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Research

Phylogenetic structure of angiosperm trees in local forest communities along latitudinal and elevational gradients in eastern North America

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Latitudinal and elevational gradients both represent thermal gradients. Assessing the consistency of the relationships between phylogenetic structure and climate between latitudinal and elevational gradients can provide insight into the mechanisms driving assembly of species from regional pools into local assemblages. The aim of this study is to compare patterns of phylogenetic structure measures for angiosperm tree species between latitudinal and elevational gradients, using a dataset of angiosperm tree species in 14 092 forest plots in eastern North America. We assessed whether these two gradients produce similar relationships between climate and phylogenetic structure, hypothesizing that they should differ in magnitude but not direction. We used correlation and regression analyses to assess the relation of measures of phylogenetic structure to elevation, latitude and climatic variables, which included minimum temperature, temperature seasonality, annual precipitation and precipitation seasonality. We found that 1) phylogenetic relatedness of angiosperm trees increases with decreasing temperature along both latitudinal and elevational gradients but the relationship between phylogenetic relatedness and temperature is steeper for elevational gradients than for latitudinal gradients; 2) the tip-weighted metric of phylogenetic relatedness (nearest taxon index) is more strongly correlated with climatic variables than the basal-weighted metric of phylogenetic relatedness (net relatedness index); 3) winter cold temperature exerts a stronger effect on community assembly of angiosperm trees than does temperature seasonality. These results suggest that winter cold temperature, rather than temperature seasonality, drives phylogenetic structure of plants in local forest communities, and that species distributions along elevational gradients are more in equilibrium with temperature, compared with those along latitudinal gradients.

Keywords: cold tolerance, community assembly, environmental filtering, niche conservatism, temperate forests, thermal gradients

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Introduction

It is broadly accepted that ecological and evolutionary processes work together to assemble local communities from species available in regional pools based on species traits linked to ecological tolerances (Wiens and Donoghue 2004, Ricklefs 2005). Phylogenetic niche conservatism, i.e. the tendency of species to retain ancestral niches, is thought to influence which species from a regional species pool can persist in a particular local community (Donoghue 2008). Since the origin of the angiosperms, Earth's climate has been predominately warmer than the present, and most major angiosperm clades originated under mainly tropical or tropical-like conditions (Behrensmeyer et al. 1992, Graham 1999), as a result, traits that are advantageous in warm environments are often ancestral whereas traits that confer cold tolerance likely evolved after the global cooling initiated in the early Eocene (~50 Mya; Graham 2011, Condamine et al. 2012), permitting some clades to persist in cold environments (Zanne et al. 2014).

Because many ecological traits are phylogenetically conserved (Donoghue 2008), evolutionary innovations conferring cold tolerance are thought to have occurred only in few clades (Ricklefs 2006). This creates an environmental filter that excludes many clades from cold climates; those that remain are likely to represent clusters of closely related species. This process is expected to result in a gradient of increasing phylogenetic relatedness (clustering) with decreasing temperature (i.e. co-occurring species tend to be more closely related in areas with colder temperatures). Minimum temperature (e.g. the mean temperature of the coldest month) is considered a major constraint for species to disperse into areas with cold climate, and thus a major driver of assembling species from a regional species pool into local communities along a thermal gradient (Hawkins et al. 2014).

Before the global cooling initiated in the early Eocene, there was little to no ice on Earth with a smaller difference in temperature from the equator to the poles and low temperature seasonality at high latitudes (Archibald et al. 2010). The global cooling strengthened not only the latitudinal gradient of temperature (i.e. temperature decreases with increasing latitude) but also the latitudinal gradient of temperature seasonality (i.e. intra-annual temperature variation increases with increasing latitude) (Latham and Ricklefs 1993a, Archibald et al. 2010). Increased seasonal variability of temperature at higher latitudes would select species that can tolerate a wider range of thermal variation. Because many ancestral clades evolved in tropical climate with no or little seasonal variation, fewer clades have evolved traits that can tolerate greater temperature seasonality. Accordingly, some authors argued that it is the temperature seasonality, rather than winter cold temperature, that determines species dispersal into areas with colder climate (e.g. higher latitudes). For example, Wiens et al. (2006) related northern distributional range limits of hylid frogs in North America to several climatic variables (including minimum temperature and temperature seasonality); they concluded that extreme winter temperature is seemingly not a critical factor to limit northern range limits of species; instead, temperature seasonality seemingly limits dispersal of many tropical clades into temperate regions.

Few of the studies that have examined the relationships between phylogenetic structure (including phylogenetic relatedness and diversity) and climate have included both minimum temperature and temperature seasonality, and these studies were conducted commonly based on latitudinal gradients (Qian et al. 2016). Because minimum temperature and temperature seasonality are strongly correlated with each other along a latitudinal gradient, the relationship of a metric of phylogenetic structure with minimum temperature (or mean annual temperature, which is usually correlated with minimum temperature very strongly) often does not differ greatly than that with temperature seasonality for latitudinal gradients (Qian et al. 2016).

Because temperature decreases with both latitude and elevation and because vegetation zonation along an elevational gradient generally mirrors that along a latitudinal gradient (MacArthur 1972, Stevens 1992), elevational gradients are commonly considered as analogs to latitudinal gradients (Körner 2000). However, unlike latitudinal gradients along which minimum temperature is strongly correlated with temperature seasonality, the two climate variables are not strongly correlated with each other along elevational gradients (Qian 2018). Thus, elevational gradients appear to be better systems for determining whether minimum temperature or temperature seasonality is a more important driver of macroecological patterns.

Previous studies have shown that cold temperature is a major factor controlling distributions of species towards higher latitudes and elevations (Huntley et al. 1989, Körner 1998). If all species are in equilibrium with current climate along both latitudinal and elevational gradients, one would expect that the temperature at the uppermost limit of a species distribution along an elevational gradient should match the temperature at the highest latitude of the species distribution along a latitudinal gradient (Randin et al. 2013, Siefert et al. 2015). In particular, one would expect that species reach the same cold temperature limits along both latitudinal and elevational gradients (i.e. Humboldt's law; Randin et al. 2013). However, because the poleward expansions of tree species after the last glaciation lag behind their potential climatic limits (Davis et al. 1986, Svenning et al. 2008) due to dispersal limitation, many tree species might have not reached their equilibrium with climate following the last glaciation (Svenning and Skov 2007). Because dispersal should be much more efficient along elevational than latitudinal gradients (Jump et al. 2009), populations of a species at the uppermost limit of an elevational gradient should be closer to equilibrium with temperature, compared to those at the northernmost limit of a latitudinal gradient. Accordingly, one would expect that species should have reached colder temperatures along elevational gradients than latitudinal gradients (Halbritter et al. 2013, Siefert et al. 2015). This would

lead to steeper relationships between measures of phylogenetic structure and temperature for elevational gradients than for latitudinal gradients.

Empirical data from latitudinal gradients have shown that phylogenetic relatedness increased and phylogenetic diversity decreased with decreasing temperature for tree species (Qian et al. 2013, 2016), which is consistent with the tropical niche conservatism hypothesis. However, mixed results have been reported for elevational gradients. For example, angiosperm woody species are more closely related to each other at higher elevations (i.e. lower temperatures) in a temperate region in Asia (Qian et al. 2014), but are more distantly related to each other at higher elevations in tropical Asia (Culmsee and Leuschner 2013, Qian and Ricklefs 2016) and tropical America (González-Caro et al. 2014, Qian and Ricklefs 2016). Because these studies were conducted in different climatic regions (e.g. tropical versus temperate regions), unique evolutionary history in each of these regions might have contributed to differences in patterns of phylogenetic relatedness between latitudinal and elevational gradients observed in these studies.

