

Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America

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Many forests of eastern North America are undergoing a species composition shift in which maples (*Acer* spp.) are increasingly important while oak (*Quercus* spp.) regeneration and recruitment has become increasingly scarce. This dynamic in species composition occurs across a large and geographically complex region. The elimination of fire has been postulated as the driver of this dynamic; however, some assumptions underlying this postulate have not been completely examined, and alternative hypotheses remain underexplored. Through literature review, and a series of new analyses, we examined underlying assumptions of the “oak and fire” hypothesis and explored a series of alternative hypotheses based on well-known ecosystem drivers: climate change, land-use change, the loss of foundation and keystone species, and dynamics in herbivore populations. We found that the oak–maple dynamic began during a shift in climate regime – from a time of frequent, severe, multi-year droughts to a period of increased moisture availability. Anthropogenic disturbance on the landscape changed markedly during this same time, from an era of Native American utilization, to a time characterized by low population densities, to Euro-American settlement and subsequent land transmutation. During the initiation of the oak–maple dynamic, a foundation species, the American chestnut, was lost as a canopy tree across a broad range. Several important browsers and acorn predators had substantial population dynamics during this period, e.g. white-tailed deer populations grew substantially concurrent with increasing oak recruitment failure. In conclusion, our analyses suggest that oak forests are reacting to marked changes in a suite of interlocking factors. We propose a “multiple interacting ecosystem drivers hypothesis,” which provides a more encompassing framework for understanding oak forest dynamics.

Many deciduous forests of eastern North America are undergoing a marked shift in species dominance. Oaks (*Quercus* spp.) were a historically dominant canopy tree in eastern North America (Dyer 2001, Abrams 2003) and are still an important constituent of the forests across a broad range (Fig. 1). Across much of this range, however, oaks are currently underrepresented in smaller size classes (Fig. 1), which is an indication of tree regeneration and recruitment failure (Lorimer 1984, Crow 1988, Loftis and McGee 1993, Goebel and Hix 1996). Many investigators have concluded that the importance of oak as a dominant forest tree is diminishing, and this loss will be accompanied by the increased importance of other species (Lorimer 1984, Host et al. 1987, Abrams 1992, Tift and Fajvan 1999). In particular, red maple *Acer rubrum* (Lorimer 1984, Host et al. 1987, Crow 1988, Abrams 1998) and sugar maple *A. saccharum* (Parker et al. 1985, Host et al. 1987, Pallardy et al. 1988, Shotola et al. 1992) exhibit an abundance of regeneration relative to their status as canopy trees (Fig. 1) suggesting a long-term increase in importance. This dominance shift has significant implications for biodiversity and ecosystems function, and has become an important

focus of research and management (Loftis and McGee 1993, McShea and Healy 2002, Spetich 2004).

Efforts to understand oak-to-maple succession have focused primarily on fire as the driver of these dynamics (Crow 1988, Abrams 1992, Van Lear and Watt 1993, Nowacki and Abrams 2008). According to the “fire and oak hypothesis” (Abrams 1992), oaks are generally fire tolerant and are promoted by surface fire, while fire intolerant maples are impeded by burning. Sharp contrast has been drawn between oaks and maples in morphological attributes related to fire tolerance (Abrams 1992). Oaks typically have thicker bark than maples which insulates trees against fire damage. In relative terms, oak seedlings build larger root systems and develop more belowground reserves (that are safe from fire), whereas maples tend to allocate carbon to aboveground growth (that is vulnerable to fire; Abrams 1992, Larson and Johnson 1998). Oaks are also considered less shade tolerant than maples (Burns and Honkala 1990) indicating a need for canopy-opening disturbances such as fire (Abrams 1992, Brose et al. 2001). Thus, there is evidence supporting the idea that oaks should be more tolerant of fire than maples, and a large literature has linked

