Global Change Biology
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Global Change Biology (2014), doi: 10.1111/gcb.12663

Is climate an important driver of post-European vegetation change in the Eastern United States?

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Abstract

Many ecological phenomena combine to direct vegetation trends over time, with climate and disturbance playing prominent roles. To help decipher their relative importance during Euro-American times, we employed a unique approach whereby tree species/genera were partitioned into temperature, shade tolerance, and pyrogenicity classes and applied to comparative tree-census data. Our megadata analysis of 190 datasets determined the relative impacts of climate vs. altered disturbance regimes for various biomes across the eastern United States. As the Euro-American period (ca. 1500 to today) spans two major climatic periods, from Little Ice Age to the Anthropocene, vegetation changes consistent with warming were expected. In most cases, however, European disturbance overrode regional climate, but in a manner that varied across the Tension Zone Line. To the north, intensive and expansive early European disturbance resulted in the ubiquitous loss of conifers and large increases of *Acer*, *Populus*, and *Quercus* in northern hardwoods, whereas to the south, these disturbances perpetuated the dominance of *Quercus* in central hardwoods. *Acer* increases and associated mesophication in *Quercus-Pinus* systems were delayed until mid 20th century fire suppression. This led to significant warm to cool shifts in temperature class where cool-adapted *Acer saccharum* increased and temperature neutral changes where warm-adapted *Acer rubrum* increased. In both cases, these shifts were attributed to fire suppression rather than climate change. Because mesophication is ongoing, eastern US forests formed during the catastrophic disturbance era followed by fire suppression will remain in climate disequilibrium into the foreseeable future. Overall, the results of our study suggest that altered disturbance regimes rather than climate had the greatest influence on vegetation composition and dynamics in the eastern United States over multiple centuries. Land-use change often trumped or negated the impacts of warming climate, and needs greater recognition in climate change discussions, scenarios, and model interpretations.

Keywords: altered disturbance regimes, climate change, conifer-northern hardwoods, land use, mesophication, oak-pine forests, subboreal forests

Received 3 April 2014 and accepted 30 May 2014

Introduction

During the time of European settlement, North America was in the grips of the Little Ice Age (LIA) – an abnormally cool period spanning the 15th–19th centuries (Fig. 1; Mann, 2002). This climate milieu should have been rather unconducive to extensive fires, yet much of the eastern United States was covered by pyrogenic vegetation types fostered by Native American burning (Abrams & Nowacki, 2008, 2014). Indeed, early immigrants to the New World did not find an untouched wilderness but rather a land under various degrees of Amerindian occupation (Mann, 2005), with populations and landscape manipulations generally increasing from north to south (Driver & Massey, 1957). Europeans effectively followed in the footsteps of Native Americans by preferentially seeking pre-existing cultural landscapes for settlement and westward expansion (Denevan, 1992; Doolittle, 2004). European settlers encountered two vastly different ecosystems divided by the Tension Zone Line (sensu Curtis, 1959; Cogbill *et al.*, 2002), with (generally) wind-based northern hardwoods on youthful glacial landscapes to the north and fire-based central hardwoods on older nonglaciated terrain to the south (Fig. 2a). In the moist pyrophobic north, the Native American footprint was limited, often concentrated around lake- and stream-side villages and interconnected trails (Patterson & Sassaman, 1988; Nowacki *et al.*, 2012). However, immediately south of the tension zone, Native American landscape manipulations were much more prevalent, promoting oak and pine dominance through broadcast burning (Delcourt & Delcourt, 1997; Abrams & Nowacki, 2008). Further west, fire controls over presettlement vegetation progressively increased as forests gave way to more open woodlands

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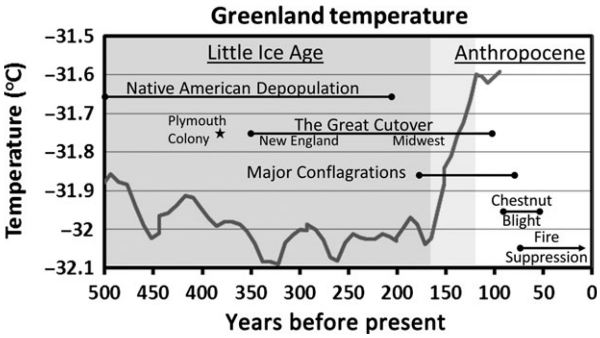


Fig. 1 The Little Ice Age to Anthropocene transition and major ecological events in North America superimposed on GISP2 Ice Core Temperature (Alley, 2004) obtained through NOAA Paleoclimatology Program and World Data Center for Paleoclimatology, Boulder, CO (ftp://ftp.ncdc.noaa.gov/pub/data/paleo/icecore/greenland/summit/gisp2/isotopes/gisp2_temp_accum_alley2000.txt).

Note: The disease-based Native American pandemic effectively started with Columbus' first voyage to the New World (Lovell, 1992; Ramenofsky, 2003), largely running its course through eastern tribes by 1800. This also co-occurred with active westward migration of Native American populations. The 'Great Cutover' arose slowly in New England from the mid-1600s, to great expansion across the Upper Midwest during the 1800s, before ending in Minnesota after 1900. The catastrophic fire era generally spans 1820–1920 to bracket the following notable fires: Miramichi Fire (ME; 1825), Peshtigo Fire (WI, MI; 1871), Michigan Fire (MI; 1881), Phillips Fire (WI; 1894), Hinckley Fire (MN; 1894), Adirondack Fire (NY; 1903), Baudette Fire (MN; 1910), and Cloquet Fire (MN; 1918) (Guthrie, 1936). Chestnut blight quickly spread north, west, and southwestward from its 1905 origins in New York City to envelope most of chestnut's range by the 1940s (see Fig. 2 of Anagnostakis, 1987)

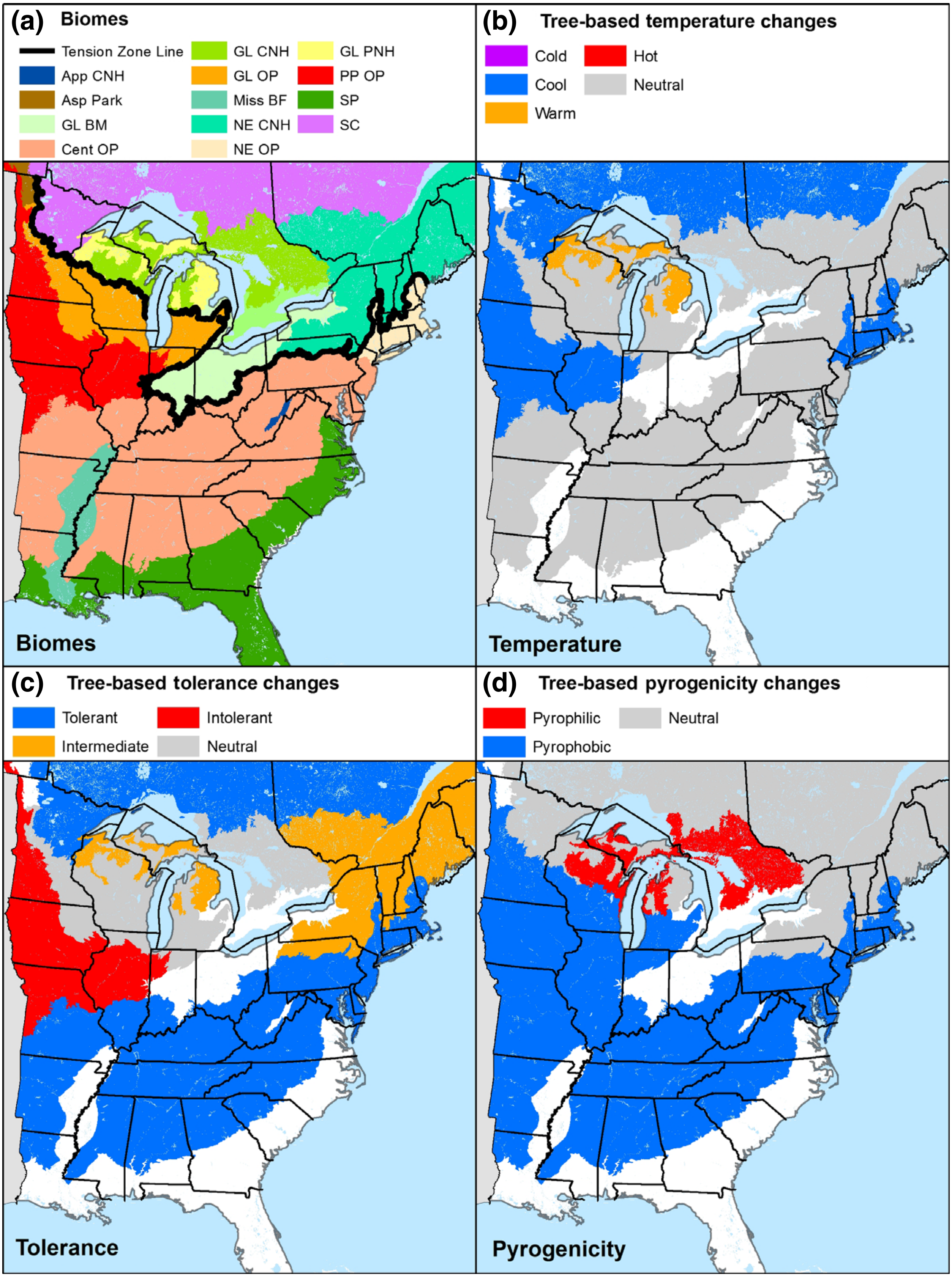
and savannas, culminating in Transeau's (1935) Prairie Peninsula – a vast fire-maintained grassland-savanna landscape where forests, based on climatic conditions, would have otherwise dominated (Anderson, 2006).

Despite a cooling and moister climate, European disturbance promoted many shade-intolerant, disturbance-adapted trees, such as aspen (*Populus*), birch (*Betula*), and oak (*Quercus*) (Russell, 1980; Nowacki *et al*., 1990; Palik & Pregitzer, 1992; Fuller *et al*., 1998; Leahy & Pregitzer, 2003). The breath and intensity of European disturbance was unprecedented, causing rates of vegetation change to be magnitudes larger than in prior millennia, leading to regional homogenization of vegetation and decoupling of long-standing climate–vegetation relations in some cases (Cole *et al*., 1998; Fuller *et al*., 1998; Schulte *et al*., 2007; Thompson *et al*., 2013). However, in terms of vegetation response, early European disturbance had less impact on areas where Native American burning and cultural landscapes existed previously. Here, the continuation of widespread disturbance from Native American to European origin fostered the dominance of midsuccessional, subclimax communities, overriding climate (as expressed by the climatic climax) for multiple millennia in the eastern United States.

