Forest Ecology and Management 475 (2020) 118406

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

A history of recurrent, low-severity fire without fire exclusion in southeastern pine savannas, USA

Monica T. Rother[a,*], Jean M. Huffman[b,d], Christopher H. Guiterman[c], Kevin M. Robertson[b], Neil Jones[d]

[a] Department of Environmental Sciences, University of North Carolina, 601 South College Road, Wilmington, NC 28403, United States
[b] Tall Timbers Research Station & Land Conservancy, Tallahassee, FL 32312, United States
[c] Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ 85721, United States
[d] Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, United States

ARTICLE INFO

Keywords:
Longleaf pine (*Pinus palustris*)
Prescribed fire
Dendrochronology
Fire history
Reference sites
Red Hills Region

ABSTRACT

The reintroduction and maintenance of historical surface fire regimes are primary goals of ecological restoration across many open, pine-dominated ecosystems in North America. In the United States, most of these ecosystems experienced long periods of fire exclusion in the 20th century, leaving few locations to serve as reference sites for ecological conditions associated with a continuous history of recurrent, low-severity fire. Here, we present a tree-ring perspective of uninterrupted surface fire activity from three pine savanna sites in the Red Hills Region of northern Florida and southwestern Georgia, USA. Our sites include two old-growth stands of longleaf pine (*Pinus palustris*): the Wade Tract on Arcadia Plantation and the Larkin Tract on Millpond Plantation. We also sampled the largely second-growth mixed pine savannas of Tall Timbers Research Station. Documentary records for burning at these sites are limited to recent decades and are often incomplete, although regional land-use traditions and scattered historical records indicate frequent fire may have persisted through the 20th century to present day. Fire-scarred cross sections from externally-scarred stumps, dead trees, and live trees provided tree-ring evidence of frequent fires occurring from the beginning of our fire-scar record in the late 19th century onward. Both fire frequency and seasonality were relatively consistent throughout time and among sites. Biennial and annual fire intervals were the most common. Most fire scars occurred in the dormant and early-earlywood portions of the rings, indicating that these fires were human-set fires during the months of January to mid-April, before the main lightning-fire season. Our findings regarding post-settlement fire frequency are consistent with previous estimates of fire frequency during earlier centuries, resulting from lightning and Native American ignitions. We recommend that our sites be used as reference sites for restoration as they are among the relatively few areas in the United States with a continuous history of frequent low-severity fire without 20th century fire exclusion.

1. Introduction

Most North American savannas, woodlands, and forests that depended on recurrent, low-severity fire to maintain their historical structure experienced a period of fire exclusion that spanned decades to over a century, depending on the location (Donovan and Brown, 2007; Pyne, 1982). Tree-ring records provide evidence of this fire-free period in open western ponderosa pine (*Pinus ponderosa*) woodlands (Swetnam and Baisan, 1996), parts of the Appalachian region (Aldrich et al., 2010; Hoss et al., 2008; Marschall et al., 2019), northern red pine (*Pinus resinosa*) forests (Engstrom and Mann, 1991; Johnson and Kipfmueller, 2016), coastal redwood (*Sequoia sempervirens*) forests (Brown and Swetnam, 1994; Greenlee and Langenheim, 1990), southeastern longleaf pine *(Pinus palustris*) savannas (Stambaugh et al., 2011a; White and Harley, 2016), and in some oak-dominated ecosystems (Stambaugh et al., 2016, 2011b), among others. Efforts to deliberately suppress wildland fire and discourage intentional burning were led by the U.S. Forest Service and began in the early 1900s with the belief that wildland fires were destroying valuable forest resources, limiting tree regeneration, and endangering human lives (Covington and Moore, 1994; Donovan and Brown, 2007; Swetnam and Baisan, 1996).

Although fire exclusion in the 20th century was widespread, fire persisted in some areas. Intentional fire (i.e., controlled burning, later called prescribed burning) continued in some fire-frequented natural

* Corresponding author.
E-mail address: rotherm@uncw.edu (M.T. Rother).

https://doi.org/10.1016/j.foreco.2020.118406
Received 30 April 2020; Received in revised form 3 July 2020; Accepted 4 July 2020

communities where people found it useful and had ownership of or access to the land. The primary purpose of intentional burning in the U.S. in the late 19th and early 20th century was for improving range for cattle and sheep and, to a lesser degree, for protecting timber (Biswell, 1989; Grelen, 1978). Continued burning of rangelands has persisted in only a few places, including in parts of Central and South Florida (Huffman and Platt, 2014; Otto, 1984) and in parts of the Great Plains such as the Flint Hills (Allen and Palmer, 2011; Hoy, 1989) and Cross Timbers (Clark et al., 2007; Shirakura et al., 2006; Stambaugh et al., 2009). Frequent fire regimes have also persisted on certain southern military installations where ignitions from ordnance complimented human and natural sources of fire in recent decades (Huffman and Platt, 2014) and in some western U.S. montane ecosystems where wildfires were not suppressed or were only partially suppressed (Fulé et al., 2003; Schoennagel et al., 2004; Stephens and Fulé, 2005). Another land use that has given impetus to the maintenance of frequent fire is hunting the northern bobwhite (*Colinus virginianus*) "quail", as this species requires frequent fire (every 1–2 years) to maintain thriving populations (Palmer and Sisson, 2017). Concentrations of quail hunting estates on local landscapes of the eastern Gulf and Atlantic Coastal Plain (Brennan, 1997; Stribling and Sisson, 2009), including the Red Hills Region of northern Florida and southern Georgia (Way, 2011), are believed to have maintained a tradition of frequent burning throughout the 20th century through to the present day. Few historical records exist that document these anthropogenic fire regimes, leaving knowledge gaps regarding the frequency, seasonal timing, and scale of burning and thus limiting their utility to inform forest restoration on nearby properties and elsewhere.

Fire-scar records developed through dendrochronological methods can provide detailed information regarding the historical fire regime of a given location (Dieterich and Swetnam, 1984; Falk et al., 2011). In areas where low-severity surface fires commonly occur, researchers analyze fire scars preserved in the annual growth rings of trees (Fig. 1). These scars form when the heat of a fire kills a portion of the cambium and the tree survives and heals from the wound. Analysis of these fire scars allows researchers to determine the frequency and seasonality of past fires, along with other fire regime characteristics. Researchers date fire scars found on individual trees and then compile that information to build site-level chronologies of fire. These methods were largely developed in the western U.S. (Arno and Sneck, 1977; Dieterich and Swetnam, 1984).

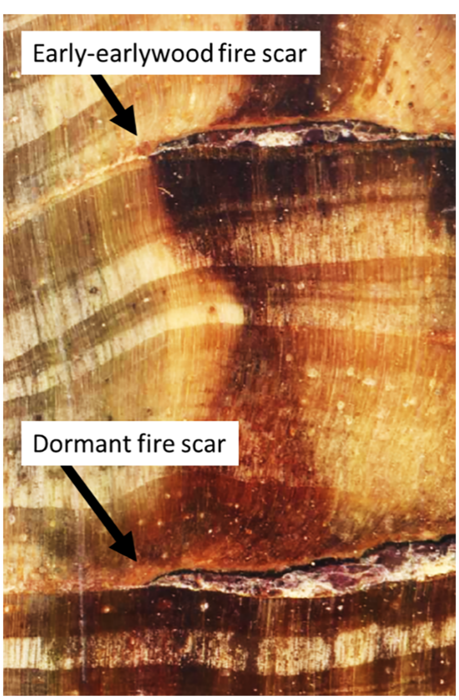

Fig. 1. Fire scars on a longleaf pine sampled at Tall Timbers. Intra-annual positioning of each scar was used to determine the season of fire. Seasonality assignments of fire scars followed Rother et al. (2018).

