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Two Centuries of Forest Compositional and Structural Changes in the Alabama Fall Line Hills

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Abstract.—Documenting changes in forest composition and structure through time and in response to disturbances strengthens our understanding of the processes that have created contemporary forest ecosystems. Results from these studies also provide the historical range of variation in forest characteristics, which is essential for establishing place-based targets for forest management. Using historical archives and current forest inventory data from the past two centuries, we quantified forest composition and structure following fundamental shifts in land use for a forest in the Fall Line Hills of Alabama (pre-European settlement (1820 and 1842), pre-industrial logging (1905), U.S. Forest Service acquisition (1943), and contemporary conditions (present)). To quantify conditions prior to European settlement, we analyzed General Land Office surveys of 1820 and 1842. We used Reed (1905) and Harper (1943) to document conditions during the early to mid-20th century. To quantify current forest conditions, we sampled 80 0.04 ha fixed area plots throughout the study area. Forest structure shifted from relatively large trees at low densities, with few small stems prior to European settlement to a relatively high density of small stems, with few large trees post-industrial logging. Although relative contributions of species varied over the past two centuries, forest composition remained relatively stable. Despite changes in land use, *Pinus palustris* remained the most common species in the forest.

Introduction

Documentation of successional and developmental processes is important in the eastern U.S. because the majority of the landscape supports secondary forests that regenerated after widespread timber harvesting sometimes coupled with other human impacts, such as grazing or row cropping, in the 20th century. Changes in disturbance regimes, the introduction of exotic pathogens, and shifts in human resource use, among other factors, are strong controls on forest composition, structure, and function and may have lasting legacies on successional and developmental pathways (Whitney, 1994; Ruffner and Abrams, 1998; Hart *et al.*, 2008). As such, forest conditions often reflect previous land-use history (Stapanian *et al.*, 1997; Foster *et al.*, 2003; Brudvig *et al.*, 2013). Throughout the eastern U.S., many stands do not resemble pre-European settlement conditions and this pattern is most often attributed to changes in land use and altered disturbance regimes that modified vegetation-environment relationships (Fralish *et al.*, 1991; Cowell, 1995; Foster *et al.*, 1998; Nowacki and Abrams, 2008). Reconstructed land-use and disturbance histories allow for a more comprehensive understanding of the conditions that created contemporary forest communities. These studies provide reference models to quantify the historical range of variation in forest conditions and provide information on forest response to exogenous disturbance events. Presettlement forest characteristics and land-use histories have been studied in the southeastern U.S. (*e.g.* Delcourt and Delcourt, 1977; Shankman and Wills, 1995; Black *et al.*, 2002; Predmore *et al.*, 2007), but no such studies have been conducted in the Fall Line Hills, a physiographic belt that spans from Mississippi to Virginia.

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The Fall Line Hills represent the transition zone between the Coastal Plain and Appalachian Highland physiographic provinces (Fenneman, 1938; Shankman and Hart, 2007). The Fall Line is a biogeographic boundary because it marks a transition between unlike physiographic provinces, representing the northward range limit for some Coastal Plain tree species and the southern range limit for some tree species common in the Appalachian Highlands (Shankman and Hart, 2007). Therefore, the Fall Line Hills region supports unique plant communities where species with ranges that do not typically overlap may co-occur. The Fall Line Hills range in width from 15 to 80 km and are widest in areas where streams have eroded through Coastal Plain sediments exposing previously underlying Appalachian formations. This region lacks historical ecological studies, which hinders forest planning efforts.

The goal of our study was to document the response of forest conditions to shifting land-use patterns over the past two centuries for a forest in the Fall Line Hills of Alabama. We analyzed historical records and conducted forest inventories for times that corresponded to fundamental shifts in land use: (1) pre-European settlement (1820 and 1842), (2) pre- industrial logging (1905), (3) U.S. Forest Service acquisition (1943), and (4) contemporary conditions. By reconstructing forest composition and structure over the past two centuries and by documenting the influences of fundamental land-use changes on forest characteristics, our results provide information on the ecological history for an understudied region. Our results may be used by forest managers to establish desired future conditions and make more informed decisions in forest planning.

METHODS

STUDY AREA

Our study was located on the Oakmulgee Ranger District of Talladega National Forest, covering portions of Tuscaloosa, Bibb, Hale, and Perry counties in west-central Alabama. The study area spanned 55,425 ha on the northwest portion of the ranger district and included Reed Brake Natural Area, a 242 ha tract reserved for research in 1975 by the U.S. Forest Service (32.942, −87.389, study sites were within a 17 km radius from location). Drastic land-use changes have occurred in the region during the past two centuries. These changes are representative of land-use shifts that occurred throughout the eastern U.S.

The Fall Line Hills region is highly dissected and characterized by sand formations that support steep slopes (Fenneman, 1938). The geology of the region is composed of the Tuscaloosa Gordo and Coker formations from the Upper Cretaceous system. The Gordo formation is comprised of cross-bedded and gravelly sand with beds of carbonaceous clay and chert and quartz pebbles, and the Coker formation consists of micaceous, fine sand, micaceous clay, and thin gravel beds of chert and quartz pebbles (Szabo *et al.*, 1988). The topography of the study area is characterized by steep, narrow ridges capped by sandstone (Reed, 1905). Elevation of the study area varies from 55 to 183 m above mean sea level. Regionally, soils are sandy, generally well-drained, and easily erodible (Reed, 1905; USDA, 2008).

Thornthwaite (1948) described the climate as humid mesothermal with short mild winters and long hot summers. Annual mean temperature for the site is 17 C, with mean temperatures of 7 C and 27 C for January and July, respectively. Annual mean precipitation is 140 cm, with mean precipitation of 13.9 cm and 11.4 cm for January and July, respectively (PRISM, 2014). The regional frost-free period typically lasts 200 d and spans from March to November (USDA, 2008).

Forests in this region were classified by Braun (1950) as *Quercus-Pinus*. Beckett and Golden (1982) used a gradient analysis to identify eight community types in the Reed Brake Natural Area within the Oakmulgee District. The most common community types were *P. palustris*-dominated, *P. taeda*-hardwoods, and *Nyssa biflora-Persea borbonia*. Other community types included *Quercus montana*, *Liquidambar styraciflua-Liriodendron tulipifera*, *P. echinata*-hardwoods, and *Q. falcata*-mixed *Quercus* communities.

Prior to European settlement, Native Americans inhabited areas along the Black Warrior River, which flows north and west of the study site. Moundville, a large political and social center for Mississippian Indians until 1700 (Maxham, 2000), is located about 13 km from the border of the Oakmulgee Ranger District. Native Americans undoubtedly influenced the forest prior to European settlement, especially given the proximity to Moundville and surrounding farmstead communities, where the majority of the Moundville polity lived (Welch, 1998). Between 1810 and 1850, European settlement expanded throughout the southeastern U.S. and the nonIndian population grew to $\geq$1.2 people km^{-2} (Frost, 1993). Early settlers commonly lived near streams and only harvested timber needed to build and provide energy for their homesteads. Widespread settlement of the area occurred from the 1860s to the 1880s (Baggett, 1993). Kaul Lumber Company purchased the land in the early 1900s and began industrial-scale production in 1912. Timber harvesting continued on the tract until 1931 when John Kaul, the owner of the lumber company, died and the company was sold. In 1935 the U.S. Forest Service created the Oakmulgee Purchase Unit, forming the current Oakmulgee Ranger District of Talladega National Forest. The Forest Service has devoted much of their management efforts to the restoration of *P. palustris*-dominated communities and the preservation of *Picoides borealis* Vieillot, a federally-listed endangered woodpecker, on the district (USDA, 2005).

DATA SOURCES AND ANALYSIS

Using historical and natural archives, we developed an ecological history that spanned two centuries divided into four fundamental land-use change periods for a forest in the Fall Line Hills of Alabama.

