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RESEARCH PAPER

Global change impacts on forest and fire dynamics using paleoecology and tree census data for eastern North America

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Abstract

• ***Key message*** **The tree census, paleopollen, fossil charcoal, human population, and climate data presented here provide unique support for important anthropogenic influences on fire over the last 2000 years in the eastern USA. This includes multiple instances of climate fire anomalies that may be best explained by the role of human-caused burning.**

• ***Context*** The coupling of paleoecological and tree census data to address larger global change questions is a novel research approach to describe and ascribe recent vegetation dynamics vis-à-vis the climate versus disturbance debate.

• ***Aims*** The aims of the study are to (1) compile and compare pre-European settlement versus modern upland arboreal pollen and tree survey data from a large number of studies in various forest regions in the eastern USA, (2) analyze fossil charcoal dating back 2000 years for the northern versus central/southern tiers of the eastern USA, and (3) compare and contrast compositional and ecophysiological attributes for both datasets and temporal changes to known climate or disturbance phenomena to elucidate global change impacts and the drivers of forest change.

• ***Methods*** We analyzed paleoecological (pollen and charcoal) and tree census studies to compare protohistoric and modern vegetation assemblage for eastern North America, including the drivers of forest change. A total of seven forest types in the north and central regions of the eastern USA were used to co-analyze fossil pollen, fossil charcoal, and tree survey data.

• ***Results*** Disparities and consistencies existed when independently assessing witness tree and pollen records. Although forests north of the tension zone line (TZL) contained mostly *Fagus*, *Pinus*, *Tsuga*, and *Acer* witness trees, pollen records were dominated, as expected, by high-pollen-producing *Pinus*, *Quercus*, *Tsuga*, and *Betula*. Here, present-day pollen and tree survey data revealed significant declines in *Fagus*, *Pinus*, *Tsuga*, and *Larix* and increases in *Acer*, *Populus*, *Fraxinus*, *Quercus*, and *Abies*. South of the TZL, both witness tree and pollen records pointed to *Quercus* and *Pinus* domination, with declines in *Quercus* and *Castanea* and increases in *Acer* and *Betula* based on present-day data. Modern assemblages comprise tree genera that are increasingly cool-adapted, shade-tolerant, drought-intolerant pyrophobes. Paleocharcoal data from 1 to 1750 AD indicate a slight increase in burning in southern forests and stable levels in the north, despite the increasing cold associated with the Little Ice Age. The most significant increase in burning followed the dramatic increase in human population associated with European settlement prior to the early twentieth century.

• ***Conclusion*** Post-1940, fire suppression was an ecologically transformative event in all datasets. Our analysis identifies multiple instances in which fire and vegetation changes were likely driven by shifts in human population and land use beyond those expected from climate alone.

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Contribution of the co-authors MDA: literature review, data compilation, data analysis, and wrote first draft of paper
GJN: literature review, data compilation, data analysis, wrote sections of the paper, and edited entire paper.

This article is part of the topical collection on *Wood formation and tree adaptation to climate*.

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1 Introduction

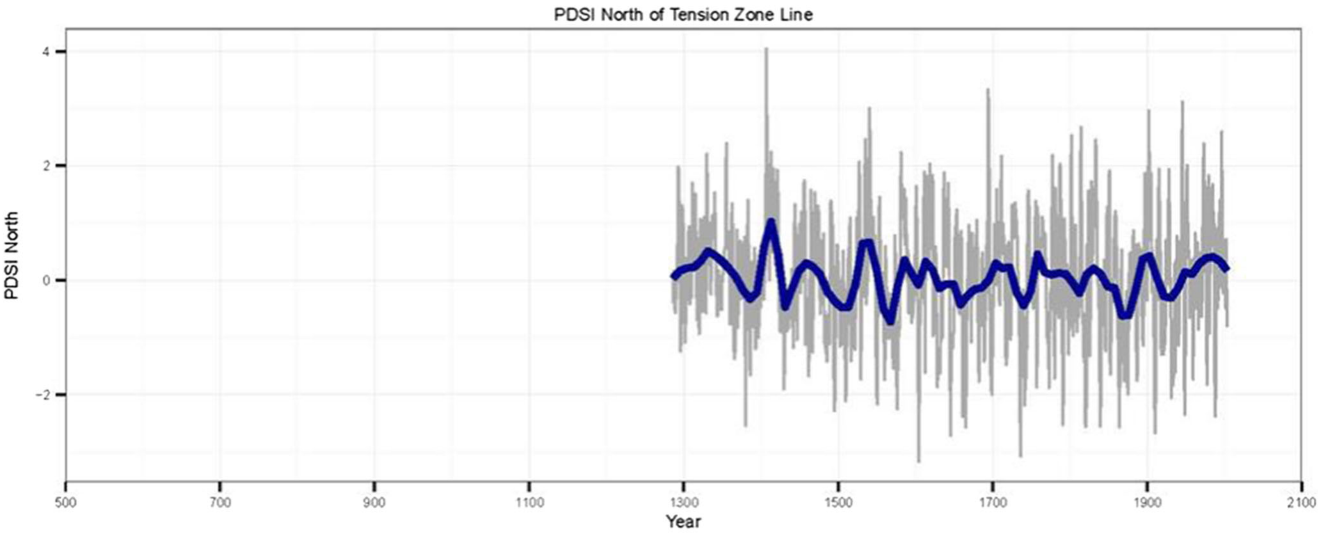
During the last five centuries, vegetation in eastern North America has been impacted by a suite of global change phenomena (Abrams and Nowacki 2008, 2015; Munoz and Gajewski 2010; McEwan et al. 2011; Woodall et al. 2013). This includes the initiation and rapid expansion of Euro-American settlement, Native American depopulation, and dramatic changes in the magnitude, extent, and type of land use practices, abrupt shifts and/or reversals in fire regimes, outbreaks of insect and disease, and significant climate change (Crosby 1976; McAndrews 1988; Denevan 1992; Whitney 1994; Parshall and Foster 2002; Foster 2004; Munoz et al. 2010). At the beginning of this five-century period, the northern hemisphere was in the midst of the Little Ice Age (LIA; ca. 1400 to 1850; Fig. 1; Mann et al. 2009) and the initial stages of European settlement took place within this climatic regime. The LIA was followed by abrupt warming associated primarily with the end of a natural cooling period coupled with increased anthropogenic modifications to atmospheric chemistry (Ruddiman 2005; Mann et al. 2009; IPCC 2013). Human populations and their impacts on vegetation through land use have also changed appreciably during the late Holocene (Denevan 1992; Abrams and Nowacki 2008; Munoz and Gajewski 2010; Nowacki et al. 2012; Munoz et al. 2014). Nevertheless, we still have only a marginal understanding of the role of climate and disturbance and their interactions with vegetation dynamics, past and present, for most regions (Rhemtulla et al. 2009). The importance of climate versus human impacts on protohistoric ecosystems in eastern North America is a highly debated issue (Munoz et al. 2010; Pinter et al. 2011; Marlon et al. 2013). One argument emphasizes the role of climate driving fire and vegetation dynamics (Parshall and Foster 2002; Shuman et al. 2004; Pederson et al. 2015); another argues that human-caused disturbance, including intentional burning, has been the primary driver, particularly during the second half of the Holocene (Guyette et al. 2006; Steyaert and Knox 2008; Nowacki and Abrams 2008, 2015). A more complete understanding of past human-fire-climate-vegetation dynamics and their anomalies requires additional research (Munoz et al. 2014; Abrams and Nowacki 2015).

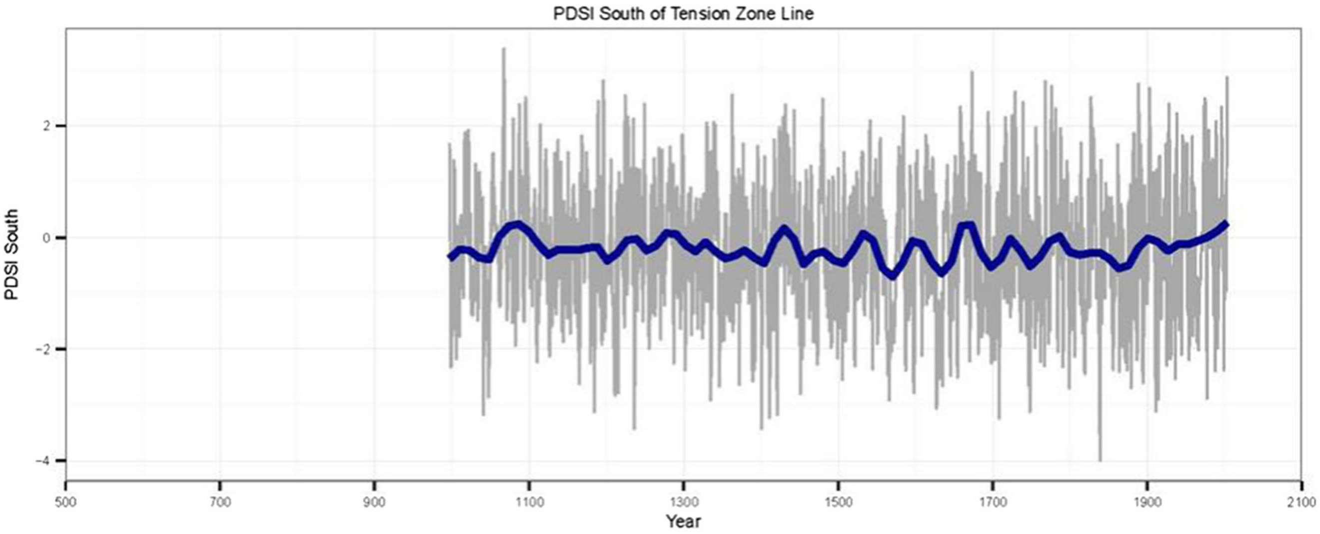
The study of fossil charcoal as an indicator of fire has helped elucidate disturbance regimes and their impacts in pollen interpretation (Patterson and Sassaman 1988; Parshall and Foster 2002). Charcoal data from sediment records can be used to provide information about past fire activity from local to global scales (Marlon et al. 2008). Nevertheless, the role of fire, including its origin, drivers, and extent in various forest types and regions, remains a contentious idea among historical ecologists (Pinter et al. 2011; Marlon et al. 2013; Abrams and Nowacki 2008, 2015). Opinions differ about the roles and relative strength of climate versus human (anthropogenic) drivers of fire, including the Early Anthropocene Burning Hypothesis. It deals with the possibility that the early human use of fire was profound, frequent, and prevalent, resulting in it becoming an early ecological driver (Ruddiman 2005; Marlon et al. 2013; Abrams and Nowacki 2015). This presumes that small populations of humans were able to burn expansive areas. Other issues that need to be resolved are the extent of lightning as an ignition source and whether burning was localized or ubiquitous in various vegetation types in the eastern USA (Ruffner and Abrams 1998; Nowacki et al. 2012).

