ÉCOSCIENCE
https://doi.org/10.1080/11956860.2018.1499282

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ORIGINALS ARTICLES

Recalling open old growth forests in the Southeastern Mixed Forest province of the United States

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ABSTRACT

Historical forests in the Southeastern Mixed Forest province of the United States have been less researched than other regions using historical tree surveys. We used 81,000 tree records from surveys during the 1800s to quantify composition of this ecological province. Upland oaks and pines comprised about 75% of all trees, with relatively equal composition. Oak composition may have comprised ≥ 45% to the northern and eastern sides of the province. Hickories were about 10% of composition and a few species were present at 1% to 2% composition. Currently, pine has increased to 49% composition; loblolly pine was 46% of all trees. Upland oaks decreased to 8% composition. Paralleling other historically oak- or pine-dominated regions, fire-intolerant species increased to 40% of composition, particularly early-successional sweetgum. Historical oak-pine forests mostly have converted to loblolly pine plantations and broadleaf forests in this region. A large extent of the eastern United States historically was dominated by oak or pine forests, which likely were open old growth forests due to a frequent, low-to-moderate severity fire regime that reduced tree densities and infrequently disturbed overstory trees. Open old growth forests should be recognized as distinct ecosystems with unique characteristics, ecological functioning, and associated management practices.

RÈSUMÈ

Les relevés historiques d'arbres ont été moins utilisés pour étudier les forêts mixtes du sud-est des États-Unis que les forêts d'autres provinces écologiques. Nous avons utilisé 81 000 mentions d'arbres provenant de relevés du XIX^{e} siècle pour quantifier la composition de cette province écologique. Les chênes de milieux secs et les pins représentaient environ 75% de tous les arbres, en proportions relativement égales. La composition en chênes pouvait être ≥ 45% au nord et à l'est de la province. Les caryers représentaient environ 10% de la composition et quelques espèces étaient présentes à 1–2%. Présentement, les pins ont augmenté à 49%; le pin à encens représentant 46% de tous les arbres. Les chênes de milieux secs ont diminué à 8%. Comme dans d'autres régions historiquement dominées par les chênes et les pins, les espèces tolérantes au feu ont augmenté à 40%, particulièrement le copalme (espèce pionnière). Les forêts historiques de chênes et de pins ont surtout été converties en plantations de pin à encens et en forêts feuillues. Une large part de l'est des États-Unis était historiquement dominée par des forêts de chênes et de pins, probablement des peuplements ouverts et âgés dus à un régime de feux fréquents et de sévérité faible à modérée qui réduisait la densité d'arbres et perturbait rarement les arbres de l'étage dominant. Les forêts ouvertes et âgées devraient être reconnues comme des écosystèmes distincts avec des caractéristiques, un fonctionnement écologique et des pratiques d'aménagement uniques.

ARTICLE HISTORY
Received 6 February 2018
Accepted 9 July 2018

KEYWORDS
Fire; General Land Office; oak; pine; regime shift; transition

MOTS CLÉS
feu; General Land Office; chêne; pin; changement de régime; transition

Introduction

Historical forests in the United States were poorly quantified by contemporaneous scientists and, indeed, scientists may not have finished formally naming species before they began cataloguing remnant uncut stands. Immigration, westward expansion after territorial acquisition, and the Industrial Revolution occurred concurrently in the United States. Therefore, the increasing non-indigenous population (i.e., 0.25 million in 1700, 5.25 million in 1800, 23 million in 1850) created a demand for cleared land, fuel, and lumber along with the tools (steam engines, steel, improved saws, railroads) to

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efficiently harvest most forests of the eastern United States during 1850–1920 (Williams 1992).

Based on surveys of historical trees during the 1800s and other historical records, large extents of oak and pine once dominated much of the eastern United States (e.g., Rostlund 1957; Williams 1992; Hanberry and Nowacki 2016; Hanberry et al. 2017). Pollen, fire, and tree ring studies tend to complement results from historical tree surveys (e.g., Delcourt and Delcourt 1987; Hart and Buchanan 2012; Copenheaver et al. 2017). Frequent, low-to-moderate severity fires filtered out fire-sensitive species, leaving oak and pine species, which have traits to allow some seedlings and saplings to survive fire. Because stand-replacing disturbances occurred less frequently than the typical life span of oaks and pines (Lorimer 2001; Seymour et al. 2002; Fowler and Konopik 2007), these ecosystems primarily were old forests, with exceptions due to Native American activities and where rare stand-replacing disturbances of fire, wind, and ice occurred. Oak and pine forest ecosystems were not a sere in a stage-based progression; instead, these ecosystems were stable in many regions spanning millennia, anchored by long-lived oak and pine species (Delcourt and Delcourt 1987; Landers and Boyer 1999).

Ecosystem structure of oak and pine forests likely was simple, consisting of an herbaceous understory and single canopy layer ranging from scattered trees in savannas to nearly continuous canopies in closed woodlands (Hanberry et al. 2014a). Both anthropogenic (Foster et al. 2004; Foster 2016) and lightning fire removed most small-diameter woody growth, creating a relatively open midstory with little woody debris, which allowed a groundlayer similar to grasslands. Open forests with a treed overstory and grassland groundlayer intermixed and merged with grasslands across the eastern US, particularly in the southern and western regions.

