

Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits

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Abstract

Rising global temperatures are suggested to be drivers of shifts in tree species ranges. The resulting changes in community composition may negatively impact forest ecosystem function. However, long-term shifts in tree species ranges remain poorly documented. We test for shifts in the northern range limits of 16 temperate tree species in Quebec, Canada, using forest inventory data spanning three decades, 15° of longitude and 7° of latitude. Range shifts were correlated with climate warming and dispersal traits to understand potential mechanisms underlying changes. Shifts were calculated as the change in the 95th percentile of latitudinal occurrence between two inventory periods (1970–1978, 2000–2012) and for two life stages: saplings and adults. We also examined sapling and adult range offsets within each inventory, and changes in the offset through time. Tree species ranges shifted predominantly northward, although species responses varied. As expected shifts were greater for tree saplings, 0.34 km yr⁻¹, than for adults, 0.13 km yr⁻¹. Range limits were generally further north for adults compared to saplings, but the difference diminished through time, consistent with patterns observed for range shifts within each life stage. This suggests caution should be exercised when interpreting geographic range offsets between life stages as evidence of range shifts in the absence of temporal data. Species latitudinal velocities were on average <50% of the velocity required to equal the spatial velocity of climate change and were mostly unrelated to dispersal traits. Finally, our results add to the body of evidence suggesting tree species are mostly limited in their capacity to track climate warming, supporting concerns that warming will negatively impact the functioning of forest ecosystems.

Keywords: climate change, eastern North America, forest inventory plots, global warming, range shifts, temperate and boreal forests, tree migration

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Introduction

Quantifying how species have responded to climate warming in recent decades is critical for understanding potential future states of ecosystems (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Chen *et al.*, 2011). Large temperature increases affecting forests at northern latitudes are raising concerns over how forest biodiversity and ecosystem functions will respond (Pedlar *et al.*, 2012; Isaac-Renton *et al.*, 2014; Trumbore *et al.*, 2015). Tree species adaptation to warmer temperatures, over longer time-scales, is expected to involve shifts in ranges, that is migration. One commonly applied approach to gain insight into how

shifts in species ranges will likely alter forest biodiversity, species distribution models, forecast tree species range responses to projected changes in climate (Iverson & Prasad, 1998; Hamann & Wang, 2006; Iverson & Mckenzie, 2013). Temperate and boreal forests are forecast to undergo dramatic compositional shifts in response to climate warming (Iverson & Prasad, 1998). Testing whether realized shifts in tree ranges match forecasts is critical, but realized latitudinal range shifts remain poorly understood, primarily due to the challenge of quantifying species occurrence at large geographic scales (Zhu *et al.*, 2012; Woodall *et al.*, 2013; Boisvert-Marsh *et al.*, 2014; Fisichelli *et al.*, 2014).

Forest inventory plot networks have proven essential to providing the large-scale species occurrence data sets needed to test how tree species ranges have responded to recent warming (Woodall *et al.*, 2009,

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2013; Zhu *et al.*, 2012, 2014). In one of the first studies probing empirical evidence for latitudinal shifts in tree species ranges, Woodall *et al.* (2009) analysed the national forest inventory plot data for the eastern United States and found that the mean latitude of seedlings was significantly farther north (>20 km) for the northern study species than the mean latitude of tree biomass – a potential signature of northward range shifts. In a subsequent study, Zhu *et al.* (2012) argued that because ranges for many of the northern species in the study of Woodall *et al.* (2009) extend north of the US–Canada border, results for dynamics at range limits may be different than those for mean latitudes. Thus, Zhu *et al.* (2012) presented a method of inference for potential changes in range limits based on the geographic distributions of saplings and adult trees. For tree species expanding their range northward in response to warming at range limits, Zhu *et al.* (2012) argue that offspring should have a more northern latitudinal distribution than adults. Results of Zhu *et al.* (2012) as well as a recent study incorporating disturbance effects (Woodall *et al.*, 2013), suggest widespread failure of tree species in eastern United States to expand ranges northward.

Further north at the temperate–boreal transition in eastern Canada, warming is greater and in turn tree species ranges may have shifted in response. In a recent study, Boisvert-Marsh *et al.* (2014) provided novel results for latitudinal range shifts in eastern tree species, focusing on inventory plots in Quebec, Canada. Repeated measurements of forest inventory plots established in the 1970s permit novel analyses by extending the analysis of range limits developed by Zhu *et al.* (2012): range limits can be compared over decades and in addition whether adult–offspring offsets in geographic space reflect temporal changes in range limits can be tested (Boisvert-Marsh *et al.*, 2014; Malis *et al.*, 2016). However, like the earlier study of Woodall *et al.* (2009), analyses completed by Boisvert-Marsh *et al.* (2014) included many tree species with northern range limits that extend far beyond the area surveyed for the forest inventory, and thus, results may be more representative of central tendency than range limits (Zhu *et al.*, 2012).

