

Mesophication of Oak Landscapes: Evidence, Knowledge Gaps, and Future Research

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Pyrophytic oak landscapes across the central and eastern United States are losing dominance as shade-tolerant, fire-sensitive, or opportunistic tree species encroach into these ecosystems in the absence of periodic, low-intensity surface fires. Mesophication, a hypothesized process initiated by intentional fire exclusion by which these encroaching species progressively create conditions favorable for their own persistence at the expense of pyrophytic species, is commonly cited as causing this structural and compositional transition. However, many questions remain regarding mesophication and its role in declining oak dominance. In the present article, we review support and key knowledge gaps for the mesophication hypothesis. We then pose avenues for future research that consider which tree species and tree traits create self-perpetuating conditions and under what conditions tree-level processes might affect forest flammability at broader scales. Our goal is to promote research that can better inform restoration and conservation of oak ecosystems experiencing structural and compositional shifts across the region.

Keywords: fire-adapted traits, flammability, mesophytic, prescribed fire, pyrophytic

Ppyrophytic, historically open-canopied oak savannas and woodlands across the central and eastern United States continue to shift structure and composition to dense, multilayered, closed-canopy forests of shade-tolerant, fire-sensitive, or opportunistic tree species (Hanberry et al. 2012, 2020b). Oaks (*Quercus* L. spp.) have dominated this region since warming and drying began following the last glaciation event (8,000–16,000 years ago; Ballard et al. 2017), covering 40%–70% of the region prior to European settlement in a woodland or savanna structure with a sparse midstory and robust, species-rich herbaceous understory (Hanberry and Nowacki 2016). Over the past several decades, however, oak importance value (IV) has declined (Fei et al. 2011, Knott et al. 2019). Mature overstory oaks account for increasing volume as they grow larger, and although seedlings establish and persist in the understory, oaks are largely absent from sapling and midstory size classes (Fei et al. 2011, Dyer and Hutchinson 2019). Instead, shade-tolerant species such as maple (*Acer* L. spp.), American beech (*Fagus grandifolia* Ehrh.), and elm (*Ulmus* L. spp.) occupy a well-developed sapling layer and midstory with increased IV coincident with a substantial reduction in understory light (less than 5%; Brose 2008) and the decline of oaks (Fei and Steiner 2007, Brewer 2016, Knott et al. 2019). Under certain conditions, canopy disturbance (e.g., windthrow, tree harvest)

encourages more opportunistic species such as tulip poplar (*Liriodendron tulipifera* L.), sweetgum (*Liquidambar styraciflua* L.), birch (*Betula* L. spp.), cherry (*Prunus* L. spp.), and sassafras (*Sassafras albidum* (Nutt.) Nees; Abrams and Nowacki 1992, Holzmüller et al. 2012, Iverson et al. 2017a).

The sapling and midstory “oak bottleneck” (Nowacki and Abrams 1992) reported across various site conditions (e.g., figure 1) indicates that these encroaching tree species will eventually replace pyrophytic oaks following mortality of the current oak overstory, generating concern about the long-term consequences for ecosystem function. Oaks are a foundation genus because of their dominance and pronounced effects on ecosystem processes (Hanberry and Nowacki 2016). Acorns constitute a portion of at least 96 avian and mammal species’ diets and are a critical winter food source for many species (McShea 2000, McShea et al. 2007). Oaks are the most important North American genus for insect herbivores, providing an essential base for terrestrial food chains (Tallamy and Shropshire 2009). The loss of oak savannas and woodlands will decrease abundance of countless wildlife species that use open-canopied areas for nesting, brooding cover, and foraging (Rodewald and Abrams 2002, Reidy et al. 2014, Starbuck et al. 2015, Harper et al. 2016, Hanberry et al. 2020b). Declining oak dominance will also alter biogeochemical cycles, because oaks strongly

