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Retrieving historical forest composition in the southern Appalachian region, United States

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A R T I C L E I N F O

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A B S T R A C T

Euro-American settlement entailed comprehensive vegetation clearing and fire exclusion, with attendant decreases in fire-tolerant oak and pine tree species and open conditions throughout the southeastern and central eastern United States. While historical tree data are locked in individual land deeds for part of the eastern United States, two assessments during 1900–1909 provided historical tree composition in the southern Appalachian region, primarily in North Carolina. According to assessments during 1900–1909, fire-tolerant oaks and American chestnut (*Castanea dentata*) were the dominant species, at about 62 % of all trees for both overlapping study extents. One century later, in current tree surveys, chestnut is no longer functionally present, due to chestnut blight (*Cryphonectria parasitica*), and oaks have decreased to 27 % of all trees, with chestnut oak (*Quercus montana*) the most abundant oak at 12 % of all trees. Red maple (*Acer rubrum*) became the most abundant species (15 % of all trees), with maples increasing from 2.5 % to 17 % of all trees. After red maple and chestnut oak, yellow-poplar (*Liriodendron tulipifera*) and sourwood (*Oxydendrum arboretum*) were the third and fourth most abundant species currently, followed by eastern white pine. Eastern white pine (*Pinus strobus*; 6.5 % of all current trees) drove the increase in the proportion of pines from 4 % (about 2 % white pines) historically to 11 % in southern Appalachian forests. Despite small fire compartments in mountainous terrain, the historical assessments documented an active fire culture, with evidence of light fire throughout 80 % of the study extent. Frequent surface fire was excluded in the region through land use and an anti-fire campaign, ensuing from national legislation during 1911. Many disturbance factors, such as chestnut blight that resulted in loss of American chestnut, influenced the rate of change by removing historically dominant species, while also modulating fire dynamics and current tree composition. The southern Appalachian region conformed to the same progression from fire-tolerant tree species to fire-sensitive tree species since Euro-American settlement and fire exclusion as most other upland regions in the eastern U.S.

1. Introduction

Tree harvest and land clearing for agriculture were among the first land use changes following Euro-American settlement in the United States. Cutting started slowly along the Atlantic Coast from Massachusetts to Virginia and expanded rapidly during the late 1860s, after the American Civil War, resulting from advancements in steam-powered technology, population growth, and westward settlement (Williams, 1989). Only 20–25 % of wood from felled trees was harvested with the remainder left as timber slash, whereas trees cleared for agricultural fields often were burned (Fernow, 1902:41–45; Ayres and Ashe, 1905; Wilson, 1908). Although efficiencies developed to reduce waste, the rate of harvest increased annually during 1850–1900, with lumber production outstripping population growth (Fernow, 1902:476–480). Indeed, this era may have had the greatest per capita wood harvest, as industrial innovation met vast forest resources consisting of large diameter trees that were hundreds of years old (Fernow, 1902; Williams, 1989).

Due to intensive tree harvest, with timber being cut faster than tree growth rates, foresters and conservationists of the time encouraged sustainability to meet the needs of future generations through establishment of forest reserves (Fernow, 1902; Holmes, 1911). Lumber extraction first decreased in the central and northern states in the eastern half of the eastern U.S., with original forests confined to mountainous, inaccessible locations, including the southern

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Appalachian Mountains from Pennsylvania south into Georgia and Alabama (Defebaugh, 1906). Fernow (1902:15–52) advocated for guarding current and future social interests through forest protection, rather than passing responsibility to future generations to recover loss of wood capital. The Forest Reserve Act of 1891 and the Sundry Civil Appropriations Act of 1897 were the first pieces of legislation to establish national forest reserves and management for ensuring a continuous supply of timber while protecting resources (Williams, 2005). The U.S. Geological Survey was funded to map forest reserves, whereas the U.S. Department of the Interior General Land Office was authorized to manage reserves until 1905, when management was transferred to the newly established U.S. Department of Agriculture, Forest Service agency (Ayres and Ashe, 1905; Holmes, 1911; Williams, 2005).

To ensure sustainable timber production, prevent soil erosion, and protect watersheds, forest reserves were purchased, accompanied by an anti-fire campaign, funded by the Weeks Act of 1911 (Holmes, 1911; Mastran and Lowerre, 1983). Deliberate burning was a long-standing cultural method of land management practiced by Indigenous peoples and Euro-Americans, in the southern Appalachian region, extending into the southeastern U.S., which still had a fire culture to clear small trees and encourage herbaceous growth for livestock rather than organized fire protection and forest fire laws (Sargent, 1884; Spillers and Eldredge, 1943; Mastran and Lowerre, 1983; Van Lear and Waldrop, 1989; Colenbaugh and Hagan, 2023). Ayres and Ashe (1905; as part of U.S. Geological Survey) surveyed 2.2 million ha during 1900 and 1901 in the southern Appalachian region (Fig. 1), with the objective of land purchase for forest reserves. Evidence of light surface fires covered approximately 1.8 million ha, or 80 % of the examined area, while 31, 500 ha had recent burns severe enough to kill the greater portion of the timber (Ayres and Ashe, 1905). In regards to open range grazing and fire, Ayres and Ashe (1905:23) noted that 'thorough protection against fire would be necessary were grazing stopped, for the accumulated vegetation would furnish a dangerous amount of fuel.' The first eastern National Forest, the Pisgah, was established during 1916 in western North Carolina, followed by purchase units that ultimately formed Nantahala, Cherokee, Chattahoochee-Oconee, and George Washington and Jefferson National Forests in this southern Appalachian region (Fig. 2; Mastran and Lowerre, 1983). To discourage intentional ignitions for tree density management, education and outreach developed through lectures, moving pictures, literature, community engagement, and employment of local residents (Mastran and Lowerre, 1983). Active fire suppression occurred through infrastructure of firefighters, fire towers, and trails, and fire protection programs and legislation (Holmes, 1911; Mastran and Lowerre, 1983).

Forest protection efforts were instituted to directly counter effects of reduced tree densities caused by fire (Holmes, 1911; Cruikshank, 1943). Fencing laws also addressed open range livestock (Haasis, 1926). Holmes (1911) found that the practice of burning the woods to improve range, by removing young trees in favor of an herbaceous plants in the understory, was worse than direct damage to young trees by livestock. The cause and effect of fire application and fire suppression was well-documented in United States Geological Survey and Forest Service reports (Ayres and Ashe, 1905; Holmes, 1911; Cruikshank, 1943). For example, Cruikshank (1943:13) summarized the before and after effects of fire protection, related to livestock: 'The damage [from oversaturation by livestock] was augmented by forest fires, set for the dual purpose of destroying the underbrush and encouraging the development of grass… With more effective Federal and State fire protection, the underbrush and young second growth in the hardwood stands restocked the land so thickly that administration of commercial herds became increasingly difficult.' Protection of young tree growth included the realization of increases by fire-sensitive tree species, such as valuable yellow-poplar and various pine species, which were different than the dominant fire-tolerant oak and pine species (Holmes, 1911; Cruikshank, 1943).

