



An indicator of tree migration in forests of the eastern United States

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ABSTRACT

Changes in tree species distributions are a potential impact of climate change on forest ecosystems. The examination of tree species shifts in forests of the eastern United States largely has been limited to simulation activities due to a lack of consistent, long-term forest inventory datasets. The goal of this study was to compare current geographic distributions of tree seedlings (trees with a diameter at breast height ≤ 2.5 cm) with biomass (trees with a diameter at breast height > 2.5 cm) for sets of northern, southern, and general tree species in the eastern United States using a spatially balanced, region-wide forest inventory. Compared to mean latitude of tree biomass, mean latitude of seedlings was significantly farther north (> 20 km) for the northern study species, while southern species had no shift, and general species demonstrated southern expansion. Density of seedlings relative to tree biomass of northern tree species was nearly 10 times higher in northern latitudes compared to southern latitudes. For forest inventory plots between 44° and 47° north latitude where southern tree species were identified, their biomass averaged 0.46 tonnes/ha while their seedling counts averaged 2600 ha⁻¹. It is hypothesized that as northern and southern tree species together move northward due to greater regeneration success at higher latitudes, general species may fill their vacated niches in southern locations. The results of this study suggest that the process of northward tree migration in the eastern United States is currently underway with rates approaching 100 km/century for many species.

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1. Introduction

Due to a doubling of pre-industrial atmospheric carbon dioxide concentrations, the world's climate is forecasted to change significantly over the next century, resulting in an increase in mean surface temperatures of 2–4.5 °C, more episodic precipitation events, and a lengthening in growing seasons (IPCC, 2007). These climate change effects are predicted to be especially prominent at middle and higher latitudes (IPCC, 2007). Climate is an important driver of forest ecosystem functions (Stenseth et al., 2002), thus changes in climate should change forest ecosystem attributes and functions. Increases in carbon dioxide concentration is expected to increase tree biomass increment through fine root and woody biomass growth (Ainsworth and Long, 2005; Norby et al., 2002, 2004). Fitness of trees is expected to be impacted by changes in absolute temperatures and the timing/amount of precipitation events (Saxe et al., 1998; Nabuurs et al., 2002; Sacks et al., 2007), along with a higher probability of

catastrophic wildfires in regions of the United States (Westerling et al., 2006). These effects on individual tree fitness are forecasted to subsequently affect tree response to stress agents such as insects and disease (Volney and Fleming, 2000; Logan et al., 2003). The combination of numerous climate change effects on forest ecosystems may ultimately be the migration of tree species (Opdam and Wascher, 2004; Walther et al., 2002).

There is evidence of past forest migration rates exceeding 50 km per century during episodes of climate change (Schwartz, 1992; Noss, 2001; Parmesan and Yohe, 2003). An important question is whether predicted future climate change will be at a rate that exceeds a tree species' capacity to migrate resulting in species extirpation/extinction or the conversion of forests to grasslands or other systems (Iverson and Prasad, 2002; Woodwell et al., 1998; Davis and Shaw, 2001). Forests may need to migrate one order of magnitude faster than in past migrations in order to adequately respond to current rates of warming (Schwartz, 1992). However, modern day fragmentation of forest ecosystems may inhibit the movement of tree species, potentially reducing tree migration capacity by one order of magnitude (Schwartz et al., 2001; Davis and Shaw, 2001; Walther et al., 2002; Opdam and Wascher, 2004).

Examination of tree species migration largely has been conducted by investigating historic ranges during the past

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millennia (for example see Davis and Shaw, 2001; Malcolm et al., 2002; McLachlan et al., 2005; Pearson, 2006) and simulating future tree species shifts (for example see Schwartz et al., 2001; Iverson and Prasad, 1998; Iverson et al., 1999, 2008; Malcolm et al., 2002; McCarty, 2001). These studies have been invaluable for not only raising awareness regarding climate change impacts on forest ecosystems, but also highlighting knowledge gaps. However, holistic assessment of these climate change effect models continues to call for refinement of modeling techniques with little or no empirical validation of these models with current data (for example see Botkin et al., 2007). Therefore, there is substantial need for developing techniques to validate extensive simulations of potential tree species shifts, which are based on poorly understood tree migration dynamics (Malcolm et al., 2002). Remote-sensing products and field-based forest inventories provide data for monitoring forest attributes across large regions. Unfortunately, remote sensing products are not well suited for identifying individual tree species across large geographic extents, especially in the understory. The alternative is to use forest inventories to track geographic ranges of tree species over a period of decades. Prior to 1999, the national inventory of United States forest land was conducted only periodically, using sample designs and data management systems that varied by state and inventory period (Gillespie, 1999). Attempts to compare historic forest inventories to contemporary inventories results are confounded by the lack of digital data (pre-1970), lack of consistent inventory methods both spatially and temporally, and sparse methods/database documentation (Woodall et al., 2008). These historic periodic forest inventories provide limited utility for accurately tracking tree species locations over time.

In 1999, an annual forest inventory was initiated by the United States Department of Agriculture, Forest Service's Forest Inventory and Analysis (FIA) program. All eastern states currently have an FIA annual forest inventory (for more information see USDA, 2007). Due to the inconsistency of periodic forest inventories, comparing the contemporary annual forest inventories to the older periodic inventories for the purpose of tracking species shifts is confounded by numerous factors (Woodall et al., 2008). First, only trees with a diameter at breast height (d.b.h.) greater than 2.54 cm can be examined since seedlings were inventoried sporadically using inconsistent sampling methodologies in periodic inventories. Second, the latitudinal shift of mature and/or established trees may be a lagging indicator of climate change effects. Attempting to compare a periodic forest inventory from 1982 to an annual inventory conducted in 2000 may not provide a sufficient period of time (only 18 years) to indicate the movement of trees with a d.b.h. greater than 2.54 cm. Furthermore, the oldest forest inventories (prior to the 1970s) are currently not digitized, restricting comparisons to current inventories. Third, in order to examine tree species shifts across large geographic extents, a multiple of state inventories need to be utilized. Because inventories were periodic prior to 1999, comparing periodic to annual inventories would mean comparing a 1978 inventory to 2001 for one state while an adjoining state might be a 1986–1999 comparison, for example. Therefore, in order to use forest inventories to assess tree species shift in the United States, the development of a more sensitive, robust, and consistent indicator is warranted.

As an alternative to the problematic process of attempting to compare tree species ranges based on annual inventories to ranges based on historic, periodic inventories, this study compares per-species tree seedling locations to locations of established, older trees, i.e., tree biomass (live trees with d.b.h. greater than 2.54 cm) using the current annual forest inventory of the eastern United States. If tree species are migrating, differences in seedling locations versus their respective biomass locations should be observed. The movement of tree line upward along an elevational

gradient has been empirically demonstrated for numerous tree species during the past century (Grace et al., 2002); perhaps a similar movement of tree species may be demonstrated northward along a latitudinal gradient. The goal of study was to develop a new indicator of tree migration through comparison of tree seedlings and biomass density/latitudinal attributes using an annual, national-level forest inventory. Specific objectives were to:

- (1) Compare the current geographic ranges of selected eastern U.S. tree species using FIA data to past range maps from Little (1971).
- (2) Compare the mean latitude for seedlings and biomass for tree species using the most recent FIA annual inventory data.
- (3) Compare the mean ratio of seedlings/ha and mean biomass/ha relative to all other species on each study plot by classes of latitude (3°).
- (4) Compare the mean seedlings/ha and mean biomass/ha in outer ranges of the species ranges (northern range greater than 90th percentile latitude of biomass and southern range less than 10th percentile latitude of biomass) and by 2° latitude classes across the entire eastern United States.
- (5) Develop recommendations for interpretation of study results and development of future indicators of tree species migration from FIA data.