In this study, we analyse a large data set with over 14 000 local forest communities to examine the relationships of phylogenetic structure of angiosperm tree species in local communities with minimum temperature and temperature seasonality, among other climatic variables, along latitudinal and elevational gradients within a single biogeographic region in eastern North America (Fig. 1). This geographic region is an ideal model system for assessing and comparing macroecological patterns along latitudinal and elevational gradients for several reasons. First, the region covers a relatively long range of temperatures (over 20°C for mean annual temperature) across a long latitudinal gradient (over 2000 km), which is ideal for assessing the effect of temperature on macroecological patterns. Second, the region includes a north–south oriented mountain system (the Appalachians), which has its highest peak at 2037 m a.s.l. and covers most of the entire length of the latitudinal gradient in eastern North America. This north–south oriented mountain system probably enhanced plant dispersal during multiple glacial–interglacial cycles of the Pleistocene (Delcourt and Delcourt 1993). Third, because the Appalachians is imbedded within the broad latitudinal gradient of eastern North America, species in forest communities along both latitudinal and elevational gradients within the region were assembled from the same regional species pool; this would have avoided the effect of differences in geological and biogeographic histories between elevational and latitudinal gradients on the assembly of species into local communities. In other words, species in all forest communities in the region, regardless of its elevation and latitude, would have been assembled from the same species pool mainly through filtering according to ecological niches of individual species (Qian et al. 2018). While often called 'environmental filtering' we note that biotic interactions also can play an important role in generating phylogenetic patterns through filtering (Mayfield and Levine 2010, Kraft et al. 2015). For example, a particular climate might be too stressful for a species only when it is also confronted with competition from better-adapted species (Crain et al. 2004). For our purposes here, it is not necessary to distinguish
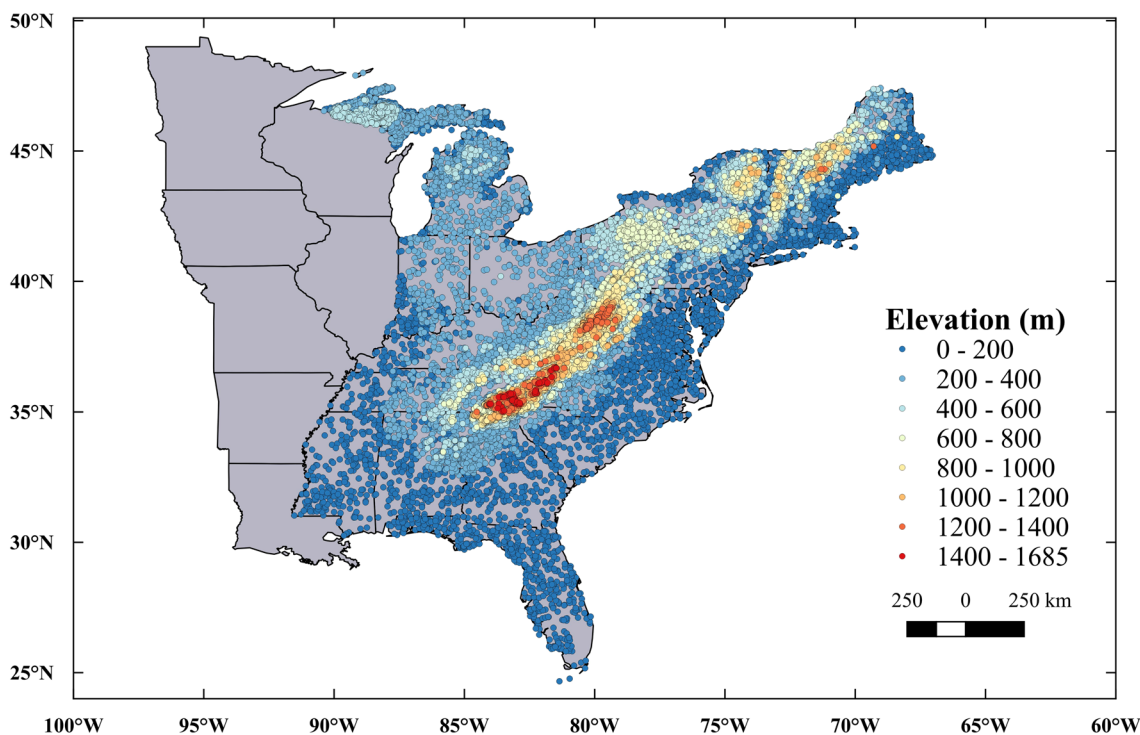

Figure 1. Map showing locations of the forest inventory plots used in this study.

between strict environmental filtering and filtering mediated by biotic interactions, so we consider both processes together under the broader term environmental-biotic filtering.

The objective of this study is to compare elevational and latitudinal gradients of phylogenetic structure for angiosperm trees to test three hypotheses. First, we predict that environmental-biotic filtering combined with phylogenetic niche conservatism will lead to more phylogenetic clustering at both higher elevations and higher latitudes. Second, leveraging the fact that temperature seasonality and minimum temperature are correlated across latitude but only weakly so across elevation, we ask which is a better predictor of phylogenetic structure. Considering that minimum temperature is closely related to cold tolerance and that many studies have frequently shown that minimum temperature is the strongest temperature-related correlate of macroecological patterns for plants (Wang et al. 2011, Hawkins et al. 2014, Qian et al. 2018), we hypothesize that minimum temperature influences phylogenetic structure more strongly than temperature seasonality (hypothesis 2). Third, considering that elevational thermal gradients are much more spatially compressed than latitudinal thermal gradients and dispersal is much more efficient along elevational than latitudinal gradients (Jump et al. 2009), species should be closer to equilibrium with climate for elevational gradients than for latitudinal gradients (Halbritter et al. 2013, Siefert et al. 2015), which should lead to stronger (steeper) relationships between phylogenetic relatedness and temperature for elevational gradients than for latitudinal gradients (hypothesis 3).

Material and methods

The data

The study area includes 24 states in the eastern United States (Fig. 1). We first divided the area into 2° latitudinal zones, between 24° and 48°, and then divided the elevational range of each latitudinal zone into elevational bands of 200 m. Following Qian et al. (2018), we extracted data for forest plots from the US Forest Service's Forest Inventory and Analysis (FIA) database (<www.fia.fs.fed.us>), and assigned each plot to a 200-m elevational band and a 2° latitudinal zone according to its location. For inclusion, a plot had to be coded as a 'natural stand' in the FIA. For those plots for which elevation was not provided in the FIA, we extracted elevations from the 30 arc-second WorldClim database (ver. 1.4, available at <www.worldclim.org>) based on the geographical coordinates of the plots, acknowledging that slight departures occur because the geographical coordinates of some sites have been slightly shifted in order to protect the privacy of landowners. When an elevational band within a latitudinal zone had more than 400 plots, we randomly selected 400 to balance sampling effort across bands. Each plot was 0.07 ha. Forest plots with fewer than two angiosperm tree species were excluded, because phylogenetic relatedness metrics used (see below) require at least two species.

