Human Ecology
https://doi.org/10.1007/s10745-018-9982-1

Structure and Composition of Historical Longleaf Pine Ecosystems in Mississippi, USA

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Abstract

Longleaf pine (*Pinus palustris*) historically was a widespread ecosystem composed of a simple tree canopy and grasslands ground layer. After widespread loss of this ecosystem due to logging and fire exclusion, little quantitative information exists about historical structure for restoration goals. We identified composition in De Soto National Forest and Pearl River County, Mississippi, USA, and density, basal area, and percent stocking in Pearl River County using General Land Office surveys and US Forest Service Forest Inventory and Analysis surveys. Historical longleaf ecosystems were about 85% pine, with lesser amounts of broadleaf evergreen and oak species. Densities were about 175 to 180 trees/ha, mean tree diameters were 45 cm, and stocking was around 60% to 65%, which suggested longleaf pines were closed woodlands. Current forests are 38% to 57% pine, primarily loblolly, while longleaf pine is 2% to 8% of composition. Indeed, current longleaf pine composition across the Coastal Plain averages 3% and does not reach 10% at smaller landscape scales. Fire-sensitive broadleaf species of water oak, sweetgum, yellow-poplar, and red maple increased from about 0.5% composition to 2% to 10% of composition. Forests became twice as dense, at about 280 trees/ha to 330 trees/ha, with mean tree diameters of 22 cm. These results characterize conversion from open old growth longleaf forests, resulting in part from human maintenance, to successional forests due to human disruption of the historical ecosystem. It is important to remember structure and composition of historical forests for restoration and recognize wholesale changes so that successional forests do not become the new social and cultural baseline.

Keywords Longleaf pine (*Pinus palustris*) · Historical ecology · USA forest service · Mississippi · Open old growth longleaf forests

Introduction

The influence of human land use and management on ecology has transformed the Coastal Plain of the southeastern United States. Longleaf pine historically dominated the Coastal Plain that extended from Texas to Virginia, an areal extent of about 56 million ha (Fig. 1, Cleland *et al.* 2007). According to historical General Land Office surveys conducted during the 1800s, pine represented 80% of total composition in portions of Alabama and Florida (Schwartz 1994; Black *et al.* 2002; Predmore *et al.* 2007) and 70% to 99% in several Georgia counties (Plummer 1975). This is in agreement with Frost (1993), who estimated longleaf pine comprised 85% of uplands in the Coastal Plain. Longleaf pine forests were open, occurring in continuous phases of savannas, open woodlands, and closed woodlands that have a grasslands understory. Wiregrass (*Aristida* spp.) and bluestem grasses (e.g.. *Andropogon* spp.) were common ground layer plants. Extraordinarily high species richness of both grasses and forbs occurred, often ranging from 150 to 300 species or more per hectare (Means 1996), with at least 96 endemic and 187 rare plants still extant in the longleaf pine understory (Walker 1993).

Today, longleaf pine forests are a critically endangered ecosystem in the United States (Noss *et al.* 1995). Longleaf pine ecosystems have declined by 98% (Noss *et al.* 1995), along with associated wildlife species, including about 30 threatened or endangered species and hundreds of sensitive species (Noss *et al.* 1995, Means 2006). The major reasons for loss were exploitative logging practices that left few seed trees for regeneration followed by fire exclusion, which resulted in

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Published online: 01 March 2018

