Chapter 3

Fire-Maintained Pine Savannas and Woodlands of the Southeastern United States Coastal Plain

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Descriptions by early naturalists provide glimpses of presettlement southeastern coastal plain landscapes. Means (1996) quoted Bartram (1791): "This plain is mostly . . . the great long-leaved pine (*P. palustris* Linn.), the earth covered with grass, interspersed with an infinite variety of herbaceous plants, and embellished with extensive savannas, always green, sparkling with ponds of water. . . . We left the magnificent savanna . . . , passing through a level, open, airy pine forest, the stately trees scatteringly planted by nature, arising straight and erect from the green carpet, embellished with various grasses and flowering plants, and gradually ascending the sand hills . . . "

Bartram's experience cannot be repeated today. Noss et al. (2015) estimated that more than 96 percent of pine savannas and woodlands (hereafter savannas), central to the North American Coastal Plain (NACP) biodiversity hot spot, have been converted to other uses by human actions or severely degraded by fire suppression. Most remaining savannas have been degraded further by logging, open-range grazing, and fire suppression. Such degraded systems have produced a history of misguided ecological ideas that often conflict with recent concepts emerging from the small number of remaining savannas that do have old-growth attributes and have been burned regularly using prescribed fires that mimic natural lightning-fire regimes (Platt 1999). Here, we present a concept of old growth for pine savannas based on three interrelated components: tree populations and ground-layer vegetation, together with feedbacks produced by both layers in the context of long-ongoing evolutionary relationships with fire.

Pine savannas with old-growth attributes exist. They do not, however, resemble old-growth forests (see chapter 1). Intact old-growth savannas

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have a characteristic two-layer physiognomy: large, often scattered overstory trees (mostly pines) above a continuous ground-layer vegetation in which grasses are aspect dominants (see figures 3-1, 3-2, 3-3). The pine populations (fire-tolerators, sensu Pausas 2017) are multiaged, ranging from recently recruited grass-stage individuals to overstory trees several centuries old. Such populations persist in an intact state only on a few high-quality sites (Varner and Kush 2004). These trees produce needles that are flame-retardant when green but incendiary when shed and dried, and, thus, they increase fire intensity and generate pyrodiversity throughout their lifespans (Platt et al. 2016). Such influence of pines on the ecosystem continues after death as large upright snags not only are repeatedly struck by lightning but also provide animal homesites. Once on the ground, logs, which can be common in nonlogged sites managed with frequent fires, provide microhabitats for animals and serve as local firebreaks, generating pyrodiversity for years before they are eventually consumed by fire (Hermann 1993). Pine savannas also contain greater ground-layer biodiversity and endemism than is typical of eastern forests, in large part resulting from a long evolutionary history of association with frequent fire in the context of relatively stable climate (Hoctor et al. 2006; Noss et al. 2015). Similar

FIGURE 3-1. Old-growth xeric sand ridge pine savanna with longleaf pine (*Pinus palustris*) in overstory and wiregrass (*Aristida stricta*) as aspect dominant in the ground layer. Croatan National Forest, North Carolina. Photo credit: R. K. Peet.

FIGURE 3-2. Old-growth flatwoods pine savanna with longleaf pines (*Pinus palustris*) and South Florida slash pines (*Pinus densa*) in the overstory. Cutthroat grass (*Panicum abcissum*) and saw palmetto (*Serenoa repens*) are aspect dominants in the ground layer. Tomlin Gully, Avon Park Air Force Base, Florida. Photo credit: W. J. Platt.

FIGURE 3-3. Old-growth upland clayhill pine savanna-woodland with longleaf pines (*Pinus palustris*) in the overstory. Wiregrass (*Aristida beyrichiana*), Indian grass (*Sorghastrum spp.*), and little blue stem (*Schizachyrium scoparium*) are aspect dominants in the ground layer. Wade Tract, Georgia. Photo credit: W. J. Platt.

high-diversity ground-layer vegetation occurs worldwide in savannas and grassland ecosystems (Parr et al. 2014; Veldman et al. 2015). The physiognomy of pine savannas also is crucial for integrity of numerous endemic animal populations known to depend on old trees and/or fire-maintained groundcover (e.g., gopher tortoises, Red-Cockaded Woodpeckers, reticulated flatwoods salamanders; Hermann 1993).

We propose that "near-natural" fire regimes are integral old-growth attributes. Frequent surface fires during late spring and early summer, when lightning fires occur most frequently (the "lightning-fire season"), maintain pine savannas with old-growth attributes (Platt 1999). Savanna vegetation is quickly altered following anthropogenic changes in fire regimes; lengthening fire-return intervals or shifting seasonal timing of fires result in changes in structure and loss of biodiversity (e.g., Palmquist et al. 2014, 2015; Platt et al. 2015). Further, with fire exclusion, regionally abundant rainfall results in closed-canopy forests (Wahlenberg 1946; Platt 1999; Beckage et al. 2009). Over the past halfcentury, studies of sites with old-growth attributes have shown that recurrent fires during the lightning-fire season maintain savanna pines, the diverse ground-layer vegetation, and the characteristic physiognomy (Fill et al. 2015; Noss et al. 2015).

