DOI: 10.1111/jbi.13108

ORIGINAL ARTICLE

WILEY Journal of Biogeography

Mean family age of angiosperm tree communities and its climatic correlates along elevational and latitudinal gradients in eastern North America

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Funding information
National Natural Science Foundation of China

Editor: Simon Scheiter

Abstract

Aim: The species comprising local communities are assembled from the species pool of the region where they are located, and environmental filtering influences which species occupy local communities based on their traits. Latitude and elevation generate two major thermal gradients, and temperature minimum and seasonality can drive community assembly, but few studies have tested if community assembly along both latitudinal and elevational gradients within the same region generates similar patterns of assembly. Here, we test hypotheses on the relations of mean family age (MFA) of angiosperm trees in local communities with environmental temperature and compare the relations between latitudinal and elevational gradients in eastern North America.

Location: USA.

Method: We used correlation and regression analyses and structure equation modelling approach to assess the relation of MFA to elevation, latitude and climatic variables, which included minimum temperature, temperature seasonality, annual precipitation and precipitation seasonality.

Results: The MFA of a local forest community decreased with increasing latitude and elevation for all gradients examined. For each gradient, the slope of the relationship between MFA and latitude or elevation was steeper for forest communities with larger values of MFA than for those with smaller values of MFA, and the standard deviation of MFA decreased with increasing latitude and elevation. MFA decreased significantly with decreasing minimum temperature for both latitudinal and elevational gradients, but the slope of the relationship between MFA and minimum temperature was steeper for elevational gradients than for latitudinal gradients. Minimum temperature had a much stronger relationship with MFA than temperature seasonality for both latitudinal and elevational gradients.

Main conclusions: Our results indicate that minimum temperature, rather than temperature seasonality, is a major driver of the pattern of decreasing MFA with increasing latitude and elevation, and the relationship between temperature and MFA is stronger (steeper) for elevational gradients than for latitudinal gradients.

KEYWORDS
cold tolerance, community assembly, environmental filtering, niche conservatism, temperate forests, thermal gradients, tropical conservatism hypothesis

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1 | INTRODUCTION

The species comprising local communities are assembled from the species pool of the region where they are located (Ricklefs, 1987), and environmental filtering plays a key role in sorting species of the regional pool into local communities based on species traits (Willis et al., 2010). Among angiosperm trees, cold tolerance is considered a major trait influencing which species in a regional pool are sorted into which local communities along thermal gradients (Hawkins, Rueda, Rangel, Field, & Diniz-Filho, 2014; Latham & Ricklefs, 1993). Because many species traits, including cold tolerance, are phylogenetically conserved (Condamine, Sperling, Wahlberg, Rasplus, & Kergoat, 2012; Crisp & Cook, 2012; Donoghue, 2008; Hawkins et al., 2014; Wiens et al., 2010), sorting species into local communities reflects the interplay between evolutionary and ecological processes (Ricklefs, 1987).

The tropical niche conservatism hypothesis (TNC), which was developed based on ideas of several workers (e.g. Farrell, Mitter, & Futuyma, 1992; Futuyma, 1998; Graham, 1999; Latham & Ricklefs, 1993; Ricklefs & Schluter, 1993) and formalized by Wiens and Donoghue (2004), provides a phylogenetic explanation for the effect of environmental filtering on community assembly along thermal gradients, particularly across latitudes. This hypothesis posits that most clades evolved in the tropics when both low and high latitudes were under tropical conditions, and can account for why the North American vegetation was dominated by clades with tropical affinities in the late Cretaceous and early Cenozoic (Graham, 1999). However, with the onset of global cooling in the Eocene, most tropical lineages were extirpated from high latitudes (Graham, 1999; Hawkins et al., 2014; Latham & Ricklefs, 1993), although some acquired adaptations enabling them to shift into the spreading temperate climates. A core measure of this historical scenario is the mean clade age (such as mean family age, MFA) of species in an assemblage (Hawkins et al., 2014; Latham & Ricklefs, 1993). The mean clade age of species in an assemblage, among other things, is predicted to decrease with decreasing environmental temperature because species assemblages in warmer environments come from both old (tropical) and young clades, whereas species in assemblages of cooler environments primarily come from young clades. Empirical data for assemblages distributed along thermal gradients across latitudes generally support this prediction (Hawkins, Rodríguez, & Weller, 2011; Hawkins et al., 2014; Qian, 2014; Qian & Chen, 2016; Qian & Ricklefs, 2016; Qian, Zhang, Zhang, & Wang, 2013; Treseder et al., 2014).

