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Barriers to natural regeneration in temperate forests across the USA

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Abstract
For millennia, natural disturbance regimes, including anthropogenic fire and hunting practices, have led to forest regeneration patterns that created a diversity of forest lands across the USA. But dramatic changes in climates, invasive species, and human population, and land use have created novel disturbance regimes that are causing challenges to securing desired natural regeneration. Climate is an ever-present background disturbance and determinant of species distribution. Changes in certain other factors such as large herbivore populations, wildfire, and pests modify forest composition and structure, and are common barriers to natural regeneration of desired species. Changes in long-standing disturbance regimes have led to the homogenization of forest landscape composition and structure. Today, forests have low regeneration potential and are low in resilience. They have reduced productivity and are prone to widespread health issues including severe forest mortality. In addition to epidemics of native invasive species due to climate change and availability of habitat at landscape scales, the continued introduction and spread of non-native pests and diseases are causing large-scale forest mortality. These ecological changes have cascading ecological consequences such as increases in severe wildfire, which pose new barriers to natural regeneration. Equally challenging are the barriers to natural regeneration that arise from social, political and economic factors. To address many of these issues requires active management that links all critical stages in the regeneration niche necessary for achieving desired regeneration to sustain forest development and production in a socially acceptable manner and economically viable market system.

Keywords Natural regeneration · North America · Silviculture · Sustainability

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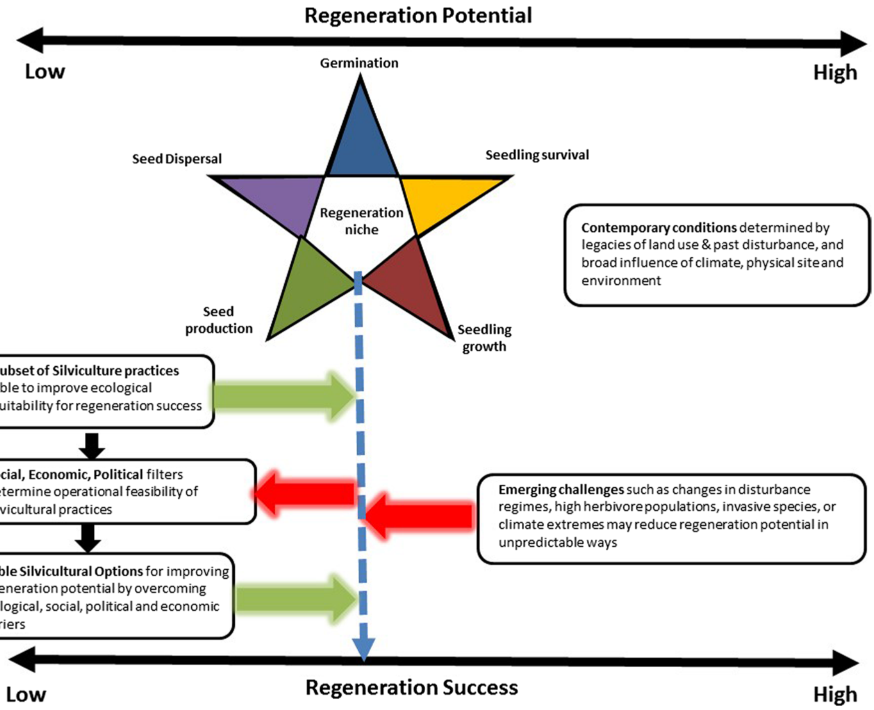

Fig. 1 The regeneration niche (star) is comprised of the developmental sequence from seed production to seedling establishment and development that occurs during stand initiation (Oliver and Larson 1996). The regeneration niche occurs somewhere between two planes: regeneration potential and regeneration success that range from low to high depending on climate, site factors, and disturbance history legacy effects on vegetation. The initial regeneration potential of a forest or species is defined by the competitiveness of the sources of regeneration (current seed, seed bank, vegetative sprouting) for each species summed for the stand (Johnson et al. 2009). Often the regeneration potential is low to moderate for desired tree species that would lead to a high to moderate probability of regeneration failure almost regardless of regeneration method. Silviculture (green arrows) can be used to increase regeneration potential, and hence, regeneration success. Barriers (red arrows) to regeneration success may arise from ecology, social, economic or political sources. Failure in anyone stage of the regeneration niche results in failure for any one species

Introduction

Securing adequate regeneration is foundational to the sustainability of forests (Dey 2014). Throughout North America and in many other places in the world, mature forests dominate rural landscapes, a legacy of land use history, especially over the past 150 years (Fig. 1) (Shifley and Thompson 2011; Pan et al. 2011; Oswalt and Smith 2014). Forest regeneration initiated by human or abiotic disturbances often results in an undesirable shift in forest composition and structure at stand and landscape scales (Hessburg et al. 2005; Schulte et al. 2007; Nowacki and Abrams 2008; Bekker and Taylor 2010; Dey 2014; Hanberry and Nowacki 2016). For example, composition and structure changes in mature forests of ponderosa pine (*Pinus ponderosa*) in the western USA or oak (*Quercus*) in the East such as increasing density of shade tolerant, fire sensitive species are causing regeneration problems for pine and oak species. In some cases, the species that are increasing in dominance such as firs (e.g., *Pseudotsuga* and *Abies*) and maples (*Acer*) are not as well-adapted to or compatible with expected future climates as are the oaks and pines (e.g., Rehfeldt et al. 2006; Brandt et al. 2014; Butler et al. 2015). To sustain the dominance of desired species and to achieve other conservation goals, managers are increasingly needing to regenerate stands within landscapes dominated by mature, dense forests under emerging challenges such as introduced and expanding invasive species and climate change (Fig. 1).

Forests can be regenerated using either natural or artificial sources of reproduction. In the USA, the majority of forest regeneration (> 90%) is from natural sources over the approximately 310 million hectares of forest land (Oswalt et al. 2014). The importance of artificial regeneration varies by region and forest type, with the majority (78%) of planting, primarily longleaf/slash pine (*Pinus palustris*/*P. elliottii*) and loblolly/shortleaf pine (*P. taeda*/*P. echinata*), occurring in the southern USA (Oswalt et al. 2014).

For successful natural regeneration, several important plant life history events must occur; thus, there are several stages of regeneration at which failure can also occur. This process of regeneration and the associated species-specific life histories have been described as the "regeneration niche", which includes stages of seed production, seed dispersal, seed germination, seedling establishment, and tree development or recruitment into the overstory (Fig. 1) (Grubb 1977; Clark et al. 1999). The regeneration niche concept suggests that the suitable, species-specific environmental conditions must occur simultaneously or in sequence to allow regeneration to happen. Understanding the silvical characteristics of tree species in relation to existing environment and regeneration needs is fundamental to forest management and has been the topic of extensive research. This body of knowledge demonstrates the ecological complexity of natural regeneration and informs managers as to the species-specific regeneration ecology (Barnes et al. 2010; Tappeiner et al. 2015; Nyland et al. 2016; Ashton and Kelty 2018).

Contemporary forest conditions are a product of the effects and interactions among historical disturbance regimes, recent climate and other factors such as physical site features that influence the regeneration environment and competitive dynamics (Fig. 1). Managing the regeneration niche to a successful conclusion requires overcoming certain ecological, social and economic barriers that can cause complete failure at various stages in the process. Emerging ecological constraints to natural regeneration occur when climate change produces unfavorable weather, changes in disturbance regimes degrade the regeneration niche, forest health threats become widespread, and/or invasive species rise to dominance. Social constraints include legislative, legal and community restrictions on forest practices; and economic constraints often determine the feasibility of applying socially acceptable forestry practices to favor desirable regeneration by meeting the ecological needs of featured species. The surviving set of silvicultural strategies, systems and practices that meet these collective needs form the basis of silvicultural prescriptions that are more likely to result in successful regeneration, the foundation of sustainable forestry.