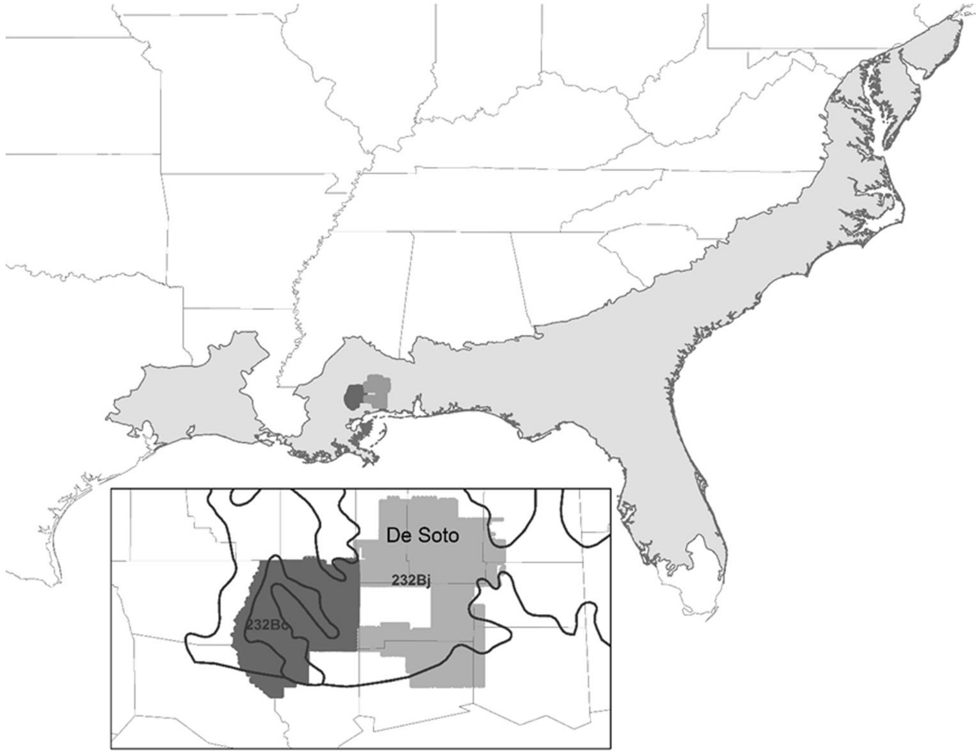

Fig. 1 The Coastal Plain of the eastern United States and the study area (darker gray and magnified in inset panel) in Mississippi. Pearl River County (dark gray to the west of De Soto National Forest) covers most of small ecological subsection of 232Bc

competition from other tree species, preventing longleaf pine establishment (Wahlenberg 1946).

Frequent, low severity fire was the historical disturbance that maintained open longleaf pine forests (Fowler and Konopik 2007). Fire return intervals ranged from almost annually to about 10 years in the Coastal Plain (Stambaugh *et al.* 2011; White and Harley 2016). Frequent fires were of low to moderate intensity because fuels did not accumulate to levels that allow for stand-replacing fires. Instead, surface fires spread across unfragmented landscapes. Lightning-ignited fires were most frequent during the late spring and early summer, while Native Americans burned during the fall, late winter, and early spring. Fire was a tool used by pre-industrial societies to open upland forests across the landscape for growth of herbaceous foods and game animals (Van Lear *et al.* 2005). Fire removed woody stems in the understory and prevented growth in the midstory, producing open forests with a simplified structure that allowed light to support an herbaceous layer on the forest floor. Fire limited overstory recruitment of tree species less fire-tolerant than longleaf pine, which develop a protective needle tuft around the terminal bud as young seedlings (i.e., the grass stage).

Longleaf pine lost the advantage as the established overstory after non-sustainable "cut-out and get-out" logging during 1880–1920. The timber industry was able to harvest the majority of longleaf pine in the southeastern United States rapidly, due to steam power, railroads, and inexpensive land prices after the Civil War (Van Lear *et al.* 2005). Pine regeneration was limited due to lack of seed trees and pine seedling consumption by feral livestock, particularly hogs that saturated the land (Frost 1993; Ware *et al.* 1993). In addition, early Euro-American settlers burned more frequently than Native Americans, sometimes biannually, preventing even longleaf pine regeneration (Stambaugh *et al.* 2011; White and Harley 2016).

Perhaps more importantly for the forest trajectory, effective fire exclusion of the frequent fire regime generally began during the 1920s. Without this filter that favored longleaf pine, many tree species were able to establish. Since fire exclusion, the area of eastern broadleaf forest or mixed broadleaf-pine forest has increased while pine-dominated forests have decreased in southeastern forests (Conner and Hartsell 2002). Dense, multistoried hardwoods resulted in loss of the herbaceous layer and species associated with open pine forests.

Nonetheless, pine plantations have become progressively common since 1952, reversing conversion to eastern broadleaf forest. In the southeastern US, pine plantations covered 0.8 million ha in 1952, 8.5 million ha in 1987, and 12 million ha in 1999 or about 50% of pinelands (Conner and Hartsell 2002; Prestemon and Abt 2002). The pulp and paper industry played a vital role in the South's post-Depression economy. Fiber from highly productive short rotation plantations of loblolly or slash pine is most profitable, although plantations of shortleaf and longleaf pine occur where multiple objectives (e.g., timber, wildlife, hunting) are of interest to the land owners.

