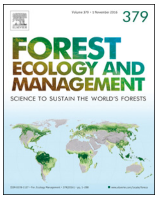
Forest Ecology and Management 472 (2020) 118256

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Open forest ecosystems: An excluded state

Brice B. Hanberry[a,*], Don C. Bragg[b], Heather D. Alexander[c]

[a] USDA Forest Service, Rocky Mountain Research Station, 8221 Mt. Rushmore Road, Rapid City, SD 57702, United States
[b] USDA Forest Service, Southern Research Station, P.O. Box 3516 UAM, Monticello, AR 71656, United States
[c] Department of Forestry, Forest and Wildlife Research Center, 775 Stone Blvd., Mississippi State University, Mississippi State, MS 39762, United States

ARTICLE INFO

Keywords:
Ecological restoration
Fire
Function
Herbaceous plants
Understory
Wildlife

ABSTRACT

Once dominant but now largely excluded from eastern North America, open forests of savannas to woodlands occupy the ecosystem gradient between grasslands and closed forests. These fire-maintained systems differ in structure, processes, and species from closed canopy, succession-driven forests that currently dominate this region. In functional open forest ecosystems, frequent, low to mixed severity and intensity surface fires limit tree regeneration, depending on factors such as overstory tree density, resulting in relatively stable structure where overstory trees co-exist with a largely herbaceous understory. Reduced and spatially variable tree densities in open forests result in unique environmental conditions and function. Trees in open forests typically represent a small fraction of the biodiversity, which instead resides in the rich herbaceous ground layer. Rather than being constrained by overstory disturbances, succession, and biological legacies, the permanently open structure and herbaceous communities of open forests support invertebrate and vertebrate species throughout their lifetimes. Transition from open to closed forests across most of eastern North America during the past century produced a "new normal," in which excluded open forests remain largely unrecognized at considerable conservation costs, particularly loss of key processes and wildlife species associated with a matrix of co-dominant tree and herbaceous layers. Management for open forests emphasizes the understory herbaceous plant community, similar to ephemeral seral stages of successional forest, rather than tree regeneration to produce an alternative outcome in structure, function, and support for biodiversity.

1. Introduction

Across most of eastern North America (south of boreal forests), severe, large-scale natural disturbances including major wildfires, windstorms, ice storms, and insect epidemics are comparatively rare, resulting in infrequent stand replacement of dominant trees in the absence of anthropogenic disturbance (Lorimer, 2001; Seymour et al., 2002; Lorimer and White, 2003; Elsner et al., 2008). Intervals between catastrophic natural disturbances in the central and southeastern United States may have ranged from hundreds to thousands of years, often with uneven and incomplete tree removal (Lorimer, 2001; Seymour et al., 2002; Ruffner and Abrams, 2003; Elsner et al., 2008). Additionally, some historical forests before intensive and extensive land use, which started with Euro-American settlement and escalated during the late 1800s, may have been more fire-, wind-, and insect-proof than currently due to lower tree densities, older more experienced individual trees, and more continuous forests without sharp edges (e.g., Mitchell and Duncan, 2009, also lower density forests may make stands less vulnerable to insects and fire exposure induces resin duct production, which helps protect against fire and insect damage). While rarity of stand-replacing disturbance should lead to widespread occurrence of closed, late successional old-growth forests, numerous reviews of historical forests, before 1900 or earlier depending on land use, have suggested that perhaps over a hundred million hectares of eastern North America (Fig. 1) were once open forests of savannas and woodlands dominated by oak (*Quercus* spp.) and pine (*Pinus* spp.; Rostlund, 1957; Denevan, 1992; Noss et al., 1995; Lorimer, 2001; Van Lear and Harlow, 2002; Hanberry and Nowacki, 2016; Hanberry et al., 2018a). Oaks once comprised $>$ 50% of all trees in the central U.S. and oaks and pine or pine alone comprised 75% of those in the southeastern U.S. (Delcourt and Delcourt, 1987; Hanberry et al., 2014; Hanberry and Nowacki, 2016; Hanberry and Dey, 2019; Hanberry et al., 2019). Other species or genera may have been dominant at local scales or have wider distributions, but at landscape scales, aside from the Lower Mississippi River Valley, no species or genera were as competitive. For example, although American chestnut (*Castanea dentata*) was considered dominant, this species comprised 2% of all trees in the central eastern US and 8% of all trees in the central Appalachian Mountains; at maximum,

---

[*] Corresponding author.
E-mail address: brice.hanberry@usda.gov (B.B. Hanberry).

https://doi.org/10.1016/j.foreco.2020.118256
Received 10 February 2020; Received in revised form 5 May 2020; Accepted 19 May 2020
0378-1127/ Published by Elsevier B.V.

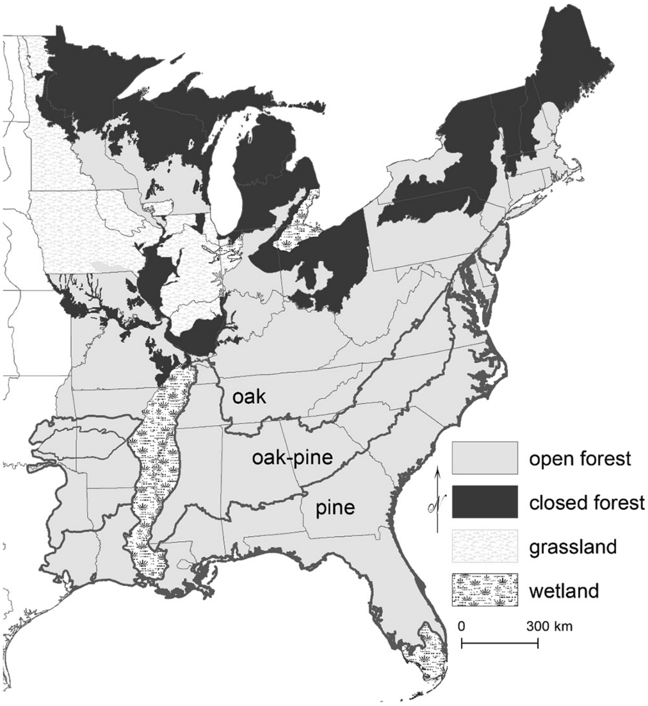


Fig. 1. Estimated historical extent of open forests in the eastern United States (modified from Hanberry and Thompson 2019 using Hanberry et al., 2014; Hanberry and Dey, 2019; Hanberry, 2020). Finer scale variation occurred due to firebreaks or fire exposure, resulting in closed forests within open forests or open forests within closed forests.

chestnut was 18% of all trees in two ecological subsections where oaks were 21% and 65% of all trees (Hanberry and Nowacki, 2016).

Based on these studies of composition, structure, and historical accounts (above), open forests rather than closed forests once were the most abundant ecosystem in eastern North America, but open forests now are a rare excluded state due to management of forests and disturbance regimes for other goals and objectives. In a literal sense, exclusion of the frequent fire disturbance regime, due to fire risk, is a challenge to continued existence of open forests (Noss et al., 1995). Metaphorically, open forests were excluded (or rejected) as an option in most contexts, likely because of their indeterminate state between grasslands and forests, which moreover contained understocked growing space rather than commercially valuable standing timber. These combined exclusions have degraded the open forest ecosystem state to such a degree that it is hardly recognizable outside of isolated remnants. Additionally, different land uses replaced forests, resulting in a smaller and fragmented forest base, and extensive clearing accelerated turnover in forest composition and structure during reforestation under different drivers. Forests affected by clearing may have a greater proportion of earlysuccessional fast-growing species than historical forests under the filtering effect of frequent fire, whereas forests specifically affected by forest management practices will favor certain species disproportionately (Hanberry, 2019). Land use history also influences groundflora presence in seed and bud banks (Abrams and Dickmann, 1982).

Loss of the historically widespread distribution of open forests throughout the eastern United States has resulted in great conservation costs. Old-growth open forest ecosystems, which contain an overstory of long-lived canopy trees and a persistent herbaceous ground layer, provide a range of light, moisture, structure, and forage favorable to many wildlife species, which lasts the lifetime of the animals (e.g., Schlossberg, 2009). A recently published analysis of long-term estimates of avian populations documented dramatic bird declines in eastern North America during the last half-century (Rosenberg et al., 2019; see also Askins et al., 2007; Hanberry and Thompson, 2019). Although conservation challenges can arise from many different factors, including agricultural intensification, habitat fragmentation, urbanization, toxic chemicals, climate change, exotic diseases, insect pests, and non-native species (e.g., domestic cats), loss of open forests also is a major contributor to declines in herbaceous species (e.g., Leach and Givnish, 1999; Van Lear et al., 2005; Rooney et al., 2008) and the vertebrates (Jackson, 1988; Means, 2007; Harper et al. 2016; Haggerty et al., 2019) and invertebrates dependent on open forests for foraging and reproducing (Folkerts et al., 1993; Grundel et al., 2010; Henderson et al., 2018; Lettow et al. 2018; Goulson, 2019; Odanaka et al., 2020).

To help address open habitat-related losses of flora and fauna, Swanson et al. (2011) recommended increased creation of early successional forests (i.e., the developmental stage between stand-replacing disturbance and re-establishment of closed forests that is similar to open forests, without the permanent tree and grass layers) in landscapes where managers have emphasized closed forest conditions (Swanson et al. 2011; Hanberry et al., 2018a). To provide a counterpart—or counterpoint—to Swanson et al. (2011), we demonstrate that degradation of the open forest spectrum in eastern North America may have a more profound impact on ecosystem processes and associated species than any lack of early successional forests. Here, we focus on differentiating open forests from other ecosystems in terms of structure and function, stability and disturbance, diversity and associated conservation costs of exclusion, and management. However, fire exclusion as a process (Nowacki and Abrams, 2008) and open forest ecosystem characteristics (Hanberry et al., 2018a) are necessarily part of extending discussion to the conservation costs of open forest exclusion. To expand the value of open forests, our goals are to: (1) describe structural and functional attributes of open forests compared to grasslands and closed canopy forests, (2) examine the stabilizing role of frequent surface fires on open forests, (3) highlight the ecological importance of open forests for biodiversity, (4) address conservation costs of open forest exclusion, and (5) discuss consequences of current management practices and benefits of management for open forests in eastern North America. Widespread restoration of open forests as a viable alternative state also deserves consideration by managers, researchers, and planners.

