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Abstract:

Longleaf pine ecosystems have experienced pronounced declines across the southeastern United States since Euro-American settlement took place in the late 19th century. These declines were primarily caused by federal fire suppression policies implemented in the 1920's, in combination with resource harvesting and land use conversion. In an absence of fire, tree species composition of frequently burned xeric ecosystems progressively becomes more mesic and fire-intolerant (*i.e.* mesophication). The change in the species composition and historic fire frequency of a montane longleaf pine ecosystem located in Sheffield Wildlife Management Area (WMA), Paulding County, Georgia was investigated. The change in forest composition was measured using modern vegetation surveys and historic "witness tree" vegetation data obtained from a georeferenced 1832 Georgia Land Lottery Survey map. The historic fire return interval was estimated using remnant longleaf stumps and dendrochronological techniques. Results from χ^2-tests indicated the modern forest is significantly more mesic and fire-intolerant than the historic forest ($p < 0.0001$), with no statistically significant difference in species composition between north- and south-facing slopes. A chronology for longleaf pine was constructed using 214 cores from extant longleaf pine and 14 relict stumps found in Sheffield WMA. Using fire scars found in seven of the preserved stumps, the historic mean fire return interval was calculated to be 5.5-years with a median return interval of 3.5-years. It was concluded that mesophication has occurred in Sheffield WMA since Euro-American settlement, and that fires were historically present in the forest but likely of low intensity and fragmented across the landscape.

Keywords: *Pinus palustris*, montane longleaf pine, mesophication, witness trees, dendrochronology, mean fire return interval

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Integrative Aspects of this Study:

This study is a descriptive ecological foray that assesses the changes in tree species composition and fire history of a longleaf pine ecosystem in northwest Georgia. Species composition shifts were calculated using standard vegetation survey techniques and data from historic plat maps developed during the 1832 Georgia Land Lottery that were digitized using GIS. Developed before the forced removal of the Cherokee People from their native lands, these historic land survey maps are an important part of American history and a useful tool to gauge the effect Euro-American settlement has had on the ecosystem. To research the fire history of northwest Georgia, dendrochronological techniques were employed to cross-date fire scarred stumps with extant longleaf pines. The combination of these methods and tools required integration of several fields outside ecology including American/Native-American history, cartography, spatial analysis techniques, plant anatomy and physiology, and ecophysiology. The results from this study would not have been achievable without the implementation and integration of these methods and tools.

Introduction:

Longleaf pine (*Pinus palustris* Mill.) ecosystems historically occupied over 37 million hectares from eastern Texas to coastal Virginia. Approximately 80% of this area was primarily longleaf and 20% was mixed species systems that included longleaf pine (Frost 1993). Euro-American settlement in the 1800s brought widespread harvesting of forest resources, large scale land conversion, and fire suppression policies in the 1920's that largely removed longleaf from the landscapes of the southeast (Noss 1989; Stephens and Ruth 2005). Approximately 3% of the historic range exists today, with 0.01% remaining as old growth stands (Varner et al. 2003; Varner and Kush 2004), making these ecosystems among the most threatened in the United States and driving interest for restoration efforts (Noss 1989).

As a keystone species of its ecosystem, longleaf pine has several adaptations that help it survive and promote fires on which it depends. Longleaf pine is shade intolerant and requires bare mineral soil to germinate, a situation that readily exists in a frequently burned system (Boyer 1990). As seedings, longleaf pine exists in a short-statured "grass stage", where they can remain for up to 10 years. In this stage, long needles surround and protect the vulnerable buds from passing fires. Saplings also develop large taproots that act as energy reserves eventually allocated to rapid above-ground growth; placing the crown above the level of most fires. Mature longleaf pines have thick fire-resistant bark and resinous pine needles. When the needles are dropped, they help promote fire and seedling regeneration between patches of grass in the understory (Brockway et al. 2005; Stambaugh et al. 2011).

In addition to their rarity across the southeastern landscape, longleaf ecosystems are notable for supporting a high level of plant and animal biodiversity. Longleaf systems can have more than 40 vascular plant species per m^2, among the most species rich of temperate ecosystems (Peet and Allard 1993). Additionally, longleaf pine systems are host to 86 species of avian and 36 species of mammal, some of which are endemic to frequently burned longleaf pine systems (Engstrom 1993). Animals that use longleaf systems as a primary habitat include the red-cockaded woodpecker (*Leuconotopicus borealis,* Vieillot, 1809), Bachman's sparrow (*Peucaea aestivalis,* Lichtenstein, 1823), brown-headed nuthatch (*Sitta pusilla,* Latham, 1790), southeastern fox squirrel (*Sciurus niger niger,* Linnaeus, 1758), southeastern pocket gopher (*Geomys pinetis*, Rafinesque, 1817), and the gopher tortoise (*Gopherus polyphemus,* Daudin, 1802) among others (Engstrom 1993; Conner et al. 1999; Tucker et al. 2006).

However, the structure and biodiversity of longleaf pine systems differ among its four ecosystem subtypes, each characterized by unique topography, hydrology, and pedology (Outcalt 2000; Peet 2006). Characterized by well drained sandy or loamy soils and relatively flat topography, the coastal plain longleaf systems are the largest and most studied of the sub-types. These systems can be found along the Atlantic and Gulf Coast from eastern Texas to Virginia (Peet 2006). Longleaf flatwood systems are found within the coastal plain but occur on more poorly drained and nutrient deficient soils (Peet 2006; Jose et al. 2010). The fall-line sandhill systems stretch along rolling hills from eastern Alabama to central North Carolina, forming a band across the historic range of longleaf pine. Occurring on mixed patches of well-drained sand and impermeable clay, fall-line sandhill systems range from extremely xeric savannahs to seepage wetlands depending on which soil type is near the surface (Peet 2006).

Among the ecosystem subtypes, montane systems exhibit the most extreme topographic variation and well developed drainage networks compared to the other ecosystem types (Peet 2006). Although it comprised only a small portion of the entire range of longleaf pine, montane longleaf forests once could be found in large parts of northern Georgia and Alabama in the Piedmont, Ridge and Valley, Cumberland Plateau, and Blue Ridge physiographic provinces (Varner et al*.* 2003; Hammond et al. 2016). Remnant old-growth montane longleaf forests are open-canopied and park-like with complex size and age structure, including mixed-aged and even-aged patches and many isolated individuals (Varner et al. 2003). The plant diversity of montane systems is unique because they exist where the native ranges of many coastal and Appalachian plant species overlap, creating assemblages of species not found elsewhere (Maceina et al 2000; Stokes et al. 2010).

Like the other longleaf types, the majority of montane longleaf was logged and the land converted to other uses. Today, most montane longleaf stands exist in isolated patches on south facing slopes and ridgetops in northeastern Alabama (Varner III et al. 2003), northwestern Georgia (Cipollini et al. 2012), and North Carolina (Watkins et al. 2017). Remnant longleaf pines can also be found intermixed with hardwood species in areas where mesic and pyrophobic species establish in the absence of regularly returning fires (*i.e*. mesophication). Over time mesophication develops a positive feedback loop that changes the understory microclimate, causes a closure of the overstory, changes competition dynamics, reduces understory diversity, and prevents the regeneration of longleaf pine and other fire dependent species (Nowacki and Abrams 2008; Hanberry et al. 2012; Kreye et al. 2013). In these closed canopy conditions sub-dominant longleaf experiences extreme growth suppression. For example, in Virginia, release events in a closed canopy system induced an annual growth increase of up to 100% in developing longleaf pines (Bhuta et al. 2008).

Compared to fire-suppressed montane longleaf, frequently burned old-growth stands (aged over 150 years) support greater diversity of plants and are often host to over 100 vascular plant species in the understory (Maceina et al. 2000; Varner and Kush 2004; Cipollini et al. 2012). Old-growth montane longleaf systems are also home to several endemic and threatened bird species including the red-cockaded woodpecker and Bachman's sparrow (Shurette et al. 2007). The high biodiversity and scarcity of these ecosystems make restoration of montane longleaf systems a priority for land managers in northern Alabama and Georgia. Additionally, restoration and management of longleaf pine stands is relatively low risk due to its natural resistances to fire, draught, and disease while also providing a profitable source of timber, pine-straw, and hunting land (Landers et al. 1995).

Restoration efforts for montane longleaf pine systems have expanded in recent years with support from federal and state resource agencies and non-profit organizations such as the Longleaf Alliance and The Nature Conservancy. For instance, there is currently an effort that began in the mid-2000's to connect disjunct patches of remnant longleaf in northern Alabama and Georgia into a corridor of managed montane longleaf systems (Stowe 2005; Georgia Forestry Commission n.d.). The goal when restoring longleaf ecosystems is not to exactly recreate the forest that existed before European contact; instead the goal is a close approximation of the historic ecosystem that will benefit associated plant and animal communities by maintaining open canopy space, removal of competing hardwood species, and a reduction of leaf litter (Brockway et al 2005). This is often achieved through a progressive reintroduction of regular fires, selective cutting of undesirable species, limited herbicide treatment, and if the forest is highly degraded, planting of longleaf pine seedlings can accelerate regeneration (Brockway et al. 2005).

The reintroduction of fire in fire-suppressed longleaf systems requires consideration of fire frequency. Although all longleaf pine forests regularly burned in the past, the mean fire return interval (MFRI) differs across the native range. Systems generally require a MFRI of around 3-7 years to persist and regenerate (Frost 1993; Ford et al. 2010; Hammond et al. 2016). However, some coastal longleaf systems in Florida have a MFRI as low as every 0.5 years (Stambaugh et al. 2011), contributing to their characteristic park-like and open canopy appearance by removing understory hardwoods, creating microhabitat pockets, and opening areas of bare mineral soil. To accurately determine the historic MFRI for a particular system, dendrochronological methods are typically employed. By cross-dating growth rings in dead longleaf stumps with those from extant trees, the fire scars in the stumps can be dated and used to determine a historical MFRI (Stambaugh et al. 2011; Huffman and Rother 2017).

Few studies investigating mesophication and associated fire histories of montane longleaf have been conducted in Alabama, North Carolina, and Virginia; and little is known about these processes in the montane systems of northwestern Georgia (Cowell 1998; Varner et al. 2003; Tuttle and Kramer 2005; Bale 2009; Klaus 2019). The goal of this study is to fill this geographical gap in knowledge, gaining a more complete understanding of montane longleaf dynamics across the region and improving the information that land managers use in restoration at the local scale.

Using a combination of vegetation surveys, historical witness tree data, and dendrochronology this study attempted to reconstruct the local historical fire patterns of Paulding County, Georgia and investigated the effects of fire suppression on the modern forest's composition. It was hypothesized that the historical forest had a MFRI between 3-7 years; which is longer than those in coastal systems and consistent with other montane systems in Georgia (Bale 2009; Klaus 2019). It was also hypothesized that mesophilic species play a more important compositional roll in the modern forest when compared to the pre-settlement forest before fire suppression policies were implemented. Finally, as south-facing slopes are inherently more xeric than north-facing slopes, it was hypothesized that mesophilic and fire-intolerant species would be more compositionally significant on north-facing slopes rather than south-facing slopes. In other words, mesophication has occurred in Sheffield Wildlife Management Area (WMA), and the effects of mesophication are more pronounced on north-facing slopes.