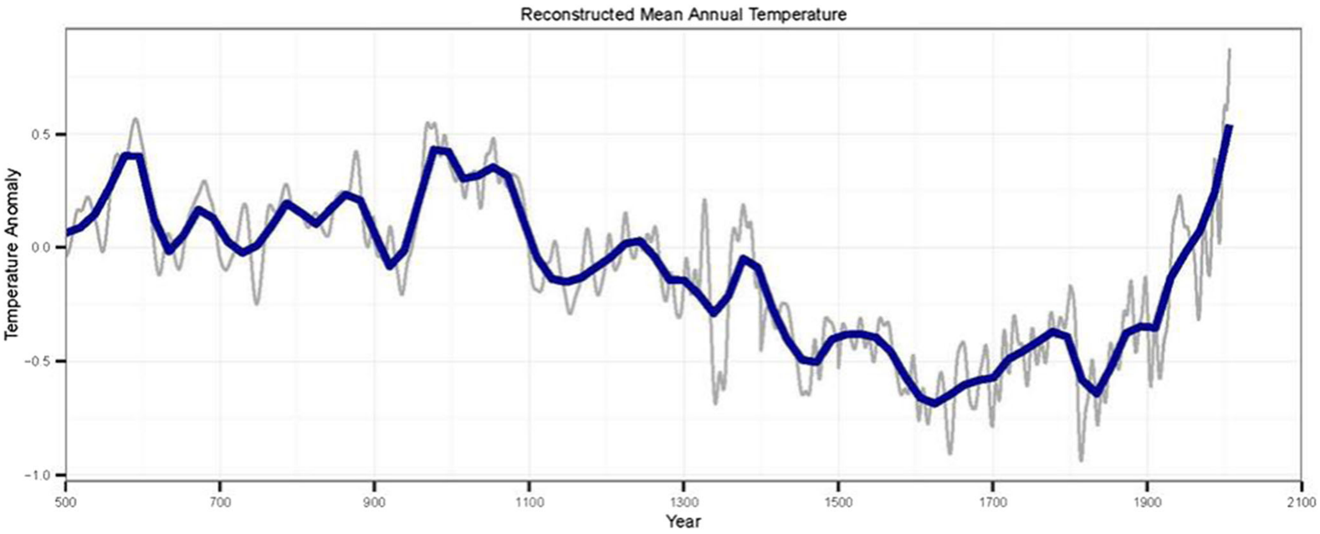
The impact of present and future climate change and other global change phenomena on world ecosystems is one of the premier research topics for ecologists and environmental scientists of this era (IPCC 2013). Research techniques in the field of historical ecology have particular relevance for assessing the impacts of climate and humans on ecosystems because what has happened in the past may provide important clues of what will happen in the future (Foster 1998; Egan and Howell 2001). For example, it is possible to study how various ecosystems responded to abrupt climate change (cooling and warming) and shifts in disturbance regimes in the past (Jackson 2006; Booth et al. 2012; Nowacki and Abrams 2015). Studies of this type have often involved the use of early land survey (witness trees and associated line notes) or paleoecology data (sediment pollen and charcoal in lakes, bogs, and caves). Comparative tree censuses using witness and modern tree data can provide fairly reliable information about forest change spanning several centuries, whereas paleoecology chronologies often span many millennia (Whitney 1994; Schulte and Mladenoff 2001; Foster 2004; Munoz et al. 2010).

Paleoecology and tree census studies have vastly contributed to our understanding of vegetation dynamics and the impacts of climate and disturbance as vegetation drivers. These include broad-scale and long-term climate change over centuries or millennia, as well as changes and interactions from both anthropogenic and natural changes in climate and perturbations. The reaction of ecosystems to global change factors can be assessed by examining the impacts of changing environmental conditions in the past, including the rise and fall of various vegetation.

Fig. 1 Climatic data (from year 500 to 2000, left to right) for the eastern ▶ USA including temperature anomaly for the northeastern USA and Palmer drought severity index (PDSI) from three sites north (top panel) and three sites south (middle panel) of the tension line. The PDSI data from the three northern locations were in Vermont, Michigan, and Wisconsin, while the three southern sites were in Virginia, south central Pennsylvania, and Kentucky. The annual PDSI values were smoothed using a 20-year running average. Climate data are from Mann et al. (2009) and the North American Drought Atlas (http://iridl.ldeo.columbia.edu/SOURCES?.LDEO/.TRL/.NADA2004/.pdsi-atlas.html)


PDSI North of Tension Zone Line
PDSI North
4
2
0
−2
500
700
900
1100
1300
1500
1700
1900
2100
Year


PDSI South of Tension Zone Line
PDSI South
2
0
−2
−4
500
700
900
1100
1300
1500
1700
1900
2100
Year


Reconstructed Mean Annual Temperature
Temperature Anomaly
0.5
0.0
−0.5
−1.0
500
700
900
1100
1300
1500
1700
1900
2100
Year

Indeed, recent paleoecological modeling studies have simulated responses to future environmental change (Jackson et al. 2009; Hannah et al. 2014). This type of information is critical to ecologists, land managers, and policy makers trying to make informed decisions about conservation, environmental change, and ecosystem resilience.

Many comparative tree studies have been amassed to assess post-European settlement changes to investigate the impacts of recent climate change on vegetation dynamics (see Appendix S1 of Nowacki and Abrams 2015). The same can be said for paleoecology studies (Davis 1963; Webb III et al. 1981; Schwartz 1989; Paciorek and McLachlan 2009). The coupling paleoecological and tree census data to address larger global change questions seems to us an important, but underutilized, research approach. The potential exists for studies to more accurately describe and ascribe recent vegetation dynamics to its causal factors, particularly in relation to the climate versus disturbance debate. A recent paper by Nowacki and Abrams (2015) presented a unique approach to untangle the role of climate versus disturbance as forest change drivers over multiple centuries. This was accomplished by categorizing major tree species/genera into temperature, shade tolerance (succession), and pyrogenicity classes based on ecophysiological characteristics, and then applying those classes to comparative studies of past and present tree censuses. In contrast, paleoecological studies have typically concentrated on documenting vegetation dynamics and their relationship to environmental changes over the Late Quaternary (Davis 1969; Webb 1983; Russell et al. 1993; Shuman et al. 2004; Williams et al. 2004). Relatively few paleoecological studies investigated the impacts of late Holocene climatic variability on vegetation dynamics.

For understanding the relative roles of climatic variability and disturbance regimes on vegetation communities, we use an approach that integrates historical and modern tree surveys with fossil pollen and charcoal data (cf. Dawson et al. 2016). Witness trees (trees used to demarcate property corners in early historical land surveys; also referred to as corner trees and bearing trees) provide a "snapshot" of forest composition during the time of land survey, spanning from the 1600s (eastern colonies) to the early 1900s (Minnesota) (Whitney 1994; Schulte and Mladenoff 2001). Although there are some shortcomings (Schulte and Mladenoff 2001; Whitney and DeCant 2001), witness tree data probably provide the best depictions of arboreal vegetation during the onset of European settlement, especially when compiled at the landscape scale (Delcourt and Delcourt 1996). Witness tree data are extensively used in historical ecology studies throughout the eastern USA (Whitney 1994). When paired with current vegetation surveys (e.g., Forest Inventory and Analysis data), changes in arboreal composition and structure can be deciphered and associated ecological drivers assigned (Nowacki and Abrams 2008, 2015).

Paleoecological data (biological and geochemical remains preserved in sedimentary archives) record environmental changes over centuries to millennia through the use of proxies. In this study, we use fossil pollen as a proxy of past vegetation composition and change (Davis 1969; Russell et al. 1993; Shuman et al. 2004; Williams et al. 2004) and fossil charcoal as a proxy of past biomass burning (Power et al. 2010; Marlon et al. 2013). The combination of these different data types should give a broader perspective of how past and projected climatic change will impact vegetation communities. More specifically, the objectives of this study are to (1) compile and compare pre-European settlement versus modern upland arboreal pollen and tree survey data from large number of studies in various forest regions in the eastern USA, (2) analyze fossil charcoal dating back 2000 years for the northern versus central/southern tiers of the eastern USA, and (3) compare and contrast compositional and ecophysiological attributes for both datasets and temporal changes to known climate or disturbance phenomena to elucidate global change impacts and the drivers of forest change.

2 Methods

A total of seven forest types in the north and central regions of the eastern USA were used to co-analyze fossil pollen, fossil charcoal, and tree survey data (Tables 1 and 2; Fig. 2). These forest types were assembled, and the tension zone line (TZL) struck using ecological subsections as base units (Cleland et al. 2007). Four of the forest types are located north of the TZL, and three forests types are located to its south (Fig. 2). The TZL is a boundary between two distinct floristic zones, in this case conifer-northern hardwood and sub-boreal to the north and oak-pine to the south (Curtis 1959). Most of the pollen chronologies used for study were extracted from Neotoma V1.0, a relational multiproxy paleoenvironmental database (Grimm 2008), with additional data extracted from published literature (Table 1). Using a criteria similar to Munoz et al. (2010), we excluded a pollen record if it (a) did not contain dated radiocarbon years within the study periods (pre-European and Little Ice Age versus modern), (b) contained a hiatus of > 500 years of accurately dated samples within the study period, (c) had no chronological control (other than the top of the core) within the study period, (d) had samples from large bodies of water (> 115 ha) or very small ponds (< 1 ha) (leaving only larger ponds and small lakes for our analysis), and (e) had samples located in present-day urban areas that might have impacted modern vegetation assemblages. By applying these criteria, we filtered our initial population of 129 pollen chronologies to 76 for this study.

Table 1 List of lake basins within each forest type included in the study with the two periods of comparison (pre-European settlement versus present day), the % of tree pollen versus total pollen (all upland vegetation) in the sample and citation. NA = not available in the Neotoma database. GL_BM = Great Lakes beech-maple; GL_CNH = Great Lakes conifer-northern hardwood; NE_CNH = Northeast conifer-northern hardwood; SC = sub-boreal conifer; Cent_OP = Central oak-pine; GL_OP = Great Lakes oak-pine; NE_OP = Northeast oak-pine

