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BERLYN REVIEW

The changing role of fire in mediating the relationships among oaks, grasslands, mesic temperate forests, and boreal forests in the Lake States

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ABSTRACT

Historically, oak forests and woodlands intergraded with southern boreal forest, temperate mesic forest, and grassland biomes, forming complex fire-mediated relationships in the Great Lakes region of Minnesota, Wisconsin, and Michigan, USA. Variability in fire recurrence intervals allowed oaks to mix with grasses or with mesic forest species in areas with high (2–10 yr) or moderate (several decades) fire frequencies, respectively. In the southern boreal forest, oak colonization was limited by cold climate. In recent decades former savannas have been largely converted to agricultural fields and the fate of oak remnants is controlled by human fire use. In mesic temperate forests, fire exclusion, wetter climate, and deer browsing have led to mesophication and increasing maple dominance. With ongoing warming, however, mesophication could reverse due to increased drought and fire frequency, and earthworm invasion, which enhances the understory environment for oak seedlings. Oaks are also likely to invade large tracts of southern boreal forest. However, deer grazing on oak seedlings will partially negate the positive influence of warming and fire. On balance, oaks have a more positive future outlook in the Lake States, as the climate becomes more favorable to oaks compared to temperate mesic and boreal forests.

KEYWORDS

Boreal forest; climate change; fire; maple; mesophication; oak; savanna; temperate forest

Introduction

Oak species interweave with the three dominant biomes of the central U.S. Lake States region: (1) evergreen forests of pine, spruce, and fir, including boreal forests and cold-temperate pine forests; (2) temperate deciduous mesic forests; and (3) grasslands, often forming oak savannas and intermingling patches of oak woodland and grassland (Curtis, 1959; Heinselman, 1996; Kruger & Reich, 1997). These interactions with other vegetation types constitute what we refer to in this paper as the oak triangle, with oak in the center and boreal forest, mesic temperate forest and grassland vegetation at the three vertices (Figure 1). This is not a geographical triangle, but instead describes the regional-scale niche of oak; oak is a component of the southern boreal forest, temperate forest, and grassland biomes, but is not a biome in itself (Frelich,

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Figure 1. The oak triangle, showing the relationships between oak and temperate mesic forest, boreal forest, and grassland/savanna. Cold-temperate pine forests and savannas are intermediate between the temperate and boreal biomes.

Reich, & Peterson, 2015). The relationships within the oak triangle have historically been regulated by fire regime and its interactions with soil type, land use, physiography, regional variation in climate, and life history characteristics of the plant species involved. This historic role of fire has been altered directly by fire exclusion, and indirectly by land-use change, and will be further altered in the future by a warming climate. Furthermore, environmental changes such as invasive species and white-tailed deer (*Odocoileus virginianus* Zimmermann, hereafter referred to as deer) grazing will work to change the way that fire interacts with oak and mediates the relationship of oak with the vegetation types in the triangle. Therefore, the future regional-scale niche of oak will be a function of multiple environmental changes including altered fire regimes and relationships with fire.

Mesophication of oak forests—characterized mainly by expansion of maple—due to fire exclusion, a regionally wetter summer climate, and deer preferentially grazing on oak seedlings, has been one of the major changes in oaks forests in the eastern United States in recent decades (McEwan, Dyer, & Pederson, 2011; Nowacki & Abrams, 2008). A second major change has been the conversion of oak savannas on sites with high soil quality to other land uses, particularly row crop agriculture, leaving only very small remnants (0.02% of the original extent in the Midwestern U.S.), mostly on sand plains (Nuzzo, 1986). These two major changes, and the uncertain future of the southern boreal forest (Frelich & Reich, 2010), raise significant issues regarding the future of oak in a warmer climate. The objective of this review and synthesis paper is to examine the historical and future dynamics of the oak triangle in the context of warming climate and the changing roles of fire. We will explore the following questions: (1) will mesophication reverse in a warmer climate and if so what role will fire play? (2) although few remain, will oak savannas expand or contract and will restoration attempts be easier or harder? And (3) how will other environmental factors interact with fire and will the net result reinforce or retard the driving force of climate change in oak forests of the Lake States region (Minnesota, Wisconsin, and Michigan, USA)?

