Assessing the potential for urban trees to facilitate forest tree migration in the eastern United States

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ABSTRACT

Latitudinal shifts in tree species distributions are a potential impact of climate change on forest ecosystems. It has been hypothesized that some tree species may become extirpated as climate change effects may exceed their migration ability. The goal of this study was to compare tree species compositions in northern urban areas to tree compositions in forestland areas in the eastern U.S. as an indicator of the potential for urban trees to facilitate future forest tree species migration. Results indicated that a number of tree species native to eastern U.S. forests of southern latitudes are currently present in northern urban forests. The biomass density (Mg/ha) of urban tree species is typically less than half of forestland densities with the majority of urban tree species found in nearby (<100 km) forestland. Urban tree propagation is often facilitated by humans, whereas the necessary pollinators and agents of tree seed dispersal in forestlands may be lacking regardless of climate change. It is suggested that urban areas may serve divergent, dual roles as both a native tree seed source and refuge for a limited number of forestland tree species, but also a facilitator of non-native tree invasion.

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1. Introduction

Due to an increase in 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 of growing seasons (IPCC, 2007). The combination of numerous climate change effects on forest ecosystems may ultimately lead to 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 to adequately respond to current rates of warming (Schwartz, 1992). In addition, 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). Monitoring current distributions of species is one of the best methods to assess climate change impacts (McLachlan et al., 2007).

Both projection models (Iverson et al., 2008) and empirical evidence (Woodall et al., 2009) have suggested that some tree populations in eastern North America may already be migrating northward. Tree species range maps from Woodall et al. (2009) display numerous examples of potential range outliers that could speed the process of tree 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 unintentionally or deliberately to meet landowner objectives (e.g., shade tree, windbreaks, or ornamentals). The very same human actions that have allowed rapid migration of non-native invasive species (e.g., *Ailanthus altissima*) could also facilitate the relatively rapid movement of native tree species in the eastern U.S. Similar to past tree species migrations that have occurred at unexpected fast rates (Clark et al., 1998), future tree migration in the U.S. may overcome barriers to migration (e.g., forest fragmentation and rapid climate change) and shift at rapid rates due to the presence of numerous "outliers" possibly identified by forest inventories.

In urban areas, many tree species have been planted. The establishment of native eastern North American tree species

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outside of their natural range occurs as ornamental plantings by urban landowners (e.g., *Catalpa speciosa* (Warder) or *Pseudotsgua menziesii* (Mirb.) in Minneapolis, MN). These plantings at latitudes higher than their respective native forest ranges may serve as a seed source for future migration of native tree populations. Conversely, the establishment of non-native tree species in urban areas may enable rapid invasion of forestlands by non-natives if climate change provides competitive advantage to non-natives (for general invasive discussion see Dukes and Mooney, 1999). The facilitation of tree migration by humans may speed the process of migration as forests respond to climate change (Aitken et al., 2008). Van der Veken et al. (2008) recently found that plant species in nurseries and gardens far exceeded their northern native range thus possibly facilitating future migration. While conservation biologists currently debate assisted migration (McLachlan et al., 2007), many plant species may have already been established by humans at higher latitudes. To date, there has been no research to examine the role that urban forests could play in facilitating future native tree population migration.

The goal of this study is to compare the species compositions of selected northern urban areas of the eastern U.S. to that of forestland tree compositions to evaluate the role that urban tree populations might serve in future tree migration scenarios. Specific objectives were to:

(1) Determine the species composition of selected (above 40th parallel) eastern U.S. major cities (Syracuse, Boston, Hartford, New York City, and Minneapolis) and compare to forestland tree composition within 100 km of city center.
(2) Determine the difference in latitudes for each tree species in each urban area between two locations: (a) the latitude of urban area center and (b) the 99th percentile latitude for each urban tree species found in eastern U.S. forestland.
(3) Determine the latitude at which each forestland tree species has the same biomass density (biomass, Mg/ha) as the same species in the study's eastern U.S. urban areas.
(4) Discuss results in terms of implications regarding future urban tree species facilitated migration and future research directions.

2. Methods

2.1. Forestland inventory data

Forestland inventory data came from the USDA Forest Service Forest Inventory and Analysis (FIA) program. The 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
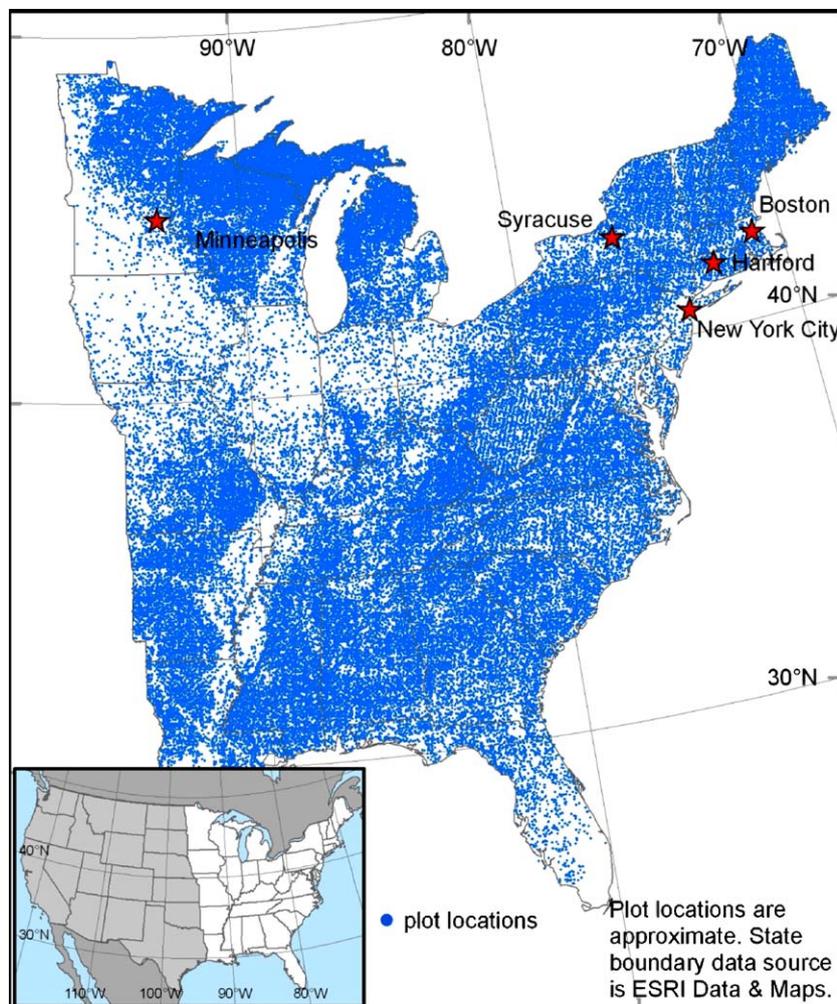

Fig. 1. Urban study areas and forestland study plots in eastern United States.

