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Source: The Journal of the Torrey Botanical Society, 149(2) : 101-121

Published By: Torrey Botanical Society

URL: https://doi.org/10.3159/TORREY-D-21-00024.1

Journal of the Torrey Botanical Society 149(2): 101–121, 2022.

Oak forests and woodlands as Indigenous landscapes in the Eastern United States

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Abstract. Land use by Indigenous people (Native Americans) and climate are primary factors affecting the dynamics of oak (*Quercus*) forests and woodlands in the eastern United States. Prior to Euro-American settlement, much of the eastern deciduous forest was dominated by oak species. The role of periodic surface burning, agriculture, and other forms of land management by Indigenous peoples is frequently noted by cultural anthropologists and historical ecologists. However, these points are often debated by paleoecologists and climate scientists. Here we present a literature review, synthesis, and data summary to investigate the role of altered land use, season of burning, and climate change in relation to pre– and post–Euro-American changes in forest composition. Human-based ignitions, as reflected by dormant-season fires, prevailed over the oak- and pine-dominated forests, with intermediate fire frequency during Indigenous periods. From the 18th century on, Euro-American populations rapidly expanded, impacting much of the eastern United States through extensive timber harvesting, land clearing, and severe fires. Starting in the 20th century, a variety of ecological influences, including agricultural land abandonment, chestnut blight, fire suppression, mesophication, and urbanization, resulted in dramatic vegetation changes in eastern landscapes. These trends have culminated in recruitment failures of most oak species on all but the most xeric sites and an increase in mid- to late-successional mesic hardwoods, most notably red maple (*Acer rubrum*), a species with very low density in our analysis of the witness tree record. We conclude that prescribed burning, agriculture, and other land uses by Indigenous peoples created a mosaicked landscape of expansive oak savannas, woodlands, and forests. A warming world over the past century should have promoted warm-adapted, fire-tolerant, xerophytic genera such as oak, hickory (*Carya*), and pine (*Pinus*) and grassland communities but instead have promoted the invasion by cool-adapted, fire-sensitive, mesophytic trees due to the absence of burning, much to the detriment of major vegetation biomes. Understanding that eastern oak and other pyrogenic ecosystems represent an Indigenous landscape strengthens our ability to best manage vegetation against the expansion of less desirable species and restore historic fire cycles through prescribed burning.

Key words: anthropology, fire, land use, Native Americans, paleoecology, *Quercus*, witness trees

Bormann and Likens (1979) compared changes in scientific thought to the "swinging pendulum of opinion." They point out that Clements's (1916) ideas of organismal succession and climatic climax theories dominated thinking during the early history of ecology in North America and then discuss the paradigm shift in response to Loucks's (1970) paper that reported the pervasive role of disturbance (specifically fire) in the sustainability of oak (*Quercus*) systems in Wisconsin. They argued that ecological thought had moved from considering the dominant role of climate to that of disturbance factors controlling vegetation development. Indeed, over the past 50 yr, ecologists have produced a vast number of scientific publications documenting the ubiquitous and recurring role of disturbance in vegetation communities around the world (White 1979; Bond *et al*. 2005; Bowman *et al*. 2011). These papers call into question the relative importance of climate in vegetation development and whether a self-perpetuating, stable end point of succession, a climax stage, is relevant for most vegetation types. However, Bormann and Likens (1979) caution that neither climate nor disturbance-based processes by themselves entirely control vegetation expression, as both factors, along with others, are important.

During the Holocene, vegetation in the eastern United States was shaped by a suite of global change phenomena. Influencing factors included rising and then oscillating temperatures; megafaunal extinction; an increasing population of Indigenous peoples followed by a sharp, pandemic-induced population collapse during the initiation and rapid expansion of Euro-American settlement;

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doi: 10.3159/TORREY-D-21-00024.1

Received for publication August 12, 2021, and in revised form October 19, 2021; first published December 14, 2021.

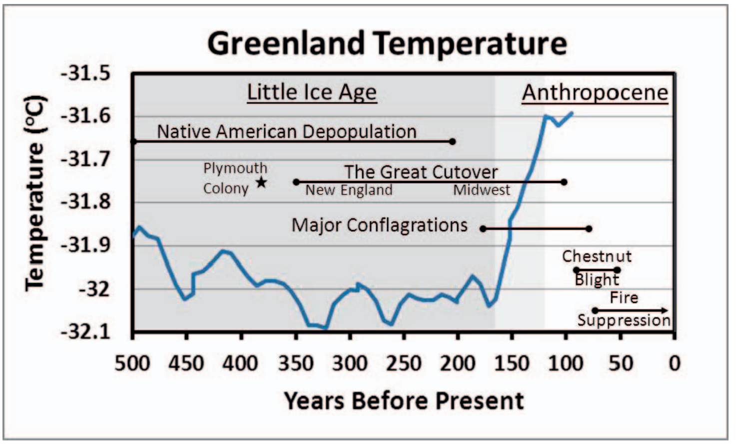

FIG. 1. Major ecological events affecting North American vegetation during the transition from the Little Ice Age to the Anthropocene superimposed on Greenland Ice Core Temperature (from Nowacki and Abrams 2015).

abrupt shifts and/or reversals in fire regimes; outbreaks of nonnative insects and disease directly affecting plants; and recent human-induced climate change (Whitney 1994; Munoz *et al*. 2010; Abrams and Nowacki 2015). During the 15th–19th centuries, the northern hemisphere was experiencing the Little Ice Age during the initial stages of European settlement (Fig. 1; Mann 2002). The Little Ice Age was followed by abrupt warming associated primarily with the end of a natural cooling period coupled with increased anthropogenic modifications to atmospheric chemistry (Intergovernmental Panel on Climate Change 2013). Human populations and their impacts on vegetation through land use have also changed appreciably during the late Holocene (Abrams and Nowacki 2008; Munoz *et al*. 2010; Nowacki *et al*. 2012).

Despite extensive research, we still have only a marginal agreement about the role of climate and disturbance and their interactions with vegetation dynamics, past and present, for most regions. The importance of climate *versus* human impacts on pre–Euro-American ecosystems in eastern North America is a highly debated issue (Abrams and Nowacki 2020; Oswald *et al*. 2020). One argument emphasizes the role of climate driving fire and vegetation dynamics, while 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; Nowacki and Abrams 2008, 2015). Thus, a more complete understanding of past human-fire-climate-vegetation dynamics and their anomalies is required. For this article, we reviewed and synthesized literature on the historical ecology of eastern oak ecosystems and season of burning, from which we conclude that these ecosystems can be best understood through the lens of Indigenous landscape management, principally fire, within the eastern climatic regions.