Fire exclusion was a gradual process, with declines in area burned

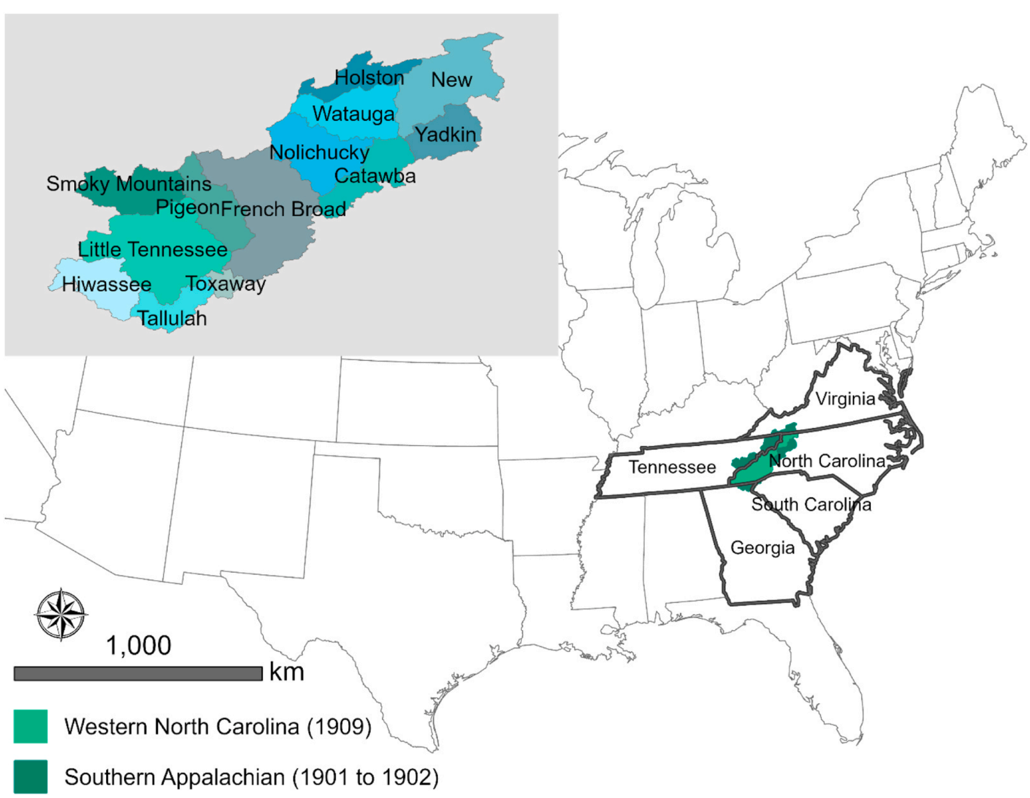

Fig. 1. The two overlapping southern Appalachian and western North Carolina study extents, which were assessed during 1900–1901 and 1909, respectively. Watersheds, rather than counties, were the assessment units in the southern Appalachians study extent (inset panel).

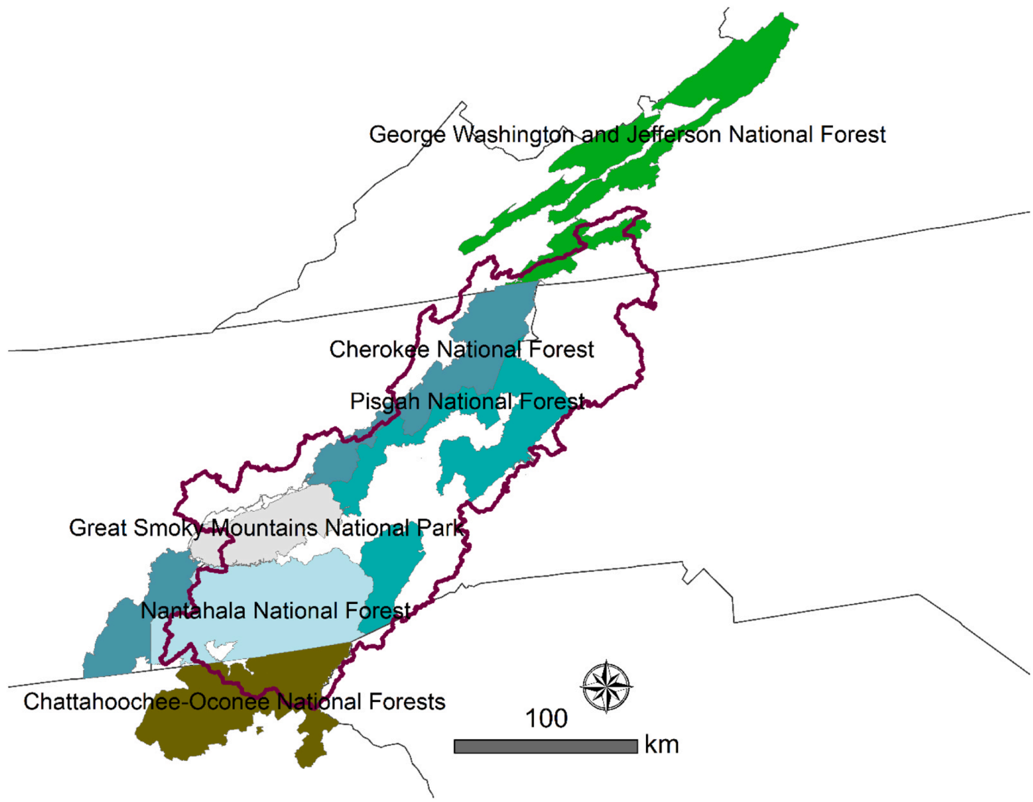

Fig. 2. Public lands cover most of this region, which contains most or all of the Cherokee, Nantahala, and Pisgah National Forests and the Great Smoky Mountains National Park, along with part of the Chattahoochee and Oconee National Forest and the George Washington and Jefferson National Forest.