The purpose of this paper is to present a national perspective and synthesis on the barriers to natural regeneration, to better understand the challenges managers face when trying to implement sustainable forest management, and to show the complex, interconnectedness of the ecological-social-economic factors that either foster or inhibit achieving desired forest conditions and landscapes through management of natural regeneration. We provide an overview of the major barriers to natural regeneration including (1) contemporary forest structure and composition that inherently has low to moderate regeneration potential, (2) negative impacts of browsing by high-density herbivore populations, (3) increasing competition and mortality from invasive species, (4) adverse impacts of changing climate on the regeneration niche and changes in disturbance regimes that favor competitors, and (5) social-economic-political factors that constrain management. We then provide examples from various regions of the USA to demonstrate both common themes and unique challenges managers encounter when they attempt to rely on natural regeneration of western coastal conifer, western ponderosa pine, eastern oak, and southern longleaf pine forests.

Barriers to natural regeneration

Understanding contemporary conditions

Before human migration to North America, changes in climate were a major determinant of species distributions by placing broad limits on the regeneration niche that was modified locally by physical factors (geology, soils, landform, topography, and hydrology) as they affect disturbance severity and competitive dynamics following wildfire, extreme weather, or insect and pathogen outbreaks that initiate regeneration (Foster et al. 2002; Camill et al. 2003; Faison et al. 2006; Patterson III 2006). Integral feedback interactions among the physical environment, climate, disturbance agents, and the vegetation itself resulted in a mosaic of forests, woodlands and savannas across the landscape.

For over 15,000 years humans have increasingly become a major driver of vegetation change, primarily through their use of fire and their impact on large herbivore populations (Dobyns 1983; Delcourt et al. 1998; Foster et al. 2002; Nelson et al. 2006; Denevan 2011; Mensing 2015). Native Americans promoted the dominance of fire-adapted, shade intolerant tree genera such as *Pinus* and *Quercus* that prospered in the favorable regeneration niches of savannas and woodlands, especially in warmer, drier regions (Agee 1993; Delcourt and Delcourt 1997; Abrams 2002; Schoennagel et al. 2004; Brown et al. 2015).

Dramatic changes in fire regimes and land use (e.g., agriculture and industrial logging) occurred over the past 400 years, resulting in rapid shifts in vegetation types and cover following European colonization of North America (Winkler 1985; Foster et al. 2002; Patterson 2006). Early European settlers continued the use of fire to manage the landscape largely for agricultural purposes, and in doing so, magnified the role of fire as a landscape disturbance agent (Guyette et al. 2002), a phenomenon that Stambaugh et al. (2018) referred to as "the wave of fire" that rolled, along with Euro-migration, from the Eastern seaboard to the Great Plains. In forested regions, an era of catastrophic fires often followed periods of major exploitative logging that occurred throughout the country during the 19th and early 20th centuries. In a matter of several decades whole regions, i.e., the Great Lakes, Midwest, South, and Pacific Northwest, were logged and burned, drastically altering the age structure and composition of the forests (Oswalt et al. 2014). This transformation of the landscape led to public concern for timber famines and calls for wildfire control, conservation and preservation.

Since the early 1900s, fire suppression on a national scale has greatly reduced the occurrence of fire and resulted in dramatic changes to vegetation. In many areas, landscape diversity has been reduced as forests recovered from timber exploitation and initial attempts to practice agriculture. More homogeneous forest conditions have developed characterized by increased density and fuel loading, more complex vertical structure, and increasing dominance by shade tolerant, fire sensitive species (Taylor and Skinner 2003; Hessburg et al. 2005; Schulte et al. 2007; Nowacki and Abrams 2008; Bekker and Taylor 2010; Hanberry et al. 2012, 2014c; Battaglia et al. 2018), including the widespread replacement of woodlands and savannas by forests in the absence of fire (Covington and Moore 1994; Hanberry 2014; Hanberry et al. 2014a, b, c; Dey et al. 2017). Successional change through shifts in species composition of naturally regenerating trees is occurring throughout the USA. Changes in regeneration niches due to new disturbance regimes are driving forests toward novel compositions. In the absence of fire, eastern oak forests (Johnson et al. 2009; Brose and Waldrop 2010; Fei et al. 2011; Nowacki and Abrams 2008, 2015), southern pine forests (Williams 1998; Welch et al. 2000), and western oak, pine, and mixed conifer forests (Covington and Moore 1994; Brown and Wu 2005; Fule et al. 2009; Cocking et al. 2012; Battaglia et al. 2018) are being replaced by shade tolerant species.

Current challenges with natural regeneration are due to the combination of historical legacy effects on the contemporary conditions within which regeneration occurs and the variety of factors that make ecological conditions for regeneration unsuitable, such as unfavorable seedbed conditions and insufficient light in the understory to promote growth and survival of the desired species. The overall effect is low regeneration potential (Fig. 1) (Johnson et al. 2009) in species that are preferred for ecological or economic reasons, and their replacement by species that are better adapted to the novel disturbance regimes operating today. In many cases, the shift in species is not considered a positive change from an economic, ecological or conservation viewpoint. At the landscape scale, the net result of changes in fire regime and land use over the past 200 years has been the homogenization of forest composition and structure that leaves landscapes low in resilience and prone to widespread forest health issues and catastrophic forest mortality, with increased barriers to natural regeneration of desired species, as evidenced by recent national forest mortality resulting from oak decline, mountain pine beetle (*Dendroctonus ponderosae*), southern pine beetle (*D. frontalis*) and large high severity wildfires.

The ecological consequences of landscape level forest mortality are significant to forest regeneration. Death of a large portion of the overstory reduces or eliminates seed sources of desired species, reduces sources of vegetative reproduction, causes problems related to limited seed dispersal, and releases competing vegetation in the understory. Catastrophic overstory mortality creates high fuel loading and hazardous wildfire conditions at potentially large scales. Wildfire size, intensity, and frequency of large fires have been increasing in the West since the 1980s (Westerling et al. 2006). The probability of potential fire increases over most of the US under future climate projections due to increasing temperature and changes in precipitation, especially in the Northern Rockies, Great Lakes, Midsouth and Northeast regions (Guyette et al. 2012, 2014). The addition of large quantities of fuels from catastrophic overstory mortality contributes to higher fire intensity (Jenkins et al. 2014). Increased fire severity and occurrence of stand replacing fires over large areas in the West poses a major obstacle to natural regeneration due to limited seed dispersal into the burn area (e.g., Chambers et al. 2016; Kemp et al. 2016; Shive et al. 2018).

High herbivore populations

Ungulate (e.g., elk and deer) browsing is an important disturbance that has long been part of the history and ecology of North America. Animal density was controlled by indigenous hunting, which minimized any adverse impact on forest regeneration, for example, it is estimated that the density of white-tailed deer (*Odocoileus virginianus*) was 2–4 deer km^{-2} before European immigration to North America (Rooney 2001). Deer at these densities are not a barrier to forest regeneration (Horsley et al. 2003; Brose et al. 2008). White-tailed deer were hunted commercially in the early 20th century to near extinction in local areas, but since that time, deer herds have increased to higher levels with > 17 deer km^{-2} in some regions, and > 40% of the northern US with population density > 4 deer km^{-2}, where they are causing serious problems with forest regeneration (Rooney and Waller 2003; Russell et al. 2017).

