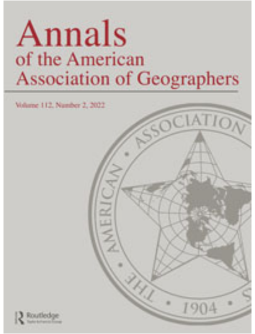

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Historical Fire Regimes and Stand Dynamics of Xerophytic Pine–Oak Stands in the Southern Appalachian Mountains, Virginia, USA

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Fire-dependent yellow pine (*Pinus*) forests are included within the temperate deciduous forest of eastern North America. These forests, which occupy dry slopes and typically contain xerophytic oaks (*Quercus*), have receded under fire suppression. Understanding historical fire regimes is essential for interpreting and managing these stands. To characterize fire history and vegetation dynamics, we conducted a dendroecological study of fire-scarred trees and age structure in pine stands at four sites in the Appalachian Mountains. Fire interval estimates suggest that before fire suppression began in the early to middle 1900s, fires occurred at approximately three- to eleven-year intervals. Short intervals were probably maintained in part by large-extent fires that spread from sparse ignition points. Fire frequency showed no long-term temporal trend (e.g., no wave of fire) from the middle 1700s through early 1900s despite land–use intensification, including industrial logging and associated wildfires during the late nineteenth and early twentieth centuries. Fire occurrence was associated with drought at two sites. Age–structure analyses evoke pyrogenic pine–oak communities that predated industrial disturbances and persisted under a regime of frequent, mixed-severity fires that was likely maintained through a positive feedback with the flammable vegetation. Competing species were established under more recent fire suppression, however, and are poised to replace the pines. *Key Words: fire frequency, fire history, mesophication, Pinus pungens, Pinus rigida.*

Few tree genera show a stronger association with fire than *Pinus*. Across North America, fire-dependent pine stands range from the longleaf pine (*Pinus palustris*) woodlands that were historically maintained by surface fires at one- to five-year intervals on the southeastern Coastal Plain to the dense jack pine (*P. banksiana*) forests that thrive under stand-replacing fires at 50- to 150-year intervals on boreal landscapes (Agee 1998; Fill et al. 2015). The fire regimes and fire ecology of longleaf pine, jack pine, and other pine-dominated ecosystems are extensively documented (e.g., Veblen, Kitzberger, and Donnegan 2000; Brown et al. 2008; Briand et al. 2015; Fill et al. 2015). In contrast, the fire regimes of xerophytic pine forests included within the broader temperate deciduous forest region of the humid eastern United States have received less attention (e.g., Williams 1998; Aldrich et al. 2010; Stambaugh et al. 2018). Improved knowledge of these fire regimes is needed, especially considering declining pine extent under the present era of fire prevention and suppression (hereafter, suppression refers to both strategies). This article contributes to an understanding of historical fire regimes and stand dynamics of montane pine-dominated stands in the southern Appalachian Mountains, where opportunities exist to restore pyrogenic vegetation across extensive federal and state conservation lands. It also advances a general understanding of fire regimes in the temperate forest region of eastern North America.

Appalachian pine stands are relatively small patches within a hardwood matrix (Figure 1). They occupy dry, south- or west-facing slopes where fire and moisture stress historically maintained pine dominance at the expense of hardwoods (Williams 1998; Lafon, Hanson, and Dwight 2019). They are dominated by yellow pines (subgenus *Diploxylon*

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Figure 1. Photograph of the dissected north slope of Brush Mountain, Virginia, looking southward. Pine stands are dark patches on the west faces of spurs.

Koehne) and typically contain xerophytic oaks, especially scarlet and chestnut oak (*Quercus coccinea* and *Q. montana*). The dominant pines are typically Table Mountain pine (*Pinus pungens*) and pitch pine (*P. rigida*) at middle elevations and shortleaf pine (*P. echinata*) at low elevations. These pines have adaptations such as thick bark and flammable foliage. The endemic Table Mountain pine also has serotinous cones. These traits are hypothesized to adapt Table Mountain pine to a "polycyclic" regime of frequent surface fires every five to seven years and canopy-opening fires approximately every seventy-five years (Frost 1998). These fires maintained open stands with blueberries (*Vaccinium*) and warm-season grasses in the understory (Harrod, Harmon, and White 2000; Croy, Bucher, and Lindblom 2018).

Such conditions are not found today under fire suppression. Aging trees dominate the overstory, and younger trees and shrubs form understory thickets that inhibit shade-intolerant pine and oak seedlings (Croy, Bucher, and Lindblom 2018). Thick duff impedes pine seedling access to mineral soil formerly exposed by fires (Williams 1998). These changes are reducing pine extent, diminishing landscape diversity, and altering wildlife habitat (Lafon, Hanson, and Dwight 2019).

National-level fire suppression was organized following industrial logging and conflagrations of the late nineteenth and early twentieth centuries (Pyne 1982; Sarvis 1993). The consequent near-exclusion of fire from eastern forests has contributed to *mesophication*: Oak and pine forests shift to maple and other mesophytes, driving a positive feedback where deepening shade and mesophytic litter reduce flammability and lead toward denser forests, less fire, and regeneration failure in oak and pine (Nowacki and Abrams 2008). Today, these changes are combatted through controlled burning, but this requires an understanding of historic forest composition, vegetation dynamics, and fire regimes, which are obscured from view by the industrial disturbances and fire suppression of the past century.

Many researchers suggest that fire was frequent under Native American and subsequent European-American occupancy (e.g., Denevan 1992; Nowacki and Abrams 2008) and was a landscape phenomenon where large-extent fires spread through the hardwood forest to encompass disjunct xerophytic stands (Stambaugh et al. 2015; Lafon et al. 2017). Some authors question this, however, proposing that fire was restricted to small xeric sites such as Appalachian ridgetops covered with oak–pine stands embedded in a broadleaf forest matrix that rarely burned (Hart and Buchanan 2012; Matlack 2013). Under this scenario, mesophication might reflect a twentieth-century shift toward a cooler, wetter climate (McEwan, Dyer, and Pederson 2011).

Another question concerns temporal changes in burning. Fire frequency might have been controlled by human activity such that burning and pyrogenic vegetation were restricted when the human presence was small during aboriginal depopulation and early European-American settlement (Williams 1998; McEwan, Dyer, and Pederson 2011; Stambaugh et al. 2018). Fire frequency would have risen thereafter, cresting with industrial logging before declining under suppression. A recent dendroecological study from Pennsylvania found evidence for this pattern based on changes in the number of fires per decade, motivating the hypothesis that a "wave of fire" swept Pennsylvania and the entire continent (Stambaugh et al. 2018). A tight coupling of fire with human activity, however, is not ubiquitous. At several fire-scar sites in the southern Appalachian Mountains, fire frequency remained high through multiple land-use phases, varying by decade but showing no long term trend before declining under fire suppression (Lafon et al. 2017). The short-term variations might reflect climatic variability, although the fire–climate relationship is weak for most fire history sites in eastern North America (e.g., Flatley et al. 2013; Stambaugh et al. 2018).

Resolving historical changes in fire frequency is important for fire management. If fire frequency peaked under industrial logging, oak and pine stands that developed in its aftermath may be industrial artifacts (Williams 1998) that do not represent previous vegetation. Conversely, if pyrogenic vegetation was maintained through a longer history of frequent fire, then evidence of this history could inform management objectives, which include restoration through controlled burning (e.g., U.S. Department of Agriculture Forest Service 2004).

Research Questions

The following questions guide our dendroecological study of fire regimes and stand dynamics of southern Appalachian pine–oak stands:

1. Fire history: (1) How frequently and extensively did fires occur historically? (2) Did fire frequency change as land use intensified over the course of European settlement and economic development? (3) Did fire occurrence vary temporally in association with climatic variations in moisture?
2. Stand dynamics: (1) Were the sites occupied by yellow pine and oak before industrial-era disturbances of the late nineteenth and early twentieth centuries? (2) Do the stands show evidence of pine age cohorts that were established after severe fires? (3) Do present species composition and age structure suggest mesophication of the stands under the suppression-era fire regime?

Method

Sites

We sampled at four sites (Griffith Knob, Little Walker Mountain, Brush Mountain, and North Mountain) located in the Jefferson National Forest (JNF, Figure 2). Each site covers 0.2 to 1.7 km^2, comprising four pine stands (Figure 3) separated by 50- to 200-m swaths of oak-dominated forest. January temperatures at the sites average between −0.4 °C and 0.0 °C, and July temperatures average 21.4 °C to 21.9 °C (PRISM 2019). Mean annual precipitation ranges from 1,012 mm to 1,175 mm and is distributed fairly evenly through the year.

The sites are in the Ridge and Valley physiographic province and are arranged at 600 to 900 m elevation along a single ridge (Figure 2) with different names over its length. The dissected north side of the ridge contains the sampled pine stands, which inhabit west-facing slopes of spurs (Figure 3). The ridge is covered with thin Berks and Weikert soils (50–85 cm; SoilWeb 2019), which are typic and lithic Dystrudepts developed on Paleozoic shale, siltstone, and sandstone (Wilkes 2002). In some places the ridge adjoins the Great Valley (Figure 2), the focus of the region's greatest human activity.

The JNF is primarily covered with an oak–pine mosaic comprising an oak forest matrix with embedded patches of pine (Simon 2013). Oak-dominated forests inhabit submesic to subxeric sites and cover approximately 73 percent of the JNF. Pine-dominated forests largely occupy dry, west-facing slopes and cover 9 percent of the JNF. The remaining 18 percent is covered mostly with mesophytic forests.