Since the late 1990s, there has been a renewed interest in longleaf pine management, conservation, and restoration. One of the major efforts is "America's Longleaf Initiative", a collaborative effort of public and private sector partners. Launched in 2009, this Initiative has a 15 year goal to increase the longleaf acreage from 1.4 to 3.2 million hectares by 2024 (Regional Working Group for America's Longleaf 2009). However, the important question for longleaf pine is restoration and management. Wahlenberg (1946) wrote: "Mismanagement of longleaf pine has been the rule rather than the exception, due to the ignorance of the unique life history and incomplete knowledge of factors determining the life and death of seedlings and hence the succession of forest types."

This study provides some idea of what that original forest probably looked like over portion of the southeastern US. Historical longleaf pine forests of the Coastal Plain often are referred to as savannas, with densities that may resemble oak savanna densities of 50–100 trees/ha (trees ≥12.7 cm; Hanberry *et al*. 2014a, b). Savannas are very continuous with grasslands, such that differentiation is difficult and perhaps unnecessary in most cases. However, rather than savannas, we suspect that longleaf pine ecosystems often were a mosaic of open and closed woodlands based on structure of restored longleaf pine ecosystems and high historical tree densities of other eastern pines due to high density establishment (Hanberry *et al*. 2014a, b). Predmore *et al.* (2007) estimated a historical density of 105 trees/ha (based on 12,600 trees total, unadjusted for surveyor bias), which suggested open woodlands, for two counties in southern Alabama with 85% pine composition. Our objective was to add to the limited information about historical longleaf pine ecosystems. We used General Land Office (GLO) surveys to determine composition in De Soto National Forest and Pearl River County, Mississippi and to quantify structural characteristics in Pearl River County (Fig. 1).

Methods

The General Land Office conducted Public Land Surveys for most of the United States during the nineteenth century. Surveyors established townships based on 36 mile^2 (1.6 × 1.6 km) sections, and at each section corner and midway along section lines, surveyors recorded two to four trees. Consequently, it is possible to reconstruct historical forests based on GLO records, using a density estimator for the point-centered quarter method (Hanberry *et al*. 2011, 2012b).

There were about 10,100 trees from surveys during circa 1810–1840 in Pearl River County (about 2500 trees) and De Soto National Forest (about 7600 trees; K. Coursey, unpublished data, De Soto National Forest; Fig. 1). In addition to using the administrative boundaries as spatial units, we used ecological boundaries of ecological subsection (Cleland *et al*. 2007; Fig. 1; note that GLO surveys were complete for subsection 232Bc but only covered a small area of 232Bj). Due to incomplete species identification, we grouped broadleaf evergreen tree species, primarily red bay (*Persea borbonia*) and sweetbay (*Magnolia virginiana*), and upland oak species, primarily red oaks.

Distances to surveyed trees were available for Pearl River County so that it was possible to calculate density, which we did for trees with diameters ≥12.7 cm. Also, bearing distance and direction were available to adjust for surveyor bias (Hanberry *et al*. 2012b) and diameter was available for calculation of basal area and percent stocking (Arner *et al.* 2001), a measure of space taken by trees. At about the 60% stocking level, forests change from open to closed woodlands (or about 55% stocking with selection of trees ≥12.7 cm; Hanberry *et al.* 2014a, b), if the midstory remains open. Alternatively at these low stocking levels, without fire, forests are considered understocked and the midstory is filled with small diameter trees and other woody growth.

We used USDA Forest Service Forest Inventory and Analysis surveys (FIA; FIA DataMart, www.fia.fs.fed.us/tools-data; Bechtold and Patterson 2005) to quantify current forest composition and structure for the entirety of the two ecological subsections (see Hanberry *et al.* 2014a, b for more detailed methods). We also displayed current longleaf pine composition across the Coastal Plain. The FIA plots typically occur every 2500 ha, and thus, similarly to GLO tree surveys, FIA surveys provide landscape scale estimates. We used expansion of tree counts at each FIA plot to calculate density per hectare and then determined mean density per subsection.