Tree populations and ground-layer vegetation are not readily reconstituted once disrupted. Flammable vegetation (sensu Mutch 1970) and vegetation feedbacks on fuels that influence characteristics of fires in the context of distinct seasonal environments have molded these fire-influenced landscapes over millions of years (Noss et al. 2015). Reintroducing fire per se is not sufficient in that fire characteristics are altered in reconstructed habitats (Robertson and Ostertag 2007). The most useful approaches to reconstruction should be ones that enhance all old-growth attributes as part of a planned program aimed at reconstituting vegetation-fire feedbacks (Fill et al. 2015).

Southeastern Pine Savannas and Woodlands in a Global Context

Pine savannas share physiognomy and frequent occurrence of fire with other savanna ecosystems (Archibald et al. 2013). Moreover, southeastern savannas share nutrient impoverishment and climatic buffering with other tropical and subtropical ecosystems designated as "Old, Climatically Buffered, Infertile Landscapes" (OCBILs; Hopper 2009, 2016). Mucina and Wardell-Johnson (2011) redefined climatic buffering as climatic stability, identified soil impoverishment as a function of landscape age, and specified predictable fire regimes (and hence, adaptation to fire) as an important aspect of OCBILs. Similar concepts regarding adaptation to frequent fire regimes have emerged in different habitats worldwide (Keeley et al. 2011; Ratnam et al. 2011), increasing recognition of ecological differences between fiery ecosystems and closed-canopy forests (Parr et al. 2014). Pine savannas exemplify how environmentally induced aspects of OCBILs can influence emergent attributes, including high biodiversity and endemism. Including the NACP, half of the 36 terrestrial biodiversity hot spots occur in OCBILs (Noss et al. 2015; Hopper et al. 2016).

Pine savannas of the southeastern US coastal plain generally occur within a relatively flat landscape on highly leached marine sediments, typically with low levels of phosphorus. The occurrence of these savanna ecosystems south of the zone of glaciation and near the climatic buffering influences of the Atlantic and/or Gulf Coast facilitated species persistence during periods of glaciation when much of the eastern North American flora was subject to significant climatic stress and consequent movement and species loss (Sorrie and Weakley 2006; Noss et al. 2015). The flora of these systems, as with other OCBILs, has ancient origins and has evolved in the context of infertile soil conditions and frequent fires. Such conditions favored dominance by a diverse set of flammable grasses and sedges, often with flat terrain and seasonal environments (sensu Platt et al. 2015), increasing the likelihood of fires spreading across herbaceous landscapes once ignited.

Globally, fiery ecosystems are disappearing. Declines are attributable primarily to decreasing occurrence of fires in fragmented landscapes (Parr et al. 2014; Noss et al. 2015). For example, Andela et al. (2017) reported a global decline of 24 percent in annually burned area over a period of less than two decades. Certainly, fire suppression has resulted in increases in woody plants (Platt et al. 2015) and decreases in diversity of the endemic-rich herb layer of many OCBILs, including pine savannas (Palmquist et al. 2014, 2015). More broadly, Pausas and Ribeiro (2017) proposed that fire regime is a primary factor explaining plant diversity around the globe, even after accounting for productivity. They suggest that fires delay competitive exclusion, increase landscape heterogeneity and generate new niches. Peet et al. (2014) made similar points for pine savannas: Fire reduces aboveground biomass, shifting from the largely asymmetric competition for light (larger plants aboveground have a disproportionate advantage) to more symmetric belowground competition where resource use is proportional to plant belowground investment. Hence conservation of OCBILs, such as pine savannas, needs to involve active management, using scientifically based prescribed fires (Fill et al. 2015).

Environmental and Biogeographic Patterns of Biodiversity

In presettlement times, pine savannas dominated the coastal plain landscape from southern Virginia to southern Florida and west to eastern Texas. While within that region there was considerable biogeographic variation (figure 3-4), longleaf pine (*P. palustris*) was the dominant tree over the vast majority of the landscape (Wahlenberg 1946; Frost 2006; Peet 2006). After review of historical documents, Frost (2006) reported that longleaf pine had dominated 52 percent of the uplands and codominated another 33.2 percent across the original range of the species. In addition, South Florida slash pine (*P. densa*) was the sole pine on sandy uplands and in what are locally called *rocklands* (savannas on limestone outcroppings) in the Florida Everglades and Keys (Schmitz et al. 2002).

We also recognize transition areas (figure 3-4) where longleaf pine shared dominance with other pines and various hardwoods. At the northeastern end of the range, most sites are relatively moist, owing to extremely low topographic relief. There, pond pine (*P. serotina*) typically was codominant. Over the inland portion of the range, including parts of the Piedmont, the southern tip of the Appalachians, and the interior coastal plain of Mississippi and Alabama, longleaf pine often shared dominance with shortleaf pine (*P. echinata*) and various oaks. At the western end of the range of longleaf pine in Louisiana and Texas, shortleaf and loblolly pine (*P. taeda*) co-occurred in upland regions; we recognize a core area of longleaf savannas with bluestem understory, transitional areas to the north with a mix of pines and hardwoods, and transitional areas to coastal prairies in the south. In central Florida, longleaf pine shared dominance with south Florida slash pine (*P. densa*). Further, oaks (*Quercus* spp.), pond cypress (*Taxodium ascendens*), and northern slash and pond pine (*P. elliottii, P. serotina*) were trees associated with savanna habitat inclusions, commonly at either the dry or wet ends of the moisture gradient, which resulted in additional heterogeneity within the broader pine savanna matrix (Peet 2006).