Nomadic hunter-gatherers inhabited southwest Virginia during the Archaic period (7000–500 BC) and possibly earlier (M. B. Kegley 1989). During the late Woodland period (AD 1000–1700), Yuchi and then Tutelo villages appeared along major streams but apparently were abandoned by about 1620 (M. B. Kegley 1989). The region seems to have been depopulated before the first European-Americans settled in the 1740s and 1750s (Egloff and Woodward 2006). Some Native American influence persisted as Cherokee and Shawnee traders, hunters, and warriors

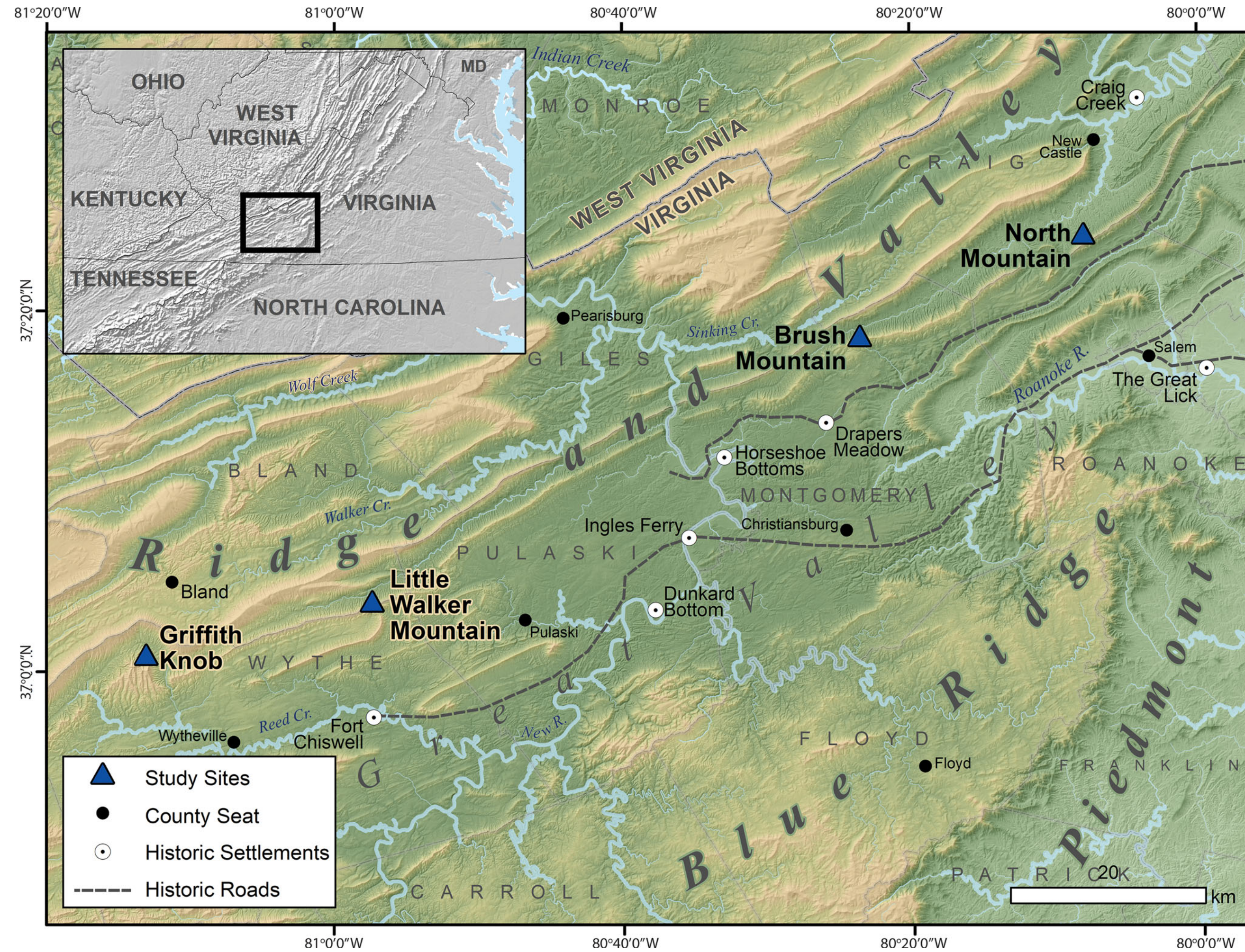

Figure 2. Study area map showing the sites and the historic settlements and roads established ca. 1740 through 1760 (F. B. Kegley 1938; M. B. Kegley 2008; Smith 1975). Present-day county seats are shown for reference.

traveled through, until the Virginians secured the frontier in the late 1700s (M. B. Kegley 1989; Egloff and Woodward 2006; Danner 2009).

Early European-American settlers probably had little influence on the four sites because they targeted good farmland beside streams in the Great Valley (cf. F. B. Kegley 1938; M. B. Kegley 1989). The two eastern sites were likely affected before the western sites, given their proximity to early travel routes and settlements (Figure 2), but all the sites were probably influenced by burning and other activities of the settlers by around 1800. Human impact intensified with industrial exploitation during the late 1800s, especially at Brush Mountain, where iron smelting, coal mining, millstone quarrying, and logging occurred from the middle 1800s through middle 1900s (M. B. Kegley 1989; Wyatt 2009; land records on file in the Supervisor's Office of the JNF, Roanoke, Virginia). Logging was the most extensive industrial operation in the area. It largely coincided with the regional logging episode of the late 1800s and early 1900s (M. B. Kegley 1989; Wyatt 2009) and had mostly removed the merchantable timber before U.S. government acquisition in 1936 to 1940 (JNF land records). The pine stands might not have been logged, however, given their poor timber quality relative to surrounding hardwood forest. No forests were logged at Little Walker Mountain, the most isolated site, which was covered with "virgin timber" when the JNF was established (JNF land records).

Field Methods

We collected full or partial cross sections from yellow pine trees with basal fire scars from areas of

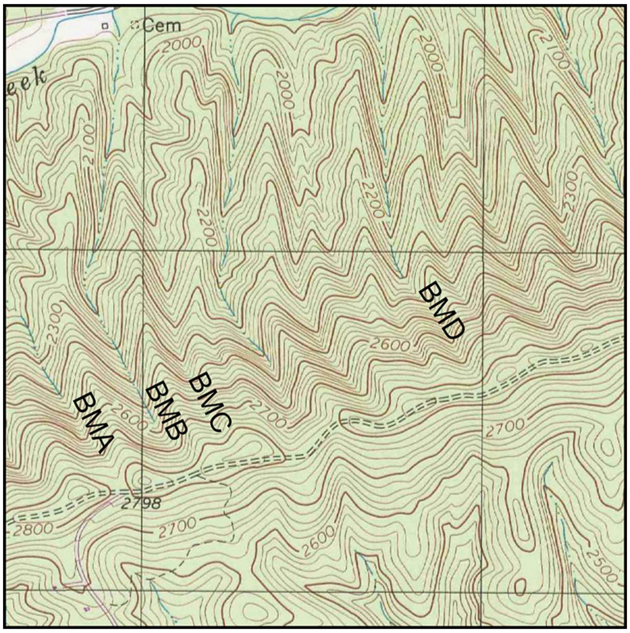

Figure 3. Section of the U.S. Geological Survey's Newport, Virginia 7.5′ topographic quadrangle (1:24,000 scale, 1998 edition) showing the Brush Mountain site.

approximately 0.5 to 3.5 ha within the four stands in each site (sixteen stands in total) between 2003 and 2005. Cross sections were collected from living trees, snags, stumps, and remnant logs (Baisan and Swetnam 1990; Grissino-Mayer et al. 2004). We supplemented our samples from Brush Mountain with fourteen fire-scarred trees collected there in 1993 (Sutherland et al. 1995).

In 1,000 m^2 (20 × 50 m) quadrats established in three stands at each site (twelve stands total), we extracted two increment cores from opposite sides at the base of each living tree measuring ≥5 cm diameter at breast height (DBH) and recorded species and DBH. For plots containing fewer than forty yellow pines, we cored additional, randomly selected yellow pines outside the plot to ensure at least forty were available for chronology development (i.e., to date fire-scarred cross sections). These additional pines were excluded from analyses of age structure and stand composition. We also inventoried saplings (DBH < 5 cm, height ≥ 50 cm) of canopy tree species in each plot but did not core them. We estimated yellow pine sapling ages by counting branch nodes on the main stem, however (Williams and Johnson 1990; Pfeffer 2005). Node count is strongly related to tree age (R^2 = 0.76; Pfeffer 2005). Additionally, we inventoried tree seedlings (height < 50 cm) in a 10 × 20 m subplot within each quadrat. Botanical nomenclature follows Kartesz and Kartesz (1980).

Laboratory Methods

Increment cores and cross sections were surfaced using progressively finer sandpaper (Speer 2010). Tree rings were cross-dated visually and then measured to the nearest 0.001 mm using a Velmex measuring system with Measure J2X software (ProjectJ2X). These measurements were used for statistical cross-dating with COFECHA software (Laboratory of Tree-Ring Research n.d.; Speer 2010).

We used the dated tree rings to assign calendar years to the fire scars in each cross section. We also designated scar seasonality according to scar position within the tree ring: dormant, early-early season, middle-early season, late-early season, and late season (Baisan and Swetnam 1990; Grissino-Mayer et al. 2004). Dormant-season scars were assigned to the ring that formed after the scar, because more fires occur in the spring than the fall fire season in the southern Appalachian Mountains (Flatley et al. 2013).

Analyses

How Frequently and Extensively Did Fires Occur Historically? Because trees are imperfect recorders of fire occurrence (Van Horne and Fule 2006), we calculated a series of fire interval metrics to assess fire frequency at each site (Aldrich et al. 2010). (1) The point fire interval assesses the recording intervals between fires on individual trees. A recording interval is defined as following the initial scar and containing intact rings such that no scars are effaced by decay or subsequent fires. (2) The stand-level composite fire interval is based on a combined record of all fires recorded within a single stand. (3) The combined-stand composite fire interval is based on a combined record of all fires recorded in all stands at a site. (4) The filtered composite fire interval considers fires that scarred at least 25 percent of the recording trees at a site, and a minimum of two trees. (5) The area-wide fire interval (Fisher, Jenkins, and Fisher 1987; Aldrich et al. 2010) assesses the frequency of spatially extensive fires that likely burned across the entire sampled area. An area-wide fire was any fire found in all recording stands at a site. Years with only one recording stand were excluded from the area-wide analysis. We used FHAES software to record, graph, and analyze fire intervals (Sutherland et al. 2017).

We calculated mean fire interval (MFI), Weibull median fire interval (WMI), standard deviation (SD), lower exceedance interval (LEI), and upper exceedance interval (UEI) for each fire interval type. Fire intervals were analyzed for the period after the first fire that was recorded on at least two cross sections (Grissino-Mayer et al. 2004). Wishing to characterize presuppression fire frequency, we omitted the period after the JNF was established in 1936 (cf. Sarvis 1993) from our calculations.