There are either complete or at least mapped interpretations from historical surveys in the Northeast, Great Lakes states, and the Midwest (Missouri, Illinois, Indiana, and Ohio), along with many studies from the Appalachian Mountains (see Hanberry and Nowacki 2016 for documentation). Indeed, researchers have duplicated efforts sometimes multiple times because much of the data have not been archived (e.g., Kilburn and Brugam 2014). Historical forests of Quebec and Ontario, Canada, similarly have been examined (e.g., Jackson et al. 2000; Danneyrolles et al. 2016). In comparison, there are few publications about historical forests during the 1800s in the Southeastern Mixed Forest ecological province of the United States, a region of 47 million ha, comprised of central Virginia and North Carolina; northern South Carolina, Georgia, Alabama, Mississippi; and parts of Louisiana, Texas, Arkansas, and Oklahoma (Cleland et al. 2007; https://data.fs.usda.gov/geodata/edw/datasets.php; Figure 1).

Here, we reconstruct forests of the under-reported Southeastern Mixed Forest ecological province (Cleland et al. 2007; Figure 1) using 81,000 tree records from historical tree surveys during the 1800s to 1850s. We then contrast historical composition of fire-tolerant upland oaks and pines to current tree composition (United States Department of Agriculture [USDA] Forest Inventory and Analysis surveys). We discuss reasons why open old growth forests are not recognized in the Southeastern Mixed Forest province and other regions in the US, despite the importance of open old growth forest ecosystems before settlement.

Methods

During the 1800s, the United States General Land Office (GLO) was responsible for surveying, platting, and selling public domain lands for settlement of Western Territories. Field notes from the GLO surveys provide a record of the leading edge of Euro-American settlement and westward expansion, and therefore land surveys capture conditions at a critical time before rapid and thorough anthropogenic transformation. The Public Land Survey System divided most Western Territories into one mile (1.6 x 1.6 km) square sections, arranged into square townships of 36 sections. Surveyors recorded two to four trees at every section corner and halfway along section lines. Georgia had a slightly different systematic land survey for which surveyors recorded one tree at each section corner and two trees along section lines (Cowell 1995). General Land Office surveyors also recorded trees encountered along section lines, which allows for examination of species bias; comparison between section trees and line trees generally shows agreement (e.g., Hanberry et al. 2014b).

We determined species composition by ecological boundaries of sections and by province for about 81,000 tree records, located in the center states of Mississippi, Alabama, and Georgia of the Southeastern Mixed Forest ecological province (Cleland et al. 2007; Figure 1). No tree distances were available and thus we were not able to estimate tree density. We used about 52,150 tree records in the Southeastern Mixed Forest province recorded during the 1820s to 1850s, of which about 850 trees in Mississippi previously were used by Peacock et al. (2008) and 39,120 trees in Alabama by Black et al. (2002). To supplement our reconstruction, we transferred Plummer's (1975) compositional tables (14,755 trees in Georgia recorded during 1805 and 1832; please note a mismatch error between species and compositional percent in the table for Meriwether County; for example, the value of 25.5% appeared to be lined with persimmon, but

