

Failure to migrate: lack of tree range expansion in response to climate change

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Abstract

Tree species are expected to track warming climate by shifting their ranges to higher latitudes or elevations, but current evidence of latitudinal range shifts for suites of species is largely indirect. In response to global warming, off-spring of trees are predicted to have ranges extend beyond adults at leading edges and the opposite relationship at trailing edges. Large-scale forest inventory data provide an opportunity to compare present latitudes of seedlings and adult trees at their range limits. Using the USDA Forest Service's Forest Inventory and Analysis data, we directly compared seedling and tree 5th and 95th percentile latitudes for 92 species in 30 longitudinal bands for 43 334 plots across the eastern United States. We further compared these latitudes with 20th century temperature and precipitation change and functional traits, including seed size and seed spread rate. Results suggest that 58.7% of the tree species examined show the pattern expected for a population undergoing range contraction, rather than expansion, at both northern and southern boundaries. Fewer species show a pattern consistent with a northward shift (20.7%) and fewer still with a southward shift (16.3%). Only 4.3% are consistent with expansion at both range limits. When compared with the 20th century climate changes that have occurred at the range boundaries themselves, there is no consistent evidence that population spread is greatest in areas where climate has changed most; nor are patterns related to seed size or dispersal characteristics. The fact that the majority of seedling extreme latitudes are less than those for adult trees may emphasize the lack of evidence for climate-mediated migration, and should increase concerns for the risks posed by climate change.

Keywords: biogeography, climate change, Forest Inventory and Analysis, latitude, presence/absence, range shift, seedling, tree migration

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Introduction

Anticipating whether or not species range limits can track climate change is a goal of global change research (Clark *et al.*, 2001; Davis & Shaw, 2001; Jackson *et al.*, 2009; Loarie *et al.*, 2009; Dawson *et al.*, 2011). Across the globe, mounting evidence confirms widespread temperature increases, particularly at high northern latitudes (IPCC, 2007). In the eastern United States, mean annual temperatures increased during the 20th century in the Midwest and Northeast, but not in the Southeast, where warming summers were balanced by cooling winters (Fig. 1a). When viewed in terms of a velocity, as has been advocated recently (Loarie *et al.*, 2009), regions in the Northeast and Upper Midwest have seen climate shifts of more than 100 km during the 20th century (Fig. 1b). As the climate warms, new regions that become available for occupation may be colonized as those no longer suitable are abandoned. Inevitable time

lags involved in plant dispersal, colonization, establishment, and maturation threaten not only rare species but also many that are abundant and provide vital ecosystem functions and services. Numerous datasets and models suggest a variety of species' responses to changing climate, but robust empirical evaluation remains challenging.

Previous studies generally agree that plants will respond to climate warming by shifting their ranges to higher elevations and latitudes (Hughes, 2000; McCarty, 2001; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Parmesan, 2006; Chen *et al.*, 2011), but only elevation responses are thus far readily apparent in data (Beckage *et al.*, 2008; Holzinger *et al.*, 2008; Kelly & Goulden, 2008; Lenoir *et al.*, 2008; le Roux & McGeoch, 2008; Bergamini *et al.*, 2009; Crimmins *et al.*, 2011; Van Bogaert *et al.*, 2011). The most recent comprehensive meta-analysis by Chen *et al.* (2011) does not include latitudinal range shifts of plants. In fact, studies of plant latitudinal range boundaries rely heavily on models at global (Thomas *et al.*, 2004), continental (Bakkenes *et al.*, 2002; Thuiller *et al.*, 2005; Meier *et al.*, 2011), and

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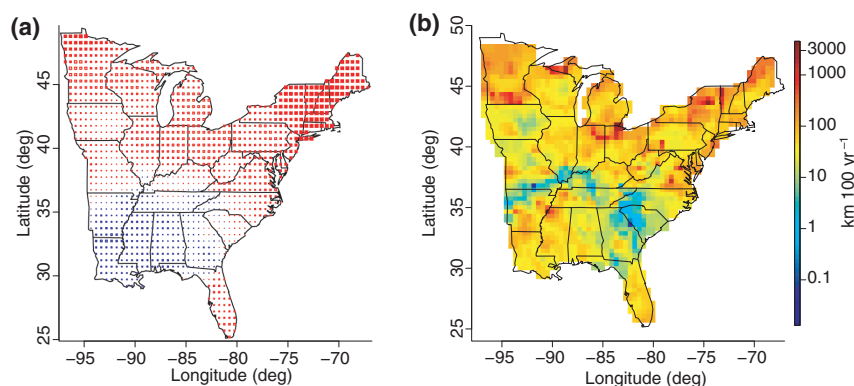


Fig. 1 Temperature change in time and space during the 20th century in the eastern United States. Data are extracted from 10 decadal mean annual temperatures from the Climate Research Unit (CRU) dataset (Mitchell & Jones, 2005). (a) Temporal trend during 1901–2000, with squares denoting the slope of the linear regression of decadal data: red – increasing trend, blue – decreasing trend; solid – significant slope with $P < 0.05$, open – insignificant slope with $P > 0.05$; and square size being proportional to the absolute value of the slope. (b) Spatial velocity of temperature change, defined as the quotient of the temporal gradient (a) and the north–south directional spatial gradient in 1991–2000 of temperature distribution (Loarie *et al.*, 2009).

regional scales (Midgley *et al.*, 2002; Broennimann *et al.*, 2006). Species distribution models in general (Guisan & Thuiller, 2005; Elith & Leathwick, 2009), and bioclimatic envelope models in particular (Pearson & Dawson, 2003; Heikkinen *et al.*, 2006) provide valuable perspectives on potential effects of climate change (Botkin *et al.*, 2007; McMahan *et al.*, 2011). However, there is little empirical evidence to support the model predictions that populations are shifting to higher latitudes.