At least some temperature-related variables change in similar ways along elevational and latitudinal gradients. For example, mean annual temperature and minimum temperature of the coldest month decrease with both latitude and elevation. Cold temperature is generally considered a major factor controlling the distribution of species towards higher elevations and latitudes (Huntley, Bartlein, & Prentice, 1989; Körner, 1998); therefore, we would expect that if all species are in equilibrium with climate, species distributions along elevational gradients are equivalent to those along latitudinal gradients in terms of temperature (Randin et al., 2013; Siefert, Lesser, & Fridley, 2015). In particular, we would expect that species reach the same cold temperature limits along both latitudinal and elevational gradients, which is described as Humboldt's law (Randin et al., 2013). However, elevational thermal gradients are much more spatially compressed than latitudinal thermal gradients; in other words, equivalent changes in temperature occur over much shorter distances for elevational gradients (Jump, Mátyás, & Peñuelas, 2009). For example, a change in temperature for an elevational distance of 10 m is equivalent to that for a latitudinal distance of *c*. 10 km (Jump et al., 2009). As a result, dispersals between contrasting climates would be more efficient along elevational gradients. This difference in dispersal between elevational and latitudinal gradients may generate climatic mismatches of species distributions between the two types of thermal gradients (Siefert et al., 2015). Because the poleward expansions of tree species in Europe and North America lag behind their potential climatic limits (Davis, Woods, Webb, & Futyma, 1986; Svenning, Normand, & Skov, 2008) due to dispersal limitation, many tree species might have not reached their equilibrium with climate following the last glaciation (Svenning & Skov, 2007). However, because dispersal should be much more efficient along elevational than latitudinal gradients (Jump et al., 2009), species should reach colder temperatures along elevational gradients than latitudinal gradients (Halbritter, Alexander, Edwards, & Billeter, 2013; Siefert et al., 2015). Comparisons of species cold thermal limits between elevational and latitudinal gradients are few, but species range limits are indeed located in colder temperatures along elevational than latitudinal gradients (e.g. Halbritter et al., 2013; Pellissier et al., 2013).

Angiosperm tree assemblages in eastern North America are ideal to comparing patterns of mean family age with respect to temperature variation between elevational and latitudinal gradients. In addition to the strong latitudinally based historical scenario for North American forests previously outlined, the major mountain system in eastern North America, the Appalachians, runs in the north–south direction, which would have facilitated species dispersal during glacial–interglacial cycles and would have maximized the match of cold range limits of species between elevational and latitudinal gradients, permitting a relatively straight-forward comparison of both patterns.

Consistent with the climatic and vegetation history of North America, Hawkins et al. (2014) found that local forest sites across the southern USA are composed of angiosperm tree species from older families than are sites further north, and of the five temperature and precipitation variables examined in their study, minimum winter temperature was the strongest correlate of the mean family age of angiosperm trees in local forests. Despite this, documenting the relationship between the mean family age of angiosperms and environmental variables along elevational gradients as well is critical to understanding the mechanisms underlying community assembly of angiosperm species, and no studies have related the mean family age of angiosperms in general and angiosperm trees in particular to elevation and environmental factors along elevational gradients in eastern North America and other temperate regions in the world.

Furthermore, comparing measures of community assembly such as mean clade age between elevational and latitudinal gradients can provide insight into mechanisms of community assembly along thermal gradients, which is central to ecology.

Here, we analyse a comprehensive data set of 13,637 local forest communities covering latitudinal gradients of *c.* 2,000 km and elevational gradients of *c.* 1,700 m in the USA east of the Mississippi River (Figure 1). The objective of this study is multifold. First, we test the hypothesis that the MFA of angiosperm trees in local forest communities decreases with increasing elevation (prediction 1), as MFA decreases with increasing latitude observed in previous studies (Hawkins et al., 2014 for the USA; Qian & Chen, 2016 for China). Second, we test the hypothesis that decreases in MFA along both elevational and latitudinal gradients primarily result from the loss of older families towards higher elevations and latitudes (prediction 2). Third, considering that dispersal is more efficient along spatially compressed elevational gradients than along latitudinal gradients, and thus, species might have reached colder sites along elevational gradients faster than latitudinal gradients, we would expect a steeper relationship between temperature and MFA for latitudinal gradients than for elevational gradients (prediction 3). Lastly, cold tolerance is considered a key trait under the tropical conservatism explanation for species distributions (Futuyma, 1998; Hawkins et al., 2014; Latham & Ricklefs, 1993), but both minimum temperature and temperature seasonality have been considered stressful thermal factors driving species distributions of plants and animals (e.g. Currie, 1991; Qian, Wang, Wang, & Li, 2007; Wang, Fang, Tang, & Lin, 2011; Wiens, Graham, Moen, Smith, & Reeder, 2006). Results of previous studies are mixed in terms of which of these two thermal factors play a more important role in driving species distributions (e.g. Qian et al., 2007; Wang et al., 2011; Wiens et al., 2006). However, few studies have assessed which of the two have played a more important role in driving community assembly, and all used latitudinal gradients as study systems (e.g. Wiens et al., 2006), across which minimum temperature and temperature seasonality can co-vary strongly. We hypothesize that minimum temperature, which is closely related with cold tolerance, plays a more important role than temperature seasonality in shaping MFA patterns (prediction 4); we evaluate this hypothesis by assessing the relative strengths of the relationships of the two temperature variables with MFA for both latitudinal and elevational gradients, along the latter of which the two temperature variables co-vary much less strongly (Jump et al., 2009; Körner, 2007).

