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Selecting tree species for testing climate change migration hypotheses using forest inventory data

C.W. Woodall[a,*], C.M. Oswalt[b], J.A. Westfall[c], C.H. Perry[a], M.D. Nelson[a], A.O. Finley[d]

[a] USDA Forest Service, Northern Research Station, St. Paul, MN, United States
[b] USDA Forest Service, Southern Research Station, Knoxville, TN, United States
[c] USDA Forest Service, Northern Research Station, Newtown Square, PA, United States
[d] Michigan State University, East Lansing, MI, United States

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ABSTRACT

The lack of objective tree species lists hinders the assessment of climate change effects on tree species distributions. The goal of this study was to develop and evaluate criteria for selecting tree species used in large-scale tree migration monitoring efforts. The results of this study indicate that tree migration conclusions are highly dependant on the species selected for examination. It was found that tree species' median latitudes or forecasted future areas provided objective criteria for development of species lists for migration hypothesis testing with the latter being insensitive to simulation error. Furthermore, only 10–15 of the top species, in terms of high median latitudes or loss in forecasted future area, are needed to maximize the sensitivity of a migration index. The use of such criteria in this study indicated a northward shift of sensitive tree populations of 27 km. It is suggested that examining species only the most likely to migrate serves as an objective starting point for migration detection. In contrast, the inclusion of all tree species commonly observed in large-scale forest inventories can obfuscate migration detection with tree species that have little ecological reason to immediately migrate in a changing climate.

1. Introduction

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 longer growing seasons (IPCC, 2007) which may in turn drive changes in forest ecosystem functions and attributes (Stenseth et al., 2002). Increases in carbon dioxide concentration are expected to increase tree biomass increment through fine root and woody biomass growth (Ainsworth and Long, 2005; Norby et al., 2002, 2004). Individual tree health 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) and more susceptibility 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 result in migration of tree species (Walther et al., 2002; Opdam and Wascher, 2004).

There is evidence of past forest migration rates exceeding 50 km per century during episodes of climate change (Schwartz, 1992; Noss, 2001; Paremsan and Yohe, 2003). Examination of tree species migration largely has been conducted by investigating historic ranges during the past millennia (for examples see Davis and Shaw, 2001; Malcolm et al., 2002; McLachlan et al., 2005; Pearson, 2006) and simulating future tree species shifts (for examples see Iverson and Prasad, 1998; Iverson et al., 1999, 2008; Schwartz et al., 2001; McCarty, 2001; Malcolm et al., 2002). More recently, Woodall et al. (2008, 2009) explored using forest inventories to examine contemporary tree migration. Woodall et al. (2009) proposed an objective indicator of tree migration where mean latitudes of a tree species' population of seedlings and biomass (trees with a d.b.h. >2.54 cm) may be compared using data from large-scale forest inventories. Using this difference in latitude (DIL) technique, a positive indication of tree migration occurs when a tree species' mean latitude of its seedling abundance is shown to be further north than its mean latitude of biomass distribution. A major unresolved issue regarding implementation of the DIL technique is the selection of species to be included in assessments using this indicator. If one were to select dozens of species unlikely to migrate for testing of climate

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[*] Corresponding author at: 1992 Folwell Avenue, St. Paul, MN 55108, United States. Tel.: +1 651 649 5141; fax: +1 651 649 5140.
E-mail address: cwoodall@fs.fed.us (C.W. Woodall).

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change hypotheses, then results using the DIL technique might indicate no migration. This postulate may be alternatively framed as: if constituent tree species in a migration index display no indications of migration then it may be assumed that most common eastern U.S. tree species are not experiencing detectable migration. Therefore, the development and evaluation of objective criteria for selecting species for inclusion in tree migration evaluations (i.e., the DIL technique) is needed.

This study postulates that tree species ideal for inclusion in migration assessments when using forest inventory data might include tree species populations with: narrow latitudinal ranges, high median latitudes, relatively abundant, endemic to northern latitudes that may be subjected to higher levels of warming, and regeneration mechanisms that facilitate reasonable rates of migration. Indeed, numerous tree migration simulations have identified tree species with the preceding attributes as migrating out of the conterminous U.S. under various climate change scenarios (Iverson and Prasad, 1998; Schwartz et al., 2001; Iverson et al., 2008). The goal of this study was to develop and assess objective criteria for selecting individual tree species for inclusion in the DIL tree migration indicator. Specific objectives were to:

(1) Assess the distribution of the DIL indicator across a large selection of abundant eastern U.S. tree species and cumulatively by individual tree species ranked by current latitudinal range, median latitude, regeneration mechanisms that facilitate migration, and forecasted changes in species' area using the low emission Hadley scenario within Iverson et al.'s (2008) potential future area models,
(2) Evaluate the sensitivity of a species migration index to simulated error of forecasted future areas (Iverson et al., 2008), and
(3) Based on initial study results, develop objective criteria for selection of tree species for inclusion in tree migration hypothesis testing.

2. Methods

2.1. Data

The USDA Forest Service 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 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 multi-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 (roughly 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 2.5 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.

