RESEARCH PAPER

How do climate and dispersal traits limit ranges of tree species along latitudinal and elevational gradients?

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ABSTRACT

Aim We compared the upper range limits of tree species along latitudinal and elevational gradients to assess the influence of specific climatic factors – winter temperature, summer temperature and growing season length – in determining species range limits. We analysed the degree and direction of climatic mismatches between latitudinal and elevational limits to determine whether mismatches could be explained by species dispersal traits.

Location Eastern North America and the Great Smoky Mountains (Tennessee and North Carolina), USA.

Methods We determined the climatic limits for each of 28 common tree species along a latitudinal gradient in eastern North America and across an elevational gradient in the Great Smoky Mountains. We calculated the degree of climatic mismatch between species limits along the two gradients and tested for relationships with species dispersal traits (seed mass, maximum height, seed and pollen dispersal mode).

Results We found strong positive relationships between species latitudinal and elevational climatic limits. Winter temperatures were much lower at species poleward limits compared with their upper elevational range limits, but there were close matches between limits for variables related to summer temperature and growing season length. The degree of climatic mismatch was influenced by species dispersal traits; species with unassisted seed dispersal and low maximum height tended to have lower latitudinal than elevational limits.

Main conclusions Our results suggest that low summer temperatures and a short growing season length limit species distributions along both latitudinal and elevational gradients, whereas winter temperature does not play a critical role. The failure of some species with poor dispersal ability to grow as far poleward as expected based on their elevational limits supports the hypothesis that historical dispersal constraints may limit species distributions along the latitudinal gradient.

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INTRODUCTION

The turnover of plant and animal species along environmental gradients is one of the oldest themes in ecology (Schimper, 1898; Whittaker, 1956; von Humboldt, 2009). Yet understanding the controls on species distributions that produce this turnover remains a central question in ecology, with important implications for predicting species range shifts in response to ongoing and predicted climate change (Jump *et al.*, 2009; Chen *et al.*, 2011).

Climate has long been recognized as a primary factor controlling the distributions of tree species, especially at their upper
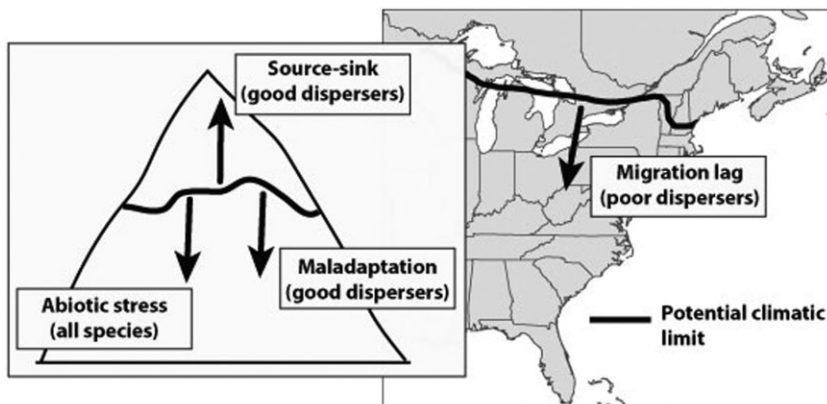
latitudinal and elevational limits (Tranquillini, 1979; Huntley *et al.*, 1989; Randin *et al.*, 2013). Several climate-based limitations have been proposed, including low winter temperatures (Sakai & Weiser, 1973), low growing season temperatures (Pigott & Huntley, 1981; Cogbill & White, 1991; Mellert *et al.*, 2011) and a shortened growing season length (Morin *et al.*, 2007; Normand *et al.*, 2009). However, in many cases it remains unclear which climate variables, and interactions between them, are responsible for setting species range limits.

A comparison of climatic thresholds along latitudinal and elevational gradients may provide insights into the factors controlling species range limits (Kollas *et al.*, 2014). A close correspondence between values of a given climatic factor at the latitudinal and elevational limits of a species would suggest that that factor plays an important role in determining those limits. In contrast, mismatch in a given factor between latitudinal and elevational limits would suggest it is not the primary limit on species distributions along one or both gradients. Recent studies comparing cold limits of plant species along elevational gradients in the Alps and latitudinal gradients in Europe have found positive relationships and close correspondences for most species (Halbritter *et al.*, 2013; Randin *et al.*, 2013), providing evidence of thermal constraints. Importantly, climatic factors differ in their relative rates of change along latitudinal and elevational gradients. In particular, sites at high elevations tend to have warmer winter minimum temperatures and longer growing seasons than high-latitude lowland sites with similar growing season temperatures (Billings, 1973). This partial decoupling of climatic changes along the two gradients allows assessment of which climatic variables match most closely between species latitudinal and elevational ranges limits, and thus are most likely to control those limits. Climatic comparisons of high-elevation and high-latitude tree lines have generally found the closest correspondence in growing season temperature (Cogbill & White, 1991; Jobbágy & Jackson, 2000; Körner & Paulsen, 2004), but whether this pattern extends to individual tree species is not known.

Although climate is thought to be the primary driver of high-latitude and high-elevation range limits of tree species, the influence of other factors may generate climatic mismatches (Randin *et al.*, 2013). A host of potentially limiting abiotic factors change differently with increasing elevation and latitude, and most of these differences are expected to create more stressful conditions for plants at high elevations. In particular, high-elevation sites are characterized by increased steepness, exposure, cloud cover, wind speed, ice deposition, UV radiation and diurnal temperature fluctuations and reduced soil depth, nutrient availability, CO_2 partial pressure and summer photoperiod – all factors that may keep tree species below their expected thermal limits (Billings, 1973). For example, Cogbill & White (1991) found that upper limits of deciduous forest and tree lines in mountain ranges in eastern North America were held below the expected climate-determined elevations due to the effects of exposure. If non-climatic abiotic stresses limit tree species distributions more strongly along elevational than latitudinal gradients, species elevational limits should be lower than their latitudinal climatic limits (Fig. 1).