An abrupt shift toward warming marked the end of the LIA (Fig. 1), a trend that continues today, enhanced by the greenhouse effect. Vegetation response to post-LIA warming did not take place in a vacuum but along with ongoing human presence, land-use change, intensive forest utilization, and insect and disease outbreaks (Whitney, 1994; MacCleery, 1996). For instance, large-scale farm abandonment throughout New England spawned a resurgence of eastern white pine (*Pinus strobus*) in the mid 19th Century (Raup, 1966). The termination of coppice harvesting by the charcoal industry at the end of the 19th Century allowed sprout-origin stands of oak, hickory (*Carya*), and chestnut (*Castanea dentata*) to mature in the central Appalachians and Ohio Valley (Nowacki & Abrams, 1992). Many of these stands where subsequently affected by chestnut blight [*Cryphonectria parasitica* (Murr.) Barr], which all but eradicated its primary host (Keever, 1953). Following catastrophic burns of the late 19th and early 20th centuries (Fig. 1), vast stands of aspen arose from the ashes of conifer-northern hardwoods in the Upper Great Lakes states (Graham *et al*., 1963; Palik & Pregitzer, 1992; Cleland *et al*., 2001). One of the most dramatic shifts has been in fire regimes, with pronounced decreases in fire frequency and intensity throughout the Central Hardwoods (Abrams, 1992). Here, most community types formerly sustained by regular fire are now at risk due to successional shifts toward shade-tolerant, fire-sensitive species and affiliated mesophication (Nowacki & Abrams, 2008; Fralish & McArdle, 2009; Hanberry *et al*., 2012a; Schumacher & Carson, 2013).

Fig. 2 Pre-European settlement vegetation biomes of North America assembled from ecological subsections of United States (Cleland *et al*., 2007) and ecological districts of Canada (Ecological Stratification Working Group, 1995) and greatest significant increasers of tree-based temperature, tolerance, and pyrogenicity classes by region. Pine-northern hardwoods are depicted by units where *Pinus* was the leading dominate presettlement tree, based largely on Schulte *et al*.'s (2007) subsection-level tree data.

Note: Abbreviations: App CNH, Appalachian conifer-northern hardwoods; Asp Park, Aspen Parklands; GL BM, Great Lakes beech-maple; Cent OP, Central oak-pine; GL CNH, Great Lakes conifer-northern hardwoods; GL OP, Great Lakes oak-pine; Miss BF, Mississippi bottomland forests; NE CNH, Northeast conifer-northern hardwoods; NE OP, Northeast oak-pine; GL PNH, Great Lakes pine-northern hardwoods; PP OP, Prairie Peninsula oak-pine; SP, Southern pines and SC, Subboreal conifers.


(a) Biomes
Tension Zone Line
App CNH
Asp Park
GL BM
Cent OP
GL CNH
GL OP
Miss BF
NE CNH
NE OP
GL PNH
PP OP
SP
SC
Biomes
(b) Tree-based temperature changes
Cold
Cool
Warm
Hot
Neutral
Temperature
(c) Tree-based tolerance changes
Tolerant
Intermediate
Intolerant
Neutral
Tolerance
(d) Tree-based pyrogenicity changes
Pyrophilic
Pyrophobic
Neutral
Pyrogenicity

This shift may have also been facilitated by lessening droughts and increasing climatic moisture in the eastern United States (McEwan *et al*., 2010).

The diverse forests of eastern North America are a reflection of a multitude of ecological settings, climatic conditions, and human interventions. Many mature forests of today essentially span two climatic periods, often originating from major disturbance events during the LIA, but growing and maturing in a warming climate in the midst of shifting economies, human attitudes toward the environment, and land use (Fig. 1; Williams, 1987; Frederick & Sedjo, 1991; MacCleery, 1996). In addition, climate change has not been uniform throughout the eastern United States, where the northern half has experienced a greater relative increase in temperature and precipitation than the southern half during the last 50–100 years (Karl *et al*., 2009; Grimm *et al*., 2013). This variation in climate may have differentially impacted north vs. south vegetation development after 1900. Much has been conjectured about the impacts of future climate change on vegetation (Bachelet *et al*., 2001; Hansen *et al*., 2001; McKenney *et al*., 2007; Iverson *et al*., 2008), yet few have directly assessed the relative importance of climate vs. human-based disturbances as currently expressed in vegetation. We need a better understanding of the role of climate–disturbance interactions in the vegetation dynamics for most regions (Munoz *et al*., 2010; Pinter *et al*., 2011). We propose to do this by (i) categorizing ecophysiological attributes for 101 major tree species/genera into temperature, shade tolerance (succession) and pyrogenicity classes, then (ii) applying those classes to comparative studies of past (presettlement) and present tree censuses to relate compositional changes to known climate or disturbance (land use) phenomena. The interpretation of compositional changes in relation to average annual range temperature, shade tolerance, and pyrogenicity allowed us to gage the relative influences of climate, known disturbance events (e.g. 'The Great Cutover' and catastrophic fire eras; Fig. 1), and altered disturbance regimes (e.g. fire suppression, mesophication) as they are actually expressed in vegetation.

Materials and methods

We identified 50 tree-census studies that compared presettlement (original land survey data) and current vegetation conditions in the eastern United States (Appendix S1). Some studies reported comparative data for multiple locations, site/cover types, or tree-size classes (e.g. Barnes, 1974; Whitney, 1987; Leahy & Pregitzer, 2003; Schulte *et al*., 2007), resulting in a total of 190 datasets available for analysis. Early tree surveys chronicle the westward progression of European land acquisition, with some dating back to the 1600s along the East Coast (Whitney & Davis, 1986; Foster *et al*., 1998; Thompson *et al*., 2013). As the typical mortality age of eastern tree species is between ≈100–300 yrs (Loehle, 1988), early 'presettlement' tallies recorded trees largely, if not exclusively, originating during the LIA period.

To transfer vegetation changes embedded in comparative tree-census datasets to meaningful metrics for tracking climate and disturbance influences, common eastern North American trees were classified by temperature, shade tolerance, and pyrogenicity based on available data, published literature, and authors' knowledge (Table 1). Temperature classes were established using actual temperature data from the Climate Change Tree Atlas (Prasad *et al*., 2007-ongoing; obtained 10/13/09 through Dr. Stephen Matthews, USFS Northern Research Station). One hundred and thirty-four tree species were sorted by the average annual temperature within their ecological range (US distribution) and divided into four temperature classes (cold = 4.1–6.6 °C; cool = 6.7 – 10.7 °C; warm = 10.8 – 13.9 °C; hot = 14.0–19.8 °C). As species were encountered in the tree-census datasets, they were added to the analytical database from this initial pool of 134 species. This helped ensure that the database was populated by species most representative of the 50 component studies. Species not recorded in the comparative datasets (or those of exceedingly low importance) were not added; these were normally rare or uncommon trees or trees outside of the scatter of component study locations. For those studies reporting tree data at the genus level, component species temperatures were averaged and assigned a temperature class at that taxonomic level (Table 1). One exception was with pine (*Pinus*), which, due to its large combined range, was subdivided into northern and southern subgroups prior to temperature class assignment. Recognizing these two subgroups was quite important so that the appropriate temperature class could be applied to datasets based on their geographical location. To assess level of disturbance (and possible indicators of human activity) recorded in tree-census datasets, species, subgenera (in the case of pine), and genera were categorized by shade tolerance (intolerant, intermediate, and tolerant) and pyrogenicity (pyrophilic and pyrophobic) based on their known life history and physiological characteristics (Table 1). The 'Silvics of North America' collection (Burns & Honkala, 1990a,b) and online Climate Change Tree Atlas (http://www.nrs.fs.fed.us/atlas/tree/tree_atlas.html; Prasad *et al*., 2007-ongoing) were extensively used to help classify trees by shade tolerance and pyrogenicity. In total, temperature, shade tolerance, and pyrogenicity were generated for 101 species, subgenera (*Pinus*), genera, and functional groups (i.e. soft hardwoods) (Table 1).

The majority of tree-census data was reported in percentages (e.g. relative abundance) or importance values that summed to 100; a perfect format for comparative analysis (Appendix S1). However, for those studies reporting data by importance value base 200 or 300 (Cottam, 1949; Zicker, 1955; Ward, 1956a,b; Nelson *et al*., 1994), tree-census data had to be first relativized (i.e. converted to importance value base 100) for presettlement and current periods. Next, these data were tallied by temperature (cold, cool, warm, hot), shade tolerance (intolerant, intermediate, tolerant), and pyrogenicity

Table 1 Common eastern North American tree species and genera classified by temperature, shade tolerance, and pyrogenicity based on literature and authors' knowledge. Average annual range temperatures derived from the Tree Atlas database (Prasad *et al.*, 2007-ongoing) were used to define temperature classes for species (cold ≤ 6.6 °C; cool = 6.7–10.7 °C; warm = 10.8–14.0 °C; hot > 14.0 °C). Range temperatures for genera/subgenera/functional groups were averaged from component species