Moderate to high densities of ungulates, such as white-tailed deer, can alter the regeneration niche by reducing tree seedling survival and growth, favoring competing vegetation through selective browsing, and inhibiting recruitment of desired species into the overstory (Tilghman 1989; Stromayer and Warren 1997; Horsley et al. 2003; Rossell et al. 2005). Density of white-tailed deer in excess of 17 deer km^{-2} is common from central Texas through the South to the Mid-Atlantic region, and in the Great Lakes (Quality Deer Management Association 2009). Deer density in excess of 5 deer km^{-2} in areas with low deer food availability, i.e., heavily forested regions, often causes forest regeneration failures (Kittredge and Ashton 1995; Horsley et al. 2003; Brose et al. 2008). In landscapes where food availability is medium to high (i.e., a mix of agriculture and forest cover), deer density thresholds associated with regeneration failures are higher (> 8–14 deer km^{-2}). Controlling deer populations by hunting, or protecting seedlings with fences or cages are the only effective means of reducing the negative impacts of deer browsing on forest regeneration. However, fencing is often cost prohibitive and changing deer hunting policy and regulation is socially complicated and difficult (Brown et al. 2000).

Invasive species—diseases, insects, and plants

Nonnative invasive species may interfere with various stages of the regeneration niche (Pimentel et al. 2005; Holmes et al. 2009; Kovacs et al. 2010; Aukema et al. 2011; Lovett et al. 2006, 2016). Many of the widely studied nonnative forest pathogens, insects and plants inhibit natural regeneration by killing seed-bearing mature trees, eating seed and seedlings, or by competing with seedlings for resources necessary for survival and growth. The death of canopy trees, creates small canopy gaps and promotes the recruitment of shade tolerant species into the overstory, often causing undesirable shifts in forest composition (Fajvan and Wood 1996; McShea and Healy 2002; Johnson et al. 2009).

Several examples of nonnative invasive pathogens that have had widespread influence on eastern forests include the chestnut blight (*Cryphonectria parasitica*) and Dutch elm (*Ophiostoma ulmi*) diseases that caused the functional loss of American chestnut and American elm (*Ulmus americana*), respectively. White pine blister rust (*Cronartium ribicola*) is a major nonnative pathogen impacting five-needled pines. The threat of nonnative invasive forest pathogens continues with the spread of sudden oak death (*Phytophthora ramorum*), which has caused widespread mortality in oak and tanoak (*Notholithocarpus densiflorus*) species along the west coast of North America (Rizzo and Garbelotto 2003; Frankel 2008), and now threatens eastern oaks, which account for more than half of all forest lands in the East (78 million ha) (Moser et al. 2009; Grünwald et al. 2012; Oswalt et al. 2014). Other major nonnative pests causing forest mortality include *Phytophthora cinnamomi*, which has been implicated as the main causal agent of rapid white oak (*Quercus alba*) mortality in the Midwest (Balci et al. 2010; Nagle et al. 2010; Reed et al. 2017) and beech bark disease, a combination of attack by a bark scale (*Cryptococcus fagisuga*) followed by infection of *Neonectria* fungi occurring in American beech (*Fagus americana*) throughout the Northeastern USA and eastern Canada (Houston 1994).

Of the nonnative invasive insects, gypsy moth (*Lymantria dispar*) is one of the most serious, having defoliated cumulatively over 32.8 million ha of forests in the East since

1924 (Sharov et al. 2002). Gypsy moth defoliations reduce acorn production by decreasing individual tree production and increasing mortality of seed bearing trees (Davidson et al. 1999; Lovett et al. 2006). Other nonnative invasive species such as the emerald ash borer (*Agrilus planipennis*) are threatening to eliminate the entire genus *Fraxinus* from forests through loss of seed bearing trees and disruption of regeneration in forest gaps that are being captured by more shade tolerant species (Cappaert et al. 2005; Poland and McCullough 2006). The list of nonnative invasive insects that invade and outbreak throughout the range of the host trees will continue to grow into the future and challenge managers to find control strategies and methods before species are lost, and forest form and function are irreversibly impaired (Waring and O'Hara 2005).

Nonnative plant species are numerous throughout the USA (Pimentel et al. 2005; Oswalt and Oswalt 2011; Miller et al. 2013). Invasive plants interfere with the regeneration of trees at practically all stages in the regeneration niche. The variety of invasive plant species in forests today exhibit a range of life history traits that can inhibit tree regeneration in different ways. They may act as interference species affecting which tree species will eventually recruit into the overstory, and often promoting the more shade tolerant species (Phillips and Murdy 1985; Nyland et al. 2006, 2007). Dense shrub canopies in the understory of closed-canopy forests reduce seedling growth and increase seedling mortality due to extreme low light, thus inhibiting the development of large, competitive reproduction (e.g., >12 mm basal diameter in oaks) that are critical to the success of genera such as *Quercus* and *Pinus* (Johnson et al. 2009). In contrast, invasive plant species that thrive in open environments are promoted by silvicultural practices such as even-aged harvesting, prescribed burning and thinning (Rebbeck 2012). Many nonnative invasive plant species are adapted to prescribed fire that is used to restore woodland and savanna conditions (Huebner 2006; Rebbeck 2012; Miller et al. 2013; Phillips et al. 2013). Large, high severity wildfires are increasingly more common in the West. They delay natural regeneration of native trees, in part, by creating conditions that favor colonization by nonnative invasive species, especially where cattle have introduced nonnative species by grazing in remote areas (Keeley 2006). Expansion of the wildland-urban interface, road building, home development and other human land use disturbances in rural forested areas increase the potential for nonnative invasive species to expand.

Several native plant species can form dense canopies after silvicultural treatments and inhibit the regeneration of desired species. For example, native ferns such as bracken (*Pteridium aquilinum*), hayscented (*Dennstaedtia punctilobula*), and New York (*Thelypteris noveboracensis*) may proliferate after harvesting and burning and cause oak/hardwood regeneration failure (Engelman and Nyland 2006). These ferns have adaptations that facilitate their regeneration following disturbances including a bank of spores in the forest floor and rhizomes buried deep in the soil. Also, high deer populations can overbrowse forest understories removing tree regeneration and provide opportunities for native ferns to rise to dominance (Horsley and Marquis 1983; Fredericksen et al. 1998; Engelman and Nyland 2006). In the Appalachian Mountains, native mountain laurel (*Kalmia latifolia*) and *Rhododendron* spp have come to dominate oak/pine forest understories in the long-term absence of fire, and they inhibit regeneration of many species that cannot tolerate the low light conditions under the shrub canopy (Phillips and Murdy 1985; Brose and Waldrop 2006, 2010). In some cases, forests become shrublands or fern glades as the overstory dies or is harvested. In the Pacific Northwest and California, shrub and tree species such as manzanita (*Arctostaphalous* spp), *Ceanothus* spp., tanoak (*Lithocarpus densiflorus*), and others are extremely competitive following fire or clearcutting. They regenerate through buried seeds or resprouting, and are generally more competitive than more desirable conifer species (Harrington 2006; McDonald and Fiddler 2010). In the Great Plains and West, disruption of historic disturbance regimes by fire exclusion and overgrazing has promoted the encroachment of native junipers (*Juniperus* spp.) into grasslands, sagebrush-steppes, aspen (*Populus* spp.) forests, and oak/pine savannas and woodlands, thereby displacing the historical natural communities (Engle et al. 1996; Wall et al. 2001; Brockway et al. 2002; Coultrap et al. 2008; Miller et al. 2008). For similar reasons, yaupon (*Ilex vomitoria*), other shrubs, and junipers have invaded oak savannas and woodlands causing regeneration and recruitment failures (Stambaugh et al. 2011a, b; Sparks et al. 2012). Once they are established in forests, either nonnative or troublesome native species can rapidly expand in the understory following mortality of canopy trees.