Results

Pine historically was 85% to 87% of total tree composition, depending on spatial unit (Table 1). That is, ecological subsection 232Bc was 85% pine while 232Bj was 87% pine. The surveyors did not attempt to differentiate pine species, unlike with other less abundant genera. The rest of tree composition was composed of bay species, or broadleaf evergreen trees, at about 4.5% to 5.5% and upland oaks at about 2.5% to 3%. Blackgum (*Nyssa sylvatica*) was about 1% to 1.5% of tree composition. Dogwood (*Cornus florida*) frequency was 1% in subsection 232Bc. Dogwood (0.74%), holly (0.72%; *Ilex* spp.), maple (0.61%; *Acer* spp.), and sweetgum (0.50%; *Liquidambar styraciflua*) were other species present in subsection 232Bj.

Currently, pine composition is 38% in subsection 232Bc and 57% in 232Bj. Loblolly pine (*Pinus taeda*) was 33% of total composition in subsection 232Bc and 38% composition in 232Bj, while slash pine (*Pinus elliottii*) added another 10%

Table 1 Historical composition (≥1%) in Pearl River County, De Soto National Forest, and ecological subsections

Tree	Count	Percent
Pearl River County		
pine	2149	86.44
bay	136	5.47
oak	60	2.41
blackgum	40	1.61
De Soto National Forest		
pine	6684	87.10
bay	353	4.60
oak	195	2.54
blackgum	81	1.06
232Bc		
pine	853	84.88
bay	57	5.67
oak	30	2.99
blackgum	16	1.59
dogwood	10	1.00
232Bj		
pine	7980	87.17
bay	432	4.72
oak	225	2.46
blackgum	105	1.15

of total composition in 232Bj (please note the small sample size for 232Bc; Table 2). Longleaf pine was 2% of composition in 232Bc and 8% in 232Bj. Without as great abundance of pine, more species were present at ≥1% of composition. The broadleaf evergreen species held relatively stable while blackgum (*Nyssa sylvatica*) increased. Water oak (*Quercus nigra)*, sweetgum, yellow-poplar (*Liriodendron tulipifera*), and red maple (*Acer rubrum*) in particular increased from about 0.5% composition to 2% to 10% of composition. Longleaf pine does not exceed 10% of composition in any subsection in the Coastal Plain (Fig. 2).

Structurally, densities and percent stocking of longleaf pine ecosystems in the two subsections were at the threshold of open to closed woodlands (Table 3; threshold values at about 175 trees/ha and 55% stocking for trees ≥12.7 cm based on open oak ecosystems; Hanberry *et al*. 2014a, b). Density was about 175 trees/ha to 180 trees/ha, after adjustment for bias from 125 trees/ha to 130 trees/ha. Basal area values of 35 to 38 m^2/ha reflect large diameter (45 cm) old growth trees with rare overstory disturbance. Stocking was around 60% to 65%, at the border between open and closed woodlands.

Currently, forests have become twice as dense, at about 280 trees/ha to 330 trees/ha (Table 3). In addition, mean tree diameters of 22 cm were 50% of historical tree diameters of 45 cm. Basal area and percent stocking consequently were low.

Table 2 Current composition (≥1%) by ecological subsection

Tree	Count	Percent	Scientific name
232Bc			
loblolly pine	131	32.51	*Pinus taeda*
blackgum	50	12.41	*Nyssa sylvatica*
water oak	38	9.43	*Quercus nigra*
sweetbay	29	7.20	*Magnolia virginiana*
sweetgum	27	6.70	*Liquidambar styraciflua*
yellow-poplar	27	6.70	*Liriodendron tulipifera*
swamp tupelo	19	4.71	*Nyssa biflora*
red maple	18	4.47	*Acer rubrum*
pondcypress	12	2.98	*Taxodium ascendens*
longleaf pine	7	1.74	*Pinus palustris*
slash pine	7	1.74	*Pinus elliottii*
shortleaf pine	5	1.24	*Pinus echinata*
black cherry	4	0.99	*Prunus serotina*
232Bj			
loblolly pine	9222	37.54	*Pinus taeda*
slash pine	2555	10.40	*Pinus elliottii*
longleaf pine	1946	7.92	*Pinus palustris*
water oak	1439	5.86	*Quercus nigra*
sweetgum	1217	4.95	*Liquidambar styraciflua*
sweetbay	1205	4.90	*Magnolia virginiana*
blackgum	940	3.83	*Nyssa sylvatica*
swamp tupelo	857	3.49	*Nyssa biflora*
yellow-poplar	657	2.67	*Liriodendron tulipifera*
red maple	580	2.36	*Acer rubrum*
laurel oak	477	1.94	*Quercus laurifolia*
southern red oak	283	1.15	*Quercus falcata*
shortleaf pine	271	1.10	*Pinus echinata*
black cherry	251	1.02	*Prunus serotina*
white oak	237	0.96	*Quercus alba*