2. Methods

2.1. Data

For more than 75 years, the USDA Forest Service Forest Inventory and Analysis (FIA) program has been charged by Congress to “make and keep current a comprehensive inventory and analysis of the present and prospective conditions of and requirements for the renewable resources of the forest and rangelands of the United States” (McSweeney-McNary Act of 1928) (Gillespie, 1999; Bechtold and Patterson, 2005). FIA is the primary source for information about the extent, condition, status and trends of forest resources across all ownerships in the United States (Smith, 2002). 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 3-phase inventory based on an array of hexagons assigned to separate interpenetrating, non-overlapping annual sampling panels (Bechtold and Patterson, 2005). 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 (Bechtold and Patterson, 2005). 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) (Smith, 2002; USDA Forest Service, 2008). Plot intensity for Phase 2 measurements is approximately one plot for every 2428 ha of land (125,000 plots nationally). 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 of at least 12.7 cm, are inventoried on forested subplots. Within each sub-plot, a 2.07 m microplot offset 3.66 m from sub-plot center is established. Within each microplot, all live tree seedlings are tallied according to species. Additionally, all trees with a d.b.h. between 2.54 and 12.7 cm are inventoried. Conifer seedlings must be at least 15.2 cm

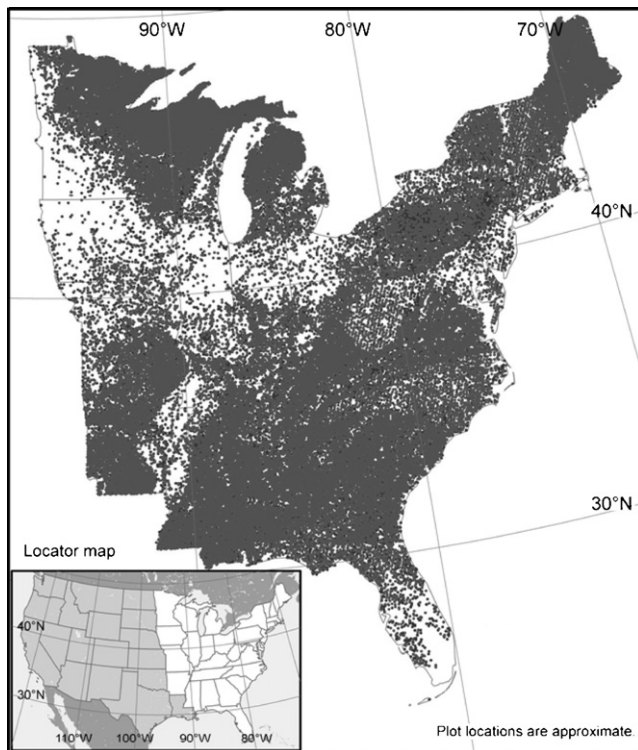


Fig. 1. Approximate study plot locations in the eastern United States, 2001–2006.

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 2.54 cm.

All inventory data is managed in an FIA database (FIADB) and is publicly available. Data for this study were taken entirely from the FIADB using the most recent annual inventory in 30 eastern states for a total of 65,953 inventory plots (Fig. 1). Annual inventories for each state were first initiated between 2001 and 2003 and run through 2006, so sample intensities may vary by state. Because FIA inventory is quasi-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.

Public law stipulates that actual plot location coordinates will not be publicly released (McRoberts et al., 2005). 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. To ensure land owner privacy, a small percentage of plots located on private lands have had their locations intentionally swapped with another private plot of close proximity (typically within a county) and ecological similarity. As these location perturbations and swaps are mandated by law and are randomly applied, these locations would be used to facilitate study repeatability while introducing no bias. Furthermore, since seedlings and biomass were measured on the same plot network, these introduced plot latitude uncertainties should not affect study results, especially when conducted over moderate to large geographic extents (McRoberts et al., 2005). While the FIA dataset may have its limitations, it represents the only dataset that can empirically address this study's questions.

2.2. Study species selection

Three sets of study species were selected: northern, southern, and general (Table 1). Fifteen northern and fifteen southern species

Table 1
Summary of study tree species.

Common name	Genus and species	Number of tree biomass plots ^a	Number of seedling plots ^b
Northern species			
Balsam Fir	<i>Abies balsamea</i>	9,575	8,432
Tamarack	<i>Larix laricina</i>	2,236	936
Black Spruce	<i>Picea mariana</i>	3,314	2,004
Red Pine	<i>Pinus resinosa</i>	2,444	417
Northern White Cedar	<i>Thuja occidentalis</i>	4,030	1,878
Sugar Maple	<i>Acer saccharum</i>	13,588	9,745
Yellow Birch	<i>Betula alleghaniensis</i>	5,343	2,455
Paper Birch	<i>Betula papyrifera</i>	8,510	2,750
Black Ash	<i>Fraxinus nigra</i>	4,040	2,834
Balsam Poplar	<i>Populus balsamifera</i>	1,595	850
Bigtooth Aspen	<i>Populus grandidentata</i>	3,580	1,006
Quaking Aspen	<i>Populus tremuloides</i>	9,762	5,119
Northern Pin Oak	<i>Quercus ellipsoidalis</i>	1,215	665
Northern Red Oak	<i>Quercus rubra</i>	11,769	6,672
American Basswood	<i>Tilia americana</i>	4,834	1,688
Southern species			
Shortleaf Pine	<i>Pinus echinata</i>	4,711	744
Slash Pine	<i>Pinus elliottii</i>	2,914	499
Loblolly Pine	<i>Pinus taeda</i>	14,108	4,652
Baldcypress	<i>Taxodium distichum</i>	590	166
Flowering Dogwood	<i>Cornus florida</i>	6,951	6,889
American Holly	<i>Ilex opaca</i>	2,074	3,307
Sweetgum	<i>Liquidambar styraciflua</i>	14,175	8,674
Yellow-poplar	<i>Liriodendron tulipifera</i>	10,020	3,582
Southern Magnolia	<i>Magnolia grandiflora</i>	363	209
Sweetbay	<i>Magnolia virginiana</i>	1,842	1,343
Southern Red Oak	<i>Quercus falcata</i>	5,411	3,695
Laurel Oak	<i>Quercus laurifolia</i>	2,505	1,553
Blackjack Oak	<i>Quercus marilandica</i>	1,156	643
Post Oak	<i>Quercus stellata</i>	7,846	6,400
Sassafras	<i>Sassafras albidum</i>	4,292	6,239
General species			
Eastern Redcedar	<i>Juniperus virginiana</i>	5,711	4,968
Eastern White Pine	<i>Pinus strobus</i>	6,240	3,389
Boxelder	<i>Acer negundo</i>	2,559	1,767
Red Maple	<i>Acer rubrum</i>	30,954	21,858
Silver Maple	<i>Acer saccharinum</i>	1,054	237
Bitternut Hickory	<i>Carya cordiformis</i>	2,754	2,698
Green Ash	<i>Fraxinus pennsylvanica</i>	6,652	5,942
Eastern Hophornbeam	<i>Ostrya virginiana</i>	5,701	6,673
White Oak	<i>Quercus alba</i>	15,433	8,839
American Elm	<i>Ulmus americana</i>	9,454	4,556

^a Number of plots where at least one tree with d.b.h. \geq 2.54 cm was observed.