2 | MATERIALS AND METHODS

The study area comprises the 24 states east of the Mississippi River (Figure 1). To balance the sampling design, we first divided the area into latitudinal zones of 2 degrees, starting at 30°, and then divided the elevational range of each latitudinal zone into elevational bands of 100 m, although most analyses were carried out with 200-m elevational bands. We extracted data for the 0.07-hectare forest plots from the US Forest Service's Forest Inventory and Analysis (FIA) database (www.fia.fs.fed.us) and assigned each plot to an elevational band of a latitudinal zone according to its location. For inclusion, a plot had to be coded as a 'natural stand' and support at least two angiosperm species. When an elevational band within a latitudinal zone had more than 200 plots, we randomly selected 200 to balance sampling effort across bands. Because gymnosperms have very different evolutionary histories than angiosperms (Graham, 1999), they were excluded, as in previous studies (e.g. Hawkins et al., 2011, 2014; Qian, 2014; Qian & Chen, 2016; Qian & Ricklefs, 2016; Qian et al., 2013). Gymnosperm tree species may dominate in some forests at high latitude and elevation, to assess the effect of removing gymnosperm tree species on our result, we conducted a set of core analyses which only used those forest plots with ≥70% of tree species being angiosperm tree species.

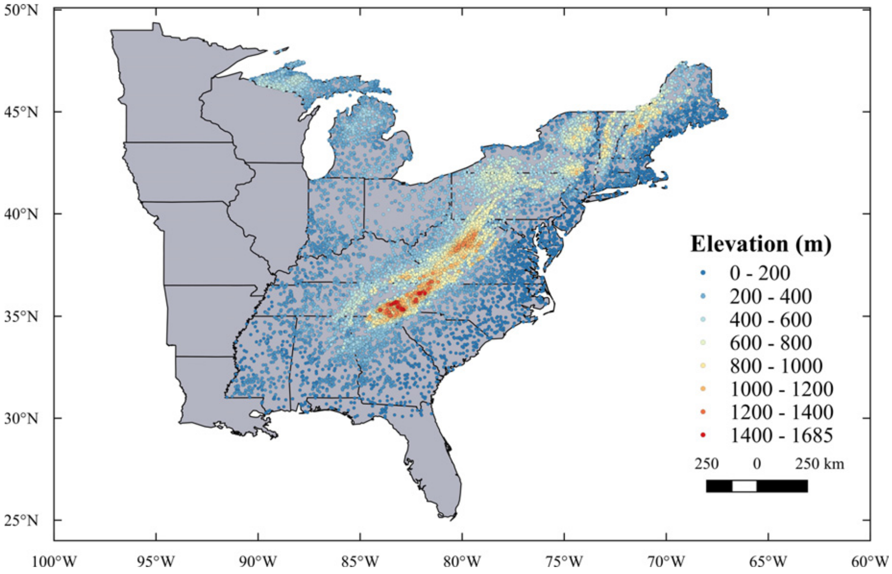


FIGURE 1 Locations of the 13,637 forest inventory plots used to investigate the relationship between mean family age and the variables of latitude, altitude and climate in this study

Botanical nomenclature of species was standardized according to The Plant List (version 1.1, www.theplantlist.org). Non-native species were excluded. For each species in each plot, we assigned it the age of the family to which the species belongs. Crown family ages were obtained from Davies et al. (2004) (available from https://github.com/camwebb/tree-of-trees/blob/master/megatrees_other/davies2004.ages). The mean family age of each forest plot was calculated as the sum of crown family ages of all species in the forest plot divided by the number of species in the forest plot, as in previous studies (e.g. Hawkins et al., 2014; Qian et al., 2013).

We related MFA of each plot to elevation, latitude, minimum temperature (MT), temperature seasonality (TS), annual precipitation (AP) and precipitation seasonality (PS). The four climatic variables are among major environmental correlates of MFA (Hawkins et al., 2014; Qian & Chen, 2016) as well as many other macroecological patterns (Qian et al., 2007; Wiens et al., 2006). For those plots for which elevation was not provided in the FIA, we extracted elevations from the 30 arc-second WorldClim database (version 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 to protect the privacy of landowners. We extracted data for the climatic variables from the 30 arc-second WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), which were BIO6, BIO4, BIO12 and BIO15, respectively.