Methods:

Site Description: Located in Paulding County, Georgia, Sheffield Wildlife Management Area (WMA) contains a population of remnant montane longleaf pine in both managed and unmanaged areas. The center of the WMA is heavily managed with regularly prescribed fires, selective cutting of hardwoods, and some herbicide treatment. Other "natural timber" areas within the WMA are either only managed with prescribed fires or have not yet been treated. Sheffield WMA is adjacent to the over 10,000-hectare Paulding Forest WMA which also contains remnant montane longleaf pine, but the area within Paulding Forest was formerly a loblolly (*P. taeda* L.) plantation and has been more heavily managed compared to Sheffield. Both of these WMAs fall within the proposed Alabama-Georgia corridor of longleaf habitat, so they are of special management interest to Georgia Department of Natural Resources (DNR). Working with "natural timber" in Sheffield WMA will allow the results of this study to be applied to Paulding Forest WMA along with large portions of northwestern Georgia that share a similar natural history.

Dendrochronology: Three sites within Sheffield WMA were selected for coring of living longleaf pines (Figure 1). The selected locations were on south facing slopes or ridgetops and each had many individuals over 40cm diameter at breast height (DBH). The three coring areas were located approximately 3km from each other and ranged in size averaging 0.768 hectares. A minimum of 50 longleaf pines were cored in each area using Haglöf increment borers. Two cores were taken from each tree perpendicular to the slope of the hill to avoid reaction wood. The cores were stored and processed according to standard dendrochronological techniques (Stokes and Smiley 1996). Core ring widths were measured using an AmScope M29 stereo microscope with 7x-45x lenses and a Velmex VRO Measuring System with Measure J2X software. The dplR statistical package in R and COFECHA were used to build the longleaf pine chronology (Grissino-Mayer 2001; Bunn 2008; Bunn 2010; Voortech 2012; R Core Team 2019; Bunn et al. 2020)

To reconstruct fire history, longleaf pine stumps were collected from the forest and the wood was examined for fire scarring. These “lighter wood” or “fat wood” stumps are protected from decomposition by hardened resin that retards microbial attack. Approximately 260 hectares of natural timber area within Sheffield WMA was surveyed for remnant stumps. Soil level, upslope direction, and the integrity of each stump was recorded along with the stump’s location, which was taken using a handheld Garmin etrex 30 GPS. From a total of 204 located, only stumps found on south-facing slopes and ridgetops that measured at least 20cm in diameter and had more than 50% of the cross-sectional area remaining were selected for removal. Priority removal was also given to stumps with visible fire damage in the wood structure. Stumps were removed by cutting with a chainsaw below the soil level and were cut into approximately 5 cm thick cross-sections both above and below the soil level (Huffman and Rother 2017). Cross sections from just above soil level were prepared using standard dendrochronological techniques (Stokes and Smiley 1996). Stump rings were measured as described above for tree cores and cross-dated to the living tree chronology using the dplR statistics package in R and COFECHA (Grissino-Mayer 2001; Bunn 2008; Bunn 2010; R Core Team 2019; Bunn et al. 2020).

<u>Vegetation surveys</u>: Shifts in vegetation composition that occurred between 1832 and the present day were investigated by comparing historical survey records from an 1832 Georgia Land Lottery maps to modern vegetation surveys conducted across Sheffield WMA. For the modern vegetation surveys, 36 circular plots (30-meter diameter) were randomly distributed across north and south-facing slopes (18 plots for each aspect) (Figure 1). To capture elevational variation in vegetation three 100 m^2 subplots located perpendicular to the contour of the slope in the upper, middle, and lower

portion of each main plot were surveyed for woody species composition (Figure 2). The DBH of each tree over 1.4 m tall in the subplots was measured. The presence of any additional species in the main plot that were not present in the subplots was also noted. Species importance value indices (IVI) were calculated among all plots, and separately for each slope (18 north and 18 south plots). These indices were calculated as: [relative density]+[relative frequency]+[relative dominance]. For species comparisons within individual plots, IVs were calculated using: [relative density]+[relative dominance].

To investigate the possibility of different mesophication rates on north and south-facing slopes, the difference in mean IV for each species between north and south facing slopes was calculated using the formula: [north IV]-[south IV]=[+N-S]. Species were classified according to ecological habit in terms of fire-tolerance and moisture-affinity, *i.e.* species were classified as either pyrophilic or pyrophobic, and either xeric or mesic according to Thomas-Van Gundy and Nowacki (2013), and Nowacki and Abrams (2015). For each species, fire-tolerance group, and moisture-affinity group, differences in IV between north- and south-facing slopes were assessed using Mann–Whitney U-tests based on the normality of the IV distribution determined using Shapiro-Wilk tests.

To compare the modern forest composition to the pre-Euro-American forest, witness tree data from a georeferenced survey map was digitized using ArcGIS (ESRI 2017). Sheffield and Paulding Forrest WMA both fall within the area covered by the 1832 Georgia Land Lottery Survey Cherokee County, Section 3, Gold District 18 survey map, originally produced on July 7, 1832 (District Plats of Survey, GA Archives). The survey map consists of square 40-acre plots. The corner of each plot and the midpoint between each corner were marked on the map with the common name of the closest tree, known as a “witness tree” (Dyer 2001). If a tree was not present at one of these points, a post would be fashioned, noting the common name of the tree used to make the post. Some trees from the historic data could only be identified to genus, as only common names were used by the surveyors. Points where only a post was present were removed from the data before analysis, leaving only witness trees. Additionally, some points were removed as the map was worn or torn in places, preventing accurate identification of the witness trees. Using the historic witness tree data and the modern vegetation surveys the relative abundance (RA) of each species and ecological habit were compared using chi-squared (χ^2) tests.

To compare different slope aspects using the historic witness tree data, digital elevation models (DEMs) obtained from the United States Geologic Survey (USGS) were used. The plat map used in this study falls on the corner of four USGS 1-arch-second (30m) DEMs, so a mosaic of the following DEMs were merged into a single raster using ArcGIS: n34w085, n34w086, n35w085, n35w086 (data.gov). The combined DEM was used to create both a slope and an aspect raster using Spatial Analyst tools included with ArcGIS. Raster values for slope and aspect were extracted at each witness tree point to determine the slope angle and aspect for the witness tree data. For comparisons of historical vegetation between aspects, only witness trees found on slopes between 7° and 23° were used to make the comparison similar to that done for the modern vegetation (all modern survey plots occurred on slopes within this range). Witness trees found on slopes with an aspect >135° and ≤315° were classified as being on a southwestern slope, while witness trees located on slopes with an aspect >315° or ≤135° were classified as being on northeastern slopes. The difference in RA across slope aspects for each species was calculated using [northeastern RA] - [southeastern RA]. Differences in the ratios of habitat classes from the historic species composition across slope aspects were assessed using a χ^2 test, while differences in mean RA were compared using Mann-Whitney tests.

Results

Dendrochronology:

Two-hundred fourteen cores were used to construct a chronology of living longleaf pine in Sheffield WMA that had coverage from the year 1912 to 2018 with a mean tree age of 76.4 years (Figure 3). The chronology of living longleaf had a mean inter-series correlation of 0.574 and a mean sensitivity of 0.281. Of the stumps located in Sheffield WMA, 14 survived processing and were able to be dated against the chronology. After the dated stumps were added, the final chronology covered 217 years from 1802 to 2018. The chronology that includes the dated stumps had a mean inter-series correlation of 0.56 and a mean sensitivity of 0.285 (Table 1). The detrended ring width index and sample depth of the chronology that includes the dated stumps is presented in Figure 4. While the stumps did not all significantly correlate with one another, each stump had several 15-year segments that significantly correlated to either the chronology of living longleaf trees, or to another stump that significantly correlated with the chronology. A total of 25 fire scars were found across 7 stumps with an average of 3.57 scars per stump (Figure 5A). Fire scars were dated across a range of years from 1855-1975, with a mean fire return interval (MFRI) of 5.5 years and a median interval of 3.5 years approximately following a Weibull distribution (Figure 6). Two fire events, occurring in 1935 and 1963, were recorded in more than one stump (Figure 5B).

<u>Modern forest composition:</u>

Results from the modern vegetation surveys show that among all plots, the three most important species by a considerable margin are black gum (*Nyssa sylvatica* Marshall, IV=48.3), sourwood (*Oxydendrum arboreum* (L.) DC., IV=45.8), and red maple (*Acer rubrum* L., IV=45.8). These are followed by longleaf pine (IV=26.9) and white oak (*Quercus alba* L., IV=26.5), while each of the other twenty species had IVs below 20 (Table 2). A few species including American chestnut (*Castanea dentata* (Marshall) Borkh.), and winged sumac (*Rhus copallinum* L.) were only found in a single plot each. Pyrophobic species importance tended to be greater, but was not statistically significantly greater, on north facing slopes ($U = 35$, $p = 0.8$) (Figure 7). Likewise, the importance for pyrophilic species tended to be higher on south-facing slopes, but this difference was not statistically significant ($U = 70$, $p = 0.2$) (Table 3). Xeric species appeared to have higher importance on south-facing slopes and mesic species appeared to have higher importance on north-facing slopes, however both of these trends were found to be not statistically significant (U = 119 and 12 respectively, p = 0.4 and 1.0 respectively) (Figure 8)

Differences in the importance of each species between aspects was examined using within-plot IVs. These comparisons showed longleaf pine as the most important species on south-facing slopes ([North IV]-[South IV] = -21.2) and sourwood as the most important on north-facing slopes ([North IV]-[South IV] = 23.6). Only 7 of the 25 species found in Sheffield WMA had a significant difference in IV between north and south-facing slopes (Table 4; Figure 9). Of these, red maple (U = 255, p = 0.003), sourwood (U = 263, p = 0.002), white oak (U = 228, p = 0.038), and chestnut oak (*Q. montana* Willd., U = 274, p < 0.001) were found to be significantly more important on north-facing slopes; while longleaf pine (U = 63, p = 0.001), southern red oak (*Q. falcata* Michx., U = 73, p = 0.001), and mockernut hickory (*Carya tomentosa* (Poir.) Nutt., U = 85, p = 0.004) were significantly more important on south-facing slopes.

<u>Historic vs. Modern Composition Comparison:</u>

A total of 2471 witness trees were identified on the 1832 Land Lottery map and positioned using ArcGIS (Figure 10). Pines (*Pinus spp.*) were by far the most abundant tree in the historic forest with a relative abundance (RA) of 0.4231, followed by red oak (*Q. rubra* Loudon, RA = 0.1518) and post oak (*Q. stellate* Wangenh., RA = 0.1174) (Table 5). After narrowing down the witness trees to individuals found on southwestern and northeastern slopes between 7° and 23°, a total of 1144 witness trees remained. This included 538 witness trees on southwestern slopes and 606 on northeastern slopes (Table 6). When comparing the RA of each species between southwest and northeast-facing slopes, pines and white oak were far more abundant on southwestern slopes than northeastern slopes. The four species with the strongest preference for northeastern slopes were black gum, red oak, American chestnut, and tulip poplar (*Liriodendron tulipifera* L.) (Figure 11). After witness trees were divided into habitat classifications, a significantly larger ratio of pyrophilic to pyrophobic species was found on southwest-facing slopes ($\chi^2 = 5.57$, $p = 0.02$). There was no difference in the ratio of moisture-affinity groups between slope aspects ($\chi^2 = 2.63$, $p = 0.1$) (Table 7). Results from Mann-Whitney U tests comparing the mean RA of each habitat class between slope aspects indicated no significant difference for any of the habitat classes (Table 8).