Did Fire Frequency Change as Land Use Intensified over the Course of European Settlement and Economic Development? To examine changes in fire frequency under differing land uses, we calculated and graphed the number of fires recorded per decade at each site, based on the combined-stand composite record. We augmented these records through analogous calculations for seven other southern Appalachian sites for which we have published fire chronologies, for a total of eleven sites, including one at Peters Mountain, Virginia, adjacent to the JNF (Hoss et al. 2008); three sites in the George Washington National Forest, Virginia, northeast of the JNF (Aldrich et al. 2010; Aldrich et al. 2014); and three sites in Tennessee and North Carolina, southwest of the JNF (Flatley et al. 2013).

In consideration of the imperfect recorder problem, we explored whether apparent temporal variations in fire frequency might simply reflect differences in the number of recording trees available at different times. Specifically, we performed linear regression analyses (Zar 1999) to relate the number of fires per decade (NF) to the number of recording trees (RT) available each decade for the eleven sites. The regression analyses were conducted for all decades before the fire-suppression era, defined as beginning in the 1930s. This data set, and others used for additional regression analyses in what follows, was found to meet regression assumptions (Zar 1999; Gotelli and Ellison 2004).

Finally, we calculated a decadal fire index (DFI) that accounts for sample size variations to permit more reliable comparisons of fire activity through time (Hoss et al. 2008; Lafon et al. 2017). DFI was calculated as the mean number of fire scars per recording tree per decade. To look for temporal changes through the presuppression era, we regressed DFI against decade (DEC), with values of DEC ranging from 1 (the 1740s) through 19 (the 1920s). DFI analyses were conducted only for the four JNF sites, because DFI for the other southern Appalachian sites is reported elsewhere (Hoss et al. 2008; Flatley et al. 2013; Aldrich et al. 2014).

Did Fire Occurrence Vary Temporally in Association with Climatic Variations in Moisture? Because DFI shows pronounced interdecadal variations, we investigated whether these differences were related to the interdecadal variations evident in the Palmer Drought Severity Index (PDSI; Cook et al. 1999). Reconstructed summer PDSI was obtained for gridpoint 247 in western Virginia. We averaged these yearly PDSI values for each decade and then regressed DFI against decadal PDSI.

To investigate the relationship of fire with interannual moisture variations, we conducted superposed epoch analysis (SEA; Swetnam and Baisan 1996) using FHAES. An autocorrelation function identified significant nonzero lag correlations in the PDSI time series. Therefore, PDSI values were prewhitened using autoregressive models based on the lowest Akaike's information criterion and significant but uncorrelated parameter estimates (Brown et al. 2008). SEA was applied to the filtered composite record at each site. We also performed SEA for regional fire years, which were fire years in at least three sites, to assess the regional synchronization of fire by drought.

Were the Sites Occupied by Yellow Pine and Oak before Industrial-Era Disturbances of the Late Nineteenth and Early Twentieth Centuries? We developed age–structure histograms from the establishment dates of trees in the plots. For cores that did not intersect the pith, we estimated tree age from the curvature and width of the innermost rings (Applequist 1958). Establishment dates were assigned to ten-year bins for graphing and the species classed into three categories: yellow pine, oak, and other species. The latter category included generally fire-intolerant, nonoak hardwoods and white pine (*Pinus strobus*; Croy, Bucher, and Lindblom 2018; Lafon et al. 2017). Additionally, for the 44 percent of fire-scarred cross sections with intact pith, we used their pith dates to estimate establishment dates and calculate tree age at first scarring.

Do the Stands Show Evidence of Pine Age Cohorts That Were Established after Severe Fires? For every stand, we identified one- or two-decade spans with at least twice the pine establishment dates as the preceding or succeeding decade. This cohort definition is consistent with dendroecological studies of other North American forests, where cohorts are typically established within two decades of a severe fire (Bergeron 2000; Sibold et al. 2007). It also matches observations of rapid postfire pine establishment after moderate- to high-severity burns in the southern Appalachian Mountains (Waldrop and Brose 1999; Lafon and Kutac 2003).

Do Present Species Composition and Age Structure Suggest Mesophication of the Stands under the Suppression-Era Fire Regime? Plot data were used to compute basal area (m^2/ha) and density (stems/ha) for each species in the tree, sapling, and seedling classes. Mesophication would be suggested if yellow pine and oak dominated the tree stratum but were less prominent among the saplings and seedlings. Additionally, we used tree establishment data in a chi-square test (Zar 1999) to examine differences in the relative frequency of establishment among the three species categories (yellow pine, oak, or other) for three time periods: frequent-fire, postfire, and mesophication (Flatley et al. 2015). The frequent-fire period spans the era before suppression. The postfire period spans four decades beginning with the decade containing the last major fire at a site, which we defined as the last fire used to calculate the filtered composite fire interval. Because the decade of the last major fire differs among sites, the postfire period begins in the 1920s at two sites and the 1930s at the other two. The four-decade span of the postfire period is meant to capture the open-stand conditions following a history of frequent burning (Flatley et al. 2015). The mesophication period covers the subsequent decades, when a more closed stand structure likely developed.

Results

Fire History

How Frequently and Extensively Did Fires Occur Historically? The pine stands in the JNF contained living and dead fire-scarred pines (four to twenty-two trees sampled per stand; Table 1) established over the past 250 years (Figure 4). Most trees were first scarred at a relatively young age (M = 22 years, range = 4–108 years). Among the respective sites, 72 to 90 percent of the scars were formed in the dormant and early-earlywood positions.

The scars record fires back to the middle or late 1700s at each site (Figures 5–8). Fires are recorded at three- to ten-year intervals for individual pine stands (stand-level composite MFI/WMI, Table 1). At the site level, they are recorded at two- to four-year intervals (combined-stand composite MFI/WMI) and six- to eleven-year intervals (filtered composite MFI/WMI). Longer estimates are provided by the point fire intervals (ten to fifteen years) and the area-wide fire intervals (twelve to thirty-two years).

Did Fire Frequency Change as Land Use Intensified over the Course of European Settlement and Economic Development? Each JNF site exhibits interdecadal variation in the number of fires (Figures 9A–9D), as do the seven sites outside the JNF (Figures 9E–9K). In general, more fires are recorded in the middle decades, especially the 1880s to the 1910s (Figure 9L). This pattern suggests an increase in fire frequency until the industrial logging peak, then a sharp decline into the suppression era. The increase, however, could simply be a sampling artifact of the number of recording trees available for different parts of the record: The number of fires per decade is positively related to the number of recording trees for ten of the eleven sites (Table 2). In fact, for the four JNF sites, DFI shows interdecadal variation but no long-term change from the middle and late 1700s until the early 1900s (Figure 10, Table 2).

Did Fire Occurrence Vary Temporally in Association with Climatic Variations in Moisture? The interdecadal variability in DFI shows no statistically significant relationships with decadal mean PDSI (Table 2) for any JNF site. Stronger relationships emerge at the interannual level (Figure 11), but the only fire–climate relationship found at more than one site is with prior-year drought at the two western sites (Figures 11A–11B, where year −1 shows a negative departure for PDSI). This association reflects negative PDSI in most years (minima of −2.98 and −3.40 for the two respective sites) combined with a lack of strongly positive PDSI values in any year (maxima = 1.14 and 1.57, respectively). In contrast, PDSI for the years with statistically insignificant associations is more evenly split between negative and positive values and also includes stronger positive values

Table 1. Fire interval calculations for the presuppression fire regime (defined for these analyses as ending in 1936)

	MFI	WMI	*SD*	LEI	UEI	Range	No. of intervals	Years covered
Griffith Knob								
Point fire interval (*n* = 73)	15.3	14.2	9.2	5.7	26.0	3–51	116	1810–1936
Stand-level composite fire interval								
Stand A (*n* = 11)	5.0	4.0	4.3	1.1	9.6	1–18	22	1810–1936
Stand B (*n* = 21)	5.2	4.5	3.5	1.5	9.3	1–13	20	1829–1936
Stand C (*n* = 22)	9.8	5.4	11.7	0.7	21.4	1–32	12	1810–1936
Stand D (*n* = 19)	4.0	3.2	3.5	0.8	7.9	1–11	26	1829–1936
Combined-stand composite fire interval	2.3	1.9	2.0	0.5	4.3	1–9	55	1810–1936
Filtered composite fire interval	8.3	7.5	5.2	2.8	14.3	1–19	14	1810–1936
Area-wide fire interval	31.7	31.4	14.8	17.7	46.1	19–48	3	1810–1936
Little Walker Mountain								
Point fire interval (*n* = 73)	11.2	9.6	8.7	3.1	20.6	2–50	86	1778–1936
Stand-level composite fire interval								
Stand A (*n* = 8)	5.2	4.9	3.0	2.1	8.7	1–17	29	1778–1936
Stand B (*n* = 6)	7.8	6.6	5.8	2.0	14.5	1–21	20	1778–1936
Stand C (*n* = 6)	7.1	6.7	4.2	2.8	11.9	3–20	18	1806–1936
Stand D (*n* = 13)	8.0	6.7	6.5	2.0	15.1	1–27	16	1806–1936
Combined-stand composite fire interval	2.9	2.7	1.9	1.0	5.2	1–10	53	1778–1936
Filtered composite fire interval	7.1	6.1	5.8	1.9	13.3	1–28	22	1778–1936
Area-wide fire interval[a]	—	—	—	—	—	—	0	—
Brush Mountain								
Point fire interval (*n* = 45)	12.9	11.5	8.6	4.1	22.7	1–50	166	1758–1936
Stand-level composite fire interval								
Stand A (*n* = 8)	8.8	6.7	7.9	1.6	17.5	1–30	14	1803–1936
Stands B and C (*n* = 25)	6.8	5.2	6.4	1.2	13.5	1–28	26	1758–1936
Stand D (*n* = 12)	7.3	5.9	6.1	1.6	14.2	1–22	24	1758–1936
Combined-stand composite fire interval	4.1	3.3	3.5	0.9	8.0	1–13	43	1758–1936
Filtered composite fire interval	11.0	9.4	7.8	3.1	20.0	1–29	16	1758–1936
Area-wide fire interval	15.3	12.6	13.3	3.5	29.3	3–46	11	1758–1936
North Mountain								
Point fire interval (*n* = 46)	12.2	10.8	8.4	3.8	21.7	1–47	74	1779–1936
Stand-level composite fire interval								
Stand A (*n* = 18)	7.0	6.0	5.2	1.9	12.9	1–21	22	1779–1936
Stand B (*n* = 8)[b]	—	—	—	—	—	—	0	—
Stand C (*n* = 4)	8.7	7.3	6.9	2.2	16.3	2–23	13	1816–1936
Stand D (*n* = 16)	4.2	3.5	3.6	1.0	8.1	1–20	36	1779–1936
Combined-stand composite fire interval	3.2	2.6	2.9	0.7	6.2	1–17	48	1779–1936
Filtered composite fire interval	8.1	6.8	6.1	2.2	14.9	1–21	18	1779–1936
Area-wide fire interval	14.7	12.0	11.6	3.4	27.9	2–37	10	1779–1936

Note: For each site and stand, *n* shows the number of fire-scarred trees included in the analysis. MFI = mean fire interval (years); WMI = Weibull median interval (years); *SD* = standard deviation (years); LEI = lower exceedance interval (years); UEI = upper exceedance interval (years).
[a]One area-wide fire was recorded at Little Walker Mountain in 1778.
[b]Stand recorded no fires during the period of analysis.

