

Decadal changes in tree range stability across forests of the eastern U.S.

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ABSTRACT

The monitoring of tree range dynamics has emerged as an important component of adaptive responses of forest management to global change scenarios such as extreme precipitation events and/or invasive species. Comparisons between the locations of adults versus seedlings of individual tree species using contemporary forest inventories is one tool widely used to assess the status of tree ranges in light of these changing conditions. With the consistent remeasurement of standard forest inventory plots across the entire eastern US occurring since the 2000s, the opportunity exists to evaluate the stability of tree ranges of focal species across a decade. Using said inventory, the northern range margins of tree distributions were examined by comparing differences (Holm-Sidak adjusted p -value = 0.2) in the 95th percentile locations of seedlings to adults (i.e., trees) by 0.5 degree longitudinal bands over nearly 10 years and by categories of canopy disturbance (i.e., canopy gap formation) for 20 study species. Our results suggest that range margins are stable for 85% of study species at both time one and at remeasurement regardless of canopy disturbance. For the very few species that had a significant difference in seedlings and adults at their range margins, there was nearly a 0.4 degree difference in latitude with seedlings being farther south irrespective of disturbance. Our findings of tree range stability across forests of the eastern US indicate a general propensity towards range contraction, especially for study species forecasted to lose range and located on disturbed sites, which may present substantial hurdles for adaptive management strategies focused on maintaining and enhancing forest ecosystem resilience in the context of global change and associated rapid climate change.

1. Introduction

Global change poses serious threats to future delivery of forest ecosystem services where changing climate (Stenseth et al., 2002; Bonan et al., 2008), land use (Metzger et al., 2006), and economies (Woodall et al., 2012) coupled with invasive species (Holmes et al., 2009) and browse impacts (Russell et al., 2017) may reduce the extent and health of forest ecosystems (Trumbore et al., 2015). The distribution of tree species is a primary driver of current and future forest extent and condition (i.e., provisioning of ecosystem services; Gamfeldt et al., 2013). Tree species define patterns of biodiversity in a given region, which in turn strongly affect levels of forest productivity and resilience in the face of global change (Botkin et al., 2007; Paquette et al., 2011). Furthermore, the adaptive response of forest managers to global change is in part limited for endemic tree species especially in areas where natural regeneration is the traditional method of regenerating forest stands (Oliver and Larson, 1996) following

disturbance or harvest activity, including numerous forest types in the eastern United States (Oswalt et al., 2014). Accurately gauging the dynamics of tree ranges in the context of forest disturbance (Liang et al., 2017) is critical for informing appropriate pathways for adapting current forest management activities in response to global change (D'Amato et al., 2011; Messier et al., 2013; Nagel et al., 2017).

Tree ranges have shifted for millennia (Clark et al., 1998; Davis and Shaw, 2001; McLachlan et al., 2005). However, the major question for resource management is if the rate of tree migration will keep pace with expected rates of climate change (Loarie et al., 2009) and other noted forcing factors of global change (Bertrand et al., 2011; Iverson and McKenzie, 2013; Vanderwel and Purves, 2014). Research suggests tree ranges may be contracting for certain species while at best migrating at a pace slower than that of expected climate change. In one of the first range margin examinations of forest tree species in the eastern US, Zhu et al. (2012) found evidence that range margins were not migrating northward as would be expected given climate change hypotheses.

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Recent results from Sittaro et al. (2017) suggest tree ranges will not be able to track the rate of expected future warming. Liang et al. (2017) emphasize that not only is climate change a driver of range margin dynamics but also interspecific competition and disturbance as the attributes of forest canopies are important controlling factors on related tree regeneration (Dobrowski et al. 2015). Fei et al. (2017) found that changes in precipitation might be causing a westward shift of certain eastern US tree species as opposed to poleward migration in response to increased moisture availability over the past few decades. When expected changes in tree ranges are combined with the influence of forest pests and pathogens, even more serious hurdles to tree range movement emerge (Thuiller et al., 2008, Rogers et al., 2017). Overall, refined monitoring techniques coupled with continuous monitoring are needed to ensure conservation of forest ecosystems in a future of expected global change.