Changing climate—direct effects on regeneration

Iverson et al. (2008) predicted the potential suitable habitat of 134 tree species' under a range of emission scenarios and climate models and found that most species may move northeastward up to 800 km in the highest emission and hottest climate change scenario. Similar predicted species shifts northward have been reported by McKenney et al. (2007), who modeled the change in species distributions to climate change scenarios for 130 North American tree species. Iverson et al. (2008) concluded that the potential habitat for half of the species studied may increase by at least 10%, whereas some species will increase in importance by at least 50%, including commercially valuable oaks and pines. Another prediction that is favorable for the future of oak is that many of its northern, mesophytic competitors, species such as the aspens, birches (*Betula* spp.), striped maple (*Acer pensylvanicum*), and sugar maple (*Acer saccharrum*) are predicted to decline with climate change.

There is some consensus among many climate models that temperature will increase an average of 0.3–0.7 °C by 2100 throughout the continental USA (IPCC 2014; Krist et al. 2014). The future climate is expected to have increases in temperature extremes. There may be a greater frequency of heat waves of longer duration, resulting in increased heat stress on trees (Allen et al. 2010; IPCC 2014). The frequency, duration and intensity of seasonal and multi-year droughts are expected to increase. Precipitation is expected to decrease in the Interior West and Southwest, and increase in the Pacific Northwest and throughout the East (Seager et al. 2007; IPCC 2014; Krist et al. 2014). There may be a greater frequency of extreme precipitation events of increasing intensity at middle latitudes. Specific changes in individual climate variables and their interactions will determine if the climate change will have a positive or adverse impact on the regeneration, abundance and dominance of any species.

Suitable temperature and adequate water supply are critical drivers of successful completion of every stage in the regeneration niche from flowering and seed production to seedling survival and growth into the overstory (Fig. 1) (Walck et al. 2011). Temperature is important in initiating flowering (Cecich and Sullivan 1999). Dry springs with low relative humidity facilitate production and dissemination of pollen, and fertilization in oaks (Sharp and Sprague 1967; Sork et al. 1993; Koenig et al. 1996; Cecich and Sullivan 1999). Adequate summer precipitation and warm temperatures increase the development of viable seed in many species (Sork et al. 1993; Koenig et al. 1996; Cecich and Sullivan 1999; Cain and Shelton 2000). In contrast, summer droughts decrease sound seed production, and increasing drought severity increases seed loss. In the fall, dry weather with low humidity promotes cone opening and seed dispersal in pines (Cain and Shelton 2000). After seed dispersal, weather that affects seed moisture content influences seed viability. For example, recalcitrant seeds of *Quercus*, *Fagus*, *Acer* and *Aesculus* require moderate to high moisture content to maintain viability (Walck et al. 2011). In contrast, seed viability in orthodox seed such as in *Pinus* is promoted at low seed moisture content. Temperature and moisture are important in both inducing seed dormancy and in breaking physical and physiological dormancy. Climate trends toward reductions in depth of snow pack and warming winter temperatures that cause early loss of snow cover expose seed and seedlings to daily freezing temperatures, desiccation (especially important for recalcitrant seed), seed predation, and seedling herbivory (Walck et al. 2011). In contrast, increases in temperature provide new regeneration opportunities for trees to invade the treeless alpine or tundra at higher elevations in mountain ranges and in northern latitudes if there is suitable soil (Hessl and Baker 1997; Walck et al. 2011).

Species can be competitive and dominate at the end of the regeneration period when a receptive environment with adequate resources are synchronously available at the signature life stages that make up the regeneration niche. For example, increasing temperature in the spring triggers flowering in oaks (Cecich and Sullivan 1999), thus high temperature events that occur earlier than in the past due to climate change can expose developing flower buds to damage or death by late spring frost events, and therefore decrease seed production. Another example of the adverse effects of asynchronous climate and tree physiology is the premature initiation of seed germination by late winter warm periods at a time when the ambient environment is not conducive to success in germination and seedling establishment, or when extreme freeze events follow germination (e.g., Timmis et al. 1994). The ecological ramifications of late spring frost damage and mortality to tree regeneration are substantial (Inouye 2000). Gu et al. (2008) concluded that late spring frost events that follow a milder winter and earlier initiation of spring are part of the climate change phenomenon. The occurrence of late spring frosts may vary by region and altitude, and the extent of damage to critical organs and tissues varies by species phenology, physiology, cold hardiness, and other inherited traits (Inouye 2000; Hänninen 2006; Augspurger 2009). Regeneration failures in desired species may be more common if climates are changing faster than tree species can adapt, or migrate to favorable climes and receptive sites.

Changing climate—disturbance interactions

Unusually high levels of tree mortality are occurring on a large scale across the US, in part, because forested landscapes are fairly homogeneous and dominated by mature forests (e.g., Wulder et al. 2006; Fan et al. 2008). Oak-hickory (*Quercus*-*Carya*) and western pine (e.g., lodgepole pine (*Pinus contorta*) and ponderosa pine) forests cover millions of hectares in North America, and they are highly susceptible to insect and disease outbreaks, which are magnified by new climate regimes that include increasing frequency of extreme weather such as droughts. Climate is contributing indirectly to mortality in ways that initiate a cascade of disturbance events that disrupt ecosystem processes and impair the forest's ability to recover through regeneration of desired species. One mechanism in which climate causes tree mortality over millions of hectares in the USA and Canada is through insect and disease outbreaks. Insects and diseases are a leading cause of tree mortality in the USA, and climate is an important determinant of the distribution and productivity of insect and disease populations (Ayres and Lombardero 2000; Logan et al. 2003; Bentz et al. 2010). For example, temperature and precipitation affect insect and disease life cycles, reproductive biology, and population growth in both positive and negative ways. Climate also influences the vigor and stress, and hence, susceptibility of the host tree species and their ability to defend against attack by insects and diseases.

Widespread insect outbreaks that have occurred over the past 40 years in western USA and Canada have caused high levels of tree mortality over tens of millions of hectares. They are expected to continue causing catastrophic mortality under future climates as insects move into new habitat made available by warming temperatures (Logan et al. 2003; Gan 2004; Allen et al. 2010; Bentz et al. 2010). Increasing temperature, and in particular, warmer winter temperatures are increasing the survival of bark beetles such as the mountain pine beetle, Douglas-fir beetle (*D. pseudotsugae*), spruce beetle (*D. rufipennis*), and the eastern (*Choristoneura fumiferana*) and western spruce budworm (*C. occidentalis*) (Logan et al. 2003; Berg et al. 2006; Hicke et al. 2006; Bentz et al. 2010). Warmer winter and spring temperatures and increased precipitation in the fall to spring period increases populations of the southern pine beetle (*Dendroctonus frontalis*) (Gan 2004). Higher temperatures may accelerate the development of insects and increase the number of generations in a year, or the frequency of outbreak populations in a decade (Bentz et al. 2010).

Higher seasonal precipitation in warm climes is often associated with vigorous populations of fungi, molds and bacteria (Ayres and Lombardero 2000). Increasing temperature, heat stress, drought, and extreme weather all work to increase physiological stress in trees, decrease tree vigor and increase tree susceptibility to insect attack and disease infection, and hence, vulnerability to mortality (Mattson and Haack 1987; Ayres and Lombardero 2000; Desprez-Loustau et al. 2006; Allen et al. 2010; Bentz et al. 2010). Climate is the major limit on the distribution of insects, and when climate change makes available new host habitat, insects are able to move readily into those areas, which based on climate predictions will be primarily northward in latitude and higher in elevation (Ayres and Lombardero 2000; Dale et al. 2001; Logan et al. 2003; Hicke et al. 2006; Bentz et al. 2010). Climate interactions with disease and insects are important factors contributing to high mortality due to forest decline events. For example, oak decline causes catastrophic mortality and regeneration problems for red oak species (*Quercus* section *Lobatae*) in eastern landscapes (Shifley et al. 2006; Kabrick et al. 2008). The magnitude of its impact is unprecedented due, in large part, to landscapes dominated by mature oak forests that are experiencing increasing drought frequency and intensity, and environmental stress such as drought, flooding and freezing temperatures (Shifley and Thompson 2011; Oswalt and Smith 2014).