^b Number of plots where at least one seedling was observed.

were selected based on abundance in the eastern U.S. and width of latitudinal ranges. There are many tree species that have narrower latitudinal ranges than this study's species; however, their relative rarity would impede statistical hypothesis testing. As a contrast to the northern and southern species, ten general species were selected based on species that are both abundant in the eastern U.S. and have the widest latitudinal ranges. The initial selection of study species was based on range maps developed by Little (1971), the same source of information used in other species migration studies (for example see Iverson and Prasad, 1998). Although numerous different combinations of study species could be selected which could alter the results of the study, it was felt that a selection of 40 common eastern tree species would minimize but not entirely eliminate subjective selection bias.

2.3. Analysis

Little's (1971) range maps were digitized for all study species to facilitate comparisons between the maximum and minimum latitudinal range as indicated by Little and current FIA tree species ranges. Although geographic ranges of many northern tree species

extend into Canada, analyses in this study were constrained to observations within the U.S. portion of these ranges for lack of comparable data inside Canada. For northern species, the minimum latitude for both seedlings and biomass as indicated by FIA data was compared to the minimum latitude as estimated by Little (1971). For southern species, the maximum latitude for both seedlings and biomass as indicated by FIA data was compared to the maximum latitude as estimated by Little (1971).

Next, the latitudes of all observations of seedlings and biomass by tree species were compared. For a given species, there were three types of possible ‘observations’ from each sample plot location: (1) both biomass and seedlings were present, resulting in equal values for both biomass and seedling latitude, (2) only biomass was present, resulting in a null value for seedling latitude, and (3) only seedlings were present, producing a null value for biomass latitude. If neither biomass nor seedlings were present, the plot was not in the domain of interest and was not included in the analyses. These types of data do not lend themselves to traditional statistical analyses. Standard *t*-tests are inappropriate due to the lack of independence between the two samples. Additionally, paired *t*-tests are precluded due to the occurrence of null values.

To conduct statistical tests, bootstrap methods (Efron, 1979) were used to estimate the standard error of the differences between mean biomass latitude and mean seedling latitude. Each bootstrap replication consisted of creating a new set of data by sampling (with replacement) from the original set of observations. From these new data, the differences in mean latitude between biomass and seedlings were computed. This process was repeated *n* times, resulting in *n* differences in means. These *n* differences were used to estimate the standard error, which provides the primary information needed for determination of statistical significance. In our analyses, we found that the estimate of the standard error stabilized after roughly 200 bootstrap replications. Thus, *n* = 200 was used for all species. Differences were assessed for statistical significance at the 95% confidence level.

To examine the density of seedlings and biomass of individual study species relative to competitors across latitudinal gradients, the ratio of study species seedlings counts or biomass to all other species seedling counts or biomass was determined for each study species on every inventory plot. For example, on all plots where at least balsam fir biomass exceeded zero, the ratio of its seedlings or biomass to the seedlings or biomass of all other tree species (including other species in this study) was determined. Means in these seedlings or biomass ratios were determined by latitude classes (3°) for northern, southern, and general species.

Finally, differences between biomass and seedlings were determined by each species’ unique outer range of latitudinal distribution. For each species, percentiles of latitude were determined for estimates of biomass of trees and numbers of seedlings/ha. The 90th percentile of biomass was assumed to be

the northern outer limit while the 10th percentile was assumed to be the southern outer limit. The means of seedlings per ha and biomass per ha was determined by species for all observations falling above or below these 90th and 10th percentiles, respectively. The mean biomass/ha and seedlings/ha in these outer ranges were incorporated into an ‘outer range ratio’ defined as:

$$ORR = \frac{SB_{90} - SB_{10}}{SB_{10}}$$

where ORR is the outer range ratio, SB_{90} is the mean biomass or mean seedlings above the 90th percentile latitude, and SB_{10} is the mean biomass or mean seedlings below the 10th percentile latitude.

Because these outer range limits of biomass and seedlings were independent observations, Wilcoxon paired *t*-tests were used to assess statistically significant differences between biomass and seedling means of the northern and southern outer ranges. If the 10th and 90th percentiles means were not statistically different (*p*-value < 0.05) then the differences were assumed to be zero. It should be noted that since the true range of many northern species extends far into Canada, that individual examination of ORRs might be misleading. To reduce misleading interpretations, ORRs were compared to each other for each species. For example, consider a northern species with biomass and seedling ORRs of 3 and 10, respectively. It would be misleading to state that this particular species has 10 times more seedlings in its northern outer range than compared to the southern range since its true outer range might lie in northern Canada. Instead, it would be stated that this species has over 3 times (10 divided by 3) more seedlings relative to biomass in the northern outer range relative to the southern range.

Finally, in order to evaluate the possible influence of truncated species ranges on study results (tree ranges extending into Canada), the mean biomass and seedlings were determined on all forestland by 2° latitude classes for all northern study species.

3. Results

Comparisons between Little’s (1971) range maps and new species ranges (based on FIA inventories) were largely inconclusive. On average, the minimum latitude for northern species biomass and seedlings was 1.2° and 0.2° lower, respectively, than Little’s ranges (Table 2), which equates to distances of about 133 and 22 km, respectively. For southern species, the FIA maximum latitude of biomass was 1.0° (111 km) higher than Little’s while the maximum latitude of seedlings was nearly the same as Little’s. An examination of a few selected species highlights the problematic nature of comparing an older census of species distributions with a contemporary sample of species locations. For tamarack, FIA’s current inventory of tree locations appears to be slightly farther north of Little’s southern range boundary with a mean latitude of

Table 2

Comparisons between species ranges according to Little (1971) and current maximum and minimum of current seedlings and biomass latitudes (°) according to FIA data.

Species	Little min. lat.	Seedling min. lat.	Biomass min. lat.	Seedling-little ^a	Biomass-little ^a
Northern species					
Balsam Fir	38.3800	39.0406	35.0196	0.6606	−3.3604
Tamarack	39.1600	42.3401	40.5472	3.1801	1.3872
Black Spruce	40.5400	42.4584	41.7029	1.9184	1.1629
Red Pine	38.6900	40.1565	38.4925	1.4665	−0.1975
Northern White Cedar	35.4100	35.7668	35.2042	0.3568	−0.2058
Sugar Maple	33.4600	29.1073	29.1073	−4.3527	−4.3527
Yellow Birch	34.7900	31.7153	32.0717	−3.0747	−2.7183
Paper Birch	35.0300	38.9462	38.5000	3.9162	3.4700
Black Ash	37.5800	35.9938	29.5840	−1.5862	−7.9960
Balsam Poplar	39.1100	41.3863	40.7435	2.2763	1.6335
Bigtooth Aspen	35.0900	37.0034	35.6855	1.9134	0.5955
Quaking Aspen	37.4800	40.0762	39.0167	2.5962	1.5367

Table 2 (Continued)