annually and concomitant increases in tree densities (Cruikshank, 1943; Spillers and Eldredge, 1943; Larson, 1956). Fire exclusion originated from land use change, of roads and agricultural fields, that prevented the spread of fire, followed by management change from active fire ignition to active fire suppression (Hanberry 2021a; Mastran and Lowerre, 1983). Decreasing annual burned area resulted in increasingly greater survival of young trees in the undergrowth, including a large proportion of young second-growth trees in the Appalachian region during the decades after initiation of active fire suppression (Cruikshank, 1943; Spillers and Eldredge, 1943; Larson, 1956). Notable forest cover in the understory already had developed by 1920 arising from initiation of active fire suppression efforts (Wilson, 1908; Mastran and Lowerre, 1983). Due to the national forestland area in the Appalachian region, fire protection was nearly complete by 1938 in western North Carolina but less so in the mountains of Georgia, at 55 % of area with fire protection (Cruikshank, 1943; Spillers and Eldredge, 1943). In the absence of frequent surface fires, other factors such as disturbances that removed dominant plants accelerated the rate of replacement by fire-sensitive tree species (i.e., succession) in the uplands, where frequent surface fires occurred prior to fire exclusion (Woods and Shanks, 1959). For example, most chestnut trees died within a few years after 1920, after the chestnut blight (*Cryphonectria parasitica*) entered the southern Appalachian region (Cruikshank, 1943). Although loss of chestnut trees played a role in increasing the rate of change, by making space available for other tree species, chestnut tree absence did not determine which species were available to replace chestnuts (Woods and Shanks, 1959). That is, chestnut tree absence did not influence whether fire-tolerant species or fire-sensitive species would survive in the understory and recruit into the overstory, because this depended on whether fire occurred to remove fire-sensitive tree species from fire-exposed locations, albeit chestnut leaf litter facilitates fire (i.e., a synergistic interaction; Kane et al., 2019; Arthur et al., 2021). Ultimately, open and closed woodlands comprised of fire-tolerant oak and pine species, with an herbaceous understory, transitioned to dense, closed forests of diverse tree species in the southern Appalachian region and throughout the southeastern and central eastern United States (Bragg et al., 2020; Hanberry 2021b).

Research on historical forests in the southern Appalachian region has been hindered by inaccessibility of tree data located in ownership deeds (Rhoades and Park, 2001). To fill a notable knowledge gap about historical forests in this region (Lafon et al., 2017), our objective was to reconstruct tree composition of the southern Appalachian region circa 1900–1909, in contrast to current tree composition, followed by consideration of how other factors than fire, such as grazing levels and the potential of sampling in different locations within the study extent, may influence measured changes in composition. We used two assessments of forest conditions in overlapping study extents: 2.2 million ha for the southern Appalachian study extent (Ayres and Ashe, 1905; as part of U.S. Geological Survey) and 1.7 million ha for the Western North Carolina study extent, contained within the broader southern Appalachian study extent (Fig. 1; Holmes, 1911; as part of U.S. Forest Service). The retrieved information increases accessibility to historical conditions for public lands that cover most of this region, which contains most or all of the Cherokee, Nantahala, and Pisgah National Forests and the Great Smoky Mountains National Park, along with part of the Chattahoochee and Oconee National Forests and the George Washington and Jefferson National Forests (Fig. 2).

2. Methods

2.1. Two overlapping study extents

The broader southern Appalachian study extent (Fig. 1) was assessed by Ayres and Ashe (1905) by 15 watersheds (mean = 144,000 ha; median = 129,000 ha) during 1900 and 1901 with the objective of purchasing land for forest reserves. The 2.6 million ha area, with 2.2 million ha examined, primarily in North Carolina, extended from southern Virginia to northern Georgia. Oak species (*Quercus alba, Q. falcata, Q. montana*, and *Q. rubra*) were by far the most abundant, with chestnut next in abundance at 17 % of all trees (Ayres and Ashe, 1905). At the time in the region, the population was 318,000 and 25 % of the land had been cleared, with farming or field abandonment in the low elevations. Transportation networks consisted of 700 km of railroad and 8000 km of poor wagon roads, which sometimes were impassable. For lumbering, forests were protected by the difficulty of access, but high-grading of the most valuable trees had started recently (Ayres and Ashe, 1905). Trees had been cut for land clearing and used locally for fuel and building supplies, rather than exported to commercial markets.

The western North Carolina study extent, a 1.7 million ha study extent contained within the broader southern Appalachian study area, was assessed during 1909, for each of 16 counties (county mean and median area about 105,000 ha; Fig. 1; Holmes, 1911). By this date, Holmes (1911:109) stated that despite high-grading to comparatively small timber, large parts of seven counties bordering Tennessee contained almost unbroken forest. Accessibility of timber largely determined whether harvest was profitable when considering transport. The fire-protected mountain coves or lowlands were most accessible and cleared for agriculture and culled of their best and most abundant trees, such as American chestnut (*Castanea dentata*), yellow-poplar (*Liriodendron tulipifera*), and some oak species (Holmes, 1911:22). In fire-exposed flat uplands, away from rivers, forests dominated by white oak (*Quercus alba*) and American chestnut had been cut due to accessibility of merchantable timber (Holmes, 1911:20). Eastern hemlock (*Tsuga canadensis*), located along higher elevation streams and northern slopes, had been harvested in the past for bark tannins (Ayres and Ashe, 1905; Holmes, 1911). At higher elevations, forests of the red oak group, American beech (*Fagus grandifolia*)-sugar maple (*Acer saccharum*) forests, and spruce forests generally remained intact (Ayres and Ashe, 1905; Holmes, 1911).

2.2. *Extraction of reporting units of watersheds or counties for study extents*

We located historical study extents with the aid of historical county boundaries (Manson et al., 2022), although most county boundaries were stable, and watersheds (USGS, 2023), which was the reporting unit for the broader southern Appalachian extent. To locate watersheds for the southern Appalachian extent, we used modern hydrological units, which at the HUC10 scale (USGS, 2023) largely corresponded to area in historical watersheds (Ayres and Ashe, 1905). We selected all counties listed for each historical watershed and then all HUC10 watersheds primarily within the counties. Then, we retained contiguous watersheds, still containing the counties, and removed any exterior watersheds if possible. This did result in a slightly wider extent, representing 2.9 million ha as opposed to 2.6 million ha, and we were not able to locate adjacency for the very small watersheds of Saluda River and First and Second Broad River basins. For the western North Carolina extent (Holmes, 1911), we selected counties by historical boundaries.

2.3. *Corroborating tree species or genera percentages*

Tree composition was reported by standing volume, by watershed in the broader southern Appalachian extent (Ayres and Ashe, 1905) or county for the western North Carolina extent (Holmes, 1911), but we simply considered the tree measurements as generally representative of the old-growth forests, and compared percentages by volume of tree species to percentages of number of trees for tree species in current forests. To help establish this approach of comparing percentages by volume to percentages by number, we compared tree species percentages from standing volume to tree species percentages for 2400 tree records in Rabun County, Georgia, where historical land lottery surveys occurred during 1820 (reported by tree species percentages; Plummer, 1975). Rabun County overlapped with the southern Appalachian study extent in the lower elevation of the Tallulah and Chattooga River basin.