The Forest Inventory and Analysis (FIA) program of the USDA Forest Service provides an extensive tree inventory for examining tree species range distribution and migration from millions of observations across the country. FIA conducts the only systematic sampling of all forest tree species at a continental scale. Although this database has been extensively used in tree range projection models (Iverson *et al.*, 2004, 2008), it has been used to evaluate potential range shifts only in highly indirect ways. Using FIA data, Murphy *et al.* (2010) found that 60% of 102 eastern US tree species have peak abundances of fitted distributions in the northern portion of their ranges. They suggested that this pattern could reflect range contraction in the south and limited expansion in the north. If ranges are more strongly limited by climate at high rather than low latitudinal limits (Dobzhansky, 1950; MacArthur, 1972; Brown *et al.*, 1996), then the opposite pattern could be expected, with strong advance in the north and limited response in the south, depending on the effects of competition with invaders advancing from the south. In addition to analyzing abundance, Woodall *et al.* (2009) compared the mean latitude of seedling and tree occurrence using FIA data throughout the eastern United States and found that northern species tend to show a shift northward, while southern species do not. They recognized

that these conclusions could be affected by their specific choice of study species (Woodall *et al.*, 2010) and their use of mean latitude, which reflects central tendency rather than range limits. Combining FIA, climate, geographic data, and several emission scenarios, Iverson *et al.* (2008) predicted that the center of suitable habitats for 134 eastern US tree species would move up to 800 km northeast. For five of the common species they analyzed, Iverson *et al.* (2004) predicted that migration in the next century will extend no more than 20 km beyond their current northern range. Taken together, these different approaches suggest that trees might be responding to climate change with latitudinal range shifts, but the evidence is indirect and not in clear agreement. The influence of global climate change on range boundaries could benefit from development of new techniques to exploit the FIA evidence at range boundaries across large spatial scales.

In this study, we develop a novel technique for examining the latitudinal difference between offspring and adults of trees at both northern and southern range limits across the eastern United States, and we evaluate the number of species showing evidence for range expansion or contraction. We then compare these patterns with changes in 20th century temperature and precipitation, as well as functional traits expected to influence migration potential, specifically, seed size and dispersal properties. We test the widely held hypothesis that trees could track climate change by migration, showing differences between offspring and adult range limits (Neubert & Caswell, 2000; Lewis *et al.*, 2006), with the largest differences between offspring and adult extent being in areas where climate change has been most pronounced. There has been substantial effort in recent years to determine whether small-seeded species have

greater migration potential than large-seeded species (reviewed by Angert *et al.*, 2011). Four mutually exclusive and all-inclusive hypotheses are summarized by a four-quadrant diagram of range shifts at northern and southern frontiers (Fig. 2):

- 1 Overall range expansion: if a species is expanding at northern and southern frontiers, then offspring will have greater latitudinal extent than adults at both range limits (I in Fig. 2), as would occur if the environment is changing in ways that benefit the species in both areas.
- 2 Northward range shift: if a species is expanding at northern frontiers and retreating from southern frontiers, then offspring will extend north of adults at the northern range limit, and adults will extend south of offspring at the southern range limit (II in Fig. 2). This is the expected response to climate warming.
- 3 Overall range contraction: if a species is contracting from northern and southern frontiers, then offspring will have less latitudinal extent than adults at both

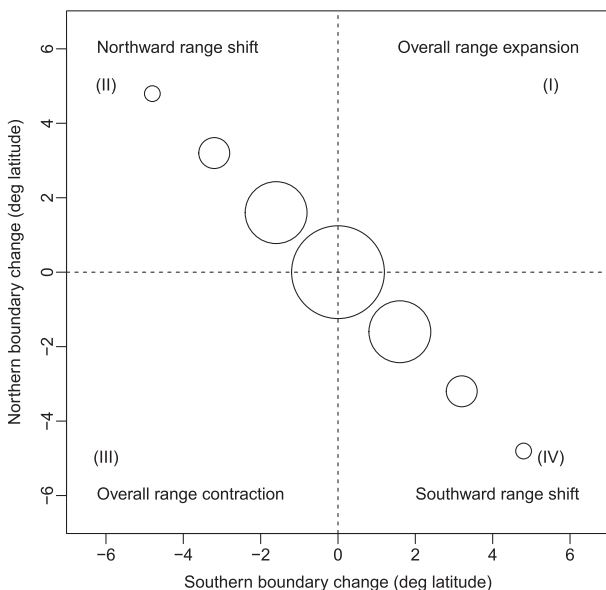


Fig. 2 Four-quadrant schematic diagram of species having greater latitudinal extent for offspring than adults (I) both at northern and southern range limits, suggesting overall range expansion; (II) at northern but not southern range limits, suggesting northward range shift; (III) at neither northern nor southern range limits, suggesting overall range contraction; (IV) at southern but not northern range limits, suggesting southward range shift. In both horizontal and vertical axes, positive value means the tendency of range expansion, while negative value means the tendency of range contraction. Each circle is a species drawn with an arbitrary center, and the diameter is proportional to the seed size, as we expect small-seeded species tend to track climate change, showing northward (II) or southward (IV) range shift, while large-seeded species tend to have no change in range limits (near the origin).

range limits (III in Fig. 2), as would occur if the environment is changing in ways that harm the species or benefit its competitors in both areas.

- 4 Southward range shift: if a species is retreating from northern frontiers and expanding at southern frontiers, then adults will extend north of offspring at the northern range limit, and offspring will extend south of adults at the southern range limit (IV in Fig. 2).