Species	Little min. lat.	Seedling min. lat.	Biomass min. lat.	Seedling-little ^a	Biomass-little ^a
Northern Pin Oak	40.2700	33.2766	36.5823	-6.9934	-3.6877
Northern Red Oak	30.7600	32.0579	31.4379	1.2979	0.6779
American Basswood	34.9400	28.9711	28.7603	-5.9689	-6.1797
	Little max. lat.	Seedling max. lat.	Biomass max. lat.	Seedling-little ^a	Biomass-little ^a
Southern species					
Shortleaf Pine	41.2000	40.3469	42.3583	-0.8531	1.1583
Slash Pine	33.4200	35.1948	36.1799	1.7748	2.7599
Loblolly Pine	39.4700	39.3078	40.5294	-0.1622	1.0594
Baldcypress	38.9400	37.6238	46.1103	-1.3162	7.1703
Flowering Dogwood	44.0600	47.7942	45.2549	3.7342	1.1949
American Holly	42.3100	45.5224	41.9657	3.2124	-0.3443
Sweetgum	41.2300	40.5288	40.9577	-0.7012	-0.2723
Yellow-poplar	44.6600	44.2302	43.2112	-0.4298	-1.4488
Southern Magnolia	35.7000	36.9175	37.1583	1.2175	1.4583
Sweetbay	42.7200	39.6307	39.8381	-3.0893	-2.8819
Southern Red Oak	40.4200	40.3811	40.9692	-0.0389	0.5492
Laurel Oak	37.3600	36.7297	39.1679	-0.6303	1.8079
Blackjack Oak	42.7400	40.9958	40.9958	-1.7442	-1.7442
Post Oak	39.6000	38.8197	41.3083	-0.7803	1.7083
Sassafras	44.8600	44.3233	47.4459	-0.5367	2.5859

^a Difference in degrees.

seedlings slightly farther north (Fig. 2a). However, there are a number of FIA tree observations substantially farther south of Little's boundary while some southern refugia identified by Little contain no FIA observations. For sugar maple and northern pin oak, the same results can be noted where ranges identified by Little and

FIA roughly overlap but with substantial outliers that could be refugia or measurement errors (Fig. 2b and c). For southern species, the same case occurs where species ranges defined by FIA inventories only approximately match Little's ranges; however, the outliers are now located to the north (Fig. 2d, e and f).

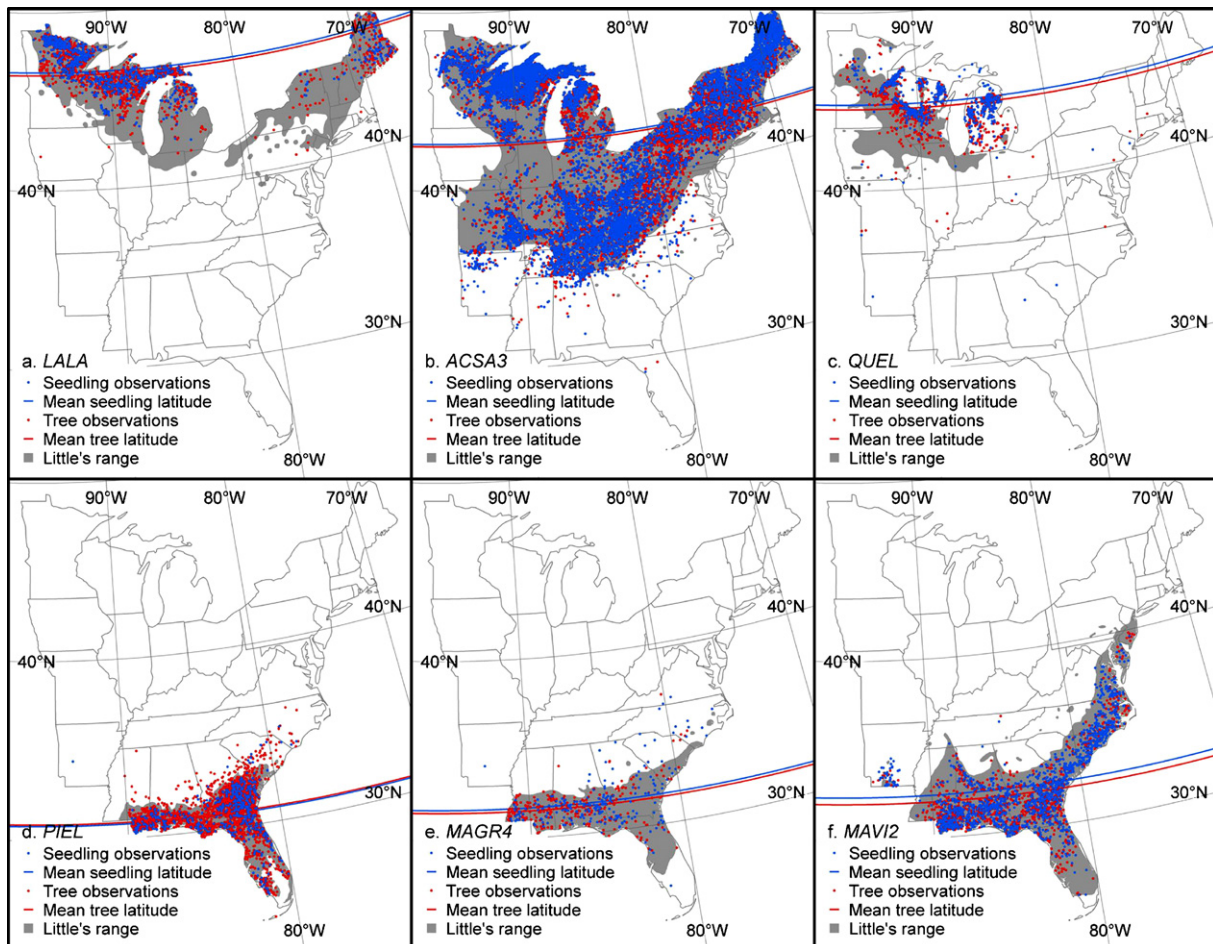


Fig. 2. Little's (1971) species ranges and plot locations for seedlings and tree biomass based on FIA data for selected species (a = tamarack, b = sugar maple, c = northern pin oak, d = shortleaf pine, e = southern magnolia, and f = sweetbay). Additionally, the mean latitude of tree seedlings and biomass based on FIA data are depicted.

Table 3

Means of seedlings and biomass, differences in degrees latitude (mean seedling latitude – mean biomass latitude; DIL), and associated bootstrap standard errors and probabilities.