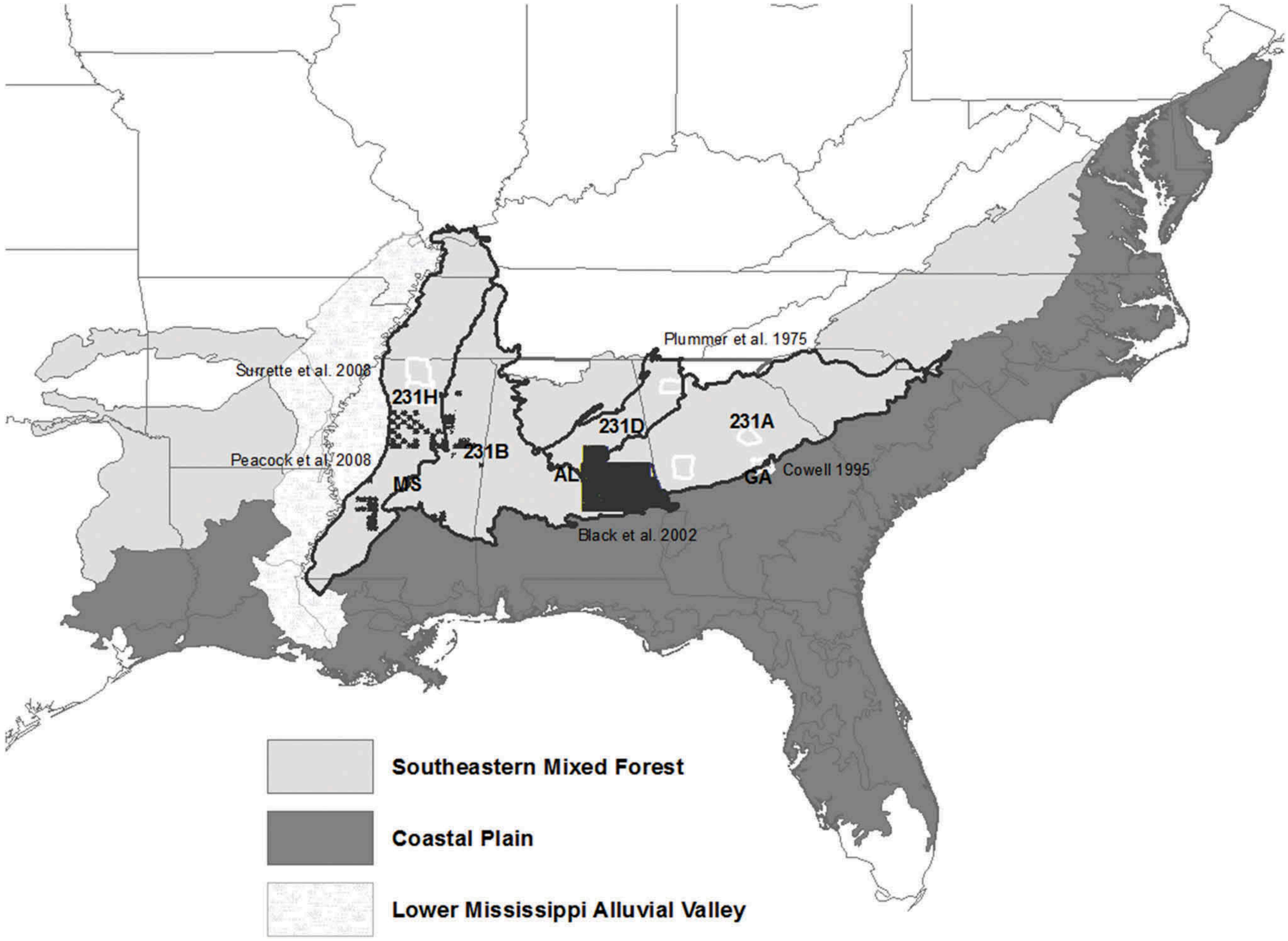

Figure 1. The Southeastern Mixed Forest ecological province of the United States and study areas (GLO survey points in black and supplementary information outlined in white by county; ecological subsections outlined in black).

matched with pine in the text) to ecological subsections (the smallest ecological unit, Cleland et al. 2007). We averaged composition weighted by sample size for any subsections that contained more than one compositional table. We then similarly transferred Cowell's (1995; 11,500 trees surveyed in Georgia during 1801 to 1804) and Surrette et al.'s (2008; 2550 upland trees in Mississippi surveyed during the 1830s and 1840s) tables for counties to ecological subsections. We again weighted composition by sample size for any subsections with more than one source of information. Note that Cowell (1995) provided records from a county that crossed ecological province lines, but we assigned values to the Southeastern Mixed Forest province because the tension zone or fall line, where prehistoric oceans occurred and soil types change, between the Southeastern Mixed Forest province and Coastal Plain is indicated by the amount of pine, which typically is > 70% in the Coastal Plain, as shown by clear partitioning in Plummer (1975).

We used USDA Forest Service Forest Inventory and Analysis surveys to quantify current forest composition. The FIA plots occur every 2500 ha and therefore provide landscape scale estimates. We limited current composition by province to ecological subsections paralleling where the GLO surveys were present, about 119,370 trees.

We also classed trees by historically common upland oaks, all pine species, hickories, and a fire-sensitive group. Despite great pine abundance, surveyors did not try to identify the pine genus by species in southern surveys, perhaps indicating that surveyors were encountering primarily one species. White oak, blackjack oak, post oak, black oak, and chestnut oak were identified, but otherwise 'red oak' and 'Spanish oak' (which we classed with red oak) may have encompassed several oak species. Thus, we grouped white oak, blackjack oak, post oak, black oak, northern red oak, southern red oak, along with less common chestnut oak and scarlet oak as upland oaks.

Results

Upland oaks and pines comprised about 75% of all trees in the central part of the province. Oaks and pines had relatively similar composition at 38% and

Table 1. Historical and current composition (trees ≥ 12.7 cm; current surveys limited to ecological subsections with historical surveys) for the Southeastern Mixed Forest province with surveys. The supplemented percent (suppl. %) includes composition from the literature.

Historical					Current			
Species	Count	Percent	Species	Suppl. %	Species	Count	Percent	Scientific name
pine	18,845	36.1	pine	31.2	loblolly pine	54,893	46.0	*Pinus taeda*
post oak	6779	13.0	post oak	15.7	sweetgum	13,351	11.2	*Liquidambar styraciflua*
hickory	5007	9.6	red oak	11.3	white oak	4298	3.6	*Quercus alba*
red oak	4868	9.3	hickory	9.4	water oak	4213	3.5	*Quercus nigra*
black oak	3123	6.0	black oak	7.6	yellow-poplar	4121	3.5	*Liriodendron tulipifera*
blackjack	2859	5.5	blackjack	4.7	red maple	3337	2.8	*Acer rubrum*
white oak	1760	3.4	white oak	4.3	shortleaf pine	2771	2.3	*Pinus echinata*
blackgum	1003	1.9	chestnut	2.2	southern red oak	2515	2.1	*Quercus falcata*
chestnut	977	1.9	dogwood	1.8	winged elm	1737	1.5	*Ulmus alata*
dogwood	774	1.5	blackgum	1.7	post oak	1697	1.4	*Quercus stellata*
Am.beech	664	1.3	sweetgum	1.1	pignut hickory	1593	1.3	*Carya glabra*
sweetgum	663	1.3	yellow-poplar	1.0	eastern redcedar	1509	1.3	*Juniperus virginiana*
ash	510	1.0	ash	0.9	blackgum	1508	1.3	*Nyssa sylvatica*
maple	439	0.8	Am.beech	0.9	mockernut hickory	1469	1.2	*Carya alba*
elm	369	0.7	maple	0.7	black cherry	1426	1.2	*Prunus serotina*
yellow-poplar	367	0.7	elm	0.6	sourwood	1316	1.1	*Oxydendrum arboreum*
holly	352	0.7	sassafras	0.5	green ash	1201	1.0	*Fraxinus pennsylvanica*
water oak	301	0.6	holly	0.4	cherrybark oak	914	0.8	*Quercus pagoda*
bay	278	0.5			American hornbeam	766	0.6	*Carpinus caroliniana*
sassafras	272	0.5			chestnut oak	714	0.6	*Quercus prinus*
ironwood	271	0.5			Virginia pine	706	0.6	*Pinus virginiana*
					flowering dogwood	697	0.6	*Cornus florida*
					black oak	634	0.5	*Quercus velutina*
					American beech	615	0.5	*Fagus grandifolia*
					American elm	576	0.5	*Ulmus americana*
					sugarberry	569	0.5	*Celtis laevigata*

Table 2. Historical and current composition by tree groups (trees ≥ 12.7 cm; current surveys limited to ecological subsections with historical surveys), for the Southeastern Mixed Forest Province and by ecological sections with surveys. The supplemented percent (suppl. %) includes composition from the literature.