Latin name	Common name	Average annual range temperature (°C)	Temperature	Shade Tolerance*	Pyrogenicity
Abies or *A.balsamea*	Balsam fir	4.4	Cold	Tolerant	Pyrophobic
Acer	Maple	9.6	Cool	Tolerant	Pyrophobic
A.negundo	Boxelder	10.7	Cool	Intermediate	Pyrophobic
A.nigrum	Black maple	9.7	Cool	Tolerant	Pyrophobic
A.pensylvanicum	Striped maple	6.7	Cool	Tolerant	Pyrophobic
A.rubrum	Red maple	11.9	Warm	Tolerant	Pyrophobic
A.saccharinum	Silver maple	9.9	Cool	Intermediate	Pyrophobic
A.saccharum	Sugar maple	8.7	Cool	Tolerant	Pyrophobic
Aesculus	Buckeye	11.3	Warm	Tolerant	Pyrophobic
A.glabra	Ohio buckeye	10.8	Warm	Tolerant	Pyrophobic
A.octandra	Yellow buckeye	11.7	Warm	Tolerant	Pyrophobic
Asimina or *A.triloba*	Pawpaw	11.8	Warm	Tolerant	Pyrophobic
Betula	Birch	8.8	Cold	Intolerant	Pyrophobic
B.alleghaniensis	Yellow birch	6.1	Cold	Intermediate	Pyrophobic
B.lenta	Black birch	10.7	Cool	Intolerant	Pyrophobic
B.nigra	River birch	13.3	Warm	Intolerant	Pyrophobic
B.papyrifera	White birch	5.1	Cold	Intolerant	Pyrophilic
Carpinus or *C.caroliniana*	Musclewood	12.8	Warm	Tolerant	Pyrophobic
Carya	Hickory	13.0	Warm	Intermediate	Pyrophilic
C.cordiformis	Bitternut	10.9	Warm	Intermediate	Pyrophobic
C.glabra	Pignut hickory	13.1	Warm	Intermediate	Pyrophilic
C.illinoensis	Pecan	15.4	Hot	Intolerant	Pyrophilic
C.laciniosa	Shellbark hickory	12.5	Warm	Intermediate	Pyrophilic
C.ovata	Shagbark hickory	11.2	Warm	Intermediate	Pyrophilic
C.texana	Black hickory	14.5	Hot	Intermediate	Pyrophilic
C.tomentosa	Mockernut	13.5	Warm	Intermediate	Pyrophilic
Castanea or *C.dentata*	Chestnut	9.8	Cool	Intermediate	Pyrophilic
Celtis or *C.occidentalis*	Hackberry	11.3	Warm	Intermediate	Pyrophobic
Cercis or *C.canadensis*	Redbud	13.0	Warm	Tolerant	Pyrophobic
Cornus or *C.florida*	Dogwood	13.8	Warm	Tolerant	Pyrophobic
Diospyros or *D.virginiana*	Persimmon	15.1	Hot	Tolerant	Pyrophobic
Fagus or *F.grandifolia*	Beech	11.0	Warm	Tolerant	Pyrophobic
Fraxinus	Ash	8.9	Cool	Intermediate	Pyrophobic
F.americana	White ash	10.3	Cool	Intermediate	Pyrophobic
F.nigra	Black ash	5.3	Cold	Intermediate	Pyrophobic
F.pennsylvanica	Green ash	11.2	Warm	Intermediate	Pyrophobic
Gleditsia or *G.triacanthos*	Honeylocust	12.6	Warm	Intolerant	Pyrophobic
Juglans		10.1	Warm	Intermediate	Pyrophobic
J.cinerea	Butternut	8.6	Cool	Intermediate	Pyrophobic
J.nigra	Black walnut	11.5	Warm	Intermediate	Pyrophobic
Juniperus or *J.virginiana*	Redcedar	13.2	Warm	Intolerant	Pyrophobic
Larix or *L.laricina*	Tamarack	4.6	Cold	Intolerant	Pyrophobic
Liquidambar or *L.styraciflua*	Sweetgum	16.1	Hot	Intolerant	Pyrophobic
Liriodendron or *L.tulipifera*	Tulip poplar	13.7	Warm	Intolerant	Pyrophobic
Maclura or *M.pomifera*	Osage orange	12.1	Warm	Intolerant	Pyrophobic
Magnolia or *M.acuminata*	Cucumbertree	11.1	Warm	Intermediate	Pyrophobic
Morus or *M.rubra*	Mulberry	13.2	Warm	Intermediate	Pyrophobic
Nyssa or *N.sylvatica*†	Blackgum	14.2	Hot	Tolerant	Pyrophobic
Ostrya or *O.virginiana*	Ironwood	10.3	Cool	Tolerant	Pyrophobic
Picea‡	Spruce	4.5	Cold	Tolerant	Pyrophobic

Table 1 (continued)

Latin name	Common name	Average annual range temperature (°C)	Temperature	Shade Tolerance*	Pyrogenicity
Pinus (northern)§	Northern pine	5.8	Cold	Intolerant	Pyrophilic
*Pinus (southern)***	Southern pine	17.1	Hot	Intolerant	Pyrophilic
P. banksiana	Jack pine	4.9	Cold	Intolerant	Pyrophilic
P. resinosa	Red pine	5.5	Cold	Intolerant	Pyrophilic
P.echinata	Shortleaf pine	15.4	Hot	Intolerant	Pyrophilic
P.elliottii	Slash pine	18.5	Hot	Intolerant	Pyrophilic
P.palustris	Longleaf pine	17.9	Hot	Intolerant	Pyrophilic
P.pungens	Table Mountain pine	11.0	Warm	Intolerant	Pyrophilic
P.rigida	Pitch pine	10.5	Cool	Intolerant	Pyrophilic
P.strobus	Eastern white pine	7.1	Cool	Intermediate	Pyrophilic
P.taeda	Loblolly pine	16.5	Hot	Intolerant	Pyrophilic
P.virginiana	Virginia pine	12.8	Warm	Intolerant	Pyrophilic
Platanus or *P.occidentalis*	Sycamore	13.1	Warm	Intolerant	Pyrophobic
Populus	Aspen	6.8	Cold	Intolerant	Pyrophilic
P.balsamifera	Balsam poplar	4.5	Cold	Intolerant	Pyrophobic
P.deltoides	Cottonwood	10.6	Cool	Intolerant	Pyrophobic
P.grandidentata	Bigtooth aspen	6.6	Cold	Intolerant	Pyrophilic
P.tremuloides	Quaking aspen	5.6	Cold	Intolerant	Pyrophilic
Prunus	Cherry	8.7	Warm	Intermediate	Pyrophobic
P.pensylvanica	Pin cherry	5.9	Cold	Intolerant	Pyrophilic
P.serotina	Black cherry	11.4	Warm	Intermediate	Pyrophobic
Quercus	Oak	12.3	Warm	Intermediate	Pyrophilic
Q.alba	White oak	12.4	Warm	Intermediate	Pyrophilic
Q.bicolor	Swamp white oak	10.3	Cool	Intermediate	Pyrophilic
Q.coccinea	Scarlet oak	12.5	Warm	Intolerant	Pyrophilic
Q.ellipsoidalis	Northern pin oak	6.7	Cool	Intolerant	Pyrophilic
Q.falcata	Southern red oak	15.7	Hot	Intermediate	Pyrophilic
Q.ilicifolia	Scrub oak	9.2	Cool	Intolerant	Pyrophilic
Q.macrocarpa	Bur oak	8.1	Cool	Intermediate	Pyrophilic
Q.marilandica	Blackjack oak	15.1	Hot	Intolerant	Pyrophilic
Q.muehlenbergii	Chinkapin oak	12.6	Warm	Intermediate	Pyrophilic
Q.nigra	Water oak	17.1	Hot	Intolerant	Pyrophilic
Q.palustris	Pin oak	11.4	Warm	Intolerant	Pyrophilic
Q.phellos	Willow oak	16.3	Hot	Intolerant	Pyrophilic
Q.prinus	Chestnut oak	11.6	Warm	Intermediate	Pyrophilic
Q. rubra	Red oak	10.3	Cool	Intermediate	Pyrophilic
Q. stellata	Post oak	15.2	Hot	Intolerant	Pyrophilic
Q. velutina	Black oak	12.1	Warm	Intermediate	Pyrophilic
Robinia or *R.pseudoacacia*	Locust	11.3	Warm	Intolerant	Pyrophobic
Salix or *S.nigra*	Willow	9.1	Cool	Intolerant	Pyrophobic
Sassafras or *S.albidum*	Sassafras	12.8	Warm	Intolerant	Pyrophilic
Taxodium or T.*distichum*	Baldcypress	17.6	Hot	Intermediate	Pyrophobic
Thuja or *T.occidentalis*	Cedar	4.5	Cold	Tolerant	Pyrophobic
Tilia or *T.americana*	Basswood	8.0	Cool	Tolerant	Pyrophobic
Tsuga or *T.canadensis*	Hemlock	7.3	Cool	Tolerant	Pyrophobic
Ulmus	Elm	11.7	Warm	Intermediate	Pyrophobic
U.alata	Wahoo	15.6	Hot	Tolerant	Pyrophobic
U.americana	American elm	10.4	Cool	Intermediate	Pyrophobic
U.rubra	Slippery elm	11.4	Warm	Tolerant	Pyrophobic

Table 1 (continued)

Latin name	Common name	Average annual range temperature (°C)	Temperature	Shade Tolerance*	Pyrogenicity
U.thomasi	Rock elm	9.3	Cool	Intermediate	Pyrophobic
Soft hardwoods††	Mesophytes	11.3	Warm	Intermediate	Pyrophobic

*Shade tolerance refers to the ability of a tree to regenerate, grow, and endure under various levels of shade. It is a general indicator of competitive ability; a multifaceted index that represents more than just light resources (e.g. root competition, growing space).

†*Nyssa* was represented by *N. sylvatica*, an enigmatic species having both pyrophilic and pyrophobic characteristics (Abrams, 2007). As it is largely increasing under current reduced fire regimes, it was designated pyrophobic, which is more representative of the genus as a whole.

‡As most presettlement surveys did not distinguish Picea species and due to their ecophysiological similarity, characteristics were averaged among the primary species (*P. mariana*, *P. glauca*, and *P.rubens*). Annual range temperature averaged from *P.mariana* (4.1 °C), *P. glauca* (4.3 °C), and *P. rubens* (5.1 °C) (not listed).

§Annual range temperature averaged from *P.banksiana* (4.9 °C), *P.resinosa* (5.5 °C), and *P.strobus* (7.1 °C).

**Annual range temperature averaged from *P.echinata* (15.4 °C), *P.elliottii* (18.5 °C), *P.palustris* (17.9 °C), and *P.taeda* (16.5 °C).

††Classifications based on averaged characteristics of *P. serotina*, *A. negundo*, *A. glabra*, *J. cinerea*, *M. acuminata*, *Ulmus*, *Celtis*, *Sassafras*, and *Platanus* specifically for Rentch & Hicks (2005).

(pyrophilic, pyrophobic) classes based on the lowest taxonomic level reported for each dataset (see Table 1 for species, subgenus, and genus classification). Absolute percentage changes were then calculated for each class by subtracting presettlement values from current values. Theoretically, absolute percentage changes within each category (temperature, tolerance, and pyrogenicity) should balance and sum to zero for each dataset. However, this occurred infrequently as many datasets had uncommon or unidentified trees (e.g. 'other or miscellaneous trees') that could not be categorized and were thus excluded. This explains why individual and summarized data presented in Appendices S2–S5 and Table 2 often do not balance (sum to zero by category).