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 sub-plots spaced 36.6 m apart in a triangular arrangement with one sub-plot in the center. All trees, with a diameter at breast height of at least 12.7 cm, are inventoried on forested sub-plots. Within each sub-plot, a 2.07 m microplot offset 3.66 m from sub-plot center is established. Within each microplot, all trees with a d.b.h. between 2.5 and 12.7 cm are inventoried. Whole tree biomass (above- and below-ground) was calculated for each tree based on methods detailed in Heath et al. (2009).

Data for this study were taken entirely from FIA's public database (FIADB version 4.0) using the most recent annual inventory in 31 eastern states on 68,252 inventory plots (Fig. 1). Annual inventories for each state were first initiated between 2001 and 2003 and run through 2006–2007, so sample intensities may vary slightly by state. Because FIA inventory is quasi-systematic with sample plots distributed across the geographic extent of each state, random variations in sample intensities should not bias assessment of tree species locations (Woodall et al., 2009).

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 similar ecological characteristics. 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, especially over 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. Urban tree inventories

Five urban areas (Boston, Hartford, Minneapolis, New York City, and Syracuse) were selected in the northern regions of the eastern United States due to the availability of relatively recent, consistent urban tree inventories. Randomly located 0.04-ha (0.1 ac) field plots were measured in the five study cities to sample the entire urban forest structure of that city (e.g., tree species composition, number of trees on all land uses): Boston, MA (year of data collection = 1996; number of plots (n) = 217), Hartford, CT (2007, n = 200), Minneapolis, MN (2004, n = 110) (Nowak et al., 2006), New York, NY (1996, n = 206) (Nowak et al., 2007), and Syracuse, NY (2004, n = 198). These cities were sampled in collaboration with various cooperators, all of whom used methods developed by the USDA Forest Service for assessing urban forests using the Urban Forest Effects (UFORE) model (e.g., Nowak and Crane, 2000; Nowak et al., 2008). Data collection included land use, tree species, stem diameter at 1.37 m above the ground, tree and crown heights, crown width, and canopy condition. These data were used to assess tree biomass by species in each city.

Whole tree biomass (above- and below-ground) for each measured tree was calculated using allometric equations from the literature (see Nowak, 1994; Nowak et al., 2002). If no allometric equation could be found for an individual species, the average of results from equations of the same genus was used. If no genus equations were found, the average of results from all broadleaf or conifer equations was used. Equations that predict above-ground biomass were converted to whole tree biomass based on root-to-shoot ratio of 0.26 (Cairns et al., 1997). Equations that compute fresh-weight biomass were multiplied by species- or genus-specific-conversion factors to yield dry-weight biomass. These conversion
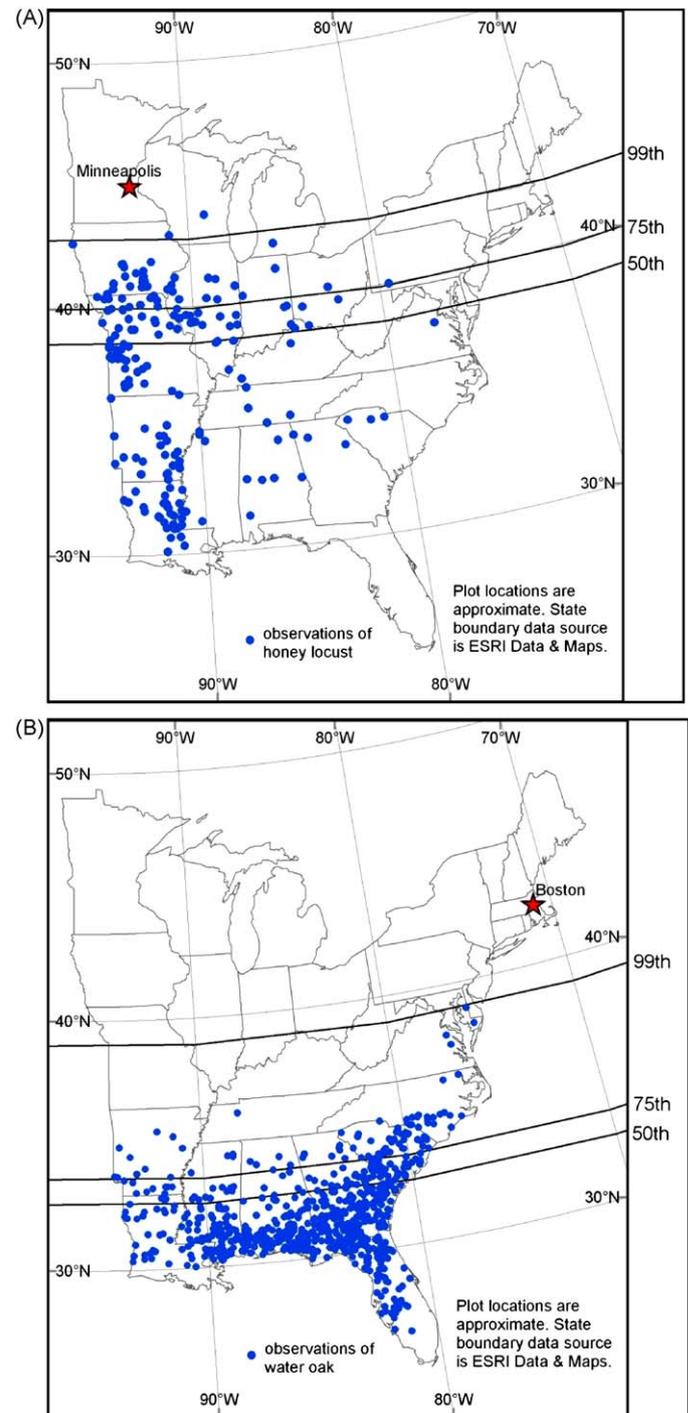