In the forests of the eastern US, the trajectory of tree monitoring techniques has greatly evolved over time from Little's (1971) seminal work delineating tree ranges in the United States to a myriad of contemporary refinements and approaches. Before the advent of remote sensing technologies (e.g., Landsat) and consistent continental-scale forest inventories (e.g., Bechtold and Patterson 2008), the quantification of tree ranges was often limited to a delineation of individual tree-species presence based on inconsistent inventories and subjective botanical descriptions summarized at coarse spatial scales (e.g., county). Although certainly adequate for basic understanding of tree species distributions, these early techniques afforded little ability to monitor tree ranges let alone enable quantitative analyses. The adoption of more consistent forest inventories in concert with publicly available digital databases enabled the statistical modeling of tree ranges with the production of dynamic tree atlases (e.g., Prasad et al., 2007, Iverson et al., 2008), which in turn informed conservation and management efforts (e.g., Iverson and McKenzie, 2013, Nagel et al., 2017). In addition to these region-wide analyses, elevational studies have greatly refined the understanding of tree species migration (e.g., Walther et al., 2005, Lenoir et al., 2009; Kelly and Goulden, 2008). In an effort to refine tree range monitoring beyond the modeling of tree distributions and elevational studies, Woodall et al. (2009) used a nationally consistent inventory to compare the distributions of seedlings versus adults as an indicator of tree range shifts. Zhu et al. (2012) built upon this work by more fully evaluating the range margins of seedlings versus adults in the context of climatic variables with Woodall et al. (2013) incorporating attributes of forest canopy disturbance in the range analyses. More recent work by Sittaro et al. (2017) and Liang et al. (2017) highlight the utility of these tree range metrics and related analyses in monitoring tree ranges in the context of global change.

Much of this prior work has been conducted in the eastern United States. It is an optimal study location given the consistent region-wide forest inventory that has been conducted for nearly 20 years (Bechtold and Patterson, 2008) in concert with a relatively diverse temperate forest and biophysical conditions (Oswalt et al., 2014). Perhaps most importantly, the remeasurement period has nearly doubled from earlier studies allowing greater statistical detection of changes in range margins combined with refined mapping. Therefore, the goal of this study was to quantify the decadal changes in range margins of major tree species in the eastern US employing the techniques used in Woodall et al. (2013) but with the important lengthening of the remeasurement period and improved mapping for visual interpretation. Specific objectives were (1) to evaluate the stability of northern range margins of selected eastern U.S. tree species by comparing latitudinal occurrences of trees and their associated seedlings by individual species at 0.5-degree lines of longitude in eastern U.S. forests across a decade-long remeasurement period and (2) to determine if said range stochasticity is influenced by forest disturbance (i.e., canopy gaps) with implications for evaluating forest ecosystem resilience and adaptive management responses.

Table 1

Study tree species common/Latin name, number of subplot observations, and forecasted change in conterminous U.S. suitable habitat (percent area) under a future Hadley Low (B1) climate scenario (see Prasad et al., 2007-ongoing). Species were assigned to one of two groups: (1) species with forecasted range loss or minimal expansion, (2) species with substantial forecasted range expansion.

Common name	Latin name	Observations	Habitat change (%)
<i>Species with range loss or minimal expansion</i>			
Sweet birch	<i>Betula lenta</i>	1709	−11.5
American beech	<i>Fagus grandifolia</i>	4267	−7.6
Sourwood	<i>Oxydendrum arboreum</i>	868	−7.1
Black cherry	<i>Prunus serotina</i>	8001	2.2
White oak	<i>Quercus alba</i>	6174	10.0
Scarlet oak	<i>Quercus coccinea</i>	1458	−23.9
Chestnut oak	<i>Quercus prinus</i>	1802	8.0
Northern red oak	<i>Quercus rubra</i>	6921	−0.1
Black oak	<i>Quercus velutina</i>	4512	13.5
American basswood	<i>Tilia americana</i>	2330	−10.7
<i>Species with substantial range expansion</i>			
Eastern redcedar	<i>Juniperus virginiana</i>	2845	66.9
Shortleaf pine	<i>Pinus echinata</i>	1230	57.6
Slash pine	<i>Pinus elliottii</i>	166	110.4
Longleaf pine	<i>Pinus palustris</i>	139	77.2
Bitternut hickory	<i>Carya cordiformis</i>	1916	85.3
Eastern redbud	<i>Cercis canadensis</i>	1176	62.0
Water oak	<i>Quercus nigra</i>	1646	74.3
Post oak	<i>Quercus stellata</i>	2137	67.4
Black locust	<i>Robinia pseudoacacia</i>	974	62.5
Winged elm	<i>Ulmus alata</i>	2515	142.6

2. Methods

As the methods in this study are largely derived from Woodall et al. (2013), methods will be succinctly summarized with detailed notes of divergence along with inclusion of new inventory data. Please refer to Woodall et al. (2013) for details unless otherwise noted below.

2.1. Study tree selection

As noted by Woodall et al. (2010), the selection of tree species in tree range shift analyses influences results, leading Woodall et al. (2013) to develop a list of 20 species for evaluation of tree range shift hypotheses in eastern forests. In short, this list only includes species with distributions largely contained within the conterminous US and with abundant observations in the seedling and overstory layers. The same tree list from Woodall et al. (2013) was used in this study along with Prasad et al.'s (2007) future potential tree habitat models under the low emission Hadley climate scenario (B1) as a conservative future (Table 1). The use of Woodall et al.'s (2013) tree species list allows not only comparison with prior study results but continued monitoring of this important ecosystem attribute across the eastern US.