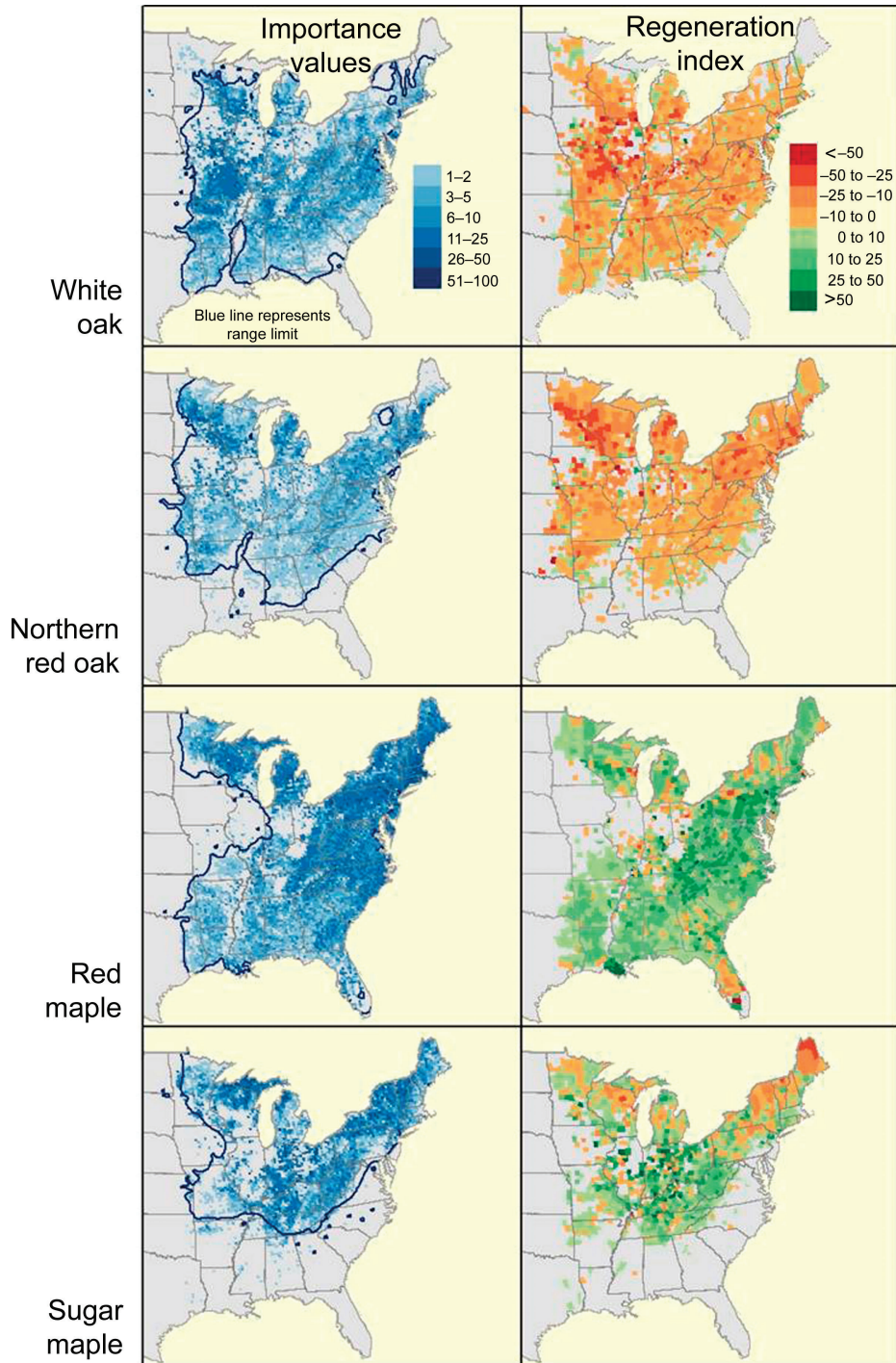


Figure 1. Present-day distribution of two oak and two maple species, and an index indicating their regeneration potential. Importance values equally weight species size (basal area) and abundance (density), with larger numbers indicating increasing importance. The Regeneration index represents the difference between each species' percentage of all small trees (<13 cm diameter) and its percentage of large trees (>38 cm diameter). Negative numbers indicate that the species is underrepresented in smaller size classes relative to its proportion of larger trees, and therefore may experience regeneration problems. Positive numbers indicate a larger proportion of smaller trees relative to larger trees for that species. In the left panel, Importance values represent the average of all USFS FIA plots occurring within each 20×20 km grid cell (Prasad et al. 2007). Range limits from Little (1971). In the right panel, tree diameter values represent averages of all USFS FIA plots occurring within each county (USFS 2007). Only species likely to attain canopy size were included when computing total tree numbers.

the initiation of the oak-maple dynamic to the absence of forest fire in these systems due to fire suppression activities and cultural changes ca 1930–1950 (Loftis and McGee 1993, McShea and Healy 2002, Spetich 2004). Fire

suppression initiated mesophication (sensu Nowacki and Abrams 2008) of these forests where maples (and other fire intolerant species) are becoming increasingly important, less light is reaching the forest floor, and regeneration

microsites are increasingly moist. The reintroduction of fire (via prescribed burning) has been initiated in a variety of locations to impede this process (Brose et al. 1999, Albrecht and McCarthy 2006, Blankenship and Arthur 2006, Bowles et al. 2007) and at least one attempt has been made to codify into law prescribed burning to promote oak (Haluska 2009).

The literature supporting an oak-to-maple transition in forests of eastern North America is deep and rigorous; however, understanding of the driver(s) of this transition is more speculative. Species-replacing ecosystem dynamics have been shown to be driven by an array of factors. For instance, spatially broad changes in species composition have been shown to be driven by climate (Jackson and Whitehead 1991, Spear et al. 1994, Delcourt et al. 1998, Schauffler and Jacobson 2002). Alterations in land-use patterns are another important factor in ecosystem dynamics (Whitney and DeCant 2003, Dyer 2010). Some species are disproportionately important in controlling ecosystems and the loss of these “foundation” species can have asymmetrically large impacts on species composition (Ellison et al. 2005). The top-down activity of fauna is important in many forests, and dynamics in “keystone” species can strongly influence forest dynamics.

We examined a suite of potential ecosystem drivers for evidence of marked variation during the time period relevant to oak-maple dynamics. To examine the basis of the oak and fire hypothesis, we assessed the published literature for evidence of fire in eastern oak forests over the past 500 yr. We also evaluated the published results from fire reintroduction experiments. We then used a combination of new data analysis and literature review to examine a variety of alternative hypotheses of oak-maple dynamics. We focused specifically on the following well-known ecosystem drivers: climate change, land-use change, the loss of foundation species, and changes in fauna (especially herbivores). The overarching goal of this research was to explore the support for a broad, multi-faceted, and flexible ecological framework for understanding oak forest dynamics.

Fire as an important disturbance process in oak forests over the last 500 years

One of the primary features of the oak-fire hypothesis is the idea that fire was an important process in oak forests over the last ca 500 yr (Brose et al. 2001). Oak dominance has been attributed to burning during this time by Native Americans, and then by Euro-American settlers, while the loss of oaks has been associated with the advent of fire suppression ca 1930 (Abrams 1992, Brose et al. 2001, Nowacki and Abrams 2008). Pre-suppression fire regimes are thought to have been largely anthropogenic in nature; lightning-ignited fires were relatively unimportant (Ruffner and Abrams 1998, Lafon et al. 2005, Mitchener and Parker 2005, Lafon and Grissino-Mayer 2007). We searched the peer-reviewed literature for data to support the idea of anthropogenic fire regimes during the centuries preceding the beginning of fire suppression.

Fire scars on tree cross-sections provide the only source of annually-resolved fire-history information in the centuries prior to Euro-American settlement (ca 1600–1800).

There have been a series of fire scar studies on the western margin of the Eastern Deciduous Forest that demonstrate the occurrence of fire in oak forests over the last 400 yr (Cutter and Guyette 1994, Guyette et al. 2002, Guyette and Spetich 2003, Stambaugh et al. 2006). We found a paucity of fire scar data from other parts of the Eastern Deciduous Forest. Buell et al. (1954) and McCarthy et al. (2001) report presettlement fires from New Jersey and Ohio, respectively, but the data come from only a single tree cross-section in each case. Shumway et al. (2001) present a fire history from 20 samples in western Maryland and report 42 fires from 1616 to 1959. In southern Indiana, Guyette et al. (2003) reported a fire history beginning in 1654 that included 84 fire scars on 27 trees. These studies, among others (Harmon 1982) offer some support for fire as a factor in presettlement oak forests, but they amount to a tiny sampling across a vast and topographically complex region. There have been numerous studies of sediment charcoal in oak forests that note the long-term presence of fire, and these studies have also found a positive correlation between charcoal and oak pollen (Delcourt et al. 1998, Foster et al. 2002). However, the temporal resolution of these studies over the last 400 yr is poor versus tree-ring based studies. Soil charcoal may be a way to identify the presence of fires in presettlement forests with higher temporal resolution, and more work of this sort is needed (Hart et al. 2008).