Fig. 2. Univariate statistics for latitude (°) of study species relative to nearby urban areas: (A) *Gleditsia triacanthos* relative to Minneapolis, MN; (B) *Quercus nigra* relative to Boston, MA.

factors, derived from average moisture contents of species given in the literature, averaged 0.48 for conifers and 0.56 for hardwoods (see Nowak et al., 2002). Open-grown, maintained trees tend to have less above-ground biomass than predicted by forest-derived biomass equations for trees of the same diameter (Nowak, 1994). To adjust for this difference, biomass results for urban trees were multiplied by a factor 0.8 (Nowak, 1994). No adjustment was made for trees found in more natural stand conditions (e.g., on vacant lands or in forest preserves).

2.3. Analysis

To compare the species composition of forestland surrounding urban study areas to that of the urban tree species composition, the latitude/longitude of each urban center was used as a center of a circle (100 km radius) to query the forest inventory. The radius of

100 km was used to reflect findings from other studies that 100 km is a maximum distance tree species might migrate over a century (Pearson, 2006). The top ten species in terms of biomass/ha for both the surrounding forestland and cities were determined for all cities. There were a number of non-native tree species (e.g., *Acer palmatum* (Thunb.)) detected in the urban inventories that were not found in the eastern U.S. forestland inventory. These species were included in an "Other Ornamentals" group because they currently have not been detected in FIA's forestland inventories. We could not explicitly investigate the dynamics of urban non-native tree species invasion of forestland because this is not occurring to any great extent in this study's urban areas except for *A. altissima* (Mill.).

In order to examine the latitudinal distributions of forestland species relative to study cities, forestland queries were limited to the eastern U.S. (Fig. 2). Although using the entire eastern U.S. to

Table 1
Top ten tree species by above-ground biomass (Mg/ha) in urban areas and in forestland areas within 100 km of city center (excluding urban lands).

City	Forestland tree species	Biomass (Mg/ha)	Sampling error (Mg/ha)	Urban tree species	Biomass (Mg/ha)	Sampling error (Mg/ha)
Syracuse	*Acer saccharum* (Marsh.)	26.540	2.654	Other Ornamentals	6.267	2.085
	Acer rubrum (L.)	23.635	2.600	*Acer saccharum*	4.907	2.067
	Fraxinus americana (Marsh.)	11.112	1.667	*Acer negundo* (L.)	3.973	1.238
	Prunus serotina (Ehrh.)	9.331	1.586	*Populus deltoids* (W. Bart.)	3.861	2.206
	Tsuga canadensis (L.)	7.557	1.587	*Salix* spp.	2.441	2.170
	Fagus grandifolia (Ehrh.)	6.500	1.365	*Quercus rubra*	2.129	1.131
	Pinus strobus (L.)	5.501	1.265	*Prunus serotina*	1.539	0.662
	Quercus rubra (L.)	4.285	1.157	*Acer saccharinum* (L.)	1.522	0.736
	Betula alleghaniensis (Britt.)	3.750	1.200	*Picea abies* (L.)	1.474	0.636
	Salix nigra (Marsh.)	3.637	1.200	*Gleditsia triacanthos* (L.)	1.216	0.718
Boston	*Pinus strobus* (L.)	35.768	3.577	Other Ornamentals	7.687	3.192
	Acer rubrum	33.237	3.656	*Quercus rubra*	7.209	1.878
	Quercus rubra	25.665	4.363	*Acer saccharum*	4.806	3.080
	Quercus velutina (Lamb.)	8.299	3.319	*Acer rubrum*	4.085	1.254
	Quercus alba (L.)	7.395	3.106	*Fagus grandifolia*	2.244	1.544
	Quercus coccinea (Muennchh.)	7.023	3.020	*Quercus palustris* (Muenchh.)	1.898	0.662
	Tsuga canadensis	6.453	2.775	*Tsuga canadensis*	1.179	0.398
	Betula lenta (L.)	4.400	2.068	*Quercus alba*	1.080	0.480
	Fraxinus americana (L.)	3.604	1.766	*Quercus velutina*	0.864	0.509
	Acer saccharum	2.444	1.271	*Acer saccharinum*	0.802	0.506
Hartford	*Acer rubrum*	28.601	2.288	*Acer saccharinum*	7.843	2.378
	Quercus rubra	27.713	2.217	*Acer rubrum*	7.804	2.536
	Pinus strobus	12.590	1.763	*Quercus palustris*	6.227	2.068
	Acer saccharum	11.660	1.749	Other ornamentals	4.549	2.890
	Tsuga canadensis	10.651	1.704	*Fagus grandifolia*	4.716	3.228
	Betula lenta (L.)	9.485	1.612	*Quercus rubra*	4.463	1.850
	Quercus velutina (Lamb.)	8.865	1.507	*Populus deltoides*	3.125	1.792
	Quercus alba	7.779	1.478	*Acer saccharum*	2.283	1.033
	Fraxinus americana	6.861	1.372	*Ailanthus altissima* (Mill.)	1.517	1.285
	Quercus coccinea	5.950	1.309	*Pinus strobus*	1.412	1.008
New York City	*Quercus rubra*	11.104	1.333	*Platanus occidentalis* (L.)	4.204	1.512
	Acer rubrum	9.449	1.228	Other ornamentals	3.978	2.248
	Quercus prinus (L.)	8.389	1.174	*Quercus rubra*	3.747	1.416
	Fraxinus americana	7.801	1.092	*Quercus palustris*	3.129	1.227
	Pinus rigida (Mill.)	6.166	1.048	*Liquidambar styraciflua*	2.447	1.180
	Quercus alba	5.693	0.968	*Morus alba*	2.094	0.875
	Betula lenta	5.319	0.957	*Robinia pseudoacacia* (L.)	1.474	0.843
	Quercus velutina	4.996	0.949	*Prunus serotina*	1.457	0.593
	Liriodendron tulipifera (L.)	4.966	0.944	*Quercus alba*	1.456	1.126
	Liquidambar styraciflua (L.)	4.080	0.816	*Ailanthus altissima*	1.114	0.389
Minneapolis	*Quercus rubra*	12.626	1.010	*Ulmus americana*	5.608	2.034
	Quercus macrocarpa (Michx.)	12.082	1.087	Other ornamentals	4.580	3.317
	Acer saccharum	7.292	0.875	*Gleditsia triacanthos* (L.)	3.767	2.566
	Quercus ellipsoidalis (Hill)	5.697	0.912	*Fraxinus pennsylvanica*	3.068	0.836
	Fraxinus pennsylvanica (Marsh.)	5.675	0.908	*Acer saccharinum*	2.404	1.473
	Tilia Americana (L.)	5.086	0.865	*Picea pungens* (Engelm.)	1.934	1.301
	Quercus alba	4.732	0.852	*Quercus macrocarpa*	1.758	1.696
	Acer saccharinum	4.285	0.814	*Catalpa speciosa* (Warder)	1.398	1.369
	Populus tremuloides (Michx.)	4.161	0.791	*Acer negundo*	1.017	0.599
	Ulmus americana (L.)	3.982	0.757	*Ulmus pumila* (L.)	0.718	0.524

