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FORUM: ISSUES, MANAGEMENT, POLICY, AND OPINIONS

OAK, FIRE, AND GLOBAL CHANGE IN THE EASTERN USA: WHAT MIGHT THE FUTURE HOLD?

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ABSTRACT

The pace of environmental and socioeconomic change over the past 100 years has been rapid. Changes in fire regimes, climate, and land use have shaped the structure and function of most forest ecosystems, including oak (*Quercus* spp. L.) forests in the eastern United States. New stressors such as air pollution and invasive species have contributed to and interacted with climate and fire to alter current forest conditions. While changing fire regimes have altered species composition of the current forest, oak regeneration is constrained by many factors that may affect future forests. Over the remainder of the twenty-first century, an accelerating pace of climate and socioeconomic changes will influence the future range of variation in Eastern oak forests. Some of these impacts will be direct, such as changes in tree growth rates, while other impacts will be indirect, such as new disturbance regimes. While it is likely that fire will be important in shaping oak forests in the twenty-first century, it is less clear exactly what that role will be. For example, it is uncertain whether our current scientific knowledge on the use of prescribed fire in oak forests will be applicable under

RESUMEN

El ritmo de los cambios ambientales y socioeconómicos en los últimos 100 años ha sido rápido. Cambios en los regímenes de fuego, en el clima y en el uso de la tierra han modelado la estructura y función de la mayoría de los ecosistemas boscosos incluyendo los bosques de roble (*Quercus* spp. L.) en el este de los EEUU. Nuevos agentes de estrés como la contaminación del aire y las especies invasoras han contribuido e interactuado con el clima y el fuego para alterar las condiciones actuales reinantes en el bosque. Mientras que el cambio en los regímenes de fuego han alterado la composición de especies en el bosque actual, la regeneración del roble está condicionada por varios factores que podrían afectar los bosques futuros. En lo que queda del siglo XXI, un ritmo acelerado de cambios climáticos y socioeconómicos influirán en el futuro rango de variación en los bosques orientales de roble. Algunos de estos impactos van a ser directos, como cambios en las tasas de crecimiento, mientras que otros impactos van a ser indirectos como nuevos regímenes de disturbios. Si bien es muy probable que el fuego sea un importante modelador de los bosques de roble en el siglo XXI, no está tan claro cuál será su rol. Por ejemplo, es incierto si nuestro conocimiento científico actual sobre el uso de quemas prescriptas novel climate and changing socioeconomic conditions. We propose that the combination of climate change, wildfire, and other disturbances will create stand conditions that favor oaks with or without management. However, management intervention (e.g., prescribed fire, thinning, or a combination) could reduce wildfire hazard, particularly in the wildland-urban interface, and create more desirable stand conditions that are resilient to future stressors such as changing precipitation patterns and warmer temperatures.

será aplicable bajo las nuevas condiciones climáticas y los cambios socioeconómicos. Nosotros proponemos que la combinación del cambio climático, los incendios y otros disturbios crearán condiciones en el rodal que van a favorecer los robles con o sin manejo. Sin embargo, las intervenciones en el manejo (por ej. quemas prescriptas, raleos o una combinación), podrían reducir el peligro de incendios, particularmente en la interfaz urbano-rural y crear condiciones deseables en el rodal que sean resilientes a futuros agentes de estrés como cambios en los patrones de precipitación y las altas temperaturas.

Keywords: *Acer*, climate change, drought, prescribed fire, *Quercus*

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INTRODUCTION

Contemporary oak (*Quercus* spp. L.) forests in the eastern United States are undergoing changes that include a greater abundance of mesophytic, fire-sensitive, and shade-tolerant tree species (Nowacki and Abrams 2008, Elliott and Vose 2011). The historic role of fire in oak forests of the eastern US has been examined by numerous investigators who generally conclude that a regime of frequent, low-intensity fires has occurred over the much of the region (e.g., McEwan *et al.* 2011, Brose *et al.* 2013, Flatley *et al.* 2013, Abrams and Nowacki 2015, Stambaugh *et al.* 2015). Fire was likely more frequent in communities adapted to (or tolerant of) fire, such as oak, mixed oak-pine (-*Pinus* spp. L.), and xeric pine-oak (Guyette *et al.* 2006, Brose and Waldrop 2014).

While fire was likely a major causal factor in the establishment and maintenance of oak forests, the mechanisms underlying these changes are complex. McEwan *et al.* (2011) suggested that fire, climate, and disturbance regimes in the nineteenth and early twentieth centuries enhanced and perpetuated oak species, whereas wetter conditions and altered fire and disturbance regimes in the twentieth century no longer favored oaks. Nowacki and Abrams (2015) concluded that post-European settlement vegetation dynamics (i.e., an increase in mesophytic species) has been driven primarily by lack of fire, with climate playing a minor role. Hence, contemporary forests are changing because successional processes are no longer arrested by fire and other disturbances, and wetter conditions favor more mesophytic species. Most notably, the expansion of more shade-tolerant *Acer rubrum* L. has been observed across most of the historical range of oak-dominated forests in the eastern US (Abrams 2005, Fei and Steiner 2007, Elliott and Vose 2011). Other non-oak species are expanding as well (Rentch *et al.* 2003, Ozier *et al.* 2006, McEwan *et al.* 2011). For example, in the southern Appalachians, Elliott and Vose (2011) documented an increase in the importance of *Liriodendron tulipifera* L. and *Betula* spp. L., and a decline in importance of several oak species (Figure 1). In the Missouri Ozarks, Hanberry *et al.* (2012) examined changes in forest composition by comparing General Land Office (GLO) records and cur-