Despite the relatively low diversity of the tree layer of southeastern pine savannas, there is considerable diversity in the composition of the ground layer, both across the region and at the local scale. Variation in the aspect-dominant grasses has been used to distinguish ground-layer divisions of pine savannas (figure 3-4). The commonly recognized core concept has been one of a ground layer with wire grass (*Aristida* spp.) as the most abundant grass. This type occupies much of the central part of the range, except for a gap in South Carolina where wire grass is absent, likely because of Pleistocene range contraction. In fact, the wire grass of the southern

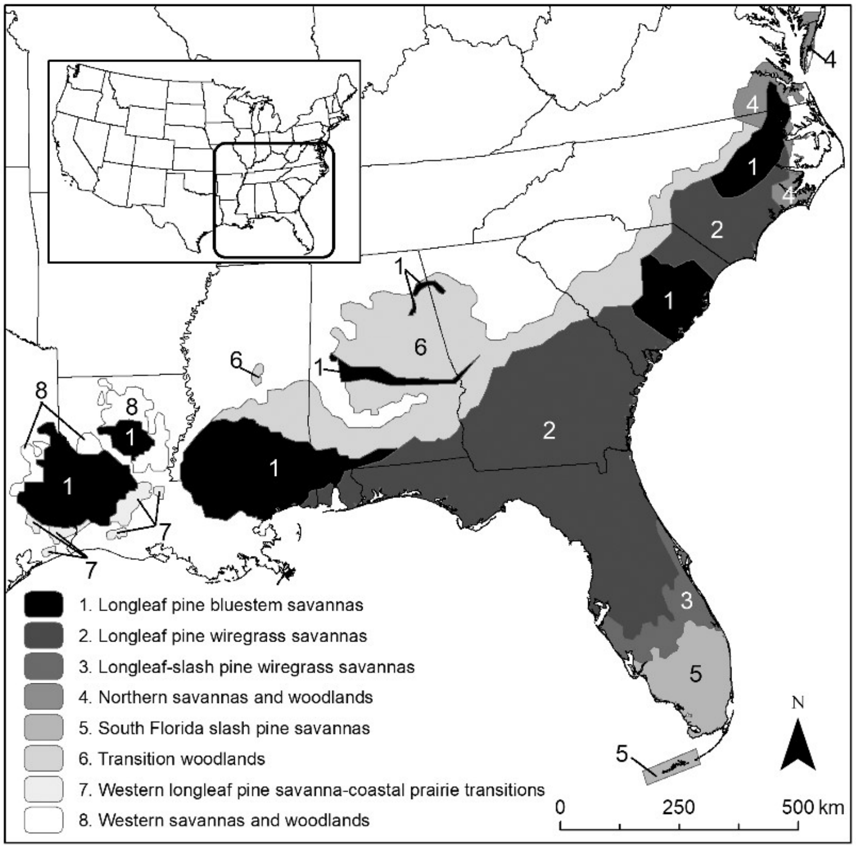

FIGURE 3-4. The ranges of different types of southeastern pine savannas in the southeastern United States. The six divisions are based on abundance of overstory trees and ground-layer grasses as described in the text. Modified from Frost (1993, 2006) and Platt (1999).

portion is morphologically distinct from the more northern wire grass and is sometimes recognized as a separate species (*Aristida beyrichiana* versus *A. stricta*). Where wire grass is not present, bluestems (*Andropogon* spp., *Schizachyrium* spp.) tend to be aspect-dominants, as in the north-central portion of North Carolina, central South Carolina, and southwest Alabama westward to Texas, as well as in the southern Florida rocklands.

Recognition of geographic regions based on grass aspect dominance does not do justice to the diversity and geographic turnover of ground-layer floristic composition in pine savannas. In contrast to near monodominance of the overstory, the ground layer commonly contains a plethora of species, including many endemics. In fact, roughly 85 percent of the many endemic plant species of the NACP occur in fire-maintained savannas or their associated inclusions (Noss et al. 2015). Most of these endemic species are narrowly distributed (Sorrie and Weakley 2006), and, as inhabitants largely of fire-maintained pine savannas, contribute to the considerable turnover in species composition, both among habitats and geographically (Carr et al. 2009; Palmquist et al. 2015).

At small scales, ground-layer diversity can be substantial. Moist, frequently burned pine savannas on silty soils typically have around 90 species per 1,000 square meters, with values often exceeding 120 (Peet et al. 2014). Similarly, well-drained silty soils can support high richness at the 1,000-square-meters scale, typically over 80 species, whereas sandy soils support less diverse longleaf types. At a scale of 1 square meter, species richness can be even more impressive. The current United States record value of 52 species in a square meter was observed in a North Carolina longleaf stand on moist, silty soils that had experienced almost annual fires for at least 75 years. After a change in management practices to somewhat lower fire frequency, smallscale richness dropped dramatically, and richness at the 1,000-square-meters scale dropped modestly (Palmquist et al. 2014). A parallel study over a 20-year period across many longleaf sites in the Carolinas found significant increases and decreases in species richness associated with increased and decreased fire frequency (Palmquist et al. 2015). These studies suggest that both local microhabitat and fire frequency influence species richness (also see Schmitz et al. 2002 for the south Florida rocklands).