2.2. Data

Nationally consistent forest inventory data from the USDA Forest Service's Forest Inventory and Analysis program (FIA; Bechtold and Patterson, 2005) served as the basis for this study. FIA applies a nationally consistent sampling protocol using a quasi-systematic design covering all ownerships in the entire nation with plots remeasured every 5–7 years in the eastern U.S. (Bechtold and Patterson, 2005). The multi-phase inventory is based on an array of hexagons assigned to separate interpenetrating, non-overlapping annual sampling panels. The first phase involves land area stratification while the second and third phase involves measuring field plots for trees and forest health indicators (e.g., soils), respectively. The focus of our study was the second phase of the inventory when permanent sample plots are visited

by field crews to measure tree and seedling attributes among a host of additional stand/site characteristics. Federally supported national plot intensity for Phase 2 measurements is approximately one plot for every 2428 ha of land (roughly 125,000 forested plots nationally). The plot design for FIA inventory plots consists of four 7.2-m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (USDA, 2016). All trees with a diameter at breast height (d.b.h.) of at least 12.7 cm are inventoried on forested subplots. Within each subplot, a 2.07 m microplot offset 3.66 m from subplot center is established where all live tree saplings are tallied according to species and all trees with a d.b.h. between 2.5 and 12.6 cm are inventoried. Seedlings are also inventoried on the microplot where conifer must be at least 15.2 cm in height while hardwood seedlings must be at least 30.5 cm in height. Once seedlings attain a d.b.h. of at least 12.7 cm they are considered saplings. Individual subplots with no anthropocentric disturbances (e.g., harvest) and fully occupied by a forest condition (i.e., no other land uses such as a settlement) at both measurement times were considered individual study observations especially as canopy gap disturbances were calculated at the subplot level (i.e., changes in microplot seedlings cannot be attributed to changes in overstory canopy nearly 40 m away on another subplot).

All study data are publicly available (FIADB, <http://apps.fs.fed.us/fiadb-downloads/datamart.html>) and were taken entirely from the

FIADB using the most recent annual inventory in 28 eastern states on a total of 57,693 subplots (Fig. 1). As more than one study species might occur on the same subplot, individual species observations (either as a seedling or tree) will total to more than the total subplots used in this study (Table 1). Annual inventories for each state were first initiated between 2002 and 2007 with subsequent re-measurement 10-years later (2012–2017) for this particular study, so sample intensities may vary by state.

2.3. Analysis

Briefly, based on methods developed in Woodall et al. (2013) with aspects adopted in recent studies (e.g., Sittaro et al., 2017), this study quantified relationships between tree and associated seedling occurrence by species across the eastern U.S. using an indicator of northern range margin shifts. The 95th percentile of seedling abundance (i.e., seedling counts) was compared to the 95th percentile of tree abundance (i.e., biomass of adults) by longitudinal bands (0.5 degrees) with study plots assigned to either gap-disturbed or non-disturbed categories. For each species, a minimum of 10 longitudinal bands and 3 observations per band were required for inclusion in analyses. In cases where the number of observations per band was insufficient to appropriately calculate a 95th percentile, the maximum observation was used which