Another important difference between latitudinal and elevational gradients is that elevational gradients are much more spatially compressed, such that equivalent changes in temperature occur over much shorter distances (Jump *et al.*, 2009). As a result, there is potential for more efficient seed and pollen dispersal between contrasting climates in mountainous regions (Sundblad & Andersson, 1995). This difference in dispersal may generate climatic mismatches between latitudinal and elevational range limits in several ways. First, evidence suggests that the expansion of tree species in Europe and North America following glacial retreat was dispersal limited (Davis *et al.*, 1986; Svenning *et al.*, 2008), such that species poleward range limits lag behind their potential climatic limits (Svenning & Skov, 2004). In contrast, dispersal should be much less limiting of species ranges along spatially compressed elevational gradients (Jump *et al.*, 2009). If this is the case, tree species should reach colder temperatures along elevational than latitudinal gradients (Randin *et al.*, 2013), and this mismatch should be greater for species with poorer seed dispersal abilities (Fig. 1). Second, depending on the strength of selection, gene flow from core (i.e. low elevation) to peripheral (i.e. high elevation) populations may prevent local adaptation at range margins (García-Ramos & Kirkpatrick, 1997; Savolainen *et al.*, 2007), potentially limiting the cold tolerance and upper elevational range of tree species (Jump *et al.*, 2009). If this is

Figure 1 Illustration of the hypothesized causes of climatic mismatch between the upper latitudinal and elevational limits of tree species. Contour lines represent the potential upper limit of a species along the elevational or latitudinal gradient based on its climatic tolerances. Arrows represent expected shifts in species limits above or below their potential climatic limit due to hypothesized mechanisms.

the case, species should reach colder temperatures along latitudinal than elevational gradients, and the mismatch should be greater for species with greater seed or pollen dispersal abilities (Fig. 1). In contrast, efficient dispersal along elevational gradients may allow populations to exceed their long-term climatic limits through source–sink dynamics (Pulliam, 1988; Halbritter *et al.*, 2013), and if this is the case, species should reach colder temperatures along elevational than latitudinal gradients, and the mismatch should be greater for species with greater seed dispersal abilities (Fig. 1).

Comparison of observed patterns of climatic mismatch between species elevational and latitudinal limits with theoretical predictions has the potential to provide novel insights into the roles of climate and dispersal in shaping species distributions. In this study, we examined the range limits of 28 common tree species along a latitudinal gradient in eastern North America and an elevational gradient in the Great Smoky Mountains of the southern Appalachians. Our specific objectives were: (1) to determine the relationship and degree of matching between species latitudinal and elevational climatic limits; (2) to assess the influence of specific climatic factors – winter temperature, summer temperature and growing season length – in determining these limits; and (3) to determine whether mismatches between latitudinal and elevational limits could be explained by species dispersal traits.

METHODS

Study area

The study was conducted across a latitudinal gradient in eastern North America (25–50° N, 60–95° W). This gradient of over 1500 km encompasses the entire range of many eastern North American tree species, transitioning from southern pines and evergreen broadleaved species to mid-latitude broadleaved deciduous species and boreal evergreen conifers in the north. For comparison with the latitudinal gradient we used an elevational gradient in the Great Smoky Mountains National Park located in the southern Appalachians of Tennessee and North Carolina, USA (35°26′–35°47′ N, 83°3′–84°0′ W; Fig. 2). The Great Smoky Mountains represent the southern extent of high peaks in eastern North America, with elevations ranging from 224 to 2024 m a.s.l. This range of elevations occurs over relatively short distances (about 15 km), creating a short steep gradient along which the turnover of tree species mirrors that of the latitudinal gradient across eastern North America (Shanks, 1954). The elevational gradient in the Great Smoky Mountains and the latitudinal gradient across eastern North America cover a similar range of summer temperature (mean July temperature ranges 14.2–26.7 °C and 13.9–28.5 °C, respectively) and growing season length (annual frost-free period 207–330 days and 142–360 days, respectively), but the range of winter temperatures is much smaller in the Great Smoky Mountains than in eastern North America (mean January temperature ranges 0.0–4.7 °C and −10.0 to 19.9 °C, respectively; Shanks, 1954; Busing *et al.*, 2005; Fridley, 2009).
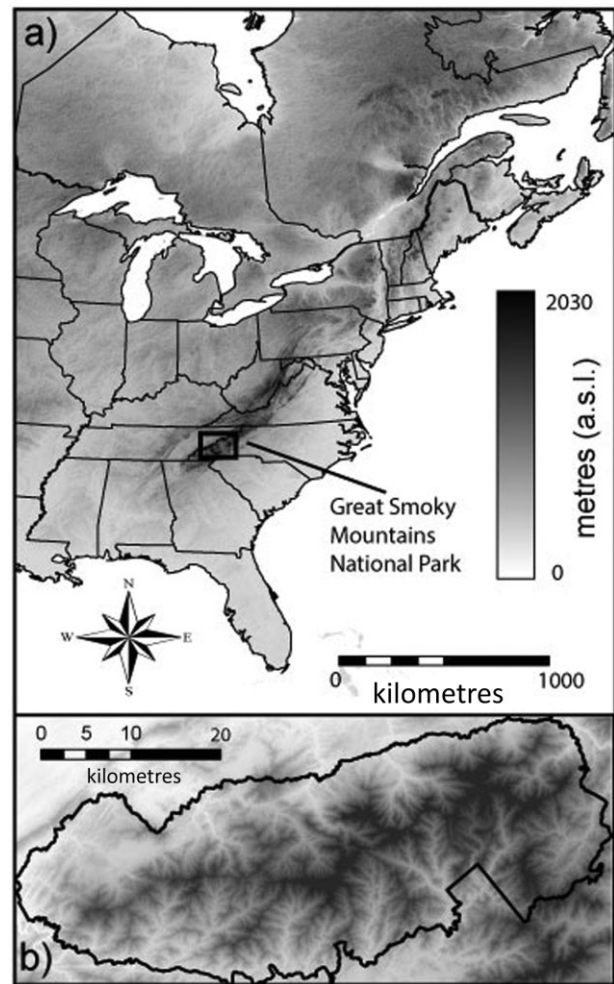

Figure 2 Map of the study area showing (a) a digital elevation model of eastern North America with the location of the Great Smoky Mountains National Park (GSMNP) and (b) enlargement of the GSMNP displaying elevational changes of > 1500 m within a spatial extent of < 10 km.