The dramatically reduced extent of southeastern pine savannas since European settlement, coupled with the apparent physiognomic simplicity of scattered pines over grass, resulted in a long period during which the vegetation of these systems received less attention than other vegetation types in eastern North America. However, in recent years, our understanding of the compositional variation of these systems has greatly expanded. This has been driven largely by the development of a comprehensive US National Vegetation Classification (USNVC), now widely employed by state and federal agencies and conservation organizations (Franklin et al. 2012). In the USNVC, associations constitute the lowest level of an eight-level hierarchy and are combined hierarchically into alliances, groups, and macrogroups. The Longleaf Pine Macrogroup contains 131 associations (table 3-1). This comes close to the 156 associations in the Appalachian-Northeast Oak-Hickory-Pine Forest and Woodland Macrogroup with many different tree species dominating the various associations across a topographically and edaphically much more complex and equally large geographic region. To provide a logical structure within which to conceptualize these many USNVC associations, Peet (2006) recognized categories that could be arranged within a two-dimensional framework of soil texture and moisture, which were subsequently incorporated as groups within the USNVC. These groups included sand barrens and xeric sandy uplands over entisols (figure 3-1), moist flatwoods over sandy spodosols (figure 3-2), silty uplands over well-drained ultisols (figure 3-3), and savannas (sensu stricto) over moist ultisols. These groups with their current official names and component alliances are shown in table 3-1, along with a group containing montane and piedmont longleaf types and a group containing thin-soil South Florida slash pine rockland savannas.

The high local diversity and large number of USNVC associations results from local co-occurrence of a great variety of small-sized, different life forms and their turnover with both geographic distance and local microhabitats (Peet 2006). Different species occupy different strata within the ground layer, such that ground-hugging rosettes co-occur with upper layer grasses and shrubs, as well as with smaller upright forbs and lianas. Different species flower at different times, so the flowering phenology presents an ever-changing display during the year, from sunbonnets (*Chaptalia tomentosa*) in January–February to the peak flowering of C_4 grasses and composites in the fall, to gentians (*Gentiana catesbaei*) in November–December (Platt et al. 1988). Different functional and phylogenetic groups characterize different portions of the longleaf savannas. Moist, silty savannas host a spectacular diversity of charismatic species such as orchids (*Calopogon* spp., *Cleistesiopsis* spp., *Plantanthera* spp., *Pogonia ophioglossoides*, *Spiranthes* spp.) and insectivorous species (*Dionaea muscipula*, *Drosera* spp., *Pinguicula* spp., *Sarracenia* spp., *Utricularia* spp.), along with a great diversity of sedges (*Rhynchospera* spp., *Scleria* spp.). Drier, silty sites support a great diversity of Fabaceae. Moist, sandy sites are renowned for their diversity of Ericaceae. Asteraceae are abundant across all these types, often with basal rosettes that facilitate winter photosynthesis. Owing to the predominance of infertile soils, annual plants are uncommon, except for a few legumes, such as partridge pea (*Chamaecrista* sp.), and a group of hemiparasites (e.g., *Agalinus* spp., *Buchnera* spp., *Schwalbea americana, Seymeria* spp.). In the end, no description can do justice to the often bewildering array of species and life forms in the pine savanna ground layer or to the high turnover of species along local soil moisture and texture gradients, as well as across the geographic region.

Role of Fire in Pine Savannas

Fire regimes across the coastal plain have been altered directly by humans and indirectly by habitat fragmentation (Wahlenberg 1946; Frost 2006). The most reliable data on presettlement fire frequency and seasonality come from scars produced in annual growth rings of old pines

TABLE 3-1. Southeastern pine savanna associations recognized in the United States National Vegetation Classification.

Alliance	*Assoc.*	*States*	*Provinces*
Dry-Mesic Loamy Longleaf Pine Woodland			
West Gulf Coastal Plain Longleaf Pine / Blackjack Oak / Bluestem Woodland	6	LA, TX	Coastal Plain
West Gulf Coastal Plain Upland Longleaf Pine / Bluestem Woodland	6	LA, TX	Coastal Plain
Southeastern Coastal Plain Longleaf Pine / Sand Post Oak / Wiregrass Woodland	6	NC, SC, GA, FL, AL, MS	Coastal Plain
Southeastern Coastal Plain Longleaf Pine / Blackjack Oak Clayhill Woodland	4	NC, SC, GA, FL, AL, MS	Coastal Plain
Southeastern Coastal Plain Upland Longleaf Pine / Wiregrass Woodland	14	NC, SC, GA, FL, AL, MS, LA	Coastal Plain
Xeric Longleaf Pine Woodland			
Longleaf Pine / Bluejack Oak Sandhill Woodland	7	LA, TX	Coastal Plain
Longleaf Pine / Turkey Oak / Pineland Three-awn Woodland	9	VA, NC, SC	Coastal Plain
Longleaf Pine / Turkey Oak / Little Bluestem Woodland	9	SC, GA, FL	Coastal Plain
Longleaf Pine / Turkey Oak - Sand Live Oak Woodland	9	GA, FL, AL	Coastal Plain
Longleaf Pine / Turkey Oak / Three-awn Woodland	3	GA, FL, AL, MS	Coastal Plain
Wet-Mesic Longleaf Pine Open Woodland			
Atlantic Coastal Plain Wet Longleaf Pine Savanna	14	NC, SC, GA, FL	Coastal Plain
West Gulf Coastal Plain Longleaf Pine Wet Savanna	3	LA, TX	Coastal Plain
East Gulf Coastal Plain Wet Pine Open Woodland	8	GA, FL, AL, MS, LA	Coastal Plain
Mesic Longleaf Pine Flatwoods - Spodosol Woodland			
Southern Coastal Plain Mesic Longleaf Pine Flatwoods	16	SC, GA, FL, AL, MS, LA	Coastal Plain

