Successional Change and Fire History in Montane Longleaf Pine-Dominated Ecosystems of Northwestern Georgia, USA

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Christopher G. Waters[1] and Matthew P. Weand[2,*]

Abstract - In the absence of fire, *Pinus palustris* (Longleaf Pine) ecosystems in the southeastern United States are vulnerable to successional change including mesophication, a process where increases in the importance of mesic and fire-intolerant species reduce biodiversity and thwart efforts to restore these systems. To determine the degree and nature of this successional trajectory at a local scale, we examined changes in species composition of a montane Longleaf Pine ecosystem in northwest Georgia using modern vegetation surveys and historical "witness tree" data. We also determined historical fire frequency using fire scars within Longleaf Pine stumps cross-dated to extant Longleaf Pine trees. Modern forest composition contained significantly more fire-intolerant taxa than the historical forest due to increased abundance of mesophytic species, especially *Acer rubrum* (Red Maple) and decline of *Pinus* spp. (pines) and some pyrophytic *Quercus* spp. (oaks). Counter to expectation, there were few differences in species composition between northeastern- and southwestern-facing slopes in modern or historical data. Fire scars indicated a historical mean fire-return interval of 5.5 years and suggest that without the reintroduction of more frequent prescribed fire, regeneration of montane Longleaf Pine is unlikely. Additional restorative techniques may also help these stands support greater biodiversity over time. For instance, co-dominance of pines and oaks in the historical forest suggests that fire-tolerant oaks should be retained in montane restoration efforts.

Introduction

Pinus palustris Mill. (Longleaf Pine) ecosystems historically occupied over 37 million hectares from eastern Texas to coastal Virginia, with Longleaf Pine dominating ~80% of this range, and mixed species systems comprising the remaining 20% (Frost 1993). Euro-American settlement in the 1800s brought widespread harvesting of forest resources and large-scale land conversion, which, along with fire-suppression policies beginning in the 1920s, largely reduced the presence of Longleaf Pine in the landscapes of the Southeast (Noss 1989, Stephens and Ruth 2005). Approximately 3% of the historical range exists today, with 0.01% remaining as old-growth stands (Varner and Kush 2004), making these ecosystems among the most threatened in the United States and driving interest for restoration efforts (Noss 1989). The eponymous keystone species of these ecosystems, Longleaf Pine, is a shade-intolerant and fire-adapted species that thrives when germinated in bare mineral soil (Boyer 1990). As a seedling, Longleaf Pine is protected from fire by its long resinous needles in a short-statured "grass stage" for up to 10 years before experiencing rapid above-ground growth (Brockway et al. 2005).

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[1]School of Environmental Studies, Tennessee Technological University, Cookeville, TN 38505. [2]Department of Ecology, Evolution and Organismal Biology, Kennesaw State University, Kennesaw, GA 30144. [*]Corresponding author - mweand@kennesaw.edu.

Four main Longleaf Pine ecotypes are recognized today, differing in topography, seasonal water availability, and soil composition (Outcalt 2000). The largest, Coastal Plain Longleaf Pine systems of the Atlantic and Gulf Coast, are characterized by well-drained sandy or loamy soils and relatively flat topography. Longleaf Pine flatwood systems are also found within the coastal plain but occur on soils that are more poorly drained and nutrient deficient (Jose et al. 2010). The fall-line sandhill systems stretch along rolling hills from eastern Alabama to central North Carolina. These systems have mixed patches of well-drained sand and impermeable clay, varying between extremely xeric savannas and seepage wetlands depending on which soil type is near the surface (Peet 2006).

The fourth ecotype, montane Longleaf Pine, exhibits the most extreme topographic variation and well-developed drainage networks compared to the other ecotypes (Peet 2006). Although this ecotype comprised only a small portion of the entire historical range of Longleaf Pine, montane Longleaf Pine forests could historically be found in the Piedmont, Ridge and Valley, Cumberland Plateau, and Blue Ridge physiographic provinces (Hammond et al. 2016). The few old-growth montane Longleaf Pine forests that exist (maintained by fire) are open-canopied and park-like with complex size and age structure (Varner et al. 2003). Today most montane Longleaf Pine stands exist in isolated patches on south-facing slopes and ridgetops in northeastern Alabama (Varner et al. 2003), northwestern Georgia (Cipollini et al. 2012), and North Carolina (Watkins 2017), where as a result of ongoing succession in the absence of fire, they may be surrounded or co-dominant with fire-intolerant and mesic hardwood species. This successional trajectory contributes to mesophication processes that prevent the regeneration of fire-dependent species (Hanberry et al. 2012, Kreye et al. 2013, Nowacki and Abrams 2008). Studies of successional change in other regional forest types have documented the increasing importance of mesic species (Cowell 1998, Tuttle and Kramer 2005); however, it is poorly understood how species composition has changed in the montane Longleaf Pine ecotype.

When maintained by fire, montane Longleaf Pine supports unique and highly biodiverse plant communities because they exist where the native ranges of many coastal and Appalachian plant species overlap, creating assemblages not found elsewhere. For instance, compared to fire-suppressed montane Longleaf Pine, frequently burned old-growth stands (aged over 150 years) support a greater diversity of plants and are often host to over 100 understory species in an area of ~25 ha (Cipollini et al. 2012, Maceina et al. 2000, Varner and Kush 2004). These old-growth systems are also home to animal species that could benefit from expansion of potential habitat, including several endemic species such as *Leuconotopicus borealis* (Vieillot) (Red-cockaded Woodpecker) and *Peucaea aestivalis* (M.H.K. Lichtenstein) (Bachman's Sparrow) (Engstrom 1993). The high biodiversity and scarcity of montane Longleaf Pine ecosystems makes expanded restoration of montane Longleaf Pine habitat a priority for land managers in northern Alabama and Georgia today.

As part of Longleaf Pine restoration efforts in northwest Georgia, this study aimed to contribute to a more complete understanding of montane Longleaf Pine successional dynamics. Knowledge regarding the historical composition of montane Longleaf Pine stands (i.e., prior to policies of fire-suppression) and their mean fire-return intervals (MFRIs) can benefit restoration efforts seeking to re-create those stand characteristics. Knowledge regarding the modern forest's composition is also important for restoration. For example, the relative abundance of mesic or fire-intolerant species in the modern forest may vary depending upon site factors such as slope and aspect and influence the success of prescribed burns through mechanisms such as leaf-litter flammability (Kreye et al. 2013).

Using a combination of historical witness-tree data, modern vegetation surveys, and dendrochronology, this study examines the successional change and fire history of montane Longleaf Pine forests where restoration is occurring in Paulding County, GA. We hypothesized that (1) mesic species play a more important compositional role in the modern forest compared to the pre-settlement forest (before fire-suppression policies were implemented), (2) mesic and fire-intolerant species would be more compositionally important on northeastern (NE)-facing slopes rather than southwestern (SW)-facing slopes in the modern forest, and (3), the historical forest had a MFRI between 3 and 7 years; which is longer than those in coastal systems and consistent with other montane systems (Bale 2009, Klaus 2019).