To increase resolution and track regional differences in compositional change and its expression in temperature, shade tolerance, and pyrogenicity, comparative tree-census studies were divided into major biomes based on dominant presettlement vegetation, and included: Northeast oak-pine, Central oak-pine, Great Lakes oak-pine, Prairie Peninsula oak-pine, Northeast conifer-northern hardwoods, Great Lakes conifer-northern hardwoods, Great Lakes pine-northern hardwoods, and Subboreal conifers (Fig. 2a). Central, Great Lakes, and Prairie Peninsula oak-pine systems were further subdivided to capture embedded wetland forests. Although depicted in Fig. 2a, we do not report data for those biomes having fewer than three studies (e.g. Appalachian conifer-northern hardwoods, Great Lakes beech-maple).

Results

During the time of European settlement, which corresponds with the Little Ice Age, forest composition in the eastern United States followed, at least in part, a temperature gradient with cold- or cool-adapted conifers and hardwoods in the north and warm- or hot-adapted oak and pine in the south (Fig. 2a, Appendices S2–S5). In addition, there was a high proportion of pyrophilic trees (e.g. oak and pine) mostly aggregated in the northeast coastal, central, and southern regions indicating the important role of presttlement (human) fires despite the cooler prevailing climate.

Northeast oak-pine systems experienced major compositional shifts between presettlement times and the present (Table 2), with *Acer* increasing dramatically across all sites (increases of 13 to 27%; Appendix B). Overall, increases in *Acer* and *Betula* (20% and 5%, respectively) were offset by decreases in *Quercus*, *Castanea*, and *Fagus* (−15%, −6%, and −3%). When expressed by temperature, tolerance, and pyrogenicity classes, these compositional changes translated to large increases in cool, shade tolerant, pyrophobes (17%, 18%, and 25%, respectively) and decreases in warm, intermediate, pyrophiles (−15%, −16%, and −24%). All of these changes were ANOVA significant (Table 3).

Trees that rose in representation were irregularly spread among many genera in Central oak-pine systems (Appendix S2), such that only *Acer* showed an appreciable increase overall (7%) (Table 2). Large increases in *Juniperus* at Missouri sites (upward to 18%) led to a marginal increase when averaged across all sites (3%). *Quercus* decreased substantially (−17%), followed distantly by *Pinus* and *Castanea* (−4% and −3%). These compositional changes expressed themselves most strongly in pyrogenicity, with a large significant decrease in pyrophiles (−22%) offset by a similar significant increase in pyrophobes (18%) (Tables 2 and 3). There was a significant shift from intermediate (−10%) to tolerant genera (8%), whereas no real trends manifested themselves in temperature due to wide-ranging and disparate changes recorded in component studies. Similar changes were found in embedded Central oak-pine wetlands (Table 2; Appendix S3), with an

Table 2 Mean absolute percentage changes (%) from pre-European settlement to present-day by arboreal vegetation and tree-based temperature, shade tolerance, and pyrogenicity classes for eight biomes and three embedded wetland systems in the eastern United States

Region or embedded wetland system (n)	Vegetation Δ		Temperature Δ				Tolerance Δ			Pyrogenicity Δ	
	Major Increasers	Major Decreasers	Cold	Cool	Warm	Hot	Intol	Inter	Tol	Pyrophile	Pyrophobe
Northeast oak-pine (10)	Acer(20), Betula(5)	Quercus(-15), Castanea(-6), Fagus(-3)	−1	17	−15	0	−1	−16	18	−24	25
Central oak-pine (33)	Acer(7), Juniperus(3)	Quercus(-17), Pinus(-4), Castanea(-3)	−2	3	−1	−4	−3	−10	8	−22	18
Central oak-pine wetlands (3)	Acer(16), Liquidambar(6), Betula(4)	Quercus(-12), Celtis (-8), Populus(-6)	0	13	−22	4	9	−18	6	−17	13
Great Lakes oak-pine (18)	Acer(9), Carya(3), Ulmus(3)	Quercus(-24)	1	−8	5	0	3	−15	10	−23	21
Great Lakes oak-pine wetlands (6)	Acer(23)	Fraxinus(-7), Larix(-6), Quercus(-3)	−15	9	5	0	−12	3	7	−2	1
Prairie Peninsula oak-pine (9)	Celtis(6), Gleditsia(5), Maclura(5)	Quercus(-39)	0	9	−13	−3	8	−15	1	−43	36
Prairie Peninsula oak-pine wetlands (3)	Acer(20), Fraxinus(3), Juniperus(3)	Ulmus(-10), Quercus (-8), Populus(-6)	0	20	−21	−4	−13	8	0	−11	6
Northeast conifer-northern hardwoods (10)	Acer(19), Prunus(5), Betula/Quercus(4)	Fagus(-23), Tsuga(-8), Picea(-5)	0	9	−11	0	5	11	−18	6	−8
Great Lakes conifer-northern hardwoods (29)	Acer(14), Populus(11), Fraxinus(3)	Tsuga(-18), Fagus(-7), Betula(-6)	2	1	−6	0	0	2	−7	9	−12
Great Lakes pine-northern hardwoods (33)	Quercus(13), Populus(12), Acer(12)	Pinus(-29), Tsuga(-10), Fagus(-4)	−13	0	10	0	−16	9	4	−2	0
Subboreal conifers (31)	Populus(15), Fraxinus(5), Acer(5)	Pinus(-18), Larix(-13), Betula(-3)	−8	4	2	0	−15	2	11	−1	−1

Table 3 Analysis of variance (ANOVA) test of presettlement and current frequency distributions for nine classes representing temperature, tolerance, and pyrogenicity for eight biomes. Arrows indicate classes with significant increases (↑) or decreases (↓) at $P \leq 0.1$; significant increases are depicted spatially in Fig. 2

Biome (n)	Class	Presettlement Mean	Current Mean	F	*P*-Value
Northeast oak-pine (10)	Cold	19.6	18.2	0.114	0.740
	Cool ↑	25.7	42.3	11.942	0.003**
	Warm ↓	51.1	36.5	5.683	0.028*
	Hot	<0.1	0.1	0.118	0.736
	Intolerant	20.0	18.6	0.138	0.715
	Intermediate ↓	59.5	43.0	5.803	0.027*
	Tolerant ↑	17.0	35.4	17.255	0.001***
	Pyrophilic ↓	72.6	48.6	18.812	<0.001***
	Pyrophobic ↑	23.8	48.5	17.690	0.001***
Central oak-pine (33)	Cold	3.6	1.4	2.584	0.113
	Cool	13.0	16.1	1.331	0.253
	Warm	62.4	61.3	0.092	0.763
	Hot	17.9	13.8	0.808	0.372
	Intolerant	23.3	20.7	0.407	0.526
	Intermediate ↓	65.3	55.6	9.126	0.004**
	Tolerant ↑	8.3	16.3	8.051	0.006**
	Pyrophilic ↓	82.3	60.2	36.075	<0.001***
	Pyrophobic ↑	14.6	32.4	25.673	<0.001***
Great Lakes oak-pine (18)	Cold	15.3	16.8	0.048	0.828
	Cool	51.4	43.6	1.393	0.246
	Warm	31.9	36.4	0.319	0.576
	Hot	0.0	0.0	x	x
	Intolerant	16.7	19.8	0.172	0.681
	Intermediate	67.4	52.5	2.429	0.128
	Tolerant	14.5	24.4	1.392	0.246
	Pyrophilic ↓	75.4	52.9	4.030	0.053*
	Pyrophobic ↑	23.1	43.9	3.760	0.061*
Prairie Peninsula oak-pine (9)	Cold ↓	0.4	0.0	12.925	0.002**
	Cool ↑	16.4	25.6	4.650	0.047*
	Warm ↓	76.6	64.1	9.599	0.007**
	Hot	6.4	3.7	0.608	0.447
	Intolerant ↑	14.2	22.1	3.421	0.083*
	Intermediate ↓	82.1	66.9	15.523	0.001***
	Tolerant	3.4	4.3	0.416	0.528
	Pyrophilic ↓	77.2	34.5	40.052	<0.001***
	Pyrophobic ↑	22.6	58.8	27.794	<0.001***
Northeast conifer-northern hardwoods (10)	Cold	18.2	18.2	<0.001	0.998
	Cool	36.1	45.5	2.746	0.115
	Warm ↓	42.1	31.1	4.249	0.054*
	Hot	<0.1	<0.1	0.200	0.660
	Intolerant ↑	9.6	14.8	3.470	0.079*
	Intermediate ↑	12.8	23.6	4.859	0.041*
	Tolerant ↓	74.0	56.4	18.093	<0.001***
	Pyrophilic	11.2	17.3	2.244	0.151
	Pyrophobic	85.2	77.6	2.576	0.126
Great Lakes conifer-northern hardwoods (29)	Cold	36.4	38.3	0.185	0.669
	Cool	48.8	49.6	0.052	0.820
	Warm ↓	14.0	7.6	4.415	0.040*
	Hot	0.0	0.0	x	x

Table 3 (continued)

Biome (n)	Class	Presettlement Mean	Current Mean	F	*P*-Value
	Intolerant	23.8	24.1	0.006	0.938
	Intermediate	9.8	12.3	1.510	0.224
	Tolerant ↓	65.5	59.0	2.941	0.092*
	Pyrophilic ↑	14.0	22.6	5.795	0.019*
	Pyrophobic ↓	85.2	72.8	11.288	0.001***
Great Lakes pine-northern hardwoods (33)	Cold ↓	60.4	47.8	8.361	0.005**
	Cool	28.4	28.6	0.004	0.948
	Warm ↑	10.5	20.7	10.646	0.002**
	Hot	0.0	0.0	x	x
	Intolerant ↓	50.7	34.8	16.632	<0.001***
	Intermediate ↑	13.5	23.0	4.830	0.032*
	Tolerant	35.1	39.2	0.737	0.394
	Pyrophilic	52.0	49.7	0.158	0.692
	Pyrophobic	47.4	47.4	<0.001	0.998
Subboreal conifers (31)	Cold ↓	88.8	81.0	8.336	0.005**
	Cool ↑	8.5	12.2	3.435	0.069*
	Warm ↑	1.9	3.8	3.173	0.080*
	Hot	0.0	0.0	x	x
	Intolerant ↓	61.5	46.4	36.614	<0.001***
	Intermediate	8.2	10.4	1.727	0.194
	Tolerant ↑	29.6	40.3	16.440	<0.001***
	Pyrophilic	41.2	40.2	0.079	0.779
	Pyrophobic	58.0	56.9	0.111	0.741

Significant differences: *≤0.1, **≤0.01, ***≤0.001.

overall increase in Acer (16%), decrease in *Quercus* (−12%), flip from pyrophiles (−17%) to pyrophobes (13%), and decrease in intermediate genera (−18%). However, there was a distinct temperature signal, with a large decrease in warm genera (−22%) and large increase in cool genera (13%).