Social-economic-political factors

Despite the challenges facing managers of natural regeneration that stem from lack of knowledge on biology, ecology and management of key species in ecosystems, the social-economic-political barriers to regeneration often override other environmental or ecological factors.

The ability to manage forests is directly affected by ownership and indirectly by public laws and policies. The ownership of forest lands in the USA varies by region. In the East, over 80% of timberlands are in private ownership while in the West, approximately 70% are owned by federal agencies (Oswalt and Smith 2014). Active forest management on federal lands has been dramatically reduced since the 1990s as evidenced by the level of timber harvesting on National Forests. In the 1960s–1970s about 28.3 million m^3 $year^{-1}$ of timber was harvested compared to $<$ 4.7 million m^3 $year^{-1}$ since 2000 (Oswalt and Smith

2014). Total forest harvest on both public and private lands is at its lowest level in the past 60 years (USDA Forest Service 2011). The reduction in harvesting on public lands results, in part, from:

- the complicated interplay between social pressure, federal regulations, available budget and resources,
- fiscal constraints due to increasing wildfire suppression costs,
- complicated coordination among agencies during environmental assessments,
- procedures that cause delays in implementation and increase the costs of management (MacCleery 2008), and
- increases in international production, especially in the pulp and paper sector, and to a lessor extent the roundwood sector (USDA Forest Service 2016).

Recent reductions in harvesting on private lands are more a result of the Great Recession of 2008 and the collapse of the housing market, but also may be due to forestry laws that limit management in individual states (Ellefson and Cubbage 1980). Currently, the annual net growth in forest volume is greater than twice the annual removals (USDA Forest Service 2011). Thus, progress through active management toward diversifying the landscape by balancing forest age structure and increasing natural community types (e.g., prairie, savanna, woodland, forest), and increasing its resilience to return to a desirable composition and level of productivity after disturbance has been substantially reduced, especially in the West where public lands dominate.

A secondary fallout from the decline in timber harvesting is the loss of capacity in logging and manufacturing industries that went out of business or moved to other regions due to uncertain and inadequate timber supplies in the Western USA, where the industry is so reliant on federal timber (Masek et al. 2011; Goergen et al. 2013). The supply of sawtimber from federal lands has also declined because resources are being diverted to fuels reduction and ecosystem restoration treatments that inherently remove trees that are unmerchantable by today's standards (MacCleery 2008). In the East, the Great Recession and housing collapse of 2008 resulted in loss of capacity in the logging and milling industries due to decreased timber supply driven by private landowners withholding their timber from the marketplace. Thus, active management is today constrained by a shortage of experienced loggers and mills. Without a strong and diverse logging and manufacturing industry, it is impossible to conduct the forest management needed to secure desired regeneration and create forest landscapes characterized by low mortality that are capable of producing their potential in wood volume and value and a host of ecosystem goods and services (forest health and productivity) in the face of future disturbances (forest resilience).

Over half of the forest lands in the USA are owned by 11.5 million private individuals, families or corporations (Butler et al. 2016). Many of these forest parcels are small with a quarter of them being < 10 ha. Most (88%) timber harvested in the US currently comes from these lands (Oswalt and Smith 2014). Traditional forest management is not a primary concern or objective of small private non-industrial landowners, and 87% of timber is harvested without a written management plan (Butler et al. 2016). In addition, many private landowners lack basic knowledge about forest management and conservation issues, and lack awareness of economic and ecological benefits of managing their properties, especially in the context of the greater landscape (Butler et al. 2016). Nearly 20% of private owners are likely to sell their properties within 5 years, which disrupts planning and implementing sustainable forest management. Reaching desired forest conditions often requires a long-term perspective and commitment that many landowners may not develop due to short land tenure (Butler et al. 2016). A break in the sequence of silvicultural practices for regeneration can result in failure due to disruption of any one of the sequential life stages in the regeneration niche at the stand level, which on a grander scale negates achieving landscape conservation objectives.

Serious efforts to regenerate desirable forests conditions by improving forest health and productivity, and creating resilient landscapes requires the participation of small private non industrial landowners, especially in the East. Getting private landowners to implement forest management and silvicultural practices needed for forest regeneration is difficult (Joshi et al. 2015; Butler et al. 2016). Barriers to forest management on private lands include lack of landowner awareness, noninvolvement of forestry professionals in management plan development, landowner concerns for negative aesthetics associated with forest practices, the personal investment required in practices that do not generate a profit, conflicts between silvicultural practices and other landowner objectives, and small parcel size that make forestry operations cost prohibitive (Knoot et al. 2010; Joshi et al. 2015; Butler et al. 2016). In most cases it takes time and investment in periodic forest treatments to secure desired regeneration. Many of these treatments (e.g., thinning, planting, vegetation management or prescribed burning) that are necessary to set the stage for successful regeneration following commercial harvest do not yield net positive revenues to the landowner. These costs must be carried for years before being offset with income from commercial thinning and harvesting.

The common timber harvest practice on private lands is diameter-limit cutting or selective cutting, which accounts for 61% of all harvesting in the US (Oswalt and Smith 2014). These harvest methods are considered high grading in that they remove the commercially valuable products without plans for regeneration or forest sustainability. They are not to be confused with the silvicultural regeneration method of single-tree selection. Diameter-limit cutting seldom results in successful regeneration of desired species, and does little to address landscape diversity, wildlife habitat, or other conservation issues (Heiligmann et al. 1985; Smith and Miller 1987; Schuler 2004; Kenefic et al. 2005). Public cost-share programs help forest planning and operations on private lands (Knoot et al. 2010), but are inadequate to meet the need required to affect landscape change. For some forestry practices (prescribed burning or herbicide application) there may be limitations to use that arise from lack of ability or capacity of the land owner to implement, state or local laws and regulations that prohibit practices or require specialized certifications, concerns over liability, or restrictions imposed by air quality standards.

Barriers to natural regeneration: regional vignettes

Coastal western hemlock-Sitka spruce forests

In the coastal region of the Pacific Northwest, from southern Alaska to northern California, the most common tree species are Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), with minor amounts of western redcedar, (*Thuja plicata*), yellow-cedar (*Callitropsis nootkatensis*) and red alder (*Alnus rubra*). The hemlock-Sitka spruce forest type occur on over 5.1 million ha in Alaska (Oswalt et al. 2014). There are few barriers to natural regeneration in this forest type and the biggest challenge for forest management is excessive regeneration that overwhelms the site. Both western hemlock and Sitka spruce are prolific seed producers; seeds are light and easily dispersed with wind and can germinate on a range of seedbed conditions (Ruth and Harris 1979; Harris 1989; Deal et al. 1991). Both species have prolific natural regeneration, particularly for western hemlock. In a recent study of hemlock and spruce seedling banks in SE Alaska, Levy et al. (2010) reported more than 20,000 spruce seedlings ha^{-1} and 200,000 hemlock seedlings ha^{-1}, with very dense, even overstocked seedling banks by management standards (Harris and Farr 1974). Because of the maritime climate, moisture is generally not a limiting factor for tree regeneration (Harris and Farr 1974; Harris 1989; Deal et al. 1991; Nowacki and Kramer 1998). Thus, the key barrier in the regeneration niche comes in the final stage of seedling growth to canopy closure and the beginning of the stem exclusion stage (Oliver and Larson 1996). Following major disturbances such as clearcutting, exceedingly high seedling density (Deal and Tappeiner 2002; Levy et al. 2010) causes long-term stagnation (e.g., 100 years) and substantial delay in stand development without further silvicultural intervention by costly precommercial thinning (Harris and Farr 1974; Alaback 1982; Tappeiner and Alaback 1989; Deal et al. 1991; Deal 2001).