2.4. *Current surveys*

The USDA Forest Service Forest Inventory and Analysis surveys (FIA; FIA DataMart 2021; Bechtold et al., 2025) quantify current forest conditions. The FIA plots occur every 2400 ha, supplying landscape scale estimates, and are surveyed on five- to seven-year cycles, varying by state. We limited composition to plots that intersected the combined southern Appalachian and western North Carolina extents, resulting in about 29,300 trees ($\geq$ 12.7 cm in diameter) on 1168 plots, surveyed during 2009–2016. Composition was based on number of trees per species relative to all trees, as a percentage.

2.5. *Similarity of surveys*

In addition to contrasting change in composition between historical and current surveys, we calculated the squared-chord distance metric between surveys (squared-chord distance $= \sum(\sqrt{P_i} - \sqrt{Q_i})^2$; where i is the ith percentage of tree groups in the two different sources, of Q and P; package philentropy; Drost, 2018; R Core Team, 2024). Historical and modern forests that differ in composition tend to have squared-chord distance ≥ 0.15, and given that thresholds divide continuous data, values between 0.12 and 0.15 indicate divergence (Overpeck et al., 1985). Due to loss of American chestnut from chestnut blight disease, we removed American chestnut from the comparisons.

3. Results

To validate application of tree percentages by volume from the assessments, we compared between the tree percentages during 1900 in the Tallulah and Chattooga River basin of the broader southern Appalachian study extent (Ayres and Ashe, 1905) and historical tree percentages during 1820 in the overlapping Rabun County. In the Tallulah and Chattooga River basin during 1900, the primary tree species were 55 % oaks, 10 % American chestnut, 7 % pines, and 7 % hickories. Similarly, in Rabun County during 1820, the primary species were 53 % oaks, 13 % chestnut, 14 % pines, and 8 % hickories. Considering that Rabun County did not contain the higher elevations of the Tallulah and Chattooga River basin and Rabun County was lacking an eastern hemlock (*Tsuga canadensis*) component that was 5 % of all trees in the Tallulah and Chattooga River basin, the predominant forest composition was similar in these areas, with a squared-chord distance of 0.065.

The broader southern Appalachian and western North Carolina study extents from the assessments also had relatively similar tree percentages (Table 1), as evidenced by a squared-chord distance of 0.069. While proportions differed, the combined percentage of oaks and American chestnut was 61–63 % of all trees for both study extents. Yellow-poplar was much more abundantly recorded in the western Carolina extent, at 8.5 % of all trees as opposed to 1.6 % of all trees in the southern Appalachian extent.

For the contrast to current tree surveys (Table 1), both historical studies had squared-chord distances of 0.157, or dissimilarities, with current surveys, despite removal of American chestnut data from comparisons because American chestnut was extirpated due to disease. In addition to loss of American chestnut, due to chestnut blight, oaks declined to 25 % of all trees in current surveys, with the most abundant oak species, chestnut oak, the second most common species at 12 % of all trees. Red maple became the most abundant species, at 15 % of all trees, increasing from an historical maple percentage of 2.5 %, which primarily was sugar maple in late-successional beech-maple forests. Pines, currently represented by eastern white pine (6.5 % of all current trees), increased from about 4 % of all trees to 11 % of all trees. Historically, white pines, such as eastern white pine, were about as common (i.e., 2 % of all trees) as yellow pines, consisting of predominantly pitch

Table 1
Percentage and rank of tree species or genera in the southern Appalachian (Southern App) study extent during 1900 and 1901, western North Carolina (North Carolina) study extent during 1909, and in the combined study extents currently, with any current species > 2 % within genera.

		Southern App		North Carolina		Current		Current species	
Genus or species	Name	%	Rank	%	Rank	%	Rank	Species	%
Quercus	oak	43.2	1	35.3	1	25.3	1		
								Q. montana	11.9
								Q. coccinea	4.7
								Q. rubra	4.2
								Q. alba	2.8
Castanea dentata	American chestnut	17.4	2	27.8	2	0.0	18		
Tsuga canadensis	eastern hemlock	4.9	3	7.7	4	3.7	7		
Pinus	pine	4.8	4	3.6	5	10.7	3		
								P. strobus	6.6
Carya	hickory	3.2	5	2.1	8	3.6	8		
								C. glabra	2.2
Betula	birch	2.8	6	1.0	13.5	6.9	6		
								B. lenta	5.0
								B. alleghaniensis	2.1
Acer	maple	2.6	7	2.6	6	16.8	2		
								A. rubrum	15.2
Tilia americana	American basswood	2.5	8	2.3	7	0.7	15		
Nyssa sylvatica	blackgum	1.8	9	0.4	16	2.4	9		
Aesculus flava	yellow buckeye	1.7	10	1.3	12	0.5	16		
Liriodendron tulipifera	yellow-poplar	1.6	11	8.5	3	9.1	4		
Fraxinus	ash	1.3	12	1.4	11	0.8	14		
Fagus grandifolia	American beech	1.0	13	1.6	10	1.4	11		
Magnolia	magnolia	0.8	14	0.7	15	2.2	10		
Picea rubens	red spruce	0.7	15	1.7	9	1.2	13		
Robinia pseudoacacia	black locust	0.7	16	0.1	17.5	1.3	12		
Oxydendrum arboreum	sourwood	0.1	17.5	0.1	17.5	7.9	5		
Abies fraseri	Fraser fir	0.1	17.5	1.0	13.5	0.4	17		

pine (*Pinus rigida*) and shortleaf pine (*Pinus echinata*). In current surveys these two pine species remained at 1.5 % of all trees, combined. Yellow-poplar and sourwood became the third and fourth most abundant species, at 9 % and 8 % of all trees, respectively.