Our final data set included 14 092 forest plots. On average, each elevational band within a latitudinal zone had 252 plots. Following Qian et al. (2018), we assembled forest plots into latitudinal gradients, each of which was constrained within 200 m in elevation (e.g. 0–200, 200–400 and 400–600 m); similarly, we assembled forest plots into elevational gradients, each of which was constrained within 2 degrees in latitude (e.g. 32–34, 34–36 and 36–38°). As in Qian et al. (2018), we focused on the three longest latitudinal gradients (1571–2532 km, i.e. those located in elevations between 0 and 600 m; Supplementary material Appendix 1 Table A2), and the three longest elevational gradients (1397–1685 m, i.e. those located in latitudes between 34 and 40°; Supplementary material Appendix 1 Table A2).

Botanical nomenclature for the angiosperms in the dataset was standardized according to The Plant List (ver. 1.1, <www.theplantlist.org>). The study plots included 149 native angiosperm tree species in 59 genera and 33 families. Non-native species were excluded from this study because this study aims to investigate the assembly of native species from the regional species pool into local communities.

Phylogeny reconstruction

The phylogenies published in Hawkins et al. (2014) and Zanne et al. (2014) include the vast majority of the 149 angiosperm tree species. We pruned each phylogeny using the species list of this study and found that the two resulting phylogenies differed to a noticeable degree. Accordingly, we generated two phylogenies for this study based on Hawkins et al.'s and Zanne et al.'s phylogenies (Supplementary material Appendix 1 Fig. A1, A2). Hawkins et al.'s phylogeny includes all genera and 141 species of this study. For the eight species that were absent from Hawkins et al.'s phylogeny, we added them to their close relatives according to various botanical literature (Flora of North America Editorial Committee 1993–2016, Zanne et al. 2014). All families and 58 genera present in the data set of this study were included in Zanne et al.'s phylogeny. The sole genus of this study that was absent from Zanne et al.'s phylogeny is *Planera* in Ulmaceae, which is a monotypic genus. Because Ulmaceae had only two genera in our data set, and the two genera would be treated as sister clades in any resolved phylogeny as we did, thus, all genera in our data set were resolved in our phylogeny generated based on Zanne et al.'s phylogeny. Most (82.6%) of the 149 species in our data set were included in Zanne et al.'s phylogeny. For the species of our data set that are absent from Zanne et al.'s phylogeny, we added them to their respective genera using the Phylomatic and BLADJ approaches (Webb et al. 2011) implemented in the S.PhyloMaker software (Qian and Jin 2016).

Phylogenetic structure metrics

Commonly used metrics to quantify phylogenetic structure include the mean pairwise distance (MPD) along the phylogenetic tree between all species in the set, the mean nearest

taxon distance (MNTD), the mean distance from each taxon to its nearest neighbor in the set, and the total branch length in the minimum spanning subtree for the set (phylogenetic diversity, PD) (Faith 1992, Webb 2000, Vellend et al. 2010). Some of these basic measures depend on the species richness of the sample. To account for the effect of species richness, it is desirable to standardize these measures according to the species richness of the sample. This standardisation leads to some of the most commonly used indices, including NRI (net relatedness index, a standardised version of MPD), NTI (nearest taxon index, a standardised version of MNTD) and PDI (phylogenetic diversity index, derived from PD) (Webb et al. 2002, 2011, Tsirogiannis and Sandel 2016). NRI and NTI measure phylogenetic relatedness among taxa at different depths in the phylogeny: NRI measures phylogenetic relatedness among taxa at both deep and shallow levels within a phylogenetic tree and emphasizes phylogenetic relatedness for major clades (e.g. orders and families) branching at deep nodes whereas NTI measures phylogenetic relatedness at a shallower level within the phylogenetic tree among taxa descending from superficial nodes. A positive NRI or NTI value indicates phylogenetic clustering whereas a negative NRI or NTI value indicates phylogenetic evenness or overdispersion. PDI standardizes the phylogenetic diversity measure of Faith (1992) with respect to species richness. A greater value of PDI represents a higher phylogenetic diversity.

NRI, NTI and PDI are commonly used in studies of community assembly (Webb et al. 2002, 2011, Cavender-Bares et al. 2009, Qian et al. 2013, 2014, 2015, 2016, Sandel and Tsirogiannis 2016, Tsirogiannis and Sandel 2016). Accordingly, we used these three metrics in this study. All the three metrics were computed using PhyloMeasures (Tsirogiannis and Sandel 2016), which uses computationally efficient algorithms described in Tsirogiannis et al. (2012, 2014), using a null model in which the species richness of each sample is maintained (i.e. the taxon shuffle approach; Kembel et al. 2010, Tsirogiannis and Sandel 2016). An important feature of these algorithms is that the calculation of NRI, NTI and PDI are not based on a resampling approximation of the mean and variance but based on exact solutions given a particular phylogenetic tree and species richness (see Tsirogiannis and Sandel 2016, and <https://cran.r-project.org/web/packages/PhyloMeasures/PhyloMeasures.pdf> for details).

For each forest plot, we calculated two sets of the phylogenetic metrics corresponding to the two phylogenies (i.e. one generated based on Hawkins et al.'s phylogeny, the other generated based on Zanne et al.'s phylogeny). Within each set of the phylogenetic metrics, three subsets of the phylogenetic metrics were calculated for each forest plot: one subset using a phylogeny that included all 149 species in this study, one subset using a phylogeny that included only those species present in the latitudinal gradient in which the forest plot was located, and the other subset using a phylogeny that included only those species present in the elevational gradient in which the forest plot was located. Thus, for each forest plot, six subsets of the three phylogenetic metrics were calculated.

Climatic data

Some important climatic variables that drive community assembly and have been broadly used in ecological studies include mean annual temperature (MAT), minimum temperature (MT), annual precipitation (AP), temperature seasonality (TS) and precipitation seasonality (PS) (Weigelt et al. 2015, Patrick and Stevens 2016, König et al. 2017). We obtained data for these climatic variables from the WorldClim database at the 30-arc-second resolution (Hijmans et al. 2005; <www.worldclim.org>) for each of the forest plots. The five climatic variables correspond to BIO1, BIO6, BIO12, BIO4 and BIO15, respectively, in the WorldClim database. Because MAT and MT are strongly correlated in our data set (r = 0.985) and because winter cold temperature is considered one of the most important factors determining distributions of plants (Wang et al. 2011, Hawkins et al. 2014), we did not use MAT in data analysis.

Statistical analysis

We conducted correlation analyses to assess the relationships between phylogenetic structure metrics and climatic variables for the whole data set including the 14 092 forest plots as well as for individual latitudinal and elevational gradients. Most of our analyses focused on the three longest latitudinal gradients located between elevations from 0 to 600 m and the three longest elevational gradients located between 34 and 40°N latitude. The relationships between phylogenetic metrics and climatic variables were compared among latitudinal and elevational gradients based on Pearson's correlation coefficient and the regression coefficient of simple regression. To more rigorously test hypothesis 2 (i.e. minimum temperature plays a more important role than temperature seasonality in shaping phylogenetic structure patterns), we simultaneously assessed the effects of minimum temperature and temperature seasonality on phylogenetic metrics while accounting for precipitation, by building a structural equation model (SEM) for each of the elevational and latitudinal gradients. In each SEM, a phylogenetic metric was the response, annual precipitation and precipitation seasonality were exogenous variables and minimum temperature and temperature seasonality were endogenous variables.