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and stumps (Rother et al. 2018). In coastal savannas, presettlement return intervals averaged 1 to 3 years with occasionally longer intervals (Wahlenberg 1946; Frost 2006), and fire scars occurred overwhelmingly during transitions from early to latewood within annual rings (Rother et al. 2018). These transitions in type of wood production occur during the lightning-fire season, at the time (May–June) when lightning-ignited fires occur most frequently throughout the coastal plain (Platt et al. 2015). These studies, together with models based on recurrent fire conditions (e.g., Guyette et al. 2012), indicate high frequencies of fires, especially during the fire season. Thus, historical fire regimes were characterized by rather predictable attributes related to frequency and season, a characteristic of OCBIL habitats more broadly.

High frequencies of prescribed fires during fire seasons in sites with old-growth attributes entrain aspects of fuels and, hence, fire characteristics. For example, short-return intervals (1 to 2 years) result in limited fuel biomass. Thus, low intensity fires consume primarily live and dead fine fuels in the ground layer. Hence, variation in fine fuel biomass and flammability of fuels have measurable effects on fire characteristics at ground level where plants have protected regenerative buds (Ellair and Platt 2013). Nonetheless, sensitivity of fire characteristics to local variation in fuel characteristics and variation in synoptic weather conditions, especially during fire seasons (Platt et al. 2015), results in a range of characteristics within and among fires (Platt et al. 2016; Dell et al. 2017).

Table 3-1. *continued*

Alliance	*Assoc.*	*States*	*Provinces*
Mesic Longleaf Pine Flatwoods - Spodosol Woodland			
Atlantic Coastal Plain Mesic Longleaf Pine Flatwoods	5	VA, NC, SC	Coastal Plain
South Florida Slash Pine Rockland			
Florida Slash Pine Rockland Woodland	4	FL	Coastal Plain
Shortleaf Pine - Oak Forest and Woodland			
Montane Longleaf Pine - Shortleaf Pine Woodland	8	NC, SC, GA, AL	Piedmont, Mountains

Vegetation-fire feedbacks modify fire regimes. Plants that contribute substantial rapidly drying biomass or increase flammability of fine fuels increase likelihoods of fires. For example, C_4 grasses grow rapidly after fire-season fires and produce aboveground biomass that dries readily, resulting in a matrix of flammable fuels (Platt 1999; Simpson et al. 2016). Leaves of woody shrubs (e.g., savanna oaks) are retained on plants, then released near the onset of the fire season, adding flammable fuels to the ground layer (Kane et al. 2008). During the fire season, this matrix of fine fuels has low ignition temperatures and combusts rapidly, producing sufficient heat to combust adjacent fuels and spread fires across landscapes under dry weather conditions (Slocum et al. 2003, 2010).

Superimposed on feedbacks produced by ground-layer plants are those produced by pines. Needles of overstory pines like longleaf pine are flame-resistant when green, but incendiary when dry (Platt 1999). Because needles are shed continually, the ground layer becomes laced with pyrogenic fuels that increase maximum temperatures and durations of heating throughout the ground layer. These fire-feedbacks generate pyrodiversity at scales capable of influencing species composition and dynamics of ground-layer vegetation (Platt et al. 2016). Pervasive fire feedbacks, especially those involving pines, have likely generated fire regimes with enhanced likelihoods of frequent (almost annual) fire-season fires.

Dynamics of Pine Savanna Plant Populations and Communities

Studies in savannas with old-growth attributes have shown that pine populations are broadly influenced by two types of disturbance. Tropical cyclones, which recur at intervals averaging about a decade along the Gulf of Mexico coast, drive stands away from demographic equilibria, shortening tree replacement cycles via differential mortality of older, larger trees, and opening space for recruitment (Platt and Rathbun 1993; Platt et al. 2000). Recurrent fires, noncatastrophic for savanna pines with thick bark and protected buds, block recruitment of hardwood trees, maintaining open space eventually colonized by pines (Platt 1999; Beckage et al. 2009). Recruitment does not occur in stands with older trees that are not burned for long periods; as pines die, open spaces become filled with hardwoods (e.g., Glitzenstein et al. 1995; Johnson et al. 2018).

In frequently burned old-growth stands, recruitment of pines involves patch dynamics. Seedlings germinate throughout stands in periodic mast years. Juvenile pines are killed by pine needle-fueled fires and thus mostly survive in open patches large enough to be devoid of shed pine needles and in which root competition from surrounding large trees is reduced (Platt and Rathbun 1993; Platt et al. 2016). In addition, fallen pines (as for example, after hurricanes) provide firebreaks that may create unburned patches in which seedlings survive (Platt and Rathbun 1993). Nonetheless, recruitment does not necessarily occur once open patches reach sufficient size for recruits to survive fires (Platt et al. 1988) because growth and survival are influenced by ground-layer vegetation (Grace and Platt 1995). Consequently, open patches often are maintained for multiple decades (Platt and Rathbun 1993; Platt 1999) before colonization and formation of patches of grass-stage pines. Once present and released from the grass stage, pines slowly grow and thin, resulting in a few trees reaching the overstory in perhaps a century. As trees grow and thinning occurs, recruitment patches merge into a matrix of randomly dispersed large trees (Noel et al. 1998).

