



Assessing the stability of tree ranges and influence of disturbance in eastern US forests

C.W. Woodall^{a,*}, K. Zhu^b, J.A. Westfall^c, C.M. Oswalt^d, A.W. D'Amato^e, B.F. Walters^a, H.E. Lintz^f

^a USDA Forest Service, Northern Research Station, Forest Inventory and Analysis Program, St. Paul, MN 55108, USA

^b Nicholas School of the Environment, Duke University, Durham, NC 27708, USA

^c USDA Forest Service, Northern Research Station, Forest Inventory and Analysis Program, Newtown Square, PA 19073, USA

^d USDA Forest Service, Southern Research Station, Forest Inventory and Analysis Program, Knoxville, TN 37919, USA

^e Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA

^f College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA

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ABSTRACT

Shifts in tree species ranges may occur due to global climate change, which in turn may be exacerbated by natural disturbance events. Within the context of global climate change, developing techniques to monitor tree range dynamics as affected by natural disturbances may enable mitigation/adaptation of projected impacts. Using a forest inventory across the eastern U.S., the northern range margins of tree distributions were examined by comparing differences in the 95th percentile locations of seedlings to adults (i.e., trees) by 0.5° longitudinal bands over 5-years and by levels of disturbance (i.e., canopy gap formation). Our results suggest that the monitoring of tree range dynamics is complicated by the limits of forest inventory data across varying spatial/temporal scales and the diversity of tree species/environments in the eastern U.S. The vast majority of tree and seedling latitudinal comparisons across measurement periods and levels of disturbance in the study were not statistically different from zero (53 out of 60 comparisons). A potential skewing of ranges towards a northern limit was suggested by the stability of northern margins of tree ranges found in this study and shifts in mean locations identified in previous work. Only a partial influence of disturbances on tree range dynamics during the course of the 5-years was found in this study. The results of this study underscore the importance of continued examination of the role of disturbance in tree range dynamics and refined range monitoring techniques given future forest extent and biodiversity implications.

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1. Introduction

Given the importance of climate as a driver of numerous forest ecosystem functions (Stenseth et al., 2002), current and forecasted changes in climate (IPCC, 2007) have the potential to substantially affect forest ecosystem attributes and functioning (Ryan et al., 2010). The culmination of numerous climate change effects may ultimately be reflected in the contraction/expansion of tree species ranges (Walther et al., 2002; Malcolm et al., 2002; Parmesan and Yohe, 2003; Botkin et al., 2007; Chen et al., 2011). Tree ranges are dynamic with substantial documentation of their change over the course of millennia (Clark et al., 1998; Davis and Shaw, 2001; McLachlan et al., 2005; Pearson, 2006), as well as over recent decades (Woodall et al., 2009; Lenoir et al., 2009). In light of contemporary climate change, several observational investigations on plant species have indicated that current rates of range shifts may be greater than historic rates with a predominant focus on

responses across elevation as opposed to latitude (Walther et al., 2005; Beckage et al., 2008; Holzinger et al., 2008; Kelly and Goulden, 2008; Lenoir et al., 2008; Harsch et al., 2009; Lenoir et al., 2009; Crimmins et al., 2011; Feeley et al., 2011; Van Bogaert et al., 2011). Correspondingly, it has been suggested that climate may change at a rate beyond the adaptability of tree species resulting in range contractions or extirpations (Clark et al., 1998; Malcolm et al., 2002; McLachlan et al., 2005; Iverson et al., 2008; Bertrand et al., 2011a). Unfortunately, latitudinal range shifts are poorly understood due to the requirement of large datasets across broad geographic scales (Woodall et al., 2009; Murphy et al., 2010; Zhu et al., 2012). Given the profound effects that climate change may have on forest biodiversity (Botkin et al., 2007) or even forest extent, monitoring the status and dynamics (e.g., effects of invasive species or disturbance effects) of tree ranges is paramount.

Due to the complex ecosystem dynamics that define current tree ranges, determining the causal agents of tree range shifts is difficult with individual tree species responding in an apparent idiosyncratic manner to climate change (Lenoir et al., 2008; Doak and Morris, 2010). The migratory response of tree species to climate

* Corresponding author. Tel.: +1 651 649 5141; fax: +1 651 649 5140.

E-mail address: cwoodall@fs.fed.us (C.W. Woodall).

change events may depend on genetic attributes (Potter and Woodall, 2012), habitat quality/continuity (i.e., forest fragmentation; Schwartz et al., 2001), demography (Anderson et al., 2009), modes of seed dispersal (Iverson et al., 2008), competition (Moorcroft et al., 2006), and response to natural disturbance (i.e., canopy gap formation; Leithead et al., 2010). The monitoring of tree species ranges can be advanced by examining their variability over short time-steps and how factors such as forest disturbance influence them.

Within closed canopy forests, there is a wider suite of temperate tree species (e.g., *Acer rubrum*) that show preferential colonization in large canopy gaps compared to species that are more common to boreal environments (e.g., *Picea mariana*) in eastern North America (Leithead et al., 2010). Thus, habitat quality, competition, demography, and species-level adaptation likely interact to affect rates of species migration. Forest canopy gaps (i.e., tree fall gaps) are caused by the death and fall of a tree of sufficient size to result in an opening of the overstory canopy (Denslow, 1980). While canopy gaps may change tree competition dynamics in a rapid manner (Scheller and Mladenoff, 2005; Leithead et al., 2010), our understanding of the effects of disturbances such as forest canopy gaps on tree range shifts at large spatial scales have often been limited to simulation studies (Scheller and Mladenoff, 2005), with only localized, empirical examinations of the effects of canopy gaps on range shifts (Leithead et al., 2010). As such, there are key knowledge gaps related to the range-wide impact of canopy gaps on changes in tree species distributions.