Field-site Description

This study examined changes in vegetation and fire history using 2 Wildlife Management Areas in Paulding County, GA (34°1'15.86"N, 84°54'12.64"W). We examined modern forest composition and fire history within Sheffield Wildlife Management Area (WMA), an ~1963-ha upland forest that includes populations of remnant montane Longleaf Pine intermixed with hardwood species. The majority of the WMA is targeted for restoration and consists of "natural timber" areas that are either only managed with prescribed burns or have not yet been treated. Prescribed burns were started within the WMAs in winter 2012, and subsequently most upland areas have been burned every 2–3 years. We examined historical forest composition (see below) across a larger area, including Sheffield WMA and the adjacent Paulding Forest WMA. Paulding Forest WMA is 10,400 ha of Longleaf Pine and *Pinus taeda* L. (Loblolly Pine) plantation forest. Both WMAs fall within a proposed corridor of Longleaf Pine habitat connecting northeast Alabama and northwest Georgia, so they are of special management interest to Georgia Department of Natural Resources (DNR; Stowe 2005).

Methods

We investigated shifts in forest composition that occurred between 1832 and 2021 by comparing historical survey records from an 1832 Georgia Land Lottery map to modern vegetation surveys conducted across Sheffield WMA. For the modern vegetation surveys, we randomly distributed 36 circular plots (30-m

diameter) across NE- and SW-facing slopes (18 plots for each aspect; see Fig. S1 in Supplemental File 1, available online at https://www.eaglehill.us/NENAonline/suppl-files/s21-4-S2791-Weand-s1, and for BioOne subscribers, at https://www.doi.org/10.1656/S2791.s1). To capture elevational variation in vegetation, we surveyed three 100-m^2 subplots located perpendicular to the contour of the slope in the upper, middle, and lower portion of each main plot for woody species composition (see Fig. S2 in Supplemental File 1). We measured the DBH of each tree >1.4 m in height in the subplots and noted the presence of any additional species in the main plot that were not present in the subplots. We calculated species importance value (IV) among all plots, and separately for each slope (18 NE-facing and 18 SW-facing plots), as

IV = (relative density) + (relative dominance) + (relative frequency),

where relative density is the percent contribution of each species to total density of all species (stems per hectare), relative dominance is the percent contribution of each species to total basal area of all species (m^2 per hectare), and relative frequency is the proportion of plots where each species was found. We also examined importance values within 2 subsets of the modern vegetation data, mature or overstory trees (greater than 15 cm DBH) and mid-story trees (less than 15 cm DBH). For species comparisons within individual plots, we calculated IVs using

IV = (relative density) + (relative dominance).

To compare NE-facing and SW-facing slopes, we calculated the difference in mean IV for each species between the 2 sets of sites as (NE-facing IV) - (SW-facing IV).

We classified species according to ecological habit in terms of fire-tolerance and moisture-affinity, i.e., as either fire-tolerant or fire-intolerant, and either xeric or mesic (Nowacki and Abrams 2015, Thomas-Van Gundy and Nowacki 2013). For each species, we assessed fire-tolerance group, and moisture-affinity group, differences in IV between NE- and SW-facing slopes using Mann–Whitney *U*-tests based on the normality of the IV distribution determined using Shapiro–Wilk tests.

To compare the modern forest composition to the pre-Euro-American forest, we digitized witness-tree data from a georeferenced survey map using ArcGIS (ESRI 2011). Sheffield and Paulding Forest WMAs both fall within the area covered by the 1832 Georgia Land Lottery Survey Cherokee County, Section 3, Gold District 18 survey map, originally produced on 7 July 1832 (District plats of survey 1805/1833). The survey map consists of square 16-ha (40-ac) plots. The corner of each plot and the midpoint between each corner were marked on the map with the common name of the closest tree (i.e., the "witness tree"; Dyer 2001). If a tree was not present at one of these points a post was fashioned by the surveyors. We removed posts from the data prior to analysis. Some trees from the historical data, including pines and hickories, could just be identified to genus as only common names were used by the surveyors. In these cases, we conducted analyses comparing the historic forest to the modern forest at the genus level. Additionally, we removed points if the map was worn or torn in places, preventing accurate identification (see Fig. S4 in

Supplemental File 1). Using the historical witness-tree data and the modern vegetation surveys, we compared the relative abundance (RA) and ecological habit of each species using chi-squared (χ^2) tests or Fisher's exact tests in the case where sample sizes were small and chi-square expected values were less than 5. We assumed that historical surveys were unlikely to record smaller trees, so we used only modern trees with DBH > 15 cm when making these comparisons. We calculated percent change in RA as ([modern RA] – [historical RA]) / [historical RA] x 100.

To compare different slope aspects using the historical witness-tree data, we used digital elevation models (DEMs) obtained from the United States Geologic Survey (USGS). The plat map used in this study falls on the corner of 4 USGS 1-arch-second (30-m) DEMs, so we merged a mosaic of the following DEMs into a single raster: n34w085, n34w086, n35w085, and n35w086 (USGS n.d.). We extracted raster values for slope and aspect at each witness-tree point to determine the slope angle and aspect for the witness-tree data. For comparisons of historical vegetation between aspects, we used only witness trees found on slopes between 7° and 23° to make the comparison similar to as was done for the modern vegetation (all modern survey plots occurred on slopes of 7–23°). We classified witness trees found on slopes with an aspect >135° and ≤315° as being on a SW-facing slope, and those on slopes with an aspect >315° or ≤135° as being on a NE-facing slope. We calculated the difference in RA across slope aspects for each species using (NE-facing RA) - (SW-facing RA). We assessed differences in the ratios of habitat classes from the historical species composition across slope aspects using a χ^2 test and compared differences in mean RA using Mann–Whitney tests.

To determine the historical MFRI, we correlated growth rings in dead Longleaf Pine stumps to cores obtained from extant trees and then dated fire scars in the stumps using this anchored ring series (Huffman and Rother 2017, Stambaugh et al. 2011). We selected 3 sites within Sheffield WMA for coring living Longleaf Pines (see Fig, S1 in Supplemental File 1). The selected locations were on SW-facing slopes or ridgetops and each had many individuals over 40 cm diameter at breast height (DBH). The 3 coring areas were located ~3 km from each other and varied in size, averaging 0.768 ha (see Fig. S1 in Supplemental File 1). We cored a minimum of 50 Longleaf Pines in each area and took 2 cores from each tree perpendicular to the slope of the hill to avoid reaction wood. The cores were stored and processed according to standard dendrochronological techniques (Stokes and Smiley 1996). We measured core ring widths using an AmScope M29 stereo microscope (Irvine, CA) with 7x–45x lenses and a Velmex VRO Measuring System (Bloomfield, NY) with Measure J2X software (VoorTech Consulting 2012). After visually cross-dating cores, we used the 'dplR' statistical package in R and COFECHA software to build the Longleaf Pine chronology (Bunn 2010, Bunn et al. 2020, Grissino-Mayer 2001, R Core Team 2019).

To reconstruct fire history, we collected Longleaf Pine stumps from the forest and examined the wood for fire scarring. These "lighter wood" stumps are protected from decomposition by hardened resin that retards microbial attack (Stambaugh et

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al. 2011). We surveyed ~260 ha of natural timber area within Sheffield WMA for remnant stumps. We recorded soil level, upslope direction, and the integrity of each stump along with the stump's location, which was taken using a Garmin etrex 30 handheld GPS (Olathe, KS). From a total of 204 located, we selected for removal only stumps found on slopes and ridgetops that measured at least 20 cm in diameter and had more than 50% of the cross-sectional area remaining. We also prioritized removal of stumps with visible fire damage in the wood structure. We removed stumps by cutting with a chainsaw below the soil level to obtain 5-cm cross sections of the oldest stem tissue (Huffman and Rother 2017). We prepared cross sections from just above soil level using standard dendrochronological techniques (Stokes and Smiley 1996). We measured stump rings as described above for tree cores and cross-dated them to the living-tree chronology using the 'dplR' statistics package in R and COFECHA (Bunn 2010, Bunn et al. 2020, Grissino-Mayer 2001, R Core Team 2019).