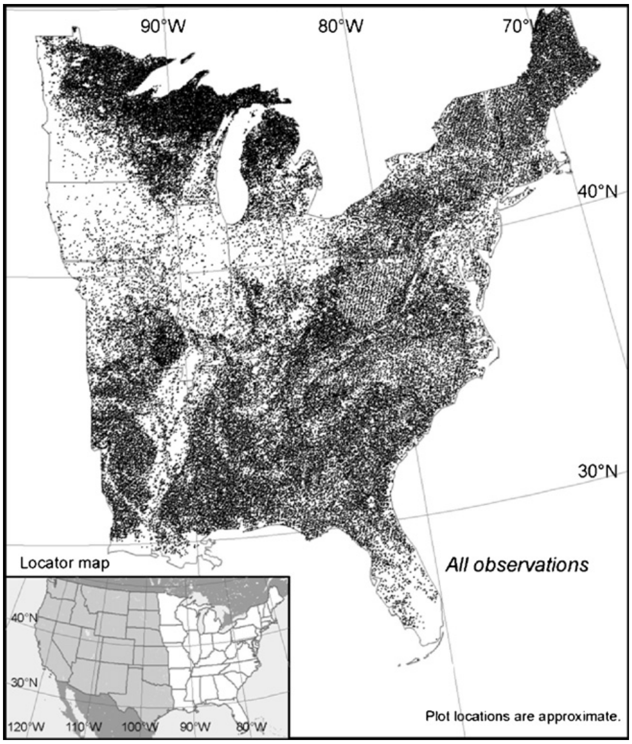

Fig. 1. Approximate study plot locations in the eastern United States, 2001–2007.

All inventory data are managed in an FIA database (FIADB) and are publicly available. Data for this study were taken entirely from the FIADB using the most recent annual inventory in 31 eastern states for a total of 72,025 observations (Fig. 1). Annual inventories for each state were first initiated between 2001 and 2003 and run through 2007, 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. It should also be noted that species' latitudinal ranges used in this study may be impacted by unequal sample intensities due to ongoing implementation of a fully annual forest inventory. It is felt that this possibility should have negligible effects on results since full implementation is nearly complete and the remaining states are random in spatial arrangement. Finally, 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. As these location perturbations are mandated by law and are randomly applied, these locations were 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).

2.2. Analysis

Given the hundreds of tree species across the eastern United States, the most common tree species with adequate sampling in a national forest inventory were selected. Two lists of the top 50 tree species in terms of total biomass and tree counts across the 31 states of the eastern United States were combined resulting in 63 unique study species (Table 1). Although most species were in both top 50 lists, some species (e.g., flowering dogwood) have low total biomass but high tree counts and vice versa.

Next, the latitudinal range, median latitude, regeneration mechanisms, and forecasted future range distributions were determined for each study species. Latitudinal range was defined as the 5th percentile latitude minus the 95th percentile latitude for each species based on tree biomass distribution to avoid the influence of measurement error. The median latitude of each tree species was simply the median latitude of tree biomass. Regeneration mechanism rankings were based on the "guild" concept provided by Prasad et al. (2007) whereby tree species are ranked according to both their ecological niche (e.g. slow-growing understory species) and masting attributes (e.g. wind-dispersed light seeds). There are 14 guilds with a guild of 1 being lightly seeded pioneer species while guilds in excess of 10 are heavy seeded, understory species. Finally, the forecasted future range areas of all study species were determined using the low emission Hadley climate scenario (Prasad et al., 2007) within Iverson et al.'s (2008) future potential tree area models.

As formulated by Woodall et al. (2009), the DIL tree migration indicator was used as an objective indicator of tree migration in this study. In order to quantify current tree migration, the mean 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. 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 (DIL). 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. DIL's were assessed for statistical significance at the 95% confidence level. For all species that had a p-value in excess of 0.05, the DIL was assumed to be 0.

The distribution of DIL's across all study species was examined through a histogram. In order to assess trends in mean DIL for various tree species lists, the cumulative mean DIL and associated standard errors was determined across classes of tree species ranked according to latitudinal range, median latitude, regeneration mechanisms, and forecasted future area distributions. Finally, in order to evaluate how errors in the species' forecasted future area distributions may affect DIL means, we randomly perturbed the simulated future area distributions by percent error classes of 5%, 10%, 15%, . . ., 50%. Using the 50% error class as an example, the observed values were perturbed by ±45–50% with the mean DIL's recomputed. This process was repeated 5000 times for each error class (the means and variances of the 50% class stabilized at about 4000 iterations). The mean DIL's of the top 10 and 25 tree species

Table 1
Summary of study tree species and observation counts (Number of plots where at least one tree with d.b.h ≥2.54 cm or seedling was observed.