Paleocological and Archaeological Findings. 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; Patterson 2006). 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 scientists (Abrams and Nowacki 2008, 2015; Pinter *et al*. 2011, Marlon *et al*. 2013). Opinions differ about the roles and relative strength of climate *versus* human (anthropogenic) drivers of fire, including the Early Anthropocene burning hypothesis. This presents the possibility that the early human use of fire was profound, frequent, and prevalent, resulting in its becoming an early ecological driver despite relatively small populations in places (Ruddiman 2005; Abrams and Nowacki 2015). Other issues that need to be resolved are the extent of lightning as an ignition source and whether burning was localized or

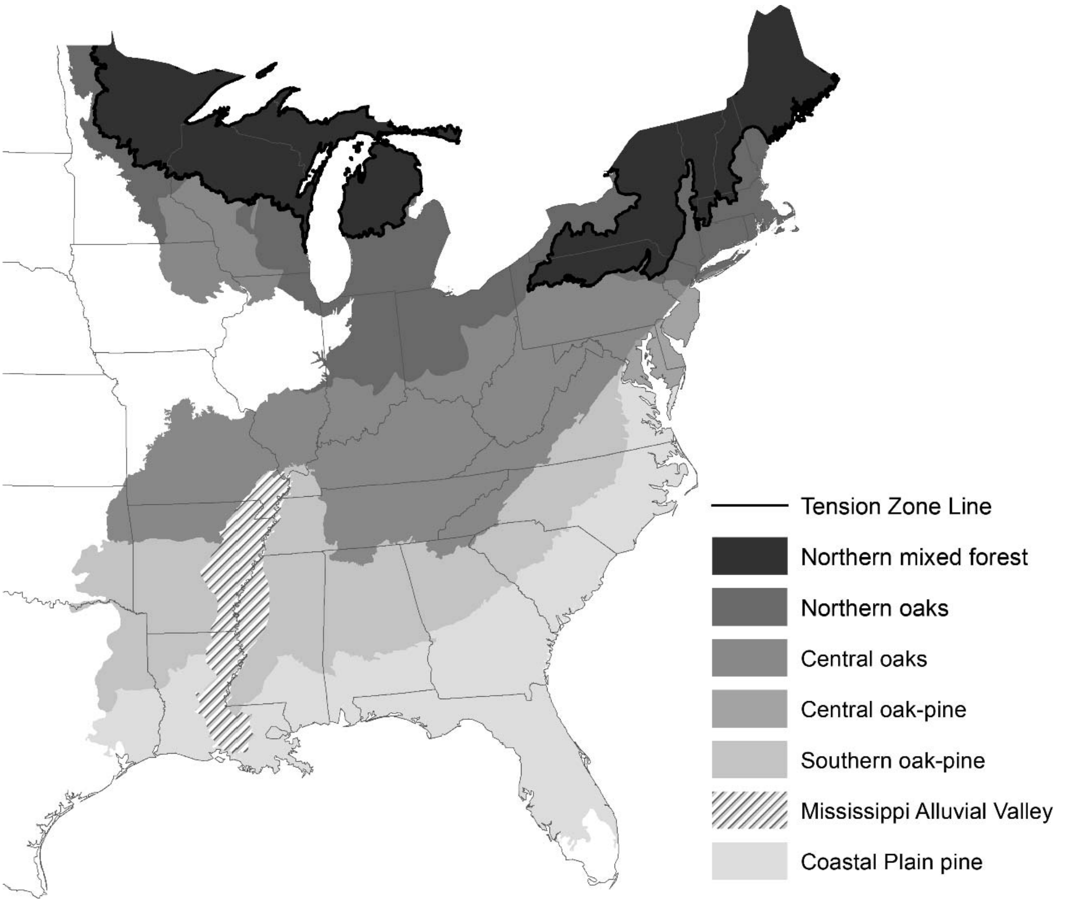

FIG. 2. Major forest types and the tension zone line (bold black line) between oak and pine forests, savannas, and woodlands, maintained by frequent surface fire, and northern mixed forests of the eastern United States. (Cleland *et al.* 2007, Hanberry and Nowacki 2016).

ubiquitous in various vegetation types in the eastern United States (Abrams and Nowacki 2008; Nowacki *et al*. 2012).

A tension zone divides the northeastern United States into two prominent forest regions: conifer-northern hardwoods to the north and oak-pine systems to the south (Cogbill 2000; Thomas-Van Gundy *et al*. 2015; Fig. 2; Table 1). Together with climate and soils, historical fire occurrence is presumed to have controlled the interface of these two major forest types. The pine component is part of a larger oak-dominated system that spans across the central portions of the eastern deciduous forest (Thompson *et al*. 2013; Hanberry and Nowacki 2016). In the region south of the tension zone, pine communities at the time of European settlement were restricted largely to predominantly infertile, glacial-derived sandy soils along the Atlantic coast or old, highly weathered, nonglaciated surfaces inland. Bromley (1935) noted the importance of pitch pine (*Pinus rigida*) plains on light, sandy soils in the original forests of southeastern Massachusetts, Cape Cod, and much of Long Island, New York. Indeed, oak, followed by pine, dominated the pollen profiles reported for this location by Oswald *et al*. (2020). Most forest ecologists believe that oak and pine are primarily light-demanding, disturbance-dependent genera that require frequent or periodic burning to sustain themselves over time (Bromley 1935; Abrams 1992, 2001). Due to their ecophysiological requirements, they would have been prevalent in more open conditions (savannas and woodlands) (Hanberry *et al*. 2018, 2020b) and only infrequent and transient members in relatively undisturbed, closed-canopy, old-growth forests as described by

Table 1. Percentages of major witness tree genera by region during the 1800s, based on averaging percentages of compiled studies by tree count and area (Hanberry and Nowacki 2016; Hanberry *et al.* 2019).

Genus	Conifer-northern hardwoods	Central and northern oak	Southern oak-pine	Southern pine
Abies	3.7	< 1	< 1	< 1
Acer	10.7	6.7	< 1	< 1
Betula	10.8	2.0	< 1	< 1
Carya	< 1	4.7	9.4	< 1
Castanea	< 1	2.1	2.2	< 1
Cornus	< 1	< 1	1.8	< 1
Fagus	9.8	6.2	< 1	< 1
Fraxinus	2.1	2.5	< 1	< 1
Larix	9.7	< 1	< 1	< 1
Liquidambar	< 1	< 1	1.1	< 1
Liriodendron	< 1	< 1	1.0	< 1
Nyssa	< 1	< 1	1.7	< 1
Persea/*Gordonia*/*Magnolia*	< 1	< 1	< 1	3.4
Picea	7.1	1.6	< 1	< 1
Pinus	15.6	5.1	31.2	75.9
Populus	5.1	2.1	< 1	< 1
Quercus	4.6	52.6	43.8	9.5
Thuja	6.1	< 1	< 1	< 1
Tsuga	9.5	2.3	< 1	< 1
Ulmus	1.7	3.0	< 1	< 1

Oswald *et al.* (2020). These expressed old-growth forest conditions are more indicative of shade-tolerant, late-successional, conifer-northern hardwood dominated by hemlock (*Tsuga*), maple (*Acer*), and beech (*Fagus*) north of the tension zone. Seemingly, the imposition of northern hardwood dynamics (wind-based, gap-phase dynamics) onto oak-pine systems without incorporating disturbance by frequent fire is common in ecology and does not allow the true driving factors of the latter to be recognized, appreciated, and incorporated into management action (Nowacki and Abrams 2015).

Many early colonists of southern New England describe open, parklike forests because of Native American burning and vegetation management (Bromley 1935). Keep in mind that this and other early observations occurred during a pandemic and forced westward relocation that profoundly and negatively disrupted Native American populations and societies (Richter 2001). Whitney (1994) reviewed the credible eyewitness accounts of Native American burning in northeastern forests and concluded that their cumulative impact was substantial. In areas of the eastern United States where General Land Office historical tree surveys are available, it is possible to calculate tree density of pre–Euro-American settlement forests based on point-center quarter sampling. These studies report the low-density, open nature of most presettlement forests and significant increase in tree density in modern-day forests, which is attributed to exclusion of fire in the mid-1900s (Fralish *et al.* 1991; Nowacki and Abrams 2008; Hanberry and Abrams 2018).