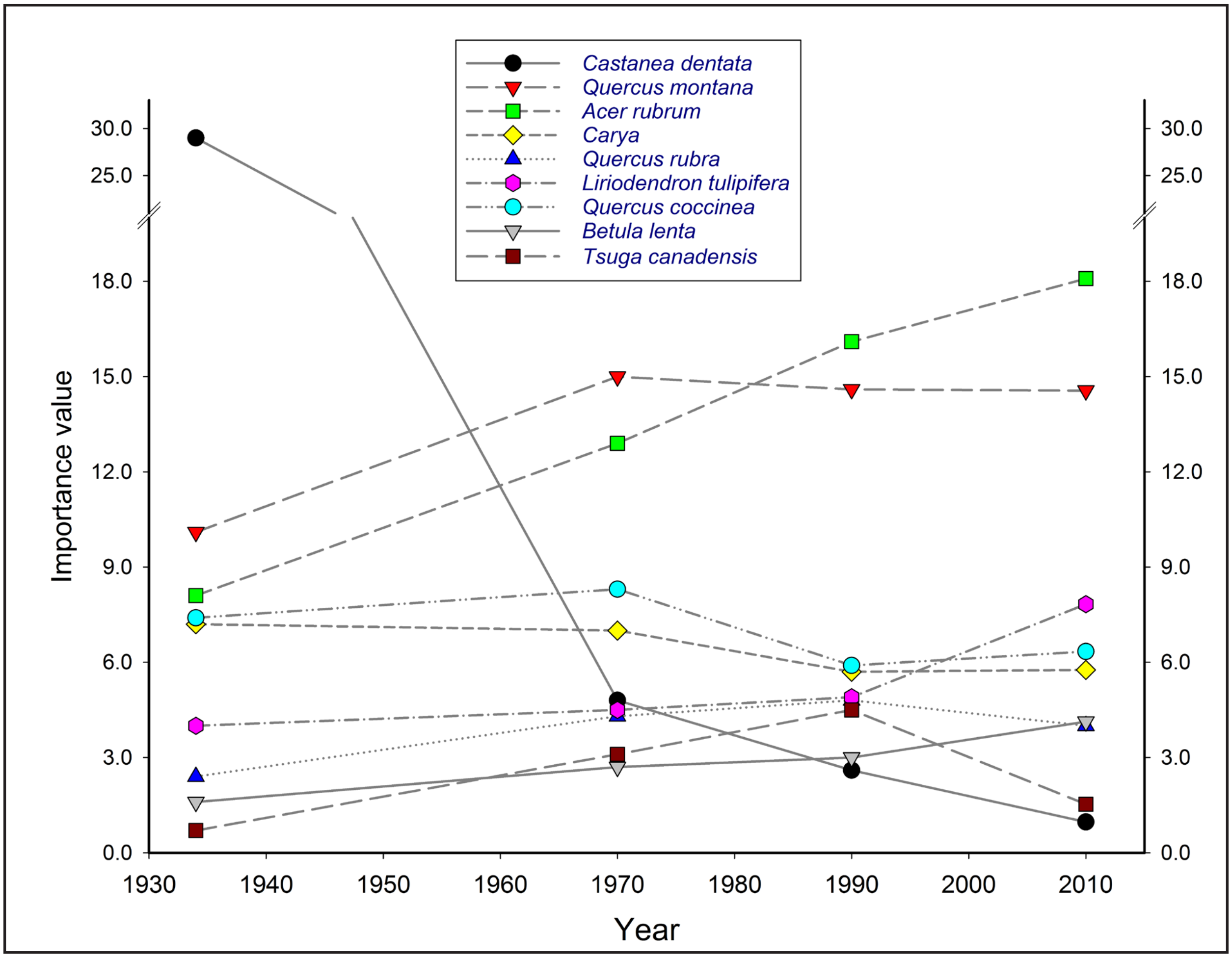

Figure 1. Changes in forest species composition in southern Appalachian forests (updated and adapted from Elliott and Vose 2011). Long-term changes for unmanaged forests; measured in 1934 to 1935, 1969 to 1973, 1988 to 1993, and 2009 to 2013 within Coweeta Basin, western North Carolina (latitude 35° 03′ N, longitude 83° 25′ W). Importance value = (relative density + relative basal area) ÷ 2.

rent USDA Forest Service Forest Inventory and Analysis (FIA) data and found that the contemporary forest condition has changed from open oak-pine savannas and woodlands to more homogeneous mixed hardwood forests over the past 50 years. They concluded that these forests would likely proceed to even denser forests of shade-tolerant species, assuming climate and disturbance regimes (such as fire) remained constant (Hanberry *et al.* 2012).

Although data are limited, the shift in composition to a greater proportion of mesophytic, fire-sensitive species in upland mixed-oak forest ecosystems across the eastern US has consequences for ecosystem function. Alexander and Arthur (2010) found that *Acer rubrum* altered hydrology and nutrient availability by changing the amount, spatial distribution, and chemical composition of stemflow and throughfall. Species also vary in litterfall decomposition rates and nutrient release, with higher decomposition rates and nutrient cycling rates generally associated with *A. rubrum* and *Liriodendron tulipifera* (Knoepp *et al.* 2005, Ball *et al.* 2009, Keiser *et al.* 2013) versus oak species.