Results

Modern forest composition

Results from the modern vegetation surveys show that among all plots, mean tree abundance was 1301 ± 80 stems/ha, with mean basal area of 33.2 ± 1.7 m^2/ha. Including all stem diameters, the 3 most important species by a considerable margin were *Nyssa sylvatica* (Black Gum; IV = 48.3)*, Oxydendrum arboreum* (Sourwood; IV = 45.8)*,* and *Acer rubrum* L. (Red Maple; IV = 45.8) largely due to their importance among stems with DBH less than 15 cm (see below and Table S1). These are followed by Longleaf Pine (IV = 26.9) and *Quercus alba* (White Oak; IV = 26.5), while each of the other 20 species had IVs less than 20. Among trees with DBH greater than 15 cm, the most important species with the exception of Sourwood (IV = 42.3) were fire-tolerant and xeric species including Longleaf Pine (IV = 57.5), White Oak (IV = 50.4), and *Quercus rubra* (Northern Red Oak; IV = 32.7). Among stems with less than 15 cm DBH in the modern survey, mesic and fire-intolerant species were by far the most important, including Red Maple (IV = 81.5), Sourwood (IV = 44.6), and Black Gum (IV = 89.2) (see Table S1 in Supplemental File 1).

The importance values of fire-intolerant species tended to be greater, but were not statistically significantly greater, on NE-facing slopes ($U = 35$, $P = 0.8$). Likewise, the importance for fire-tolerant species tended to be higher on SW-facing slopes, but this difference was not statistically significant ($U = 70$, $P = 0.2$). Xeric species appeared to have higher importance on SW-facing slopes, and mesic species appeared to have higher importance on NE-facing slopes, but both of these trends were found to be not statistically significant ($U = 119$ and 12, respectively, $P = 0.4$ and 1.0, respectively).

Differences in the importance of each species between aspects were examined using within-plot IVs (see Table S2 in Supplemental File 1). These comparisons showed Longleaf Pine as the most important species on SW-facing slopes ([NE IV] - [SW IV] = -21.2) and Sourwood as the most important on NE-facing slopes

([NE IV] - [SW IV] = 23.6). Only 7 of the 25 species found in Sheffield WMA had a significant difference in IV between NE- and SW-facing slopes. Of these, Red Maple ($U = 255$, $P = 0.003$), Sourwood ($U = 263$, $P = 0.002$), White Oak ($U = 228$, $P = 0.038$), and *Q. montana* (Chestnut Oak, $U = 274$, $P < 0.001$) were found to be significantly more important on NE-facing slopes; while Longleaf Pine ($U = 63$, $P = 0.001$), *Q. falcata* (Southern Red Oak, $U = 73$, $P = 0.001$), and *Carya tomentosa* (Poir.) Nutt. (Mockernut Hickory, $U = 85$, $P = 0.004$) were significantly more important on SW-facing slopes.

Historical vs. modern composition comparison

A total of 2471 witness trees were identified on the 1832 Land Lottery map and positioned using ArcGIS (see Fig. S4 in Supplemental File 1). *Pinus* spp. (pines) were by far the most abundant tree in the historical forest with an RA of 0.4231, followed by Northern Red Oak (RA = 0.1518) and *Q. stellata* (Post Oak; RA = 0.1174). After narrowing down the witness trees to individuals found on SW- and NE-facing slopes between 7° and 23°, a total of 1144 witness trees remained, including 538 witness trees on SW-facing slopes and 606 on NE-facing slopes (Table S3). When comparing the RA of each species between SW- and NE-facing slopes, pines and White Oak were far more abundant on SW-facing slopes than NE-facing slopes. The 4 species with the strongest preference for NE-facing slopes were Black Gum, Northern Red Oak, *Castanea dentata* (American Chestnut), and *Liriodendron tulipifera* (Tulip Poplar). After witness trees were divided into habitat classifications, a significantly larger ratio of fire-tolerant to fire-intolerant species was found on SW-facing slopes ($\chi^2 = 5.57$, $P = 0.02$). There was no difference in the ratio of moisture-affinity groups between slope aspects ($\chi^2 = 2.63$, $P = 0.1$). Results from Mann–Whitney U tests comparing the mean RA of each habitat class between slope aspects indicated no significant difference for any of the habitat classes.

Comparing the historical relative abundance of each species to what is found in the modern forest (modern trees with DBH > 15 cm), there is evidence of a shift to a more mesic and fire-intolerant composition. The importance of some mesic and fire-intolerant species increased by orders of magnitude relative to the historical importance (maples increased 835%, Sourwood increased 1738%) and the importance of xeric, fire-tolerant pines declined by 41% (Table 1). However, among fire-tolerant oaks, some species increased while others decreased. Declines in the importance of other species both mesic (*Fagus grandifolia* [American Beech], *Fraxinus* spp. [ashes]) and xeric (American Chestnut, Post Oak) occurred because there were no modern trees greater than 15 cm DBH.

A Fisher's exact test comparing the species composition of historical and modern forests showed a statistically significant difference ($P < 0.001$). Species counts were divided once again into habitat classes according to their moisture-affinity and fire-tolerance. The complete results of the χ^2 tests comparing the historical and modern abundance of each habitat class are presented in Table 2. The modern forest was significantly more fire-intolerant ($\chi^2 = 76.1$, $P < 0.0001$), but not more mesic than the historical forest.

Table 1. The change in relative tree species abundance (RA) from 1832 to 2019 in Paulding County, GA. The habitat classification of each species used in data analysis is also presented here. Historical count is the abundance of each species identified in 1832 Georgia Land Lottery survey maps. Modern count is abundance among 36 plots surveyed in 2019. Percent change in RA was calculated as (Modern RA – Historical RA) / Historical RA x 100. Only trees with greater than 15 cm DBH were used in the modern count.