Human presence dates back at least 15,000 years BP in the Americas (Braje *et al.* 2017), and their effects on ecosystems were immediate through the mass killing and eventual extirpation of megafauna. By deploying a combination of forces, some of which were new (weapons and dogs), these first arrivals proved fatal on a naive prey base (Nowacki *et al.* 2012). The enormity of this mass extinction event is staggering, with 34 megafaunal genera going extinct in North America, including all mammals > 1,000 kg and two mammalian orders (*Perissodactyla* and *Proboscidea*) eliminated (Koch and Barnosky 2006). Changes in principal disturbance agents from megaherbivores to human fire were practically seamless in North America, with the importance of fire (as measured in charcoal) increasing proportionally with megafauna decrease (measured in dung fungal spores; Gill *et al.* 2009). The switch to fire may have substantially lessened the ecological changes expected from megaherbivore loss since fire can be considered a "herbivore" of sorts (consuming vegetation *via* flame instead of by mouth; see Bond and Keeley 2005). For instance, herbivory and fire are analogous in that both are strong vegetation regulators, promoting open conditions (grasslands, shrublands, and savannas) and early-successional plants at the expense of closed-canopy forests and late-successional plants. However, fire differs from herbivory in several important aspects. First, herbivory selects against highly edible/digestible plants within certain height windows (animal reach), whereas fire indiscriminately consumes dead and living material (regardless of protein value) at all heights from ground to treetop provided there is flame access (Bond and Keeley 2005). Nutrient cycling obviously differs contingent on the digested remains (ashes *vs*. dung). Finally, herbivory promotes inedible and/or highly defended plants through avoidance, whereas fire promotes plants with specific physiological traits (*e.g*., thick bark, sprouting, cone serotiny, and smoke-induced germination). Altogether, the cascade from megaherbivory to a human-based fire regime led to unique developmental pathways and plant communities during the Holocene. Two different mechanisms operated in tandem, thus (a) allowing formerly herbivory-suppressed plants to rebound (*i.e*., relaxation) while (b) promoting fire-adaptive plants (Gill *et al*. 2009).

It is at this time, when principal disturbance agents shifted from megaherbivores to human-based fire, that Indigenous peoples became a "keystone species," managing the land for optimal food resources (Abrams and Nowacki 2008). Indigenous peoples profoundly influenced vegetation not only *via* burning but also through land clearing for settlements and agriculture (Nowacki *et al*. 2012). Review articles by Abrams (2002) and Lorimer and White (2003) remarked how stable oak has been over the past 9,000 yr in the eastern forests and that paleocharcoal was abundant in most oak sites prior to Euro-American settlement. Paleoecologists have frequently included charcoal measurements in sediment analyses since the 1970s (Swain 1973). The long-term sustainability of oak and/or pine systems has been attributed to Native American burning (Gleason 1913; Cottam 1949; Pyne 1983). A widespread conversion from mainly open woodlands to closed-canopy oak forests occurred after the cessation of Indigenous burning following Euro-American settlement. Delcourt and Delcourt (1997) argued that human cultural evolution has resulted in the transformation of much of the southeastern United States from natural to cultural landscapes over the past 5,000 yr. Population estimates for Indigenous peoples increased from less than 100,000 at 12,000 BP to 3.2 million by 250 BP, with Native American depopulation from the mid-1500s to 1800 following Euro-American colonization (Hart and Buchanan 2012; Marlon *et al*. 2013).

In paleochronologies of 2,500 to 3,500 yr for the influence of fire on oak, chestnut, and pine forests in north-central Massachusetts, Foster *et al*. (2002) concluded that "fire was an important but varying force shaping vegetation patterns at the regional, landscape and stand scale in central New England. Given that fire ignitions are inferred to be largely anthropogenic in origins this also implies that the New England landscape must be considered controlled, at least in part, by cultural, as well as natural and environmental factors over past millennia." In Deep Pond located in Suffolk County, Long Island, New York, oak and pine forests were sustained for 2,180 yr with moderately high fire activity (Patterson 2006), hardly a signature from mainly lightning-strike ignitions. Frequent Indigenous burning on the island of Martha's Vineyard, Massachusetts, may have been responsible for the coincidence of high charcoal values and high oak and grass pollen percentages. Abundant charcoal with abundant oak and grass pollen was also found in postsettlement sediments. Parshall and Foster (2002) reported that presettlement fires were clearly most common in the pitch pine-oak forests along the warmer New England coastal region, especially on the outwash plains of Cape Cod, Martha's Vineyard, and Long Island. Pitch pine is shade intolerant and does not regenerate well under shade and in thick leaf litter, so fires of all intensities can encourage stand establishment. However, they concluded that while Indigenous populations were higher along the coast of New England, the high occurrence of fires in pitch pine and oak forests in these locations can be explained by the climatic, edaphic, and fuel conditions without attributing a higher incidence of burning by people. They do not explain the ignition source for these coastal fires.

Fires in oak forests are typically low- to moderate-intensity understory burns, and the signatures of charcoal produced from such events may be hard to detect or erode in the sedimentary record (Abrams and Seischab 1997). Therefore, sediment cores may provide accurate records of only intense and/or high-magnitude fire events (Stocks and Kauffman 1997; Hart and Buchanan 2012; Abrams and Nowacki 2020). Indeed, a comparative study at the same site concluded that many fires recorded in the fire-scar record did not appear in the paleoecological record (Whitlock *et al*. 2004). Nevertheless, there is abundant sediment charcoal evidence in the paleoecological literature indicative of extensive fires throughout much of the eastern United States during the Holocene. Using data from a network of sites throughout the eastern United States, Power *et al*. (2008) reported that paleocharcoal increased from 14,000 to 9,000 BP and then remained fairly constant during the remainder of the Holocene.

In the cool and humid Northeast, a region not particularly conducive to fire, strong linkage exists between the distribution of fire-adapted oak (with high-sediment charcoal) and Native villages and associated activities (Fuller *et al*. 1998). A 3,500-yr history of oak and (formerly) chestnut in north-central Massachusetts reported high charcoal values indicative of forest fires (Foster *et al*. 2002). A paleoecological study of the Hudson Highlands in southeastern New York revealed that high oak pollen percentages were associated with continuous charcoal influx during the Holocene (Maenza-Gmelch 1997). During the Medieval Climatic Optimum (1,100–700 BP), pine and oak dominance was associated with high charcoal in the Hudson Valley of New York (Pederson *et al*. 2005). Subsequent cooling during the Little Ice Age was associated with decreased pine and charcoal, increased birch, but stable levels of oak. Analysis of sediment pollen and charcoal evidence from the past 2,000 yr for conifer-northern hardwood forests across a longitudinal gradient in the northeast and north-central United States and southern Ontario reveal oak incursions with increased fire (Clark and Royall 1996). The most western forests in Minnesota and Wisconsin were dominated by oak, birch, and pine, and evidence of past fires was most abundant in these forests. Farther east, the sites were increasingly dominated by beech, hemlock, yellow birch, and spruce, and amounts of sediment charcoal decreased. Clark and Royall (1995) reported on the transformation of northern hardwood (beech-maple) forests to white pine-oak forests in response to Iroquois cultivation and burning during the 1400s at Crawford Lake in southern Ontario, Canada. Indeed, based on paleocharcoal data, the occurrence of fire was unusually high for this cool, wet period.

Paleoecological investigations in eastern Tennessee and North Carolina revealed that oak and pine dominated during the past 1,500 to 4,000 yr (Delcourt 1987; Delcourt and Delcourt 1997). Charcoal influx was continuous during the period and increased from past to present in response to increasing human populations. A study using soil charcoal in southern Appalachian forests indicated that fires occurred regularly over the past 4,000 yr, peaked at 1,000 BP with the appearance of Woodland Tradition Indigenous peoples, and occurred across the range of dry oak-pine–dominated ridges to mesic hardwood forest (Fesenmyer and Christensen 2010). In addition, these authors report only one fire record between 10,570 and 4,000 BP. Considering the oak and pine dominance in this region dates back 5,000–10,000 BP, this suggests that the evidence of earlier fires eroded over time. However, soil charcoal dating to 6,735 BP was reported for the Cumberland Plateau of Tennessee (Hart *et al*. 2008).