Old-growth pine populations persist but cannot be viewed as in demographic equilibria. Projections for population changes over time based on individual-tree demography in sites with old-growth attributes suggest rapidly growing populations (Platt et al. 1988), but projections for population changes based in patch-based demography suggest spatially heterogeneous populations whose dynamics are driven by rates of disturbance, such as hurricane frequency (Platt and Rathbun 1993). Indeed, dynamics of old-growth pine populations most likely varied in spatial and temporal structure, with tree replacement cycles much shorter along coasts with associated frequent lightning storms and tropical cyclones than in inland areas more protected from such disturbance.

Pine savannas with old-growth attributes also contain hardwood trees and shrubs that occur mainly in the ground layer (Platt 1999). Established plants commonly resprout after fire (e.g., Schafer and Just 2014), forming clusters of clonal stems (Platt et al. 2015). For example, oak populations (e.g., *Quercus laevis*, *Q. margarettae*) often contain genetic individuals with aggregated clonal stems. Some species (e.g., *Quercus minima, Q. elliottii, Castanea pumila, Morella pumila, Ilex glabra, Vaccinium stamineum*) do not have arboreal stages as large as congeners in surrounding forests. These species appear to have lost tree stages and gained underground geoxylic structures as evolutionary responses to frequent fire, as hypothesized for some woody species in other savanna habitats (e.g., Simon et al. 2009; O'Donnell et al. 2015).

Populations of hardwoods have enigmatic status in frequently burned old-growth pine savannas. Although the presence of species without tree stages suggests long evolutionary relationships with fire, increases in abundance have been designated as shrub encroachment attributed to human disturbance (see review in Platt et al. 2015). Past logging and fire suppression are proposed to have released populations of native hardwood trees once fire intensity was reduced (e.g., Glitzenstein et al. 1995; Gilliam and Platt 1999). As a result, reduction of hardwoods has been a perennial focus of both silvicultural and restoration efforts (e.g., Platt et al. 2015), though a limited amount of research has pointed to concerns about conservation practices that aim to reduce hardwoods (Hiers et al. 2014). Hypotheses regarding shrub-tree population structure and dynamics have emerged from studies of sites with old-growth attributes (e.g., Grady and Hoffman 2012). These hypotheses have been based on the idea that hardwood trees are unlikely to survive repeated fires fueled by pyrogenic pine needles, but may persist in open areas away from pines (Platt et al. 2016). Thus, spatial heterogeneity of hardwood tree populations may have depended on the spatial distribution of pyrogenic pines (Ellair and Platt 2013). This concept may provide an approach useful in conservation of hardwood tree populations in sites with old-growth attributes.

Dynamics of populations and relations to fire are less well-known for ground-layer species than trees. Meristematic tissues of most grasses and forbs (and seeds in some monocarpic species) are protected by location at or below ground level. Ground-layer plants, especially C_4 grasses, tend to respond postfire with rapid aboveground growth and reproduction, as well as often by clonal growth (e.g., Platt et al. 1988; Fill et al. 2012; Peet et al. 2014). These studies indicate that ground-layer plant populations in sites with old-growth attributes, as in many savannas (Lamont et al. 2011; Clarke et al. 2013), tend to be persistent over time despite recurrent fires. The resulting direct regeneration involves only minor changes in species composition of pine savannas following fires. In contrast, even a modest reduction in fire frequency can result in a layer of dead grasses shading the ground, significantly reducing the smallscale diversity of herbaceous plants. Smallscale disturbances, such as hot spots resulting from the burning of downed trees or localized animal disruptions (e.g., gopher tortoises), also may be important in regeneration by both longleaf pine and ground-layer plants (Hermann 1993; Grace and Platt 1995).

Remaining Old-Growth Pine Savannas and Woodlands

We identified old-growth southeastern pine savanna sites based on the three components of old growth: tree populations, intact ground-layer vegetation, and a prescribed fire regime with attributes producing ecological conditions postulated to have occurred historically. A fourth important attribute of an old-growth landscape is sufficient extent and habitat heterogeneity for viable populations of plants and animals to have persisted in a fiery landscape. Employing all four of these criteria, remaining old-growth pine savanna occurs only as clusters of sites in the Red Hills region of southern Georgia (Wade Tract and surrounding and nearby conservation easements that maintain high-quality pine savanna landscapes) and on Eglin Air Force Base (Patterson Natural Area and nearby high-quality tracts).