Several approaches have been used to empirically assess large-scale shifts in current tree ranges, including examinations of tree occurrence across elevational gradients (Kelly and Goulden, 2008; Lenoir et al., 2008), comparisons of tree ranges from historical and contemporary inventories (Woodall et al., 2008), and comparisons of seedling and adult tree extent (Lenoir et al., 2009; Woodall et al., 2009), or some combination thereof. Numerous aspects of tree ranges have been examined, such as measures of tree range central tendency (Woodall et al., 2009) or tree range limits (Zhu et al., 2012). Taken together, refined understanding of the variability of tree range margins over short time-steps may be acquired through development of techniques that empirically assess tree range expansion/contraction and naturally occurring interactions across large scales. Using a large-scale forest inventory to examine northern range limits by life stage (i.e., seedlings versus adults; see Woodall et al., 2009), while considering the effect of recent tree canopy gaps, offers the potential to refine the monitoring of tree latitudinal ranges. Therefore, the two objectives of this study were (1) to evaluate the stochasticity (i.e., range expansion or retreat) of northern range limits of eastern U.S. tree species by comparing latitudinal occurrences of trees and their associated seedlings by individual tree species at 0.5-degree lines of longitude in eastern U.S. forests and (2) to determine if said stochasticity is influenced by forest disturbance (i.e., canopy gaps).

2. Methods

2.1. Study tree selection

The selection of tree species for the purpose of evaluating indicators of range shifts can influence study results (Woodall et al., 2010). Numerous species selection criteria were established in an effort to objectively accomplish study objectives. First, lists of the most common tree species in the eastern U.S. were determined: top 50 in terms of tree abundance and top 50 in terms of seedling abundance (for a total of 62 tree species). Second, species were eliminated from this list of common tree species whose range (according to Little, 1971) substantially extended beyond the

49th parallel into Canada. At most, tree species could only have portions of their northern limits well-below the 49th parallel (e.g., southeastern Ontario). It is hoped that this criterion would negate many of the statistical censorship issues inherent with tree ranges that extend into Canada as there is no consistent forest inventory across the international border. Third, all tree species were ordered according to the forecasted range expansion/contraction as simulated within Prasad et al.'s (2007–ongoing) future potential tree habitat models using the low emission Hadley climate scenario (B2). Through combination of all these criteria, two study species lists (10 species each) were created: (a) common tree species with no substantial component of their range in Canada and likely to experience either a loss in range or minimal range expansion in the U.S. under a future climate scenario and (b) common tree species with no substantial component of their range in Canada and likely to experience substantial range expansion in the U.S. under a future climate scenario (Table 1). It can be hypothesized that trees forecasted to have the greatest future range expansion or contraction (i.e., future range change) might demonstrate the greatest contemporary northern margin variability potentially exacerbated by disturbances.

2.2. Data

The USDA Forest Service's Forest Inventory and Analysis (FIA) program is the primary source for information about the extent, condition, status and trends of forest resources across all ownerships in the U.S. (Bechtold and Patterson, 2005). FIA applies a nationally consistent sampling protocol using a quasi-systematic design covering all ownerships in the entire nation (Bechtold and Patterson, 2005). FIA operates a multi-phase inventory based on an array of hexagons assigned to separate interpenetrating, non-overlapping annual sampling panels. In Phase 1, land area is stratified using aerial photography or classified satellite imagery to increase the precision of estimates using stratified estimation. Remotely sensed data may also be used to determine if plot locations have forest land cover; forest land is defined as areas at least 10% stocked with tree species, at least 0.4 ha in size, and at least 36.6 m wide. In Phase 2, permanent fixed-area plots are installed in each hexagon when field crews visit plot locations that have accessible forest land. Field crews collect data on more than 300 variables, including land ownership, forest type, tree species, tree size, tree condition, and other site attributes (e.g., slope, aspect, disturbance, land use) (USDA Forest Service, 2008). Plot intensity for Phase 2 measurements is approximately one plot for every 2428 ha of land (roughly 125,000 plots nationally) which is remeasured every five years in the eastern U.S. Briefly, 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. 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. Within each microplot, all live tree seedlings are tallied according to species. Additionally, all trees with a d.b.h. between 2.5 and 12.7 cm are inventoried. Conifer seedlings must be at least 15.2 cm in height with a root collar diameter less than 2.5 cm. Hardwood seedlings must be at least 30.5 cm in height with a root collar diameter less than 2.5 cm. Individual subplots with no anthropogenic disturbances (e.g., harvest) and fully occupied by a forest condition (i.e., no other land uses such as agricultural) at both measurement times were considered individual study observations. As an objective of this study is to evaluate the effect of disturbance (e.g., canopy gap formation) on seedling/tree range variability across northern range margins, it was felt that subplots needed to be examined individually as opposed to pooling data from all the subplots within one FIA inventory plot.

Table 1

Study tree species common/Latin name, number of subplot observations, and forecasted change in conterminous U.S. range (percent area) under a future Hadley Low (B2) climate scenario (see Prasad et al., 2007–ongoing). Species assigned to one of two groups: (1) species with forecasted range loss or minimal expansion, and (2) species with substantial forecasted range expansion.