Region	Site name	Periods of comparison	Tree pollen presettlement %	Tree pollen present %	Publication
GL_BM	Barry Lake, ON	1674 and 1967	98.8	71.0	McAndrews (1984)
GL_BM	Cranberry Lake, ON	1595 and 1975	83.5	71.4	NA
GL_BM	Fudger Lake, OH	1447 and 1967	83.0	37.1	Shane (1991)
GL_BM	Hams Lake, ON	1644 and 1981	96.7	85.5	Bennett (1987)
GL_BM	High Lake, ON	1563 and 1950	97.8	98.6	Fuller (1995)
GL_BM	Humber Pond 5, ON	1611 and 1975	22.1	72.4	Weninger and McAndrews (1989)
GL_BM	Humber Pond 7, ON	1563 and 1973	5.2	63.9	NA
GL_BM	Parrott's Pond, ON	1561 and 1976	56.9	67.9	McCarthy (1986)
GL_BM	Pond Mills Pond, ON	1498 and 1950	94.8	64.8	McAndrews (1981)
GL_BM	Silver Lake, OH	1550 and 1960	93.7	51.8	Ogden III (1966)
GL_BM	Van Nostrand Lake, ON	1570 and 1950	95.2	65.7	McAndrews (1973)
GL_BM	Wylde Lake, ON	1609 and 1975	98.5	84.9	NA
GL_CNH	Hell's Kitchen Lake, WI	1593 and 1960	96.2	86.3	Kneller and Peteet (1993)
GL_CNH	Spirit Lake, MI	1575 and 1970	98.4	94.8	Woods and Davis (1989)
GL_CNH	Wood Lake, WI	1493 and 1950	92.3	87.3	Heide (1981)
GL_CNH	Demont Lake, MI	1567 and 1937	96.1	83.6	Ahearn (1976)
GL_CNH	Capitola Lake, WI	1553 and 1956	90.1	60.3	Calcote (2003)
GL_CNH	Hemlock Lake, WI	1559 and 1984	96.1	78.3	Calcote (2003)
GL_CNH	Lorraine Lake, MI	1630 and 1983	95.8	95.7	Calcote (2003)
GL_CNH	Morrison Lake, MI	1615 and 1970	97.6	88.0	Calcote (2003)
GL_CNH	McDonald Lake, MI	1594 and 1983	98.8	92.9	Calcote (2003)
GL_CNH	Lake O'Pines, WI	1606 and 1990	98.4	92.2	Ewing (2000)
NE_CNH	Basin Pond, ME	1555 and 1960	98.7	86.6	Gajewski (1983)
NE_CNH	Clear Pond, NY	1583 and 1960	99.0	91.8	Gajewski (1985)
NE_CNH	Conroy Lake, ME	1586 and 1967	98.1	86.9	Gajewski (1983)
NE_CNH	Heart Lake, NY	1589 and 1950	98.9	90.1	Whitehead and Jackson (1990)
NE_CNH	Ely Lake, PA	1596 and 1965	99.7	59.2	Gajewski (1985)
NE_CNH	Giles Lake, PA	1560 and 1984	98.8	87.1	Russell et al. (1993)
NE_CNH	Gould Pond, ME	1368 and 1979	99.7	76.2	Jacobson Jr et al. (1987)
NE_CNH	Kinsman Pond, NH	1428 and 1950	98.9	94.2	Spear (1981)
NE_CNH	Lake Lacawac, PA	1572 and 1984	97.8	91.3	Russell et al. (1993)
NE_CNH	Loon Pond, ME	1516 and 1977	99.0	91.4	Jacobson et al. (unpublished)
NE_CNH	Mansell Pond, ME	1571 and 1980	99.1	91.9	Almquist-Jacobson and Sanger (1995)
NE_CNH	North Pond, MA	1571 and 1950	98.7	89.0	Whitehead and Crisman (1978)
NE_CNH	Poland Spring Pond, ME	1593 and 1978	98.2	88.9	Jacobson et al. (unpublished)
NE_CNH	Ross Pond, ME	1600 and 1972	90.3	86.7	Kellogg (1991)
NE_CNH	Silver Lake, PA	1561 and 1967	95.7	83.5	Russell et al. (1993)
NE_CNH	Sinkhole Pond, ME	1470 and 1976	90.6	92.5	Jacobson et al. (unpublished)
NE_CNH	Spring Lake, PA	1596 and 1950	96.2	71.4	NA
NE_CNH	Upper South Branch Pond, ME	1589 and 1950	97.3	94.4	Anderson (1979)
NE_CNH	Basswood Road Lake/Splan Pond, ME	1481 and 1950	97.8	91.0	Mott (1975)
SC	Bob Lake, MN	1568 and 1959	91.2	84.6	NA
SC	Goldsmith Lake, MN	1568 and 1959	94.2	81.8	NA
SC	Hostage Lake, MN	1331 and 1980	89.1	80.8	Almendinger (1985)
SC	Hug Lake, MN	1592 and 1964	95.2	86.6	Swain (1974)

Table 1 (continued)

Region	Site name	Periods of comparison	Tree pollen presettlement %	Tree pollen present %	Publication
SC	Irvin Lake, MN	1589 and 1982	89.2	87.4	Alwin (1982)
SC	Mud Lake, MN	1441 and 1980	86.2	80.2	Almendinger (1985)
SC	Portage Lake, MN	1588 and 1938	89.6	75.5	NA
SC	Siseebakwet South, MN	1557 and 1978	91.0	81.8	Alwin (1982)
SC	Wentzel's Pond, MN	1491 and 1980	74.8	69.4	Almendinger (1985)
Cent_OP	Anderson Pond, TN	1518 and 1950	77.9	72.9	Delcourt (1979)
Cent_OP	Black Pond, TN	1526 and 1974	87.7	68.2	Cridlebaugh (1984)
Cent_OP	Hack Pond, VA	1510 and 1950	97.0	97.3	Stuiver (1969)
Cent_OP	Jackson Pond, KY	1472 and 1975	56.6	58.4	Wilkins (1985)
Cent_OP	Quarles Pond, VA	1396 and 1950	72.8	78.7	Craig (1969)
Cent_OP	Tuskegee Pond, TN	1589 and 1945	40.7	46.8	Cridlebaugh (1984)
GL_OP	Bossuot Lake, MN	1550 and 1963	57.2	49.5	McAndrews (1968)
GL_OP	Frains Lake, MI	1541 and 1950	96.2	73.2	Kerfoot (1974)
GL_OP	Radtke Lake, WI	1630 and 1950	93.8	69.1	Webb (1983)
GL_OP	Rutz Lake, MN	1593 and 1953	46.4	48.2	Waddington (1969)
GL_OP	Wintergreen Lake, MI	1574 and 1970	99.5	72.5	Manny et al. (1978)
GL_OP	Pretty Lake, IN	1518 and 1950	97.4	67.8	Ogden III (1969)
NE_OP	Carbuncle Pond, RI	1545 and 1950	98.0	70.5	NA
NE_OP	Duck Pond, MA	1523 and 1950	81.5	78.3	Winkler (1985)
NE_OP	Greenwater Pond, MA	1530 and 1950	89.5	76.1	NA
NE_OP	Pasacaco Pond, RI	1596 and 1950	84.8	72.0	NA
NE_OP	Rogers Lake, CT	1470 and 1950	92.2	68.4	Davis and Deevey Jr. (1964)
NE_OP	Linsley Pond, CT	1583 and 1971	88.4	89.3	Brugam (1978)
NE_OP	Eagle Pond, MA	1459 and 2000	88.8	48.7	Foster et al. (2002b)
NE_OP	Duarte Pond, MA	1570 and 2000	95.9	70.9	Foster et al. (2002a)
NE_OP	Wickett Pond, MA	1495 and 1984	78.0	92.4	Francis and Foster (2001)
NE_OP	Little Mirror Lake, MA	1582 and 1985	93.2	90.7	Fuller et al. (1998)
NE_OP	Silver Lake, MA	1588 and 1988	95.1	94.2	Fuller et al. (1998)
NE_OP	Aino Pond, MA	1589 and 1987	93.0	85.1	Fuller et al. (1998)
NE_OP	Jemima Pond, MA	1512 and 1999	77.3	60.1	Parshall and Foster (2002)

We used the Neotoma age-depth information for our chronologies, which typically use the European settlement horizon as a chronological control. Whenever possible, we used age-depth models based on calibrated 14C dates, but for this time period, there is not a major difference between radiocarbon and calibrated ages. Arboreal pollen percentages for selected taxa (Table 3) were calculated using the terrestrial pollen sum (Table 1). First, we eliminated all herb and shrub pollen; then, the remaining tree pollen were relativized for each species with the total tree pollen count equal to 100%. Taxonomic resolution of pollen data were reduced to the genus level in arboreal taxa where species-level identification were made (e.g., *Acer saccharum* and *Acer rubrum* were aggregated to *Acer*) because most records are not identified beyond the genus level. The protohistoric period encompasses Native American occupation during the Little Ice Age (ca. 1400 to 1850 AD), while the contemporary period reflects post-Euro-American land use and climate change after ca. 1850.

Charcoal data are from the Global Charcoal Database (GCD, v. 2) (Daniau et al. 2012), including 13 records from north of 42° N latitude (2430 samples) and 11 records south of 42° N latitude (428 samples), and were used to reconstruct trends in biomass burning for the eastern USA during the past 2000 years (Table 2). Data from the GCD are typically standardized to produce anomalies from a shared base period for multiple records. Standardizing the charcoal values makes comparisons possible across many records, despite differences in specific particle size classes measured, lab, and analytical methodologies. For standardization, each record was

Table 2 Sites used for paleocharcoal analysis by region. The northern and southern zones were divided at 43° N latitude across the eastern USA (see map in Fig. 2)

Region	Site name, state	Publication
North	Steel Lake, MN	Nelson et al. (2004)
North	Hell's Kitchen, WI	Clark and Royall (1996)
North	Ferry Lake, WI	Jensen et al. (2007)
North	Sharkey, MN	Geiss et al. (2003)
North	Basin, ME	Clark and Royall (1996)
North	Kimble, MN	Geiss et al. (2003)
North	Round Pond, NY	Clark unpublished
North	Pout Pond, NH	Clark and Hussey (1996)
North	Lily Pond Warwick, MA	Fuller et al. (1998)
North	Aino Pond, PA	Fuller et al. (1998)
North	Otter Pond, PA	Fuller et al. (1998)
North	Green Pond, PA	Fuller et al. (1998)
North	Little Pond Bolton, PA	Fuller et al. (1998)
South	Ely, PA	Clark and Royall (1996)
South	Howes Prairie Marsh, IN	Cole and Taylor (1995)
South	Binnewater, NY	Robinson et al. (2005)
South	Cliff Palace Pond, KY	Delcourt and Delcourt unpublished
South	Curt Pond, KY	Delcourt and Delcourt unpublished
South	Black Pond, TN	Delcourt and Delcourt unpublished
South	Tuskegee Pond, TN	Delcourt and Delcourt unpublished
South	Mound G Pond, TN	Delcourt and Delcourt unpublished
South	Horse Cove Bog, NC	Delcourt and Delcourt unpublished
South	Cahaba Pond, AL	Delcourt and Delcourt unpublished
South	Lake Tulane, FL	Watts and Hansen (1988)

"presampled" to a common temporal window (10 years in this case). A weighted mean was calculated if multiple values existed within a given 10-year period for each record. The presampled records were subsequently rescaled, transformed, and converted to *z* scores following the protocol detailed in Power et al. (2010) and implemented via the PfTransform (paleofire) function in the paleofire R package (Blarquez et al. 2014). A base period of 2000–200 cal year BP was used to calculate the *z* scores. The standardized and normalized charcoal records were then smoothed using a 200-year window width with the pfCompositeLF (paleofire) function to create a composite for the northern and southern zones, divided at 42° N latitude, and for the entire eastern USA, along with 5% and 95% bootstrap confidence intervals.

Climatic data was compiled and synthesized for the eastern USA, including temperature anomaly for the northeastern USA and Palmer drought severity index (PDSI) from three sites north and three sites south of the tension line. The east–west gradient of PDSI data are from three northern locations that were in Vermont, Michigan, and Wisconsin while the three southern sites were in Virginia, south central Pennsylvania, and Kentucky. The annual PDSI values were smoothed using a 20-year running average. The mean annual temperature and PDSI data were obtained from Mann et al. (2009) and the North American Drought Atlas (http://iridl.ldeo.columbia.edu/SOURCES?.LDEO/.TRL/.NADA2004/.pdsi-atlas.html), respectively. Temperature data were obtained by extracting data from the paleoclimate dataset reconstructed by Mann et al. (2009) covering grid cells in the eastern USA.

For tree census data, we identified 52 studies in the eastern USA that produced a total of 192 datasets available for analysis (Nowacki and Abrams 2015). Early tree surveys chronicle the westward progression of European land acquisition, with some dating back to the seventeenth century along the Atlantic Coast (Whitney and Davis 1986; Foster et al. 1998; Thompson et al. 2013). These are divided into two time periods, the early historic (1620 to 1850 AD) and contemporary (1940 to 2000 AD), making these as similar as possible with the paleopollen data.

