the mean correlation coefficient based on the mean *P*-value.

RESULTS

At the continental scale, latitude was negatively and strongly to moderately correlated with MINT ($r = -0.921$), tree species and family richness (-0.648 and -0.766 , respectively), MFAW (-0.762), and PSV (-0.889), and was positively and moderately correlated with NRI (0.729) (Table 1; Figs 1 & 2). Conversely, MINT was positively correlated with tree species and family richness (0.636 and 0.747 , respectively), MFAW (0.715), and PSV (0.846), and was negatively correlated with NRI (-0.714) (Table 1; Figs 1 & 2). PSV was negatively correlated with NRI (-0.828). Ages of angiosperm families in North America varied greatly, ranging from 25.23 to 135.41 million years old. The mean age of angiosperm families within a quadrat decreased with increasing latitude and thus with decreasing temperature, regardless of whether MFA or MFAW was used, but MFAW was more strongly correlated with latitude and MINT than was MFA (Table 1).

When each observed value of PSV or NRI was compared with a distribution of 1000 null communities, over 80% of the 1175 quadrats across North America were significantly phylogenetically clustered ($P < 0.05$), and only 6% of the quadrats were significantly evenly distributed across the phylogeny of North American angiosperm trees, regardless of which phylogenetic

Table 1 Pearson's correlation coefficients among latitude (LAT), minimum temperature (MINT), species richness (SR), family richness (FR), mean family age (MFA), species-weighted mean family age (MFAW), phylogenetic species variability (PSV) and net relatedness index (NRI) for angiosperm trees in North America ($n = 1175$).

| | LAT | MINT | SR | FR | MFA | MFAW | PSV |
|------|-------|-------|-------|-------|-------|-------|-------|
| MINT | -0.92 | | | | | | |
| SR | -0.65 | 0.64 | | | | | |
| FR | -0.77 | 0.75 | 0.97 | | | | |
| MFA | -0.40 | 0.41 | 0.54 | 0.52 | | | |
| MFAW | -0.76 | 0.72 | 0.65 | 0.70 | 0.75 | | |
| PSV | -0.89 | 0.85 | 0.73 | 0.82 | 0.53 | 0.83 | |
| NRI | 0.73 | -0.71 | -0.55 | -0.68 | -0.30 | -0.64 | -0.83 |

metric was used. Clearly, angiosperm tree species within quadrats were more phylogenetically related at higher and colder latitudes (Table 1; Figs 1 & 2).

When data were analyzed separately for each of the three longitudinal bands, patterns on the relationships of latitude and MINT with species and family richness, MFA and measures of phylogenetic relatedness at the band scale were generally consistent with those at the continental scale (Table 2). On average, latitude explained the same amount of the variation in the six variables in the three longitudinal bands as did MINT, which was 58.4% in both cases (i.e. the average of 18 squared correlation coefficients in either LAT or MINT in Table 2).

The vast majority of the correlations between either latitude or MINT and each of the six variables were significant ($P < 0.05$) after accounting for spatial autocorrelations, regardless of which method was used to account for spatial autocorrelation (Table S1). Specifically, when Method 1 was used, all the 48 relationships were significant ($P < 0.05$); when Method 2 was used, 44 of the 48 correlations were significant ($P < 0.05$), and another two were marginally significant ($P < 0.07$; Table S1). The strength of correlations based on all samples of a data set was nearly identical to that based on only 5% of the samples of the data set ($|r| = 0.730 \pm 0.183$ SD vs. 0.731 ± 0.185 for the correlations between latitude and the six variables in the four data sets; $|r| = 0.728 \pm 0.170$ vs. 0.728 ± 0.171 for correlations between MINT and the six variables in the four data sets; Table S1). This result indicates that in general 5% of the sample size of an original data set can very well represent the entire original data set.

DISCUSSION

Our finding that the angiosperm tree flora of North America is strongly phylogenetically structured, i.e. tree species are more phylogenetically clustered in areas with lower MINT, provides direct support to a key prediction of the phylogenetic niche conservatism hypothesis. Few studies have examined geographic variation of phylogenetic relatedness of species at a broad geo-

Figure 1 Spatial variation in phylogenetic species variability (PSV) (a) and net relatedness index (NRI) (b).