		Historical			Current	
Province	Group	Count	Percent	Suppl. %	Count	Percent
	upland oak	19,541	37.5	43.8	9271	7.8
	pine	18,845	36.1	31.2	58,993	49.4
	other	8760	16.8	15.5	47,317	39.6
	hickories	5007	9.6	9.4	3787	3.2
Section	Group	Count	Percent	Suppl. %	Count	Percent
231A	upland oak	6994	38.7	46.7	3069	9.4
	pine	6222	34.4	28.9	16,512	50.8
	other	2531	14.0	13.7	11,916	36.6
	hickories	2314	12.8	10.8	1027	3.2
231B	upland oak	6483	30.6	30.6	2859	5.8
	pine	9687	45.8	45.8	25,805	52.4
	other	3716	17.6	17.5	19,251	39.1
	hickories	1285	6.1	6.1	1364	2.8
231D	upland oak	1538	33.9	38.9	1269	17.5
	pine	2069	45.6	36.2	3469	47.8
	other	473	10.4	15.4	2065	28.5
	hickories	460	10.1	9.5	452	6.2
231H	upland oak	4526	54.0	61.4	2074	6.8
	pine	867	10.3	8.9	13,207	43.6
	other	2040	24.3	19.0	14,085	46.5
	hickories	948	11.3	10.7	944	3.1

36%, respectively, using the tree points (Tables 1 and 2; see Table 1 for most scientific names; Appendix A). After incorporation of supplementary information (average weighted by sample size) from historical tree surveys in northern Mississippi and eastern Georgia, oak percentage increased to 44% and, consequently, pine percentage decreased to 31%.

Hickories, including both upland and wetland species, were about 10% of composition. Because oaks, pines, and hickories were about 85% of composition, only a few species, such as blackgum, American chestnut (*Castanea dentata*), dogwood, sweetgum, and American beech, were present at 1% to 2% composition. Additionally, supplementary information made little change to these values.

Currently, pine has increased to 49% composition in the province due to loblolly pine plantations; loblolly pine was 46% of all trees. Upland oaks have decreased to 8% composition and hickories have decreased to 3% composition. Other fire-intolerant species have increased to 40% of composition, mostly sweetgum, but also water oak, yellow-poplar, red maple, winged elm, and eastern redcedar.

Discussion

Historically, the Southeastern Mixed Forest province was dominated by oak and pine (combined total of 75%; Table 2). The oak to pine ratio was relatively even in the central part of the province, although oak presence was greater to the northern and eastern sides of the province in less sandy soils, based on supplementary information locations (see Figure 1). After incorporation of supplementary information from northern Mississippi and eastern Georgia, oak percentage increased to 44% and pine percentage decreased to 31%. Pines became more common in the southern part of the province and may have reached greatest abundance in the western part of the province in Arkansas (Mohr and Roth 1897; Mattoon 1915; Bragg 2002). Hickories were 10% of composition, which was an abundant genus compared to the other non-pine, non-oak species. This may help explain why early ecologists and foresters considered hickory to be a major associate of oak (Hanberry and Nowacki 2016). Nonetheless, oaks and pines each outnumbered hickories by almost four trees to one. An oak-pine-hickory forest designation probably is no more explanatory than simply oak-pine forests. Similarly, description of the province as southeastern mixed forests implies a variety of different broadleaf tree species, which was not the case historically. In addition, southeastern mixed forests would equally well describe the current vegetation of the Coastal Plain (e.g., Hanberry et al. 2018).

Because of different lines of evidence, most of the historical pine in the Southeastern Mixed Forest province is believed to be shortleaf pine, mixed with some amount of loblolly pine in wetlands, and even longleaf pine (e.g., Bragg 2002). Historical accounts typically identify shortleaf pine when pines are differentiated (Nelson 1957). The earliest forestry reports provide accounts of extensive shortleaf pine forests still remaining in the western side of this province in Arkansas and Louisiana and present shortleaf pine as the most abundant tree species (Mohr and Roth 1897; Mattoon 1915; Bragg 2002). Moreover, because upland oaks and pines dominated historical uplands, it follows that there was a fire regime that filtered out fire-sensitive species, such as loblolly pine that required protection from fire by wetlands, before they could establish, and also that surveyed pines were fire-tolerant shortleaf pine in the Southeastern Mixed Forest province (Fowler and Konopik 2007). Upland oaks, shortleaf pine, and longleaf pine have adaptations to low- and moderate-severity, high-frequency fire that removed other species.

The Southeastern Mixed Forest province historically was demarcated to the north by oak-dominated forests, with very little pine presence, and to the south by the longleaf pine-dominated Coastal Plain, where soils have a high sand content (Hanberry and Nowacki 2016). The ecological tension zone between the Coastal Plain and Southeastern Mixed Forest province marked the transition between oak-pine forests and pine-dominated forests. Plummer (1975) demonstrated the strong spatial partitioning within Bibb County, Georgia, where there was ≥ 90% pine in the Coastal Plain and 15% to 30% pine in the Southeastern Mixed Forest province.