Species distributions

Data on tree species distributions in the Great Smoky Mountains National Park originated from a systematic vegetation survey of the park conducted from 1935 to 1938 (MacKenzie & White, 1998). The survey consisted of 1378 rectangular 0.08-ha plots located randomly within the park. This remains the only study to date that has sampled the entire park, encompassing the full elevational gradient. In each plot, woody plants were identified to species and classified as trees (> 10 cm diameter at breast height) or shrubs. For our analysis, we included only species that occurred as trees in at least 50 plots and had an upper elevational limit within the park, which we defined as having a maximum elevation below the 95th percentile of plots in the dataset. The final species list included 28 species, representing many of the most common hardwood and conifer species in the Great Smoky Mountains and eastern North America (Table 1).

For tree species distributions in eastern North America we used digitized versions of Little's (1971) tree species range maps

Table 1 Climatic limits (2.5% quantiles) of 28 study species along latitudinal gradient in eastern North America (ENA) and elevational gradient in the Great Smoky Mountains (GSM) based on January mean temperature, July mean temperature and frost free days (FFD). The mismatch between the latitudinal and elevational limit is given for each climate variable. Positive mismatches indicate elevational limits are colder (or have fewer FFD) than latitudinal limits. Negative mismatches indicate elevational limits are warmer (or have more FFD) than latitudinal limits. Species are sorted from the highest to the lowest elevational limit.

Species	January mean temp. (°C)			July mean temp. (°C)			FFD (days year^{-1})		
	Latitudinal limit	Elevational limit	Mismatch	Latitudinal limit	Elevational limit	Mismatch	Latitudinal limit	Elevational limit	Mismatch
Betula lenta	−7.59	−1.37	−6.22	18.65	16.56	2.09	130.05	120.24	9.81
Acer saccharum	−15.95	−1.29	−14.66	16.37	16.69	−0.32	97.89	120.73	−22.84
Aesculus flava	−2.17	−1.28	−0.88	20.16	16.70	3.46	154.85	120.94	33.91
Acer pensylvanicum	−14.24	−1.26	−12.98	16.32	16.74	−0.42	109.41	121.38	−11.98
Prunus serotina	−11.60	−1.25	−10.36	18.25	16.77	1.48	124.53	121.79	2.73
Tsuga canadensis	−13.28	−1.15	−12.13	17.13	16.92	0.21	113.87	122.43	−8.57
Halesia tetraptera	−0.47	−0.97	0.50	20.25	17.23	3.02	155.90	125.40	30.50
Acer rubrum	−15.37	−0.91	−14.45	16.72	17.32	−0.60	106.97	126.83	−19.86
Quercus rubra	−15.28	−0.91	−14.36	16.93	17.32	−0.40	108.05	126.83	−18.78
Robinia pseudoacacia	−3.69	−0.76	−2.93	19.82	17.57	2.25	153.09	127.17	25.93
Fraxinus americana	−12.97	−0.75	−12.22	17.42	17.59	−0.17	118.88	127.21	−8.33
Tilia americana	−14.94	−0.62	−14.32	17.48	17.80	−0.33	110.52	133.70	−23.18
Magnolia fraseri	−4.18	−0.56	−3.62	18.52	17.91	0.61	147.24	133.99	13.25
Quercus alba	−9.78	−0.52	−9.26	19.26	17.98	1.28	139.26	137.37	1.89
Magnolia acuminata	−5.08	−0.41	−4.67	19.31	18.17	1.15	139.89	139.40	0.49
Sassafras albidum	−5.21	−0.40	−4.82	20.32	18.19	2.13	154.39	139.40	14.99
Quercus montana	−5.73	−0.39	−5.33	19.71	18.19	1.52	148.01	139.40	8.61
Quercus velutina	−7.75	−0.32	−7.43	20.10	18.31	1.79	151.44	139.64	11.80
Oxydendrum arboreum	−1.76	−0.19	−1.57	20.71	18.53	2.17	161.84	146.27	15.57
Nyssa sylvatica	−5.27	−0.19	−5.08	20.29	18.54	1.76	153.76	146.31	7.46
Carya glabra	−5.25	−0.15	−5.10	20.64	18.61	2.04	157.12	147.00	10.13
Carya alba	−4.41	−0.03	−4.39	20.69	18.80	1.89	157.17	149.53	7.63
Pinus rigida	−7.45	0.01	−7.46	19.29	18.86	0.43	141.32	149.64	−8.32
Cornus florida	−4.92	0.04	−4.97	20.56	18.92	1.64	155.44	149.87	5.57
Liriodendron tulipifera	−5.22	0.09	−5.31	20.20	19.00	1.20	154.47	150.60	3.87
Quercus coccinea	−5.62	0.10	−5.72	19.88	19.01	0.87	149.08	150.75	−1.67
Pinus strobus	−16.90	0.65	−17.55	16.38	19.94	−3.55	98.30	160.91	−62.61
Pinus virginiana	−3.96	0.66	−4.62	19.97	19.95	0.02	154.30	160.93	−6.63

(http://esp.cr.usgs.gov/data/little). Although dated, these maps remain the definitive source for the ranges of North American tree species. We compared all results using these data with an alternative data source of species distributions using plot data collected between 2001 and 2006 from the United States Department of Agriculture Forest Inventory and Analysis Program (FIA; http://www.fia.fs.fed.us) and Canada's National Forest Inventory (NFI; https://nfi.nfis.org). Both approaches produced similar results, but we only report results based on Little's species range maps because we believe these provide more accurate estimates of species poleward range limits due to increasingly sparse coverage of Canadian plot data with increasing latitude. Sparse plot coverage at higher latitudes resulted in the poleward range limits of some species being at lower latitudes than limits provided by Little's range maps.

Climate data

We extracted daily minimum and maximum temperatures from 1980 to 2010 for each 0.5° × 0.5° grid cell in eastern North America from Daymet (http://daymet.ornl.gov). We obtained similar daily temperature data from six weather stations in or near Great Smoky Mountains National Park that spanned the entire elevational gradient of the park (Fridley, 2010). Weather station data were then used to calculate linear lapse rates of temperature along the elevational gradient which enabled us to calculate daily minimum and maximum temperatures for each of the vegetation plots in the Great Smoky Mountains. While these climate data are not from the same time period as the species distribution data we used, temperatures in the Great Smoky Mountains have remained relatively stable over the past century (Fig. S1 in Supporting Information), meaning that these estimates of species climatic distributions were accurate. Further, Lesser & Fridley (unpublished data) found a lack of warming in the Great Smoky Mountains that agrees with other studies that have observed no significant warming across much of the south-eastern United States (Portmann *et al.*, 2009; Meehl *et al.*, 2012).