Pre-European settlement.—To quantify pre-European settlement forest characteristics, we used records from the General Land Office (GLO) Public Lands Survey System from 1820 and 1842. The PLSS divided land into 93 km^2 townships arranged in a grid system extending from multiple meridians in each state. Each township was divided into 36 sections. While walking the borders of these sections, the surveyors recorded four trees at each section corner using the point-center quarter method (Cottam and Curtis, 1956) and two trees at each 0.8 km (half-mile) post (Bourdo, 1956). Potential bias exists in survey notes because of individual surveyor's preference for a certain species or for larger trees (Bourdo, 1956), but potential bias of individual surveyors in Alabama is unknown because few GLO studies have been conducted in the state.

The study area was initially surveyed by the GLO in 1820 and the earliest settlement deeds in Bibb and Hale counties date to the early portion of the decade (Baggett, 1993). Therefore, the land was surveyed prior to formal European settlement. Some of the original field notes of 1820 were destroyed by a fire at the land survey office in Florence, Alabama. In 1842 surveyors retraced 132 points for which the original field notes had been lost using the same methods as the 1820 survey. We speculate any impacts of early settlers were localized to homesteads, which were clustered near streams, and the resurveyed lines of 1842 reflected conditions prior to widespread settlement and European impacts. Using the GLO surveys of 1820 and 1842, we documented the witness tree taxa, witness tree location (distance and azimuth from section corner), and the general site description (soil class, forest type, open woods, and locations of streams and *Arundinaria* spp. brakes) for each township, range, and section in our study area. From the species common names listed in the original surveys, we referenced Weakley (2012) to obtain current binomials.

We georeferenced each surveyed corner in the study area (n = 726) and used a digital elevation model overlay in a geographic information system to classify each corner by topographic position as either: (1) ridgetop and upper slope, (2) south to west facing mid-slope, (3) north to east facing mid-slope, or (4) lower slope and bottomland. The goal of our topographic characterization was to categorize composition and structural conditions across a moisture gradient, which is a strong control on forest composition and structure in this region (Shankman and Wills, 1995; Ruffner and Abrams, 1998; Elliott *et al.*, 1999). We calculated relative frequencies for each taxon mentioned in the original land surveys using these topographic categories. For each witness tree taxon, we formed a 2×4 contingency table, tallying taxon presence and absence by topographic position and calculated the G^2 statistic to test for independence between witness tree taxon and topographic position (Strahler, 1978). For taxa with significant relationships ($P < 0.05$), we calculated standardized residuals (Haberman, 1973). The standardized residual values indicate if a species is more or less likely to occur on a certain topographic position (Whitney, 1990; Ruffner and Abrams, 1998). Total forest density across all topographic classifications was calculated using the Morisita (1957) density estimator and the distances of each witness tree from its corresponding section corner. To minimize estimator bias and more accurately represent the actual density of the presettlement forest, we applied correction factors for biased density estimates recommended by Hanberry *et al.* (2011) for the Morisita density estimator. We georeferenced locations where surveyors noted 'open woods' (*i.e.* woodland structures) and used the relative frequency of these labeled corners to calculate the percent of land occupied by woodland structures. We used a *t*-test to determine significant difference between the average distance between witness tree and section corners for corners labeled "open woods" against those without this designation. Locations of *Arundinaria* spp. brakes were also mapped based on surveyors' notes.

Pre-industrial logging.—To document change in forest conditions after European settlement prior to industrial timber harvesting, we used data collected by Reed (1905). Reed (1905) quantified the composition and structure of 28,517 ha of land in the Bibb County tract, which is located within our study area, to make recommendations for the Kaul Lumber Company's management plan. His analysis divided parcels into *P. palustris* lands, bottomlands, and unwooded lands. On *P. palustris* lands, Reed (1905) documented species and diameter of all *P. palustris* stems greater than 3 cm diameter at breast height (DBH) and all *P. taeda*, and *P. echinata* stems greater than 15 cm DBH. On bottomlands, Reed (1905) documented stems of commercially important hardwood species greater than 25 cm DBH and used the same size classes for the three *Pinus* spp. Reed (1905) stated the number of hectares within each tract that were unwooded but provided no additional information for unwooded lands. Portions of the tract in which few *P. palustris* stems were present or in which the forest had been severely disturbed were not surveyed. For our land cover descriptions, we only incorporated data from stems greater than 25 cm DBH because this size threshold was identical for all listed species.

U.S. Forest Service acquisition.—To describe characteristics of the forest following industrial timber harvesting in the early 20th century, we reviewed data from Harper (1943). Harper (1943) provided a qualitative observation of the forest, listing species by importance and describing general forest characteristics and environmental gradients. We summarized the content of these qualitative observations to describe forest conditions following intensive

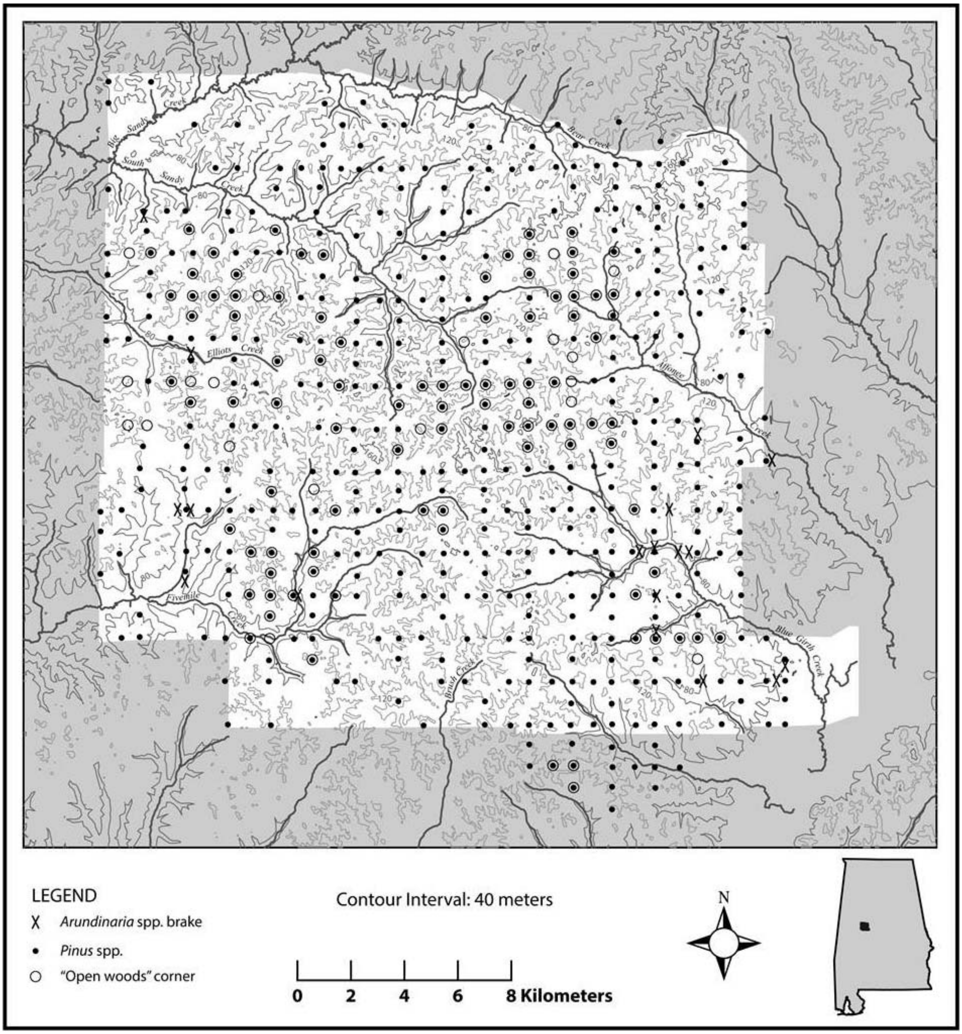

FIG. 1.—Map of pre-European settlement forest composition and structure on the Oakmulgee Ranger District, Talladega National Forest, Alabama. The shaded portion of the inset map represents the study area. Points represent section corners and half-corners of the GLO survey (1820 and 1842) with corresponding species and site descriptions. *Arundinaria* spp. brakes noted by surveyors along transects are shown

timber harvesting practices of the early 20th century and after the acquisition of the Oakmulgee Purchase Unit by the U.S. Forest Service.

