

A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum

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Abstract. We present a reconceptualization of forests in eastern North America by differentiating the ecological characteristics of open oak (*Quercus*) and pine (*Pinus*) forests from closed successional and old-growth forests. Despite historical abundance of savannas and woodlands, the fundamental ecology of open forest ecosystems remains ill-defined when compared to either closed forests or grasslands. Open forests were characterized by simple internal stand structure consisting of a single stratum of variably spaced, often very old overstory trees and limited midstory, maintained by understory disturbance that controlled tree regeneration and allowed instead a taxonomically rich herbaceous groundlayer. In contrast, closed forests have dense woody growth throughout the vertical profile, limiting herbaceous plants. To provide further clarity about these ecosystems, we developed a canopy closure spectrum model dependent on the interactions between prevailing disturbance regimes of the historical and current eras, which affect either the tree understory (regeneration) or overstory, and tree traits of fire and shade tolerance. Recognition of different stand structures, disturbance regimes, and their interrelationships should expand understanding of open forests and limit ecological misunderstandings and restoration misapplications, thereby improving management of these once historically extensive ecosystems.

Key words: fire; forest management; old-growth; savannas; succession; woodlands.

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INTRODUCTION

Ecologists have long explained vegetative patterns through conceptual models of relationships between the biotic and the abiotic, linkages between structure and function, community change over time, and anthropogenic influences (Clements 1916, Gleason 1926, Tansley 1935, Whittaker 1953, Quarterman and Keever 1962, Connell and Slatyer 1977). Over the past century, scientists have repeatedly reconsidered forest

succession and dynamics (Clements 1916, Gleason 1926, Egler 1954, Pickett 1976, Noble and Slatyer 1980, Glenn-Lewin et al. 1992, Carey and Curtis 1996, Oliver and Larson 1996, Franklin et al. 2002, Bormann and Likens 2012). While much has been learned, opportunities to reinterpret the past, refine the present, and model the future remain even in prominent ecosystems from well-studied regions. For instance, how characteristic and extensive were the classical closed-canopy, old-growth forests of shade-tolerant

maples (*Acer*), beech (*Fagus*), hemlock (*Tsuga*), or magnolia (*Magnolia*) in eastern North America? A growing body of evidence documents that much of this region had been dominated—for thousands of years—by open, old-growth forests of less shade-tolerant oak (*Quercus*) and pine (*Pinus*), and not just on xeric sites (Delcourt and Delcourt 1987, Burns and Honkala 1990*a, b*, Hanberry and Nowacki 2016, Hanberry and Abrams 2018, Hanberry et al. 2018*a, b*).

In many, if not most, of these historical open forests, canopy-dominant trees also varied considerably in age. Unfortunately, very few of these old, multi-aged, open forests survived as functionally intact examples to the present day (Hanberry and Abrams 2018). Most ecology and forest management texts consider only closed successional forests (i.e., forests with tree development throughout the vertical profile that have not developed typical old-growth structure or shade-tolerant composition) as the predominant vegetative cover in eastern North America, and focus

on stand dynamics driven by differences in tree shade tolerance and other related forest characteristics (Oliver and Larson 1996, Barnes et al. 1997, Perry et al. 2008). While this may be the case for most of these landscapes today (given their long-term lack of fire and disturbance regimes dominated by timber management), this view of ecosystem response is limited and largely unsuitable for the conceptualization and restoration of open forest conditions (Hanberry et al. 2018*b*). We believe that recognition of open old-growth forests, controlled by a disturbance regime (i.e., regular surface fires) that regulates tree success in the understory, has been lacking perhaps because the transition from open forests to closed forests either occurred gradually enough over such an extended time frame as to be imperceptible to most observers or was thought to conform to successional stages in closed forests.

Our objective is to reevaluate this paradigm by differentiating between open and closed (both

Box 1. Glossary

Closed Forests: High-density forests comprised of trees that fill the vertical profile because there is no control of tree regeneration. Canopies may be closed in fully stocked forests, but gap dynamics in old-growth forests may open canopies and frequent overstory disturbance may result in understocked forests comprised of dense, small diameter trees, where the overstory is not separated from the midstory and the canopy may not be closed. Overstory trees primarily are shade-tolerant species in old-growth forests. Closed forests are more abundant now, after historically extensive open forests transitioned to closed forests.

Open Forests: Low-density forests (typically between 10% and 75% of full stocking, with densities ranging from 50 to 250 trees/ha) where herbaceous vegetation is dominant under the overstory, with limited tree growth throughout the midstory because tree regeneration is controlled by fire, or other understory disturbances that remove small diameter woody stems. Overstory canopies vary from widely spaced in savannas to continuous in closed woodlands. Overstory trees characteristically are fire-tolerant species. Because most historical forests were dominated by fire-tolerant species, and based on contemporaneous accounts and other lines of evidence, open forests probably were widespread historically.

Successional Forests: Forests undergoing structural development after overstory removal in areas larger than gaps. Typically, overstory tree disturbance is too frequent to allow time for the slower process of compositional change to shade-tolerant species. Successional forests tend to contain greater tree species richness than old-growth forests that are limited to fire-tolerant or shade-tolerant species. Currently, successional forests are abundant, particularly in the southeastern United States, due to frequent overstory disturbance.

Old-growth Forests: Forests that have achieved characteristic structure and composition typical of either closed or open old-growth forests, after overstory trees have established. Closed old-growth forests are noted for complex and varied canopy structure, and shade-tolerant species, such as *Fagus grandifolia*. Open old-growth forests contain an overstory tree layer of fire-tolerant species. Old-growth structure and composition are rare currently and common in the past.

successional and old-growth) forests (see Box 1 for a glossary of terms). To further illustrate these unique differences, we develop a forest spectrum model based on canopy closure in eastern North America to extend well-described conceptualizations of successional forests (Carey and Curtis 1996, Oliver and Larson 1996, Franklin et al. 2002, Bormann and Likens 2012). We then summarize our reconceptualization of these open forests to help prevent potential misapplications of terminology and techniques developed for closed forests in their restoration. Through better understanding of the ecological patterns and processes underpinning historical open forest ecosystems, we believe scientists can improve the framework required to describe, restore, and manage functional modern-day examples of open forests.

THE FOREST CLOSURE SPECTRUM MODEL

A complete canopy closure spectrum arises from complex relationships between species autecology (including traits of fire, shade, and harvest tolerance), site conditions, and disturbance regimes. The spectrum for closed forests (top of Fig. 1) follows a trajectory of shade tolerance-mediated development after a stand-replacing disturbance removes overstory trees. On the other end of the spectrum, open forests (bottom of Fig. 1) are fundamentally shaped by frequent surface fires, rather than shade tolerance, that regulate the stem density and taxonomic composition of all strata (under-, mid-, and overstory). Understanding the dynamics of these different portions of the openness spectrum is key to

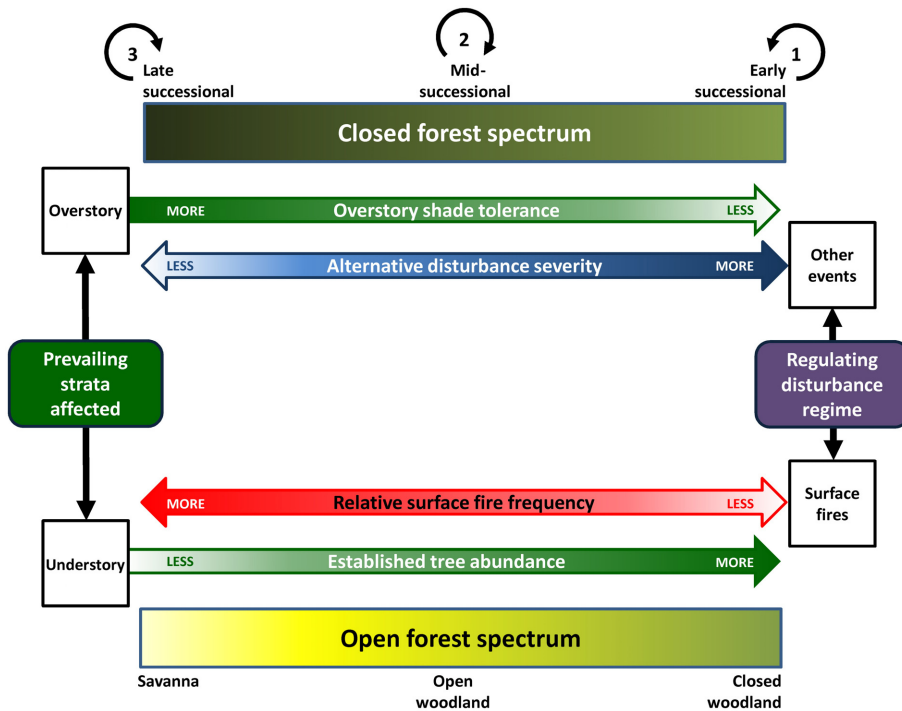


Fig. 1. A forest spectrum model for eastern North America. This paper concentrates on the open forest state of the spectrum, for which frequent surface fire is the dominant regulating disturbance regime. Historically, factors that varied (e.g., climate patterns, ignition frequencies, fuel load accumulations, fire severities) dictated the frequency of surface fires, which in turn largely controlled the abundance of established trees and the local expression (savanna, open woodland, closed woodland) of the open forest spectrum. Surface fires affect the understory disproportionately in open forests, particularly those dominated by fire-tolerant taxa such as oaks and pines. Prolonged fire exclusion pushes open forests into the closed forest spectrum, resulting in a new suite of disturbance regimes to dictate overstory dynamics. Different stable states within the varying dominant successional stages (1, 2, or 3) can be sustained by the appropriately influential disturbance regime(s).

understanding the forests of eastern North America, past and present.