Due to its location, spatial extent and temporal depth, the forest inventory of Quebec offers a unique opportunity to examine eastern tree species migration at the northern boundary of the temperate and boreal forests. In a previous study, Boisvert-Marsh *et al.* (2014) examined range shifts of Quebec tree species; however, only 6 of the 11 species studied have northern range limits within the Quebec forest plot network. Given the rarity of spatially expansive, long-term temporally replicated

forest inventory data sets, we revisit this data set and extend the analysis to 16 species. Furthermore, we aim to link quantification of range shifts with the underlying causes of success or failure to migrate by examining external drivers of change such as climate warming as well as species dispersal traits (Angert *et al.*, 2011; Chen *et al.*, 2011; Zhu *et al.*, 2012). The aim of this study was to test for evidence for range shifts of tree species and to determine whether there exists a correlation of these changes with warming and dispersal potential. We hypothesized that (i) tree species ranges are expanding northward, with greater changes for saplings than adults; (ii) the velocity of tree migration is less than the velocity of climate warming; and (iii) a correlation exists between the velocity of tree migration and their dispersal potential.

Materials and methods

Forest inventory plot data

The Quebec forest inventory plot network covers most of the forested areas of Quebec, exclusive of noncommercial, high-latitude and low-density forests in the north (Fig. 1; MRNFQ 2006). Since the 1970s, a total of 12 300 permanent sample plots have been established and measured by the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFPQ). In the first cycle of the inventory from 1970–1978, 7155 plots were established. To maximize the number of years covered between two measurements (to detect long-term changes), we selected plots that were measured in the first cycle of the inventory and subsequently also measured between 2000 and 2012. This yielded a total of 5719 plots with a mean of 32 years between sampling (Fig. 1, Fig. S1; Map tiles by Stamen Design, under CC BY 3.0).

Plots are circular with a radius of 11.28 m and an area of 400 m². Within each plot, trees larger than 9 cm in diameter at breast height (DBH, measured at 1.3 m height on the stem) are identified to species, measured and their vitality noted. In our analysis, we refer to these individuals larger than 9 cm as adults. Saplings are defined by three size categories with a combined span of 1 to 9 cm in diameter and were recorded within one subplot with a radius of 3.57 m (40 m²) that lies within the centre of the main plot. In this analysis, we use the smallest sapling size class, which ranges from 1 to 3 cm in diameter.

Criteria for inclusion of tree species in the range analysis

Our analysis focuses on 16 tree species that were selected based on: (i) a threshold for abundance and (ii) species northern range limits. Species represented by at least 1000 adult trees distributed over a minimum of 50 inventory plots in both inventory periods were included (Table S1). The threshold for species inclusion strikes a balance between having a sufficient number of individuals of a species represented in plots so that one can define the distribution and excluding less common

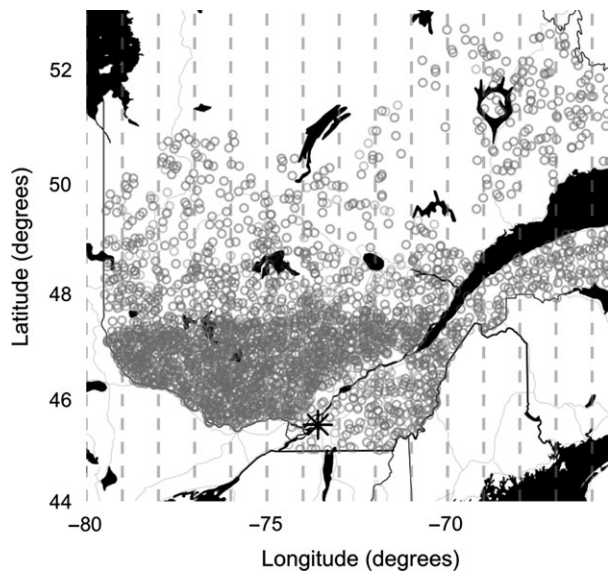


Fig. 1 Distribution of the 5719 Quebec forest inventory plots utilized in the current study that were measured in the first inventory cycle (1970–1978) and subsequently recently re-measured (2000–2012). Individual plots are represented by open grey circles. Solid black areas are water bodies, and the asterisk shows the location of the city of Montréal, Québec.

species that are not as well represented in the data. We argue here that including less common species is important to understanding threats of climate change to biodiversity.

To assess whether the northern range limit of a tree species could be quantified using the Quebec forest inventory data, we compared range maps for each species (USGS, 1999), with the northern extent of the forest inventory plot network. If the northern range limit was found to be much further north than the most northern inventory plots, it was not included in our analyses. This resulted in our exclusion of five species *B. papyrifera*, *P. glauca*, *P. mariana*, *A. balsamea*, *P. tremuloides* included in the analysis of Boisvert-Marsh *et al.* (2014) (Fig. S2). Accordingly, we included species whose northern range limit lie within the geographic extent of the forest inventory plot network (Fig. S3). In addition, we used a less stringent abundance threshold for the inclusion of a tree species than that of Boisvert-Marsh *et al.* (2014). Thus, our analysis contains novel results for 10 tree species: *Betula populifolia*, *Quercus rubra*, *Fraxinus americana*, *Fraxinus nigra*, *Ulmus americana*, *Populus grandidentata*, *Tilia americana*, *Picea rubens*, *Pinus strobus* and *Tsuga canadensis*. Finally, by including data from more recent inventories, the average number of years between plot sampling was increased to 32 years compared to 22 years reported in Boisvert-Marsh *et al.* (2014).