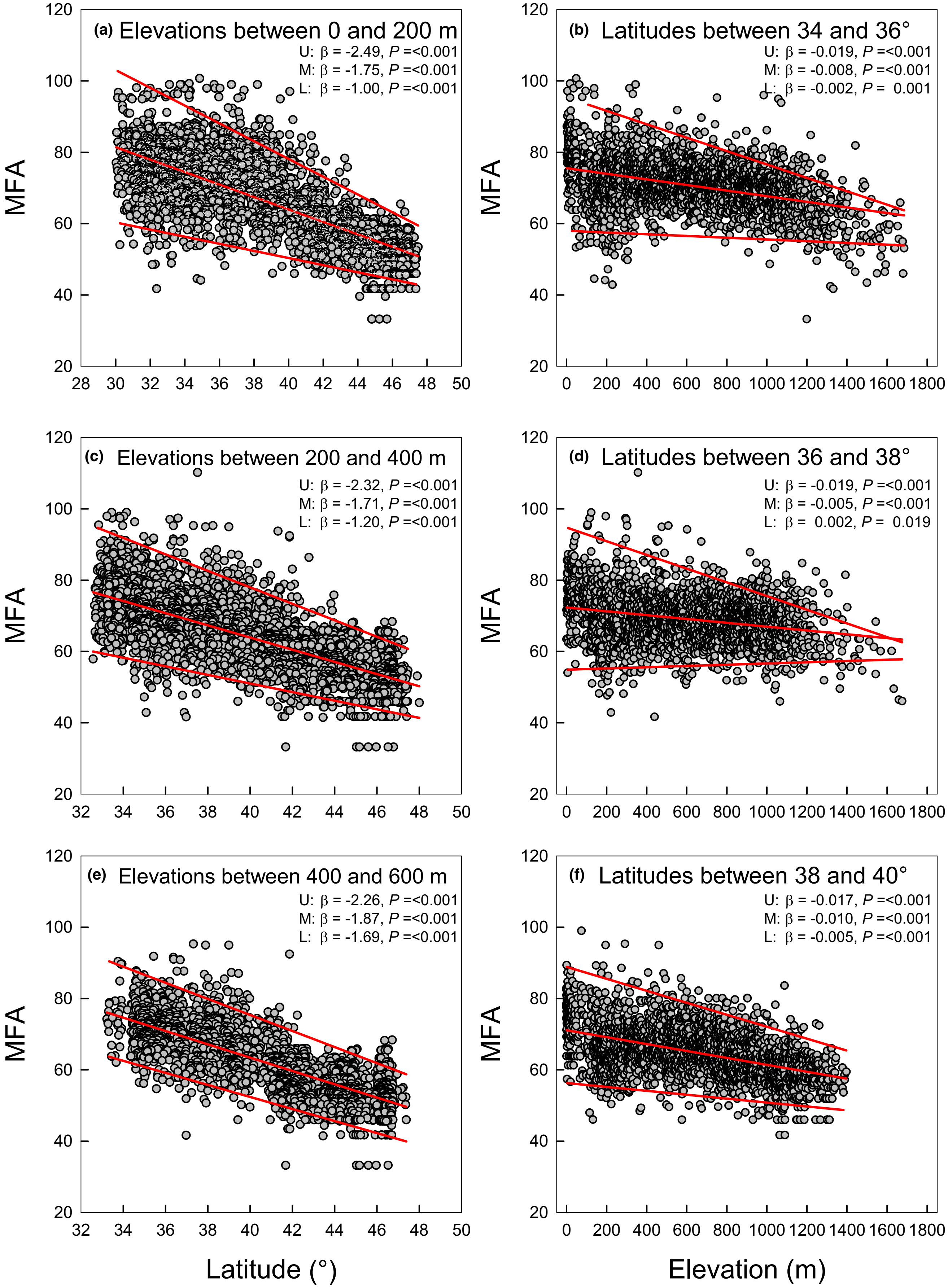
To test prediction 1 (i.e. MFA of angiosperm trees in local forest communities decreases with increasing elevation, as with latitudinal gradients), we used correlation and regression analyses to assess the relation of MFA to elevation, latitude and the climatic variables. To test prediction 2 (i.e. plots in low latitudes or elevations comprise species in both young and old families and older families drop out of communities more frequently than younger families towards higher latitudes or elevations), we related the standard deviation of MFA to latitude or elevation. A pattern of decreasing standard deviation of MFA with increasing latitude or elevation, in combination with the pattern predicted by prediction 1, would be consistent with the hypothesis. In this test, we assembled the single longest latitudinal gradient and the longest elevational gradient in the study area. Specifically, for the latitudinal gradient, species in all forest plots located in elevations <600 m were binned into 1-degree latitudinal zones; for the elevational gradient, species in all forest plots located in latitudes between 34° and 38° were binned into 100-m elevation bands. To test prediction 3 (i.e. a steeper relationship between temperature and MFA for latitudinal gradients than for elevational gradients), we compared coefficients of regressions of MFA against temperature between latitudinal and elevational gradients. Finally, we tested prediction 4 (i.e. minimum temperature plays a more important role than temperature seasonality in shaping MFA patterns) by simultaneously assessing the effects of minimum temperature and temperature seasonality on MFA while accounting for precipitation, we built structural equation models (SEMs) in which MFA was the response, annual precipitation and precipitation seasonality were exogenous variables and minimum temperature and temperature seasonality were endogenous variables. An SEM allows simultaneous testing of direct and indirect effects between predictor and response variables and thus enables evaluation of hypothesized causal relationships (Grace, 2006). We focused on three longest latitudinal gradients at low elevations (i.e. 0–200 m, 200–400 m and 400–600 m in elevation) and three longest elevational gradients (located at 34–36°, 36–38° and 38–40° in latitude) for all analyses.

All species in our data set appeared in more than one plot. It has been shown that a moderate to large number of repeated co-occurrences of species across plots generate artifactually strong relationships between species attributes and the environment when aggregated at the community level (Peres-Neto, Dray, & ter Braak, 2016; Zelený & Schaffers, 2012). We conducted a randomization analysis to assess whether this issue is with this study. Specifically, we (1) randomly shuffled family ages assigned to all species, (2) substituted family age of each species in each forest plot with its randomized family age and re-calculated MFA for each forest plot, (3) used the randomized MFA values to run regressions of MFA against latitude (for latitudinal gradients) or elevation (for elevational gradients) and (4) repeated the randomization 1,000 times to obtain 1,000 null regression coefficients for each latitudinal or elevational gradient. We then determined where the observed coefficient of each latitudinal or elevational gradient lies with respect to the null distributions. We used systat (Wilkinson, Hill, Welna, & Birkenbeuel, 1992) for traditional statistical analyses and the r package 'lavaan' 0.5–20 (cran.r-project.org/web/packages/lavaan) for the SEM analyses.