Currently, forests are dominated by loblolly pine, most planted. Loblolly pine was 46% of all trees, which was greater than historical pine composition. Upland oaks decreased to 8% composition, even though white oak composition remained stable. Other, primarily fire-intolerant species increased to 40% of composition, mostly sweetgum. Two other winners under recent fire-free conditions in the Southeastern Mixed Forest province, and in the eastern US overall, were red maple and eastern redcedar (Nowacki and Abrams 2008, 2015). Red maple has increased within eastern forests, and would be even more abundant if loblolly pines were not planted, whereas eastern redcedar has increased principally into more open ecosystems (Hanberry et al. 2014b; Hanberry and Hansen 2015).

During the past 100 years, open oak and pine forest ecosystems have transitioned to closed forests that contain a variety of previously minor species (Nowacki and Abrams 2008, 2015). The greatest decline has occurred in longleaf pine (*Pinus palustris*), which historically constituted the principal species of primarily (75%) pine forests in the Coastal Plain of the southeastern US (Hanberry and Nowacki 2016). Now, in the Coastal Plain, longleaf pine only is about 3% of total trees, while planted loblolly and slash pines (*P. taeda* and *P. elliottii*) contribute to about 55% overall pine composition (Hanberry et al. 2018; Hanberry, unpublished from USDA Forest Inventory and Analysis surveys; FIA; www.fia.fs.fed.us/

tools-data; Bechtold and Patterson 2005). Fire-tolerant oak species correspondingly have decreased in the eastern US, albeit not to the extreme of longleaf pine.

Oak and pine decreases signal loss of open forests maintained by fire (Abrams 1992). Fire exclusion as an active policy began early in the 1900s, resulting in release of woody vegetation into the midstory, closing the forest, and replacing the grasslands component of open forests (Nowacki and Abrams 2008; Hanberry and Abrams 2018). Prior to modern fire exclusion policy, Native American peoples indirectly and directly managed localized stands resulting in measurable changes in forest composition (Foster et al. 2004; Foster and Cohen 2007; Fowler and Konopik 2007; Foster 2016). Most of these forested landscapes were logged and converted to agriculture after Euro-American settlement, which may have accelerated conversion to fire-intolerant species during reforestation after agricultural abandonment (Bragg 2002). In particular, loblolly pine historically was relegated to wetlands, which provided protection from fire and also from agriculture, and became a colonizer of old fields after agricultural abandonment (Bragg 2002).

Due to the absence of landscape-scale burning, the transition of fire-dependent oak and pine ecosystems to closed broadleaf forests is common across the eastern United States (Nowacki and Abrams 2008, 2015; Hanberry and Abrams 2018). A mixture of species with a range of drought and light tolerances and a range of other traits, excluding fire tolerance, have established in current forests. These forests are young, comprised of small-diameter trees, and currently successional after overstory tree removal, rather than the old growth of the past. The current maintenance of pine plantations through agroforestry prevents succession and state shifts towards broadleaf forests. Pine plantations are on short rotations, which does not allow structural development to older forests.

Why are open old forests forgotten?

Oak-pine forest covered the Southeastern Mixed Forest province and additionally oaks in the central eastern US and pine in the Coastal Plain dominated most of the forested United States in the past (Figure 2; Williams 1992; Hanberry and Nowacki 2016; Hanberry et al. 2017). The most parsimonious reason that historical forests were 50% to 85% fire-tolerant oaks and pines was because of documented frequent, low-to-moderate severity fire that effectively filtered out fire-intolerant species (Rostlund 1957; White and Lloyd 1998; Landers and Boyer 1999; Fowler and Konopik 2007; Hart and Buchanan 2012). Consistent with historical oak and pine dominance in forests with a recurrent surface fire regime, there may have been more open forests composed of fire-tolerant species historically in the United States than closed forests (e.g., Williams 1992; Hanberry and Nowacki 2016; Hanberry et al. 2017). In addition to favoring oak and pine species, low-to-moderate severity fire provides a mechanism to largely remove small-diameter trees in the understory, keeping understories open and tree densities low. Without recorded tree distances, we were not able to estimate density, but there is evidence of low-density forests from similar ecosystems (Hanberry et al. 2014a; Hanberry et al. 2018). Typically, including oak-shortleaf pine forests in Missouri, oak and pine forests were open, with tree densities not exceeding 250 trees per ha (diameters ≥ 13 cm) and a relatively unoccupied midstory (e.g., Hanberry et al. 2014a).

Historical accounts of the southeastern United States mention plains, savannas, open forests, grazing lands, and fields, and the presence of a large herbivore, American bison (*Bison bison*; e.g., Rostlund 1957; Bragg 2002; for historical accounts). For example, Rostlund (1957) concluded that two kinds of forest were described by explorer accounts:

> One kind of forest was "high and dense," obviously a forest dominated by stands of mature timber and difficult to pass through because of heavy undergrowth … How widespread they were in aboriginal time is hard to say, but it can be said that there are not very many references in the early historic record to forests of this type. It is almost certain that the "forest primeval" was not nearly so universal in pre-colonial time as seems to have been commonly believed a generation or two ago. The second type of forest was a sunlit wood, claro y abierto, the "open airy grove" of Bartram, with trees so far apart and so clear of underbrush that horses could freely gallop from glade to glade … Comments in this vein are found in so many of the old narratives, and in reports from so many different parts of the Southeast, that one can hardly avoid drawing the conclusion that open woodland with little or no underbrush must have been the most common type of forest. Some of the early observers speculated upon the reason for the open character of the forest, and suggested that the cause was the Indian practice of burning the woods at frequent intervals (p.407).