Closed vs. open forests

Closed successional forests are defined as dense stands undergoing progressive stages of development from the relatively rapid and orderly transition of a temporarily deforested stand to a continuously canopied forest structure. First a brief, non-forested stage occurs, consisting of a mixture of herbaceous and woody stems, followed by a young forest stage after establishment of tree seedlings and/or sprouts, and then a mid-successional stage during self-thinning mortality of the young forest. In late successional stands, dominant trees differentiate into an overstory, which may close. Where overstory disturbance is infrequent, internal complexity develops from variable patterns in vertical and horizontal structure, including gaps, patches of trees of variable age, and an abundance of large live trees, snags, and downed woody debris (Fig. 1). With time, internal stand structural change is followed by compositional change chiefly driven by species tolerance to shade. Factors such as gap size variability, microsite variation, regeneration sources (stump or root sprouts, seeds), the persistence of advance reproduction, and herbivore influences also impact compositional change. However, overstory disturbance generally is too frequent, particularly in the southeastern United States, to allow composition change to increasingly shade-tolerant taxa, characterized in eastern North America by species such as American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), eastern hophornbeam (*Ostrya virginiana*), and southern magnolia (*Magnolia grandiflora*).

Before the advent of metal tools and mechanization that greatly facilitated timber harvesting, stand-replacing disturbances tended to be infrequent and small scale (Seymour et al. 2002, Lorimer and White 2003, Elsner et al. 2008) compared to current frequency of overstory removal. This allowed for the widespread development of old-growth forests across much of eastern North America. When severe wind storms or other major disturbances occurred that could fell large trees, overstory damage likely occurred in small gaps or patchily, very unlike comprehensive removal in clear cuts (Seymour et al. 2002). Typical estimates of stand-replacing disturbances,

generally by wind or crown fire, range from hundreds to thousands of years (Seymour et al. 2002, Lorimer and White 2003, Schulte and Mladenoff 2005, Hanson and Lorimer 2007, Elsner et al. 2008). For example, in northern hardwood forests, disturbances that removed 30–60% of the canopy occurred on 300- to 400-yr rotations, or about once during expected tree lifespans (Hanson and Lorimer 2007). In the past, with stand-replacing disturbances <0.2 ha in size occurring about every 100 yr in the closed forests of the northeastern United States and 2 ha openings forming every 200 yr (Seymour et al. 2002), early successional stages of <15 yr appeared on about 1–3% of the landscape and an equivalent 1–3% of trees in the 15–30-yr age class (Lorimer and White 2003). Today, tree growth occupies the vertical profile of the forests, even if the overstory is not closed due to gap dynamics or differentiated by dominant trees in understocked stands as a result of timber management practices—whether through overstory thinning or low-density plantings.

Even though most closed forests in eastern North America prior to Euro-American settlement had a dominant old-growth component, some were fundamentally and perpetually successional, at least in structure. This included riparian forests subject to major flooding and boreal forests that terminated and reinitiated every 50–150 yr due to relatively frequent severe fires (Heinselman 1981) or major insect outbreaks (e.g., spruce budworm [*Choristoneura fumiferana*] in balsam fir [*Abies balsamea*] forests; Blais 1983). Boreal forests also may have been constrained to structural succession because abundant seeds and/or sprouts from short-lived overstory trees, either remaining within or adjacent to disturbed areas, caused regenerating stands to resemble prior conditions. Additionally, in areas where old-growth had been in place for an extended period and early successional species were rare, late successional species probably were the colonizers after disturbance (e.g., beech forests in Indiana; Lindsey 1961). In these last two examples, the resistance to compositional change due to abundance of a few tree species has been termed a legacy lock (Johnstone et al. 2010).

However, closed canopy (either old-growth or successional) forests of this region represent only part of a wider spectrum of forest structure

(Fig. 1). In contrast to the dense, often vertically complex closed forests, open forests are characterized by simple internal stand structure, consisting of a single stratum of persistently understocked overstory trees and limited midstory (Hanberry et al. 2014a, b). In open forests, overstory trees may be widely dispersed (in savannas) or nearly continuous (in closed woodlands; Hanberry et al. 2014a). This openness and constrained tree growth permit the development of a typically diverse and abundant groundlayer dominated by grasses, sedges, and forbs. The combination of an open overstory and a robust herbaceous understory produced distinctive ecosystems of high ecological value, often with critical regulatory influences on adjoining ecosystems (Jones et al. 2018).

Disturbance-based drivers of the forest closure spectrum

Although climate, site conditions, and herbivory may constrain the potential species pool in any given region, regional composition reflects the natural disturbance regime (Staver and Levin 2012). Most of the old-growth forests, whether open or closed, of eastern North America found prior to widespread Euro-American settlement were cleared prior to 1930 and now forests in this region are driven by stand-replacing disturbances that occur at intervals of less than a century (Seymour et al. 2002, Pan et al. 2011). Modern landscapes in eastern North America are covered by successional forests that are an outcome of decades of agricultural clearing and then abandonment, timber harvesting, eventual implementation of effective fire suppression, development of silvicultural practices focused on full stocking and a preferred commercial species, or other land uses that continue to alter the forest communities. Forest composition in these successional stands is now largely driven by tolerance to different shade levels and timber management and other land uses.

Unlike closed forests driven by overstory dynamics related to canopy tree removal and shade tolerance, open forests are shaped by limitations in woody plant establishment by frequent, low-intensity surface fires. Characteristics of the fire regime that drives open forest development are subject to a degree of variation as a function of fire return interval and seasonality, burn intensity and duration, fuel structure (e.g., vertical and horizontal patterns) and flammability, along with

other attributes that contribute to the ecology of fuels (Mitchell et al. 2009). When coupled with this ecology, a shared characteristic of historically dominant oak and pine species is their ability to tolerate frequent, low-intensity fire and to encourage frequent surface fires. Other factors, such as drought and soil limitations, may cause enough tree mortality to produce persistent open forests at smaller spatial and temporal scales, but will not favor only fire-tolerant oak and pine species throughout large regions. As for large herbivores, white-tailed deer (*Odocoileus virginianus*) densities are at or above historical highs, but while they may be selectively affecting certain tree species, deer are not browsing forests sufficiently to prevent some type of closed forests from developing (Rooney and Waller 2003, Bradshaw and Waller 2016, Russell et al. 2017).

Frequent fire regimes and open forests

Frequent surface fires acted on the understory to limit establishment and canopy recruitment of fire-tolerant trees and largely excluded fire-sensitive tree species. Note that fire-tolerant species are not immune from effects of burning; rather, they are generally tolerant enough for some of their propagules to eventually escape the deleterious effects of fire by reaching maturity. Escaped individuals can be patchy in their spatial distribution, as the result of highly localized protected sites, inconsistent fire intensity, or chance. Non-lethal fire events can repeatedly injure trees, slowing growth rates for years or even decades. Even the most fire-tolerant species may fail to establish new seedlings under very frequent fire during most years (albeit successful regeneration only is necessary after a lifetime of centuries). As an example, the annual fires that once swept across much of longleaf pine's (*Pinus palustris*) original distribution could eliminate virtually all new longleaf seedlings; the right combination of conditions was needed to permit even a few seedlings to sufficiently establish a belowground presence to tolerate burning (Chapman 1932, Wahlenberg 1934, Garren 1943). This may have led to some early ecologists and foresters to recommend fire suppression as a means to permit longleaf pine to reclaim cutover forests from sprouting scrub oaks (Pessin 1933, Johnson and Hale 2002).

When very frequent, few trees persisted and maintenance of savannas and grasslands was

assured. Toward the opposite end of the open forest spectrum, less frequent or more irregular fire return intervals allowed more establishment of trees, resulting in an increasingly closed woodland structure. In addition to frequency, factors such as intensity, duration, fuels, and timing (season) of burning, and vegetation and site interactions with fires affect tree establishment. Internal feedback mechanisms within the ecosystem also helped to maintain frequent fires (Hanberry et al. 2014b). For instance, open forests are exposed to heat and wind conducive to fire; furthermore, their herbaceous layer and leaf litter spread surface fire by providing fuel continuity necessary for effective surface fires (Pecot et al. 2007). Frequent fires regulated the accumulation of fuel, thereby fire-tolerant species could persist once sufficiently large, with exposure to high severity, overstory-replacing fire disturbances being uncommon. Open forests are resistant to severe fires as the lack of midstory and breaks in canopy continuity restricts the extent or propagation of high severity events. The open structure, low densities, and physiological responses to fire also may diminish the influence of most catastrophic disturbances such as windthrow or insect outbreaks. Long-term maintenance of an open forest state also was facilitated by the actions of herbivores (especially large ungulates) and climate and site conditions, which cannot be too wet to ignite or too dry to produce fire fuels.

Fire also consumes the mechanical barrier of coarse woody debris, leaf litter, and other organic matter on the forest floor that can reduce the emergence of some species, especially grasses. In addition to reducing establishment barriers, fire allows more light to reach the mineral soil. Light intensity on the forest floor is principally a function of overstory tree density, which in open forests is controlled by the fire regime. Understory openness can be further accentuated when overstory fire-tolerant oaks and pines rapidly self-prune their lower branches, often due to fire-induced branch loss. The understory light regime is an important factor that influences the composition and dynamics of the groundlayer vegetation. In longleaf pine savannas, the negative effects of fire exclusion on groundlayer diversity are primarily a function of duff accumulation, while shade cast by the midstory is of secondary importance (Hiers et al. 2007). Fewer barriers and

increased soil temperature and its fluctuations (Iverson and Hutchinson 2002) may also contribute to increased germination from the seed bank (Facelli and Pickett 1991).