Comparing the historical relative abundance of each species to what is found in the modern forest indicates an overall shift to a more mesic and fire-intolerant composition. Maple (*Acer spp.*) experienced a 5708% increase in RA, while sourwood and black gum saw a 1553% and 531% increase in RA respectively. Of the species that were found in the modern forest, the largest decreases in RA were from American chestnut (-97%), post oak (-96%), and pines (-80%) (Table 5). Using the number of individuals of each species in a χ^2 test, the difference in species composition was found to be highly statistically significant ($p < 0.0001$). Species were divided once again into habitat classes according to their moisture-affinity and fire-tolerance (Table 9). The results of the χ^2 tests comparing the historic and modern abundance of each habitat class is presented in Table 10. The modern forest is both significantly more mesic ($\chi^2 = 394$, $p < 0.0001$) and significantly more fire-intolerant ($\chi^2 = 1342$, $p < 0.0001$) then the historic forest.

<u>Discussion</u>:

The hypotheses of this study were 1) the upland forest in northwest Georgia, represented by Sheffield WMA, has experienced mesophication since Euro-American settlement, 2) the effects of mesophication were more pronounced on north-facing slopes, and 3) the historic MFRI was between 3 and 7 years, being longer than the MFRI's found in coastal longleaf systems. Results from this study support all three hypotheses to some degree. The forest in Sheffield WMA as of 2019 is significantly more mesic and fire-intolerant than the forest found in northwest Georgia in 1832, as evidenced by the shift in ratios of xeric:mesic and fire-tolerant:fire-intolerant habitat classes (Table 9 and 10). While there is not a significant difference in the importance of the overall habitat classes between slopes in the modern forest (Table 3), some species are significantly more important on either north or south-facing slopes in ways that are consistent with their habitat classifications, e.g. mesophilic *A. rubrum* is more important on north-facing slopes (Table 4). Finally, the historic MFRI was estimated to be on a 5.5-year cycle, falling within the expected range for a montane longleaf pine system (Figure 6).

<u>Mesophication - Changes in Xeric and Pyrophilic Species</u>

Pines were by far the most abundant species in the historic forest (Table 5). Because pines are early successional and disturbance adapted species in the southeastern US (Brockway et al. 2005), this abundance suggests disturbance played a large role in shaping the historic community structure. While pines overall have experienced a large decline in RA, longleaf pine remains as one of the most important members of the modern forest community and the second most important species on south-facing slopes (Table 2 and 4). Extant mature longleaf pine in Sheffield WMA are likely remnant individuals that germinated before wide-spread fire suppression policies were implemented in the 1920's. The cores taken from living longleaf pines on average dated to 1945 (Table 1; Figure 3). During data collection for the modern vegetation surveys, no longleaf pine regeneration was observed in any of the "natural timber" areas (areas where restoration or other manipulations are not known to have occurred for several decades).

The large relative abundance of pyrophilic oaks in the historic forest is an important finding of this study that has implications for restoration of montane longleaf. All species of oak with the exception of black oak (*Q. velutina* Lam.), experienced an overall decline in relative abundance between sampling periods (Table 5). Although oaks have long been recognized as co-occurring with montane longleaf (Mohr 1901; Harper 1905; Peet and Allard 1993), decades of restoration practices have commonly used fire, herbicides and thinning to eliminate all hardwood species (Boyer 1990; Kush et al. 1999; Brockway and Outcalt 2000). However, this approach is changing, and in coastal and sandhill longleaf systems pyrophilic oak species are receiving increasing recognition for their contribution to biodiversity and ecological place in longleaf restoration (Hiers et al. 2014; Loudermilk et al. 2016). For example, oaks may act as nurse trees that moderate soil temperatures and increase microhabitats that support insect diversity. (Hiers et al. 2014; Loudermilk et al. 2016). Because montane systems are generally more mesic than coastal longleaf systems, it makes sense that they would support more hardwood species like oaks. The historical co-dominance of pines and oaks found in this study suggests a role for pyrophilic oaks in montane ecosystem restoration. As restoration efforts for longleaf pine communities expand across northwest Georgia an effort to preserve populations of pyrophilic oaks within each longleaf pine community could have benefits similar to those found in sandhill communities. However, retaining oaks could create extra challenges for restoration of montane longleaf forests. Selective removal of only a subset of hardwoods could be more expensive and time consuming.

<u>Mesophication - Changes in Mesic and Pyrophobic Species</u>

The most pronounced importance change from a single mesic species was the massive establishment of maple since 1832 (presumably red maple, as no other species were found in the modern survey). Since Euro-American settlement, red maple has experienced an over 5000% increase in relative abundance in northwest Georgia (Table 5). While maple constituted a small part of historical upland communities, fire suppression may have allowed it to flourish in areas where frequent fires previously excluded its establishment, as found in other areas of the eastern US (Lorimer 1984). Possessing multiple traits typically associated with generalist invasive species (e.g. early maturation age, high reproductive capacity, and the ability to establish in different successional states), red maple was able to quickly propagate from habitats that were sanctuaries from fire before wide-spread fire suppression policies were implemented (Lambers and Clark 2005; Alexander & Arthur 2010). Although red maple is not considered fire-tolerant, the relationship of red maple and fire is complex. After a history of fire-suppression, established mature maple can persist and out-grow some oak species even under a periodic fire regime (Green et al. 2010; Keyser et al. 2018). Ultimate explanations for red maple's spread are varied and include factors such as new fire regimes, introduced species, climate change, and modern wildlife management practices (Fei and Steiner 2007).

Along with maple, sourwood and black gum also experienced large increases in relative abundance, about 1500% and 500% respectively (Table 5). The only modern species with a higher mean IV on south facing slopes than longleaf pine is black gum (Table 4), which currently exists primarily as a mid-story species in Sheffield WMA (Sutton 2019). While these species were classified according to Thomas-Van Gundy and Nowacki (2013) as xeric and fire-intolerant in this study, there is some evidence they have a moderate fire-tolerance (Abrams 2007; Keyser et al. 2018; Vander Yacht et al. 2019). However, the fire-tolerance of sourwood and black gum does not compare to the competitive advantage truly pyrophilic species (e.g. oaks and pine) would have in a frequently burned system. The prevalence of red maple, sourwood and black gum in the modern forest are a challenge for restoration aiming to produce longleaf dominated upland communities. More work is needed to determine their responses to disturbances including fire. Greater understanding of these responses could help minimize the use of expensive restoration manipulations such as selective herbicide treatments or mechanical removals.

<u>Mesophication – Changes between slope aspects</u>

Counter to the hypothesis, there were not strong differences in mesophication between slope aspects. I expected greater mesophication on north-facing slopes because mesophile species originating in bottomlands could have gradually propagated up these cooler, more shaded slopes faster as compared to south-facing slopes. It should be noted that although not statistically significant, modern north-facing slopes tended to have greater importance of mesic- and pyrophobic species compared to south-facing slopes (Table 3; Figure 7 and 8). In the historic forest, there was a greater ratio of pyrophilic:pyrophobic trees on south-western facing slopes compared to north-eastern slopes (Table 7), but otherwise there are no significant differences in relative abundance of habitat classes between slopes (Table 8). Species differences in relative abundance between slopes were generally less pronounced in the historic forest, and greater in the modern forest (Figure 9 and 11), suggesting that the historic forest may have been more homogeneous compared to the modern forest. Greater homogeneity would be expected if the landscape was "managed" to some extent, for instance through widespread use of fire by Native Americans or early Euro-American settlers. Perplexingly, the relative abundance of red oak and white oak on opposing slope aspects switched since 1832 (Figure 12). In the historic data, white oak was more prevalent on south-facing slopes and red oak was more prevalent on north-facing slopes (Figure 11), while in the modern forest, white oak is more prevalent on north-facing slopes and red oak is more prevalent on south facing slopes (Figure 9). In the absence of fire or other management, ongoing mesophication should create stronger vegetation differences between north and south-facing slopes in the future.

Other Factors Affecting Forest Composition

Aside from mesophication associated with fire-suppression, many other changes have likely affected the modern forest's composition. Factors including the spread of forest pests and pathogens, changes in climate and wildlife, and human activity influence forest composition across the southeastern US. For instance, a major factor that influenced the change in species composition over the past 200 years is the functional extinction of American chestnut due to logging and blight. American chestnut exists today as small shoots in the understory re-sprouting from root collars established before the chestnut blight killed nearly all mature American chestnut trees (Paillet 2002; Elliot and Swank 2008). Based on the historic witness tree data, chestnut was among the most abundant species in upland areas on both northeastern and southwestern slopes (Table 6). While it cannot be directly ascertained from this study, it is important to ask which species, if any, filled the niche opened with the loss of American chestnut. Changes in species composition from disease, fire, or logging have been observed to induce an advancement in ecological succession (Abrams and Nowacki 1992). It is possible that the loss of chestnut, logging of canopy dominants, and the implementation of fire suppression policies at approximately the same time contributed to the increased importance of mesic and other sub-dominate hardwood species.

Considerations in Comparisons of Historic vs Modern Vegetation

When comparing historical witness tree data with modern vegetation surveys, interpretation must be cautious. There are many factors that could influence the results of the comparison, particularly those regarding the historic surveyors who recorded the witness trees. Species misidentification, methodological inconsistencies, and surveyor bias in tree identification and location are difficult to account for, especially in forests with non-uniform densities (Black and Abrams 2001; Kronenfeld and Wang 2007).

Additionally, the accuracy and resolution of witness tree positions in the landscape must be considered. Efforts to determine the true position of these trees can be compromised by either mistakes made by the surveyors, or from the resolution of the DEM used. The DEM used to assign a slope and aspect to each witness tree in this study was of 1 arc-second (approximately 30 meter) resolution. Because fine topographic detail below this resolution is not currently available, a witness tree could appear to be on a slope aspect that is incorrect. To account for this possibility, the witness tree data was subset into two broad slope aspect categories, northeast-facing (>315° or ≤135°) and southwest-facing (>135° and ≤315°). Based on personal observation of northwest Georgia forests (e.g. the modern survey plots were 30m in diameter and only encompassed one slope aspect per plot), it seems unlikely the topography would change drastically enough (i.e. from north to south facing) within a

30m resolution cell to create mis-located witness trees. In the future, the acquisition of expanded finer resolution data could improve the determination of witness tree locations.