Species	Historical count	Historical RA	Modern count	Modern RA	% change in RA	Moisture affinity	Fire tolerance
Acer spp. (maples)	10	0.0040	14	0.0374	835%	Mesic	Intolerant
Liriodendron tulipifera L. (Tulip Poplar)	36	0.0146	11	0.0294	102%	Mesic	Intolerant
Cornus florida L. (Flowering Dogwood)	13	0.0053	3	0.0080	52%	Mesic	Intolerant
Diospyros virginiana L. (Eastern Persimmon)	5	0.0020	0	0.0000	-100%	Mesic	Intolerant
Euonymus atropurpureus Jacq. (Eastern Burningbush)	5	0.0020	0	0.0000	-100%	Mesic	Intolerant
Fagus grandifolia Ehrh. (American Beech)	34	0.0138	0	0.0000	-100%	Mesic	Intolerant
Fraxinus spp. (ashes)	16	0.0065	0	0.0000	-100%	Mesic	Intolerant
Ilex opaca Aiton (American Holly)	1	0.0004	0	0.0000	-100%	Mesic	Intolerant
Liquidambar styraciflua (Sweetgum)	19	0.0077	0	0.0000	-100%	Mesic	Intolerant
Magnolia acuminata (L.) L. (Cucumbertree)	3	0.0012	0	0.0000	-100%	Mesic	Intolerant
Morus spp. (mulberries)	4	0.0016	0	0.0000	-100%	Mesic	Intolerant
Ulmus spp. (elms)	10	0.0040	0	0.0000	-100%	Mesic	Intolerant
Oxydendrum arboreum (L.) DC. (Sourwood)	23	0.0093	64	0.1711	1738%	Xeric	Intolerant
Nyssa sylvatica Marshall (Black Gum)	87	0.0352	11	0.0294	-16%	Xeric	Intolerant
Juglans nigra L. (Black Walnut))	3	0.0012	0	0.0000	-100%	Xeric	Intolerant
Prunus serotina Ehrh. (Black Cherry)	3	0.0012	0	0.0000	-100%	Xeric	Intolerant
Quercus falcata Michx. (Southern Red Oak)	42	0.0170	22	0.0588	246%	Xeric	Tolerant
Q. alba L. (White Oak)	105	0.0425	53	0.1417	233%	Xeric	Tolerant
Q. velutina Lam. (Black Oak)	23	0.0093	10	0.0267	187%	Xeric	Tolerant
Q. Montana Willd. (Chestnut Oak)	69	0.0279	26	0.0695	149%	Xeric	Tolerant
Carya spp. (hickories)	51	0.0206	19	0.0508	146%	Xeric	Tolerant
Q. marilandica Münchh. (Blackjack Oak)	50	0.0202	7	0.0187	-8%	Xeric	Tolerant
Q. rubra L. (Northern Red Oak)	375	0.1518	37	0.0989	-35%	Xeric	Tolerant
Pinus spp. (pines)	1041	0.4213	93	0.2487	-41%	Xeric	Tolerant
Q. stellata Wangenh. (Post Oak)	290	0.1174	4	0.0107	-91%	Xeric	Tolerant
Castanea dentate (Marsh.) Borkh. (American Chestnut)	152	0.0615	0	0.0000	-100%	Xeric	Tolerant
Juniperus virginiana L. (Eastern Red Cedar)	1	0.0004	0	0.0000	-100%	Xeric	Tolerant

Dendrochronology

We constructed a chronology of living Longleaf Pine in Sheffield WMA using 214 cores that had coverage from the year 1912 to 2018 with a mean tree age of 76 years. The chronology of living Longleaf Pine had a mean inter-series correlation of 0.574 and a mean sensitivity of 0.281. Of the stumps located in Sheffield WMA, 14 survived processing and were able to be dated against the chronology. After the dated stumps were added, the final chronology covered 217 years from 1802 to 2018 (Fig. 1). The chronology that includes the dated stumps had a mean inter-series correlation of 0.56 and a mean sensitivity of 0.285 (Table 3). While the stumps did not all significantly correlate with one another, each stump had several 15-year

Table 2. Counts of tree species in Paulding County, GA, grouped by 2 habitat classifications (moisture affinity and fire tolerance) from historical maps and modern vegetation surveys. Chi-squared (χ^2) tests were used to detect significant shifts between historical and modern counts within each habitat dichotomy.

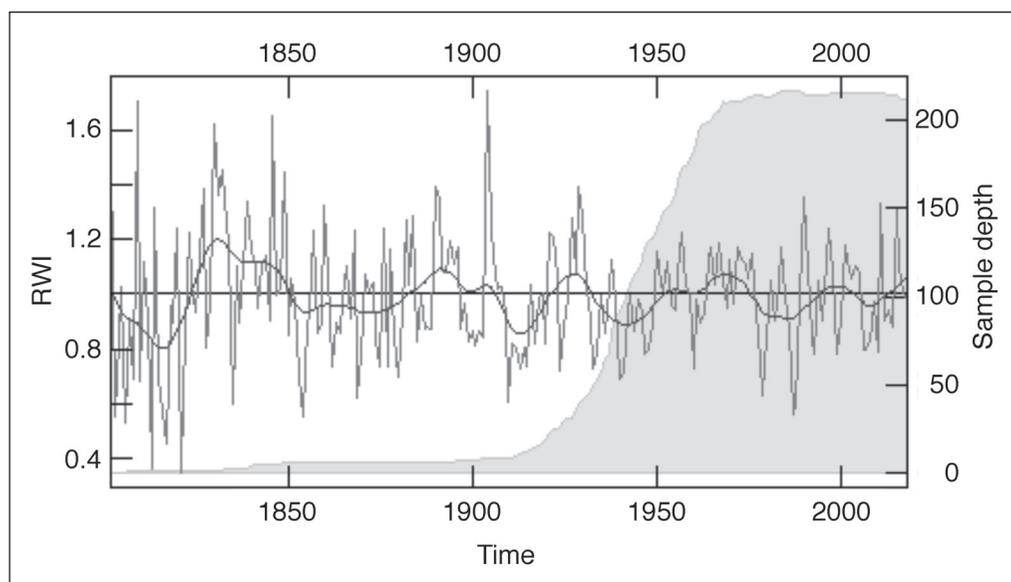| Habitat group	Historical count	Modern count	χ^2	P
Moisture affinity				
Xeric	2315	346	0.6	0.46
Mesic	156	28		
Fire tolerance				
Tolerant	2199	271	76.1	<0.0001
Intolerant	272	103		

Figure 1. The ring width index (RWI) and sample depth for Longleaf Pine trees and relict stumps in Paulding County, GA. The shaded grey area represents the sample depth present at each year from 1802 to 2018, the jagged grey line is the average relative ring growth, and the smoothed black line represents the detrended relative yearly growth using the spline method.

segments that significantly correlated to either the chronology of living Longleaf Pine trees, or to another stump that significantly correlated with the chronology. A total of 25 fire scars were found across 7 of the 14 stumps, with an average of 3.57 scars per stump. Fire scars were dated across a span of years from 1855 to 1975, with a MFRI of 5.5 years and a median interval of 3.5 years approximately following a Weibull distribution (Fig. 2B). Two fire events, occurring in 1935 and 1963, were recorded in more than 1 stump (Fig. 2A).

Discussion

Our results show support for all hypotheses to some degree. The montane Longleaf Pine systems we examined experienced an increase in the importance of mesic species since Euro-American settlement, especially on NE-facing slopes. And our analysis of fire scars in remnant stumps indicates a longer historical fire-return interval compared to coastal Longleaf Pine systems. We discuss the each of these main results in the sections below.

Successional changes in xeric and fire-tolerant species

Pines were by far the most abundant taxa in the historical forest (Table 1). Because pines are early successional and disturbance-adapted species in the southeastern US (Brockway et al. 2005), this abundance suggests disturbance played a large role in shaping the historical community structure. While pines overall have experienced a large decline in RA, Longleaf Pine remains as one of the most important members of the modern forest community and the second most important species on SW-facing slopes (see Table S2 in Supplemental File 1). On average, extant mature Longleaf Pines dated to 1945 and are therefore likely remnant individuals that germinated either before widespread fire-suppression policies were implemented or possibly following periods of intense logging that created conditions promoting fire. While national fire-suppression policies began in the 1920s, it is unknown when these policies took hold or how strongly they were enforced in the rural areas of northwest GA (see dendrochronology section below). Very little Longleaf Pine regeneration was observed in any of the "natural timber" areas of the study site (i.e., areas where restoration or other manipulations are not known to

Table 3. Chronology statistics from Longleaf Pine trees and relict stumps in in Sheffield Wildlife Management Area, Paulding County, GA.