Spatial heterogeneity and the open forest spectrum

Although vertical structural diversity is low in most open forests, considerable spatial heterogeneity arises from varying tree density in the form of vegetation phases of savannas and woodlands at landscape scales (Hanberry et al. 2016). Variation in fuel loading helps to regulate the impacts of fire on tree establishment success (Loudermilk et al. 2012) and the dispersion between overstory trees creates greater horizontal heterogeneity in canopy closure and stand density than found in closed forests (Hanberry et al. 2014a, 2016). Uniform or random spacing typically may occur as individual trees claim the growing space around them, but factors such as differential fire severity, fire energy release driven by overstory contributions to fuels, patterns in fine-scale environmental gradients, and/or remnants of persistent soil seed banks may lead to patches of aggregated trees and clustered arrangements (Dell et al. 2017). Additionally, dense pine establishment in particular may result in groups of trees that periodically fill overstory gaps. On the most open end of the spectrum, it may be difficult—and essentially unnecessary—to distinguish treed savannas from grasslands that contain various forest configurations, such as riparian forests, groves, scattered trees, and trees in shrub form.

Spatial heterogeneity in overstory tree distribution and differential fire energy release produced by fuels heterogeneity also play key roles in structuring understory conditions (O'Brien et al. 2008, Dell et al. 2017). A wide range in canopy closure produces gradients in light, water, wind, and fire exposure, which favor different plant traits and result in differing groundlayer composition. Overstory trees and understory herbaceous plants are functionally linked through interactions of fuel spatial distribution and subsequent energy release (O'Brien et al. 2008, Dell et al. 2017). Open forests have elements of grasslands because the growing space is not captured by trees, allowing for a diverse shade-intolerant herbaceous cover. Hence, open forests represent interfaces where key

system properties change discontinuously, resulting in different ecosystem function. The term ecotone may be synonymous with interface, given the understanding that open forests are unique and emergent ecosystems in their own right, analogous to wetlands at the interface of aquatic and terrestrial ecosystems.

A sparse to absent woody midstory further distinguishes closed woodlands from closed forests. The limited open forest midstory owes its reduced woody vegetation to the frequent consumption of small diameter woody stems, seedling trees in particular, by fire. Fire favors herbaceous vegetation primarily by killing or greatly stunting woody vegetation, thereby limiting its abundance and allowing light to reach the forest floor. Fire's impact on woody stems is a function of its frequency, season of burn, and distribution across sites, with frequent growing-season burns causing the greatest mortality, especially where certain fuels have accumulated (Waldrop et al. 1992, Glitzenstein et al. 1995, Drewa et al. 2002, Mitchell et al. 2009). Woody plants also struggle to establish because of a continuous herbaceous groundlayer that presents a remarkably challenging competitive environment for seedlings (Scholes and Archer 1997). There are also elements of the fuel structuring that occur in at least some open forests that contribute to under- and midstory vegetation patterns. For example, recent work has shown that longleaf pine cones burn hotter and longer than other fine fuels, producing areas of higher fire radiative energy that contribute to variation in fuel consumption, plant mortality, and other pyrogenic impacts that can influence forest structure (O'Brien et al. 2016).

UNDERSTANDING HISTORICAL OPEN OAK AND PINE FORESTS OF EASTERN NORTH AMERICA

With the preceding paragraphs on the comparative structure, function, and dynamics of the forest closure spectrum for background, we now take the opportunity to reconceive of the historical forest conditions of eastern North America with an emphasis on the nature of open forests. Our objective of this section is to link the dominant (driving) disturbance regimes of the past with the observations (both historical and contemporary) of the composition, complexity,

dynamics, and their interactions on the open oak and pine forests in eastern North America, where their canopy closure spectrum ranges from sparsely treed savannas to open woodlands to closed woodlands.

Species composition and dominance

The open oak- and pine-dominated forests that characterized much of eastern North America for thousands of years arose from widespread, surface fire-driven disturbance regimes (Beilmann and Brenner 1951, Prentice et al. 1991, Abrams 1992, Grimm and Jacobson 1992, Overpeck et al. 1992, Earley 2004, Williams et al. 2004, Frost 2006, Arthur et al. 2012, Hanberry and Abrams 2018). This long history of fire helped shaped the dominance of these taxa over large scales. In many places, oaks comprised 30–80% (or more) of the stems across deciduous forests of eastern North America, while most other hardwood species were relatively minor components. For example, upland oaks comprised approximately 55% of past forests in the eastern broadleaf forest region and 65% of the trees in prairies bordering eastern forests (Goring et al. 2016, Hanberry and Nowacki 2016). Most of these open forests were dominated by a relatively limited number of upland oak species. White oak (*Quercus alba*) and lesser amounts of black (*Quercus velutina*, or perhaps other taxa in the red oak subgroup) were common throughout the region; chestnut oak (*Quercus prinus*) and northern red oak (*Quercus rubra*) were more dominant in the east; post oak (*Quercus stellata*), bur oak (*Quercus macrocarpa*), and blackjack oak (*Quercus marilandica*) in the interior; and southern red oak (*Quercus falcata*) in the south (Schnur 1937, Hanberry et al. 2012, 2013, Faison and Foster 2014, Greenberg et al. 2016).

Likewise, taxonomically simple open forests comprised of pine or mixed oak–pine also dominated much of the southeastern United States. Longleaf pine defined open forests across millions of hectares of the Lower Coastal Plain from Texas to Virginia (Frost 1993, Earley 2004, Hanberry et al. 2018a). In these open forests, longleaf often contributed in excess of 75% of total composition (Hanberry and Nowacki 2016, Hanberry et al. 2018a). For those Lower Coastal Plain areas with few longleaf pine, it was not uncommon for some species of scrub oaks (e.g., turkey oak [*Quercus laevis*] and/or blackjack oak) to

dominate the open woodlands (Pessin 1933). Indeed, in moderate amounts these scrub oaks can play a vital contributing role in helping longleaf pine reestablish on some xeric sites (Loudermilk et al. 2016). Oaks and shortleaf pine (*Pinus echinata*), sometimes with a component of loblolly pine (*Pinus taeda*), dominated open forest ecosystems across much of the Upper Coastal Plain, Piedmont, and Interior Highland (Ouchita and Ozark) regions (Bragg 2008, Hanberry and Nowacki 2016). Loblolly pine and slash pine (*Pinus elliottii*) flatwoods across the Coastal Plain of the southern United States, pine (*P. elliottii* var. *densa*, *Pinus caribaea*, and numerous other species and varieties) systems in southern Florida and the Caribbean, and longleaf pine woodlands in the extreme southern Appalachian Mountains represent additional examples of open pine forests in this region (O'Brien et al. 2008). Pine-dominated open forests or barrens occurred in

Canada, the northern Lake States, New England, and the Mid-Atlantic regions, often associated with sandy or stony soils, comprised of jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), pitch pine (*Pinus rigida*), and occasionally eastern white pine (*Pinus strobus*; e.g., Forman 1979, Heinselman 1981, Whitney 1986).

Age complexity in historical open forests

The age structure of many old southern pine forests is usually quite complex (Platt et al. 1988, Gilliam and Platt 1999, Varner et al. 2003, Bragg 2004, Varner and Kush 2004, Pederson et al. 2008), a function of often episodic or sporadic canopy recruitment. For example, historical longleaf pine forests (Fig. 2) were characterized by an overstory that included large, old (>200 yr) trees, more-or-less continuously recruited via small canopy gaps prior to fire exclusion. Scattered across these old stands are overstory gaps



Fig. 2. Example of an uneven-aged open old-growth forest: longleaf pine on the Greenwood Plantation in southern Georgia. Frequent fire controls tree regeneration, with only scattered saplings of the old (>150 yr) dominant overstory species present.

containing a handful of persistent, often fire-stunted, slow-growing longleaf saplings, with occasional pole-sized pines that have reached a large enough size to resist fires and not be suppressed by overstory shade. These fire-resistant longleaf pine saplings are suggestive of the heterogeneity also present in many open forests—they have a multi-aged overstory akin to that of old-growth closed forests. This was especially true in the deep sands of the Wade Tract of southwest Georgia where Platt et al. (1988) documented the continuous gap-phase recruitment of longleaf pine throughout its centuries-long recorded history. Others have noted larger even-aged cohorts of longleaf to be present but uncommon (Varner et al. 2003, Pederson et al. 2008).

Open oak forest ecosystems also followed this same developmental pattern with multiple age classes in an otherwise vertically simple overstory (Fig. 2). For instance, dendrochronological studies in some remnant old-growth oak forests have shown relatively continuous recruitment prior to fire suppression (Abrams and Copenheaver 1999, Rentch et al. 2003, Bragg et al. 2012, Hart et al. 2012, McEwan et al. 2014). These studies also noted that gap-scale recruitment of white and chestnut oak recruitment often required multiple release events during canopy ascension. These releases were likely caused by small-scale canopy disturbances, for example, death of individual trees or patches of several trees. When infrequent, crown-replacing events, caused by wind, ice, insects, drought, or high severity fire, created larger gaps, it was possible to recruit bigger patches of even-aged seedlings (Rentch et al. 2003). These large-scale canopy disturbances could be more common in xeric oak-pine stands with a history of frequent fire (King and Muzika 2014).

In part, the development of open, uneven-aged old-growth forests was possible because many of the dominant tree species, including white oak, post oak, bur oak, longleaf pine, and shortleaf pine, can live for well over 300 yr. This is much longer than most other species considered early seral in eastern North America and helped to produce the age complexity of open forests. The long-term persistence of open forests depends on the rare, sometimes synchronous, combination of circumstances that allowed fire-tolerant advanced reproduction to accumulate in the understory,

sometimes for decades. Because extensive areas were not frequently replaced by catastrophic disturbances, open forests achieved age heterogeneity as this advanced regeneration opportunistically replaced canopy trees that died.

Low severity fire and its influence

In the past, much of eastern North America was exposed to frequent, low severity fires (Frost 1998, Guyette et al. 2012). Although the controlling influence of this pyrogenic disturbance regime has been questioned by some (Pederson et al. 2014), we believe that in many areas the transition from open to closed forests was a direct consequence of successful widespread fire exclusion, starting after 1910 and ramping up in the 1930s. Prior to active suppression, fires generally burned every 5–20 yr across much of eastern North America (Lafon et al. 2017, Stambaugh et al. 2018), and sometimes as often as every year or two in the Lower Coastal Plain where the fine fuels in the form of graminoids and leaf litter (especially pine straw) accumulated quickly enough to carry fire (Glitzenstein et al. 1995, 2003, Stambaugh et al. 2018) and prevent tree regeneration from capturing growing space. Fire regime variation across space and time allowed for different vegetative states, from savannas to woodlands, transitions between these states, and the periodic recruitment of new overstory trees.