Common name	Genus and species	Observation	Common name	Genus and species	Observation
Balsam fir	*Abies balsamea*	11548	Green ash	*Fraxinus pennsylvanica*	10756
Eastern redcedar	*Juniperus virginiana*	8785	American holly	*Ilex opaca*	4874
Black spruce	*Picea mariana*	3681	Black walnut	*Juglans nigra*	3895
Red spruce	*Picea rubens*	3284	Sweetgum	*Liquidambar styraciflua*	17786
Shortleaf pine	*Pinus echinata*	4967	Yellow-poplar	*Liriodendron tulipifera*	12062
Slash pine	*Pinus elliottii*	3271	Sweetbay	*Magnolia virginiana*	2767
Longleaf pine	*Pinus palustris*	1704	Blackgum	*Nyssa sylvatica*	14188
Red pine	*Pinus resinosa*	2679	Swamp tupelo	*Nyssa biflora*	2691
Eastern white pine	*Pinus strobus*	8037	Eastern hophornbeam	*Ostrya virginiana*	9918
Loblolly pine	*Pinus taeda*	16461	Sourwood	*Oxydendrum arboreum*	5547
Virginia pine	*Pinus virginiana*	3461	Sycamore	*Platanus occidentalis*	2187
Baldcypress	*Taxodium distichum*	963	Bigtooth aspen	*Populus grandidentata*	4066
Northern white-cedar	*Thuja occidentalis*	4429	Quaking aspen	*Populus tremuloides*	11241
Eastern hemlock	*Tsuga canadensis*	5465	Black cherry	*Prunus serotina*	24100
Striped maple	*Acer pensylvanicum*	3690	White oak	*Quercus alba*	19125
Red maple	*Acer rubra*	41685	Scarlet oak	*Quercus coccinea*	5014
Silver maple	*Acer saccharinum*	1186	Southern red oak	*Quercus falcata*	8133
Sugar maple	*Acer saccharum*	16984	Cherrybark oak	*Quercus pagoda*	2037
Yellow birch	*Betula alleghaniensis*	6478	Laurel oak	*Quercus laurifolia*	3375
Sweet birch	*Betula lenta*	3413	Bur oak	*Quercus macrocarpa*	2584
Paper birch	*Betula papyrifera*	9756	Water oak	*Quercus nigra*	11634
American hornbeam	*Carpinus caroliniana*	6279	Willow oak	*Quercus phellos*	3076
Bitternut hickory	*Carya cordiformis*	4767	Chestnut oak	*Quercus prinus*	5201
Pignut hickory	*Carya glabra*	9594	Northern red oak	*Quercus rubra*	15833
Shagbark hickory	*Carya ovata*	5286	Post oak	*Quercus stellata*	7125
Mockernut hickory	*Carya tomentosa*	10168	Black oak	*Quercus velutina*	11380
Eastern redbud	*Cercis canadensis*	3641	Black locust	*Robinia pseudoacacia*	2806
Flowering dogwood	*Cornus florida*	11016	Sassafras	*Sassafras albidum*	9110
Hawthorn	*Crataegus* spp.	3477	American basswood	*Tilia Americana*	5643
American beech	*Fagus grandifolia*	10955	Winged elm	*Ulmus alata*	8369
White ash	*Fraxinus americana*	14069	American elm	*Ulmus americana*	12419
Black ash	*Fraxinus nigra*	4964			

according to these perturbed future area distributions were computed.

3. Results

The differences in species' seedling and biomass mean latitudes (DIL) were determined for all study species (Table 2). Twenty seven of the studies' species had DIL's that were statistically greater than 0, indicating a possible shift northward for approximately one half of the species examined. Eleven species had *p*-values in excess of 0.05, thus they were assigned DIL values of zero in subsequent analyses. The statistically significant DIL values ranged from −1.24° (Hawthorn) to 1.32° (American Hornbeam). Difference in latitude values were normally distributed with the majority (46) of study species having DIL's from −0.4 to 0.4° (Fig. 2).

The latitude range (5th–95th percentile) was determined for each study species (Table 3). As would be expected, there was considerable variation in mean latitudes ranging from a very

Table 2
Difference in latitude results (mean seedling latitude – mean biomass latitude) and associated bootstrap standard errors and probabilities for all study species, eastern U.S.