Population estimates for the eastern USA were obtained from the HYDE 3.1 global population dataset (Klein Goldewijk et al. 2011) by aerially averaging data from grid cells between 25° N and 49° N latitude and 95° E and 65° E longitude. Temperature data were obtained by extracting data from the paleoclimate dataset reconstructed by Mann et al. (2009) covering grid cells in the eastern USA.

2.1 Data analysis

Major tree genera in eastern North American (16 genera distributed across the seven forest types in our study region) were classified by temperature, shade tolerance, and pyrogenicity (including drought tolerance) based on available data, published literature, and authors' knowledge (Table 3). Temperature classes were established using actual temperature data from the Climate Change Tree Atlas (Prasad et al. 2007–ongoing). Each tree genus was classified into one of four temperature classes (cold, cool, warm, and hot) based on the average annual temperature within its ecological range (US distribution; Nowacki and Abrams 2015). Genera were also categorized by shade tolerance (intolerant, intermediate, and tolerant) and pyrogenicity (pyrophilic and pyrophobic) based on their known life history and physiological characteristics (Table 3). Individual tree percentages from pollen and survey data were tallied by temperature (cold, cool, warm), shade tolerance (intolerant, intermediate, tolerant), and pyrogenicity (pyrophilic, pyrophobic) classes based on the lowest taxonomic level reported for each dataset. All of the genera classified as pyrophilic were also classified as drought tolerant (Burns and Honkala 1990); thus, changes in pyrogenicity are indicative of changes in

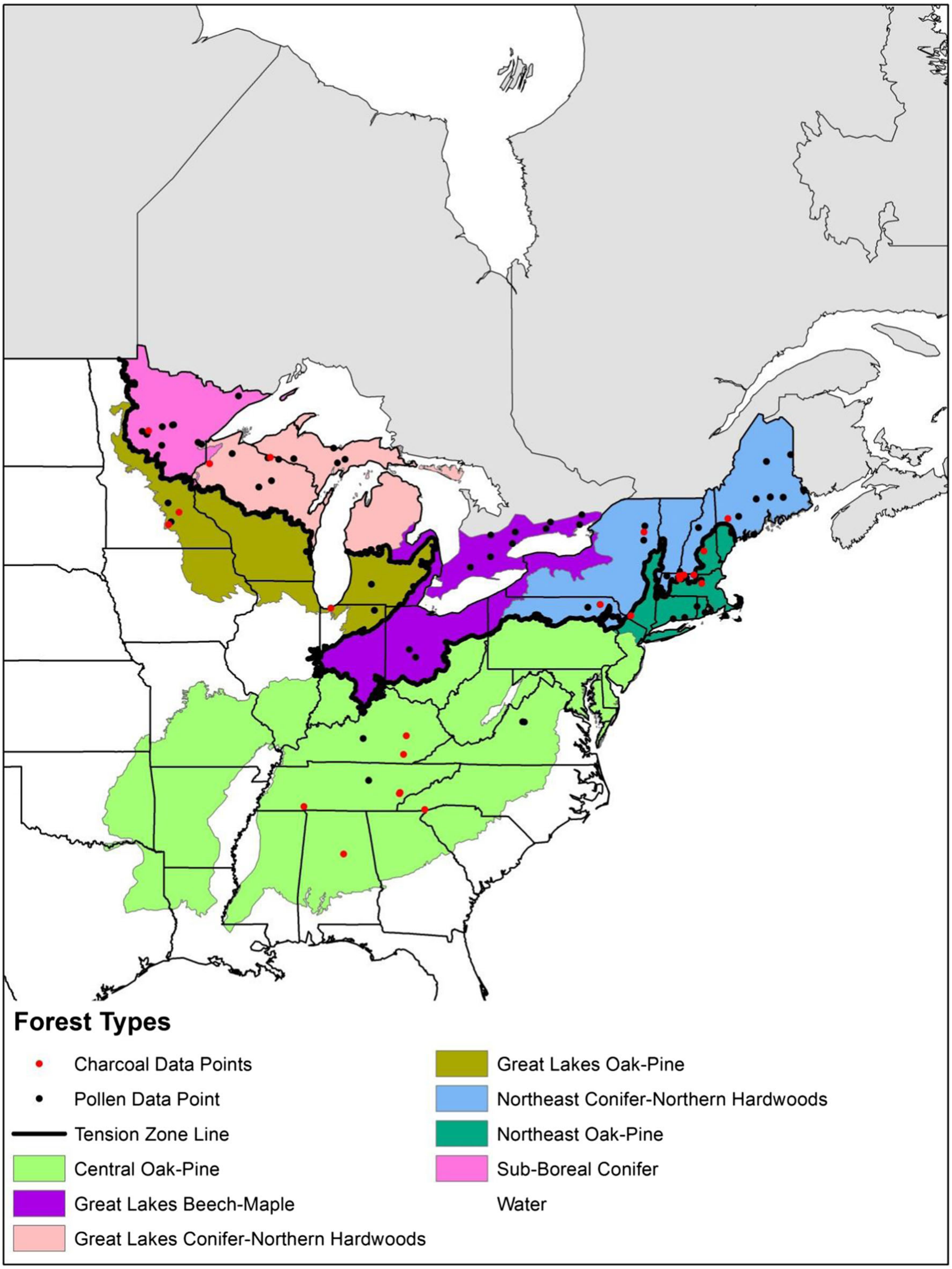


Fig. 2 Pre-European settlement forest biomes of North America assembled from ecological subsections of USA, pollen study site, and tension zone locations (Cleland et al. 2007; Nowacki and Abrams 2015). Black dots are the location of the paleopollen study sites (Table 1), and red dots are the location of paleocharcoal study sites (Table 2)

climate conditions and drought tolerance. Absolute percentage changes were then calculated for each class by subtracting protohistoric from contemporary abundances, and two-tailed *t* tests were performed between the two time periods to test for statistical differences in both the pollen and tree survey data.

Table 3 Common eastern North American tree genera classified by temperature, shade tolerance, and pyrogenicity (adapted from Nowacki and Abrams (2015)). Average annual range temperatures (in parentheses) 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). Range temperatures for genera were averaged from component species. Pollen representation in sediment samples is based on Prentice and Webb III (1986). Pyrophilic genera are also classified as drought tolerant (including moderately drought tolerant, indicated with DT

Latin name	Common name	Temperature	Shade tolerance	Fire-drought tolerance	Pollen representation
Abies	Fir	Cold (4.4)	Tolerant	Pyrophobic	Low
Acer	Maple	Cool (9.6)	Tolerant	Pyrophobic	Low
Betula	Birch	Cold (8.8)	Intolerant	Pyrophobic	High
Carya	Hickory	Warm (13.0)	Intermediate	Pyrophilic-DT	Intermediate
Castanea	Chestnut	Cool (9.8)	Intermediate	Pyrophilic-DT	Unknown
Fagus	Beech	Warm (11.0)	Tolerant	Pyrophobic	Intermediate
Fraxinus	Ash	Cool (8.9)	Intermediate	Pyrophobic	Low
Larix	Larch	Cold (4.6)	Intolerant	Pyrophobic	Low
Picea	Spruce	Cold (4.5)	Tolerant	Pyrophobic	Low
Pinus (mostly *strobus* type)	Pine	Cold (5.8)	Intolerant	Pyrophilic-DT	High
Populus	Aspen	Cold (6.8)	Intolerant	Pyrophilic-DT	Low
Quercus	Oak	Warm (12.3)	Intermediate	Pyrophilic-DT	High
Thuja	Cedar	Cold (4.5)	Tolerant	Pyrophobic	Low
Tilia	Basswood	Cool (8.0)	Tolerant	Pyrophobic	Low
Tsuga	Hemlock	Cool (7.3)	Tolerant	Pyrophobic	Intermediate
Ulmus	Elm	Warm (11.7)	Intermediate	Pyrophobic	High

3 Results

PDSI was consistently higher (less droughty) in northern forests than southern, where it was typically above and below zero, respectively (Fig. 1a, b). However, PDSI generally increased after about 1900 in southern regions, but within the historic range of variability. Temperatures across the eastern USA declined from 500 to ~ 1700 AD and abruptly increased thereafter (Fig. 1c).

Pollen assemblages from the Great Lakes beech-maple (*Fagus-Acer*) forest are dominated by oak (*Quercus*) and pine (*Pinus*) in the protohistoric and contemporary periods because these genera are high-pollen producers (Tables 3 and 4). Inconsistent with the principal components by which this forest type was named (sensu Braun 1950), beech and maple, with intermediate and low pollen production, were vastly underrepresented in the pollen record. However, protohistoric tree surveys supported the forest type designation, with elevated occurrences of beech and maple followed by oak, although this is based on only two sites. Arboreal pollen assemblages exhibited little change over the study period, but tree survey data document a large decline in beech (− 29%). Pollen assemblages in the protohistoric Great Lakes conifer-northern hardwood biome were dominated by high-pollen producers of pine and birch (*Betula*) and intermediate pollen producer hemlock (*Tsuga*), whereas the tree survey data indicate that these forests were dominated by pine, hemlock, and maple (Table 4). In this region, tree survey data document significant changes in 11 species with the largest increases for maple, aspen (*Populus*), and oak and largest decreases for pine and hemlock. Although no statistically significant changes in the relative abundances were found in any of the pollen taxa, the direction of change for the important genera (maple, pine, and hemlock) correspond to that found in the tree survey data.

Protohistoric pollen assemblages in the Northeast conifer-northern hardwoods exhibited high abundances of birch, pine, hemlock, oak, and beech (Table 4), whereas tree survey data indicated that these forests were disproportionally beech dominated, followed hemlock and maple. Over the period of study, the pollen data document statistically significant declines in the abundances of hemlock and beech and increases in birch and maple, all of which correspond to trends observed in the tree survey record. Protohistoric pollen assemblages in sub-boreal conifer forests were again dominated by high-pollen producers pine and birch, while tree survey data document a diverse forest community dominated by pine, larch (*Larix*), spruce (*Picea*), and birch (Table 4). Over the period of record, sub-boreal forest pollen assemblages document statistically significant increases in oak, aspen, and ash (*Fraxinus*), whereas tree survey data statistically document a more robust array of compositional shifts, with significant increases in aspen, ash, maple, and fir (*Abies*) and decreases in pine, larch, and birch.