Finally, the historical surveys encompassed a much larger area than the modern survey and likely recorded a more diverse sample of trees from a greater number of habitats. The modern sampling focused on upland “natural timber” habitats within the Sheffield WMA where longleaf pine was likely to occur, and where management has not occurred in several decades. Sampling on a broader scale would be extremely difficult as much of the land in northwest Georgia is privately held and does not consist of “natural timber.” To make the historical and modern comparison more accurate, the historic data was subset to only include witness trees on slopes within the same range as the modern survey plots (>7° and <23°), which hypothetically restricted all historical data to upland forests. Considering that upland forests are where xeric and fire-tolerant species would be expected to persist, this makes the pronounced effects of mesophication found in Sheffield WMA even more striking.

Fire History and Dendrochronology – Fire Return Intervals

Consistent with the hypothesis, cross-sections of longleaf stumps recovered from Sheffield WMA show evidence of fire return intervals that are longer than those of coastal longleaf systems. Twenty-five fire scars were identified across seven successfully dated stump cross-sections. These scars represented fires that occurred from 1855 to 1975 with a MFRI of 5.5 years. Although the sample size of stumps was small, half of the stumps that survived processing contained fire scars. Therefore, fire was likely prevalent but variable across the landscape, as would be expected in montane longleaf systems. Two fires were recorded in more than one stump, providing evidence supporting the accuracy of the cross-dating.

However due to the low sample size, it is difficult to determine if the MFRI calculated here has been over or under-estimated. Comparing this study to others, the MFRI calculated for Sheffield WMA is slightly longer than what has been calculated in other montane systems. A study using similar methods conducted in Sprewell Bluffs WMA, GA calculated a historic MFRI of 3 distinct time periods: pre-1840, 1840-1915, and post-1915. The MFRI of each of these time periods was found to be 2.6, 1.2, and 11.4 years respectively (Klaus 2019). Another study conducted at Choccolocco Mountain calculated the MFRI to be 3.2 years from 1653-1831 and 2.5 years from 1832-1940 (Bale 2009). Variations in MFRI across the region could be caused by differences in local precipitation, drought, lightning strikes, or human activity (Frost 1998).

Fire History and Dendrochronology – Growth Dynamics of Extant Longleaf

Results from the dendrochronological analyses suggest most longleaf in Sheffield WMA germinated in the 1940-1950s, with the oldest tree dating to 1911 and no regeneration in natural timber areas since the 1970s (Figure 2). The mean number of rings in each core was 72.5 ± 1.1, meaning the average time of establishment was at least 72 years ago but due to the fact that longleaf pine may exist in the "grass stage" for the first few years of its life, an exact time of germination cannot be determined. Therefore, only a minimum estimate of age can be determined. Regardless, these stands are all approximately even aged and relatively young (Figure 3). Longleaf pines are known to live up to 500 years, but rarely achieve lifespans this long due to the disturbance driven systems they inhabit (Boyer 1990; Brockway et al. 2005). The oldest trees in old-growth, mixed-aged stands at Choccolocco Mountain, AL (Mountain Longleaf National Wildlife Refuge) are ~250 years old but the majority of trees are 85 years of age or less (Varner et al 2003). It is unknown how the growth trends of relatively young, even-age stands differ from old-growth, and mixed-aged stands in the region, and there are few examples available for comparison. Indeed, this study is the first to examine growth trends in degraded longleaf stands rather than old growth or those that have been restored. As of 2020 there were only two chronologies of montane longleaf in the International Tree Ring Database (ncdc.noaa.gov), both old-growth stands, the first from Choccolocco Mountain (Guyette et al. 2012), and the second from

Lavender Mountain, GA (Pederson et al. 2012). Over the period common between Choccolocco Mountain and Sheffield WMA chronologies (1912-2006), ring-width indices were significantly correlated ($R = 0.4$, $p < 0.001$), however there was poor correlation between Sheffield WMA and Lavender Mountain chronologies ($R = 0.01$, $p=0.9$) over their common period (1912-2003). More studies of montane longleaf stands of different ages and disturbance histories are needed to further understand the relationship between these factors and tree growth.

The Sheffield chronology did not have any strong growth trends in the most recent 50 years (Figure 2), and no trees originating since the 1970s, both suggesting few stand-wide disturbances have occurred, *i.e.* disturbances causing multiple tree mortality, subsequent growth release in surviving individuals, and new recruitment in seedling and saplings. Storms causing windthrow are important for creating gaps that allow for regeneration. Lipps (1967) suggested that ice storms were major mortality agents at Lavender Mountain, and Varner et al. (2003) estimated that gaps from storms are created at the rate of 2 per ha-1 per decade at Choccolocco Mountain. Using this estimate, the stands examined in Sheffield WMA have a mean size of 0.78 ha, so at least 7 gap-creating disturbances would be expected since 1970. Additionally, it is unknown how much self-thinning has occurred. Like disturbance, self-thinning opens space in the canopy required for longleaf pine to regenerate in the understory (Stokes et al 2010). Occasional dead and dying longleaf pines were observed in the stands, but as previously stated no evidence of regeneration was observed in the understory of the “natural timber” areas. Without restoration or natural disturbances that create sufficient gaps, stands like these seem destined to be replaced by hardwood species over time.

<u>Fire History and Dendrochronology – Stump Cross-Dating</u>

The cross-dated stumps tended to be older than the living trees having an average ring count of 86.6 ± 3.2 and the oldest cross section had 189 rings. While there was poor correlation among all stumps, each stump significantly correlated to either the chronology of living longleaf; or to another stump that also significantly correlated with the living chronology. The lack of correlation between stumps is probably due to the low sample size obtained in this study (Table 1). With this low sample size, exogenous signals in the growth trends are harder to detect. The stumps had an overall higher mean sensitivity than the cores from extant trees (Table 1), which could have also contributed to difficulties detecting a common growth trend. Of the over 200+ stumps located in Sheffield MWA, only a handful remained intact enough to be considered useable in analysis. As remnant stumps decompose, burn, or become weathered by other means across northwest Georgia, time is running out to expand on the result of this study or conduct similar studies in other longleaf systems (Huffman and Rother 2017).

Conclusions

The vegetation analysis in this study supports the hypothesis that mesophication has occurred across Sheffield WMA since the implementation of fire-suppression policies following the Clarke-McNary Act of 1924 (Stephens and Ruth 2005). The fire scars found in remnant longleaf stumps suggest that fire was likely prevalent yet variable across the historic landscape, and the chronology of extant longleaf suggests that disturbances since the 1970s were apparently not severe enough to allow for regeneration that would create the diversity of stand age-structures found in reference montane longleaf systems.

A lack of modern fires has allowed mesophication to progress over time, but the current state of mesophication could be reversed through the reintroduction of periodic fires. As restoration efforts expand in northwest GA and northeast AL, it is likely that these types of stands (even aged, encroached on by hardwoods) will be encountered by managers. As fire is reintroduced into management areas with even-aged longleaf stands, these remnant trees serve as a genetic resource to cross breed with younger plants upon reproductive maturity (e.g. planted seedlings) and will help create the mixed-aged stands found in old-growth montane longleaf. Additionally, selective removal of some hardwood species while leaving pyrophilic oaks could lead to restorations with more diverse habitats, more closely resembling the historic forest and supporting additional biodiversity.

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Tables:

Table 1: Chronology statistics from longleaf pine trees and relict stumps in in Sheffield Wildlife Management Area, Paulding County GA.

	Cores	Stumps	Cores + Stumps
Total number of series	214	14	228
Number of years covered	107	189	217
Range of years covered	1912-2018	1802-1990	1802-2018
Mean inter-series correlation	0.574	0.241	0.56
Mean ring width (mm)	2.29	1.64	2.23
Ring width standard deviation (mm)	1.083	0.865	1.054
Mean autocorrelation	0.728	0.574	0.718
Mean sensitivity	0.281	0.358	0.285
Percentage of flagged series	12.70%	86.07%	16.90%
Mean DBH ± Standard Error (cm)	41.2 ± 0.6	-	-

Table 2: Among-plot importance values (IV) of tree species in Sheffield Wildlife Management area, Paulding County GA.

Species	Importance Value
Nyssa sylvatica	48.3
Oxydendrum arboreum	45.8
Acer rubrum	45.8
Pinus palustris	26.9
Quercus alba	26.4
Quercus rubra	17.0
Carya glabra	15.8
Quercus montana	10.6
Cornus florida	10.0
Quercus falcata	8.9
Pinus taeda	8.1
Liriodendron tulipifera	6.0
Carya tomentosa	6.0
Pinus virginiana	4.8
Quercus velutina	4.4
Quercus marilandica	3.4
Quercus stellata	2.4
Sassafras albidum	2.1
Fagus grandifolia	2.1
Pinus echinata	1.9
Prunus serotina	0.8
Magnolia macrophylla	0.8
Castanea pumila	0.5
Rhus copallinum	0.5
Unknown	0.4

Table 3: Mean importance values (IV) and standard errors (SE) for moisture-affinity and fire-tolerance classes of tree species from north and south facing slopes in Paulding County, GA. Differences in IV between slopes were tested with Mann-Whitney U-tests.

	North-facing			South-facing				
	Mean IV		SE	Mean IV		SE	U	p
Moisture-Affinity								
Mesic	15.9	±	11.0	9.2	±	4.9	12	1.00
Xeric	13.8	±	4.7	14.1	±	3.7	119	0.40
Fire-Tolerance								
Pyrophile	8.8	±	3.2	11.9	±	3.5	70	0.22
Pyrophobe	23.2	±	9.5	15.3	±	6.3	35	0.80

Table 4: Within-plot mean species importance values (± SE), and associated Mann-Whitney tests (U) comparing North and South facing slopes in Paulding County GA. $p < 0.05$ indicates a significant difference between slopes. Species marked by an * were only found in one plot.

Species	North			South			U	p
Acer rubrum	42.6	±	5.8	19.1	±	4.6	255	0.003
Carya glabra	10.2	±	2.5	8.0	±	1.8	175	0.701
Carya tomentosa	0.5	±	0.4	5.5	±	1.7	85	0.004
*Castanea pumila**	0.0	±	0.0	0.6	±	0.6	153	0.345
Cornus florida	7.2	±	3.1	6.9	±	2.9	146	0.604
Fagus grandifolia	0.4	±	0.3	0.8	±	0.5	151	0.581
Liriodendron tulipifera	6.5	±	3.1	3.0	±	1.4	175	0.603
Magnolia macrophylla	0.0	±	0.0	0.6	±	0.5	144	0.163
Nyssa sylvatica	31.2	±	3.6	35.8	±	3.9	130	0.323
Oxydendrum arboreum	40.5	±	6.3	16.9	±	4.6	263	0.001
Pinus echinata	0.0	±	0.0	4.0	±	2.4	135	0.080
Pinus palustris	6.4	±	2.3	27.7	±	4.8	63	0.001
Pinus taeda	2.9	±	1.6	12.0	±	6.3	126	0.149
Pinus virginiana	1.9	±	0.9	4.8	±	2.1	140	0.389
Prunus serotina	0.6	±	0.5	0.0	±	0.0	180	0.163
Quercus alba	21.8	±	4.0	10.2	±	2.9	228	0.038
Quercus falcata	0.8	±	0.6	16.0	±	4.2	73	0.001
Quercus marilandica	0.9	±	0.6	3.5	±	1.8	128	0.145
Quercus montana	16.0	±	3.8	0.6	±	0.6	274	0.000
Quercus rubra	7.1	±	1.7	15.2	±	5.5	139	0.460
Quercus stellata	0.7	±	0.7	3.1	±	1.4	128	0.098
Quercus velutina	1.5	±	1.0	4.2	±	1.5	116	0.058
*Rhus copallinum**	0.0	±	0.0	0.4	±	0.4	153	0.345
Sassafras albidum	0.2	±	0.2	1.1	±	0.5	135	0.163
Unknown*	0.2	±	0.2	0.0	±	0.0	171	0.345

Table 5: The change in relative tree species abundance (RA) from 1832 to 2019 in Paulding County, GA. The habitat classification of each species used in data analysis is also presented here. The results of a χ^2 test applied to the historic and modern species counts indicates a significant shift in species composition ($p<0.0001$).