Tree species	Mean seedling latitude (°)	Mean biomass latitude (°)	DIL (°)	DIL SE (°)	*t*	Probability
Balsam fir	46.0095	46.0853	−0.0758	0.0090	−8.4037	<0.001
Eastern redcedar	35.9834	36.5485	−0.5651	0.0373	−15.1492	<0.001
Black Spruce	46.7393	46.7368	0.0024	0.0162	0.1505	0.8805
Red spruce	44.9218	44.8786	0.0432	0.0203	2.1273	0.0346
Shortleaf Pine	34.8013	34.5993	0.2020	0.0635	3.1822	0.0017
Slash pine	30.655	30.7319	−0.0769	0.0553	−1.3890	0.1664
Longleaf pine	31.8671	31.7042	0.1629	0.0815	1.9989	0.047
Red Pine	45.4607	45.2686	0.1922	0.0636	3.0219	0.0028
Eastern white pine	43.1911	43.0218	0.1693	0.0536	3.1567	0.0018
Loblolly pine	33.2556	33.3208	−0.0652	0.0193	−3.3763	0.0009
Virginia pine	36.0456	36.3318	−0.2862	0.0484	−5.9079	<0.001
Baldcypress	32.1483	32.0193	0.1290	0.1536	0.8399	0.402
Northern white-cedar	46.1646	46.0193	0.1453	0.0221	6.5811	<0.001
Eastern hemlock	43.3309	42.8959	0.4350	0.0595	7.3146	<0.001
Striped maple	43.3127	43.1007	0.2120	0.0654	3.2401	0.0014
Red maple	39.1311	39.8713	−0.7402	0.0303	−24.4684	<0.001
Silver maple	40.2962	41.1289	−0.8327	0.2344	−3.5522	0.0005
Sugar maple	42.4914	42.3539	0.1375	0.0262	5.2540	<0.001
Yellow birch	44.9369	44.6440	0.2929	0.0364	8.0526	<0.001
Sweet birch	40.0891	39.8633	0.2258	0.0661	3.4170	0.0008
Paper birch	45.9419	45.7901	0.1518	0.0259	5.8656	<0.001
American hornbeam	37.7515	36.4356	1.3160	0.0664	19.8223	<0.001
Bitternut hickory	39.4203	39.5577	−0.1374	0.0642	−2.1390	0.0337
Pignut hickory	36.0611	36.5066	−0.4455	0.0386	−11.5410	<0.001
Shagbark hickory	38.7979	38.8010	−0.0031	0.0640	−0.0487	0.9612
Mockernut hickory	35.4868	35.9003	−0.4135	0.0327	−12.6547	<0.001
Eastern redbud	36.6826	36.8499	−0.1673	0.0518	−3.2339	0.0014
Flowering dogwood	36.1085	35.6118	0.4968	0.0313	15.8521	<0.001
Hawthorn	38.4112	39.6541	−1.2429	0.1383	−8.9852	<0.001
American beech	40.7688	40.2949	0.4739	0.0415	11.4321	<0.001
White ash	40.6794	40.6380	0.0415	0.0375	1.1044	0.2708
Black ash	46.2365	45.9340	0.3025	0.0242	12.5180	<0.001
Green ash	38.9512	39.0378	−0.0866	0.0694	−1.2475	0.2137
American holly	34.1838	34.3875	−0.2038	0.0482	−4.2248	<0.001
Black walnut	39.068	38.8587	0.2093	0.0980	2.1364	0.0339
Sweetgum	33.6561	33.6924	−0.0363	0.0162	−2.2434	0.026
Yellow-poplar	36.119	36.0516	0.0674	0.0348	1.9330	0.0546
Sweetbay	32.395	32.0203	0.3746	0.0521	7.1900	<0.001
Blackgum	35.5336	35.4969	0.0367	0.0292	1.2595	0.2093
Swamp tupelo	32.3321	32.2472	0.0849	0.0742	1.1442	0.2539
Eastern hophornbeam	40.5129	40.9216	−0.4087	0.0571	−7.1643	<0.001
Sourwood	35.8631	35.6038	0.2592	0.0361	7.1907	<0.001
Sycamore	35.8859	36.6765	−0.7905	0.1611	−4.9085	<0.001
Bigtooth aspen	44.9178	44.4084	0.5095	0.0637	7.9984	<0.001
Quaking aspen	46.0486	45.8636	0.1850	0.0175	10.5948	<0.001
Black cherry	39.571	39.2192	0.3518	0.0430	8.1733	<0.001
White oak	37.0316	37.4117	−0.3802	0.0319	−11.9069	<0.001
Scarlet oak	36.8328	37.1596	−0.3269	0.0485	−6.7373	<0.001
Southern red oak	33.7992	34.1693	−0.3702	0.0295	−12.5559	<0.001
Cherrybark oak	33.2757	33.5323	−0.2566	0.0623	−4.1177	0.0001
Laurel oak	31.6754	31.578	0.0974	0.0360	2.7049	0.0074
Bur oak	45.577	44.9085	0.6685	0.0971	6.8822	<0.001
Water oak	32.7041	32.6432	0.0609	0.0176	3.4724	0.0006
Willow oak	33.9288	34.0494	−0.1206	0.0509	(2.3708	0.0187
Chestnut oak	37.2196	37.5600	−0.3404	0.0420	(8.1051	<0.001
Northern red oak	40.8104	40.6762	0.1342	0.0457	2.9407	0.0037
Post oak	34.9866	35.2379	−0.2513	0.0404	−6.2164	<0.001
Black oak	37.6027	38.1147	−0.5120	0.0411	−12.4530	<0.001
Black locust	37.918	38.1418	−0.2238	0.1040	−2.1525	0.0326
Sassafras	36.8242	37.5858	−0.7616	0.0418	−18.2017	<0.001
American basswood	44.0135	43.4555	0.5580	0.0799	6.9834	<0.001
Winged elm	34.4151	34.4376	−0.0224	0.0242	−0.9257	0.3557
American elm	40.2414	40.3487	−0.1073	0.0597	−1.7979	0.0737