Anthropological understanding of Native Americans living in the Eastern Deciduous Forest suggests fire was an important, and frequently used, land management tool (Cronon 1983, Williams 1989, Denevan 1992, Doolittle 1992, Whitney 1994, Krech 1999). The oak-fire hypothesis relies upon Native American burning of forests, and on the idea of a relatively continuous burn regime during the transition from Native American to Euro-American land use (Abrams 1992, Brose et al. 2001). We found strong evidence that this transition, in fact, was marked by a century of atypically low Native American populations due to pandemics that swept through native societies well ahead of Euro-American settlement activities (Lovell 1992). Some work suggests that by the time Euro-Americans began crossing the Appalachian Mountains in significant numbers, indigenous populations had been decimated and their social structures had been shattered by plague (Denevan 1992, Milner et al. 2001). Milner et al. (2001) concluded that by the mid-1600s “large portions of the region were unoccupied or, at best, saw few permanent settlements” (p. 14), with populations instead concentrated along productive coastal areas and river valleys. If large areas of eastern North America were depopulated for ca 150 yr from the mid-1600s to the beginning of serious western settlement activities by Euro-Americans ca 1800 (Kelton 2002), this would have had substantial implications for anthropogenic landscape processes such as fire. In fact, this absence of humans in the landscape might be reflected by Guyette et al. (2003) who found a 126-yr gap in the fire regime from 1675 to 1800 in southern Indiana. Guyette et al. (2002) identify a “Depopulated Native American” era of low fire occurrence prior to Euro-American settlement in the Ozark Mountains. However, early Euro-American settlers provided numerous accounts of Native American burning in some regions, so there must have been fire

activity on the landscape. If the landscape was largely depopulated, it is possible that few ignitions swept across large areas, such that even low population numbers could influence wide areas of forest. Nevertheless, our literature review left us with the following question: what is the likelihood of an anthropogenic fire regime, sufficiently widespread, frequent and intense to limit regeneration of maples across a vast and topographically complex region, in a landscape that was largely depopulated for > 125 yr?

In the more recent past, we found direct evidence suggesting a link between fire and oak. Euro-American ignition fires ca 1875–1940 were frequent and spatially extensive (Guyette et al. 2002) and marked by oak regeneration and recruitment (McEwan et al. 2007, Hutchinson et al. 2008). For instance, in an oak forest of west Virginia, Schuler and McClain (2003) found seven fires from 1869 to 1962, and in Ohio, Sutherland (1997) reported frequent fires ca 1870–1930. McEwan et al. (2007) found that from ca 1875 to 1940 fires occurred at a frequency of 6–7 yr in oak forests of Kentucky and Ohio. This period of frequent fire was followed by the virtual elimination of fire as a landscape process ca 1940, and is coincident with the initiation of maple recruitment (Hutchinson et al. 2008).

In summary, we found strong evidence for fire in oak forests associated with Euro-American activity, but support for presettlement fire east of the Mississippi is more speculative. A period of frequent fire ca 1875–1940 was followed by a virtual absence of fire after ca 1940. We found a paucity of fire history data across much of eastern North America prior to 1800, especially east of the Mississippi River. There is evidence of Native American use of fire in eastern North America, but implications of cataclysmic population losses associated with plagues that swept through Native American populations 150 yr prior to Euro-American settlement have not been sufficiently addressed. Further work is needed that can 1) extend our understanding of fire history in oak forests prior to 1800,

and 2) deepen understanding of the transition from Native American to Euro-American land-use.

Results of experiments using fire to establish oak and impede maple

Experiments in which fire is applied to forests, and the responses of oaks and maples are measured, represent one of the more direct tests of the oak and fire hypothesis. There have been numerous studies that used a variety of burning techniques and combinations with other forms of disturbance. We examined the published fire experiment literature and asked the following question: “does reintroduction of fire promote oak recruitment and act as a filter for maple regeneration?”

We found that the influence of prescribed fire on oak-maple dynamics has been inconsistent (Table 1). Single fires have been largely ineffective at promoting oak regeneration, and sometimes yield the opposite of the intended effect by increasing the density of red maples seedlings. For instance, Albrecht and McCarthy (2006) document a strongly positive response of red maple to a single prescribed fire, with little response by oaks in Ohio forests (Table 1). Working in Kentucky, Kuddes-Fischer and Arthur (2002) found an initial increase in oak seedling density following a single prescribed fire that was matched by an increase in density of other seedlings, including red maple. After two years, oak seedling mortality had increased and its density returned to pre-treatment levels, but red maple density remained elevated. Elliot et al. (1999) detailed a complex response of oak and maple to a single prescribed fire depending on landscape position and fire intensity in North Carolina. Red maple seedling density generally increased following fire, as did that of oak seedlings, while sapling response was variable depending on landscape position and fire intensity. In Missouri, Huddle and Pallardy (1999)

Table 1. Summary of results from representative prescribed fire experiments in oak forests of eastern North America. Impacts of prescribed fire are simplified to depict significant increases or decreases in density as reported in the publication. Increases are represented by an upward pointing triangle, decreases by a downward pointing triangle, no significant change is indicated by an equals sign. Oaks in the white oak group (*Leucobalanus*) and sugar maple are grey triangles, red oaks (*Erythrobalanus*) and red maple are black triangles. Sites are state postal abbreviations. The “Burns” column details the maximum number of fires in any given study. Empty cells indicate that the taxa were not present, not measured, or not reported in the publication.

Study	Site	Burns	Oaks		Maples	
			Seedling	Sapling	Seedling	Sapling
Single-burns						
Albrecht and McCarthy (2006)	OH	1	= =	= =	▲	
Elliot et al. (1999)	NC	1	▲ ▲	▼ ▼	▲	▼ ▼
Huddle and Pallardy (1999)	MO	1	▼ ▼		▼	
Kuddes-Fischer and Arthur (2002)	KY	1	= =		▲	▼ ▼
Multiple burns						
Arthur et al. (1998)	KY	2	▲ ▲	▲ ▲	▲	▲
Blake and Schuette (2000)	MO	4		=		=
Blankenship and Arthur (2006)	KY	3	▲ ▲	▲ ▲	▲	▲
Hutchinson et al. (2005)	OH	4	= =	= =	= =	= =
Burning and thinning						
Albrecht and McCarthy (2006)	OH	1	= =	= =	▲	▲
Brose and Van Lear (1998)	VA	1		▲ ▲		▼
Kruger and Reich (1997)	WI	2	▲	▲	▼ ▼	▼ ▼
Iverson et al. (2008)	OH	2	▲ ▲	▲ ▲	▼	▼
McGee et al. (1995)	NY	2	▼	▼		

found higher survivorship and a stronger sprout response in red oak seedlings than in red maple which was similar in performance to white oak; all three species had greater mortality in burned conditions than in a control. This cursory overview reflects the overall conclusion from prescribed fire experiments that single burns are often ineffective at promoting oaks and impeding maples (Table 1).