Species	Historic Count	Historic RA	Modern Count	Modern RA	% Change in RA	Moisture-Affinity	Fire-Tolerance
Acer spp.	10	0.0040	330	0.2350	5707.91%	Mesic	Intolerant
Carya spp.	51	0.0206	105	0.0748	262.35%	Xeric	Tolerant
Castanea dentata	152	0.0615	3	0.0021	-96.53%	Xeric	Tolerant
Cornus florida	13	0.0053	50	0.0356	576.91%	Mesic	Intolerant
Diospyros virginiana	5	0.0020	0	0.0000	-100.00%	Mesic	Intolerant
Euonymus atropurpureus	5	0.0020	0	0.0000	-100.00%	Mesic	Intolerant
Fagus grandifolia	34	0.0138	7	0.0050	-63.77%	Mesic	Intolerant
Fraxinus spp.	16	0.0065	0	0.0000	-100.00%	Mesic	Intolerant
Ilex opaca	1	0.0004	0	0.0000	-100.00%	Mesic	Intolerant
Juglans nigra	3	0.0012	0	0.0000	-100.00%	Xeric	Intolerant
Juniperus virginiana	1	0.0004	0	0.0000	-100.00%	Xeric	Tolerant
Liquidambar styraciflua	19	0.0077	0	0.0000	-100.00%	Mesic	Intolerant
Liriodendron tulipifera	36	0.0146	31	0.0221	51.55%	Mesic	Intolerant
Magnolia acuminata	3	0.0012	0	0.0000	-100.00%	Mesic	Intolerant
Magnolia macrophylla	0	0.0000	3	0.0021	N/A	Mesic	Intolerant
Morus spp.	4	0.0016	0	0.0000	-100.00%	Mesic	Intolerant
Nyssa sylvatica	87	0.0352	312	0.2222	531.16%	Xeric	Intolerant
Oxydendrum arboreum	23	0.0093	216	0.1538	1552.84%	Xeric	Intolerant
Pinus spp.	1041	0.4213	117	0.0833	-80.22%	Xeric	Tolerant
Prunus serotina	3	0.0012	3	0.0021	76.00%	Xeric	Intolerant
Quercus alba	105	0.0425	70	0.0499	17.33%	Xeric	Tolerant
Q. falcata	42	0.0170	28	0.0199	17.33%	Xeric	Tolerant
Q. marilandica	50	0.0202	10	0.0071	-64.80%	Xeric	Tolerant
Q. montana	69	0.0279	38	0.0271	-3.07%	Xeric	Tolerant
Q. rubra	375	0.1518	47	0.0335	-77.94%	Xeric	Tolerant
Q. stellata	290	0.1174	7	0.0050	-95.75%	Xeric	Tolerant
Q. velutina	23	0.0093	17	0.0121	30.08%	Xeric	Tolerant
Rhus copallinum	0	0.0000	3	0.0021	N/A	Xeric	Intolerant
Sassafras albidum	0	0.0000	7	0.0050	N/A	Xeric	Tolerant
Ulmus spp.	10	0.0040	0	0.0000	-100.00%	Mesic	Intolerant

Table 6: The number and relative abundance (RA) of each witness tree species on southwestern and northeastern slopes.

Species	**Southwestern Count**	**Southwestern RA**	**Northeastern Count**	**Northeastern RA**
Acer spp.	2	0.0037	4	0.0066
Carya spp.	9	0.0167	11	0.0182
Castanea dentata	35	0.0651	48	0.0792
Cornus florida	3	0.0056	5	0.0083
Diospyros spp.	1	0.0019	1	0.0017
Euonymus atropurpureus	2	0.0037	2	0.0033
Fagus grandifolia	10	0.0186	12	0.0198
Fraxinus spp.	1	0.0019	2	0.0033
Ilex opaca	0	0.0000	1	0.0017
Liquidambar styraciflua	2	0.0037	4	0.0066
Liriodendron tulipifera	6	0.0112	15	0.0248
Magnolia acuminata	0	0.0000	3	0.0050
Morus rubra	2	0.0037	0	0.0000
Nyssa sylvatica	17	0.0316	31	0.0512
Oxydendrum arboreum	5	0.0093	7	0.0116
Pinus spp.	227	0.4219	236	0.3894
Prunus serotina	1	0.0019	0	0.0000
Quercus alba	38	0.0706	23	0.0380
Quercus falcata	11	0.0204	15	0.0248
Quercus marilandica	17	0.0316	13	0.0215
Quercus montana	26	0.0483	23	0.0380
Quercus rubra	72	0.1338	92	0.1518
Quercus stellata	43	0.0799	50	0.0825
Quercus velutina	6	0.0112	5	0.0083
Ulmus spp.	2	0.0037	3	0.0050

Table 7: Historic witness tree counts by slope aspect and habitat group. Results from a χ^2 test comparing each habitat group on opposing slopes are also presented here.

Habitat Group	Historic Count			
	Southwest	Northeast	χ^2	p
Moisture-Affinity				
Xeric	507	555	2.63	0.1
Mesic	31	51		
Fire-Tolerance				
Pyrophile	484	516	5.57	0.02
Pyrophobe	54	90		

Table 8: The mean relative abundance (RA) ± standard error (SE) of witness trees in each habitat class. Results from Mann-Whitney (U) tests comparing the RA between northwestern and southeastern slopes are also presented here.

	Southwest-facing			Northwest-facing				
Habitat Group	RA		SE	RA		SE	U	p
Water-affinity								
Xeric	7.25	±	3.09	7.62	±	3.08	71	0.72
Mesic	0.58	±	0.16	0.78	±	0.23	48	0.64
Fire Tolerance								
Pyrophile	9.00	±	3.87	8.51	±	3.65	51	0.97
Pyrophobe	0.77	±	0.24	1.14	±	0.38	72	0.54

Table 9: The historic and modern mean relative abundance (RA) ± standard error, of tree species in Paulding County GA, grouped by two habitat classifications (moisture-affinity and fire-tolerance) from historical maps and modern vegetation surveys.

Habitat Group	Historic Mean RA			Modern Mean RA		
Moisture-affinity						
Xeric	0.0551	±	0.0251	0.0412	±	0.0151
Mesic	0.0049	±	0.0013	0.0231	±	0.0179
Fire Tolerance						
Pyrophile	0.0742	±	0.0344	0.0267	±	0.0083
Pyrophobe	0.0061	±	0.0020	0.0378	±	0.0185

Table 10: Counts of tree species in Paulding County GA, grouped by two habitat classifications (moisture-affinity and fire-tolerance) from historical maps and modern vegetation surveys. Chi-squared (χ^2) tests were used to detect significant shifts between historical and modern counts within each habitat dichotomy.

Habitat Group	Historic Count	Modern Count	χ^2	p
Moisture-affinity				
Xeric	2315	983	394.02	<0.0001
Mesic	156	421		
Fire Tolerance				
Pyrophile	2199	449	1342.25	<0.0001
Pyrophobe	272	955		

Figures:

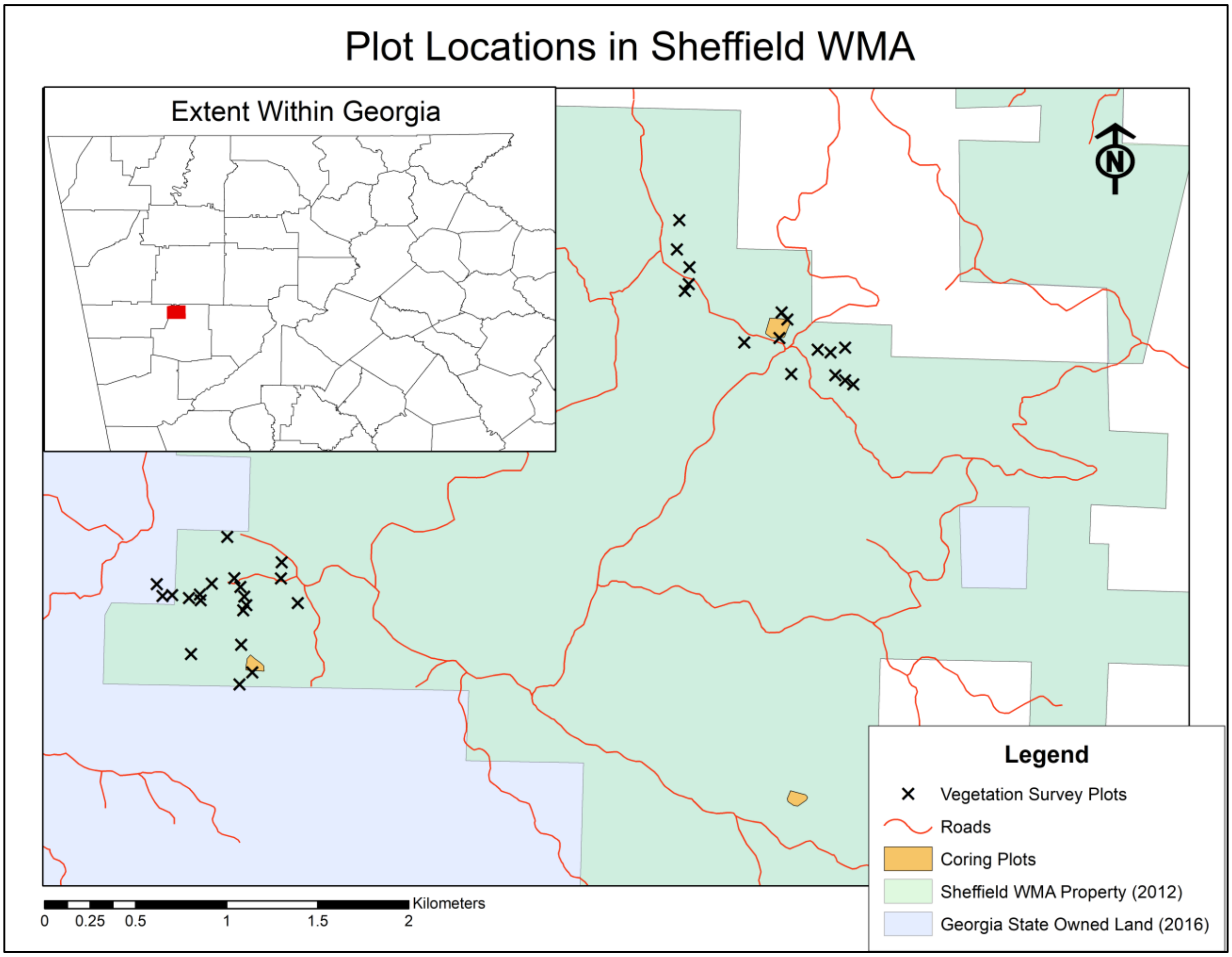

Figure 1: A map of Sheffield Wildlife Management Area in Paulding County GA, including the locations of plots used for dendrochronology analysis of living longleaf pines and modern vegetation surveys.