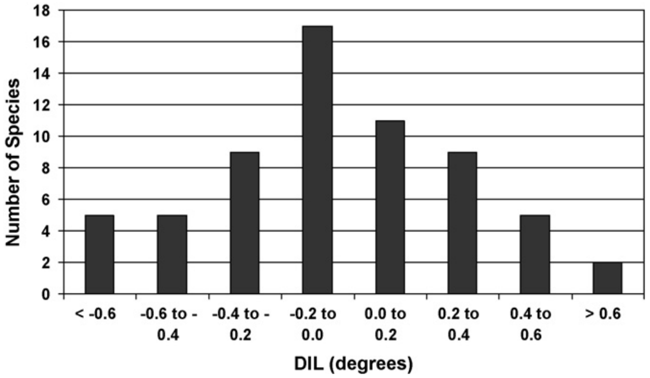

Fig. 2. Histogram of difference in latitude (DIL) values for all study species, eastern United States.

narrow range of 3.53° for black spruce to 15.48° for green ash. The majority of species had latitude ranges between 5° and 10°. Some species such as cherrybark oak have a narrow range well below the Canadian border (Fig. 3a). Other species, such as sugar maple, have a very wide latitudinal range that extends into Canada (Fig. 3b). In the case of cherrybark oak, there is one noteworthy observation in Minnesota, evidence as to why our study formulated species' ranges as 5th–95th percentile latitudes. The median latitudes ranged from 30.79° for slash pine to 46.54 for black spruce. The majority of study species had median latitudes between 35° and 45°. The plurality of study species had regeneration mechanism rankings of 5 or 6 indicating a moderate ability to migrate. Species such as red and silver maple are lightly seeded pioneer species and thus had the highest rankings, while heavy seeded understory species such as sweetbay and eastern redbud had the lowest rankings. Finally, the forecasted change in area occupied in the eastern U.S. by study species under the low Hadley climate scenario indicated that black spruce lost the most area (−78.3%) while winged elm was forecasted to gain the most area (142.6%). Twenty-one of the 63 study species were simulated to lose area under this future climate scenario.

Cumulative mean DIL's across classes of study species ranked according to increasing latitudinal range, decreasing median latitude, decreasing ability to migrate (increasing regeneration score), and decreasing loss in forecasted future area were determined (Fig. 4a–d). Species ranked according to their median latitude and forecasted area change demonstrated the largest mean DIL scores when the top 10–15 ranked species were included. The highest DIL of approximately 0.25° was attained when using the top 15 species ranked according to decreasing median latitude. Species with the highest rankings according to decreasing ability to migrate had negative DIL values. Curiously, if the rankings of forecasted future area change are reversed (increasing losses in future area) a mean DIL of −0.19° is attained for the top 20 species. All cumulative means, regardless of ranking criteria, stabilized around zero after 40 or more species were included in the cumulative mean.

If one were to use only the top 10 or 25 species forecasted to lose the most area, mean DIL's were not strongly affected by errors in forecasted future species' areas under the low Hadley climate scenario (Fig. 5). When only the top 10 species in terms of forecasted loss in area were included in the mean DIL, the mean DIL was stable across forecasted species area errors ranging from 5% to 50%.

4. Discussion

The process of selecting tree species for comprehensive testing of migration hypotheses is highly subjective. Based on the results of this study, if one were to select a completely random assortment of tree species for an indicator of migration the ultimate conclusion

Table 3
The latitude range (*L*, degrees, 5th percentile latitude – 95th percentile latitude), median latitude (degrees, *M*), regeneration mechanisms (*R*), and forecasted future area using the low Hadley climate scenario (percent, *H*) by tree species in 31 states of eastern U.S.