Repeated burning has yielded mixed results for oak regeneration and recruitment (Table 1). On a Kentucky site that had experienced two fires, Arthur et al. (1998) document a near doubling of red maple density in the seedling and sapling layers. Following the fires, red maple seedling density was $>2 \times$ greater than all other seedling species combined, and $>4 \times$ that of all oak species (Table 1). In a separate study, Blankenship and Arthur (2006) found that three prescribed fires promoted oak regeneration, but also increased the density of understory red maples. Red maple had vastly higher understory densities following the fires, and Blankenship and Arthur (2006, p. 143) mention that “[t]he long-term consequences of repeated burning on oak regeneration are not clear”. Hutchinson et al. (2005) applied four fires to a southeastern Ohio oak forest and noted that (p. 224) “fire did not alter the competitive status of oak + hickory seedlings relative to that of shade-tolerant seedlings in either a consistent or substantial manner”. Red maple did exhibit mortality immediately following fires, but rebounded aggressively while understory sugar maple and oak density were not significantly influenced (Hutchinson et al. 2005). Blake and Schuette (2000) found no significant effect of prescribed fire on either white oak or sugar maple in an oak forest of Missouri (Table 1). It is important to note that burning conditions in most prescribed fires are probably markedly different than during ca 60-yr period of fire and oak regeneration from ca 1870 to 1930 when burning was frequent and sometimes intense (Guyette et al. 2002, McEwan et al. 2007).

Studies that impose forest thinning in association with prescribed fires have been more successful, but results have also varied (Table 1). In central Virginia, Brose and Van Lear (1998) found that prescribed fire following shelterwood harvesting in a Virginia forest increased oak density and decreased density of red maple. In contrast, McGee et al. (1995) worked in a New York site that had experienced a shelterwood cut in 1976 and subsequently been burned twice. They found (p. 166): “[i]n general, the status of *Quercus rubra* among competing tree regeneration species . . . was not improved by the use of prescribed fire, or fire in conjunction with shelterwood seed cutting”. This finding was supported by Albrecht and McCarthy (2006) who examined oak and maple dynamics in Ohio sites that had been thinned and burned. They found no positive effects of fire, thinning or a combination of the two on oak regeneration. Instead, potential competitors including red maple, sassafras *Sassafras albidum* and yellow-poplar *Liriodendron tulipifera* were stimulated. The application of more intensive disturbance has been more successful in shifting the understory balance toward dominance by oaks (Table 1). Kruger and Reich (1997) report a marked decrease of sugar maple abundance and an increase in abundance of red oak following forest clearing and two successive, annually-applied prescribed fires in Wisconsin. Iverson et al. (2008) found that a second fire on the Ohio

sites used by Albrecht and McCarthy (2006) increased oak seedling and sapling regeneration and reduced density of red maple. Iverson et al. (2008) noted that both the timing of the fire (relative to significant acorn crop production) and landscape position were critical, with xeric sites experiencing greater oak regeneration and recruitment.

In summary, we found that the effectiveness of prescribed fire for impeding oak-maple succession has varied widely. Fire interacting with other disturbance processes has been more effective. Our review of the literature suggests that continued experimentation is needed to fully vet the efficacy of fire as a restoration tool in oak forests. One of the potentially most important limitations of these studies is their relatively short time-frame. It may take several decades before oaks benefit from fire and other disturbance treatments (Kittredge and Ashton 1990). Future work is needed that extends experimental time series of prescribed fire. Other potentially fruitful approaches for furthering our understanding of fire in oak forests include: 1) burning experiments that intentionally manipulate the intensity of fire to better mimic a range of potential conditions for that process and 2) continuing experimental combinations where fire is coupled with other forms of forest disturbance.

Alternative and interacting drivers of oak forest dynamics

Climate variability in eastern oak forests over the last 500 years

Regional climate variation creates discernable pattern in forest dynamics and broad geographic synchrony in forest species replacement. For example, in Minnesota the transition from oak woodlands to richer, mesic forest appears to have been driven by long-term climate change (Grimm 1983, 1984, Clark 1988). Throughout New England, spruce (*Picea*) increased in abundance over the last ca 2000 yr in response to centennial and millennial scale cooling (Davis et al. 1980, Gajewski 1987, Jackson and Whitehead 1991, Spear et al. 1994, Schaffler and Jacobson 2002). Long-term drought patterns, in particular, have been shown to increase disturbance rates and initiate alterations of species composition. For instance, a 30-yr megadrought in northeastern Utah is thought to have resulted in the significant dieback of forest dominants and initiated a transition to a pinyon pine ecosystem as climatic conditions changed (Gray et al. 2006). Droughts in the 1990s induced tree mortality and pushed back the forest border in the southwestern U.S. (Allen and Breashears 1998), and a severe drought favored *Austrocedrus chilensis* recruitment over *Nothofagus dombeyi* in a mixed Patagonian forest (Suarez and Kitzberger 2008). In these systems, and a variety of others (Gajewski 1998, Gajewski et al. 2006, Jackson 2006), long-term shifts in climate have been important triggers for species replacement – is there a discernable shift in climate associated with the ongoing oak-maple dynamic?

We investigated the potential role of climate in oak-maple dynamics by reconstructing annual to multi-decadal variations in drought over the last 500 yr across a large portion of the eastern oak forest (Fig. 2). Eighteen grid