Quantifying evidence for range shifts

In the first part of the analysis, we examined whether northern range limits for 16 tree species changed between the first and recent inventory. Species ranges were examined in 1° wide longitudinal bands and were defined using the distribution of

the plot latitudes where each species occurs. Strictly defined, the range limit in each band is the maximum of the distribution; however, because the maximum (100th percentile) is sensitive to extreme values, we calculated the 95th percentile. Hereafter, we refer to this as the 95th percentile of latitudinal occurrence. Following Zhu *et al.* (2012), the latitudinal difference distributions (LDD) for each species at its northern distribution edge can be calculated as

$$\text{LDD}_j^{\text{life stage}} = q_j^{(2\text{nd time class})} - q_j^{(1\text{st time class})}$$

where for every 1° wide longitudinal band (j) the species' 95th percentile of latitudinal occurrence (q) in the 1st time class is subtracted from the species' 95th percentile of latitudinal occurrence in the 2nd time class, and where life stage is either adults, saplings, or adults and saplings combined. Positive mean LDD indicates a northward shift of the northern distribution edge.

As the location of saplings in relation to adults has previously been assumed to indicate range shifts (Zhu *et al.*, 2012), we also tested how differences between sapling and adult LDD's varied within and between inventories as follows:

$$\text{LDD}_j^{(1\text{st time class})} = q_j^{(\text{sapling 1st time class})} - q_j^{(\text{adults 1st time class})}$$

$$\text{LDD}_j^{(2\text{nd time class})} = q_j^{(\text{sapling 2nd time class})} - q_j^{(\text{adults 2nd time class})}$$

where in every 1° wide longitudinal band (j) the 95th percentile of latitudinal occurrence (q) of adult trees is subtracted from the 95th percentile of latitudinal occurrence of the offspring. Positive mean LDD indicates saplings being distributed further north than adult trees. As we expect offspring that extend further north or south than adult trees to be an indicator for northward or southward range shift, positive mean LDD for the 95th percentile would imply a range expansion at the northern distribution edge. To examine whether species LDD varied from east to west or exhibited other spatial patterns, we separated species range shifts into positive and negative and examined whether distinct trends with longitude were present.

To determine whether the definition of the range limit or the width of the latitudinal band influenced the results, the analysis was repeated with 90th and 99th percentiles and with bands 0.5° wide, but the results were qualitatively unaffected.

Relationships between range shifts, climate change and seed dispersal traits

To determine whether tree species range shifts were related to the degree of warming, we tested for a correlation between the mean LDD of tree species and the change in mean annual surface temperature between the two time classes. We focused on temperature because in previous work on tree species ranges just to the south of Quebec precipitation change was not influential (Zhu *et al.*, 2012). Surface temperature data covering 1961 to 2000 were obtained from the Climate Research

Unit (CRU) and used to calculate the linear temperature trends for each longitudinal band (Mitchell & Jones, 2005). We included data for 1961 to 1970 (prior to the onset of the inventory in 1970) to capture temperatures influencing saplings recorded in the first inventory. The correlation between mean LDD and temperature change for every species q in each growth stage x was calculated as follows:

$$\rho(T, \text{LDD})_{q,x} = \text{cor}(\Delta T_j, \text{LDD}_{q,x,j})$$

where ΔT is the temperature change between 1960 and 2000 within each longitudinal band (j). Relationships were linear and nonparametric methods (Spearman's or Kendall's tau) yielded similar results.

The velocity of temperature change is the velocity required for a species to move in order to maintain constant temperature conditions. We also examined the relationship between species range shifts over time (km yr^{-1}) and climate warming at range limits represented as the spatial velocity of temperature change in km yr^{-1} for the area under investigation and its surroundings (Loarie *et al.*, 2009).

$$\text{spatial velocity}[\text{km yr}^{-1}] = \frac{\text{temporal gradient}[\text{C yr}^{-1}]}{\text{spatial gradient}[\text{C km}^{-1}]}$$

The temporal gradient was calculated using the change in mean annual surface temperature between 1961 and 2000. To calculate the spatial gradient (C km^{-1}), we used the average maximum technique for a 3×3 raster cell neighbourhood with each cell having a side length of 0.5° and using the average annual temperature for the period 1961 to 2000. The method was modified to fit different cell widths at different latitudes (Loarie *et al.*, 2009). The spatial gradient was calculated in ARCGIS (version 10.3.1; Esri Deutschland GmbH) using weighted focal statistics. We calculated the correlation between mean LDD and 20th century temperature for species that were present in at least four longitudinal bands by taking into account the spatial velocity at the particular maximum latitudinal extent for each species and each longitudinal band.

To test whether dispersal traits were related to changes in species northern range limits (Angert *et al.*, 2011; Zhu *et al.*, 2012), we used data from the USDA Natural Resources Conservation Service's PLANTS database to compare mean LDD with two functional traits, seed size and seed spread rate (NRCS, 2010). Seed size was calculated as the reciprocal of seed per pound in an average seed lot and converted to grams per seed (NRCS, 2010). Seed spread rate is an ordinal variable (slow, moderate or rapid) that is intended to capture a species ability to spread relative to other species with the same growth habit (NRCS, 2010). Characteristics in the PLANTS database have been compiled from the scientific literature, grey literature, agency documents and the knowledge of plant specialists. Therefore, values for a trait such as seed spread rate should be thought of as approximations, given that they are not derived from precise measurements or experiments, but from field observations and estimates from the literature. Moderate and slow spread rates were both represented by seven species, and the rapid spread rate was only represented by two species (namely, *Betula populifolia* and *Ulmus americana*). We thus included these with the species with moderate

spread and refer to the combination as moderate-fast. All analyses were conducted in R version 3.2.2 (R Core Team 2015).