The removal or limitation of frequent fire was quickly observed by early foresters as one of the best opportunities for increasing forest stocking (Mattoon 1922) and hence became one of the first, and most universal, silvicultural recommendations available to interested landowners. This recommendation countered centuries of prior practice. Widespread human use of fire in the past to reshape the environment has been well-documented in the eastern United States (Williams 2005). Early explorer William Bartram described (Harper 1998:141–142) parts of the southeastern Coastal Plain as

... a vast forest of the most stately Pine trees that can be imagined, planted by nature at a moderate distance, on a level, grassy plain enamelled [sic] with a variety of flowering shrubs... [t]his sublime forest continued for five or six miles... for in all of flat countries of Carolina and Florida... the waters of the rivers are, in some degree, turgid, and have a dark hue, owing to the annual firing of the forests and plains...

Bartram's use of the term "firing" fits the well-documented use of fire by prehistoric peoples to influence forested ecosystems (Denevan 1992, Delcourt and Delcourt 1997, Delcourt et al. 1998, Abrams and Nowacki 2008, Journey 2012). Hilgard (1860:349) also noted the outcome of this practice in the longleaf pine-dominated southern third of Mississippi:

The herbaceous vegetation and undergrowth of the Longleaf Pine Region is hardly less characteristic than the timber. Whenever the regular burning of the woods, such as practiced by the Indians...the pine forest is almost destitute of shrubby undergrowth, and during the growing season appears like a park, whose long grass is often very beautifully interspersed with brilliantly tinted flowers.

Oak-dominated ecosystems in the Central Hardwoods region were regulated by frequent surface fires in the same fashion. In 1750, Jesuit missionary Father Louis Vivier described (Vivier 1900:207–209) the lands along the Mississippi River as:

...bordered, throughout nearly the whole of its course, by two strips of dense forests, the depth of which varies more or less from a half a league to four leagues. Behind these forests the country is more elevated, and is intersected by plains and groves, wherein the trees are almost as thinly scattered as in our public promenades. This is partly due to the fact that the Savages set fire to the prairies toward the end of autumn, when the grass is dry; the fire spreads everywhere and destroys most of the young trees.

The woods burning practices of Native Americans were continued and even intensified by Euro-American settlers (Guyette et al. 2002, Arthur et al. 2012). For example, William Dunbar, a Scottish immigrant and early settler in the Natchez, Mississippi area (Berry et al. 2006:41), wrote of the haze commonly encountered in the lower Mississippi River Valley during the latter months of the year, attributing it to:

...a common practice [sic] of the Indians and [Euro-american] Hunters, of firing the woods, plains [sic] or savannahs; the flames often extending themselves some hundred miles, before the fire is extinguished...

It is important to note that improperly applied burning could be detrimental to ecosystem integrity, as was noted by Hilgard (1860:361):

In their natural state, as received from the hands of the Indians, the Pine Woods were one great pasture

—as, in thinly settled regions, they still are. Nor is it, generally, the ranging of cattle which has destroyed the pasturage in other regions, but simply the injudicious burning of the woods, at seasons when the fire would destroy not only the dry leaves, but also parch the *heart* and *roots* of the grasses...The beautiful, park-like slopes of the Pine Hills are being converted into a smoking desert of pine trunks...

Under regulated anthropogenic application and in conjunction with edaphic and topographic conditions, low severity surface fire was the primary stabilizing mechanism for most open forest systems (Bray 1906, Heyward 1939, Garren 1943, Beilmann and Brenner 1951, Forman 1979, Abrams 1992, Earley 2004, Frelich et al. 2015, Veldman et al. 2015).

Under- and midstory composition and dynamics

In general, open oak and pine forests of eastern North America are characterized by a productive and diverse groundlayer vegetation, dominated by herbaceous perennials (~90%) and often containing species of high conservation value (Drew et al. 1998, Leach and Givnish 1999, Kirkman et al. 2001). Open forests have been described as grasslands with trees, but in some oak savannas, Leach and Givnish (1999) suggested that forblands would be more accurate given their dominance by a diverse community of forbs. In the Lower Coastal Plain of eastern North America, the forb- and graminoid-dominated groundlayer of frequently burned longleaf pine savannas can be extremely diverse, with 25–35 species occurring per square meter (Walker and Peet 1984, Peet and Allard 1993). Where conditions are such that longleaf pine flatwood sites burn less frequently (Fig. 3), certain fire-tolerant shrubs (e.g., saw palmetto [*Serenoa repens*], wax myrtle [*Morrellia cerifera*], gallberry [*Ilex glabra*]) quickly tend to dominate open forest understories (Glitzenstein et al. 1995). Open oak ecosystems maintained by fire support two to three times the small-scale species richness of unmanaged closed oak forests in the same region (Leach and Givnish 1999, Knapp et al. 2015).

The groundlayer of closed oak forests is dominated by shade-tolerant perennial herbs or spring ephemerals that complete much or all of their annual carbon assimilation before canopy closure (Neufeld and Young 2003). In open oak forests, abundance and diversity of groundlayer



Fig. 3. Difference between annually burned longleaf pine flatwood site (foreground) vs. an open stand that has not burned in over a decade (background). When fire return intervals approach or exceed 10 yr in this type, the woody understory includes a number of shrub species in addition to saw palmetto to the exclusion of most other herbaceous species and produces a much more intense fire when burned.

vegetation are related to canopy cover across a fire frequency gradient in oak savannas. Cool-season (C_3) graminoids, notably panic grasses (*Dichanthelium* spp.) and upland sedges (*Carex* spp.) are also common in some open oak forests

and these increase with repeated burning (Taft 2003, Hutchinson et al. 2005). With increasing canopy cover, the cover of forbs and especially grasses decreases and species diversity also declines (Peterson et al. 2007, Peterson and Reich

2008). However, the reduction of grass dominance is not always a problem in some open forests. As an example, forbs that flower in the summer or fall require moderate to high light levels characteristic of open oak forests (Nelson 2010). Hence, for forbs such as composites (Asteraceae) and legumes (Fabaceae) to dominate oak savannas, the partial shade cast by the overstory must limit coverage by C_4 grasses and frequent fires need to reduce the dominance of woody plants.

Similarly, in open longleaf pine forests, groundlayer species richness is inversely related to tree basal area and canopy cover, both factors that are influenced by fire frequency (Veldman et al. 2014). However, compared to open oak forests, the herbaceous flora of open pine forests tends to be more dominated by grasses, particularly C_4 grasses (Masters et al. 1996, Brockway and Lewis 1997, Kirkman et al. 2001). In fact, ecological classifications often include the dominant C_4 grass in the nomenclature (e.g., longleaf pine-wiregrass [*Aristida*] savannas, shortleaf pine-bluestem [*Andropogon*] woodlands). While often less abundant than the grasses, forbs still contribute much to the diversity in open pine forests, with composites and legumes again being major groups (Drew et al. 1998). Woody plants (tree seedlings/sprouts and shrubs) may also be a significant component of the groundlayer vegetation except in a regime of long-term annual or near-annual burning (Bowles et al. 2007, Peterson et al. 2007, Knapp et al. 2015).

Long-term annual or biennial dormant season fires can also exclude woody plants from the groundlayer vegetation in many ecosystems in eastern North America (Knapp et al. 2015). Fire-tolerant tree species evolved a number of adaptations for persistence under a frequent fire-mediated disturbance regime, including thick, insulating bark on mature trees, high flammability constituents in the bark, foliage, and other aboveground tissues, cone serotiny, self-pruning of lower branches, the ability to resprout multiple times after topkilling, and other unique mechanisms, such as the grass stage found in longleaf pine (Gignoux et al. 1997, Fonda 2001, Bond and Keeley 2005, Kane et al. 2008, Mitchell et al. 2009). Although fires may lethally heat soil-stored seeds (Wiggers et al. 2013) or destroy propagules and even advanced regeneration

(Mitchell et al. 2009), germination of some hard-coated seeds (e.g., legumes) is stimulated by heat (Cushwa et al. 1968, Bradstock and Auld 1995). Prescribed fire has been shown to trigger the germination of seed-banking species in oak woodlands and forests (Taft 2003, Hutchinson et al. 2005) and in shortleaf pine woodlands (Sparks et al. 1998). Indeed, fire energy release driven by overstory-derived fuels appears to have the greatest positive impact on diversity in relatively open-canopied, frequently burned stands (Dell et al. 2017).

However, low-stature woody vegetation is not always absent from even the most open forests; both fire-tolerant shrubs and trees may be present and occasionally formed a patchy scrub groundlayer. Shrublands comprised of oak sprouts or grubs, top-killed by fire, were described for the eastern prairie-forest interface (Lindsey 1961). Across much of the Coastal Plain of the southeastern United States, travelers and GLO surveyors frequently mentioned oak and pine scrubs in the open forestlands they traversed during the 19th century (Bragg 2002). Dr. Charles Mohr (quoted in Sargent 1884:539) described such a community near Shreveport, Louisiana:

The rolling uplands that which extend to the edge of the [Red River]. . . bear an open growth of oaks. . . The undergrowth in these woods is scanty, and consists for the most part of seedling oaks.

Dey et al. (2017) noted that this fire-stunted advance tree regeneration is critical to the eventual replacement of the overstory dominants that eventually succumb to any of a number of causes. Shortleaf pine has a comparable capacity to resprout from top-killed seedlings (Mattoon 1915), and longleaf pine's grass stage is a different manifestation of this established tree regeneration pool. Regardless of species, the ability of these advanced regeneration pools to replace overstory trees requires some respite from the frequent surface fires.