	Cores	Stumps	Cores + stumps
Total number of series	214	14	228
Number of years covered	107	189	217
Range of years covered	1912–2018	1802–1990	1802–2018
Mean inter-series correlation	0.574	0.241	0.560
Mean ring width (mm)	2.29	1.64	2.23
Ring width standard deviation (mm)	1.083	0.865	1.054
Mean autocorrelation	0.728	0.574	0.718
Mean sensitivity	0.281	0.358	0.285
Mean DBH ± standard error (cm)	41.2 ± 0.6	-	-

have occurred for several decades). Conversely, Loblolly Pine was more common in lower size classes (see Table S2 in Supplemental File 1).

The large relative abundance of fire-tolerant oaks in the historical forest is an important finding of this study with implications for restoration of montane Longleaf Pine. Several species of xeric and fire-tolerant oaks experienced a decline in relative abundance between sampling periods (Table 1), and oaks were of low importance among mid-story trees with <15 cm DBH (see Table S2 in Supplemental File 1). Although oaks have long been recognized as co-occurring with montane Longleaf Pine (Mohr 1901), decades of restoration practices have commonly used fire, herbicides, and thinning to eliminate many hardwood species (Boyer 1990, Brockway and Outcalt 2000, Kush et al. 1999). However, this approach is changing, and in coastal and sandhill Longleaf Pine systems, fire-tolerant oak species are receiving increasing recognition for their contribution to biodiversity and ecological place in Longleaf Pine restoration (Hiers et al. 2014, Loudermilk et al. 2016). For example, oaks may act as nurse trees that moderate soil temperatures and increase microhabitats that support insect diversity (Hiers et al. 2014, Loudermilk et al. 2016).

Figure 2. (A) A timeline of fire scars in Longleaf Pine stumps from Sheffield Wildlife Management Area, Paulding County, GA. The timespan covered by each stump is represented by the horizontal lines with intersecting vertical lines representing fire scars at that corresponding year. Stump identifications are placed on the *y*-axis. A composite of all dated fire scars is along the *x*-axis. (B) The distribution of interval durations (in years) between fire scars in Longleaf Pine stumps. The mean fire-return interval (MFRI) was 5.5 ± 0.94 (mean ± SE) years.

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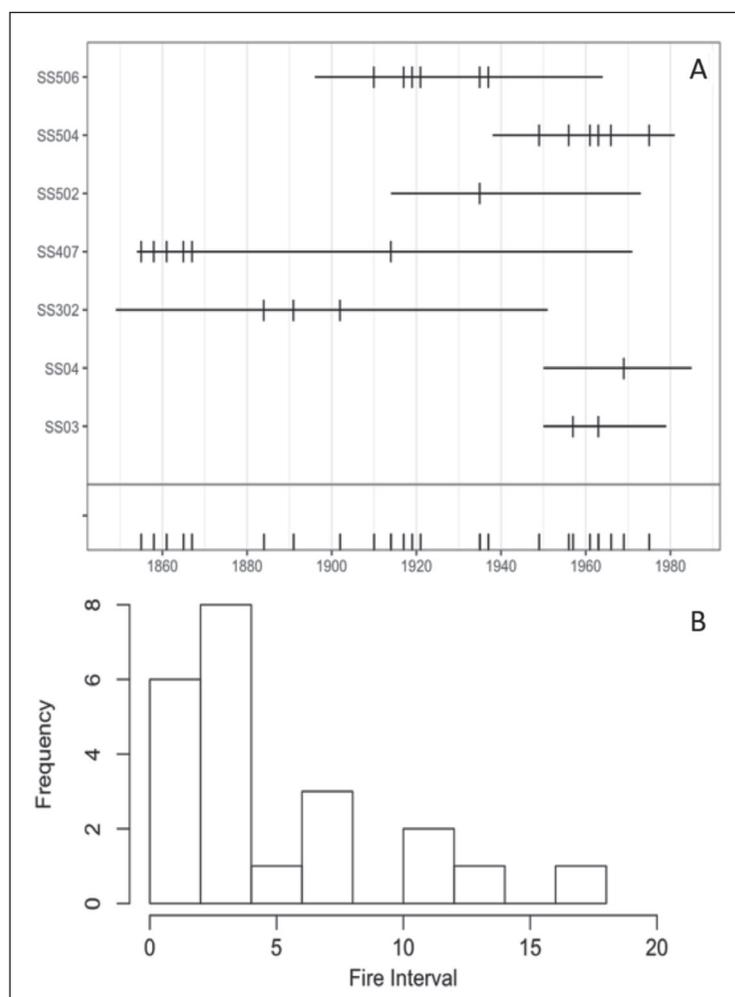
The historical co-dominance of pines and oaks found in this study suggests a role for fire-tolerant oaks in montane ecosystem restoration. As restoration efforts for Longleaf Pine communities expand across northwest Georgia, an effort to preserve populations of fire-tolerant oaks within each Longleaf Pine community could have benefits similar to those found in sandhill communities.

Successional changes in mesic and fire-intolerant species

The most pronounced change from a single mesic species was the massive establishment of maples since 1832 (presumably Red Maple, as no other species were found in the modern survey). Since Euro-American settlement, maples have experienced a >800% increase in relative abundance in northwest Georgia (Table 1). While maples constituted a small part of historical upland communities, a period of infrequent fire may have allowed it to encroach into areas where frequent fires previously excluded its establishment, as found in other areas of the eastern US (Lorimer 1984). Possessing multiple traits typically associated with generalist invasive species (e.g., early maturation age, high reproductive capacity, and the ability to establish in different successional states), Red Maple was able to quickly propagate from habitats that were sanctuaries from fire before widespread fire suppression policies were implemented, or in the absence of active suppression, fires became infrequent for other reasons (Alexander and Arthur 2010, Lambers and Clark 2005). Although Red Maple is not considered fire-tolerant, the relationship of Red Maple and fire is complex. After a history of relatively infrequent fire, established mature maples can persist and out-grow some oak species even under a periodic fire regime (Green et al. 2010, Keyser et al. 2018). Ultimate explanations for the spread of Red Maple are varied and include factors such as new fire regimes, introduced species, climate change, and modern wildlife management practices (Fei and Steiner 2007).

Along with maples, Sourwood also experienced a large increase in relative abundance, ~1700% (Table 1). While mature Black Gum (i.e., >15 cm DBH) slightly declined in relative abundance compared to the historical survey, it is the most important mid-story species in these stands today (see Table S1 in Supplemental File 1). On SW-facing slopes, the only modern species with a higher mean IV than Longleaf Pine is Black Gum (see Table S2 in Supplemental File 1). While Sourwood and Black Gum were classified as xeric and fire-intolerant in this study, there is some evidence they have a moderate fire-tolerance (Keyser et al. 2018). The prevalence of Red Maple, Sourwood, and Black Gum in the modern forest are a challenge for restoration aiming to produce Longleaf Pine-dominated upland communities. More work is needed to determine their responses to disturbances including fire. Greater understanding of these responses could help minimize the use of expensive restoration manipulations such as selective herbicide treatments or mechanical removals.