Results

Changes in northern range limits over three decades

LDD was positive for the majority of the species for both sapling and adult life stages, indicating a general pattern of northern shifts in tree species ranges (upper right quadrant; Fig. 2). For saplings, 13 of 16 species or 81% showed positive values for LDD. Results were similar for adults, with 10 of 16 species or 63% showing positive values for LDD (Fig. 2). LDD was generally larger for saplings than for adult trees: mean LDD for saplings across all species was 0.0967° (10.75 km), whereas it was 0.0387° (4.30 km) for adult trees. The largest positive LDD, 0.4074° (34.5 km), was observed for the sapling stage of *Tilia americana* (Fig. 2, Table S2). A large negative LDD, -0.4268° (-36.18 km), was observed for the adult stage of *Fraxinus americana*, which was also unique in that both saplings and adult life stages exhibited negative LDD (Fig. 2).

Mapping the distribution of positive and negative range shifts for saplings and adults, neither positive nor negative range shifts exhibited evidence of being substantially longitudinally biased for either saplings or adults (Fig. 3; Fig. S4). Also evident from the map showing changes within each longitudinal band was that positive shifts were more dominant for saplings (Fig. 3a, b) compared to adults (Fig. 3c, d). Few changes were observed between -69° and -65° where one finds the St. Lawrence River as well as limited coverage of the area immediately north of the St. Lawrence (Fig. 3, Fig. 1).

We found evidence that at both the beginning of the inventory in 1970 as well as three decades later (c. 2000–2012), range offsets predominated: adult tree species northern range limits were greater than saplings for nearly all species, resulting in generally negative values for sapling–adult range offsets. Mean LDD for adults vs. saplings across all species was -0.242° (27 km) in 1970, whereas it was -0.153° (17 km) in 2000–2012 (Fig. 4). For a large majority of tree species, the sapling–adult range offset decreased over time, although the change was quite small in a few cases (Fig. 4). For a few tree species, the sapling–adult offset increased with time (Fig. 4). In particular, *Betula populifolia* and *Ulmus americana* were characterized by large changes, which for *B. populifolia* was dominated by one longitudinal band (Fig. S5). However, in general, species responses described above were consistent across the range of longitudes within the study area (Fig. S5).

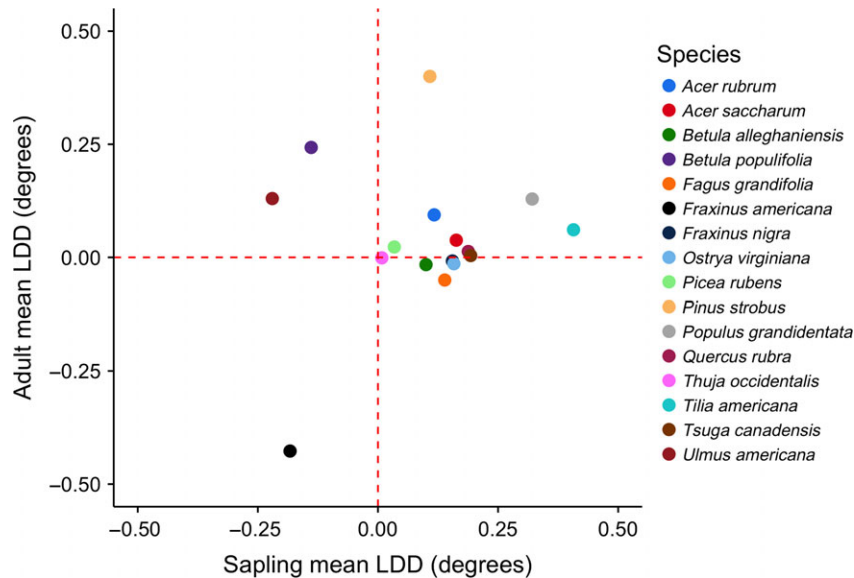


Fig. 2 Changes in temperate tree species northern range from 1970–2000 for saplings and adults. Range changes are described by the 95th percentile latitudinal distribution difference (LDD; units are decimal degrees). Means are calculated from values for 1° longitudinal bands covering the area shown in Fig. 1. Where shifts were prevalent (~46° latitude), a difference of 0.5° latitude corresponds to a distance of 55.6 km (see Fig. 3). [Colour figure can be viewed at [wileyonlinelibrary.com](#)]