We further evaluate the hypotheses that species with greater dispersal ability might spread more rapidly under climate change (Clark *et al.*, 2001; Angert *et al.*, 2011; Nathan *et al.*, 2011), and small-seeded species might show greater northward (II) or southward (IV) range shifts than large-seeded species (near the origin in Fig. 2).

While providing perhaps the most direct evidence for subcontinental scale range shifts for a large number of species, it is important to recognize limitations of FIA data, and the fact that no analysis can definitively determine migration patterns. We compare results of our analysis with other empirical and modeling studies, recognizing how sampling designs, successional trends, and source-sink dynamics can influence study of adult and offspring distributions.

Materials and methods

Our analysis concerns the latitudinal extent of offspring and adults from FIA data distributed longitudinally across the eastern United States, combined with 20th century temperature and precipitation change, as well as seed size and dispersal properties. A population that is migrating north in response to warming is expected to have offspring extending to higher latitudes than adults in regions that have warmed over the last century, but not in regions where climate has remained essentially constant. This is the signature of an expanding population front, as predicted by all models of migration (Okubo, 1980; Neubert & Caswell, 2000; Clark *et al.*, 2001; Lewis *et al.*, 2006). Likewise, a population retreating from a warming southern boundary is expected to have adults south of the southern extent of new recruitment by offspring. This is the basic assumption behind recent analyses of Woodall *et al.* (2009), but analyzed in our study at the range boundaries themselves. Lenoir *et al.* (2009) used this assumption when comparing seedling and adult distributions to detect altitudinal range shifts. In the following sections, we summarize our methods, including the FIA sampling design, the longitudinal band analysis (LBA) to detect range shifts, and comparisons of range shifts, climate change, and functional traits.

Forest inventory data

The FIA program is the primary source for information on the extent, condition, status, and trends of forest resources in the

United States (Smith *et al.*, 2009). FIA applies a nationally consistent sampling protocol covering all ownerships across the United States, resulting in national sample intensity of one plot per 2428 ha (Bechtold & Patterson, 2005) within forest lands (i.e. homogenous forest cover classes to reduce estimate uncertainty). Sample intensities vary somewhat by state; however, because the inventory is systematic, varying sample intensities do not bias assessment of tree species locations (McRoberts *et al.*, 2005). Forested land is defined to be >0.4 ha in area and 36.6 m in width, with at least 10% tree cover. FIA inventory plots in forested conditions consist of four 7.2 m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (Bechtold & Patterson, 2005). All trees (standing live and dead) with a diameter at breast height (dbh) of at least 12.7 cm, are inventoried on forested subplots. Within each subplot, a 2.07 m radius microplot offset 3.66 m from subplot center is established where only live trees with a dbh between 2.5 and 12.7 cm are inventoried. Within each microplot, all live tree seedlings are tallied according to species. Conifer seedlings must be at least 15.2 cm in height with a root collar diameter <2.5 cm. Hardwood seedlings must be at least 30.5 cm in height with a root collar diameter <2.5 cm. Inherent in any large-scale forest inventory, there is measurement error associated with tree species identification. The FIA program has a quality assessment and quality control program associated with the national inventory that monitors measurement error and continuously seeks to reduce said errors (Pollard *et al.*, 2006; USDA Forest Service, 2011). Nationally, FIA field crews have attained at least 95% repeatability of tree species identification with nearly 9% of all inventory plot measurements remeasured for this repeatability assessment (ca. 2010).

In this analysis, FIA data were extracted from annual inventories (1999–2008) in 31 eastern states for a total of 43 334 inventory plots from FIADB version 4.0 on 16 March 2010 (available online <http://fia.fs.fed.us/>; Fig. 3). Because we focus on range limits, we used Little's digitized geographic range maps (USGS, 1999) to restrict analysis to the 92 species having their entire geographic range within the eastern United States (Table S1 in Supporting Information includes the complete species list). To compare species in different life stages (offspring vs. adult), we followed the FIA definition, dividing the data into two types of subgroups, (i) seedling (dbh < 2.5 cm) vs. tree (dbh > 2.5 cm), and (ii) sapling (2.5 cm < dbh < 12.7 cm) vs. large tree (dbh > 12.7 cm). In other words, we conducted two offspring vs. adult comparisons: seedling vs. tree, and sapling vs. large tree.

Longitudinal band analysis

We developed a LBA for comparing occurrences of offspring vs. adults across the full northern and southern frontiers for each species. To allow for variation in migration response along range limits, we stratified the 43 334 FIA plots into longitudinal bands 1° wide, from 98° to 68°W spanning the geographic extent of the eastern United States (Fig. 3). For each longitudinal band, we determined the 5th and 95th percentiles of latitudinal occurrence for all species for each of the life

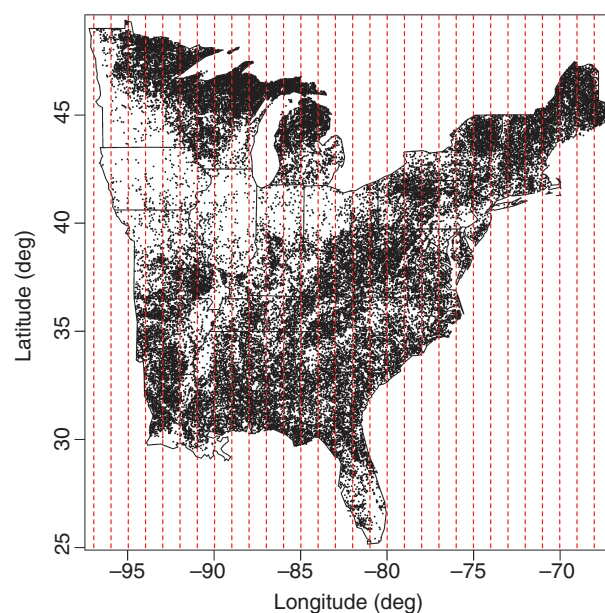


Fig. 3 Approximate Forest Inventory and Analysis plot locations (black points) and one degree longitudinal study bands (red dashed lines) in the eastern United States.