Common name	Latin name	Observations	Range change (%)
<i>Species with range loss or minimal expansion</i>			
Sweet birch	<i>Betula lenta</i>	3256	–11.5
American beech	<i>Fagus grandifolia</i>	10,170	–7.6
Sourwood	<i>Oxydendrum arboreum</i>	4229	–7.1
Black cherry	<i>Prunus serotina</i>	19,153	2.2
White oak	<i>Quercus alba</i>	16,645	10.0
Scarlet oak	<i>Quercus coccinea</i>	4427	–23.9
Chestnut oak	<i>Quercus prinus</i>	5622	8.0
Northern red oak	<i>Quercus rubra</i>	15,717	–0.1
Black oak	<i>Quercus velutina</i>	10,426	13.5
American basswood	<i>Tilia americana</i>	5012	–10.7
<i>Species with substantial range expansion</i>			
Eastern red cedar	<i>Juniperus virginiana</i>	6188	66.9
Shortleaf pine	<i>Pinus echinata</i>	3218	57.6
Slash pine	<i>Pinus elliotii</i>	1450	110.4
Longleaf pine	<i>Pinus palustris</i>	779	77.2
Bitternut hickory	<i>Carya cordiformis</i>	3882	85.3
Eastern redbud	<i>Cercis canadensis</i>	2719	62.0
Water oak	<i>Quercus nigra</i>	5677	74.3
Post oak	<i>Quercus stellata</i>	4600	67.4
Black locust	<i>Robinia pseudoacacia</i>	1689	62.5
Winged elm	<i>Ulmus alata</i>	4899	142.6

The attributes of a seedling microplot should correlate well with the attributes of the surrounding subplot (e.g., canopy gaps).

All inventory data are managed in an FIA database (FIADB, <http://apps.fs.fed.us/fiadb-downloads/datamart.html>) and are publicly available. Data for this study were taken entirely from the FIADB using the most recent annual inventory in 28 eastern states on a total of 64,854 subplots (derived from 37,482 plots) (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 1998 and 2003 with subsequent re-measurement 5-years later, so sample intensities may vary by state. Because the FIA inventory is systematic with sample plots distributed across the geographic extent of each state, varying sample intensities will not bias assessment of tree species locations, it will only affect the precision of the estimates. Finally, public law stipulates that actual plot location coordinates will not be publicly released (McRoberts et al., 2005).

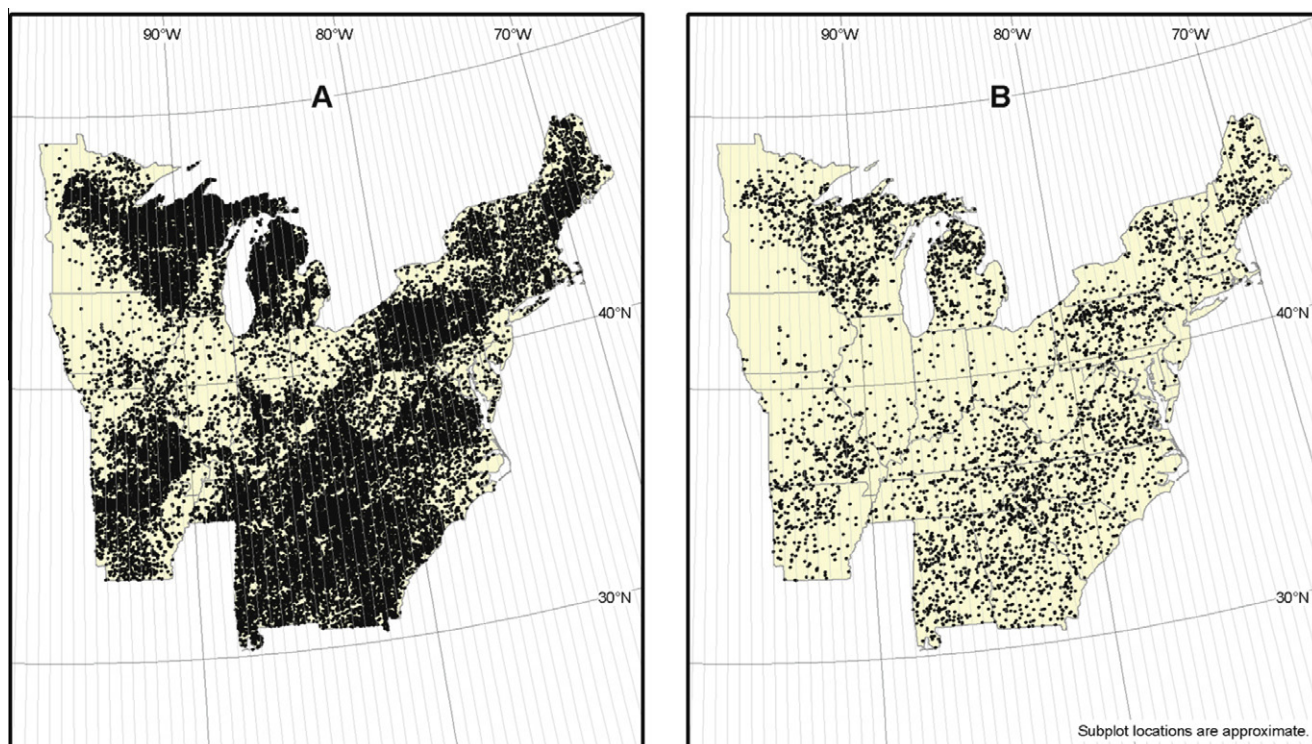


Fig. 1. Study observation locations (A) non gap-disturbed forested subplots, (B) gap disturbed forested subplots.

As such, the longitude and latitude of most plot locations in this study have been perturbed in an unbiased direction not exceeding 1.67 km, and typically within a 0.8 km radius of the actual plot location. As these location perturbations are mandated by law and are randomly applied, these locations were used to facilitate study repeatability while introducing no bias.

