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# The Longleaf Tree-Ring Network: Reviewing and expanding the utility of *Pinus palustris* Mill. Dendrochronological data

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**Abstract**

The longleaf pine (*Pinus palustris* Mill.) and related ecosystem is an icon of the southeastern United States (US). Once covering an estimated 37 million ha from Texas to Florida to Virginia, the near-extirpation of, and subsequent restoration efforts for, the species has been well-documented over the past *ca.* 100 years. Although longleaf pine is one of the longest-lived tree species in the southeastern US—with documented ages of over 400 years—its use has not been reviewed in the field of dendrochronology. In this paper, we review the utility of longleaf pine tree-ring data within the applications of four primary, topical research areas: climatology and paleoclimate reconstruction, fire history, ecology, and archeology/cultural studies. Further, we highlight knowledge gaps in these topical areas, for which we introduce the Longleaf Tree-Ring Network (LTRN). The overarching purpose of the LTRN is to coalesce partners and data to expand the scientific use of longleaf pine tree-ring data across the southeastern US. As a first example of LTRN analytics, we show that the development of seasonwood chronologies (earlywood width, latewood width, and total width) enhances the utility of longleaf pine tree-ring data, indicating the value of these seasonwood metrics for future studies. We find that at 21 sites distributed across the species' range, latewood width chronologies outperform both their earlywood and total width counterparts in mean correlation coefficient (RBAR = 0.55, 0.46, 0.52, respectively). Strategic plans for increasing the utility of longleaf pine dendrochronology in the southeastern US include [1] saving remnant material (*e.g.,* stumps, logs, and building construction timbers) from decay, extraction, and fire consumption to help extend tree-ring records, and [2] developing new chronologies in LTRN spatial gaps to facilitate broad-scale analyses of longleaf pine ecosystems within the context of the topical groups presented.

**Keywords**

tree ring, savanna ecology, climatology, climate reconstruction, fire, archaeology

> "Even though I came from longleaf country in Alabama and in my later years had learned more and more about the subject, I realized how little I really knew—and how much more I had to learn and how much more remained for science to discover—about the American South's signature tree."
>
> *E.O. Wilson In memoriam, foreward,* Finch et al. (2012)

## Introduction

The tragic plight and subsequent efforts to restore longleaf pine (*Pinus palustris* Mill.) in the southeastern United States have been well-documented over the last several decades. Longleaf pine is a foundation species for the different longleaf pine ecosystems that once-collectively spanned an estimated 37 million ha (Frost, 2007), making it one of the largest ecosystem assemblages in North America during the late Holocene. Euro-American colonization of the southeastern US brought about detrimental land use practices—such as widespread logging, fire suppression, habitat fragmentation, and a host of other exploitative practices that have reduced the pre-colonial range to just over 4 million ha (Oswalt and Guldin, 2021) (Figures 1 and 2). As one of the longest-lived tree species in the southeastern US, with average ages (e.g., 300-400 + years) second only to bald cypress (*Taxodium distichum* Rich.; e.g., Stahle et al., 2012), longleaf pine is highly valued within the discipline of dendrochronology for the scientific information embedded within its rings. As the science of dendrochronology progresses, coeval with current and impending climate and environmental change, there is a need to review the current knowledge of the species and expand the utility of tree-ring data, especially within the context of ongoing restoration efforts.

Following the earliest descriptive literature on longleaf pine (e.g., Bartram, 1791; Williams, 1837; Michaux, 1857; Gosse, 1859), much of the initial research was focused on the economic value and exploitation of its ecosystem Ashe (1894); Schwarz (1907); Harper (1913), particularly for the naval stores Gamble (1921); Cary (1928); Harper (1944) and timber industries Harper (1928); Wahlenberg (1946).

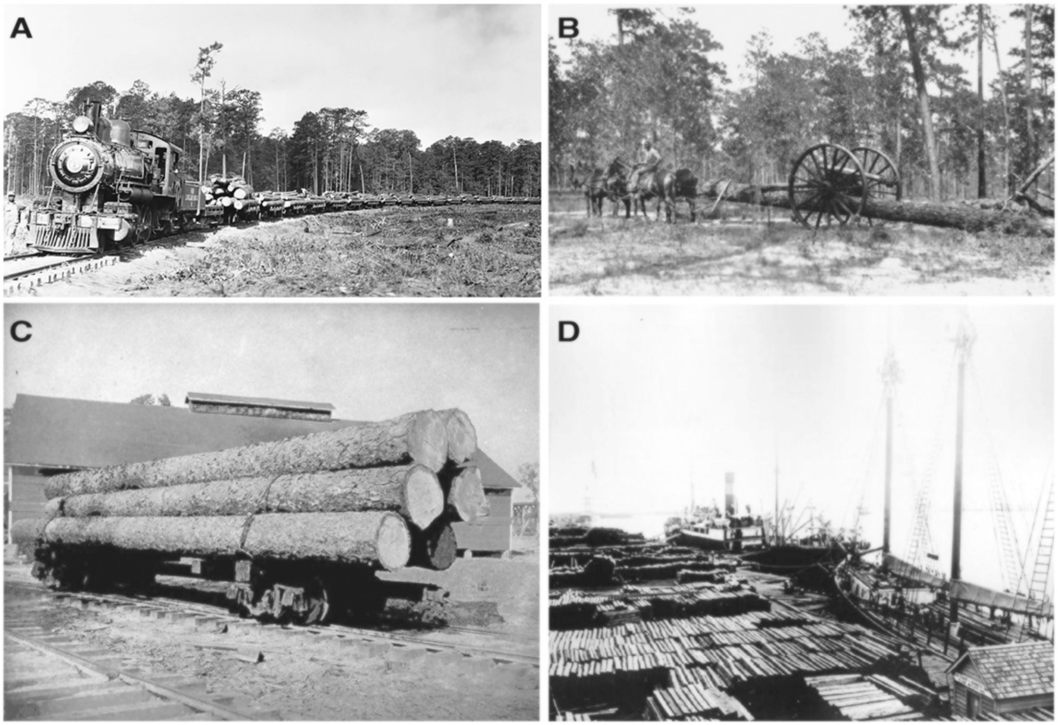

**Figure 1.** Early photographs of widespread logging and distribution of longleaf throughout the southeastern US. (a) Newly-harvested longleaf logs headed to a lumber mill near Weirgate, Texas ca. 1930. (b) Harvesting longleaf pine ca. 1915 near De Leon Springs, Florida with horse and wagon. (c) A link-and-pin rail car along the Escambia Railway loaded with virgin longleaf pine near Century, Florida ca. 1925. (d) Stacks of milled longleaf pine ready for shipping at a port near Fernandina, Florida ca. 1900. Photographs in panel A from University of North Texas Libraries, Portal to Texas History, and B, C, and D from the Florida State Photographic Collection.

A growing volume of literature, which has seen resurgence in recent decades, has focused on longleaf biogeography and natural history (Mohr, 1897, 1901; Frost, 1993; Earley, 2004; Stambaugh et al., 2017). Noted for its role as a foundation species in a variety of ecosystems that were once extensive throughout the southeastern Gulf and Atlantic Coastal Plain, longleaf are now reduced to the point of being listed as a globally endangered species and one of the U.S.'s most endangered ecosystems (Noss and Scott 1995).

## Natural history and exploitation

Longleaf pine is the key component to a wide range of savanna and woodland ecosystems (Platt, 1999; Oswalt et al., 2012; Peet et al., 2018) across the primary physiographic regions of the southeastern US (e.g., Atlantic and Gulf Coastal Plains, Piedmont, Ridge and Valley, Cumberland Plateau, Blue Ridge), from coastal locations to elevations approximately 600 m.a.s.l. (Figure 3; Boyer, 1990; Stout and Marion 1993; Stowe et al., 2002). Accounts from the early 18$^{th}$ through early 20$^{th}$ centuries indicate that longleaf pine was dominant across much of this range. Longleaf pine ecosystems, while shaped by edaphic and climatic factors, are ubiquitously maintained by frequent surface fire (Chapman, 1932; Heyward, 1939; Bridges and Orzell, 1989; Brockway et al., 2007; Platt, 1999; Stambaugh et al., 2011); hence, longleaf pine has developed several reproductive and morphological adaptations to fire,