Changes in species composition can also influence productivity and growth responses to climate variability. For example, Hart *et al.*

(2012) analyzed climate-growth relationships in the Cumberland Plateau and suggested that *Acer rubrum* is more sensitive to warmer and dry conditions than oaks. Elliott *et al.* (2015) used a combination of dendrochronology and long-term, on-site climate records to evaluate climate-growth relationships of six dominant hardwood species in the southern Appalachians of North Carolina. They found differences in climate sensitivities that corresponded with xylem anatomy, in which mesophytic species with diffuse-porous xylem (*Acer rubrum*, *Liriodendron tulipifera*, and *Betula lenta* L.) were generally more sensitive to precipitation distribution (such as small storms and dry spell length) than xeric or semi-mesophytic species (*Quercus alba* L., *Q. montana* Willd., and *Q. rubra* L.) with ring-porous xylem (Elliott *et al.* 2015). In southern Indiana, Roman *et al*. (2015) found that carbon accumulation in oak species was less impacted by a severe drought than were *Acer saccharum* Marshall, *Liriodendron tulipifera*, and *Sassafras albidum* (Nutt.) Nees. Fewer studies are available that assess the impacts of drought on mortality in eastern US forests and the relationships are complex and multifactored. For example, Dietz and Moorcroft (2011) analyzed long-term forest mortality patterns and found that factors such as stand characteristics and air pollution were stronger drivers of mortality patterns than climate variation. However, in a study examining species-specific mortality patterns across the southeastern US, Klos *et al.* (2009) found a much higher mortality rate in mesophytic species (*Acer* spp., *Betula* spp., *Fagus grandifolia* Ehrh., *Liriodendron tulipifera, Magnolia* spp. L., *Nyssa* spp. L.) versus oak species under severe drought conditions. Taken together, these observational data suggest that mesophytic species are more vulnerable to drought both in terms of reduced growth and higher mortality, and hence may be disproportionately impacted by rising air temperatures and changing drought regimes expected with climate change. A key question is how these new drought regimes will interact with fire (wildfire and prescribed fire) to shape forest structure and function.

Because of the historic role of fire in eastern US oak forests, many researchers have assessed the potential for re-introducing fire to alter species composition, with an overall objective of increasing oak dominance and regeneration, while decreasing more mesophytic species. The thick bark of many oak species imparts resistance to fire for larger trees, while a well-developed root system imparts fire resilience in smaller-stemmed advanced regeneration by promoting aggressive re-sprouting (Nowacki and Abrams 2008, Brose and Waldrop 2014). Overall, most studies indicate that frequent fires are required to kill non-oak species (Hutchinson *et al.* 2012, Arthur *et al.* 2015) and that oak regeneration is enhanced if fire is used in combination with other treatments such as thinning (Brose *et al.* 2013, Brose and Waldrop 2014). While fire appears to be a viable tool for oak management in contemporary forests, prescribed fire is currently used over a small fraction of the range of mixed-oak forests (Melvin 2012). As a result, if current climate and other disturbance regimes are upheld, it is likely that the pattern of increasing mesophytic and fire-intolerant species maintaining or gaining dominance in mixed-oak forests will continue in the eastern US (McEwan *et al.* 2011).

APPROACH

Several recent papers have raised questions about how climate change and other factors (e.g., invasive species) will impact oak forests and interact with prescribed fire and other restoration efforts (Arthur *et al.* 2012, Hart and Buchanan 2012, Dey 2014); however, to our knowledge, there are no definitive experiments or studies that can be drawn upon for direct inferences. When responses are understood at a mechanistic level, the ability to extrapolate beyond historical observations and to model ecosystem dynamics is improved, but not without uncertainty. An alternative is to synthesize our current understanding of species responses to observed climate variability and altered disturbance regimes and project how these responses might shape the structure and function of future forests under new climate and disturbance regimes. Hence, this hypothesis-based approach provides a starting point for decisions about potential management and restoration approaches, while recognizing that uncertainty requires monitoring and adaptations as additional observations and experiments accumulate. For example, a reasonable hypothesis is that the rapid pace and magnitude of climate change will influence competitive dynamics and regeneration patterns among species (Clark *et al.* 2014*a*) and increase wildfire frequency and area burned (Flannigan *et al*. 2009, Slocum *et al.* 2010*a*, Liu *et al.* 2012, Flannigan *et al.* 2013), all of which will favor oaks. Alternatively, more severe drought and an expanding wildland-urban interface may reduce the ability to utilize prescribed fire in the future (Mitchell *et al.* 2014), limiting the ability of managers to use fire as a management tool to help shape the structure and function of future oak forests.

An important question facing land managers is how to manage oak forests in anticipation of the direct and indirect effects of future climate change that include changes in wildfire regimes and potential limits to the use of prescribed fire. To address this question, we synthesized existing literature to examine two propositions for the eastern US: 1) climate change will facilitate the re-establishment of oak dominance in hardwood forests; and 2) management intervention can be used to accelerate re-establishment of oak forests, but an increase in oak dominance will occur with or without management. Through these propositions, we advance the concepts that management interventions will be more effective under changing climate regimes and management will be necessary to sustain ecosystem services in future oak forests.

PROPOSITIONS

Proposition 1:
Climate Change Will Facilitate an Increase in Oak Dominance in Hardwood Forests of the Eastern US

As discussed by McEwan *et al.* (2011), causal factors underlying changes in eastern US oak forests over the past century are complex, but changes in precipitation regimes (i.e., reduced drought severity and frequency; Pederson *et al.* 2015) and disturbance regimes (Nowacki and Abrams 2015) were likely major driving variables in the twentieth century. With a reduction in widespread fire and other disturbances, more mesophytic, shade-tolerant, and fire-sensitive species have taken advantage of these wetter conditions over the past century, with some suggestion that changes in the structure of the canopy and litter promotes a self-perpetuating mesic environment that provides a competitive advantage (Abrams 2005, Nowacki and Abrams 2008, Alexander and Arthur 2010, Kreye *et al.* 2013). Whether these changes will be sufficient to offset the impacts of drier and warmer conditions projected for the future is unknown. Global Climate Models (GCMs) indicate that the climate of the eastern US will experience increasing temperatures and associated evapotranspiration throughout the twenty-first century (IPCC 2014, Melillo *et al.* 2014). Predicting changes in precipitation is challenging and highly uncertain; however, in general, models predict an increased number of consecutive dry days for many areas within the range of Eastern oak forests (Walsh *et al.* 2014). Bedel *et al.* (2013) concluded that conditions in southern and mid-south regions of the US will likely become drier overall, given a warmer environment during future spring and summer seasons (Figure 2; http://nca2014.global-