The oak species involved in the region of interest are principally northern red oak (*Quercus rubra* L.), bur oak (*Q. macrocarpa* Michx.), northern pin oak (*Q. ellipsoidalis* E.J. Hill), white oak (*Q. alba* L.), and black oak (*Q. velutina* Lam.). Other species found in association with oaks include sugar maple (*Acer saccharum* Marshall), red maple (*A. rubrum* L.), American basswood (*Tilia Americana* L.), yellow birch (*Betula alleghaniensis* Britton), hemlock (*Tsuga Canadensis* (L.) Carrière), and beech (*Fagus grandifolia* Ehrh.) in the mesic forests; white pine (*Pinus strobus* L.) and red pine (*P. resinosa* Aiton) in transitional temperate-boreal forests; jack pine (*P. banksiana* Lambert), white spruce (*Picea glauca* (Moench) Voss), black spruce *(P. mariana* (Miller) BSP), balsam fir (*Abies balsamea* (L.) Miller), paper birch (*Betula papyrifera* Marshall), and aspen (*Populus tremuloides* Michx.) in the boreal forest; grasses such as little bluestem (*Schizachyrium scoparium* (Michx.) Nash), big bluestem (*Andropogon gerardii* Vitman), and many forbs in native grasslands; and exotic cool season (C_3) grasses in abandoned-field grasslands. The review begins with a general discussion of how fire historically regulated the relationship between oak and the three vegetation types of the oak triangle, and then examines how other environmental factors affect the role of fire and the interactions between oak and the other three vegetation types, and how climate change may further impact the overall niche of oak.

Variability in fire frequency and the oak triangle

Species traits, such as bark thickness and ability to sprout, interact with the temporal and spatial variability of fire to regulate the balance between vegetation types along a gradient of fire frequency (Figure 2). The duration of heat from flames necessary to kill cambium beneath the bark of a tree is a function of the square of bark thickness, and resistance to heat that may girdle the tree can range from a minute or less for small saplings of thin-

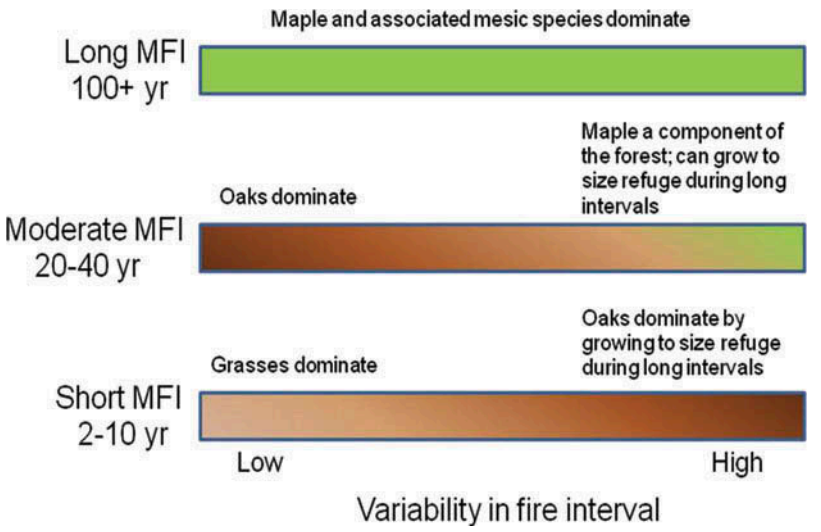

Figure 2. Fire frequency (MFI = mean fire frequency) and variability as regulators of the relationships of oak forest with grasslands and temperate mesic forests. Note that oaks can dominate in areas with short average fire intervals and high variability or with moderate fire intervals and low variability.

barked species to 30 min or more for large individuals of thick-barked species (Michaletz & Johnson, 2007). Furthermore, variability in fire frequency potentially works in favor of species that need longer intervals in an interaction of two species groups where one group can withstand shorter intervals than the second group (Figure 2).

For oaks, the ability to form seedlings that re-sprout from underground rootstocks (also known as grubs; Curis, 1959), allows persistence of oaks in very frequently burned grasslands. These individuals can then take advantage of a longer-than-average interval between fires due to chance climatic events or spatial variability, where small areas at spatial extents from a few meters (boulders, gopher mounds, fuel variability) to tens of meters (slope, aspect, wet spots) experience lower fire intensity than the surrounding areas during a burn (Franklin, Robertson, & Fralish, 1997; Thaxton & Platt, 2006), to grow to a size at which the bark thickness will protect them from further damage. Reaching a size that confers resistance to fire-induced mortality is referred to here as a 'size refuge'. Oaks that reach a size refuge can go on to become mature trees while fires continue to occur. Perfect spatial and temporal uniformity of fire at short intervals of a few years would exclude oaks, but this can rarely be achieved in nature or even in areas with regular prescribed fire—therefore some oaks can persist (Peterson & Reich, 2001). Shrubs such as American hazel (*Corylus Americana* Walter) also interact with fire frequency (Pelc, Montgomery, & Reich, 2011) and the shrubs can inhibit oak regeneration, making oak savannas a mixture of shrubs, grasses, and trees that can be unstable over time, at least at the relatively small spatial extents of most study plots (Brudvig & Asbjornsen, 2008).