Common name	*L*	*M*	*R*	*H*	Common name	*L*	*M*	*R*	*H*
Balsam fir	3.8915	46.1275	5	−41.2	Green ash	15.4780	38.3191	10	17.4
Eastern redcedar	9.1960	36.4347	4	66.9	American holly	7.5231	34.2592	5	28.5
Black Spruce	3.5293	46.5420	5	−78.3	Black walnut	7.8422	38.7677	7	25.6
Red spruce	3.8271	44.9697	5	−19.3	Sweetgum	6.5892	33.4750	8	36.8
Shortleaf pine	5.9688	34.5970	4	57.6	Yellow-poplar	8.2882	36.2852	8	15.6
Slash pine	4.8359	30.7924	8	110.4	Sweetbay	6.4480	31.4533	13	23.7
Longleaf pine	5.6783	31.2761	4	77.2	Blackgum	9.3700	35.5901	13	19.0
Red pine	5.3802	45.3224	4	−22.0	Swamp tupelo	6.5603	31.8395	13	32.0
Eastern white pine	10.9437	44.0361	9	−24.6	Eastern hophornbeam	14.7004	42.4627	5	13.2
Loblolly pine	6.0584	33.1905	3	50.6	Sourwood	6.1187	35.7402	5	−7.1
Virginia pine	5.7783	36.4071	4	21.2	Sycamore	8.5291	37.1119	9	57.0
Baldcypress	7.4690	31.5867	9	29.0	Bigtooth aspen	6.9576	44.7501	2	−46.5
Northern white-cedar	3.7789	46.0348	5	−33.9	Quaking aspen	5.3838	46.0309	2	−40.0
Eastern hemlock	10.8788	43.6913	5	−20.7	Black cherry	14.2138	39.8344	11	2.2
Striped maple	10.2016	44.0454	5	−32.8	White oak	11.8383	37.0483	6	10.0
Red maple	15.1760	40.4877	1	0.3	Scarlet oak	7.5092	37.0684	6	−23.9
Silver maple	10.1668	41.6911	1	34.4	Southern red oak	6.4681	34.0522	6	43.7
Sugar maple	10.4846	43.1569	5	−18.7	Cherrybark oak	5.8762	33.3501	6	29.4
Yellow birch	5.6781	45.0957	9	−36.4	Laurel oak	5.7012	31.5438	6	53.4
Sweet birch	7.5734	40.7144	9	−11.5	Bur oak	7.8491	45.6668	6	28.2
Paper birch	4.7604	45.9124	7	−41.1	Water oak	4.6135	32.6032	6	74.3
American hornbeam	14.3998	35.2991	5	16.4	Willow oak	6.2651	33.7984	6	34.1
Bitternut hickory	10.4704	39.3030	6	85.3	Chestnut oak	7.2492	37.4368	6	8.0
Pignut hickory	9.2247	36.6734	6	17.8	Northern red oak	11.7774	40.8604	6	−0.1
Shagbark hickory	9.5409	38.7111	6	31.3	Post oak	6.7461	35.3012	6	67.4
Mockernut hickory	7.6400	36.0174	6	18.7	Black oak	10.1992	37.5959	6	13.5
Eastern redbud	6.8146	37.1936	13	62.0	Black locust	7.0622	38.0928	12	62.5
Flowering dogwood	8.0264	35.7668	10	20.7	Sassafras	9.6278	37.6194	12	36.8
Hawthorn	13.7570	40.8830	13	−3.0	American basswood	10.4365	44.5579	5	−10.7
American beech	13.2524	41.2626	5	−7.6	Winged elm	5.6342	34.3813	1	142.6
White ash	10.6015	40.8507	10	25.8	American elm	14.4674	40.6061	1	16.1
Black ash	4.9053	46.0811	10	−25.8					

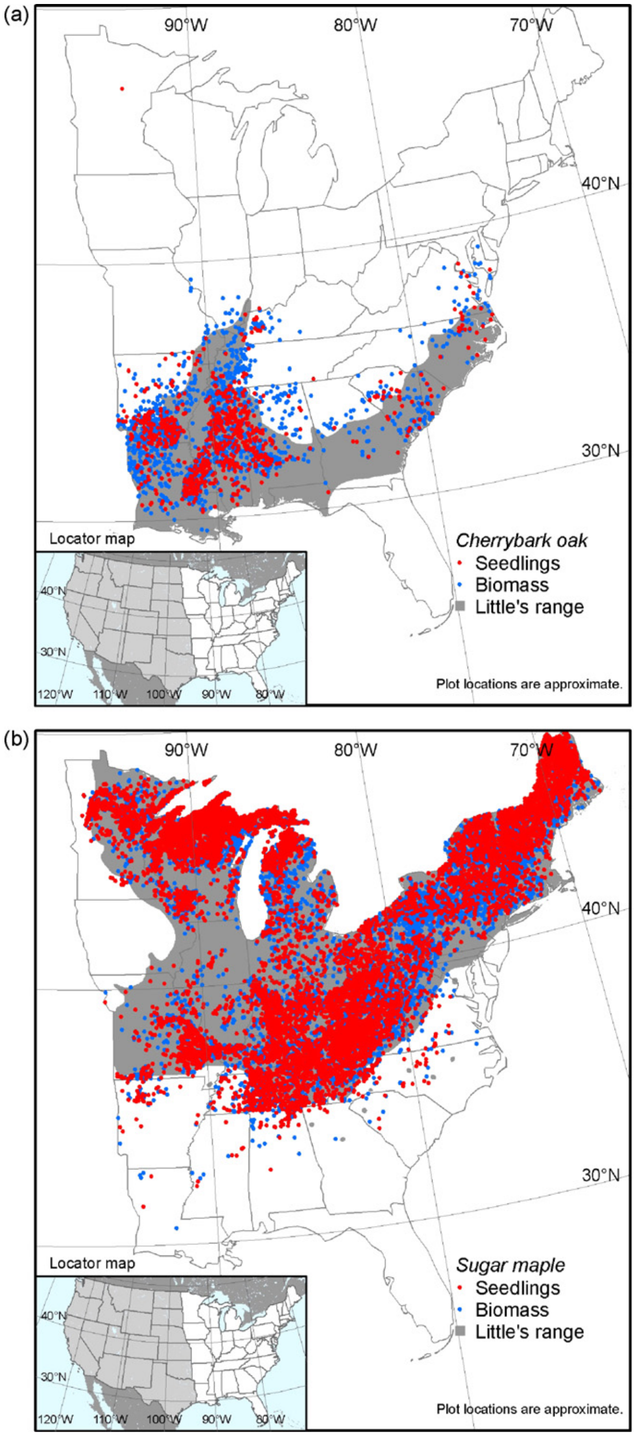

Fig. 3. Distribution of tree biomass and seedling observations for (a) cherrybark oak and (b) sugar maple along with an overlay of historic species ranges (shaded grey) described by Little (1971).