Few fire-scar records have been developed in pine savannas of the southeastern U.S. In the case of longleaf pine, only three published research articles are available, one based in the Kisatchie National Forest, Louisiana (Stambaugh et al., 2011a), one in the DeSoto National Forest, Mississippi (White and Harley, 2016), and a montane longleaf pine study at Sprewell Bluff Wildlife Management Area, Georgia (Klaus, 2019). A handful of additional studies are reported in theses, dissertations, or reports (Bale, 2009; Henderson, 2006; Huffman, 2006; Huffman and Platt, 2014). Studies in savannas dominated by slash pine (*Pinus elliottii*) and south Florida slash pine (*Pinus densa*) (nomenclature from Weakley, 2015) are also available (Harley et al., 2013; Huffman et al., 2004). The relative lack of fire-scar research in southern pine savannas is related to many factors, including limited availability of remnant material such as old stumps and dead trees, a western focus among scientists conducting this type of research, and a general misperception that longleaf pine does not form fire scars. The region's need for expanded fire-history research using methods customized for its ecosystems is underscored by it having some of the highest historical fire frequencies on the continent owing to frequent lightning ignitions and a long and complex history of anthropogenic burning.

In the present study, we aimed to develop fire histories using fire-scar data for three sites in the Red Hills Region of northern Florida and southwestern Georgia (Fig. 2, Fig. 3, Table 1). Given the well-known tradition of burning by private landowners in this region, we expected to document frequent fire activity over the last century or more at each of our study sites. We hoped to provide direct evidence of the fire regime during this period that could support and enhance written and oral accounts of continual burning, which would further demonstrate the unique value of these communities as reference sites for restoration. Our sample locations included two old-growth stands of longleaf pine: the Wade Tract on Arcadia Plantation and the neighboring Larkin Tract on Millpond Plantation. The Wade Tract is well-known as a rare, remnant old-growth stand that already serves as a reference site for restoration (Noel et al., 1998; Varner and Kush, 2004), although prescribed fires have been closely monitored and documented only over the last few decades. Our third site is within the largely second-growth old-field pine savannas of Tall Timbers Research Station, where research and conferences have focused on fire ecology since its establishment in 1958.

2. Methods

2.1. Study area

The Red Hills Region is situated in northern Florida and southwestern Georgia, within the North American Coastal Plain (Noss et al., 2014). Historically, this region was dominated by fire-maintained longleaf pine (Platt, 1999) and shortleaf pine savannas and woodlands (Clewell, 2013; Ostertag and Robertson, 2007). Vegetation communities were characterized by widely-spaced trees and a species-rich herbaceous ground layer including abundant cover by grasses (Platt, 1999). The long-term fire regime prior to European settlement is believed to have consisted of frequent fires ignited by both lightning and Native Americans (Komarek, 1964, 1967). A large portion of the region was used for row crop agriculture until around the turn of the 20th century, and most farming was abandoned by the 1930s (Paisley, 1968). Beginning in the late 19th century, much of the land was consolidated into estates for hunting the northern bobwhite, which included a strong tradition of frequent prescribed burning, primarily in the late winter and early spring following the hunting season and before the nesting season (Crawford and Brueckheimer, 2012; Stoddard,

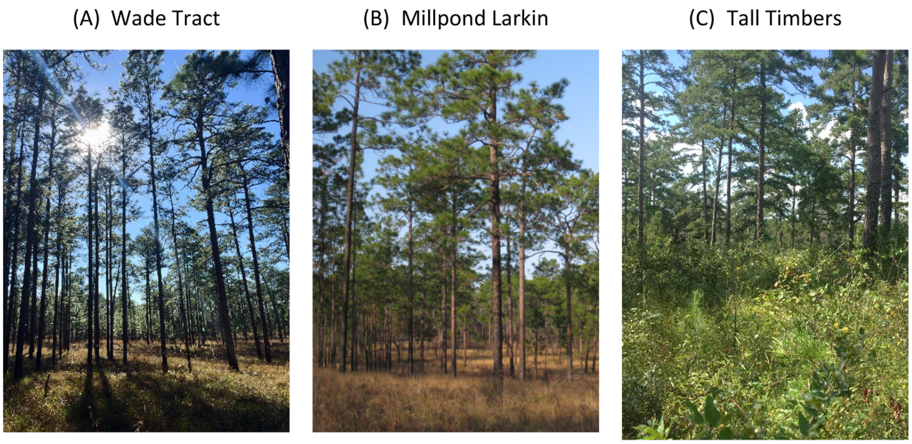

Fig. 2. Photographs of the three study sites: (A) Wade Tract, (B) Millpond Larkin, and (C) Tall Timbers. At these sites and in much of the Red Hills Region, prescribed fires have long been used to maintain open stand conditions and herbaceous vegetation. This management regime promotes a species-rich understory and provides quality habitat for wildlife. These sites may serve as useful reference areas for restoration.

1931). Currently, upland areas within the region are dominated by pine communities typically managed with biennial or annual prescribed fire, most of which are old-field pine communities. A smaller subset of the region is intact, native (never plowed) longleaf pine savanna (Ambrose, 2001; Ostertag and Robertson, 2007), of which a few areas retain old-growth trees (> 200 years old). For this study, we selected three sites with no known recent history of fire exclusion, including two old-growth longleaf pine sites (The Wade Tract and Millpond Larkin) and Tall Timbers, a second-growth, largely old-field site (Fig. 2, Fig. 3, Table 1).

Our two northern sites, the Wade Tract and Millpond Larkin, lie on adjacent properties in Thomasville, Georgia. They are located on what was once a single parcel of land that was purchased in 1903 by Jeptha Homer Wade II to be used as a large hunting property called Millpond Plantation. After 1961, the original Millpond Plantation was divided into three sections. The western section, now called Arcadia Plantation, includes the Wade Tract Preserve (hereafter, "the Wade Tract"), a rare 84-ha stand of old-growth longleaf pine. This site was never logged or used for agriculture and remains under a management regime and conservation easement to protect old-growth characteristics (Crawford and Brueckheimer, 2012). Prescribed fire is the only management at this site. The Millpond Larkin site consists of a 55-ha stand located 2 km east of the Wade Tract, on Millpond Plantation. It is dominated by mature and old-growth longleaf pine that are selectively harvested for timber, maintaining pine basal area per unit area within a range of about 5–15 m^2 ha^{-1}. Like the Wade Tract, this site was never cleared for agriculture and is under conservation easement, with frequent fire as the currently predominant management regime. Longleaf pine stands that lack significant logging, agriculture, and fire exclusion are extremely rare throughout the distribution of the species. The Wade Tract, and to a lesser degree other Red Hills Plantations, are already considered reference sites for restoration (Noel et al., 1998; Varner and Kush, 2004).