We used SYSTAT (Wilkinson et al. 1992) to conduct correlation and regression analyses, and used the R package 'lavaan' ver. 0.5-20 (<https://cran.r-project.org/web/packages/lavaan/>) to conduct the SEM analyses.

Results

For a given phylogenetic metric, values of the metric calculated based on the phylogeny derived from Hawkins et al.'s phylogeny were strongly correlated with those based on the phylogeny derived from Zanne et al.'s phylogeny. For example, for values of phylogenetic metrics calculated using a full phylogeny with all the 149 species of this study, the

correlation coefficient was 0.986, 0.977 and 0.984 for NRI, NTI and PDI, respectively (n = 14 092 in all cases). This suggests that results of data analysis based on either phylogeny would be nearly identical. In order to achieve more robust results, we calculated the mean of paired values derived from the two phylogenies for each forest plot and used the resulting mean values in data analyses.

When the whole data set with all 14 092 forest plots of this study was considered, NRI and NTI were strongly and positively correlated with each other (r = 0.816, p < 0.001), and were both strongly and negatively correlated with PDI (r = −0.957 and −0.935, respectively; p < 0.001 in both cases). NRI and NTI were negatively correlated with minimum temperature, annual precipitation and precipitation seasonality and were positively correlated with temperature seasonality (Fig. 2). In contrast, PDI was positively correlated with minimum temperature, annual precipitation and precipitation seasonality, and was negatively correlated with temperature seasonality (Fig. 2).

When data were analyzed for each latitudinal or elevational gradient based on the species pool of each gradient, the relationships between minimum temperature and each of the three phylogenetic metrics were consistent among the six gradients (Fig. 3). Specifically, minimum temperature was negatively correlated with NRI and NTI and was positively correlated with PDI for all the six gradients (Fig. 3). However, the relationship between each of the other three climatic variables and each of the three phylogenetic metrics was not consistent among the six gradients. For example, annual precipitation was negatively correlated with NRI in five of the six g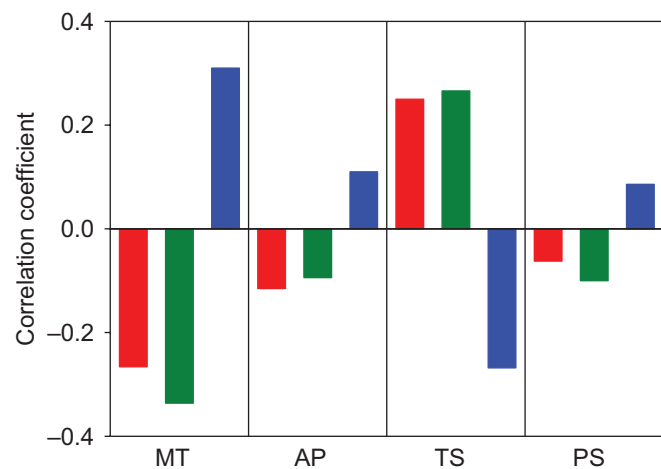radients, but was positively correlated in the other gradient (Fig. 3b). Similarly, precipitation seasonality was positively correlated with PDI in three of the six gradients and was negatively correlated with two of the other three gradients (Fig. 3c, e). The mean of absolute values of correlation coefficients with climatic variables reported in Fig. 3 was 0.141 for NRI and 0.181 for NTI. Thus, in general, the relationships were stronger for NTI than for NRI (Fig. 3, Supplementary material Appendix 1 Table A1). Of the four climatic variables, minimum temperature was most strongly correlated with NTI for both latitudinal and elevational gradients (Supplementary material Appendix 1 Table A1). On average, the relationships between the phylogenetic metrics and the climatic variables were significantly stronger for the latitudinal gradients than for the elevational gradients (mean and SD of absolute values of correlation coefficients: 0.213 ± 0.078 for the former versus 0.108 ± 0.077 for the latter; t-test, p < 0.001). Of the three latitudinal gradients (Fig. 3), the strongest relationship between NTI and minimum temperature was found for the latitudinal gradient located between 400 and 600 m in elevation (Fig. 3, 4). Of the three elevational gradients, the strongest relationship between NTI and minimum temperature was found for the elevational gradient located between 36 and 38° in latitude (Fig. 3, 4). Accordingly, we will focus on these two gradients in some analyses.

The mean of absolute values of the 18 correlation coefficients for each climatic variable reported in Fig. 3 was 0.224, 0.123, 0.175 and 0.120, respectively, for minimum temperature, annual precipitation, temperature seasonality and precipitation seasonality. Thus, of the four climatic variables examined, minimum temperature was the most important climatic correlate of phylogenetic relatedness and diversity for local angiosperm tree assemblages in eastern North America.

When the effects of minimum temperature and temperature seasonality on the three phylogenetic metrics were compared, minimum temperature not only had a stronger effect but also had a more consistent direction of relationship between latitudinal and elevational gradients than temperature seasonality (Fig. 5). For example, minimum temperature was negatively correlated with NRI and NTI and positively correlated with PDI for both latitudinal and elevational gradients (Fig. 5). In contrast, the directions of the relationships between temperature seasonality and either NTI or PDI for latitudinal gradients were opposite to those for elevational gradients (Fig. 5).