Although deer browsing and herbivory are usually not major problems for western hemlock and Sitka spruce because of excessive regeneration, herbivory on preferred species such as western redcedar and yellow-cedar regeneration can limit their regeneration. Hence, their regeneration success may require planting seedlings and protecting them with shelters. Yellow-cedar has some particular challenges for regeneration. Yellow-cedar can regenerate by seed or asexually by layering. However, its natural regeneration failures occur due to poor seed and cone production, and loss of layering capacity due to yellow-cedar decline that is associated with climate change (Hennon et al. 2009, 2016). Thus, planting of yellow-cedar cuttings (stecklings) may be required for successful regeneration. Another species of increasing importance in this forest type is red alder. Alder is a shade intolerant pioneer species with rapid juvenile growth and is frequently found following disturbances such as logging, avalanches and landslides, or in riparian zones (Wipfli et al. 2002; Deal et al. 2004). Natural regeneration via seed is not assured and red alder is normally planted to ensure adequate stocking where alder is desired (Harrington et al. 1994).

Ponderosa pine forests of the western USA

Ponderosa pine (*Pinus ponderosa*) occurs on 9.3 million ha in the West (Oswalt et al. 2014). In the Colorado Front Range (CFR), the easternmost mountain range of the southern Rocky Mountains, ponderosa pine forests are dominant at elevations between 1700 and 2800 m, mixing with scattered Rocky Mountain juniper (*Juniperus scopulorum*) at the lower elevations and Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) at elevations exceeding 2000 m (Peet 1981). Specific climatic conditions (e.g., temperature and moisture) are major determinants of ponderosa pine success in each of the stages in the regeneration niche (Feddema et al. 2013; Petrie et al. 2016, 2017), often resulting in highly episodic natural regeneration (Brown and Wu 2005; Boyden et al. 2005; League and Veblen 2006; Shepperd et al. 2006). The reproductive stages of flowering and cone development span over 2 years, and they are promoted by cool, wet springs, warm, wet summers, and warm winters (Mooney et al. 2011; Feddema et al. 2013; Savage et al. 2013; Petrie et al. 2017). Currently, on the Colorado Front Range, good seed crops occur every 4–6 years but even in years with high seed production, seed viability is often 50% and highly predated by small mammals (Shepperd et al. 2006). Successful seed germination is influenced by soil moisture availability, growing degree days, and above freezing temperatures. Seedling germination and establishment is highest when air and soil temperatures range from 20° to 25 °C and when precipitation and moisture availability are average or above average for the local area (Petrie et al. 2016). A decrease in seedling germination and establishment occurs when temperatures exceed 25 °C and soil water potential falls below −4 MPa (Petrie et al. 2016). Late spring or early fall freezes can also negatively impact germinants and seedling establishment.

In addition to climatic factors, light availability influences ponderosa pine regeneration success. Ponderosa pine is shade-intolerant. Historically, wildfires kept forests relatively open (Brown et al. 2015; Battaglia et al. 2018) and kept the more shade tolerant Douglas-fir at low densities allowing sufficient amount of light to reach the forest floor. However, with the advent of fire exclusion from these frequent fire-dependent forests, tree density has increased and shifted forests toward more closed-canopied conditions (Brown et al. 2015; Battaglia et al. 2018). This has impacted the ability of ponderosa pine to compete with Douglas-fir (or white fir (*Abies concolor*), grand fir (*Abies grandis*), or red fir (*Abies magnifica*) in other regions of the Western USA).

Another consequence of increased tree density is the increase in wildfires that burn across large, contiguous areas, resulting in substantial areas with no overstory tree survival (Chambers et al. 2016; Fornwalt et al. 2016; Rother and Veblen 2016). Since ponderosa pine does not have serotinous cones, does not vegetatively sprout, and has short-lived seeds in the seed bank (Oliver and Ryker 1990), post-fire regeneration is dependent on seeds from surviving trees. After wildfires, Chambers et al. (2016) found that regeneration density decreased exponentially as distance from surviving forests increased; the majority of regeneration was found within 50 m of the seed-bearing trees. As wildfires in ponderosa pine dominated forests continue to have components of large high severity patches that exceed hundreds or thousands of hectares (Chambers et al. 2016; Stevens et al. 2017), we will continue to have areas without successful natural ponderosa pine regeneration.

Although proximity to seed source is important, the change in environmental conditions following a high severity fire also impacts regeneration success. The loss of overstory combined with bare, blackened soils create higher daytime and lower nighttime surface temperatures, increased wind speeds, and increased evaporation, which can lead to desiccation of seedlings (Feddema et al. 2013; Rother et al. 2015; Petrie et al. 2016). In addition, sprouting of aspen (*Populus tremuloides)*, gambel oak (*Quercus gambleii)*, shrubs, and herbaceous plants can inhibit successful ponderosa pine regeneration (Bonnet et al. 2005; Collins and Roller 2013).

Successful ponderosa pine regeneration in high severity burn areas also has to contend with the chance of another wildfire burning in the same area too soon. In high severity burn areas, surface fuel loads are often elevated due to the amount of overstory tree mortality (Keyser et al. 2008; Fornwalt et al. 2018). Ponderosa pine growth on the Colorado Front Range is slow, often taking 20–25 years to reach the height of 1.3 m (Shepperd et al. 2006). Although ponderosa pine is known to have high resistance to fire due to its thick bark, this resistance is size dependent, with bark thickness increasing as trees grow larger in diameter (Keyser et al. 2006; Hood and Lutes 2017). Seedling and sapling sized ponderosa pine are highly susceptible to the flame lengths observed in a wildfire (Battaglia et al. 2009), especially in areas with high surface fuel loads.

Oak forests of the eastern USA

In the East, oak forest types occur on 79 million ha and account for more than half of the forest lands (Oswalt et al. 2014). Paleoecological studies have revealed that oak has been the dominant genus in forests of this region for millennia (Abrams 2002; Hanberry and Nowacki 2016). Despite the long-term dominance of oak, it is experiencing regeneration failure on many but the most xeric sites (Johnson et al. 2009; Fei et al. 2011). Although a single causal mechanism may explain oak regeneration failure in a stand, the ubiquitous pattern of oak regeneration failure across a wide range of site conditions is attributed to multiple interacting factors such as altered disturbance regimes, climate change, herbivory, insects and diseases, invasive species, and competing vegetation (McEwan et al. 2011).

Oak is a species-rich genus in the East and oak species vary considerably in silvical characteristics, but most seem to have some commonality in their regeneration ecology. Acorn production is not usually limiting to oak regeneration because oak forests are of an age that is generally associated with good production (Downs 1944; Downs and McQuilken 1944). However, as forests continuing aging, as they are throughout the East (Shifley and Thompson 2011; Shifley et al. 2012; Oswalt and Smith 2014), seed production will start declining in senescent older trees, and thus become a limitation to regeneration. Predation of acorns by insects, small mammals, birds and deer, and herbivory of seedlings and saplings by animals and insects can limit oak regeneration. Oak masting events provide enough seed to satiate predators, thus allowing some seed to germinate and develop into seedlings. Acorn production is erratic and large oak seed crops are usually produced every 2–10 years (Dey 2002). White-tailed deer are the most influential herbivore in eastern oak forests (Healy and McShea 2002). White-tailed deer population density is at unprecedented levels in many parts of the eastern oak forest region, and is likely a novel limiting factor on oak regeneration by both acorn consumption and seedling browsing (Crete 1999). Over browsing by white-tailed deer is directly responsible for oak regeneration failure in some stands (Tilghman 1989; McWilliams et al. 1995; Dey 2014).