Increases of *Acer* at many Great Lakes oak-pine sites (Appendix S2) were reflected in its overall score (9%), followed by gains in *Carya* (3%) and *Ulmus* (3%) (Table 2). *Quercus* experienced a sizeable decrease overall (−24%), although there were some exceptions in Wisconsin (Barnes, 1974). Compositional changes registered most greatly in pyrogenicity, with significant decreases in pyrophiles (−23%) and significant increases in pyrophobes (21%) (Tables 2 and 3). Although a switch from intermediate (−15%) to tolerant genera (10%) and cool-temperature (−8%) to warm-temperature genera (5%) was evident (Table 2), these changes were insignificant (Table 3). Within embedded wetlands (Table 2; Appendix S3), a huge increase in *Acer* was found (23%), offset by subtle decreases in *Fraxinus, Larix*, and *Quercus* (−7%, −6%, and −3%, respectively). Great Lakes wetlands displayed shifts from intolerant (−12%) to tolerant genera (7%) and from cold- (−15%) to cool- and warm-temperature genera (9% and 5%, respectively). Pyrogenicity, however, did not change.

In the Prairie Peninsula, represented exclusively by Missouri sites (Appendix S2), a wide variety of genera showed increases, including *Celtis* (6%), *Gleditsia* (5%), *Maclura* (5%), *Juniperus* (4%), *Acer* (4%), and *Fraxinus* (3%) (latter three genera not tabularly reported). A large decrease in *Quercus* was consistent across all sites, with an average relative decrease of −39% (Table 2). These compositional changes extremely affected pyrogenicity, with a huge significant loss of pyrophiles (−43%) matched by a large significant gain in pyrophobes (36%) (Tables 2 and 3). Significant losses in shade-intermediate and warm genera (−15% and −13%, respectively) were offset by gains in shade-intolerant and cool genera (8% and 9%). Embedded wetland forests (Table 2 and Appendix S3) experienced a large increase in *Acer* (20%) and decreases in *Ulmus, Quercus*, and *Populus* (−10%, −8%, and −6%, respectively). In general, these compositional changes translated to shifts from warm, intolerant, pyrophiles (−21%, −13%, and −11%) to cool, intermediate, pyrophobes (20%, 8%, and 6%).

Acer and *Fagus* had reciprocal responses in Northeast conifer-northern hardwoods (Table 2 and Appendix S4), with *Acer* gains on all sites (averaging 19%) offset by huge losses in *Fagus* on all but one site (averaging −23%). *Prunus, Betula*, and *Quercus* experienced small increases (5%, 4%, and 4%, respectively), whereas two principal conifers diagnostic to this forest type, *Tsuga* and *Picea*, both decreased (−8% and −5%). Compositional changes manifested in shifts from warm, shade tolerant, pyrophobes (−11%, −18%, and −8%, respectively) to cool, intolerant/intermediate, pyrophiles (9%, 5%/11%, and 6%). However, shifts in pyrogenicity were not significant (Table 3).

Great Lakes conifer-northern hardwoods (Table 2 and Appendix S4) experienced sizeable increases in *Acer* and *Populus* across most sites (averaging 14% and 11%, respectively), a large decrease in *Tsuga* (−18%), and moderate decreases in *Fagus* and *Betula* (−7% and −6%). Here, as in the Northeast, conifer-northern hardwoods displayed similar decreases in warm, tolerant, pyrophobes (−6%, −7%, and −12%, respectively). These changes were significant (Table 3) along with an increase in pyrophiles (9%).

Nearly all sites within the Great Lakes pine-northern hardwoods (Table 2 and Appendix S4) experienced sizeable gains in *Quercus*, *Populus*, and *Acer* (averaging 13%, 12%, and 12%, respectively). The large increase in *Quercus* is distinctly different from all other systems. These increases largely came at the expense of *Pinus* (−29%), followed by *Tsuga* and *Fagus* (−10% and −4%, respectively). The switch from *Pinus* to *Quercus* dominance largely drove a significant transition from cold and intolerant genera (−13% and −16%, respectively) to warm and intermediate genera (10% and 9%) (Tables 2 and 3). The shift toward warm genera was also facilitated by the increase in *Acer rubrum*; a warm-temperature species. No change in pyrogenicity was detected.

Conifer loss was clearly evident in the Subboreal systems of northern Minnesota (Table 2 and Appendix S5), whereby large decreases in *Pinus* and *Larix* (−18% and −13%, respectively) were offset mainly by *Populus* (15%) and less so by *Fraxinus* and *Acer* (both 5%). These compositional changes translated into significant decreases in cold, intolerant genera (−8% and −15%, respectively) and significant increases in cool/warm, tolerant genera (4%/2% and 11%) (Tables 2 and 3). The conifer-to-broadleaf switch did not alter pyrogenicity, as the principal change genera (*Pinus*, *Populus*) were pyrophilic. Subboreal conifers outside of Minnesota (i.e. Subboreal conifers ‘other’; Appendix S5) had strong increases in *Betula* and *Populus* (20% and 18%, respectively), offset by a large decrease in *Abies* (−24%) and lesser decreases in *Thuja* (−10%) and *Pinus* (−3%). Here, the compositional changes had a major effect on tolerance and pyrogenicity, with large shifts from tolerant pyrophobes (−33% and −43%, respectively) to intolerant pyrophiles (both 44%), but not on temperature, representing a continuation of cold and cool genera dominance.

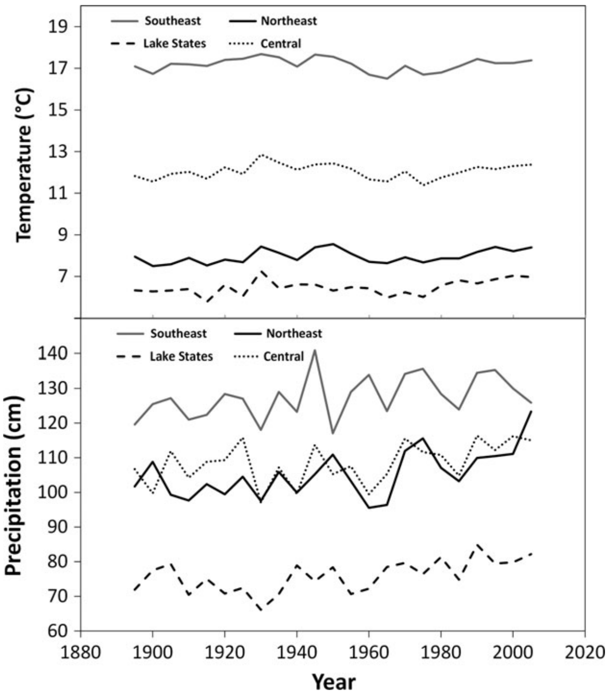


Fig. 3 Five-year running average annual temperature and precipitation data from 1895 to 2010 for four geographical regions of the eastern United States. Data as obtained from NOAA National Climate Date Center (http://www7.ncdc.noaa.gov/CDO/CDODivisional Select.jsp#).

Note: Northeast = ME, NH, VT, MA, RI, CT, NY, PA, NJ, DE and MD; Lake States = MI, WI, MN and IA; Central = WV, OH, IN, IL, MO, KY and TN; Southeast = VA, NC, SC, GA, FL and AL

Significant linear regressions ($P < 0.05$) across timeline include:
Northeast Temperature = −2.77 +0.00551(year)
Lake States Temperature = −3.96 + 0.00536(year)
Southeast Precipitation = −18.5 + 0.0747(year)
Northeast Precipitation =−146 + 0.129(year)
Lake States Precipitation = −81.1+ 0.0804(year)
Central Precipitation = −48.2 + 0.0803(year)

Regional temperature and precipitation trends (1895–2010) for four major geographical regions in eastern United States reveal that the southeast United States is warmer and wetter than all other regions (Fig. 3). The Lake States was the driest of the four regions, but only slightly cooler than the Northeast. Between 1895 and 2010, temperature increased significantly ($P < 0.05$ using regression analysis) in the Northeast and Lake States, but not in the Southeast or Central regions. Precipitation significantly increased in all four regions during this period (Fig. 3). A large uptick of warming took place after 1980 (see figure 6 of Shen *et al*., 2012), prompting us to compare climate changes from 1895 to 1979 vs. 1980 to 2010 (Table 4). Between these two periods, average annual temperature increased most in the Lake States

Table 4 Pre- and post-1980 average annual temperature (°C) and average total precipitation (cm) and the actual and percent change between those two periods for four major regions in the eastern United States

	Lake States	Northeast	Central	Southeast
Annual Temperature (°C)				
1895–1979 mean	6.36	7.90	12.02	17.17
1980–2010 mean	6.88	8.27	12.19	17.23
Actual change	0.52	0.37	0.17	0.06
Percent change	8.2%	4.7%	1.4%	0.3%
Annual Precipitation (cm)				
1895–1979 mean	74.32	103.30	106.99	126.78
1980–2010 mean	80.64	111.94	112.94	129.32
Actual change	6.32	8.64	5.95	2.54
Percent change	8.5%	8.4%	5.6%	2.0%

(8.2%), followed by the Northeast (4.7%), and least in the Central (1.4%) and Southeast (0.3%) regions. Precipitation followed a similar pattern by increasing most in the Lake States and Northeast (8.5 and 8.4%), intermediate in the Central Region (5.6%), and least in the Southeast (2.0%). Thus, during the last 115 years, the two northern regions have become warmer and wetter relative to their southern counterparts. The magnitude of temperature change estimated from the Greenland dataset associated with Anthropocene warming (≈0.45 °C increase from 170 to 120 years ago; Fig. 1) is comparable to the warming actually recorded in the Northeast and Lakes States after 1895 (0.37 and 0.52 °C; Table 4). It is worth noting that abrupt warming (possibly signaling the start of the Anthropocene) started about 1910 based on instrument data (http://www.ncdc.noaa.gov/paleo/globalwarming/instrumental.html). This contrasts with Greenland Ice core data showing that abrupt warming started about 1850 (Fig. 1).