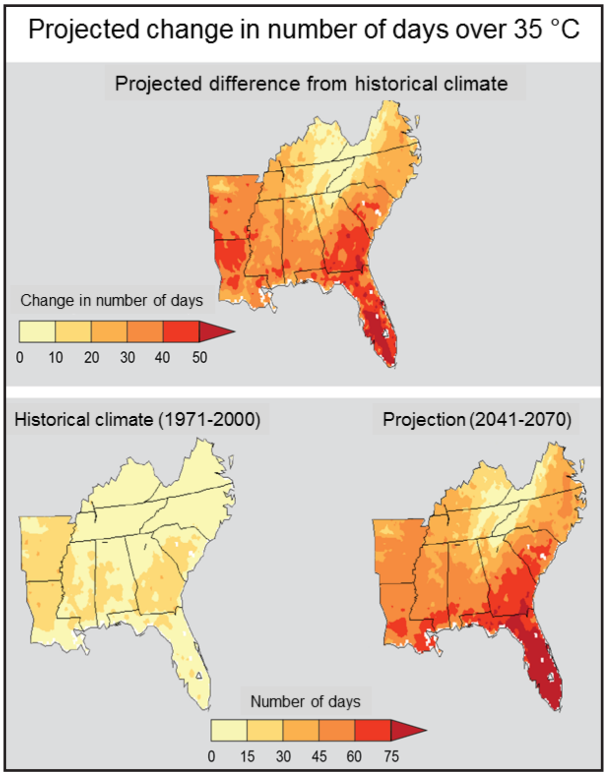

Figure 2. Projected future temperature across the southeastern US reflects the increase in number of days above 35 °C (from: http://nca2014.globalchange.gov/report/regions/southeast).

change.gov/report/regions/southeast). Higher temperatures and altered precipitation patterns will likely result in changes in tree growth rates, mortality rates, competition, and species interactions, all of which can modify the distribution of tree species in favor those more adapted to xerophytic conditions (Klos *et al.* 2009, Clark et *al.* 2012, Clark *et al.* 2014*b*, Elliott *et al.* 2015, Zolkos *et al.* 2015).

Historically, drought has been a major driver of large-scale tree mortality in the eastern US (Pederson *et al*. 2014) and recent studies have reported an increase in drought- and heat-related mortality across the globe and in the US (Allen *et al.* 2010, van Mantgem *et al.* 2013, Williams *et al.* 2013); however, drought tolerance varies considerably among species (Meinzer *et al.* 2013). The physiological basis regulating differential species responses to drought is largely driven by variation in the ability of tree species to survive long periods with substantial soil water deficits or high vapor pressure deficits (VPD), or both (Domec *et al.* 2015, McDowell and Allen 2015). This survival depends (in part) on stomatal control (the ability of leaf stomata to close when VPD is high) and on the hydraulic systems of trees (the ability to move soil water from roots to the leaves). Trees that have a high degree of stomatal sensitivity to VPD and maintain leaf or xylem water potentials well above critical water potentials are classified as more isohydric, whereas trees that allow actual leaf or xylem water potentials to fall throughout the day and approach critical water potentials are classified as anisohydric (Klein 2014). High VPD can stress the water-conducting system and elicit stomatal closure. Excessively high transpiration in response to greater VPD can result in cavitation (or air bubbles), which restricts water transport (Sperry 2011). Hence, severe drought can cause irreparable cavitation in the xylem, resulting in hydraulic failure and subsequent desiccation of foliage (Tyree and Sperry 1989, McDowell *et al.* 2011). Alternatively, trees can close their stomata to reduce the risk of hydraulic failure, but stomatal closure results in diminished photosynthesis that can reduce tree growth and lead to carbon starvation and eventual tree death (McDowell *et al.* 2011).

Another factor determining vulnerability to cavitation among species is xylem anatomy, with ring-porous xylem being more vulnerable to cavitation than diffuse-porous or tracheid xylem anatomies. In eastern US oak forests, mesophytic species (e.g., *Acer* spp., *Liriodendron tulipifera,* and *Nyssa* spp.) are typically isohydric, diffuse-porous, whereas oaks are anisohydric, ring-porous (Table 1). These differences in stomatal conductance and xylem anatomy also influence whole-tree transpiration rates, with significantly greater water use by diffuse-porous species than ring-porous species under the same climatic and environ-

Table 1. Common tree species across the eastern United States classified by hydrotype (mesophytic, semi-mesophytic, or xerophytic)[a], xylem anatomy (diffuse-porous, ring-porous, semi-ring-porous, or tracheid)[b], and stomatal control (isohydric or anisohydric)[c]. Classifications were extracted from the literature; [a] hydrotype (Flatley *et al.* 2015), [b] xylem anatomy (Ewers *et al.* 2007) and [c] stomatal control (Roman *et al.* 2015).