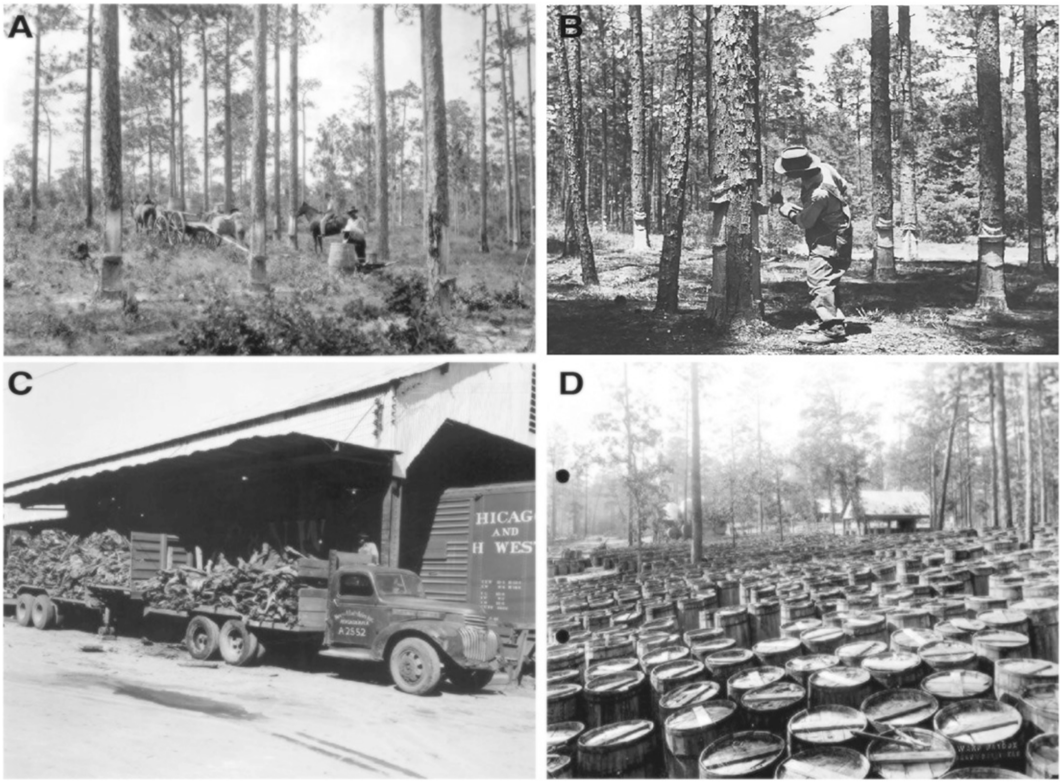


**Figure 2.** Early 20th century photographs of the naval stores industry across the southeastern US. (a) Typical scene of a naval stores operation from *ca.* 1920s northern Florida. (b) Cupping a tree in an Alabama longleaf pine forest for turpentine gum production *ca.* 1930–1949. (c) After widespread logging, stumps were removed from the ground and transported to a processing facility, such as the one shown here of Newport Industries, Pensacola, Florida *ca.* 1956. (d) A naval stores distillery in Florida *ca.* 1910 showing the rosin yard, where raw pitch was stored in wooden barrels for turpentine processing. Photographs in panels A, C, and D from the Florida State Photographic Collection and B from the Alabama Department of Archives and History.

such as the presence of needle tufts that insulate terminal buds, thick bark to protect against heat transfer, and self-pruning

lower branches to prohibit crown fires (Boyer, 1990; Landers et al., 1995). Scores of federally protected species inhabit longleaf pine ecosystems (Walker, 1993; Zion et al., 2019). Notably, certain longleaf pine habitats—based on, for example, tree density, size, age, structure, and ground cover—act as optimal niche gestalts by allowing the endangered Red-cockaded Woodpecker (*Picoides borealis* Vieillot) to not only persist, but to thrive (Jackson, 1994; Engstrom and Sanders, 1997; Conner et al., 2001; James et al., 2001; Shaw and Long, 2007; Kaiser et al., 2020).

The naval stores (i.e., pitch, rosin, tar, and turpentine) industry began in the early 1600s in Virginia (Frost 2007). The earliest production focused on using naturally preserved stumps and other *lightwood*—also colloquially termed *fatwood*, *fat lighter*, or *lighter knot*—due to the high amount of resin and hence ease of catching fire for pitch and tar manufacturing. During the colonial period, the naval stores industry in the southeastern US, particularly in North and South Carolina, was not only an important part of the regional economy, but also a

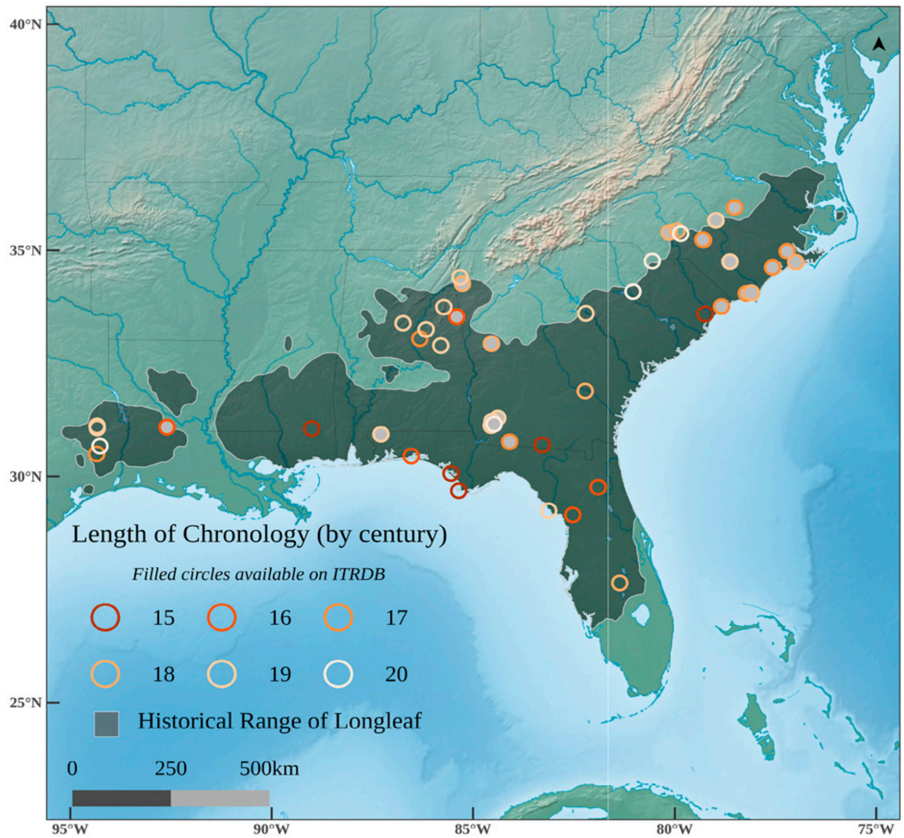


**Figure 3.** Spatial and temporal distribution of longleaf pine tree-ring data compiled by the LTRN. Historical, native range of longleaf pine across the southeastern US (from Little Jr 1971) shown as a gray polygon, with tree-ring records included on the ITRDB denoted by a filled circle. Length of chronology is binned to the starting century of each record. Figure generated using the R Statistical Software (v4.2.1; R Core Team, 2022). For interpretation of the references to colours in this figure legend, refer to the online version of this article.

critical source of pitch and tar to western Europe for the use of sealing wooden vessels. Throughout the 19th to mid-20th century, industry methods and production continuously expanded across much of the southeastern US (Outland III 2004; Barnett 2019). Although harvesting longleaf pine for timber began during the colonial period for shipbuilding (Mundo et al., 2022), the most extensive cutting prior to the 1830s was primarily for agricultural land clearing, especially along the Atlantic Coastal Plain (e.g., US States of Virginia, North Carolina, and South Carolina). For most of the 19th century, intensive logging was generally restricted to stream courses and railroad corridors (Frost 2007). However, with the naval industry demand and the expansion of railways across the region, nearly all the remaining longleaf pines were logged and exported to other regions of the US and abroad (Oswalt, et al., 2012). After the *ca.* 1930s, much of the cutover land was converted to agriculture or, in some locations, longleaf pine was replaced with loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm.) pine plantations.