Charcoal amount was also influenced by landform and climate. A paleoecological study of the eastern Highland Rim and adjacent Cumberland Plateau of Tennessee documented that pine and spruce forest converted to oak domination about 15,000 to 12,000 BP (Delcourt 1979). Oak dominance, followed by ash and hickory, persisted for the remainder of the Holocene, including further increases in oak after 5,000 BP. On the Allegheny Plateau of Maryland, spruce and pine forests at the beginning of the Holocene gave way to pine-oak (5,000 BP) and then oak-chestnut forests (2,000 BP) (Maxwell and Davis 1972). A study of sites ranging from Maine to Virginia reported the occurrence of fire on drier upland and coastal plain sites dominated by oak and pine dating back to 6,000 BP, although some sites lacked substantial fire evidence (Patterson 2006). Charcoal levels were lower on more mesic sites but were more elevated on almost all sites after Euro-American settlement. A synthesis of sedimentary charcoal records for the northeastern United States and eastern Canada reported peak charcoal around 9,500 BP, a large decline until 6,500 BP, and an increase to the present day (Marlon *et al*. 2013). In the central United States, charcoal levels were low at the beginning of the Holocene, peaked at about 3,500 BP, and then declined to the present day. As mentioned previously, oak dominance in Indiana started about 10,500 BP, associated with a large increase in charcoal levels after megafaunal extinction (Gill *et al*. 2009).

Evidence for Indigenous Burning and Land Use. A diverse array of studies demonstrate the long-term interconnectedness of prehistoric human cultures and the ecosystems they inhabited throughout the eastern United States (reviewed in Delcourt and Delcourt 2004; Abrams and Nowacki 2008). In the Northeast, there was a divergence in human-environment relations in that the Indigenous populations of northern New England were mostly nonagricultural hunters and gatherers (including fishing) due to unfavorable climate and poor soils, while populations to the south practiced extensive agriculture (Cronon 1983). Patterson and Sassaman (1988) concluded that there were significant burning and agricultural fields near protohistoric Native American settlements and that a high density of Native populations existed in the coastal area of southern New England and Long Island. In a study of regional forest dynamics in north-central Massachusetts, Foster *et al*. (1998) reported that "prehistorical Indian activity in the region had adopted maize agriculture by approximately 1,200 BP and were utilizing a mixture of hunting, food gathering, and small-scale agriculture at the time of European contact." One potential broad-scale Native impact was the use of fire to clear settlements, to maintain fields, and to improve wildlife habitat. Paleoecological data from Massachusetts indicate that Indigenous populations were greater and that fire was more frequent and/or intense at lower elevations, maintaining high abundances of oak (Fuller *et al*. 1998). For a study of many sites in the northeastern United States, Munoz *et al*. (2010) reported that prior to Euro-American settlement, human population level increased in response to the widespread adoption of maize agriculture during the late Woodland period. Despite this evidence, paleoecologists have equivocated that "during times when Native populations were relatively high, we found no evidence for forest clearance, elevated use of fire, or widespread agriculture" (Oswald *et al*. 2020).

Human-facilitated tree dispersal has been recognized prior to European arrival on the North American continent based on a variety of data sources. For instance, the anomalous northward expansion of warm-based American chestnut (*Castanea dentata*) during the Neoglacial Cooling period was documented through pollen records (Russell 1987), which corresponded to archaeological evidence of seed movement of valued trees by Indigenous peoples (Snow 1980). A similar northward expansion of pecan (*Carya illinoinensis*) by human vectors is suspected in the Midwest (Bettis *et al*. 1990), undoubtedly due to its high food value by Indigenous peoples (Hall 2000). By combining Native American variables with original land survey records, Tulowiecki and Larson (2015) found that Native American variables significantly improved the predictive performance of species distribution models for mast-bearing American chestnut, oak, and hickory. Comparable positive associations to Indigenous settlement and land use were found in northwestern Pennsylvania, a strong indication that Indigenous peoples actively selected for these disturbance-adapted genera (Black *et al*. 2006). Molecular genetics applied to pawpaw (*Asimina triloba*), producer of the largest edible fruit of any North American tree, suggests that Indigenous peoples played an important role in long-distance dispersal, extending its distribution beyond the southern limits of the Laurentide Ice Sheet (Wyatt *et al*. 2021). At the community level, the existence of certain vegetation types has been ascribed to Indigenous people, particularly oak savannas occurring in locations where mesic hardwoods should have otherwise prevailed in northeastern Wisconsin (Dorney and Dorney 1989). Similarly, by including Native Americans as a variable (rather than just using environmental variables), model improvements of the spatial distribution of oak savannas in western New York led Tulowiecki *et al*. (2020) to conclude that former oak savannas can be attributed largely to Indigenous land use. In stepwise fashion, these studies linking Indigenous activity to local vegetation expression can serve as a basis to project early human influences at even larger "ecoregional" scales across eastern North America (Abrams and Nowacki 2008; Nowacki and Abrams 2015).

Fire Scars. Modern-day lightning-strike density does not adequately explain the predominance and persistence of fire-adapted oak-pine systems. Lightning-strike density is relatively low over most of the eastern United States, and when strikes do occur, they are normally associated with rain events. In contrast, lightning-strike density is quite high in southern coastal regions, concentrated in the states of Georgia and Florida (Abrams and Nowacki 2008; Holle and Brooks 2019). However, lightning storms are restricted largely to the summer growing season, when humidity is high and vegetation flammability is low. To help distinguish between natural "lightning" and human-based ignitions, fire-scar data can be implemented where seasonality has been recorded.

The importance of Indigenous ignitions is reflected in fire-scar data across the eastern United States (Table 2). Differentiating between Indigenous *versus* natural (lightning) ignitions proves difficult due to inherent overlap; the former take place year-round, whereas the latter are restricted largely to summer thunderstorms, which is further confounded by differing season lengths due to latitude (longer south, shorter north). As such, dormant-season fires can be confidently attributed to Indigenous ignitions, whereas growing-season fires could be either natural or Indigenous. Thus, even though Indigenous burns would be underrepresented, comparing dormant- to growing-season burns serves as a conservative way to estimate the importance of Indigenous ignitions relative to natural ignitions. These comparative estimates can be derived only from fire-scar data sets that include seasonality (Table 2). Fire seasonality is determined by examining fire scars relative to their tree-ring position, with dormant-season fires being recorded between annual tree rings and growing-season fires occurring during active tree-ring formation.

In the Northeast, dormant-season fires far outnumbered growing-season fires, representing 33–88% of all fire scars. These percentages and the margins of difference between dormant- and growing-season burns would be sizably greater if fires with undetermined seasonality were removed. Mean fire intervals (MFIs) ranged from 1.8 to 20.0 yr across all time periods. The Northeast, where the European-based "wave of fire" was first recognized (Stambaugh *et al*. 2018), was supported by shorter MFIs after European settlement (Table 2). Coincidentally, consistent with increasing human-based fire, the percentage of dormant-season fires rose during the European settlement period.

In the central and southern Appalachians, dormant-season fires were demonstrably more common than growing-season fires, reaching 100% in places (Table 2). Mean fire intervals were short throughout this region, ranging from 1.9 to 13.1 yr. And, where reported, the wave of fire associated with European settlement was evident, displaying a U-shaped MFI trend from pre-European through European settlement to fire suppression eras (LaForest 2012; Stambaugh *et al*. 2020). Similar fire demographics were found in the adjacent Central Hardwoods, with the predominance of dormant-season fires and short MFIs ranging from 1.5 to 16 yr. The wave of European settlement fire (shorter MFIs) was evident on all but two sites (Saltwell Hollow and Lemm Swamp, Tennessee; Stambaugh *et al*. 2016), the latter oddly showing the reverse trend. The northern pines of the Midwest were characterized by dormant-season burns (four of five sites) and short MRIs of 6.3–20 yr.