Species	Hydrotype[a]	Xylem anatomy[b]	Stomatal control[c]
Acer rubrum L.	Mesophytic	Diffuse	Isohydric
Acer saccharum Marshall	Mesophytic	Diffuse	Isohydric
Acer pensylvanicum L.	Mesophytic	Diffuse	Isohydric
Betula alleghaniensis Britton	Mesophytic	Diffuse	Isohydric
Betula lenta L.	Mesophytic	Diffuse	Isohydric
Betula papyrifera Marshall	Mesophytic	Diffuse	Isohydric
Carya spp. Nutt.	Semi-mesophytic	Semi-ring	Intermediate
Fagus grandifolia Ehrh.	Mesophytic	Diffuse	Isohydric
Fraxinus spp. (*americana, pennsylvanica*) L.	Mesophytic	Ring	Anisohydric
Liriodendron tulipifera L.	Mesophytic	Diffuse	Isohydric
Magnolia spp. (*acuminata, fraseri*) L.	Mesophytic	Diffuse	Isohydric
Nyssa sylvatica Marshall	Semi-mesophytic	Diffuse	Intermediate
Oxydendrum arboreum (L.) DC.	Semi-mesophytic	Ring	Intermediate
Pinus spp. (*rigida* Mill., *taeda* L., *echinata* Mill., *pungens* Lamb., *virginiana* Mill.)	Xerophytic	Tracheid	Isohydric
Pinus palustris Mill.	Xerophytic	Tracheid	Isohydric
Pinus strobus L.	Semi-mesophytic	Tracheid	Isohydric
Prunus serotina Ehrh.	Semi-mesophytic	Ring	Anisohydric
Quercus alba L.	Xerophytic	Ring	Anisohydric
Quercus coccinea Münchh.	Xerophytic	Ring	Anisohydric
Quercus montana Willd.	Xerophytic	Ring	Anisohydric
Quercus rubra L.	Semi-mesophytic	Ring	Anisohydric
Quercus velutina Lam.	Semi-mesophytic	Ring	Anisohydric
Robinia pseudoacacia L.	Semi- mesophytic	Ring	Isohydric
Tilia Americana L.	Mesophytic	Diffuse	Isohydric
Tsuga canadensis (L.) Carrière	Mesophytic	Tracheid	Anisohydric

mental factors (Ford *et al.* 2011*a*, von Allmen *et al*. 2015, Vose *et al.* 2016). Some of these factors may translate into different growth sensitivities to climate variability (von Allmen *et al*. 2015). For example, recent studies examining growth responses to climate variability suggest that stem wood growth is generally more sensitive to dry periods in diffuse-porous species versus ring-porous species (Pederson *et al.* 2012, Brzostek *et al.* 2014, Elliott *et al.* 2015). Despite being anisohydric, drought tolerance of oak trees is facilitated by deep rooting depths (Abrams 1990, Meinzer *et al.* 2013) and other physiological adaptations that facilitate stable water use and xylem pressure (McCulloh *et al.* 2010, Meinzer *et al.* 2013, von Allmen *et al.* 2015).

Taken together, these physiological and morphological differences help provide a mechanistic understanding for field observations of reduced growth and higher mortality in mesophytic species (*Acer rubrum*, *Liriodendron tulipifera*, and *Betula lenta*) versus oak species (*Quercus alba*, *Q. montana*, and *Q. rubra*) under severe drought conditions. Hence, if drought frequency and severity increase as projected in GCMs (IPCC 2014, Melillo *et al.* 2014), these observed differences in drought tolerance between diffuse-porous and ring-porous species are likely to influence forest dynamics over large areas of the eastern US. These dynamics will be driven by a combination of direct effects (e.g., changes in competitive ability due to climate variation; Pederson *et al.* 2015) and indirect effects resulting from altered disturbance regimes (Nowacki and Abrams 2015). Predicting future species composition in oak forests is challenging; however, modeling approaches suggest that temperate forest stands will see an increase in oaks over the next 50 to 100 years due to altered climate conditions (Bachelet *et al.* 2003, Clark *et al.* 2014*b*). An increased oak component could result from reduced growth and higher mortality of mesophytic, diffuse-porous species relative to oak species; however, longer-term and sustained changes will also require successful oak regeneration (Abrams 2005, Fei *et al.* 2011) and the ability of oaks to outcompete other xerophytic species that will also be favored under drier conditions (Table 1). The challenges of oak regeneration under current climate conditions and disturbance regimes are well documented (Brose *et al.* 2013, Brose and Waldrop 2014). Although it is difficult to predict how increased drought frequency and severity will impact oak recruitment in the future, some studies suggest that oak regeneration will be favored. For example, Ibáñez *et al.* (2007) suggested that *Quercus rubra* recruitment would benefit under climate change conditions that result in warmer and drier conditions. In addition, more frequent and severe fires (as defined by Keeley 2009) resulting from drier fuels and greater fuel loads could also favor oak regeneration (Blankenship and Arthur 2006, Brose *et al.* 2013).

Fires in the eastern US could increase in frequency and area burned during periods of low precipitation and high temperatures (Lafon and Quiring 2012). Compared to the earlier period of 1979 to 1996, fire season length has increased across the globe during the period 1996 to 2013, in which temperatures, length of rain-free intervals, and wind speeds were more pronounced and significantly related to fire season length (Jolly *et al.* 2015). For example, fire season length has shown a significant increase in the eastern US Coastal Plains (Jolly *et al.* 2015). Over the last decade, this region has witnessed a substantial increase in wildfires and a group of large fires in Okefenokee National Wildlife Refuge, the Osceola National Forest, and adjacent lands burned ~243 000 ha in 2007 (Georgia Forestry Commission 2007). Several models using GCMs coupled with indices of fire danger have predicted significant increases in wildfire area burned and fire severity, particularly in the Northern Hemisphere, including the southeastern US (Lafon and Quiring 2012, Liu *et al.* 2012, Bedel *et al.* 2013, Flannigan *et al.* 2013, Mitchell *et al.* 2014). These models converge on the projection that mixed-oak forests in the eastern US will likely experience greater prolonged dry periods, increased wildfire risk, and larger areas burned.