Because the relationship between a phylogenetic metric and minimum temperature was strongest for NTI, compared to those for the other two phylogenetic metrics, our SEM analyses focused on NTI. When minimum temperature and temperature seasonality were simultaneously related to NTI while accounting for annual precipitation and precipitation seasonality, minimum temperature exerted a much stronger effect on NTI than temperature seasonality for all the six latitudinal and elevational gradients (compare absolute values of standardized path coefficients within each panel in Supplementary material Appendix 1 Fig. A4). Furthermore, the direction of the relationship between NTI and minimum temperature was consistent among the SEMs of all latitudinal
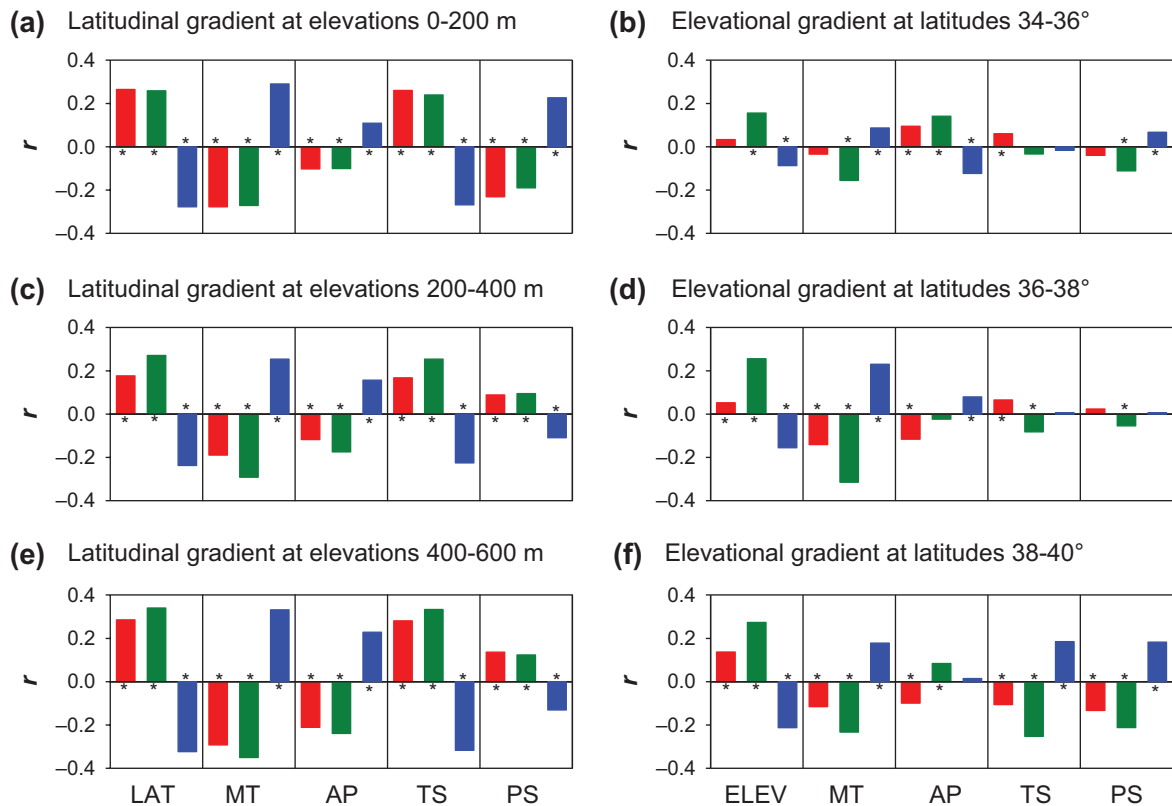

Figure 2. Correlation coefficient between phylogenetic structure metrics (net relatedness index, NRI: nearest taxon index, NTI; standardized phylogenetic diversity index, PDI) and climatic variables (minimum temperature, MT; annual precipitation, AP; temperature seasonality, TS; precipitation seasonality, PS) for angiosperm trees in the 14 092 local forest communities examined in this study. The three bars in each of the four segments represent three phylogenetic structure metrics (NRI, red; NTI, green; PDI, blue). p-values < 0.001 in all cases.

(a) Latitudinal gradient at elevations 0–200 m

(b) Elevational gradient at latitudes 34–36°

(c) Latitudinal gradient at elevations 200–400 m

(d) Elevational gradient at latitudes 36–38°

(e) Latitudinal gradient at elevations 400–600 m

(f) Elevational gradient at latitudes 38–40°

Figure 3. Correlation coefficient (r) between phylogenetic structure metrics (net relatedness index, NRI; nearest taxon index, NTI; standardized phylogenetic diversity index, PDI) and latitude (LAT), elevation (ELEV) or climatic variables (minimum temperature, MT; annual precipitation, AP; temperature seasonality, TS; precipitation seasonality, PS) for angiosperm trees in local forest communities along latitudinal (a, c and e) or elevational (b, d and f) gradients in eastern North America. The three bars in each of the five segments in a panel represent three phylogenetic structure metrics (NRI, left and red; NTI, middle and green; PDI, right and blue). An asterisk above or below a bar represents the significance level of p < 0.05. The number of forest plots for each gradient is shown in Supplementary material Appendix 1 Table A2.

and elevational gradients (i.e. negative relationships in all SEMs), whereas the direction of the relationship between NTI and temperature seasonality was inconsistent among the six SEMs (Supplementary material Appendix 1 Fig. A4).

The regression slope (coefficient) of NTI against minimum temperature was significantly steeper for elevational gradients than for latitudinal gradients (Table 1; mean ± SD: −0.154 ± 0.071 for the former versus −0.058 ± 0.012 for the latter, t-test, p < 0.05). This is true regardless of whether NTI was calculated based on the species pool that included only those species restricted to a particular gradient under investigation or based on the species pool that included all the 149 species of this study (compare Table 1 with Supplementary material Appendix 1 Table A2). These results indicate that along a thermal gradient from warm to cold temperature, phylogenetic relatedness of species in assemblages increased more quickly for elevational gradients than for latitudinal gradients.

Discussion

Our results have shown that the phylogenetic relatedness of angiosperm tree species in forest communities increases with

decreasing temperature and precipitation (Fig. 2) and this pattern generally holds for both latitudinal and elevational gradients (Fig. 3), supporting the tropical niche conservatism hypothesis. We found several conspicuous patterns in this study, which we discuss below.

The relationship between temperature and NRI or NTI for the elevational gradients of this study is consistent with those in other temperate regions but contrary to those in tropical regions

We found that both NRI and NTI were negatively correlated with minimum temperature along elevational gradients, as along latitudinal gradients, for angiosperm trees in eastern North America, indicating that tree species in assemblages at higher elevations were more closely related, regardless of whether tip-weighted or basal-weighted metric of phylogenetic relatedness was considered. This finding is consistent with our hypothesis 1 and findings of previous studies for plant assemblages along elevational gradients in temperate regions (Li et al. 2014, Qian et al. 2014). However, our finding is contrary to those for tree species assemblages along elevational gradients in tropical regions. For example,
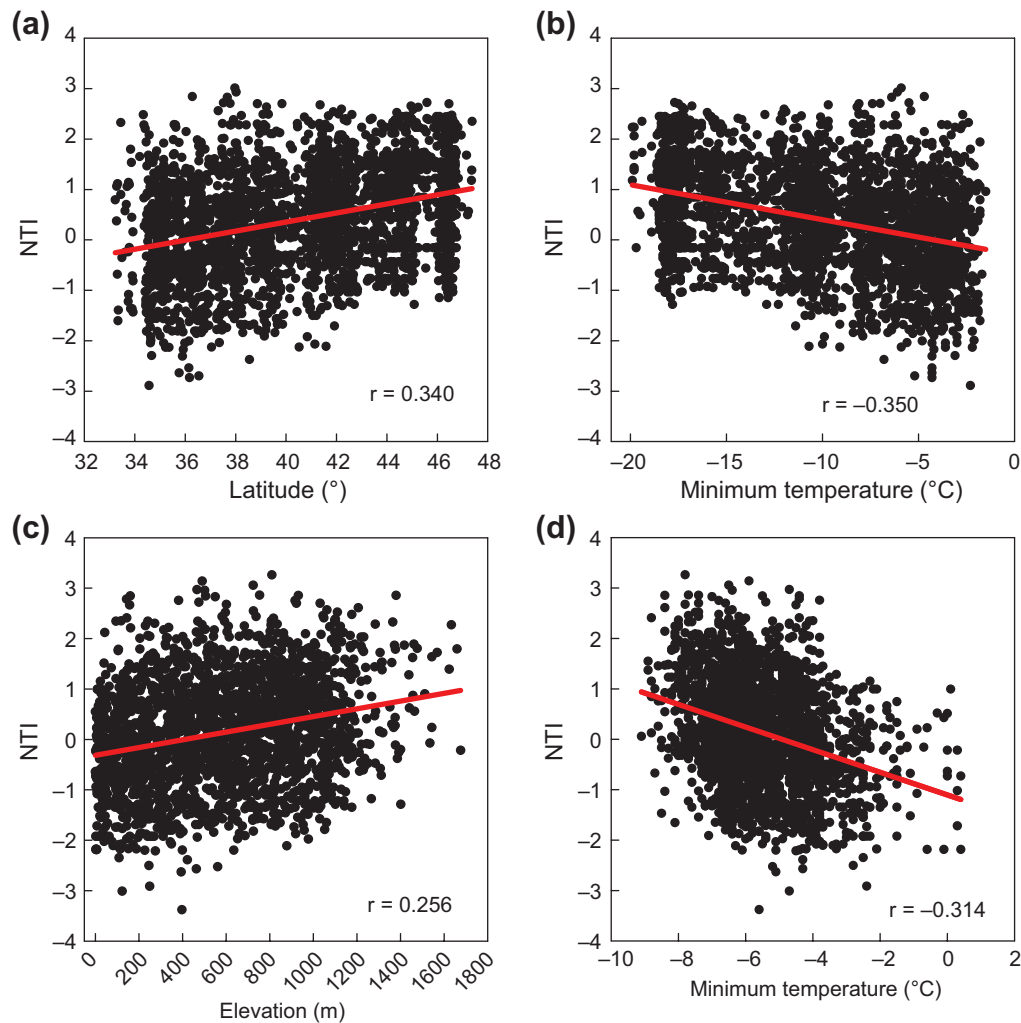
Figure 4. Relations of nearest taxon index (NTI) of angiosperm tree assemblages with latitude, elevation and minimum temperature along a selected latitudinal gradient (between elevations 400–600 m; panels a and b) and a selected elevational gradient (between latitudes 36–38°N; panels c and d), along which NTI was most strongly correlated with minimum temperature among the three gradients of each type (i.e. latitudinal versus elevational; Fig. 3).