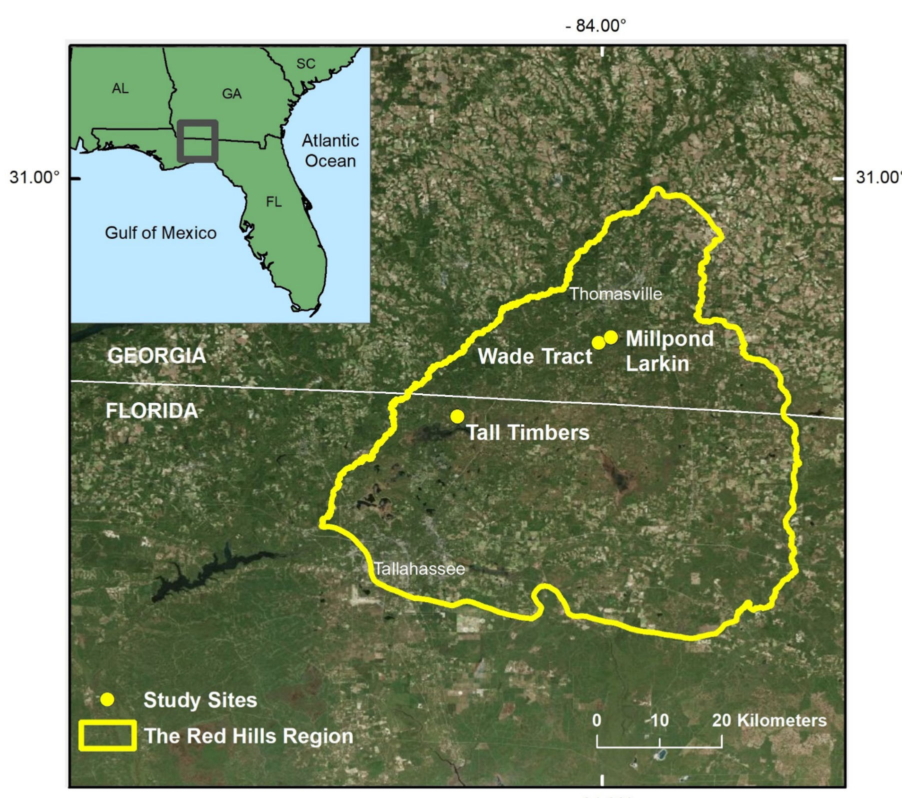

Fig. 3. Study area including the three study sites within the Red Hills Region of southwestern Georgia and northern Florida.

Table 1
Characteristics of each study site and of the fire-scar samples collected.

Site	Location (Lat, Long, in decimal degrees)	General vegetation type	Elevation	Species sampled	Trees dated (*n*)	Fire scars (*n*)
Wade Tract	30.77, −83.99	Old-growth longleaf pine savanna	70 m	Longleaf pine	10	129
Millpond Larkin	30.76, −84.00	Mature and old-growth longleaf pine savanna	75 m	Longleaf pine	9	83
Tall Timbers	30.66, −84.21	Old-field pinelands dominated by loblolly pine and shortleaf pine; patches of longleaf pine	65 m	Longleaf pine Shortleaf pine	11	204
				Total	30	416

The Tall Timbers site is located between Tallahassee, Florida and Thomasville, Georgia. The majority of this property consists of old-field (post-agricultural) upland pine communities. In most areas, the overstory is dominated by loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) that became established in fields abandoned from the end of the American Civil War (1865) to the 1930s, based on historical accounts (Crawford and Brueckheimer, 2012; Paisley, 1968), aerial photographs dating back to 1931, and understory vegetation types (Ostertag and Robertson, 2007). The understory species composition at Tall Timbers overlaps considerably with that of native sites, although the dominant vegetation at Tall Timbers has a higher composition of forbs and off-site broadleaf tree species and lacks native community indicator species including wiregrass (*Aristida beyrichiana*) (Glitzenstein et al., 2012; Ostertag and Robertson, 2007). These areas are thought to have been burned at least once every two years since the abandonment of agriculture, but documentation of specific prescribed fires did not begin until the 1990s. Some areas on the property also have longleaf pine in the canopy. The history of these locations is less clear, given that longleaf pine typically, but not always, fails to recolonize disked fields after abandonment. There is no evidence from aerial photography that these locations with longleaf pine are old fields, but current vegetation suggests a history of significant soil disturbance. All pine stands have been managed with two selective timber harvests in the past century, maintaining pine basal area per unit area within a range of about 8–15 m^2 ha^{-1}.

The geology and soils of our sites share commonalities. All three sites are characterized by karst topography with rolling hills ranging in elevation from 25 to 90 m above sea level. Soils are formed in Pliocene sediments of the Miccosukee Formation (Lawton et al., 1976; Sanders, 1981). Soils at all sites are loamy sands in the Ultisol order with kandic (low-activity clay) subhorizons, specifically fine-loamy, kaolinitic, thermic Typic Kandiudults (Norfolk, Orangeburg, Faceville series), Plinthic Kandiudults (Dothan, Fuquay series), or Arenic Kandiudults (Lucy series) (USDA Natural Resource Conservation Service Web Soil Survey (https://websoilsurvey.nrcs.usda.gov/)). Locations without a history of agriculture retained the sandy surface horizons characteristic of these series, while post-agricultural locations were variously eroded to the loam or clay-loam horizons.

2.2. Field and laboratory methods

We relied on standard dendrochronological field methods for reconstructing fire history at our three sites (Arno and Sneck, 1977; Dieterich and Swetnam, 1984; Falk et al., 2011; Farris et al., 2013). In each location, we searched for fire-scarred trees with visible evidence of repeated scarring. This method of sampling is used in most tree-ring based fire histories and ensures that the fire history is relatively complete (Fulé et al., 2003; Van Horne and Fulé, 2006). However, given that open wounds leave resinous southern pine trees susceptible to lethal burning in subsequent fires, these open wounds often contain only a relatively recent (< 150 year) record of fire in the Red Hills Region, at least in areas where we have sampled (Huffman and Rother, 2017). We used a chainsaw to collect full cross sections from remnant material including stumps, logs, and dead trees. No live trees were sampled at the Wade Tract or Millpond Larkin. At Tall Timbers, live trees were sampled opportunistically in association with planned thinning on the property. In the laboratory, we sanded each sample with progressively finer sandpaper to improve the visibility of the tree rings.

There are differences among our sites in terms of how fires spread across the landscape. The Wade Tract site is currently divided by a dirt road into two similarly sized units covering a total of 160 ha. Within each unit, flammable vegetation is relatively continuous and ignited fires typically burn most the unit. All trees that we sampled except for two have been in the same burn unit for as far back as we can tell, approximately one century, based on historical aerial photographs, aerial lidar scans, and the lack of early successional vegetation that would indicate old roads or firebreaks. We assume that adjacent units on the same property were burned under approximately the same fire regime according to the common land use objectives. At Millpond Larkin, flammable vegetation was generally continuous in the area sampled and we expect that fires that scarred individual trees typically burned across most of the site. In contrast, the Tall Timbers property has been broken into dozens of smaller, 5–15 ha blocks of land throughout its history for ease of fire management and to benefit northern bobwhite and other wildlife species (Palmer and Sisson, 2017). We sampled across several of these relatively small burn units and thus, at this property, fire scars on individual trees do not represent fires that burned across most of the site.