(maxima of 2.20–2.59 at Griffith Knob and 2.24–3.36 at Little Walker Mountain).

Stand Dynamics

Were the Sites Occupied by Yellow Pine and Oak before Industrial-Era Disturbances of the Late Nineteenth and Early Twentieth Centuries? Age–structure histograms (Figure 12) provide evidence for preindustrial occupancy by yellow pine and oak, although most trees established subsequently. Pith dates of fire-scarred trees indicate preindustrial pine establishment (Figure 4).

Do the Stands Show Evidence of Pine Age Cohorts That Were Established after Severe Fires? Yellow pine cohorts are evident for at least two stands within each site (Figure 12). Pith dates of fire-scarred trees (Figure 4) suggest large cohorts in certain decades at Griffith Knob and Brush Mountain. In general, linking pine cohorts to

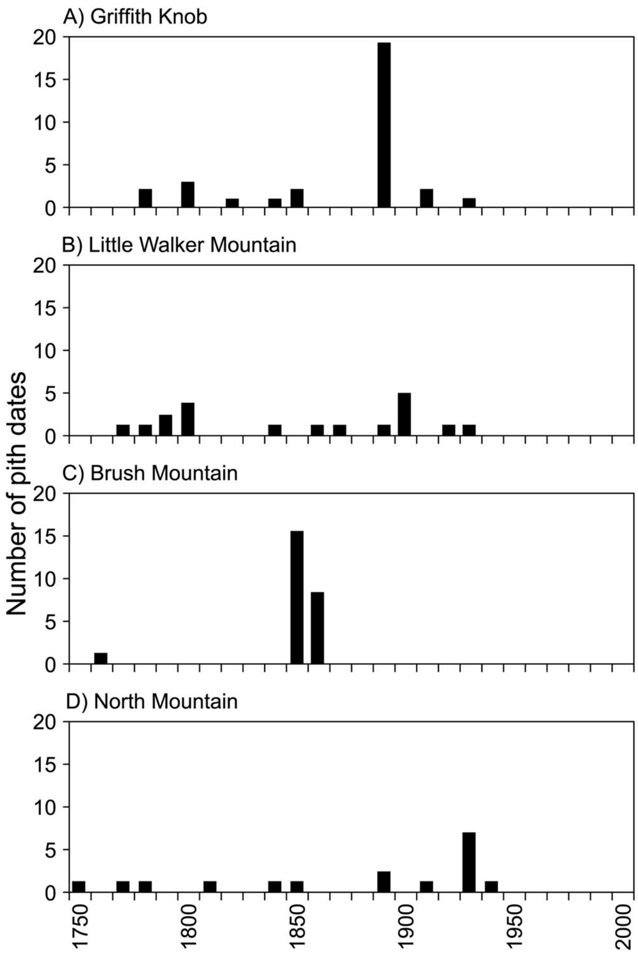

Figure 4. Number of pith dates per decade for fire-scarred pine cross sections.

specific fires is difficult, because high fire frequency means that trees were established with multiple fires. A major fire at Brush Mountain in 1853, however, might provide an exception to this statement, because it was followed by three decades of minimal fire activity that coincided with pine establishment.

Do Present Species Composition and Age Structure Suggest Mesophication of the Stands under the Suppression-Era Fire Regime? Stand composition and age structure are consistent with succession toward more mesophytic, fire-intolerant associations. Table Mountain pine and chestnut oak dominated the tree stratum (Table 3), but species such as northern red oak (*Quercus rubra*), black gum (*Nyssa sylvatica*), and red maple (*Acer rubrum*) were more abundant among the saplings and seedlings (Table 4). Age structure data (Figure 12, Figure 13) show that yellow pine and oak established under frequent burning and in the postfire decades. The other species, however, were largely established under fire suppression. Therefore, the relative frequency of establishment among the tree categories (yellow pine, oak, or other) varied across the three fire regime periods, $\chi^2(4) = 138.4$, $p < 0.05$. Yellow pines predominated in the frequent-fire period, oak in the postfire period, and other species in the mesophication period (Figure 13).

Discussion

Fire History

Relatively short fire intervals typified the pine–oak stands before fire suppression. Precise intervals cannot be determined because trees do not record fires perfectly (Van Horne and Fule 2006), but MFI/WMI estimates suggest a range that probably contains the actual values. At the lower end, a minimum of two years is indicated by the combined-stand composite MFI/WMI, a widely reported metric (e.g., Baisan and Swetnam 1990; Flatley et al. 2013; Aldrich et al. 2014; Margolis 2014; Whitehair et al. 2018; Marschall et al. 2019) based on the full sample of trees at a site. It incorporates the most thorough record of fire and would represent the typical fire interval for this vegetation if every fire burned the entire site. It might, however, underestimate fire interval length because some fires probably did not cover the whole landscape. At the upper end, the point fire interval indicates that the maximum MFI/WMI for any point on the landscape was about fifteen years, but this is almost certainly an overestimate because individual trees do not record all fires that burn them (Van Horne and Fule 2006). Therefore, a two- to fifteen-year range encompasses the extreme endpoints bounding the probable MFI/WMI. This range can be narrowed using other MFI/WMI measures. The stand-level composite MFI/WMI (three to ten years) gives reasonable estimates because it is based only on the small area sampled in a stand (0.5–3.5 ha). The filtered composite MFI/WMI (six to eleven years) is also a reliable estimate (Van Horne and Fule 2006). These two measures therefore suggest typical fire intervals within the three- to eleven-year range. Such intervals resemble those found in other sites in the Appalachian Mountains and vicinity (e.g., Flatley et al. 2013; Aldrich et al. 2014; Stambaugh et al. 2018; Kuppinger and Rich 2020) and therefore suggest

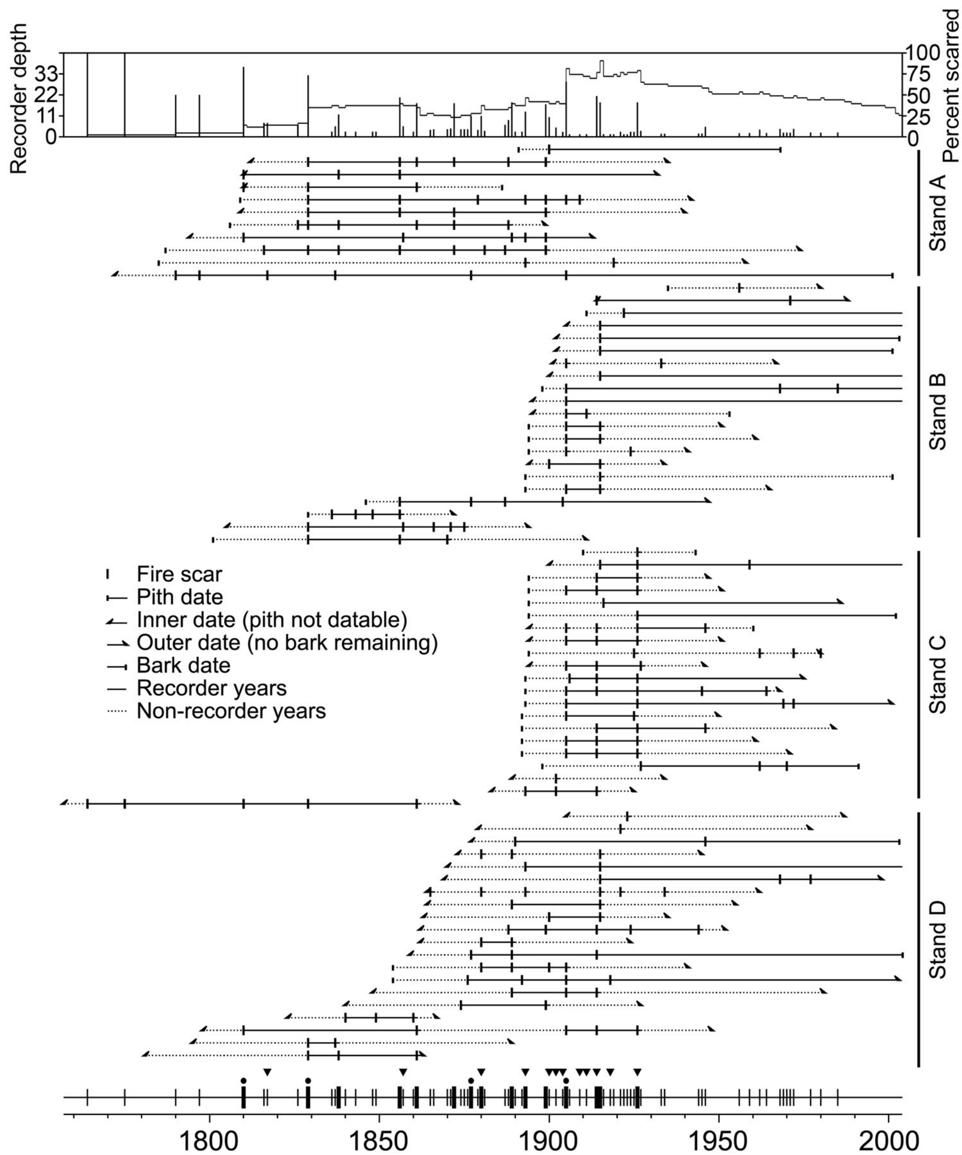

Figure 5. Fire chart for Griffith Knob, showing annually dated fire scars for each cross section. In the small upper graph, the line indicates the number of recording trees and the histogram bars depict the percentage of recording trees scarred. In the main chart, horizontal lines show the time spanned by each tree and vertical hatches represent dated fire scars. The horizontal line at chart bottom represents the composite record of all fires. On this line, thin vertical lines represent less extensive fires, thick vertical bars represent fires recorded by ≥25 percent of recording trees, solid circles show area-wide fire years, and triangles designate regional fire years.

that the fire regime at these JNF sites was typical for the region.