Fire suppression efforts spanning most of the 20$^{th}$ century contributed to the mesophication of longleaf pine habitats (i.e., hardwood dominated woodlands), presenting a challenge for conservation and restoration that include prescribed fire (Gilliam and Platt

1999; Varner III et al. 2005; Ryan et al., 2013). Other important conservation and management issues include habitat destruction by invasive and non-native species, such as feral hogs (*Sus scrofa* L.), which were first introduced by the Spanish in the 1500s and whose numbers increased exponentially by the late 20th century (Wood and Roark 1980; Frost 1993, 1997; Lipscomb 1989). Fortunately, a renewed and growing interest in longleaf pine for timber and habitat conservation has occurred over the past few decades. Today, numerous range-wide conservation and restoration strategies exist to help guide public and private landowners in longleaf pine reestablishment (e.g., Sellers et al., 2021; Oluoch et al., 2021). Such widespread efforts include The Longleaf Alliance—a consortium aimed at guiding longleaf restoration, stewardship, and conservation using science-based outreach, partnership engagement, and on-the-ground assistance—as well as targeted Federal programs that provide incentives to private landowners for planting longleaf pine in lieu of commercial forest species such as loblolly and slash pine. Along with the renewed interest in restoring longleaf pine habitat across the southeastern US over the past *ca.* 30 years, researchers have discovered the scientific value of longleaf pine tree-ring records and their contribution to better understanding the structure and function of longleaf pine ecosystems, among other related topics.

Longleaf pine meets many requirements as a valued species within the field of dendrochronology. For example, longleaf pine [1] is a long-lived and widely distributed tree in the southeastern US and is a primary component of savannas and woodlands, including coastal plain and montane environments, from eastern Texas to southern Virginia, [2] has annual ring-width growth that is highly responsive to climate and environmental fluctuations, [3] is a recorder of fire activity, and [4] was widely used as a construction material for historical structures. Because of its high resin content, remnant longleaf pine material is often well-preserved and abundant across the southeastern US landscape, and timber from this species was commonly used for construction beginning in the 18th century. These factors allow for the development of long tree-ring chronologies (> 500 years) from remnant, archaeological, and living longleaf pine in Georgia and Louisiana (Stambaugh et al., 2011), Mississippi (White and Harley 2016; Herrmann et al., 2016; Harley et al., 2017a; Bregy et al., 2022), North Carolina (Maxwell et al. 2021), and Florida (Harley et al., 2017b). Despite these positive attributes, tree-ring research using longleaf pine (for purposes other than silviculture) has been relatively limited compared to other species in the southeastern US, such as bald cypress (e.g., Stahle et al., 2012). As an example, only 20 site-unique records have, so far, been contributed to the International Tree-Ring Data Bank (ITRDB; Mendely Data doi: 10.17632/dm8mdvnfmy.1). Given the broad utility of longleaf within the discipline of dendrochronology, additional tree-ring collections throughout its range—especially in the context of a data network—would facilitate deeper understandings of this iconic species within the context of natural history.

The Longleaf Tree-Ring Network (LTRN) is both a collection of individuals and a database currently consisting of over 35 researchers in academia, conservation, land management, and government who have come together with the goal to expand the scientific use of longleaf pine tree-ring data across its range within the southeastern US and beyond. This project seeks to: [1] provide a review of longleaf pine-specific dendrochronological research to highlight the status of the science and identify knowledge gaps within the bounds of primary topical applications (**Climate**, **Fire**, **Ecology**, and **Archaeology/ Cultural Studies**), [2] increase public availability of unpublished longleaf pine tree-ring chronologies, [3] update and extend previously-developed records, [4] develop new records within geographic areas without representation, [5] explore the development of longleaf pine tree-ring records based on new and emerging tree-ring methods (e.g., earlywood/ latewood and false ring chronologies), and [6] promote the value and utility of longleaf pine tree-ring records to stakeholders who may benefit from awareness of their potential application (e.g., researchers in relevant fields, land managers and/or owners). We also report here our initial development of a database of tree-ring chronologies, progress on making chronologies and associated data (e.g. plot-level vegetation data) available for research, and current efforts on developing new records, including records based on emerging methods.

## Primary applications in dendrochronology

### Climate

Longleaf pine holds tremendous potential for contributing to proxy-based paleoclimate reconstructions in the southeastern US, though this potential has only been realized in recent decades. Early examinations of longleaf pine radial growth were conducted in the early 1900s (e.g., Schwarz 1907); however, the influence of climate on the species was not examined in detail until the 1990s (Platt et al., 1988; Devall et al., 1991; West et al., 1993). Two primary factors likely contributed to the slow development of longleaf pine dendrochronological analyses. First, early dendrochronological research in the southeastern US emphasized examination of exceptionally long-lived species such as bald cypress (Stahle et al. 1985, 1998; Stahle and Cleaveland 1992), a species that grows throughout much of the longleaf pine range, has a lifespan upwards of 2000 years and is sensitive to variations in spring and summer precipitation and streamflow (Stahle et al., 2012; Therrell et al., 2020). As a point of reference, a current search (November 2022) for publicly available bald cypress chronologies on the ITRDB yields 45 compared to 22 for longleaf pine. Consequently, the perceived value of bald cypress as the primary source of paleoclimate information likely delayed the investigation of longleaf pine for dendroclimatology. A second contributing factor to the lack of longleaf pine tree-ring studies is likely related to the difficulty in crossdating the annual growth rings of longleaf pine relative to many other species. Highly sensitive growth patterns of longleaf pine, coupled with an abundance of intra-annual variations in latewood density (i.e., false rings) that can easily be misconstrued as annual rings, creates distinct challenges for developing absolutely-dated and robust chronologies from the species (Henderson and Grissino-Mayer 2009; Patterson et al., 2016).

Longleaf pine grows in sandy or rocky soils, and despite having a deep taproot, their overall root system is relatively shallow (Miller et al., 2006; Crockett et al., 2010). The root system architecture, however, enables individuals in certain xeric habitats to be highly sensitive to changes in precipitation and soil moisture. While the annual growth patterns of longleaf pine have been underappreciated as paleoclimatic proxy, several recent studies have successfully used longleaf pine for climate applications (e.g., Mitchell et al., 2020; Collins-Key and Altman, 2021; Maxwell et al., 2021; Stambaugh et al., 2021; Bregy et al., 2022), indicating the potential of this species for future paleoclimatic studies.

Initial studies examining longleaf pine climate sensitivity identified precipitation as the dominant climatic factor influencing radial growth (Lodewick 1930; Coile 1936). Little further analysis of this climate sensitivity was conducted until the late 20$^{th}$ century, when subsequent research showed positive, reliable relationships between radial growth and variability in soil moisture and precipitation (Zahner 1989; Devall et al., 1991; Meldahl et al., 1999). Continued work corroborated these relationships across much of the historical range of longleaf pine (Foster and Brooks 2001; Henderson and Grissino-Mayer 2009; Patterson et al., 2016). Additionally, Bhuta et al. (2009) found a positive and significant relationship between winter (January and February) temperatures and ring width at the northern latitudinal range limit of longleaf pine in Virginia.

The consistent response of longleaf pine to precipitation across the species' range led to the inclusion of the species in paleoclimatic reconstructions of drought (Ortegren 2008; Cook et al., 2010; Pederson et al., 2012), particularly as an integral driver of some of the drought reconstruction models of the North American Drought Atlas (Cook et al., 1999). Similarly, the sensitivity of the species to growing season soil moisture resulted in the incorporation of longleaf pine chronologies in a 285-years (1700–1985) streamflow reconstruction of the Flint River in Georgia, USA (Knight et al., 2004). The connection between longleaf pine and streamflow is indirect, as both streamflow and longleaf pine growth respond to changes in water balance, rather than longleaf pine responding to direct changes in streamflow. Further work expanding on this indirect relationship has used longleaf pine as a predictor to reconstruct streamflow in various areas of the southeastern US (Harley et al., 2017b; Maxwell et al., 2017).Harley et al. (2017b) used a multi-species tree-ring network to reconstruct Suwannee River (Florida) discharge during the period 1550–2005. Notably, they found that longleaf pine chronologies ($n$ = 10) outperformed those from seven other species ($n$ = 31), including bald cypress ($n$ = 15), for the average relative explained variance in the reconstruction model, which demonstrates the value that drought-sensitive longleaf pines have for providing pre-instrumental estimates of climate and streamflow across the southeastern US.

Further advances in the dendroclimatology of longleaf pine have benefitted from the development of seasonwood (e.g., earlywood and latewood) chronologies and subsequent examinations of differential seasonal growth in the species. The majority of interannual radial growth variability for longleaf pine is in the latewood zone, and latewood width has proven more sensitive than total ring width to hydroclimate variability, particularly summer and fall precipitation (Meldahl et al., 1999; Henderson and Grissino-Mayer 2009; Gentry et al., 2010; Patterson et al., 2016; Mitchell et al., 2019). Several studies have found a positive relationship between total ring width of longleaf pine and spring precipitation (Slack et al., 2016; Collins-Key and Altman 2021; Stambaugh et al., 2021), yet storm events that produce large amounts of precipitation are most likely the main driver behind this relationship, with more rainfall yielding a wider-than-average latewood growth band, and hence a wide total annual ring (Gentry et al., 2010; Knapp et al., 2016; Mitchell et al., 2019). In the southeastern US, tropical cyclones (TCs) are the most common type of storm that produce large quantities of rainfall during the latewood-growth season (Mitchell et al., 2019).