Using the daily temperature data, we derived climatic variables representing factors hypothesized to control species upper latitudinal and elevational range limits: winter cold, growing season length and growing season temperature. To quantify winter cold, we calculated the mean daily temperature of the coldest month (January) and the mean annual absolute minimum temperature. We quantified the length of the growing season using two metrics: (1) annual frost-free days (FFD), the period between the last frost (daily minimum temperature < 0 °C) of the spring and first frost of the autumn, and (2) growing season length (GSL), the period beginning when daily mean temperature exceeded 5 °C for five consecutive days and ending when daily mean temperature fell below 5 °C for five consecutive days (Kollas *et al.*, 2014). We quantified growing season temperature using two metrics: (1) mean daily temperature during the warmest month (July), and (2) growing season temperature (GST), the mean daily temperature during the growing season as defined above. We also calculated the number

of annual growing degree-days (GDD), which takes into account both the length and temperature of the growing season, as the cumulative annual sum of daily mean temperature minus a base temperature of 10 °C.

For reasons of data availability, we used air temperature to quantify potential thermal constraints on tree species, but previous work has found that soil temperature rather than air temperature is critical for determining the position of the tree line (Körner & Paulsen, 2004). However, root-zone and canopy temperatures are highly correlated, particularly when integrated over periods of a week or more (Körner & Paulsen, 2004), so we believe that the use of soil temperature data would not have had a strong impact on our findings.

Data analysis

For each species, we calculated climatic limits along the latitudinal and elevational gradients as the 0%, 2.5% and 5% quantiles of the distribution of climatic values of species occurrences in eastern North America and the Great Smoky Mountains. Results of subsequent analyses were similar regardless of which quantile was used, so we only report results based on the 2.5% quantiles.

We tested the relationship between species climatic limits along latitudinal and elevational gradients using major axis regression. We also calculated the mismatch between latitudinal and elevational limits of each species for each climatic variable as the difference between the latitudinal and elevational climatic limit. Positive mismatches indicate that species limits are higher, and thus colder, along the elevational gradient than the latitudinal gradient. Conversely, negative mismatches indicate that species limits are lower, and thus warmer, along the elevational gradient than the latitudinal gradient. We tested whether the average mismatch across all species for each climatic variable was significant using paired *t*-tests. To visually assess mismatches, we superimposed species elevational climatic limits onto the latitudinal gradient, and vice versa. For each species, this allowed us to create contour lines indicating a species' expected range limit along a given gradient based on its climatic limits on the other gradient (Figs 3 & S2).

Next, we assessed whether the degree of mismatch could be explained by species dispersal traits. We selected four traits related to dispersal ability: maximum height, seed mass and seed (wind, animal or unassisted) and pollen (wind or animal) dispersal mode. Seed dispersal distance is known to be positively related to plant height and negatively related to seed mass (Nathan *et al.*, 2002; Thomson *et al.*, 2011). Wind-dispersed seed has been shown to generally disperse much farther than animal-dispersed or unassisted seed (Wilson & Traveset, 2000), although this trend is complicated by some animals (birds) generally having much greater dispersal distances than others such as ants (Horvitz & Le Corff, 1993). Species were also categorized as having wind- or animal-assisted pollen dispersal, with pollen dispersal distances expected to be greater for wind-dispersed species. Dispersal trait data were derived from Burns & Honkala (1990) and the Seed Information Database (Royal Botanic
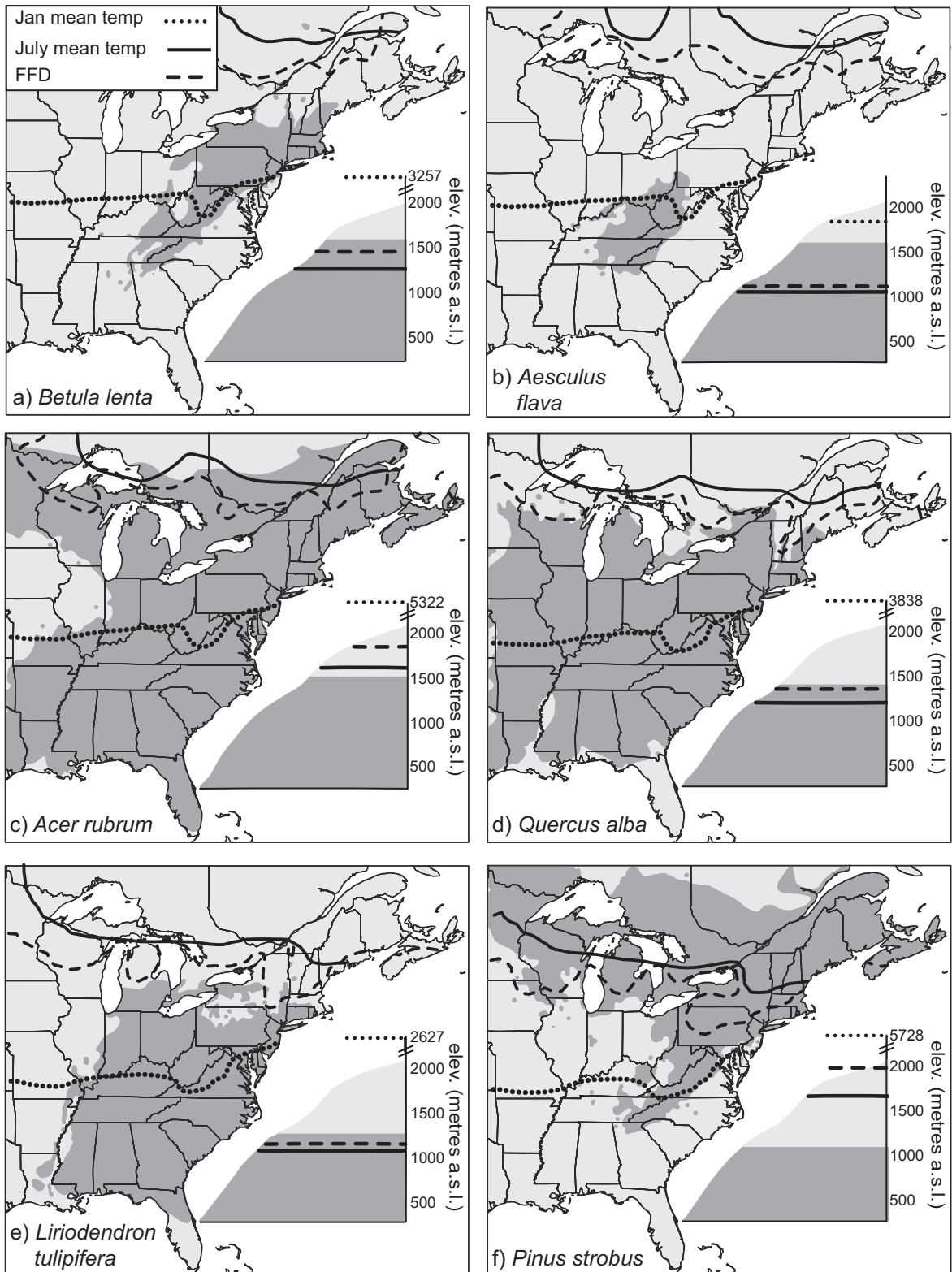
Figure 3 Distributions of six representative tree species, (a) *Betula lenta*, (b) *Aesculus flava*, (c) *Acer rubrum*, (d) *Quercus alba*, (e) *Liriodendron tulipifera*, and (f) *Pinus strobus*, in eastern North America and along an elevational gradient in the Great Smoky Mountains (inset profile). Species distribution is shown with dark grey shading. Contour lines on maps show a species' expected poleward range limit based on its corresponding climatic limit along the elevational gradient. Horizontal lines on elevation profiles show a species' expected upper limit based on its corresponding latitudinal climatic limit in eastern North America. Climatic limits are shown for January mean temperature (dotted line), July mean temperature (solid line) and frost free days (dashed line).