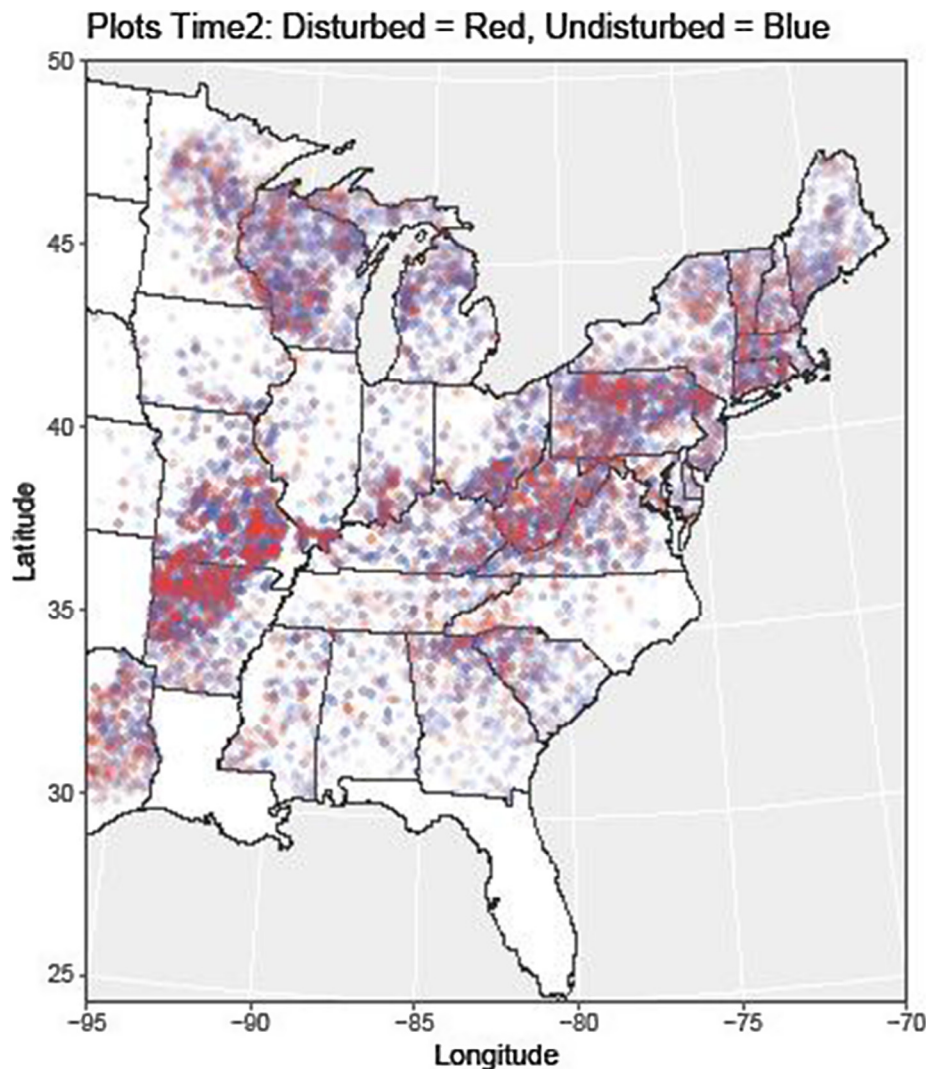


Fig. 1. Study observation locations for either gap-disturbed (red) or undisturbed (blue) forests over remeasurement period between time 1 and 2. (Note: Given the map's spatial scale, more than one subplot can occur at each plot location). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reduces the precision but should not bias results. Taken together, the medians of the 95th percentile latitudinal locations of seedlings and trees were compared (for each study species) across all longitudinal bands as an indicator of northern range margin fluctuations over time. Differences in live tree exposed crown area (ECA; i.e., canopy gap disturbance) over time was determined by assigning all tree species to ECA species group models developed by Lorimer and Frelich (1989). Canopy gap-disturbed subplots were defined as having less ECA at time two than time one with all other study observations being considered non-gap disturbed subplots. A difference between the canopy gap disturbance techniques applied in Woodall et al. (2013) and this study was dropping inclusion of trigonometric functions that enabled calculation of distance from tree mortality on a subplot to seedlings on the microplot. Such a difficult calculation reduced the repeatability of this study and did not afford any appreciable increase in resolution in describing disturbance dynamics below the subplot scale.

In order to test the null hypothesis that the difference in latitude between the 95th percentile of seedling occurrence and the 95th percentile of tree occurrence did not differ significantly from zero, Wilcoxon signed-rank tests were conducted for time 1, time 2 non-disturbed, and time 2 disturbed observations by each study species. The Wilcoxon test was chosen due to small sample sizes for a limited number of study species and/or examination of the data revealed some cases of deviation from normality. Due to the number of tests performed, a Holm-Sidak multiple comparison adjustment to the resulting p-values was applied. The Holm (1979) sequential rejection procedure was implemented by first ordering the p-values from smallest to largest. The Sidak (1967) adjustment to the p-values was then calculated from $p_s = 1 - (1 - p_w)^k$ where p_s is the Sidak adjusted p-value, p_w is the original Wilcoxon p-value, and $k = m - i + 1$ (m = total number of tests, i = rank position). Thus, the p_s calculation takes into account the ranking. Finally, following rank order from highest to lowest, a statistically significant difference is concluded when $p_s \leq \alpha$. At the first occurrence of $p_s > \alpha$ and for all subsequent tests lower in the rank order, the determination is no statistical difference. For these tests, $\alpha = 0.20$ was chosen to maintain a reasonable level of confidence in avoiding Type I errors while also recognizing the importance of avoiding Type II errors in environmental monitoring (Mapstone, 1995).

3. Results

The median differences in the 95th percentile latitudes between trees and seedlings (Table 2) were usually (14 out of 20 species) negative (indicating that trees were observed farther north than seedlings); however, these differences were only statistically significant for three species in time 1 (eastern red cedar [*Juniperus virginiana*], short-leaf pine [*Pinus echinata*], and post oak [*Quercus stellata*]), with these three tree species located on average 0.14 degrees farther north than associated seedlings on average (Table 3). All three of these study species are expected to undergo an expansion of suitable habitat in the eastern US under future climate scenarios (Table 1). On plots where there was a loss in canopy cover (i.e., disturbance) over the re-measurement period, all three significant latitudinal differences (white oak [*Quercus alba*], black oak [*Quercus velutina*], and post oak [*Quercus stellata*]) resulted in trees being farther north than seedlings (i.e., lack of regeneration) by an average of 0.42 degrees (Table 3). For non-disturbed plots at time 2 there were also three species (Table 2; scarlet oak [*Quercus coccinea*], black oak, and black locust [*Robinia pseudoacacia*]) that demonstrated potential range margin contraction with trees being located 0.32 degrees farther north than associated seedlings on average (Table 3).