Membership of species/subgenera/genera/functional groups within temperature, shade tolerance, and pyrogenicity classes were not equally distributed, with greatest representation in warm (43 of 101), intolerant (40), and pyrophobic (58) classes (Table 5). Moreover, temperature, shade-tolerant, and pyrogenicity classifications were not necessary independent parameters as evidenced by membership counts. Cold-temperature trees tended to be shade intolerant, cool- and warm-temperature trees tended to be shade intermediate and pyrophobic, whereas hot-temperature trees were often shade intolerant and pyrophilic. Nevertheless, the largest number of pyrophilic trees was found in warm-hot climates. When comparing shade tolerance with pyrogenicity, shade-intolerant trees tended to be pyrophilic, whereas shade-tolerant trees were exclusively pyrophobic.

Discussion

Climate change as a scientific endeavor has risen to epic proportions commensurate with world interest, with real and surmised impacts covering all aspects of life (ecological, economic, and socio-political). Long-publicized predictions of climate change effects on vegetation are now starting to reveal themselves (Hughes, 2000), particularly at high altitudes and latitudes where subtle changes in temperature are greatly magnified in glacier retreat, permafrost melting, and tree-line shifts (Oerlemans, 1994; Hinzman *et al*., 2005; Walther *et al*., 2005; Beckage *et al*., 2008; Harsch *et al*., 2009; Stroup *et al*., 2014). However, at more temperate locations, vegetation change has lagged in part due to ecological inertia (entrenchment due to plant longevity, plasticity, and resilience; Pielou, 1991; Woodall *et al*., 2009; Zhu *et al*., 2012).

Confounding interpretations further is the fact that climate change (changes in precipitation, temperature, and general weather patterns) has not been uniform, but varies geographically, thus affecting vegetation communities and attendant plants differently. Moreover, a number of anthropogenic disturbances have affected vegetation concurrent with recent climate change (past ≈100 years), with profound and long-lasting effects (as already pointed out in the Introduction) clouding vegetation–climate relations. In all, vegetation represents an amalgamation of all these phenomena to various degrees (climate, land use, disturbance events) – factors that are difficult to tease apart. Here, we attempt to meet this challenge by reporting the relative contributions of climate and disturbance as expressed in post-European vegetation change by tracking trees by temperature, shade tolerance, and pyrogenicity classes. We found that climate controls large-scale biogeographical patterns as the number of tree species/subgenera/genera increased from cold to warm affinities paralleling available energy gradients (Currie & Paquin, 1987). The number of pyrophilic trees were highest in warm- and hot-temperature classes (Table 5), reflecting the higher frequency of presettlement fires in the south (Guyette *et al*., 2006). Therefore, the presettlement biomes of the eastern United States are a product of both climatic and fire variation, grading from shade-tolerant, fire-sensitive conifer-northern hardwoods in the north to intolerant, pyrophytic, oak-pine systems in the south (Fig. 2a; Nowacki & Abrams, 2008). European land use and disturbances have substantially altered these established relationships across all

Table 5 Membership matrix (based on count) showing relations among temperature, shade tolerance, and pyrogenicity classes for 101 species/subgenera/genera/functional groups. Class headers show total membership in parentheses. Strong associations are bolded and underlined in the matrix

	Shade Tolerance Class			Pyrogenicity Class	
	Intolerant (40)	Intermediate (38)	Tolerant (23)	Pyrophilic (43)	Pyrophobic (58)
Temperature Class					
Cold (16)	**11**	2	3	8	8
Cool (25)	6	**12**	7	8	**17**
Warm (43)	12	**21**	10	15	**28**
Hot (17)	**11**	3	3	**12**	5
Shade Tolerance Class					
Intolerant (40)	x	x	x	**26**	14
Intermediate (38)	x	x	x	17	21
Tolerant (23)	x	x	x	0	**23**

biomes, leading to novel vegetation types and successional trajectories.

Oak-pine biome

Oak-dominated ecosystems with pine, hickory, and chestnut associates historically spanned the central portion of the United States from the Atlantic Coast to the Central Plains (Fig. 2a). Based on multiple independent lines of evidence (including historical accounts, charcoal stratigraphy, fire-scar data, tree-life history, and ecophysiological traits), fire played a prominent role in the formation and long-term maintenance of this biome (Abrams, 1992, 2002; Lorimer, 2001; Spetich *et al.*, 2011). Commensurate with a precipitation–moisture gradient from west (dry) to east (moist), the historical structure of component ecosystems generally graded from open savannas to closed-canopy forests. The fact that oaks and associates were able to maintain dominance eastward under progressively wetter conditions (where the competitive effect of shade-tolerant species is stronger) underscored the importance of human ignitions in presettlement times (Guyette *et al.*, 2006; Abrams & Nowacki, 2008, 2014).

Comparative analyses of presettlement vs. current forest composition in the glaciated Northeast region revealed prodigious increases of maple (*Acer*) at the expense of oak and chestnut. The tremendous impact of chestnut blight was evident in the outright loss of chestnut in forest overstories (Anagnostakis, 1987). Although the loss of chestnut in the early 1900s may have initially favored oak and hickory (Keever, 1953; McCormick & Platt, 1980), that advancement seems to have been short-lived and supplanted by shade-tolerant maple for many years now. When expressing compositional shifts in terms of temperature, shade tolerance, and pyrogenicity properties of component tree species, a strong mesophication signal appeared whereby warm-temperature, shade-intermediate pyrophiles are being increasingly replaced by cool-temperature, shade-tolerant pyrophobes in an era of fire suppression (Fig. 2; Nowacki & Abrams, 2008). The strong increase in cool genera (+17%) at the expense of warm genera (−15%) starkly contrasts with a warming climate in which temperature increased relatively more in the Northeast than in central and southeastern states (Table 4). The correlated increase in precipitation may have mitigated the warming effect to further promote cool, shade-tolerant mesophytes (McEwan *et al.*, 2010).

The Central and Great Lakes oak-pine systems behaved similarly, with moderate increases in maple and sizable decreases in oak. Compositional changes were most strongly expressed in decreased pyrogenicity, and less so by tolerance (from intermediate to shade tolerant). Tree-based temperature changes were mixed and subtle, with replacement species seemingly derived from an array of temperature classes. Moreover, red maple (*Acer rubrum*) may have had a neutralizing influence, being a warm-based replacement species of warm-based oak. Overall, these trends are consistent with ongoing fire suppression and mesophication previously documented within these regions (Fralish & McArdle, 2009; Hanberry *et al.*, 2012a,b). The relative dryness of the Lakes States and warmth of the central and southeast regions (Fig. 3) may have inhibited the development of cool-affinity, mesophytic, replacement species here relative to the cool and moist Northeast.

The largest decreases in oak (−39%) and pyrogenicity (−43%) occurred within the Prairie Peninsula – a former mix of tallgrass prairie and oak savannas having the most frequent and intense fire regime in eastern North America. This massive decrease in fire importance coincides with past depictions of fire regime change (see Fig. 2 of Nowacki & Abrams, 2008). Here, fire suppression benefitted shade-intolerant genera, consistent with successional theory and pioneer invasion of open lands. Also, recent field and pasture abandonment has allowed a wide variety of fire-sensitive species to colonize and flourish here (Hanberry *et al*., 2014). As in the Northeast, significant shifts from warm to cool genera were encountered (Fig. 2b), a trend opposite to that expected in a warming climate. It is interesting to note that the Prairie Peninsula is a region that is cool and moist enough to support closed-canopy forests, a fact that became the subject of ecological interest dating back a century or more (Gleason, 1913; Grimm, 1984). Subsequent research revealed that the Prairie Peninsula formed about 8700 BP as a result of early Holocene warming and Native American burning that converted the forests to grasslands (Anderson, 2006). Thus, it is no surprise that recent fire suppression in the region has caused a reversion back to forest vegetation, despite Anthropocene warming.

The wetlands possessed both similarities and dissimilarities to their surrounding oak-pine uplands. These embedded systems, mainly wet riparian zones that historically burned less, often harbored a rich array of mesophytes (e.g. *Acer*, *Fraxinus, Celtis, Ulmus*) (Fahey *et al*., 2014). As such, fire suppression had reduced effects, with these lowlands experiencing more subtle decreases in oak and pyrogenicity relative to their upland counterparts. Due to low fire receptivity and topographic protection from historical fire, these rich, mesic bottomlands were probably more structurally advanced (higher density; less open) upon European arrival, conditions favoring shade-tolerant mesophytic regeneration and recruitment. Collectively, embedded wetlands converged on cool genera, however from different directions based on region (at the expense of warm genera in Central and Prairie Peninsula regions and cold genera in the Great Lakes). The lack of directional shifts in this regard suggests that compositional changes did not track climate *per se*, but were driven primarily by individual species response, primarily cool-temperature maples [silver maple (*Acer saccharinum*), boxelder (*Acer negundo*), sugar maple (*Acer saccharum*)], to the prevailing moist/fertile site conditions in the absence of fire (Dunn, 1987; Nelson *et al*., 1994; Barnes, 1997; Cowell, 1998; Knutson & Klaas, 1998; Cook, 2005; Hanberry *et al*., 2012b). The current composition, structure, and disturbance dynamics of these riparian areas do not mirror presettlement conditions, lying far outside the historical range of variability (Fahey *et al*., 2014).

In summary, the effects of fire suppression and the associated mesophication were universally present in comparative datasets for the entire oak-pine biome. All uplands exhibited huge shifts from pyrophilic to pyrophobic genera, with shade-tolerant genera being the usual benefactors. Changes in temperature classes were less consistent; however, the most pronounced changes were conversions from warm to cool genera – a trend inconsistent with climatic warming. In the oak-pine biome, human-based disturbances and fire suppression completely overwhelmed the effects of any temperature-related vegetation shifts.