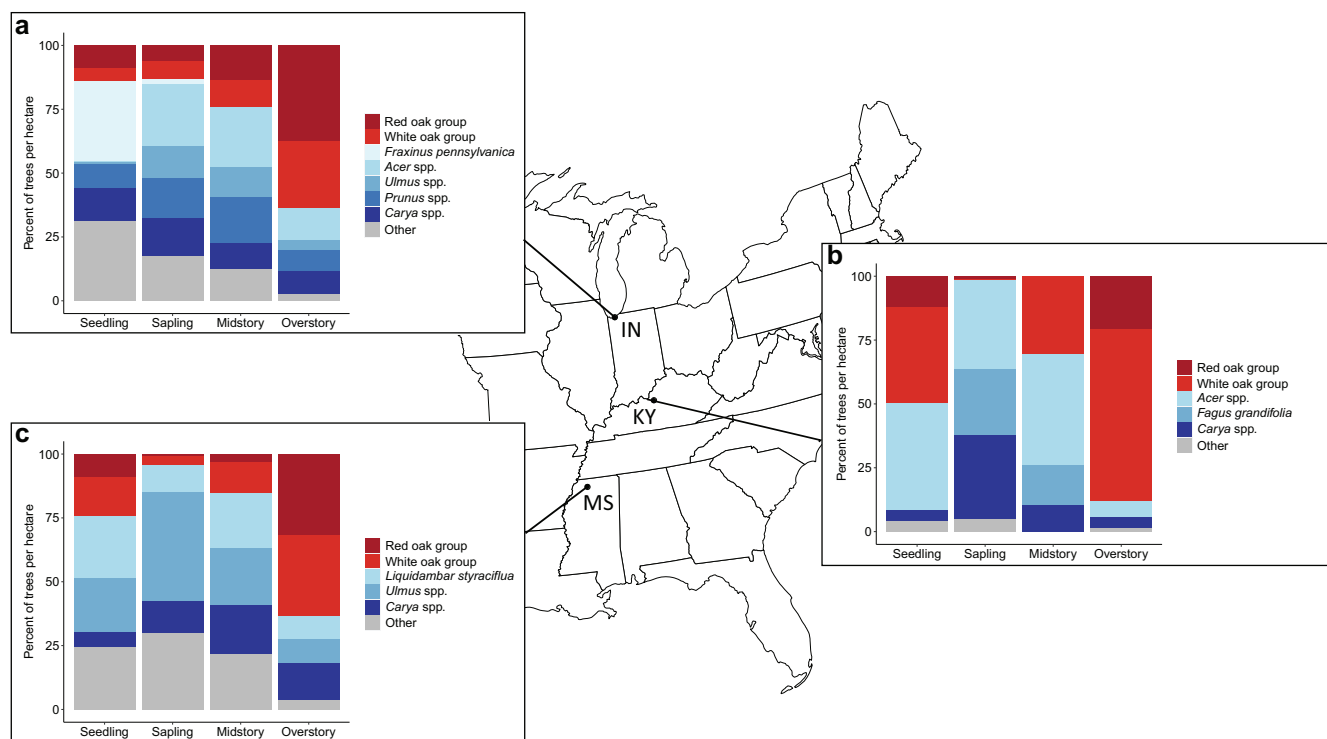


Figure 1. Case studies in upland oak forest sites in the central and eastern United States (from north to south) at (a) Indiana Dunes National Park, Indiana (IN), (Sanders and Grochowski 2013), (b) Bernheim Arboretum and Research Forest, Kentucky (KY), and (c) Spirit Hill Farm, Mississippi (MS), indicate a bottleneck in the sapling (less than 10 centimeters diameter at breast height [cm DBH]) and midstory (10–20 cm DBH) size class distribution of oak trees. Overstory (more than 20 cm DBH) oak trees and seedlings (shorter than DBH height) are often abundant. These data suggest low oak recruitment and indicate that shade-tolerant, fire-sensitive, or opportunistic tree species are poised to replace oaks following overstory mortality.

influence precipitation distribution (Alexander and Arthur 2010, Siegert et al. 2019) and nutrient cycling through their crown, bark, and leaf litter traits (Alexander and Arthur 2010, 2014). Therefore, declining oak dominance and transition to a closed-canopy forest state will inevitably lead to a loss of multiple ecosystem functions.

Intentional fire exclusion beginning in the 1930s is often cited as an important cause of declining oak dominance. The “fire-oak hypothesis” posits that periodic, low- to moderate-intensity surface fires maintain upland oak dominance by reducing competition from fire-sensitive species and maintaining a highly flammable herbaceous fuel bed beneath a relatively open canopy (Abrams 1992). Oak adaptations, which often include thick bark, prolific resprouting capacity, low to moderate shade tolerance, and drought tolerance, facilitate their persistence in fire-prone environments (Abrams et al. 1995, Brewer 2001). Once established, oak crown, bark, and leaf litter traits perpetuate a warmer, drier, and more flammable understory, promoting oak self-replacement under conditions of periodic fire (figure 2a; Lorimer 1985, Nowacki and Abrams 2008, Dickinson et al. 2016, Varner et al. 2016). In contrast, the “mesophication hypothesis” (figure 2b; Nowacki and Abrams 2008) proposes that fire exclusion encourages the densification of stands by understory and midstory

individuals of shade-tolerant, fire-sensitive, or highly opportunistic tree species (i.e., mesophytes), whose traits create shadier, cooler, and wetter understory conditions and a leaf litter fuel bed that dampens fire, allowing mesophytes to self-perpetuate while hindering oaks and other pyrophytic species (e.g., *Pinus* L. spp.). The fire-oak and mesophication hypotheses differ from traditional forest successional theory, which focuses primarily on changing light conditions and individual species’ shade tolerance (Watt 1947, Peet and Christensen 1987), because they recognize that feedback loops between trees and their understory environment modify growing conditions and fire potential.

In recent decades, the fire-oak hypothesis has gained considerable attention among researchers and managers, with prescribed fire being increasingly used across the region to promote oak regeneration (Hutchinson et al. 2005b, Arthur et al. 2012, Brose et al. 2013, Waldrop et al. 2016). Many studies show that fire alone is insufficient to promote oak regeneration because the low-intensity late dormant-season fires often conducted in this region have little impact on stand structure and understory light (Arthur et al. 2015, Carter et al. 2015), only top-kill small trees (less than 10 centimeters diameter at breast height), and do not reduce resprouting from competition (Waldrop et al. 2016). Furthermore, many closed-canopy

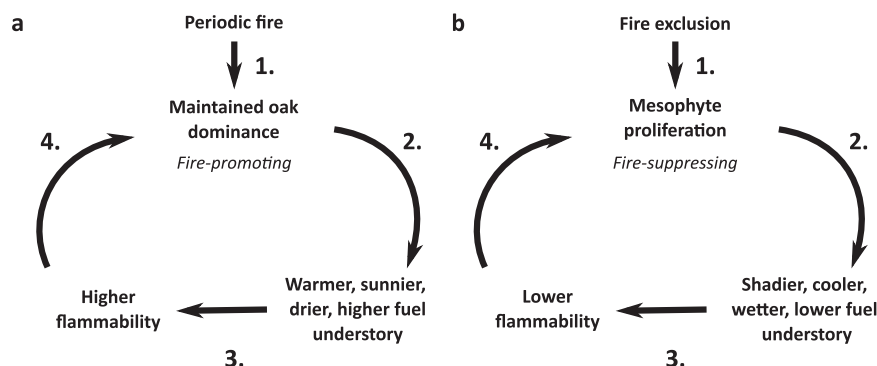


Figure 2. Conceptual models depicting the various self-perpetuating phases of (a) the fire-oak hypothesis (Abrams 1992) and (b) the mesophication hypothesis (Nowacki and Abrams 2008).

stands in which these fires are implemented have insufficient oak advance regeneration (Dey and Fan 2009), a prerequisite for oak success (Johnson et al. 2019). Consequently, multiple disturbances (e.g., fire plus thinning or herbicide) that open the canopy and reduce competition create the best opportunity for advance regeneration to accumulate and become competitive. Oak recruitment into the canopy is then possible after a fire-free interval, which permits additional oak development and fire resistance, followed by additional overstory removal (Dey and Schweitzer 2018). Despite the utility of these generalized prescriptions, fire remains an evasive tool to promote oak regeneration on many sites (Johnson et al. 2019). Therefore, there remains a need for experimental studies that assess how fire and other silvicultural practices can be applied to restore desired forest conditions.