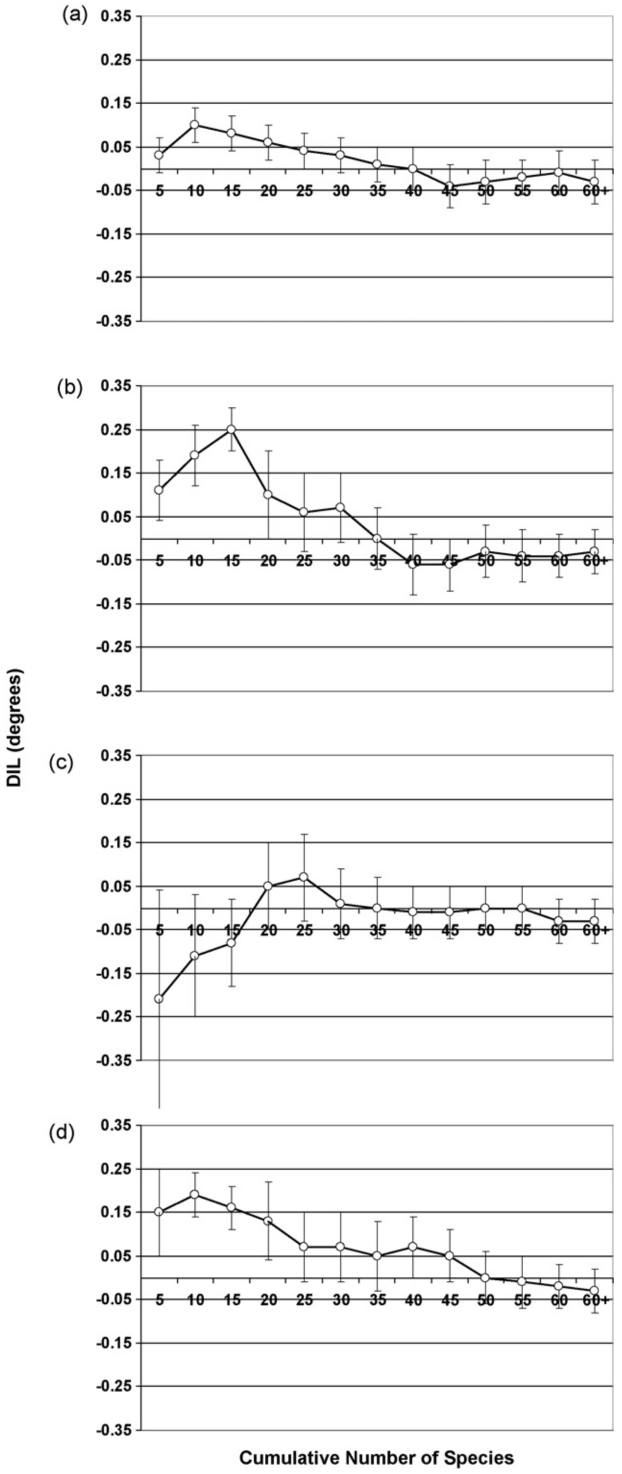

Fig. 4. Cumulative DIL (difference in seedling and biomass mean latitudes) means and associated standard errors by increasing number of included tree species ranked by (a) tree increasing latitude range, (b) decreasing median latitude, (c) decreasing migratory ability (regeneration mechanisms, see guilds in Iverson et al., 1999), and (d) decreasing loss in future area simulated (Iverson et al., 2008) under the low Hadley climate scenario.

would be of little or no migration. Further confounding would occur if one were to select a random and large selection of species (>40 species) to test migration hypotheses. The results of our study suggest using only limited lists (<20 species) of species most likely to migrate when testing tree migration hypotheses. Additionally, if one were to use a systematic nationwide forest inventory to monitor possible tree migration, the selected species should be relatively abundant to afford an adequate level of statistical rigor.

As an initial exploration of developing tree lists for testing of migration hypotheses, various individual (e.g., tree regeneration capabilities) and population attributes (e.g., latitudinal range) were examined. The optimal species for serving as an early detection species of migration are ones that have relatively narrow latitudinal ranges and inhabit high latitudes. There is the possibility that tree species future area distribution models (e.g., Iverson et al., 2008) may provide a robust mechanism for selecting

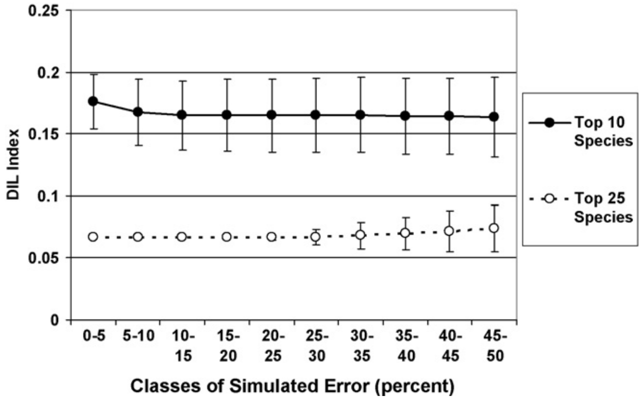

Fig. 5. Changes in mean DIL by classes of simulated error in forecasted future species' area distributions (low Hadley climate scenario) for the top 10 and 25 species (ranked according to forecasted decreasing loss in forecasted area).