Culmsee and Leuschner (2013) showed that both NRI and NTI for trees in forests along an elevational gradient in tropical Asia are positively correlated with temperature. González-Caro et al. (2014) studied trees in forests across a broad Colombian elevational gradient and found that both NRI and NTI are positively correlated with temperature variables (including minimum temperature). Across a broader geographic extent, Qian (2018) found that NRI and NTI are negatively correlated with elevation and positively correlated with mean annual temperature for trees in forests across an elevation gradient in tropical South America. Qian and Ricklefs (2016) proposed that for tropical elevational gradients, niche convergence might have played a primary role in driving community assembly, leading to a pattern of decreasing phylogenetic relatedness towards high elevation. Findings from the present study and those examining patterns of phylogenetic relatedness for angiosperms along elevational and latitudinal gradients in temperate regions (Qian et al. 2013,

2014, 2016, Li et al. 2014, Qian and Sandel 2017) suggest that niche conservatism has played a primary role in driving phylogenetic community assembly for plants along both latitudinal and elevational gradients in temperate regions, at least in the Northern Hemisphere.

Climatic variables are correlated with NTI more strongly than with NRI

Our analysis has shown that NTI, which measures tip-weighted phylogenetic relatedness, tends to co-vary with climatic variables more strongly than does NRI, which is measured as the mean of phylogenetic distances and thus gives basal nodes more weight, compared to NTI. Traits that confer tolerance to cold and dry climates are generally conserved at more basal clades or high taxonomic levels such as orders and families in angiosperms (Wiens and Donoghue 2004). This would suggest a stronger climatic relation with
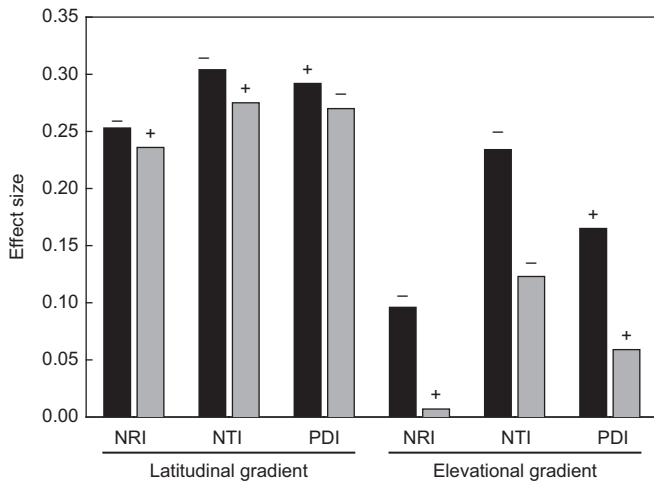
Figure 5. Comparison between effects (absolute values of correlation coefficient) of minimum temperature (black bar) and temperature seasonality (grey bar) on three phylogenetic metrics (NRI, net relatedness index; NTI, nearest taxon index; PDI, phylogenetic diversity index). Each effect size represents the mean value for three latitudinal or elevational gradients reported in Fig. 3. A plus or minus sign on a bar represents a positive or negative effect, respectively.

NRI than with NTI, opposing the pattern that we found. However, the pattern found in this study that NTI is more strongly related to climatic variables (particularly temperature) than NRI has also been observed in previous studies. For example, Culmsee and Leuschner (2013) found that NTI is more strongly correlated with elevation (a surrogate of temperature) than NRI for tree species in forest communities in Malesia ($r^2 = 0.66$ for NTI versus 0.47 for NRI). Patrick and Stevens (2016) found that ses.MNTD (equivalent to $-1 \times$ NTI) is correlated with mean temperature, temperature seasonality and precipitation seasonality more strongly than ses.MPD (equivalent to $-1 \times$ NRI) for bats in North American deserts.

If phylogenetic clustering in cold climate arises because only a few clades evolve the trait innovations necessary to

Table 1. Slopes for simple linear regressions of nearest taxon index (NTI) against minimum temperature (MT, °C) for latitudinal and elevational gradients. NTI was calculated using the species pool that included only the species of the study gradient.

Gradient	Length	n	Slope	p
1) Latitudinal gradients				
Gradient at elev. 0–200 m	2532 km	3532	−0.045	< 0.001
Gradient at elev. 200–400 m	1713 km	3000	−0.061	< 0.001
Gradient at elev. 400–600 m	1571 km	2719	−0.069	< 0.001
2) Elevational gradients				
Gradient at lat. 34–36°	1685 m	2388	−0.084	< 0.001
Gradient at lat. 36–38°	1675 m	2238	−0.225	< 0.001
Gradient at lat. 38–40°	1397 m	2405	−0.152	< 0.001

survive cold temperatures, it is still possible that these few clades will be scattered widely across the phylogeny. If that is the case, NTI will provide a better reflection of the clustering pattern than either NRI or PDI, both of which will include deep nodes in the tree and therefore not represent as clearly the difference between a cold- and warm-adapted community.