Tree Species	Mean seedling latitude (°)	Mean biomass latitude (°)	DIL (°)	DIL std error (°)	<i>t</i>	Probability
Northern species						
Balsam Fir	46.0507	46.1134	-0.06273	0.00856	-7.3254	<0.0001
Tamarack	46.6022	46.4344	0.16781	0.04045	4.1486	<0.0001
Black Spruce	46.7449	46.7537	-0.00875	0.01935	-0.452	0.6517
Red Pine	45.4347	45.3262	0.10844	0.07231	1.4996	0.1353
Northern White Cedar	46.1811	46.026	0.15508	0.02331	6.6532	<0.0001
Sugar Maple	42.5951	42.4646	0.13049	0.02989	4.3653	<0.0001
Yellow Birch	45.0886	44.7692	0.31942	0.03809	8.3864	<0.0001
Paper Birch	45.9538	45.8532	0.10058	0.02501	4.0217	0.0001
Black Ash	46.2295	45.9319	0.29755	0.02529	11.7649	<0.0001
Balsam Poplar	46.7751	46.7601	0.01505	0.03908	0.3852	0.7005
Bigtooth Aspen	44.9413	44.4827	0.45863	0.05265	8.7102	<0.0001
Quaking Aspen	46.0649	45.8983	0.16666	0.01925	8.6586	<0.0001
Northern Pin Oak	44.7858	44.5289	0.25692	0.05319	4.83	<0.0001
Northern Red Oak	40.9422	40.6619	0.28036	0.053	5.2897	<0.0001
American Basswood	44.1252	43.5621	0.56314	0.07098	7.9335	<0.0001
Southern species						
Shortleaf Pine	34.8385	34.6197	0.21882	0.062	3.5296	0.0005
Slash Pine	30.7891	30.8788	-0.08972	0.05352	-1.6763	0.0952
Loblolly Pine	33.3603	33.4212	-0.06091	0.02348	-2.5939	0.0102
Baldcypress	32.566	32.6555	-0.08954	0.16239	-0.5514	0.582
Flowering Dogwood	36.04	35.588	0.452	0.03065	14.7477	<0.0001
American Holly	34.2866	34.4571	-0.17051	0.04645	-3.6712	0.0003
Sweetgum	33.765	33.8105	-0.04554	0.01703	-2.6741	0.0081
Yellow-poplar	35.9757	35.8718	0.10396	0.03563	2.9182	0.0039
Southern Magnolia	31.6884	31.5213	0.16706	0.09369	1.7831	0.0761
Sweetbay	32.3927	32.0147	0.37794	0.05901	6.4046	<0.0001
Southern Red Oak	33.949	34.3028	-0.35376	0.02985	-11.851	<0.0001
Laurel Oak	31.8125	31.7383	0.07419	0.03941	1.8825	0.0612
Blackjack Oak	35.2057	35.4993	-0.29359	0.08978	-3.2701	0.0013
Post Oak	32.7991	32.7575	0.0416	0.01575	2.641	0.0089
Sassafras	36.8747	37.6347	-0.76001	0.04077	-18.6436	<0.0001
General species						
Eastern Redcedar	35.9859	36.5081	-0.52211	0.03767	-13.8609	<0.0001
Eastern White Pine	43.2909	43.1032	0.18764	0.05187	3.6176	0.0004
Boxelder	39.3821	40.0446	-0.66245	0.1028	-6.4438	<0.0001
Red Maple	39.3472	40.0209	-0.67364	0.03233	-20.836	<0.0001
Silver Maple	40.3507	41.1991	-0.8484	0.21813	-3.8894	0.0001
Bitternut Hickory	39.3981	39.5341	-0.13607	0.06193	-2.1971	0.0292
Green Ash	39.1459	39.3761	-0.23021	0.06402	-3.5958	0.0004
Eastern Hophornbeam	40.7255	41.122	-0.39653	0.05973	-6.6387	<0.0001
White Oak	37.1121	37.4261	-0.31391	0.03338	-9.4048	<0.0001
American Elm	40.3908	40.588	-0.19717	0.06003	-3.2842	0.0012

Using FIA's annual inventory, comparisons of mean latitudes for both seedlings and biomass by groups of northern, southern, and general species indicated latitudinal shifts for many species (Table 3). Eleven of 15 northern species demonstrated a potential shift northward as indicated by their mean latitude of seedlings being significantly (p -value < 0.05) higher than their mean latitude of biomass. Only one northern tree species (balsam fir) had a statistically significant lower mean seedling latitude compared to tree biomass of only 0.06°. In contrast, only 5 out of 15 southern species and 1 out of 10 general species had a mean seedling latitude significantly (p -value < 0.05) higher than the mean latitude of biomass. Assuming a value of zero for species where their difference in mean latitude (degrees) between biomass and seedlings was not statistically different from zero, the average northward shift between seedlings and biomass for northern species was 0.19° or 21 km. In contrast, southern and general species had mean latitudes of seedlings lower than that of tree biomass by 0.03° and 0.38°, respectively. Some of the species with the largest statistically significant (p -value < 0.05) shifts northward in seedlings versus biomass were American basswood (0.56°), bigtooth aspen (0.46°), flowering dogwood (0.45°), sweetbay (0.38°), yellow birch (0.32°), black ash (0.30°), and northern red oak (0.28°). Some of the species with the largest

statistically significant (p -value < 0.05) shifts southward in seedlings versus biomass were silver maple (0.84°), sassafras (0.76°), red maple (0.67°), boxelder (0.66°), eastern redcedar (0.52°), and eastern hophornbeam (0.39°).

In order to more thoroughly evaluate the success or failure of tree regeneration across the full latitudinal gradient in the eastern United States, the mean ratio of each individual study species seedlings/ha and biomass/ha to all the other tree species was examined by classes of latitude (Fig. 3). For northern species, the ratio of tree biomass greatly exceeded the ratio of seedlings across all latitude classes indicating that species' regeneration may only be adequate in comparison to its associated site occupancy. This phenomena was stark for northern species north of 38° where the ratio of seedlings was roughly half that of the tree biomass ratio. Southern species demonstrated extremely poor regeneration relative to stand occupancy in the southernmost latitude (seedlings less than half the ratio of their respective biomass) but experienced a high regenerative success in the higher latitudes (seedling ratios exceeding 50 times the biomass ratio). General tree species had seedling and tree ratios closely match each other at the lower and highest latitudes but had indications of less regeneration in latitudes ranging from 38° to 47° (seedlings close to 2/3 the ratio of their respective biomass).

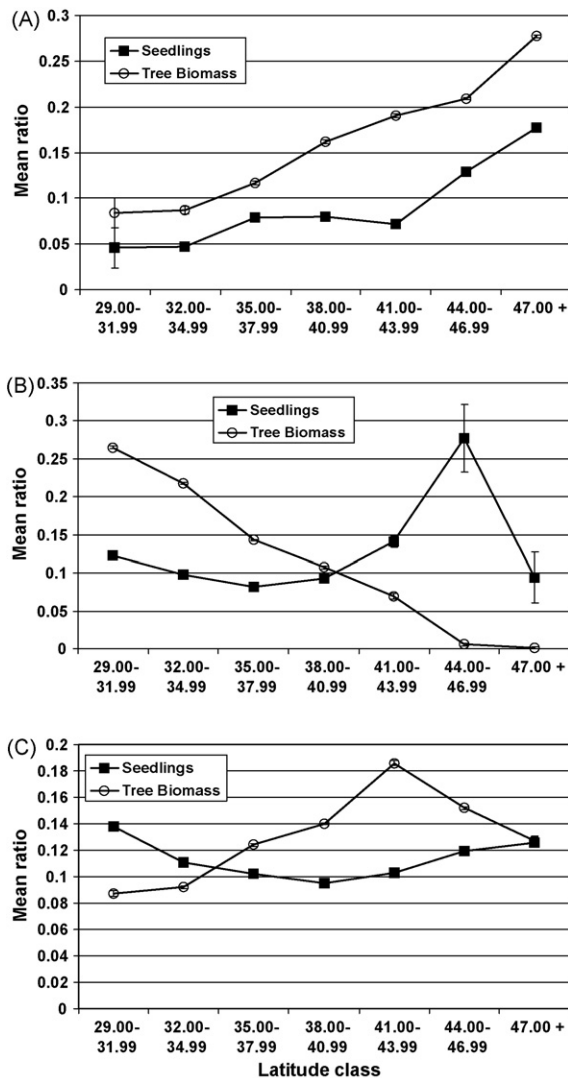


Fig. 3. Means and standard errors of ratios of each individual study species seedling or biomass to all other species seedlings or biomass on each study plot by latitude class (3°) in the eastern United States (A = Northern Species, B = Southern Species, C = General Species). A mean ratio of 0.5 for seedlings would indicate that on average the seedling counts for each study species accounted for half of the total seedling counts on all plots.