To better capture the range of diversity in persisting old-growth southeastern pine savannas, we compiled a list of tracts with more than one old-growth attribute. We started with a list compiled by Varner and Kush (2004), wherein they identified 15 old-growth sites covering 5,094 hectares. Natural ground-layer vegetation was maintained on only 9 sites; the rest were undergoing ground-layer restoration. In our list (table 3-2), we indicate dominant vegetation types, and for tracts containing old-growth tree populations, the current estimate of acreage. Sites with old tree populations and a long-term history of frequent fire are important for understanding natural fire dynamics of these ecosystems. We identified seven sites that have both old-growth tree populations and a long history of frequent fires. Five occur in Florida and one each in North Carolina and Georgia. In a second list, we identify sites with old-growth trees but with degraded or uncertain ground-layer conditions (also see Johnson et al. 2018). It is possible that a few of these belong in our first list or will shift to that list with recurrent prescribed fires. These sites are spread across Alabama, Florida, Georgia, and North Carolina, and none is particularly large. Finally, we compiled a list of sites with relatively intact ground-layer vegetation, regularly managed with fire and an overall extent of over 10,000 hectares. For this list, we include 14 longleaf and 2 slash pine sites. These all have the potential to regain old-growth tree populations if properly managed, using frequent, fire-season fires. All these large sites are on a military base, national forest, or national wildlife refuge. Additional areas of extensive but more degraded longleaf vegetation are identified in the Range-Wide Conservation Plan for Longleaf Pine compiled by the Regional Working Group for America's Longleaf.

TABLE 3-2. Examples of nearly old-growth pine savanna vegetation of the southeastern Coastal Plain and adjacent areas. Vegetation types are defined at the bottom of the table.

Site	*State*	*Area-ha*	*Veg Type*
Sites with old-growth trees and ground-layer vegetation			
Croatan National Forest, Pringle Road	NC	20	SH
Wade Tract / Red Hills Plantations	GA	3200	CL
Eglin Air Force Base	FL	3650	SH & FW
Goethe State Forest	FL	75	FW or SH
Platt Branch	FL	160	FW
Venus Flatwoods	FL	40	FW
Tomlin Gully (Avon Park Air Force Base)	FL	200	FW
Sites with old-growth trees but uncertain or degraded ground-layer vegetation			
Arnett Branch	NC	46	MT
Boyd Tract	NC	24	CL
Bonnie Doone Tract	NC	65	CL
Camp LeJeune Tract	NC	20	SH
Appling Tract / Moody Preserve	GA	120	CL, SH
Brooksville / Big Pine Tract	FL	170	SH, CL
Tiger Creek	FL	2	SH
Mountain Longleaf National Wildlife Refuge	AL	45	MT
Horn Mountain	AL	20	CL
Longleaf sites with old-growth ground-layer vegetation and area cumulatively >10,000 ha			
Frances Marion National Forest	SC		FW, SH
Camp LeJeune	NC		SH, FW, SV
Fort Bragg	NC		SH
Fort Gordon	GA		SH
Fort Stewart	GA		SH, FW, SV
Fort Benning	GA		SH, CL
Eglin Air Force Base	FL		SH, FW
Avon Park Air Force Base	FL		FW, SV

continued on next page

Maintenance of Southeastern Pine Savanna Ecosystems in the Future

Pervasive human-induced changes in fire regimes have now broadly disrupted the long vegetation-fire coevolution of pine savannas. As a result, nearly all savannas have shifted away from old-growth conditions (Fill et al. 2015). Because of wildfire exclusion, remaining tracts with even some characteristics of old growth have only prescribed fire regimes, and those often differ markedly from lightning-fire regimes,

Table 3-2. *continued*

Site	*State*	*Area-ha*	*Veg Type*
Longleaf sites with old-growth ground-layer vegetation and area cumulatively >10,000 ha			
Apalachicola National Forest / St. Marks National Wildlife Refuge	FL		FW, SH, SV
Ocala National Forest	FL		SH, FW
Osceola National Forest / Okefenokee National Wildlife Refuge	FL		SH, FW
Kisatchie National Forest / Fort Polk	LA		CL
De Soto National Forest	MS		SH, CL
Conecuh National Forest	AL		SH, CL
Slash Pine Sites with >10,000 ha old-growth ground-layer vegetation			
Everglades National Park	FL		SH, FW, SV, RK
Big Cypress National Park	FL		SH, FW, SV

Veg Type Key

CL: Clay/Loam	Dry-Mesic Loamy Longleaf Pine Woodland (NVC G009)
FW: Flatwoods	Mesic Longleaf Pine Flatwoods - Spodosol Woodland (NVC G596)
MT: Montane	Shortleaf Pine - Oak Forest & Woodland (NVC G012)
RK: Rockland	South Florida Slash Pine Rockland (NVC G005)
SH: Sandhill	Xeric Longleaf Pine Woodland (NVC G154)
SV: Savanna	Wet-Mesic Longleaf Pine Open Woodland (NVC G190)

with shifts in seasonality and frequency (cf. Platt et al. 2015). The small size of most old-growth sites makes it difficult to represent the full range of natural heterogeneity (Hoctor et al. 2006; Sorrie and Weakley 2006). This fragmentation, as well as increasing urbanization surrounding old-growth sites, affects the ability of managers to conduct prescribed fires. In the future, further land-use changes may threaten maintenance of old-growth conditions and restoration of degraded sites. Urbanization in the region is expected to increase markedly, leading to increased fragmentation (Terando et al. 2014) and the possibility of cascading effects that result in future prescribed fire becoming increasingly difficult due to a combination of fuel accumulation and fragmentation in a human-dominated matrix.