Differences between slope aspects

Counter to our hypothesis, there were not strong differences in the importance of mesic species between slope aspects. A greater importance of mesic species was

expected on NE-facing slopes because mesic species originating in bottomlands could have gradually propagated up these cooler, more-shaded slopes faster as compared to SW-facing slopes. It should be noted that although not statistically significant, modern NE-facing slopes tended to have a slightly greater importance of mesic- and pyrophobic species compared to SW-facing slopes (Fig. 3). In the historical forest, there was a greater ratio of fire-tolerant:fire-intolerant trees on SW-facing slopes compared to NE-facing slopes, but otherwise no significant differences in habitat classes between slopes. Species differences in relative abundance between slopes were generally less pronounced in the historical forest and greater in the modern forest, suggesting that the historical forest may have been more homogeneous compared to the modern forest. Greater homogeneity would be expected if the pre-settlement landscape was uniformly managed (i.e., Native Americans may have burned NE- and SW-facing slopes with similar frequency). For restoration efforts, these historical results indicate that while remnant montane Longleaf Pine is most often found on SW-facing slopes, both SW- and NE-facing slopes can support montane Longleaf Pine.

Considerations in comparisons of historical vs. modern vegetation

When comparing historical witness-tree data with modern vegetation surveys, interpretation must be cautious. There are many factors that could influence the results of the comparison, particularly those regarding the historical survey-ors who recorded the witness trees. Species misidentification, methodological
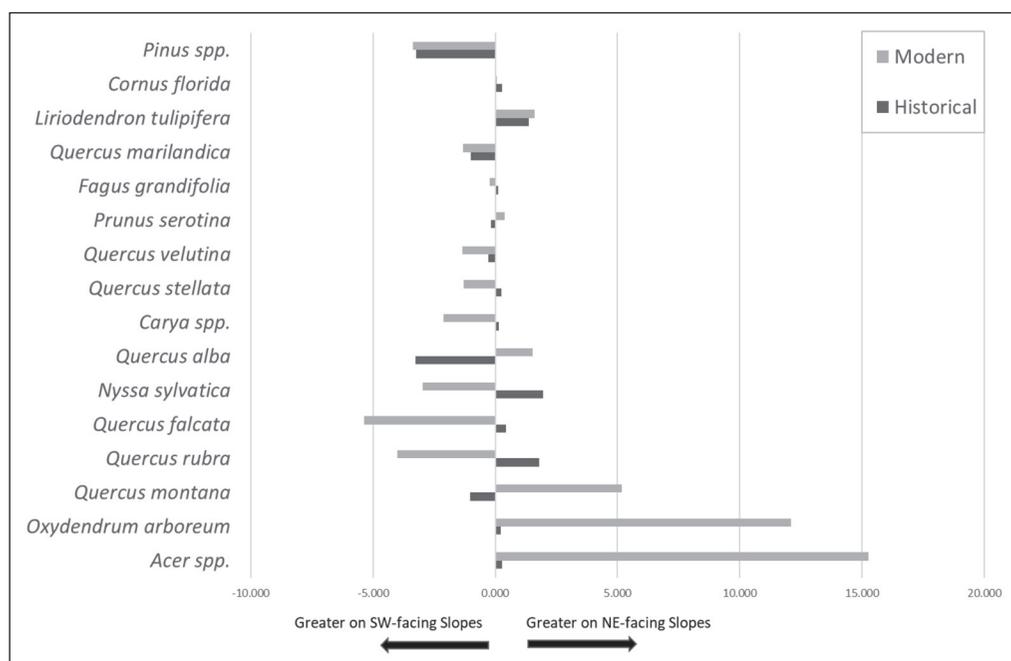

Figure 3. The difference in relative abundance between NE- and SW-facing slopes from the historical and modern vegetation surveys. Species are ordered by the change in difference from the historical data to the modern data.

inconsistencies, and surveyor bias in tree identification and location are difficult to account for, especially in forests with non-uniform densities (Black and Abrams 2001, Kronenfeld and Wang 2007). Additionally, the accuracy and resolution of witness-tree positions in the landscape must be considered. Efforts to determine the true position of these trees can be compromised by either mistakes made by the surveyors or from the resolution of the DEM used. The DEM used to assign a slope and aspect to each witness tree in this study was of 1 arc-second (~30 m) resolution. Fine topographic detail below this resolution is not currently available, so a witness tree could appear to be on a slope aspect that is incorrect. To account for this possibility, the witness-tree data was subset into 2 broad slope-aspect categories, NE-facing (>315° or ≤135°) and SW-facing (>135° and ≤315°). Based on personal observation of northwest Georgia forests (e.g., the modern survey plots were 30 m in diameter and only encompassed 1 slope aspect per plot), it seems unlikely the topography would change drastically enough (i.e., from NE- to SW-facing) within a 30-m–resolution cell to create mis-located witness trees. In the future, the acquisition of expanded finer-resolution data could improve the determination of witness-tree locations. Finally, the historical surveys encompassed a much larger area than the modern survey and likely recorded a more diverse sample of trees from a greater number of habitats. To make the historical and modern comparison more accurate, the historical data was subset to only include witness trees on slopes with the same span of steepness as the modern survey plots (>7° and <23°), which hypothetically restricted all historical data to upland forests. Considering that upland forests are where xeric and fire-tolerant species would be expected to persist, the pronounced effects of successional change are even more striking.

Fire-return intervals

Although our sample size of Longleaf Pine stumps was small, half of the stumps that survived processing contained fire scars that indicated a fire return interval that is longer (mean = 5.5 years) than the 1–7-year MFRI of coastal Longleaf Pine systems. Therefore, fire was likely prevalent but variable across the landscape, as would be expected in montane Longleaf Pine systems with dissected and undulating topography. With low sample-size and because not all fires scar trees, it is difficult to determine if the MFRI calculated here has been over- or underestimated as compared to other montane systems in the region. A study using similar methods conducted in western Georgia calculated a historical MFRI of 3 distinct time periods: pre-1840, 1840–1915, and post-1915. The MFRI of each of these time periods was found to be 2.6, 1.2, and 11.4 years, respectively (Klaus 2019). Another study conducted at Choccolocco Mountain, AL, calculated the MFRI to be 3.2 years from 1653 to 1831 and 2.5 years from 1832 to 1940 (Bale 2009). Variations in MFRI across the region could be caused by differences in local precipitation, drought severity, lightning strikes, or human activity (Frost 1998).

The cross-dated stumps tended to be older than the majority of living trees, and the lack of correlation among stumps is probably due to the low sample size (Table 3). With this low sample size, exogenous signals in the growth trends are

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harder to detect. The stumps had an overall higher mean sensitivity than the cores from extant trees, which could have also contributed to difficulties detecting a common growth trend. Of the over 200 stumps located, fewer than 30 remained intact enough to be considered useable in analysis. As remnant stumps decompose, burn, or weather by other means across northwest Georgia, it will be difficult to expand on the results of this study or conduct similar studies in other Longleaf Pine systems (Huffman and Rother 2017). Despite small sample size, the detection of fire scars during the era of supposed fire suppression (e.g., 1920–1960) confirms that fire was not completely excluded in this region of Georgia.