The fidelity between latewood ring growth and late-season precipitation has supported a recent advance in studies that use longleaf pine data for TC research. Multiple tree-ring metrics (e.g., latewood width, $\delta^{18}O$) from longleaf pine have been shown to be particularly sensitive to TC rainfall; thus, can be used for reconstructions of TC events, a field known as *paleotempestology* (Liu and Fearn 1993, 2000; Emanuel, 2008; Wallace et al., 2014; Muller et al., 2017), or more specifically, dendrotempestology (Dinulica et al., 2012; Tucker 2015; Tucker and Pearl 2021). Gentry et al. (2010) were the first to note the sensitivity of longleaf pine latewood width to TC rainfall in Texas. Paleoclimate reconstructions of TC precipitation have since incorporated longleaf pine seasonwood (Knapp et al., 2016; Soule´ et al., 2021) and more recently, adjusted latewood (LWadj; Maxwell et al. (2021); Bregy et al. (2022)). LWadj is calculated by removing the influence of early season climate on latewood width (Meko and Baisan 2001) and is shown to be more sensitive to climate than raw, unadjusted latewood width (Soule´ et al., 2021). Using LWadj from longleaf pine, recent TC studies identified an increase in extreme rainfall years over time (Maxwell et al., 2021), and further, the large-scale oceanic and atmospheric controls of TC rainfall (Bregy et al., 2022). In addition to latewood width and LWadj, other longleaf pine ring-width metrics have been linked to TCs, including growth suppression due to tree damage (Trouet et al., 2016; Zampieri et al., 2020; Collins-Key and Altman 2021), and inter-annual density fluctuations (i.e., false rings) (Mitchell et al., 2019), created when heavy precipitation from “drought-busting” TCs brings additional water availability late in the growing season, inducing earlywood production for a second time in a single year (Maxwell et al., 2012). The examination of $\delta^{18}O$ stable isotope values from cellulose of longleaf pine latewood has been linked to TC activity (Miller et al., 2006). To date, the ability of isotopic tree-ring records to capture TC activity is mixed with multiple studies showing promise (Miller et al., 2006; Mora et al., 2007; Labotka et al., 2016), but other sites showing false negatives and positives and other difficulties therein (Lewis et al., 2011). However, isotopic methods have only been used on three sites, and thus the feasibility of using $\delta^{18}O$ to estimate TC activity from longleaf pine remains unclear and warrants more examination.

The breadth of research that examines longleaf pine ring-width sensitivity to extreme rainfall events underscores the value of the species in the field of climatology and paleoenvironmental reconstruction.

We contend that demonstrating the reliability of this particular climate sensitivity is critical to engaging in a major challenge of dendroclimatology: capturing extreme wet years. During such years, multiple extreme rainfall events occur, and the soil becomes saturated. Tree radial growth is often unresponsive to saturation/excess moisture (e.g., Fritts 1976), making hydroclimatic reconstructions for those years difficult, although possible as demonstrated for other locations and species (Coulthard et al., 2016; Nguyen and Galelli 2018; Nguyen et al., 2021). Longleaf pine can inhabit well-drained soils that rarely experience sustained saturation. As a result, longleaf pine can record multiple extreme events in one growing season and may therefore complement tree-ring data from other species by capturing the full extent of anomalously wet years. We emphasize that longleaf pine has strong potential as a paleoclimatic proxy, particularly for hydroclimate extremes. Promising avenues within this context include [1] paleotempestology and [2] targeting the storm season to augment other species, particularly in a high-resolution (sub-annual) framework.

## *Fire*

Longleaf pine is one of the most fire-adapted species in North America. At the seedling stage, small trees maintain a grass-like architecture wherein the stem remains < 50 cm tall and the apical bud is protected from fire by a dense cluster of long (20−40 cm) green needles (Wahlenberg, 1946; Brown 1964).

This protracted stage can last ca. 5−25 years (Bruce, 1959), allowing the seedlings to develop a robust root system. At a certain point in time, around when the stem reaches 2.5 cm diameter, the seedlings undergo a rapid vertical growth surge that thrusts the apical bud out of the range of surface fire. This “bolting” period lasts for several years, after which the trees can reach >5 m in height and begin to mature. As they grow, longleaf pine trees develop thick bark that resists heat damage (Heyward 1939; Gilliam and Platt 1999; Barnett 1999), although cambial damage from passing fires is common, particularly when trees are young, allowing for tree-ring reconstructions of fire history, especially if the earliest growth years can be extracted in samples (Huffman and Rother 2017).

Longleaf pine ecosystems are fire maintained. Given the high vegetative productivity of the southeastern US, longleaf stands often include abundant surface fuels that can be cured to burn in a relatively short and dry weather window. Furthermore, the pine litter and the associated herb and shrub understory is highly flammable and promotes frequent, low-severity fire (Fonda 2001; Platt et al., 2016). These frequent surface fires preclude other, less fire-adapted species from being recruited into the canopy.

Regular burning inhibits heavy fuel accumulation and ladder fuel structure. This reduces the risk of high-severity fires that reach the crown and maintains communities where longleaf pine is commonly the sole dominant tree in areas otherwise occupied by herbaceous and shrub communities (Heyward 1939; Lavoie et al., 2010).

Despite being one of the most fire-dependent tree species, surprisingly little quantitative data exist on historical fire regimes in longleaf pine ecosystems. The historical fire regime for the longleaf pine ecosystem is estimated to be 1–4 years (Frost 1993, 1998; Guyette et al., 2012; Glitzenstein et al., 1995, 2003; Stambaugh et al., 2011; White and Harley 2016; Kirkman et al., 2017; Palmquist et al., 2015; Gilliam and Platt 1999; Schafer et al., 2015). A recent assessment of geographic distribution of fire-scar studies in North America revealed a spatial concentration of studies in western forests, particularly in ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) and dry mixed conifer forests (Margolis et al., 2022). Relative to other low-elevation pine species in eastern North America (e.g., shortleaf pine (*Pinus echinata* Mill.), pitch pine (*Pinus rigida* Mill.), red pine (*Pinus resinosa* Sol. ex Aiton), few published tree-ring–based studies of longleaf pine fire history exist. We are aware of only four refereed articles that used crossdated fire scars to reconstruct fire history located in Louisiana (Stambaugh et al., 2011), Mississippi (White and Harley 2016), Georgia (Klaus 2019), and northern Florida/southern Georgia (Rother et al., 2020). A few additional studies are available as dissertations, theses, or reports (Huffman 2006; Henderson 2006; Bale 2009; Huffman and Platt 2014). The study of longleaf pine fire history is still in its infancy, and amplifying research efforts in this capacity will yield increased spatial and temporal variability of longleaf pine fire dynamics and regimes, which provides critical information to the restoration and management of longleaf ecosystems. Enormous potential exists to develop additional fire histories of significant length given that the trees are long-lived, and the high resin content slows decomposition and can allow stumps to persist on the landscape for a century or more (Stambaugh et al., 2011). For the southeastern region, longevity (e.g., 400 + years) in fire information is needed to extend prior to pre-Euro-American colonization, although shorter records also provide valuable information regarding post-settlement fire regimes.

The dearth of tree-ring based fire-history studies using longleaf pine is related to numerous factors. First, the loss of approximately 97% of the historical longleaf pine range—half of which is in private landholdings—has fragmented suitable study areas for this type of work (Oswalt and Guldin 2021). Old-growth stands are now rare (Varner and Kush 2004). Second, even in places where ecosystems remain in a longleaf pine cover type, old stumps and other remnant material needed for multi-century fire-history reconstructions (Ferris 1912; Hawley 1921; Barnett 2019) are left to decay or are consumed by fire.

Third, longleaf pine does not regularly produce repeated external scarring (i.e., “cat faces”; Figure 4(a) and (c)) as is commonly found on other pine species (Brockway 2005; Outcalt and Brockway 2010; Huffman and Rother 2017). This could be driven by the lower-intensity fires that characterize these systems; heating along the trunk may remain below thresholds that would produce an open wound. Even when scarred, longleaf pine heals rapidly, often closing over wounds in a few years (Figure 4(c)). These limitations can be overcome to produce high-quality tree-ring reconstructions of fire in the southeastern longleaf and associated pine ecosystems. This region is a frontier for tree-ring–based fire histories given the previous concentration of research in the western US (Margolis et al., 2022).