Pollen assemblages in the oak-pine forests south of the TZL (including the Central, Great Lakes, and Northeast regions) are dominated by oak and pine over

Table 4 Pre-European settlement (protohistoric) and present-day percentages and temporal change of pollen and tree surveys for the major tree genera in forest types north of the tension zone line. Number of sites for pollen and survey trees, respectively, is in parentheses. Forest type abbreviations are found in Table 1

Forest type (no. of sites)	Species	Fossil pollen (%)			Tree survey (%)		
		Protohistoric	Present	Absolute change	Protohistoric	Present	Absolute change
GL_BM (13; 2)	*Acer*	4.89	3.21	−1.68	15.50	17.85	2.35
	Betula	9.59	12.56	2.97	1.25	1.55	0.3
	Carya	2.76	2.58	−0.18	6.55	10.20	3.65
	Fagus	6.70	4.46	−2.24	33.00	3.85	−29.15
	Fraxinus	4.11	3.68	−0.43	7.20	8.95	1.75
	Pinus	17.81	18.39	0.58	1.15	0.10	−1.05
	Quercus	26.99	25.68	−1.31	10.90	8.75	−2.15
	Tsuga	7.26	4.11	−3.15	x	x	x
	Ulmus	7.25	7.57	0.32	5.00	13.10	8.1
GL_CNH (10; 62)	*Abies*	0.42	0.81	0.39	1.68	3.61	1.93***
	Acer	2.31	3.38	1.08	15.11	27.82	12.71***
	Betula	25.11	28.44	3.33	9.73	6.21	−3.52**
	Thuja	0.08	0.64	0.56	5.73	6.63	0.9
	Fagus	1.27	0.41	−0.86	6.98	1.52	−5.46***
	Fraxinus	1.15	1.68	0.53	1.45	3.82	2.37***
	Larix	0.40	0.83	0.44	3.31	0.79	−2.52***
	Picea	1.36	1.71	0.36	2.08	2.57	0.49
	Pinus	36.86	27.58	−9.27	28.67	11.19	−17.48***
	Populus	0.99	3.46	2.48	2.00	13.68	11.68***
	Quercus	7.41	8.46	1.06	3.06	11.10	8.04***
	Tsuga	14.51	8.75	−5.76	15.99	2.52	−13.47***
	Ulmus	2.51	2.89	0.39	1.70	0.94	−0.76*
NE_CNH (19; 10)	*Abies*	1.18	1.39	0.20	1.41	1.49	0.08
	Acer	1.83	2.62	0.79*	12.70	31.47	18.77***
	Betula	25.49	32.48	6.99*	7.15	10.98	3.83
	Thuja	1.45	1.44	−0.01	0.33	0.43	0.1
	Fagus	10.22	5.53	−4.69**	34.79	11.36	−23.43***
	Fraxinus	1.37	2.05	0.68	2.37	4.18	1.81
	Larix	0.17	0.23	0.06	0.06	0.07	0.01
	Picea	6.88	6.02	−0.86	6.92	1.91	−5.01
	Pinus	17.82	15.28	−2.54	3.55	4.71	1.16
	Populus	0.38	0.82	0.44	0.35	2.93	2.58**
	Quercus	10.48	13.13	2.64	5.12	8.87	3.75
	Tsuga	15.93	6.87	−9.05**	15.87	7.96	−7.91*
	Ulmus	0.91	1.43	0.52	0.91	0.57	−0.34
SC (9; 31)	*Abies*	0.90	0.85	−0.06	5.93	10.56	4.63***
	Acer	0.73	0.92	0.20	2.11	6.86	4.75***
	Betula	18.11	22.76	4.64	13.36	10.04	−3.32*
	Thuja	0.94	0.78	−0.16	5.79	7.14	1.35
	Fagus	x	x	x	x	x	x
	Fraxinus	0.66	1.86	1.21*	1.30	6.64	5.34***
	Larix	0.42	0.29	−0.13	17.84	4.79	−13.05***
	Picea	9.50	6.36	−3.14	15.17	14.01	−1.16
	Pinus	52.01	40.80	−11.21	25.00	7.22	−17.78***
	Populus	0.97	3.32	2.35*	9.79	24.85	15.06***
	Quercus	5.51	10.44	4.93*	1.32	2.75	1.43
	Tsuga	0.35	0.06	−0.30*	x	x	x
	Ulmus	0.88	1.36	0.48	0.97	0.49	−0.48
Average change				2.08%			5.93%
No. of sign. changes				8			22

***$P < 0.001$

**$P < 0.01$

*$P < 0.05$

the period of study, with few significant shifts in the abundances of any genera documented (Table 5). Correspondingly, tree survey data recorded the same dominants over the period of record. However, tree

Table 5 Pre-European settlement (protohistoric) and present-day percentages and temporal change of pollen and tree surveys for the major tree genera in forest types south of the tension zone line. Number of sites for pollen and survey trees, respectively, is in parentheses. Forest type abbreviations are found in Table 1

		Fossil pollen (%)			Trees surveys (%)		
Forest type (no. of sites)	Species	Protohistoric	Present	Absolute change	Protohistoric	Present	Absolute change
Cent_OP (7; 33)	*Acer*	0.61	5.47	4.86	3.50	10.47	6.97***
	Betula	1.57	1.91	0.34	0.66	1.19	0.53
	Carya	5.95	5.52	−0.43	6.53	8.16	1.63
	Castanea	2.63	1.68	−0.96	2.90	0.15	−2.75***
	Fagus	0.24	0.15	−0.09	2.31	2.30	−0.01
	Fraxinus	2.53	3.75	1.22	1.20	1.62	0.42
	Pinus	24.67	20.50	−4.17	8.47	4.40	−4.07
	Populus	0.14	0.47	0.33	0.09	0.61	0.52
	Quercus	47.95	43.37	−4.58	64.31	47.16	−17.15***
	Tilia	0.15	0.05	−0.10	0.27	0.17	−0.1
	Tsuga	0.22	0.11	−0.10	0.79	0.29	−0.5
	Ulmus	0.94	2.41	1.47	1.38	2.80	1.42*
GL_OP (6; 18)	*Acer*	1.56	2.81	1.26	6.05	15.19	9.14*
	Betula	4.26	4.11	−0.15	1.36	1.48	0.12
	Carya	3.71	4.75	1.04	0.43	3.16	2.73
	Castanea	x	x	X	x	x	x
	Fagus	3.99	2.48	−1.51	2.63	3.34	0.71
	Fraxinus	4.55	3.97	−0.58	1.64	2.83	1.19
	Pinus	5.49	9.93	4.43	11.24	9.32	−1.92
	Populus	0.15	0.54	0.39	5.55	6.60	1.05
	Quercus	57.36	48.65	−8.72	57.49	33.77	−23.72*
	Tilia	1.34	1.58	0.25	4.70	6.24	1.54
	Tsuga	0.18	0.04	−0.15	0.01	0.00	−0.01
	Ulmus	5.61	8.42	2.82	4.35	7.07	2.72
NE_OP (13; 10)	*Acer*	2.14	2.74	0.60	6.00	26.03	20.03***
	Betula	16.08	17.31	1.23	2.46	7.90	5.44**
	Carya	2.94	2.43	−0.51	4.20	2.26	−1.94
	Castanea	3.00	1.35	−1.65	6.53	0.35	−6.18***
	Fagus	5.49	3.53	−1.95	4.49	1.60	−2.89*
	Fraxinus	1.23	1.31	0.07	2.30	2.43	0.13
	Pinus	19.12	22.38	3.26	16.81	15.62	−1.19
	Populus	0.07	0.08	0.01	1.17	0.62	−0.55
	Quercus	34.67	36.94	2.27	43.84	29.12	−14.72*
	Tilia	0.06	0.00	−0.06	0.11	0.05	−0.06
	Tsuga	5.70	2.43	−3.27*	5.52	7.34	1.82
	Ulmus	1.01	0.92	−0.09	1.32	1.09	−0.23
Average change				1.57%			3.89%
No. of sign. changes				1			11

***$P < 0.001$

**$P < 0.01$

*$P < 0.05$

survey data did record significant declines in oak and chestnut and significant increases in maple. In most cases, the direction of change recorded in tree surveys paralleled those in the pollen record.

Compositional differences between pollen and tree survey data were generally consistent with differences in pollen productivity (Table 3), with high-pollen-producers pine, birch, and oak overrepresented and low-pollen-producers maple and aspen underrepresented relative to tree survey data. Overall, forests north of the TZL were dominated by genera typical of conifer-northern hardwoods, including pine, birch, beech, hemlock, and maple. Forests south of the TZL were dominated by oak followed by pine in both data types. Here, high-pollen-producing pine and birch were overrepresented and low-pollen-producing maple and aspen were underrepresented in the pollen record relative to tree surveys.

Tree genera were partitioned into temperature, shade tolerance, pyrogenicity (including drought classes) and applied to pre-European fossil pollen and witness tree data (Fig. 3). The Great Lakes beech-maple pollen data were dominated by warm-adapted trees that were evenly split between two shade-tolerant classes (intolerant and intermediate) and both fire/drought classes. Witness trees from the same forest type had few cold-adapted, intolerant pyrophiles. The Great Lakes conifer-northern hardwood pollen data were dominated by cold-adapted, shade-intolerant (early successional) trees that were nearly evenly split between pyrophiles and pyrophobes. Witness trees differed from this by having had a higher proportion of cool-adapted, shade-tolerant, drought-intolerant/

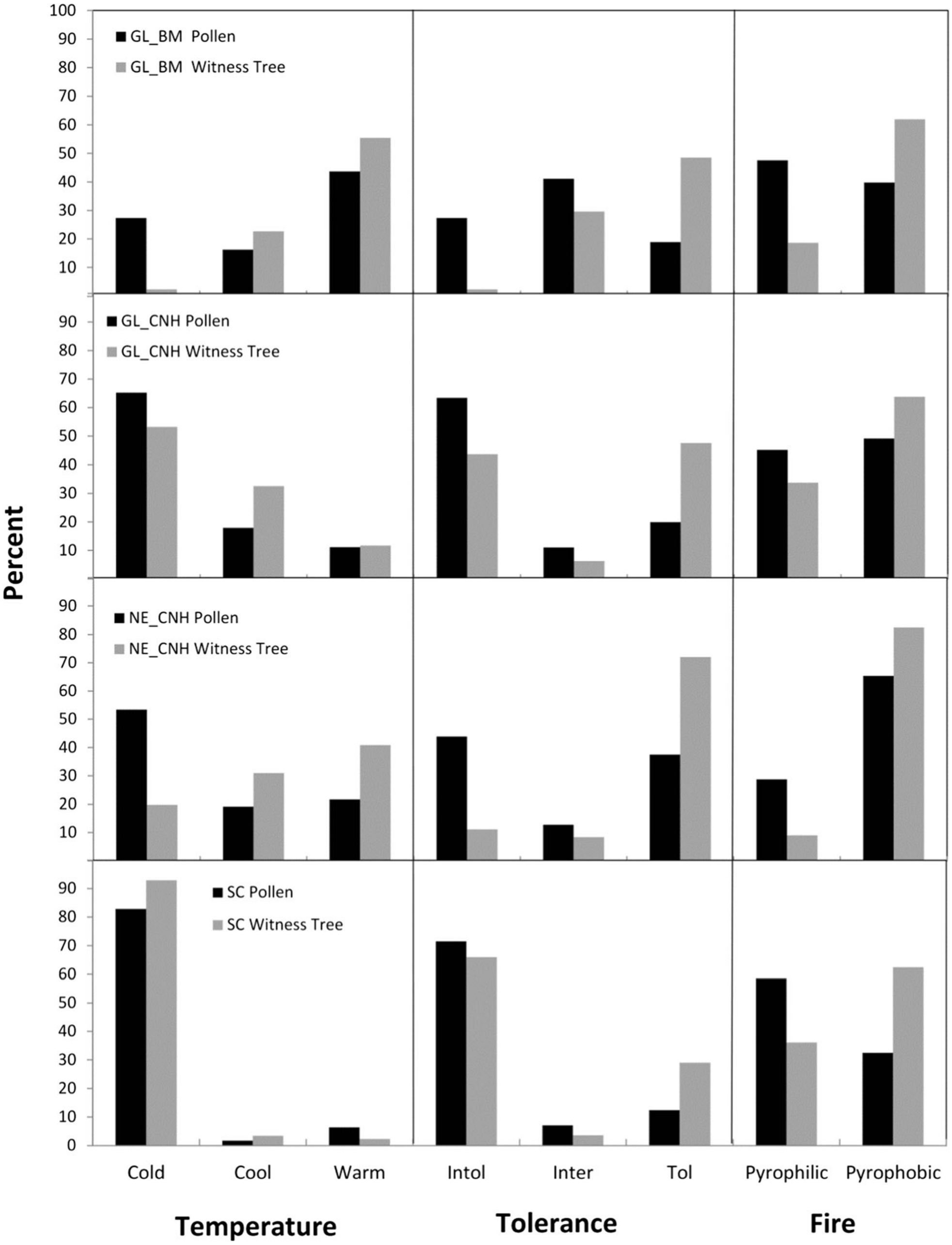


Fig. 3 Tree genera percentage in each of the ecophysiological classes for pollen versus witness tree data from forest biomes north of the tension zone line. Pyrophilic genera are also rated as drought tolerant; pyrophobic are drought intolerant (low to moderate)

pyrophobic trees. In protohistoric Northeast conifer-northern hardwoods, pollen data was dominated by cold-adapted, drought-intolerant pyrophobes that were evenly split between shade intolerant and tolerant trees. Witness trees had a higher proportion of cool- and warm-adapted, shade-tolerant pyrophobes. The sub-boreal forest was greatly dominated by cold-adapted, shade-intolerant trees with more drought-tolerant pyrophiles in the pollen data and more drought-intolerant pyrophobes in the witness tree data.