Discussion

Compositional and Structural Changes

Historically, pine was about 85% of total tree composition, predominantly longleaf pine although loblolly pine probably was present with lesser amounts of other pine species. We assume the majority of pine trees were longleaf pine, in agreement with 1) other research (e.g., Frost 1993; Schultz 1997), 2) the weight of historical evidence (e.g., Mohr and Roth 1897; Mattoon 1915) and cultural identity and remembrance, and 3) lack of species identification for pine by historical surveyors, which may indicate that they were encountering a very common pine species. Schultz (1997) estimated that loblolly composed a small fraction of historical southern forests, with pure stands totaling scarcely 2 million ha. We are not aware of evidence against historical predominance by longleaf

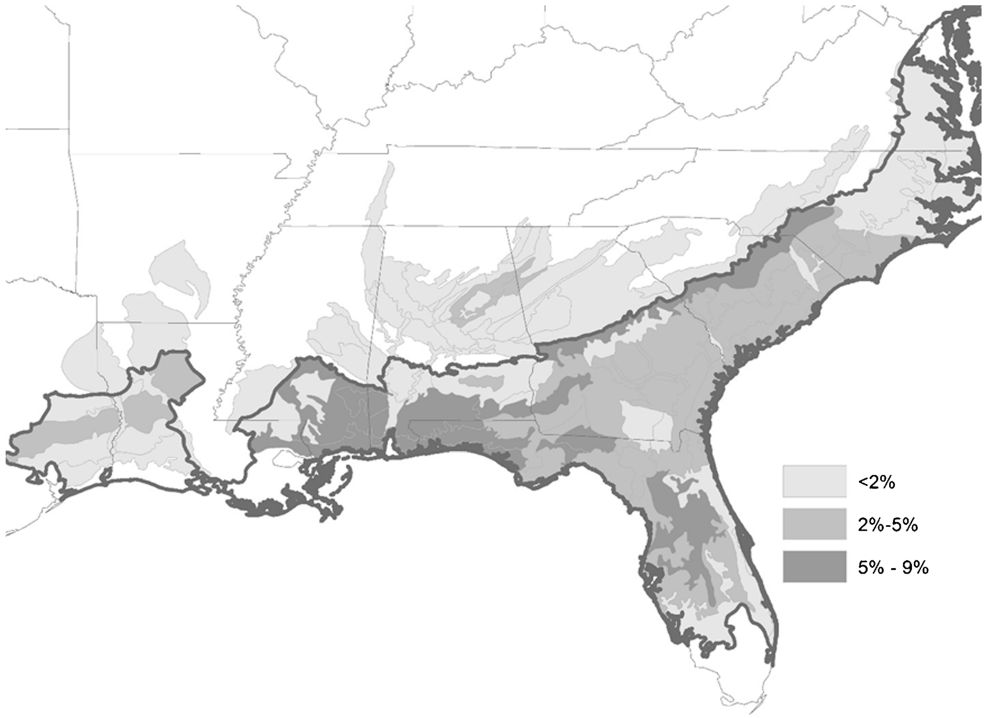

Fig. 2 Current composition (percent of all trees, using FIA surveys) of longleaf pine in the Coastal Plain

pine in the Coastal Plain before Euro-American settlement. In addition to pine, oaks also were present, surviving to reach adult diameters in small spots where fire was less frequent. Broadleaf evergreen tree species represented fire-protected wetlands embedded in a pine matrix. Although not delineated here, canebrakes were recorded in the GLO surveyor notes.