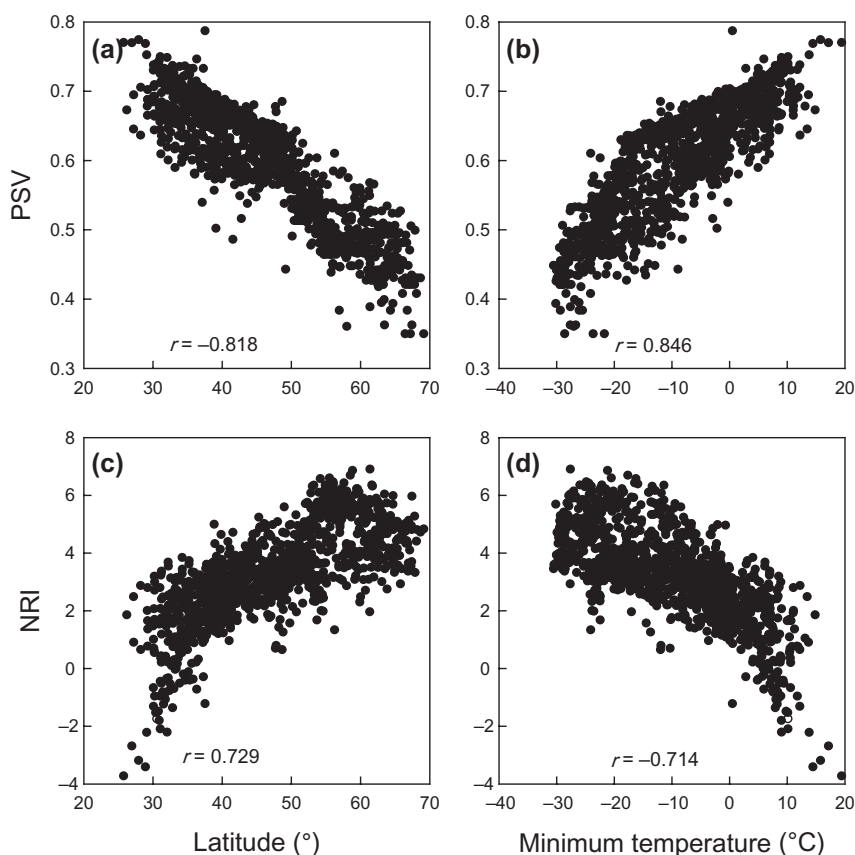
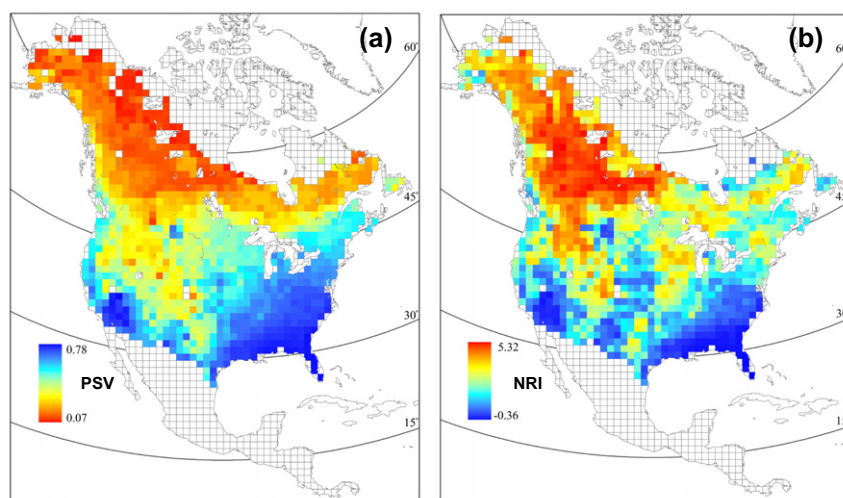