Oak seedlings that germinate from acorns may exist in the understory in mature forests for several years, but are ultimately dependent on canopy disturbance that provides adequate light for growth and increased competitiveness (Carvell and Tryon 1961). New oak seedlings have slow juvenile shoot growth due to preferential carbon allocation to their roots (Johnson et al. 2009). This strategy puts them at a competitive disadvantage in certain disturbance regimes. Infrequent, small-scale, low intensity disturbances that create small canopy gaps, favor shade tolerant species, and infrequent but catastrophic damage to the overstory releases shade tolerant species in the understory and promotes regeneration of pioneer competing species. Oak seedlings and seedling sprouts can persist in the understory of forests if there is adequate light (Dey 2014). Known as advance reproduction, they are the primary source for oak regeneration, and may be competitive if they are relatively large and well-established at the time of regeneration release (Johnson et al. 2009). Larger oak trees can produce sprouts if they are cut in a harvest and stump sprouts are the most competitive source of regeneration, but sprouting capacity declines rapidly in larger and older oak trees and not all oak trees produce stump sprouts (Weigel and Peng 2002).

One of the most common limiting factors to oak regeneration and its recruitment into the overstory is inadequate sunlight for oaks to develop into large, competitive regeneration, either before being released as advanced reproduction or after release in stand initiation (Lorimer 1993; Dey 2014). Oaks are moderately tolerant to intolerant of shade depending on species, and oak advanced reproduction typically grows well in 20–50% of full sunlight (Dey 2002). However, in most mesic and submesic oak forests throughout the East, the midstory and understory contain a high density of shade-tolerant stems (e.g., red maple (*Acer rubrum*), sugar maple (*A. saccharum*) and American beech) that reduce light to < 5% of full sunlight, insufficient for survival or growth of oak seedlings. In mature forests, there may be thousands of small (< 15 cm tall) oak seedlings, but they are not competitive during regeneration. Partial harvesting releases the shade tolerant understory, but when oak forests are clearcut without adequate oak advance reproduction, regeneration is often dominated by fast-growing pioneer species such as yellow-poplar (*Liriodendron tulipifera*), birches and aspens.

Changes in disturbance regimes, climate, and herbivore pressure, and introduction of nonnative invasive species are associated with increasing abundance of shade-tolerant stems in the understory and midstory of oak forests that limits oak regeneration (Johnson et al. 2009; McEwan et al. 2011). It is commonly reported that oak forests were more open in the past than they are today due to a regime of frequent low-intensity surface fires and periodic mixed-severity fires that inhibited regeneration of fire-sensitive species, competing vegetation and formation of a midstory canopy (Abrams 1992; Hanberry et al. 2014b; Stambaugh et al. 2015). Under a fire regime, any factor that causes overstory mortality creates an opening and frees up space for oaks to grow up into. Fire preferentially favors oaks over its competitors because oak has many fire adaptations. The association between widespread frequent fire and long-term dominance of oak is known as the fire-oak hypothesis (Abrams 1992; Arthur et al. 2012). Many oak species are adapted to frequent fire regimes because they have relatively thick bark to protect the cambium from lethal temperatures, readily sprout if the shoot is killed by fire, they can compartmentalize fire injuries and resist stem decay, and they are better adapted to surviving on droughty, fire-prone sites than their competitors (Abrams 1992; Stambaugh et al. 2015). But in the absence of fire, canopy disturbances release the shade tolerant species in the understory, and if the gap is large enough, provide regeneration opportunities for competing pioneer species.

Nonnative invasive plants, pests, and pathogens also present barriers to oak regeneration. For example, Chinese privet (*Ligustrum sinense*), bush honeysuckle (*Lonicera maackii*), and common buckthorn (*Rhamnus cathartica*) are shade-tolerant, nonnative invasive plants that can create monocultures in oak forest understories may inhibit oak regeneration by limiting available light (Hartman and McCarthy 2008; Schulte et al. 2011; Hart and Holmes 2013). Gypsy moth (*Lymantria dispar*) is an nonnative invasive pest that defoliates oak trees and hinders oak regeneration by killing seedlings and saplings and by reducing acorn production through mortality or reduced tree vigor in sexually mature oak trees (Gottschalk 1989). In addition, the native oak decline complex, an intricate interaction among climate, fungi and insects, is a chronic barrier to oak regeneration by killing mature trees. Catastrophic mortality can occur over tens or hundreds of thousands of hectares (Oak et al. 2004; Shifley et al. 2006; Kabrick et al. 2008). Death of overstory oaks by decline decreases acorn production substantially, reduces the potential for overstory trees to produce sprouts, and releases the dominant shade tolerant regeneration in the understory. The future is for oak decline to continue as a major forest health problem because of the expected increasing occurrence and severity of drought, increasing heat stress, increases in precipitation that will promote fungal populations, and a maturing oak forest landscape across the East (LeBlanc and Foster 1992). Left unmanaged, these stands will continue to experience regeneration failure in the desired oak species and succession toward more shade tolerant species.

Changes in climate through the Eastern Deciduous Forest Region have also hindered oak regeneration. McEwan et al. (2011) found that throughout the region that growing season moisture increased and maximum summer temperature decreased during the 20th Century. Increased precipitation and reduced maximum temperatures may have influenced regeneration patterns in oak-dominated systems (McEwan et al. 2011; Pederson et al. 2013; 2015). Additionally, relative to the four centuries prior, droughts of the last century were less frequent and intense while consecutive years of abundant moisture were more common and intense (McEwan et al. 2011; Pederson et al. 2013). Multi-year, severe droughts (i.e. megadroughts) were relatively common from 1500 to 1900 (Cook et al. 2010; McEwan et al. 2011). Oaks are generally drought resistant and thus, droughts may favor oak regeneration by killing drought-sensitive species such as maples and other shade-tolerant mesophytes, and thereby increasing light to oaks in the regeneration layer (Abrams 1990). Some researchers have hypothesized that this long megadrought-free period may have, in part, allowed drought-sensitive species to reach threshold densities and/or sizes that they may no longer be as sensitive to drought conditions. For example, red maple intercepts precipitation at higher rates than many co-occurring species in oak stands and thus, directs a disproportionate amount of water as stem flow to the center of the root network (Alexander and Arthur 2010). Additionally, the leaves and woody material of red maple decompose faster than oak litter (MacMillan 1988; Abrams 1990), and an increase in this relatively fast decaying organic matter is expected to increase infiltration capacity of the soil, increase soil moisture holding capacity, and modify soil nutrient pools thereby creating more mesic site conditions that favor oak competitors (Nowacki and Abrams 2008).