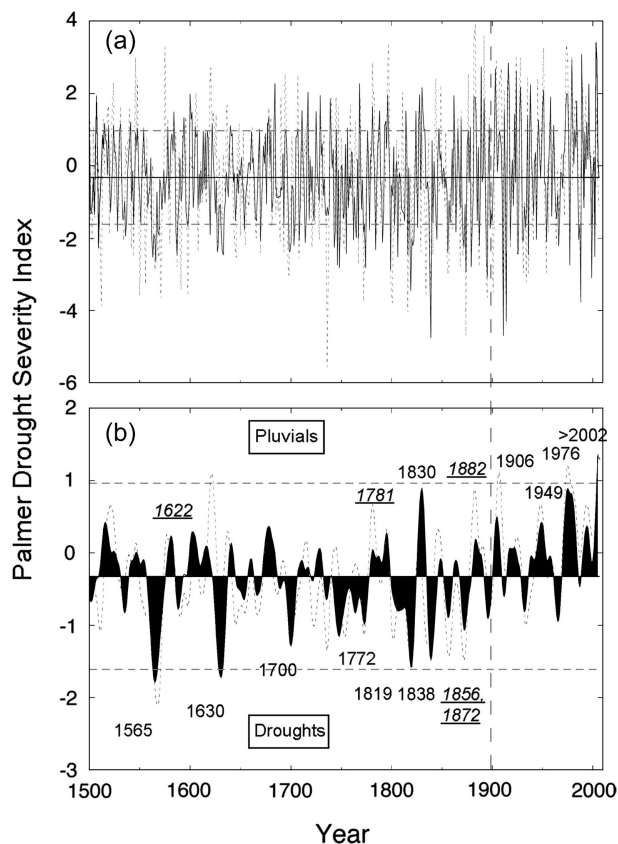


Figure 2. Drought since 1500 across a large portion of the eastern oak forest. The top figure (a) shows annual reconstructions of the Palmer Drought Severity Index (Cook and Krusic 2004, Cook et al. 2004) across our eastern (solid curve) and western (dashed curve) study areas (Fig. 3). The horizontal black solid line is the long-term mean and the horizontal grey dashed lines represent ± 1 standard deviation from the mean. The bottom figure (b) shows the annual reconstruction smoothed with a 15-yr spline to emphasize multi-annual to decadal-scale droughts. Significant drought and pluvial events are labeled with events solely in the western region in italics and underlined. >2002 indicates the pluvial from 2002–2005, the end of the current reconstructed record. Gray, vertical dashed line is a reference line for the year 1900.

points from the North American Drought Atlas (identified in Fig. 3), a network using tree-ring records to reconstruct the Palmer Drought Severity Index (PDSI; Cook and Krusic 2004, Cook et al. 2004), were combined to reconstruct separate drought histories for the western and eastern halves of our region of focus (Fig. 2a). The annual records were then smoothed using a 15-yr spline to examine decadal-scale drought (Fig. 2b). To investigate the potential influence of climate during the observed oak-to-maple transition, we used instrumented climate data (PRISM Group 2008) and compared a period during which oak regeneration was strong (1911–1940) to a more recent period in which maple regeneration vastly exceeded that of oaks (1971–2000; Fig. 3). To specifically test the potential role of drought stress in regeneration dynamics, 1) spring and summer precipitation and 2) maximum summer temperature were compared; these are two of the most important climatic factors in drought stress and calculation of PDSI (Palmer 1965).

Our analyses identified a substantial change in moisture availability across the eastern oak forest over the last 500 yr. While no record-long trend is apparent in the annual reconstruction (Fig. 2a), the smoothed drought record reveals four centuries of frequent and intense drought, followed by ca 100 yr of reduced drought and increased moisture availability (Fig. 2b). The era of intense and frequent decadal-scale drought starts with two megadroughts (smoothed droughts that drop below -1 SD of the long-term mean) centered on 1565 and 1630 (Fig. 2b). Six additional multi-year droughts were centered on 1700, 1772, 1819, 1838, 1856 and 1872. Following 1872 there are no droughts of similar magnitude or duration (Fig. 2b).

Over the last century, droughts have become less frequent and less severe, and continuous years with abundant moisture availability (pluvials) have become more frequent and more intense (Fig. 2b). Of the eight pluvials with a PDSI >0.25 lasting more than three years, five have occurred since 1880, with four since 1900 (Fig. 2b). In fact, the only pluvials of this magnitude prior to 1880 are centered on 1830 in the east, and 1622 and 1781 in the western portion of our study area (regions shown in Fig. 3). These time-series of drought reveal increased moisture availability over the last 100 yr concomitant with the oak-to-maple transition.

Our analysis of climate in the 20th century, as indicated by instrumental records, corroborates our finding from the tree-ring reconstruction, that the last century has been characterized by increased moisture availability (Fig. 3). Comparison of climatic averages from 1971–2000 to those of 1911–1940 revealed a pattern of increased growing season precipitation and decreased maximum summer temperatures. Within the central oak region, average growing season (March–August) precipitation is 6.4% greater and average summer maximum temperatures (June–August) are 0.5°C cooler. An examination by region shows that the eastern area is 3% wetter and 4°C cooler, while the western area is 10% wetter and 5°C cooler. Increased precipitation in combination with reduced maximum temperatures could reduce moisture-stress of plants in a biologically meaningful way.

The 400-yr period of frequent and intense droughts between 1500 and 1900 could have favored oaks over mesophytic species such as maple. In fact, recent work suggests that growth rates of oaks were reduced less than mesophytic species under drought condition in the southeastern U.S. (Klos et al. 2009). Moreover, oaks exhibit declining rates of mortality with increasing severity of drought, the opposite of the trend found for mesophytic species like maples (Olano and Palmer 2003, Klos et al. 2009). Therefore, extended and more intense droughts (e.g. 1565, 1630, 1700; Fig. 2b) could have acted as a regeneration filter against drought-sensitive maples, reducing competition and allowing for oak recruitment.

The decadal-scale droughts indicated by our reconstruction (Fig. 2b) may have also favored oaks by increasing light on the forest floor. A number of studies in the eastern U.S. (Hursh and Haasis 1931, Jenkins and Pallardy 1995, Pedersen 1998, Olano and Palmer 2003), and in oak forests specifically (Stringer et al. 1989), have shown droughts to be a trigger for tree mortality. The droughts identified in our reconstructions are vastly more

Average climate change (1971–2000 vs 1911–1940)

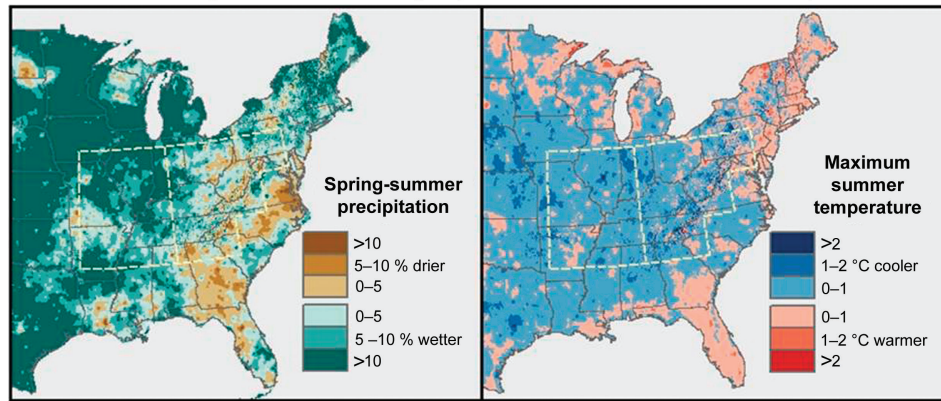


Figure 3. Climate change in the eastern U.S. derived from annual (1911–1940) and normal (1971–2000) climate data (PRISM Group 2008). In the left panel, green areas experienced wetter spring-summer conditions 1971–2000 compared to 1911–1940; in the right panel, blue areas experienced cooler summer temperatures over these same periods. Spring is defined here as March–May, and summer as June–August. Yellow lines define the western and eastern areas of the central oak region used for the PDSI reconstructions in Fig. 2.

severe than those associated with these studies (Fig. 2b), suggesting an increased likelihood of drought-related tree mortality, increased frequency and size of tree-fall gaps, and increased light availability at the forest floor (Clinton et al. 1994, Suarez and Kitzberger 2008). These conditions favor oak regeneration and recruitment in modern forest stands (Abrams 1992, Brose et al. 2001).