South of the TZL, pre-European Central oak-pine forests were composed mostly of warm-adapted, shade-intermediate, drought-tolerant pyrophiles, with a slightly higher proportion of cold and shade-intolerant trees in the pollen versus witness tree data (Fig. 4). The Great Lakes oak-pine forest too was dominated by warm-adapted, shade-intermediate, drought-tolerant pyrophiles in both datasets. The Northeast oak-pine forest had a fairly even distribution of tree species across all ecophysiological classes, but tended to be dominated by warm-adapted, shade-intermediate pyrophiles, more so in the witness tree record (Fig. 4). Pollen data had somewhat more cold-adapted, intolerant and drought-intolerant pyrophobic trees. Overall, forests south of the TZL contained a higher proportion of warm-adapted, shade-intermediate, drought-tolerant and pyrophilic trees prior to European settlement, whereas northern forests were dominated by cold-adapted, shade-intolerant species that were fairly evenly split between pyrophobes and pyrophiles. However, in the north, witness tree data consistently had higher values for shade-tolerant, drought-intolerant, and pyrophobic genera, which can be attributed to differential pollen production among genera.

Comparing mean pre- and post-European settlement changes in the transformed ecophysiology data, the Great Lakes beech-maple forests exhibited a decrease in warm-adapted, shade-tolerant, drought-intolerant pyrophobes in both data types (Table 6). Temporal changes in the Great Lakes conifer-northern hardwood forest included an increase in warm-adapted, shade- and drought-tolerant pyrophilic survey trees, whereas pollen data showed a decline in drought-tolerant pyrophilic trees and neutral shade tolerance changes. Northeast conifer-northern hardwoods had a decrease in warm-adapted, shade-tolerant trees and an increase in drought-tolerant pyrophiles in both datasets. The sub-boreal conifers exhibited an increase in cool and warm-adapted and shade-tolerant trees and a decline in drought-tolerant pyrophiles, the latter only in pollen data. South of the TZL, Central oak-pine forest type had a decline in warm, intolerant,

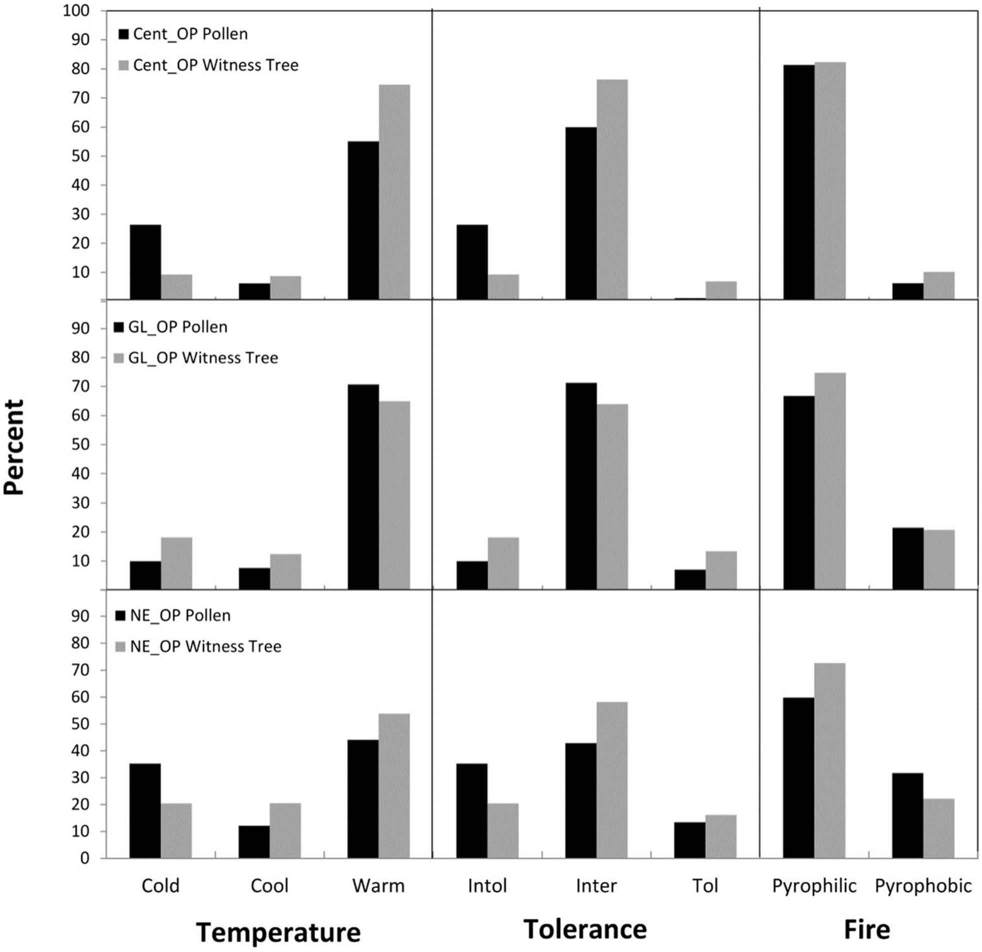


Fig. 4 Tree genera percentage in each of the ecophysiological classes for pollen versus witness tree data from forest biomes south of the tension zone line. Pyrophilic genera are also rated as drought tolerant; pyrophobic are drought intolerant (low to moderate)

Table 6 The mean percent change (as an absolute value) and the overall direction of change in the three ecophysiological classes (pyrogenicity and drought tolerance combined) from pre-European settlement to modern day in pollen and tree survey data for each forest type north ($n = 4$) and south ($n = 3$) of the tension zone line, including a grand mean for each biome. Forest type cells without an arrow had neutral changes for that parameter. See Table 1 for forest type abbreviations

North	GL_BM		GL_CNH		NE_CNH		SC		North average	
Absolute	Pollen	Tree survey	Pollen	Tree survey	Pollen	Tree survey	Pollen	Tree survey	Pollen	Tree survey
Temperature	4.07↓	8.13↓	2.16↑	4.24↑	4.47↓	11.81↓	4.74↑	8.44↑	3.86	8.16
Tolerance	4.07↓	12.97↓	4.07	12.97↑	7.46↓	10.07↓	4.81↑	11.65↑	5.10	11.91
Pyrogenicity/drought	2.55↑	8.55↑	3.09↓	4.79↑	2.95↑	9.79↑	3.34↓	1.62	2.98	6.19
South	Cent_OP			GL_OP		NE_OP			South average	
Absolute	Pollen	Tree survey		Pollen	Tree survey	Pollen	Tree survey		Pollen	Tree survey
Temperature	4.02↓	7.06↓		3.94↓	10.06↓	3.03↓	14.07↓		3.66	10.39
Tolerance	3.78↑	8.60↑		3.42↓	9.74↑	3.09↓	14.18↑		3.43	10.84
Pyrogenicity/drought	8.70↓	15.28↓		2.39↓	18.64↓	3.42	22.92↓		4.84	18.94

drought-tolerant/pyrophilic trees in both datasets (Table 6). In the Great Lakes oak-pine forest type, tree composition exhibited an overall decline in temperature and drought/fire adaptation and an increase in shade tolerance in the tree survey data. Ecophysiological changes in Northeast oak-pine forests varied between pollen and witness tree data, while both data types showed a general cooling of temperature adaptation they differed in the direction or lack of changes in shade and drought tolerance and pyrogenicity. Across all three ecophysiological classes, the magnitude of temporal change (as an absolute value) was significantly greater ($P < 0.001$) for tree surveys than for pollen data. The overall temporal change was also somewhat higher in southern versus northern forests (Table 6). In most cases, the direction of change was similar between pollen and witness tree data. Northern forests were highly variable in terms of temperature, tolerance, and pyrogenicity/drought changes, going up in two and down in two forest types. In contrast, southern forests exhibited an overall decline in temperature adaptation and drought/ pyrogenicity but were inconsistent in shade-tolerant changes. In five of seven forest types, aggregated tree genera registered temperature declines from past to present and moved in the opposite direction of the prevailing post-1820 warming (Table 6; Fig. 1).

Trends in standardized charcoal accumulation rates (the charcoal index) show different trajectories in biomass burning in the northern and southern zones of the eastern USA (Fig. 5). In the north, variations in standardized charcoal accumulation rates show relatively minor variations from 1 to 1750 AD, with the maximum occurring between 1 and 200 AD and the minimum occurring around 1200 AD. After European settlement, around 1750 AD, charcoal levels increased rapidly towards present. Confidence intervals in the most recent decades expand substantially from their previous range, indicating increased variability in the time series. In the southern zone, the charcoal records are much lower resolution (i.e., each sediment core was sampled less frequently than what is typical in the north), and as a result, there are less than one fifth of the samples than what is available in the north. Nevertheless, the combined data from the southern zone show a gradual upward trend from 1 to 1750 AD, with the minimum around 1 AD and the pre-European maximum around 700 AD. After 1750 AD, charcoal levels in the southern zone form a parabola, increasing rapidly, cresting around 1900, then declining thereafter. Taken as a whole (24 records; 2858 samples), the eastern US standardized charcoal index shows a flat trend, until the large increase in burning during the European settlement era. A decline in recent centuries is also evident in the south and the eastern USA as a whole. Population from the HYDE 3.1 database shows a gradual increase from 1 to 1500 AD. Population declines from 1500 to 1600 AD (consistent with the Native American pandemic), increases slightly from 1600 to 1700 AD, and shows a rapid increase subsequently towards present after European colonization. The initial increase in charcoal predated abrupt warming that started about 1820 (Figs. 1 and 5).