Long-term prescribed fire experiments in open oak and pine forests provide further insights into how the structure, composition, and diversity of the groundlayer vegetation varies under different fire regimes. In oak savannas and woodlands in the upper Midwest, groundlayer diversity and the abundance of herbaceous vegetation were shown to be maximized in a regime of biennial

fires over a period of >30 yr (Peterson et al. 2007, Peterson and Reich 2008). Similarly, in the Missouri Ozarks, Knapp et al. (2015) showed that frequent burning for >60 yr in oak woodlands led to a diverse groundlayer with a vigorous herbaceous component, which was in sharp contrast to the depauperate flora of nearby unburned woodlands. In the Coastal Plain, where growing-season fires ignited by lightning or people are much more common, the relationship between frequent fire in open pine forests and a productive groundlayer vegetation has been recognized for a very long time (Stoddard 1931). Multiple studies have compared the long-term (>40 yr) effects of different fire regimes on community composition of open forests. Waldrop et al. (1992) demonstrated that the abundance of herbaceous vegetation, particularly grasses, was much greater with annual burning than periodic burning (3–7-yr return) in South Carolina loblolly pine stands. Similarly, long-term frequent burning (1–3-yr intervals) in both Georgia longleaf pine flatwoods and Florida longleaf pine savannas promoted a diverse and productive groundlayer dominated by grasses (Brockway and Lewis 1997, Glitzenstein et al. 2012).

Shorter-term studies in a variety of open forests also show increases in groundlayer/seed bank diversity and the abundance of herbaceous vegetation after repeated fires (Taft 2003, Hutchinson et al. 2005, Bowles et al. 2007, Holzmüller et al. 2009) or the combination of mechanical thinning and prescribed fire (Royo et al. 2010, Kinkead et al. 2013, Lettow et al. 2014, Sharma et al. 2018). For example, short-term groundlayer flora response to thinning and repeated burning has been documented in shortleaf pine woodlands in the Ouachita Mountains of Arkansas. These restoration treatments have greatly increased the density and biomass of both grasses and forbs (Masters et al. 1996, Sparks et al. 1998). Taken together, these studies show that fire return intervals of <5 yr may be necessary to sustain a productive and diverse groundlayer in open oak and pine forests. However, less frequent fire may sustain an open forest groundlayer community when tree growth is more severely limited by the environment, for example, the excessively drained or shallow soils found in barrens (Anderson et al. 2007).

PUTTING IT ALL TOGETHER: A RECONCEPTUALIZATION OF OPEN FORESTS

The preceding sections were intended to help (re)define the concept of open oak and pine forests in eastern North America, particularly addressing simple overstory structure and species-rich understories compared to closed successional forests that now dominate the region. Open forest ecosystems should be recognized as a currently missing portion of the spectrum between closed successional forests and grasslands. We advocate that most open forests were widespread and stable ecosystems, in the sense that these forest types have been present for thousands of years and the simple stand structure and monotypic composition do not vary much when overstory trees live for centuries, with intermediate and emergent properties resulting from the intersection of two ecosystems that share a disturbance regime. Open forests are now a missing portion of the forest spectrum in eastern North America, given the uniqueness and historical importance of open oak and pine forests, largely as a consequence of societal decisions regarding forest land management priorities over the past century.

Lack of recognition of open forests reinforces the notion that closed forests are the archetypal forest in eastern North America, thereby resulting in misunderstandings that have reduced effective research and conservation of remaining open forest ecosystems. Conventional concepts of succession and closed forests are deeply embedded in American ecology and forestry, which makes it difficult to determine all the implications and consequences of applying that body of knowledge to a different ecosystem. However, the reconceptualization of community types in eastern North America is not without precedent (Mitchell et al. 2006). For instance, after archetypal closed old-growth forests were accepted as an alternative state to closed successional forests, identification of stand features and species associated with closed old-growth forests occurred, along with understanding of different stand dynamics and management techniques than those that occur in closed successional forests (Franklin et al. 2002). After a long and often difficult process, acknowledgment of the ecologically unique attributes of old-growth forests

helped provide better protection and management of the remaining resource.

We believe that ecological terms and silvicultural methods developed for successional closed forests, such as shade tolerance, even- and uneven-aged management, and vertical layers *as applied to open forest ecosystems* are ultimately inconsistent with their most appropriate use. For example, even-aged management has been the dominant strategy for regenerating closed oak stands throughout the eastern United States for more than 50 yr (Johnstone et al. 2010). However, even-aged management is a term for successional forests, which are influenced by overstory disturbance and rapid change following disturbance as a function of varying degrees of shade tolerance. Development and application of open forest management with a specific focus on maintaining relatively constant stocking through thinning and prescribed fire is more appropriate, and although practiced at small scales, is not yet realized to be an option to even-aged management.

Hence, to minimize problems arising from misapplications, we offer the following concepts to separate open oak and pine forests from closed forests in eastern North America, with clarifications of potential misunderstandings:

1. Open forests once dominated large areas for thousands of years, and closed forests were much less abundant across the region. *Clarification of potential misunderstanding:* Contemporary characterizations of eastern North America as being densely forested by late successional species in the past, with only scattered areas of open oak and pine forest, are a misrepresentation of historical forest conditions.
2. Successional forests are undergoing the developmental stages of reforestation after stand-replacing disturbance that eventually can develop into closed old-growth forests. However, stand-replacing disturbances were much less frequent historically than currently. *Clarification of potential misunderstanding:* Despite current abundance of closed successional forests, old-growth ecosystems—both open and closed—were historically much more common due to less overstory disturbance than currently (mainly, less harvesting).
3. Closed forests represent only one end of a spectrum of forest structure. The open portion of the forest density spectrum is itself a gradient ranging from savannas to closed woodlands. *Clarification of potential misunderstanding:* Open forests historically provided variation in canopy closure, an attribute now typically lacking in eastern forests.
4. Open forests characteristically have a simple vertical structure. However, tree density and arrangement provided horizontal heterogeneity, particularly at landscape scales. *Clarification of potential misunderstanding:* In open forests, a largely single layer canopy structure with some spatial heterogeneity in stocking is most desirable, rather than the achievement of multiple vertical layers across the entire stand that is considered a hallmark of success for many restoration efforts in closed forests.
5. Unlike closed forests, fire tolerance—not shade or drought tolerance—is the primary reason that oak and pine species dominated open forests historically. Fires targeted understory tree growth. Although there are other agents, such as drought and soil limitations that cause mortality of small diameter trees, these factors are localized in spatial or temporal scale. *Clarification of potential misunderstanding:* Shade tolerance historically was much less important in maintaining the long-term dominance of open oak and pine forests.
6. Fire-tolerant oak and pine species typically have maximum lifespans of multiple centuries, allowing for their gradual recruitment into the canopy during occasional fire-free intervals that permitted fire-tolerant oaks and pines to grow out of the most vulnerable stages. *Clarification of potential misunderstanding:* Regeneration only needs to be occasional and timely, while temporally and spatially continuous recruitment of understory trees is detrimental to the herbaceous groundlayer.
7. Historical open forests were generally stable both as forest types that occurred for thousand years and as old-growth stands, similar to closed old-growth, with limited change in structure and composition due to infrequent large-scale overstory

disturbances. This relative stability occurred over much of the region because stand-replacing disturbances occurred less frequently than tree lifespans while frequent fire filtered out the less fire-tolerant taxa. *Clarification of potential misunderstanding:* Fire-tolerant tree species, especially those with considerable longevity, can form open old-growth even though they would be classified as shade-intolerant, early-successional species in closed forests. A simple (single layer) overstory does not imply it must also be even-aged; many different age classes can exist, either in groups or scattered across the forest.

8. Because of the discriminating action of frequent fire, tree diversity is often relatively low—sometimes a virtual monoculture—in old-growth open forests, dominated by taxa specially adapted to persist through repeated burns. *Clarification of potential misunderstanding:* While high tree diversity is often considered one of the desired outcomes following restoration, in most open forests a return to fewer but more fire-adapted species is a better metric of success.
9. Open forests are inherently bipartite systems with both forest and grassland components that interact functionally, particularly through the process of fire. *Clarification of potential misunderstanding:* Open forests represent interaction between grasslands and forests, suggesting that indicators of “naturalness” in closed old-growth forests, such as a multi-layered canopy and an undisturbed forest floor that limits the success of shade-intolerant herbaceous species, are undesirable in open forests.
10. Restoration of open forests can be considered successful only if both the overstory structure and understory composition are returned—and sustained—to an approximation of what had been present. *Clarification of potential misunderstanding:* While some restoration efforts rely solely on mechanical or even chemical methods to control certain aspects of the vegetation, these treatments cannot reproduce the full range of influences of frequent fire, from filtering less fire-tolerant tree species to encouraging a diverse community of forbs and grasses.

CONCLUSIONS

We offer a new conceptualization of historical forest condition and dynamics for eastern North America when fire was frequent and widespread. During this period, forest structure was often in the open part of the canopy closure spectrum due to frequent fire's limitations on understory woody stem recruitment. Tree density heterogeneity varied across environmental/fire frequency gradients, and the groundlayer was productive and diverse. These open forests also contained a simple overstory structure and low diversity oak and pine composition that nevertheless resulted in old-growth. Today, loss of frequent fire means that open oak and pine forest ecosystems have declined precipitously in the eastern North America (Noss et al. 1995, Hanberry and Abrams 2018, Hanberry et al. 2018b), and similar open forest ecosystems such as ponderosa pine (*Pinus ponderosa*) and Oregon white oak (*Quercus garryana*) in the western United States are also imperiled. Functional open oak and pine forests persist only when and where circumstances permit application and sustenance of the needed fire regime.