In addition to climate change and fire risk predictions, future projections indicate rapid land use and land cover changes, with 12 to 17 million hectares of new development by 2060 (Wear and Greis 2013). These changes are driven in large part by increase in human population (Figure 3a), and urbanization is greatest at the periphery of urban centers, expanding the wildland-urban interface (WUI) (Fig-

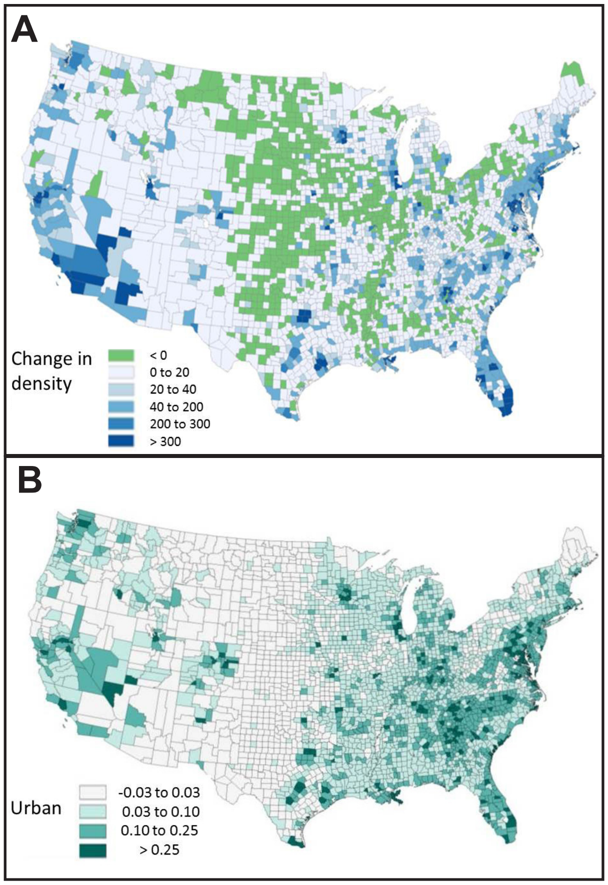

Figure 3. (A) Projected changes in human population density (by county) from the time period 1997 to 2060 (Wear 2011). Data are the change in people per square kilometer (values are approximate after unit conversions and rounding) under the International Panel on Climate Change (IPCC) A1B emissions scenario. Areas in green denote areas where population density is projected to decrease. (B) Forecasted change in the proportion of the county in urban land use, A1B scenario, 1997 to 2060 (Wear 2011).

ure 3b, Wear 2011) through many areas of the Eastern oak forest range. This increasingly fragmented landscape may decrease opportunities for prescribed burning due to a larger WUI (Mitchell *et al.* 2014), while at the same time predicted hotter, drier conditions seem likely to increase wildfire risk (Krawchuk *et al.* 2009, Marlon *et al.* 2009, Liu *et al.* 2012), causing concerns for the safety and health of an expanding population in the WUI.

Proposition 2: Management Intervention May Accelerate Re-Establishment of Oak Forests, but Oak Dominance Will Increase with or without Management

If projections of future climate and fire interactions are correct for the eastern US (Flannigan *et al*. 2009; Slocum *et al*. 2010*a*, *b*; Liu *et al.* 2012; Mitchell *et al.* 2014), we propose that changes in the frequency and severity of droughts and wildfire will favor oaks over the long term with or without management. A key question for land managers is whether they should anticipate and help guide these dynamics using management tools such as prescribed fire (Ryan *et al.* 2013) and thinning over shorter time scales or allow them to unfold without intervention over longer time scales (Figure 4). More frequent and severe wildfires may reduce tree vigor (Clark *et al.* 2012, Arthur *et al.* 2015), accelerate decomposition and nutrient losses (Trammell *et al.* 2004, Knoepp *et al.* 2009, Alexander and Arthur 2010, Nave *et al.* 2011, Elliott *et al.* 2012), and decrease net primary productivity and carbon accumulation and storage (Brzostek *et al.* 2014). If these dynamics occur, the resulting condition of these highly disturbed forest ecosystems may be inconsistent with management goals. As an alternative, management actions could be used to facilitate a more rapid transition to greater oak dominance, which would, in turn, create stands more resistant and resilient to these future climate stressors (Millar *et al.* 2007), while providing a greater level of ecosystems services. We recognize that our propositions are simplifications of highly complex relationships that depend on the interaction of factors such as local site conditions (e.g., xeric vs. mesic upland oak stands), initial species composition, and historical and contemporary disturbance regimes that could yield a variety of potential outcomes in time and space (*sensu* alternative stable states; Nowacki and Abrams 2008). For example, under low and moderate