Pine densities of about 175 trees/ha to 180 trees/ha, after increases for surveyor bias, and stocking of about 60% to 65% suggested a forest ecosystem phase of closed woodlands, but at the threshold between open and closed woodlands (Hanberry *et al.* 2014a). To our knowledge, only Predmore *et al.* (2007) have estimated longleaf pine density using historical tree surveys. Their estimate of 105 trees/ha, without density increases for surveyor bias that caused surveyors not to select the nearest trees, likely quantified open woodlands. A range of open and closed woodlands probably occurred across the region, intermixed with grasslands and pine savannas and localized closed canopy wetland forests and canebrakes. Because the Coastal Plain covers a large extent, a variety of longleaf pine-dominated ecosystems have been described (e.g., Peet and Allard 1993), varying with soil and topography.

Historical tree densities were greater than savannas, even though longleaf pine ecosystems often are referred to as longleaf pine savannas. Native American populations collapsed, perhaps by up to 95%, shortly after exposure to small pox and other diseases introduced by European explorers, and villages and clearings were abandoned (Fowler and Konopik 2007). However, fire frequencies may not have decreased (Stambaugh *et al.* 2011), due to adoption of burning practices by early Euro-American settlers. That is, forest densities may have been as influenced by fire before settlement as during historical surveys of the 1800s. Woodlands in this study may be representative of widespread longleaf woodlands, particularly in more fertile and wet soils. In addition, openness of the midstory may have created an illusion of lower densities in forests.

Historical trees were old growth due to limited frequency of overstory disturbance before industrialization (Lorimer

Table 3 Structure (trees ≥12.7 cm; density in trees/ha; BA = basal area, m^2/ha) of historical longleaf pine ecosystems and current forests by subsection

Subsection	Density	Low	High	Unadjusted	Diameter	BA	Low	High	Stocking	Low	High
Historical											
232Bc	182	113	224	132	46	38	23	46	66	41	81
232Bj	174	108	215	126	45	35	21	43	61	38	75
Current											
232Bc	282				22	12			33		
232Bj	330				22	15			39		

2001; Elsner *et al.* 2008), resulting in large diameter trees (mean 45 cm diameter) and high basal areas. Historical diameter distributions generally are not possible to correct for surveyor bias for trees of moderate size that could be blazed and contained the potential for longevity. Nonetheless, given typical longevity for longleaf pine is 300 hundred years, trees had time to develop large stems, particularly in productive soils. Furthermore, due to understory tree removal by fire, historical forests probably contained few smaller trees.

Currently, forests are 38% and 57% pine in the two ecological subsections. Although ecological subsection 232Bc is small and thus, there is a small sample size, the 38% pine composition is representative of forests without forest management and pine plantations. In contrast, subsection 232Bj (i.e., De Soto National Forest) is representative of management for pine in the Coastal Plain, which overall contains about 55% pine.

Longleaf pine was 2% and 8% of composition in the two subsections, while longleaf is 3% of composition in the Coastal Plain (Fig. 2). De Soto National Forest is managed for longleaf pine, which consequently increases longleaf pine composition in the subsection, compared to the influence of loblolly and slash pine plantations. Even if longleaf pine was simply the majority of historical pine composition, for example, only 50% of all trees, the loss of longleaf still is extreme. Longleaf pine composition signifies a bipartite ecosystem composed of grasslands and trees, which is no longer present across the region.

Current forests, particularly in the southeastern US where overstory disturbance is frequent for the forest product industry, are successional forests. Successional forests contain dense, small diameter trees with a thick midstory of regenerating trees or other woody growth. Because of fire exclusion and overstory disturbance due to extensive harvesting during 1850–1920, pine plantation rotations of <35 years, continued harvest or clearing for other land uses, and cycles of farm abandonment, current tree diameters are small.