stages (seedling vs. tree, and sapling vs. large tree). In other words, 5% of the occurrences are at lower latitudes than the 5th percentile and at higher latitudes than the 95th percentile. The distributions of these percentiles across longitudinal bands were compared between stages to evaluate the assumption that offspring distributions extend to higher or lower latitudes than adults. We calculated the difference for longitudinal pairs of offspring and adults, yielding latitudinal difference distributions (LDD) at northern and southern boundaries for each species. For the x th latitudinal percentile,

$$\text{LDD}_{j,x} = q_{j,x}^{(\text{offspring})} - q_{j,x}^{(\text{adult})}, \quad (1)$$

where $q_{j,x}$ is the latitude corresponding to percentile x in longitudinal band j . At a northern frontier, positive $\text{LDD}_{j,x}$ is consistent with northern expansion, because it implies that offspring extend further north than adults. At a southern frontier, positive $\text{LDD}_{j,x}$ is consistent with northward retreat (southern contraction). The mean of LDD at a range boundary (north or south) summarizes the mean latitudinal difference between small and large size classes. For each species, we summarized two mean LDD values, one at northern and one at southern frontiers.

With this explanation of the LBA method, underlying motivation is straightforward. Our analysis of offspring and adult latitudinal extents is fundamentally an examination of distributional extremes. The extreme value of a distribution has no statistical confidence assigned to it, because it is observed once. Likewise, a comparison of locations for the extreme offspring latitude with the extreme adult latitude has no statistical uncertainty associated with it. However, by comparing these extreme events from a number of longitudinal bands

(i.e. the LDDs of Eqn 1) we introduce replication and the potential to evaluate the relationship between offspring and adults along their range margins across areas that have experienced different degrees of 20th century warming (Fig. 1). It further introduces the potential for modeling, as LDDs may depend on the degree of climate change or other variables associated with each band (next section). To evaluate sensitivity to a specific percentile, we repeated the analysis not only for the 5th and 95th percentiles of latitudes, but also for north and south extremes (the 0th and 100th percentiles), and the 10th and 90th percentiles. The sensitivity to discretizing longitude was assessed by repeating the analysis at 0.5°, 1°, and 2° wide longitudinal bands.

Climate change and functional trait data

To determine if the tendency to expand or contract is related to the degree of climate change in a region, we compared the mean of LDD with 20th century climate change from the Climate Research Unit (CRU) high resolution climate data, version 2.1 (Mitchell & Jones, 2005). Based on more than seven sources of meteorological station records, the CRU data are gridded with a spatial resolution of 0.5° × 0.5°, and temporal resolution of 10 decades (1900–2000). Analysis was completed for the two most commonly used climate variables, mean annual temperature and mean annual precipitation. We first calculated 20th century linear trends (slopes) for temperature and precipitation change for each longitudinal band location $q_{j,x}$ in Eqn (1). For each species, we determined the correlation between LDD and trends in temperature or precipitation,

$$\begin{aligned}\rho_T &= \text{cor}(\text{LDD}_{j,x}, \Delta T(q_{j,x})) \\ \rho_P &= \text{cor}(\text{LDD}_{j,x}, \Delta P(q_{j,x}))\end{aligned}\quad (2)$$

where ΔT is temperature change and ΔP is precipitation change for offspring locations ($q_{j,x}$). At the northern frontier, positive ρ_T (ρ_P) is evidence that range expansion occurs where temperature (precipitation) increase has been greatest. At the southern frontier, positive ρ_T (ρ_P) is evidence that range contraction occurs where temperature (precipitation) increase has been greatest. We used correlation for these comparisons, because there was no evidence of nonlinearity.

The correlations between climate change and spread can be made more transparent by placing them on the same dimensions, translating climate change over time to climate velocity (Loarie *et al.*, 2009). Over much of the eastern US canopy forests date from the early 20th century. Seedlings in our data sets established approximately a century later. The velocity of climate change with latitude y is obtained from rate of change and the climate gradient (Fig. 1b),

$$\frac{dy}{dt} = \frac{dT}{dt} / \frac{dT}{dy}\quad (3)$$

We compared the mean LDD value for each species with the velocity of climate change at its range limit.

To determine whether or not dispersal characteristics can explain the tendency to expand or contract, as being hypothesized in recent studies (Angert *et al.*, 2011; Nathan *et al.*, 2011), we compared mean LDD from the LBA method with plant

functional trait data from the USDA Natural Resources Conservation Service's PLANTS database (USDA NRCS, 2010). We compared range expansion or contraction potential with two functional traits, (i) seed size, which is the reciprocal of seed per pound in an average seed lot, and (ii) seed spread rate, which is an ordinal variable (slow, moderate, or rapid) intended to describe the capability to spread compared with other species with the same growth habit (USDA NRCS, 2010).

All analyses were performed in R version 2.12.1 (R Development Core Team, 2010).

Results

Use of LBA to identify relationships consistent with range shifts is illustrated by example species, followed by summaries for the entire dataset. LDDs from the seedling vs. tree comparison (Eqn 1) show contrasting patterns for two species at northern range limits (Fig. 4): expansion for *Ilex opaca* (American holly) and contraction for *Diospyros virginiana* (common persimmon). For *Ilex opaca*, seedlings (red) occur well north of the range for trees (blue, Fig. 4a and b). If the northern extent of seedlings represents a sink population, then seeds are dispersed to and germinate at these latitudes, but do not survive to adulthood. This would occur, for example, if temperatures were too low to support populations of the species (e.g. bird-dispersed seeds germinate but do not survive). An alternative explanation is that the range is expanding. It is unlikely that seedlings could long survive winter temperatures too low to support adult trees. Note that this is not one of the horticultural species of *Ilex* typically sold in nurseries. It is thus possible that *Ilex opaca* has expanded its range to take advantage of warming climate in the upper Midwest (Fig. 1a).