The Southeast has the highest frequency of lightning strikes in the United States, and that was reflected in fire-scar seasonality (Table 2). Here, growing-season fires surpassed dormant-season fires in many cases. Again, since Indigenous-set fires can occur throughout the year, a portion of growing-season fires may in fact be attributed to humans but undeterminable. Mean fire intervals were short, ranging from 1.8 to 9.0 yr, the longer MFIs associated with recent fire suppression (Huffman 2006; White and Harley 2016). It should be noted that in the Southeast, biannual fires have been documented and may been prevalent in the past (Stambaugh *et al*. 2011a).

Dormant-season burning prevailed throughout the south-central states of Oklahoma and Texas across all time periods. The reduction and elevation of MFIs were evident at many sites across time. Consistent hallmarks of the European-based "wave of fire" followed by fire suppression occurred throughout the eastern United States (Table 2).

In summary, human-based ignitions, as reflected by dormant-season fires, prevailed over the oak- and pine-dominated portions of the eastern United States, with intermediate MFIs during Indigenous periods, the shortest MFIs during European settlement, and the longest MFIs during recent fire suppression. Even though fire occurrence is associated with drought, as often reported (including Oswald *et al*. 2020), the fire-scar record indicates that drought-induced fires are not fully realized without broad-scale human ignitions (Guyette *et al*. 2006). Pyne (1984) concluded that lightning produced a small proportion of the ignitions in the Northeast. The low occurrence of lightning across the East is inconsistent with the existence of vast fire-based vegetation formations and suggests that Native American ignitions were highly important (Abrams and Nowacki 2008, 2015).

Table 2. Literature documenting fire-scar seasonality and mean fire intervals by region. NR = Not Reported.

Site and state	Forest type	Citation	Time period	Dormant season (%)	Growing season (%)	Undetermined (%)	Mean fire interval (yr)
Northeast							
Baxter Mountain, Adirondack Mountains, NY	Pine	Abadir *et al*. 2019	1689–1997	34	23	43	16.2
Potter Mountain, Adirondack Mountains, NY	Pine	Abadir *et al*. 2019	1611–2014	39	10	51	20.0
Long Branch Hill, PA	Oak-pine	Brose *et al*. 2013	1630–2010	72	28	0	19.4
Slate Run, PA	Oak-pine	Brose *et al*. 2013	1620–2010	88	8	4	14.0
Upper Dry Run, PA	Oak-pine	Brose *et al*. 2013	1630–2010	50	50	0	10.9
PA	Oak-pine	Stambaugh *et al*. 2018	Pre-European settlement (1592–1819)	60	24	16	6.2–17.8
			Post-European settlement (1755–1914)	73	9	18	3.2–6.3
SGL088, Juniata and Perry counties, PA	Pine	Marschall *et al*. 2016	Pre-European settlement (1663–1754)	53	5	43	5.6
			Post-European settlement (1755–1914)	58	0	42	4.2
SGL107, Juniata County, PA	Pine	Marschall *et al*. 2016	Pre-European settlement (1644–1754)	33	5	62	12.0
			Post-European settlement (1755–1914)	57	3	41	4.0
Tioga, PA	Oak-pine	Marschall *et al*. 2019	Pre-European settlement (1620–1794)	60	3	37	4.1
			Post-European settlement (1795–1914)	63	3	34	1.8
Central and southern Appalachians							
Brymer Mountain, AL	Pine	Guyette *et al*. 2010	1550–1940	92	7	1	2.6–2.7
Choccolocco Mountain, AL	Pine	Guyette *et al*. 2010	1547–2006	97	3	1	2.5–3.2
Johns Mountain Wildlife Mgmt. Area, GA	Oak-pine	Stambaugh *et al*. 2020	Pre-European settlement (1673–1834)	100	0	0	5.3
			European settlement (1834–1935)	83	17	0	2.3
			Fire exclusion (1935–1979)	100	0	0	6.0
Savage River State Forest, MD	Oak	Shumway *et al*. 2001	1589–1992	91	9	0	7.6
Linville Mountain, NC	Oak-pine	Flatley *et al*. 2015	1701–2009	56	19	25	4.0–13.1
House Mountain, TN	Oak-pine	Flatley *et al*. 2013	1742–2009	59	19	22	2.6–9.8
Licklog Ridge, TN	Oak-pine	Flatley *et al*. 2015	1723–2009	68	7	25	2.2–9.1
Gold Mine Trail, TN	Oak-pine	LaForest 2012	Pre-European settlement (1684–1834)	67	NR	NR	11.6
			European settlement (1835–1934)	61	NR	NR	1.9
			Fire suppression (1935–2007)	40	NR	NR	8.8
Rabbit Creek, TN	Oak-pine	LaForest 2012	Pre-European settlement (1700–1834)	88	NR	NR	7.9
			European settlement (1835–1934)	84	NR	NR	1.9
			Fire suppression (1935–2008)	63	NR	NR	8.1
Pine Mountain Trail, TN	Oak-pine	LaForest 2012	Pre-European settlement (1710–1834)	83	NR	NR	10.3
			European settlement (1835–1934)	84	NR	NR	2.3
			Fire suppression (1935–2007)	44	NR	NR	6.7
Reddish Knob, VA	Oak-pine	Aldrich *et al*. 2014	1671–1913	57	44	0	4.6–12.5
Kelly Mountain, VA	Oak-pine	Aldrich *et al*. 2014	1638–1921	86	14	0	3.7–7.8
Peters Mountain, VA	Oak-pine	Hoss *et al*. 2008	1867–1976	94	6	0	2.5

Table 2. Continued.

Site and state	Forest type	Citation	Time period	Dormant season (%)	Growing season (%)	Undetermined (%)	Mean fire interval (yr)
Mill Mountain, VA	Oak-pine	Aldrich *et al*. 2010	1704–2003	90	10	0	5.4
Brush Mountain, VA	Oak-pine	DeWeese 2007	1732–2002	90	10	0	4.1
Griffith Knob, VA	Oak-pine	DeWeese 2007	1750–2004	72	28	0	2.3
Little Walker Mountain, VA	Oak-pine	DeWeese 2007	1694–2004	79	21	0	2.8
North Mountain, VA	Oak-pine	DeWeese 2007	1736–2003	84	16	0	3.2
Pike Knob Preserve, WV	Oak-pine	Hessl *et al*. 2011	1770–2010	74	26	0	8.6
New River Gorge National River, WV	Oak-pine	Maxwell and Hicks 2010	1898–2005	100	0	0	4.0
Central hardwoods							
Nye Cabin, IA	Oak	Guyette *et al*. 2010	1699–1860	85	NR	NR	5.0
Kankakee Sands, IL	Oak	Considine *et al*. 2013	1930–2007	54	38	8	1.5–2.3
Angel Hollow, KY	Oak-pine	Stambaugh *et al*. 2020	Pre-European settlement (1740–1834)	33	67	0	5.0
			European settlement (1834–1935)	85	15	0	3.8
Land Between the Lakes, KY	Oak	Guyette *et al*. 2010	1688–2005	100	0	0	5.2
Pine Camp, KY	Pine	Guyette *et al*. 2010	1790–2005	96	4	0	5.0
Allegheny/Cumberland Plateaus, OH and KY	Oak	McEwan *et al*. 2007	1870–1940	84	16	0	2–16
Vinton County, OH	Oak	Sutherland 1997	Post-European settlement (1856 onward)	69	31	0	5.4
Ohio Hills, OH	Oak	Hutchinson *et al*. 2008	1870–1933	93	7	0	9–14.5
Savage Gulf State Natural Area, TN	Oak-pine	Stambaugh *et al*. 2020	Pre-European settlement (1659–1834)	92	8	0	4.4
			European settlement (1834–1935)	71	29	0	2.5
			Fire exclusion (1935–2018)	22	78	0	13.7
Huckleberry Ridge, TN	Oak	Stambaugh *et al*. 2016	Pre-European settlement (1721–1834)	100	0	0	3.3
			European settlement (1834–1926)	99	1	0	2.5
			Military use (1926–2003)	100	0	0	NR
Rowland Creek Headwaters, TN	Oak	Stambaugh *et al*. 2016	Pre-European settlement (1727–1834)	100	0	0	3.9
			European settlement (1834–1926)	100	0	0	3.2
			Military use (1926–2003)	100	0	0	10.3
Saltwell Hollow, TN	Oak	Stambaugh *et al*. 2016	Pre-European settlement (1631–1834)	97	3	0	4.5
			European settlement (1834–1926)	100	0	0	8.4
			Military use (1926–2004)	91	9	0	6.6
Lemm Swamp, TN	Oak	Stambaugh *et al*. 2016	Pre-European settlement (1701–1834)	97	3	0	5.2
			European settlement (1834–1926)	100	0	0	10.3
			Military use (1926–2004)	100	0	0	5.7
Kleinschmidt Woods, WI	Oak	Wolf 2004	1804–2000	53	46	0	6.3

Table 2. Continued.