Because shifts in tree species locations may be most evident within their outer ranges of latitude, the attributes of their seedlings and biomass was examined within their outer ranges defined by the 10th and 90th percentile latitude of their respective biomass (Table 4). Most northern species had many times more seedlings/ha relative to biomass/ha within their northern outer range compared to their southern range. These results were especially stark for northern pin oak in its northern outer range which when compared to the southern outer range had approximately 50% less biomass but nearly 12 times greater seedling counts. On average, all northern species seedlings/ha were 3.5 times higher at northern outer ranges compared to the southern outer range while biomass/ha was only 0.3 times higher. For southern and general species, ORRs were very similar.

In order to explore the possible effects of species range truncation on study results, the mean biomass and seedlings were estimated by latitude classes for northern species (Fig. 4). Ten of the fifteen northern study species had their mean biomass and seedling densities peak before the 49th parallel. For most species, seedling and biomass means tended to trend closely with each

other across latitude classes; however, some species have notable seedling shifts northward (sugar maple, yellow birch, northern red oak, American basswood). No species demonstrated a noticeable shift southward except for a two latitude classes of northern red oak. If only species with a mean biomass peaking before the 49th parallel are used to determine a mean difference in degrees between biomass and seedling for northern species (Table 2), seedlings demonstrate a northward shift of 0.24° (27 km).

4. Discussion

When examining the possible migration of tree species, the most obvious method is to compare locations of tree species over time. FIA's annual inventory may be used to define current tree ranges and subsequently compared to historic range maps. The most widely used historic range maps are those developed by Little (1971). This study's results indicated that comparing historic range maps to current forest inventory data is problematic. First, historic maps were an attempted census of tree locations with little documentation of methods and totally lacking estimates of uncertainty. Second, contemporary forest inventories are a sample of tree locations which have a high probability of missing isolated tree species refugia. Nationally, FIA field crews correctly identify tree species 95% of the time (Pollard et al., 2006) but species identification errors can also be a concern. These two issues combine to reduce our confidence in species' absolute maximum and minimum latitudes. All it takes is one small refugia to confound comparisons: they may or may not have been censused by historic surveys and have a low probability of being sampled by contemporary forest inventories.

From examination of actual inventory measurements overlaid with historic range maps an important note emerges: it is evident that there are potential range outliers that could speed the process of tree species migration. By some mechanism, tree species have been established far beyond their typical range limits. One hypothesis is that tree species non-native to certain ecosystems have been established by humans either by accident or deliberately to meet landowner objectives (e.g., shade tree, windbreaks, or ornamentals). The very same unintentional human actions that have allowed rapid migration of non-native invasive species (e.g., tree-of-heaven) could also facilitate the relatively rapid movement of native tree species in the eastern United States. Not unlike some past tree species migrations that have occurred at unexpected fast rates (Clark et al., 1998), future tree migration in the United States may overcome barriers to migration (e.g., forest fragmentation and rapid climate change) and shift at fast rates due to the presence of numerous "outliers" possibly identified by forest inventories.

In order to avoid the confounding factors present in using historic censuses or inventories of forest trees, this study promulgated the use of current observations of tree seedlings and biomass as an indicator of tree migration. Because individual trees do not move, the hypothesis is that if indeed tree species are migrating northward in response to climate change, then tree seeds and other propagules should be producing seedlings northward ahead of their seed-producing tree biomass. In contrast, the regeneration of tree species should be diminishing in their southernmost locations while established live tree biomass persists. Additionally, given the fact that northern latitudes are currently experiencing the greatest increases in temperature, this study's indicator should show the greatest shift and fecundity in tree seedlings for northern species. When comparing tree seedling and biomass dynamics across latitudinal gradients, we found compelling evidence that northern trees may be migrating northward in the eastern United States. Out of 15 northern study species, 11 were found to have their mean latitude of seedlings significantly higher than their respective biomass. If northern

Table 4

Means and associated standard errors for biomass/ha and seedlings/ha, along with outer range ratios, for study species at northern (>90th percentile latitude) and southern (<10th percentile latitude) edge of latitudinal range.