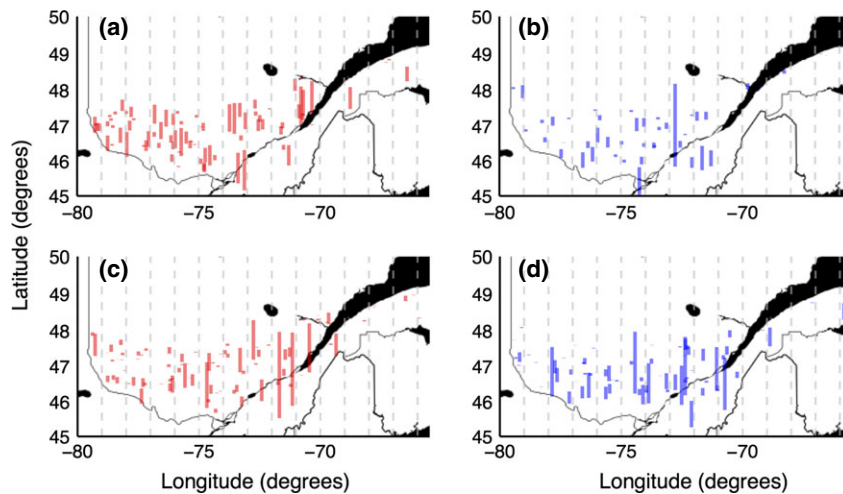


Fig. 3 Map of changes in temperate tree species ranges from ~1970 to 2000 for (a, b) saplings and (c, d) adult trees. Northern range shifts are shown in red (at left), and southern shifts in blue (at right). A line is drawn to represent the change for each tree species within a band, and the lines are jittered to reduce overlap. Range limits were assessed in 1° longitudinal bands (indicated by grey-dotted lines). [Colour figure can be viewed at [wileyonlinelibrary.com](#)]

Linking range shifts, climate warming and dispersal traits

Long-term climate warming at range limits and LDD were mostly weakly correlated, and not correlations were mostly not significant (Table 1). However, for some species such as *Acer rubrum* and *Acer saccharum* northern ranges expanded, LDD correlated with

climate warming, and sapling LDD and its correlation with climate were larger than adults.

Mean spatial velocity at species northern range limits varied between 1.45 and 2.28 km yr⁻¹ for adults and between 1.04 and 2.65 km yr⁻¹ for saplings (Fig. 5). Results for adults and saplings combined resembled those for adults. Spatial velocity of temperature change surpasses the mean latitudinal difference distribution

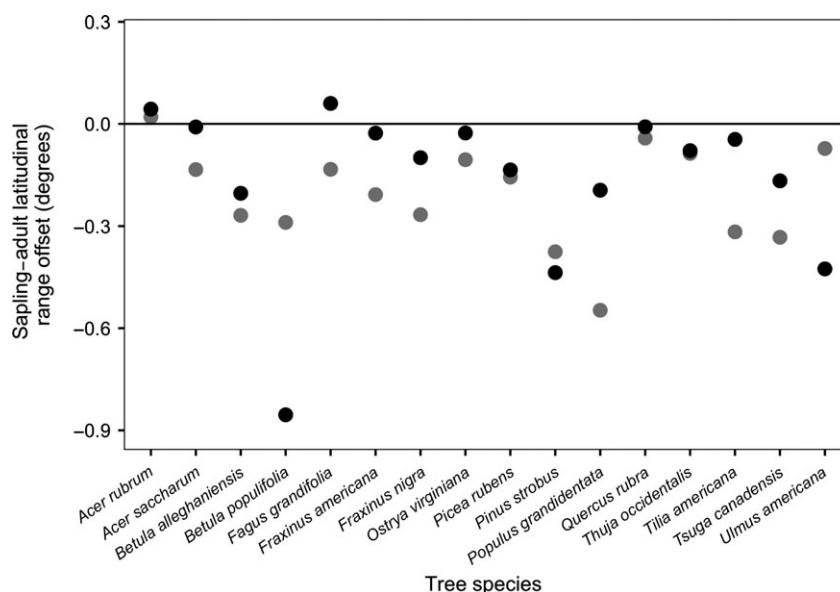


Fig. 4 Mean tree species sapling–adult range offsets in degree latitude for 1970 (in grey) and 2000 (in black). The offset was calculated by subtracting the adult 95th percentile latitude from the sapling 95th percentile latitude; thus, negative values indicate adult ranges are more northern than saplings.

Table 1 Tree species mean northern range shifts (LDD; km yr⁻¹) and the correlation between the slope of climate warming for 1960–2000 (ΔT) and LDD ($Cor_{\Delta T-LDD}$). Data are presented for saplings and adults. Pearson correlations presented; sample size (n), P -value (P)