Climate change also is likely to impact all aspects of old-growth characteristics of pine savannas. Increases in temperature are likely in the region by the end of the century (USGCRP 2017). Changes in precipitation are more uncertain but include the possibility of increases in average precipitation along the Atlantic Coast and decreases in the western part of the coastal plain (USGCRP 2017). Nonetheless, even increased precipitation, when combined with temperature increases, could result in increased potential evapotranspiration and drought. Growth and survival of pines should be less sensitive to drought than for other tree species. Increased cloud-ground lightning strikes and more intense tropical storms could concurrently shift age-size class distributions of pines and facilitate tree replacement cycles (Romps et al. 2014), but seedling establishment could become hampered by moisture stress, especially on xeric sites (Loudermilk et al. 2016). The likelihood of altered water cycles and water availability in the future means that small wetlands within these ecosystems may be particularly vulnerable to climate change. The importance of these wetland habitats for many endemic species, their current rarity as part of frequently burned landscapes, and their vulnerability to climate change make them a major priority for conservation of old growth in the future. Decreased water availability may also pose substantial constraints on fire prescriptions, especially in drier conditions, as on xeric soils and in the west gulf portion of the coastal plain.

Despite the potential for increasing threats and vulnerability, we suggest a high likelihood that savannas with old-growth characteristics will be maintained, and even expanded, across the region. We now have a solid base of data from sites with old-growth attributes upon which to base restoration and management. Several types of conservation partnerships that focus on pine savanna restoration have begun in the southeastern United

States. Regional partnerships between federal agencies and a range of public and private stakeholders have identified restoration of pine ecosystems and prescribed fire regimes, mimicking natural fires as key strategies for conservation in the region. Examples include Landscape Conservation Cooperatives and the Southeast Conservation Adaptation Strategy. Region-wide plans for conservation have identified priority landscapes for restoring pine savannas that span all major geographic regions of southeastern pineland. And indeed, implementation teams have begun restoring pine savannas in every state in the range.

Research on the ecology and management of the remaining old-growth savannas can provide a wealth of knowledge to guide management and conservation efforts based on prescribed fire regimes that restore old-growth attributes produced by vegetation-fire feedbacks. For example, research on the effects of fire on old-growth sites suggests that restoration of savanna characteristics cannot be done simply by reestablishing fire. When fires alone (and especially if not conducted during the fire season) are reestablished in long-unburned sites, they do not restore the savanna species composition, especially in the ground layer. Moreover, they can have other unintended consequences on community characteristics such as increased mortality of overstory trees or proliferation of woody shrubs, thus leading to de novo ecosystems (Varner et al. 2005; Platt et al. 2015b). Full restoration of savannas often should include thinning dense overstory trees (Noel et al. 1998) and reestablishment of ground-layer savanna species, especially those that produce important vegetation-fire feedbacks (Fill et al. 2015; Platt et al. 2016).

Moving pine savanna restoration forward requires careful integration of knowledge of past evolution with uncertainties about the future. Overall, recognition of the long evolutionary history of these ecosystems in association with fire, coupled with knowledge of the extreme heterogeneity of species and community composition and dynamics at multiple scales derived from research in existing old-growth sites, should be useful in developing concepts for restoration despite the uncertainties of future environmental conditions. Acceptance of variability in environmental conditions over space and time, while also guaranteeing that responses to specific environmental conditions molded by past evolution are maintained, should be important if remaining and restored sites are to be resilient to future change (Hiers et al. 2014; Fill et al. 2015). Maintaining and restoring fires, and especially vegetation-fire feedbacks integral to the evolutionary history of pine savannas, will be especially important for the future of pine savanna ecosystems.

Conclusion

Contemporary old-growth concepts emerged from study of closed-canopy temperate forests. Generally, "old growth" denotes forested areas dominated by populations of trees with limited anthropogenic mortality. Forests containing such older trees are hypothesized to resemble those present historically and to persist if situated in a spatial context that supports natural patterns of regeneration driven by ongoing gap dynamics punctuated by relatively infrequent disturbances. In southeastern pine savannas, old-growth attributes provide a framework of core concepts integral to the ecology and evolution of the species, ecosystems, and landscapes comprising the NACP hot spot of biodiversity. Study of old-growth pine savannas has been instrumental in shifting ecological paradigms in those ecosystems from pine savannas as early successional ecosystems maintained by natural and human disturbances to persistent ecosystems molded over millions of years of coevolution with fire as an endogenous ecological process. These ecosystems with high biodiversity and endemism persist after natural fires, while key species exert feedbacks, continually modifying the natural ecological process of fire, resulting in a high diversity of species indigenous to these unique fiery ecosystems. These emergent concepts provide scientifically based guides for ongoing conservation initiatives to increase and maintain substantial areas of old-growth pine savannas and woodlands, supporting biodiversity and endemic species in a sustainable way.

To achieve these goals, it will be necessary to preserve and manage large areas with careful restoration of fire regimes that mimic the natural fire regimes that occurred under presettlement conditions. The substantial geographic turnover in composition across the coastal plain and the large number of local endemic species means that a large and dispersed network of preserves managed in accordance with locally modified fire regimes will be needed. If these goals are accomplished, then old-growth trees, ground-layer vegetation and the indigenous animals should be able to maintain persistent populations. The major challenges are likely to be the fragmented nature of most of the landscape, the relatively modest number of large tracts with an intact ground layer that has burned frequently, and the increasing difficulty of using fire on wildlands imbedded in human development. But, we emphasize it is possible, given the foundation laid by our increased understanding of the old-growth attributes of pine savannas and woodlands, and that on-going initiatives are leading us in the right direction.

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