2.3. Analysis

This study combines aspects of analytical procedures from a variety of work. Based on Woodall et al. (2009), seedling abundance (i.e., seedling counts) was compared to tree abundance (i.e., biomass of adults) as an indicator of northern range margin shifts. Based on Zhu et al.'s (2012) longitudinal band analysis (LBA), changes in range margins (i.e., expansion or contraction) may be examined by separating a tree's range into longitudinal bands and comparing latitudinal percentiles of seedling and tree locations across all bands. In this process, longitudinal bands serve as replication. Finally, based on work by Leithhead et al. (2010), the influence of canopy gap formation was determined by assigning study plots to either a gap-disturbed or a non-disturbed category. Based on these previous studies, variations of these approaches were developed to accomplish study objectives. First, only the northern latitudinal distribution of seedlings/trees was examined. As the Gulf of Mexico and Atlantic Ocean serve as a natural southern barrier to tree range shifts, full expression of tree range shifts is confounded along with the lack of remeasured inventory plots in Florida, Louisiana, and Mississippi. Second, the width of longitudinal bands and specific percentiles can vary (Zhu et al., 2012). As Zhu et al. (2012) found, the width of the longitudinal bands and selection of percentile did not have an effect on tree range shift conclusions. The longitudinal band width of 0.5° and the 95th percentile distribution of tree species latitude were selected in this study as the 95th percentile reduces the possible impact of measurement errors inherent in a national-scale inventory (i.e., hundreds of field crew measuring a million trees). For each species, a minimum of 10 longitudinal bands and three 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. Although more conservative criteria (e.g., >3 observations per band) should be considered for future applications of this study's technique, as an initial exploration we balanced the need for maximizing observations within longitudinal bands with replication among bands. 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 stochasticity over time.

All study observations (i.e., subplots) were assigned to one of two disturbance categories: canopy gap-disturbed and non canopy gap-disturbed. It was postulated that changes in tree exposed crown area (ECA) in proximity to seedling monitoring plots (i.e., FIA microplots) would be indicative of canopy gap-disturbances. A parsimonious approach to identifying canopy-gap disturbed subplots was adopted that combines crown area calculations with an indicator of mortality close to seedling measurements. First, differences in live tree ECA between time one and two was determined by assigning all tree species to ECA species group models developed by Lorimer and Frelich (1989). Second, to exclude mortality (i.e., reductions in ECA over time) that was far from the microplot seedling measurements, the weighted mean (by tree diameter) distance of tree mortality from microplot center was determined. Initial examinations between ECA reductions and seedling counts indicated that mortality greater than 5 m from microplot center was not highly correlated with seedling occurrence/change. Combining these two metrics, canopy gap-disturbed subplots were de-

fined as having less ECA at time two than time one and a mean weighted tree mortality distance to microplot center less than 5 m. All other study observations were considered non-gap disturbed subplots. Our LBA was used to compare the locations of seedlings to trees at both time one and two across a 5-years remeasurement interval. If northern range limits were stochastic one would expect seedlings to be farther away from their associated adults (i.e., trees) at time 2 compared to the difference at time 1 (and vice versa). The 5-years interval was used to assess disturbance impact on short-term range variability. We made no attempt to compare only trees or only seedlings between time 1 and 2 (i.e., range shift) because the 5-years interval may be too short to detect species range shift.

In order to test the null hypothesis that the difference in the 95th percentile of seedling latitudinal occurrence minus the 95th percentile of tree latitudinal occurrence was not significantly different from zero, Wilcoxon signed-rank tests were conducted (p -value < 0.1) for time 1, time 2 non-disturbed, and time 2 disturbed observations by each individual 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. As it can be argued that some of the study species overlap across the plot network, a Bonferroni adjustment was conducted to this study's alpha level of 0.1 resulting in an multiple-test adjusted alpha level of 0.005 (assuming 20 study species equaled 20 multiple tests).

3. Results

Medians of differences between the 95th percentile latitude of seedling and tree occurrence across longitudinal classes for individual study species (negative number indicates trees farther north than seedlings) suggested northern range limit stability for most study species over a short time-step (5-years) (Table 2). Across all measurement periods and disturbed or non-disturbed plots, 53 out of 60 seedling versus tree comparisons were not significantly different from zero (p -value \geq 0.005). When viewing seedling versus tree comparisons where there was a significant difference (p -value \leq 0.005), 4 out of the 7 comparisons suggested that trees were farther north than their associated seedlings (i.e., range retreat). For time 1, time 2 undisturbed, and time 2 disturbed subplots, shortleaf pine (*Pinus echinata*), eastern red cedar (*Juniperus virginiana*), and black oak (*Quercus velutina*) had the largest significant difference (alpha \leq 0.005) between their 95th percentile of seedling and tree locations (-0.910° [-100.5 km], -0.429° [-47.4 km], and -0.435° [-48.1 km], respectively) indicating possible northern range margin retreat.

The spatial distribution of subplot observations and 95th percentiles across longitudinal bands were examined for two study species. Chestnut oak (*Quercus prinus*) has reasonable agreement among the locations of the 95th percentile of its associated seedlings and trees within each longitudinal band (Fig. 2, as indicated by the $y = x$ diagonal) both at time 1 and for undisturbed time 2 subplots indicating northern range limit stability. On disturbed subplots the vast majority of chestnut oak seedling and tree latitudinal pairs within the longitudinal bands still suggested range stability despite a difference of -0.355° (-39.2 km) (Table 2, p -value = 0.0151). In contrast, eastern red cedar had indications of northern range margin retreat due to disparity in locations of the 95th percentile of its associated seedlings and trees within each longitudinal band (Fig. 3, as indicated by the $y = x$ diagonal) at time 1 (-0.429° [-47.4 km], p -value < 0.001) but results at time 2 non-disturbance (-0.344° [-38.0 km], p -value = 0.0116) and disturbance (-0.374° [-41.3 km], p -value = 0.0437) categories still suggested no statistical difference.

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 (1998–2004) and at time 2 (5-years subsequent to time 1) for both non-disturbed and disturbed subplots (with or without canopy gaps). Negative values indicate median latitudes of adult trees are further north than seedling median latitudes. (Note: IQR = interquartile range, *n* = number of longitudinal bands).