Short fire intervals could have been maintained through a spectrum of plausible burning scenarios. At one end of the spectrum is a scenario with a high density of small-extent fires, each contained within a single pine stand. This pattern would resemble the hypothesis (Matlack 2013) that fires in the Appalachian Mountains burned oak–pine forest on dry ridgetops but did not spread into the surrounding "mesic deciduous forest" matrix. The hypothesis would need modification to account for the observed vegetation pattern of the Ridge and Valley, where pine stands primarily occupy mountain slopes, not ridgetops, and are embedded within a matrix of oak forest instead of mesophytic forest, which is largely confined to lower slopes, valleys, and ravines. Under this scenario, each pine stand burned independently of the other stands because fires rarely spread through the surrounding oak forest. This seems improbable because it would require an extraordinarily high ignition density on a regular

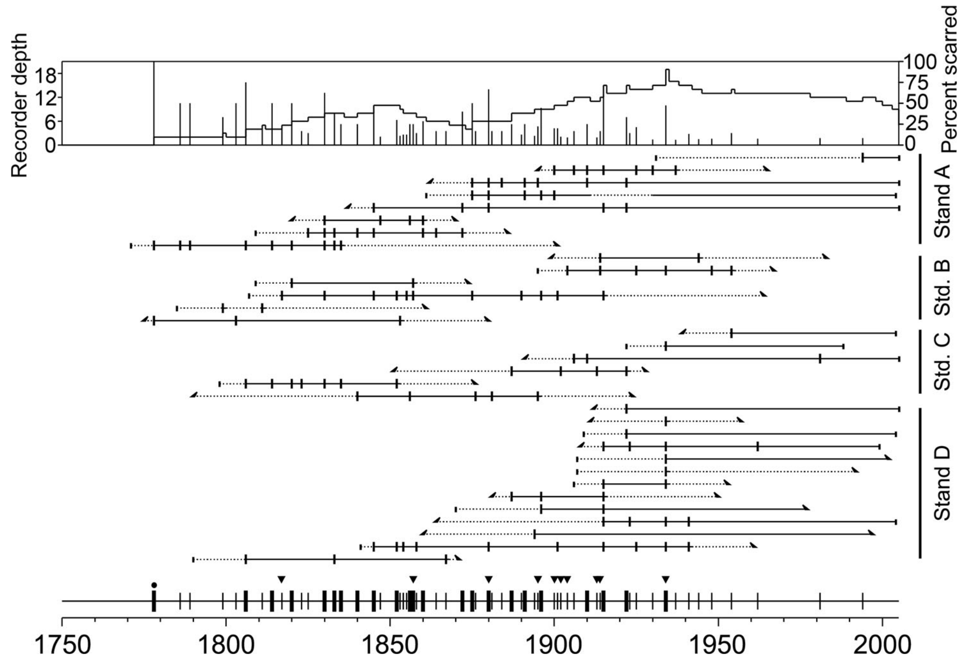

Figure 6. Fire chart for Little Walker Mountain. Thin vertical lines represent less extensive fires, thick vertical bars represent fires recorded by ≥25 percent of recording trees, solid circles show area-wide fire years, and triangles designate regional fire years.

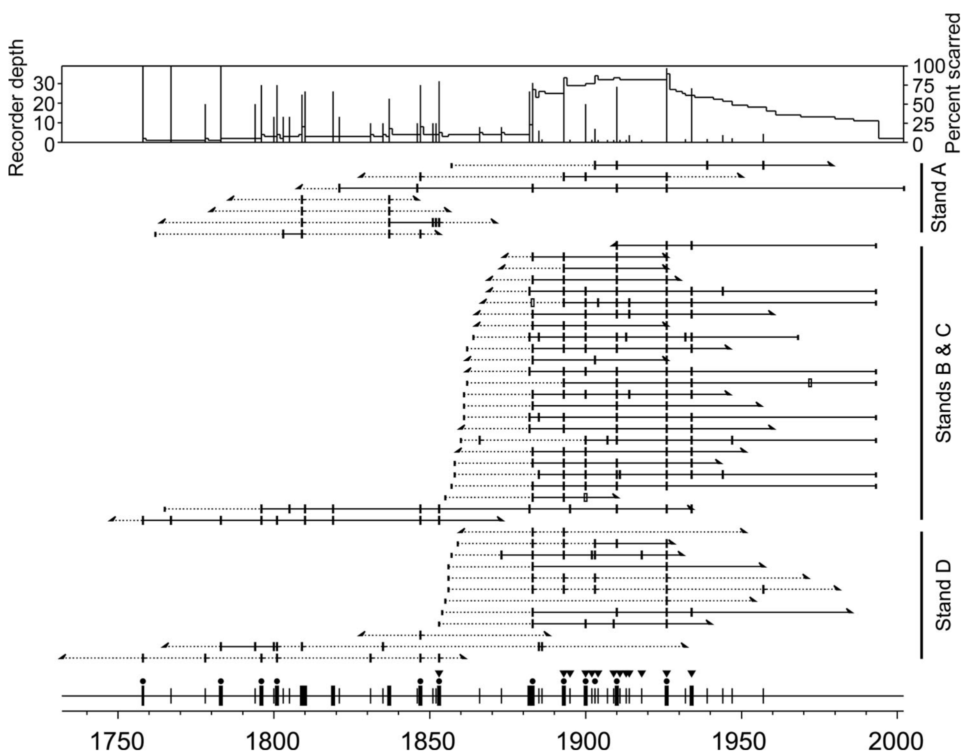

Figure 7. Fire chart for Brush Mountain. Thin vertical lines represent less extensive fires, thick vertical bars represent fires recorded by ≥25 percent of recording trees, solid circles show area-wide fire years, and triangles designate regional fire years.

basis to maintain frequent burning through small-extent fires (Lafon et al. 2017). Burning to promote blueberries or other resources might account for a relatively high ignition density, but the assumption that fires did not spread outside the pine stands contradicts observations that some oak species produce flammable litter (Nowacki and Abrams 2008; Kreye et al. 2013; Babl et al. 2020) that can carry fire over

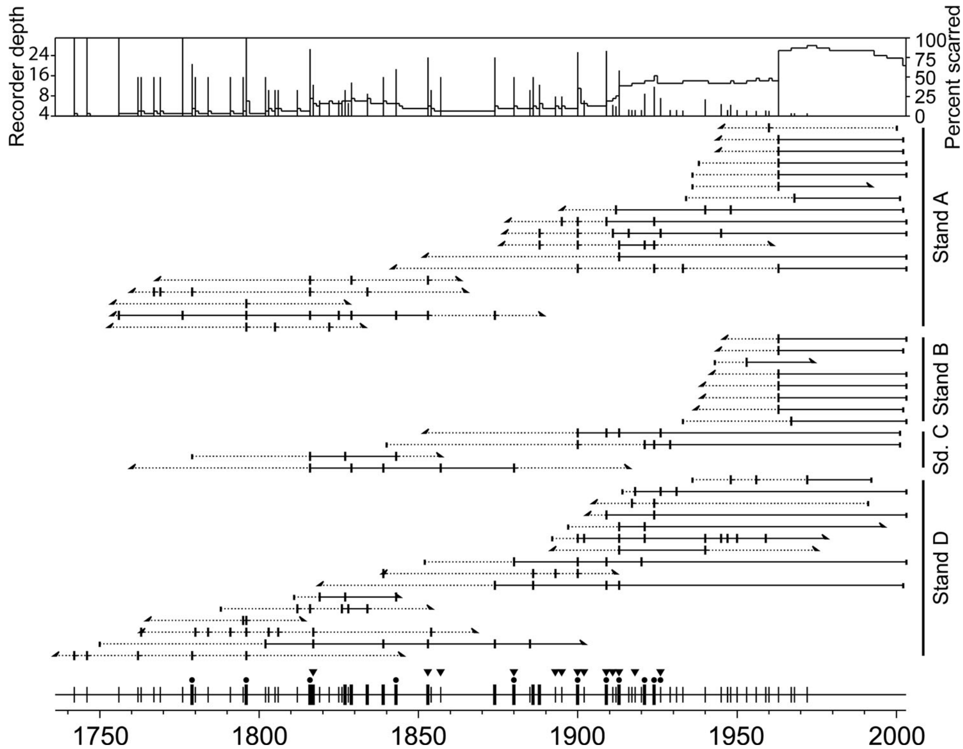

Figure 8. Fire chart for North Mountain. Thin vertical lines represent less extensive fires, thick vertical bars represent fires recorded by ≥25 percent of recording trees, solid circles show area-wide fire years, and triangles designate regional fire years.

large areas during the dry, windy conditions common in spring and fall (Flatley, Lafon, and Grissino-Mayer 2011; Lafon et al. 2017).

At the other end of the spectrum is a scenario where frequent burning was maintained by fires spreading from relatively sparse ignition points to encompass large areas of the oak–pine mosaic. This scenario of landscape-level burning would have been especially important during the 1700s, when Native American activities were waning and the European-American presence remained small. Anthropogenic ignitions were likely sparse during this time. Lightning ignitions might have also been sparse, because ignition points are widely scattered and lightning-ignited fires can only burn large areas when they spread extensively beyond the ignition site; for example, during dry weather (Lafon et al. 2017). Frequent burning would have become less dependent on large-extent fires as anthropogenic activities intensified over the nineteenth and early twentieth centuries, providing ignitions for multiple small fires that, in combination with larger fires, burned the pine stands and much of the oak–forest matrix on a frequent basis. Large-extent fires undoubtedly still controlled the fire regime, because most burning in any fire regime is accomplished by a handful of the largest fires (Pyne 1982).

Although we cannot precisely discern the size of fires from our data, area-wide fires provide evidence consistent with the spread of fire through the 0.2 to 1.7 km^2 areas sampled for this study. Fires might have extended well beyond these study area boundaries. Fire compartments—areas through which a fire can spread unimpeded (Frost 1998)—can extend for many kilometers along a mountain slope and into the adjacent valleys (C. Frost, consultant with Blue Star Consulting, personal communication, October 12, 2015; Lafon et al. 2017). Fire scars are commonly observed on old oaks and other trees growing on dry mountainsides between pine stands and even on lower slopes (Flatley et al. 2013). These wounds, now mostly decayed, bear witness to the spread of fire through large compartments.