Minimum temperature exerts a stronger effect on community assembly than does temperature seasonality

The environmental stress (tolerance) hypothesis has been commonly considered as a major mechanism driving species distribution (Latham and Ricklefs 1993b). However, some studies (Wiens et al. 2006) have reported that temperature seasonality is more strongly correlated with species distribution than minimum temperature. Because nearly all the studies that have investigated the relative importance of minimum temperature and temperature seasonality on species richness and distribution were conducted across latitudes and because minimum temperature and temperature seasonality are strongly and negatively correlated along latitudinal gradients (e.g. r = −0.957, −0.972 and −0.984 for the three latitudinal gradients examined in this study), the independent effect of each of the two climatic variables cannot be determined for latitudinal gradients. In this study, minimum temperature and temperature seasonality along elevational gradients are not negatively correlated with each other; instead, they are weakly and positively correlated (r = 0.401, 0.264 and 0.357 for the three elevational gradients examined in this study). Our results showed that phylogenetic relatedness of angiosperm trees was more strongly correlated with minimum temperature than with temperature seasonality for both latitudinal and elevational gradients and this difference was reinforced for elevational gradients (Supplementary material Appendix 1 Table A1). This result is consistent with our hypothesis 2. Furthermore, minimum temperature has consistent relations with phylogenetic metrics among latitudinal and elevational gradients but temperature seasonality does not (Fig. 3). Qian et al. (2018) explored patterns of mean family age for angiosperm tree assemblages along latitudinal and elevational gradients in eastern North America; they also found that minimum temperature is correlated to mean family age more strongly and more consistently than temperature seasonality. Thus, their and our findings support the notion that cold temperature extreme plays a more important role than temperature seasonality in driving community assembly (Qian et al. 2007, Wang et al. 2011).

Phylogenetic relatedness increases with decreasing temperature more quickly for elevational gradients than for latitudinal gradients

We found that the slope of the relationship between phylogenetic relatedness and minimum temperature was steeper for elevational gradients than for latitudinal gradients (Table 1).

This suggests that phylogenetic relatedness is in equilibrium with temperature in a greater degree for elevational gradients than for latitudinal gradients in eastern North America. This is consistent with our hypothesis 3 and findings of some previous studies focusing on other measures of plant community structure. For example, Qian et al. (2018) found that the slope of the relationship between mean family age and minimum temperature for angiosperm tree assemblages in eastern North America is steeper for elevational gradients than for latitudinal gradients. Halbritter et al. (2013) compared latitudinal and elevational range limits of plant species in Europe and found that species reach a colder climate limit along the elevational gradient, compared to the latitudinal gradient, suggesting that plants on elevational gradients are closer to equilibrium with temperature than those on latitudinal gradients. However, our finding appears to be contrary to those of Siefert et al. (2015), who found that minimum temperature (measured as January mean temperature) is substantially higher at the high-elevation limit than at the high-latitude limit for nearly all 28 tree species examined in eastern North America. However, we noticed that January mean temperature at high elevations was over-estimated for all angiosperm tree species in their study. For example, the January mean temperature at the high-elevation limit of *Acer rubrum* was −0.9°C on an elevational gradient in Siefert et al. (2015) but this species appeared in numerous forest plots with January mean temperature of −2.2°C or lower (based on the WorldClim database at the 30 arc-second resolution; Hijmans et al. 2005) on the same elevational gradient in our study. There is a need to examine how well minimum temperature at the highest elevation of a species matches that at the northernmost latitude of the species in eastern North America based on accurately documented climate data and a great number of plant species.

Conclusions

We examined patterns of phylogenetic structure for a large number of local angiosperm tree assemblages distributed along elevational and latitudinal gradients in eastern North America. Our analyses revealed several conspicuous patterns. First, phylogenetic relatedness of angiosperm trees increases with decreasing temperature along elevational gradients, which is consistent with those observed for plants on elevational gradients in other temperate regions but contrary to those observed in tropical regions. Second, tip-weighted metric of phylogenetic relatedness is more strongly correlated with climatic variables than basal-weighted metric of phylogenetic relatedness, suggesting that recent diversification has played an important role in shaping patterns of phylogenetic structure for angiosperm trees in eastern North America. Third, winter cold temperature exerts a stronger effect on community assembly of angiosperm trees than does temperature seasonality, suggesting that cold tolerance is a more important driver of community assembly of angiosperm trees, compared with temperature seasonality. Lastly, the relationship between phylogenetic relatedness and temperature is steeper for elevational gradients than for latitudinal gradients, suggesting that species distributions along elevational gradients are more in equilibrium with temperature, compared with those along latitudinal gradients. Our conclusions are based on only angiosperm tree species. Different organismal groups may show different patterns of phylogenetic structure along geographical and environmental gradients, e.g. angiosperms versus gymnosperms (Ma et al. 2016, Qian et al. 2019), woody angiosperms versus herbaceous angiosperms (Kubota et al. 2017), or plants versus animals (Graham et al. 2009, González-Caro et al. 2014). Future studies should determine if the patterns that we have observed here for angiosperm trees along latitudinal and elevational gradients in eastern North America are repeated in other organismal groups.

Data availability statement

All data used in this study have been published and are accessible to readers from the cited sources.

References

Archibald, S. B. et al. 2010. Seasonality, the latitudinal gradient of diversity and Eocene insects. – Paleobiology 36: 374–398.

Behrensmeyer, A. K. et al. 1992. Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals. – Univ. of Chicago Press.

Cavender-Bares, J. et al. 2009. The merging of community ecology and phylogenetic biology. – Ecol. Lett. 12: 693–715.

Condamine, F. L. et al. 2012. What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. – Ecol. Lett. 15: 267–277.

Crain, C. M. et al. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. – Ecology 85: 2539–2549.

Culmsee, H. and Leuschner, C. 2013. Consistent patterns of elevational change in tree taxonomic and phylogenetic diversity across Malesian mountain forests. – J. Biogeogr. 40: 1997–2010.

Davis, M. et al. 1986. Dispersal versus climate: expansion of *Fagus* and *Tsuga* into the Upper Great Lakes region. – Vegetatio 67: 93–103.

Delcourt, P. A. and Delcourt, H. R. 1993. Paleoclimates, paleovegetation and paleoflora during the Late Quaternary. – In: Flora of North America Editorial Committee (eds), Flora of North America north of Mexico. Oxford Univ. Press, vol. 1, pp. 71–94.

Donoghue, M. J. 2008. A phylogenetic perspective on the distribution of plant diversity. – Proc. Natl Acad. Sci. USA 105: 11549–11555.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. – Biol. Conserv. 61: 1–10.

Flora of North America Editorial Committee 1993–2016. Flora of North America north of Mexico. – Oxford Univ. Press.

González-Caro, S. et al. 2014. Phylogenetic alpha and beta diversity in tropical tree assemblages along regional scale environmental gradients in northwest South America. – J. Plant Ecol. 7: 145–153.

Graham, A. 1999. Late Cretaceous and Cenozoic history of North American vegetation north of Mexico. – Oxford Univ. Press.

Graham, A. 2011. The age and diversification of terrestrial New World ecosystems through Cretaceous and Cenozoic time. – Am. J. Bot. 98: 336–351.

Graham, C. H. et al. 2009. Phylogenetic structure in tropical hummingbird communities. – Proc. Natl Acad. Sci. USA 106: 19673–19678.

Halbritter, A. H. et al. 2013. How comparable are species distributions along elevational and latitudinal climate gradients? – Global Ecol. Biogeogr. 22: 1228–1237.

Hawkins, B. A. et al. 2014. Community phylogenetics at the biogeographical scale: cold tolerance, niche conservatism and the structure of North American forests. – J. Biogeogr. 41: 23–38.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – Int. J. Climatol. 25: 1965–1978.