3 | RESULTS

The MFA of a local forest community decreases with increasing latitude and elevation for all the six gradients examined (Figure 2), supporting prediction 1. For each of the gradients, the regression slope of the relationship between MFA and latitude or elevation was steeper for forest communities with larger values of MFA than for those with smaller values of MFA (compare the upper line with the lower line of each panel in Figure 2), indicating that the trend of decreasing MFA with increasing latitude or elevation resulted primarily from the loss of species in old families towards high latitudes or elevations. This is consistent with that of the analysis relating the

FIGURE 2 Relationship of mean family age (MFA) of angiosperm trees in forest communities with latitude (left column) or elevation (right column) in eastern North America. In each plot, the middle line is the least squares fit to all data points, and upper and lower lines are the least square fit to the 10 data points with largest and smallest values of MFA, respectively, in each 1-degree latitudinal zone (the three plots in the left column) or each 100-m elevational band (the three plots in the right column). Regression coefficient (β) and significance (*p*) of each regression were indicated (U, upper line; M, middle line; L, lower line)


(a) Elevations between 0 and 200 m
U: β = -2.49, P =<0.001
M: β = -1.75, P =<0.001
L: β = -1.00, P =<0.001
(b) Latitudes between 34 and 36°
U: β = -0.019, P =<0.001
M: β = -0.008, P =<0.001
L: β = -0.002, P = 0.001
(c) Elevations between 200 and 400 m
U: β = -2.32, P =<0.001
M: β = -1.71, P =<0.001
L: β = -1.20, P =<0.001
(d) Latitudes between 36 and 38°
U: β = -0.019, P =<0.001
M: β = -0.005, P =<0.001
L: β = 0.002, P = 0.019
(e) Elevations between 400 and 600 m
U: β = -2.26, P =<0.001
M: β = -1.87, P =<0.001
L: β = -1.69, P =<0.001
(f) Latitudes between 38 and 40°
U: β = -0.017, P =<0.001
M: β = -0.010, P =<0.001
L: β = -0.005, P =<0.001
MFA
20
40
60
80
100
120
28
30
32
34
36
38
40
42
44
46
48
50
0
200
400
600
800
1000
1200
1400
1600
1800
Latitude (°)
Elevation (m)

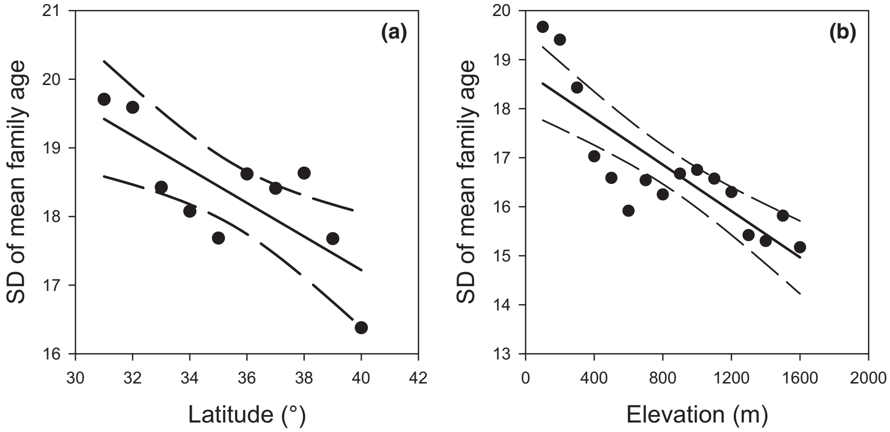


FIGURE 3 Relationship of standard deviation (*SD*) of mean family age of angiosperm trees in forest communities with latitude (a) or elevation (b) in eastern North America. Each dot in panel (a) represents *SD* of mean family age for forest plots within each 1-degree latitudinal zone below 600 m in elevation; each dot in panel (b) represents *SD* of mean family age for forest plots within each 100-m elevational band constrained between 34° and 38°N latitude. For each linear regression (solid line), broken lines indicate the 95% confidence intervals of the mean

standard deviation of MFA with latitude or elevation, which showed that the standard deviation of MFA decreased with increasing latitude and elevation (Figure 3), supporting prediction 2.

MFA decreased significantly with decreasing minimum temperature ($p < .001$) for both latitudinal and elevational gradients (Table 1). However, the regression slope of the relationship between MFA and minimum temperature was steeper for elevational gradients than for latitudinal gradients (Table 1), inconsistent with prediction 3. About 17% of the forest plots used in this study had 30% or more tree species being gymnosperms. When these forest plots were excluded from the analysis, the result remained the same qualitatively (compare Table 1 with Appendix S1).