Figure 2 Relations of phylogenetic species variability (PSV) and net relatedness index (NRI) with latitude and minimum temperature for angiosperm tree assemblages (quadrats, $n = 1175$) in North America.

graphic extent, and, to our knowledge, our study is the first to examine phylogenetic relatedness of plant species in regional assemblages along the gradients of MINT across a continental region. Kooyman *et al.* (2011) examined phylogenetic relatedness of woody plants in local assemblages (c. 0.1–0.5 ha) in tropical and subtropical regions in eastern Australia but they did not relate measures of phylogenetic relatedness to climatic variables in general and MINT in particular. Giehl & Jarenkow (2012)

examined phylogenetic relatedness of trees in local assemblages (c. 1 ha) constrained to only about 10° in latitude in tropical and subtropical regions in South America. Phylogenetic niche conservatism hypothesis in general and tropical conservatism hypothesis in particular (Wiens & Donoghue, 2004) have been formulated to explain differences in species diversity between tropical and temperate regions but neither Kooyman *et al.* (2011) nor Giehl & Jarenkow (2012) included temperate regions.

Table 2 Pearson's correlation coefficients of latitude (LAT) and minimum temperature (MINT) with species richness (SR), family richness (FR), mean family age (MFA), species-weighted mean family age (MFAW), phylogenetic species variability (PSV) and net relatedness index (NRI) for angiosperm trees in eastern ($n = 279$), central (343) and western (553) quadrats in North America.

| Category | Eastern | | Central | | Western | |
|----------|---------|-------|---------|-------|---------|-------|
| | LAT | MINT | LAT | MINT | LAT | MINT |
| SR | -0.95 | 0.93 | -0.62 | 0.62 | -0.67 | 0.69 |
| FR | -0.98 | 0.97 | -0.77 | 0.77 | -0.82 | 0.81 |
| MFA | -0.78 | 0.77 | -0.43 | 0.43 | -0.21 | 0.28 |
| MFAW | -0.89 | 0.87 | -0.63 | 0.61 | -0.73 | 0.75 |
| PSV | -0.93 | 0.92 | -0.84 | 0.82 | -0.89 | 0.91 |
| NRI | 0.81 | -0.82 | 0.74 | -0.73 | 0.67 | -0.71 |

Nevertheless, both Kooyman *et al.* (2011) and Giehl & Jarenkow (2012) found that woody species in subtropical and warm temperate samples are more phylogenetically clustered than those in tropical samples, which is consistent with our finding.

Algar *et al.* (2009) is, to our knowledge, the only study that examines the relationship between phylogenetic relatedness and MINT for animals in regional assemblages at a broad geographical (continental) extent. They found a positive relationship between PSV and MINT for treefrogs in the New World. Their result is consistent with ours. Other previous studies on animals at a broad geographical extent examined the relationship between phylogenetic relatedness and latitude (instead of temperature). For example, Hortal *et al.* (2011) compared NRI values of scarab assemblages between northern and southern latitudes in southern Europe with a narrow range ($\sim 20^\circ$) of latitudes. Although they found that the average of NRI values per quadrat is smaller in the south than that in the north, there appears to lack a clear gradient of increasing NRI with increasing latitude in the eastern half of their study area (their Fig. S3).

We used two metrics (i.e. PSV and NRI) to quantify the phylogenetic relatedness of angiosperm trees in each regional assemblage in North America. Although these two metrics are strongly correlated, it appears that the latitudinal gradient of phylogenetic structure goes more smoothly when PSV was used, compared with that using NRI (Fig. 1). Quadrats along the northern edge of boreal biome may be less phylogenetically clustered, compared with those located south of them, and this pattern is clearer when NRI was used as a measure of phylogenetic relatedness (Fig. 1). Boreal biome originated 10–4 Ma (Graham, 1999; Willis & McElwain, 2002; Fine & Ree, 2006), and thus is relatively young, compared with other major biomes in North America. This suggests that in addition to MINT, range edges of angiosperm trees in northern boreal forest zone are set by other factors, which may include, but not be limited to, permafrost soils and short growing season. Across the longitu-