Large-extent fires are also suggested where the two most distant stands at a site record fire during the same year, even though the fire is not recorded in an intervening stand. At Little Walker Mountain, for example, an 1806 fire was identified in stands A and D (Figure 6) and the intervening stand C but not in stand B. Similar cases are seen in the other

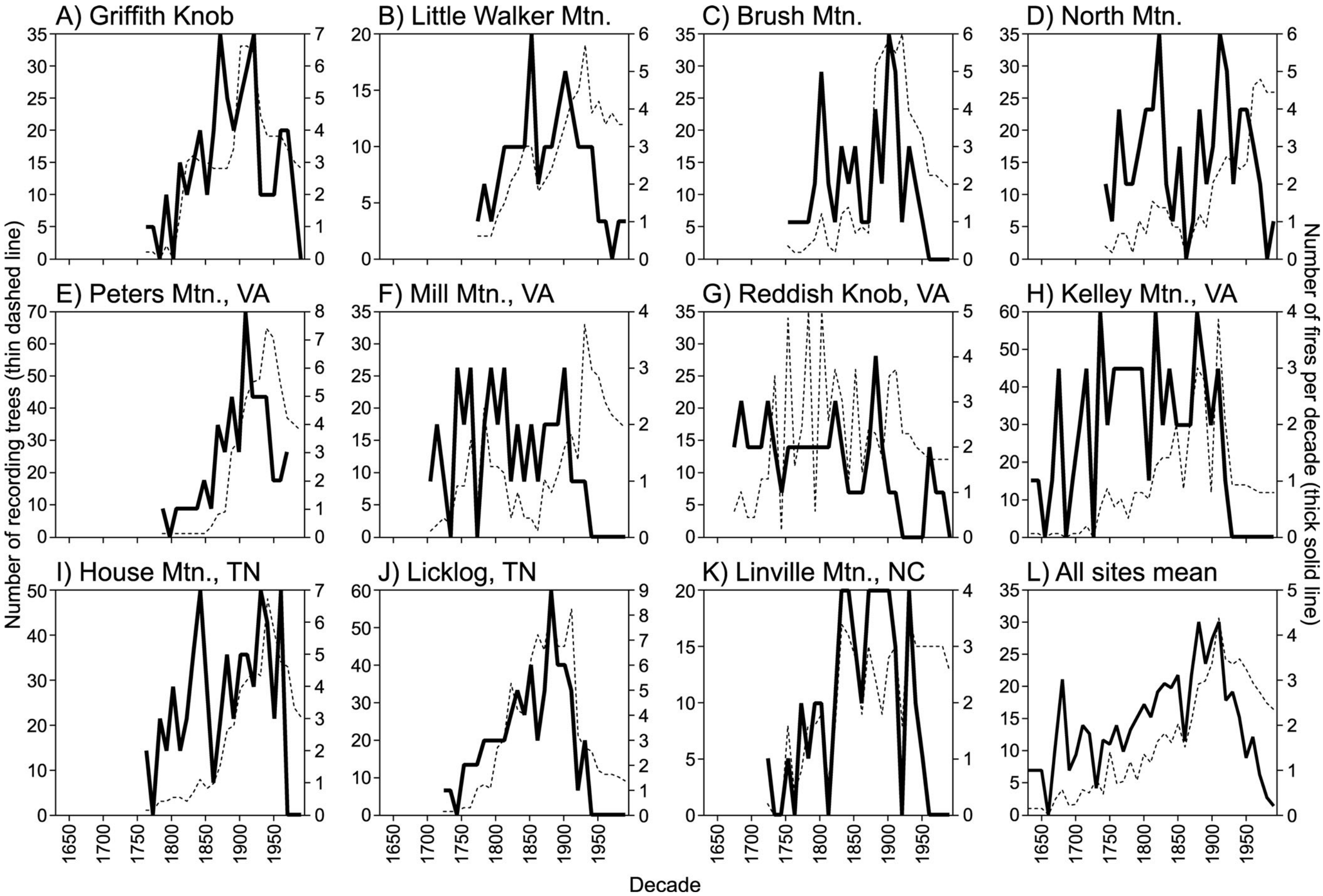

Figure 9. Number of recording trees (dashed line) and fires (solid line) for the Jefferson National Forest sites (A–D) and the seven additional sites (E–K). (L) Average values for the eleven sites.

sites. Given the small sample size of fire-scarred trees in each stand (e.g., one recording tree at the aforementioned stand B in 1806), there is a high probability that the fires burned the intervening stands but left no remaining evidence. In most cases, synchronous burning of multiple stands on the same mountain slope probably indicates that a single fire burned them all. This interpretation is analogous to the reconstruction of large-extent fires using fire-scarred trees on mountainous landscapes of the western United States (e.g., Baisan and Swetnam 1990; Everett et al. 2000; Fule et al. 2003; Grissino-Mayer et al. 2004). Even today in the Appalachian Mountains, wildfires can spread through the hardwood–pine mosaic until they are contained (Flatley, Lafon, and Grissino-Mayer 2011). They must have spread more readily through the flammable, unfragmented landscapes of the past.

A positive feedback can be envisioned where frequent, extensive fires supported open stands with flammable oak and pine litter and combustible grass–shrub understory that fostered the spread of fire (Harrod, Harmon, and White 2000; Nowacki and Abrams 2008; Aldrich et al. 2014). Such a feedback is consistent with recent empirical work in southeastern U.S. forests, where stand conditions associated with burning, mechanical thinning, or both promote conditions of fuel moisture, tree litter composition, and herbaceous fuel biomass that are conducive to fire (Kreye et al. 2018; Vander Yacht et al. 2019; Babl et al. 2020). This feedback could help explain the consistent level of burning through different levels of human activity: Conditioned by a history of fire that predated European settlement, vegetation continued to carry fire over the landscape at short intervals even after Native American depopulation and before large European-American impact. Subsequent population expansion and more intensive land use would have introduced denser ignitions that might have yielded smaller individual fires. Some of the fires represented by only one or a few scars might have been of small extent, especially if

Table 2. Results of the regression analyses conducted for this study

Site	Regression model	R^2
Relationship of NF to the number of RTs per decade for sites across the region. The analyses cover the decades from the beginning of the record through the 1920s.		
Griffith Knob, VA	NF = 0.161 × RT + 1.120	0.65*
Little Walker Mountain, VA	NF = 0.232 × RT + 1.229	0.52*
Brush Mountain, VA	NF = 0.065 × RT + 1.575	0.29*
North Mountain, VA	NF = 0.278 × RT + 1.214	0.50*
Peters Mountain, VA	NF = 0.113 × RT + 1.176	0.74*
Mill Mountain, VA	NF = 0.085 × RT + 1.073	0.24*
Reddish Knob, VA	NF = −0.002 × RT + 1.924	0.00
Kelley Mountain, VA	NF = 0.034 × RT + 1.634	0.19*
House Mountain, TN	NF = 0.076 × RT + 2.590	0.22*
Licklog Ridge, TN	NF = 0.093 × RT + 1.256	0.71*
Linville Mountain, NC	NF = 0.247 × RT − 0.068	0.72*
Mean of all sites	NF = 0.111 × RT + 1.124	
Relationship of DFI to DEC for the Jefferson National Forest sites. Values of DEC range from 1 (for the 1740s) through 19 (for the 1920s).		
Griffith Knob, VA	DFI = − 0.010 × DEC + 0.942	0.04
Little Walker Mountain, VA	DFI = − 0.002 × DEC + 0.899	0.00
Brush Mountain, VA	DFI = − 0.026 × DEC + 1.197	0.15
North Mountain, VA	DFI = − 0.013 × DEC + 1.056	0.08
Relationship of DFI to decadal PDSI for the Jefferson National Forest sites. The analyses cover the decades from the beginning of the record through the 1920s.		
Griffith Knob, VA	DFI = − 0.182 × PDSI + 0.761	0.09
Little Walker Mountain, VA	DFI = − 0.081 × PDSI + 0.849	0.02
Brush Mountain, VA	DFI = 0.121 × PDSI + 0.968	0.02
North Mountain, VA	DFI = 0.215 × PDSI + 1.015	0.13

Note: NF = number of fires/decade; RT = recording trees; DEC = decade; DFI = decadal fire index; PDSI = Palmer Drought Severity Index.
*Significant at the 0.05 level.

constrained by other recently burned patches where fuel had been consumed. Alternatively, they could indicate low-intensity burns that covered a large area but were not intense enough to scar many trees.

Regardless of the mechanisms responsible for their high frequency, fires continued to burn at a consistent level through the period of record until the advent of fire suppression. This long-term consistency matches the DFI patterns for other southern Appalachian sites (Hoss et al. 2008; Flatley et al. 2013; Aldrich et al. 2014) and implies that the region was not swept by a wave of fire that built up during European-American settlement and crested with the extractive industry (McEwan, Dyer, and Pederson 2011; Stambaugh et al. 2018). Instead, the evidence for such a wave in the southern Appalachian region appears to be an artifact of sample size. Whether this is also the case in other areas of the eastern United States with an apparent wave of fire needs exploration. A sample size artifact might exist, for example, in some of the Pennsylvania sites of Stambaugh et al. (2018), given that sample size varies substantially over the period of record. Regardless of those particular sites, fire scar studies from across North America demonstrate that the wave-of-fire model does not apply universally. It seems relevant to some areas (e.g., the Ozark Plateau and the Colorado Front Range) where fire frequency increased under European-American agriculture, logging, or mining activities (Veblen, Kitzberger, and Donnegan 2000; Guyette, Muzika, and Dey 2002). In the Sierra Nevada, however, fire activity rose after aboriginal depopulation (Taylor et al. 2016), and it subsequently fell in the Sierra Nevada and through much of the southwestern United States with intensified livestock grazing that depleted the fine fuels that had carried fire over the landscape (e.g., Baisan and Swetnam 1990; Fule et al. 2003; Grissino-Mayer et al. 2004; Taylor et al. 2016). The only near-universal pattern across the continent is the reduced fire frequency under suppression.