In contrast to the period 1500–1900, which was characterized by drought conditions that likely favored oaks, the last century of frequent and intense pluvial conditions should have favored maples. Maples, and other mesophytic species, are better adapted than oaks to a moister climate. They are more tolerant of shade, and seedlings exhibit aboveground carbon allocation, allowing for faster initial growth. The wetter climate conditions revealed by our analyses may have favored mesophytic vegetation, initiating the positive feedback loop of the mesophication hypothesis (Nowacki and Abrams 2008), which posits increasingly unfavorable conditions for oaks as regeneration microsites become increasingly shady and mesic.

In conclusion, our long-term climate reconstruction suggests 400 yr of frequent and intense droughts followed by a century of moister conditions. This transition in climate is synchronous with an apparent increase in the competitive status of maples and reduced oak regeneration. Understanding of oak-maple dynamics could be enhanced by work that addresses this pattern. Further work is needed to test the hypothesis that severe droughts suppress recruitment of maple (and other mesophytic species) and can generate oak recruitment pulses. Reconstructions of historical drought patterns and oak regeneration are a critical initial step in this process. Experimentation to elucidate the influence of varying moisture conditions in the competitive relationship between oaks and mesophytic would also be useful such as 1) field experiments that hold other factors constant while varying water availability, and 2) greenhouse or common garden experiments that test the relative competitive ability of oaks and maples under varying water regimes.

Euro-American land-use dynamics and oak forest formation

Anthropogenic disturbance is a known driver of long-term dynamics in a wide array of ecosystems. In forests, clearing and agricultural development have the potential to sharply alter the long-term compositional trajectory of the re-vegetating ecosystem. For instance, forest clearing creates opportunities for tree species that are adapted for high-light environments (Matlack 1997, Dyer 2001, 2010, Foster et al. 2003, Whitney and DeCant 2003); after taking advantage of an opportunity created by open conditions, some species can persist as forest dominants for centuries. Even though forest successional patterns are known to be strongly influenced by historical land use, its role in oak-maple dynamics is underexplored.

We used literature review and GIS analysis of county-level decennial census data to quantify land-use change in the Eastern Deciduous Forest. We assessed land cover data from 1850, 1880 and 1930 to estimate land-clearance activity during a known period of successful oak establishment. We used GIS to depict (Fig. 4) estimated percent forest cover in each county for each of the three years, using data from the Historical Census Browser (2004). For 1850, percentages reflect “unimproved” vs “improved” land, where improved land includes land cleared for various uses (e.g. crops, grazing) or that was lying fallow following use (Haines and ICPSR 2004). Percentages for 1880 are based upon “unimproved woodland and forest” and “other unimproved” land, versus “improved land” for tillage, meadows, and pastures. Values for 1930 are based upon “woodland not pastured” vs cropland, pasture, and all other land. Because the only data available are those collected in the census, all percentages (for all years) are based on the proportion of land-use within farm holdings. Thus, our analysis may underestimate total forest cover in the eastern U.S. because some land that was not held in farms could have been woodland.

We found that in 1850 forest cover was still high across much of the eastern U.S. (Fig. 4). Forest land decreased

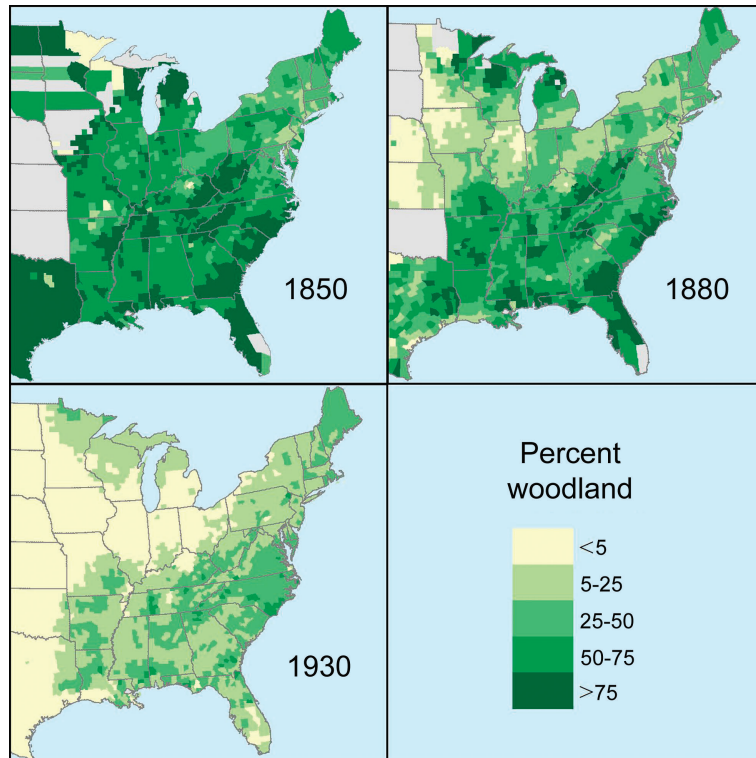


Figure 4. Land cover change in the eastern U.S., derived from county-level U.S. decennial censuses. See text for details. Data obtained from Historical Census Browser (2004).

substantially between 1850 and 1880, but the landscape still had large forested portions (Fig. 4). In contrast, by 1930 most of the Eastern Deciduous Forest had been cleared (Fig. 4). This cartographic analysis indicates rapid and widespread forest clearing, especially between 1880 and 1930, corroborating other findings for eastern North America that suggest broad-scale, intensive forest clearing took place in contemporary oak forests. In fact, we found literature support for the idea that much of eastern North America had been extensively (and repeatedly) deforested (Greeley 1925). Even steep slopes were occasionally cleared and farmed (Kalisz 1986), and grazing in forest understories by cattle and hogs was common (Cronon 1983, Williams 1989, Whitney 1994). This period of intense forest harvesting was concomitant with a period of oak regeneration. In nine forest sites in Kentucky and Ohio, McEwan et al. (2007) found that most oaks in the region initiated between 1880 and 1930 and that most of these forests were recovering from stand-replacing events. Forest clearance and agricultural utilization of this scale and intensity may have represented a novel disturbance in many eastern forests (Cronon 1983, Whitney 1994, Foster et al. 1998). Reforestation subsequently characterized much of eastern North America in the 20th century (Williams 1989).