2.3. Data analysis

We crossdated each sample to ensure that annual growth rings and fire scars were correctly assigned the year of formation (Speer, 2010; Stokes and Smiley, 1968). Sanded samples were first scanned at 1200 dpi resolution with a flatbed scanner. Crossdating relied on a previously developed master chronology from an old-growth pine savanna on Greenwood Plantation in Thomasville, Georgia, within 30 km of our sampling locations (Pederson et al., 2012). We used the software program CooRecorder (version 8.1, Larsson, 2016) to mark and measure annual growth rings. Rings were then visually crossdated against the master chronology. We also used Cofecha software (Holmes, 1983) to verify ring measurements and crossdating against the master chronology. Growth abnormalities including false rings and some missing rings created challenges for crossdating, particularly for samples with fewer than 100 rings. Samples that could not be crossdated were not included in the study.

Fire scars were dated based on their occurrence within the crossdated annual growth rings. Whenever feasible, we assigned seasonality to the fire scars based on the intra-ring position of the fire scar (Fig. 1) (Baisan and Swetnam, 1990). We used a seasonality classification system previously developed in southern pine savannas of longleaf pine, slash pine, and south Florida slash pine (Rother et al., 2018). This system works well for pines with relatively even ratios of earlywood to latewood and with a lightning-fire season that corresponds to the transition from earlywood to latewood. It includes the following positions: 1) dormant (D), for the position between the previous year's latewood and current year's earlywood; 2) early-earlywood (EE), for the first half of earlywood; 3) late-earlywood (LE), for the second half of earlywood; 4) transition (T), for the area where trees change from producing earlywood to latewood; 5) early-latewood (EL), for the first half of latewood; and 6) late-latewood (LL), for the second half of latewood. In that same study, cambial phenology data were analyzed to provide estimates of the time of year associated with each fire-scar position, and these estimates inform our interpretation of seasonality in the present study.

We used our fire-scar records from individual trees to build site-level chronologies of fire. Information from each fire-scarred tree was first entered into a Microsoft Access© database customized for producing FHX files (the most common file format for fire-history data from tree rings). Our fire-history data include recording and non-recording periods of time for each tree sampled. This method of distinguishing between recording and non-recording years is used because trees that experience fire may not always have fire scars in the year of fire (Falk et al., 2011; Gutsell and Johnson, 1996; Stephens et al., 2010). Recording periods typically initiate when a portion of the vascular cambium is exposed by an injury that enhances further susceptibility to wounding for the remainder of the tree's life. However, subsequent periods of non-recording can occur in areas of the wood where fire scars are broken or burnt off or where the tree is able to completely heal over the scar and thereafter has reduced susceptibility to scarring. Fire frequency in our study was calculated based on recorder years only, using the mean fire interval (MFI). The period of analysis for MFI calculations was truncated to the time window that included at least two recording trees; this excluded the earliest parts of the fire-scar chronologies.

Data analysis utilized the R computing program (R Development Core Team, 2019) using the *burnr* library (version > 0.5.0, Malevich et al., 2018). We used *burnr* to compute fire intervals, analyze seasonality, and create graphics for the fire histories. For purposes of this study, *burnr* was updated to include fire-scar positions customized for southern pinelands (Rother et al., 2018). We did not calculate the MFI for Tall Timbers because recorded fires probably did not burn across the entire study site since sampling occurred across numerous different burn units. However, we presume that fire regimes recorded in the studied units are representative of other units on the property given that they were managed for the same purpose. For the Wade Tract, we calculated fire interval statistics for both the entire site and for the unit that was most heavily sampled (contained 8 out of 10 samples); individual fires ignited on a given day may have burned across both units or in one of the two units. For Millpond Larkin, individual fires could have burned across the entire sampled area and thus a single MFI was calculated for that site.

3. Results

We crossdated and analyzed fire-scarred cross sections from a total of 30 trees across our 3 sites (Table 1). Most trees contained numerous fire scars (range: 2–27; mean: 14) and in total 416 fire scars were dated. At the Wade Tract and Millpond Larkin, our samples came exclusively from longleaf pine, whereas at Tall Timbers trees sampled were both longleaf pine ($n = 5$) and shortleaf pine ($n = 6$). An additional 4–11 trees per site were sampled but were not included in the present study either because of problems with crossdating or because the tree was not sufficiently old to be of interest (less than 50 years old).

Our tree-ring record of fire history indicates that low-severity surface fires occurred frequently throughout the study period at our three sites (Fig. 4). At the Wade Tract, the MFI for all 10 trees combined was 1.8 years for the period of analysis (1882–1997). When we considered only the 8 trees on the larger unit (the green colored trees in Fig. 4), the