At the mesic forest vertex of the triangle, mean fire intervals were historically much longer, and in contrast to the grassland vertex, variability in fire interval works against oak. Although regular mean fire intervals of 20–40 yr would work against mesic species such as sugar maple and basswood (which have very thin bark and high likelihood of fire-induced mortality for the first few decades of life), a chance longer interval of 50–80 yr would allow some tree species of mesic habitats to become mature individuals that could reach a size refuge. This allows these species to become a permanent member of the forest community, with the potential for coexistence of mesic species such as sugar maple and American basswood in an oak-dominated forest (Abrams, Ruffner, & DeMeo, 1998). Exclusion of fire for a century or more can allow mesic species to completely take over the understory (Aldrich, Parker, Romero-Severson, & Michler, 2005). In such forests, multiple fires at relatively short intervals over several decades would be necessary to eliminate maple reproduction for a long enough time for a new cohort of oak to become established to ensure successful restoration to oak (Albrecht & McCarthy, 2006; McEwan, Hutchinson, Long, Ford, & McCarthy, 2007). As fire intervals continue to lengthen, more and more mesic species will be successful, with feedbacks on fuel structure and humidity of the forest floor environment that reinforce mesic species dominance (Abrams, 2005). When fire intervals exceed a few centuries, the issue is whether any oak will persist, although moderately shade-tolerant oak species such as northern red oak and white oak can persist at low levels of dominance through occasional capture of canopy gaps. Stands of oak can also exist embedded within a landscape matrix of maple-basswood forest as a result of rare severe fires that occur in wind-thrown mesic forests (Frelich et al., 2015).

Historically, fire frequency likely regulated the balance between oaks and pines in areas with a climate suitable for both groups of species. There is no fire frequency (or intensity) that would eliminate oaks but allow pines to continue growing in cold-temperate areas of

the northern Lake States (such as mixed white, red and jack pine forests, or the pine-oak barrens described by Curis, 1959). On the other hand, a high fire frequency can keep pines out. Pines are unable to root sprout as compared to oaks. Furthermore, the absence of fire for 20–30 yr is required for white pine to grow large enough to escape mortality in a subsequent fire—that much time is needed for pines to grow tall enough so that foliage is not scorched, with bark thick enough to avoid basal scorch (Tester, Starfield, & Frelich, 1997). High-intensity fires characteristic of red and white pine-dominated forests top-kill oaks, but cannot exclude oaks since they can persist as grubs. On savanna-like pine and oak barrens, frequent low-intensity fires leave oak root systems alive and, due to short flame lengths, cannot scorch well-established open-coned jack pines enough to kill them. Recruitment to large, resistant size classes for both pine and oak probably depended on irregularly variable temporal and spatial characteristics of the fire regime, allowing coexistence due to the equal contributions of pine resistance to fire versus oak persistence through fire (Nowacki & Abrams, 2008).

Moving north into the southern boreal forests, oaks become limited by climate. Winter minimum temperatures in the range of −40 to −50°C cause death of cambial cells and trunk injury even to very hardy deciduous trees such as oaks (Sakai & Weiser, 1973). Winter minimum temperatures in this range were historically common in southern boreal forests such as the Boundary Waters Canoe Area Wilderness of northern Minnesota (Heinselman, 1996). The absence of oaks along the north shore of Lake Superior in Minnesota, where winter minimum temperatures never reach the lows that they do inland from the Great Lakes, shows that cool summer conditions and limited growing degree days can also throw the competitive balance from temperate oak and maple species to boreal species, with fire or extreme cold having little impact on this aspect of the temperate-boreal ecotone (Fisichelli, Frelich, & Reich, 2012; Walker, Davis, & Sugita, 2002). Therefore, oaks are either stunted by winter cold compared to the pines that grow much taller, and/or by short summers in the southern boreal forest, and acorn production is a limiting factor (Morin, Augspurger, & Chuine, 2007). The oaks can survive high-intensity fires that are common in boreal jack pine forests, but cannot dominate due to their short stature and inability to compete with the massive post-fire recruitment of jack pine.