4 Discussion

The disparities of using pollen-based versus tree census data, and their inherent differences, in vegetation reconstruction have been previously recognized by paleoecologists (Dawson et al. 2016). Pollen data are parsed from accumulations of particulate matter cast from large catchments that collect incrementally over long-time periods. When considering species differences in pollen production, dissemination and preservation, differential rates of deposition and mixing of sediments over time, radiocarbon-dating uncertainties, and the segment sizes required to gain adequate pollen counts, it is not surprising that the resulting data are rather low spatiotemporal resolution (within-core samples often spanning multiple

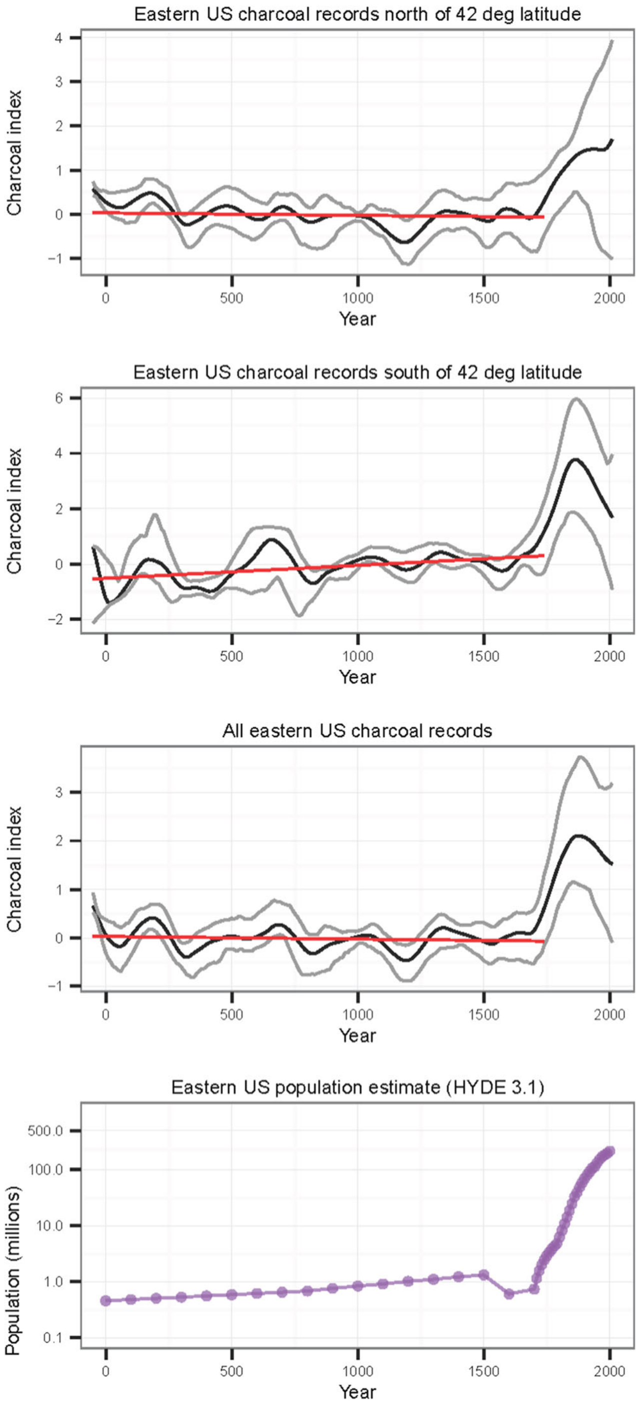


Fig. 5 Eastern North America biomass burning (charcoal index) trends for regions **a** north of tension zone line, **b** south of tension zone line, and **c** entire eastern USA, all smoothed with a 250-year (black) line and shown with 95% bootstrap confidence interval (gray lines) and a linear regression line for data between year 0 and 1700. Panel **d** is the estimated human population for the eastern USA from year 0 to 2000 (from the HYDE 3.1 global population dataset (Klein Goldewijk et al. 2011))

years representing hundreds of hectares of depositional input). Exceptions occur where varves exist in sediment samples. In contrast, survey or census data are obtained from the direct measure of living trees surrounding a specific point at a specific time, thus resulting in high spatiotemporal resolution. However, this method has its limitations as well. For instance, witness trees have their own set of species selection biases contingent on tree size, wood durability and commercial value, surveyor instructions and partialities, and ease of reach and scribing survey trees (Bourdo 1956; Whitney 1994; Black and Abrams 2001; Schulte and Mladenoff 2001). Despite their respective weaknesses, both data types are invaluable to the understanding of historical ecology, particularly when used in the proper context. This compilation adds to this discussion by quantifying the disparities among these two data types in forest reconstruction and tracking compositional change over time, with cautions and remedies.

Our reconstruction of forest composition from fossil pollen versus tree surveys revealed important similarities and differences between the two data types. The disparities can be largely explained by genera variations in pollen production and dispersal (Table 3). Almost universally, high-pollen producers (birch, pine, and oak) were over represented, intermediate pollen producers (beech, hemlock, and elm) were adequately represented, and low-pollen producers (fir, maple, and aspen) were underrepresented in pollen records relative to tree surveys. Discrepancies were most stark and numerous north of the TZL where low-pollen-producing genera (fir, maple, cedar, ash, larch, and aspen) were more abundant, and thus largely underrepresented in pollen records relative to other genera (Table 4). Indeed, the biggest disparity between the two data types existed in the Great Lakes beech-maple protohistoric forest, which was dominated by oak and pine as pollen versus beech and maple as witness trees (the later consistent with the forest type's namesake). Discrepancies were less apparent in oak-pine forests south of the TZL, having reasonably similar pollen and tree survey composition and dominance except for the high-pollen-producing birch. Paleoecologists have long recognized the incongruence between tree pollen counts and tree census data (Fagerlind 1952; Potzger et al. 1956; Davis and Goodlett 1960), and have made corresponding adjustments in their interpretation of forest composition and dominance, including pollen correction factors (Davis 1963; Andersen 1970; Prentice and Webb III 1986; Jackson and Williams 2004). We used correction factors to categorize pollen-to-tree census relationships (Table 7). Although correction factors seem like an attractive method to recalibrate pollen to better equate/correspond to tree census data, problems exist with that approach as (1) the relationship between vegetation and pollen percentage is not linear, (2) a linear correction factor assumes an intercept of zero (e.g., zero pollen percent = tree absence), and (3) the relationship between vegetation and pollen percentage is not constant across space or time (pers. comm, Dr. Samuel Munoz, November 26, 2014). However, correction factors are valuable in that they capture the magnitude of difference

Table 7 Correction factors by tree genera by individual study and summarized (averaged) by continent and for all studies. Pollen representation relative to tree census data were based on the following correction factor ranges: underrepresented > 1.25 (blue), representative = 0.75–1.25, and overrepresented < 0.75 (orange). Final genera designations of underrepresented, representative, or overrepresented were based on correction factors from all studies (last column)

Genus	Pollen Representation Relative to Tree-Census Data	Curtis (1959) [NA]	Davis (1963) [NA]	Andersen (1967) [Europe]	Janssen (1967) [NA]	Livingstone (1968) [NA]	Andersen (1970) [Europe]	Webb et al. (1981) [NA]	Bradshaw (1981) [Europe]	Heide and Bradshaw (1982) [NA]	European Studies	North American Studies	All Studies
Abies	Underrepresented	0.300	7.143		2.179	3.125	1.000	8.667		3.600	1.000	4.169	3.716
Acer	Underrepresented	12.600	5.263		10.794	5.263	2.000	10.000		4.489	2.000	8.068	7.201
Alnus	Overrepresented		0.048	0.500			0.250		1.111		0.620	0.048	0.477
Betula	Overrepresented	0.683	0.179	0.250	0.349	0.208	0.250	0.373	0.108	0.262	0.203	0.342	0.296
Carpinus	Overrepresented						0.330				0.330		0.330
Carya	Representative							1.389		0.667		1.028	1.028
Cupressaceae	Underrepresented							2.333				2.333	2.333
Fagus	Representative		0.667	1.000		1.075	1.000	1.500	1.111	2.154	1.037	1.349	1.215
Fraxinus	Underrepresented	NA	2.083	2.000	0.876	2.000	2.000	3.071	0.526	0.167	1.509	1.639	1.590
Juglans	Overrepresented							0.500				0.500	0.500
Larix	Underrepresented		120.482		131.250			5.500				85.744	85.744
Ostrya/ Carpinus	Underrepresented		2.326		2.398							2.362	2.362
Picea	Underrepresented	0.200	1.724		3.391	1.351	0.500	1.765		0.286	0.500	1.453	1.317
Pinus	Overrepresented	0.100	0.005		0.451	0.147	0.250	0.153	0.164	1.004	0.207	0.310	0.284
Populus	Underrepresented		25.641		23.333			16.375		2.154		16.876	16.876
Quercus	Overrepresented	NA	0.004	0.250	0.455	0.007	0.250	0.659	1.000	0.609	0.500	0.347	0.404
Salix	Overrepresented							0.182	1.111		1.111	0.182	0.646
Taxus	Overrepresented								0.769		0.769		0.769
Thuja	Underrepresented	NA	3.571							34.000		18.786	18.786
Tilia	Underrepresented	5.500	27.778	2.000	2.197		2.000	7.750		1.250	2.000	8.895	6.925
Tsuga	Representative	2.095	0.833			0.217		0.629		1.720		1.099	1.099
Ulmus	Overrepresented	0.250	0.909		0.839	0.038	0.500	1.271		0.125	0.500	0.572	0.562

(thus the scope of the problem) between pollen records and tree census data at the species/genera level. Palynologists are developing more robust and elaborate methods to close the gap between pollen and actual tree census data (Paciorek and McLachlan 2009; Sugita et al. 2006, 2010).

When evaluating temporal variation in forest composition and dominance, we found that the finer resolution of tree census data captured many important changes in genera abundance not seen in the pollen data. This included the well-documented declines in oak and chestnut and increases in maple census trees south of the TZL (Nowacki and Abrams 2008). North of the TZL, census trees routinely showed significant declines in beech and pine and increases in maple and aspen, changes that were only marginally evident in pollen data. While these compositional shifts make sense ecologically (see below), it is important to point out that witness tree surveys are very different in methodology and point location from current tree surveys. The greatest methodological departures occur in the far eastern portions of the USA (original 13 colonies) where metes-and-bounds surveys were conducted, and property corners were oftentimes marked by widely and irregularly spaced, single trees (Thomas-Van Gundy and Nowacki 2013). The General Land Office Survey (GLO), conducted from Ohio westward, generally recorded two to four witness trees at section and quarter-section corners and at river crossings ("meander posts") (Bourdo 1956; Whitney 1994; Black and Abrams 2001). The point-based tree data recorded by GLO surveys differ substantially from modern-day surveys (e.g., Forest Inventory and Analysis) which often use replicated fixed-area plots within forest stands. In contrast, tree variation in fossil pollen is recorded using a uniform analytical technique often from a single sediment core from a lake or bog, which minimizes spatial-temporal errors. Witness trees often only make up a small portion of any one forest or location, whereas paleoecological data are derived from a larger geographic catchment representing both local and regional vegetation (Jackson 1994; Fuller et al. 1998). However, individual witness tree warrants were often combined into connect drafts to increase number of survey trees and geographic area relative to a single tract of land. Nevertheless, when interpreting these types of data, one should be aware of the inherent differences among pollen, witness tree, and modern forest surveys.