2. Structural and functional attributes of open forest ecosystems

We define open forests as a fire-dependent bilayer ecosystem consisting of a single overstory dominated by fire-tolerant tree species and an herbaceous ground layer, with limited midstory shrub and tree cover (Fig. 2; see also Hanberry et al., 2018a). The single tree layer constrained the complexity and dimensionality of internal stand structure; however, open forests ecosystems varied from nearly treeless savannas to closed woodlands that spanned the spectrum between grasslands and well-stocked, closed canopy forests (Hanberry et al., 2018a). Tree density of larger diameter trees ($\geq$12.7 cm) ranged from $>$ 50 trees/ha to $<$ 250 trees/ha (basal area of 5–30 m^2/ha), with a corresponding range of canopy cover, generally from 40% to nearly continuous (90%; Hanberry et al., 2014). In eastern North America,[1] frequent surface fires, which typically occurred every 2–25 years, removed most woody understory stems in open forests, thereby limiting midstory

---

[1] Although this paper focuses on the eastern U.S., open pine and oak forests also occur in western North America (e.g., the still abundant ponderosa pine, *Pinus ponderosa*, forests and some rare oak remnants; Hanberry et al., 2017). Furthermore, similar to the alternatives of open and closed forest states in temperate forests with moderate precipitation, depending on presence of fire (Hanberry et al., 2018b), savanna and forest systems both co-occur in tropical zones where precipitation and nutrient availability are great enough to support trees with the open savanna state resulting from fire (Higgins et al., 2000; Cardoso et al., 2018; Charles-Dominique et al., 2018). In other words, the open state is distributed globally where frequent surface fires shape ecosystems.

Fig. 2. Open forests with a bilayer of trees and herbaceous grasslands in southern pines (a) and central oaks (b) of the eastern United States.

development (Wade et al., 2000; Hanberry et al., 2018a; Landfire, 2020). The resulting high light environment and frequent pyrogenic perturbations allowed formation of a diverse, forb- and grass-dominated understory, which further contributed to openness of the ecosystem by providing fine fuels to sustain surface fires (Hanberry et al., 2018a). Continual presence of both large trees and a dense ground layer helped to suppress woody regeneration; woody shrub biomass in open forests usually was low, except for sclerophyllous shrubs (Hanberry et al., 2018a).

The influence of overstory trees in an otherwise grass- or forb-dominated ecosystems is critical to the open forest spectrum (Fig. 3). Many ecological processes, including light and water availability; carbon (C) partitioning, storage, and flux; nutrient dynamics; and environmental stability change markedly as tree cover changes along the spectrum from grasslands to closed forests (Fig. 4). For example, the overstory trees in open forests reduce sunlight, temperature, and wind velocities, increase relative humidity, and contribute nutrient-rich stemflow and leaf litter to underlying soils, often resulting in spatially variable light, moisture, and nutrient environments when compared to treeless grasslands (Brudvig and Asbjornsen, 2009; Hanberry et al., 2018a). Contrasted with the closed canopy end of the spectrum, open forests receive more sunlight and experience more extreme temperatures and greater wind velocities (Hanberry et al., 2018a), but have lower relative humidity and lower nutrient inputs via stemflow, and generally slower decomposition and nutrient mineralization rates (characteristics comparable to early successional forests; e.g., Swanson et al., 2011).

Spatial patterns of woody plants also influence patterns of rainfall distribution and water cycling along the open forest spectrum. Tree canopies intercept and alter precipitation distribution, especially during leaf-on and small rainfall events (Haworth and McPherson, 1995; Siegert et al., 2019), which can impact soil water availability beneath them (Levia and Frost, 2006; Levia et al., 2011). Under light precipitation, canopy interception may reduce underlying surface soil moisture while during heavy rain events, tree leaves and branches capture and redistribute water, which can drip from the surfaces onto the soils below, thereby increasing underlying surface soil moisture (Ko and Reich 1993; Haworth and McPherson 1995; Scholes and Archer 1997, Siegert et al., 2019). Trees also funnel rainwater down their branches and stems, leading to high water inputs near the bole of the tree and a zone of high surface soil moisture (Haworth and McPherson 1995) and increased nutrient inputs (Levia and Herwitz 2000). Thus, as woody dominance increases, precipitation distribution will become more heterogeneous with zones of increased water and nutrient inputs near trees. Furthermore, tree cover influences the rate at which surface soils dry following a rainfall event, with rates increasing with decreasing tree cover (Brudvig and Asbjornsen, 2009).

In general, aboveground net primary productivity (ANPP) increases with increased woody plant dominance (Reich et al., 2001a,b; Norris et al. 2001; Knapp et al., 2008), as trees invest heavily in aboveground tissues to outgrow their competitors and maximize light capture, leading to higher aboveground C pools as biomass accumulates over time (Reich et al., 2001a,b; Knapp et al., 2008; McKinley and Blair, 2008). Belowground net primary productivity (BNPP) may either increase (Reich et al., 2001a,b) or decrease (McCulley and Jackson, 2012) with increased woody cover, depending on the fire regime, water availability, and tree species composition. Fine root standing biomass typically declines with increasing tree cover (Reich et al., 2001a,b; McCulley and Jackson, 2012), and coarse root biomass increases (McKinley and Blair, 2008). While trees have shallow, lateral roots beneath their canopies in open forests, most fine root biomass in these systems derives from grasses that dominate the interspaces between tree canopies (Scholes and Archer 1997). Grasses tend to concentrate their roots in the top 30 cm of soil (Schenk and Jackson 2002a; Nippert et al., 2012) as a strategy to increase nutrient and water uptake (Schenk and Jackson 2002b), especially following pulsed rainfall events in relatively dry environments (McNaughton et al. 1998). However, with frequent fire, soil C pools in grasslands and open forest may be less than in undisturbed closed forests (McKinley and Blair 2008).

Woody plant influences on biogeochemistry also vary along the open forest spectrum. For instance, throughfall and stemflow chemistry can differ between pyrophytic tree species common to open forests and fire-sensitive trees common to closed forests, thereby affecting biogeochemistry differently (Alexander and Arthur, 2010). Tree in-filling into woodlands has been shown to reduce forest floor development, soil C pools, and fuel mass if litter quality and decomposition rates of encroaching species are high, such as when fire-sensitive broadleaf tree species invade oak woodlands (Alexander and Arthur, 2014) and eastern redcedar (*Juniperus virginiana*) invades tallgrass prairie (Norris et al., 2001; McCulley and Jackson, 2012). Nitrogen (N) cycling often increases following woody plant encroachment. Differences in N cycling between open and closed forests can be pronounced if open forests are frequently burned and closed forests are not. While fire often causes a temporary (< 1 year) increase in plant available NH_4^+ and NO_3^- (Wan et al., 2001), frequent (i.e., annual) surface fires in grassland systems have been shown to suppress N availability by reducing the quality and amount of soil organic N (Ojima et al., 1994). N pools in aboveground biomass increase with increased woodiness, along with greater transfer of N to the forest floor via litterfall (Reich et al., 2001a,b; Norris et al., 2007; McKinley and Blair, 2008). Annual net N mineralization rates in soils often increase with higher levels of woody cover, due to higher lability of tree leaf litter compared to that of grasses (Reich et al., 2001a,b; McKinley and Blair, 2008; McCulley and Jackson, 2012). For example, bunchgrass leaf litter often decomposes more slowly than that of oaks (Osono et al. 2014). This is more apparent when litter quality (e.g., C:N ratio or lignin content) differences

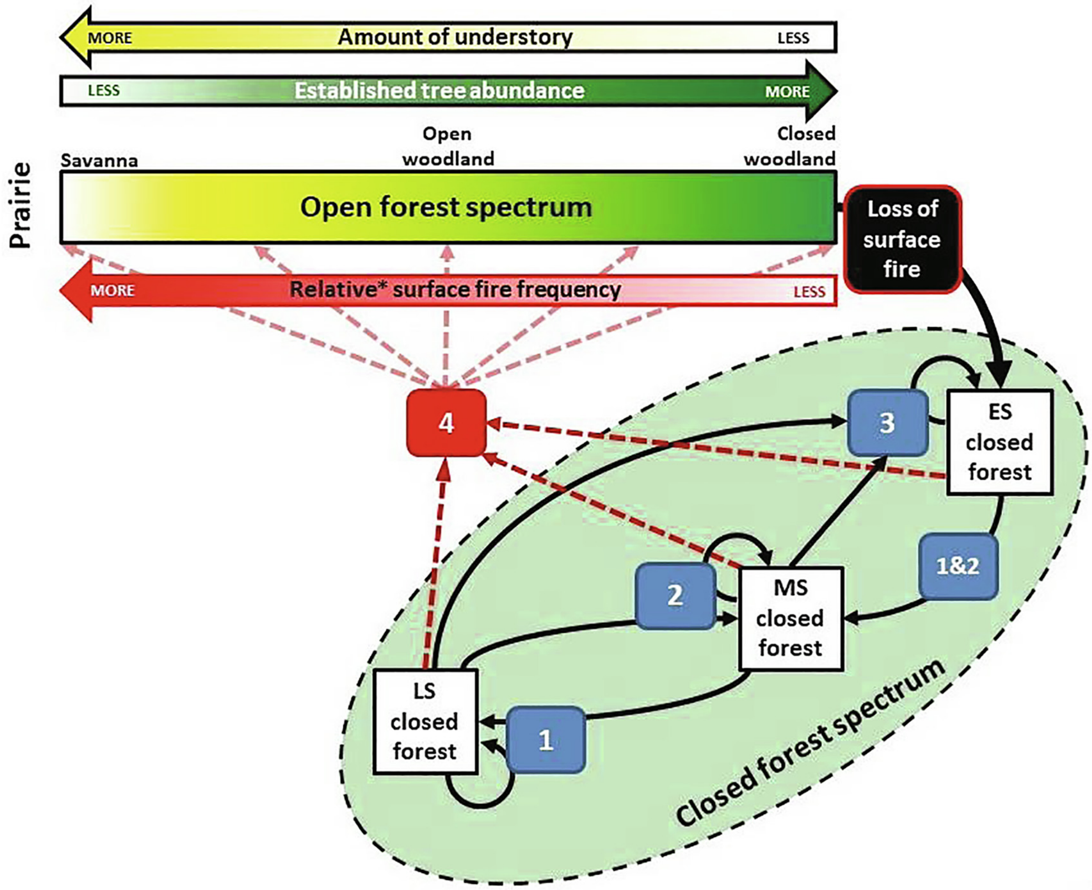


Fig. 3. The open forest spectrum (adapted from Hanberry et al., 2018a), including pathways of internal transition (between varying degrees of openness) and the development of closed canopy forests following traditional successional trajectories with the loss of effective surface fires. Relative surface fire frequency is in reference to how site conditions influence the necessary frequency of surface fires to maintain open conditions (lower productivity sites typically require fewer fires per time period). Transition mechanisms between various states of openness include 1: no major disturbance(s), individual tree mortality, shade tolerance-driven succession; 2: intermediate disturbance(s), small gaps insufficient to support early successional (ES) tree species; 3: stand-replacing disturbance, return of ES species, possible retention (biological legacies) of mid (MS) and late successional (LS) tree species; 4: resumption of frequent surface fire, opening of closed canopy.