Maintenance and restoration of oak landscapes will be best informed through a better understanding of the role of fire exclusion and fire-vegetation feedback loops in initiating and sustaining the structural and compositional shifts observed today. Researchers often attribute diminishing oak dominance to mesophication, but they are usually referring only to the well-documented proliferation of fire-sensitive, shade-tolerant, or other opportunistic tree species and decline of oaks (figure 2b, phase 1), with little empirical evidence for other parts of the hypothesis (figure 2b, phases 2–4). Without this support, the observed shifts in forest structure and composition could just as likely result from alternative mechanisms (e.g., climate change; McEwan et al. 2011, Pederson et al. 2015, Dyer and Hutchinson 2019) or their interactions with fire exclusion. Furthermore, there is a paucity of information regarding the potential self-perpetuating mechanisms that unfold to affect forest flammability once mesophytes establish, but these feedback loops could help explain why implementing fire and reducing mesophyte encroachment are increasingly difficult on many sites (Ryan et al. 2013, Dickinson et al. 2016, Kreye et al. 2018b, Hanberry et al. 2020a). In the present article, our primary objectives are to review each phase of the mesophication process, explore support for the hypothesis and key knowledge gaps, and pose additional

avenues for research on the role of mesophication in developing current and future oak landscapes. Ultimately, our goal is to encourage research that can better inform restoration and conservation of oak ecosystems across the central and eastern United States.

A step-by-step look at the mesophication hypothesis

Below, we discuss each phase of the hypothesized mesophication process as shown in figure 2b.

Phase 1: Fire exclusion, mesophyte spread, and declining oak dominance.

Phase 1 of the mesophication hypothesis (figure 2b) speculates that long-term fire exclusion from oak landscapes fostered mesophyte proliferation, leading to increased competition with oaks and reduced oak recruitment into the canopy. This idea has been the focus of several reviews detailing the historical and ecological rationale behind the fire-oak hypothesis (e.g., Abrams 1992, Nowacki and Abrams 2008, Arthur et al. 2012, Brose et al. 2013). Key links between oak dominance and fire prevalence are paleoecological pollen and charcoal records that show that oak presence increased following the last glacial event during a period of climate warming and drying that was often accompanied by widespread fire (Hart et al. 2008, Ballard et al. 2017); upland oak morphological and physiological traits indicate their evolution with fire, often including thick bark, efficient wounding response, and precocious growth of sprouting stems following a top-kill when not shaded (Abrams 1992, Varner et al. 2016); dendrochronological analyses of fire scars confirm widespread, frequent fires during or just prior to the establishment of current upland oak overstories (Guyette et al. 2006, McEwan et al. 2007, 2011, Stambaugh et al. 2016); stand reconstructions reveal failed oak regeneration and increased mesophyte establishment following fire exclusion in uplands beginning in the 1930s (Shumway et al. 2001, Hutchinson et al. 2008); and witness tree and historical accounts document a prevalence of oak-dominated open savannas and woodlands and a scarcity of mesophytic closed-canopy forests in uplands (Brewer 2001, Hanberry et al. 2012, 2014, Dey and Kabrick 2015). Combined, this evidence points to a strong influence of fire exclusion on observed structural and compositional shifts across upland oak landscapes.

Although fire exclusion undoubtedly contributed to these shifts, it is important to recognize that other environmental and biological changes that co-occurred with fire exclusion could have exacerbated these shifts by limiting fire potential or favoring mesophytes over oaks. Many of these have been reviewed elsewhere (e.g., McEwan et al. 2011, Pederson et al. 2015, Vose and Elliott 2016, Abrams and Nowacki 2019), including a recent review by Hanberry et al. (2020a) that details mechanisms, patterns, and evidence

for several potential drivers of forest shifts; therefore, we limit our discussion to important points. Notably, climate has been exceptionally wet with reduced drought severity and frequency during the last century (McEwan et al. 2011, Pederson et al. 2013, 2015, Kutta and Hubbart 2018). This may have reduced fire frequency and favored growth and survival of diffuse-porous mesophytes over ring-porous oaks (Elliott et al. 2015, Pederson et al. 2015, Maxwell and Harley 2017, Au et al. 2020). Repeated high grading and other selection systems would have favored shade-tolerant species over oaks in the absence of fire (Abrams and Nowacki 1992, Dey 2014). Herbivory from white-tailed deer (*Odocoileus virginianus* Zimmermann) has limited oak regeneration on many sites (Thomas-Van Gundy et al. 2014, McWilliams et al. 2018, Kelly 2019); fire exclusion may have reduced available forage, making oaks a preferred browse, subsequently shifting the competitive advantage to mesophytes. Prior to European settlement, however, herbivory by eastern wood bison (*Bison bison pennsylvanicus* Shoemaker), eastern elk, (*Cervus canadensis canadensis* Erxleben), and other herbivores common in the region likely interacted with fire to maintain dominance of pyrophytic trees and an open-canopied structure (Hanberry 2019, Hanberry et al. 2020b, Mueller et al. 2020), similar to other savanna and woodland ecosystems (Scogings and Sankaran 2020). The loss of passenger pigeons (*Ectopistes migratorius* Linnaeus) and American chestnut (*Castanea dentata* (Marshall) Borkh.) may have hindered oaks by altering canopy structure and forest flammability. Large flocks of passenger pigeons perched atop forest canopies created pulses of woody fuels and large canopy gaps by breaking limbs (Ellsworth and McComb 2003), and American chestnut was among the most flammable upland species in the region (Elliott and Swank 2008, Kane et al. 2020). Pronounced atmospheric nitrogen deposition in the central and eastern United States since industrialization (approximately in the 1850s) has also been associated with increased growth and survival of some mesophytes compared to oaks (Thomas et al. 2010, Wallace et al. 2007). Therefore, even if fire is the keystone disturbance that maintained oak savannas and woodlands (Hanberry et al. 2020a), other factors likely interacted to initiate oak decline in the past. We contend that successfully managing for upland oak regeneration today depends most on understanding current-day limitations to fire, which may hinge on the vegetation–fire feedback loops that act to promote or suppress fire as discussed below in phases 2–4.