These diminishment are masked to a large degree by the relative abundance of oak and pine in North American forests; however, the closed oak and pine forest ecosystems present today are fundamentally different than those that dominated in the past. Indeed, very few managed landscapes remain dominated by open forests, having transitioned during the last century to increasingly dense stands comprised of fire-intolerant species in all strata (thus, many vertical layers) and a woody rather than herbaceous understory (Goebel and Hix 1996, McCarthy et al. 2001, Bragg 2004, Fraver and Palik 2012, Dey et al. 2017, Hanberry and Abrams 2018). Efforts to arrest this degradation and restore self-replacing oak- and pine-dominated ecosystems have had limited success (Dey et al. 2017), due in part to our imperfect understanding of the structure and dynamics of these systems. We have also largely lost the ability to reference actual functioning examples to address this challenge. Most of the few unmanaged old-growth remnants left have long since lost their original open forest structure, providing few useful models for scientists and managers to reference.

The disappearance of open forests, especially at scale and across many different landscapes, has had many significant conservation implications. Unlike the currently dominant closed successional forests, explicit connections between historical open forests and biodiversity forged over thousands of years cannot be easily replicated. Taxa associated with the open forests of eastern North America, such as the now-extirpated eastern elk (*Cervus canadensis canadensis*), many early successional birds (Johnson and Hale 2002, Reidy et al. 2014), butterflies and other pollinators (Campbell et al. 2007, Wood et al. 2011), groundlayer taxa (Kirkman et al. 2001, Mitchell et al. 2006), and myriads of other species that depended on open forests have declined steeply having failed to find the closed successional forests acceptable habitat. Only recently have conservation-driven objectives (e.g., recovery of endangered species) begun to influence forest management practices. For example, large-scale habitat restoration of open pine forests dominated by large, mature trees for red-cockaded woodpeckers (*Picoides borealis*) has helped to at least temporarily arrest the decline of that endangered species. However, even this conservation success story does not inherently capture enough of the needed dynamics to ensure the long-term stability of these restoration efforts. A better understanding and greater awareness of the attributes of these unique open oak and pine forests therefore are needed to ensure improvements in their management and restoration.

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LITERATURE CITED

- Abrams, M. D. 1992. Fire and the development of oak forests. *BioScience* 42:346–353.
- Abrams, M. D., and C. A. Copenheaver. 1999. Temporal variation in species recruitment and dendroecology of an old-growth white oak forest in the Virginia Piedmont, USA. *Forest Ecology and Management* 124:275–284.
- Abrams, M. D., and G. J. Nowacki. 2008. Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. *Holocene* 18:1123–1137.
- Anderson, R. C., J. S. Fralish, and J. M. Baskin. 2007. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, Cambridge, UK.
- Arthur, M. A., H. D. Alexander, D. C. Day, C. J. Schweitzer, and D. L. Loftis. 2012. Refining the oak-fire hypothesis for management of oak-dominated forests in the eastern United States. *Journal of Forestry* 110:257–266.
- Barnes, B. V., D. R. Zak, S. R. Denton, and S. H. Spurr. 1997. *Forest ecology*. John Wiley and Sons, New York, New York, USA.
- Beilmann, A. P., and L. G. Brenner. 1951. The recent intrusion of forests in the Ozarks. *Annals of the Missouri Botanical Garden* 83:261–282.
- Berry, T., P. Beasley, and J. Clements. 2006. *The forgotten expedition, 1804–1805: the Louisiana purchase journals of Dunbar and Hunter*. Louisiana State University Press, Baton Rouge, Louisiana, USA.
- Blais, J. R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Canadian Journal of Forest Research* 13:539–547.
- Bond, W. J., and J. E. Keeley. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* 20:387–394.
- Bormann, F. H., and G. Likens. 2012. *Pattern and process in a forested ecosystem*. Springer-Verlag, New York, New York, USA.
- Bowles, M. L., K. A. Jacobs, and J. L. Mengler. 2007. Long-term changes in an oak forest’s woody understory and herb layer with repeated burning. *Journal of the Torrey Botanical Society* 134:223–237.
- Bradshaw, L., and D. M. Waller. 2016. Impacts of white-tailed deer on regional patterns of forest tree recruitment. *Forest Ecology and Management* 375:1–11.
- Bradstock, R. A., and T. D. Auld. 1995. Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* 32:76–84.
- Bragg, D. C. 2002. Reference conditions for old-growth pine forests in the Upper West Gulf Coastal Plain. *Journal of the Torrey Botanical Society* 129:261–288.
- Bragg, D. C. 2004. Composition, structure, and dynamics of a pine-hardwood old-growth remnant in southern Arkansas. *Journal of the Torrey Botanical Society* 131:320–336.
- Bragg, D. C. 2008. The prominence of pine in the Upper West Gulf Coastal Plain during historical times. Pages 29–54 in L. M. Hardy, editor. *Freeman*

- and Custis Red River Expedition of 1806: two hundred years later, *Bulletin of the Museum of Life Sciences*, Number 13. Louisiana State University in Shreveport, Shreveport, Louisiana, USA.
- Bragg, D. C., D. W. Stahle, and K. C. Cerny. 2012. Structural attributes of two old-growth Cross Timbers stands in western Arkansas. *American Midland Naturalist* 167:40–55.
- Bray, W. L. 1906. Distribution and adaptation of the vegetation of Texas. *Bulletin of the University of Texas, Scientific Series*, No. 10, Austin, Texas, USA.
- Brockway, D. G., and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96:167–183.
- Burns, R. M., and B. H. Honkala. 1990a. *Silvics of North America*, Vol. 1, Conifers. U.S.D.A. Forest Service Agriculture Handbook 654, Washington, D.C., USA.
- Burns, R. M., and B. H. Honkala. 1990b. *Silvics of North America*, Vol. 2, Hardwoods. U.S.D.A. Forest Service Agriculture Handbook 654, Washington, D.C., USA.
- Campbell, J. W., J. L. Hanula, and T. A. Waldrop. 2007. Effects of prescribed fire and fire surrogates on floral visiting insects of the Blue Ridge province in North Carolina. *Biological Conservation* 134:393–404.
- Carey, A. B., and R. O. Curtis. 1996. Conservation of biodiversity: a useful paradigm for forest ecosystem management. *Wildlife Society Bulletin* 24:610–620.
- Chapman, H. H. 1932. Some further relations of fire to longleaf pine. *Journal of Forestry* 30:602–604.
- Clements, F. E. 1916. *Plant succession: an analysis of the development of vegetation*. Publication 242, Carnegie Institution of Washington, Washington, D.C., USA.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119–1144.
- Cushwa, C. T., R. E. Martin, and R. L. Miller. 1968. The effects of fire on seed germination. *Journal of Range Management* 21:250–254.
- Delcourt, P. A., and H. R. Delcourt. 1987. Late-Quaternary dynamics of temperate forests: applications of paleoecology to issues of global environmental change. *Quaternary Science Reviews* 6:129–146.
- Delcourt, H. R., and P. A. Delcourt. 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. *Conservation Biology* 11:1010–1014.
- Delcourt, P. A., H. R. Delcourt, C. R. Ison, W. E. Sharp, and K. J. Gremillion. 1998. Prehistoric human use of fire, the Eastern Agricultural Complex, and Appalachian oak-chestnut forests: paleoecology of Cliff Palace Pond, Kentucky. *American Antiquity* 63:263–278.
- Dell, J. E., L. A. Richards, J. J. O'Brien, E. L. Loudermilk, A. T. Hudak, S. M. Pokswinski, B. C. Bright, J. K. Hiers, B. W. Williams, and L. A. Dyer. 2017. Overstory-derived surface fuels mediate plant species diversity in frequently burned longleaf pine forests. *Ecosphere* 8:e01964.
- Denevan, W. M. 1992. The pristine myth: the landscape of the Americas in 1492. *Annals of the Association of American Geographers* 82:369–385.
- Dey, D. C., J. M. Kabrick, and C. J. Schweitzer. 2017. Silviculture to restore oak savannas and woodlands. *Journal of Forestry* 115:202–211.
- Drew, M. B., L. K. Kirkman, and A. K. Gholson Jr. 1998. The vascular flora of Ichauway, Baker County, Georgia: a remnant longleaf pine/wiregrass ecosystem. *Castanea* 63:1–24.
- Drewa, P. B., W. J. Platt, and E. B. Moser. 2002. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. *Ecology* 83:755–767.
- Earley, L. S. 2004. *Looking for longleaf: the fall and rise of an American forest*. University of North Carolina Press, Chapel Hill, North Carolina, USA.
- Egler, F. E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio* 4:412–417.
- Elsner, J. B., T. H. Jagger, and K. Liu. 2008. Comparison of hurricane return levels using historical and geological records. *Journal of Applied Meteorology and Climatology* 47:368–374.
- Facelli, J. M., and S. T. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* 57:1–32.
- Faison, E. K., and D. R. Foster. 2014. Did American chestnut really dominate the eastern forest? *Arnoldia* 72:18–32.
- Fonda, R. W. 2001. Burning characteristics of needles from eight pine species. *Forest Science* 47:390–396.
- Forman, R. T. T., editor. 1979. *Pine barrens: ecosystem and landscape*. Academic Press, New York, New York, USA.
- Franklin, J. F., et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155:399–423.
- Fraver, S., and B. J. Palik. 2012. Stand and cohort structures of old-growth *Pinus resinosa*-dominated forests of northern Minnesota, USA. *Journal of Vegetation Science* 23:249–259.
- Frelich, L. E., P. B. Reich, and D. W. Peterson. 2015. Fire in upper Midwestern oak forest ecosystems: an oak