When examining examples that show how 95th percentile latitudes for trees and seedlings vary by 0.5 degree longitude bands, it is apparent that the differences are not uniformly distributed along the range margins (Figs. 2 and 3). For black oak, there is an increased potential for range contraction along the eastern edge of its extent

(southern Maine, to western Pennsylvania) at time 1 (Fig. 2a) that persists through time 2 both for sites that were non-disturbed (Fig. 2b) and disturbed over the re-measurement period (Fig. 2c). Post oak exhibited a reasonably stable range margin at time 1 (trees farther north than seedling by only 0.1 degrees, Table 2) across most longitudinal bands, particularly in the western portion of its range (Fig. 3a). However, by time 2, post oak had distinct separations between trees and seedlings (0.6 degrees) at disturbed locations especially along its eastern range margin (New Jersey to western Kentucky).

When examining results across all species and times, study tree species margins appeared to be stable for 17 of 20 (85%) of study species at both time one and at re-measurement regardless of canopy disturbance (Table 3). For the three study species with a significant difference in seedlings and adults at their range margins, there was a 0.416 versus 0.326 degree difference in latitude, on disturbed versus non-disturbed sites respectively, with seedlings occurring farther south. When examining the results in the context of forecasted optimal future locations given climate simulations, the species forecast to lose extent under future climate scenarios had nearly twice the difference (-0.17 versus -0.33 degrees) in the displacement of seedlings relative to trees if the canopy was disturbed (Table 3).

4. Discussion

Since being proposed nearly a decade ago (e.g., Woodall et al., 2009), the use of tree demography information (i.e., seedlings versus trees) from large-scale forest inventories to assess and monitor contemporary tree ranges has been successfully adopted (Iverson and McKenzie, 2013) across a number of studies. Sittaro et al. (2017) used tree demography (trees versus saplings) in eastern North America to assess range margins extending well into Canada. Dobrowski et al. (2015) used tree demography to assess tree recruitment dynamics in western US forests while Monleon and Lintz (2015) also used demography in western US forests to suggest ranges were shifting due to climate change. As was exhibited in our study, indicators of tree range dynamics can be re-assessed over time using newly acquired inventory data in comparison to the oldest compatible inventories. Examining changes in the relationships between trees and seedlings across time may provide one of the most sensitive indicators of tree range dynamics across large spatial domains (e.g., the eastern U.S.) given the ephemeral nature and plasticity of tree regeneration.

Our study found continued stability of northern tree range margins for selected study species in eastern U.S. forests in a manner similar to Woodall et al. (2013). The stability of tree ranges can also be viewed as a failure to shift (Zhu et al., 2012) given the various global change factors that affect forests, ranging from changing climate (Monleon and Lintz, 2016) to changing land use patterns (Metzger et al., 2006) and related legacies (Nowacki and Abrams, 2015). Perhaps most interestingly, for all instances in our study when there was a statistical difference in latitudes of seedlings versus adults, the seedlings were located further south than associated trees. At least for the northern range margins there remains a potential for range contraction when trees die. For trees whose ranges are forecasted to contract in the future due to climate change, forest disturbance (i.e., loss of canopy cover) appeared to exacerbate the latitudinal separation between trees and seedlings along these northern range margins. Such failure to migrate or even loss of range extent due to disturbance cannot be primarily attributed to climate change (e.g., Nowacki and Abrams, 2015). Although not examined in this study, there may be numerous factors inhibiting the regeneration of tree species when disturbances reduce canopy cover. In the aftermath of disturbance invasive plant species may be opportunistic invaders (Trumbore et al., 2015) in combination with other pests and pathogens (Rogers et al., 2017). Moreover, many areas of the eastern forest contain dense understory conditions resulting from the proliferation of non-native and native plant species creating significant bottlenecks to the successful recruitment of canopy species (Royo and

Table 2

Medians (degrees) of differences between the 95th percentile latitude of seedling and tree occurrence across 0.5-degree longitudinal bands for individual study species across the eastern U.S. Differences reported at time 1 (2002–2007) and at time 2 (~10 years subsequent to time 1) for both non-disturbed and disturbed observations (with or without canopy gaps). Negative values indicate trees are further north than seedlings with significant results in bold (p-value < 0.2). (Note: IQR = interquartile range, n = number of longitudinal bands).