Phase 2: Mesophytes create a shadier, cooler, more humid understory with higher fuel moisture, and lower fuel loads than oaks. During phase 2 of the mesophication hypothesis (figure 2b), mesophytes create a shadier, and consequently cooler and more humid, understory with higher fuel moisture and consistently lower fuel loads than oaks. A shadier, and consequently cooler, understory is typically assumed because species encroaching into oak landscapes are often shade-tolerant, and shade-tolerant species usually have higher

leaf area and a deeper crown than oaks (Babl et al. 2020). These traits maximize light capture and survival in low light (Valladares and Niinemets 2008) but also obstruct light from reaching the forest floor (Canham et al. 1994), especially with stand densification. High tree density and deep shade can promote higher understory humidity by reducing wind speeds, decreasing forest floor vapor pressure deficit, and reducing evaporation rates (Siegert and Levia 2011). Reduced drying rates in these conditions can then increase fine fuel moisture (Kreye et al. 2018a). However, fuel moisture variations under light conditions and structural arrangements common beneath oaks and mesophytes have not been investigated.

Mesophytes could further increase fuel moisture by influencing how rainwater is captured and spatially redistributed to the forest floor. Differences in bark morphology, bark water storage capacity, and crown geometry affect rainwater partitioning into stemflow (i.e., water that runs down trunks), throughfall (i.e., water that drips from crowns), and interception (i.e., water captured by crowns; Park and Cameron 2008, Van Stan et al. 2016). Smoother and thinner-barked species such as red maple (*Acer rubrum* L.) and American beech funnel 2–20 times more rainfall as stemflow compared to rougher-barked oak species (Alexander and Arthur 2010, Siegert and Levia 2014), which may create a zone of higher fine fuel moisture in the immediate area surrounding their boles (figure 3a, 3b). However, the denser, deeper crowns of mesophytes relative to oaks also increase canopy interception and reduce throughfall inputs (Siegert et al. 2019). Even though the shallower, sparser crowns of oaks may increase throughfall, the small increase in throughfall inputs is likely dispersed across a large portion of the forest floor and more readily evaporated. Whether or not this imbalance of canopy water inputs between oaks and mesophytes affects fuel moisture heterogeneity in a way that dampens fire remains unknown, but canopy influences may be especially important in the relatively moist forest ecosystems of this region.

However, differences in rooting depth and water use efficiency between mesophytes and oaks could also affect fuel moisture. Soil moisture in the rooting zone directly contributes to live fuel (i.e., ground-layer vegetation) moisture by determining water availability for transpiration and tissue hydration (Qi et al. 2012) and affects moisture of dead fine fuels (i.e., leaf litter) by acting as a lower boundary for water and energy (i.e., soil heat) exchange (Matthews et al. 2006). Compared to oaks, mesophytes are often more shallowly rooted (Gaines et al. 2015, Matheny et al. 2017), suggesting more water withdrawal from shallower soil horizons, with maples using about twice as much water as oaks (Wullschleger et al. 2001, Von Allmen et al. 2015). This may lead to drier soils beneath mesophytes that may reduce fine fuel moisture and increase flammability. Differences in tree water use are also affected by climate, because the water use of mesophytes can decline to equal or lower than oaks under soil moisture stress (Meinzer et al. 2013, Von Allmen et al. 2015). Notably, seasonal water use depends on