Successful fire-history reconstructions have adapted common approaches or devised new ones to better fit with longleaf pine ecology and the process of fire in longleaf pine ecosystems. The classic fire-scar approach of target-sampling only stumps, snags, and other specimens with evidence of repeated external scarring is difficult in longleaf pine ecosystems. In recent years, researchers have increasingly included cross sections from trees that are not externally scarred but contain internal (buried) scars (Huffman 2006; Stambaugh et al., 2011; White and Harley 2016; Huffman and Rother 2017) (Figure 4(c)). This approach is more time intensive as the basal areas of stumps are excavated for sampling near ground level and multiple full cross sections are collected vertically along the stump axis and analyzed (Huffman and Rother 2017) (Figure 4(b)). Despite being more tedious, this method of fire scar vertical-position analysis has been shown to yield more comprehensive fire regime information, as demonstrated by the bi-annual fire frequency evidence found in Louisiana by Stambaugh et al. (2011) and in Mississippi by White and Harley (2016). These buried scars are often relatively small, and care must be taken to ensure that fire scars are properly distinguished from other injuries (Huffman 2006; White and Harley 2016). In some cases, litter and/or soil accumulation, especially in fire-suppressed stands, may result in fire scars that are slightly below the current surface, nearer to the root-shoot boundary at the time of fire.

Finally, the seasonality of fire in longleaf pine ecosystems both past and present is an area of high interest among land managers, researchers, and other stakeholders. The intra-annual position of a fire scar within a tree ring allows the researcher to estimate the approximate time of year, or season (e.g., spring, summer, and dormant) of the burn (Dieterich and Swetnam 1984; Rother et al., 2018). Thus far, the existing fire-scar studies in longleaf pine show substantial variation in seasonality across time and space. In some areas, such as in southern Mississippi (White and Harley 2016) and northern Florida (Huffman 2006) a greater proportion of growing season fires occur near or at the transition of earlywood to latewood and are suggestive of a lightning-dominated fire regime (Rother et al., 2018). By contrast, in areas where the fire-scar record is strongly dominated by dormant season events, fires were likely due to human ignitions, at least in the time window examined (e.g.,Stambaugh et al., 2011; White and Harley 2016). Dormant and early-spring fires are most common on some private lands on the Georgia-Florida border where


**Figure 4.** Scar analysis on a fire-scarred, remnant longleaf pine stump. All panels demonstrate the importance of the height at which fire-scar analysis is conducted on a cat face. Fast-moving ground fires typically scar live longleaf pine lower on the cat face, or open scar wounds (a). A dendropyrochronological researcher uses a chainsaw to collect a cross section from a remnant longleaf pine stump as low as possible towards the root-shoot interface, sometimes requiring excavation around the stump. Inset (c) shows a polished section collected from the lowest possible plane above the root-shoot-interface of (b), following the methods of Huffman and Rother (2017). For interpretation of the references to colours in this figure legend, refer to the online version of this article.

prescribed fires are applied every one to 2 years for management of quail populations for hunting (Rother et al., 2020). The ability to associate a certain fire-scar position with a time of year can be improved through insights from cambial phenology studies (e.g., Rother et al., 2018) or comparisons of fire events with known dates to the fire-scar record.

Although the importance of frequent, low-severity fire in longleaf pine ecosystems is well understood, we contend that current knowledge regarding the variability of fire regimes across the range of longleaf pine is limited. There is often a single story being told about longleaf pine and fire rather than a more nuanced account of how fire frequency, seasonality, and other aspects of the fire regime varied with elevation, latitude, proximity to range edge, forest composition, and other important factors. Fire has been the focus of many dendroecological analyses of longleaf pine forests because of its important ecological role in maintaining these systems. Studies have shown that fire suppresses growth of the apical and lateral meristems during the event year, but often results in growth increases over subsequent years. After the initial and short-term growth suppression, a more prolonged release occurs due to the increases in soil nutrient deposition and the creation of more open canopy conditions, which in turn moderates competition and encourages recruitment of longleaf pine saplings to upper canopy positions (Ames et al., 2015; Ford et al., 2010; Slack et al., 2016). Additional dendroecological analyses of fire-growth relaitonships as well as tree-ring based fire histories should shed light on the spatial and temporal variability of fire activity in longleaf pine ecosystems and allow land managers to make more informed decisions regarding the application of fire as a restoration and management tool.

## Ecology

The ecological amplitude of longleaf pine allows for distinct variations in the structure and composition of the communities that make up the longleaf pine ecosystems. These systems are dependent on abiotic factors (*e.g.,* climate and soil) which, through the complex role of fire on the overstory and understory components of the community, set it apart from other temperate forested ecosystems in North America (Peet 2007; Ratnam et al., 2011). Dendroecological studies provide more in-depth and long-term approaches to untangling how abiotic variables can influence longleaf pine radial growth across ecosystems and help define the foundational composition, structure, and dynamics of longleaf pine ecosystems. For land managers, such insights can improve restoration and conservation-focused decision making by providing the land-use and natural disturbance history of a site when little to no information is available.

Ecological investigation of longleaf systems through the use of tree-ring analysis began in the late 1980s and continues throughout the geographic range today. Despite being understudied throughout much of the 20th century prior to the *ca.* 1980s (Frost 1993; Oswalt et al., 2012), recent efforts by scientists and land managers in the Coastal Plain led to a more comprehensive understanding of the community composition, stand structure, climatic variation, and effects of fire frequency and seasonality in longleaf pine ecosystems, such as in Alabama (Kush et al., 1999; Meldahl et al., 1999), Florida (Platt et al. 1988, 2016; Rebertus et al., 1993; Olson and Platt 1995; Gilliam and Platt 1999; Noel et al., 1998; Robertson et al., 2019), Georgia (Pederson et al., 2008; Rutledge et al., 2021), Mississippi (Devall et al., 1991; White and Harley 2016), South Carolina, and Texas (Henderson and Grissino-Mayer 2009) (Figure 5; Table 1). Each of the studies listed in Table 1 provides understanding of tree growth and development, stand dynamics and disturbance histories, forest productivity, tree biology, abiotic and biotic influences on tree growth, reproduction, and mastecology at their respective locations displayed in Figure 5. However, continued work is needed to provide more context to these research topics from other areas across the range of longleaf such as Louisiana, peninsular Florida, coastal North Carolina, and montane longleaf forests of Alabama, northern Georgia, and western North Carolina (Figure 5). A more holistic and comprehensive approach targeting spatial gaps across the range can aid scientists and land managers in developing strategies for management, including considerations for carbon markets and climate change.

Within the subfield of dendroecology, growth-change detection is a powerful analysis that can elucidate direct effects of past disturbance agents on tree growth. In this analysis, statistically-anomalous criteria

are applied to growth ring patterns, thereby highlighting the occurrence and duration of rapid increases or decreases in growth. Applying this analysis across multiple vegetation plots in forests provides a better understanding of the frequency and severity of historical endogenous and exogenous disturbances (Nowacki and Abrams 1997). When applied stand-wide, numerous studies have successfully applied growth-change detection on longleaf pine tree rings for the purposes of better understanding how historical environmental events (*e.g.,* logging, tornadoes, and TCs) influenced the ecological trajectory of the stand (Bhuta et al., 2008; Pederson et al., 2008; West et al., 1993). Greenberg and Simons (1999) used dendroecological methods to first determine stand structure and composition, then explored how oaks (*Quercus* spp.) influenced longleaf pine growth. They highlight that spatial patchiness and the variability of fire frequency, seasonality, and intensity are important components in maintaining longleaf pine ecosystem dynamics. Curtin et al. (2020) employed tree-ring analysis to reconstruct individual tree height growth patterns in an attempt to understand the effects of overstory competition on canopy recruitment.

While longleaf pine is generally thought of as being shade-intolerant, this work showed the persistence of midstory trees in high-density stands. Gap-phase dynamics and the growth patterns of trees positioned in the middle and lower portions of the canopy after being released from overstory tree competition warrants further investigation due to the uncertainty of how trees in this vertical stratum operate within the overall dynamics of the stand.