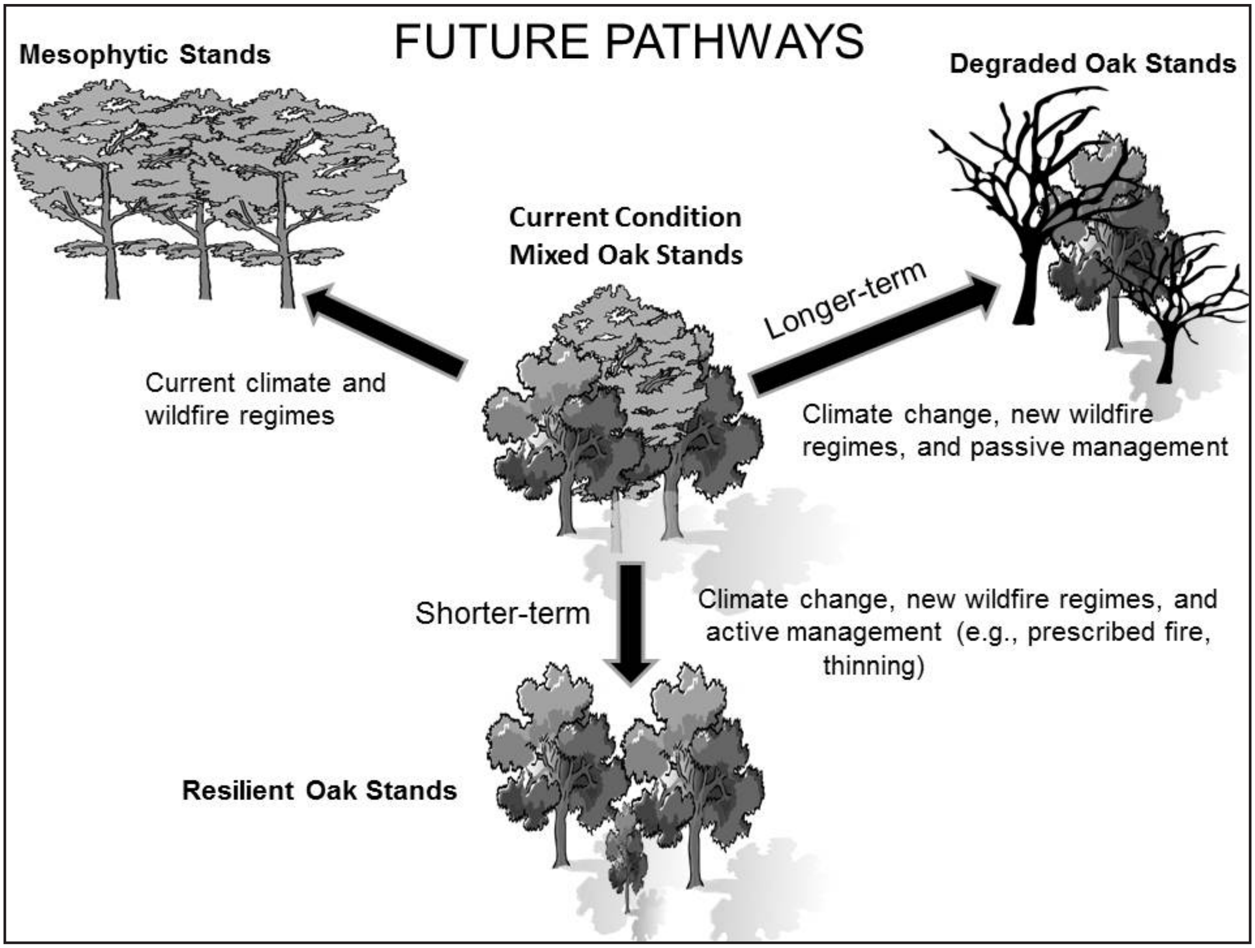

Figure 4. Conceptual diagram of future pathways to more oak-dominated forests with passive management or active management intervention (see Agee 2002). With passive management, stand structure and function will be driven by drought and wildfire that will favor oaks; however, the stands will be less vigorous and poorer quality. As an alternative, active management would facilitate and sustain desirable stand conditions that are more resistant and resilient to current and future droughts and wildfire. Active management could include selective removal of mesophytic species with thinning and prescribed fire.

precipitation deficits, mesic upland stands may have sufficient soil water availability to buffer low and moderate deficits, but they would reach a threshold at high precipitation deficits in which ecosystem condition would decline due to accelerated mortality of mesophytic species (Figure 5a). In contrast, under high precipitation deficits, xeric upland sites may be less prone to threshold responses than mesic upland sites because they have a greater proportion of drought-adapted xerophytic species. Active management (prescribed fire, thinning, or a combination) could be used to modify species composition in favor of more drought tolerant species and reduce water demand, both of which would decrease drought vulnerability and impacts on ecosystem condition (Figure 5b).

It is difficult to predict changes in the vulnerability to invasive species; however, known (and unknown) invasive species could interact with drought and create new fire regimes that dramatically alter structure and function. For example, the expansion of the highly flammable cogongrass (*Imperata cylindrical* [L.] P. Beauv.) in the US coastal plain forests could

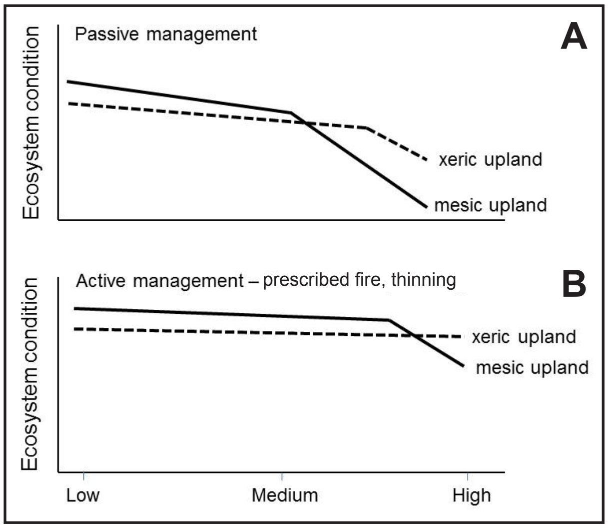

Figure 5. Ecosystem condition with (A) passive management and (B) active management (e.g., thinning, prescribed fire, or a combination of the two; see Agee 2002). Relationships between drought and forest condition are complex and driven by differences in site conditions, current stand structure and composition, and historical and current disturbance regimes. For example, within the continuum of site conditions that support oak forests, we hypothesize that ecosystem condition (based on metrics such growth rate, mortality) on mesic upland sites will be more resilient to low and moderate levels of precipitation deficit relative to xeric upland sites; however, at high precipitation deficits, ecosystem condition on mesic uplands will degrade in a "threshold response" due to high rates of tree mortality. Xeric upland oak sites will be inherently more resistant and resilient to drought at all levels due to a greater proportion of dry site oaks (e.g., white oak [*Q. alba*], scarlet oak [*Q. coccinea*]). Active management could be used to maintain a higher level of ecosystem condition and reduce the magnitude of response to drought.