The oak triangle in a changing environment

Oak forest dynamics have been on a trajectory of change over the last three centuries (McEwan et al., 2011). Frequent burning by Native Americans and Passenger pigeon (*Ectopistes migratorius* L.) consumption of red oak acorns, which favored white oaks over red oaks, are no longer in force across the landscape. Red oak did well after European settlement (ca 1875–1940) due to cutting of pine or mesic forests, followed by slash burning and abandonment of land, in a landscape context with low levels of deer grazing on oak seedlings and minimal consumption of acorns by deer, black bear (*Ursus americanus* Pallus), and turkey (*Meleagris gallopavo* L.) (McEwan et al., 2011). Since the period of red oak establishment, fires have been very infrequent, facilitating concurrent mesophication and invasion of second-growth oak forests by maple and other mesic tree species. In the southern parts of the Lake States, the reduction in fire frequency occurred due to exclusion of fire by a severely fragmented landscape with isolated patches of oak

forest and savanna in an agricultural matrix, combined with fire suppression. In the contiguously forested parts of the region—that regenerated back to forests either directly after clearing or later on after abandonment of farms—fire frequency decreased due to suppression, wetter climate, and changes in understory environment to more shady and humid conditions.

A trajectory of change will continue in the future. The region is projected to experience warming of 2–3° C by the mid-21st century and perhaps twice that by the end of the century, accompanied by increasing frequency and intensity of droughts (Galatowitsch, Frelich, & Phillips-Mao, 2009). Deer will become more abundant in the northern areas where their numbers were previously limited by cold conditions.

European earthworm invasions are reengineering the region's soils. Except for coarse sands and acidic soils, the earthworms occupy >80% of the Lake States' landscape, and are likely to occupy all suitable soils within a few decades (Fisichelli, Frelich, Reich, & Eisenhauer, 2013). The principal impacts of earthworm invasion relevant to oak forests are consumption of the organic horizon (which helps warm and dry the soil), leaching of the key nutrients N and P, and facilitation of invasive plant species that can compete with oak seedlings (Frelich et al., 2012). In addition, there are strong interactive effects among deer, earthworms, and invasive plants (Dávalos, Nuzzo, & Blossey, 2015) that may affect oak seedling success, although their impact on oak has not been studied. Two introduced tree diseases and pests of oak, sudden oak death (*Phytopthora ramorum* Werres, De Cock, & Man in't Veld) and bur oak blight (*Tubakia iowensis* sp.nov.), could eventually play an important role in oak forests of the region; however, little is known about how these may affect oaks in the Lake States at this time. A third introduced disease, oak wilt (*Ceratocystis fagacearum*), has infected substantial acreages of oak forests in the southern Lake States Region, and although it is absent from the large contiguously forested parts of the region, it is not known how the disease will spread in a warmer climate. The net effect of all of these changes will alter the relationship of the oak species group with fire, and consequently its relationships with grasslands, mesic, and boreal forests.

Warmer temperatures will favor oak in interactions with both boreal species and mesic tree species (Heinselman, 1996; Reich et al., 2015, Figure 3; Walker et al., 2002). Increased drought frequency and intensity will work directly in favor of oak in interactions or competition with other tree species in boreal and mesic temperate forests, and these direct effects will be reinforced by the indirect effects of drought through increased fire frequency; similar patterns of change occurred when drought frequency increased in the past (Booth, Jackson, Sousa, Sullivan, Mickley & Clifford, 2012). Future fire frequency and behavior will be impacted by landscape configuration created by human settlement, ownership, and land-use patterns. In southern Lake States areas dominated by cities and row crops, fires are unable to spread across the landscape and firefighters have excellent and rapid access to fires by roads, allowing effective suppression. The vast majority of forest lands in the region, however, are in large contiguous tracts of public forest ownership in national, state, and county forests in the northern Lake States, where fire control is very difficult or impossible during severe droughts, allowing large wildfires to spread across the landscape in recent years (Frelich & Reich, 2010). Thus, in areas currently occupied by southern boreal or northern mesic forest, future fires are likely to increase in frequency and size, which will open space for the spread of oak species (northern red oak, northern pin oak, bur oak), which are already present in low to intermediate numbers in