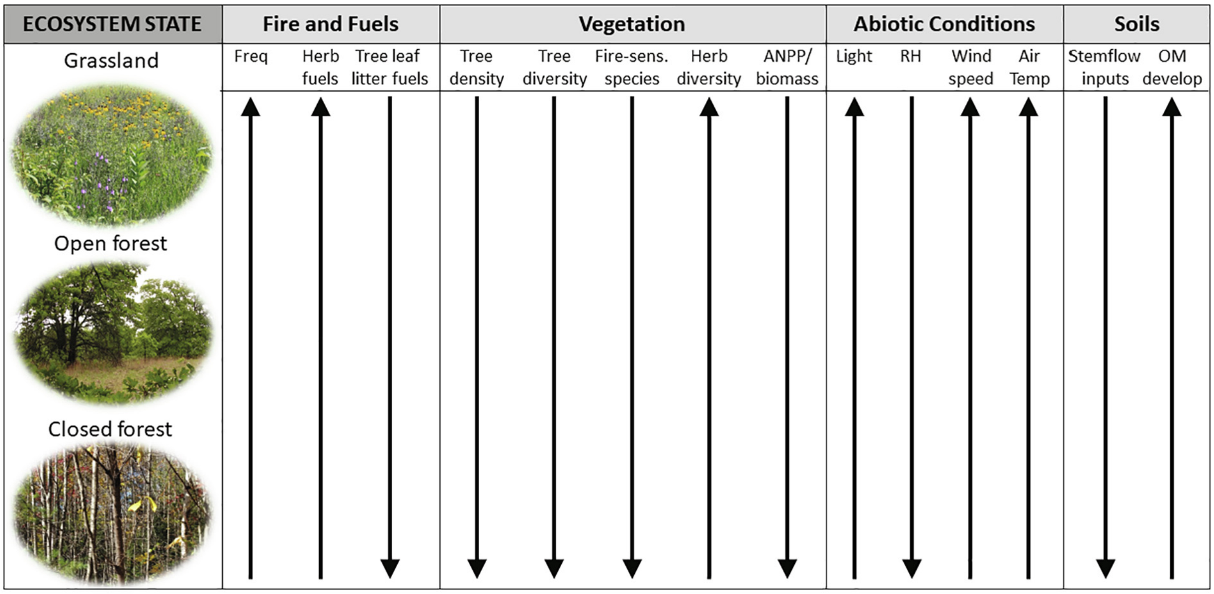


Fig. 4. Generalized changes (increases toward arrowhead) in fire and fuels, vegetation characteristics, abiotic conditions, and soils across the spectrum from treeless grasslands to open forests (i.e., savannas and woodlands) to closed forests (ANPP = aboveground net primary productivity; RH = relative humidity; OM = organic matter).

exist between trees previously associated with open forests and encroaching fire-sensitive species (Alexander and Arthur, 2014; Finzi et al., 1998).

3. Fire as a stabilizing disturbance in open forests

Frequent surface fire is the primary process that maintains open forest structure, composition, functionality, and stability (see also Peterson and Reich, 2008) by inhibiting dense, multiple tree layers that block light transmittance to the forest floor and out-compete herbaceous plants for growing space (Higgins et al., 2000; Peterson and Reich, 2008; Hanberry et al., 2018a). Recognition of this vegetative response led to fire's adoption as a tool for habitat manipulation by Native Americans, who used it to modify vegetation patterns in eastern North America to sustain their foodways and other cultural practices (Denevan, 1992; Denevan, 2011). Later Euro-American settlers adopted the use of fire and even expanded it as a labor-saving tool that supported their pastoralism and desire to clear forests (amongst other reasons; e.g., Hickman 1962), only to later see a remarkably thorough reversal of fire use to fire exclusion as it became considered a liability to human life, health, property, and timber resources (Read, 1943; Johnson and Hale, 2002; Cohen, 2008).

Fire shaped composition through selective filtering of species pools (Hanberry, 2019). The oak and pine genera in particular contain species that are competitive under low severity fire regimes, based on historical abundance (Hanberry and Nowacki, 2016). The fire-tolerant tree species characteristic of open forests are well-adapted to frequent fire, with traits such as hotter burning and/or more flammable litter (Williamson and Black, 1981; Kreye et al., 2013, 2018), protected buds (e.g., longleaf pine; Heyward, 1939), thick, fire-resistant bark (southern pines; Hare, 1965), and ability to resprout from the stump or roots if top-killed by fire when small (e.g., shortleaf pine (Mattoon, 1915) and many hardwoods, including oaks (e.g., Clark and Hallgren, 2003). In open oak forests, usually a few oak species were dominant in an area, although white oak (*Q. alba*) was most abundant (Hanberry and Nowacki, 2016). Much of the central eastern US consisted of black (*Q. velutina*), bur (*Q. macrocarpa*), chestnut (*Q. montana*), post (*Q. stellata*), and/or white oak woodlands (Schnur, 1937; Fralish, 2004). In the Cross Timbers ecoregion, which covers millions of hectares from southern Kansas through Oklahoma into Texas and even extreme western Arkansas, a complex of post oak and blackjack oak (*Q. marilandica*) woodlands, savannas, and prairies occurred, with only minor components of other hardwoods and conifers (Dyksterhuis, 1948). Across the southern US, longleaf pine (*Pinus palustris*) once dominated tens of millions of hectares of savannas and woodlands across the Lower Coastal Plain (Smith et al., 2000; Hanberry et al., 2018c). Similarly, a few upland oaks mixed with shortleaf pine (*Pinus echinata*) covered similarly vast areas of open forests in the Upper Coastal Plain and Interior Highland regions (Hanberry and Nowacki, 2016; Hanberry et al., 2019). Woodland composition may be affected by seasonality of burn as well as frequency, as oaks appear to be more vulnerable than pines to growing season burns (Glitzenstein et al., 1995).

Most tree species are sensitive to frequent fire, although they may have adaptations to establish after severe fires, such as reproduction by wind-dispersed seeds (e.g., sweetgum, *Liquidambar styraciflua*) or rapid growth (e.g., loblolly pine, *Pinus taeda*; Hanberry, 2019). Persistence of less fire-tolerant species in frequently burned landscapes occurred primarily in sheltered environments such as isolated wetlands, riparian corridors, talus slopes, or bluffs where fire was less frequent (Gleason, 1922; Hanberry et al., 2012; Hanberry, 2020). Scattered individuals of fire-intolerant trees and shrubs also can originate due to dispersal from closed canopy forests in these fire-protected areas of the landscape (Gleason, 1922; Hanberry et al., 2012).

Prior to onset of effective fire exclusion, fire return intervals in the open oak and pine forests of eastern North America in general ranged between 2 and 25 years, depending on the suite of species present, ecology of fuels, and the nature of the ignitions (Glitzenstein et al., 1995; Wade et al., 2000; Fralish and McArdle, 2009; Glitzenstein et al., 2012). Historical fire return intervals typically were about 5–25 years in oak open forests (Landfire, 2020). Historical fire return intervals typically were about 2 to 5 years in longleaf pine open forests and up to 7 years in shortleaf pine open forests (Frost, 1998; Wade et al., 2000; Glitzenstein et al., 2012; Guyette et al., 2012; Landfire, 2020). Very frequent fire return intervals (those from 1 to 4 years) prevent establishment of all but the most fire-tolerant tree species with adaptations that allow vulnerable seedlings to persist, such as longleaf pine tree seedlings that have long needles to protect large buds (Wade et al., 2000). Variable, but periodically extended, fire return intervals allow occasional overstory recruitment needed under otherwise frequent surface fire regimes (Hanberry et al., 2018a).

Resilient internal feedbacks emerged between fire, vegetation, and environmental conditions (Hanberry et al., 2012). Open forests allow transmission of light and wind, which help in either producing fuels, drying fuels for ignition, or spreading fire. That is, high light allows development of a continuous herbaceous layer, which dries readily in the sun and wind, to fuel frequent surface fires that remove small diameter trees and maintain open forests (Hanberry et al., 2014; Hanberry et al., 2018a). Trees interspersed in open forests also contribute fuels (from fine to coarse), and their distribution and impacts on flammability and burning patterns contribute to observed variation in fire effects. For example, fuel ecology research on longleaf pine-dominated open forests has shown the role that "perched" pine needles (those draped over grasses and other vegetation) play in helping to carry hotter surface fires across sites rapidly, while cones and coarse woody debris provide longer burning, hotter, smoldering fuels that create different microsites for plant germination (Williamson and Black, 1981; Hiers et al., 2009; Mitchell et al., 2009). The fire-tolerant tree species characteristic of open forests are well-adapted to frequent fire, with traits such as hotter burning and/or more flammable litter (e.g., longleaf pine needles; Williamson and Black, 1981; Kreye et al., 2013, 2018), which facilitates return of fire (Beckage et al., 2009). Variation in fire regimes is amplified by environmental gradients of soil moisture and site topography that alter exposure to fire (Hanberry et al., 2018a). All fire regimes have elements of stochasticity in their frequency, intensity, and extent that are influenced by available fuel characteristics, environmental amendments by vegetation (e.g., sun and wind breaks, water concentration or removal), soils, climate, weather fluctuations, water bodies, rock, and topographic firebreaks (Swanson, 1981; Hanberry, 2020).