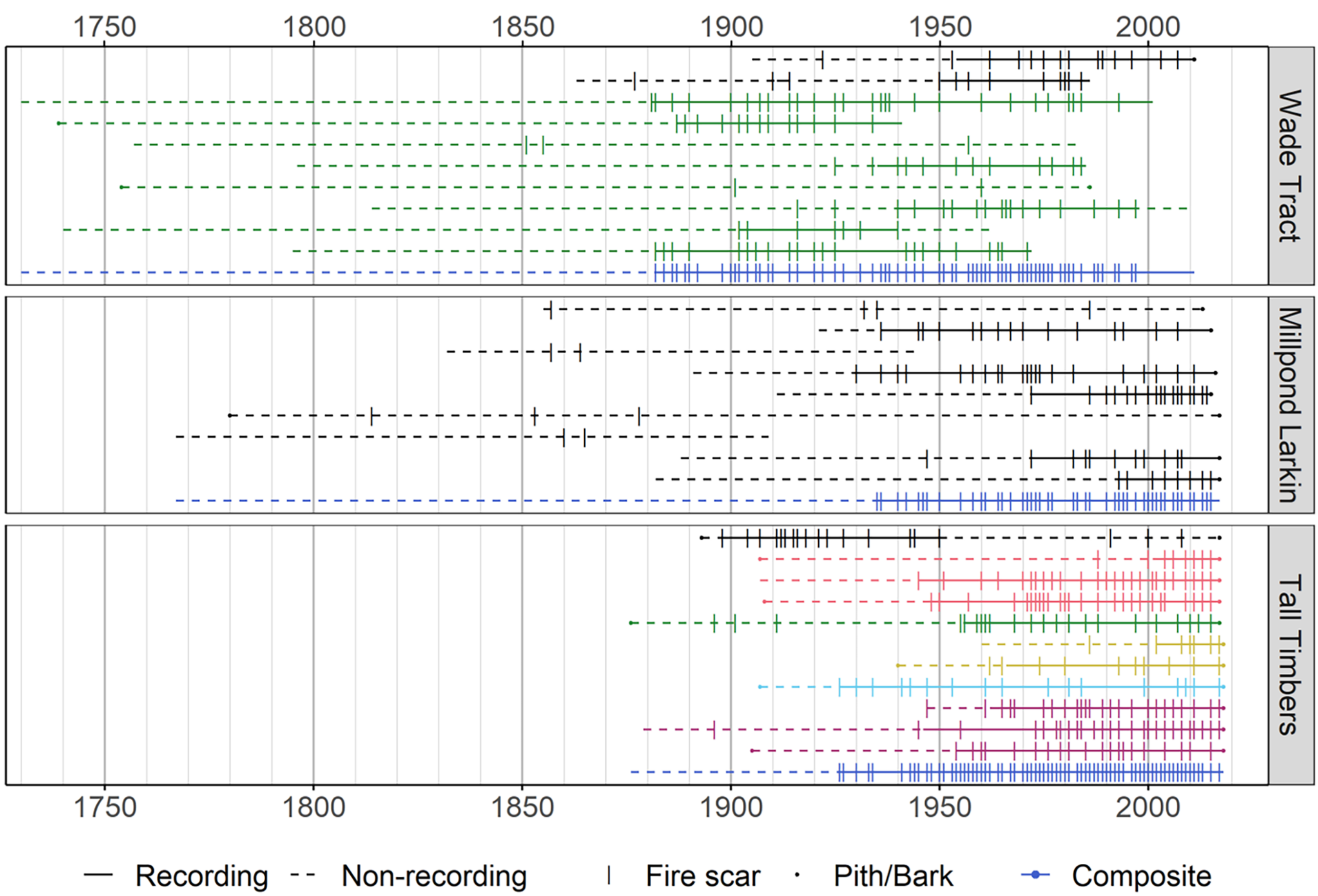

Fig. 4. Fire histories for each site. Horizontal lines show the time series of an individual tree or the site composite (in dark blue). Solid lines indicate that the tree was recording fire while dashed lines indicate years of non-recording. Vertical tick marks represent fire scars. The composite fire-scar series includes all fire events during the period in which two or more trees are recording fire. Color-coding of trees indicates shared burn units within the site. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

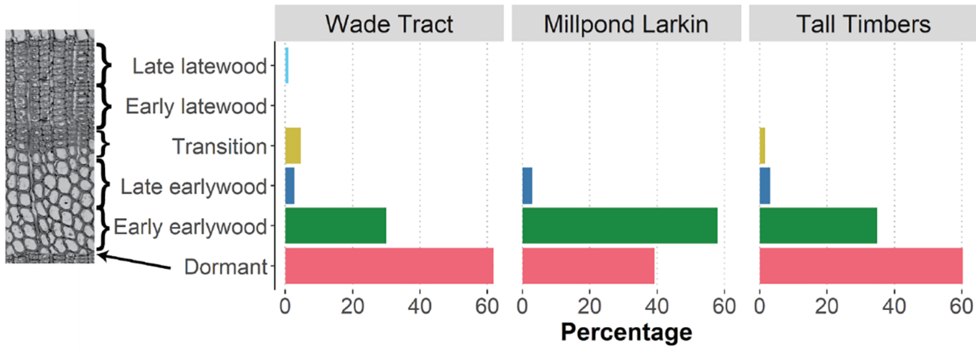

Fig. 5. Fire scar seasonality across the three study sites. Intra-annual fire scar positions were assigned based on the system described in Rother et al. (2018), depicted at the far left (microtome image provided by G. Harley).

MFI was 2.1 years. At Millpond Larkin, the MFI for all 9 trees combined was 1.8 years for the period of analysis (1935–2015). At Tall Timbers, trees within individual burn units, as color coded in Fig. 4, recorded fires at frequencies comparable to the other sites. For example, the single longleaf pine that recorded the oldest fires at the site (TT04) recorded 15 fires in a 53-year period of continuous recording (1898–1950; point fire return interval = 3.5 years). As another example, 3 other trees from a shared burn unit that recorded fire during more recent decades documented 37 fires in a 64-year period of continuous recording (1954–2017; MFI for these 3 trees only = 1.8 years). The earliest fire documented in our study occurred in 1814 at Millpond Larkin while the most recent fires occurred in 2017 at Tall Timbers. At all three sites, periods of annual burning were common during the period of analysis. At the Wade Tract, 51% of fire intervals were annual when all 10 trees were included while 38% were annual when we considered the 8 trees in the larger unit only. At Millpond Larkin, 55% of fire intervals were annual. Longer intervals without fire (> 10 years) are present at the Wade Tract and Millpond Larkin but were restricted to periods of the fire-history records when sample depth was insufficient to accurately characterize fire frequency (prior to 1882 at the Wade Tract and prior to 1935 at Millpond Larkin).

We were able to assign a season to most of the fire scars found in our samples (83–93%, depending on site). For these scars, the seasonal timing varied among sites and through time, although most fires occurred in the dormant and early-earlywood positions (Fig. 5). Of the scars with a known seasonality classification, > 90% occurred in the dormant and early-earlywood positions combined (92% at the Wade Tract, 95% at Tall Timbers, and 97% at Millpond Larkin). Most scars in other positions occurred in more recent years of the record (1980s to present) and were primarily in the late-earlywood and transition positions.

4. Discussion

We document a record of uninterrupted, frequent fire over the last century or more in three pine savanna sites of the Red Hills Region. While most tree-ring based fire history studies in the U.S. include a pronounced period of fire exclusion in the 20th century (e.g., Stambaugh et al., 2011a; Swetnam and Baisan, 1996; Taylor et al., 2016), we documented fires at our sites approximately every couple of years during this period (early 20th century onward at Tall Timbers and Millpond Larkin, late 19th century onward at the Wade Tract). This is not surprising for the Red Hills Region given the strong tradition of burning among landowners, particularly to promote northern bobwhite habitat. Many landowners in the region also value the benefits of frequent fire for providing habitat for rare and endangered species, conservation of natural communities, aesthetics, and protection of timber resources from wildfire. Although our findings of uninterrupted fire are unusual for open, pine-dominated ecosystems of North America, other records of continuous fire regimes have been documented, as reviewed in the introduction. Given the pervasiveness of fire exclusion, our sites represent unique reference sites for guiding restoration of natural communities degraded by the absence of fire.

The lack of fire scars in our study area prior to the 19th century should not be interpreted as evidence of an absence of fire historically. Instead, this pattern reflects limitations of the available tree-ring evidence. We targeted stumps, dead trees, and some live trees (live tree sampling at Tall Timbers only) that exhibited external signs of repeated scarring. The external wounding typically resulted from initial mechanical injuries caused by people, including from impacts by land-management equipment and deliberate cuts to inspect wood grain. These wounds enabled us to develop a relatively complete record of fire for the last century or more, but they generally do not provide a means for detecting earlier fires in longleaf pine savannas (Huffman and Rother, 2017). Open wounds that are typically targeted for tree-ring based fire histories do not develop readily in longleaf pine (Huffman, 2006; Huffman and Rother, 2017; Stambaugh et al., 2011a). Additionally, when large open wounds do form, they usually do not persist for long periods because they are highly resinous and increase tree susceptibility to mortality in subsequent fires (Huffman and Rother, 2017). Our sample size per site could be small given how often these sites were burned. Further sampling could add fire events to the chronology, extend the fire chronology further back in time, and potentially reveal an even higher fire frequency during the last century or more.