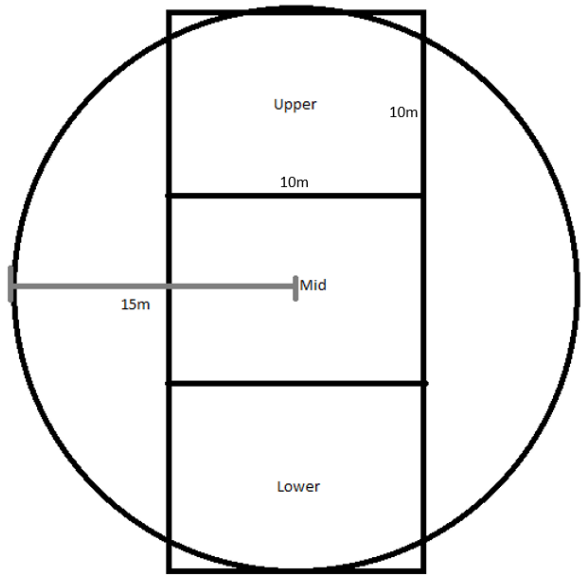

Figure 2: Vegetation plot design used to survey tree species in Sheffield Wildlife Management Area, Paulding County GA. Each tree in the three sub-plots was identified and the DBH was measured. The presence of additional species in the large circular plot not found in the subplots were also be indexed.

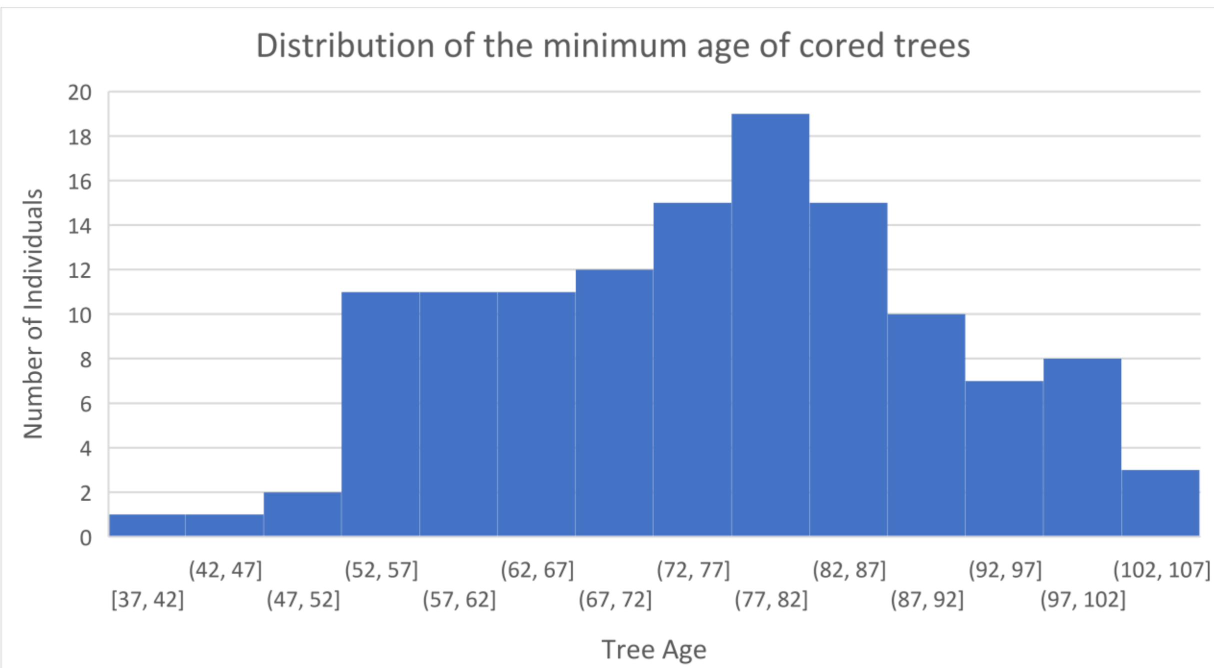

Figure 3: A histogram showing the distribution of the minimum possible age of each tree represented in the chronology of living longleaf pine (mean = 76.4 years, standard error= ±1.3).

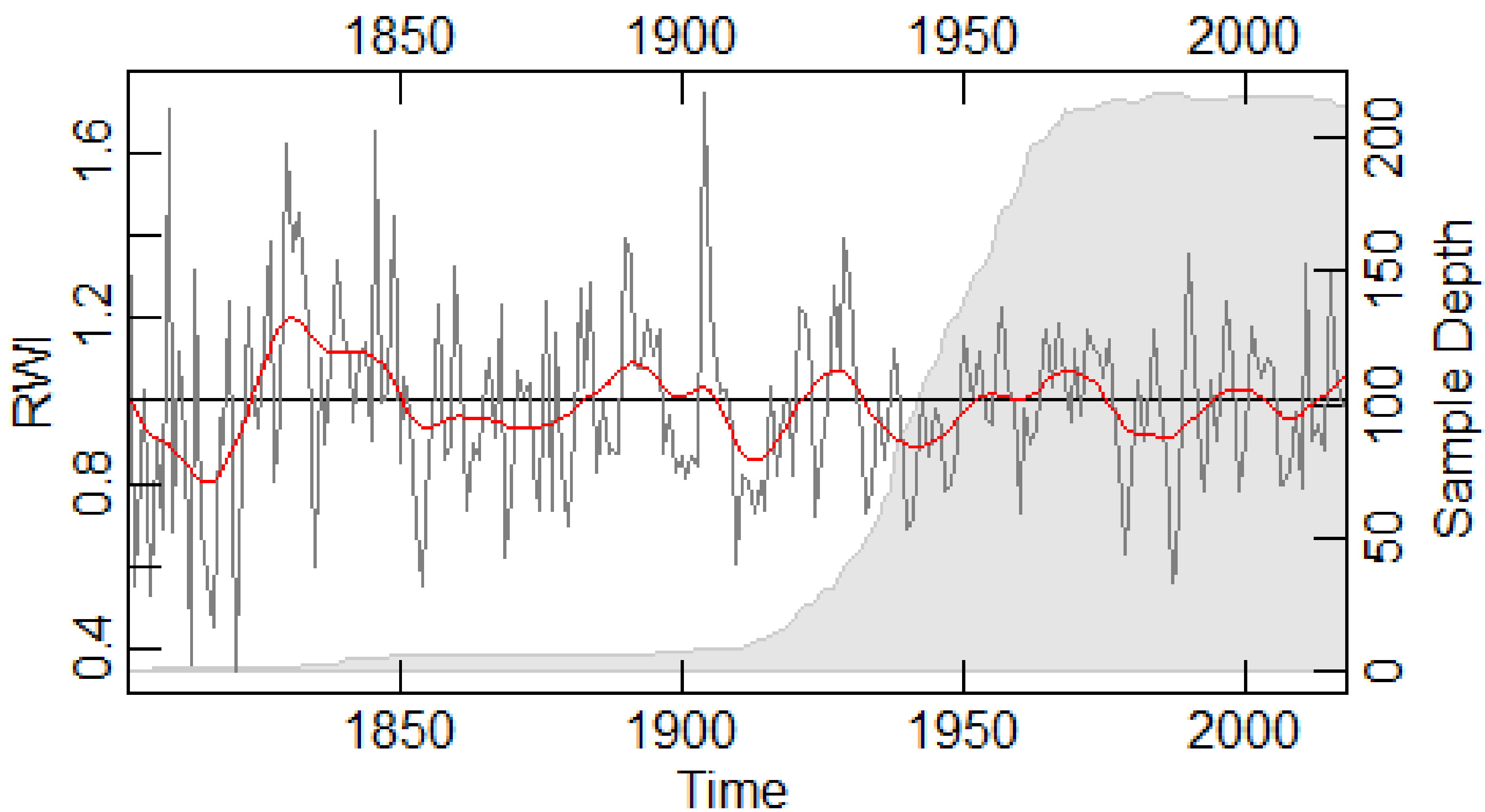

Figure 4: The ring width index (RWI) and sample depth for longleaf pine trees and relict stumps in Paulding County, Georgia. The shaded grey area represents the sample depth present at each year from 1802 to 2018, the grey line is the average relative ring growth, and the red line is the detrended relative yearly growth using the spline method.

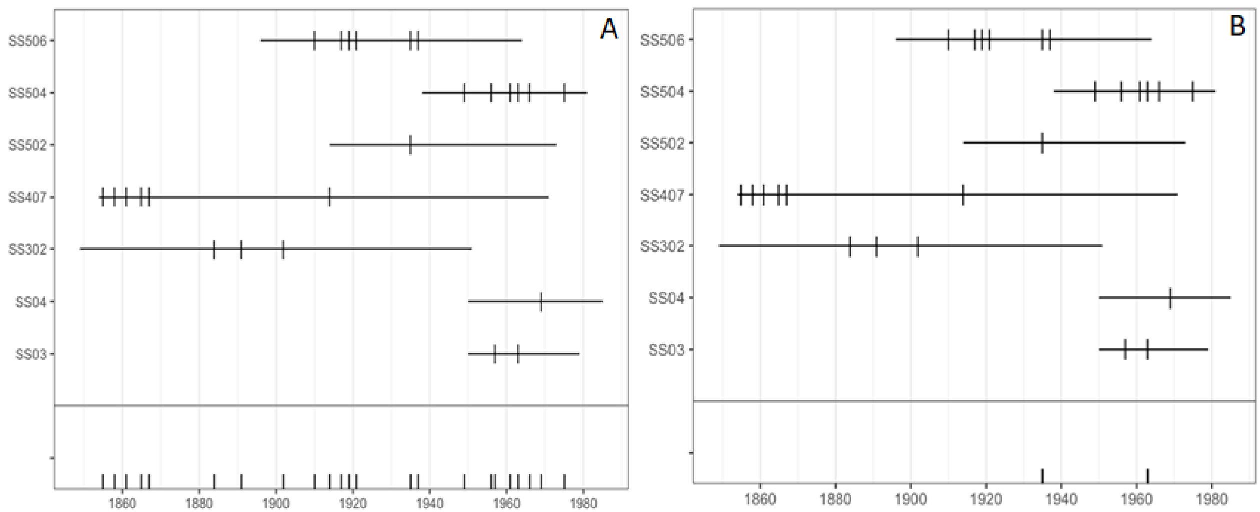

Figure 5: Timeline of fire scars in longleaf pine stumps from Sheffield Wildlife Management Area, Paulding County GA. The timespan covered by each stump is represented by the horizontal lines with intersecting vertical lines representing fire scars at that corresponding year. A composite of all dated fire scars is along the x-axis. A composite of all fire scars can be found on the x-axis in panel A, while composite of fires recorded in more than one stump can be found on the x-axis of panel B.