Bragg (2002) determined similar structure from early explorer accounts: 'Using these historical sources as a guide, the virgin pine forests often appeared as open stands, with extensive grass and forb understories only occasionally interrupted by clumps of shrubs and tree saplings (p. 284).'

The historical range of bison provides an approximation of the extent of open forests and grasslands in the United States, albeit bison and bison remains have not been recorded in parts of Atlantic Coastal Plain longleaf pine and southern New England oaks (Gates

Figure 2. Regions dominated by historical oak and pine, which probably were open old growth forests. Other regions did not have a frequent low-severity fire regime because of climate limitations on fire, or alternatively, in flat dry grasslands, fire was too frequent to allow tree establishment.

et al. 2010). Although there are many potential drivers of open forest conditions, including herbivory, we believe the past presence of American bison was more of a consequence of open forests than a driver primarily because open forests occurred where bison were not present and bison are grazers rather than browsers (Hanberry and Abrams 2018). Additionally, despite current high populations of a browser, white-tailed deer (*Odocoileus virginianus*), herbivores have not controlled tree establishment that has created high-density closed forests at landscape scales.

Nonetheless, open oak and pine forest characteristics do not parallel typical well-described 'old growth' forests with multiple canopy layers of the Pacific Northwest and other temperate wet or cold forests (Franklin and Van Pelt 2004; Brūmelis et al. 2011; Donato et al. 2012). Litigation concerning wildlife species of old growth forests primarily drew attention to closed old forests, characterized by internal vertical and horizontal complexity due to fine-scale stand dynamics (Franklin and Van Pelt 2004; Kane et al. 2011; Donato et al. 2012). Research on closed old growth forests may have become so influential and archetypical that it obscured other types of old growth, such as open forests. Similar litigation for wildlife in open longleaf pine forests and research about old growth forests in the eastern United States has not become as well known or well covered in various publication outlets. During the 1990s, the USDA Forest Service and collaborators developed old growth definitions for the eastern United States, starting with a generic definition: 'Old growth encompasses the later stages of stand development that typically differ from earlier stages in a variety of characteristics which may include tree size, accumulations of large dead woody material, number of canopy layers, species composition, and ecosystem function (p. 51)' (White and Lloyd 1998). These efforts used old growth remnants to develop descriptions of 35 forest cover types, including oak and pine subtypes such as a xeric pine and pine-oak woodlands (Murphy and Nowacki 1997) and combinations such as longleaf and slash pine (Landers and Boyer 1999), with an emphasis on complete representation of most eastern tree species (e.g., Tyrrell et al. 1998), rather than a focus on historically dominant forest types. Indeed, White and Lloyd (1998) noted that a pine-oak forest type was not included as a type on dry-mesic sites. Tyrrell et al. (1998) developed a radar chart of a total of 15 attributes typically associated with old growth (e.g., tree density of forest rather than lower-density woodlands and savannas, late successional status, abundance of snags and coarse woody debris) to demonstrate how closely each ecosystem type resembled the core concept of old growth.

Although it is clear that old growth definitions vary among ecosystem types (Tyrrell et al. 1998), separation between open and closed forests has not been differentiated because closed forest attributes of successional status, shade tolerance, and structural features consistently are criteria for old growth (Tyrrell et al. 1998). Oak and pine forests are not successional or ephemeral under a fire regime and minimal disturbance of the overstory (Landers and Boyer 1999; Lorimer 2001; Seymour et al. 2002), as evidenced by presence in historical pollen studies from thousands of years ago and dominance during the 1800s, which represented trees that had established hundreds of years ago (Delcourt and Delcourt 1987; Landers and Boyer 1999; Hanberry and Nowacki 2016). Oak and pine are not shade-tolerant, but that does not matter in an open forest with a fire regime that removes shade-tolerant species. A fire regime also consumes understory biomass, resulting in different structural features than closed forests. Open forests did exhibit steady state dynamics and gap dynamics because they had similar frequency of overstory disturbance as closed old growth forests in the eastern US (Lorimer 2001; Seymour et al. 2002).

Closed forests are a foundation of society, ecology, and silviculture whereas open forests do not match ecological, silvicultural, and cultural standards of forests. Differential structure is relatively unrecognized in ecological and silvicultural literature, perhaps in part because open pine and oak forests are remnants and have been forgotten through cultural amnesia. Compared to closed forests, internal structure of savannas and woodlands was simple, consisting of low-density, large-diameter trees with a single canopy layer (Hanberry et al. 2014a). However, structural variation in terms of canopy closure across the landscape was greater than closed forests (Hanberry and Abrams 2018). The herbaceous groundlayer provided diversity along with a continuum of forest structure that varied in openness due to different fire exposure and other environmental gradients. The dual nature of open forests, intermediate between grasslands and forests, may seem irregular compared to fully stocked forests of temperate zones or inconsistent with ecological succession to climax forests.

Management recommendations based on developing characteristics of old, closed-canopy forests diminish the importance of other, more open types of historical treed communities. One common recommendation for management of forests to prevent standardization is development of internal structural complexity, such as continuous foliage distribution to fill vertical canopy gaps (Fischer et al. 2006; Lindenmayer et al. 2006). This is an appropriate recommendation for late-successional forest ecosystems, where time without catastrophic disturbance produces closed forests with fine-scale variation within stands, but development of woody density is antithetical to open forest ecosystems, which have a simple structure of overstory trees and limited woody development in the midstory and understory, allowing herbaceous plants to capture growing space. Likewise, tree debris on the forest floor, while a desired indicator of time without disturbance in closed old growth forests, interferes with herbaceous growth that is a component of open forests. Time since fire and other factors will influence the amount and spatial heterogeneity of tree debris and woody understory layers.