Site and state	Forest type	Citation	Time period	Dormant season (%)	Growing season (%)	Undetermined (%)	Mean fire interval (yr)
Upper Midwest							
Menominee Indian Reservation, WI	Pine	Sands and Abrams 2011	1822–2007	76	NR	NR	6.4–20.0
Grindle Lake, WI	Pine	Guyette *et al*. 2016	1664–1923	76	24	0	10.4
Waubee Lake, WI	Pine	Guyette *et al*. 2016	1707–1864	88	12	0	6.3
Airport Road, WI	Pine	Guyette *et al*. 2016	1655–1925	17	83	0	12.9
Moquah Barrens, WI	Pine	Guyette *et al*. 2016	1591–1937	79	21	0	12.8
Southeast							
Wade Tract, GA	Pine	Rother *et al*. 2020	1882–1997	62	38	0	1.8
Millpond Larkin, GA	Pine	Rother *et al*. 2020	1935–2015	39	61	0	1.8
Tall Timbers, FL	Pine	Rother *et al*. 2020	1898–1950	60	40	0	3.5
De Soto National Forest, MS	Pine	White and Harley 2016	European settlement (1760–1879)	37	65	0	4.3
			Logging era (1880–1935)	31	68	0	4.2
			Fire suppression era (1936–1979)	25	75	0	8.0
			Management era (1980–2013)	69	31	0	3.4
St. Joseph Bay Preserve, Gulf County, FL	Pine	Huffman 2006	Pre-European settlement (1592–1830)	0	100	0	NR
			European settlement (1831–1883)	21	78	0	NR
Little St. George Island, FL	Pine	Huffman 2006	Early (1866–1904)	20	80	0	4.0
			Middle (1927–1945)	0	100	0	4.0
			Recent (1963–1999)	20	80	0	9.0
South-central							
Cache Creek, OK	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1637–1899)	97	1	1	6.5
			Post-European settlement (1901–2010)	95	5	0	19.3
Deep Fork, OK	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1704–1899)	73	5	22	4.5
			Post-European settlement (1900–2016)	89	0	11	7.5
French Lake, OK	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1712–1899)	76	2	22	4.4
			Post-European settlement (1901–2005)	83	3	14	5.2
Okmulgee Game Management Area, OK	Oak	DeSantis *et al*. 2010	1750–2005	95	5	0	2.7
Hollis Canyon, OK	Oak	Stambaugh *et al*. 2016	Pre-European settlement (1727–1850)	92	0	8	8.8
			Conflict/settlement (1850–1901)	85	0	15	3.6
			Public ownership (1901–2010)	88	0	12	10.7
French Lake, OK	Oak	Stambaugh *et al*. 2016	Pre-European settlement (1712–1850)	69	2	29	6.3
			Conflict/settlement (1850–1901)	84	3	13	2.4
			Public ownership (1901–2005)	83	3	14	5.2

Table 2. Continued.

Site and state	Forest type	Citation	Time period	Dormant season (%)	Growing season (%)	Undetermined (%)	Mean fire interval (yr)
Rain Gauge Flat, OK	Oak	Stambaugh *et al*. 2016	Pre-European settlement (1746–1850)	81	0	19	6.5
			Conflict/settlement (1850–1901)	77	15	8	3.2
			Public ownership (1901–2009)	83	9	9	16.7
Cache Creek, OK	Oak	Stambaugh *et al*. 2016	Pre-European settlement (1637–1850)	100	0	0	12.3
			Conflict/settlement (1850–1901)	93	4	2	2.7
			Public ownership (1901–2010)	95	5	0	19.3
Hollis Canyon, OK	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1720–1899)	87	0	13	6.9
			Post-European settlement (1901–2010)	88	0	13	10.7
Keystone, OK	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1772–1907)	71	15	15	4.1
			Post-European settlement (1908–2001)	67	23	10	2.0
Tully Hollow, OK	Pine	Rooney and Stambaugh 2019	Pre-European settlement (1650–1889)	91	3	6	3.0
			European settlement (1890–1925)	88	13	0	2.1
			Recent use (1925–1992)	86	0	14	16.8
Okmulgee Wildlife Management Area, OK	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1750–1899)	70	5	25	4.3
			European settlement (1900–1988)	58	2	39	1.7
			Recent use (1989–2005)	68	0	32	1.8
Rain Gauge Flat, OK	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1746–1899)	80	5	15	5.0
			Post-European settlement (1901–2009)	83	9	9	16.7
Tallgrass Prairie Preserve, OK	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1770–1871)	50	8	42	3.5
			European settlement (1871–1914)	65	4	30	2.2
			Recent use (1915–1989)	72	23	5	1.3
Tishomingo National Wildlife Refuge, OK	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1736–1842)	82	3	15	3.4
			European settlement (1842–1946)	87	3	10	4.9
			Recent use (1946–2015)	100	0	0	7.4
Purtis Creek State Park, TX	Oak	Stambaugh *et al*. 2011b	1690–1924	100	0	0	8.1
Bastrop State Park, TX	Oak-pine	Stambaugh *et al*. 2017	Pre-European settlement (1653–1829)	46	27	27	10.9
			European settlement (1830–1890)	25	58	17	4.9
			Regional development (1891–1940)	67	24	9	2.4
			Fire suppression (1941–2011)	50	0	50	NR
Bastrop State Park, TX	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1653–1829)	58	16	26	10.9
			European settlement (1830–1940)	57	25	20	3.4
			Recent use (1941–2011)	75	25	0	NR
Hagerman National Wildlife Refuge, TX	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1707–1842)	42	6	52	4.4
			European settlement (1842–1946)	76	2	22	2.8
			Recent use (1946–2015)	82	6	12	3.3
Purtis Creek State Park, TX	Oak	Rooney and Stambaugh 2019	Pre-European settlement (1690–1820)	88	0	12	6.7
			European settlement (1820–1924)	100	0	0	9.8

Fire Scar *versus* Paleocharcoal Studies. A series of fire-scar studies were conducted on old-growth mixed forests in northern and central Pennsylvania, culminating in a synthesis paper by Stambaugh *et al*. (2018). These authors described a wave of anthropogenic fire from Native American occupation (dating back to 1592) and depopulation through Euro-American settlement and industrialization to declining fire use during the 20th century. The mean fire return intervals ranged from 5 to 18 yr prior to Euro-American settlement and from 3 to 6 yr following Euro-American settlement up until the fire suppression era. Paleocharcoal studies sometimes report very low levels of historic charcoal in the same region where fire scar data indicate frequent fire. For example, a kettle lake in north-central Pennsylvania, surrounded by hemlock-oak, had very low levels of sediment charcoal (Clark and Royall 1996). These data contrast with the high-frequency fire-scar data (using pine) in the region (Stambaugh *et al*. 2018). It has been argued that charcoal produced by low-intensity surface fires may not adequately register in the sediment record compared to more severe surface or crown fires of conifer-dominated forests (Abrams and Seischab 1997; Stocks and Kauffman 1997; Abrams and Nowacki 2020). This includes studies in which both fire scar and paleocharcoal were compared in concert (Whitlock *et al*. 2004).