A contrasting pattern was found for *Diospyros virginiana* (Fig. 4c and d). Seedlings (red) do not extend as far north as trees (blue), as would be expected for a range contraction. This pattern is apparent across the full northern frontier, from Missouri to Delaware. Current information does not identify whether lack of *Diospyros* seedlings at the northern frontier results from recent climate change, land use change, or other factors. These direct comparisons were extended to all the study's 92 species.

Across all species, patterns consistent with range contraction at both northern and southern boundaries predominate. This pattern is especially pronounced for the seedling vs. tree comparison, but it is also evident for the sapling vs. large tree comparison. The quadrant diagram (Fig. 5) shows species having greater latitudinal extent for seedlings than trees at both northern and southern range limits (I), at northern but not southern range limits (II), at neither northern nor southern range

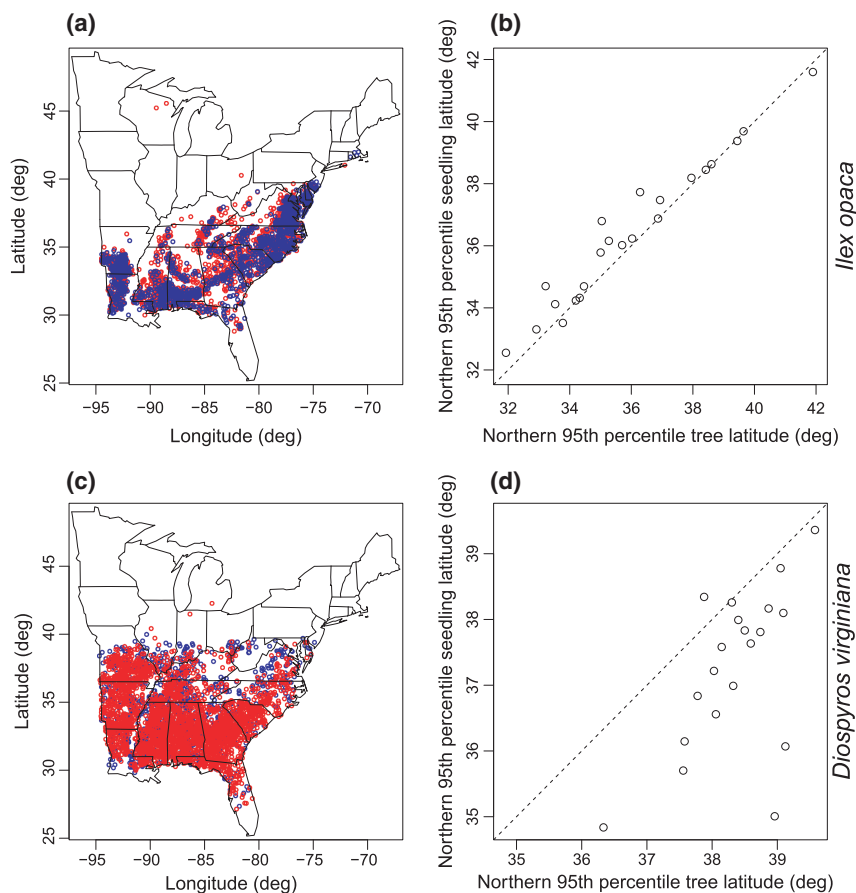


Fig. 4 Seedling and tree range difference at the northern range limit of two example species, *Ilex opaca* (a, b) and *Diospyros virginiana* (c, d). (a) and (c) All plot locations of seedlings (red) and trees (blue). (b) and (d) Differences between seedling and tree 95th percentile latitudes in each longitudinal band. Points above the 1 : 1 line in *Ilex opaca* (b) indicate longitudinal bands where seedlings are located further north than trees, as would be expected if there is expansion at the northern range limit. Points below the 1 : 1 line in *Diospyros virginiana* (d) indicate longitudinal bands where trees occur further north than seedlings, as would be expected if there is contraction at the northern range limit. For clarity in the figure, seedlings (red) are overlaid with trees (blue) in *Ilex opaca* (a), whereas trees (blue) are overlaid with seedlings (red) in *Diospyros virginiana* (c).

limits (III), or at southern but not northern range limits (IV). The largest proportion of species has lower seedling latitudinal extent than trees at northern boundaries, and higher latitudinal extent than trees at southern boundaries – in other words, contraction at both boundaries. In the seedling vs. tree comparison, 54 out of 92 species (58.7%) show this pattern consistent with range contraction (III in Fig. 5). In the sapling vs. large tree comparison, 60 out of 92 (65.2%) species show this pattern (Fig. S1).

The other three cases contain fewer species (Fig. 5). In the seedling vs. tree comparison, 19 out of 92 species (20.7%) are consistent with range expansion in the north and contraction in the south (II in Fig. 5), whereas 15 out of 92 species (16.3%) are consistent with range expansion in the south and contraction in the north (IV in Fig. 5). In other words, slightly more species are consistent with a northward range shift (II in

Fig. 2) than with a southward range shift (IV in Fig. 2). In the sapling vs. large tree comparison, 12 out of 92 species (13%) show the pattern consistent with northward range shift, and 16 out of 92 species (17.4%) show the pattern consistent with southward range shift (Fig. S1).