Gardens Kew, 2014). We tested relationships between species dispersal traits and elevational versus latitudinal climatic limit mismatch using linear regressions.

Our approach assumes that dispersal ability is related to a species' standard seed dispersal mode. However, non-standard dispersal vectors have been shown to contribute substantially to long-distance dispersal (Higgens *et al.*, 2003; Nathan *et al.*, 2008). For example, blue jays may have played an important role in the post-glacial migration of fagaceous species (*Quercus*, *Fagus*) otherwise considered to be poor dispersers (Johnson & Webb, 1989). Long-distance dispersal events, however, represent only a small proportion of dispersal events (Nathan, 2006). Our conservative estimates of species range margins, based on Little's range maps (Little, 1971), do not account for outlying, disjunct populations, which may be more greatly influenced by long-distance and non-standard dispersal. Thus, species distribution limits, as we have calculated them here, are more likely to be dictated by local dispersal using standard mechanisms.

RESULTS

Climatic limits and mismatches

Overall, there was a positive relationship between species climatic limits along latitudinal and elevational gradients, with species that reached colder temperatures along a latitudinal gradient also having colder elevational limits for each of the included climate variables (Table 1, Fig. 4). The one significant outlier was *Pinus strobus* (white pine) which had a much warmer elevational limit than would be predicted by its latitudinal limit (Table 1, Fig. 3f). At the opposite extreme (although not a significant outlier), *Aesculus flava* (yellow buckeye) consistently had a latitudinal limit that was warmer than predicted by the elevational limit (Table 1, Fig. 3b).

Significant positive relationships between latitudinal and elevational limits were found for all tested climate variables (Table 2); however, because of high correlations between climate variables we focus the remaining analysis on January mean temperature, July mean temperature and FFD, as these had the strongest relationships and lowest mismatch values among variables representing winter temperature, growing season temperature and growing season length, respectively. (Table 2).

Of these climatic variables, mismatches between latitudinal and elevational range limits were greatest for January mean temperature (Table 1), with species reaching much colder winter temperatures along the latitudinal gradient than the elevational gradient (Figs 3, 4a & S2). The average January mean temperature at the poleward limit across study species was −8 °C, while the average at the upper elevational limit was −0.5 °C, resulting in an average mismatch across all species of −7.6 °C (paired *t*-test, $P < 0.001$; Table 2). The mismatch tended to be greater for species with more poleward and higher limits (Fig. 4a).

Elevational and latitudinal limits of July mean temperature and FFD both showed much closer correspondence. Species limits for July mean temperature were strongly correlated, with

a major axis regression slope of 0.38 (0.52 with *P. strobus* removed; Table 2). The average July mean temperature at the poleward limit across study species was 19 °C, compared with 18 °C at the upper elevational limit (Table 1), resulting in an average mismatch of < 1 °C (paired *t*-test, $P = 0.006$; Table 2). There was a slight tendency for species to have colder elevational than latitudinal limits, and these mismatches tended to be greater for species with more equatorial latitudinal limits and lower elevational limits (Fig. 4b).

Species limits for FFD were also strongly correlated, with the slope from the major axis regression being 0.35 (0.52 with *P. strobus* removed; Table 2). The average number of FFD at the poleward limit was 137.4 days while the average at the upper elevational limit was 137 days (Table 1), producing a non-significant mismatch of only 0.4 days (paired *t*-test, $P = 0.93$; Table 2). For FFD, species were more equally split on either side of the 1:1 line, as opposed to the other variables where most species fell on one side or the other (Fig. 4). Species with more equatorial and lower limits tended to have a shorter growing season (fewer FFD) at their elevational than their latitudinal limit (Fig. 4c). Conversely, species that occurred farther poleward and higher on the elevational gradient tended to have a longer growing season (more FFD) at their elevational than their latitudinal limit (Fig. 4c).

Effects of dispersal traits on climatic mismatch

Linear regression showed no significant relationship between climatic mismatch and either seed mass or pollination mode (Table S2). Dispersal mode and maximum height both showed significant relationships with climatic mismatch (Fig. 5, Table S2). For all climatic variables, the mismatch between latitudinal and elevational limits became more negative (i.e. latitudinal limits became colder relative to elevational limits) with increasing height and with the transition from unassisted seed dispersal to animal dispersal to wind dispersal (Fig. 5). Mismatches were negative across all dispersal groups and heights for January mean temperature, indicating that the latitudinal limits were colder than elevational limits. However, species with unassisted seed dispersal (relatively poor dispersers) had the smallest levels of mismatch, whereas wind-dispersed species (relatively good dispersers) had the highest levels of mismatch (Fig. 5a, b). Tree height showed the same pattern, with shorter species (relatively poor dispersers) having the smallest levels of mismatch, while the tallest species had the highest levels of mismatch (Fig. 5a, b).