Contemporary conditions.—To quantify current forest composition and structure, we established 80 0.04 ha fixed-area plots stratified along the same topographic gradient used to describe pre-European settlement forests (20 plots each on ridgetops and upper slopes, south to west facing mid-slopes, north to east facing mid-slopes, and lower slopes and bottomlands) distributed throughout the entire forest. Species, DBH, and canopy class were

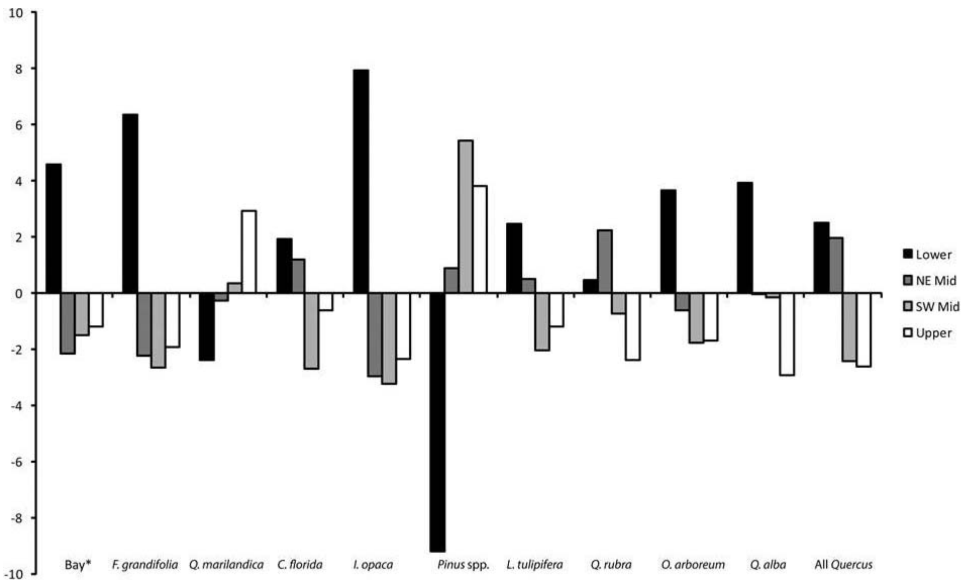

FIG. 2.—Significant associations ($P < 0.05$) of taxa on varying topographic positions on the Oakmulgee Ranger District, Talladega National Forest, Alabama. Values correspond to the likelihood of a species occurring on the given topographic position. * Either *P. borbona* or *M. virginiana*

recorded for each stem ≥10 cm DBH. Canopy classes included overtopped (crown restricted from above), intermediate (crown extends to the lower level of the canopy), codominant (crown forms a level canopy stratum), and dominant (crown extends above the canopy stratum) (Oliver and Larson, 1996). Snags, snapped stems, and uprooted stems were not included in our analysis. Relative frequency, relative density, and relative dominance were calculated for each species recorded on these plots.

RESULTS

PRE-EUROPEAN SETTLEMENT

Pinus spp., *Quercus* spp., and *Carya* spp. were the most commonly occurring stems in the presettlement forest (Table 1). *Pinus* spp. were the most commonly occurring taxa across all topographic positions and were distributed throughout the entire study area (Fig. 1). On lower slopes and bottomlands, *Q. stellata, Q. rubra,* and *Ilex opaca* were the second most commonly occurring taxa (all had equal values). On north and east facing mid-slopes, *Q. rubra* was the second most commonly occurring species. On south and west facing mid-slopes, *Q. stellata* was the second most commonly occurring species. *Quercus marilandica* was the second most commonly occurring species on ridgetops and upper slopes. We estimated the total tree density of the presettlement forest to be 370 stems ha^{-1}. Corners that the surveyors described as "open woods" occurred throughout the study area and represented 16% of all corners (Fig. 1). The proportion of corners with 'open woods' descriptions varied by topographic position with bottomland, north and east facing slope, south and west facing slop, and ridgetop corners having 12%, 21%, 15%, and 15% "open woods" corners, respectively. The average distance from a witness tree to a section corner was not

TABLE 1.—Relative frequencies (% of corners at which species occurred) of pre-European settlement forest species at all section corners and half-corners (n = 726) by topographic position on the Oakmulgee Ranger District, Talladega National Forest, Alabama

	Topographic sites				
	Mesic →			Xeric	
Taxa	Lower slope	NE mid slope	SW mid slope	Upper slope	Total
Pine (*Pinus* spp. L.)	43.7	70.7	83.9	83.5	68.3
Red Oak (*Quercus rubra* L.)	12.7	16.1	10.4	5.2	11.8
Post Oak (*Q. stellata* Wangenh.)	12.7	10.2	11.9	12.2	11.7
Hickory (*Carya* spp. Nutt.)	10.8	9.8	5.2	7.0	8.4
Dogwood (*Cornus florida* L.)	10.3	9.3	3.1	6.1	7.4
Blackjack (*Q. marilandica* Münchh.)	3.3	6.3	7.3	13.0	6.7
Chestnut (*Castanea dentata* Marshall (Borkh.))	7.0	7.3	4.1	6.1	6.2
White Oak (*Q. alba* L.)	11.3	5.9	3.6	—	5.9
Black Oak (*Q. velutina* Lam.)	8.0	6.3	3.1	5.2	5.8
Black Gum (*Nyssa sylvatica* Marshall)	7.5	6.8	3.6	2.6	5.5
Holly (*Ilex opaca* Aiton)	12.7	0.5	—	—	3.9
Sourwood (*Oxydendrum arboreum* (L.) DC.)	7.5	2.9	1.6	0.9	3.6
Maple (*Acer* spp. L.)	5.2	2.9	1.6	0.9	2.9
Beech (*Fagus grandifolia* Ehrh.)	8.5	0.5	—	—	2.6
Bay*	6.6	0.5	1.0	0.9	2.5
Poplar (*Liriodendron tulipifera* L.)	4.7	2.9	0.5	0.9	2.5
Sweet Gum (*Liquidambar styraciflua* L.)	3.8	2.4	1.0	—	2.1
Chinquapin (*Castanea pumila* (L.) Mill.)	2.8	2.4	1.0	0.9	1.9
Spanish Oak (*Q. falcata* Michx.)	2.3	2.4	1.0	—	1.7
Chestnut Oak (*Q. montana* Willd.)	0.9	2.0	1.0	—	1.1
Water Oak (*Q. nigra* L.)	2.8	0.5	—	—	1.0
Bullbay (*Magnolia grandiflora* L.)	1.9	0.5	0.5	—	0.8
Persimmon (*Diospyros virginiana* L.)	1.4	1.5	—	—	0.8
Ash (*Fraxinus* spp. L.)	0.9	1.5	—	—	0.7
Cucumber (*Magnolia acuminata* (L.) L.)	0.9	0.5	1.0	—	0.7
Gum**	1.4	0.5	—	—	0.6
Sassafras (*Sassafras albidum* (Nutt.) Nees)	0.9	0.5	—	—	0.4
Birch (*Betula* spp. L.)	0.9	—	—	—	0.3
Sycamore (*Platanus occidentalis* L.)	0.5	0.5	—	—	0.3
Hazel (*Alnus serrulata* (Aiton) Willd.)	0.5	—	—	—	0.1
Hornbeam (*Carpinus caroliniana* Walter)	—	0.5	—	—	0.1
Swamp Oak (*Q. bicolor* Willd.)	—	0.5	—	—	0.1
Sweet Elm (*Ulmus* spp. L.)	0.5	—	—	—	0.1
Willow Oak (*Q. phellos* L.)	0.5	—	—	—	0.1

* Either *Persea borbonia* (L.) Spreng or *Magnolia virginiana* L.