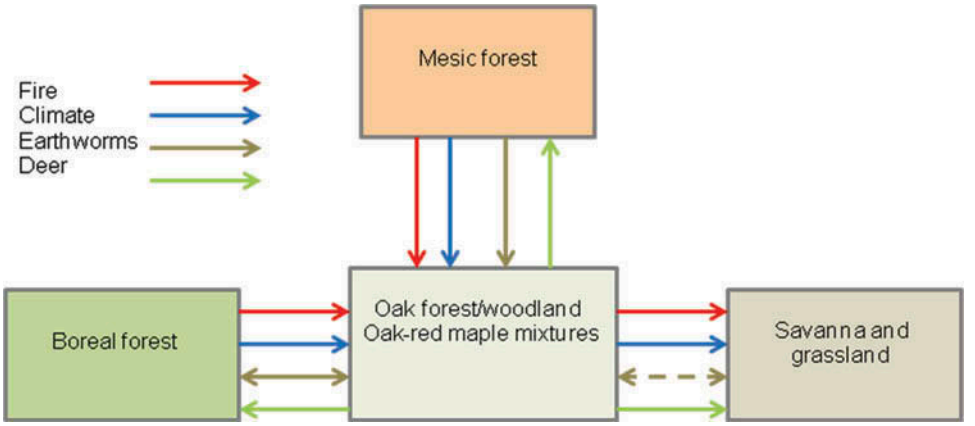

Figure 3. Relationship between oak and mesic forest, boreal forest and grassland/savanna, as influenced by drivers of change expected to have large impacts during the 21st century. Dotted line indicates the hypothesized relationship that is not yet supported by published research.

numerous locations within these forests (Curis, 1959; Friedman & Reich, 2005; Heinselman, 1996). Oaks can spread rapidly due to distribution by the Blue jay (*Cyanocitta cristata* L.), which can move acorns up to 1.9 km in a single flight (Johnson & Webb, 1989). However, it may still take oak species like white oak and black oak (the latter currently confined to the southern Lake States) decades to a few centuries to reach the northern portions of the temperate mesic forest and southern boreal forest (Matthews, Iverson, Prasad, Peters, & Rodewald, 2011).

In the southern boreal forest, warmer summers (and the accompanying longer growing seasons allowing maturation of acorns) and lack of winter damage to the cambium of the oaks will allow oaks to use the growing season more efficiently than they can now. This will lead to large increases in height growth (Reich et al., 2015) and mature stature of oaks, allowing them to effectively compete with boreal conifers in post-fire regeneration. Oaks are not browsed by the current large herbivore, the moose (*Alces alces* L.), but are preferred for browsing by deer, which are likely to replace moose as the climate becomes warmer (Frelich et al., 2012). Therefore, deer could be a force opposing the effects of a warming climate and more frequent fires on tree colonization patterns (Fisichelli et al., 2012), by reducing the height growth of oaks and possibly preventing the recruitment of oaks into the future canopy (Figure 3). However, the relative lack of human fragmentation in the southern boreal forest and the presence of wolves will likely lead to a mosaic of deer densities across the landscape, so that oaks are likely to be able to take advantage of future fires in many locations.

Earthworm invasion will have contrasting effects on oak success in invading the southern boreal forest. Successful germination of northern red oak is enhanced by lack of leaf litter (Garcia, Bañuelos, & Houle, 2002), so that European earthworms will help oaks by creating bare mineral soil seedbed conditions as deciduous species increase in abundance in the boreal forest, even in the absence of fire. However, the lack of leaf litter will also reduce fuel loads and contiguity, possibly muting the expected future increases in fire frequency to an unknown extent. In addition, red maple is somewhat more tolerant to cold than the oak species invading the southern boreal forest, as suggested by its slightly

more northerly range limit (Walters & Yawney, 1990), and is equally responsive to warming and longer growing season (Reich et al., 2015); moreover, the species is also able to take advantage of forest floor conditions created by earthworms. Therefore, red maple may have a head start prior to the expected increase in oak abundance.