Evidence consistent with expansion at both northern and southern limits is least well represented. Only four out of 92 species (4.3%) have lower 5th and higher 95th percentiles for seedlings than for trees (I in Fig. 5). The same percentage (4.3%), albeit a different set of four species, was obtained for comparisons of saplings vs. large trees (Fig. S1).

In sum, our results suggest a pattern consistent with the following ranking in terms of number of species: overall range contraction > northward or southward range shift > overall range expansion. For species having comparisons consistent with range contraction, the magnitude of the latitude shift is greater for the

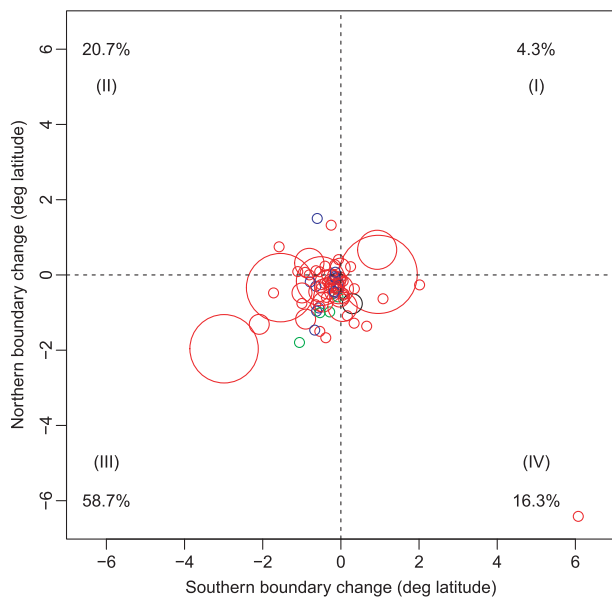


Fig. 5 Latitudinal range change at southern (5th percentile) and northern (95th percentile) boundaries from the seedling vs. tree comparison. Four quadrats bear the same meaning as Fig. 2. Each circle is a species, scaled to its seed size, with the color of seed spread rate (red – slow, blue – moderate, green – rapid, black – no data) from PLANTS database (USDA NRCS, 2010). Percentages in the four quadrats summarize the proportion of species falling into the corresponding cases. Detailed latitudinal differences for all species are shown in Table S1.

seedling vs. tree than for the sapling vs. large tree comparisons. This result is robust, being consistent across 0.5°, 1°, and 2° longitudinal bandwidths and for percentiles 0th and 100th (maximum and minimum), 5th and 95th, and 10th and 90th. Across all 92 species the average range contraction was 0.37° (42 km) at northern boundary, and 0.26° (29 km) at southern boundary for the seedling vs. tree comparison.

The relationship between LDD and 20th century climate trends (Eqn 2) shows a similar pattern for both offspring vs. adult comparisons. For the seedling vs. tree comparison, 62.2% of species have positive ρ_T at northern limits, implying that ranges expanded most where temperature increase was greatest, and 44.4% have positive ρ_T at southern limits, implying that ranges contracted most where temperature increase was greatest. For the sapling vs. large tree comparison, these percentages are 61.1% and 44.4%, respectively (Table S2). There was no relationship between expansion patterns and precipitation change.

Contrary to the common assumption that migration potential is determined by seed characteristics, the LBA shows no relationship between range expansion or contraction and functional traits (i.e. seed size and seed spread rate). Most species classified as large seeded

and slow spread potential fall in the category of overall reduction in range size (circle sizes and colors in III of Fig. 5). Small-seeded species occur in all four categories, including overall range expansion or contraction and northward or southward range shift.

Discussion

Despite caveats that must apply to any analysis of forest plot data, evidence for climate-driven migration is essentially absent in this large analysis that considers distributions of offspring and adults across geographic gradients in climate change. Patterns are more consistent with range contraction of eastern US tree species than with northward migration. The results based on the direct comparisons of seedlings and trees at range limits do not inspire confidence that tree populations are tracking contemporary climate change. If the seedling class integrates up to a decade or more of climate history (seedling banks range up to several decades in age), and trees integrate up to a century, then northward migration in response to warming would result in seedlings displaced to the north of mature individuals of the same species. The greater the warming, the greater the expected displacement. Likewise, retreat from southern boundaries is expected where warming has reduced the competitive advantage previously enjoyed in a cooler climate. This assumption is the basis for a large number of analyses of climate and migration (Okubo, 1980; Neubert & Caswell, 2000; Clark *et al.*, 2001; Lewis *et al.*, 2006), but massive inventories of both seedlings and adults have not been analyzed in this way. The majority of species in our analysis shows a pattern consistent with range contraction at both northern and southern range limits. Some species are consistent with the expected but much debated poleward range shift (Parmesan & Yohe, 2003; Chen *et al.*, 2011). Range expansion at both northern and southern frontiers is observed for the smallest proportion of species among the four possible cases (Fig. 5). Due to FIA's sampling intensity, this study provides perhaps the most robust assessment of tree migration potential. Moreover, failure to find evidence that seedlings extend as far north as adults and absence of a relationship to local climate changes suggests cause for concern, given the temperature trends already underway during the 20th century (Fig. 1). Before discussing implications we consider some of the important caveats of an analysis like this.

Sources of uncertainty, limitations, and caveats

The factors that could influence patterns we quantified here include (i) sampling effects and data limitations,

(ii) successional changes, and (iii) sink populations beyond the range where the population is viable. The caveats that follow could apply to any of the many recent studies reporting evidence of range shifts, but are rarely considered.

Due to the inherent limits of FIA data (Woodall *et al.*, 2009), the comparison of the presence/absence data could be biased if there is a higher probability of finding offspring than adults or vice versa. Our analysis that includes not only seedlings and trees but also saplings and large trees (see Forest inventory data), reduces this risk – our results are similar for both comparisons. We further relied on the fact that the sample size is massive. A range of different stand ages will contribute variation to patterns we analyze, but not necessarily overwhelm them. The large sample sizes for both seedlings and trees can help to overcome bias toward particular life stages. However, the fact that sample sizes are substantial does not insure that plot design can be ignored. The 54 m² seedling sample area is still much smaller than the 673 m² tree plot (Bechtold & Patterson, 2005), but seedlings can occur at much higher densities.