When minimum temperature and temperature seasonality were simultaneously related to MFA while accounting for annual precipitation and precipitation seasonality, minimum temperature had a much stronger relationship with MFA than temperature seasonality for both latitudinal and elevational gradients (Figure 4). Specifically, for the latitudinal gradients, the standardized coefficients of minimum temperature on MFA were stronger than that of temperature seasonality by a factor of 3.56; for the elevational gradients, the effect of minimum temperature on MFA was stronger than that of temperature seasonality by a factor of 3.18. Thus, the results are consistent with prediction 4.

The evaluation of the 'similarity issue' identified by Zelený and Schaffers (2012) indicated that species occurrences cannot account for the observed links between MFA and the physical environment. The mean value of 1,000 null regression coefficients for a latitudinal or elevational gradient was zero for the three elevational gradients and was zero or nearly zero for the three latitudinal gradients (ranging from −0.012 to 0.010). Five of the six observed regression coefficients reported in Figure 2 (regression lines indicated as 'M') fell outside of 2 standard deviation units of the randomized regression coefficients, and the observed regression coefficient for the other gradient (i.e. the elevational gradient at latitude 36–38°) was close to 2 standard deviation units of the randomized regression coefficients (i.e. −0.005 vs. −0.006).

TABLE 1 Results of regressions of mean family age (MFA) of angiosperm trees in forest communities against minimum temperature for latitudinal and elevational gradients in eastern North America

	N	Intercept	Slope	R^2	*p*
Latitudinal gradient					
0–200 m elevation	3077	74.657	0.149	0.554	<.001
200–400 m elevation	3000	75.994	0.147	0.558	<.001
400–600 m elevation	2719	76.460	0.140	0.593	<.001
Elevational gradient					
34–36° latitude	2397	77.267	0.173	0.173	<.001
36–38° latitude	2245	78.224	0.163	0.106	<.001
38–40° latitude	2405	82.915	0.229	0.254	<.001

4 | DISCUSSION

We found empirical support for three of all four predictions we tested, providing a clearer understanding of the ecological and evolutionary forces affecting the structure of forest communities in the temperate zone. The eastern USA is an ideal geographical system for assessing phylogenetic and other macroecological patterns along latitudinal and elevational gradients for several reasons. First, the eastern USA covers a relatively long thermal gradient (a range of *c.* 20°C for mean annual temperature) with diverse forest communities (Barbour & Billings, 1999). A long thermal gradient would be ideal for assessing the effect of temperature on macroecological patterns. Second, the Appalachians, which reach an altitude of 2,037 m, run in