Although there are many economic and social reasons that limit restoration opportunities, restoration for open oak and pine forests currently may be most limited by lack of widespread recognition of these forests as distinct ecosystems with unique ecological functions and management needs. Even researchers and managers familiar with the historical range of longleaf pine may not realize that there are alternative forest conditions to successional and old growth closed forests presented in ecological and silvicultural literature. The open spectrum of forests, which historically occurred at landscape scales, is now missing and may contribute to declines in forbs, pollinators, and bird species dependent on a grassland component in forests. It is possible and sometimes desirable to produce forests with more exposed conditions and grassland vegetation than those provided by closed forests with multiple vertical layers, while avoiding problems associated with clearcuts. Additionally, management options exist beyond even-aged and uneven-aged management practices developed for closed forests. Open forest management is focused on maintenance of the overstory and prevention of tree regeneration and midstory development through practices such as prescribed burns and understory thinning.

Conclusion

The historical Southeastern Mixed Forest province historically was dominated by two genera, oak and pine, comprising about 75% of total composition. Upland oak and pine composition may be about equal, with some spatial variation particularly due to ecological tension zones of oaks to the north and pines to the south. That is, oaks became more abundant in the northern part of the province toward the oak region of the central eastern US and pines became more prominent in the southern part of the province closer to the longleaf pine region of the flat, sandy soils in the Coastal Plain. These historical forests have converted primarily to young closed broadleaf forests and loblolly pine plantations.

Open old growth forests should be acknowledged as a distinct ecosystem with its own ecological functioning and associated management practices. Ecologists and foresters generally have overlooked an ecologically important ecosystem, and thus have not interpreted adequately the full range of forest diversity (Hanberry and Abrams 2018). Because current forests are closed-canopied and valued as a timber-producing resource, closed forests have been well described in terms of ecological succession and by forest management models and goals. However, successional ecosystems are an outcome of frequent overstory disturbance by humans, and we may need to consider implications of historically stable systems that are open. Characteristics of closed forests are very different from open forest ecosystems, which contain both overstory trees that cover the complete spectrum of canopy cover and an herbaceous groundlayer, with very little vertical development. Recognition of open forests that are not forest alone but include a grasslands component has ecological and management consequences for a set of ideas that have been established based on closed forests.

Acknowledgments

This paper may not reflect views of the USDA Forest Service. We thank anonymous reviewers.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

There was no funding for this research.

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Appendix A. Historical (≥ 0.5%) and current composition, by ecological section and species (trees ≥ 12.7 cm)