Conifer-northern hardwood biome

Northern hardwoods (*Acer, Fagus, Tilia*), either solely or mixed with various conifers (*Tsuga, Pinus, Picea, Thuja*), historically formed a contiguous block across the boundary with Canada (Fig. 2). Normally associated with rich, mesic locations, conifer-northern hardwoods were often referred to as 'asbestos forests' as their cool, heavily shaded understories and moisture-laden leaf cask greatly retarded fire (Vogl, 1967; Bormann & Likens, 1979). Here, forest dynamics were largely wind driven, with multi-cohort stands being most prominent from recurring light- and moderate-severity wind disturbances (Frelich & Lorimer, 1991; Fraver & White, 2005; Hanson & Lorimer, 2007; Stueve *et al*., 2011). One exception is pine, which largely benefits from fire (Maissurow, 1935; Stearns, 1950; Abrams, 2001). Pine representation generally increases westward with decreasing precipitation, being particularly abundant on sandy glacial outwash plains where it often formed nearly pure stands. Due to its ecological distinctiveness, pine-dominated forests were tracked separately from northern hardwoods comprised of more 'mesophytic' conifers such as *Tsuga canadensis* (hemlock). This allowed us to better tie replacement species to site conditions, with cool-based sugar maple being the principal maple species regenerating within mesic conifer-northern hardwoods and warm-based red maple within more xeric pine-northern hardwoods (Nowacki *et al*., 1990).

The effects of the Great Cutover, which swept east to west across this biome from the late 1700s to 1900 (Fig. 1), along with subsequent high-intensity burns and ongoing forest practices were clearly embedded in the comparative datasets. The loss of conifers ('deconiferization'; Mladenoff & Stearns, 1993; Cole *et al*., 1998; Schulte *et al*., 2007) was manifested across the entire biome, with hemlock being the leading decreaser in conifer-northern hardwoods and pine in the pine-northern hardwoods. Widespread and recurrent human disturbances coupled with beech bark disease (Evans *et al*., 2005; Morin *et al*., 2007) negatively affected beech (*Fagus*), with declines proportional to its presettlement abundance. Maple and aspen (the latter especially westward) were major benefactors of large-scale forest disturbance across the regions (Cole *et al.*, 1998; Schulte *et al.*, 2007; Thompson *et al.*, 2013). Collectively, these disturbance-related compositional changes translated to consistent shifts in temperature, tolerance, and pyrogenicity in both Northeast and Great Lakes conifer-northern hardwoods, with large declines in warm-temperature, shade-tolerant, pyrophobes. The collective shift toward less shade-tolerant pyrophilic genera is consistent with the effects of intense cutting and burning on a late-successional climax forest (Cleland *et al.*, 2001). Here too, the shifts from warm to cool and/or cold genera run counter to the expected effects of a warming climate.

The Great Lakes pine-northern hardwoods represented a bastion of eastern white pine, an easily floatable, superior timber species that was preferentially sought and cut (Abrams, 2001). Here, the devastating combination of intensive cutting and burning was evident (Elliott, 1953; Kilburn, 1960a; Whitney, 1987; Cleland *et al.*, 2001). The removal of large seed trees and subsequent burning of vulnerable regeneration largely depleted the pine component in favor of sprouting hardwoods, specifically oak, aspen, and maple (largely warm-temperature red maple). The conversion from northern pines (cold-temperature, shade-intolerant pyrophiles) to oaks (warm-temperature, shade-intermediate pyrophiles) caused a major change in the temperature and shade-tolerance properties of the forest, with distinctive shifts from cold to warm genera, and from shade-intolerant to intermediate genera, while pyrogenicity remained constant. Based on the historical record (Elliott, 1953; Kilburn, 1960a; Whitney, 1987), this temperature shift as expressed in vegetation change is actually an artifact of the preferential removal of overstory (cold) pine and replacement by (warm) oak and red maple rather than an actual indicator of warming.

Subboreal conifer biome

Comprised of a mix of conifers (*Pinus, Picea, Larix*) and broadleaf trees (*Betula* and *Populus*), the presettlement forests of northern Minnesota closely resembled the boreal forest of Canada (Fig. 2). Here, the 'Great Cutover' terminated its westward march around 1900 (Fig. 1), leading to a temporal compression of many different types of European land alterations. The area was first affected by logging, catastrophic slash fires, and land clearance, followed by fire suppression, pulpwood (coppice) clear-cutting, and farm abandonment (Baker, 1992; Frelich & Reich, 1995; Scheller *et al.*, 2005; White & Host, 2008). These European interventions combined to invoke distinct flora changes throughout the region. For instance, the proportion of needled vs. broadleaved trees has basically flipped from historical to current times (Laurentian Mixed Forest Province; Hanberry *et al.*, 2012b). At the community level, there has been a virtual disappearance of pine and larch (*Larix)* types, largely supplanted by aspen-dominated stands, many with no presettlement antecedent (Friedman & Reich, 2005; Hanberry *et al.*, 2012b). The meteoric rise in aspen is indicative of intense and recurrent site disturbance, consistent with its reputation as being a shade-intolerant, sprout-based, fire follower (Graham *et al.*, 1963; Cleland *et al.*, 2001). Recent increases in shade-tolerant maple (principally red maple and sugar maple) and ash (*Fraxinus*) have been ascribed to fire suppression and associated mesophication (Hanberry *et al.*, 2012b). In the comparative datasets, these compositional changes were most strongly expressed in shifts from intolerant to tolerant genera, followed by shifts from cold to cool and warm genera; the latter consistent with the greater relative warming in northern regions. On sites further east ('other' subboreal conifers; Appendix S5), both birch and aspen increased substantially at the expense of conifers (*Abies, Thuja*, and *Pinus*). This vegetation change translated to strong shifts from shade-tolerant pyrophobes to shade-intolerant pyrophiles, but not in temperature.

The tension zone line

As early European populations increased and spread from the East Coast inland, they encountered two vastly different ecosystems: conifer-northern hardwood forests in the north and oak-pine systems in the south (Fig. 2a). Early on, conventional wisdom held climate as the main driver as the boundary between the two systems generally paralleled latitude in the New England area (Raup, 1937). Though the exact timing might have differed, the type and sequence of European disturbances were similar throughout the East, with land clearance by cutting and burning often followed by agriculture where feasible (Frederick & Sedjo, 1991; MacCleery, 1996). This disturbance-based transformation of the landscape started out rather humbly at Plymouth settlement in 1620 (Harper, 1918; Hawes, 1923), gaining momentum as it spread westward over three centuries and spanning the transition between the Little Ice Age and climatic warming (Fig. 1). Due to their distinct ecology, these two biomes responded differently to this vast and unprecedented wave of human disturbance.

To the north, presettlement conifer-northern hardwoods coalesced in a cool, moist temperate climate (which naturally suppressed fire) under a wind-driven disturbance regime. Catastrophic disturbances were rare with exceedingly long return times: 800 (fire) and

1150 years (wind) in Maine (Lorimer, 1977), 980–3190 years (wind) in New York (Seischab & Orwig, 1991), 1000–2000 years (wind) in Pennsylvania (Whitney, 1990), 648–1295 years (fire and wind) in Michigan (Whitney, 1986), and 1210–1360 years (wind) in Wisconsin (Canham & Loucks, 1984; Schulte & Mladenoff, 2005). Rather, light to moderate wind storms are characteristically common, allowing multi-cohort stands of late-successional species to dominate presettlement landscapes (Frelich & Lorimer, 1991; Fraver & White, 2005; Hanson & Lorimer, 2007). Overall, conifer-northern hardwoods were fairly stable systems thought to be in quasi-equilibrium with their environment, effectively representing the climatic climax. Here, the perturbations wrought by Europeans so strongly contrasted the naturally low disturbance environment of this system that their impact was immediate and devastating. The effects of cutting and burning activities were clearly embedded in the comparative datasets, with shade-tolerant pyrophobes (*Fagus, Tsuga, Picea*) greatly diminishing. This combination of disturbance agents proved particularly lethal to conifers, with large seed trees eliminated by cutting and regeneration consumed by fires (a one-two punch), leading to widespread deconiferization and promotion of sprouting hardwoods throughout the north (Elliott, 1953; Kilburn, 1960b; McIntosh, 1972; Cole *et al*., 1998; Zhang *et al*., 2000; Leahy & Pregitzer, 2003; Schulte *et al*., 2007). Shade-intermediate and intolerant pyrophiles in particular, like oak and aspen, largely benefitted from unbridled European disturbance (Nowacki *et al*., 1990; Palik & Pregitzer, 1992). The increase of cold-adapted aspen is particularly striking considering that the Lake States experienced the largest degree of warming (about 8%, Table 4). Apparently, a critical ecological threshold waits as climate change models have future suitable habitat for aspen being eliminated from the conterminous United States by the year 2100 (Iverson & Prasad, 1998, 2002).

Curiously, shade-tolerant maple responded remarkably well, possessing the largest percent increases in conifer-northern hardwood systems consistent with previous findings (McIntosh, 1972; Schulte *et al*., 2007; Thompson *et al*., 2013). This trend runs counter to the prediction of its future status (Iverson & Prasad, 1998, 2002). Seemingly, maple is dually benefiting from immediate gains in second-growth representation while being well positioned for further gains through understory release as shade-intolerant (aspen-birch) forest types age and disintegrate. This later recruitment pulse, which distantly follows initial European disturbance, essentially represents the understory reinitiation stage of Oliver & Larson (1996). Furthermore, maple might have benefitted through the exploitation of niches vacated by other late-successional trees. Indeed, a number of factors have combined to curb the rebound of other shade-tolerant competitors, such as climatic warming, drought, budworm, and acid deposition on spruce (*Picea*; Johnson, 1983; Hornbeck & Smith, 1985; Hamburg & Cogbill, 1988), and deer overbrowsing, hemlock wooly adelgid, seedbed alteration, and seed-tree elimination for hemlock (Alverson *et al*., 1988; Mladenoff & Stearns, 1993; Orwig *et al*., 2002). Being a resilient sprouter and warm-adapted, the prospects of beech expansion similar to or even greater than maple seemed assured, yet has been unrealized due to beech bark disease (McIntosh, 1972; Evans *et al*., 2005; Morin *et al*., 2007). Within the genus *Acer*, the super-generalist red maple (Abrams, 1998) might be better poised for the future being a warm-adapted species as compared to sugar maple, which is cool-adapted (Table 1). Climate change predictions by Iverson & Prasad (1998; see their table 3) seem to bear this out, with red maple maintaining its distribution (though still dropping in importance) but sugar maple decreasing markedly in this regard. As with aspen, sugar maple is predicted to be largely eliminated from the conterminous United States by the end of this century (Iverson & Prasad, 1998, 2002).