Fire frequency also depends on fuel availability and continuity. Consistent surface fires require both a wet period to produce sufficient herbaceous vegetation to provide much of the fine fuels needed to carry fire over the landscape and a dry period to allow their ignition (Shuman et al., 2016; Hanberry et al. 2018b). Less productive sites (e.g., those with xeric and/or nutrient poor soils) by definition produce less vegetation during the same time interval as more productive sites and thus, may burn less frequently than more productive locations because of a slower return of the fine fuels needed to carry fire. These sites also tend to be less prone to woody plant reestablishment. On xeric and/or nutrient poor sites, tree leaf litter can also help provide fuel continuity when a fairly continuous herbaceous groundcover fails to develop under open woodlands.

Spatial variation of tree arrangement, density, and canopy closure also is complex across gradients of fire exposure (e.g., Higgins et al., 2000; Hanberry and Dey, 2019). Trees in open forests may display a range of spatial patterns from random to clustered to uniform, interspersed in a mosaic of densities ranging from very sparsely stocked savannas to open woodlands to relatively closed forests (Hanberry et al., 2018a). This variation influences nature of fine fuel loading, type, and distribution, due to the replacement of fine fuels from the herbaceous component by fine fuels from trees and an increase in fuel moisture (Kane et al., 2008; Kreye et al., 2018).

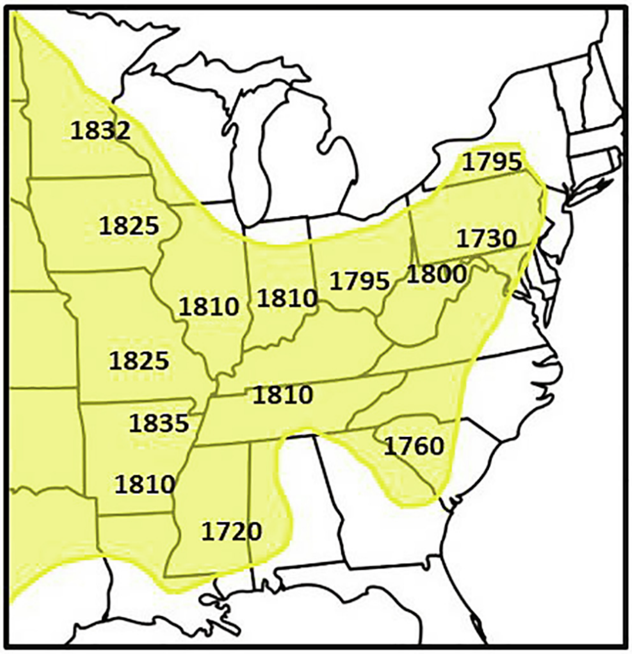


Fig. 5. Historical distribution of American bison (*Bison bison*) in the eastern US (shaded region), with estimated years of extirpation adapted from map and dates in Farrand (1904, p. 63).

The historical stability of open oak and pine forests in eastern North America, which resisted transition to closed forests for thousands of years under varying fire regimes and climate (Delcourt and Delcourt, 1987; Van Lear and Harlow, 2002), is a testament to positive feedbacks between vegetation and frequent surface fire regimes cultured over millennia. Open forests can exist in a relatively stable (non-successional) state through several generations of long-lived tree species with only minor compositional and structural changes over time (Hanberry et al., 2018a). Hence, old-growth open forests usually have an uneven-aged tree component that is stable and dominated by fire-tolerant species heretofore considered to be early seral because of their relative intolerance of shade (Hanberry et al., 2018a). This contrasts with conventional precepts of old-growth forests in eastern North America of late seral stands dominated by shade-tolerant canopy species.

Exclusion of frequent surface fires is a destabilizing force for open forests (Hanberry et al., 2018b). Fire exclusion is an active process via fire suppression and containment of human-caused ignitions, and furthermore, highly fragmented modern landscapes are dominated by land uses and fuel load discontinuities that passively suppress surface fires and limit fire spread (e.g., Guyette et al. 2002; Schertzer et al. 2015). Closed forests likewise act as firebreaks by moderating environmental conditions and further disrupting continuity of fine fuels needed to allow fire ignition and spread (Beckage et al., 2009; Odion et al., 2010). Extended fire-free periods allow for establishment of less fire-tolerant woody plants and development of closed forests (Peterson and Reich, 2001; Cardoso et al., 2018; Charles-Dominique et al., 2018; Hanberry et al., 2018b). Tree density in closed forests is sufficient to suppress grasses, forbs, and other herbaceous understory plants (Maynard and Brewer, 2013; Brewer et al., 2015; Charles-Dominique et al., 2018). Closed conifer forests, such as those found across the southern pine region, produce large amounts of highly flammable fine fuels (e.g., pinestraw, cones, bark, twigs), but with fire exclusion, these fine fuels accumulate and inhibit herbaceous vegetation. The litter of fire-sensitive tree species often is not flammable (Kreye et al 2013, 2018; Babl et al., 2020) and decomposes quickly (Alexander and Arthur 2014). Tree influences on water inputs and drying rates will contribute to wetter fuels in closed forests, further suppressing fire. As enough fire-sensitive species establish in an open forest, the transformed community is able to resist reversion to its original open state by facilitating increasingly favorable conditions for fire-sensitive species, producing a feedback mechanism (i.e., mesophication) that further alters fuel behavior and ecology (Nowacki and Abrams, 2008; Hiers et al., 2009).

4. Biological diversity of open forests

Diversity largely arises from the herbaceous component and affiliated fauna and fungi of these complex ecosystems. Open forests of eastern North America do not have great arboreal richness or diversity, as only a few tree genera tend to dominate these ecosystems (Hanberry et al. 2018a). The simple overstory structure of open forests allows light to the forest floor, while fire removes mechanical barriers of trees and vegetation debris, providing favorable conditions for many different types of grasses and forbs (Maginel et al., 2019). Although dominant herbaceous taxa may be wiregrass (*Aristida* spp.) and saw palmetto (*Serenoa repens*) in the eastern region of longleaf pine savannas and bluestem (*Andropogon* spp., *Schizachyrium* spp.) in other pine and/or oak woodlands, the largest, most intact examples of uncultivated savannas and woodlands contain thousands of grasses and forb species, and even small, isolated, disturbed remnants may contain hundreds of species (Walker, 1993; Leach and Givnish, 1999; Bader, 2001). Numerous species associated with open forests have been compiled into indicator plant lists (e.g., Packard, 1988; Walker, 1993; Leach and Givnish, 1999; Bader, 2001). In contrast, closed forests may lack most of these herbaceous species, particularly ones that increase after burning because of requirements for fire (i.e., heat or smoke or reduced competition) to germinate, such as geraniums and lupines, which are used by butterflies (Martin et al., 1975; Abrams and Dickmann, 1982; Dunwiddie, 1998).

Open forests possess multiple and complex environmental gradients other than surface fire effects, such as differences in moisture and light availability, soil nutrients, nutrient cycling, and herbivores, which favor a different suite of herbaceous species than grasslands and particularly closed forests. Open forest conditions including increased shade under trees (which increases water availability), a reduced growing season, water seasonality, and perhaps cold winter stress appear to increase representation of C_3 grasses, sedges, and shrubs relative to open grasslands (Leach and Givnish, 1999; Peterson et al., 2007). Herbivores of open forests but not closed forests may have influenced species composition and abundance (Meagher, 1986; Anderson, 2006). For example, American bison (*Bison bison*), which were extirpated from the eastern US by the early 1800s (Fig. 5; Farrand, 1904; Meagher, 1986), were almost exclusively grazing mammals, with a strong preference for grasses, sedges, and only occasionally forbs and rarely woody plants (Meagher, 1986; Anderson, 2006).

Larger scale community patterns resulting from the influence of fire patterns and site conditions also are incorporated in open forests but typically absent from the current matrix of closed forests. For instance, other now greatly reduced herbaceous-dominated treeless ecosystems, such as cane (primarily *Arundinaria gigantea*) “brakes”, wetlands, blackland prairies, glades, barrens, balds, and other kinds of grassland communities often were interspersed and blended into open forests (Kirkman et al., 2001; Bragg, 2003; Estes et al., 2016; Hanberry, 2020). These embedded ecosystems provided additional spatial heterogeneity and taxonomic richness, and are but one of numerous gradients supporting high biodiversity.

Open forests further support community diversity through their influence on food webs, or food resources for consumers, and habitat requirements. Light, open structure, and herbaceous plants are important for many species of insects, birds, and small mammals (Johnson and Hale, 2002; Campbell et al., 2007; Wood et al., 2011), which provide critical ecosystem services, such as pollination and control of forest pests. Herbaceous foliage, fruits and seeds (including mast from oak and pine trees), and associated insects feed many types of birds, amphibians and reptiles, invertebrates, and mammals (Hunter et al., 2001; McShea et al., 2007; Hanberry and Thompson 2019), while the lack of a midstory additionally allows maneuverability for some bird species to prey on insects and small mammals. Unique fungi and lichen also are present in open forests and grasslands (Foltz et al., 2013; Morse and Sheard, 2020). Some fungi, primarily ascomycetes, may require fire to germinate, similar to some herbaceous plants (Claridge et al., 2009). Post-fire fungi stabilize soil and capture nitrogen, assisting re-establishment of herbaceous cover after fire (Claridge et al., 2009).