** Either *N. sylvatica* or *L. styraciflua*

significantly different (P = 0.47) for corners described as "open woods" versus those not described as "open woods." Species-environment analysis illustrated that *Persea borbonia* or *Magnolia virgniniana*, *Fagus grandifolia*, *Ilex opaca*, *Oxydendrum arboretum,* and *Q. alba* exhibited a strong positive relationship with lower slope positions, and *Pinus* spp. exhibited a negative association with lower slopes (Fig. 2). *Pinus* spp. and *Q. marilandica* exhibited a strong positive association with ridgetop and upper slope positions.

TABLE 2.—Density of forest species on the Bibb County tract in central Alabama from Reed (1905). Area (ha) of unwooded land is included in the total density. Nomenclative from Reed (1905)

	Density (stems/ha)		
Taxa	Longleaf	Bottomland	Total
Longleaf pine (*P. palustris*)	65.8	2.6	51.7
Loblolly pine (*P. taeda*)	8.0	40.2	10.6
Shortleaf pine (*Pinus echinata*)	3.7	1.3	3.0
White oaks (*Q. Leucobaus*)	—	5.0	0.5
Black oaks (*Q. Erythrobalanus*)	—	7.4	0.8
Red gum (*Liquidambar styraciflua*)	—	12.2	1.3
Yellow-poplar (*Liriodendron tulipifera*)	—	5.1	0.6
Other hardwoods	—	28.9	3.1
Total	77.5	102.9	71.8

PRE-INDUSTRIAL LOGGING

The tract was divided into *P. palustris* land (22,284 ha), bottomland (3082 ha), and unwooded land (3151 ha). Total density of stems >25 cm was 72 stems ha^{-1} across all forest classifications, including unwooded lands (Table 2). Excluding unwooded lands, total density of such stems was 81 ha^{-1}. *Pinus palustris* was the most commonly occurring species on *P. palustris* lands, whereas *P. taeda* was the most commonly occurring species on bottomlands (Table 2). Bottomland areas had a higher density of stems >25 cm than *P. palustris* lands (Table 2). Of the total tract, 43% of the land had been previously logged and 15% had been boxed for turpentine (Fig. 3). Reed (1905) recommended that the Kaul Lumber Company raise the previous lower diameter limit to 46 cm to yield the best financial returns.

U.S. FOREST SERVICE ACQUISITION

The majority of the study area occurred within Harper's (1943) Central *P. palustris* Hills region (Fig. 4). This region was described as highly fragmented and scattered throughout the Central *Pinus* Belt that extended across the state, corresponding with the Fall Line Hills. The *P. palustris* Hills were bordered by the *P. taeda* Belt, the Coal Basin Region, and the Eutaw Belt. Harper (1943) listed the most common species in the *P. palustris* Hills as *P. palustris* in the uplands, *P. taeda* in valleys, and *M. virginiana* in riparian zones of small streams. Evergreen stems, primarily *P. palustris,* comprised about half of all stems. Ridgetop canopies were composed of *P. palustris* with an understory and mid-story composed of *Q. marilandica, Q. laevis, Q. incana* W. Bartram, and *Q. stellata*. Although *Q. incana* is only described in Harper (1943), the species commonly grows in *P. palustris* ecosystems in the midstory layer. Several hardwood species and other *Pinus* species grew on lower slopes and valleys. The southeastern portion of the study area was classified by Harper (1943) as part of the *P. taeda* Belt. This area was dominated by *P. taeda, P. echinata,* and *M. virgniana. Pinus palustris* was present in this region, but was less dominant than *P. taeda* and *P. echinata.*

CONTEMPORARY CONDITIONS

The contemporary forest was dominated by *P. palustris, P. taeda,* and *Q. montana* (Table 3). *Pinus palustris* had the highest relative density of any species and *P. taeda* had the highest relative frequency. Basal area for the forest was 26.3 m^2 ha^{-1} and tree

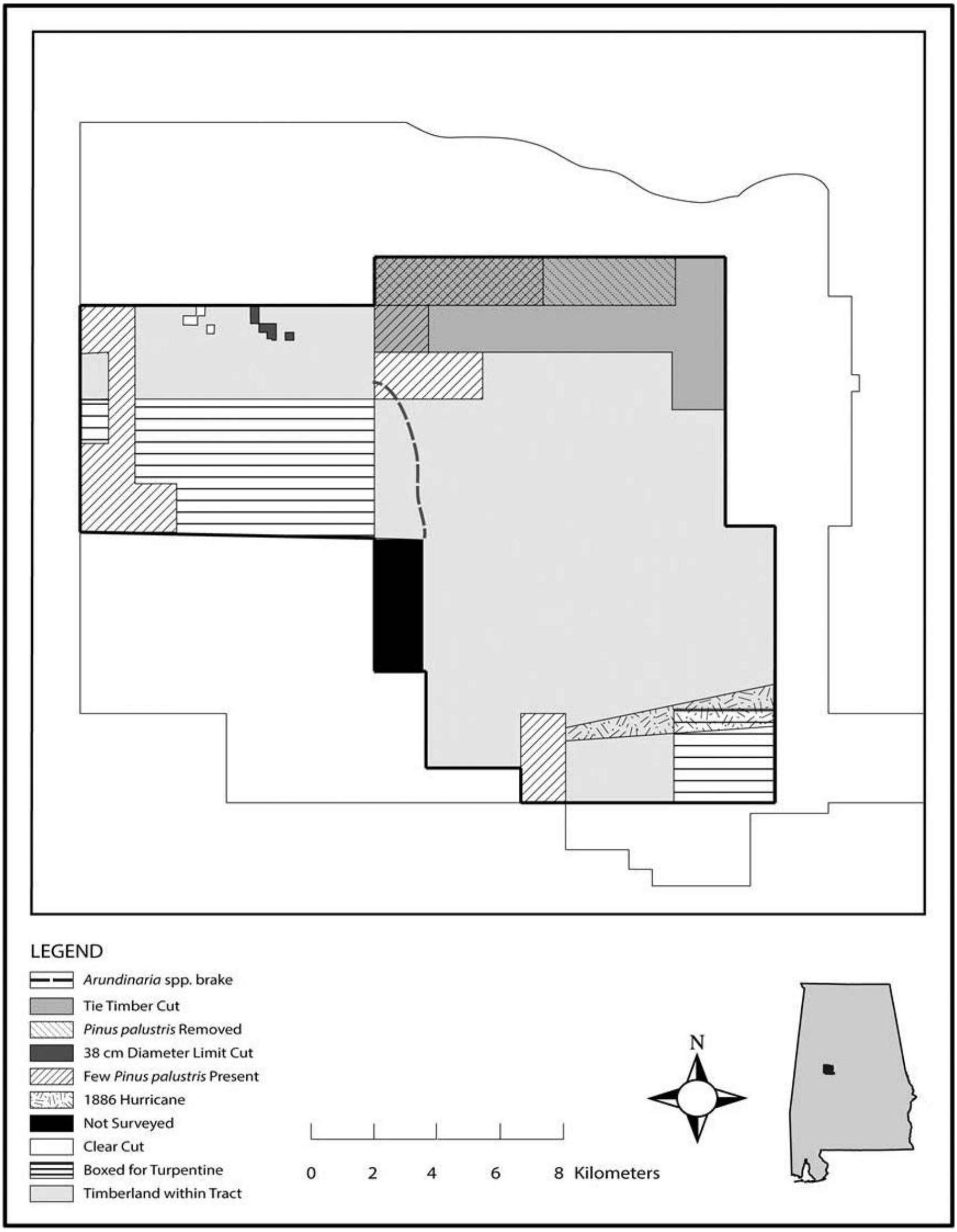

FIG. 3.—Map of Bibb County (Alabama) tract from Reed (1905). The fine border surrounding the Bibb County tract represents the Oakmulgee Ranger District, Talladega National Forest. Notable observations from the site description are indicated