Species	90th latitude	Mean bio	Std error	Mean seed	Std error	10th latitude	Mean bio	Std error	Mean seed	Std error	Biomass ORR ^a	Seed ORR ^b
Northern species												
Balsam Fir	47.7732	5.08	0.20	1367.99	60.98	44.5938	10.46	0.47	1626.57	71.21	-0.51	-0.16
Tamarack	48.2279	16.77	1.39	617.74	77.95	44.7083	9.27	0.89	259.34	52.62	0.81	1.38
Black Spruce	48.2140	13.77	1.01	2048.79	228.12	45.3027	9.56	0.78	1135.43	118.77	0.44	0.80
Red Pine	47.3886	22.54	1.72	54.94	10.99	43.5157	24.61	2.07	18.15	6.23	-0.08	2.03
Northern White Cedar	47.7472	21.20	1.14	1341.28	112.26	44.6532	14.54	0.94	147.75	24.05	0.46	8.08
Sugar Maple	46.5757	32.48	1.03	5407.16	222.13	36.9973	10.65	0.45	700.69	28.24	2.05	6.72
Yellow Birch	46.7422	15.12	0.79	600.91	63.03	41.9036	12.39	0.79	126.43	17.88	0.22	3.75
Paper Birch	47.8178	9.84	0.50	327.35	29.52	43.9348	9.11	0.41	131.64	21.42	0.08	1.49
Black Ash	47.8393	11.49	0.80	2435.08	184.49	44.0192	7.53	0.48	659.62	91.36	0.53	2.69
Balsam Poplar	48.4310	10.32	1.00	1117.92	309.88	45.1105	7.07	0.65	415.37	69.11	0.46	1.69
Bigtooth Aspen	46.5745	12.83	1.04	270.85	38.87	41.4056	13.59	0.91	77.19	13.47	-0.06	2.51
Quaking Aspen	47.8947	18.14	0.66	1778.37	127.68	43.8425	10.88	0.44	264.71	21.47	0.67	5.72
Northern Pin Oak	46.0377	9.24	1.32	1526.58	214.60	42.9388	17.51	1.85	118.39	27.63	-0.47	11.89
Northern Red Oak	45.8664	16.15	0.64	582.18	28.69	35.4926	10.50	0.45	191.33	10.19	0.54	2.04
American Basswood	46.7593	12.77	0.68	301.54	35.07	37.9158	10.14	0.68	109.13	14.34	0.26	1.76
Southern species												
Shortleaf Pine	37.1862	15.41	0.99	102.17	13.30	32.1072	15.15	0.93	72.02	12.93	0.02	0.42
Slash Pine	32.3424	24.47	1.94	139.87	36.46	29.5134	25.52	1.69	96.08	16.16	-0.04	0.46
Loblolly Pine	35.6505	39.05	1.22	348.92	60.91	31.3805	29.36	0.91	240.69	21.81	0.33	0.45
Baldcypress	35.8108	45.48	8.29	162.79	74.56	29.8490	41.87	7.22	200.43	68.65	0.09	-0.19
Flowering Dogwood	38.4118	1.22	0.07	626.28	43.64	32.4320	2.00	0.10	179.77	10.47	-0.39	2.48
American Holly	37.7819	4.11	0.46	579.79	47.65	31.3688	1.55	0.20	291.99	18.27	1.65	0.99
Sweetgum	36.5789	12.44	0.49	438.45	41.61	31.6026	8.18	0.33	350.50	17.48	0.52	0.25
Yellow-poplar	38.9769	24.42	1.00	173.17	16.46	32.4356	12.61	0.65	96.19	9.25	0.94	0.80
Southern Magnolia	32.4384	5.20	2.22	166.41	27.13	30.4706	3.06	0.69	267.58	71.03	0.70	-0.38
Sweetbay	34.8302	1.98	0.23	393.40	40.07	30.3824	7.24	0.91	357.94	40.08	-0.73	0.10
Southern Red Oak	37.0082	11.94	0.90	177.69	13.83	31.7475	6.15	0.51	327.79	33.32	0.94	-0.46
Laurel Oak	33.6408	9.64	1.00	295.95	53.06	29.7779	16.71	1.52	569.48	61.45	-0.42	-0.48
Blackjack Oak	37.8813	5.87	0.67	363.42	79.30	32.7344	3.16	0.43	197.35	19.89	0.86	0.84
Post Oak	34.5155	6.50	0.40	319.86	16.92	31.0383	9.82	0.50	466.21	25.73	-0.34	-0.31
Sassafras	41.1207	4.61	0.33	1095.41	85.17	33.9277	0.81	0.06	502.48	22.37	4.69	1.18
General species												
Eastern Redcedar	38.9869	5.06	0.31	227.03	28.05	33.4762	2.28	0.15	266.39	12.95	1.22	-0.15
Eastern White Pine	46.4025	11.99	0.72	265.56	24.25	36.9031	16.94	1.14	551.23	55.73	-0.29	-0.52
Boxelder	45.0356	5.10	0.44	413.24	59.47	33.9058	4.57	0.48	419.47	43.09	0.12	-0.01
Red Maple	46.3293	13.28	0.31	1480.34	47.76	32.9533	5.48	0.18	447.05	12.07	1.42	2.31
Silver Maple	44.6364	34.59	4.33	375.08	118.85	37.1104	12.41	2.58	192.16	36.84	1.79	0.95
Bitternut Hickory	43.7767	5.12	0.49	421.80	36.36	35.7141	4.47	0.51	200.30	16.94	0.15	1.11
Green Ash	45.9969	5.57	0.34	1087.76	70.09	32.9563	7.08	0.47	345.75	25.06	-0.21	2.15
Eastern Hophornbeam	46.4371	2.21	0.12	1257.01	69.77	33.6367	2.31	0.12	381.82	22.88	-0.04	2.29
White Oak	43.2257	16.60	0.50	693.58	49.30	33.4724	10.26	0.41	209.66	10.03	0.62	2.31
American Elm	45.6532	2.40	0.10	294.50	29.56	34.4585	4.71	0.24	135.92	9.42	-0.49	1.17

Italicized means indicate non-significant difference between the 10th and 90th means at the $p = 0.05$ level.

^a Biomass outer range ratio = (mean biomass/ha above 90th percentile latitude – mean biomass/ha below 10th percentile latitude)/mean biomass/ha above 90th percentile latitude.

^b Seedling outer range ratio = (mean seedlings/ha above 90th percentile latitude – mean seedlings/ha below 10th percentile latitude)/mean seedlings above 90th percentile latitude.

study species with a substantial amount of their range in Canada are removed from this analysis, the shift northward is even more evident (0.19° versus 0.24°). Only one northern species (balsam fir) was found to have seedlings with a mean latitude significantly lower than its associated biomass. Some studies have indicated that forest fragmentation and rapid rates of climate change may impede tree migration (Davis and Shaw, 2001) while other studies have noted instances of tree species ability to rapidly migrate (Clark et al., 1998). This study found that the mean latitude of seedlings relative to mean standing tree biomass was approximately 21 km farther north for northern species. This finding of 21 km is very close to a finding by Iverson et al. (2004) that the first 20 km of tree migration has the highest probability of colonization. Assuming that most of these seedlings are less than 20 years old, then one could conclude that some of these northern tree species may be able to move up to 100 km northward per century. Although this conclusion would also have to assume that this study's shift in mean latitude corresponds to a shift in species' outer ranges, it might confirm a wide range of simulation results

(Parmesan and Yohe, 2003; Malcolm et al., 2002; Iverson and Prasad, 1998; Iverson et al., 2008). Furthermore, these results appear to confirm work by Malcolm et al. (2002) that tree species migration rates will be highest at the highest latitudes with the northernmost species moving at a rate of 100 km/century.

Northern species may be not only migrating the farthest, but they may be also experiencing tremendous regeneration relative to their biomass at their northernmost locations. For both northern and southern species, there are indications of less robust regeneration in their lower latitudes. Obviously trees do not actually migrate; their seedlings experience survival in northern locations while succumbing to mortality in southern locations. Given the results of this study, not only have seedlings already shifted northward for most of this study's northern species, the preponderance of seedlings in northern locations compared to southern locations relative to tree biomass indicates that this northward migration will continue.

In contrast to northern species, the southern and general species did not demonstrate a shift northwards. Southern species