Common Name	Time 1				Time 2: Non-disturbed				Time 2: Disturbed			
	Median	IQR	n	p-value	Median	IQR	n	p-value	Median	IQR	n	p-value
Sweet Birch	-0.1568	0.325	24	0.7486	-0.0412	0.4254	22	0.3534	-0.1347	0.6443	8	0.9971
American beech	0.0000	0.0887	47	0.9819	0.0000	0.0456	46	0.9974	-	-	0	-
Sourwood	-0.2190	0.7192	17	0.6718	-0.0289	0.4232	13	0.8271	0.0000	0.3069	3	0.9989
Black cherry	0.0670	0.5631	55	0.9438	0.0339	0.3380	54	0.2194	0.0000	0.6722	11	0.9994
White oak	-0.0060	0.6041	50	0.9278	-0.0014	0.4556	44	0.7970	-0.3052	0.8149	16	0.1290
Scarlet oak	-0.1335	0.4656	24	0.3652	-0.2842	1.5372	21	0.0978	-0.0412	0.7881	7	0.9989
Chestnut oak	-0.0002	0.3562	27	0.9678	-0.0003	0.2602	29	0.4748	-0.0850	0.8431	13	0.6267
Northern red oak	0.0495	0.5548	57	0.9446	0.0400	0.6483	56	0.4128	0.0002	0.8532	6	0.9999
Black oak	-0.0686	0.7193	47	0.3441	-0.0532	0.9099	46	0.0944	-0.3498	1.4479	17	0.1010
American basswood	-0.0503	0.4188	27	0.2541	-0.0146	0.5145	20	0.9829	-0.1672	0.5797	14	0.4515
Eastern redcedar	-0.1582	2.3938	43	0.1765	-0.0623	1.8995	38	0.2789	-0.7730	2.7429	17	0.2414
Shortleaf pine	-0.1771	0.4089	15	0.0662	-0.0139	0.5665	7	0.8171	-0.1654	0.1519	10	0.9990
Slash pine	-1.0143	1.1588	3	0.9844	-	-	1	-	-	-	0	-
Longleaf pine	-0.2027	0.3627	2	0.9688	-	-	3	-	-	-	0	-
Bitternut hickory	0.0761	1.4039	40	0.9861	0.0056	2.0911	38	0.9931	0.4715	2.2621	12	0.7640
Eastern redbud	-0.0956	0.8385	21	0.9852	0.0553	1.8245	13	0.9857	-	-	0	-
Water oak	0.0005	0.4589	37	0.4854	0.0000	0.4320	33	0.9957	-0.0005	0.9971	4	0.9999
Post oak	-0.0992	0.5145	25	0.1037	-0.0005	0.4281	19	0.9879	-0.5920	0.7725	18	0.0346
Black locust	-0.0698	1.1632	17	1.0000	-0.6392	2.7076	11	0.1162	-1.3977	0.2762	9	0.9981
Winged elm	0.0387	0.3347	29	0.3593	0.0305	0.3889	29	0.3513	0.0001	0.4413	5	0.9999

Carson, 2006). When this dynamic is combined with the preferential selection of native tree species by herbivores (Russell et al., 2017), one would expect range expansion of native tree species to be severely limited, especially when combined with extreme weather events (e.g., droughts) that are expected in areas of the eastern US (USGCRP, 2017). For oak species in particular, which constitute the majority with significant displacement of seedlings relative to adults (Table 2), successful regeneration may require specific combinations of light, fire, or moisture, that are increasingly rare over recent decades for forests in the eastern US (Nowacki and Abrams, 2008, Iverson et al., 2017). As suggested by Fei et al. (2017), changes in successional trajectories of eastern US forests over past decades may be of equal importance to expected future climate change in terms of shaping the distributions of future forest ranges.

Fei et al. (2017) have raised an important tree range monitoring consideration which is poleward versus east/westward migration. Our results align somewhat with Fei et al.'s (2017) findings in that for angiosperms exhibiting potential contraction there was a lack of expansion in the eastern US with a potential westward expansion. In our study, post and black oak appeared to have range contraction along the eastern seaboard of the US with range stability (i.e., alignment between

adults and seedlings) in the western portion of their ranges. The range stability or contraction we have found for almost all tree species in our study suggests serious future limitations to maintaining tree species diversity in eastern US forests when combined with future global change factors expected to affect this region. For example, more extreme future climate change events (i.e., more episodic precipitation events) and an increasing prevalence of non-native forest pests and diseases in the eastern US (Lovett et al. 2016; USGCRP, 2017), are expected to increase levels of canopy disturbance in this region. These mortality events in combination with other factors driving regeneration dynamics such as deer browse (Russell et al., 2017), create great uncertainty regarding future regeneration dynamics and generate a significant need for refinement of our understanding of the interaction between disturbance, climate change, and tree recruitment dynamics.

The majority of tree species examined require moderate canopy disturbance for recruitment; however, the lack of recruitment observed for several oak species in this study highlights the importance of disturbance history in affecting contemporary regeneration response. In particular, the importance of fire in stimulating oak recruitment is well documented (e.g., Knapp et al., 2015). Exclusion of fire from much of the eastern US over the past century has led to the development of

Table 3

Summary of differences between 95th percentile latitudinal occurrences between seedlings and trees (degrees, negative value indicates 95th percentile of tree latitudinal occurrence farther north than 95th percentile latitudinal occurrence of seedlings). A difference of zero was assigned for each species when the seedling and tree latitudinal differences was not statistically different (p-value < 0.2) from zero. Results grouped by forecasted changes in future conterminous U.S. range under a Hadley Low (B1) climate scenario (Prasad et al., 2007-ongoing), time period, and disturbance category (disturbed or non-disturbed with canopy gaps).