Common name	Time 1				Time 2: non-disturbed				Time 2: disturbed			
	Median	IQR	<i>n</i>	<i>p</i> -Value	Median	IQR	<i>n</i>	<i>p</i> -Value	Median	IQR	<i>n</i>	<i>p</i> -Value
Sweet birch	0.000	0.291	29	0.8593	−0.017	0.303	27	0.5114	0.000	0.742	11	1.0000
American beech	0.000	0.108	49	0.6626	0.000	0.077	49	0.3602	0.000	0.104	40	0.3500
Sourwood	0.000	0.280	25	0.5597	0.040	0.204	24	0.1815	0.000	1.079	15	0.5693
Black cherry	0.048	0.381	56	0.0493	0.023	0.400	54	0.2577	0.085	1.276	41	0.0046
White oak	0.008	0.500	51	0.6861	−0.021	0.454	51	0.3087	−0.122	1.037	38	0.0225
Scarlet oak	−0.014	0.636	36	0.4249	−0.152	0.880	35	0.0152	−0.200	0.744	12	0.7002
Chestnut oak	0.000	0.350	32	0.8414	0.000	0.291	30	0.8448	−0.355	1.320	20	0.0151
Northern red oak	0.122	0.460	58	0.0008	0.130	0.319	58	0.0008	0.049	0.806	46	0.1528
Black oak	0.012	0.422	45	0.5500	−0.036	0.771	48	0.0129	−0.435	2.185	29	<0.0001
American basswood	−0.028	0.334	46	0.0167	0.000	0.206	40	0.4994	−0.037	0.401	14	0.0942
Eastern red cedar	−0.429	2.718	38	<0.0001	−0.344	3.790	39	0.0116	−0.374	1.557	26	0.0437
Shortleaf pine	−0.910	2.288	26	<0.0001	−0.208	1.638	25	0.0063	–	–	–	–
Slash pine	−0.136	0.453	12	0.2402	−0.295	0.712	10	0.0078	–	–	–	–
Longleaf pine	−0.167	0.358	15	0.0017	−0.051	0.741	12	0.0371	–	–	–	–
Bitternut hickory	−0.009	0.951	40	0.1258	−0.173	1.200	41	0.0342	0.000	0.410	18	0.6257
Eastern redbud	−0.130	0.890	34	0.9791	−0.058	0.714	33	0.7136	–	–	–	–
Water oak	0.0001	0.268	33	0.5783	−0.028	0.320	33	0.5915	−0.057	0.994	20	0.9661
Post oak	−0.173	0.893	45	0.0320	−0.200	0.548	33	0.0846	−0.260	1.123	13	0.0371
Black locust	−0.357	1.720	26	0.0875	−0.717	1.851	27	0.0214	–	–	–	–
Winged elm	0.000	0.283	35	0.3760	0.000	0.302	36	0.2947	0.000	1.349	18	0.2334

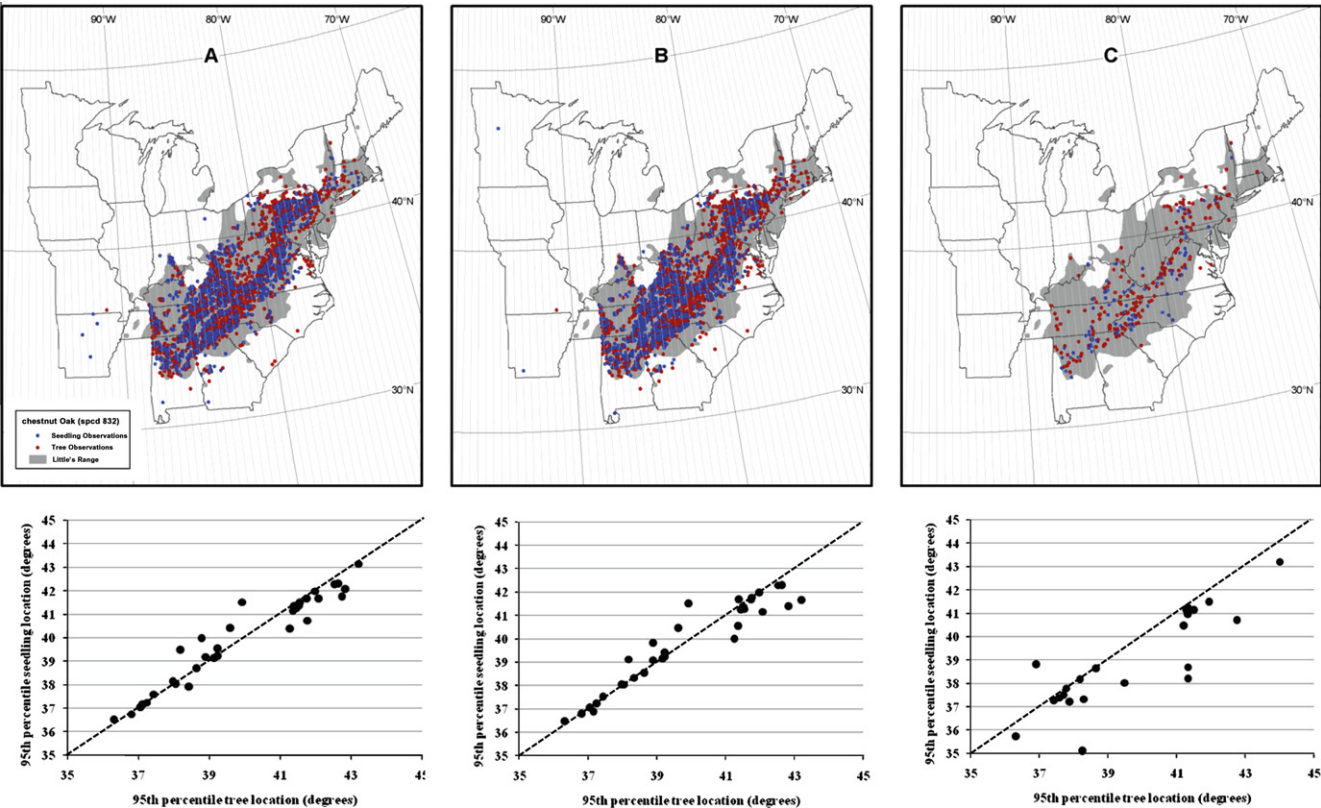


Fig. 2. 95th percentile of seedlings and trees by 0.5-degree longitude class for chestnut oak in the eastern U.S.: (A) Time 1: all subplots. (B) Time 2: non-disturbed subplots. (C) Time 2: disturbed subplots. (Note: given the map's spatial scale, more than one subplot can occur at each plot location).