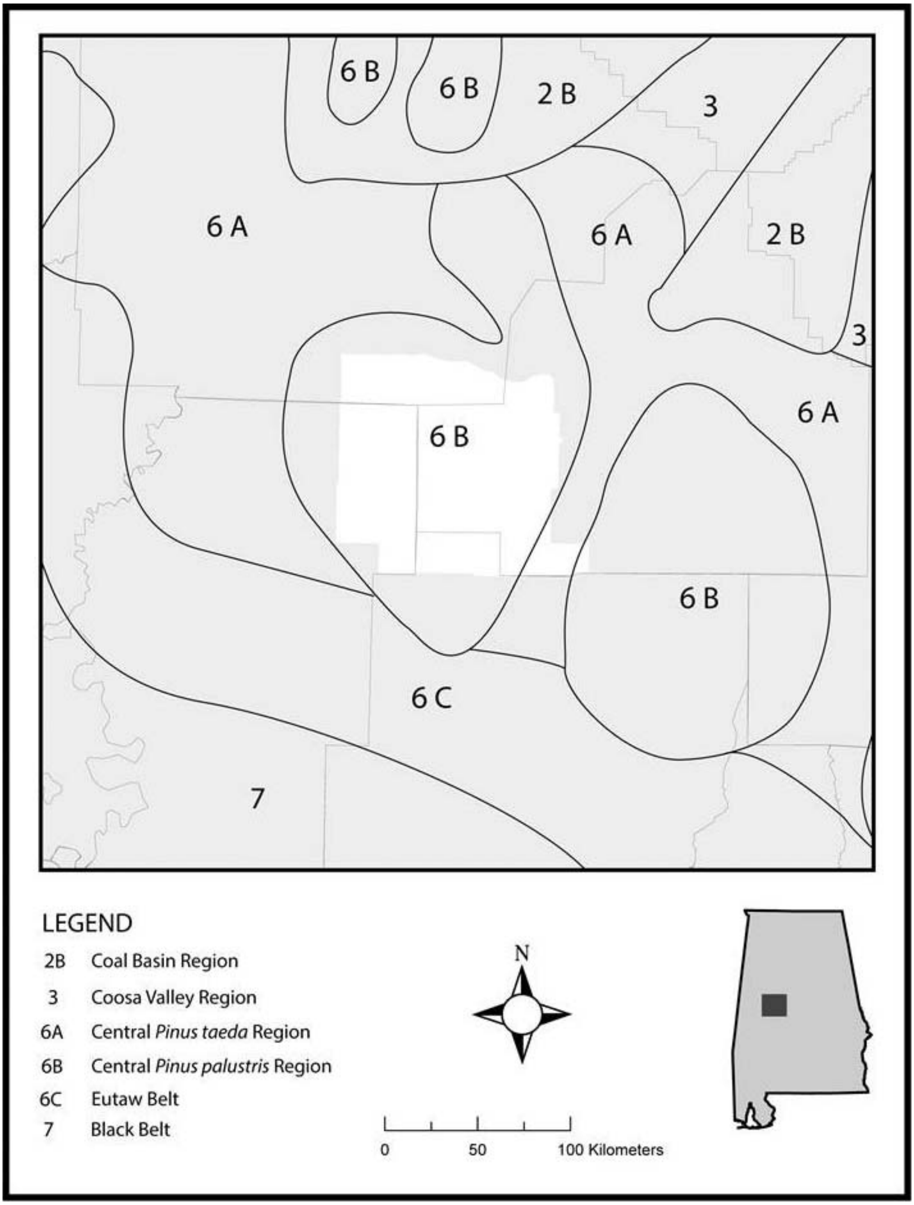

FIG. 4.—Forest classifications of west-central Alabama based on Harper (1943). The white region represents the Oakmulgee Ranger District, Talladega National Forest, Alabama

density was 493 stems ha^{-1}. Basal area for *P. palustris, P. taeda,* and *Q. montana* was 8.1 m^2 ha^{-1}, 4.0 m^2 ha^{-1}, and 2.4 m^2 ha^{-1}, respectively. Density for *P. palustris, P. taeda,* and *Q. montana* was 128 stems ha^{-1}, 61 stems ha^{-1}, and 46 stems ha^{-1}, respectively. Density of stems $\geq$10 cm DBH was greatest on ridgetops and upper slopes and lowest on bottomlands and lower slopes, whereas basal area was greatest on ridgetops and upper slopes and lowest on south and west facing slopes (Table 3). Across all topographic classes, density of stems ≥25 cm DBH was 173 ha^{-1}. Diameter distribution formed an inverse J-shaped curve with the smallest size class dominated by species other than *Pinus* spp. and *Quercus-Carya* spp., and all other size classes dominated by four *Pinus* spp. (Fig. 5). The forest overstory was dominated by *Pinus* spp., while *Quercus* spp. and *Carya* spp. dominated the intermediate class and other hardwoods composed the majority of the overtopped class (Fig. 6).

DISCUSSION

PRE-EUROPEAN SETTLEMENT

In pre-European settlement forests, *Pinus* spp. were the most commonly occurring taxa across all topographic positions. Because the genus was not divided into species in the early survey, we could not determine the specific compositional distribution of presettlement *Pinus* spp. However, we suspect that the majority of *Pinus* stems on ridgetops and upper slope positions with poor, sandy soils were *P. palustris* and that the majority of *Pinus* stems in lower slope positions with more fertile soils were *P. taeda* (Harper, 1943; Shankman and Wills, 1995).

We concluded, prior to European settlement, the forest was largely closed canopy based on our estimated tree density from the GLO surveys. Based on rules established by the GLO for surveyors, we assumed witness trees were most likely stems greater than 25 cm DBH (Bourdo, 1956). However, patches of woodland and perhaps even savanna-like structures likely existed, roughly comprising 16% of the area as noted by surveyors (Fig. 2). The distances from corner points to witness trees did not significantly differ between corners marked "open woods" and those not marked "open woods." We suggest locations recorded as "open woods" were those that lacked mid-story or understory strata and were characterized by large canopy trees with an open understory resembling a woodland structure. Distances between corners and witness trees should not have differed if the primary difference between "open woods" was the presence or absence of a mid-story layer. Because witness trees were likely large and easily noticeable, surveyors may have passed over smaller trees in favor of larger ones.

Arundinaria spp. brakes have been present in the study area since at least the 1820s, prior to widespread European settlement. Original surveyors noted multiple *Arundinaria* spp. brakes which spanned over a hectare in extent along the surveyed section boundaries (*see* Fig. 1), with many stems growing 3–4 m height (Platt and Brantley, 1997). In the southeastern U.S., *Arundinaria* spp. brakes were typically found in unwooded alluvial plains or in areas with savanna-like structures (Platt and Brantley, 1997). *Arundinaria* spp. brakes were historically maintained by fires that occurred approximately every 10 y that eliminated competing woody stems. Shorter fire return intervals favor pyrophilic trees and shrubs and inhibit primary growth of *Arundinaria* spp. (Hughes, 1957; Gagnon, 2009). Bale *et al.* (2008) described the mean fire interval (MFI) of an Alabama montane *P. palustris* system to have been 11 y, between 1575 and 1700. The MFI decreased to 3 y from 1725 until the early 1900s (Bale *et al.*, 2008). Although the documented presettlement MFI of 3 y would hypothetically support fire-tolerant trees and shrubs over *Arundinaria* spp., fire was likely less frequent in bottomland and lower slope positions, which would have allowed the *Arundinaria* spp. brakes to be maintained in these areas prior to settlement (Cowell, 1995; Shankman and Wills, 1995; Bale *et al.*, 2008).