- forest restoration and management handbook. USDA Forest Service General Technical Report PNW-914. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pages 17–43 in S. M. Hermann, editor. The longleaf pine ecosystem: ecology, restoration, and management, Proceedings of the Tall Timbers Fire Ecology Conference, Number 18. Tall Timbers Research Station, Tallahassee, Florida, USA.
- Frost, C. C. 1998. Presettlement fire frequency regimes of the United States: a first approximation. Pages 70–81 in T. L. Pruden and L. A. Brennan, editors. 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.
- Frost, C. C. 2006. Chapter 2: history and future of the longleaf pine ecosystem. Pages 9–42 in S. Jose, E. J. Jokela, and D. L. Miller, editors. The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, New York, USA.
- Garren, K. H. 1943. Effects of fire on vegetation of the southeastern United States. *Botanical Review* 9:617–654.
- Gignoux, J., J. Clobert, and J.-C. Menaut. 1997. Alternative fire resistance strategies in savanna trees. *Oecologia* 110:576–583.
- Gilliam, F. S., and W. J. Platt. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (Longleaf pine) forest. *Plant Ecology* 140:15–26.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:7–26.
- Glenn-Lewin, D. C., R. K. Peet, and T. T. Veblen. 1992. Plant succession: theory and prediction. Chapman & Hall, New York, New York, USA.
- Glitzenstein, J. S., W. J. Platt, and D. R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. *Ecological Monographs* 65:441–476.
- Glitzenstein, J. S., D. R. Streng, R. E. Masters, K. M. Robertson, and S. M. Hermann. 2012. Fire-frequency effects on vegetation in north Florida pine-lands: another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. *Forest Ecology and Management* 264:197–209.
- Glitzenstein, J. S., D. R. Streng, and D. D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and northeast Florida, USA. *Natural Areas Journal* 23:22–37.
- Goebel, P. C., and D. M. Hix. 1996. Development of mixed-oak forests in southeastern Ohio: a comparison of second-growth and old-growth forests. *Forest Ecology and Management* 84:1–21.
- Goring, S. J., et al. 2016. Novel and lost forests in the upper midwestern United States, from new estimates of settlement-era composition, stem density, and biomass. *PLoS ONE* 11:e0151935.
- Greenberg, C. H., B. S. Collins, W. H. McNab, D. K. Miller, and G. R. Wein. 2016. Introduction to natural disturbances and historic range of variation: type, frequency, severity, and post-disturbance structure in Central Hardwood forests. Pages 1–32 in C. H. Greenberg and B. S. Collins, editors. Natural disturbances and historic range of variation: type, frequency, severity, and post-disturbance structure in Central Hardwood forests USA. Springer, New York, New York, USA.
- Grimm, E. C., and G. L. Jacobson. 1992. Fossil-pollen evidence for abrupt climate changes during the past 18 000 years in eastern North America. *Climate Dynamics* 6:179–184.
- Guyette, R. P., R. M. Muzika, and D. C. Dey. 2002. Dynamics of an anthropogenic fire regime. *Ecosystems* 5:472–486.
- Guyette, R. P., M. C. Stambaugh, D. C. Dey, and R.-M. Muzika. 2012. Predicting fire frequency with chemistry and climate. *Ecosystems* 15:322–335.
- Hanberry, B. B., and M. D. Abrams. 2018. Recognizing loss of open forest ecosystems by tree densification and land use intensification in the Midwestern USA. *Regional Environmental Change* 18:1731–1740.
- Hanberry, B. B., K. Coursey, and J. S. Kush. 2018a. Structure and composition of historical longleaf pine ecosystems in Mississippi, USA. *Human Ecology* 46:241–248.
- Hanberry, B. B., R. F. Brzuszek, H. T. Foster II, and T. J. Schauwecker. 2018b. Recalling open old growth forests in the Southeastern Mixed Forest province of the United States. *Écoscience*. <https://doi.org/10.1080/11956860.2018.1499282>
- Hanberry, B. B., D. C. Dey, and H. S. He. 2012. Regime shifts and weakened environmental gradients in open oak and pine ecosystems. *PLoS ONE* 7:e41337.
- Hanberry, B. B., H. S. He, and S. R. Shifley. 2016. Loss of aboveground forest biomass and landscape biomass variability in Missouri, US. *Ecological Complexity* 25:11–17.
- Hanberry, B. B., D. T. Jones-Farrand, and J. M. Kabrick. 2014a. Historical open forest ecosystems in the Missouri Ozarks: reconstruction and restoration targets. *Ecological Restoration* 32:407–416.

- Hanberry, B. B., J. M. Kabrick, and H. S. He. 2014*b*. Densification and state transition across the Missouri Ozarks landscape. *Ecosystems* 17:66–81.
- Hanberry, B. B., and G. J. Nowacki. 2016. Oaks were the historical foundation genus of the east-central United States. *Quaternary Science Reviews* 145:94–103.
- Hanberry, B. B., B. J. Palik, and H. S. He. 2013. Winning and losing tree species of reassembly in Minnesota's mixed and broadleaf forests. *PLoS ONE* 8: e61709.
- Hanson, J. J., and C. G. Lorimer. 2007. Forest structure and light regimes following moderate wind storms: implications for multi-cohort management. *Ecological Applications* 17:1325–1340.
- Harper, F., editor. 1998. *The travels of William Bartram*. University of Georgia Press, Athens, Georgia, USA.
- Hart, J. L., S. L. Clark, S. J. Torreano, and M. L. Buchanan. 2012. Composition, structure, and dendroecology of an old-growth *Quercus* forest on the tablelands of the Cumberland Plateau, USA. *Forest Ecology and Management* 266:11–24.
- Heinselman, M. L. 1981. Fire and succession in the conifer forests of northern North America. Pages 374–405 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest succession: concepts and application*. Springer-Verlag, New York, New York, USA.
- Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. *Ecology* 20:287–304.
- Hiers, J. K., J. J. O'Brien, R. E. Will, and R. J. Mitchell. 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. *Ecological Applications* 17:806–814.
- Hilgard, E. W. 1860. *Report on the geology and agriculture of the state of Mississippi*. E. Barksdale, State Printer, Jackson, Mississippi, USA.
- Holzmüller, E. J., S. Jose, and M. A. Jenkins. 2009. The response of understory species composition, diversity, and seedling regeneration to repeated burning in southern Appalachian oak-hickory forests. *Natural Areas Journal* 29:255–262.
- Hutchinson, T. F., R. E. Boerner, S. Sutherland, E. K. Sutherland, M. Ortt, and L. R. Iverson. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. *Canadian Journal of Forest Research* 35:877–890.
- Iverson, L. R., and T. F. Hutchinson. 2002. Soil temperature and moisture fluctuations during and after prescribed fire in mixed-oak forests, USA. *Natural Areas Journal* 22:296–304.
- Johnson, A. S., and P. E. Hale. 2002. The historical foundations of prescribed burning for wildlife: a southeastern perspective. Pages 11–23 in W. M. Ford, K. R. Russell, and C. E. Moorman, editors. *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, Pennsylvania, USA.
- Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* 16:1281–1295.
- Jones, C. N., D. L. McLaughlin, K. Henson, C. A. Haas, and D. A. Kaplan. 2018. From salamanders to greenhouse gases: Does upland management affect wetland functions? *Frontiers in Ecology and the Environment* 16:14–19.
- Jurney, D. H. 2012. Anthropology of fire in the Ozark Highland Region. Pages 12–33 in D. C. Dey, M. C. Stambaugh, S. L. Clark, and C. J. Schweitzer, editors. *Proceedings of the 4th Fire in Eastern Oaks Conference*. General Technical Report NRS-P-102, USDA Forest Service, Newtown Square, Pennsylvania, USA.
- Kane, J. M., J. M. Varner, and J. K. Hiers. 2008. The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeters. *Forest Ecology and Management* 256:2039–2045.
- King, C. B., and R. M. Muzika. 2014. Historic fire and canopy disturbance dynamics in an oak-pine (*Quercus-Pinus*) forest of the Missouri Ozarks (1624–2010). *Castanea* 79:78–87.
- Kinkead, C. O., J. M. Kabrick, M. C. Stambaugh, K. W. Grabner. 2013. Changes to oak woodland stand structure and ground flora composition caused by thinning and burning. Pages 373–383 in G. W. Miller, et al., editors. *Proceedings, 18th Central Hardwood Forest Conference*. USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.
- Kirkman, L. K., R. J. Mitchell, R. C. Helton, and M. B. Drew. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany* 88:2119–2128.
- Knapp, B. O., K. Stephan, and J. A. Hubbart. 2015. Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, USA. *Forest Ecology and Management* 344:95–109.
- Lafon, C. W., A. T. Naito, H. D. Grissino-Mayer, S. P. Horn, and T. A. Waldrop. 2017. *Fire history of the Appalachian region: a review and synthesis*. Gen. Tech. Rep. SRS-219. USDA Forest Service, Southern Research Station, Monticello, Arkansas, USA.
- Leach, M. K., and T. J. Givnish. 1999. Gradients in the composition, structure, and diversity of remnant