Immediately to the south of the Tension Zone (Fig. 2a), large-scale European disturbances aligned better with the historical disturbance regime of oak-pine, which was fire-based (Abrams, 1992; Nowacki & Abrams, 2008). Here, cutting and burning practices allowed the prominent hardwoods (oak, hickory, chestnut) to initially flourish, often through vigorous sprouting. In some areas, the high frequency of cutting and burning largely depleted nonsprouting pines through seed-tree removal and consumption of its regeneration by fire (Nowacki & Abrams, 1992; Abrams, 2001). This was certainly the case on lands used for charcoal production in the central United States, where stands were cut every 20–30 years and uncontrolled burns were common (Mikan & Abrams, 1995). In the east, fire suppression activities started in the early 1900s and ramped up appreciably after World War II (see Fig. 3 of Nowacki & Abrams, 2008). For instance, in Pennsylvania, roughly 405 000 ha burned in 1908 (single year) compared with 3,400 ha during the entire 1980 decade, representing a 1000-fold decrease in area burned (Abrams & Nowacki, 1992). It was this recent decline in landscape burning that allowed maple to increase in oak-pine systems, with greatest increases occurring in the most mesic locales, specifically in the humid Northeast and along riparian (wetland) corridors of the other, more westward biomes. Maple development in the central oak-pine biome, while present, may have been slowed by the inherently warmer and drier climate (Abrams, 1998). In this light, Fralish & McArdle's

(2009) claim that the Illinois Ozark Hills will be the first contiguous oak-dominated forest region to convert to mesophytic dominance was probably premature, as maples in the Northeast oak-pine region are increasing much more rapidly, presumably due to cooler and wetter conditions. Among all tree species, red maple has increased the most in eastern forests during the last half century via forests succession (Abrams, 1992; Fei & Steiner, 2007). As a warm-adapted species, red maple's increase in northern forests is consistent with a warming climate trend, whereas its increase in central forests is more temperature neutral (principally replacing warm-based oaks). In either case, however, its increase is probably best explained by fire suppression rather than climate change, although variation in regional climate has seemingly impacted the speed and degree of red maple expansion.

The boundary between conifer-northern hardwoods and oak-pine biomes is part of the Tension Zone Line (Potzger, 1947; Curtis, 1959; Hushen *et al.*, 1966; Cogbill, 2000; Fig. 2a). Witness-tree data have greatly improved our understanding of its presettlement location and the ecological reasons for its existence in the Northeast (Cogbill *et al.*, 2002). Consequently, its long recognition as a fire-based boundary in its western sectors (Wisconsin; Curtis, 1959) has been extended to New England where it is now considered more of a process (fire) and edaphic demarcation (C.V. Cogbill, personal communication, 17 March 2014). The long-established activities of Native Americans were indelibly etched in its boundary, which oscillates up large river corridors corresponding to locations of Native American habitation and transportation (Black *et al.*, 2006). The Tension Zone Line makes for a convenient general boundary for understanding European effects on the land. To the north, European disturbance made late-successional, largely fire-proof, conifer-northern hardwood forests more shade intolerant and pyrogenic, whereas south of it, recent fire suppression has made former pyrogenic oak-pine systems more shade tolerant and pyrophobic. However, any 'newly' created oak forests to the north are likely to be only one generation and will revert back over time to something resembling the presettlement hardwood forest (Nowacki *et al.*, 1990; Abrams, 1992). The Tension Zone Line also marks the general boundary between differential changes in warming and precipitation after 1900, whereby northern forests have become increasingly warmer and wetter, and forests to the south have experienced less change in climate. These differences, coupled with variation in tree species responses to post-European human activities, have led to very different ecological outcomes between the two regions.

Considerations for climate change modeling

Many climate models project that continued warming will promote oak and pine and negatively affect replacement species, such as maple, in the eastern United States (Iverson & Prasad, 1998, 2001, 2002; McKenney-Easterling *et al.*, 2000; Brandt *et al.*, 2014), yet this pattern was not seen in the vegetation datasets amassed and analyzed in this study. Ironically, just the opposite was true in most cases. This is a bit perplexing, considering that disturbances release growing space and facilitate species invasion (e.g. aspen; Landhäusser *et al.*, 2010). One would think that there would have been ample opportunity for climate-induced species replacement to occur and be detected over the past century. Perhaps not enough time has elapsed for climate change to manifest itself in long-lived arboreal vegetation, as reported in several comprehensive Forest Inventory Analysis (FIA) studies (Woodall *et al.*, 2009; Zhu *et al.*, 2012). Indeed, the long time frames affiliated with our comparative datasets, spanning hundreds of years, may largely drown out climate change-induced species shifts that might be just appearing. However, Hanberry's (2013) recently published study that records species changes for a shorter, 20–30-year period (a condensed period of time when climate changes have been most vigorous) shows the same principal trends, with all reported maples significantly increasing (*A. rubrum*, *negundo*, and *saccharum*) and oaks (*Q. alba, rubra*, and *velutina*) significantly decreasing. The same pattern was found by Fei *et al.* (2011), who reported that between 1980 and 2008, eight of 25 oak species decreased significantly throughout the eastern United States, including the two most prevalent white oak species (*Q. alba* and *stellata*) and red oak species (*Q. rubra* and *velutina*). Much of this decrease has been matched with increases in red maple (Abrams, 1998; Fei & Steiner, 2007).

The rise in mainly cool-adapted, shade-tolerant, pyrophobic taxa in the eastern United States runs counter to climate warming and is best explained by fire suppression. It is possible that sugar maple, a cool northern species which has been in decline for several decades due to a suite of factors (e.g. insect, disease, acid rain; Horsley *et al.*, 2002), may exhibit further declines as a result of climate warming. However, we believe that warm-based red maple, whose range includes almost the entire eastern United States, has not and will not be ill-affected by past and future climate warming, within reasonable expectations, and will continue to replace oak species throughout the biome in the absence of the reintroduction of fire or other analogous silvicultural treatments (Barnes, 2009). Compared to the industrial logging, catastrophic fire, and chestnut blight regimes from the 1700s to the early 1900s (Fig. 1), the fire suppression era (post-1930 to present-day) is characterized by relative quiescence in the extent and intensity of disturbances. This has allowed forest succession to proceed to a greater extent in most oak and pine forests relative to past millennia when this process was held in check by Native American burning. One would think that this reduced disturbance regime over the past 80+ years would have resulted in forest change being controlled primarily by climate, but the results of this article suggest otherwise. We conclude that the vast majority of forest ecosystems are still not in equilibrium with the prevailing climate due to past disturbance regime legacies. Because forest succession is a relatively slow process, often times requiring several centuries to reach the late stages, we predict that eastern United States forests are still a long way from being predominantly controlled by and reflective of climate.

One fundamental problem with climate change models predicting future vegetation changes is the assumption that species distributions and importance (starting points for model runs) are in equilibrium with climate which, in reality, they are often not due to past disturbance. Indeed, many species are currently in the midst of actively readjusting to the removal of fire across vast portions of the eastern United States, with fire-sensitive, shade-tolerant species increasing in importance and expanding to their true climatic envelope and fire-adapted, shade-intolerant/intermediate species decreasing in importance and contracting in range in the absence of burning. These ecological trends are abundantly apparent in comparative tree-census datasets and similar in magnitude the profound changes in species distribution that took place following glacial retreat at the beginning of the Holocene (cf. Munoz *et al*., 2010). For species undergoing range expansion and shifts in importance, climate envelopes based on current distributions may need to be recalculated for ecological parameters used in climate change models (Prasad *et al*., 2007-ongoing), especially for mesophytes released from fire restrictions of the past. Moreover, model outputs need to account for the near-obligatory requirement of pyrogenic species to have landscape fire to exploit expanded climatic envelopes as projected for oak and southern pine (Iverson & Prasad, 1998, 2001, 2002). It was intentional human ignitions who largely drove fire regimes in the presettlement times in much of the eastern United States and without those ignitions fire occurrence would have been greatly reduced (Guyette *et al*., 2006; Abrams & Nowacki, 2008), even under somewhat warmer and drier conditions. There is little evidence to support widespread lightning-caused fires in the eastern United States, outside of Florida, due to a lack of dry lightning (Abrams & Nowacki, 2008, 2014). The true ecophysiological requirements of species and the pivotal role of historical fire need to be better integrated into future climate change scenarios (inputs, outputs, interpretations) to improve the predictive power of models and their ecological relevance (e.g. King *et al*., 2013). In this vein, potential exists for the well-researched classifications established here for temperature, shade tolerance, and pyrogenicity (Table 1) to serve as a unifying template for future interpretation of ecological and palynological datasets.

Acknowledgements

We thank Chris Bouma for his help with NOAA climate data analysis and presentation and Dan Wendt and Jeff Muehleck of the US Forest Service for GIS assistance. Cecil Frost, Michael Schafale, Diane Burbank, and David Cleland provided guidance on presettlement vegetation regions. Drs. Louis Iverson and Stephen Matthews of the US Forest Service, Northern Research Station generously provided species/genus temperature averages from their Tree Atlas database. Lastly, we extend an appreciative thanks to Drs. Lisa Schulte and Brice Hanberry for providing raw tree-census data stemming from their past work (Schulte *et al*., 2007; Hanberry *et al*., 2012a,b). The above acknowledgements do not imply manuscript endorsement.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Descriptive information of comparative tree-census studies of the eastern United States used in this study.

Appendix S2. Dominant presettlement and current vegetation (top 3) and relative change by composition, temperature, shade tolerance, and pyrogenicity of four major oak-pine systems in the eastern United States.

Appendix S3. Dominant presettlement and current vegetation (top 3) and relative change by composition, temperature, shade tolerance, and pyrogenicity of three embedded oak-pine wetlands in the eastern United States.

Appendix S4. Dominant presettlement and current vegetation (top 3) and relative change by composition, temperature, shade tolerance, and pyrogenicity of three major conifer-northern hardwoods biomes in the eastern United States.

Appendix S5. Dominant presettlement and current vegetation (top 3) and relative change by composition, temperature, shade tolerance, and pyrogenicity of subboreal conifer systems in the eastern United States.