dinal gradient of North America, the phylogenetic relatedness of tree species in the western band (particularly along its coast) appears to be more heterogeneous than that of the eastern band, regardless of which phylogenetic metric was used (Fig. 1). This may be partly because the west is physiographically very heterogeneous, and the west coast has a more maritime climate and partly because conifers-dominated forests may have some additional impact on the nature of angiosperm forest representatives, and needle-leaf forests are more prevalent at a wider range of latitudes in the west than in the east. All these may have resulted in lower correlations of MINT and latitude with measures of phylogenetic relatedness in the west, compared with the east (Table 2). Another plausible reason for the lower correlations in the west is that a large area of biotic refugium in Alaska during the Last Glacial Maximum may have weakened the general unidirectional dispersal gradient from the south to the north after the glaciation that occurred in the other two longitudinal bands of North America.

Our study showed that over 80% of regional tree assemblages in North America north of Mexico were significantly phylogenetically clustered. Our study area is primarily restricted to latitudes north of 30° N. We did not include typical tropical assemblages of trees in our study due to lack of data at the spatial scale examined. Because significant phylogenetic evenness is found for woody plants in wet tropical forests (Kooyman *et al.*, 2011), we expect that if our study had included a large number of regional tree assemblages from wet tropical regions south of 30° N, particularly those near the equator, the proportion of regional tree assemblages showing phylogenetic clustering structure would be markedly reduced and a substantial proportion of the regional tree assemblages south of 30° N would have shown a random or overdispersed phylogenetic structure.

Our study showed that ages of families are positively correlated with MINT, regardless of whether MFA or MFAW was used. This relationship is consistent with the prediction of the phylogenetic niche conservatism hypothesis. In a global analysis, Hawkins *et al.* (2011) reported a diagram showing a latitudinal gradient of family ages for arborescent angiosperms in North America based on family lists, but they examined neither the relationship between family age and temperature nor the relationship of species-weighted family age with latitude and temperature. Moreover, because their classification of angiosperm families into three groups (i.e. families with arborescent plants only, families with herbaceous plants only and families with both arborescent and herbaceous plants) includes errors for some families (e.g. they treated Poaceae as a herbaceous family but this family includes about 1400 woody species of bamboos) and their arborescent families include not only tree families but also families with only shrubs and/or lianas, it is not clear the degree to which the pattern of family ages found in their study is comparable to that found in our study, although both studies have shown the general trend of decreasing family ages with latitude. Stevens (2006) found that the average relative age of New World leaf-nosed bats decreases with increasing latitude. Ricklefs & Schluter (1993) showed that the clades that made up

bird assemblages in a tropical locality in Panama are approximately twice as old as the clades that comprised a bird assemblage in a temperate locality (Illinois, USA). Our finding that family ages are negatively correlated with latitude is consistent with the latitudinal gradient of taxon ages reported in previous studies (e.g. Ricklefs & Schluter, 1993; Stevens, 2006; Hawkins *et al.*, 2011).

In conclusion, the phylogenetic niche conservatism hypothesis postulates links among environment, evolutionary history and species diversity. The present study tested two major predictions of the phylogenetic niche conservatism hypothesis, and the results of this study support these predictions: species tend to be more phylogenetically clustered and ages of clades tend to be younger in colder regions, compared with those in warmer regions. These patterns suggest that the composition of tree species in each regional assemblage is determined by the similarity of phylogenetically constrained ecological niches (e.g. cold tolerance) among species in the regional assemblage through habitat filtering processes.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1. Map showing the division of North America into eastern (red), central (green) and western (blue) longitudinal bands.

Table S1. *P*-values based on two methods to account for spatial autocorrelation.

BIOSKETCH

Hong Qian's research is multidisciplinary and particularly lies at the interface of ecology and biogeography. His research involves a wide range of spatial scales (from local to global) and a variety of taxa (e.g. bryophytes, vascular plants, vertebrates and invertebrates). For this article, H.Q. initiated the study, performed statistic analyses and wrote the manuscript, Y.Z. and X.W. compiled data and produced maps, J.Z. performed phylogenetic analyses and randomization analyses, and all authors contributed substantially to revisions.

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