Many palynological studies have reported substantial changes in forest composition from the pre-European settlement to present day. After European settlement, forests in the northeast had considerably less beech, chestnut, hickory, and hemlock and more birch, spruce, and fir (Russell and Davis

2001; Munoz et al. 2010). In this study, we also found that hemlock and beech pollen declined and that of birch increased in the Northeast conifer-northern hardwood forest. Former chestnut-hemlock forests in north-central Massachusetts are now dominated by oak as a result of human activity, including the introduction of chestnut blight (Fuller et al. 1998; Foster et al. 2002b). Following European settlement in New England, conifer-hardwood forests had declines in hemlock and beech and increases in white pine or pitch pine that invaded the open and abandoned forests (Parshall and Foster 2002). In our study, pine pollen dominated most forest types, but did not change significantly, likely reflecting its status as a high-pollen-producing species (Davis and Goodlett 1960). In southeastern New York, forests exhibited a decline in pine (mostly *Pinus strobus*) and an increase in birch and oak (Pederson et al. 2005). A substantial increase in yellow birch (*Betula alleghaniensis*) pollen during the late Holocene in the western Great Lakes region is attributed to a wetter climate (increased lake levels; Jackson and Booth 2002). In this study, birch pollen did not increase significantly following European settlement in the Great Lakes forests. A broad-scale study by Gajewski (1987) reported that hemlock and beech declined in northern New England while expanding in the Midwest over the past 500 years. This is consistent with the significant pollen declines in our Northeast conifer northern hardwoods, but we found no such increase of these genera in the Great Lakes beech-maple and conifer-northern hardwoods (spanning the Midwest). Davis et al. (1998) reported that former pine forests in northern Wisconsin and Michigan became dominated by hemlock and northern hardwoods in more recent years. Our Great Lakes-conifer-northern hardwood forests were dominated by these species (including birch), both pre- and post-European settlement, with pine and hemlock exhibiting non-significant declines.

Pollen records indicate that strong climate-vegetation relations existed prior to European arrival in certain segments of North America (Watts 1979; Shuman et al. 2004; Gill et al. 2009; Munoz et al. 2010). However, climatic controls of vegetation seemingly dissipated during the onset of European settlement, with humans (disturbance) becoming the primary driver of compositional change and leading to regional vegetation homogenization (Fuller et al. 1998; Foster et al. 1998). This post-European disruption of climate-vegetation relationships was recently corroborated in comparative tree survey data, whereby compositional changes have been attributed to changes in land use history rather than climate (Nowacki and Abrams 2015). The synchrony of European population expansion and Native American depopulation differed on the North American continent. Native American populations started declining from the very instant of European arrival driven largely by introduced diseases (Crosby 1976; Dobyns 1993). Starting along travel route of DeSoto's 1539–1542 expedition and from early settlements along the East Coast, an ensuing pandemic was unleashed, quickly sweeping across America along major travel corridors and decimating Native American populations throughout the sixteenth and seventeenth centuries (Richter 2001; Mann 2005). Coupled with intertribal conflicts and social upheavals, population reductions of 80–90% likely happened among Native Americans. In many locations, this "wave of death" preceded European settlement by a hundred years or more, especially west of the Appalachians.

Extensive settlement of the eastern USA was not complete until about 1850, effectively expanding westward from the East Coast (Hart and Buchanan 2012). Concurrent with European settlement, the exploitation of forests occurred at an ever-increasing pace until the early twentieth century (Whitney 1994; Abrams 2003; Nowacki and Abrams 2008; Rhemtulla et al. 2009). Most of the eastern seaboard and the Ohio Valley were already logged at least once by the mid-nineteenth century. By 1920, approximately 99% of the original forest was gone. Not only were the original forests cut, but there was a large loss of forest area to land clearing for agriculture during the nation-building period. The "Great Cutover" logged billions of board feet of timber in the eastern and western USA and produced vast areas covered in "slash" (logging debris; Whitney 1994; Abrams 2003; Nowacki and Abrams 2008). As the slash dried, huge wildfires followed, which burned with an intensity not experienced in the original forest (Pyne 1982; Fig. 2). These fires ushered in the fire suppression (Smokey Bear) era in the USA starting in the 1930s. The most noticeable feature of the 2000-year fire history here is a large increase in burning during the past ~ 300 years associated with European land clearance for agriculture. Biomass burning peaked between 1800 and 1900 AD based on historical records, followed by substantial declines after ca. 1940.

The charcoal index between 1 and 1750 AD in this study suggests stable levels of burning in the north and a slight increase in the south. It is interesting to note that southern forests exhibited a slight increase in burning associated with the Medieval Warm Period (ca. 950 to 1250 AD) but did not decline with the LIA (ca. 1350–1850; Mann et al. 2009). In northern forests, the charcoal index dipped between 1000 and 1200 AD and then increased at the start of the LIA, the opposite of what would be expected from climate control. However, the greater abundance of samples in the north makes north/south comparisons difficult. Munoz et al. (2010) reported a steep rise in burning after 1000 AD that continued through the LIA in the northeastern USA. A synthesis of pre-European fire return intervals for the eastern USA report a north to south trend, with generally longer fire frequency in the cool north (> 16 years) and shorter in the hot south (< 2 years; Guyette et al. 2012). A slight increase in fires in the southern zone prior to 1750 AD corresponds with a gradual increase in Native American populations estimated during that time, so the increased burning may have been due to a growing number of human-set fires.

Based on fire-scar data for the eastern USA, the major factors controlling late Holocene differences in fire regimes are human population density, culture, and annual drought (Guyette et al. 2006, 2012). For the period between 1650 and 1930, these authors report stable levels of burning in the Northeast and Midwest and increased burning in the Upper Lake States and Central Plains, with no decline as a result of the Little Ice Age. The fossil charcoal trend here also indicates that there was no significant decline in burning in either the northern or southern zone, which would be expected if changing Native American populations controlled charcoal levels. The absence of a decline is also somewhat surprising given that the general ubiquity of reduced biomass burning observed elsewhere in the Americas has a result of simultaneous depopulation and cooling climate (Power et al. 2012; Stambaugh et al. 2013). In southeast New York, for example, transitioning to the LIA resulted in pine forests converting to spruce and hemlock and a corresponding decline in paleocharcoal relative to during the Medieval Warm Period (Pederson et al. 2005). Variations in temperature or drought, however, are not a good explanation for the pre-European settlement increase in biomass burning in the southern zone because the paleoclimate data suggest that conditions became progressively cooler after 1100 AD (Fig. 1), which would not explain increased fires. This suggests a disconnect whereby human burning often trumped climate, even in the face of depopulation (Abrams and Nowacki 2015). Moreover, it has been argued that few people can be responsible for burning large areas (Kay 2007; Bond and Keeley 2005; Pinter et al. 2011). Climate warmed after 1600 before an abrupt decline in the early 1800s without much noticeable impact on charcoal abundance. This was followed by another period of accelerated warming after ca. 1840 that persists to the present day. The abrupt and sustained increase in charcoal starting in the early 1700s predates the latest warming phase but is highly consistent with the increase in human population and associated activities (cf. Parshall and Foster 2002; Munoz et al. 2010; Marlon et al. 2013). The large decrease in fire after 1940, mainly attributed to active fire suppression via the Smokey Bear campaign (Abrams 2010), occurred during a significant warming period and may represent another important fire-climate disconnect. However, the decline of burning may have been facilitated by lessening frequency and intensity of drought after 1930 (Fig. 1; McEwan et al. 2011). The impact of severe drought and drought lessening is apparently quite important in the ecological history of the eastern USA. In the Big Woods of Minnesota, a transition from savanna woodlands to closed deciduous forest has been attributed to early (ca. AD 1300) drought reducing fuels and the impact of fire (Shuman et al. 2009). Pulse of tree recruitment at the subcontinental scale during droughts of the late 1600s was severe enough to open large canopy gaps in the eastern broadleaf forests and impact forest composition (Pederson et al. 2014).

The resilience of eastern forests that followed the clearcut and catastrophic fire era, as indicated by the results of this study, reinforces the disturbance attributes for most of its species (Nowacki and Abrams 2008). Nevertheless, there was the near eradication of chestnut, which was once an associate of oak along the Appalachian Mountains from the chestnut blight (*Cryphonectria parasitica*; Whitney 1994). However, generally low levels of chestnut were recorded in the pollen and witness tree records in this study, and its relative pollen production is unknown (Table 2; Steve Jackson personal communication October 2014). It has been suggested that the abundance of chestnut might have been overemphasized in the past, especially at regional scales (Hanberry and Nowacki 2016).

We recorded a large decline in pine, hemlock, and larch (in the sub-boreal forest), called "deconiferization," which is attributed to intensive logging and their inability to reproduce sprout vegetatively (Abrams 2001; Nowacki and Abrams 2008). The Great Lakes region experienced a large increase in aspen, an aggressive pioneer tree species, as a direct result of clearcutting and burning the original conifer-northern hardwood forests (Nowacki and Abrams 2008). Large increases also occurred in maples, 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 and Abrams 2015). While evident in our witness tree data, the apparent lack of this response in pollen data is likely due to maple having low-pollen presence in sediment records (Prentice and Webb III 1986). Moreover, the paleochronologies used here had an average ending date of 1966 and thus often do not capture the last half-century of forest change.

The more aggressive of the maple species, particularly over the last 50 years, is red maple which is now a dominant tree over much of the eastern USA (Abrams 1998). The dramatic rise of red maple has been attributed to a suite of factors, including the extensive and repeated logging during the late nineteenth and early twentieth centuries, the loss of chestnut, the suppression of understory burning, and increased precipitation (Abrams 1992; Abrams 1998; Fei and Steiner 2007; McEwan et al. 2011). We can add increase in temperature as a driver for this warm-adapted maple as compared with sugar maple. The increase in red maple is believed to be one of several important factors responsible for oak decline in the eastern USA, which is mostly evident south of the TZL in this study. The coincidence of active fire suppression, a warming climate, and lessening of drought during the twentieth century make moisture attributions difficult. For example, there is little evidence in the paleoecology literature that maple (including red maple) significantly increased to become a forest dominant during past wet periods prior to twentieth century (Gajewski 1987; Russell et al. 1993; Foster et al. 2002; Pederson et al. 2005). In contrast, tree survey studies indicate that red maple responded quite quickly to fire suppression after 1940 (Larsen 1959; Lorimer 1984; Abrams 1992; Shumway et al. 2001). Following European settlement, the pollen and tree survey data used here revealed changes in the ecophysiological environment indicative of an overall cooling and loss of pyrogenicity and drought and increase in shade tolerance. This is consistent with a mesophication of forests in the eastern USA, which has been primarily attributed to the decline of burning after 1940 (Nowacki and Abrams 2008, 2015). The overall cooling is particularly noteworthy because forests are becoming more mesic despite general warming over the period of study.

In conclusion, paleoecological (pollen and charcoal), tree census, land use history, and climate data used in concert in this study provided a more robust interpretation of historical ecology than possible with only one data type by compensating for inherent weaknesses in each data type. The charcoal, human population, and climate data provided important support for the anthropogenic fire hypothesis over the last 2000 years in the eastern USA, including multiple instances of climate-fire disconnects that may be best explained by the role of human-caused burning.

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Data availability Raw data were generated in the lab of MDA. Derived data supporting the findings of this study are available from the corresponding author [MDA] on request.

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