- oak savannas in southern Wisconsin. *Ecological Monographs* 69:353–374.
- Lettow, M. C., L. A. Brudvig, C. A. Bahlai, and D. A. Landis. 2014. Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. *Forest Ecology and Management* 329:89–98.
- Lindsey, A. A. 1961. Vegetation of the drainage-aeration classes of northern Indiana soils in 1830. *Ecology* 42:432–436.
- Lorimer, C. G., and A. S. White. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. *Forest Ecology and Management* 185:41–64.
- Loudermilk, E. L., J. K. Hiers, S. Pokswinski, J. J. O'Brien, A. Barnett, and R. J. Mitchell. 2016. The path back: Oaks (*Quercus* spp.) facilitate longleaf pine (*Pinus palustris*) seedling establishment in xeric sites. *Ecosphere* 7:e01361.
- Loudermilk, E. L., J. J. O'Brien, R. J. Mitchell, W. P. Cropper Jr., J. K. Hiers, S. Grunwald, J. Grego, and J. C. Fernandez-Diaz. 2012. Linking complex forest fuel structure and fire behaviour at fine scales. *International Journal of Wildland Fire* 21:882–893.
- Masters, R. E., C. W. Wilson, G. A. Bukenhofer, and M. E. Payton. 1996. Effects of pine-grassland restoration for red-cockaded woodpeckers on white-tailed deer forage production. *Wildlife Society Bulletin* 24:77–84.
- Mattoon, W. R. 1915. Life history of shortleaf pine. *USDA Bulletin* 244.
- Mattoon, W. R. 1922. Longleaf pine. *USDA Bulletin* 1061.
- McCarthy, B. C., C. J. Small, and D. L. Rubino. 2001. Composition, structure and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. *Forest Ecology and Management* 140:193–213.
- McEwan, R. W., N. Pederson, A. Cooper, J. Taylor, R. Watts, and A. Hruska. 2014. Fire and gap dynamics over 300 years in an old-growth temperate forest. *Applied Vegetation Science* 17:312–322.
- Mitchell, R. J., J. K. Hiers, J. O'Brien, S. B. Jack, and R. T. Engstrom. 2006. Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. *Canadian Journal of Forest Research* 36:2724–2736.
- Mitchell, R. J., J. K. Hiers, J. O'Brien, and G. Starr. 2009. Ecological forestry in the southeast: understanding the ecology of fuels. *Journal of Forestry* 107:391–397.
- Nelson, P. W. 2010. The terrestrial natural communities of Missouri. Missouri Department of Conservation. Missouri Natural Areas Committee, Jefferson City, Missouri, USA.
- Neufeld, H. S., and D. R. Young. 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests. Pages 38–90 in F. Gilliam, editor. *The herbaceous layer in forests of eastern North America*. Oxford University Press, Oxford, UK.
- Noble, I. R., and R. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43:5–21.
- Noss, R. F., E. T. LaRoe, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. U.S. Department of the Interior, National Biological Service, Washington, D.C., USA.
- O'Brien, J. J., J. K. Hiers, M. A. Callahan Jr., R. J. Mitchell, and S. B. Jack. 2008. Interactions among overstory structure, seedling life-history traits, and fire in frequently burned neotropical pine forests. *AMBIO: A Journal of the Human Environment* 37:542–547.
- O'Brien, J. J., E. L. Loudermilk, J. K. Hiers, S. M. Pokswinski, B. Hornsby, A. T. Hudak, D. Strother, E. Rowell, and B. C. Bright. 2016. Canopy-derived fuels drive patterns of in-fire energy release and understory plant mortality in a longleaf pine (*Pinus palustris*) sandhill in northwest Florida, USA. *Canadian Journal of Remote Sensing* 42:489–500.
- Oliver, C. D., and B. C. Larson. 1996. *Forest stand dynamics*. Updated edition. John Wiley and Sons, New York, New York, USA.
- Overpeck, J. T., R. S. Webb, and T. Webb. 1992. Mapping eastern North American vegetation change of the past 18 Ka – No-analogs and the future. *Geology* 20:1071–1074.
- Pan, Y., J. M. Chen, R. Birdsey, K. McCullough, L. He, and F. Deng. 2011. Age structure and disturbance legacy of North American forests. *Biogeosciences* 8:715–732.
- Pecot, S. D., R. J. Mitchell, B. J. Palik, E. B. Moser, and J. K. Hiers. 2007. Competitive responses of seedlings and understory plants in longleaf pine woodlands: Separating canopy influences above and below ground. *Canadian Journal of Forest Research* 37:634–648.
- Pederson, N., J. M. Dyer, R. W. McEwan, A. E. Hessl, C. J. Mock, D. A. Orwig, H. E. Rieder, and B. I. Cook. 2014. The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs* 84:599–620.
- Pederson, N., J. M. Varner, and B. J. Palik. 2008. Canopy disturbance and tree recruitment over two centuries in a managed longleaf pine landscape. *Forest Ecology and Management* 254:85–95.

- Peet, R. K., and D. J. Allard. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification. Pages 45–81 in S. M. Hermann, editor. Proceedings of the Tall Timbers Fire Ecology Conference, No 18. Tall Timbers Research Station, Tallahassee, Florida, USA.
- Perry, D. A., R. Oren, and S. C. Hart. 2008. Forest ecosystems. JHU Press, Baltimore, Maryland, USA.
- Pessin, L. J. 1933. Forest associations in the uplands of the lower Gulf Coastal Plain (longleaf pine belt). *Ecology* 14:1–14.
- Peterson, D. W., and P. B. Reich. 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. *Plant Ecology* 194:5–16.
- Peterson, D. W., P. B. Reich, and K. J. Wrage. 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *Journal of Vegetation Science* 18:3–12.
- Pickett, S. 1976. Succession: an evolutionary interpretation. *American Naturalist* 110:107–119.
- Platt, W. J., G. W. Evans, and S. L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *American Naturalist* 131:491–525.
- Prentice, I. C., P. J. Bartlein, and T. Webb. 1991. Vegetation and climate change in eastern North America since the last glacial maximum. *Ecology* 72:2038–2056.
- Quarterman, E., and C. Keever. 1962. Southern mixed hardwood forest: climax in the southeastern Coastal Plain, U.S.A. *Ecological Monographs* 32:167–185.
- Reidy, J. L., F. R. Thompson, and S. W. Kendrick. 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *Forest Ecology and Management* 313:34–46.
- Rentch, J. S., M. A. Fajvan, and R. R. Hicks. 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. *Forest Ecology and Management* 184:285–297.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181:165–176.
- Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* 91:93–105.
- Russell, M. B., C. W. Woodall, K. M. Potter, B. F. Walters, G. M. Domke, and C. M. Oswalt. 2017. Interactions between white-tailed deer density and the composition of forest understories in the northern United States. *Forest Ecology and Management* 384:26–33.
- Sargent, C. S. 1884. Report on the Forests of North America (Exclusive of Mexico). U.S. Department of the Interior Census Office, Government Printing Office, Washington, D.C., USA.
- Schnur, G. L. 1937. Yield, stand, and volume tables for even-aged upland oak. USDA Technical Bulletin 560.
- Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517–544.
- Schulte, L. A., and D. J. Mladenoff. 2005. Severe wind and fire regimes in northern forests: historical variability at the regional scale. *Ecology* 86:431–445.
- Seymour, R. S., A. S. White, and P. G. deMaynadier. 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management* 155:357–367.
- Sharma, A., K. K. Bohn, S. Jose, and D. L. Miller. 2018. Seed bank-vegetation dynamics along a restoration management gradient in pine flatwoods ecosystems of the Florida Gulf Coast. *Natural Areas Journal* 38:26–43.
- Sparks, J. C., R. E. Masters, D. M. Engle, M. W. Palmer, and G. A. Bukenhofer. 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. *Journal of Vegetation Science* 9:133–142.
- Stambaugh, M. C., J. M. Marschall, E. R. Abadir, B. C. Jones, P. H. Brose, D. C. Dey, and R. P. Guyette. 2018. Wave of fire: an anthropogenic signal in historical fire regimes across central Pennsylvania, USA. *Ecosphere* 9:e02222.
- Staver, A. C., and S. A. Levin. 2012. Integrating theoretical climate and fire effects on savanna and forest systems. *American Naturalist* 180:211–224.
- Stoddard, H. L. 1931. The bobwhite quail: its habits, preservation and increase. C. Scribner's Sons, New York, New York, USA.
- Taft, J. B. 2003. Fire effects on community structure, composition, and diversity in a dry sandstone barrens. *Journal of the Torrey Botanical Society* 130:170–192.
- Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16:284–307.
- Varner, J. M., and J. S. Kush. 2004. Remnant old-growth longleaf pine (*Pinus palustris* Mill.) savannas and forests of the southeastern USA: status and threats. *Natural Areas Journal* 24:141–149.
- Varner, J. M. III, J. S. Kush, and R. S. Meldahl. 2003. Structural characteristics of frequently-burned

- old-growth longleaf pine stands in the mountains of Alabama. *Castanea* 68:211–221.
- Veldman, J. W., L. A. Brudvig, E. I. Damschen, J. L. Orrock, W. B. Mattingly, and J. L. Walker. 2014. Fire frequency, agricultural history and the multivariate control of pine savanna understorey plant diversity. *Journal of Vegetation Science* 25:1438–1449.
- Veldman, J. W., et al. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment* 13:154–162.
- Vivier, L. 1900. Letter from Father Vivier of the Society of Jesus, to a father of the same society [Original manuscript 1750]. Pages 200–229 in R. G. Thwaites, editor. *The Jesuit relations and allied documents*. Volume 69. Burrows Brothers, Cleveland, Ohio, USA.
- Wahlenberg, W. G. 1934. Effect of fire and grazing on soil properties and the natural reproduction of longleaf pine. *Journal of Forestry* 33:331–337.
- Waldrop, T. A., D. L. White, and S. M. Jones. 1992. Fire regimes for pine-grassland communities in the southeastern United States. *Forest Ecology and Management* 47:195–210.
- Walker, J., and R. K. Peet. 1984. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55:163–179.
- Whitney, G. G. 1986. Relation of Michigan's presettlement pine forests to substrate and disturbance history. *Ecology* 67:1548–1559.
- Whittaker, R. H. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecological Monographs* 23:41–78.
- Wiggers, M. S., L. K. Kirkman, R. S. Boyd, and J. K. Hiers. 2013. Fine-scale variation in surface fire environment and legume germination in the longleaf pine ecosystem. *Forest Ecology and Management* 310:54–63.
- Williams, G. W. 2005. References on the American Indian use of fire in ecosystems. USDA Forest Service. https://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/nrcs144p2_051334.pdf
- Williams, J. W., B. N. Shuman, T. Webb, P. J. Bartlein, and P. L. Leduc. 2004. Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes. *Ecological Monographs* 74:309–334.
- Wood, E. M., A. M. Pidgeon, C. Gratton, and T. T. Wilder. 2011. Effects of oak barrens habitat management for Karner blue butterfly (*Lycaeides samuelis*) on the avian community. *Biological Conservation* 144:3117–3126.