Dendromastecology is a productivity-related sub discipline of dendroecology that links analyses of growth patterns (releases and/or suppressions) to annual mast production in trees (Speer 2001). For

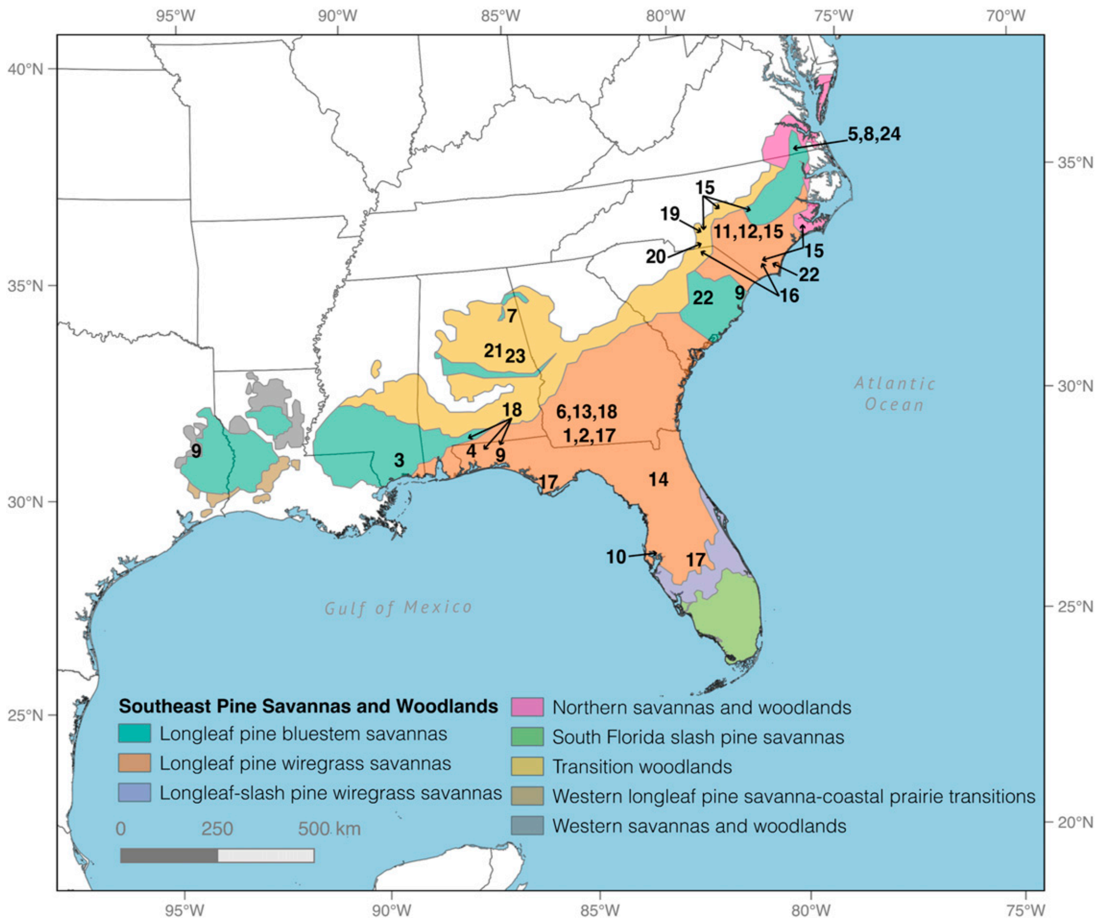


**Figure 5.** Map of dendroecological studies utilizing longleaf pine tree rings in southeastern pine savannas and woodlands (Peet et al., 2018). Key to Paper IDs #1−24 displayed in the map are located in Table 1. Figure generated in QGIS v3.26. For interpretation of the references to colours in this figure legend, refer to the online version of this article.

longleaf pine, cone production during masting events is related to radial growth of the prior year, and lower stand densities can lead to increased masting rates and production (Patterson and Knapp 2016, 2018). Using methods similar to those employed by dendromastecology studies, dendroentomology focuses on studying and identifying effects of past insect outbreaks on radial growth of trees (e.g., Swetnam and Lynch 1993; Speer 2001). To date, we have found no peer-reviewed, tree-ring studies that have analyzed insect, disease, or pathogenic effects on longleaf. The limited research on these processes are important areas for research as each, singularly or as compounded events, will likely strongly impact the trajectory of these ecosystems and the species itself, especially as the climate changes.

As climatic conditions continue to change, disentangling the effects of human and natural disturbances on longleaf pine radial growth and forest composition and structure are critical along two fronts: longleaf pines positioned [1] at higher elevation sites and [2] along range margins (Iverson and Prasad 2002; Prasad et al., 2020). Compared to Coastal Plain locations, less is known about the dendroecology of montane longleaf pine communities within the Piedmont

**Table 1.** Published dendroecological studies of longleaf pine. Complete list of published dendroecological studies of longleaf pine and key that accompanies Figure 5 (searched 12 March 2021). Sources were found using the following search arguments: ALL=(longleaf OR (*Pinus* AND *palustris*)) AND (dendroecology OR dendrochronology OR treering OR tree-ring OR (age AND structure)) in Web of Science.

| Map ID | Reference | Map ID | Reference |
|---|---|---|---|
| 1 | Platt et al. (1988) | 13 | Knoepp et al. (2015) |
| 2 | West et al. (1993) | 14 | Slack et al. (2016) |
| 3 | Devall et al. (1991) | 15 | Patterson et al. (2016) |
| 4 | Meldahl et al. (1999) | 16 | Patterson and Knapp (2016) |
| 5 | Bhuta et al. (2008) | 17 | Rother et al. (2018) |
| 6 | Pederson et al. (2008) | 18 | Patterson and Knapp (2018) |
| 7 | Varner et al. (2003) | 19 | Mitchell et al. (2019) |
| 8 | Bhuta et al. (2009) | 20 | Kaiser et al. (2020) |
| 9 | Henderson and Grissino-Mayer (2009) | 21 | Kressuk et al. (2020) |
| 10 | Ford et al. (2010) | 22 | Soule´ et al. (2021) |
| 11 | Mattingly et al. (2012) | 23 | Bhuta and Kennedy (2021) |
| 12 | Ames et al. (2015) | 24 | Eberhardt et al. (2022) |

and Ridge and Valley ecoregions, in part, because of a legacy of timbering practices in these areas (Varner and Kush 2004). Of the studies that do exist in montane stands, Patterson and Knapp (2016) inventoried longleaf pine in a North Carolina Piedmont community, while others have looked extensively at woody stem structure and dynamics in longleaf pine communities along the Alabama Ridge and Valley (Varner et al., 2003) and the Alabama Piedmont (Bhuta and Kennedy 2021; Kressuk et al., 2020).

Studies that investigate climate-growth relationships, and how these relationships interact with fire and other disturbances—particularly at the western, southern, and northern range margins—are necessary because the direction and magnitude of climate change (*e.g.,* warmer, cooler, drier, and wetter) will have varying impacts on the growth and ecology of different populations across the species' range. Due to historical widespread logging, old-growth longleaf trees are rare, and thus most older samples are found as remnant stumps. Improving our ability to identify the species of remnant stumps or downed woody debris accurately and correctly from among the various southern yellow pines that often co-occur across the southeastern US (*e.g.,* longleaf, shortleaf, loblolly, and slash) will increase our understanding of the species' growth requirements and natural history. Methods for differentiating remnant longleaf pine from other southern, yellow pine species using tree rings have been demonstrated (Eberhardt et al., 2022; please see Archaeology/Cultural Studies section for further discussion) as have the mechanisms of heartwood formation (Allen and Hiatt 1994), but more replication is needed to solidify these techniques and better understand their application across the species range. Continued work is needed to provide additional context to these research topics from other areas across the species range in montane longleaf pine forests of Alabama, northern Georgia, and the Carolinas, as well as peninsular Florida, coastal North Carolina, and Louisiana. A more landscape-scale approach to ecological analysis of longleaf pine which represents all parts of the species' range may aid scientists and land managers in [1] understanding the stand dynamics and disturbance histories of a site when no other historical records are available, [2] understanding how disturbance can impact a site and be used, in turn, for better management, [3] making more informed decisions when conservation and restoration is a management goal, and [4] developing best management practices for carbon markets and climate change adaptation.

As a final thought, a better understanding of false ring production, particularly during the juvenile stages of growth (*ca.* grass and bolting stages) is needed for stand-age dynamics studies. Because longleaf pine can persist in the grass stage (as seedlings) for up to 20 years (Bruce, 1959) with minimal height growth (Pessin 1934; Boyer 1990), methods to determine definitive age are needed to examine year of germination and recruitment rates over time. False ring production is widespread in the species and some evidence points to climatic relationships, particularly with TCs (Mitchell et al., 2019), as is discussed in the **Climate** section. Understanding what mechanisms that control ring production in the grass and bolting stage, and false ring production are important next steps for dendroecological research across these systems.