Other ornamentals: currently non-invasive, non-native tree species planted as ornamentals.

assess future migration may ignore future migration routes, it is beyond the scope of this study to forecast migration routes given the myriad of attributes (e.g., shape, composition, and context) that define functioning biological corridors (Rosenberg et al., 1997) for the multitude of tree species in this study. The distributional statistics of the 99th percentile of forestland tree latitudes in the entire eastern U.S. minus the city center latitude was determined for every urban tree species in every study city (where species co-occurred in urban and forestland areas). Finally, a truncated linear regression model was developed for every urban tree species in the eastern U.S. (where species co-occurred in urban and forestland areas). The model determined the latitude at which the urban tree species whole tree biomass density (oven-dry weight) was equivalent to the forestland whole tree biomass density:

$$E(LAT) = b_0 + b_1(BIO) + e$$

where E() is the statistical expectation, *LAT* is latitude in degrees, b_x are coefficients to be estimated, *BIO* is the whole tree biomass (Mg/ha), and *e* is the random error term.

The data were truncated at the median latitude of each species, as we were only interested in predicting the northern latitude where the urban and forested biomass densities were equivalent. Because this truncation results in biased parameter estimates in least squares regression (Maddala, 1986), the linear regression models were fitted using SAS PROC QLIM. This procedure accounts for the truncation by adjusting the likelihood of each observation by the area of the truncated portion of the distribution (Long, 1997). Using the model coefficients, the equivalent latitude of forestland having the same biomass density as urban trees was determined for each tree species in each city. No models were included in results where the standard error of the coefficients exceeded the coefficients themselves.

3. Results

Approximately 42% of the top ten tree species in terms of biomass/ha in urban areas matched the top ten tree species in forestland areas within 100 km of city centers (Table 1). The percentage of top ten tree species matches were 30, 50, 40, 30, and 40% for Syracuse, Boston, Hartford, New York City, and Minneapolis, respectively. The biomass density (biomass/ha) of tree species was typically two to five times greater for the same species in forestland areas as compared to nearby urban areas. The highest tree biomass density for any individual tree species in each forestland area (100-km radius around each study city) ranged from 11.1 to 35.8 Mg/ha. In contrast, the highest individual tree species biomass density in each urban area ranged from 4.2 to 7.8 Mg/ha. The biomass/ha sampling errors for both forestland and urban areas were roughly equivalent in absolute terms.

The 99th percentile latitude of every tree species was compared to the latitude of every city center latitude (latitudinal differences) and summarized by city. The 99th percentile latitude was assumed to be the upper northern range of each species. Well over 75% (third quartile) of tree species in urban areas are found in forestland farther north in latitude (Table 2). With the exception of New York City, roughly 10% of tree species in urban areas were farther north of the northern limit of corresponding species in forestlands. For many of these tree species, such as *Gleditsia triacanthos* (L.) relative to Minneapolis and *Q. nigra* (L.) relative to Boston (Fig. 2a and b), the northern range limit of forestland species was substantially (>2°) farther south than the same species in northern urban areas. In total, 19 urban trees species (out of 81 unique tree species) in this study were farther north than their respective native latitudinal ranges in forestland areas (unique species across all urban study areas) (Table 3). Some of the tree

species farthest north in urban areas as compared to native forestland distributions were: *Magnolia* spp. (3.26°, Syracuse), *Cornus florida* (L.), *Q. nigra* (5.49, Boston), *Quercus virginiana* (Mill.) (8.36°, Boston), *Liquidambar styraciflua* (L.) (1.91°, New York City), *Catalpa speciosa* (Warder) (2.49°, Minneapolis), *Aesculus glabra* (Willd.) (3.22°, Minneapolis) (Table 3). New York City only had three tree species in urban areas farther north than the tree's respective northern forestland range limit. In contrast, Syracuse, Boston, and Minneapolis had over 10% of urban tree species north of the 99th percentile latitudinal distribution of the same tree species in forestland areas for a cumulative total of 23 species. It should be noted that the invasive tree species *A. altissima* was detected in Syracuse and Boston farther north of its current range in forestland within the eastern U.S.

Table 2
Univariate statistics of latitudinal differences (°) between urban tree species (city center latitude) and 99th percentile latitude of the same species in forestland areas of the eastern U.S. (positive differences indicate urban tree species farther north of forestland northern limit). Counts of unique urban tree species, including use of "other ornamentals" group, by city: Syracuse (52), Boston (63), Hartford (48), New York City (48), and Minneapolis (31).

Statistic	Cities				
	Syracuse	Boston	Hartford	New York City	Minneapolis
Max	3.26	8.36	1.99	1.91	3.22
90th	1.10	0.41	0.02	−0.96	2.08
Q3	−1.14	−0.97	−1.87	−2.21	−0.43
Median	−3.37	−3.87	−4.16	−5.37	−2.00
Q1	−4.57	−5.03	−5.56	−6.53	−3.12
10th	−5.18	−5.86	−6.43	−7.89	−3.57
Min	−5.71	−6.42	−6.99	−8.20	−3.91

Table 3
Latitudinal differences between latitude of cities and 99th percentile latitude of forestland for study tree species where 99th percentile latitude for each individual species is less than city latitude.