4. Discussion

4.1. Key findings

Historical tree data are locked in individual land deeds for part of the eastern United States, but forest assessments during the first decade of the 1900s can supply missing information of quantified tree composition, particularly in mountains that were the last locations to be cleared of original forests. Tree species composition was recorded in the southern Appalachian region, within two overlapping study extents during the first decade of the 1900s, which occurred prior to initiation of federal fire suppression policy and extensive timber harvest, due to inaccessibility of timber in the mountains (Ayres and Ashe, 1905; Holmes, 1911). The two assessments helped illustrate the historical dominance by fire-tolerant oaks and American chestnut (61–63 % of all trees), with 80 % of area mapped that had evidence of recent surface fires (Ayres and Ashe, 1905; Holmes, 1911). The assessments described frequent fire that kept small diameter woody sprouts and seedlings in check and, in consequence, controlled overstory and midstory densities, particularly of fire-sensitive species (Ayres and Ashe, 1905; Holmes, 1911). Composition has become dissimilar after fire exclusion and harvest, as red maple specifically has increased, along with sourwood, yellow-poplar, and eastern white pine, with consequent decreases in percentage of oaks. American chestnut was extirpated rapidly after entry of chestnut blight into the southern Appalachian region during 1920 (Cruikshank, 1943). These historical assessments of the early 1900s, while later than General Land Office surveys conducted during the 1800s and the onset of fire exclusion due to land use change, supply another line of evidence that supports historical upland dominance by fire-tolerant tree species across the southern Appalachian region and the central eastern and southeastern U.S. in general, with attendant increases in fire-sensitive tree species after fire exclusion, excepting the northern parts of the northernmost states (Hanberry et al., 2013; Hanberry et al., 2019; Bragg et al., 2020).

Findings of oak dominance under frequent burning followed by establishment of fire-sensitive tree species under fire exclusion also aligned with other studies in the region (Flatley et al., 2015; Lafon et al., 2017). Harrod et al. (1998) completed a chronosequence between 1936–1995 in xeric forests with exposure to historical fires, not the protected coves, in the western Great Smoky Mountains National Park. During the 1930s, mean canopy density, basal area, and richness were low, relative to later fire-suppressed sites, but increased rapidly during the first few decades of fire exclusion and then remained nearly constant between the 1970s and 1995. During this interval, the relative density of other species, prominently red maple and eastern white pine, increased at the expense of oaks, which decreased from 40 % to 27 % of canopy trees. These values almost perfectly corresponded to values from the southern Appalachian study extent, for which oaks decreased from 43 % to 27 % of all trees. Similarly, during 1938 in North Carolina, the upland hardwood type, or typical forest cover in the Appalachian region, was estimated as 20 % red oaks (i.e., Erythrobalanus), 22 % white oaks (Leucobalanus), and 21 % (dead) chestnut, not very different than the 1900–1901 estimates for the broader southern Appalachian extent (Ayres and Ashe, 1905; Cruikshank, 1943). During 1982–1984 inventories of North Carolina, which was relatively pine-dominated outside of the Appalachian region, yellow-poplar became the single most abundant broadleaf tree species, with concurrent increases in eastern white pine and red maple (Ashe, 1897; Sheffield and Knight, 1986). Additionally, the sequence of rapid tree densification, and expansion, within decades after fire exclusion has been reported for this region and surroundings (Ashe, 1897; Moore, 1910; Flatley et al., 2015; Lafon et al., 2017). The change in composition was delayed proportionally to the percentage of fire-tolerant tree species already present, but eventually fire-tolerant tree species were out-competed by colonizing species when under different land use and disturbance filters (Flatley et al., 2015).

Even though densities of forests dominated by oaks and American chestnuts under frequent fire regimes were not quantified in the historical assessments, qualitative descriptions were that repeated fires, due to continued control of the young tree growth but not larger diameter trees, had greatly reduced tree densities to open woods, although a range of densities occurred along a gradient from fire-exposed locations to fire-protected locations in the lowlands (e.g., cove forests; Ayres and Ashe, 1905:18, 181). Ayres and Ashe (1905) uniquely described second growth and undergrowth in 190 subdivisions of 14 watersheds. In locations where fires had been skipped during the past several years, and forests also high-graded, sprouts of oaks and sourwood occurred along with seedlings from other species, with thick establishment of white pine in old fields, which Holmes (1911) also noted. While the lack of sourwood in the historical assessments may represent bias against a smaller tree species that was less merchantable, Ayres and Ashe (1905:124) detailed abundant sourwood in the second growth and undergrowth notes, due to plentiful regeneration, rather than itemized as timber trees, with notes such as 'Second growth consists largely of scrub pine [*P. virginiana*, Virginia pine] associated with black [*P. rigida*, pitch pine] and white pines, and sourwood and chestnut sprouts…. Sourwood forms the undergrowth to a large extent in badly burned woods; *Kalmia* is occasionally found.' Dense laurel (*Rhododendron*) typically grew along streams and on the north slopes. Generally, the presence of a surface fire regime (as documented by Ayres and Ashe, 1905), which controls tree seedlings, in conjunction with a high percentage of fire-tolerant tree species, such as oak and pine species, American chestnut, and to a lesser extent, hickories, indicated that overstory and understory tree densities were less than without fire (Ayres and Ashe, 1905; Harrod et al., 2000). Furthermore, herbaceous groundcover, due to regular fire, provided enough forage to sustain livestock, until fire protection increased tree stocking (Cruikshank, 1943)

In addition to sourwood, other tree species became dominant during the past century. Maple species comprised just 2.5 % of historical trees. Holmes (1911:26) stated that both sugar maple and red maple were minor in abundance and commercial value ('unimportant'), but sugar maple was a component of mesic forests in coves and cooler slope aspects, along with American beech due to their similar success as late-successional species. Sugar maple represented a greater percentage of the historical landscape than red maple (Ayres and Ashe, 1905). Holmes (1911:26) furthermore observed of red maple that: 'Sprouts and seedlings are abundant, and, owing to their vitality, form a large portion of the young growth where fires kill off other trees.' This observation demonstrated the current difficulty of controlling red maple with low severity fires. Similar to red maple, white pine increased from about 2 % of all trees historicall to about 6.5 % of all trees currently, in part because white pine reproduces well in old fields and unburned woods, with rapid growth of young trees (Ayres and Ashe, 1905; Holmes, 1911), which results in success under fire exclusion and land use. The historical composition of yellow-poplar was unclear, due to an estimate of 1.5 % of all trees from Ayres and Ashe (1905) and 8.5 % from Holmes (1911). Yellow-poplar was harvested through some limited high-grading, at the time of the assessments, and cleared for agricultural land use, but so were other tree species, such as oaks and chestnut (Ayres and Ashe, 1905). Yellow-poplar may have been more concentrated in the North Carolina study extent (Ayres and Ashe, 1905). Yellow-poplar also may have been overestimated by Holmes (1911) and underestimated by Ayres and Ashe (1905). Yellow-poplar likely has increased, following fire exclusion, given fire-sensitivity of this species and increased yellow-poplar currently in the southeastern U.S. compared to abundance in historical General Land Office surveys (Hanberry et al., 2019), or even increased yellow-poplar detected in modern forest inventories (Sheffield and Knight, 1986).