Although we were unable to reconstruct pre-settlement fire regimes at our sites, the fire frequency we document in the Red Hills Region is consistent with longer fire regime reconstructions from longleaf pine savannas elsewhere. Several tree-ring studies have shown that pre-19th century mean fire intervals were also less than five years (Huffman, 2006; Stambaugh et al., 2011a; White and Harley, 2016; Bale, 2009). Additionally, the evolutionary ecology of longleaf pine savannas highlights the important role that frequent fire played in shaping native community assemblages and structure (Fill et al., 2015; Platt et al., 2016). Longleaf pine require open stand structures facilitated and maintained by fire and exhibit several traits conducive to fitness in a landscape characterized by frequent fire, including thick bark and highly flammable needle cast (Frost, 2006; Keeley and Zedler, 1998; Noss, 2018; Stambaugh et al., 2017). Experimental studies that document changing vegetation patterns under differing burn regimes also demonstrate that frequent fire is required to maintain open pine savannas with herbaceous understories in this region (Clewell, 2011; Glitzenstein et al., 2012; Waldrop et al., 1992). Based on available prior research, we conclude that the high fire frequency during our period of record (fires every *c.* 2 years) is likely aligned with the longer-term fire regime at these sites, although subtle shifts in the historical fire regime through time may have occurred based on land-use changes and objectives. For example, burning to provide forage for cattle, a likely land use in non-agricultural areas of the Red Hills for about two centuries prior to the northern bobwhite hunting period, typically involved annual winter burning (Akerman, 2007; Paisley, 1968), whereas Native American burning and lightning ignitions may have been more variable in frequency and season (Stambaugh et al., 2017). Current recommendations of burning every 1–3 years in southeastern pine savannas (Kirkman and Jack, 2017) are generally consistent with both our findings of human-set fires in the last century or more and other tree-ring studies that document pre-settlement fire frequency (Huffman, 2006; Stambaugh et al., 2011a; White and Harley, 2016; Bale, 2009). That said, local land managers must carefully decide what frequency of prescribed fire is most appropriate for meeting multiple land-use objectives with consideration of vegetation community type, current vegetation conditions, feasibility, and safety.

The seasonality of fires we document is consistent with our expectation that fires during the period of analysis were human-set. The vast majority of fire scars occurred within the dormant and early-earlywood positions. Based on a previous cambial phenology study (Rother et al., 2018), historical accounts from the Red Hills Region (Crawford and Brueckheimer, 2012), and limited prescribed fire records for these sites, we estimate that most fires occurred in the months of January through mid-April. The main lightning fire season peaks later in May–August, although some lightning fires can occur year-round in this region (Komarek, 1964, 1967; Rother et al., 2018). In the modern day, the likelihood of widespread lightning-ignited fire is significantly reduced by human activities including the use of prescribed fire, the suppression of wildfires, and the fragmentation of the landscape which inhibits fire spread. Native Americans also burned this landscape in earlier centuries (Frost, 2006; Van Lear et al., 2005), but the timing and frequency of those fires prior to European settlement remains unclear. Currently, land managers who conduct prescribed burns vary in their perspectives regarding the seasonal timing of fire. Our findings suggest that very frequent dormant and early-earlywood fires can maintain open conditions at old-growth longleaf pine sites. However, the specific effects and tradeoffs between prescribed fires applied in different seasons in specific community types is a subject of continued study. As with fire frequency, land managers must weigh many considerations when making decisions regarding the seasonal timing of prescribed fire, and different approaches may be warranted for different sites.

5. Conclusion

We present a unique tree-ring perspective of uninterrupted frequent surface fires at sites that should serve as valuable references for restoration of pine savanna ecosystems. The fires we documented were probably entirely human-set as part of the long tradition of deliberate burning to promote open, pine-dominated communities with high plant species richness for northern bobwhite populations. Our sites, along with other pine savannas in the Red Hills Region, were likely continuously burned from prior millennia to the current day by a historical series of ignition sources including lightning, Native Americans, ranchers and farmers, and managers of northern bobwhite. In this light, the two native longleaf pine sites (Wade Tract, Millpond Larkin) provide a rare vision into what ecosystem structure and composition can be maintained by recurrent fire in the absence of fire exclusion, intensive soil disturbance, and industrial logging. The largely old-field site at Tall Timbers Research Station additionally suggests to what degree pine savanna ecosystems can be restored using continuous frequent fire as the primary management tool, given that these communities provide habitat for many imperiled wildlife species (Cox and McCormick, 2016; Cox and Slater, 2007; Palmer and Sisson, 2017). Old field land is far more common than native longleaf pine savanna both in the Red Hills Region (Ambrose, 2001) and throughout the distribution of longleaf pine (Frost, 2006; Oswalt et al., 2012), so the fire history and prescribed fire management of these areas should not be overlooked. Our findings underscore the importance for supporting the cultural tradition of frequent fire in southeastern pine savannas for their long-term sustainability. This specifically includes policies and regulations that support landowner use of prescribed fire, the retention of large, intact burnable parcels under single ownership, hunting of fire-dependent species (e.g. northern bobwhite), and incentives for promoting ecosystem services through burning. Our study emphasizes the continuing importance of dendrochronological research for highlighting the role of fire in maintaining valuable ecological reference sites and establishing goals for restoration of historical fire regimes.

CRediT authorship contribution statement

Monica T. Rother: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing - original draft, Funding acquisition. **Jean M. Huffman:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Christopher H. Guiterman:** Methodology, Software, Data curation, Formal analysis, Visualization, Funding acquisition, Writing - review & editing. **Kevin M. Robertson:** Conceptualization, Funding acquisition, Resources, Writing - review & editing. **Neil Jones:** Visualization, Investigation, Writing - review & editing.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

Acknowledgements

We would like to thank the Sedgwick and Wade families for supporting this study and providing access to Millpond Plantation and the Wade Tract for sampling. We also appreciate the support of Tall Timbers Research Station in approving collection on that property. Research was supported by funding from the G.G. Wade Charitable Trust and Tall Timbers Research Station. We thank Eric Staller and Andrew Chase for assistance with wood collection on Tall Timbers and William Platt and R. Todd Engstrom for help with wood collection on the Wade Tract. We also thank Megan Husain, Andrew Cunningham, Dylan Lockard, and Joshua Faylo for assisting with processing samples, and Steven Malevich for help in updating burnr for our analyses.

References

Akerman, J.A., 2007. Florida Cowman: A History of Florida Cattle Raising. Cattlemen's Association, Kissimmee, Florida.
Aldrich, S.R., Lafon, C.W., Grissino-Mayer, H.D., DeWeese, G.G., Hoss, J.A., 2010. Three centuries of fire in montane pine-oak stands on a temperate forest landscape. Appl. Veg. Sci. 13, 36–46.
Allen, M.S., Palmer, M.W., 2011. Fire history of a prairie/forest boundary: more than 250 years of frequent fire in a North American tallgrass prairie. J. Veg. Sci. 22, 436–444.
Ambrose, C.E., 2001. Remnants of a Forest: Mapping and Inventory of Ground Cover in the Red Hills Region of South Georgia and North Florida. Tall Timbers Research Station, Tallahassee, Florida.
Baisan, C.H., Swetnam, T.W., 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. Canadian J. Forestry Res. 20, 1559–1569.
Arno, S.F., Sneck, K.M., 1977. A Method for Determining Fire History in Coniferous Forests in the Mountain West. General Technical Report, INT-GTR-42. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.
Bale, A.M., 2009. Fire Effects and Litter Accumulation Dynamics in a Montane Longleaf Pine Ecosystem (Master's Thesis). University of Missouri, Columbia, Missouri.
Biswell, H.H., 1989. Prescribed Burning in California Wildlands Vegetation Management. University of California Press, Berkeley, California.
Brennan, L.A., 1997. Northern bobwhite population trends at Groton Plantation, South Carolina, 1957–1990. Tall Timbers Research Station, Tallahassee, Florida.
Brown, P.M., Swetnam, T.W., 1994. A cross-dated fire history from coast redwood near Redwood National Park, California. Can. J. For. Res. 24, 21–31.
Clark, S.L., Hallgren, S.W., Engle, D.M., Stahle, D.W., 2007. The historic fire regime on the edge of the prairie: a case study from the Cross Timbers of Oklahoma. In: Tall Timbers Fire Ecology Conference Proceedings, vol. 23, pp. 40–49.
Clewell, A.F., 2011. Forest succession after 43 years without disturbance on ex-arable land, northern Florida. Castanea 76, 386–394.
Clewell, A.F., 2013. Prior prevalence of shortleaf pine-oak-hickory woodlands in the