It is important to consider whether or not there are nonclimatic obstacles to migration. Species faced with physiographic barriers to migration (e.g. close to coastlines, parent material heterogeneity, and mountains) should be interpreted carefully, because they may be more limited by geography than climate (Bakkenes *et al.*, 2002; Clark *et al.*, 2011). Species with range limits close to boundaries of the sample region may bias results. Our analysis includes few northern species, because they may extend their ranges into Canada. Careful attention to caveats yields conclusions robust to the widths of longitudinal bands (0.5°, 1°, or 2°), or the latitudinal percentiles (0th and 100th, 5th and 95th, or 10th and 90th).

The possibility that successional change and sink populations could be mistaken for range expansion has to be considered as an alternative explanation. Seedlings can expand in areas where trees are rare or absent as successional species reinvade or recruitment declines with stand development. Successional changes could affect our results in at least two ways. Light demanding species can be common in forest overstories where recruitment of the same species in shaded understories is rare. Alternatively, early successional stands could support recruitment of light-demanding species at sites where few individuals have reached the adult stage. In both cases, a biased representation of particular stand ages could affect results in ways that are difficult to anticipate. There is also potential for interactions. Presence of seedlings following recovery from disturbance would be especially confusing if there were a strong

correlation between recent disturbance and climate change. Although there is substantial heterogeneity in land use across the eastern United States, much of the entire region is dominated by 20th century afforestation. We expect that land cover has contributed to patterns we report, but we are unaware of systematic geographic trends could explain our results. We examined LDD by shade-tolerance classes and did not find a tendency for shade tolerant species to be expanding more than shade intolerant species.

Heterogeneous habitats may create sink populations for seedlings, outside the range of adult trees being supported by continual seed inputs (Pulliam, 1988). While possible in principle, the bulk of seed for most species falls close to adults and long-distance dispersed seed faces competition from copious seed produced by local plants. Moreover, seedlings may be more sensitive to climate variation than adults (Grubb, 1977; Harper, 1977). Thus, although we cannot ignore the possibility of sink populations, we assume that such effects would not dominate the broad geographic patterns we report. If there are sink populations, our method would mistake them for range expansion. In other words, sink populations could not be an explanation for failure to find the range shifts predicted by climate change.

Comparison with other FIA studies

By directly analyzing tree and seedling distributions at range boundaries, our analysis of latitudinal extent addresses limitations of previous studies. Previous analyses using FIA data suggest that both seedlings and trees have higher abundance in the northern latitudes than the southern latitudes within their geographic ranges, which could be interpreted as a signature of northward tree migration (Woodall *et al.*, 2009; Murphy *et al.*, 2010), but could also represent responses to a whole range of variables. Abundance and occupancy patterns (Murphy *et al.*, 2006, 2010) might not provide evidence of range shifts, because geographic range is defined by boundaries, not abundance or occupancy within boundaries (Cox & Moore, 2010, pp. 204, 38–40). Despite different approaches and assumptions, Murphy *et al.* (2010) suggested that the most common response could be range contraction in the south and limited expansion in the north, leading to a possible overall range size reduction.

Woodall *et al.*'s (2009) comparison of mean latitudes for seedlings and trees could likewise miss dynamics at population frontiers. Range shifts in response to climate change are expected to occur at the leading (northern) or trailing (southern) edges, with the changes in mean latitude being sensitive to other factors. Woodall *et al.* (2009) also examined maximum and minimum

latitudes. Still, Woodall *et al.*'s (2009) results are consistent with range contraction in this analysis. At the southern range limits of northern species, 12 out of 15 species show greater minimum latitude for seedlings. At the northern range limits of southern species, 10 out of 15 species show greater maximum latitude for trees (table 2 in Woodall *et al.*, 2009). Many of the 40 species they studied have ranges that are not contained within the eastern United States (especially for northern species) so dynamics at northern range limits are unknown (Woodall *et al.*, 2010). To minimize these effects on the analysis, we included all species having entire ranges within the study area (see Forest inventory data).

Climate change has already been large (Fig. 1) – we do not have to wait decades to evaluate whether or not climate change is affecting migration. Our finding that the majority of species may experience range contraction at both northern and southern limits does not square with the expectation that species will migrate rapidly north in response to climate change. Many models predict rapid tree migration (Clark, 1998; McKenney *et al.*, 2007), but some do not (Clark *et al.*, 2001, 2003; Nathan *et al.*, 2011). Iverson *et al.*'s (2008) habitat distribution model predicts that 61–68 of 134 species will increase at least 10%, and 50–58 species will lose at least 10% of their area-weighted importance value. Some of these predictions are consistent with our comparisons of offspring and adults (e.g. *Acer nigrum* and *Juglans cinerea*). On the other hand, Iverson *et al.* (2004) predicted that migration potential at northern range limit for *Diospyros virginiana*, *Liquidambar styraciflua*, *Oxydendrum arboreum*, *Pinus taeda*, and *Quercus falcata* would be limited to within 20 km of the area currently occupied. Our analysis of these species all show contraction at northern limits, in general agreement with Iverson *et al.*'s (2004) expectation that migration potential is limited.