PRE-INDUSTRIAL LOGGING

Timber harvesting and turpentine production began in the late 19th and early 20th centuries. According to Reed (1905), prior to 1905, trees were harvested based on a lower diameter limit of 38 cm DBH. Because only stems above 25 cm were recorded in Reed (1905), we assumed that all witness trees were at least 25 cm DBH by the time of harvest. Therefore, it is likely that many of the original witness trees were removed during the logging operations prior to Reed (1905), given the previous diameter limit cut of 38 cm.

Pinus palustris was the dominant species in the forest when Kaul Lumber Company gained ownership. Sites with large proportions of *P. taeda* and *P. echinata* were less valued than *P. palustris* by the Kaul Lumber Company. Reed (1905) only mentioned three species (*P. palustris, P. taeda, P. echinata*) found on *P. palustris* lands, and grouped hardwoods into broad categories (*Quercus Leucobalanus* spp., *Quercus Erythrobalanus* spp., *L. styraciflua, L. tulipifera,* and other hardwoods) in bottomlands because the Kaul Lumber Company, for whom the plan was written, focused on *P. palustris* production. Hardwoods composed a large portion of stems on bottomlands (66% of all stems) prior to industrial logging, but were not surveyed on *P. palustris* lands. Hardwood species may have been present on *P. palustris* lands, but were not mentioned in Reed (1905).

Assuming that all witness trees were >25 cm DBH, a conservative estimate, density of large stems (>25 cm) decreased from 1820 to 1905 by ca. 80%. Reed (1905) noted that logging had occurred in the area since the establishment of the Mobile and Ohio Railroad in 1897. Logging impacts were localized rather than widespread as *P. palustris* was selectively harvested from sites that were relatively easy to access (Reed 1905). In the early 1900s, an annual fire return interval was promoted to reduce fuel loading and protect timber from potentially dangerous fires. Concurrently, early European settlers also boxed *P. palustris* for turpentine near home sites. Reed (1905) stated that the selective harvesting of *P. palustris*, boxing trees for turpentine production, and a shorter fire return interval had largely removed *P. palustris* from private landholdings on the tract at the time of the report (Fig. 2). These impacts may have resulted in the removal of some original witness trees and therefore, lowered density of large trees in the forest.

Reed (1905) noted the abundance of *Arundinaria* spp. brakes had declined from the time of the GLO surveys to the early 1900s and he attributed this to an increase in fire frequency. However, *Illicium floridanum* Ellis, a species that most commonly occurs in marshy areas, was relatively abundant in riparian zones in the early 20th century, where *Arundaria* spp. brakes were found in presettlement forests. Reed (1905) remarked that only one *Arundinaria* spp. brake remained in the center of the Bibb County tract (Fig. 2), which "in some places forms dense, almost impenetrable thickets over 0.4 km (0.25 mile) in width" (p. 48). This *Arundinaria* spp. brake occurred near the current Reed Brake Natural Area. Portions of the forest that were described prior to European settlement as dense *Arundinaria* spp. brakes, were described by Reed (1905) as young stands dominated by *L. styraciflua* and *M. virginiana.*

Reed (1905) commented tornadoes and other strong wind events often impacted the forest, especially portions on ridgetops, but occasionally left a path in which all timber was broken or uprooted. Reed (1905) cited the hurricane of 1886 as the most noteworthy example of an exogenous disturbance which had major and lasting impacts. The wind uprooted or broke almost every stem in the 1000 ha storm track. After 18 y, at the time of the report, minimal reproduction had occurred in the area, which Reed (1905) attributed to frequent fires and a paucity of seed trees. On the majority of the damaged area, *Quercus, Carya,* and other hardwood saplings occurred at high densities, but *P. palustris* saplings were found only in small, scattered patches (Abrams and Scott, 1989). Some relatively large areas

TABLE 3.—Relative frequency (% of plots on which species occurred), relative density (% contribution of species to total density), and relative dominance (% contribution of species to total basal area) for current forest species across varying topographic positions on the Oakmulgee Ranger District, Talladega National Forest, Alabama

	Topographic Sites														
	Mesic									Xeric					
	Lower Slope			NE Mid Slope			SW Mid Slope			Upper Slope			Total		
Taxa	Rel. Freq.	Rel. Den.	Rel. Dom.	Rel. Freq.	Rel. Den.	Rel. Dom.	Rel. Freq.	Rel. Den.	Rel. Dom.	Rel. Freq.	Rel. Den.	Rel. Dom.	Rel. Freq.	Rel. Den.	Rel. Dom.
Pinus palustris	30.0	4.3	9.8	80.0	17.3	24.2	60.0	29.1	35.7	70.0	46.6	53.7	60.0	25.9	31.0
Pinus taeda	60.0	12.1	18.1	65.0	12.7	14.3	65.0	9.7	13.0	55.0	14.8	15.4	61.3	12.4	15.3
Quercus montana	45.0	10.4	5.6	55.0	15.5	18.2	20.0	7.3	7.8	25.0	5.0	4.7	36.3	9.3	9.0
Quercus rubra	35.0	4.3	4.3	70.0	8.0	11.3	35.0	2.6	5.7	40.0	3.7	6.5	45.0	4.6	7.0
Liriodendron tulipifera	55.0	6.6	11.5	40.0	3.1	6.0	10.0	3.1	1.6	10.0	0.4	0.5	28.8	3.1	5.0
Carya spp.	70.0	9.5	9.3	60.0	8.0	4.7	35.0	3.4	1.7	40.0	5.9	2.9	51.3	6.6	4.8
Liquidambar styraciflua	70.0	11.8	6.6	35.0	6.7	4.0	40.0	6.5	5.1	35.0	2.2	1.6	45.0	6.5	4.3
Quercus falcata	45.0	4.3	5.7	25.0	2.6	3.3	50.0	3.7	5.5	20.0	0.9	1.6	35.0	2.7	3.9
Pinus echinata	30.0	4.3	7.2	20.0	1.0	1.8	35.0	4.2	6.7	15.0	0.7	0.5	25.0	2.4	3.9
Oxydendron arboreum	75.0	7.2	3.6	45.0	6.2	3.1	45.0	7.1	3.8	25.0	2.2	1.1	47.5	5.5	2.8
Quercus alba	40.0	8.1	7.4	30.0	3.1	1.7	15.0	0.8	0.4	25.0	1.7	0.7	27.5	3.2	2.6
Quercus stellata	45.0	4.3	3.0	35.0	2.3	1.6	35.0	5.0	3.8	30.0	2.6	1.8	36.3	3.5	2.5
Quercus marilandica	—	—	—	5.0	0.5	0.2	25.0	4.2	2.6	30.0	4.6	3.7	15.0	2.5	1.6
Quercus vellutina	15.0	0.9	0.5	10.0	0.8	1.3	5.0	0.8	1.2	5.0	1.7	1.6	8.8	1.1	1.1
Pinus virginiana	5.0	0.3	0.6	5.0	0.5	0.2	10.0	3.1	2.1	10.0	1.3	1.6	7.5	1.3	1.1
Nyssa sylvatica	20.0	1.4	1.8	25.0	1.8	0.5	35.0	2.1	0.6	20.0	0.9	0.3	25.0	1.5	0.8
Acer rubrum	40.0	4.9	1.8	5.0	0.3	0.3	5.0	0.5	0.5	10.0	0.9	0.4	15.0	1.5	0.7
Acer flordianum Champ.) Pax	5.0	0.6	1.4	20.0	1.6	0.5	5.0	0.3	0.1	—	—	—	7.5	0.6	0.5
Cornus florida	10.0	0.6	0.1	35.0	3.1	0.7	40.0	2.4	0.5	30.0	2.8	0.7	28.8	2.3	0.5
Fraxinus americana L.	10.0	0.6	0.2	15.0	1.8	1.0	5.0	0.3	0.4	5.0	0.2	0.0	8.8	0.7	0.4
Quercus nigra	10.0	0.6	0.6	—	—	—	10.0	1.8	0.7	—	—	—	5.0	0.6	0.3
Diospyros virginiana	—	—	—	5.0	0.5	0.3	—	—	—	5.0	0.2	0.5	2.5	0.2	0.2
Sassafras albidum	—	—	—	20.0	1.0	0.4	10.0	0.8	0.2	5.0	0.2	0.0	8.8	0.5	0.2
Prunus serotina Ehrh.	15.0	0.9	0.3	10.0	0.5	0.2	5.0	0.3	0.1	—	0.2	—	7.5	0.4	0.1