Longleaf pine forests of the southern USA

At the time of European settlement, longleaf pine forests were among the most extensive ecosystems in North America, occupying an estimated 37 million hectares of forests, woodlands, and savannas throughout the southeastern USA (Frost 1993, 2007; Oswalt et al. 2012). Longleaf pine has been considered a difficult species for natural regeneration success due in part to characteristics of its regeneration ecology. Seed production is variable spatially and temporally (Haymes and Fox 2012; Guo et al. 2016), with good seed crops occurring approximately every 4–7 years (Croker and Boyer 1975; Boyer 1990). Longleaf pine seeds germinate quickly, often within a week of reaching the ground (Boyer 1990; Brockway et al. 2007). The condition of the seedbed is important, as longleaf pine seeds require contact with mineral soil for germination (Boyer 1990). Following germination, seedlings develop in a "grass stage" that is characterized by allocation of growth to the root system and stem thickness, with needles surrounding the terminal bud but no stem elongation. This morphology is considered an adaptation to frequent surface fire (O'Brien et al. 2008; Keeley 2012; Pile et al. 2017a) but can put longleaf pine at a competitive disadvantage relative to taller species in the absence of fire. Longleaf pine seedlings may persist in the grass stage from 2 to over 10 years, depending on growing conditions, but have commonly been reported to begin stem elongation when the root collar diameter approaches 2.5 cm (Boyer 1990; Knapp et al. 2006), however, variability in this threshold has also been noted (Ramsey et al. 2003). Following emergence from the grass stage, rate of recruitment is reduced by competition (Boyer 1993), although longleaf pine has been noted to persist in a suppressed state for long periods and then respond to release (Boyer 1985; Curtin 2017).

Legacy effects of historical land use determine conditions under which contemporary natural regeneration occurs, with longleaf pine exemplary of several particular challenges. Through a variety of past land use decisions, including forest conversion to agriculture, widespread logging, extraction of naval stores (turpentine, rosin, tar and pitch), urban development, and the development of plantation forestry, the extent of longleaf pine was reduced to approximately 3% of its presettlement representation by the end of the 20th century (Frost 2007). The removal of mature longleaf pine trees as a seed source eliminated the possibility for natural regeneration throughout much of its range, while open range hogs decimated the abundance of longleaf pine seedlings throughout the region during the 1800 s. The once dominant longleaf pine type was, in part, due to a frequent (1–6 years on average) fire regime across its range (Van Lear et al. 2005; Huffman 2006; Frost 2007; Stambaugh et al. 2011a, b). But, the fire exclusion policies of the 1900 s further reduced longleaf pine regeneration success and allowed for increased abundance of species that compete with longleaf pine regeneration, an effect that persists as a barrier today.

Past challenges with natural longleaf pine regeneration could be attributed to misunderstanding or disregard for the species' regeneration ecology (Frost 2007). However, extensive research has greatly informed our understanding of longleaf pine ecosystem function and regeneration needs (see Jose et al. 2007; Kirkman and Jack 2017 for compilations), suggesting shifts in regeneration limitations from ecological to social and operational constraints. For example, scientists and managers universally acknowledge the importance of fire for regeneration success. Fire is critical to several stages in the regeneration niche, including creating a seedbed for germination and reducing the competitive ability of other species, and fire interacts with other ecosystem components to maintain overall ecosystem function (Mitchell et al. 2009). However, the ability to use fire for forest management is not just an ecological decision but largely dictated by policy decisions, social acceptance, and available resources (Ryan et al. 2013; Kobziar et al. 2015). At a broad scale, land ownership further contributes to patterns of natural regeneration success. The majority of extant longleaf pine is under private ownership, while management objectives compatible with natural longleaf pine regeneration and the ability to achieve those objectives operationally are more commonly realized on public lands (Oswalt et al. 2012).

In the future, the ability to maintain a frequent fire regime will likely remain a barrier to natural regeneration of longleaf pine, although several other factors present possible future challenges. Habitat suitability models generally suggest that longleaf pine may be relatively well-positioned for future climate (Prasad et al. 2007), although the effects of climate change on specific life history processes, such as cone production, are not well understood (Guo et al. 2016). Despite longleaf pine's association with xeric sites, dry extremes have been associated with seedling mortality (Allen 1954; Knapp et al. 2013; Loudermilk et al. 2016), raising questions regarding impacts of future climate variability on regeneration success. In addition, the southeastern US is prone to aggressive plant invasion, with specific challenges from species that may respond favorably to prescribed fire (e.g., cogongrass (*Imperata cylindrica*); MacDonald 2004) or affect the ability to use prescribed fire due to changes to fuel dynamics (e.g., Chinese tallow (*Triadica sebifera*); Pile et al. 2017b). However, longleaf pine may be successfully regenerated naturally using a variety of silvicultural approaches (Mitchell et al. 2006), suggesting flexibility for forest management in the future.

Conclusion

Natural regeneration is very much a function of the *whims* of nature, i.e., all the stochastic events that collectively affect regeneration in significant ways and seldom results in desired conditions without management. Variations in seed availability, germination conditions, competition, climate effects, herbivory, and other factors all combine to cause highly variable and often unpredictable forest regeneration outcomes. Active forest management to regenerate desirable forests on a much larger scale than current levels is needed to set the landscape on a trajectory toward increased health, productivity and resilience. Environmental stresses and forest perturbations are causing severe mortality and regeneration failures across regional landscapes because our nation's forests (330 million hectares) are relatively homogeneous and thus vulnerable to insect and disease outbreaks, extreme weather events, wildfires and changing climate. Balancing forest age structure by regenerating desired forest compositions is fundamental to conserving native diversity, sustaining production of forest goods and services, and increasing ecosystem and landscape resilience to future stresses and disturbances. It will be difficult to achieve these goals given the current level of regeneration harvesting occurring on public lands and the methods of harvesting that predominate on private lands.

A central objective in using natural regeneration is getting adequate numbers of desirable trees. These desirable trees can be too many or too few, and this involves species, form, size, and position in the stand. Desirable numbers are typically defined as a range of stocking that will meet management objectives, and other constraints related to stocking, as the stand develops. The added cost of enrichment planting when the natural regeneration is too low, or the cost of thinning when density is too high, represent a significant economic barrier to regeneration success. This can be a barrier to natural regeneration when funds are limited or when achieving a minimum stocking is required.

Barriers to natural regeneration operate at the individual, stand/community and landscape scales. They affect tree regeneration through physiology and ecology mechanisms and processes, and include social, political and economic factors. Changes in land use history over the past 400–500 years have left a legacy in forest composition and structure that are foundational to current forest health, productivity and landscape resilience problems. Novel disturbance regimes, homogeneous landscape conditions, invasive species and changing climates challenge our ability to naturally regenerate forests that often have low to moderate regeneration potential to begin with.

Each tree species has ecological needs for natural regeneration. This is complicated enough in that we may not fully understand the silvical needs of desired species and major competing species. Successful regeneration involves the sequential achievement of the stages in the regeneration niche, from flowering and seed production, to recruitment into canopy dominance at crown closure. Inadequate ecological conditions can lead to natural regeneration failure at any stage in the regeneration niche. Specific factors that challenge contemporary management include: (1) ecological change: climate, invasive species, herbivory, insects/diseases and wildfire, which cause widespread forest mortality and disrupt regeneration, and (2) human change: social, political, economic, which affect our ability to manage the forest. Additionally, a regulatory structure may create disincentives for using natural regeneration approaches by requiring minimum numbers of trees in a specified time-frame. There are lots of places in the natural regeneration process for failures—it is a complex ecology within a complex social and management decision system. However, these challenges should not discourage us or cause delay in our plans and efforts to manage for resilient, healthy and productive forest systems that provide for the conservation of our natural heritage and provide for our social well-being. A strong and diverse timber industry and forest products manufacturing sector is essential to implementing silvicultural prescriptions for successful natural regeneration and overcoming financial barriers to management on a local to national scale. New markets for small diameter and low quality forest resources are needed to increase profitability and encourage forest owners to engage in active management to improve the regeneration niche and increase regeneration potential and success.

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