Tallahassee Red Hills. Castanea 78, 266–276.
Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. J. Forest. 92, 39–47.
Cox, J.A., McCormick, J.K., 2016. New insights from an attempt to reintroduce red-cockaded woodpeckers in northern Florida. J. Field Ornithol. 87, 360–370.
Cox, J.A., Slater, G.L., 2007. Cooperative breeding in the brown-headed nuthatch. Wilson J. Ornithol. 119, 1–8.
Crawford, R.L., Brueckheimer, W.R., 2012. The legacy of a Red Hills hunting plantation. In: Tall Timbers Research Station & Land Conservancy. University Press of Florida, Gainesville, Florida.
Dieterich, J.H., Swetnam, T.W., 1984. Dendrochronology of a fire-scarred ponderosa pine. Forest Sci. 30, 238–247.
Donovan, G.H., Brown, T.C., 2007. Be careful what you wish for: the legacy of Smokey Bear. Front. Ecol. Environ. 5, 73–79.
Engstrom, B.F., Mann, D.H., 1991. Fire ecology of red pine (*Pinus resinosa*) in northern Vermont, U.S.A. Can. J. For. Res. 21, 882–889.
Falk, D.A., Heyerdahl, E.K., Brown, P.M., Farris, C., Fulé, P.Z., McKenzie, D., Swetnam, T.W., Taylor, A.H., Van Horne, M.L., 2011. Multi-scale controls of historical forest-fire regimes: new insights from fire-scar networks. Front. Ecol. Environ. 9, 446–454.
Farris, C.A., Baisan, C.H., Falk, D.A., Van Horne, M.L., Fulé, P.Z., Swetnam, T.W., 2013. A comparison of targeted and systematic fire-scar sampling for estimating historical fire frequency in south-western ponderosa pine forests. Int. J. Wildland Fire 22, 1021–1033.
Fill, J.M., Platt, W.J., Welch, S.M., Waldron, J.L., Mousseau, T.A., 2015. Updating models for restoration and management of fiery ecosystems. For. Ecol. Manage. 356, 54–63.
Frost, C., 2006. History and future of the longleaf pine ecosystem. In: The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York, New York, pp. 9–48.
Fulé, P.Z., Heinlein, T.A., Covington, W.W., Moore, M.M., 2003. Assessing fire regimes on Grand Canyon landscapes with fire-scar and fire-record data. Int. J. Wildland Fire 12, 129–145.
Glitzenstein, J.S., Streng, D.R., Masters, R.E., Robertson, K.M., Hermann, S.M., 2012. Fire-frequency effects on vegetation in north Florida pinelands: another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. For. Ecol. Manage. 264, 197–209.
Greenlee, J.M., Langenheim, J.H., 1990. Historic fire regimes and their relation to vegetation patterns in the Monterey Bay area of California. Am. Midl. Nat. 124, 239–253.
Grelen, H.E., 1978. Forest grazing in the South. J. Range Manage. 31, 244–250.
Gutsell, S., Johnson, E., 1996. How fire scars are formed: coupling a disturbance process to its ecological effect. Can. J. For. Res. 26, 166–174.
Harley, G.L., Grissino-Mayer, H.D., Horn, S.P., 2013. Fire history and forest structure of an endangered subtropical ecosystem in the Florida Keys, USA. Int. J. Wildland Fire 22, 394–404.
Henderson, J.P., 2006. Dendroclimatological Analysis and Fire History of Longleaf Pine (*Pinus palustris* Mill.) in the Atlantic and Gulf Coastal Plain (PhD Dissertation). The University of Tennessee, Knoxville, Tennessee.
Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 69–78.
Hoss, J.A., Lafon, C.W., Grissino-Mayer, H.D., Aldrich, S.R., DeWeese, G.G., 2008. Fire history of a temperate forest with an endemic fire-dependent herb. Phys. Geogr. 29, 424–441.
Hoy, J., 1989. Controlled pasture burning in the folklife of the Kansas Flint Hills. Great Plains Quart. 9, 231–238.
Huffman, J.M., 2006. Historical fire regimes in southeastern pine savannas (PhD Dissertation). Louisiana State University, Baton Rouge, Louisiana.
Huffman, J.M., Platt, W.J., 2014. Fire History of the Avon Park Air Force Range: Evidence from Tree Rings. Unpublished contract report submitted to Avon Park Air Force Range, Avon Park, Florida.
Huffman, J.M., Platt, W.J., Grissino-Mayer, H.D., Boyce, C.J., 2004. Fire history of a barrier island slash pine (*Pinus elliottii*) savanna. Natural Areas J. 24, 258–268.
Huffman, J.M., Rother, M.T., 2017. Dendrochronological field methods for fire history in pine ecosystems of the Southeastern Coastal Plain. Tree-ring Res. 73, 42–46.
Johnson, L.B., Kipfmueller, K.F., 2016. A fire history derived from *Pinus resinosa* Ait. for the Islands of Eastern Lac La Croix, Minnesota, USA. Ecol. Appl. 26, 1030–1046.
Keeley, J.E., Zedler, P.H., 1998. Evolution of life histories in *Pinus*. In: Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, pp. 219–249.
Kirkman, L.K., Jack, S.B., 2017. Ecological Restoration and Management of Longleaf Pine Forests. CRC Press, Boca Raton, Florida.
Klaus, N., 2019. Fire history of a Georgia montane longleaf pine (*Pinus palustris*) community. Georgia J. Sci. 77, 1–13.
Komarek, E.V., 1964. The natural history of lightning. In: Tall Timbers Fire Ecology Conference Proceedings, vol. 3, pp. 139–183.
Komarek, E.V., 1967. The nature of lightning fires. In: Tall Timbers Fire Ecology Conference Proceedings, vol. 7, pp. 5–41.
Larsson, L., 2016. CooRecorder and Cdendro programs of the CooRecorder/Cdendro package version 8.1.
Lawton, D.E., Moye, F.J., Murray, J.B., O'Connor, M.J., Penley, H.M., Sandrock, G.S., 1976. Geologic Map of Georgia. Georgia Department of Natural Resources, Geologic and Water Resources Division, Georgia Geological Survey.
Malevich, S.B., Guiterman, C.H., Margolis, E.Q., 2018. burnr: Fire history analysis and graphics in R. Dendrochronologia 49, 9–15.
Marschall, J.M., Stambaugh, M.C., Jones, B.C., Abadir, E., 2019. Spatial variability of historical fires across a red pine–oak landscape, Pennsylvania, USA. Ecosphere 10, 1–21 e02978.
Noel, J.M., Platt, W.J., Moser, E.B., 1998. Structural characteristics of old- and second-growth stands of longleaf pine (*Pinus palustris*) in the Gulf Coastal Region of the U.S.A. Conserv. Biol. 12, 533–548.
Noss, R.F., 2018. Fire ecology of Florida and the Southeastern Coastal Plain. University Press of Florida, Gainesville, Florida.
Noss, R.F., Platt, W.J., Sorrie, B.A., Weakley, A.S., Means, D.B., Costanza, J., Peet, R.K., 2014. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. Diversity Distribut. 21, 236–244.