City	Species	Latitude difference (°)
Syracuse	*Aesculus glabra* (Willd.)	1.30
	Ailanthus altissima[a]	1.12
	Carya glabra (L.)	0.44
	Catalpa speciosa	0.57
	Cornus florida (L.)	1.29
	Gleditsia triacanthos	0.33
	Magnolia spp.	3.26
	Platanus occidentalis (L.)	1.04
Boston	*Aesculus glabra*	0.60
	Ailanthus altissima[a]	0.41
	Carya tomentosa (Sarg.)	0.86
	Cornus florida	0.59
	Magnolia spp.	2.56
	Platanus occidentalis	0.34
	Quercus nigra	5.49
	Quercus virginiana (Mill.)	8.36
Hartford	*Acer* spp.	0.97
	Aesculus glabra	0.02
	Cornus florida	0.02
	Magnolia spp.	1.99
	Nyssa sylvatica (Marsh.)	0.10
New York City	*Liquidambar styraciflua*	1.91
	Magnolia spp.	0.89
	Quercus stellata (Wangenh.)	1.65
Minneapolis	*Aesculus glabra*	3.22
	Catalpa speciosa	2.49
	Celtis occidentalis	0.11
	Gleditsia triacanthos	2.25
	Juglans nigra	0.72
	Juniperus virginiana	0.30
	Morus alba (L.)	1.90

[a] Non-native tree species.

Table 4
Truncated regression coefficients for city and tree species pairs for which the equivalent latitude (latitude of forestland with the same biomass/ha as the northern city) was lower than the latitude of the city along with the difference in latitude between the city and equivalent latitude (mean latitudinal differences are provided when tree species were in more than one city).

Cities	Species	Regression coefficients				Sigma	Lat. Diff.
		b0	SE	b1	SE		
SYR	*Picea abies*	42.8829	0.6665	−0.0129	0.0105	1.6382	0.18
MPLS	*Pinus strobus*	44.2971	0.1207	−0.0018	0.0016	1.6782	0.66
MPLS	*Acer rub rum*	44.6852	0.0227	−0.0176	0.0007	2.0583	0.28
BOST, HART	*Betula lenta*	41.6351	0.0623	−0.0090	0.0017	1.0200	0.42
BOST, HART, NYC	*Carpinus caroliniana* (Walter)	37.9585	0.3516	−0.3124	0.0615	5.0758	3.63
SYR	*Carya cordiformis* (Wangenh.)	41.8470	0.1105	−0.0190	0.0044	2.2221	1.21
SYR, BOST, NYC	*Carya glabra* (Mill.)	35.0227	0.4127	0.0070	0.0051	3.0783	6.99
SYR, BOST, HART	*Carya ovata* (Mill.)	39.6996	0.1842	−0.0049	0.0040	2.5679	2.68
BOST, HART, MPLS	*Celtis laevigata* (L.)	35.6323	1.1685	−0.0519	0.0221	3.8226	6.82
SYR, BOST, HART, NYC	*Cornus florida*	36.1100	0.1689	−0.0702	0.0224	2.2903	5.85
SYR, BOST	*Crataegus* spp.	42.1069	0.2265	−0.0223	0.0204	2.0964	0.58
MPLS	*Fraxinus pennsylvanica*	43.6740	0.0600	−0.0125	0.0024	2.7340	1.33
SYR, BOST, HART, NYC, MPLS	*Gleditsia triacanthos*	38.9932	0.2066	0.0161	0.0037	1.5138	3.54
SYR, BOST, HART, NYC, MPLS	*Juglans nigra* (L.)	37.8348	0.4197	0.0188	0.0062	2.7480	4.71
NYC	*Liquidamb ar styraciflua*	32.2218	0.2170	0.0137	0.0023	2.6632	8.41
NYC	*Liriodendron tulipifera*	35.9321	0.1587	0.0111	0.0013	2.2287	4.74
SYR, BOST, HART, NYC	*Magnolia* spp.	36.9065	0.2105	0.6187	0.0667	0.1706	5.00
SYR, BOST, HART	*Carya glabra*	41.6718	0.8125	−0.1366	0.0500	2.1331	0.75
SYR, HART	*Morus rubra* (L.)	38.3127	0.3020	0.0554	0.0170	2.5998	4.07
HART, NYC	*Nyssa sylvatica*	35.6775	0.1550	0.0411	0.0056	2.5903	5.54
SYR, BOST, HART, NYC	*Platanus occidentalis*	37.3484	0.2331	0.0106	0.0029	1.8362	4.59
SYR, BOST, MPLS	*Populus deltoides* (Marsh.)	42.2852	0.2758	−0.0059	0.0033	1.8899	1.17
MPLS	*Prunus serotina*	43.2019	0.0404	−0.0444	0.0021	2.2626	1.76
SYR	*Prunus americana* (Marsh.)	38.5248	1.4391	0.1982	0.1874	4.6619	4.51
SYR, BOST, HART, NYC, MPLS	*Quercus alba*	38.8167	0.6930	−0.0465	0.0056	5.7117	3.77
HART	*Quercus coccinea*	29.8035	1.9544	0.0168	0.0089	4.1852	11.96
BOST	*Quercus nigra* (L.)	31.4501	0.2662	−0.0152	0.0039	2.0653	10.89
MPLS	*Quercus rubra*	43.8888	0.0449	−0.0082	0.0008	2.1062	1.07
NYC	*Quercus stellata* (Wangenh.)	36.5421	0.0429	0.0089	0.0012	1.1910	4.13
SYR, BOST, NYC	*Quercus velutina*	34.4194	0.5929	0.0233	0.0041	4.4503	7.59
SYR, BOST, HART, NYC	*Robinia pseudoacacia*	37.0854	0.4500	0.0318	0.0054	2.4983	4.84
SYR	*Salix nigra*	39.7456	0.2901	0.0098	0.0071	3.8808	3.29
BOST, NYC	*Sassafras albidum*	37.7582	0.2172	0.0436	0.0089	2.4129	3.73
MPLS	*Ulmus americana*	44.0634	0.0464	−0.0590	0.0053	2.1101	1.23
SYR	*Ulmus rubra* (Muhl.)	37.9071	0.4298	0.0254	0.0160	3.4719	5.13

Lat. Diff. = latitudinal differences (°), b1 = Mg/ha, SE = associated standard errors (Mg/ha). City abbreviations: Syr = Syracuse, Bost = Boston, Hart = Hartford, Mpls = Minneapolis, NYC = New York City.