Species group	Time/Disturbance	Total number of study species	Number of study species with significant difference*	Mean differences (degrees)
Range loss/minimal expansion	Time 1	10	0	-
	Time 2: Non-Disturbance	10	2	-0.1687
	Time 2: Disturbance	8	2	-0.3275
Substantial range expansion	Time 1	10	3	-0.1448
	Time 2: Non-Disturbance	9	1	-0.6392
	Time 2: Disturbance	7	1	-0.5920
All	Time 1	20	3	-0.1448
	Time 2: Non-Disturbance	19	3	-0.3255
	Time 2: Disturbance	15	3	-0.4160

* Differences between 95th percentile latitudinal occurrences of seedlings and trees (p-value < 0.20).

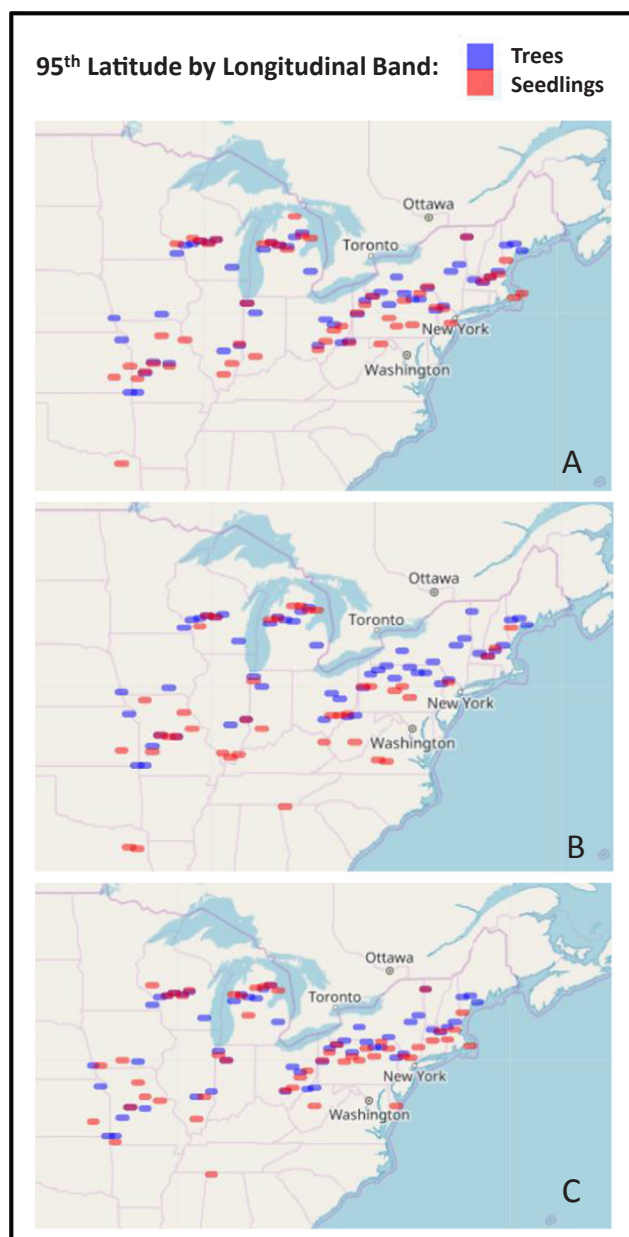


Fig. 2. 95th percentile latitudes of seedlings (red) and trees (blue) by 0.5-degree longitude class for black oak in the eastern U.S.: (A) Time 1: all subplots, (B) Time 2: non-disturbed subplots, (C) Time 2: disturbed subplots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

regeneration layers dominated by shade-tolerant, fire-sensitive species, particularly *Acer rubrum*, largely at the expense of oak regeneration (Nowacki and Abrams, 2008). Overstory *Quercus velutina*, *Quercus alba*, and *Quercus stellata* observed at northern range edges are largely an artefact of historic, intensive land use and fire (Thompson et al., 2013), with contemporary disturbances largely serving to recruit non-oak species in these locations. Although projections of future habitat suitability for these species suggest an increase in suitable areas north of current range margins (Prasad et al., 2007), our findings underscore the importance of accounting for recruitment dynamics and changes in land-use and disturbance regimes (Nowacki and Abrams, 2015) when anticipating future forest conditions. In particular, managers interested in increasing the representation of these species as part of adaptive strategies will also need to include prescribed fire or other site preparation techniques to ensure regeneration conditions are suitable for