TABLE 3.—Continued

	Topographic Sites														
	Mesic									Xeric					
	Lower Slope			NE Mid Slope			SW Mid Slope			Upper Slope			Total		
Taxa	Rel. Freq.	Rel. Den.	Rel. Dom.	Rel. Freq.	Rel. Den.	Rel. Dom.	Rel. Freq.	Rel. Den.	Rel. Dom.	Rel. Freq.	Rel. Den.	Rel. Dom.	Rel. Freq.	Rel. Den.	Rel. Dom.
Juniperus virginiana L.	5.0	0.3	0.2	—	—	—	—	—	—	5.0	0.2	0.0	2.5	0.1	0.1
Quercus hemispherica W. Bartram ex Willd.	—	—	—	—	—	—	5.0	1.0	0.2	—	—	—	1.3	0.3	0.1
Betula lenta L.	5.0	0.3	0.1	5.0	0.5	0.1	—	—	—	—	—	—	2.5	0.2	0.1
Magnolia virginiana	5.0	0.3	0.2	—	—	—	—	—	—	—	—	—	1.3	0.1	0.0
Magnolia acuminata	5.0	0.3	0.1	—	—	—	—	—	—	—	—	—	1.3	0.1	0.0
Magnolia macrophylla Michx.	5.0	0.3	0.1	—	—	—	—	—	—	—	—	—	1.3	0.1	0.0
Quercus laevis Walter	—	—	—	—	—	—	—	—	—	5.0	0.2	0.1	1.3	0.1	0.0
Vaccinium arboreum Marshall	—	—	—	10.0	0.5	0.1	—	—	—	—	—	—	2.5	0.1	0.0
Quercus michauxii Nutt.	5.0	0.3	0.0	—	—	—	—	—	—	—	—	—	1.3	0.1	0.0
Density (stems ha^{-1})	—	**433**	—	—	**484**	—	—	**478**	—	—	**576**	—	—	**493**	—
Dominance (basal area (m^2 ha^{-1})	—	—	**27.2**	—	—	**26.5**	—	—	**22.8**	—	—	**28.5**	—	—	**26.3**

Bold values – indicate total density and dominance for all species across each topographic site

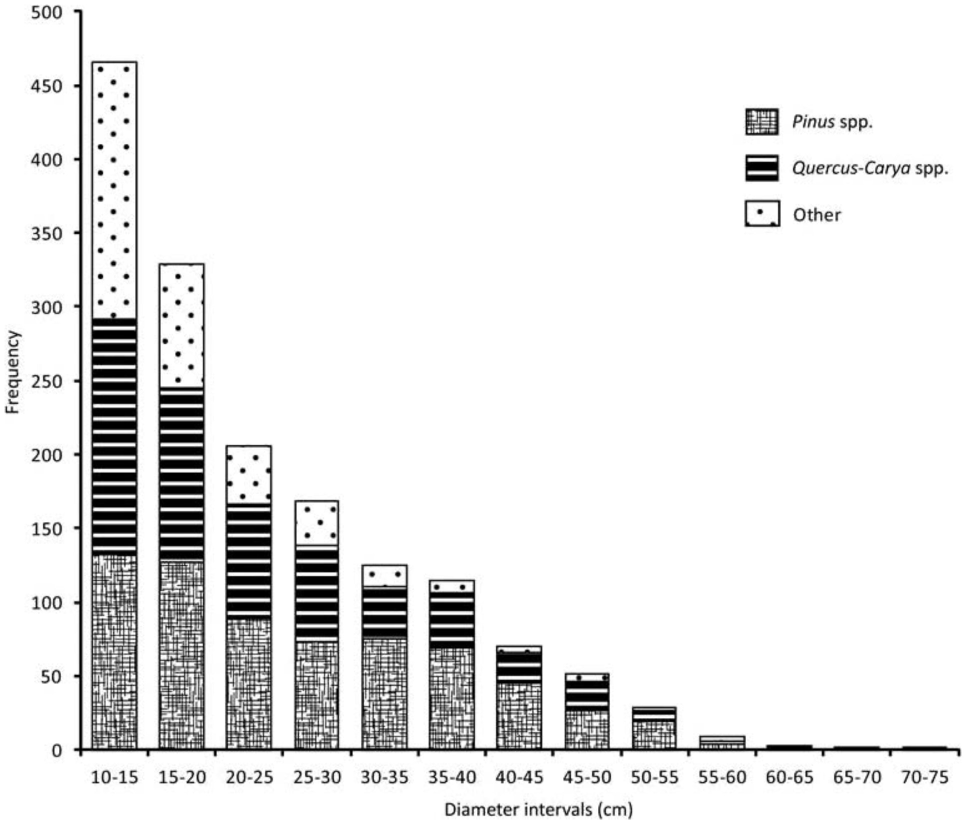

FIG. 5.—Diameter distribution for *Pinus* spp., *Quercus* and *Carya* spp, and other species in the current forest on the Oakmulgee Ranger District, Talladega National Forest, Alabama

within the damaged path supported bunch grasses, but few woody stems existed. Notably, Reed (1905) stated that few *Pinus* stems were affected by *Dendroctonus frontalis* Zimmerman and the damage was so minimal that he considered it to be unimportant.

Prior to the fire suppression movement, land managers used fire to reduce fuel loadings in the forest. Reed (1905) stated that nearly the entire tract was burned annually. Prior to harvesting operations, the Kaul Lumber Company promoted fires on an annual basis to reduce fuels and prevent a catastrophic fire that could damage timber. During periods of no rain from late summer until early spring, fire ignitions were frequent. Reed (1905) stated that the short rotation of these fires damaged the forest in three ways: "(1) the impoverishment of the soil and the consequent loss in rate of growth of timber, (2) the prevention of the reproduction of the [*P. palustris*], and (3) the gradual destruction of the large trees" (p. 13).