Section	Species	Count	Percent	Species	Count	Percent	Scientific name
231A	pine	6222	34.4	loblolly pine	15,222	46.8	*Pinus taeda*
	post oak	2803	15.5	sweetgum	3833	11.8	*Liquidambar styraciflua*
	hickory	2314	12.8	yellow-poplar	1662	5.1	*Liriodendron tulipifera*
	red oak	1660	9.2	white oak	1492	4.6	*Quercus alba*
	black oak	1542	8.5	water oak	1442	4.4	*Quercus nigra*
	chestnut	670	3.7	shortleaf pine	901	2.8	*Pinus echinata*
	white oak	483	2.7	red maple	841	2.6	*Acer rubrum*
	blackjack	462	2.6	southern red oak	746	2.3	*Quercus falcata*
	blackgum	291	1.6	sourwood	526	1.6	*Oxydendrum arboreum*
	dogwood	180	1.0	pignut hickory	492	1.5	*Carya glabra*
	maple	172	1.0	post oak	412	1.3	*Quercus stellata*
	beech	160	0.9	mockernut hickory	410	1.3	*Carya alba*
	poplar	150	0.8	winged elm	399	1.2	*Ulmus alata*
	sweetgum	120	0.7	black cherry	382	1.2	*Prunus serotina*
	sassafras	96	0.5	flowering dogwood	328	1.0	*Cornus florida*
	ash	93	0.5	blackgum	277	0.9	*Nyssa sylvatica*
	sourwood	83	0.5	Virginia pine	226	0.7	*Pinus virginiana*
				scarlet oak	224	0.7	*Quercus coccinea*
				eastern redcedar	222	0.7	*Juniperus virginiana*
				green ash	216	0.7	*Fraxinus pennsylvanica*
				chestnut oak	199	0.6	*Quercus prinus*
				black oak	178	0.5	*Quercus velutina*
				northern red oak	178	0.5	*Quercus rubra*
231B	pine	9687	45.8	loblolly pine	24,446	49.6	*Pinus taeda*
	post oak	2205	10.4	sweetgum	5176	10.5	*Liquidambar styraciflua*
	red oak	1570	7.4	water oak	1821	3.7	*Quercus nigra*
	hickory	1285	6.1	red maple	1534	3.1	*Acer rubrum*
	blackjack	1278	6.0	yellow-poplar	1485	3.0	*Liriodendron tulipifera*
	white oak	695	3.3	white oak	1352	2.7	*Quercus alba*
	black oak	692	3.3	shortleaf pine	896	1.8	*Pinus echinata*
	blackgum	404	1.9	southern red oak	881	1.8	*Quercus falcata*
	sweetgum	350	1.7	blackgum	784	1.6	*Nyssa sylvatica*
	beech	311	1.5	eastern redcedar	723	1.5	*Juniperus virginiana*
	ash	277	1.3	post oak	620	1.3	*Quercus stellata*
	holly	210	1.0	mockernut hickory	564	1.1	*Carya alba*
	dogwood	198	0.9	pignut hickory	487	1.0	*Carya glabra*
	water oak	196	0.9	winged elm	487	1.0	*Ulmus alata*
	elm	192	0.9	sourwood	475	1.0	*Oxydendrum arboreum*
	bay	182	0.9	green ash	465	0.9	*Fraxinus pennsylvanica*
	chestnut	164	0.8	sweetbay	423	0.9	*Magnolia virginiana*
	maple	154	0.7	black cherry	414	0.8	*Prunus serotina*
	poplar	125	0.6	sugarberry	378	0.8	*Celtis laevigata*
	sassafras	104	0.5	water tupelo	362	0.7	*Nyssa aquatica*
				cherrybark oak	360	0.7	*Quercus pagoda*
				American hornbeam	352	0.7	*Carpinus caroliniana*
				swamp tupelo	317	0.6	*Nyssa biflora*
				willow oak	309	0.6	*Quercus phellos*
				laurel oak	223	0.5	*Quercus laurifolia*
231D	pine	2549	36.2	loblolly pine	2828	39.0	*Pinus taeda*
	post oak	1119	15.9	sweetgum	408	5.6	*Liquidambar styraciflua*
	hickory	672	9.5	chestnut oak	364	5.0	*Quercus prinus*
	black oak	579	8.2	white oak	347	4.8	*Quercus alba*
	red oak	545	7.7	Virginia pine	305	4.2	*Pinus virginiana*
	blackjack	231	3.3	yellow-poplar	242	3.3	*Liriodendron tulipifera*
	white oak	215	3.1	pignut hickory	212	2.9	*Carya glabra*
	blackgum	167	2.4	shortleaf pine	202	2.8	*Pinus echinata*
	chestnut	162	2.3	sourwood	196	2.7	*Oxydendrum arboreum*
	sweetgum	94	1.3	southern red oak	194	2.7	*Quercus falcata*
	ash	85	1.2	red maple	187	2.6	*Acer rubrum*
	poplar	75	1.1	mockernut hickory	179	2.5	*Carya alba*
	beech	72	1.0	post oak	177	2.4	*Quercus stellata*
	dogwood	71	1.0	black cherry	147	2.0	*Prunus serotina*
	elm	52	0.7	longleaf pine	134	1.8	*Pinus palustris*
	chestnut oak	40	0.6	black oak	126	1.7	*Quercus velutina*
				water oak	94	1.3	*Quercus nigra*
				blackgum	92	1.3	*Nyssa sylvatica*
				scarlet oak	91	1.3	*Quercus coccinea*
				winged elm	75	1.0	*Ulmus alata*

(*Continued*)

(Continued).

Section	Species	Count	Percent	Species	Count	Percent	Scientific name
				northern red oak	74	1.0	*Quercus rubra*
				blackjack oak	73	1.0	*Quercus marilandica*
				green ash	72	1.0	*Fraxinus pennsylvanica*
				eastern redcedar	52	0.7	*Juniperus virginiana*
				flowering dogwood	43	0.6	*Cornus florida*
231H	red oak	1402	16.7	loblolly pine	12,397	40.9	*Pinus taeda*
	post oak	1267	15.1	sweetgum	3934	13.0	*Liquidambar styraciflua*
	hickory	948	11.3	white oak	1107	3.7	*Quercus alba*
	blackjack	888	10.6	water oak	856	2.8	*Quercus nigra*
	pine	867	10.3	winged elm	776	2.6	*Ulmus alata*
	black oak	485	5.8	red maple	775	2.6	*Acer rubrum*
	white oak	472	5.6	shortleaf pine	772	2.5	*Pinus echinata*
	dogwood	364	4.3	yellow-poplar	732	2.4	*Liriodendron tulipifera*
	blackgum	248	3.0	southern red oak	694	2.3	*Quercus falcata*
	beech	171	2.0	eastern redcedar	512	1.7	*Juniperus virginiana*
	sweetgum	156	1.9	cherrybark oak	508	1.7	*Quercus pagoda*
	ironwood	146	1.7	post oak	488	1.6	*Quercus stellata*
	elm	118	1.4	black cherry	483	1.6	*Prunus serotina*
	holly	113	1.3	green ash	448	1.5	*Fraxinus pennsylvanica*
	ash	101	1.2	pignut hickory	402	1.3	*Carya glabra*
	maple	90	1.1	blackgum	355	1.2	*Nyssa sylvatica*
	poplar	72	0.9	black willow	316	1.0	*Salix nigra*
	chestnut	65	0.8	mockernut hickory	316	1.0	*Carya alba*
	sassafras	56	0.7	American elm	312	1.0	*Ulmus americana*
	hornbeam	46	0.5	American hornbeam	290	1.0	*Carpinus caroliniana*
	water oak	41	0.5	eastern hophornbeam	271	0.9	*Ostrya virginiana*
				American beech	253	0.8	*Fagus grandifolia*
				boxelder	224	0.7	*Acer negundo*
				American sycamore	184	0.6	*Platanus occidentalis*
				slippery elm	174	0.6	*Ulmus rubra*
				baldcypress	163	0.5	*Taxodium distichum*
				sugarberry	151	0.5	*Celtis laevigata*
				willow oak	145	0.5	*Quercus phellos*