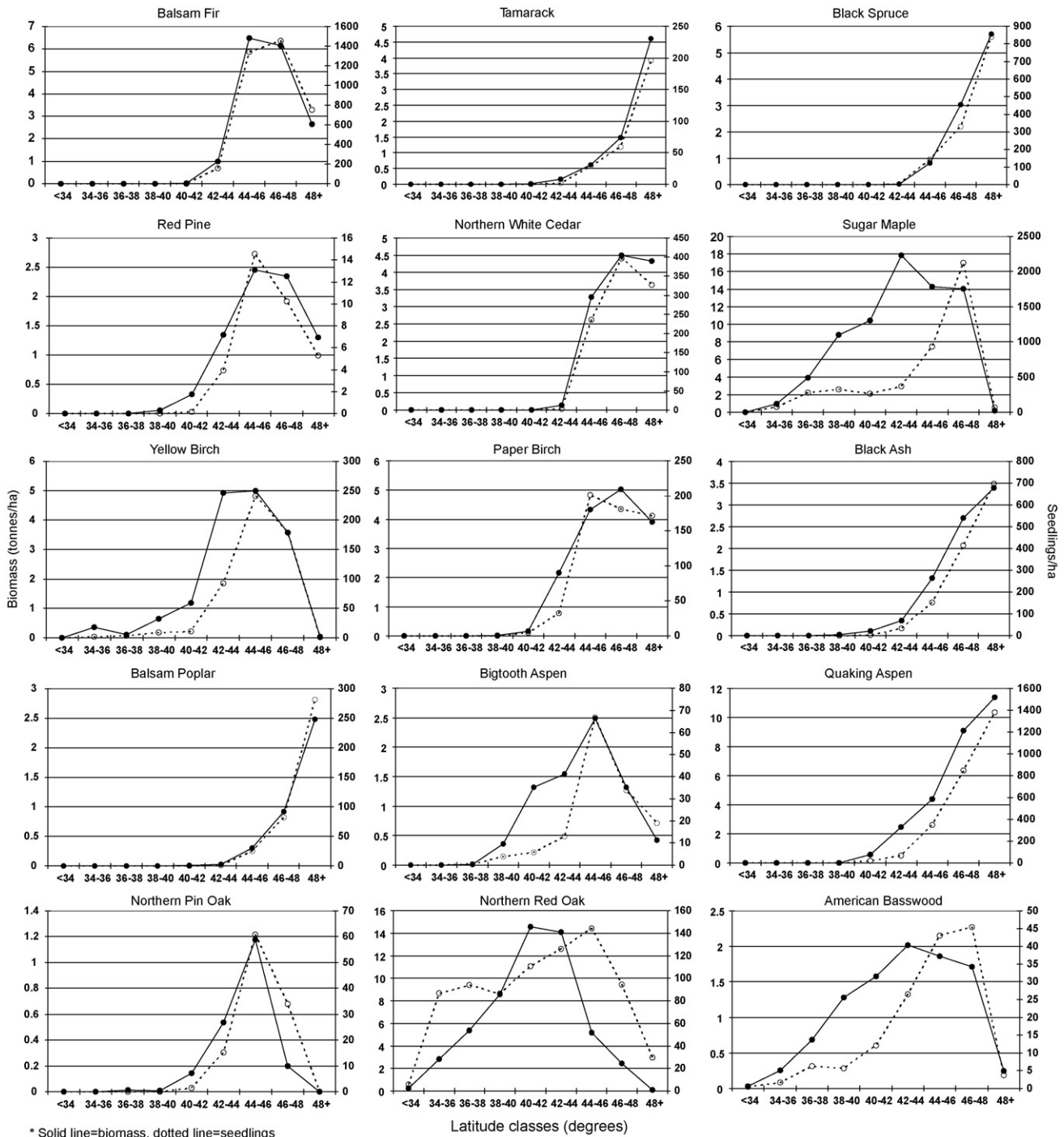


Fig. 4. Mean biomass (tonnes/ha) and seedlings (counts/ha) on forestland in the eastern United States by 2° latitude classes and northern study species.

had almost no difference between mean latitudes of seedlings and tree biomass when considering all species. However, when examining the ORRs of southern and northern study species, southern species seedlings appeared to be less numerous relative to their tree biomass in southern latitudes compared to northern latitudes. So, although there are currently no evident shifts in seedling locations, there appears to be a higher density of southern species seedlings at higher latitudes. General species had the surprising results of showing a lower mean seedling latitude than tree biomass despite no indications from other analyses that general species have higher seedling counts in lower latitudes. Based on these results it may be surmised that southern tree

species are not currently migrating northward despite better regeneration success in northern latitudes. In contrast, general species demonstrate an expansion southward despite indications that seedlings are not occurring in greater numbers in southern latitudes.

If northern species are migrating out of southern locations, southern species are remaining spatially static, and general species may be expanding southward, then what tree population dynamics do these results indicate? We propose the hypothesis that as northern species migrate out of middle and northern latitudes, the southern and general species will fill these vacated niches. Southern species are already demonstrating a ratio of

seedling to competitor seedling counts 5000 times greater than the ratio of their tree biomass to competitor biomass in one northern latitude class (44–47°). Although southern tree species may not be currently moving out of their southern latitude niches, they may be experiencing successful regeneration at their northern locations and may serve as a source of early colonists to facilitate rapid tree migration in the future (Clark et al., 1998; Malcolm et al., 2002). Given that southern species are experiencing less regeneration at their southern latitudes (less than 35°) it can be hypothesized that either general species or new species currently outside the latitudinal gradient will fill the vacated niches. Indeed, general species demonstrated a possible shift southward in their seedlings respective to their tree biomass, indicating that general tree species may be filling niches that may be vacated by southern species.

This study's indicator of tree migration has many caveats that deserve exploration in future research efforts. First, the selection of study species is subjective and may affect study results. Efforts should be extended to develop a standard list of species to be used as an "index" of climate change effects. Large-scale forest inventory data may be used to develop tree migration indices that contain species with narrow latitudinal ranges (e.g., northern pin oak, bigtooth aspen). Second, latitude was only used as a surrogate for temperature in this study and may be confounded by elevation in the eastern United States. The possible effects of both longitude and elevation on this study's indicator should be explored. Third, just because there are fewer seedlings at lower latitudes compared to northern latitudes does not necessarily mean regeneration is failing. . . their survival rates may just be higher or there may be mast periodicity. Unfortunately, there is a lack of literature regarding the survival of tree seedlings for the multitude of species and stand/site conditions in this study. Nonetheless, the incorporation of seedling survival/mortality into the study's indicator should be explored. As an alternative, seedling counts might be replaced by mean latitudes for age-weighted biomass. Fourth, this study ignores the effect of interspecific competition or forest health/management issues across latitudinal gradients. Regeneration may be failing at southern locations not due to increasing temperature, but to unique competition effects, the prevalence of forest pests (e.g., gypsy moth), or active forest management. Fifth, there is inherent but small measurement error in tree species identification during a large-scale forest inventory. Therefore, utilizing as many observations as possible and avoiding use of maximum or minimum observations should reduce the impact of these errors on study results. Sixth, the true ranges of many tree species in this study are not contained by the coterminous United States. Many northern species extend far into Canada necessitating incorporation of Canadian forest inventory data if one wished to examine the complete latitudinal range of northern tree species. Unfortunately, the disparity in Canadian and United States forest inventory sample designs may preclude such an effort. Therefore, this study attempted to create species shift metrics solely based on United States forest inventory data. The results indicated that this study may be underestimating the migration of northern species through the inclusion of study species that proliferate in Canada. Hence, our assertions of northern tree species migration may be conservative. Seventh, tree species' ability to migrate may be dependent on seed weights and dispersal mechanisms. Therefore, the incorporation of migration anisotropy (due to prevailing winds) and tree seed weights may help improve future migration models. Finally, this study utilized means in its indicator analyses. Just because a mean latitude may shift does not necessarily translate into a corresponding maximum or minimum shift in latitude, hence changes in species' ranges. Also, distances of migrations following paths other than directly north or south would be underestimated by our

approach. Further evaluation of the dynamics between mean shifts in tree locations versus changes in outer range boundaries should be examined. Despite numerous caveats, it is felt that the inclusion of 40 tree species and over 65,000 inventory plots reduced study subjectivity and minimized any biases. This indicator should be refined for future use, meanwhile this study's results should initiate dialogue regarding climate change effects on forest ecosystems that may have already occurred.

5. Conclusions

This study empirically explored possible tree migration in the eastern United States by comparing tree seedlings to their respective forest stand biomass of trees with a d.b.h. ≥ 2.54 cm using a current annual inventory across 30 states. This indicator of tree migration suggested that most northern study species are exhibiting a northward migration. Over 70% of this study's northern species have mean locations of seedlings significantly farther north than their respective biomass. Southern species demonstrated no significant shift northward despite greater regeneration success in northern latitudes while general species showed a possible expansion southward. Given current tree regeneration trends identified in this study, the process of tree migration may continue or accelerate with a rate up to 100 km per century for numerous northern tree species. Given these stark results and the multitude of caveats that surround this new indicator of tree species shift, future research is highly warranted.

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