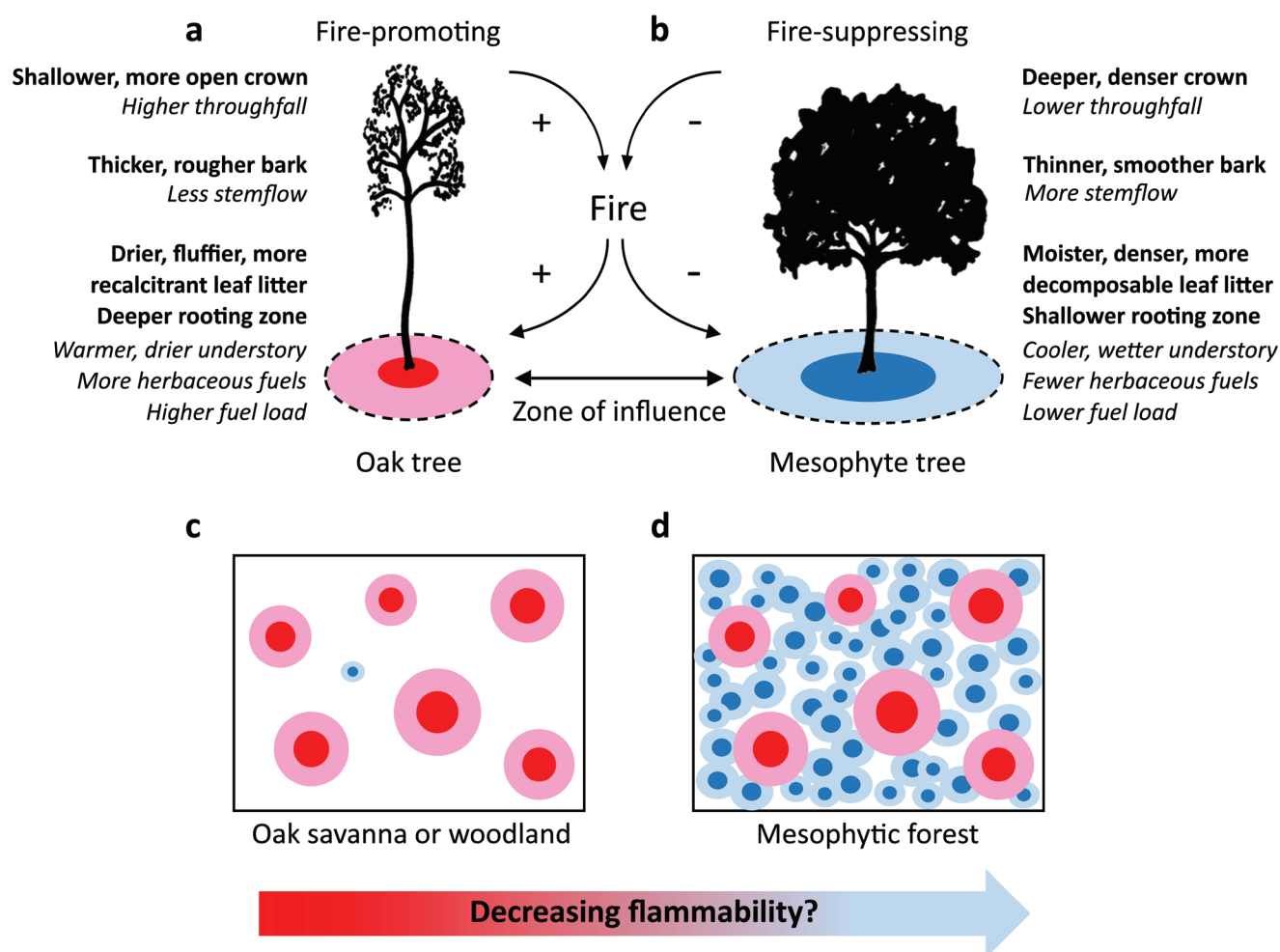


Figure 3. Tree traits (in bold) and potential contributions (in italics) to vegetation–fire feedback loops that act to either promote or suppress fire through changes in understory microclimate, throughfall or stemflow inputs, root water uptake, and fuel type, moisture, and load within zones of influences beneath the crowns of individual oak (a) and mesophyte (b) trees. Lighter colors represent individual tree traits affecting a zone at least the size of the crown, whereas darker colored zones are affected also by bark traits. Oaks, which are generally larger, have wider zones than mesophytes. These tree-level zones likely interact with those of other tree species and ground-layer vegetation to create a gradient in forest flammability that differs between relatively open-canopied oak savannas and woodlands (c) and closed-canopy, mesophytic forests (d), and therefore potential for prescribed fire restoration at the stand scale.

differing physiological constraints among species that are likely site specific (Meinzer et al. 2013). For example, water use declined more in overstory (Matheny et al. 2017) and midstory red maple (Oren and Pataki 2001) compared to co-occurring overstory oaks during soil drydown periods. Therefore, fine fuel moisture, especially in the rooting zone of trees, could partially reflect tree species' differences in water uptake from surface soils, but the net impact of these contributions has not been explored empirically.

Mesophytes may also increase fuel moisture and reduce fuel loads through their leaf litter and wood traits (Nowacki and Abrams 2008). For example, leaf litter of mesophytic species often adsorbs more water or dries slower compared to pyrophytic species, including oaks (Kreye et al.

2013). Increasing the presence of mesophytic litter into pyrophytic oak litter fuel beds increases the amount of water adsorbed, resulting in wetter litter beds throughout the drying process until beds reach equilibrium moisture content (Kreye et al. 2018b, McDaniel et al. 2021). These differential moisture responses are linked to differences in leaf morphology. Mesophytes tend to have smaller, thinner leaves that do not curl after abscission (figure 4), leading to higher fuelbed bulk density and moisture retention (Dickinson et al. 2016, Babl et al. 2020). Mesophytes also often have leaf litter that decomposes faster than that of upland oaks (Alexander and Arthur 2014), which could reduce fuel loads (Dickinson et al. 2016) and increase fuel moisture by reducing litter interception and increasing soil