Considerable short-term variability in fire activity is evident, however. Interannual variability is linked to climate for our two western study sites, where

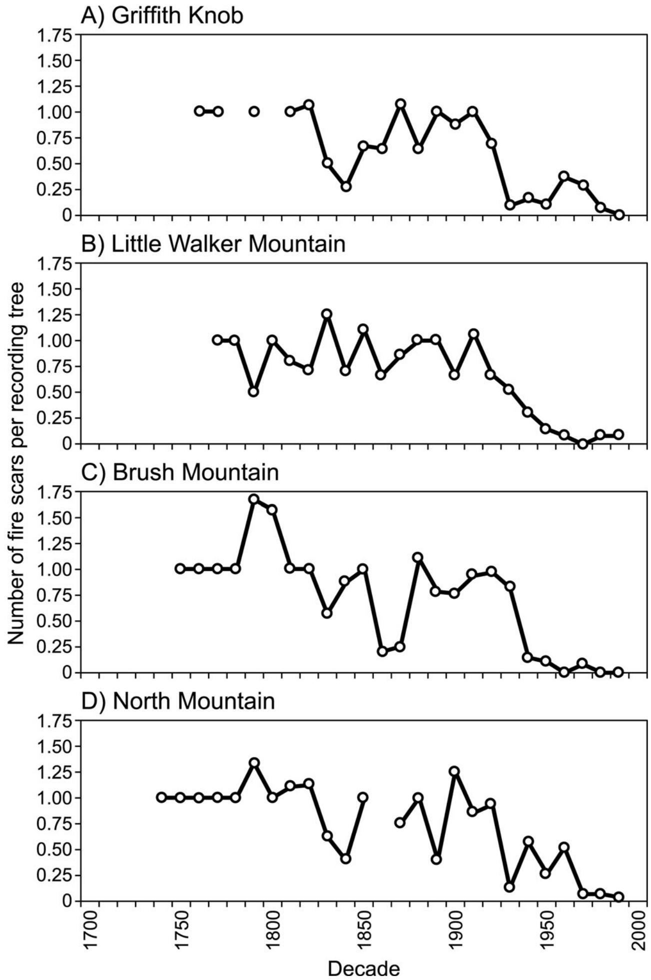

Figure 10. The decadal fire index for each Jefferson National Forest site. A missing value indicates an absence of recording trees in the corresponding decade.

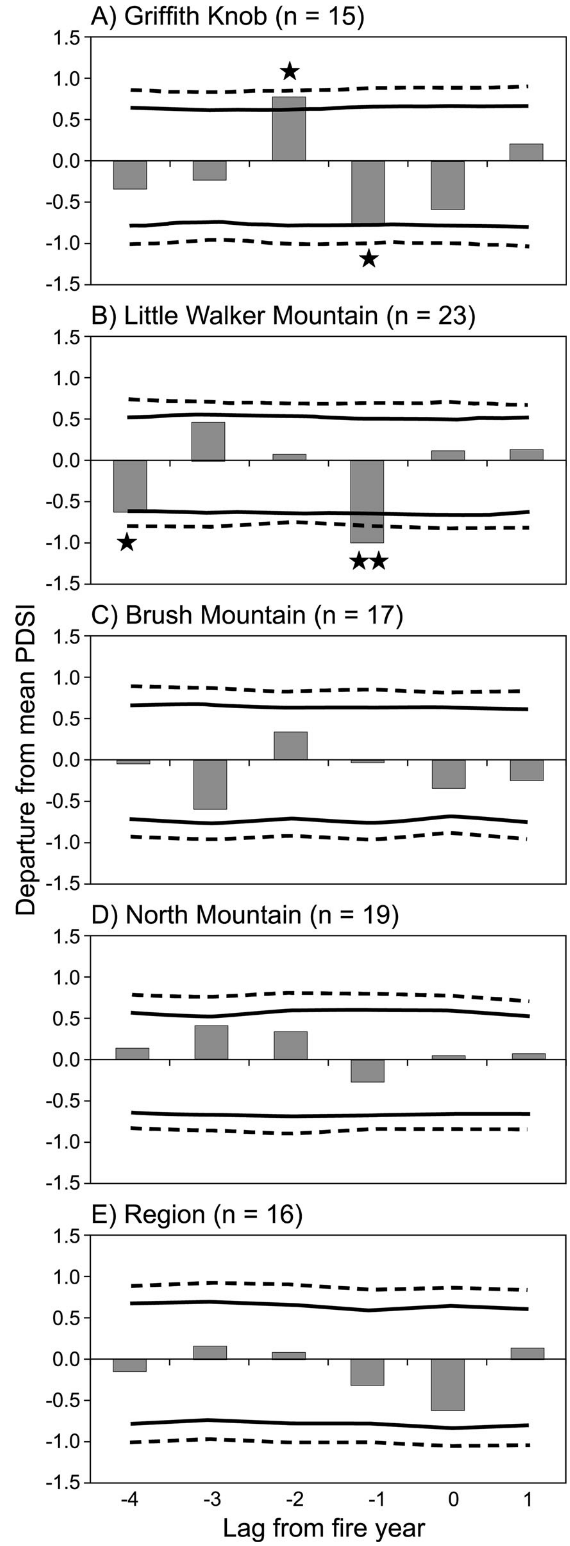

Figure 11. Summary of superposed epoch analysis for major fires. The PDSI for fire years is compared to mean PDSI conditions through the record. Solid and dashed lines indicate confidence intervals (0.05 and 0.01 levels, respectively). Sample sizes refer to the number of fire years analyzed. PDSI = Palmer Drought Severity Index.

SEA indicates a relationship with prior-year drought. Although this relationship emerges at only two sites, it is consistent with a fire–drought link for present-day fires in the Appalachian Mountains (Lafon et al. 2017) and probably reflects autumnal fires recorded by dormant-season scars that formed after dry summers. The seasonal mismatch between PDSI reconstructions (summer) and fires (predominantly fall and spring; Lafon et al. 2017) probably lessens the statistical link between fire and climate (Aldrich et al. 2014) and helps explain the weak fire–drought relationships of the two eastern sites. Human influences could also be at play. People might have overwhelmed the climate influence by choosing not to burn in drought years but to burn in dry windows within wetter years when fuels were dry enough to burn but not to feed damaging wildfires (Schuler

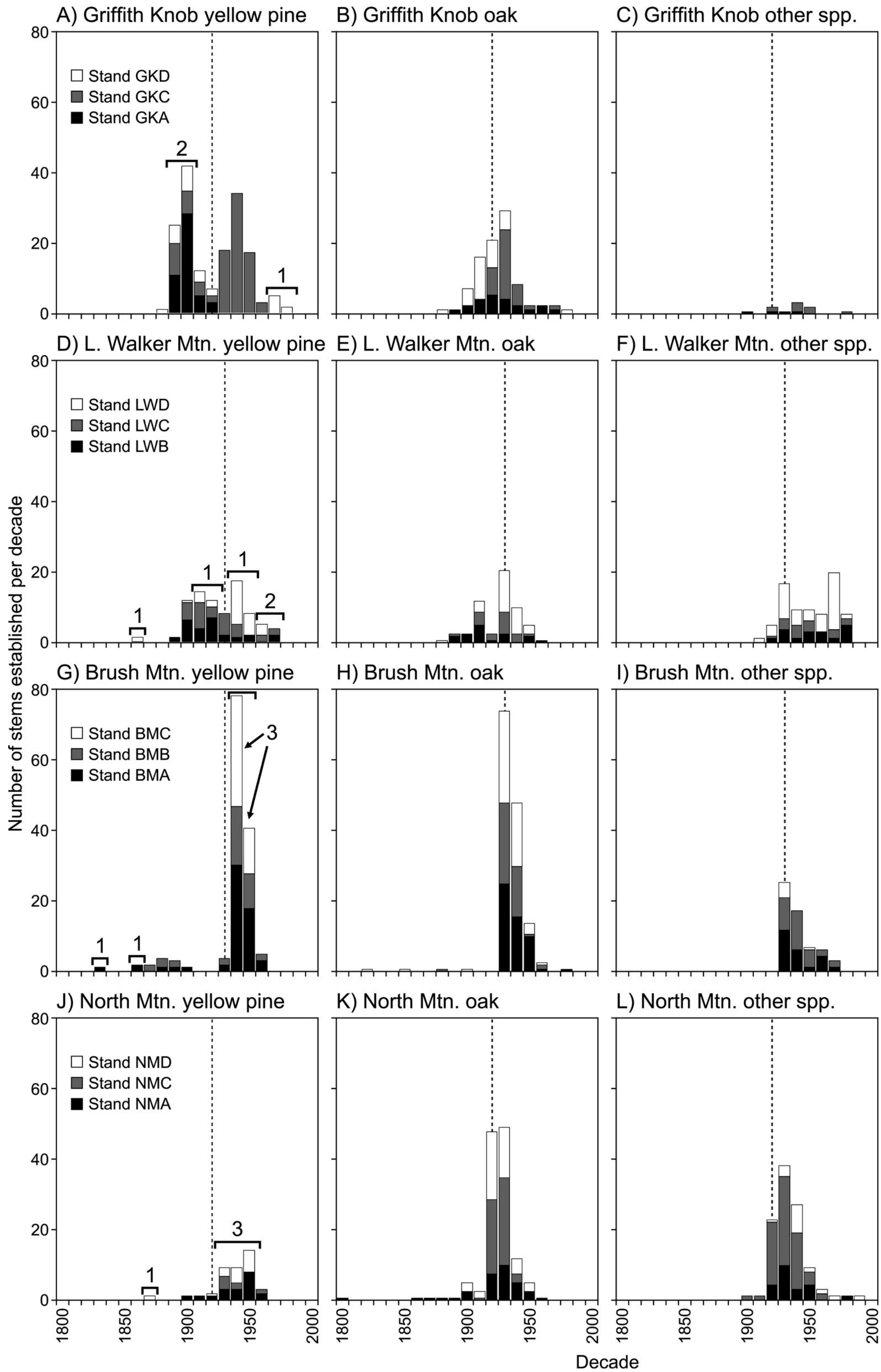

Figure 12. Age structure for the major tree groups. Each row of graphs corresponds to a site. Different bar shading represents different stands. Vertical dashed lines indicate the decade of the last major fire (last fire used to calculate the filtered composite fire interval). The numbers with brackets indicate how many stands had a distinct pine cohort (as defined here) for the bracketed decades. *Note:* One pre-1800 oak tree was cored at North Mountain (in the 1770–1779 decade) but is excluded from these graphs.