Key topics for future dendroecological studies (of equal importance) include [1] further understanding mechanisms of false ring production, [2] susceptibility/vulnerability to insect/fungal pathogens (*e.g,.* heart rot and other diseases), [3] further studies into masting drivers and mechanisms, [4] deeper exploration of the complex biotic interactions between longleaf pine and other species, such as *Quercus* spp. (*c.f.*(Greenberg and Simons 1999)), [5] carbon cycling, [6] biogeographic studies of tree response at the western, northern, and southern range boundaries, [7] understanding what mechanisms facilitate vertical growth from grass to juvenile life stages, [8] expanding the spatial coverage of plot-level longleaf pine dendroecological data (Figure 5), and [9] ensuring plot-level demographic data collected for ecological applications is available via the DendroEcological Network (Rayback et al., 2020). Understanding how a changing climate will impact these topics is also an overarching goal in using dendroecology on longleaf pine.

## *Archaeology/cultural studies*

Dendroarchaeology incorporates techniques of tree-ring science to date and assign a provenance (i.e., determine the source of origin) to historical structures or artifacts (Figure 6). Not only does this disciplinary subfield develop valuable historical information, but as discussed in this section, recent studies show that important climatological and ecological information can be obtained from historical timbers, especially given the history of timber harvesting and construction since Euro-American colonization throughout the eastern US (De Graauw 2017; De Graauw and Hessl 2020). In the southeastern US, longleaf pine was commonly used as a construction material, such that an estimated 75% of colonial era homes, and up to 33% of all lumber manufactured through the late 1800s, was derived from longleaf pine (Varner and Kush 2004). Due to its resin content and high specific gravity relative to other pine species (Koch 1972), longleaf pine has served in a wide range of applications such as pilings, joists, and trestles where high strength and rot resistance was paramount before the advent of pressure-treated lumber. These properties led to a surge in demand for longleaf pine timbers during the middle 18th through early 19th centuries and contributed to longleaf pine being one of the most harvested tree species in the US during this period (Finch et al., 2012; Kellogg 1909; Smith et al., 2000). However, despite the extensive use of longleaf pine in construction, the species remains underrepresented in dendroarchaeology studies. At present, only seven peer-reviewed studies have dated historical structures containing longleaf pine timbers that include six dwellings and one crib dam (Van De Gevel et al., 2009; Grissino-Mayer et al., 2010; Garland et al., 2012; Harley et al., 2017a, 2018; Leland et al., 2021; Patterson et al., 2021). This collection excludes unpublished theses, dissertations, and gray literature, such as technical reports from commercial dendroarchaeology performed by the Oxford Tree-Ring Laboratory. Several important themes emerge from the published literature. First, all but one study (Leland et al., 2021) used reference chronologies that are not publicly available, such as those from Eglin Air Force Base, Florida (Harley et al., 2018), Lake Louise, Georgia (Grissino-Mayer et al., 2010; Garland et al., 2012), DeSoto National Forest, Mississippi (Harley et al., 2017a; Patterson et al., 2021), and Hope Mills, North Carolina (Van De Gevel et al., 2009). Second, dendroarchaeological


**Figure 6.** Examples of historic longleaf pine timbers from across the U.S. (a) A researcher uses a handsaw to collect a section from a dugout canoe in Laurinburg, NC. (b) Coffin plank boards extracted from the unmarked grave sites associated with the Asylum Hill Cemetery (*ca.* 1855–1935) on current grounds of the University of Mississippi Medical Center, Jackson, MS (Herrmann et al., 2016; Malis et al., 2022). (c) A researcher uses a Pressler© GmbH dendroarchaeology bit (Gestern, Germany) attached to a variable-speed hand drill to collect a 12-mm diameter core from a longleaf pine timber near Tupelo, Mississippi (Patterson et al., 2021). (d) An undated longleaf pine structure on a private ranch near Zolfo Springs, Hardee County, Florida, which is near the southern range limit of the species. (e) A cache of longleaf pine timbers from the Terminal Warehouse in New York, NY, the origins of which were sourced in a provenance study to the southeastern US (Leland et al., 2021). For interpretation of the references to colours in this figure legend, refer to the online version of this article.

dating of historical longleaf pine timbers has relied on a relatively small number of long reference chronologies that are not yet publicly available. Making such records publicly available via the ITRDB would serve to facilitate additional dendroarchaeological research across the southeastern US.

A primary limitation to the dendroarchaeological dating of longleaf pine timbers and artifacts is the lack of publicly available, multi-centennial, seasonally-resolved chronologies throughout the range of the species. Excluding private collections and other datasets that will be added later to public archives as part of the LTRN, only 27 longleaf chronologies representing 23 unique sites across the range are available on the ITRDB (as of November 2022, Figure 3; Mendely Data doi: 10.17632/dm8mdvnfmy.1). Two of these chronologies, Jeffries Smokehouse in North Carolina (Barefoot 1996) and the Terminal Warehouse in New York (Leland et al., 2021), are from archaeological collections. Between these datasets are large spatial data gaps; many historical structures that may be identified for future study will be hundreds of kilometers away from the nearest available reference chronology (Figure 3, ITRDB chronologies, e.g., Garland et al., 2012). Temporal data gaps are also a limitation to dating historical longleaf pine timbers. Multi-century chronologies are necessary to overlap with the historical periods in question, and

Contemporary old-growth stands are rare due to extensive logging during the late 1800s (Frost 1993). While most of the longleaf pine chronologies available on the ITRDB are multi-centennial in length, few extend prior to 1750, which is necessary (e.g., having enough overlap between the historical timbers and the reference chronology) in most cases to visually and statistically crossdate structures or artifacts as recent as the early 1800s. Of the 25 longleaf pine chronologies developed from living trees currently available on the ITRDB, only 11 predate 1700 CE. While additional, multi-centennial chronologies are needed for dendroarchaeological dating and provenancing, data from historic timbers, as well as from remnant wood, have the potential to extend chronologies beyond 1700 CE, feeding back into improved capabilities to date historic structures and artifacts, and for ecological and climate applications.

Recent improvements in the dating certainty of longleaf pine materials includes the development of seasonally-resolved chronologies and the ability to identify longleaf pine from other southern US yellow pines (e.g., shortleaf and loblolly pine), as discussed in the **Climate** and **Ecology** sections, respectively. Specific to dendroarchaeology, longleaf pine latewood chronologies have proven useful where total ring-width data have not. For example, Patterson et al. (2021) used latewood widths to date the Walker House in Tupelo, Mississippi, after unsuccessfully attempting total ring-width. Despite this potential, only half of the longleaf pine ITRDB chronologies are seasonally resolved ($n = 12$). In addition to developing a more spatially-extensive network of longleaf pine chronologies, increasing the availability of seasonally-resolved data could prove to be transformative in southeastern US dendroarchaeology and allow for the dating of previously undateable structures and artifacts across the region. Another recent advance is the ability to identify southern yellow pine remnant material (see Wahlenberg, 1946; Eberhardt et al., 2022). Proper identification of tree species is important for choosing appropriate reference chronologies in the field of dendroarchaeology, and remnant material derived from the various southern yellow pines can be difficult to distinguish from one another. Recently, Eberhardt et al. (2022) provided a method to distinguish longleaf pine from other southern yellow pine species using quadratic discriminant analyses of pith and second-ring diameter. When adopted for dendroarchaeology, this method will be useful for determining species-specific building materials and identifying longleaf pine used outside the former range of the species. Finally, the field of dendroarchaeology is advancing to including new dating techniques (e.g., X-ray computed tomography, strontium isotopes, and quantitative wood anatomy) for crossdating and provenancing wood (Dom´ınguez-Delma´s et al., 2020), and we anticipate these methods will improve the accuracy and capabilities of dating longleaf pine material.

The LTRN will improve dendroarchaeological dating for a number of applications. A more expansive tree-ring network increases the likelihood of dating additional structures and reduces reliance on spatially-distant chronologies. The network will also allow for strengthened dendro provenancing of longleaf pine material found outside the range of the species (e.g., Leland et al., 2021; Mundo et al., 2022). While results from these studies are interesting in their own right, information beyond tree-ring data, such as improved insights into timber trade, workmanship, and wood preference can be acquired to reveal the spatial footprint and evolution of exported pine material through time. Another benefit of the improved network will be the use of archaeological material in climatological and ecological research. Dendroarchaeological data have the potential to extend existing chronologies farther into the past (Cook et al., 2015; Matheus et al., 2017), informing a broader context of environmental change (e.g., in the development of drought atlases). Other potential advances include analyses of range-wide crossdating and climate sensitivity of longleaf pine. Thus far, a composite southern Mississippi latewood chronology (Harley et al., 2017a; Patterson et al., 2021) that contains house and coffin timbers (Herrmann et al., 2016), was used by Bregy et al. (2022) for dendroclimatic applications along the broader US Gulf Coastal Plain. Though not using longleaf pine, De Graauw and Hessl (2020) compiled data from 18 log structures to examine forest recruitment and dynamics—a practice that can be adopted for longleaf pine. In all, the potential to develop long, climate- or ecology-sensitive tree-ring proxy data from longleaf pine increases with the addition of historic timbers, for which the absolute dating depends on the spatiotemporal extension of the LTRN.