The results of individual species differences were pooled to generate means by species group (e.g., forecasted range loss/expansion) and time/disturbance (Table 3). Mean differences (zero assigned to each difference not statistically different from zero, *p*-value < 0.005) between trees and their associated seedlings over the 5-years time-step were only slightly different from zero. Due to the variability and weak results, no

robust conclusions can be drawn regarding expansion/contraction hypotheses. However, slight tendencies were apparent such as non-disturbed forests demonstrating range stability with cases of northward expansion. Disturbed forests also tended to have northern margin stability, but with a few instances of range contraction. Range expansion was only found at time 1 and for non-disturbed forests, suggesting a slight

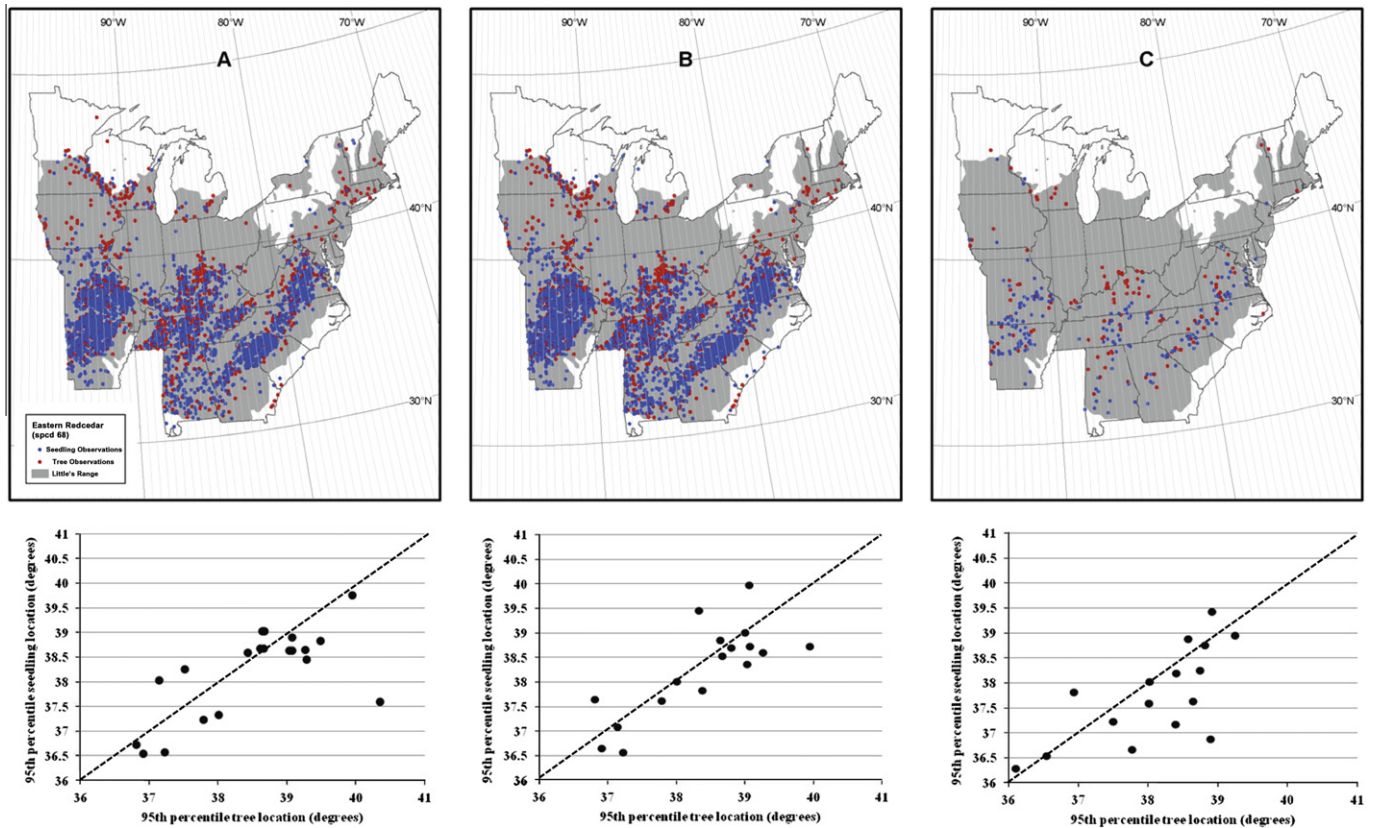


Fig. 3. Maps of study observations and 95th percentile of seedlings and trees by 0.5-degree longitude class for eastern red cedar in the eastern U.S.: (A) Time 1: all subplots. (B) Time 2: non-disturbed subplots. (C) Time 2: disturbed subplots. (Note: given the map's spatial scale, more than one subplot can occur at each plot location).