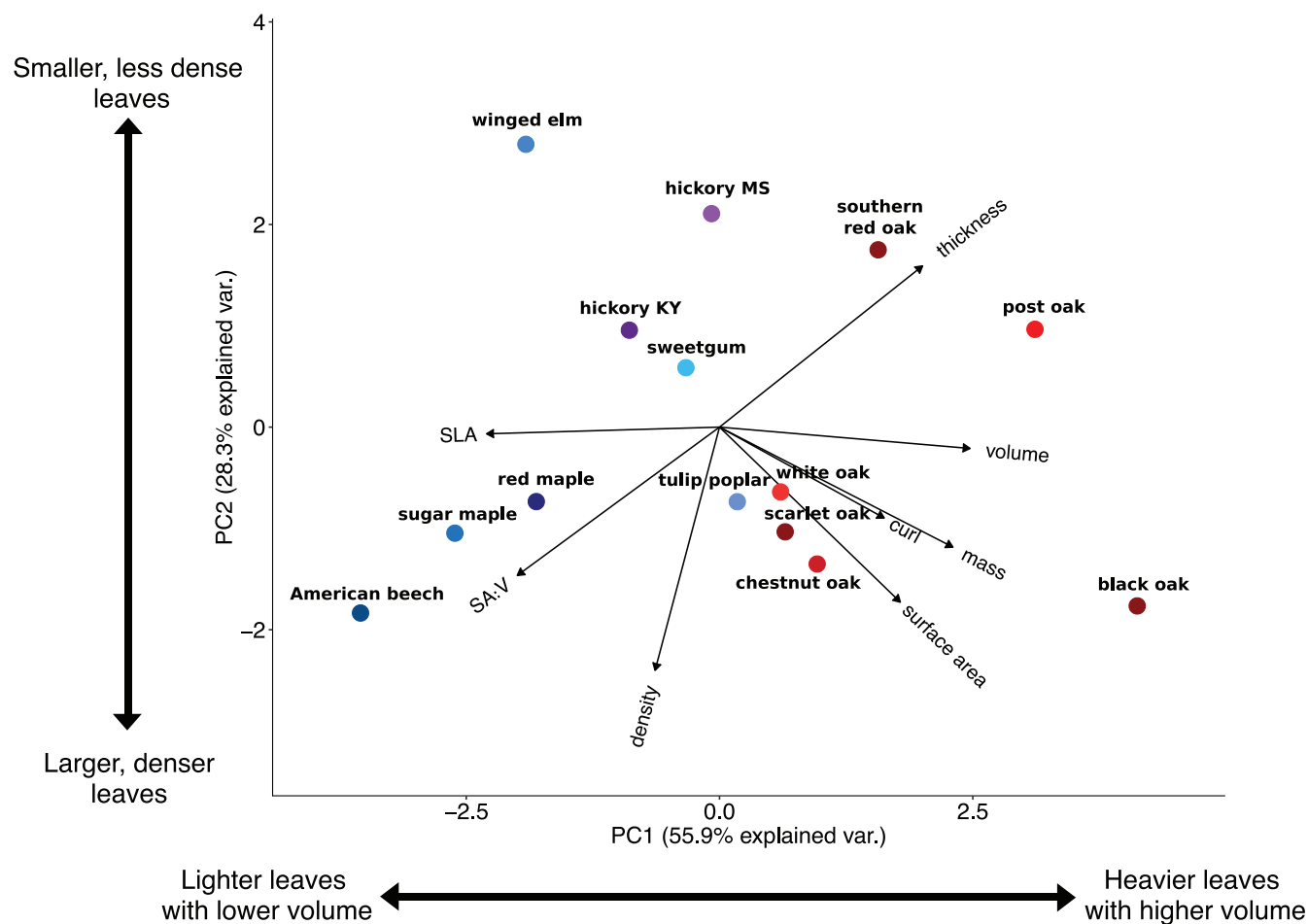


Figure 4. Principal component analysis (PCA) biplot of litter traits measured on leaf litter of oaks (shades of red) and nonoaks (shades of blue and purple) collected at Bernheim Arboretum and Research Forest, Kentucky (KY), in the United States (black oak, chestnut oak, scarlet oak, white oak, tulip poplar, red maple, sugar maple, American beech, hickory [pignut hickory, mockernut hickory]; see Babl et al. 2020 and the supplemental material for details) and Spirit Hill Farm, Mississippi (MS), in the United States (post oak, southern red oak, sweetgum, winged elm, hickory [pignut hickory, mockernut hickory, bitternut hickory, shagbark hickory]; see McDaniel et al. 2021 and the supplemental material for details). Points indicate the mean PCA score for each species, and the length of the vector arrow represents the strength of the associated trait's correlation with principal components. Abbreviations: Mass, dry mass; SLA, specific leaf area; SA:V, surface area to volume ratio.

organic matter content (Berg 2000), which increase water infiltration and soil water holding capacity (Hudson 1994). Oaks also tend to generate more coarse woody debris and produce higher density wood, leading to slower wood decomposition rates compared to nonoaks such as hickories (*Carya* L. spp.) and maples (MacMillan 1988), but wood traits and their impacts on fuel conditions have been less explored than those of leaf litter.

Although several studies focus on leaf litter differences among mesophyte and oak species (Kane et al. 2008, Kreye et al. 2013, 2018b, Babl et al. 2020, McDaniel et al. 2021), a more shaded understory beneath mesophytes could also reduce fuel moisture and loads by altering ground-layer vegetation cover. Closed-canopy forests typically contain sparse, species-poor ground-layer vegetation (Hutchinson et al. 2005a, Brewer et al. 2015). Warm-season grasses

(e.g., *Andropogon* L. spp., *Schizachyrium* Nees spp.) that were common in the understory of fire-maintained, oak-dominated open woodlands in the Mid-South and in less mesic locations (Brewer 2001, Brewer et al. 2015) are now largely restricted to edges, canopy gaps, or xeric sites of fire-excluded oak forests because these grasses do not tolerate shade and deep leaf litter (Maynard and Brewer 2013). Furthermore, leaf litter of bunchgrasses common in open-canopied woodlands or grasslands often decomposes more slowly than that of oaks (Osono et al. 2014), indicating ground-layer vegetation with a significant bunchgrass component may be key for sustaining fire in open-canopied, oak-dominated systems (Brewer and Rogers 2006).

Phase 3: A shadier, cooler, wetter, and lower fuel understory environment beneath mesophytes reduces flammability. During phase 3

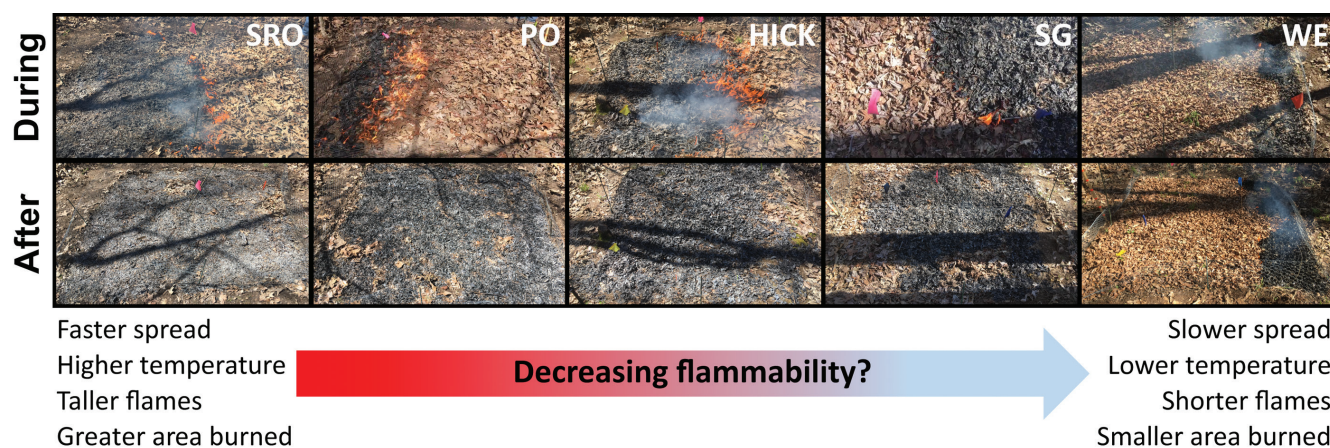


Figure 5. Leaf litter flammability experiment conducted at Spirit Hill Farm, Mississippi, in the United States (see McDaniel et al. 2021 and the supplemental material for details). The images show plots (3 square meters) of constructed single species fuel beds during (the top panels) and after (the bottom panels) a late dormant season burn conducted in March 2019.