Mismatches for July mean temperature were generally positive, indicating that species latitudinal limits were warmer than expected based on elevational limits. However, the mismatch was significantly less for wind-dispersed and taller species (Fig. 5c, d). A similar pattern was observed for mismatches in FFD, with shorter species and those with unassisted seed dispersal having a greater number of FFD at their latitudinal than their elevational limits (Fig. 5e, f). Mismatches were generally smaller for taller species and those with animal-dispersed seed, but there was a slight tendency for tall and wind-dispersed species to have
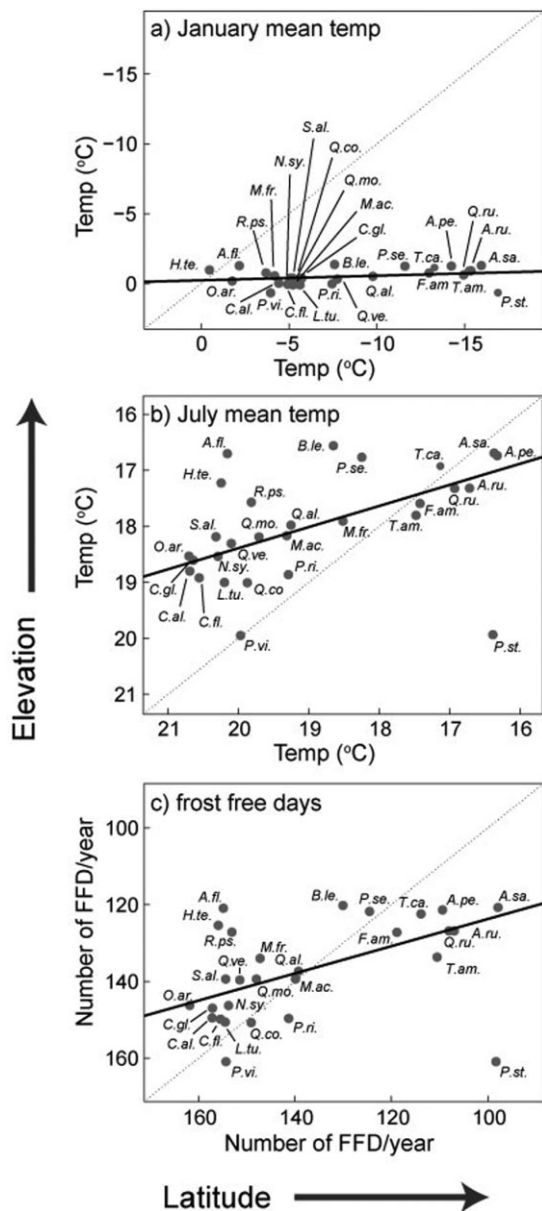
Figure 4 Relationship between climatic limits (2.5% quantile) of 28 eastern North American tree species along latitudinal and elevational gradients for (a) January mean temperature, (b) July mean temperature, and (c) frost free days. Solid lines represent the major axis regression line (regression coefficients given in Table 2). Species falling above the dotted 1:1 line have colder elevational limits than latitudinal limits. Species falling below the dotted line have warmer elevational limits than latitudinal limits. Species codes: *Betula lenta* (*B.le.*), *Acer saccharum* (*A.sa.*), *Aesculus flava* (*A.fl.*), *Acer pensylvanicum* (*A. pe.*), *Prunus serotina* (*P. se.*), *Tsuga canadensis* (*T. ca.*), *Halesia tetraptera* (*H. te.*), *Acer rubrum* (*A. ru.*), *Quercus rubra* (*Q. ru.*), *Robinia pseudocacia* (*R. ps.*), *Fraxinus americana* (*F. am.*), *Tilia americana* (*T. am.*), *Magnolia acuminate* (*M. ac.*), *Sassafras albidum* (*S. al.*), *Quercus montana* (*Q. mo.*), *Quercus velutina* (*Q. ve.*), *Oxydendrum arboretum* (*O. ar.*), *Nyssa sylvatica* (*N. sy.*), *Carya glabra* (*C. gl.*), *Carya alba* (*C. al.*), *Pinus rigida* (*P.ri.*), *Cornus florida* (*C. fl.*), *Liriodendron tulipifera* (*L. tu.*), *Quercus coccinea* (*Q. co.*), *Pinus strobus* (*P. st.*), *Pinus virginiana* (*P. vi.*).

Table 2 Slope and R^2 from major axis regression analysis of elevational versus latitudinal climatic limits for 28 eastern North American tree species. Climate variables are January mean temperature, July mean temperature, annual minimum temperature, frost free days (FFD), growing season length (GSL), growing season temperature (GST) and growing degree days (GDD). The mean mismatch across the 28 species between latitudinal and elevational limits is shown for each climate variable. Values in parentheses are for the same analysis with outlier (*Pinus strobus*) removed.

Variable	Slope	R^2	Mismatch
Jan mean temp (°C)	0.03* (0.08***)	0.08 (0.49)	7.57*** (7.76***)
Jul mean temp (°C)	0.38** (0.52***)	0.18 (0.60)	−0.97** (−0.97**)
Ann min temp (°C)	0.06** (0.12***)	0.11 (0.51)	6.91*** (7.05***)
FFD	0.35** (0.52***)	0.18 (0.61)	−0.41 (−0.38)
GSL	0.10* (0.26***)	0.08 (0.51)	59.3*** (62.1***)
GST	1.06** (0.92***)	0.20 (0.54)	−1.37*** (−1.38***)
GDD	0.24** (0.42***)	0.14 (0.59)	129.6 (146.1*)

Significant at: *$P < 0.1$, **$P < 0.05$, ***$P < 0.001$.

negative mismatches, indicating that these species had latitudinal limits with fewer FFD than their elevational limits.