Ostertag, T.E., Robertson, K.M., 2007. A comparison of native versus old-field vegetation in upland pinelands managed with frequent fire, South Georgia, USA. In: Tall Timbers Fire Ecology Conference Proceedings, vol. 23, pp. 109–120.
Oswalt, C.M., Cooper, J.A., Brockway, D.G., Brooks, H.W., Walker, J.L., Connor, K.F., Oswalt, S.N., Conner, R.C., 2012. History and Current Condition of Longleaf Pine in the Southern United States. General Technical Report, SRS-166. General Technical Report-Southern Research Station, USDA Forest Service, Asheville, North Carolina.
Otto, J.S., 1984. Traditional cattle-herding practices in southern Florida. J. Am. Folklore 97, 291–309.
Paisley, C., 1968. From Cotton to Quail: An Agricultural Chronicle of Leon County, Florida, 1860–1967. University of Florida Press, Gainesville, Florida.
Palmer, W.E., Sisson, C.D., 2017. Tall Timbers' Bobwhite Quail Management Handbook. Tall Timbers Press, Tallahassee, Florida.
Pederson, N., Bell, A.R., Knight, T.A., Leland, C., Malcomb, N., Anchukaitis, K., Tackett, K., Scheff, J., Brice, A., Catron, B., Blozan, W., Riddle, J., 2012. A long-term perspective on a modern drought in the American Southeast. Environ. Res. Lett. 7, 1–8 014034.
Platt, W.J., 1999. Southeastern pine savannas. In: Savannas, Barrens, and Rock Outcrop Plant Communities of North America, pp. 23–51.
Platt, W.J., Ellair, D.P., Huffman, J.M., Potts, S.E., Beckage, B., 2016. Pyrogenic fuels produced by savanna trees can engineer humid savannas. Ecol. Monogr. 86, 352–372.
Pyne, S.J., 1982. Fire in America: A Cultural History of Wildland and Rural Fire. University of Washington Press, Seattle, Washington.
R Development Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Rother, M.T., Huffman, J.M., Harley, G.L., Platt, W.J., Jones, N., Robertson, K.M., Orzell, S.L., 2018. Cambial phenology informs tree-ring analysis of fire seasonality in Coastal Plain pine savannas. Fire Ecol. 14, 164–185.
Sanders, T.E., 1981. Soil Survey of Leon County, Florida. US Department of Agriculture, Soil Conservation Service and Forest Service.
Schoennagel, T.L., Veblen, T.T., Romme, W.H., 2004. The interaction of fire, fuels, and climate across Rocky Mountain Forests. Bioscience 54, 661–676.
Shirakura, F., Sasaki, K., Arévalo, J.R., Palmer, M.W., 2006. Tornado damage of *Quercus stellata* and *Quercus marilandica* in the Cross Timbers, Oklahoma, USA. J. Veg. Sci. 17, 347–352.
Speer, J.H., 2010. Fundamentals of Tree-ring Research. University of Arizona Press, Tucson, Arizona.
Stambaugh, M.C., Guyette, R.P., Godfrey, R., McMurry, E.R., Marschall, J.M., 2009. Fire, drought, and human history near the western terminus of the Cross Timbers, Wichita Mountains, Oklahoma, USA. Fire Ecol. 5, 51–65.
Stambaugh, M.C., Guyette, R.P., Marschall, J.M., 2011a. Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. J. Veg. Sci. 22, 1094–1104.
Stambaugh, M.C., Guyette, R.P., Marschall, J.M., Dey, D.C., 2016. Scale dependence of oak woodland historical fire intervals: contrasting The barrens of Tennessee and Cross Timbers of Oklahoma, USA. Fire Ecol. 12, 65–84.
Stambaugh, M.C., Sparks, J., Guyette, R.P., Willson, G., 2011b. Fire history of a relict oak woodland in northeast Texas. Rangeland Ecol. Manage. 64, 419–423.
Stambaugh, M.C., Varner, J.M., Jackson, S.T., 2017. Biogeography: an interweave of climate, fire, and humans. In: Ecological Restoration and Management of Longleaf Pine Forests. CRC Press, Boca Raton, Florida, pp. 17–38.
Stephens, S.L., Fry, D.L., Collins, B.M., Skinner, C.N., Franco-Vizcaino, E., Freed, T.J., 2010. Fire-scar formation in Jeffrey pine - mixed conifer forests in the Sierra San Pedro Martir, Mexico. Can. J. For. Res. 40, 1497–1505.
Stephens, S.L., Fulé, P.Z., 2005. Western pine forests with continuing frequent fire regimes: possible reference sites for management. J. Forest. 103, 357–362.
Stoddard, H.L., 1931. Bobwhite Quail; Its Habits, Preservation and Increase. Charles Scribner's Sons, New York, New York.
Stokes, M.A., Smiley, T.L., 1968. An Introduction to Tree-ring Dating. University of Arizona Press, Tucson, Arizona.
Stribling, H.L., Sisson, D.C., 2009. Hunting success on Albany, Georgia plantations: the Albany Quail Project's modern quail management strategy. In: National Quail Symposium Proceedings, vol. 6, pp. 338–347.
Swetnam, T.W., Baisan, C.H., 1996. Historical fire regime patterns in the southwestern United States since AD 1700. Historical fire regime patterns in the southwestern United States since AD 1700, 11–32.
Taylor, A.H., Trouet, V., Skinner, C.N., Stephens, S., 2016. Socioecological transitions trigger fire regime shifts and modulate fire–climate interactions in the Sierra Nevada, USA, 1600–2015 CE. Proc. Natl. Acad. Sci. 113, 13684–13689.
Van Horne, M.L., Fulé, P.Z., 2006. Comparing methods of reconstructing fire history using fire scars in a southwestern United States ponderosa pine forest. Can. J. For. Res. 36, 855–867.
Van Lear, D.H., Carroll, W.D., Kapeluck, P.R., Johnson, R., 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. For. Ecol. Manage. 211, 150–165.
Varner, J.M., Kush, J.S., 2004. Remnant old-growth longleaf pine (*Pinus palustris* Mill.) savannas and forests of the southeastern USA: status and threats. Nat. Areas J. 24, 141–149.
Waldrop, T.A., White, D.L., Jones, S.M., 1992. Fire regimes for pine-grassland

communities in the southeastern United States. For. Ecol. Manage. 47, 195–210.
Way, A.G., 2011. Conserving Southern Longleaf: Herbert Stoddard and the Rise of Ecological Land Management. University of Georgia Press, Athens, Georgia.
Weakley, A.S., 2015. Flora of the Southern and Mid-Atlantic States. University of North Carolina, Chapel Hill, North Carolina.
White, C.R., Harley, G.L., 2016. Historical fire in longleaf pine (*Pinus palustris*) forests of south Mississippi and its relation to land use and climate. Ecosphere 7, 1–17 e01458.