Fire typically creates greater contrasts in vegetation types than contrasts under fire exclusion (Hanberry et al., 2013; Flatley et al., 2015; Hanberry 2021b). In mountainous areas, fires amplify zonal patterns based on elevation and aspect, due to correspondence with a gradient of protection to exposure in fire frequency (Flatley et al., 2015). Barriers to fire ignition and spread such as rough topographies, cooler temperatures at higher elevations and north-facing aspects, and stream valleys effectively dissected the mountains into smaller fire compartments, resulting in less frequent fires than flatter topographies (Frost, 1998; Lafon et al., 2017). However, fire burned frequently in the Appalachian region before fire exclusion (Van Lear and Waldrop, 1989; Harmon, 1982; Harrod et al., 2000; Fesenmyer and Christensen, 2010; Van Lear and Waldrop, 1989; Lafon et al., 2017; Arthur et al., 2021). Fire compartments were large enough to enclose entire mountainsides, and spotting of embers allowed fires to cross into adjacent fire compartments (Lafon et al., 2017). Indeed, Flatley et al. (2015) detected increased tree recruitment and decreased oak percentage since the onset of fire exclusion even in protected cove sites, indicating that fires previously had maintained more open conditions. Without fire, tree species that were limited to coves and bottomlands, stream sides, and high elevation northern slopes protected from fire were able to expand into areas that had frequent fire historically (Flatley et al., 2015).

4.2. Considering potential non-fire influences on before and after comparisons

Numerous ecological and anthropogenic factors may have influenced fire dynamics (i.e., dampening or facilitating fire via antagonistic and synergistic interactions), the rate of change from fire-tolerant to fire-sensitive tree species, and current composition of fire-sensitive species in the southern Appalachian region (i.e., successional replacement; Woods and Shanks, 1959; Kane et al., 2019; Hanberry et al., 2020; Arthur et al., 2021). Fire and fire exclusion offer a primary framework for interpreting the before and after comparisons of the shift from fire-tolerant tree species to fire-sensitive tree species (Hanberry et al., 2020; Arthur et al., 2021). Nonetheless, American chestnut and chestnut blight, herbivory by native herbivores and livestock, land use change, and climate variability likely interacted with fire dynamics to shape forest composition. For example, chestnut loss opened growing space to other tree species and the loss of flammable chestnut leaves made the forest floor less flammable (Kane et al., 2019; Arthur et al., 2021), accelerating transition to increased tree densities of diverse tree species after fire exclusion (Woods and Shanks, 1959). Transition in composition was delayed proportionally to the percentage of fire-tolerant tree species, which provided propagules and advance regeneration, present in forests (Flatley et al., 2015). Fire exclusion provided the necessary conditions for fire-sensitive species to expand, while other disturbances modulated the rate and trajectory of change.

In the presence of fire and varying browsing severity from the one remaining native large herbivore of the white-tailed deer (*Odocoileus virginianus*), fire-tolerant tree species dominated most of the uplands, with fire-sensitive tree species restricted to fire-protected sites in the Appalachian region of the southeastern U.S. (Ayres and Ashe, 1905; Holmes, 1911; Bragg et al., 2020; Hanberry and Faison, 2023). Despite initiation of active fire exclusion, the transition from oaks and chestnut to fire-sensitive species required several decades even with additional disturbances that acted synergistically with fire exclusion, including tree clearing, targeted harvesting of oak, agricultural cultivation, overgrazing, and the loss of American chestnut due to blight. Measurable changes from oak dominance to fire-sensitive species became evident during the 1970s and 1980s in the Appalachian region (Sheffield and Knight, 1986; Harrod et al., 1998). The counterfactual situations are not available of all potential drivers happening under continued frequent surface fires or alternatively, no potential drivers happening under fire exclusion. However, if these disturbances occurred with frequent surface fires, fire-sensitive tree species still would remain largely limited to fire-protected locations (Ayres and Ashe, 1905; Holmes, 1911). Even though commercial timber operations targeted specific species, including yellow-poplar and oak species (Holmes, 1911; Larson, 1956), fire-sensitive tree species can only survive and recruit into the overstory at great densities in most upland locations when fire is excluded. Indeed, if all the oak trees were logged, and advance regeneration removed, fire-sensitive tree species still will not survive frequent surface fires. If only fire exclusion had occurred without removal of vegetation, the progression would have been measured in tree generations, as the dominant trees slowly lost growing space to other tree species, rather than decades that reflected slow diminishment of annual area burned due to gradual fire exclusion combined with growing space opened by land disturbance (Woods and Shanks, 1959; Sheffield and Knight, 1986; Harrod et al., 1998).

Multiple other drivers such as climate change, loss of American chestnut to introduced chestnut blight (*Cryphonectria parasitica*), which entered the southern Appalachian region about 1920 and killed most chestnut trees within a few years (Cruikshank, 1943), and overabundance of white-tailed deer have been proposed as important drivers to increase tree densities of fire-sensitive species (McEwan et al., 2011). Unlike fire exclusion, climate was not outside of natural range of variation during the progression from open forests of fire-tolerant tree species to closed forests of diverse fire-sensitive tree species (Hanberry et al., 2020). The same progression ensued outside of the limited range of abundant American chestnut, which was never more dominant than oaks at landscape scales, and chestnut loss does not cause fire-sensitive species to withstand frequent surface fires (Hanberry et al., 2020). While chestnut was not a cause for whether fire-sensitive tree species were limited to locations protected by fire or not, disturbances that removed dominant fire-tolerant tree species, or herbaceous vegetation, will open up growing space and accelerate transition in species under fire exclusion (Woods and Shanks, 1959). Rather than overabundance, deer populations at the time were recovering from near extirpation, with lesser deer population densities and extirpation of the other wide-ranging large herbivores during the interval of transition (Hanberry et al., 2020; Hanberry and Faison, 2023). With the advent of humans and fire management to the North American continent, shortly followed by the extinction of numerous species of true megaherbivores, the influence of fire probably became primary, with secondary support by the few remaining megaherbivores (Hanberry and Faison, 2023; Pedersen et al., 2023). Offering a partial explanation for loss of control of small diameter tree densities, deer are native large herbivores that act as understory (i.e., limited in height relative to overstory trees) disturbances, interacting with surface fire, another understory disturbance, to help control small diameter tree densities, but herbivory preferences cannot explain historical dominance by fire-tolerant species and transition to fire-sensitive species (Hanberry and Abrams, 2019; Hanberry and Faison, 2023).