DISCUSSION

Comparison of species range limits along latitudinal and elevational gradients of similar environmental change provides a unique opportunity to study the factors controlling species distributions. By comparing upper limits of tree species along a latitudinal gradient in eastern North America and an elevational gradient in the Great Smoky Mountains, our study investigates the climatic factors that limit species ranges and how dispersal traits may influence these limits. If the same climatic factors are largely responsible for dictating range limits, there should be close correspondence of species limits between gradients (Jump *et al.*, 2009; Randin *et al.*, 2013; Kollas *et al.*, 2014). Large degrees of mismatch in climatic limits between the two gradients would suggest that factors other than, or in conjunction with, climate were also responsible for controlling range limits (McGlone, 1996; Ricklefs, 2004). We found a close correspondence of climatic variables related to growing season length and summer temperature at species upper latitudinal and elevational range limits, consistent with the hypothesis that common growing season length and temperature thresholds limit species distributions along both gradients. In contrast, we found large degrees of mismatch for variables associated with winter temperature, suggesting that winter cold tolerance is not the primary factor influencing range limits. Our results also show that climatic mismatches between species latitudinal and elevational range limits can be explained by traits related to dispersal ability. The observed mismatch patterns are consistent

Figure 5 Relationships between dispersal traits (dispersal mode (a,c,e) and maximum height (b,d,f)) and climatic mismatch between latitudinal and elevational range limits for 28 eastern North American tree species. Results are shown for mismatch in January mean temperature (a,b), July mean temperature (c,d), and frost free days (e,f). Positive mismatches indicate colder elevational limits than latitudinal limits. Negative mismatches indicate warmer elevational limits than latitudinal limits. A zero value (dotted line) indicates no mismatch. For panels (a), (c) and (e) thick black bars represent median mismatch values, boxes represent first and third quartiles, whiskers extend to the most extreme values that are within 1.5 times the interquartile range from the box and open circles represent outliers. For panels (b), (d) and (f) solid black lines represent best fit lines from simple linear regression. Results of linear models (P and R^2) are shown for each trait–mismatch relationship.
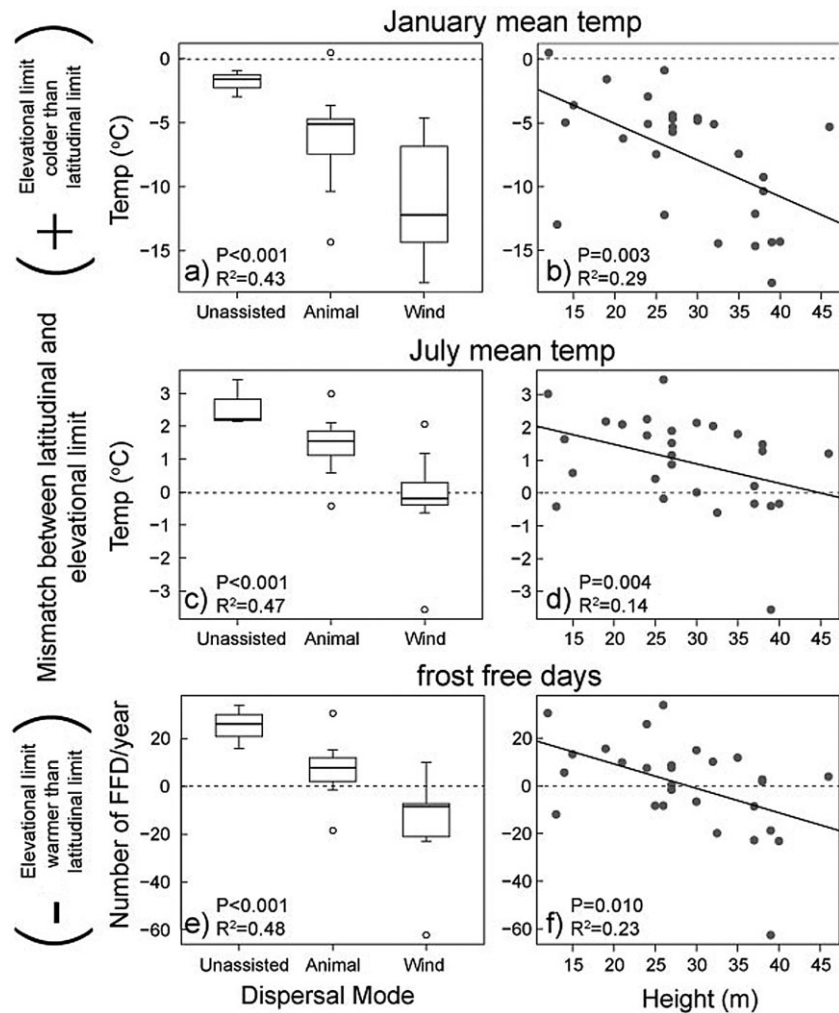
with predictions under the hypothesis that historical dispersal limitation restricts the poleward range limits of poorly dispersing species.

Climatic limits

Climatic limitations on species range limits have the potential to operate in several ways. First, low winter temperatures may limit species ranges by causing freezing injury. For example, Sakai & Weiser (1973) found that the freezing resistance of North American trees correlated well with minimum winter temperature at their poleward range limits, providing evidence that cold hardiness was a major factor determining species distributions. In contrast, our finding of large mismatches in winter temperatures between species latitudinal and elevational limits suggests that cold tolerance was not the primary limiting factor governing range limits. In particular, winter temperatures were much warmer at upper elevational limits compared with poleward limits for most species, suggesting that species distributions in the Great Smoky Mountains were not limited by winter temperatures. Kollas et al. (2014) found similar results in a comparison of elevational and latitudinal gradients in Europe, where

there were also high degrees of mismatch between species limits with regard to winter temperatures for seven broad-leaved tree species. Our results do not rule out the possibility that cold winter temperatures constrain species at high latitudes, either alone or through interactions with other factors, but previous studies of temperate tree species in Europe and North America have found that poleward limits are better explained by other climatic variables such as spring frost or growing season length (Morin et al., 2007; Kollas et al., 2014).