have substantial impacts on fire regimes and fire behavior (Lippincott 2000) in that region. Invasion by *Microstegium vimineum* (Trin.) A. Camus, a non-native annual grass, resulted in a positive invasion-fire feedback in which biomass and recruitment of the invasive species were greater in burned than unburned deciduous forests (Wagner and Fraterrigo 2015). Similarly, more severe fires that expose mineral soil could facilitate establishment of a wide variety of light-seeded species. The conditions created by changing climate, along with other global changes such as elevated CO_2, more fragmented landscapes, and invasive plant and animal species, will likely create novel structural and functional characteristics (Hiers *et al.* 2012) that are not analogous to most of the oak forests that existed prior to mesophication (*sensu* Nowacki and Abrams 2008). Exactly how these external drivers will shape the structure and functions of eastern US oak forests is unknown. This uncertainty emphasizes the need to closely monitor forest change and responses to management actions in order to adapt to unanticipated outcomes.

What types of management actions could be implemented in current forests to help facilitate the transition to more resistant and resilient oak forests in the future? Prescribed fire will continue to be a critical management tool in oak forests (Ryan *et al.* 2013); however, there will be challenges to using prescribed fire in an increasingly human-dominated landscape (Figure 3b; Mitchell *et al.* 2014). More variable climate conditions may also result in greater and more flammable fuels, especially if drought increases mortality (Klos *et al.* 2009). These changing conditions emphasize the need for collaborative partnerships between land managers and researchers to conduct large-scale experiments, monitor change and effectiveness, and implement adaptive management as needed. As a starting point, some guidance is provided by the large number of prescribed fire studies in eastern US oak forests. For example, Brose and Waldrop (2014) reviewed the literature over the past 50 years and concluded that oak regeneration is most successful after multiple growing-season fires and after a substantial reduction in overstory density. The success of using fire to alter species composition is variable; however, a common theme is that single, low-intensity fires often increase the importance of mesophytic species

(Elliott *et al.* 1999, Blankenship and Arthur 2006). Like oak regeneration, multiple fires are more likely to promote mature oak forests (Hutchinson *et al.* 2012), although frequent or mixed-severity fires can reduce the vigor of surviving oaks. In addition to favoring oak dominance, reducing density of mesophytic species will likely create stands that are more drought tolerant and resistant to large-scale mortality from changing climatic conditions. Oaks also have the added benefit of requiring less water for evapotranspiration, and hence greater water yield would be expected in stands that have perennial or ephemeral streams (Ford *et al.* 2011*b*, von Allmen *et al.* 2015, Vose *et al.* 2016). This could have important implications for creating stand conditions that sustain ecosystem services, such as water supply, under drier conditions. In areas where prescribed fire is not feasible (e.g., WUI areas), stand structure could be altered by mechanical or herbicide removal of mesophytic species.

CONCLUSIONS

Restoration ecology has been guided by the notion of historical reference conditions (e.g., Falk *et al.* 2006, Stanturf *et al.* 2014). Similarly, the concept of desired future conditions has often been referenced by historical observations and experiences of land managers (e.g., Druckenbrod *et al.* 2006, Dey and Schweitzer 2014). Recently, both of these concepts have been challenged because the rapid pace of environmental changes will create novel conditions in which historical reference conditions are not appropriate and desired future conditions are not achievable (Hobbs *et al.* 2014, Golladay *et al.* 2015, Hanberry *et al.* 2015). In the case of oak restoration, using prescribed fire could be viewed as an example of congruence among historical reference conditions, desired future conditions, and achievable future conditions. This congruence is possible because the reference condition (i.e., oak-dominated forests) was created under climatic conditions and disturbance regimes that are likely to be represented in the coming decades as a result of climate warming in the eastern US.

If an increase in oak dominance is the primary desired future condition, then only passive management may be required as we hypothesize that an increase in drought, wildfire frequency and severity, and other disturbances will favor oaks over mesophytic species in the long term (Figure 5). However, these new disturbance regimes may result in undesirable changes (e.g., reduced biomass and productivity, invasive species) in forest structure and function and decrease ecosystem services provided by oak forests. Instead of passive management, we advocate for active management (Agee 2002) to facilitate a more rapid transition to oak dominance that could alleviate some of the negative impacts of severe droughts and wildfire on forest health and productivity, while at the same time protecting or enhancing ecosystem services such as streamwater quantity and quality. The primary constraint will be a growing WUI that will ultimately limit the widespread application of prescribed fire and increase pressure to prevent and extinguish wildfires.

While our propositions are based on synthesis and interpretation of the scientific literature, several unknowns could further shape these future oak-dominated forests, such that novel structural and functional characteristics may emerge that will require adaptive management and restoration strategies (Hiers *et al.* 2012). For example, invasive species (insects, plants, diseases) and other global changes such as elevated CO_2 could play a role in forest dynamics and disturbance regimes. In addition, if future wildfires are more frequent and severe, then reduced tree vigor and nutrient loss could decrease stand productivity. We propose that the combination of climate change, wildfire, and other disturbances will create stand conditions that favor oaks with or without management. However, management intervention (e.g., prescribed fire, thinning, or a combination) could reduce wildfire hazard, particularly in the WUI, and create more desirable stand conditions that are resilient to future stressors such as changing precipitation patterns and warmer temperatures. Like most projections of the future, we acknowledge that there is uncertainty in our propositions and surprises are likely. While some of this uncertainty may be reduced through additional field observations, results from new experiments, and better models, monitoring, and adaptive management will be critical components of any management activity.

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