Growth dynamics of extant Longleaf Pine

The Longleaf Pine stands in this study are even aged and relatively young (Fig. S3 see Supplemental File). Although the oldest tree dated to 1911, mean tree age was 72.5 ± 1.1 years, putting the time of establishment in the 1940s–1950s. Older trees may have served as seed sources for the larger cohort that established during this time, likely following a period of logging, fire, or other disturbance. Longleaf Pines are known to live up to 500 years, but rarely achieve lifespans this long due to the disturbance-driven systems they inhabit (Boyer 1990). As of 2003, the oldest trees in old-growth, mixed-aged stands at Mountain Longleaf National Wildlife Refuge on Choccolocco Mountain, AL, were ~250 years old, but the majority of trees were ≤85 years of age (Varner et al. 2003).

It is unknown how the growth trends of relatively young, even-age stands differ from old-growth, and mixed-aged stands in the region, and there are few examples available for comparison. This study is the first to examine growth trends in degraded Longleaf Pine stands rather than old growth or those that have been restored. As of 2022, there are only 2 chronologies of montane Longleaf Pine in the International Tree Ring Database (ncdc.noaa.gov), both old-growth stands: the first from Choccolocco Mountain, AL (Guyette et al. 2012), and the second from Lavender Mountain, GA (Pederson et al. 2012). Over the period common between Choccolocco Mountain and Sheffield WMA chronologies (1912–2006), ring-width indices were significantly correlated ($R = 0.4$, $P < 0.001$); however, there was a poor correlation between Sheffield WMA and Lavender Mountain chronologies ($R = 0.01$, $P = 0.9$) over their common period (1912–2003). More studies of montane Longleaf Pine stands of different ages and disturbance histories are needed to further understand the relationship between these factors and tree growth. Beyond the scope of restoration, understanding growth trends in a diversity of stand types has particular importance for climate-change research seeking to model how Longleaf Pine stands will accrue and sequester carbon over time.

Endogenous and exogenous disturbance are both important mechanisms influencing stand-growth dynamics as they involve tree mortality, subsequent growth release in surviving individuals, and new recruitment in seedling and saplings (Stokes et al. 2010). Our chronology comprised of mature Longleaf Pine did not have any strong growth trends in the most recent 50 years (Fig. 1), and no trees originating since the 1970s. The lack of mid-canopy or sapling Longleaf Pine

trees within the sites used for coring suggests few stand-wide disturbances or that very little self-thinning and regeneration have occurred. This trend was also observable in the larger, modern forest survey where dead or dying mature Longleaf Pine, mid-canopy trees, or saplings were only occasionally observed. Indeed, mean Longleaf Pine DBH was 35.6 cm, and no Longleaf Pine had a DBH of less than 10 cm (stand-structure data not shown). Without restoration, natural disturbances, or self-thinning events that create sufficient canopy gaps, stands like these seem destined to be replaced by hardwood species over time.

Conclusions

As a result of the absence of fire and other disturbances that could allow for Longleaf Pine regeneration, succession increased the importance of mesic species in the remnant montane Longleaf Pine forests examined here. Without reintroduction of regular fires, the even-aged stands of Longleaf Pine likely cannot support the biodiversity found in historical montane Longleaf Pine systems. However, as restoration efforts expand in northwest Georgia and northeast Alabama and these heavily mesophied stands are encountered, their remnant trees serve as a genetic resource to cross breed with younger plants upon reproductive maturity (e.g., planted seedlings), eventually helping to create the mixed-aged stand structures found in old-growth montane Longleaf Pine. Additionally, selective thinning of some hardwood species while retaining fire-tolerant oaks could lead to forests with more diverse habitats that more closely resemble the historical forest and support additional biodiversity.

Literature Cited

Alexander, H.D., and M.A. Arthur. 2010. Implications of a predicted shift from upland oaks to Red Maple on forest hydrology and nutrient availability. Canadian Journal of Forest Research 40(4):716–726.

Bale, A.M. 2009. Fire effects and litter accumulation dynamics in a montane Longleaf Pine ecosystem Ph.D. Dissertation. University of Missouri, Columbia, MO. 109 pp.

Black, B.A., and M.D. Abrams. 2001. Influences of Native Americans and surveyor biases on metes and bounds witness-tree distribution. Ecology 82(9):2574–2586.

Boyer, W.D. 1990. *Pinus palustris* Mill. Longleaf Pine. Silvics of North America 1:405–412.

Brockway, D.G., and K.W. Outcalt. 2000. Restoring Longleaf Pine–Wiregrass ecosystems: Hexazinone application enhances effects of prescribed fire. Forest Ecology and Management 137(1–3):121–138.

Brockway, D.G., K.W. Outcalt, D.J Tomczak, and E.E. Johnson. 2005. Restoration of Long-leaf Pine ecosystems. General Technical Report SRS-83. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. 34 pp.

Bunn, A.G. 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28(4):251–258.

Bunn, A.G., M. Korpela, F. Biondi, F.Campelo, P. M´erian, F. Qeadan, and C. Zang. 2020. dplR: Dendrochronology Program Library in R. R package version 1.7.1. Available online at https://cran.r-project.org/web/packages/dplR/index.html.

Cipollini, M.L., J. Culberson, C. Strippelhoff, T. Baldvins, and K. Miller. 2012. Herbaceous plants and grasses in a mountain Longleaf Pine forest undergoing restoration: A survey and comparative study. Southeastern Naturalist 11(4):637–668.

Cowell, C.M. 1998. Historical change in vegetation and disturbance on the Georgia Piedmont. American Midland Naturalist 140(1):78–89.

District plats of survey. 1805/1833. District plats of survey, survey records, Surveyor General, RG 3-3-24, Georgia Archives. Available online at https://dlg.usg.edu/record/gaarchives_dmf.

Dyer, J.M. 2001. Using witness trees to assess forest change in southeastern Ohio. Canadian Journal of Forest Research 31(10):1708–1718.

Engstrom, R.T. 1993. Characteristic mammals and birds of Longleaf Pine forests. Pp. 127–138, *In* S.M. Hermann (Ed.). Proceedings of the Tall Timbers fire ecology conference. Vol. 18. Tall Timber Research, Inc., Tallahassee, FL. 418 pp.

Environmental Systems Research Institute (ESRI). 2011. ArcGIS Desktop: Release 10. Redlands, CA.

Fei, S., and K.C. Steiner. 2007. Evidence for increasing Red Maple abundance in the eastern United States. Forest Science 53(4):473–477.

Frost, C.C. 1993. Four centuries of changing landscape patterns in the Longleaf Pine ecosystem. Pp. 17–43, *In* S.M. Hermann (Ed.). Proceedings of the Tall Timbers fire ecology conference. Vol. 18. Tall Timber Research, Inc., Tallahassee, FL. 418 pp.

Frost, C.C. 1998. Presettlement fire frequency regimes of the United States: A first approximation. Pp. 70–81, *In* T.L. Pruden and L.A. Brennan (Eds.).Fire in ecosystem management: Shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology Conference Proceedings. Vol. 20. Tall Timber Research, Inc., Tallahassee, FL. 459 pp.

Green, S.R., M.A. Arthur, and B.A. Blankenship. 2010. Oak and Red Maple seedling survival and growth following periodic prescribed fire on xeric ridgetops on the Cumberland Plateau. Forest Ecology and Management 259(12):2256–2266.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: A manual and tutorial for the computer program COFECHA. Tree-Ring Research 57(2):205–221.