Low summer or growing season temperatures have previously been shown to constrain species distributions by limiting growth and development (Pigott & Huntley, 1981; Mellert et al., 2011). For example, Pigott & Huntley (1981) found that the poleward limit of *Tilia cordata* (small-leaved basswood) in Britain corresponded with summer temperatures that were too low to permit fertilization and ovule development. Summer temperatures have also been shown to explain the upper elevational limits of tree species in the Bavarian Alps (Mellert et al., 2011), elevations of spruce–fir ecotones of mountain ranges in eastern North America (Cogbill & White, 1991) and the position of alpine tree lines world-wide (Körner, 1998; Körner & Paulsen, 2004). Short growing season length, alone or

in combination with a low growing season temperature, may also place physiological limitations on tree species. Using a process-based model, Morin *et al.* (2007) determined that poleward distributions of temperate trees in North America were most often limited by insufficient GDD to undergo fruit ripening or flowering. Similarly, Normand *et al.* (2009) found that a short growing season limited the upper latitudinal and elevational range limits of European plants. We found similar results in our study, with July mean temperature and growing season length limits having the highest correspondence between the latitudinal and elevational gradients. These findings support the hypothesis that common thresholds for growing season temperature and/or length influence species limits along both gradients. The close correlation between growing season length and summer temperature in our study system makes it difficult to disentangle their effects using our approach. Experimental tests are required to determine whether growing season length, summer temperature or a combination of the two most strongly limit tree establishment and growth at species poleward and high-elevation range limits.

Causes of mismatches between elevational and latitudinal limits

Although summer temperature and growing season length generally corresponded well between species upper latitudinal and elevational limits there was not a perfect match for all species. We found that the degree of mismatch was strongly linked to species dispersal traits, with poorer-dispersing species – those with unassisted seed dispersal and low maximum height – tending to have lower, and thus warmer, latitudinal limits than expected based on their elevational climatic limits. This pattern is consistent with the hypothesis that historical dispersal limitation may have influenced the poleward distributions of species with limited dispersal ability. The species with mismatch patterns most consistent with the historical dispersal limitation hypothesis include *Aesculus flava*, *Halesia tetraptera*, *Robinia pseudoacacia* and *Oxydendrum arboreum*. These species had latitudinal limits well below their elevational climatic thresholds and traits associated with poor dispersal ability (short to medium height and unassisted dispersal or animal-dispersed seed). Further, their ancestral distributions are located in the southern Appalachians (Burns & Honkala, 1990), meaning that they have had far more time to disperse up the elevational gradient in the Great Smoky Mountains than to move poleward along the latitudinal gradient following the last glacial period. Post-glacial migration lag has been implicated as a leading cause of European tree species not filling their potential climatic niches (Svenning & Skov, 2004) and has also been proposed to limit the poleward distribution of *Picea glauca* (white spruce) in eastern North America (Payette, 2007).

An alternative explanation for mismatches between species elevational and latitudinal climatic limits is that long dispersal distances relative to the scale of climatic variation in mountainous regions allow species to exceed their fundamental climatic niches through source–sink dynamics (Pulliam, 1988; Halbritter

et al., 2013). We cannot completely rule out this possibility in our study, but we do not believe it is a major cause of the observed mismatches. If species were able to extend their elevational limits upwards by maintaining sink populations above their long-term climatic limits, we would expect mismatches between elevational and latitudinal limits to be higher for species with the greater dispersal ability, the opposite of the observed pattern. Another possible explanation for why species with poor dispersal ability had warmer latitudinal than elevational limits is that low gene flow along the broad latitudinal gradient may restrict genetic variation, and thus adaptation, in range edge populations (Alleaume-Benharira *et al.*, 2006). We believe that this is an unlikely cause of the observed mismatch patterns, for two reasons. First, population genetics studies show that gene flow is extensive for most forest tree species (Savolainen *et al.*, 2007). Second, if low gene flow limits poleward range expansion we would expect mismatches to be greatest for species with low pollen dispersal ability, since gene flow by pollen dispersal is typically much more extensive than gene flow by seed dispersal (Ennos, 1994). However, we observed no relationship between species pollen dispersal mode and climatic mismatches.

Interestingly, one species, *Pinus strobus* (white pine), showed a significantly different pattern from any of our other study species, with an elevational limit well below its latitudinal climatic thresholds. *Pinus strobus* can be categorized as a good disperser based on its height and dispersal mode (Table S1), and its observed mismatch pattern is consistent with the hypothesis that high dispersal rates, and hence high gene flow, along the short elevational gradient prevent adaptation to cold temperatures found at high elevations. Previous studies have found limited genetic differentiation among populations along elevational gradients (Ohsawa & Ide, 2008), perhaps due to extensive pollen flow. For example, Sundblad & Andersson (1995) found no differentiation in cold hardiness in *Pinus sylvestris* (Scots pine) across an elevational gradient, despite significant differentiation across the latitudinal range of the species. Although no studies to our knowledge have compared the cold hardiness of *P. strobus* populations across elevational or latitudinal gradients, common garden studies have shown that southern Appalachian seed sources grow faster than individuals from any other part of *P. strobus*'s range (Wendel & Smith, 1990). The failure of *P. strobus* to grow at high elevations in the Great Smoky Mountains may reflect the tradeoff between cold hardiness and growth observed in many tree species (Loehle, 1998; Koehler *et al.*, 2012), such that fast-growing, low-elevation genotypes are not capable of surviving at higher elevations with colder temperatures and a shorter growing season. Further tests of this hypothesis would involve direct comparisons of gene flow and local adaptation to climate in *P. strobus* populations along the latitudinal and elevational gradients.

CONCLUSIONS

Our results demonstrate that there is a positive relationship between the latitudinal and elevational climatic limits of eastern

North American trees – species that grow at higher latitudes also grow at higher elevations. Comparison of the high-latitude and high-elevation limits of tree species suggests that low summer temperatures and a short growing season length limit species distributions along both gradients, whereas winter temperature probably does not play a critical role. We also demonstrate that the degree of climatic mismatch between elevational and latitudinal range limits can be explained by species dispersal traits. In particular, species with poor dispersal ability did not grow as far poleward as expected based on their elevational limits, suggesting that historical dispersal constraints may have limited the post-glacial expansion of some species. These findings have implications for how individual species may respond to current and ongoing climate shifts. Based on climate predictions for the coming century, all of the climatic range limits we identify here are expected to shift poleward and up in elevation (Colwell *et al.*, 2008). Our analysis suggests that poorly dispersing species may not adequately track climate shifts along the latitudinal gradient in eastern North America. The inability to keep pace with suitable climate space combined with the contraction of trailing range edges may put these species at increased risk compared with better dispersers.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

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

Figure S1 Climate trends (1900–2011) in Great Smoky Mountain National Park for January mean temperature, July mean temperature, and frost free days.

Figure S2 Distributions of study species in eastern North America and along the elevational gradient in the Great Smoky Mountains.

Table S1 Dispersal traits of study species.
Table S2 *P*-values for effects of species traits on latitude–elevation climatic mismatch.

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