Table 3

Summary of differences between 95th percentile latitudinal occurrences between seedlings and trees (degrees, negative mean 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 < 0.005) from zero. Results grouped by forecasted changes in future conterminous U.S. range under a Hadley Low (B2) 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 (°)
Range loss/minimal expansion	Time 1	10	1	0.012
	Time 2: non-disturbance	10	1	0.013
	Time 2: disturbance	10	2	−0.035
Substantial range expansion	Time 1	10	3	−0.151
	Time 2: non-disturbance	10	0	0.000
	Time 2: disturbance	5	0	0.000
All	Time 1	20	4	−0.069
	Time 2: non-disturbance	20	1	0.007
	Time 2: disturbance	15	2	−0.023

* Differences between 95th percentile latitudinal occurrences of seedlings and trees (p -value < 0.005).

negative influence of disturbance on the northern margin of tree ranges.

4. Discussions

There appears to be a lack of latitudinal range expansion along the northern range frontiers of tree species examined in this study suggesting contemporary range stability over short time-steps for most study species. The tendencies for disturbances to either have minimal effect on ranges (for species forecasted to gain range under future climatic scenarios) or slight reduction in range (for species forecasted to lose range under future climatic scenarios) demonstrates the role that disturbances may play in future tree

ranges. The nuanced results also demonstrate the difficulties that lie ahead for monitoring tree ranges given the complex of individual tree species' traits, response to disturbance, demography, and response to a changing climate. As Gaston's (2009) discussion highlighted and has been found in this study, the limits to species' ranges are quite variable with static persistence, abrupt changes to viable populations, or a gradual waning (i.e., contraction). Although past evaluations of tree regeneration in detailed research plots over short time steps (<5-years) has indicated potential patterns in range shifts (Leithead et al., 2010), the monitoring of national-scale tree ranges may require substantial time steps (>5-years) to detect statistically significant differences across a variety of species and environments.

Our results suggest the absence of substantial range expansion at most species' northern range limits, a result consistent with Zhu et al. (2012). This analysis is one of the few studies examining latitudinal range shifts of many plant species. Contemporary range shifts are frequently observed from elevational shifts in mountain regions, and then mirrored to latitudinal shifts based on altitude-for-latitude substitution (Jump et al., 2009). We confirm the validity of this logic, but suggest that range shifts could be several orders of magnitude greater in distance if upward elevational shifts are translated into latitudinal shifts. For example, Colwell et al. (2008) demonstrated that a 1 °C increase in mean annual temperature corresponds to ~167 m elevational difference, but with a ~145 km latitudinal difference (Fig. 1 in Jump et al., 2009). In the eastern U.S., the climate change velocity (i.e., the required migration distance for species to keep pace with climate change) is much greater in areas with minimal topography (e.g., Midwest and Coastal Plains) than mountainous ones (e.g., Appalachian Mountains) (Fig. 2 in Loarie et al., 2009). The much greater latitudinal distance required for trees to offset climate change may exceed the seed dispersal capacity, making it much more difficult to migrate northward than upwards. Furthermore, there could also be substantial lags between climate change and tree range response, implying that the leading edge migration rates will not keep pace with the rate of climate change. Despite the nearly 1000 km northward shift in temperature isolines across parts of the eastern U.S. over the course of the last century (Fig. 1b in Zhu et al., 2012), this study did not find northern margin expansion. This potential migration lag could be explained by the spatial fragmentation of the forested landscape (Bertrand et al., 2011) with resultant local refugia promoted by diversity in physiography across the landscape (Dobrowski, 2011). Entwined within these dynamics are the non-climatic factors (e.g., soil) and biotic interactions (e.g., competition) that may also contribute to species specific range shift patterns.

The general characteristic of northern range margin stability found in this study with a slight tendency towards contraction (especially in disturbed forests) is in contrast to the simulations by Iversen et al. (2008), which suggest range retreat for only a few tree species under the Hadley Low (B2) future climate scenario, while the vast majority of their future modeled habitats suggest northern range margin expansion. However, the future scenarios are for climates potentially centuries from the present which may not compare to the stochasticity seen over a 5-years time-step. Present day empirical indicators of tree range shifts should be used in concert with bioclimatic envelope models for robust monitoring of contemporary tree ranges. The use of field-based assessments of range shifts allows for a detection of community-level successional and developmental dynamics potentially overlooked by species-specific models heavily influenced by climatic conditions. Given the complex dynamics inherently associated with plant ranges (e.g., ontogenetic niche shifts, see Bertrand et al., 2011b; confounding abiotic factors such as soils, see Urbietta et al., 2011), further conclusions from this study are limited suffice to say that the monitoring of all life stages of trees may be critical to mitigating potential climate change effects.

Canopy gap disturbances may facilitate the northern range limit retreat of some study species, especially for species forecasted to lose areal extent under future climate scenarios (e.g., scarlet oak, *Quercus coccinea*). The few species with significant differences in seedling versus tree locations for species forecasted to lose their range indicated a slight influence of disturbance increasing the northern range margin retreat of tree species (0.012 to −0.035° [1.33 to −3.87 km]). Emerging work by Van Bogaert et al. (2011) suggests a similar finding that disturbance may be a stronger controlling factor on tree ranges than recent climatic trends. If the slight trends identified in this study (e.g., influence of disturbance

and lack of northern margin expansion) became more pronounced over longer time intervals (e.g., >5 years) coupled with global climate change possibilities (e.g., stressors such droughts; Running, 2008) then forest extent could be at risk for reductions and/or loss of tree species diversity in the future. The question remains as to whether the regeneration of tree species can successfully establish themselves beyond their current ranges (Zhu et al., 2012) or if this study's findings are reflective of normal offspring population dynamics in response to varying abiotic factors (Urbietta et al., 2011). If indeed tree ranges have a greater propensity for contraction, species range predictions generated from niche models may not adequately describe the complexity of mechanisms behind species ranges (Dawson et al., 2011), in particular tree regeneration.