Abbreviations: HICK, hickory (including pignut, mockernut, shagbark); PO, post oak; SG, sweetgum; SRO, southern red oak; WE, winged elm.

of the mesophication process (figure 2b), the shadier, cooler, and wetter understory environment created by mesophytes reduces flammability because of both overstory shading and the compositional and structural shifts that affect leaf morphology and fuel bed moisture and loads (see phase 2). Laboratory experiments that burned dry leaf litter of several oak, pine, and mesophytic tree species reveal consistent patterns. Upland pines and oaks burn with greater intensity and higher fuel consumption, and extinguish more rapidly (Kane et al. 2008, Dickinson et al. 2016). In contrast, nonoak species such as sweetgum and eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch.), and lowland oak species, such as water oak (*Q. nigra* L.), burn poorly, with shorter flames and lower fuel consumption (Mola et al. 2014, Kreye et al. 2018b). In laboratory studies that manipulated moisture conditions to represent humid conditions common in the region (Kreye et al. 2018a), burning across drying sequences or at contrasting “wet versus dry” conditions led to similar patterns observed from dry lab burns, suggesting flammability differences persist under different moisture regimes. Species that dry more rapidly also tend to burn with greater intensity (Kreye et al. 2013, Mola et al. 2014). Dickinson and colleagues (2016) manipulated leaf litter fuel beds to be oak- or maple-dominated over 4 years in the field and found maple fuel beds had less mass and higher bulk density than oak fuel beds, resulting in lower flammability in laboratory experiments. Late dormant season burns of single-species fuel beds of oaks and encroaching nonoak species under field conditions revealed similar trends (figure 5; McDaniel et al. 2021). The mechanisms for these oak–mesophyte differences across studies likely include leaf morphology and fuelbed packing (see phase 2; figure 4).

In addition to tree leaf litter, herbaceous species that respond positively to canopy openings in oak forests and

woodlands (e.g., warm-season grasses) can affect fire behavior through surface fuel decomposition rates, seasonal variation in flammability, and other fuel characteristics (Bragg 1982, Platt et al. 1991, Brewer and Rogers 2006). Late summer wildfires in north Mississippi forests (mostly dominated by oaks and pine) were associated with dry conditions or the presence of warm-season grasses (Brewer and Rogers 2006), a trend supported by relative failures in implementing late growing-season prescribed fires in closed-canopy oak forests lacking warm-season grasses (Brewer et al. 2015).

Phase 4: Shadier, cooler, and moister conditions and reduced flammability beneath mesophytes promote mesophyte regeneration while hindering oak regeneration. Phase 4 of the mesophication process posits that shadier, cooler, and moister conditions with reduced flammability beneath mesophytes promote mesophyte regeneration and spread while hindering that of oaks (figure 2b). In general, shade-tolerant mesophytes have higher growth and photosynthetic rates and survival under shadier, moister conditions and more rapidly take advantage of changing light availability (Gottschalk 1994) compared to principally shade-intolerant upland oaks. In contrast, oaks are most competitive under drier, higher light conditions (Dey and Parker 1997, McDonald et al. 2003) and slower to respond to changing light levels (Dillaway et al. 2007). Oaks do well on more mesic sites, but only if light levels are sufficiently high and mesophyte competition is low, which is typically not the case on current-day sites that lack fire. Consequently, oaks are often outcompeted on high-quality mesic sites, resulting in successful regeneration only on lower quality xeric sites in the absence of fire (Kabrick et al. 2008). In the few studies assessing whether mesophyte canopies are associated with increased regeneration of conspecifics versus oaks and vice versa, mesophyte regeneration had high survival and growth beneath both

mesophyte and oak overstories, whereas oak regeneration did well beneath conspecifics but poorly beneath mesophytes (Canham et al. 1994, McDonald et al. 2003, Allen et al. 2018). These patterns are often associated with crown traits and differences in the light environment beneath mesophytes and oaks (see phase 1). However, changes in mycorrhizal associations with fire exclusion and changing species composition could also affect oak regeneration. Fire-adapted oaks associate with ectomycorrhizal (ECM) fungi, whereas many mesophytes associate with arbuscular (AM) mycorrhizae. These associations create fuel conditions that promote (ECM) or suppress (AM) fire, and they are also essential for seedling growth and survival (Carpenter et al. 2020). For example, oak seedlings planted near stump sprouts of mature oaks had greater ECM colonization and growth and higher concentrations of nitrogen and phosphorus than those planted near stump sprouts of mature maples (Dickie et al. 2002). We know of no studies directly linking increased survival or growth of conspecifics beneath mesophytes to reduced flammability.

Future research and conclusions

Testing the mesophication hypothesis and its role in declining oak dominance can help us plan for when and where fire and other management tools most effectively promote oak regeneration. To this end, we need to further explore several key aspects of the hypothesis:

To what degree do tree-scale, self-perpetuating processes influence flammability and tree regeneration? The present article highlights how key tree traits act to either reinforce or suppress fire (figure 3), but our understanding of these processes remains limited. For example, strong evidence exists for reduced flammability with the loss of pyrophytic fine fuels, from both leaf litter (figure 5) and herbaceous groundcover, but major gaps remain in scaling these small-scale, mostly laboratory-based studies to *in situ* wildland fires. In addition, there are likely unexplored temporal components affecting the degree to which species' impacts on flammability matter. For instance, species differences in leaf litter fuels may be more pronounced immediately following litterfall and decline over time because of decomposition (Stambaugh et al. 2011, Weir and Limb 2013), potentially making tree species' effects on flammability more evident during early versus late dormant or growing season fires. Furthermore, increased stemflow inputs near thinner-barked mesophytes could create a zone of high fine fuel moisture near the bole of the tree, at least temporarily following a rainfall event, but no studies have connected this tree trait and precipitation characteristics to flammability. A zone of dampened flammability adjacent to thinner-barked mesophytes could be especially important in these relatively moist forest ecosystems given that many prescribed fires are conducted within a few days of a precipitation event (Wade and Lunsford 1989, Waldrop and Goodrick 2012).