The mesophication (i.e. mapleization) of oak forests that has been so widespread in the temperate forest biome in recent decades could be reversed by future warmer temperatures and higher drought frequency. For example, sugar maple-dominated forests in Sylvania Wilderness Area in Upper Michigan are already experiencing a lack of reproduction due to a combination of drought and deer grazing (Salk et al., 2011). Earthworms could also help reverse mesophication by accomplishing part of the effects of fire via removing the duff layer. Earthworms also discriminate heavily against sugar maple, a major competitor of oaks on mesic sites (Frelich et al., 2012). However, one thing earthworms cannot do that fire can is to kill the other major maple species, red maple. Red maple germination is enhanced by a forest floor environment with exposed mineral soil, and is more tolerant of the relatively dry and nutrient-poor surface soil conditions created by earthworms than sugar maple (Walters & Yawney, 1990). As previously mentioned, earthworms could potentially oppose future increases in fire frequency by altering the fuel bed on the forest floor. Therefore, earthworms are likely to favor red maple along with oaks in the future temperate mesic forest, just as mentioned above for the boreal forest. In addition, red maple also can re-sprout after one or two fires, as well as attain large enough sizes to resist the types of low-intensity fires that commonly occur on mesic sites (Albrecht & McCarthy, 2006), and has the ability to rapidly capture gaps on a variety of types of sites (Fei & Steiner, 2009). Thus, unless higher-intensity fires occur in the future, oak–red maple mixtures are an expected outcome of the suite of future environmental changes in both the current southern boreal and northern temperate forests. Higher-intensity fires could be facilitated by creating fuel beds with high masses, such as tree tops after a harvest or canopy wind throw, and by expected future increases in drought severity.

The expected changes in the future environment will have significant impacts on the conservation of now rare oak savannas (Figure 3). Increasing drought frequency will work directly against oak in interactions with grasses (Davis et al., 1999), and the neighborhood effects of grasses (Wright et al., 2013), deer grazing, and in some cases low nutrients and/or lack of mycorrhizae (Dickie, Schnitzer, Reich, & Hobbie, 2007; Peterson & Reich, 2001) will work together to reduce the aggressiveness with which oak invades grasslands in the future. Because most of the savanna landscape has been converted to farms, these interactions mostly only take place on a few sites that were not suitable for agriculture. The rarity of these sites, however, makes the outcome of changing climate on them more important to the conservation of native communities than indicated by the small proportion of the landscape they occupy. The role of fire on these sites is mostly controlled by cultural behavior (Guyette, Muzika, & Dey, 2002), especially the desire to maintain a rare vegetation type, which is opposed by costs and the negative impacts on the surrounding lands associated with conducting prescribed burns on small isolated parcels of land. However, vast tracts of contiguous publicly owned forest land just to the north of the remnant savannas, including sand plains and shallow-to-bedrock sites such as the Boundary Waters Canoe Area Wilderness, represent a potentially large acreage of land that, without the threat of conversion to agriculture, could support future oak savannas in a warmer climate (Frelich & Reich, 2010). Rapid change from forest to savanna caused by

cascades of multiple factors influenced by climate, including tree–grass interactions, fuel-fire feedbacks, and drought-induced mortality of trees, has been shown to be a reasonable expectation from the paleoecological record of response to past climate changes and the modeling of future climates (Jeffers, Bonsall, Brooks, & Willis, 2011; Umbanhowar, Jr., Camill, Geiss & Teed, 2006).

Conclusions

The interactions among oak species, boreal forest, temperate mesic forest, and grasslands have historically been continuously shifting with changing climate and human land use, and will continue to do so in the future. The spatial pattern and extent of the future oak component of the three major biomes depend not only on climate and fire, but also on how the role of fire will be changed by novel environmental filters such as deer browsing and earthworm invasion. More research is needed on how deer and earthworms, as well as exotic diseases of oak, will respond to a warming climate and interact with fire.

Climate change will favor an overall northward and eastward expansion in potential suitable habitat for oak species (Iverson, Prasad, Matthews, & Peters, 2008). This is likely to include an expanded niche for oaks within the mesic forests in the interior of the temperate forest biome, and replacement of southern boreal forest by oaks and red maple (Frelich et al., 2012; Reich et al., 2015). Full or partial reversal of mesophication (depending on the magnitude of warming) within the temperate forest biome is expected, although it is hard to imagine not ending up with mixed red maple–oak forests in the future due to size refuge effects of red maple that protect mature trees from fire, and disease, deer, and earthworm effects that will partially oppose the positive effects of increased fire frequency on oak seedling recruitment.

Despite these difficulties, when taken in the context of the landscape of the Lake States, these factors only partially oppose the positive impacts of fire on oak species. Combined with climate change, the net impact of future fires is likely to enhance the positive effects of fires that do occur on oak species. In addition, there will likely be more opportunities for ecologically significant natural and prescribed fires (Frelich et al., 2015). This will help land managers restore oak as a component of the mesic forest, and potentially to enhance the natural savannification of areas currently occupied by boreal and temperate forests. This in turn may enhance—or at least minimize the loss of—diversity at the landscape scale due to projected climate change in the Lake States during the 21st century.

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