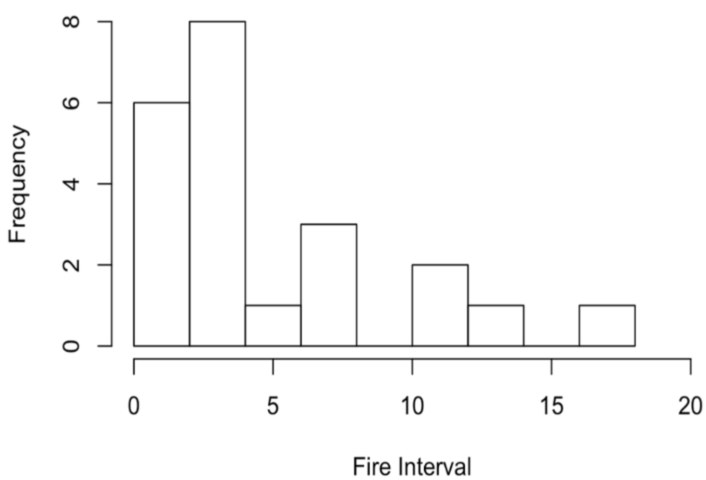

Figure 6: The distribution of intervals (years) between fire scars in seven longleaf pine stumps. The mean fire return interval (MFRI) was 5.5 ± 0.94 years.

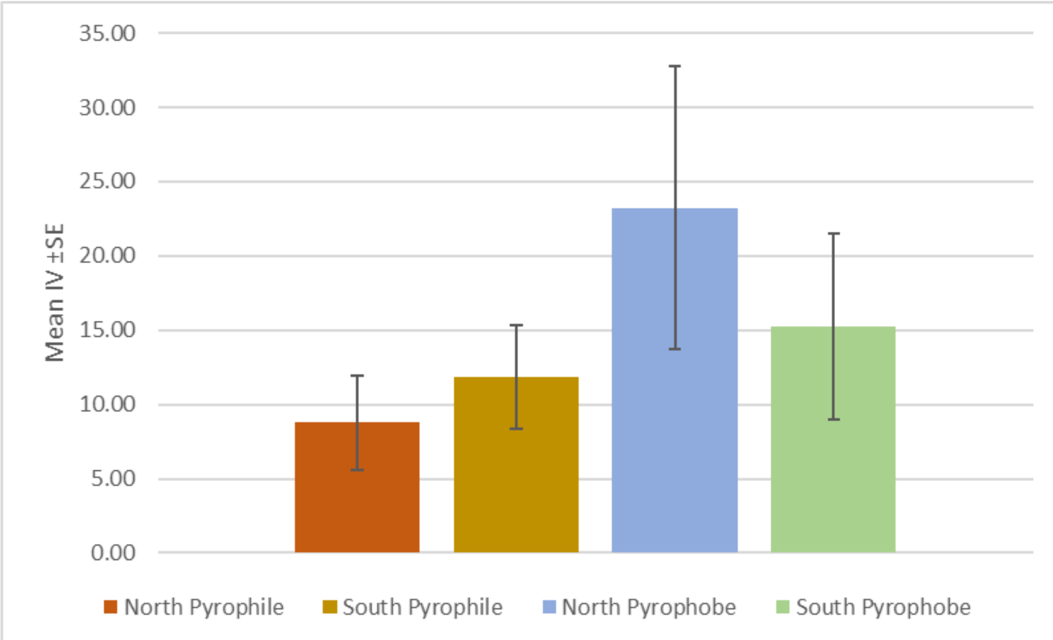

Figure 7: Mean importance value (IV) and standard errors for tree species in Sheffield WMA grouped by fire-tolerance and slope aspect.

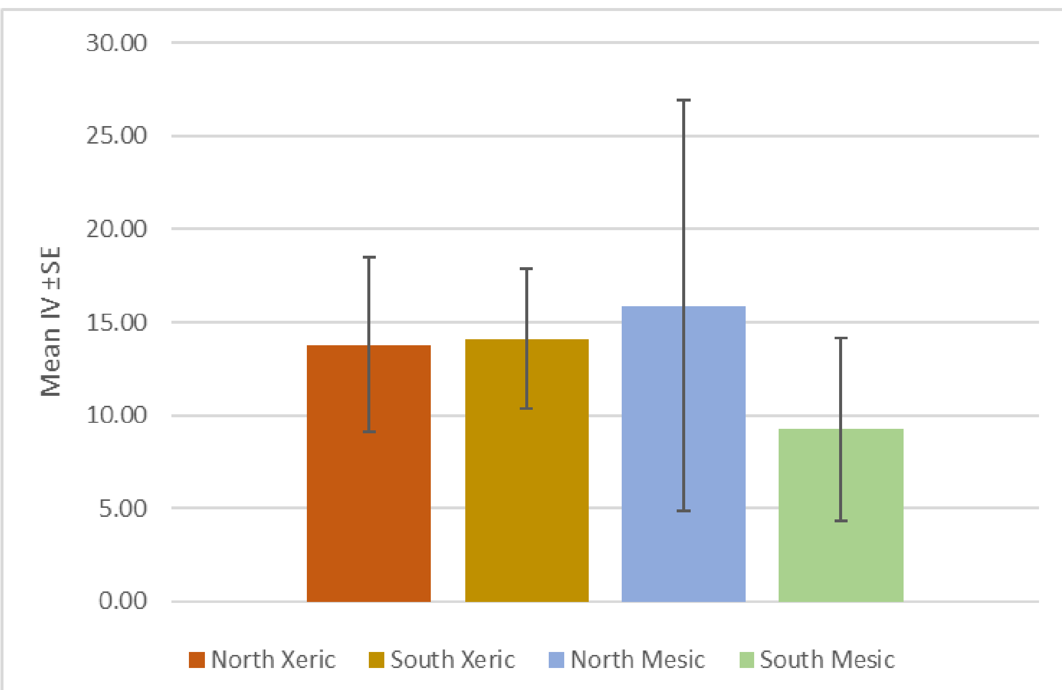

Figure 8: Mean importance value (IV) and standard errors for tree species in Sheffield WMA grouped by moisture-affinity and slope aspect.

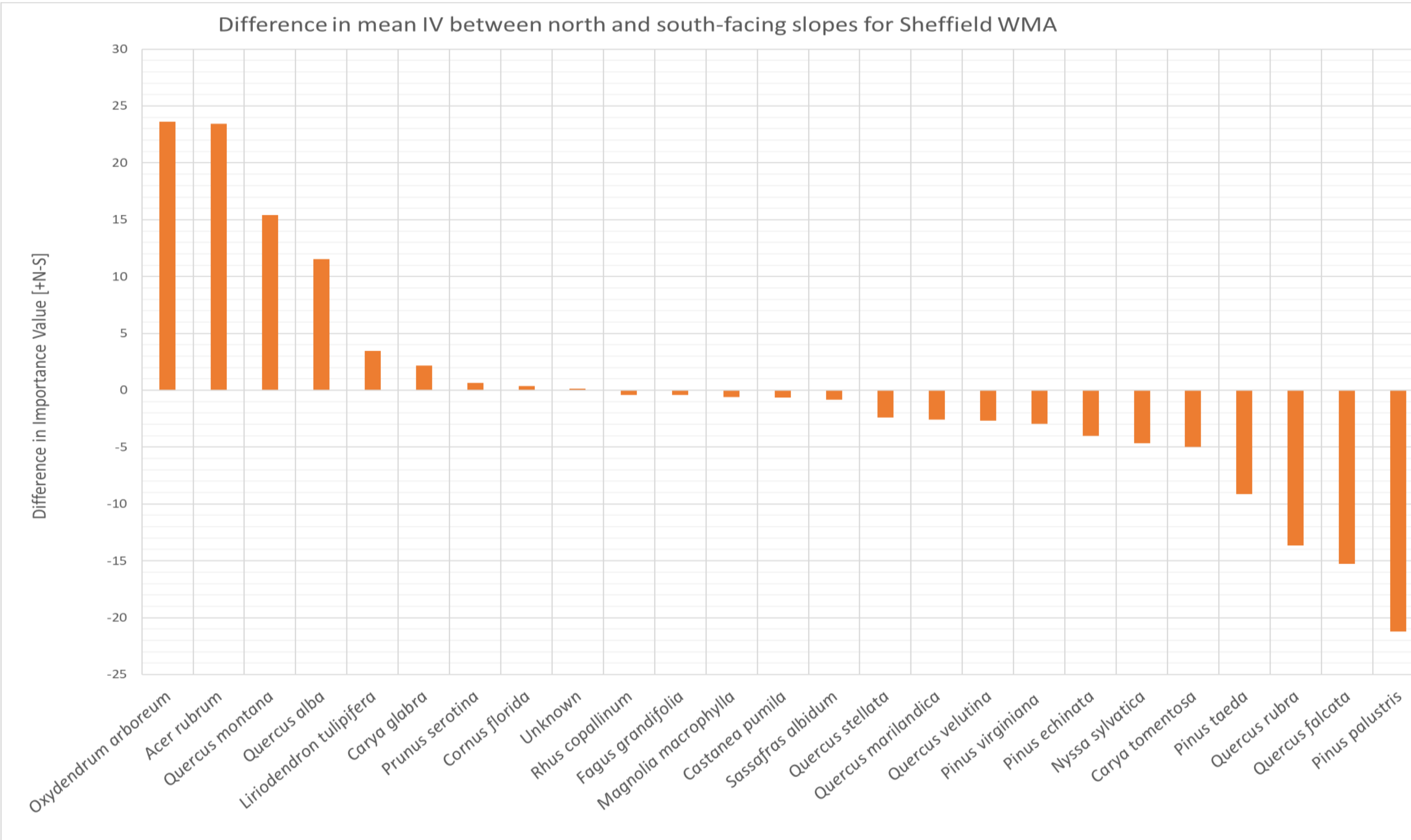

Figure 9: The difference in mean within-plot IV between north and south-facing slopes for Sheffield WMA. Positive values indicate higher importance on north-facing slopes and negative values indicate higher importance on south-facing slopes. There is a general trend of mesic and fire-intolerant species exhibiting higher importance on north-facing slopes, while xeric and pyrophilic species tend to have higher importance on south-facing slopes. Most of the differences between species importance by slope aspect were found to be insignificant.