How do vegetation–fire feedback loops vary among tree species? We typically group tree species into broad

categories (e.g., pyrophyte versus mesophyte, hardwood versus conifer), but species clearly differ in traits associated with flammability (figure 4), ability to persist in fire-prone environments (Varner et al. 2016), and tolerance of varying climatic conditions (Iverson et al. 2019). We need to understand these differences and then develop modeling approaches that take into account contributing factors to determine which encroaching species are most problematic in terms of their impacts on forest flammability and growing conditions and their resistance to various restoration approaches. For example, red maple's "generalist" abilities (Abrams 1998) and prolific resprouting capacity even following multiple fires (Schweitzer et al. 2019) allow this "mesophyte" to do well across a variety of sites and climates (Iverson et al. 2017b, Maxwell et al. 2019), whereas sugar maple (*Acer saccharum* Marshall), also often categorized as a "mesophyte," is much less prolific. As such, more aggressive management efforts such as thinning plus herbicide or growing season burns (Brose and Van Lear 1998) may be needed to reduce the clump resprouting of red maple but might be unnecessary if the encroaching mesophyte were sugar maple. Furthermore, most models that predict flammability rely on general fuel types (e.g., hardwood litter) or plant functional types (e.g., temperate broadleaf deciduous) that cannot capture species-level differences in flammability, although they clearly exist. Therefore, understanding species-level interactions with the fire regime and other factors such as climate could help managers devise targeted approaches for promoting desired species while controlling problematic ones.

Can these self-perpetuating processes propagate to stand and landscape scales? Individual trees of any size affect understory conditions through their crown, bark, and leaf litter traits, i.e., "zones of influence" (figure 3a, b). If understory conditions affect fuel moisture and loads, then these tree-level zones should eventually converge and interact with those of other tree species and ground-layer vegetation to influence forest flammability (figure 3c, 3d), and therefore potential for prescribed fire restoration at the stand or landscape scale. Understanding these inherently spatial processes will likely require development of spatial models to tease out the complexity of interacting individuals of various species and sizes.

Are these self-perpetuating elements strong enough to overcome broad scale phenomena, such as climate change and its interaction with fire potential? Future increases in drought frequency and severity are likely to favor oaks over mesophytes on many sites (Vose and Elliott 2016, Iverson et al. 2017b) both by increasing fire activity and by limiting the growth of water-loving mesophytes (Brzostek et al. 2014). Flammability differences between oaks and mesophytes also may be masked under conditions of drought (Stambaugh et al. 2011) when growth responses to these conditions may be more pronounced (Lafon and Quiring 2012). However, if fires are more common during drought years and fires are only needed every few years to keep encroaching mesophyte

density low, flammability differences may be inconsequential. However, our ability to use prescribed fire could be limited during drought because of an increased interface between urban space and wildland and corresponding safety concerns (Mitchell et al. 2014, Vose and Elliott 2016). Alternatively, some areas in the region are predicted to experience heavy, pulsed rainfall events with climate change (Walsh et al. 2014), which could foster mesophyte spread on these sites or limit the timing or location of prescribed fire implementation. An increased understanding of tree-level, self-perpetuating processes and their temporal and spatial dynamics could clarify their importance during extreme climatic events.

Are the forest structural and compositional shifts observed today simply the result of fire exclusion or do other factors come into play? For example, implementation of dormant season prescribed fire in closed-canopy stands where most oak regeneration is suppressed has little positive impact, but these are the conditions under which most fires in the region are conducted (Brose et al. 2013). In contrast, growing season fires, especially when conducted in relatively open stands, have shown promise for reducing mesophyte competition, releasing oak reproduction, promoting an herbaceous fuel bed (Brose and Van Lear 1998, Gruchy et al. 2009, Brose et al. 2013), and providing a pulse of high-quality forage when nutritional demands of herbivores such as white-tailed deer are high (Lashley et al. 2011, 2015), which could be important for curtailing browse impacts on oak regeneration, particularly if mesophytes and oaks differ in their nutritional status. However, the potential critical importance of fire phenology and this vegetation–fire–herbivory interaction have been largely overlooked, likely because growing season fires are often avoided because of narrow burn windows (Chiodi et al. 2018) and high fuel moisture under shading from leaf cover (Harper et al. 2016). If growing season fires are key for promoting oaks over mesophytes, then management efforts could aim to create the conditions most conducive to implementing these fires (e.g., canopy removal to increase light to understory, reduce relative humidity, and dry out fuels).

In our review, we found considerable support for mesophication's role in declining oak dominance, but questions remain regarding each phase of the hypothesized mesophication process. Current upland oak forests with dominant oak overstories, dense, mesophytic midstories and sapling layers, and leaf litter-dominated fine fuels are arguably a novel ecosystem state. Shifting this state back to open-canopied savannas and woodlands with an herbaceous fuel bed by reintroducing fire alone, the primary disturbance thought to induce this shift, has been shown mostly ineffective (Arthur et al. 2012, Brose et al. 2013). This may be because there has been insufficient time for fire restoration efforts to have an effect, because fire exclusion interacts with other factors to limit oak regeneration, or because feedback loops between mesophytes and their understory reduce flammability and promote their own persistence, decreasing the effectiveness

of fire restoration and mesophyte removal. Therefore, there remains a need for wide-ranging discussions among fire ecologists and practitioners about how to successfully sustain or restore desired composition, structure, and ecological state using innovative and integrated approaches that focus not only on restoring fire but that account for fire's interaction with climate change, wildlife, and vegetation traits that act to reinforce or suppress fire's role across the landscape.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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