In summary, we found evidence that oak forests experienced substantial disturbance were substantially disturbed by clearing and agricultural activity. The most intense time of disturbance overlaps with a period of widespread oak regeneration and recruitment, i.e. 1880–1930. Fires were frequent during this time period (Guyette et al. 2002, McEwan et al. 2007); however, fire is one piece of a broader anthropogenic landscape impact, and intensive land-clearing

is sufficient to influence long-term forest dynamics in the absence of fire, or any other factor. More work is needed to separate the tangled ecological effects of forest harvesting and forest fire. Specific lines of inquiry include: 1) experiments that induce intense and repeated forest harvesting, followed by reforestation, while excluding fire, 2) historical reconstructions in stands that were repeatedly cleared and then reforested, but where fires were not present, and 3) work in old-growth forests that have data supporting a long-term dynamic in fire, but no change in land-use.

The loss of a foundation species and 20th century variation in forest competition

The loss of “foundation species” can have a disproportionately large influence on forest dynamics and lead to substantial alterations in species composition (Ellison et al. 2005). The American chestnut was a foundation species in eastern North America (Ellison et al. 2005) comprising >50% of the basal area in some forests (Braun 1950). By the late-1930s, the pathogenic fungus *Cryphonectria parasitica* had devastated chestnut throughout much of its range and it presently exists almost exclusively as occasional sprouts and saplings (Paillet 2002). The loss of chestnut initiated forest dynamics in areas where it had been a dominant species (Keever 1953, Woods and Shanks 1959, Good 1968), and its loss is simultaneous with the initiation of the oak-maple dynamic. Is there evidence of maples being promoted by the loss of chestnut? We searched a series of publications focused on chestnut replacement for data that could elucidate the potential role of chestnut blight in the initiation of oak-maple dynamics.

We found consistent and striking evidence in the published literature that the loss of chestnut was associated with an increase in maple. For instance, Mackey and Sivec (1973) indicated a shift in species composition toward sugar maple, red maple and black cherry *Prunus serotina* following the chestnut blight in western Pennsylvania. In New Jersey, Good (1968) found that red maple was abundant in areas where chestnut replacement was underway, noting that on northwest-facing midslopes red maple was “tremendously important” (p. 248) making up more than half the total tree seedling density. Keever (1953) noted similar patterns in North Carolina. In the Great Smoky Mountains, Woods and Shanks (1959) found that red maple was an important species replacing American chestnut and proposed specifically that the loss of chestnut promoted gap-capture by red maples (p. 358): “*Acer rubrum* is widely distributed throughout the forests of the Smokies at all altitudes. Seeds are shed in great abundance and germination percentage is usually high so that young seedlings are numerous. However, mortality is great and usually only a very small fraction of these develop to maturity. When the chestnuts died, the openings in the canopy admitted more light than usual and a larger proportion of the seedlings survived. At the same time a larger proportion of advance regeneration grew to maturity.”

Our literature search revealed evidence that the loss of American chestnut accelerated red maple succession in at least some locations (Keever 1953, Woods and Shanks 1959, Good 1968). Since oak seedlings are suppressed by tall understory vegetation (Lorimer et al. 1994), this facilitation of red maple seedlings could have indirectly led to suppression of oaks. Lines of inquiry that could further understanding of the role of chestnut blight in oak forest dynamics include: 1) field studies that examine forest dynamics within plots where chestnut was present (which can be reconstructed in some cases by the presence of coarse woody debris) versus where chestnut was absent, 2) tree-ring analysis to reconstruct maple canopy accession and correlate the timing with chestnut loss (which is often dated in historical documents within a given area), and 3) assays that examine competition among chestnut, oak and maples to assess the potential role of chestnut loss in maple accession.

Wildlife population dynamics and 20th century variation in herbivory and frugivory

Pressure from herbivores and frugivores can have a marked influence on forest structure and composition, and is known to drive long-term dynamics in some systems. To explore links between changing wildlife population levels and the oak-maple dynamic we conducted a literature review focusing on prominent herbivores and frugivores in oak forests. Were there substantial dynamics in populations of species likely to influence the competitive balance between oaks and maples over the last 150 yr?

We found strong evidence that a variety of wildlife species known to influence forest succession had highly variable populations across eastern North America over the past 150 yr. Perhaps most important among these species are white-tailed deer *Odocoileus virginianus*, which

have been identified as a keystone herbivores in eastern forests due to their capacity to influence forest regeneration (Stromayer and Warren 1997, Waller and Alverson 1997, Rooney and Waller 2003, Cote et al. 2004). By 1900, the number of white-tailed deer in eastern North America reached a nadir of 1–2 million (McCabe and McCabe 1997). Deer numbers rebounded dramatically in the 20th century, and in many places vastly exceed presettlement densities (Leopold et al. 1947, Miller et al. 2003, Cote et al. 2004). Rooney and Waller (2003) found that red oak seedling densities declined as a function of white-tailed deer browse pressure, and Strole and Anderson (1992) report that deer were preferentially selecting white oak with a relatively low preference for sugar maple. Yuska et al. (2008) found that deer exclosure increased the survivorship and size of oak seedlings in the absence of other factors. In addition to potential browse pressure, the preferred food of white-tailed deer in autumn is acorns, which can make up 70–80% of their diet (Rue 1989, Healy 1997). There is clear evidence, therefore, to link dynamics in deer populations to oak seedling establishment and survival.

Other wildlife populations experienced dramatic fluctuations over the time period relevant to oak-maple dynamics. The passenger pigeon *Ectopistes migratorius* may have played a role in oak dominance in presettlement forests. Before the mid-1800s, its population was estimated to be 3–5 billion individuals, with the primary breeding area in the central and northern hardwood regions of the Eastern Deciduous Forest. The weight of roosting birds would lead to substantial breakage in the forest canopy, increasing light to the forest floor, and potentially favoring shade-intolerant species such as oak (Ellsworth and McComb 2003). The passenger pigeon was driven to extinction, eliminating what may have been an important disturbance factor in oak forests (Ellsworth and McComb 2003). Oak acorns are associated with a complex web of interactions among weevils, birds, rodents and other species (Semel and Anderson 1988, McShea 2000). Long-term population numbers of some of these species are not known; however, many species that are influential on oak seedling establishment and persistence had population changes similar to white-tailed deer. For instance, the wild turkey *Meleagris gallopavo*, which may impact oak regeneration through disturbance of the forest floor and frugivory, went through a population dynamic that included extremely low numbers in the early 1900s, and rapidly rebounding populations since then (Kennemar et al. 1992, Steffen et al. 2002, Rinkes and McCarthy 2007). The pressure on acorn crops created by rebounding wildlife populations may have been exacerbated by the loss of American chestnut mast associated with the blight.