5. Conservation costs of an excluded state

Loss and degradation of open forests has contributed to widespread and often irreversible declines in the biodiversity in eastern North America, with some species and subspecies closely associated with and likely influential on open forests now extinct. While the loss of charismatic megafauna (such as eastern wood bison, *Bison bison pennsylvanicus*; eastern cougar, *Puma concolor couguar*; and eastern elk, *Cervus canadensis canadensis*) is the most apparent result of decline of open forests, the greatest extinction rates have probably occurred in rich herbaceous layers of many open forests (Leach and Givnish, 1999; Gilliam, 2007). Many historically uncomplicated open forests are experiencing dramatic increases in arboreal richness and decreases in herbaceous richness as less fire-tolerant tree species invade (e.g., Hoff et al., 2018). For instance, Rogers et al. (2008) found about a 25% plant species density decline in remnant oak savannas since the 1950s, without offsetting increases in native shade-adapted species. Plant endemism in longleaf pine savannas may reach 40%, resulting in hundreds of species of conservation concern including a number of threatened orchid species (Van Lear et al., 2005). Specific examples of threatened, endangered, or rare plant species associated with open habitats are too numerous to list in this synthesis paper, but include tinytim (*Geocarpon minimum*), rough-leaved loosestrife (*Lysimachia asperulaefolia*), American chaffseed (*Schwalbea americana*), smooth coneflower (*Echinacea laevigata*), Michaux's sumac (*Rhus michauxii*), and sandplain gerardia (*Agalinis acuta*; Norquist, 1987; Harper et al., 1997).

In addition, many rare and declining vertebrates depend on open forests, or fare best under the "early successional" conditions of understocked forests with a significant herbaceous understory. For example, frequently burned open conditions supply the heat exposure and ground layer generally required by reptiles, such as the federally threatened gopher tortoise (*Gopherus polyphemus*). About 17 amphibian species are longleaf pine specialists, including the federally threatened flatwoods salamander (*Ambystoma cingulatum*; Means et al., 2004). Open conditions also are suitable for the near-extinct red wolf (*Canis rufus*) and small mammals of species concern such as Sherman's fox squirrel (*Sciurus niger shermani*; Van Lear et al., 2005; McShea et al., 2007).

Of the vertebrates, few are more reliant on open forests than birds. Birds have evolved specific habitat criteria to survive and reproduce successfully, even though constraints may vary during different semi-seasonal activities, such as nesting and migration (Hunter et al., 2001). Some bird species occupy open conditions during the breeding season, while other species may take advantage of resources in open conditions after fledging. Most bird species that nest in open areas, about 130 species in eastern North America, have been declining (Hunter et al., 2001), and taxa associated with grasslands, especially those along the Mississippi River flyway, have declined precipitously since 1970 (Rosenberg et al., 2019). These species commonly are termed early successional; however, they may be more properly termed disturbance-dependent or open forest (Askins, 2001; Hunter et al., 2001; Hanberry and Thompson, 2019). Indeed, early successional bird species may have relied more on the once extensive and previously stable open forest ecosystems than transient early successional forests or gaps in late successional forests.

Numerous species of invertebrates are also highly dependent on open forests. Xeric longleaf pine savannas alone contain at a minimum 4000 terrestrial arthropod species, of which 10% are endemic (Folkerts et al., 1993). For example, many invertebrates, including the federally endangered Karner blue butterfly (*Lycaeides melissa samuelis*) and multi-state listed frosted elfin (*Callophrys irus*) and regal fritillary (*Speyeria idalia*) butterflies, rely on flowers of herbaceous plants abundant in open forests (Henderson et al., 2018). However, high rates of endemism and loss of open forests and floral resources are not the only challenge facing open forest species. Rapid declines in many insect populations (globally) have signaled a crisis, perhaps due to a substantial extinction debt accruing from cumulative resource use and many other human impacts rather than a single responsible factor, including habitat loss and degradation, loss of floral resources and poor nutritional quality of available flowers; these factors occur with loss of open forests (Tilman et al., 1994; Winfree et al., 2009; Potts et al., 2010; Koh et al., 2016).

6. Managing for open forests

Conventionally managed closed forests are dominated by valuable trees, as compared to an undesirable underutilization of (tree) growing space by an herbaceous ground layer in open forests. A different set of drivers and responses control closed forests because disturbances, primarily logging, impact the overstory without restraining tree regeneration, resulting in tree domination rather than coexistence with an herbaceous layer (Hanberry et al., 2018a; see also Fig. 3). Hence, frequent overstory tree removal by harvesting (Pan et al., 2011) has become the predominant driver of eastern forests, resulting in continual successional cycles, sometimes with biological legacies of mid- or late successional species remaining.

Management for early successional ecosystems can produce "highly desirable" attributes, specifically a rich herb layer, which are limited in many landscapes (Hansen et al. 1991; Swanson et al., 2011, p. 123; Hanberry et al., 2018a). Today, early successional forests represent about 10–15% of timberlands in the eastern U.S. (down from over 50% less than a century ago but likely still greater than historical representation), not including additional sources of early successional vegetation resulting from various land uses or agricultural conversion and abandonment (Trani et al., 2001; Lorimer and White, 2003; Pan et al., 2011; Hanberry and Thompson, 2019). While conversion of mature closed forest to more open early successional forest condition may offer some respite to declining species, early successional forests by their definition are fleeting and besides, result from frequent harvest and perpetuate closed forest cycles. As trees capture growing space from herbaceous vegetation, relocation is not possible for established plants and unstable conditions potentially reduce animal survival and reproduction (Schlossberg, 2009). Early successional habitats that arise following some forms of timber harvesting have been suggested as sufficient replacements for the conservation costs imposed by closed forests (e.g., Swanson et al., 2011), but evidence (described above) suggests that this is not likely the case as plants, animals, and other taxa did not evolve under contemporary forest management and land use practices. While early successional forests provide conditions similar to open forests, the environmental stability and persistence of open forests is a key difference.

Unlike early successional forests, open forests are not ephemeral or transitional. The longevity (established trees can live hundreds of years while some herbaceous understory plants lived decades) and persistence via self-replacement provides a constancy that grants open forest-affiliated plant and animal species dependent on high light environments access to predictable resources throughout their lifetimes, rather than a need to colonize ever-shifting early successional forests (e.g., Schlossberg, 2009). Indeed, the concept of "early successional species" may need to be reframed as "open forest species" for management purposes, given abundance of open forests and rarity of early successional forests in historical landscapes and other lines of evidence, with consequent redirection of management and conservation of these birds from early successional forests to open forest ecosystems (Hanberry and Thompson, 2019). Restoration of open forests, with their blended grass, forb, and arboreal components, spatial variability, and long-term stability when properly maintained offers a more permanent solution for conserving species than reliance on managing for early successional closed forests. For example, restoration of open forests for the endangered red-cockaded woodpecker (*Picoides borealis*) has provided large areas of habitat suitable for the many other species (Stephens et al., 2019).

A growing body of research and practice focuses on restoration of open forests with a focus on groundflora management, continuity of the overstory, and control of tree regeneration (McIntyre et al., 2010; Reid et al., 2020; Bragg et al., this special issue). Tools include fire, thinning, and herbicides, with recognition that the overstory and ground layer also provide a powerful control (by capturing available resources) on tree regeneration (Hanberry et al., 2017; Hanberry et al., 2018a). Multiple cycles of burning and thinning may be necessary, as a single prescribed burn or a burn of too low severity will not likely be successful at controlling tree regeneration, even that of fire-sensitive species, many of which are capable of resprouting following top-kill, given feedbacks in closed forests (Brose et al., 1999; Albrecht and McCarthy, 2006; Alexander et al., 2008, Green et al., 2010). Nonetheless, silvicultural interventions required to support open forest maintenance should decrease over time as open conditions stabilize.

Although the economics are not as favorable as conventional systems, the Stoddard-Neel system maintains an open forest structure using prescribed fire and occasional harvest of large longleaf pines (i.e., single tree selection), while timber prices are high, to generate modest revenues and meet non-economic objectives (McIntyre et al., 2010) while in the Missouri Ozarks, investment in pine-oak open forest management resulted in $2.20 of local economic activity for every dollar spent (Song and Aguilar, 2015). Variable retention forestry practices or thinning produce a better approximation of historical open forest ecosystems than clearcuts while fulfilling both ecological and economic objectives. Variable retention leaves varying densities of residual overstory trees with the intention of permanent tree retention, that is, overstory trees always remain in stands, whereas other partial harvesting systems, such as shelterwood and multiple/deferment cuttings may leave high levels of tree retention, but eventually remove the entire overstory.

Recognizing management for open forests as an alternative option will require a general shift in our precepts of acceptable forest conditions. The lucrative nature of forest management for timber harvest and incentives to boost stand stocking and shorten rotation length, plus fire exclusion and landscape fragmentation for agricultural, residential, and industrial purposes to support a burgeoning population, make it highly unlikely that large-scale restoration of historical fire regimes and open forests will be possible. Nonetheless, restoration efforts may restore lost processes, rare conditions, and declining species.

7. Conclusions

Open forest states of savannas and woodlands once dominated much of eastern North America due to frequent, low to mixed severity surface fires. From the earliest years of forestry in North America, fires were viewed as impeding economic development and forest sustainability, and hence retrogressive, contributing to current conservation challenges for open forest ecosystems (e.g., Bruner, 1930). Today, fires are infrequent, rarely occurring more than once a decade, and open forests now are as excluded from the region's landscapes as the frequent burns or thinnings required to maintain them. This exclusion has considerable ecological costs, including altered ecological function and environmental conditions with associated declines in abundance and richness of herbaceous plants and animal populations. Early successional forests offer only a partial solution because they are temporally fleeting and do not supply sufficient and ecologically appropriate long-term conditions to sustain natural processes inherent to open forests. Open forest structure, in contrast, provides relative stable conditions for a diversity of plant and animal species throughout their lifetimes.