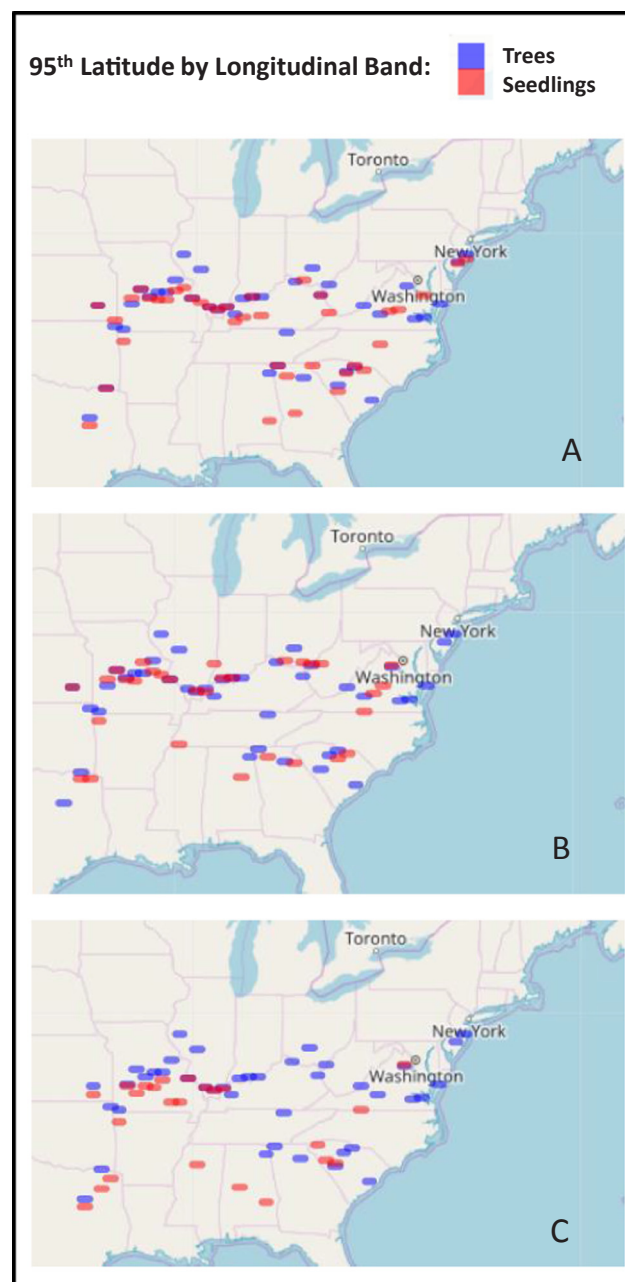


Fig. 3. 95th percentile latitudes of seedlings (red) and trees (blue) by 0.5-degree longitude class for post oak in the eastern U.S.: (A) Time 1: all subplots, (B) Time 2: non-disturbed subplots, (C) Time 2: disturbed subplots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

recruitment of these species (Iverson et al., 2017).

The lack of adequate regeneration to advance tree ranges along northern margins or even range contraction in the case of disturbance may hamper forest management activities. Natural regeneration is often relied upon in silvicultural systems employed in the northeastern US (Oliver and Larson, 1996). The regeneration failure of in situ tree species when canopies are disturbed may not only reduce tree diversity and hence resiliency of forest stands to global change (Messier et al., 2013, Gamfeldt et al., 2013), but also reduce the success of adaptive forest management activities (e.g., Millar et al., 2007). Adaptive management objectives often include artificial establishment of predominantly southern tree species in northern locations as a means to transition a forest to a new condition in anticipation of climate change

(Nagel et al., 2017). By their very definition, such stand transition management activities (Millar et al., 2007, Nagel et al., 2017) require a more extensive list of tree species for consideration (whether through artificial or natural regeneration), which may not be possible given the results of contemporary tree range analyses such as ours. Although these introduced species may be adapted to future climate conditions, similar factors limiting in situ species in these locales (e.g., competition, herbivory) will likely affect regeneration success of future climate-adapted species and should be considered as part of adaptive silviculture strategies.

5. Conclusions

Continued evaluation of indicators of northern range margin stability in forests of the eastern US suggest a lack of regeneration north of current tree distributions for a majority of tree species examined in this study regardless of how forecasted distributions aligned with future climate simulations. For the few species that exhibited potential northern range contraction, disturbance appeared to exacerbate that difference. This disparity in 95th percentile latitudinal occurrence of trees and seedlings appeared to be more pronounced in the eastern portion of the northern range margins with trees markedly farther north suggesting hurdles to tree regeneration. As a hypothesis for further evaluation, since these disparities are located in closer proximity to the Atlantic Ocean in contrast to the central US where climate projections are more extreme, perhaps regeneration challenges could be more attributed to advanced stand age, browse impacts, invasive species, and urbanization/parcelization. Overall, the demonstrated stability of northern range margins suggest future constraints on the ability of trees to track climate change with serious implications for adaptive forest management that relies on a more expansive species list (i.e., both in situ and novel tree species) for successful forest management operations.

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