Regarding grazing levels and severity of herbivory, oversaturation by livestock can remove advance regeneration of the dominant oak and chestnut trees (i.e., 60 % of all trees during 1900–1909) and also herbaceous vegetation (Holmes, 1911; Frost and Harrold 2013). The Appalachian region was open range during the 1900–1909 assessments, with areas of overgrazing (Ayres and Ashe, 1905; Holmes, 1911). Currently (i.e., year 2013), about 10 % of the study extent was classified as pasture (Dewitz, 2023). However, during 1900–1909, fire still was administered to reduce tree densities, increasing forage for cattle (i.e., evidence for fire on 80 % of the study extent; Ayres and Ashe, 1905). After national public lands were purchased during the 1920s, and fire protection was enacted, public grazing also was restricted (Cruikshank, 1943). But after fire protection, young tree establishment in the absence of fire was so prolific that forage was not available, as forests closed in the understory, making forests unsuitable for cattle (Cruikshank, 1943). Tree regeneration superseded overgrazing. Grazing or browsing at a variety of different severity levels occurs with native large herbivores, as characteristics of natural disturbance regimes (Hanberry and Faison, 2023).

A possibility is that historical assessments measured different locations than current surveys. During 1900 and 1909, 25 % of the land had been cleared, with farming or field abandonment in the low elevations, because mountain regions are marginal for agricultural use (Ayres and Ashe, 1905; Holmes, 1911). Currently (i.e., year 2013), 0.3 % of the combined study extent was classified as cultivated crops (Dewitz, 2023). During 1900–1909, the non-agricultural area was forestland, estimated around 75 %, and currently, forests cover 78 % of the combined study extent (Ayres and Ashe, 1905; Holmes, 1911). This is remarkably consistent, although resulting from 60 % of the combined study extent as protected national public lands. Because agriculture occurred in the low, flat elevations, forests were located in rugged areas during the historical assessments (Ayres and Ashe, 1905). Currently, forests also were in the most rugged locations (i.e., greater than 500 mean ruggedness value whereas cultivated crops were located where mean ruggedness was 114, comparable to high intensity development in the region; Amatulli et al., 2020). The placement of surveys was similar between the two sampling periods, away from flat locations and with similar forest productivity and conditions, that is, not likely to favor a different subset of tree species.

When fire-tolerant species decrease as fire-sensitive species increase, fire exclusion is the most parsimonious explanation (Hanberry et al., 2020). Frequent surface fire is a direct mechanism to remove small diameter trees (Maxwell, 1910; Spillers and Eldredge, 1943). Indigeous stewards and early Euro-America settlers applied fire to manage rangelands and open forests for game animals (*Odocoileus virginianus*, *Cervus canadensis*, *Bison bison*) and livestock (Maxwell, 1910; Spillers and Eldredge, 1943). With frequent surface fire, fire-sensitive tree species were relegated to locations protected from fire such as coves and floodplains (Ayres and Ashe, 1905; Holmes, 1911; Cruikshank, 1943; Harrod et al., 1998; Arthur et al., 2021). Fire was applied in the past because fire was effective in reducing tree densities (Maxwell, 1910; Spillers and Eldredge, 1943). Likewise, fire protection practices were mandated to increase tree stocking, which was the expected response that was noted immediately after fire exclusion (Ayres and Ashe, 1905; Wilson, 1908; Cruikshank, 1943). Land management transfer from Native Americans, who applied fire to reduce tree densities, to Euro-Americans, who suppressed fire application to increase tree densities, directly resulted in increased tree densities and tree species diversity (Hanberry et al., 2020).

5. Conclusions

Historical land surveys from the 1800s or earlier are not available in the southern Appalachian region, yet historical tree assessments from the early 1900s fill in the gap to quantify historical forest composition before the major land use changes of tree removal and fire exclusion. Despite the inherently small fire compartments of mountainous terrain, fires were frequent enough to maintain historical dominance by oaks and American chestnut. Descriptions of the undergrowth indicated primarily open forests, with scant growth of young trees due to control by fires. The proportion of fire-sensitive tree species, particularly red maple and eastern white pine, has increased relative to fire-tolerant species since the onset of fire exclusion. While many modulating factors may have facilitated this progression by removing dominant, fire-tolerant tree species and shaping fire dynamics and current tree composition, frequent surface fires and subsequent exclusion provide a framework through which compositional shifts from fire-tolerant tree species to fire-sensitive tree species can be interpreted. The southern Appalachian region exhibited the same progression from fire-tolerant tree species to fire-sensitive tree species as most other upland regions in the eastern U. S., following Euro-American settlement and gradual fire exclusion.

CRediT authorship contribution statement

J. Adam Warwick: Writing – review & editing. **Hanberry Brice:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

All data sources are publicly available.

References

Amatulli, G., McInerney, D., Sethi, T., Strobl, P., Domisch, S., 2020. Geomorpho90m, empirical evaluation and accuracy assessment of global high-resolution geomorphometric layers. Sci. Data 7, 1–18.

Arthur, M.A., Varner, J.M., Lafon, C.W., Alexander, H.D., Dey, D.C., Harper, C.A., Horn, S.P., Hutchinson, T.F., Keyser, T.L., Lashley, M.A., Moorman, C.E., Schweitzer, C.J., 2021. Fire ecology and management in eastern broadleaf and Appalachian forests. In: Greenberg, C.H., Collins, B. (Eds.), Fire ecology and management: Past, present, and future of US forested ecosystems. Springer International Publishing, Cham, Switzerland, pp. 105–147.

Ashe, W.W.. 1897. Forests of North Carolina. M. I. & J. C. Stewart, Winston, North Carolina.

Ayres, H.B., Ashe, W.W., 1905. The southern Appalachian forests. Department of the Interior US Geological Survey, Washington, D.C.

Bechtold, W.A., Patterson, P.L., 2005–2025. The enhanced forest inventory and analysis program—national sampling design and estimation procedures. Usda forest service. Southern Research Station, Asheville, NC. https://doi.org/10.2737/SRS-GTR-80.

Bragg, D.C., Hanberry, B.B., Hutchinson, T.F., Jack, S.B., Kabrick, J.M., 2020. Silvicultural options for open forest management in eastern North America. For. Ecol. Manag. 474, 118383.

Colenbaugh, C., Hagan, D.L., 2023. After the fire: potential impacts of fire exclusion policies on historical cherokee culture in the Southern Appalachian mountains, USA. Hum. Ecol. 51 (2), 291–301.

R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria..

Cruikshank, J.W. 1943. North Carolina forest resources and industries. US Department of Agriculture Forest Service, Government Printing Office, Washington, D.C.

Defebaugh, J.E. 1906. History of the Lumber Industry of America. American Lumberman, Chicago, Illinois.