Because the 99th percentile of a forestland tree species latitudinal range may be considered an outlier, models were developed to estimate the latitude at which forestland tree species have a biomass density equivalent to that of urban trees in the eastern U.S. (Table 4, Fig. 3a and b). The equivalent latitude model adequately represented the Gaussian distribution of species' latitudinal distributions truncated at their respective median latitude (Fig. 4). Thirty five tree species in forestland areas had densities equivalent to that of urban areas at latitudes farther south of city center latitudes. The differences in city center latitudes and forestland equivalent latitudes ranged from 0.18 to 11.96°. Some of the tree species with the greatest differences in equivalent latitude and city center latitudes were: *Quercus velutina* (Lamb.) (Syracuse, Boston, New York City; 7.59°), *Quercus coccinea* (Muennchh.) (Hartford; 11.96°), *Q. nigra* (Boston; 10.89°), and *Liquidambar styraciflua* (New York City; 8.41°), and *Carya glabra* (Mill.) (Syracuse, Boston, New York City; 6.99°) (where a tree species was found in multiple cities a mean difference in latitudes is presented).

4. Discussion

Urban areas possess diverse populations of tree species, many of which are native to the eastern U.S. These urban areas may contain numerous native tree species farther north than their current ranges, thus potentially serving as a seed source along a potential migration corridor. In theory, the same mechanism that enables urban areas to serve as a means of propagation for invasive species might facilitate the migration of native tree species. The key to this hypothesis is that the tree species composition of urban areas contains numerous species farther north of their respective current ranges. This study found that urban areas could possibly facilitate future migration for only a limited set of forestland tree species for a number of reasons.

First, species compositions of urban trees are very similar to that of surrounding forestland areas. Through comparisons of the tree compositions of urban areas and surrounding forestland areas, it is evident that urban areas are refugia for limited numbers of tree species. For the cities in this study, 30–50% of the tree species representing the majority/plurality of tree biomass in a city can be found in surrounding forestland. The remaining tree species are either purely ornamentals (e.g., *Acer platanoides*) or infrequent/understory native tree species (e.g., *Celtis laevigata*). The ability of urban trees to facilitate migration is constrained by the preponderance of urban tree biomass being composed of ornamentals, less competitive understory tree species, and/or tree species similar to that of surrounding forests. However, if eastern U.S. climate changes to conditions that provide competitive advantages to ornamentals then these currently non-invasive ornamentals could invade forestlands.

Second, few species in urban areas are farther north of the outer range of native tree species' ranges. This study found that over 75% of the native tree species in cities were within the latitudinal range of their respective forestland range. Only a few tree species in urban areas were found to be farther north of their forestland ranges in the eastern U.S. *Magnolia* spp. and *Catalpa speciosa* may
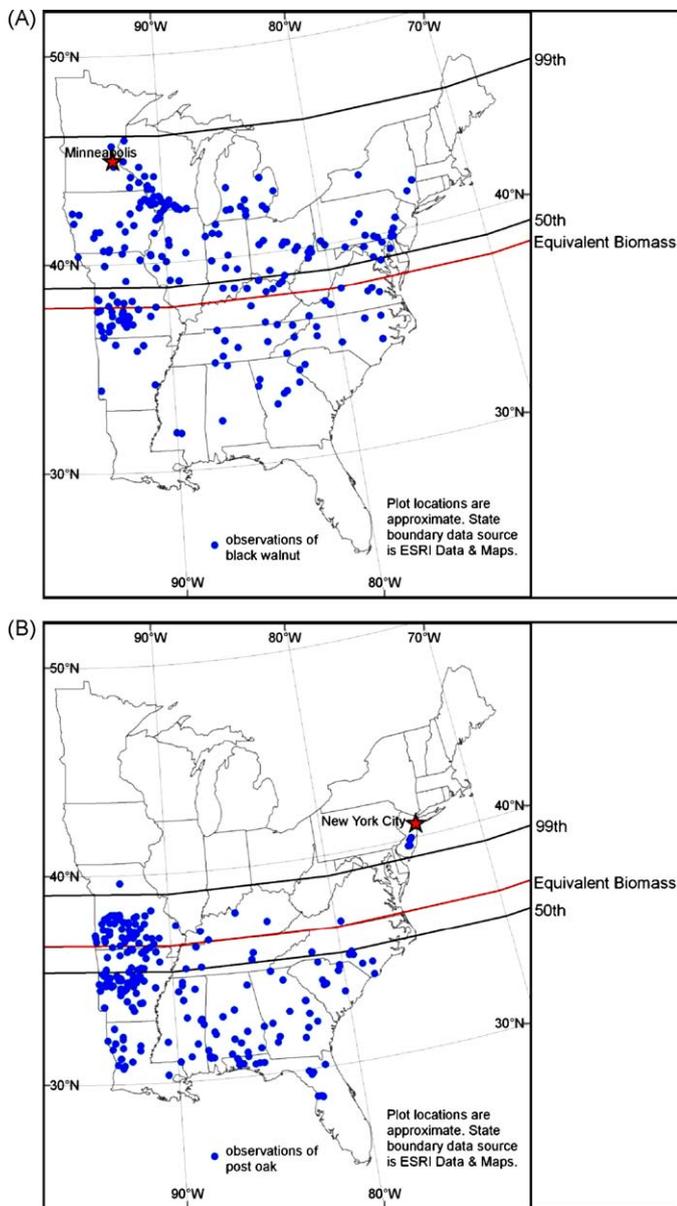
Fig. 3. Estimated equivalent latitude where forestland biomass of study species equals biomass/ha of species in nearby urban areas: (A) *Juglan nigra* relative to Minneapolis, MN; (B) *Quercus stellata* relative to New York City, NY.
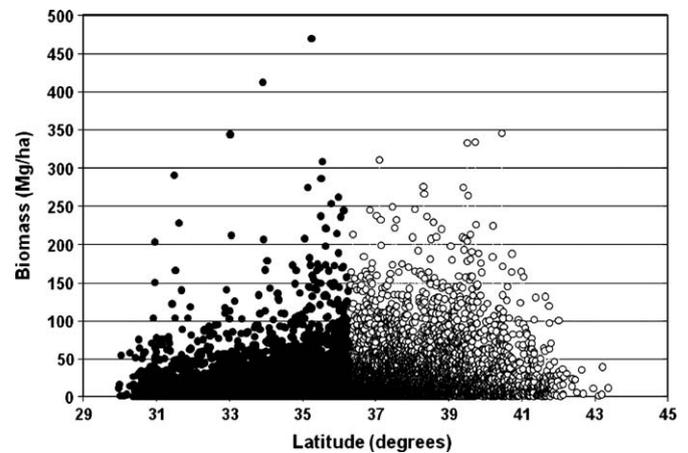