Conversion from Open Pine Forests and Current Management

Historically, frequent low severity fires prevented broadleaf tree establishment, which occurs without understory disturbance. Open pine ecosystems without a fire regime transition to closed broadleaf forests in the eastern United States, as displayed by reduction in pine composition from 85% of total trees to 38% or 57%, if supplemented by planted loblolly pine (Conner and Hartsell 2002, Hanberry *et al.* 2014a, b). Closed broadleaf forests are an alternative state (i.e., potential vegetation) with dense canopy layers that block light from reaching the understory to support an herbaceous layer. Once closed broadleaf forests establish, restoration of the open forest state is difficult because thinning of overstory trees to allow light penetration will release trees in the understory. Restoration through prescribed burns occurs at small scales, due to the complexity of burning as a management tool, and there is little economic incentive to set fire to the landscape frequently, and therefore, fire-tolerant longleaf and shortleaf pines continue to decrease (Van Lear *et al.* 2005). Currently, a decade of prescribed burning appears to restore open longleaf pine ecosystems and specialist bird species (Steen *et al.* 2013).

Recent land conversion to pine plantations counteracts the state transition to closed broadleaf forests. The southeastern US is an exception to on-going compositional replacement of pine and oaks by fire-sensitive species because pine composition has increased during past decades due to loblolly and slash pine plantations (Conner and Hartsell 2002). The South is the "wood basket" of the United States, the greatest source of forest products in terms of both area and volume (Haynes 2002). Unlike restoration of open pine ecosystems, there are great economic incentives to convert closed broadleaf forests to pine plantations, redirecting a process that shifts forests away from pine species to broadleaf species.

Intensive management of southern pine plantations has increased productivity and yield of plantations, but is a concern where forest biological diversity historically was associated with the ground layer. Pine plantations probably are a closer analogue than closed broadleaf forests to historical open pine ecosystems. Due to long growing seasons and fast pine growth, pine plantations are on short rotations of <35 years; regular stand-replacing disturbance results in regenerating stands and active management provides tree thinning. Open ecosystems (i.e., clearcuts) and open forest ecosystems (i.e., thinned plantations) thus are present, albeit ephemeral and altered. Common site preparation practices include planting improved stock, herbicide use, fertilization, and mechanical bed treatment. The objective is to reduce competition for pine seedlings and to encourage pine growth, which consequently hastens canopy closure and results in a preponderance of young closed-canopy stands. Management to control broadleaf tree regeneration extends the duration of open forest ecosystems with an herbaceous ground layer; conversely, if management intensity is too great (i.e., site preparation with herbicide applications and mechanical treatments, followed by further herbicide applications after planting) then plantations will be dominated by fast-growing pines with little ground layer development or wildlife presence (i.e., "dirt and pine," Hanberry *et al.* 2012a).

Pine plantations create habitat for early successional species, but given that the Coastal Plain was instead open old growth forests that were stable for at least hundreds, if not thousands of years, the large number of associated and now rare species probably require stable open forests. Resemblance to stable open pine ecosystems can be increased by retention of trees at harvest to provide a continuous overstory of large diameter trees and establishment of skips and gaps between planted trees to keep an open understory. With enough time and retention of any longleaf pines within or surrounding pine plantations through multiple rotations, scattered large diameter trees will develop, perhaps eventually becoming attractive to red-cockaded woodpeckers, which select live, old pine trees for long term cavities (Means 2006).

Conclusions

Historical forests of the Coastal Plain were dominated by pine, primarily longleaf. A much-debated question in longleaf pine ecosystem restoration is "what did the original longleaf pine forest look like?" This study showed pine densities consistent with open and closed woodlands of large diameter trees. The open and simple structure, maintained by frequent fire, supported a ground layer of grasslands and great species diversity. Without fire, similarly to other historically open oak- and pine-dominated regions of the US, forests have converted to a variety of fire-sensitive species or been planted in loblolly and slash pine. In addition, forests currently are successional, composed of dense, small diameter trees. Closed forest ecosystems do not provide the open structure required by light-demanding herbaceous plants and wildlife associates.

It remains important to remember historical ecosystems with high conservation value, so that cultural amnesia does not shift baselines to acceptance of new normals. Closed successional forests, while abundant today, are not representative of historical ecosystems and clearcut management perpetuates current forests. Initiatives such as the Longleaf Alliance help raise the profile of longleaf ecosystems so that they are recognized and restored. Nonetheless, conversion of intact old growth remnants with threatened and endangered plants and insects persists.

Acknowledgements Views in this paper do not necessarily reflect those of the USDA Forest Service.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflicts of interest.

The authors approved the manuscript and are responsible for interpretation of results and for any errors contained in this paper.

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