Historical forests were 'not just about the trees' (Matonis and Binkley, 2018). Excluding open forests with their herbaceous component from the conversation in ecological science and management practice limits our ability to understand and restore these important ecosystems to eastern North America. Recognition of their historical role and current absence is important, as open forests bridge the canopy spectrum between grasslands and closed forests. Embracing open forests also makes sense under anticipated future climatic conditions, which are generally assumed to be warmer, with less predictable precipitation and potentially more extreme events across much of eastern North America (USGCRP, 2018). After all, oak and pine forests have stood the test of fluctuating and often extreme climates over thousands of years (Delcourt and Delcourt, 1987). The growing influence of climate change makes open forest restoration more pressing because the dominant oaks and pine trees of this ecosystem extend to the most southern US and hence may represent the taxa expected to do best (e.g., Iverson et al., 2008). Given that increased temperature and precipitation extremes fall within the habitat envelope of oaks and pines (along with most of their associated species), restoring open forests comes with inherent advantages. Rather than overlooking the open forest state as an aberration, including this excluded state on the landscape and in our management portfolios may prevent future forest degradation and additional loss of species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank reviewers for their contribution to the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118256.

References

Abrams, M.D., Dickmann, D.I., 1982. Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan. Can. J. Bot. 60, 946–954.

Albrecht, M.A., McCarthy, B.C., 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. For. Ecol. Manage. 226, 88–103.

Alexander, H.D., Arthur, M.A., 2010. Implications of a predicted shift from upland oaks to red maple on forest hydrology and nutrient availability. Can. J. For. Res. 40 (4), 716–726.

Alexander, H.D., Arthur, M.A., 2014. Increasing red maple leaf litter alters decomposition rates and nitrogen cycling in historically oak-dominated forests of the eastern US. Ecosystems 17 (8), 1371–1383.

Alexander, H.D., Arthur, M.A., Loftis, D.L., Green, S.R., 2008. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. For. Ecol. Manage. 256 (5), 1021–1030.

Anderson, R.C., 2006. Evolution and origin of the Central Grasslands of North America: climate, fire, and mammalian grazers. J. Torrey Bot. Soc. 133 (4), 626–647.

Askins, R.A., 2001. Sustaining biological diversity in early successional communities: The challenge of managing unpopular habitats. Wildl. Soc. Bull. 29, 407–412.

Askins, R.A., Chávez-Ramírez, F., Dale, B.C., Haas, C.A., Kerkert, J.R., Knopf, F.L., Vickery, P.D., 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. Ornithol. Monographs 64, 1–46.

Babl, E.K., Alexander, H.D., Siegert, C.M., Willis, J.W., 2020. Could canopy, bark, and leaf litter traits of encroaching non-oak species influence future flammability of upland oak forests? For. Ecol. Manage. 458, 117731.

Bader, B.J., 2001. Developing a species list for oak savanna/oak woodland restoration at the University of Wisconsin-Madison Arboretum. Ecol. Restoration 19, 242–250.

Beckage, B., Platt, W.J., Gross, L.J., 2009. Vegetation, fire, and feedbacks: a disturbance-mediated model of savannas. Am. Nat. 174, 805–818.

Bragg, D.C., 2003. Natural presettlement features of the Ashley County, Arkansas area.

Am. Midland Natural. 149 (1), 1–20.

Bragg, D.C., Hanberry, B.B., Hutchinson, T.F., Jack, S., Kabrick, J.M., This volume. Open forest management: an alternative silvicultural system.

Brewer, J.S., Abbott, M.J., Moyer, S.A., 2015. Effects of oak-hickory woodland restoration treatments on native groundcover vegetation and the invasive grass, *Microstegium vimineum*. Ecol. Restoration 33, 256–265.

Brose, P., Van Lear, D., Cooper, R., 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. For. Ecol. Manage. 113, 125–141.

Brudvig, L.A., Asbjornsen, H., 2009. The removal of woody encroachment restores biophysical gradients in Midwestern oak savannas. J. Appl. Ecol. 46, 231–240.

Bruner, E.M., 1930. Forestry and forest fires in Arkansas. University of Arkansas Cooperative Extension Circular 281. 30 p.

Campbell, J.W., Hanula, J.L., Waldrop, T.A., 2007. Effects of prescribed fire and fire surrogates on floral visiting insects of the Blue Ridge province in North Carolina. Biol. Conserv. 134, 393–404.

Cardoso, A.W., Oliveras, I., Abernethy, K.A., Jeffery, K.J., Lehmann, D., Edzang Ndong, J., McGregor, I., Belcher, C.M., Bond, W.J., Malhi, Y.S., 2018. Grass species flammability, not biomass, drives changes in fire behaviour at tropical forest-savanna transitions. Front. Forests Global Change 1, 6.

Charles-Dominique, T., Midgley, G.F., Tomlinson, K.W., Bond, W.J., 2018. Steal the light: shade vs fire adapted vegetation in forest–savanna mosaics. New Phytol. 218, 1419–1429.

Claridge, A.W., Trappe, J.M., Hansen, K., 2009. Do fungi have a role as soil stabilizers and remediators after forest fire? For. Ecol. Manage. 257, 1063–1069.

Clark, S.L., Hallgren, S.W., 2003. Dynamics of oak (*Quercus marilandica* and *Q. stellata*) reproduction in an old-growth Cross Timbers forest. Southeast. Nat. 2 (4), 559–574.

Cohen, J., 2008. The wildland-urban interface problem: a consequence of the fire exclusion paradigm. Forest History Today 14, 20–26.

Delcourt, P.A., Delcourt, H.R., 1987. Late-Quaternary dynamics of temperate forests: Applications of paleoecology to issues of global environmental change. Quat. Sci. Rev. 6, 129–146.

Denevan, W.M., 1992. The pristine myth: the landscape of the Americas in 1492. Ann. Assoc. Am. Geogr. 82 (3), 369–385.

Denevan, W.M., 2011. The "Pristine Myth" revisited. Geogr. Rev. 101 (4), 576–591.

Dunwiddie, P.W., 1998. Ecological management of sandplain grasslands and coastal heathlands in southeastern Massachusetts. Tall Timbers Fire Ecol. Conference Proc. 20, 83–93.

Dyksterhuis, E.J., 1948. The vegetation of Western Cross Timbers. Ecol. Monogr. 18 (3), 325–376.

Elsner, J.B., Jagger, T.H., Liu, K.-B., 2008. Comparison of hurricane return levels using historical and geological records. J. Appl. Meteorol. Climatol. 47, 368–374.

Estes, D., Brock, M., Homoya, M., Dattilo, A., 2016. A guide to the grasslands of the Mid-South. USDA Natural Resources Conservation Service, Tennessee Valley Authority, Austin Peay State University, and the Botanical Research Institute of Texas. 27 p. Available online at: https://www.segrasslands.org/guide-to-the-grasslands-of-the-midsouth, last accessed 23 September 2019.

Farrand, L., 1904. Basis of American History, 1500-1900. Volume 2 in The American Nation, A History, A.B. Hart, ed. Harper & Brothers, Publishers, New York, NY. 303 p.

Finzi, A.C., Van Breemen, N., Canham, C.D., 1998. Canopy tree–soil interactions within temperate forests: species effects on soil carbon and nitrogen. Ecol. Appl. 8 (2), 440–446.

Folkerts, G.W., Deyrup, M.A., Sisson, D.C., 1993. Arthropods associated with xeric longleaf pine habitats in the southeastern Unites States: a brief overview. In: Hermann, S.M. (Eds.), The Longleaf Pine Ecosystem: Ecology, Restoration, And Management. Proceedings of the Tall Timbers Fire Ecology Conference, No. 18. Tall Timbers Research, Tallahassee, Florida, pp. 159–192.

Foltz, M.J., Perez, K.E., Volk, T.J., 2013. Molecular phylogeny and morphology reveal three new species of *Cantharellus* within 20 m of one another in western Wisconsin, USA. Mycologia 105, 447–461.

Fralish, J.S., 2004. The keystone role of oak and hickory in the central hardwood forest. In: Spetich, M.A. (Ed.), Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability. USDA Forest Service General Technical Report SRS-73. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp 78-87.

Fralish, J.S., McArdle, T.G., 2009. Forest dynamics across three century-length disturbance regimes in the Illinois Ozark Hills. Am. Midl. Nat. 162, 418–449.

Frost, C.C., 1998. Presettlement fire frequency regimes of the United States: a first approximation. In: Pruden, T.L., Brennan, L.A. (Eds.), Fire in Ecosystem Management: Shifting the Paradigm from Exclusion to Prescription. Tall Timbers Fire Ecology Conference Proceedings 20, Tall Timbers Research Station, Tallahassee, Florida, USA, pp 70–81.

Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57, 845–858.

Gleason, H.A., 1922. The vegetational history of the Middle West. Ann. Assoc. Am. Geograph. 12, 39–85.

Glitzenstein, J.S., Platt, W.J., Streng, D.R., 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecol. Monogr. 65, 441–476.

Glitzenstein, J.S., Streng, D.R., Masters, R.E., Robertson, K.M., Hermann, S.M., 2012. Fire-frequency effects on vegetation in north Florida pinelands: another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. For. Ecol. Manage. 264, 197–209.

Goulson, D., 2019. The insect apocalypse, and why it matters. Curr. Biol. 29 (19), R967–R971.

Green, S.R., Arthur, M.A., Blankenship, B.A., 2010. Oak and red maple seedling survival and growth following periodic prescribed fire on xeric ridgetops on the Cumberland Plateau. For. Ecol. Manage. 259, 2256–2266.

Grundel, R., Jean, R.P., Frohnapple, K.J., Glowacki, G.A., Scott, P.E., Pavlovic, N.B., 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. Ecol. Appl. 20 (6), 1678–1692.

Guyette, R.P., Muzika, R.M., Dey, D.C., 2002. Dynamics of an anthropogenic fire regime. Ecosystems 5, 472–486.

Guyette, R.P., Stambaugh, M.C., Dey, D.C., Muzika, R.-M., 2012. Predicting fire frequency with chemistry and climate. Ecosystems 15, 322–335.

Haggerty, C.J.E., Crisman, T.L., Rohr, J.R., 2019. Direct and indirect effects of pine silviculture on the larval occupancy and breeding of declining amphibian species. J. Appl. Ecol. 56 (12), 2652–2662.