Tree species	LDD (km yr ⁻¹)	$Cor_{\Delta T-LDD}$	n	P	LDD (km yr ⁻¹)	$Cor_{\Delta T-LDD}$	n	P
	Adults				Saplings			
<i>A. rubrum</i>	0.265	0.14	16	0.61	0.329	0.59	16	0.02
<i>A. saccharum</i>	0.108	0.15	16	0.58	0.461	0.45	16	0.08
<i>B. alleghaniensis</i>	-0.046	0.44	16	0.09	0.281	-0.38	11	0.25
<i>B. populifolia</i>	0.687	0.34	5	0.57	-0.391	-0.98	3	0.14
<i>F. grandifolia</i>	-0.141	0.58	11	0.06	0.391	-0.39	10	0.26
<i>F. americana</i>	-1.206	-0.22	7	0.63	-0.518	0.82	5	0.09
<i>F. nigra</i>	-0.022	0.09	13	0.76	0.438	-0.36	10	0.31
<i>O. virginiana</i>	-0.039	-0.19	9	0.63	0.446	-0.02	6	0.98
<i>P. rubens</i>	0.064	0.23	12	0.48	0.095	0.04	9	0.91
<i>P. strobus</i>	1.131	0.13	13	0.68	0.304	-0.23	6	0.66
<i>P. grandidentata</i>	0.365	0.04	12	0.89	0.908	-0.48	8	0.23
<i>Q. rubra</i>	0.036	-0.07	9	0.87	0.531	-0.63	5	0.25
<i>T. occidentalis</i>	-0.003	0.15	16	0.59	0.022	0.03	15	0.91
<i>T. americana</i>	0.172	0.44	8	0.27	1.151	0.49	4	0.51
<i>T. canadensis</i>	0.012	-0.03	9	0.93	0.544	0.37	8	0.37
<i>U. americana</i>	0.368	0.12	9	0.75	-0.621	0.76	4	0.24

(converted into km yr⁻¹) of nearly all species, irrespective of life stage (Fig. 5). For most species, spatial velocity of temperature at range limits exceeded the pace of tree species range shifts by a factor of two (Fig. 5). Two exceptions were for saplings of *Tilia americana* (1.5 km yr⁻¹) and for *Populus grandidentata* (0.98 km yr⁻¹) (Fig. 5).

Tree species seed mass was not related to mean latitudinal differences across all life stages (Fig. S6). Contrary to expectation, mean values for range shifts for

species characterized by potentially faster seed spread rates were smaller than those characterized by slow seed spread rates and this pattern was consistent across all life stages (Table S4).

Discussion

Quantifying tree species responses to recent climate warming is an essential step in refining predictions of

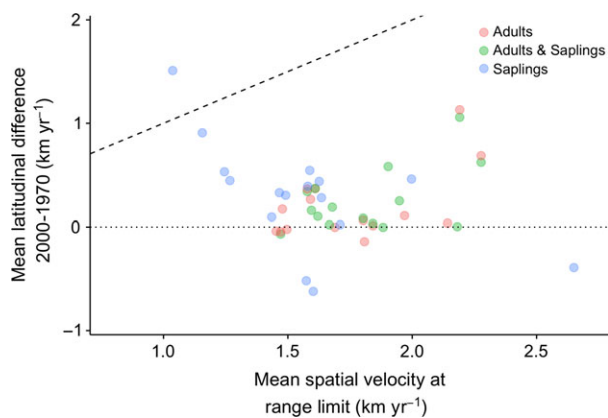


Fig. 5 Comparison of mean latitudinal difference per tree species in km yr^{-1} for different life stages with the mean spatial velocity of temperature at the range limit of tree species. The dotted line indicates no change between 2000 and 1970 in range; the dashed line indicates the 1 : 1 relationship between the calculated spatial velocity of temperature at the range limit and the species mean range shift in km per year between 2000 and 1970. [Colour figure can be viewed at wileyonlinelibrary.com]

the future composition and function of forest ecosystems. To our knowledge, our study is one of the largest conducted to date, both in temporal and geographic scope, exploring empirical evidence for eastern North American tree species range expansion. We provide evidence for a predominantly northward migration of tree species with saplings exhibiting faster range expansion than adult trees as predicted. These changes in range were however weakly correlated with seed dispersal traits and species exhibited variable and mostly weak and nonsignificant patterns with climate warming. Importantly, despite evidence for an overall pattern of northern expansion, migration was greatly outpaced by the spatial velocity of temperature change.

In this study, we extended an analysis of range limits developed by Zhu *et al.* (2012) by including a temporal dimension. We thus employed methods consistent with their approach: range boundaries were based on the 95th percentile latitude and species with range boundaries within the boundaries of the forest plot network were included. Accordingly, a number of northern species were excluded namely, *Abies balsamea*, *Picea mariana*, *Populus tremuloides*, *Picea glauca* and *Betula papyrifera*. While a recent study utilizing the Quebec forest inventory data included these species (Boisvert-Marsh *et al.*, 2014), our comparison of the northernmost plot locations and tree species range maps (USGS, 1999) suggested that their range limits lie far beyond the northern limits of the forest plot network, precluding conclusions of range shifts. As argued by Zhu *et al.* (2012): 'Abundance and occupancy patterns (Murphy *et al.*, 2006, Murphy *et al.*, 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)'. Similarly, we would therefore caution against the interpretation of the 90th percentile latitude as the range limit for *Abies balsamea*, *Picea mariana*, *Populus tremuloides*, *Picea glauca* and *Betula papyrifera* as defined by Boisvert-Marsh *et al.* (2014) given that their northern range limit does not lie within the Quebec forest plot network and emphasize the importance of employing clear definitions of 'distribution' and 'range' in future studies of range limits.