tree species lists for objective migration hypothesis testing efforts (i.e., the DIL technique). It was unexpected to find that despite the hundreds of tree species in the eastern United States, perhaps only a little more than ten species serve as sensitive indicators of tree migration when using a national forest inventory. We suggest using the top 10–15 species in terms of median latitude and/or forecasted future area as initial tree lists for monitoring migration such as with the DIL technique (Woodall et al., 2009). Coupling this methodology with an annual forest inventory across the eastern United States provides a continuous monitoring framework for early detection of tree migration.

Perhaps the most revealing result from this study was that future species potential distributions and current empirical indicators of tree population shifts are not mutually exclusive in monitoring tree populations in a changing climate. Future tree distribution simulations informed the process of selecting species most likely to migrate and subsequently included in testing current migration hypotheses. Although most nations/regions will not have future tree distribution models available to them, incorporating aspects of these models into species selection (e.g., median latitude) may help winnow tree species lists to ones most likely to migrate. Surprisingly, current tree migration monitoring results were not sensitive to errors in forecasted future area if one were to use forecasted changes in area to select the top species for inclusion in DIL testing. Given the wide divergences in forecasted area changes of species in this study (−78% to 143%), a 50% error in forecasted areas did not substantially change migration results. An inordinate amount of error would need to be incorporated into forecasted future area models to suggest spruce and birches would not migrate in a warming climate.

Despite our attempts to develop objective tree lists for migration monitoring efforts, we must acknowledge the hurdles and caveats that others should address when adopting our methods in other regions/countries. First, given the limited latitudinal range of most nations and the resulting incompatibility of their forest inventories with the full species distribution, most nations probably cannot develop a robust indicator of tree migration using forest inventories. There is a tree species range conundrum that needs to be overcome. Early detection species should be abundant at high latitudes but not too far into the higher latitudes where their ranges may be truncated by natural/political borders. Second, the number of species selected for inclusion in an early detection program is somewhat subjective even if an objective index for ranking species is developed. There is a balance of selecting only tree species most likely to migrate in combination with sufficient abundance in a forest inventory to provide for statistical rigor. Our study had over 75,000 forest inventory observations of 63 tree species but ended up suggesting only 10–15 species for inclusion in a migration index. Other regions/nations with less intensive forest inventories and/or tree species diversity may be substantially limited in their ability to develop a tree migration detection system. Third, the tree migration detection methodology presented in this study is only one method for monitoring climate change effects on tree populations. As has been evidenced from numerous other studies, the monitoring of tree species along elevational gradients (Grace et al., 2002; Lenoir et al., 2008) or through remote-sensing efforts (Naesset and Nelson, 2007) may prove superior to this study's methods in any one region's or nation's unique situation. Finally, this study only examined the sensitivity of migration hypothesis testing to tree species lists for northward migration. As found in Woodall et al. (2009), wide-ranging and/or niche-insensitive species (e.g., red maple) may expand southward as climate sensitive species migrate northward. The testing of southward migration hypotheses in the northern hemisphere would require a new set of species list selection criteria apart from those proposed in this study.

Finally, this study focused on assessing the migration of climate sensitive species to higher latitudes in response to climate change. In contrast, the migration of climate insensitive tree species to lower latitudes to fill vacated niches may serve as an alternative indicator of tree migration. This study found that if one were to use the top twenty tree species in terms of forecasted area gains (e.g., winged elm) there would be an observed southward shift of 21 km as indicated by DIL. Given the cost and statistical hurdles with tracking tree species' populations as they possibly migrate out of regions/nations, the monitoring of climate insensitive, common tree species to detect lower latitude range shifts may provide alternative methodology for climate change effects monitoring.

5. Conclusions

Given the sometimes contentious issue of monitoring climate change effects on forest ecosystems, objective criteria for selecting tree species for tree migration hypothesis testing is paramount. A random selection of common tree species in the eastern U.S. would most likely indicate no migration, while selection of species with proclivities for migration may present divergent results due to northward or southward shifts. Out of the 63 study species in this study, only 10–15 were suggested for inclusion in tree migration hypothesis tests based on their median latitudes. Selection of species lists based on forecasted future area models also serves as an adequate criterion for objectively selecting species for migration hypothesis testing and is relatively insensitive to simulation error. There are various techniques available to regions/nations for monitoring their tree species distributions possible response to climate change; however, basic requirements appear to be a recurring forest inventory that samples regeneration, forest ecology information regarding individual species attributes (climate sensitive versus insensitive), and a reasonable range in latitude. For nations in high latitudes, the migration monitoring of climate sensitive species to higher latitudes may be the most efficient strategy. In contrast, nations at middle/low latitudes may find the migration of climate insensitive species into lower latitudes to be a monitoring possibility.

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