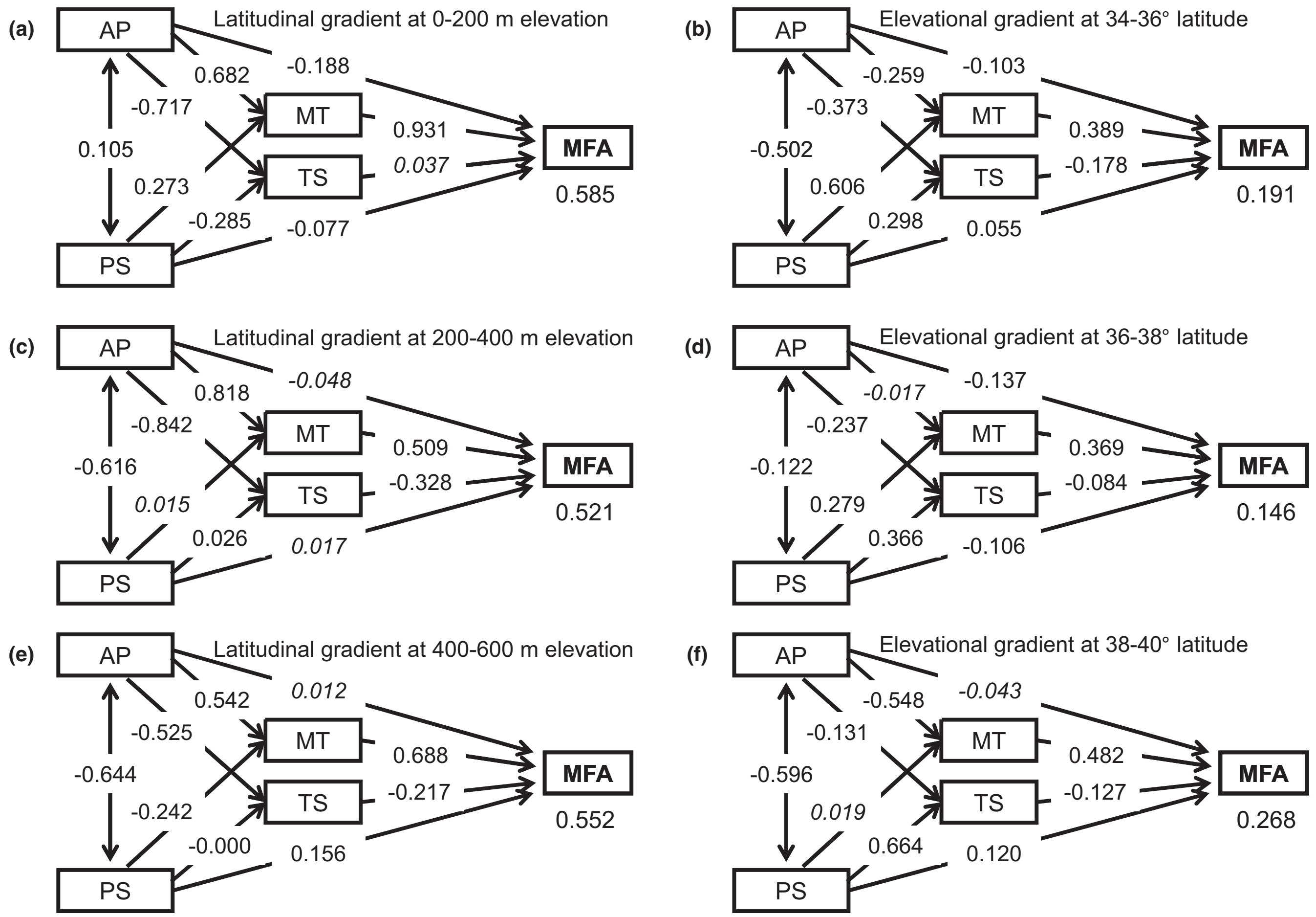


FIGURE 4 Structural equation models (SEMs) showing relationships among annual precipitation (AP), precipitation seasonality (PS), minimum temperature (MT) and temperature seasonality (TS) in explaining the variation in the mean family age (MFA) of angiosperm trees in forest communities along latitudinal gradients (a, c and e) and elevational gradients (b, d and f) in eastern North America. Numbers on arrow lines are standardized path coefficients; numbers below boxes for MFA are R^2 values. Numbers in italic type are not significant ($p > .05$)

the north–south direction and cover much of the entire length of the latitudinal gradient of the eastern USA. The Appalachians first formed roughly 480 MYA, and once reached elevations similar to those of the Alps in Europe and the Rocky Mountains in western North America before natural erosions (Pulsipher & Pulsipher, 2014). Thus, elevational thermal gradients in the Appalachians well developed before the origin of angiosperms (Takhtajan, 1969). This would have allowed a 'full' development of elevational gradients of angiosperm distributions based on species ecological niche. Third, because the Appalachians were and are imbedded within the latitudinal gradient of eastern North America, through multiple glacial–interglacial cycles during the past 350,000 years (Delcourt & Delcourt, 1993), species distributed at high elevations and latitudes during interglacial periods were presumably intermingled at low elevations during glacial periods. This would have minimized the effect of difference in geological histories between elevational and latitudinal gradients on assembling species into local communities. Species in all forest communities in the eastern USA, regardless of its elevation and latitude, were assembled from the same species pool through environmental filtering based on ecological niches of individual species. The present study extends the study of Hawkins et al. (2014) by comparing the relationships between mean family age and climate in forest communities between latitudinal and elevational gradients.

We found that the mean family age of angiosperm tree species in local forest communities decreases with elevation, consistent with our prediction 1. We also found that mean family age decreases with decreasing minimum temperature along latitudinal gradients in the eastern USA. This finding is consistent with the finding of Qian et al. (2013) for angiosperm tree species in North America at a regional scale (quadrats of 12,100 km^2). Our finding is also consistent with those of previous studies relating mean family age and minimum temperature for angiosperm woody or tree species in local forest communities along latitudinal gradients in other continents. For example, Qian (2014) found that the mean family age of angiosperm woody species in local forest communities is positively correlated with minimum temperature along a latitudinal gradient in South America, while Qian and Chen (2016) found that the mean family age of angiosperm tree species in local forest communities decreases with decreasing minimum temperature along a latitudinal gradient in China. Overall, these findings from different studies are consistent with the prediction of the TNC (Latham & Ricklefs, 1993; Wiens & Donoghue, 2004).

Similarly, we found that the mean family age for angiosperm tree species in local communities is also positively correlated with minimum temperature along elevational gradients. This is consistent with the prediction of the TNC (Latham & Ricklefs, 1993; Wiens & Donoghue, 2004) but is contrary to the findings of Qian (2014), Qian (2017) for forest communities along elevational gradients in tropical regions. The mean family age of angiosperm tree species is negatively correlated with minimum temperature for communities along an elevational gradient in tropical Asia (Qian, 2016). Similarly, the mean family age of angiosperm woody (primarily tree) species is negatively correlated with temperature for communities along an elevational gradient in tropical South America (Qian, 2014). The contrasting patterns of the mean family age and temperature between temperate and tropical elevational gradients might reflect different mechanisms of community assembly. For tropical elevational gradients, niche convergence appears to be a dominant mechanism in assembling species from a regional pool into local communities (Qian & Ricklefs, 2016). In contrast, for temperate elevational gradients, niche conservatism has played a key role in assembling species of a regional pool into local communities. This is partly because multiple glacial–interglacial cycles during the Quaternary forced species of high elevations to move to low elevations and to intermingle with species from high latitudes during glacial periods and then forced the newly formed mixtures of species from latitudinal and elevational gradients to move to high latitudes and high elevations during interglacial periods, species in local communities at both higher latitudes and higher elevations were assembled through environmental filtering acting along with niche conservatism mechanisms. Thus, the mean family age of species along temperate elevational gradients is expected to decrease with decreasing temperature, as along latitudinal gradients.