## Conclusions and future work

### The longleaf tree-ring network

Our review of the literature within the context of the utility of longleaf pine tree rings in the natural and cultural sciences, in part, revealed the need for a collaborative research working group focused on broad-scale analyses as applied specifically to climate, fire, ecology, and archaeology. Along with the goals of the LTRN mentioned previously, we developed an initial database of 98 complete, extant chronologies across the range of longleaf pine not yet included on the ITRDB (Figure 3; Mendely Data doi: 10.17632/dm8mdvnfmy.1). Across the LTRN, we highlight spatial gaps in the [1] longleaf pine-bluestem savannas of Louisiana; Mississippi, and North Carolina, [2] longleaf pine-wiregrass savannas of southeastern Alabama, and south-central Georgia and [3] transition woodlands of south-central Alabama. Along with filling gaps in data, we implore researchers to consider a few critical needs of future longleaf studies: developing seasonwood chronological data, and the importance of collecting and archiving remnant longleaf material to safeguard against loss of material, and hence scientific information, to decomposition or fire consumption. The collection and addition of remnant material will also serve to maximize chronology development at each study site. Most of the longleaf pine chronologies in the LTRN begin in the 17th and 18th centuries (Figure 3). Yet, a few records extending to the 15th and 16th centuries are located in the northwest Florida panhandle and coastal South Carolina, and represent specific studies that have targeted the collection of remnant material (Henderson and Grissino-Mayer, 2009; Maxwell et al., 2021; Harley et al., 2018).

### Seasonwood chronologies

Developing seasonwood (i.e., earlywood, latewood) chronologies from longleaf pine is another critical need that spans all discussed topics and is one of the primary foci of the LTRN. To this end, the following analysis highlights the superiority of seasonwood chronologies over total ring width. We analyzed the variability of latewood width (LWW), earlywood width (EWW), and total ring width (TRW) from 21 sites included in the LTRN (three of which are currently available via the ITRDB), distributed across the widest possible expanse of the range as currently available, and representative of various habitats (e.g. montane, coastal; Figure 7). We detrended each seasonwood chronology for the 21 sites with a horizontal mean line, which acted to standardize all measurements and decrease artifacts from early-aged growth anomalies that are common with raw values while still preserving growth patterns and frequencies and used the standard chronology for subsequent analyses. We find that at all 21 sites included in the analysis, LWW chronologies outperform both their EWW and TRW counterparts in the mean correlation coefficient (RBAR = 0.55, 0.46, 0.52, respectively). Both the probability density functions and box plots show that LWW chronologies had higher frequency of both narrower-than-average and wider-than-average growth rings—which are termed *marker rings* and represent a stronger environmental or climatic signal shared amongst trees in each collection (Fritts 1976; Stokes 1996)—as revealed by the tail ends of the distributions (gray arrows). Previous work demonstrates this phenomenon at the local scale (Meldahl et al., 1999; Henderson 2006; Gentry et al., 2010; Patterson et al., 2016; Mitchell et al., 2019). Our analysis across the longleaf range demonstrates that this property holds up across the southeastern US. Hence, any future chronology development of longleaf pine should include seasonwood measurements as standard, no matter the research goal.

### Collecting and archiving remnant longleaf

We highlight the scientific need to develop new and longer tree-ring records from this species across the broadest possible extent of the species' range both within the southeastern US and from historic timber material outside its natural distribution. Yet, given the widespread exploitation of the species since Euro-American colonization, old longleaf pine

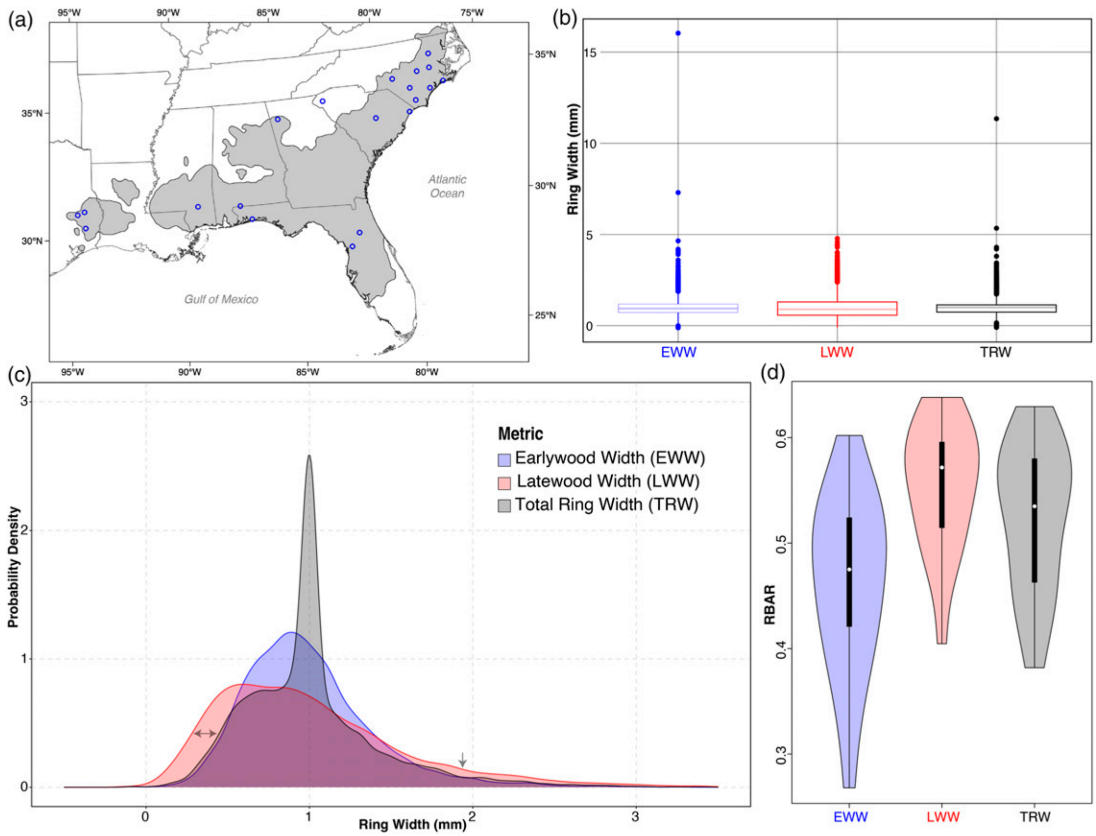


**Figure 7.** LTRN longleaf pine seasonwood chronology variability across the species range (A). (B) Box plots and (C) probability density functions of earlywood widths (EWW; blue), latewood widths (LWW; pink), and total ring widths (TRW; gray) for 21 seasonwood chronologies of the LTRN distributed across the historical range of longleaf (inset map in (A); Little Jr (1971)). (D) Mean correlation coefficient (*r*-value; RBAR) among measured series of earlywood widths (EWW; blue), latewood widths (LWW; pink), and total ring widths (TRW; gray) for all 21 seasonwood chronologies. The frequency of marker rings (i.e., abnormally narrow or wide growth rings) is higher in LWW chronologies consistency across the 21 sites included in this analysis (gray arrows), highlighting the need for developing longleaf seasonwood chronologies for the species as opposed to only TRW, which is currently the standard. For interpretation of the references to colours in this figure legend, refer to the online version of this article.

forests are rare. Many of the areas that still contain old living longleaf pine trees have already been identified and studied, but remnant material is often overlooked. The decomposition rate for woody material in the southeastern US is rather quick, yet yellow pine stumps, particularly longleaf pine, more than 500 years old still exist in many areas because of the high resin content of the species. In addition to the eventual loss of remnant material from weathering, stumps and logs are incinerated during fire events. Collecting and archiving remnant longleaf pine material in the southeastern US is needed for the purpose of bolstering current and future research projects focused on better understanding climate change, producing accurate predictions, identifying risks and vulnerabilities, and informing decisions of how humans will adapt to future changes to our climate system. Thus, we highlight the critical need for a campaign to *Save the Stumps*, especially by broadcasting to private landowners and public land managers the scientific value of remnant longleaf pine material. Like all physical tree-ring samples, adequately archiving such material is important for future analyses.

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## Data availability

Information on all longleaf tree-ring data compiled by the LTRN are included on the public data repository at: Harley, Grant (2022), "Longleaf Tree-Ring Network Working Data Set", Mendeley Data, V1, doi: 10.17632/dm8mdvnfmy.1

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