Huntley, B. et al. 1989. Climatic control of the distribution and abundance of beech (*Fagus* L.) in Europe and North America. – J. Biogeogr. 16: 551–560.

Jump, A. S. et al. 2009. The altitude-for-latitude disparity in the range retractions of woody species. – Trends Ecol. Evol. 24: 694–701.

Kraft, N. J. et al. 2015. Community assembly, coexistence and the environmental filtering metaphor. – Funct. Ecol. 29: 592–599.

Latham, R. E. and Ricklefs, R. E. 1993a. Continental comparisons of temperate-zone tree species diversity. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities. Univ. of Chicago Press, pp. 294–314.

Latham, R. E. and Ricklefs, R. E. 1993b. Global patterns of tree species richness in moist forests: energy–diversity theory does not account for variation in species richness. – Oikos 67: 325–333.

Li, X.-H. et al. 2014. Phylogenetic clustering and overdispersion for alpine plants along elevational gradient in the Hengduan Mountains Region, southwest China. – J. Syst. Evol. 52: 280–288.

Kembel, S. W. et al. 2010. Picante: R tools for integrating phylogenies and ecology. – Bioinformatics 26: 1463–1464.

König, C. et al. 2017. Dissecting global turnover in vascular plants. – Global Ecol. Biogeogr. 26: 228–242.

Körner, C. 1998. A re-assessment of high-elevation treeline positions and their explanation. – Oecologia 115: 445–459.

Körner, C. 2000. Why are there global gradients in species richness? Mountains might hold the answer. – Trends Ecol. Evol. 15: 513–514.

Kubota, Y. et al. 2017. Phylogenetic properties of Tertiary relict flora in the east Asian continental islands: imprint of climatic niche conservatism and in situ diversification. – Ecography 40: 436–447.

Ma, Z. et al. 2016. Phylogenetic assemblage structure of North American trees is more strongly shaped by glacial–interglacial climate variability in gymnosperms than in angiosperms. – Ecol. Evol. 6: 3092–3106.

MacArthur, R. H. 1972 Geographical ecology: patterns in the distribution of species. – Harper and Row.

Mayfield, M. M. and Levine, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. – Ecol. Lett. 13: 1085–1093.

Patrick, L. E. and Stevens, R. D. 2016. Phylogenetic community structure of North American desert bats: influence of environment at multiple spatial and taxonomic scales. – J. Anim. Ecol. 85: 1118–1130.

Qian, H. 2018. Climatic correlates of phylogenetic relatedness of woody angiosperms in forest communities along a tropical elevational gradient in South America. – J. Plant Ecol. 11: 394–400.

Qian, H. and Jin, Y. 2016. An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. – J. Plant Ecol. 9: 233–239.

Qian, H. and Ricklefs, R. E. 2016. Out of the tropical lowlands: latitude versus elevation. – Trends Ecol. Evol. 31: 738–741.

Qian, H. and Sandel, B. 2017. Phylogenetic structure of regional angiosperm assemblages across latitudinal and climatic gradients in North America. – Global Ecol. Biogeogr. 26: 1258–1269.

Qian, H. et al. 2007. Environmental determinants of amphibian and reptile species richness in China. – Ecography 30: 471–482.

Qian, H. et al. 2013. Latitudinal gradients in phylogenetic relatedness of angiosperm trees in North America. – Global Ecol. Biogeogr. 22: 1183–1191.

Qian, H. et al. 2014. Phylogenetic structure and phylogenetic diversity of angiosperm assemblages in forests along an elevational gradient in Changbaishan, China. – J. Plant Ecol. 7: 154–165.

Qian, H. et al. 2015. Evolutionary and ecological causes of species richness patterns in North American angiosperm trees. – Ecography 38: 241–250.

Qian, H. et al. 2016. Phylogenetic structure and ecological and evolutionary determinants of species richness for angiosperm trees in forest communities in China. – J. Biogeogr. 43: 603–615.

Qian, H. et al. 2018. Mean family age of angiosperm tree communities and its climatic correlates along elevational and latitudinal gradients in eastern North America. – J. Biogeogr. 45: 259–268.

Qian, H. et al. 2019. Phylogenetic dispersion and diversity in regional assemblages of seed plants in China. – Proc. Natl Acad. Sci. USA 116: 23192–23201.

Randin, C. F. et al. 2013. Do the elevational limits of deciduous tree species match their thermal latitudinal limits? – Global Ecol. Biogeogr. 22: 913–923.

Ricklefs R. E. 2005. Phylogenetic perspectives on patterns of regional and local species richness. – In: Bermingham, E. et al. (eds), Tropical rainforests: past, present and future. Univ. of Chicago Press, pp. 16–40.

Ricklefs, R. E. 2006. Evolutionary diversification and the origin of the diversity–environment relationship. – Ecology 87: S3–S13.

Sandel, B. and Tsirogiannis, C. 2016. Species introductions and the phylogenetic and functional structure of California's grasses. – Ecology 97: 472–483.

Siefert, A. et al. 2015. How do climate and dispersal traits limit ranges of tree species along latitudinal and elevational gradients? – Global Ecol. Biogeogr. 24: 581–593.

Stevens, G. C. 1992. The elevational gradient in altitudinal range, an extension of Rapoport's latitudinal rule to altitude. – Am. Nat. 140: 893–911.

Svenning, J.-C. and Skov, F. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? – Ecol. Lett. 10: 453–460.

Svenning, J.-C. et al. 2008. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. – Ecography 31: 316–326.

Tsirogiannis, C. and Sandel, B. 2016. PhyloMeasures: a package for computing phylogenetic biodiversity measures and their statistical moments. – Ecography 39: 709–714.

Tsirogiannis, C. et al. 2012. Efficient computation of popular phylogenetic tree measures. – Lecture Notes Comput. Sci. 7534: 30–43.

Tsirogiannis, C. et al. 2014. New algorithms for computing phylogenetic biodiversity. – Lecture Notes Comput. Sci. 8701: 187–203.

Vellend, M. et al. 2010. Measuring phylogenetic biodiversity. – In: Magurran, A. E. and McGill, B. J. (eds), Biological diversity: frontiers in measurement and assessment. Oxford Univ. Press, pp. 193–206.

Wang, Z. et al. 2011. Patterns, determinants and models of woody plant diversity in China. – Proc. R. Soc. B 278: 2122–2132.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. – Am. Nat. 156: 145–155.

Webb, C. O. et al. 2002. Phylogenies and community ecology. – Annu. Rev. Ecol. Syst. 33: 475–505.

Webb, C. O. et al. 2011. Phylocom: software for the analysis of phylogenetic community structure and character evolution, with phylomatic, ver. 4.2. – <https://phylodiversity.net/phylocom/>.

Weigelt, P. et al. 2015. Global patterns and drivers of phylogenetic structure in island floras. – Sci. Rep. 5: 12213.

Wiens, J. J. and Donoghue, M. J. 2004. Historical biogeography, ecology and species richness. – Trends Ecol. Evol. 19: 639–644.

Wiens, J. J. et al. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. – Am. Nat. 168: 579–596.

Wilkinson, L. et al. 1992. SYSTAT for Windows: statistics. – SYSTAT, Evanston.

Zanne, A. E. et al. 2014. Three keys to the radiation of angiosperms into freezing environments. – Nature 506: 89–92.