Dewitz, J., 2023. National land cover database (NLCD) 2021 products. U.S. Geological Survey data release. https://doi.org/10.5066/P9JZ7AO3.

Drost, H.G., 2018. Philentropy: information theory and distance quantification with R. J. Open Source Softw. 3 (26), 765.

Fernow, B.E., 1902. Economics of forestry: a reference book for students of political economy and professional and lay students of forestry. Crowell, New York, United States.

Fesenmyer, K.A., Christensen Jr, N.L., 2010. Reconstructing holocene fire history in a Southern Appalachian forest using soil charcoal. Ecology 91 (3), 662–670.

Flatley, W.T., Lafon, C.W., Grissino-Mayer, H.D., LaForest, L.B., 2015. Changing fire regimes and old-growth forest succession along a topographic gradient in the great smoky mountains. For. Ecol. Manag. 350, 96–106.

Frost, C.C., 1998. Presettlement fire frequency regimes of the United States: a first approximation. In fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecol. 20, 70–81.

Frost, C.C., Harrold, C., 2013. Historic fire regimes and presettlement vegetation of Big South Fork National Recreation Area, Tennessee & Kentucky. Report for the National Park Service, Oneida, Tennessee.

Haasis, F.W., 1926. The decreasing importance of forest grazing in the Southern Appalachian region. J. For. 24 (5), 533–534.

Hanberry, B.B., 2021a. Timing of tree density increases, influence of climate change, and a land use proxy for tree density increases in the eastern United States. Land 10 (11), 1121.

Hanberry, B.B., 2021b. Transition from fire-dependent open forests: alternative ecosystem states in the southeastern United States. Diversity 13 (9), 411.

Hanberry, B.B., Abrams, M.D., 2019. Does White-tailed deer density affect tree stocking in forests of the eastern United States? Ecol. Process. 8 (1), 1–12.

Hanberry, B.B., Faison, E.K., 2023. Re-framing deer herbivory as a natural disturbance regime with ecological and socioeconomic outcomes in the eastern United States. Sci. Total Environ. 868, 161669.

Hanberry, B.B., Palik, B.J., He, H.S., 2013. Winning and losing tree species of reassembly in Minnesota's mixed and broadleaf forests. PLoS One 8 (4), e61709.

Hanberry, B.B., Brzuszek, R.F., Foster, H.T., Schauwecker, T.J., 2019. Recalling open old growth forests in the southeastern mixed forest province of the United States. Écoscience 26 (1), 11–22.

Hanberry, B.B., Abrams, M.D., Arthur, M.A., Varner, J.M., 2020. Reviewing fire, climate, deer, and foundation species as drivers of historically open oak and pine forests and transition to closed forests. Front. For. Glob. Change 3, 56.

Harmon, M., 1982. Fire history of the westernmost portion of great smoky mountains national park. Bull. Torre Bot. Club 74–79.

Harrod, J., White, P.S., Harmon, M.E., 1998. Changes in xeric forests in Western great smoky mountains national park, 1936-1995. Castanea 63, 346–360.

Harrod, J.C., Harmon, M.E., White, P.S., 2000. Post-fire succession and 20th century reduction in fire frequency on xeric Southern Appalachian sites. J. Veg. Sci. 11 (4), 465–472.

Holmes, J.S., 1911. Forest conditions in western North Carolina. Edwards & Broughton, Raleigh, North Carolina.

Kane, J.M., Varner, J.M., Saunders, M.R., 2019. Resurrecting the lost flames of American chestnut. Ecosystems 22 (5), 995–1006.

Lafon, C.W., Naito, A.T., Grissino-Mayer, H.D., Horn, S.P. and Waldrop, T.A., 2017. Fire history of the Appalachian region: a review and synthesis. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Larson, R.W., 1956. The timber supply situation in Georgia. US Department of Agriculture Forest Service, Government Printing Office, Washington, D.C.

Manson, S., Schroeder, J., Van Riper, D., Kugler, T., Ruggles, S., 2022. IPUMS national historical geographic information system: version 17.0 [dataset]. IPUMS, Minneapolis, MN.

Mastran, S.S., Lowerre, N. 1983. Mountaineers and rangers: a history of Federal forest management in the Southern Appalachians, 1900–1981. U.S. Department of Agriculture, Forest Service, Washington, DC.

Maxwell, H., 1910. The use and abuse of forests by the virginia Indians. William Mary Coll. Q. Hist. Mag. 19 (2), 73–103.

McEwan, R.W., Dyer, J.M., Pederson, N., 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography 34 (2), 244–256.

Moore, W.M., 1910. Forest conditions in south carolina. Gonzales and Bryan, Columbia, South Carolina.

Overpeck, J.T., Webb, T.I., Prentice, I.C., 1985. Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. Quat. Res. 23, 87–108.

Pedersen, R.Ø., Faurby, S., Svenning, J.C., 2023. Late-Quaternary megafauna extinctions have strongly reduced mammalian vegetation consumption. Glob. Ecol. Biogeogr. 32 (10), 1814–1826.

Plummer, G.L., 1975. 18th century forests in Georgia. Bull. Ga. Acad. Sci. 33, 1–19.

Rhoades, C.C., Park, A.C., 2001. Pre-blight abundance of American chestnut in kentucky. J. Am. Chestnut Found. 15 (1), 36–44.

Sargent, C.S. 1884. Report on the forests of North America (exclusive of Mexico). US Government Printing Office, Washington, DC.

Sheffield, R.M., Knight, R.M. 1986. North Carolina's forests. US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station.

Spillers, A.R. and Eldredge, I.F., 1943. Georgia forest resources and industries. US Department of Agriculture Forest Service, Government Printing Office, Washington, D.C.

USDA Forest Inventory and Analysis FIA DataMart. 2021. Available online: http://www.fia.fs.usda.gov/tools-data/ (accessed on 18 October 2023).

USGS. 2023. TNM Download (v2.0). Available at http://apps.nationalmap.gov/downloader/#/ Accessed 16 July 2023.

Van Lear, D.H., Waldrop, T.A. 1989. History, uses, and effects of fire in the Appalachians. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, North Carolina.

Williams, G., 2005. The USDA forest service – the first century. U.S. Department of Agriculture, Washington, DC.

Williams, M., 1989. Americans and their forests: a historical geography. Cambridge University Press.

Wilson, J., 1908. Report of the secretary of agriculture on the Southern Appalachian and White mountain watersheds. U.S. Government Printing Office, Washington, DC.

Woods, F.W., Shanks, R.E., 1959. Natural replacement of chestnut by other species in the great smoky mountains national park. Ecology 40 (3), 349–361.