U.S. FOREST SERVICE ACQUISITION

The introduction of commercial logging on the tract and increased human population density from 1905 to 1943 resulted in large tracts being cleared, although actual forest density is unknown for this time. Based on the descriptions of Harper (1943), *Pinus palustris*

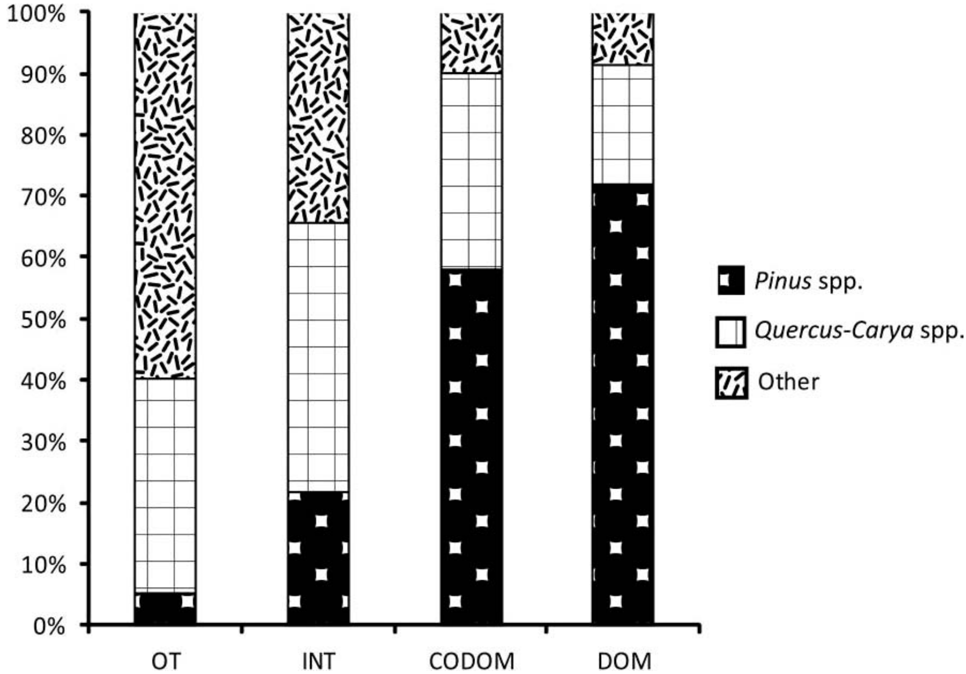

FIG. 6.—Vertical structure distribution of *Pinus* spp., *Quercus* and *Carya* spp., and other species in the current forest on the Oakmulgee Ranger District, Talladega National Forest, Alabama (OT = overtopped stems, INT = intermediate stems, CODOM = codominant stems, DOM = dominant stems)

occupied similar sites as in presettlement forests, but the number of *P. palustris* dominated stands most likely declined because the species was favored by Kaul Lumber Company. However, Harper (1943) stated *P. palustris* remained the most commonly occurring species in this region, despite the widespread removal of stems in the previous decades.

Although relative density and dominance of species changed with land-uses, the species present in the forest remained the same from pre-European settlement period, except for the loss of *Castanea dentata,* which occurred on 6% of all section corners. Harper (1943) noted *Cryphonectria parasitica* (Murrill) Barr (chestnut blight) appeared in Alabama in 1928 and by 1943 nearly all *C. dentata* in the state were affected. The introduction of *C. parasitica* directly altered the composition of the forest and effectively eliminated *C. dentata* trees from the canopy in this region and over its entire range.

Harper (1943) noted, beginning in 1922, the *P. palustris* Hills were protected from fire. Unlike Reed (1905) and previous forest scientists, who argued fires were destructive, Harper (1943) was among the first to acknowledge the benefits of fire to *P. palustris* regeneration and protection from pathogens. During the fire suppression period, large clearings resulted in the regeneration of *Quercus* spp., *P. taeda,* and *P. echinata* but very few *P. palustris* stems (Harper, 1943). Fire suppression also promoted pathogens such as *Scirrhia acicola* (Dearn.) Siggers, a needle blight that affects *P. palustris* seedlings and saplings and weakens their leaves (Chapman, 1932; Harper, 1943). The disease was first noted after fire suppression began but declined after the restoration of fire (Siggers, 1934; Derr and Melder, 1970).

The introduction of grazing animals by European settlers was described as a novel disturbance to the landscape by Harper (1943). Many gullies of the Central *P. palustris* Hills resulted from accelerated erosion caused by introduced domestic hooved animals. Prior to European settlement, no rooting animals were found in American forests. However, *Sus scrofa* L., introduced by settlers for use as livestock, uprooted tree seedlings including *P. palustris* and were generally destructive to the forest.

CONTEMPORARY CONDITIONS

The current forest was dominated by *P. palustris,* similar to forest conditions of the past two centuries, but composition and structure differed from previous forest conditions. *Pinus palustris* and *P. taeda* had the highest relative densities and dominances of all species. *Pinus* spp. were more frequently observed on ridgetops and mid-slope positions, whereas hardwoods were more prevalent on lower slope positions.

Stem density increased from 1905 to present. We note, however, that we did not sample every stand in the forest and stem density varies spatially; therefore, our results reveal general trends. For stems ≥25 cm DBH, tree density of the entire forest was 173 stems ha^{-1}. The increase in density of stems above 25 cm from the early 1900s forest (72 stems ha^{-1}) and current forest was likely because of the management of the forest for timber production and removal of large stems by Kaul Lumber Company and continued timber production by Talladega National Forest. Contemporary forests exhibited a higher density of smaller stems, typical of early stages of structural development, compared to pre-European settlement forests, which included larger trees at wider spacings and a lower tree density (quadratic mean diameter would have been higher in the presettlement forest). These changes may be attributed to shifts in both land-use and natural disturbance regimes (Fralish *et al.*, 1991; Nowacki and Abrams, 2008).

Active fire suppression remained in effect from the middle to the late 20th century. With the introduction of a prescribed burning program by the U.S. Forest Service, the MFI for most *P. palustris* dominated stands returned to ca. 3 y. Although the re-introduction of fire in the forest may increase *P. palustris* resistance to *S. acicula,* the occurrence of this disease is predicted to increase with expanded *P. palustris* restoration (Ward and Misretta, 2002).

Over the past two centuries, many observations have noted wind disturbances, highlighting the influence of wind as a disturbance agent on forest composition and structure in the Fall Line Hills. For example, in 2011, two EF-1 tornadoes and one EF-3 tornado damaged roughly 1000 ha of the forest. The U.S. Forest Service salvaged the damaged timber to reduce the fire risk and insect damage to *P. borealis* habitat and to attempt to recoup financial losses (Ragland, 2011). Pathogens and invasive species have continued to affect forests since the report of pathogen introduction by Harper (1943). Widespread outbreaks of *D. frontalis* occurred on a decadal basis, with the most recent happening from 2008 to 2011. These outbreaks were most frequent in planted and unmanaged *P. taeda* stands. *Pinus taeda* decline, premature death between ages 30 to 50 y, has been documented on the forest. Individuals on south and west facing slopes and slopes with a higher percent grade were more likely to experience decline (Eckhardt and Menard, 2008). Density for *P. taeda* was lowest on south and west facing slopes, which corresponded to the trend of *P. taeda* decline. Altered forest conditions and increased human activity throughout the landscape increased the frequency of alien invasive plant species, notably *Ligustrum sinense* Lour., *Imperata cylindrica* (L.) P. Beauv., and *Wisteria sinensis* (Sims) DC., in the current forest. Invasive wildlife species were also present in the contemporary forest, the most problematic of which, because of rooting, was *S. scrofa,* introduced by early European settlers.

SUMMARY

Reconstructing forest history allows managers and land users to understand fully how the forest has been impacted by humans. We used four discrete periods in time corresponding to major shifts in land-use history to compose the chronological changes of a montane *P. palustris* forest in the Fall Line Hills. Forest structure has been affected by both natural and human disturbances since European settlement. In the early 19th century, the forest structure was characterized by relatively large trees at low densities, with few small stems. After widespread land clearings and altered land uses throughout the 20th century, the contemporary forest structure was characterized by a relatively high density of small stems and few large trees, resembling an earlier stage of stand development. Although tree density varied over the past two centuries, forest composition remained relatively stable. *Pinus palustris* remained the most commonly occurring species on the site since pre-European settlement and *Quercus* spp. and *Carya* spp. have composed a large portion of the forest for over 200 y. Our study not only documented the changes in forest composition and structure in response to different land uses, but also chronicled changing attitudes regarding fire and other disturbances through the 20th century. The response of forest communities to anthropogenic and natural disturbances emphasizes the importance of previous land use on current and future forest conditions. Reconstructed historical ecologies are important for guiding forest planning by providing the ecological context of past and present conditions and compositional and structural changes therein.

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