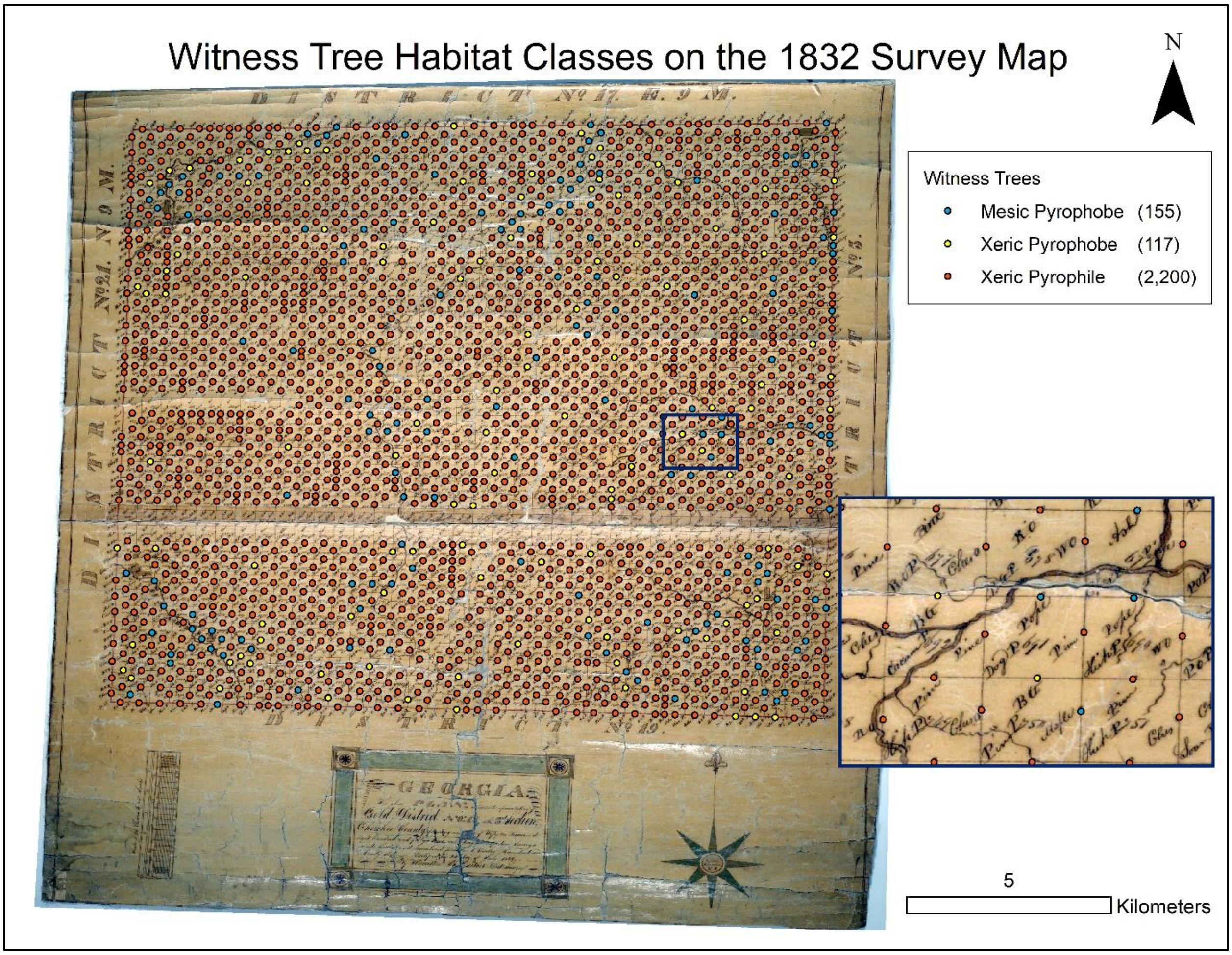

Figure 10: A map showing witness tree points in reference to their positions on the historic survey map. Some points were not used due to worn spots or tears in the map. Interestingly, Mesic pyrophobes (blue points) and xeric pyrophobes (yellow points) appear to occur mostly along the major streams, while xeric pyrophiles (orange points) occur throughout the map.

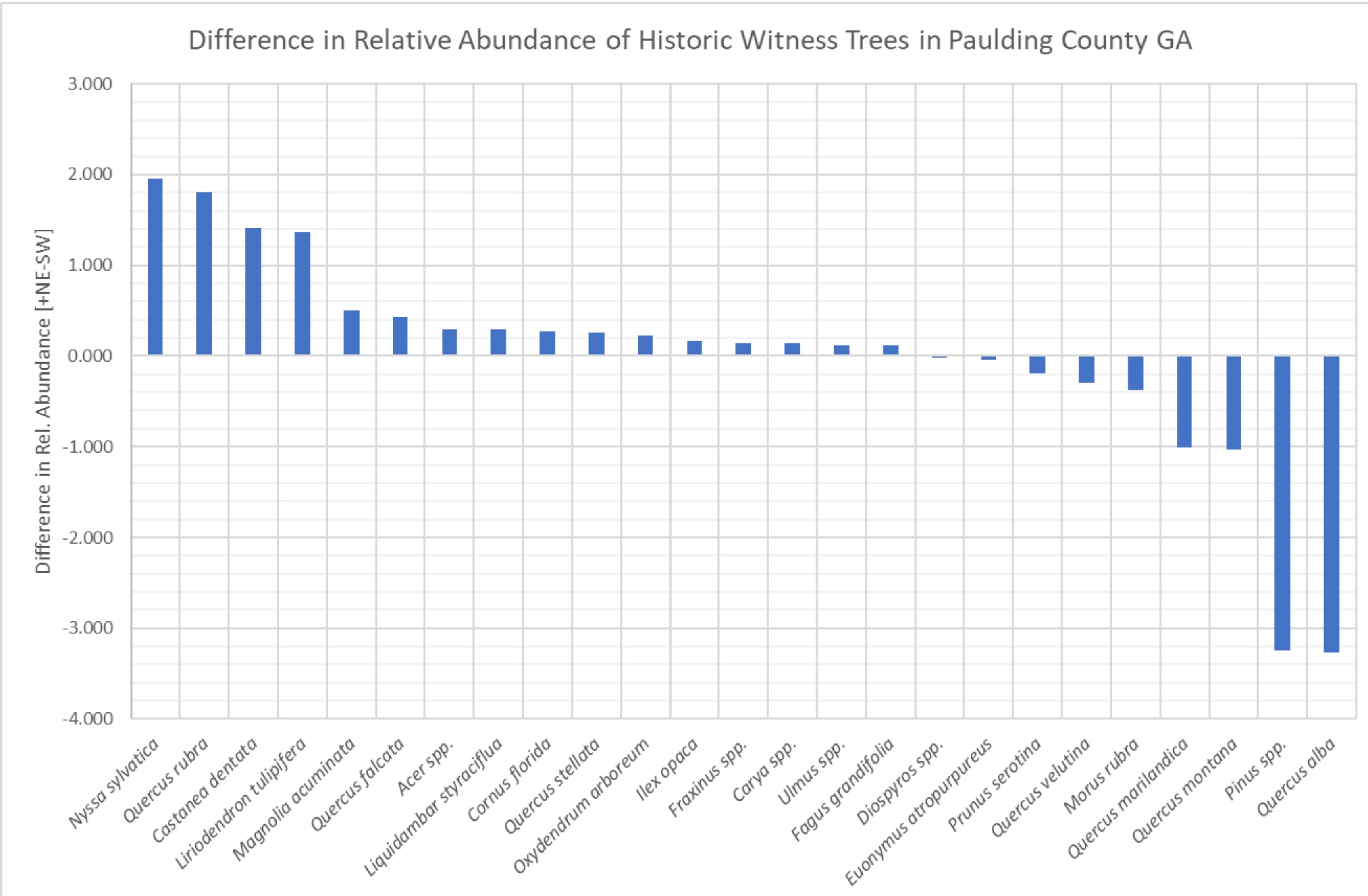

Figure 11: Difference in relative abundance of historical witness trees on northeast (NE) and southwest (SW) facing slopes. Differences were calculated as +NE-SW.

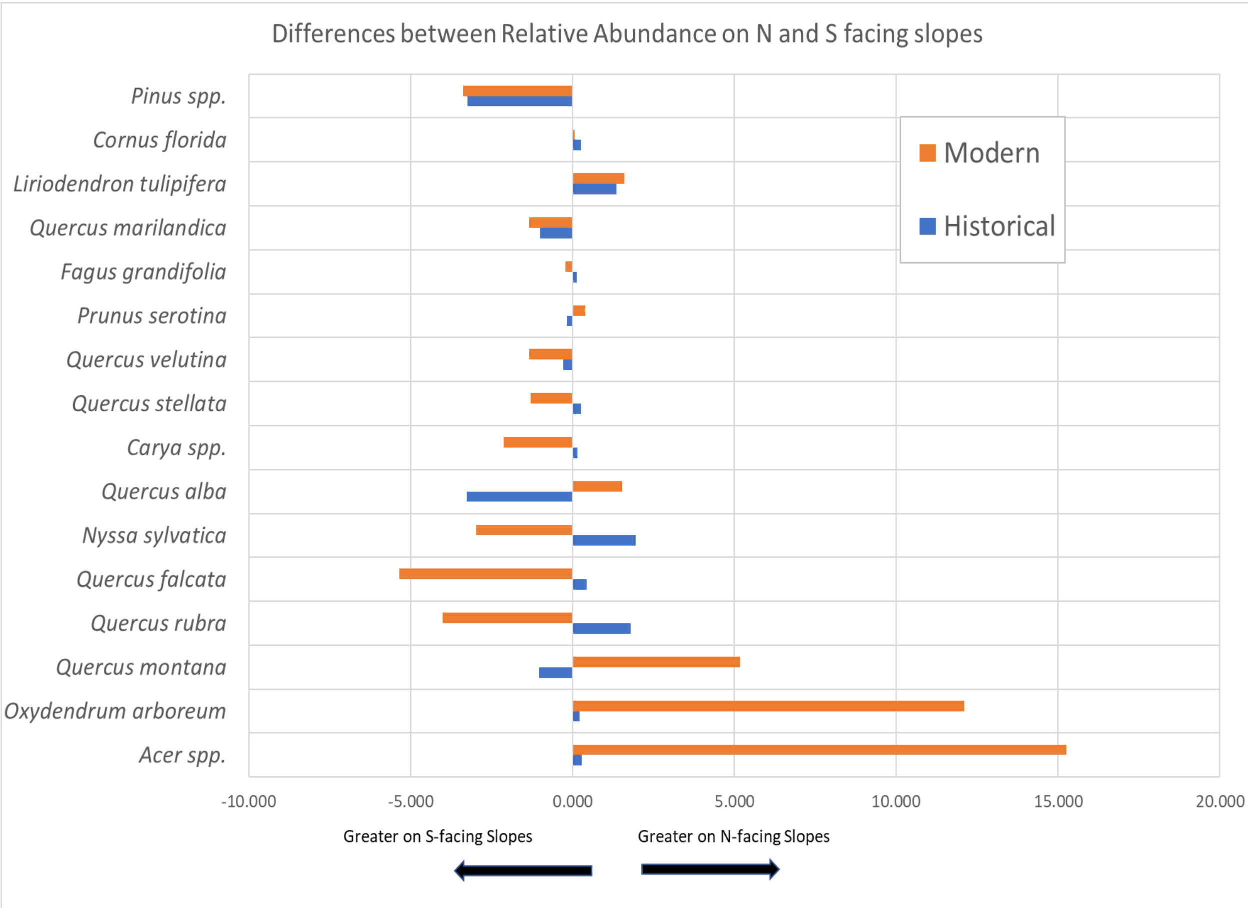

Figure 12: The difference in relative abundance between north and south-facing slopes from the historic and modern vegetation surveys. Species are ordered by the change in difference from the historic data to the modern data.