We found that for both latitudinal and elevational gradients, the regression slope of the relationship between MFA and latitude or elevation was steeper for communities with larger values of MFA than for those with smaller values of MFA (Figure 2) and that the standard deviation of MFA decreased with increasing latitude and elevation (Figure 3). Both results indicate that the phylogenetic structure of tree communities primarily reflects a loss of old families towards high latitudes or elevations rather than the replacement of old families by young families when moving to higher latitudes or elevations. In other words, communities at low latitudes and elevations comprise both old and young families but old families in forest communities drop off gradually towards high latitudes or elevations. This pattern is consistent with our prediction 2.

Our results showed that the regression slope of the relationship between MFA and minimum temperature was steeper for elevational gradients than for latitudinal gradients. As a result, at a particular minimum temperature, MFA is lower for the elevational gradient than for the latitudinal gradient, which is inconsistent with our prediction 3. This suggests that angiosperm tree species have reached a colder climate limit along latitudinal gradients than along elevational gradients, although we acknowledge that our analyses do not directly compare species at their upper latitudinal and elevational limits. 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. In contrast, Siefert et al. (2015) 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. For example, for the 24 angiosperm tree species examined in their study, January mean temperature at their high-elevation limits is, on average, higher than that at their high-latitude limits by about 7°C (−0.60 vs. −7.69°C). They suggest that winter temperature does not play a critical role in limiting species distributions at high latitudes and elevations. However, several studies (e.g. Hawkins et al., 2014; Qian et al., 2007; Wang et al., 2011) have suggested that minimum temperature has played a critical role in shaping distributional limits of species. We believe that minimum temperature is a key determinant for tree distributions towards both high latitude and high elevation, but differences in some environmental factors between latitudinal and elevational gradients (Körner, 2007) might have caused mismatches in minimum temperatures of species distributions at high latitude and elevation. Some climatic features unique to elevational gradients (e.g. decreasing atmospheric pressure and increasing radiation towards high elevation) might be important factors, in addition to minimum temperature, limiting tree species distribution at high elevation.

We used the structure equation modelling approach to simultaneously assess the relative importance of minimum temperature and temperature seasonality on MFA while accounting for precipitation. We found that minimum temperature has a much stronger relationship with MFA than does temperature seasonality for both latitudinal and elevational gradients. This result is consistent with our prediction 4 and the prediction of the TNC (e.g. Futuyma, 1998; Ricklefs & Schluter, 1993; Wiens & Donoghue, 2004). Our finding is also consistent with that of Wang et al. (2011) for woody plants in China and that of Qian et al. (2007) for amphibians and reptiles in China. However, our finding differs from that of Wiens et al. (2006) for hylid frogs in North America. Wiens et al. (2006) related northern distributional range limits of 12 species to several climatic variables (including minimum temperature and temperature seasonality) using multiple regression analyses and found that temperature seasonality was retained in more regression models than minimum temperature. Accordingly, they concluded that extreme winter temperature is seemingly not a critical factor to limit northern range limits of species, and they considered their finding contrary to the prediction by others (e.g. Futuyma, 1998; Ricklefs & Schluter, 1993). However, Wiens et al.'s (2006) study was constrained to a narrow range of low latitudes and thus a short latitudinal gradient. More importantly, their study area was generally restricted to tropical climates, where temperatures do not generally fall to 0°C. For example, the northern range limits of all six species in their primary analysis were located in latitudes south of the Tropic of Cancer, within the latitudes where water is often more critical than temperature (Hawkins et al., 2003).

We suggest that a robust test invoking minimum temperature should include areas in temperate climates. Our study is located entirely in temperate climates and found that temperature seasonality has a much weaker relationship with the mean family age of species in forest communities, compared to extreme winter temperature.

In conclusion, we found the following patterns in this study: (1) mean family age decreases with increasing latitude or elevation, (2) decrease in MFA along both elevational and latitudinal gradients primarily results from the loss of old families towards higher elevations or latitudes (see Hawkins et al., 2014 for discussion of range shifts in species from older angiosperm groups in response to climate change beginning in the Paleogene), (3) the relationship (regression slope) between minimum temperature and MFA is steeper for elevational gradients than for latitudinal gradients and (4) minimum temperature plays a more important role than temperature seasonality in shaping MFA patterns for both latitudinal and elevational gradients. The patterns observed in this study are fully consistent with an historical explanation for local community structure driven by the global processes reflecting the origin of angiosperms and post-Eocene climate change, a link long argued in the ecological literature (Ricklefs, 1987) but still perhaps not fully appreciated.

ACKNOWLEDGEMENTS

We are grateful to three anonymous reviewers for constructive comments on the manuscript. J.Z. was supported by the National Natural Science Foundation of China (Grant No. 31670439), 'Thousand Young Talents' Program in China, and East China Normal University.

DATA ACCESSIBILITY

The data used in this study can be accessed freely.

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BIOSKETCHES

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Author contributions: H.Q. conceived the idea, designed the study and wrote the article; J.Z. prepared the data; H.Q., B.A.H. and J.Z. analyzed the data and participated in revising the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Qian H, Zhang J, Hawkins BA. Mean family age of angiosperm tree communities and its climatic correlates along elevational and latitudinal gradients in eastern North America. *J Biogeogr*. 2017;00:1–10. https://doi.org/10.1111/jbi.13108