Impacts of Euro-American Settlement and the Little Ice Age (1600–1900). The timing of Native American depopulation and Euro-American settlement differed significantly between regions, starting in the 1600s for the East Coast and continuing into the early 1900s for the Central Plains (Nowacki *et al*. 2012). Extensive settlement of the eastern United States was not complete until 1850 (Hart and Buchanan 2012). Euro-American settlement coincided with the Neoglacial Cooling period during the Little Ice Age (*ca*. 1600–1900), when temperatures were at or near their lowest point during the past 8,000 yr (Fig. 1). Following Euro-American settlement, land clearing and the cutting of the forests for building material and firewood ensued (MacCleery 1992; Whitney 1994). Momentum increased with a rising population and wood demands of the charcoal iron industry; this escalated into the "Great Cutover" during the 19th century. The forest was recognized for its importance for industrialization, agriculture, and the basis of material progress. Iron furnaces in the United States date back to the early 1700s, and their peak activity was in the mid-19th century, primarily in the Central Hardwoods (MacCleery 1992). Other industrial uses of wood included railroads, mines (props), shipbuilding, and manufacturing, although the largest consumption remained for domestic uses. Most of New England, New York, the Eastern Seaboard, and the Ohio Valley were already logged at least once by the mid-19th century. Approximately 99% of the original forest was gone by 1920.

Prior to 1850, commercial forestry in the eastern United States was typically limited to small sawmills in most towns (MacCleery 1992). The subsequent increasing demands for timber led to the large-scale commercialization of the forest industry by the mid-19th century, including steam-powered saws and railroad logging. Logging escalated, leading to the height of the clear-cut era from 1850 to 1920. Not only were the original forests cut, but there was a large loss of forest area to land clearing (agriculture) during the nation-building period. It has been estimated that 66 million ha of U.S. forests were cleared for agriculture by 1860. Between 1850 and 1920, the forested area of the eastern United States declined by approximately 40%. The loss of forested land to agricultural clearing ranged from 22% to 76% (averaging 50%) in 12 eastern states (Whitney 1994). Areas left in old-growth forests totaled less than 0.5%. The Great Cutover produced extensive stumplands covered in logging debris (slash). As the slash dried, huge wildfires followed, burning with an intensity not experienced in the original forest (Pyne 1984). These fires ushered in the fire suppression (Smokey Bear) era in the United States starting in the 1930s (Fig. 1; Abrams 2010).

20th-Century Abrupt Warming and Smokey Bear. The mid- and late 19th century brought forth dramatic changes in climate and land-use history in the eastern forest. The Little Ice Age came to an end about 1850, after which temperatures and greenhouse gases increased (Mann *et al*. 1998; Fig. 1). However, the warmest years have occurred mainly in the past four decades. In the United States, temperatures have increased by about 0.73 °C in the past century, but warming has been most pronounced in the northern tier, moderate in the central tier, and least in the southern tier (Tebaldi *et al*. 2012; Nowacki and Abrams 2015).

The clear-cut and catastrophic fire eras peaked in the early 1900s but started to dissipate in the

1920s and 1930s (Nowacki and Abrams 2008). The huge wildfires that occurred, particularly the Great Fire of 1910 in Montana and Idaho and the Peshtigo Fire in Wisconsin, contributed to the idea that fires needed to be suppressed (van Wagtendonk 2007). The U.S. Forest Service was established in 1905, and one of its primary tasks was to suppress all fires on the forests it administered. The National Park Service, established in 1916, took a similar approach to national parks. By 1934, a policy of extinguishing all fires by 10:00 am of the next burning period was implemented (named the "10 am policy"). Smokey Bear and the slogan "Only YOU Can Prevent Forest Fires" was created to garner public support for the strict fire suppression policy. This policy resulted in a dramatic decline in the area burned in the eastern United States from about 11 million ha in the early 1940s to less than 1 million after 1970 (Nowacki and Abrams 2008). More recently, however, a moderate amount of burning, estimated from satellite sensors, has occurred in the Southeast between 2000 and 2006, and this activity is predicted to increase in the future (Hawbaker *et al*. 2013). In contrast to more northern states, fire activity in the Southeast is being facilitated by having more pyrogenic vegetation (*e.g*., pine-oak, herbaceous wetlands), a warmer climate, a continued burning culture, and a higher incidence of lightning fires.

The 20th-century exclusion of fire was a pivotal event in the ecological history of eastern forests, allowing climate-based natural succession to ensue, something that was held in check with Indigenous fire regimes. In the absence of surface fires, forest succession produces an increase in shade-tolerant species, and multistoried, closed canopies develop that increase the intensity of high (overstory) and low (understory) shade. This change in species composition and microclimate also altered the leaf litter and fuel bed properties and pyrogenicity tendencies of the understory, making most forest less conducive to burning (Nowacki and Abrams 2008). This mesophication process dominated by cool-based replacement species runs counter to the abrupt warming that has taken place during the past century. Indeed, many of the oak replacement species promoted by fire suppression and mesophication, which include red maple, black gum (*Nyssa sylvatica*), and black birch (*Betula lenta*), are predicted to decrease because of global warming (Fig. 3; Abrams 1998; Prasad *et al*. 2007–present). Their climate-based analysis has not incorporated the impacts of human fire suppression and other land-use practices now shaping eastern forests.

Human practices during the past century described in this section have directly or indirectly impacted nearly every forest in the eastern United States. In many cases, the forest response has been counter to what one would have anticipated by the increased warming during the most recent period. The deconiferization of eastern mixed forests has been a major force for species change, including shifts in species temperature classes, but this has much more to do with a lack of sprouting ability in conifers than it does with climate change (Abrams 2001). In addition, the warm- and hot-adapted species that dominated the central oak-pine region have declined in favor of later-successional mesophytic trees (especially maples) more representative of cool northern climes. The overwhelming increase in red maple is quite evident when comparing its sparse distribution at the time of European settlement (Table 1) *versus* its present-day dominance in eastern forests, particularly in the northern oak region (Fig. 3; Abrams 1998). Maples present in northern hardwood and oak forests prior to European settlement were largely sugar maple (*Acer saccharum*; Abrams and Ruffner 1995; Cogbill 2000). Thus, most forests in the eastern United States are changing (*via* succession and mesophication) against the tide of prevailing warming over the past century. The evidence suggests that the main driver of these changes is fire exclusion rather than climate or other factors (Nowacki and Abrams 2015; Hanberry *et al*. 2020a).