Fig. 4. Truncated regression dataset for *Liriodendron tulipifera* in eastern U.S. with observations below the median latitude represented by solid circles and observations above the median latitude represented by open circles.

be much farther north of their current forestland ranges in northern urban areas; however, they typically do not constitute major components of forests within their native ranges. The negative impacts of rapid climate change and tree migration could only be minimally ameliorated by the propagation of a few minor forestland tree components farther north.

Third, the relatively low levels of tree biomass in urban areas compared to forestland areas raises doubts that urban areas would be able to serve as a robust seed source to a viable, expanding tree populations. For a few native tree species, there are mature trees in urban areas farther north in their potential migration corridor; however, their densities are a fraction of the biomass found in self-sustaining forestland tree populations. For a number of native tree species, the biomass density (biomass/ha) of forestland trees was over five times greater than their respective species in urban areas. If tree species were extirpated, then urban trees that are maintained through irrigation, fertilization, and suppression of competitive effects might possibly serve as a seed source. In

addition to the numerous benefits that urban trees provide to metropolitan citizenry (e.g., aesthetics, soil stabilization, and energy conservation), they may also have the potential to serve as seed source in a changing climate. However, the progeny of all urban tree species (native and non-native) may have been selected by humans for traits (e.g., aesthetic flowering qualities) that might place them at a competitive disadvantage in forestland ecosystems. Additionally, ornamental tree propagation in urban areas is often facilitated by humans, whereas in forestland areas the necessary pollinators and agents of seed dispersal may be lacking no matter how climate may change. A few forestland tree species such as *Gymnocladus dioicus* (L.) and *Maclura pomifera* (Raf.) have long since lost their original seed dispersers due to millennia of evolution and climate change (Barlow, 2000). These "relics" of ancient forest ecosystems are now primarily propagated through human means, the same fate that current forestland tree species might meet in urban areas if extreme climate change occurs.

Fourth, urban areas could serve as a facilitator of invasive tree expansion. Although not an explicit objective of this study since the FIA inventory only detected a handful of invasive tree species. The aggressive invasive tree species, *A. altissima*, was a top ten tree species in term of biomass density in New York City and Hartford. Additionally, it was one of the few forestland tree species found outside its current latitudinal range in northern cities (Syracuse, 1.44°; Boston, 0.73°; Hartford, 0.16°). Invasive tree species establish themselves in the highly disturbed areas of urban settings (Call and Nilsen, 2003). Sometimes they are even tended by urban landowners as fast-growing trees that may have sprouted for free in a backyard (Radoff, 2008). The road networks emanating from urban areas may provide corridors for these invasive tree species (*A. altissima* chapter, Woodall et al., 2005). Beyond obvious invasive species, current non-invasive ornamental urban tree species could become invasive if climate changes in their favor. Taken in combination, urban tree populations should be monitored for invasive species dispersal through native tree populations as climate changes.

Future research on urban tree planting that assists migration is suggested by the results of this study. While Van der Veken et al. (2008) found that European nurseries may broadly assist plant migration in their study areas, urban trees may only minimally assist forest ecosystem adaptation to future climate change in the northern U.S. primarily due to their species composition. Urban tree planting programs could be revised to foster the planting of middle/southern latitude forestland species (with small populations, fragmented ranges, and/or low fecundity; Aitken et al., 2008) in northern urban areas in anticipation of climate change. However,

urban areas are not the only areas planted with native tree species for purposes other than regenerating forestland areas. Future study of tree species in agroforestry landscapes (e.g., windrows and hedgerows) and suburban areas (e.g., boulevards and parking lots) is suggested. These tree resources have already been identified as providing valuable ecosystem services in terms of carbon sequestration (Perry et al., 2009)—could they aid native tree migration?

This study only examined a few selected urban areas where systematic tree inventories were available, thus results may only serve as an indicator of the potential of urban tree populations to facilitate forest tree migration. Within that caveat, it may be tentatively concluded that for the majority of native tree species in forestland areas, urban areas will only serve as a minimal source of propagation if migration is necessitated by climate change. Unfortunately, urban areas might enable relatively rapid expansion of aggressive invasive tree species (e.g., A. altissima) to the detriment of less competitive native tree species. Future research is suggested to expand the objectives of this study to non-urban areas of tree plantings such as windrows in agricultural areas and boulevards in suburban settings. Under a climate change scenario of necessitated rapid migration, urban areas may serve a dual role both as a facilitator of non-native tree invasion and as a seed source or refuge for native tree species that may be dispersed along migration pathways.

Acknowledgements

References

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1, 95–111.

Barlow, C., 2000. The Ghosts of Evolution: Nonsensical Fruit, Missing Partners, and Other Ecological Anachronisms. Basic Books, New York City, p. 291.

Bechtold, W.A., Patterson, P.L., 2005. The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures, Gen. Tech. Rep. SRS-80. USDA Forest Service, Asheville, NC, 85 p.

Cairns, M.A., Brown, S., Helmer, E.H., Baumgardner, G.A., 1997. Root biomass allocation in the world's upland forests. Oecologia 111, 1–11.

Call, L.J., Nilsen, E.T., 2003. Analysis of spatial patterns and spatial association between invasive tree-of-heaven (Ailanthus altissima) and the native black locust (Robinia pseudoacacia). The American Midland Naturalist 150, 1–14.

Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G.A., Lewis, M., Lynch, J., Pacala, S., Prentice, C., Schupp, E.W., Webb, T., Wyckoff, P., 1998. Reid's paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. Bioscience 48, 13–24.

Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to quaternary climate change. Science 292, 673–679.

Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? Trends in Ecology and Environment 14, 135–139.

Heath, L.S., Hansen, M., Smith, J.E., Miles, P.D., Smith, B.W., 2009. Investigation into calculating tree biomass and carbon in the FIADB using a biomass expansion factor approach. In: McWilliams, W., Moisen, G., Czaplewski, R., comps. Forest Inventory and Analysis (FIA) Symposium 2008; October 21–23, 2008; Park City, UT. Proc. RMRS-P-56CD. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO. 26 p.

IPCC, 2007. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Avery, B., Tignor, M., Miller, H.L. (Eds.), Climate change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom/New York, NY, USA, 996 p.

Iverson, L.R., Prasad, A.M., 2002. Potential redistribution of tree species habitat under five climate change scenarios in the eastern U.S. Forest Ecology and Management 155, 205–222.

Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. Forest Ecology and Management 254, 390–406.

Long, J.S., 1997. Regression Models for Categorical and Limited Dependent Variables, vol. 7. SAGE Publications, Thousand Oaks, CA, p. 328.

Maddala, G.S., 1986. Limited-dependent and Qualitative Variables in Econometrics. Cambridge University Press, Cambridge, England, p. 401.

McLachlan, J.S., Hellmann, J.J., Schwartz, M.W., 2007. A framework for debate of assisted migration in an era of climate change. Conservation Biology 21, 297–302.

McRoberts, R.E., Holden, G.R., Nelson, M.D., Liknes, G.C., Moser, W.K., Lister, A.J., King, S.L., Lapoint, E.B., Coulston, J.W., Smith, W.B., Reams, G.A., 2005. Estimating and circumventing the effects of perturbing and swapping inventory plot locations. Journal of Forestry 103, 275–279.

Noss, R.F., 2001. Beyond Kyoto: forest management in a time of rapid climate change. Conservation Biology 15, 578–590.

Nowak, D.J., 1994. Atmospheric carbon dioxide reduction by Chicago's urban forest. In: McPherson, E.G., Nowak, D.J., Rowntree, R.A. (Eds.), Chicago's urban forest ecosystem: results of the Chicago Urban Forest Climate Project. Gen. Tech. Rep. NE-186. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA, pp. 83–94.

Nowak, D.J., Crane DE, 2000. The urban forest effects (UFORE) model: quantifying urban forest structure and functions. In: Hansen, M., Burk, T. (Eds.), Proceedings: Integrated tools for natural resources inventories in the 21st century. IUFRO Conference, 16–20 August 1998, Boise, ID, General Technical Report NC-212. U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, MN, pp. 714–720.

Nowak, D.J., Crane, D.E., Stevens, J.C., Ibarra, M., 2002. Brooklyn's urban forest. General Technical Report NE-290. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, 107 p.

Nowak, D.J., Hoehn, R., Crane, D.E., Stevens, J.C., Walton, J.T., 2006. Assessing urban forest effects and values: Minneapolis' urban forest. Resource Bulletin NE-166. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, 20 p.

Nowak, D.J., Hoehn, R., Crane, D.E., Stevens, J.C., Walton, J.T., 2007. Assessing urban forest effects and values: New York City's urban forest. Resource Bulletin NRS-9. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, 24 p.

Nowak, D.J., Hoehn, R.E., Crane, D.E., Stevens, J.C., Walton, J.T., Bond, J., 2008. A ground-based method of assessing urban forest structure and ecosystem services. Arboriculture and Urban Forestry 34, 347–358.

Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscapes and biogeographical scale levels in research and conservation. Biological Conservation 117, 285–297.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Pearson, R.G., 2006. Climate change and the migration capacity of species. Trends in Ecology and Evolution 21, 11–113.

Perry, C.H., Woodall, C.W., Liknes, G.C., Schoeneberger, M.M., 2009. Filling the gap: improving estimates of working tree resources in agricultural landscapes. Agroforestry Systems 75, 91–101.

Radoff, A., 2008. Personal communication. National Geographic, Washington, DC.

Rosenberg, D.K., Noon, B.R., Meslow, E.C., 1997. Biological corridors: form, function, and efficacy. Bioscience 47, 677–687.

Schwartz, M.W., 1992. Modeling effects of habitat fragmentation on the ability of trees to respond to climatic warming. Biodiversity and Conservation 2, 51–61.

Schwartz, M.W., Iverson, L.R., Prasad, A.M., 2001. Predicting the potential future distribution of four tree species in Ohio using current habitat availability and climatic forcing. Ecosystems 4, 568–581.

Smith, W.B., 2002. Forest inventory and analysis: a national inventory and monitoring program. Environmental Pollution 116, S233–S242.

USDA Forest Service, Forest Inventory and Analysis National Core Field Guide, Version 4.0. (2008). [Online], available at www.fia.fs.fed.us/library/field-guides-methods-proc (verified 20 Feb 2008), USDA Forest Service, Forest Inventory and Analysis National Office, Arlington, VA.

Van der Veken, S., Hermy, M., Vellend, M., Knapen, A., Verheyen, K., 2008. Garden plants get a head start on climate change. Frontiers in Ecology and the Environment 6, 212–216.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Woodall, C.W., Oswalt, C.M., Westfall, J.A., Perry, C.H., Nelson, M.D., Finley, A.O., 2009. An indicator of tree migration in forests of the eastern United States. Forest Ecology and Management 257, 1434–1444.

Woodall, C.W., Johnson, D., Gallion, J., Perry, C.H., Butler, B.J., Piva, R., Jepsen, E., Nowak, D.J., Marshall, P., 2005. Indiana's Forests, 1999–2003 Part A. Resource Bulletin NC-RB-253A. USDA Forest Service North Central Research Station, St. Paul, MN, 95 p.

Woodwell, G.M., MacKenzie, F.T., Houghton, R.A., Apps, M., Gorham, E., Davidson, E., 1998. Biotic feedbacks in the warming of the Earth. Climatic Change 40, 495–518.