Relationship with climate change and functional traits

The fact that most species appear to be contracting at both northern and southern range limits is not consistent with the expectation that temperature change during the 20th century should allow for rapid spread (Fig. 6). At the northern frontier, in particular, calculations using climate observations suggest that species may need to migrate hundreds of km northward to track warming temperatures in the eastern United States (Fig. 1b). However, making the reasonable assumption that the LDD observed in this study represents dynamics on a 100 year scale, our results suggest that most species have not tracked 20th century temperature change (below the 1 : 1 line in Fig. 6).

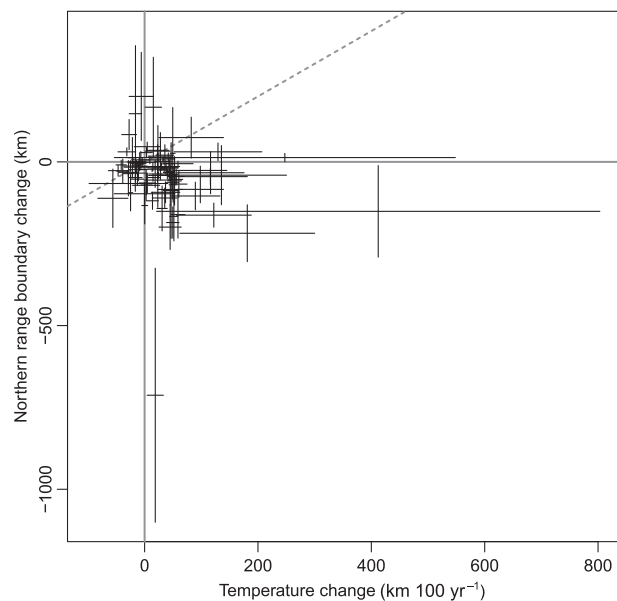


Fig. 6 Temperature change during the 20th century (calculated as Fig. 1b) in comparison with latitudinal difference between seedlings and trees at northern range boundary (calculated in longitudinal band analysis). Each crosshair is a species with mean \pm standard error. Positive temperature change means temperature distribution moving to the north, while negative means moving to the south. Positive northern range boundary change means species is consistent with expansion at the northern range limit, while negative means contraction. Species above the 1 : 1 line (gray dashed) suggest tracking temperature change.

Our results should not be interpreted to say that climate has no effect on species range limits. Sixty-two percent of species at northern boundaries and 44% at southern boundaries are positively correlated with temperature change (Table S2). There is no relationship with precipitation change. Many variables affecting these boundaries could preclude the large geographic shifts needed to track climate. For example, adults might be controlled by annual mean temperature and precipitation, but offspring might be driven by temperature variabilities and extremes, growing season temperature or drought, spring precipitation, first-last day of frost, and so forth. Soils, disturbance, and land use change could provide a backdrop for species interactions, including competition, herbivore, and disease. If habitat destruction, degradation, and fragmentation resulted from land use change are proximate factors limiting response to climate (Hof *et al.*, 2011), vulnerability could shift from human effects in the near term to climate change in the near future.

Clark *et al.* (2003) emphasized that species range shifts cannot be predicted from seed dispersal characteristics and life history. The empirical evidence presented here should not be misinterpreted to say that

seed characteristics have no impact. This study shows that most large-seeded species have patterns consistent with overall range contraction at both northern and southern range limits (Fig. 5), a pattern that is suggestive of an effect, but different from the expected capacity to track warming at northern range limits. Like us, the meta-analysis of Angert *et al.* (2011) showed that seed mass and seed dispersal mode have low explanatory power for range shifts of Swiss alpine plants. Crimmins *et al.* (2011) found that altitudinal range shifts of California plant species are unrelated to life-form, physiognomy, dispersal mechanism, and fire adaptation. Such studies do not establish that seed traits are unimportant, because they are comparisons across rather than within species. Seed traits could have an impact on spread of many species without emerging as 'significant' predictors of spread across species. The result that species-level traits do not correlate with migration potential suggests that use of seed size as an indicator of which species may track climate could be of limited utility.

Slow migration potential from models, experiments, and observational data

Model predictions that tree responses to climate change would be slow and unpredictable (Clark *et al.*, 2003) motivated an extensive seedling study to evaluate performance of residents and potential invaders (Ibanez *et al.*, 2008, 2009). Invasion of new regions means that rare seeds traveling long-distances face competition from overwhelming numbers of locally produced seed. To overcome these odds, rare dispersers require local microsites where they are clearly superior to residents (Clark *et al.*, 2003), or locally disturbed sites, where local seed rain from potential competitors is low (Fastie, 1995). Models that make some effort to incorporate the many sources of uncertainty do not predict the rapid spread that comes from simple projection of dispersal kernels (Clark *et al.*, 2001, 2003). Fourteen thousand seedlings of residents and potential invaders were planted and followed in competition for light and soil moisture, in gaps and in the forest understory, from southeastern Piedmont to northern hardwoods (Ibanez *et al.*, 2008, 2009). Potential invaders consisted of species from warmer latitudes or elevations, likely to migrate north in response to contemporary climate change (Fig. 1). Results showed no advantage to potential invaders, certainly not the dominance needed if they were to overcome the numerical disadvantages required for rapid spread. Results of widespread seedling experiments on invasion (Ibanez *et al.*, 2008, 2009) coupled with the FIA record of offspring-adult comparisons (this analysis) would appear to support model

results that predict migration rates far below those required to track contemporary climate change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Latitudinal range change at southern (5th percentile) and northern (95th percentile) boundaries from the sapling vs. large tree comparison.

Table S1. Mean latitudinal range expansion (positive) or contraction (negative) at the northern and southern boundaries for the seedling vs. tree and sapling vs. large tree comparisons (species mean of LDD in Eqn 1).

Table S2. Correlation between species range shift and 20th century temperature change at the northern and southern boundaries for the seedling vs. tree and sapling vs. large tree comparisons (ρ_T in Eqn 2).

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