Conclusion. As the Holocene progressed, Indigenous populations increased and became a major ecological force on the continent, as vividly expressed through megafaunal extinction and fire ignitions. The areas south of the tension zone likely changed to cultural control by the mid-Holocene at least and probably earlier (Delcourt *et al*. 1986; Abrams and Nowacki 2008, 2015; Nowacki *et al*. 2012). A combination of warm climate during the Holocene Thermal Maximum and increasing Indigenous populations (and their use of fire) acted in concert to promote warm-/hot-adapted tree species in the vast central and southern regions. Around 3,300 BP, however, the Neoglacial Cooling period started, with cooling

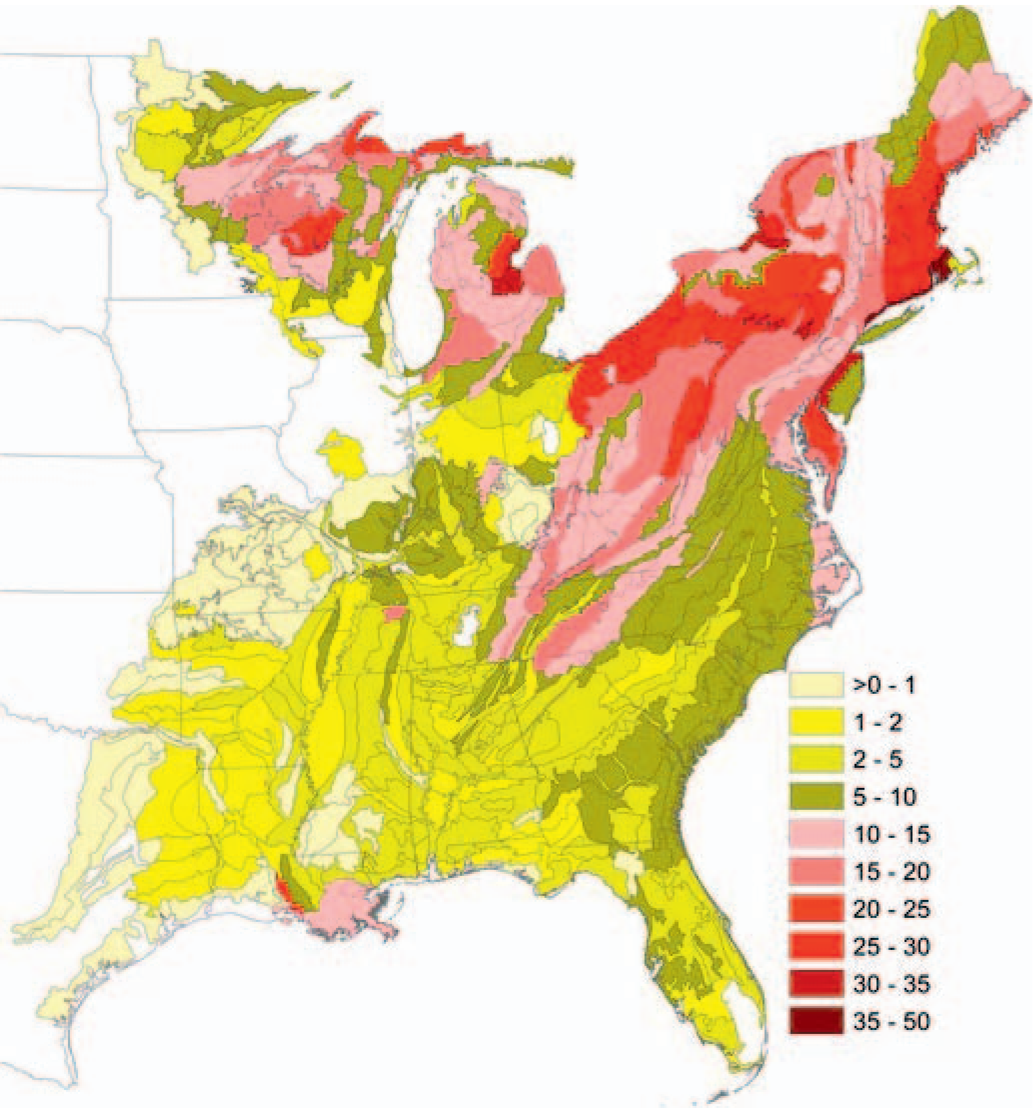

FIG. 3. Current percentage of red maple in the eastern United States (Forest Inventory and Analysis 2021) by ecological subsection (Cleland *et al.* 2007).

intensifying through the Little Ice Age period (ending about 1900) with embedded periods of warming (*e.g*., Medieval Warm period; Fig. 1). Here, high levels of fire and warm/hot central/southern and pyrogenic tree species persisted during Neoglacial cooling, representing a climate-fire-vegetation anomaly.

The clear-cut and catastrophic fire era in the eastern United States spanned the Little Ice Age and the start of abrupt warming after 1900. The fact that so much burning took place during the latest and coldest stages of the Neoglacial Cooling period (associated with the Great Cutover) indicates a lack of climate control. Strict fire suppression policies after 1930 ushered in a new era of forest dynamics for the eastern United States, facilitating a successional replacement across vast areas of fire-dependent oak and pine forests (Cottam 1949; Abrams 1992; Nowacki and Abrams 2008). The oak-pine replacement process is most aggressive in the northern half of the eastern biome, where a suite of shade-tolerant and mesophytic tree species exist in large numbers (Abrams 1998). Farther west and south, the warmer and drier conditions prevent the fast-paced oak-to-maple conversion process seen elsewhere, although understory composition (of shade-tolerant trees) indicates that changes are forthcoming (Abrams 1992; Moser *et al*. 2006; Burton *et al*. 2010). The mesophication process over the half century or more has promoted mostly northern-affinity, late-successional, mesophytic tree species, which runs counter to the climatic warming. This process is promoting a suite of tree species that are predicted to decrease and/or migrate northward at the expense of southern-affinity species because of climate change (Prasad *et al*. 2007–present).

Presently, oak and pine edaphic climaxes are restricted to very dry and/or nutrient-poor sites (*e.g*., barrens, rocky ridges, glacial outwash, coastal plains, and Central Plains), but those sites often contain flammable vegetation and are prone to burning (Lafon *et al*. 2005). Even though more compositionally stable, vast changes in structure from open- to closed-canopy forests have ensued. On better-quality sites, most oak and pine forests are not a climax type and will be successionally replaced in the absence of periodic fire (Loucks 1970; Abrams 1992; Nowacki and Abrams 2008). This is true today and likely applies to oak and pine ecology for the entire Holocene. Therefore, claiming long-term upland oak or pine stability on sites without recurring fire (*e.g*., Clark and Royall 1996; Patterson 2006; Oswald *et al*. 2020) is problematic because it lacks modern-day analogues. A few localized exceptions exist, such as a mesic red oak (*Quercus rubra*) forest in North Carolina that has little evidence of fire prior to 1950 (van de Gevel *et al*. 2012). Nevertheless, this forest is now transitioning to sugar maple dominance against the tide of global warming.

The role of historic fires in shaping world vegetation is front and center in the long-running climate-disturbance debate. Both climate and humans are major drivers of fire, with fire formerly controlling vegetation expression within a climate envelope, especially south of the tension zone. The incidence of fire increased with the rise of humans in many locations, and the world would be a very different place in terms of both climate and vegetation without fire (Bond *et al*. 2005; Bowman *et al*. 2011). Nonetheless, the opinion that Indigenous land use (fire, clearing, agriculture, and so on) played a minor role in the forest/vegetation dynamics is not uncommon among paleoecologists (Power *et al*. 2008; Marlon *et al*. 2013; Oswald *et al*. 2020). Fires are not singularly human or climate but rather caused by a combination of both, except in some very rare cases. Native people are ecosystem architects, managing ecosystems to sustain their needs for food and shelter. Indigenous people used fire to create and sustain grain-producing grasslands and burned the vast expanses of mast-producing oak and hickory forests in the eastern United States to prevent their conversion to less desirable closed forests. Whether purposefully started or by accident, there was little incentive for Indigenous peoples to put them out given the limited tools they had and knowledge that fire would most likely benefit all surrounding habitats. Indeed, oak management by Native Americans is not unique to the eastern United States. There is also extensive documentation of Indigenous people using fire in western oaks for many of the same reasons described for the East, including keeping forests open for oak regeneration, reducing undesirable species, and increasing mast production (reviewed in Mensing 2006). The weight of evidence demonstrates that the extensive expanses of oak, hickory, pine, savanna, and grasslands, among others, in the eastern and central United States were primarily managed landscapes created and sustained by and for the needs and desires of the Indigenous people.

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