Realized shifts in tree ranges and model predictions

Over long timescales tree species adaptation to warmer temperatures is expected to involve shifts in ranges. In particular, northern forests such as temperate and boreal forests are expected to undergo dramatic compositional shifts in response to climate warming. Species distribution models are commonly applied to forecast the magnitude of species range shifts in responses to projected changes in climate (Iverson & Prasad, 1998; Iverson *et al.*, 2004; Hamann & Wang, 2006). Testing whether realized shifts in tree ranges match forecasts is a key step in assessing and refining forecasts and models (Iverson & McKenzie, 2013). A number of studies have examined evidence for range expansion at smaller geographic and temporal scales. For example, temperate species such as *A. rubrum* and *A. saccharum*, whose limits fall near the southern border of the boreal forest, have been shown to establish in boreal forests (Barras and Kellman 1998, Leithead *et al.* 2010). Gamache & Payette (2005) found that *Picea mariana* treelines expanded significantly in Quebec but found a lack of correlation between tree establishment and climatic variables; however, this species was excluded in the present study because the range limit is outside the forest plot network.

Species distribution models forecast future species range limits based on calibrated relationships between species occurrence or abundance and climatic variables thought to influence species performance. Here we compare our estimates for realized range shifts with forecasted changes for tree species examined in the present study. Using climate envelope approach models, McKenney *et al.* (2007) predict potential northward central range shifts of several hundred kilometres for 130 North American tree species until the end of the century. Specifically, for the species examined in the present study, *Tilia americana*, *Acer saccharum*, *Ostrya virginiana*, *Quercus rubra*, *Fraxinus americana*, *Betula alleghaniensis*, *Pinus strobus* and *Acer rubrum*, McKenney *et al.* (2007) predict northward latitudinal shifts in range centres to vary from a high of 9.2° to a low of

7.6°, respectively. Taking *Tilia americana* as an example, because it had one of the largest northern range shifts -0.4° latitude over ~ 30 years ($0.013^\circ \text{ yr}^{-1}$) – we find a stark contrast with the predicted change of 9.2° over 100 years is seven times larger ($0.092^\circ \text{ yr}^{-1}$). While the exact values should of course be viewed only as indicators of potential range dynamics, it is still clear that a large discrepancy exists between estimates of realized range shifts and forecasted range shifts, suggesting that tree range expansion in eastern North America will likely fail to keep pace with climate warming at northern range limits.

The forest inventory and analysis data of the United States are used extensively in examining tree species distributions at large geographic scales (Woodall *et al.*, 2009, 2013; Murphy *et al.*, 2010; Zhu *et al.*, 2012, 2014; Nock *et al.*, 2013; Monleon & Lintz, 2015). Murphy *et al.*'s (2010) examination of abundance patterns of 102 eastern North American tree species predicts limited range expansion at the northern edge. Comparing the mean latitudes of seedling density and tree biomass, Woodall *et al.* (2009) drew a similar conclusion and suggested that the majority of northern temperate species of the same area are migrating northward due to greater regeneration success at higher latitudes. However, results from the study of Zhu *et al.* (2012), which focused exclusively on species with range limits within the eastern United States and not extending north into Canada, were consistent with the suggestion of limited range expansion (or stability) at the northern edge and concurrent range contraction at the southern range limit as a general trend for tree species in the eastern United States (Murphy *et al.*, 2010).

Temporal replication within forest inventory occurrence data allows for quantification of how sapling–adult offsets change between inventory periods. Our analysis suggested that sapling range limits for most species are more southern relative to adults (Fig. 4). Within the inferential framework of Zhu *et al.* (2012), this would suggest that the ranges of these species are contracting. However, we show that indeed species ranges are generally moving northward and that in accordance with the comparisons within life stages the adult–sapling range offset decreased between inventory periods. For some species, saplings were north of adults as expected or there was very little difference (Fig. 4). However the question remains, why are saplings ranges more southern for the other species, even when temporal analysis indicates a northward range expansion over time? This pattern, also previously identified by Boisvert-Marsh *et al.* (2014), may possibly resulting from ‘pulse’ or episodic recruitment followed by retarded recruitment resulting from changes in conditions (Brown & Wu, 2005; Urbietta *et al.*, 2011).

Alternatively, also potentially relevant are findings that suggest that climate conditions that are optimal for juvenile trees may be warmer (i.e. more southern) than for adults (Zhu *et al.*, 2014). This ontogenetic difference in temperature optimums could also be responsible for the offset observed in the first time period, with a shift through time towards reduced offsets between adults and saplings in the second time period. Further attention to this pattern is warranted and highlights the importance of long-term temporally replicated data when addressing complex ecological systems. As Zhu *et al.* (2012) previously stated, analyses of the United States Forest inventory and analysis (FIA, <http://www.fia.fs.fed.us/recent-load-history/index.php>) data are among the most robust assessments of tree species migration potential. Unfortunately, many inventories, including the FIA, lack the temporal depth present in the Quebec forest inventory which is a key aspect of ‘robustness’, in addition to criteria such as geographic extent and the number of species included (Kerr *et al.*, 2007; Parmesan *et al.*, 2011; Monleon & Lintz, 2015). In the future, re-census within the FIA plot network is sure to provide insightful data – especially as the length of the monitoring period increases.