Table 3. Mean tree basal area (m^2/ha) and density (stems/ha) across the three plots at each site

	Griffith Knob		Little Walker Mountain		Brush Mountain		North Mountain	
	Basal area	Density	Basal area	Density	Basal area	Density	Basal area	Density
Acer rubrum	<0.1	7	0.2	40	0.1	37	<0.1	13
Carya glabra	<0.1	3						
Nyssa sylvatica	0.2	27	0.5	117	0.6	163	1.5	340
Pinus pungens	14.7	533	9.9	273	12.8	460	5.0	123
Pinus rigida	0.2	3						
Pinus strobus	<0.1	3	0.8	100				
Pinus virginiana	0.1	17			0.1	7	0.3	10
Quercus alba	0.3	23						
Quercus coccinea	0.8	67	0.6	23	1.3	87	3.7	137
Quercus montana	4.1	173	3.2	137	8.2	410	5.0	263
Quercus rubra	0.6	23	0.6	37	<0.1	3	1.1	43
Quercus velutina	0.4	13			0.1	3	0.1	3
Robinia pseudoacacia							<0.1	3
Total	21.4	893	15.8	727	23.2	1,170	16.8	937

Table 4. Mean sapling and seedling density (stems/ha) across the three plots at each site

	Griffith Knob		Little Walker Mountain		Brush Mountain		North Mountain	
	Saplings	Seedlings	Saplings	Seedlings	Saplings	Seedlings	Saplings	Seedlings
Acer rubrum	27	433	43	833	40	733	153	1,217
Carya glabra	7	367						
Castanea dentata	7	17	17	117	3		3	33
Fagus grandifolia		17						
Nyssa sylvatica	17		117	67	317	117	1,127	600
Pinus pungens	437	133	307	83	17		30	
Pinus rigida	7	50						
Pinus strobus	60	17	143	17	3			
Pinus virginiana	53	83						
Quercus alba	23	283	3		3		33	17
Quercus coccinea	330	650	3			133		850
Quercus montana	13	583		600	13	2,500	130	167
Quercus rubra	37	1,567	20	133	10	117	3	133
Quercus velutina		750	50			83	3	
Robinia pseudoacacia	13		50	50				
Tsuga canadensis	10		3					
Total	1,040	4,950	757	1,900	407	3,683	1,483	3,017

and McClain 2003; Flatley et al. 2013). Although people might have intentionally burned more remote areas, including the western sites in our study area, fire was probably less useful because of less convenient access to berry patches or other fire-maintained resources. Therefore, the burning of these sites must have depended more heavily on dry conditions that enabled accidentally or naturally ignited fires to spread into them. This interpretation is consistent with other fire history studies in the southern Appalachian Mountains, where burning was not statistically related to drought (e.g., Schuler and McClain 2003; Flatley et al. 2013; Aldrich et al. 2014) except at two remote locations in the Ridge and Valley of Virginia (Aldrich et al. 2014).

Stand Dynamics

Plot-based age structure and composition, combined with establishment dates of fire-scarred trees, evoke pyrogenic pine–oak communities that occupied the sites under frequent burning. Such vegetation

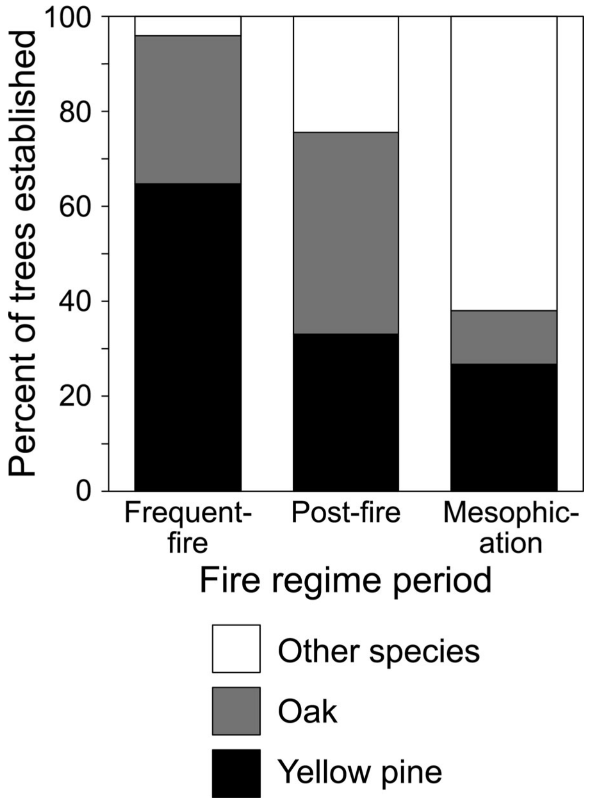

Figure 13. The percentage of each major tree group established in the three fire regime periods.

was present before the industrial-era disturbances. In fact, pine stands likely occupied these slopes for centuries or millennia through a pine–fire feedback that dates back to the Pleistocene (Lafon, Hanson, and Dwight 2019). Although logging and the accompanying wildfires benefited pine and oak reproduction (Williams 1998), the stands are not artifacts of industrial disturbances. The fire-scarred cross sections substantiate this interpretation because they preserve remnants of old pine age classes that are scattered sparsely through the stands and are infrequently detected in the 1,000 m^2 plots.

The stands include multiple cohorts that apparently established after occasional fires of moderate severity. These fires, along with ice storms and southern pine beetle outbreaks (Lafon and Kutac 2003), created patches of varying disturbance severity within or between stands such that relatively intact canopy alternated with large gaps. This disturbance regime would have fostered tree establishment episodes more frequently than a regime of occasional stand-replacing fires. Moreover, frequent surface fires would have maintained relatively open stands that enabled pine establishment without the need for large gaps. This scenario is consistent with a polycyclic fire regime, albeit with the fire cycles differing less strongly in frequency or severity than proposed by Frost (1998): Relatively mild surface fires occurred every few years and were punctuated by mixed-severity fires at intervals of perhaps one to four decades. Similar fire regimes likely existed in other montane pine stands, as suggested by tree establishment data from the southern Blue Ridge Mountains of Tennessee, Georgia, and South Carolina (Brose and Waldrop 2006; Flatley et al. 2013).

Brush Mountain is notable for its mid-1800s cohort, which follows an 1853 fire that could have been unusually severe and provided open conditions that favored pine regeneration. A potential indicator of its high severity is the paucity of fire-scarred cross sections predating the fire in stands B, C, and D. The fire might have consumed most of the older fire-scarred material. Perhaps of greater ecological significance, however, is the reduced burning during the subsequent three decades. Whether the two minor fires recorded during this span were severely limited in extent or were simply mild or patchy fires that proved ineffective at scarring trees cannot be determined. Regardless, the general lack of fire gave tree seedlings time to grow large enough to survive subsequent fires, which scarred the trees after frequent burning resumed in 1882. Consequently, almost all of the fire-scarred trees we sampled date to the 1850s and 1860s, even though the cored trees show that pine establishment continued afterward. These cored trees likely survived in small unburned or lightly burned patches within the larger burned perimeter. Such patchiness is common for wildfires (Kolden et al. 2012) and represents another level of spatial heterogeneity with important consequences for pyrogenic vegetation dynamics.

The twentieth-century pulse in tree establishment, observed at all four sites and at other Appalachian locations at the beginning of the fire suppression era (Williams and Johnson 1990; Brose and Waldrop 2006; Aldrich et al. 2010; Flatley et al. 2015), reflects favorable establishment conditions in open stands that had previously been maintained by frequent fire. With fire no longer common, pines, oaks, and other taxa readily established in the open stands until they became overcrowded. This establishment pulse did not coincide with climatic wetness, as proposed by some researchers (McEwan, Dyer, and

Pederson 2011). In fact, most of the trees date to the relatively dry decades of the 1920s through 1950s, not wetter decades such as the 1910s or 1970s (cf. PDSI available from National Centers for Environmental Information 2019). This finding supports the argument (Nowacki and Abrams 2015) that fire suppression, not climate change, is the primary driver of mesophication.

At the time of our sampling in 2003 to 2005, Table Mountain pine and chestnut oak remained dominant in the overstory, which was probably denser than in the past owing to the large cohort of pine and oak established with the onset of fire suppression. Historically, such cohorts would have been thinned by subsequent fires. The understory, meanwhile, shifted to a more diverse tree assemblage that includes fire-intolerant species such as black gum, red maple, and white pine This compositional shift likely portends a long-term successional change in overstory composition consistent with mesophication. Litter and shade cast by these species will gradually reduce forest flammability and diminish the likelihood of burning.

Conclusion

Frequent burning and pyrogenic vegetation did not originate during the industrial era in the southern Appalachian Mountains. Fires occurred frequently before extensive European-American land use and industrialization such that a distinct wave of fire is not evident. The wave-of-fire model seems to apply only in certain regions of the United States and is therefore not a generally applicable hypothesis. Rather, the fire history of any region depends on its particular circumstances of history and geography. This study and others from the southern Appalachian region suggest that frequent burning was maintained by large-extent fires, ignited by people and lightning, that burned across the mountain slopes and spread through a flammable vegetation mosaic to encompass the pine stands and surrounding hardwood forests. The flammable mosaic was itself a consequence of fire history, a result of a positive feedback where fire promoted open stands of oak and pine with combustible litter. These forests were burned primarily by surface fires that impeded the establishment of mesophytic species. As fires passed through the pine stands, however, they sometimes burned with greater severity and generated large openings where pine cohorts became established. Thus, the historical fire regime of the pine stands appears to have been a polycyclic fire regime.

Suppressing this fire regime disrupted the fire–vegetation feedback and contributed to the development of dense stands where conditions no longer favor the long-term maintenance of pine, oak, and other fire-dependent taxa. For resource managers seeking to restore the historical pyrogenic vegetation (e.g., U.S. Department of Agriculture Forest Service 2004), controlled burning will be necessary. Low-severity, low-risk burns, however, might not suffice because they will not adequately thin the dense vegetation that inhibits the establishment and growth of shade-intolerant oak and pine. More severe fires or mechanical thinning might also be needed. Our results suggest the Appalachian pine stands are resilient to occasional high-severity fires.

This study contributes to a growing body of evidence demonstrating the historical importance of fire across the temperate forest region of eastern North America. This region harbors tree species with serotinous cones, thick bark, and other fire adaptations that imply a long history of fire. This work and other recent fire scar studies provide explicit evidence of that fire history. They demonstrate that fire occurred frequently in the past and that it helped maintain fire-dependent vegetation until the historical fire regimes were disrupted in the twentieth century.

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