We found a noteworthy synchrony between regeneration failure in oaks and changing populations of wildlife species known to influence forest succession. These species were uncommon during the early 1900s when oak forests were initiating across much of the region. During this time, the absence of these seedling browsers and seed predators could have facilitated oak regeneration. In the mid-to-late 1900s, when oak regeneration problems began, the population numbers of many species were rapidly increasing (Healy 1997). Lines of inquiry that could further understanding of the role of wildlife populations in oak forest dynamics

include: 1) reconstructions of species-specific patterns in long-term tree recruitment in areas with a good record of deer populations, 2) experimental studies that assess particular activities of wildlife species on oak forest dynamics (Rinkes and McCarthy 2007), and 3) experiments that manipulate density of herbivores while simultaneously examining other forest disturbances (e.g. studies of burning associated with herbivore density manipulation).

Multiple interacting ecosystem drivers and oak forest dynamics

A rich literature supports the idea of an ongoing, widespread, oak-maple dynamic in the Eastern Deciduous Forest (Fig. 1; Lorimer 1984, Parker et al. 1985, Host et al. 1987, Crow 1988, Pallardy et al. 1988, Shotola et al. 1992, McEwan and Muller 2006). This transition began in the early 1900s and has, apparently, accelerated since then (Fig. 5a; Abrams 1998, Nowacki and Abrams 2008). In working to understand the drivers of this process, at the broadest level, we found that the oak-maple dynamic is associated with a substantial climatic shift – from a time of frequent, severe, multi-year droughts to a period of increased moisture availability and cooler summer temperatures (Fig. 5b). The oak-maple transition also took place within the context of broad-scale and intensive land-use change. Forest cover was drastically reduced during a period of intensive disturbance when oak forests were establishing, but this was followed in many areas by reforestation synchronous with increasing dominance by maples (Fig. 5c).

Fire was an important process during the establishment and recruitment of trees that currently compose the overstory of many oak-dominated forests in eastern North America (Abrams 1992; Fig. 5d). Fire was present in presettlement oak forests (McCarthy et al. 2001, Shumway et al. 2001, Guyette et al. 2002), although its extent, frequency and intensity is currently unknown due to a lack of annually resolved fire-history data from that period in these forests (Fig. 5d). Fire peaked in intensity and frequency during the early 1900s, and then virtually vanished as a landscape process with the advent of fire suppression, forest fragmentation and other cultural changes (Fig. 5d; Brose et al. 2001). During this same time period, mammalian herbivores and frugivores populations were highly dynamic (Fig. 5e). The passenger pigeon was probably a significant disturbance factor in eastern forests, and its populations crashed from exceedingly large numbers to extinction in a brief period of time (Fig. 5e). This was followed by similar declines in the populations of herbivores and frugivores, whose populations have been rebounding during the period in which oak regeneration has been limited. Any of these landscape processes (Fig. 5a–e) are individually sufficient to influence long-term forest dynamics.

In conclusion, our literature assessment and new analyses, suggest that eastern oak forests are in a state of reaction to multiple, interacting, ecosystem drivers. The factors involved in oak-to-maple dynamics include, but are not limited to, drought regime dynamics, land-use change, changes in fire, the loss of American chestnut, and changing herbivore populations. Future work that tests

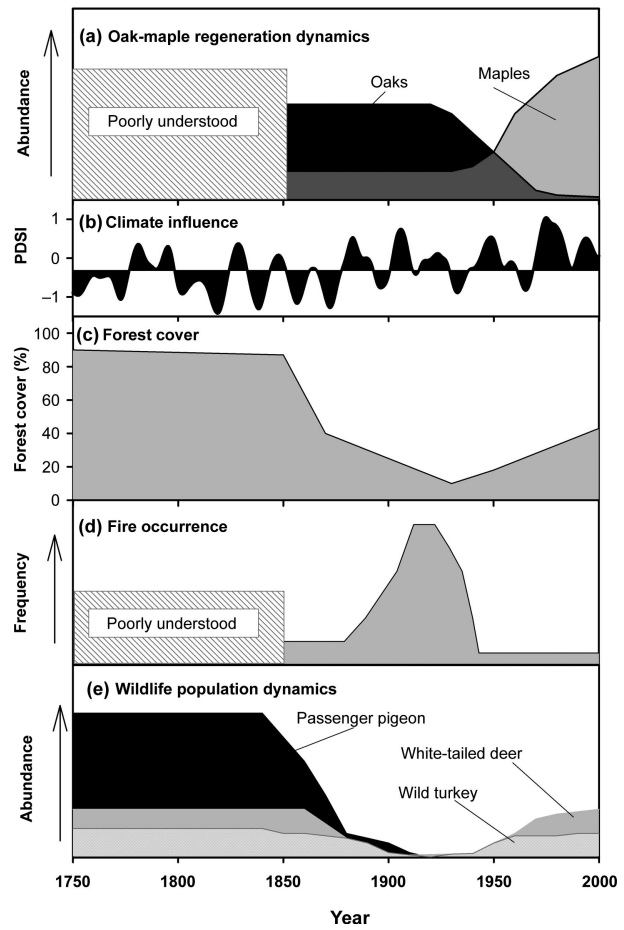


Figure 5. Time-line of concomitant changes in oak forests since 1750. All panels are estimates derived from historical data and are intended to illustrate general trends. Panel (a) derives from the oak-maple dynamics literature and depicts regeneration dynamics. Panel (b) is a Palmer Drought Severity Index (PDSI) reconstruction using a 15-yr spline (see text for detail; Fig. 2b). Forest cover (panel c) is estimated from the Historical Census Browser (2004). Fire occurrence (panel d) is a general estimate derived from the literature, and particularly the fire-history reconstruction of McEwan et al. (2007). Wildlife population data from representative species are derived from historical accounts (see text for details), and depicts general, relative, trends (Panel e).

alternative hypotheses within the multiple interacting drivers framework could profitably expand our understanding of oak-to-maple succession, and further elucidate the complex mechanisms of deciduous forest dynamics.

Acknowledgements – Robert Muller, Morgan Varner, Amy Hessl, Sarah Alverson, Amy Hruska, Amy Goff-Yates, Mary Dyer and two anonymous reviewers provided helpful comments on previous versions of this manuscript.

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