Hanberry, B.B., 2019. Recent shifts in shade tolerance and disturbance traits in forests of the eastern United States. Ecol. Process. 8, 32.

Hanberry, B.B., 2020. Defining the historical northeastern forested boundary of the Great Plains grasslands in the United States. Professional Geograph. 72, 1–8.

Hanberry, B.B., Dey, D.C., 2019. Historical range of variability for restoration and management in Wisconsin. Biodivers. Conserv. 28, 2931–2950.

Hanberry, B.B., Nowacki, G.J., 2016. Oaks were the foundation genus of the east-central United States. Quat. Sci. Rev. 145, 94–103.

Hanberry, B.B., Thompson III, F.R., 2019. Open forest management for early successional birds. Wildl. Soc. Bull. 43, 141–151.

Hanberry, B.B., Dey, D.C., He, H.S., 2012. Regime shifts and weakened environmental gradients in open oak and pine ecosystems. PLoS ONE 7, e41337.

Hanberry, B.B., Jones-Farrand, D.T., Kabrick, J.M., 2014. Historical open forest ecosystems in the Missouri Ozarks: Reconstruction and restoration targets. Ecol. Restoration 32, 407–416.

Hanberry, B.B., Bragg, D.C., Hutchinson, T.F., 2018a. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. Ecosphere 9, e02431.

Hanberry, B.B., Abrams, M.D., White, J.D., 2018b. Is increased precipitation during the 20th century statistically or ecologically significant in the eastern US? J. Land Use Sci. 13, 259–265.

Hanberry, B.B., Coursey, K., Kush, J.S., 2018c. Structure and composition of historical longleaf pine ecosystems in Mississippi, USA. Human Ecol. 46, 241–248.

Hanberry, B.B., Brzuszek, R.F., Foster II, H.T., Schauwecker, T.J., 2019. Recalling open old growth forests in the Southeastern Mixed Forest province of the United States. Écoscience 26, 11–22.

Hanberry, B.B., Kabrick, J.M., Dunwiddie, P.W., Hartel, T., Jain, T.B., Knapp, B.O., 2017. Restoration of temperate savannas and woodlands. In: Murphy, S., Allison, S. (Eds.), Routledge Handbook of Ecological and Environmental Restoration. Routledge, New York, NY, pp. 142–157.

Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991. Conserving biodiversity in managed forests. Bioscience 41 (6), 382–392.

Hare, R.C., 1965. Contribution of bark to fire resistance of southern trees. J. Forest. 63 (4), 248–251.

Harper, C.A., Ford, W.M., Lashley, M.A., Moorman, C.E., Stambaugh, M.C., 2016. Fire effects on wildlife in the Central Hardwoods and Appalachian regions, USA. Fire Ecol. 12 (2), 127–159.

Harper, M., Trame, A.M., Fischer, R.A., Martin, C.O., 1997. Management of longleaf pine woodlands for threatened and endangered species. USACERL Technical Report 98/21, US Army Corps of Engineers Construction Engineering Research Laboratories, Champaign, IL. 153 p.

Haworth, K., McPherson, G.R., 1995. Effects of *Quercus emoryi* trees on precipitation distribution and microclimate in a semi-arid savanna. J. Arid Environ. 31 (2), 153–170.

Henderson, R.A., Meunier, J., Holoubek, N.S., 2018. Disentangling effects of fire, habitat, and climate on an endangered prairie-specialist butterfly. Biol. Conserv. 218, 41–48.

Heyward, F., 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20 (2), 287–304.

Hickman, N.W., 1962. Mississippi Harvest: Lumbering in the Longleaf Pine Belt, 1840–1915. University of Mississippi, Oxford, MS, pp. 306.

Hiers, J.K., O'Brien, J.J., Mitchell, R.J., Grego, J.M., Loudermilk, E.L., 2009. The wildland fuel cell concept: an approach to characterize fine-scale variation in fuels and fire in frequently burned longleaf pine forests. Int. J. Wildland Fire 18, 315–325.

Higgins, S.I., Bond, W.J., Trollope, W.S.W., 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. J. Ecol. 88, 213–229.

Hoff, D.L., Will, R.E., Zou, C.B., Lillie, N.D., 2018. Encroachment dynamics of *Juniperus virginiana* L. and mesic hardwood species in Cross Timbers forests of north-central Oklahoma, USA. Forests 9 (2), 75.

Hunter, W.C., Buehler, D.A., Canterbury, R.A., Confer, J.L., Hamel, P.B., 2001. Conservation of disturbance-dependent birds in eastern North America. Wildl. Soc. Bull. 29, 440–455.

Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manage. 254 (3), 390–406.

Jackson, J.A., 1988. The southeastern pine forest ecosystem and its birds: past, present, and future. In: Jackson, J.A. (Ed.), Bird Conservation 3. Univ. of Wisconsin Press, Madison, WI, pp. 119–159.

Johnson, A.S., Hale, P.E., 2002. The historical foundations of prescribed burning for wildlife: a southeastern perspective. In: Ford, W.M., Russell, K.R., Moorman, C.E. (Eds.). Proceedings: The Role of Fire for Nongame Wildlife Management and Community Restoration: Traditional Uses and New Directions. Gen. Tech. Rep. NE-288. USDA Forest Service, Northeastern Research Station, Newtown Square, PA, pp 11-23.

Kane, J.M., Varner, J.M., Hiers, J.K., 2008. The burning characteristics in southeastern oaks: discriminating fire facilitators from fire impeders. For. Ecol. Manage. 256, 2039–2045.

Kirkman, L.K., Mitchell, R.J., Helton, R.C., Drew, M.B., 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. Am. J. Bot. 88 (11), 2119–2128.

Knapp, A.K., McCarron, J.K., Silletti, A.M., Hoch, G.A., Heisler, J.C., Lett, M.S., Blair, J. M., Briggs, J.M., Smith, M.D., 2008. Ecological consequences of the replacement of native grassland by Juniperus virginiana and other woody plants. In: Van Auken, O. W. (Ed.), Western North American Juniperus Communities. Ecological Studies, vol 196. Springer, New York, NY, pp. 156-169.

Ko, L.J., Reich, P.B., 1993. Oak tree effects on soil and herbaceous vegetation in savannas and pastures in Wisconsin. Am. Midl. Nat. 130, 31–42.

Koh, I., Lonsdorf, E.V., Williams, N.M., Brittain, C., Isaacs, R., Gibbs, J., Ricketts, T.H., 2016. Modeling the status, trends and impacts of wild bee abundance in the United States. PNAS 113, 140–145.

Kreye, J.K., Varner, J.M., Hiers, J.K., Mola, J., 2013. Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. Ecol. Appl. 23 (8), 1976–1986.

Kreye, J.K., Varner, J.M., Hamby, G., Kane, J.M., 2018. Mesophytic litter dampens flammability in fire-excluded pyrophytic oak-hickory woodlands. Ecosphere 9, e02078.

Landfire, 2020. Biophysical settings. Available online at: https://www.landfire.gov/national_veg_models_op2.php, last accessed 4 May 2020.

Leach, M.K., Givnish, T.J., 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. Ecol. Monogr. 69, 353–374.

Lettow, M.C., Brudvig, L.A., Bahlai, C.A., Gibbs, J., Jean, R.P., Landis, D.A., 2018. Bee community responses to a gradient of oak savanna restoration practices. Restor. Ecol. 26 (5), 882–890.

Levia Jr, D.F., Frost, E.E., 2006. Variability of throughfall volume and solute inputs in wooded ecosystems. Prog. Phys. Geogr. 30 (5), 605–632.

Levia Jr, D.F., Herwitz, S.R., 2000. Physical properties of water in relation to stemflow leachate dynamics: implications for nutrient cycling. Can. J. For. Res. 30 (4), 662–666.

Levia, D.F., Keim, R.F., Carlyle-Moses, D.E., Frost, E.E., 2011. Throughfall and stemflow in wooded ecosystems. In: Levia, D.F., Carlyle-Moses, D.E., Tanaka, T. (Eds.), Forest Hydrology and Biogeochemistry. Springer, Dordrecht, pp. 425–443.

Lorimer, C.G., 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. Wildl. Soc. Bull. 29, 425–439.

Lorimer, C.G., White, A.S., 2003. Scale and frequency of natural disturbances in the northeastern US: Implications for early successional forest habitats and regional age distributions. For. Ecol. Manage. 185, 41–64.

Maginel, C.J., Knapp, B.O., Kabrick, J.M., Muzika, R.M., 2019. Landscape-and site-level responses of woody structure and ground flora to repeated prescribed fire in the Missouri Ozarks. Can. J. For. Res. 48, 1004–1014.

Martin, R.E., Miller, R.L., Cushwa, C.T., 1975. Germination response of legume seeds subjected to moist and dry heat. Ecology 56, 1441–1445.

Matonis, M.S., Binkley, D., 2018. Not just about the trees: Key role of mosaic-meadows in restoration of ponderosa pine ecosystems. For. Ecol. Manage. 411, 120–131.

Mattoon, W.R. 1915. Life history of shortleaf pine. USDA Bull. 244. 46 p.

Maynard, E.E., Brewer, J.S., 2013. Restoring perennial warm-season grasses as a means of reversing mesophication of oak woodlands in northern Mississippi. Restor. Ecol. 21, 242–249.

Means, D.B., 2007. Vertebrate faunal diversity of longleaf pine ecosystems. In: Jose, S., Jokela, E., Miller, D. (Eds.), the Longleaf Pine Ecosystem. Springer, New York, NY, pp. 157–213.

McCulley, R.L., Jackson, R.B., 2012. Conversion of tallgrass prairie to woodland: Consequences for carbon and nitrogen cycling. Am. Midl. Nat. 167, 307–321.

McIntyre, R.K., Jack, S.B., McCall, B.B., Mitchell, R.J., 2010. Financial feasibility of selection-based multiple-value management on private lands in the South: A heuristic case study approach. J. Forest. 108, 230–237.