The trends we detected in northern range margins also highlight the importance of integrating an understanding of how successional trajectories depend on past land-use and disturbance patterns. Such interactions should be characterized given the stochasticity of tree species ranges and the challenge they pose with respect to mechanistic understanding and modeling. For example, our approach detected slight northern range margin retreat for eastern red cedar at time 1; however, these patterns likely reflect successional versus climatic dynamics. In particular, this species typically colonizes abandoned fields and ultimately succeeds to later successional forest species over time, independent of climate conditions (Meiners and Gorchoy, 1998). Similarly, the lack of expansion for chestnut oak and shortleaf pine on disturbed plots reflects successional dynamics, as regeneration from these canopy species are unable to compete with seedlings of more shade tolerant species, including red maple (Abrams, 1992; Bragg and Shelton, 2011). These findings underscore the importance of accounting for community dynamics in conjunction with individualized, climate-based predictions for a given species.

Given the diversity of tree species and forest conditions across the eastern U.S., numerous caveats and suggested future tree range monitoring research can be suggested. First, the 5-years re-measurement period is a relatively short time frame. Statistical power to infer tree range migration dynamics may be increased by re-examining this study's findings over longer lengths of time. Furthermore, the source-sink population dynamics of tree populations (Pulliam, 1988), especially at northern range margins, are not fully understood for all the species in this study. Natural fluctuations in tree fecundity might be misinterpreted for range retreat. Second, although the northern range limit censorship issue (i.e., the Canadian border) will probably not be overcome, the southern ranges of eastern tree species should be examined in the context of Gulf of Mexico as a barrier to migration and its effects on tree ranges. Third, changes in exposed crown area across time and distance from seedlings were incorporated into a canopy gap-disturbance indicator in this study; however, future work should explore the development of refined gap-disturbance metrics within the U.S.'s national inventory. Finally, this study did not establish relationships between indicators of tree range shifts and climatic/management variables. Emerging research suggests that tree regeneration indeed may be a sensitive indicator of climate change in forest ecosystems (Leak and Yamasaki, 2010; Treyger and Nowak, 2012). As tree regeneration can be episodic and related to climate/management variables, its incorporation into future tree range models may further elucidate tree range shift dynamics. It can be further speculated that although future habitat models (Iversen et al., 2008) may predict northern range margin expansion based on consistent changes in climate parameters (i.e., increasing mean temperatures), the potential of increased climatic variability (McLaughlin et al., 2002) may reduce successful tree regeneration (Urbietta et al., 2011) resulting in sink populations.

Finally, past work has indicated that mean location of seedlings relative to trees may be farther north, thus indicating a northward shift (Woodall et al., 2009). In contrast, examination of the outer northern ranges of tree species in this study and others (Zhu et al., 2012) appear to indicate range stability and/or retreat for study species. Do these results conflict? It can be hypothesized that tree species regeneration within current ranges may be more successful at higher latitudes, but demonstrating an inability to establish in the northern fringe or beyond their current range. In concert with this trend, it may be possible that regeneration is failing at a species very southern extent (i.e. classic range contraction). By analyzing abundance data, Murphy et al. (2010) suggests that North American tree species may experience loss of southern ranges coupled with limited northern range expansion resulting in a loss of species total extent. The northward skewing of seedlings versus trees (i.e., adults) over time may create the situation where mean seedling locations are at higher latitudes compared to mean tree latitudes, but their 95th percentiles may be converse (Fig. 4). Both statistics of central tendency (Woodall et al., 2009) and range margins (i.e., this study) may need to be considered simultaneously to more accurately monitor possible tree range shifts and identify potential “tipping points” (Doak and Morris, 2010). The shifting of temperature isolines across the study area (Zhu et al., 2012) raises the possibility that tree regeneration may continue to be skewed towards its northern range margin if warming trends continue. Coupled with these statistical issues regarding range monitoring, the substantial tree species diversity, diverse geography, and anthropogenic footprint across the eastern U.S. forests may create wide-ranging and often species-specific responses to not only canopy gap disturbances events but also global climate change.

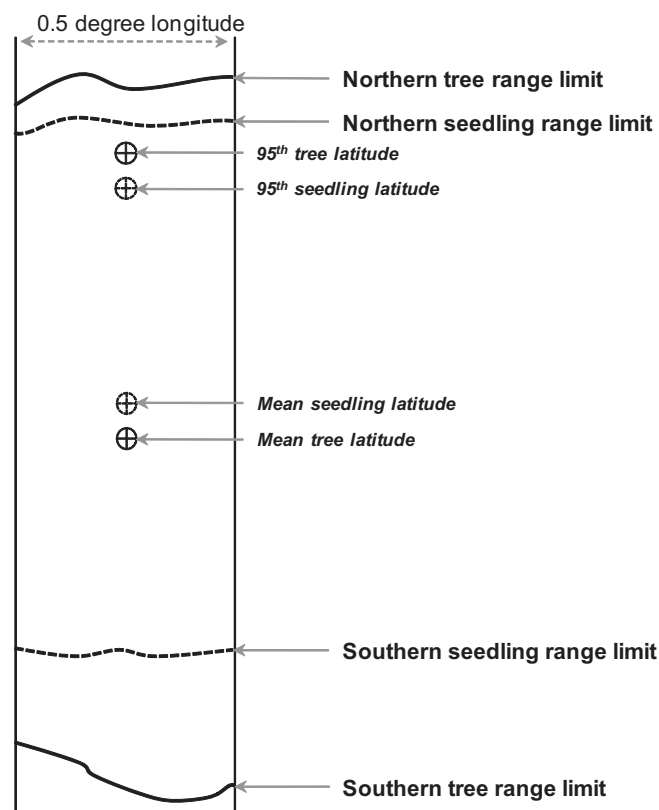


Fig. 4. Illustration of ranges of seedlings and trees for a tree species experiencing range contraction while median latitude shifts northward.

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