Understanding drivers of change in tree species ranges

Previous studies have found that species vary greatly in their rates of change, suggesting that individual species traits, acting in concert with external drivers of change, govern individual species range shifts (Chen *et al.*, 2011). For the six tree species common to this study and to the study of Boisvert-Marsh *et al.* (2014) – *A. rubrum*, *A. saccharum*, *F. grandifolia*, *T. occidentalis*, *O. virginiana*, *B. alleganiensis* – qualitatively similar results were obtained for range expansion, despite subtle methodological differences. However, unlike Zhu *et al.* (2012) or the present study, no attempt was made to directly relate observed changes in tree species ranges to dispersal traits or to climate warming (Boisvert-Marsh *et al.*, 2014). Recent examinations of the relationship between seed dispersal traits and migration tendencies determined low explanatory power for species’ range shifts (Angert *et al.*, 2011). This is in accordance with our results showing that contrary to the expectation that dispersal traits should be correlated with range dynamics, both seed mass and a qualitative measure of seed spread rate were not related to tree species northern range expansion. Similarly, Zhu *et al.* (2012) previously reported no relationship between dispersal traits and range changes for a very large sample of eastern North American tree species, albeit for which northern range boundaries were predominantly stable. We emphasize that the analysis employed by Zhu *et al.*

(2012) and which is adopted here is clearly an initial foray into understanding the role of dispersal in range shifts and what traits can predict species dispersal capacities (Aubin *et al.*, 2016).

Importantly, direct comparison of the pace of tree species northern range expansion in the present study with the spatial velocity of climate change places the observed northward range expansion in context: tree species are generally moving northward, but at a much slower pace than the warming climate (Fig. 5, Fig S7). The differing northern range shifts observed for species in this study supports evidence from previous research where the velocity of migration was found to be species-specific (Corlett & Westcott, 2013). Furthermore, our results also cast some doubt on the notion that dispersal traits are useful in predicting which species will be able to migrate better (Corlett & Westcott, 2013). Duchesne & Ouimet (2008) analysed the ecological response (growth, mortality and recruitment) of tree species populations in Quebec using the forest inventory data from 1970 to 2005. Their study led them to conclude that responses of tree population dynamics to global environmental changes can be very complex or even misleading considering the confounding effects of other disturbance agents. Future studies should start to link not only species traits with successful range expansion within particular regions, but also test for the influence of a wider range of factors. For example, factors that could have an important influence include: forest management activity that creates or limits recruitment opportunities, natural disturbances that may create opportunities or barriers for sapling recruitment (Woodall *et al.*, 2013), introduced pathogens that are known to influence species distributions such as spruce budworm or the emerald ash borer (Liang & Fei, 2014), or potential dispersal barriers such as built-up areas or natural features. We questioned whether the emerald ash borer (*Agrilus planipennis*) might account for the remarkable results for *Fraxinus americana* observed here (Fig. 2). Although present in natural forests, that ash borer has mostly affected urban areas and the area of infestation is still limited to the south of the Province. Alternatively, issues with misclassification of *Fraxinus americana* with congeners between inventories remains a possibility but are unlikely at such a large scale. Given that *F. americana* is among the three species with the least coverage (in plot numbers in which saplings or adults are present), we think the result should therefore be interpreted with care. While analyses with rarer species may thus leave some questions open regarding the true nature of a result, we suggest that such results may act as a first warning that could be followed up with supplemental surveys that would help to distinguish statistical issues from true changes in ranges. Further experimental work

will likely aid in clarifying trends and drivers of changes, but contending with the number of species and large areas involved presents significant challenges (Ibáñez *et al.*, 2006, 2009; Solarik *et al.*, 2016).

While identifying and disentangling the drivers of range dynamics presents a significant challenge for future work, results of our study clearly support a growing body of evidence which suggests that tree range expansion in eastern North America will likely fail to keep pace with climate warming at northern range limits. We foresee potential for harmonizing provincial scale data sets in Canada, as well as at the national scale in North America. Doing so would prevent researchers from dropping species from analyses because the northern or southern range limit is on the opposite side of the border, thus facilitating future work on tree species ranges at still larger geographic scales and importantly trailing edges for many northern species in eastern North America (Jump *et al.*, 2009).

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Supporting Information

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

Table S1 Summary of the number of plots occupied by each of the 16 included tree species, separated by growth stage and time class.

Table S2 Range offsets and mean 95th percentiles of latitudinal occurrence for each of the 16 tree species.

Table S3 Dispersal traits, northern range limit change and the spatial velocity of climate warming for different life stages of the 16 tree species.

Table S4 Comparison of mean changes in tree species northern range limits for species with slow vs. moderate–fast seed spread rate.

Figure S1 Histogram of distribution of the number of years separating the two inventories of the forest plot network for the 5719 plots used in the analysis of tree species range shifts.

Figure S2 Range maps for tree species with northern range limits lying beyond the northern limits of the Quebec forest inventory plot network but which appear in the study of range limits of Boisvert-Marsh *et al.* (2014).

Figure S3 Range maps for the 16 tree species with northern range limits within the Quebec forest inventory plot network and included in the present study.

Figure S4 Variation in the latitudinal difference distribution for 16 tree species with longitude for two life stages.

Figure S5 Variation in tree species sapling–adult range offset in degrees latitude with longitude.

Figure S6 Comparison of mean latitudinal difference per tree species in km yr^{-1} for different life stages with seed weight. Seed weight values for each tree species represented in the plot are given in Table S3.

Figure S7 Climate warming in Quebec, Canada for 1961–2000 based on gridded ($0.5^\circ \times 0.5^\circ$) temperature data.