McKinley, D.C., Blair, J.M., 2008. Woody plant encroachment by *Juniperus virginiana* in a mesic native grassland promotes rapid carbon and nitrogen accrual. Ecosystems 11 (3), 454–468.

McNaughton, S.J., Banyikwa, F.F., McNaughton, M.M., 1998. Root biomass and productivity in a grazing ecosystem: the Serengeti. Ecology 79 (2), 587–592.

McShea, W.J., Healy, W.M., Devers, P., Fearer, T., Koch, F.H., Stauffer, D., Waldon, J., 2007. Forestry matters: Decline of oaks will impact wildlife in hardwood forests. J. Wildl. Manage. 71, 1717–1728.

Meagher, M., 1986. Bison bison. Mammalian Species 266, 1–8.

Means, D.B., Dodd Jr, C.K., Johnson, S.A., Palis, J.G., 2004. Amphibians and fire in longleaf pine ecosystems: Response to Schurbon and Fauth. Conserv. Biol. 18, 1149–1153.

Mitchell, R.J., Duncan, S.L., 2009. Range of variability in southern coastal plain forests: its historical, contemporary, and future role in sustaining biodiversity. Ecol. Soc. 14, 17.

Mitchell, R.J., Hiers, J.K., O'Brien, J., Starr, G., 2009. Ecological forestry in the Southeast: understanding the ecology of fuels. J. Forest. 107 (8), 391–397.

Morse, C.A., Sheard, J.W., 2020. *Rinodina lecideopsis* (Teloschistales, Physciaceae) a new endemic species from the central United States related to *R. bischoffii*. The Bryologist 123, 31–38.

Nippert, J.B., Wieme, R.A., Ocheltree, T.W., Craine, J.M., 2012. Root characteristics of C 4 grasses limit reliance on deep soil water in tallgrass prairie. Plant Soil 355, 385–394.

Norris, M.D., Blair, J.M., Johnson, L.C., 2001. Land cover change in eastern Kansas: litter dynamics of closed-canopy eastern redcedar forests in tallgrass prairie. Can. J. Bot. 222, 214–222.

Norris, M.D., Blair, J.M., Johnson, L.C., 2007. Altered ecosystem nitrogen dynamics as a consequence of land cover change in tallgrass prairie. Am. Midland Naturalist 158 (2), 432–446.

Norquist, C., 1987. Endangered and threatened wildlife and plants; threatened status for *Geocarpon minimum*. Fed. Reg. 52 (115), 22930–22933.

Noss, R.F., LaRoe, E.T., Scott, J.M., 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. US Department of the Interior, Washington (DC). Biological Report 28.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and 'mesophication' of forests in the eastern United States. Bioscience 58, 123–138.

Odanaka, K., Gibbs, J., Turley, N.E., Isaacs, R., Brudvig, L.A., 2020. Canopy thinning, not agricultural history, determines early responses of wild bees to longleaf pine savanna restoration. Restor. Ecol. 28, 138–146.

Odion, D.C., Moritz, M.A., DellaSala, D.A., 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. J. Ecol. 98, 96–105.

Ojima, D.S., Schimel, D.S., Parton, W.J., Owensby, C.E., 1994. Long-and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry 24 (2), 67–84.

Osono, T., Azuma, J., Hirose, D., 2014. Plant species effect on the decomposition and chemical changes of leaf litter in grassland and pine and oak forest soils. Plant Soil 376, 411–421.

Packard, S., 1988. Just a few oddball species: restoration and rediscovery of the tallgrass savanna. Restoration Manage. Notes 6, 130–224.

Pan, Y., Chen, J.M., Birdsey, R., McCullough, K., He, L., Deng, F., 2011. Age structure and disturbance legacy of North American forests. Biogeosciences 8, 715–732.

Peterson, D.W., Reich, P.B., 2001. Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. Ecol. Appl. 11, 914–927.

Peterson, D.W., Reich, P.B., 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. Plant Ecol. 194, 5–16.

Peterson, D.W., Reich, P.B., Wrage, K.J., 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. J. Veg. Sci. 18, 3–12.

Potts, S.G., Beismeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353.

Read, A.D., 1943. Forestry in the Deep South. Ames Forester 31, 43–52.

Reid, J.L., Holmberg, N.J., Albrecht, M., Arango-Caro, S., Hajek, O., Long, Q., Trager, J., 2020. Annual understory plant recover dynamics in a temperate woodland mosaic during a decade of ecological restoration. Nat. Areas J. 40 (1), 23–34.

Reich, P.B., Peterson, D.W., Wedin, D.A., Wrage, K., 2001a. Fire and vegetation effects on productivity and nitrogen cycling across a forest–grassland continuum. Ecology 82, 1703–1719.

Rogers, D.A., Rooney, T.P., Olson, D., Waller, D.M., 2008. Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 89 (9), 2482–2492.

Ruffner, C.M., Abrams, M.D., 2003. Disturbance history and stand dynamics along a topographic gradient in old-growth hemlock-northern hardwood forests of the Allegheny Plateau, USA. Nat. Areas J. 23, 98–113.

Schenk, H.J., Jackson, R.B., 2002a. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. J. Ecol. 90 (3), 480–494.

Schenk, H.J., Jackson, R.B., 2002b. The global biogeography of roots. Ecol. Monogr. 72 (3), 311–328.

Schnur, G.L., 1937. Yield, stand, and volume tables for even-aged upland oak forests. USDA Technical Bulletin 560. 87 p.

Siegert, C.M., Drotar, N., Alexander, H.D., 2019. Spatial and temporal variability of throughfall in an upland oak-hickory forest. Geosciences 9 (405), 1–13.

Song, N., Aguilar, F.X., 2015. Economic impacts of the implementation of the Missouri Pine-Oak Woodlands Restoration Project at the Mark Twain National Forest, 2012-2019: A project of the Collaborative Forest Landscape Restoration Program. Report to the USDA Forest Service Mark Twain National Forest, Rolla, MO.

Stephens, S.L., et al., 2019. Is fire "for the birds"? How two rare species influence fire management across the US. Front. Ecol. Environ. 17, 391–399.

Swanson, F.J., 1981. Fire and geomorphic processes. In: Mooney, H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J.E., (Eds.), Fire Regimes and Ecosystem Properties: Proceedings of the Conference. General Technical Report WO-GTR-26. US Department of Agriculture, Forest Service, Washington, D.C., pp 401–420.

Reich, P.B., Peterson, D.W., Wedin, D.A., Wrage, K., 2001b. Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. Ecology 82, 1703–1719.

Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., Stanton, J.C., Panjabi, A., Helft, L., Parr, M., Marra, P.P., 2019. Decline of the North American avifauna. Science 366 (6461), 120–124.

Rostlund, E., 1957. The myth of a natural prairie belt in Alabama: an interpretation of historical records. Ann. Assoc. Am. Geogr. 47 (4), 392–411.

Schertzer, E., Staver, A.C., Levin, S.A., 2015. Implications of the spatial dynamics of fire spread for the bistability of savanna and forest. J. Math. Biol. 70, 329–341.

Schlossberg, S., 2009. Site fidelity of shrubland and forest birds. Condor 111, 238–246.

Scholes, R.J., Archer, S.R., 1997. Tree-grass interactions in savannas. Annu. Rev. Ecol. Syst. 28 (1), 517–544.

Seymour, R.S., White, A.S., deMaynadier, P.G., 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. For. Ecol. Manage. 155, 357–367.

Smith, G.C., Patterson, M.W., Trendell, H.R., 2000. The demise of the longleaf-pine ecosystem. Southeastern Geographer 40 (1), 75–92.

Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Front. Ecol. Environ. 9, 117–125.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371, 65–66.

Trani, M.K., Brooks, R.T., Schmidt, T.L., Rudis, V.A., Gabbard, C.M., 2001. Patterns and trends of early successional forests in the Eastern United States. Wildl. Soc. Bull. 29, 413–424.

USGCRP (U.S. Global Change Research Program), 2018. Impacts, risks, and adaptation in the United States: Fourth National Climate Assessment, Volume II. Reidmiller, D.R., Avery, C.W., Easterling, D.R., Kunkel, K.E., Lewis, K.L.M., Maycock, T.K., Stewart, B. C., eds. U.S. Global Change Research Program, Washington, DC, USA, 1515 pp.

Van Lear, D.H., Carroll, W.D., Kapeluck, P.R., Johnson, R., 2005. History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk. For. Ecol. Manage. 211, 150–165.

Van Lear, D.H., Harlow, R.F., 2002. Fire in the eastern United States: influence on wildlife habitat. In: Ford, W.M.; Russell, K.R.; Moorman, C.E. (Eds.), Proceedings: the role of fire for nongame wildlife management and community restoration: traditional uses and new directions. Gen. Tech. Rep. NE-288. U.S. Dept. of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, pp. 2-10.

Wade, D.D., Brock, B. L., Brose, P. H., Grace, J.B., Hoch, G. A., Patterson III, W.A., 2000. Fire in eastern ecosystems. In: Brown, James K.; Smith, Jane Kapler, (Eds.), Wildland Fire in Ecosystems: Effects of Fire on Flora. Gen. Tech. Rep. RMRS-GTR-42-vol. 2. U. S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, pp. 53-96.

Walker, J., 1993. Rare vascular taxa associated with the longleaf pine ecosystems: patterns in taxonomy and ecology. In: Hermann, S. M. (Eds.), The Longleaf Pine Ecosystem: Ecology, Restoration, And Management. Proceedings of the Tall Timbers Fire Ecology Conference, No. 18. Tall Timbers Research, Tallahassee, Florida, pp. 105-125.

Wan, S., Hui, D., Luo, Y., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol. Appl. 11, 1349–1365.

Williamson, G.B., Black, E.M., 1981. High temperatures of forest fires under pines as a selective advantage over oaks. Nature 293 (5834), 643–644.

Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., Aizen, M.A., 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90, 2068–2076.

Wood, E.M., Pidgeon, A.M., Gratton, C., Wilder, T.T., 2011. Effects of oak barrens habitat management for Karner blue butterfly (*Lycaeides samuelis*) on the avian community. Biol. Conserv. 144, 3117–3126.