Guyette, R.P., M.C. Stambaugh, D.C. Dey, and R.M. Muzika. 2012. Predicting fire frequency with chemistry and climate. Ecosystems 15(2):322–335.

Hanberry, B.B., B.J. Palik, and H.S. He. 2012. Comparison of historical and current forest surveys for detection of homogenization and mesophication of Minnesota forests. Landscape Ecology 27(10):1495–1512.

Hammond, D.H., J.M. Varner, Z. Fan, and J.S. Kush. 2016. Long-term stand dynamics of old-growth mountain Longleaf Pine (*Pinus palustris*) woodlands. Forest Ecology and Management 364:154–164.

Hiers, J.K., J.R. Walters, R.J. Mitchell, J.M. Varner, L.M. Conner, L.A. Blanc, and J. Stowe. 2014. Ecological value of retaining pyrophytic oaks in Longleaf Pine ecosystems. The Journal of Wildlife Management 78(3):383–393.

Huffman, J.M., and M.T. Rother. 2017. Dendrochronological field methods for fire history in pine ecosystems of the Southeastern Coastal Plain. Tree-Ring Research 73(1):42–46.

Jose, S., S. Ranasinghe, and C.L. Ramsey. 2010. Longleaf Pine (*Pinus palustris* Mill.) restoration using herbicides: Overstory and understory vegetation responses on a coastal plain flatwoods site in Florida, USA. Restoration Ecology 18(2):244–251.

Keyser, T.L., V.L. McDaniel, R.N. Klein, D.G. Drees, J.A. Burton, and M.M. Forder. 2018. Short-term stem mortality of 10 deciduous broadleaved species following prescribed burning in upland forests of the southern US. International Journal of Wildland Fire 27(1):42–51.

Klaus, N. 2019. Fire history of a Georgia montane Longleaf Pine (*Pinus palustris*) community. Georgia Journal of Science 77(2):5.

Kreye, J.K., J.M Varner, J.K. Hiers, and J. Mola. 2013. Toward a mechanism for eastern North American forest mesophication: Differential litter-drying across 17 species. Ecological Applications 23(8):1976–1986.

Kronenfeld, B.J., and Y.C. Wang. 2007. Accounting for surveyor inconsistency and bias in estimation of tree density from presettlement land-survey records. Canadian Journal of Forest Research 37(11):2365–2379.

Kush, J.S., R.S. Meldahl, and W.D. Boyer. 1999. Understory plant community response after 23 years of hardwood control treatments in natural Longleaf Pine (*Pinus palustris*) forests. Canadian Journal of Forest Research 29(7):1047–1054.

Lambers, J.H.R., and J.S. Clark. 2005. The benefits of seed banking for Red Maple (*Acer rubrum*): Maximizing seedling recruitment. Canadian Journal of Forest Research 35(4):806–813.

Lorimer, C.G. 1984. Development of the Red Maple understory in northeastern oak forests. Forest Science 30(1):3–22.

Loudermilk, L.E., J.K. Hiers, S. Pokswinski, J.J. O'Brien, A. Barnett, and R.J. Mitchell. 2016. The path back: Oaks (*Quercus* spp.) facilitate Longleaf Pine (*Pinus palustris*) seedling establishment in xeric sites. Ecosphere 7(6):e01361.

Maceina, E.C., J.S. Kush, and R. Meldahl. 2000. Vegetational survey of a montane Longleaf Pine community at Fort McClellan, Alabama. Castanea 65(2):147–154.

Mohr, C. 1901. Plant Life of Alabama- An Account of the Distribution, Modes of Association, and Adaptions of the Flora of Alabama, Together With a Systematic Catalogue of the Plants Growing in the State. US National Herbarium, Washington, DC. 921 pp.

Noss, R.F. 1989. Longleaf Pine and Wiregrass: Keystone components of an endangered ecosystem. Natural Areas Journal 9(4):211–213.

Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience, 58(2):123–138.

Nowacki, G.J., and M.D. Abrams. 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? Global Change Biology 21(1):314–334.

Outcalt, K.W. 2000. The Longleaf Pine ecosystem of the South. Native Plants Journal 1(1):42–53.

Pederson, N., A.R. Bell, T.A. Knight, C. Leland, N. Malcomb, K.J. Anchukaitis, K. Tackett, J. Scheff, A. Brice and W. Blozan. 2012. A long-term perspective on a modern drought in the American Southeast. Environmental Research Letters 7(1):014034.

Peet, R.K. 2006. Ecological classification of Longleaf Pine woodlands. Pp. 51–93, *In* S. Jose, E.J. Jokela, And D.L. Miller (Eds.).The Longleaf Pine Ecosystem. Springer, New York, NY. 438 pp.

R Core Team 2019. R: A language and environment for statistical computing. Version 4.0.0. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://www.R-project.org/.

Stambaugh, M.C., R.P. Guyette. and J.M. Marschall. 2011. Longleaf Pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. Journal of Vegetation Science 22(6):1094–1104

Stephens, S.L., and L.W. Ruth. 2005. Federal forest-fire policy in the United States. Ecological Applications 15(2):532–542.

Stokes, M.A., and T.L. Smiley. 1996. An Introduction to Tree-ring Dating. University of Arizona Press. Tucson, AZ. 73 pp.

Stokes, T.A., L.J. Samuelson, J.S. Kush, M.G. Farris, and J.C. Gilbert. 2010. Structure and diversity of Longleaf Pine (*Pinus palustris* Mill.) forest communities in the Mountain Longleaf National Wildlife Refuge, northeastern Alabama. Natural Areas Journal 30(2):211–225.

Stowe, J. 2005. Connecting the Longleaf Pinelands of Northeast Alabama and Northwest Georgia: Our last chance for corridors to protect the special things. Pp. 18–19, *In* M.L. Cipollini (Comp.). Proceedings of the Second Montane Longleaf Pine Conference Workshop. Berry College, Mount Berry, GA. 49 pp.

Thomas-Van Gundy, M.A., and G.J. Nowacki. 2013. The use of witness trees as pyro-indicators for mapping past fire conditions. Forest Ecology and Management 304:333–344.

Tuttle, J.P., and E.A. Kramer. 2005. Appendix J. Georgia Historic Vegetation Reconstruction Pilot Project. Institute of Ecology, University of Georgia, Athens, GA. 25 pp.

United States Geologic Survey. n.d. Data catalog. Data.gov. Available online at https://catalog.data.gov/dataset/usgs-1-3-arc-second-contour-downloadable-data-collection. Accessed 25 June 2020.

Varner, J.M., and J.S. Kush. 2004. Remnant old-growth Longleaf Pine (*Pinus palustris* Mill.) savannas and forests of the southeastern USA: Status and threats. Natural Areas Journal 24(2):141–149.

Varner, J.M., III, J.S. Kush, and R.S. Meldahl. 2003. Structural characteristics of frequently-burned old-growth Longleaf Pine stands in the mountains of Alabama. Castanea 68(3):211–221.

Watkins, K.E. 2017. Examining Longleaf Pine spectral properties to remotely map relict stands in central North Carolina. Ph.D. Dissertation. University of North Carolina, Greensboro, NC. 51 pp.

VoorTech Consulting. 2012. MeasureJ2X V5. Available online at http://www.voortech.com/projectj2x/release/index.html.