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Fire Ecology

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Fire history and vegetation data reveal ecological benefits of recent mixed-severity fires in the Cumberland Mountains, West Virginia, USA

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Abstract

Background: Without periodic fire, fire-adapted plant communities across the Central Hardwood Forest Region (CHF) in the USA have undergone significant changes in forest structure and species composition, most notably a decrease in oak regeneration and herbaceous diversity and an increase in shade-tolerant, fire-sensitive tree species. In this study, we conducted a comparative analysis of two mixed pine-oak (*Pinus-Quercus)* forests with different land management histories in the Cumberland Mountains of southern West Virginia where fire ecology and fire effects are understudied. We reconstructed the fire history of both sites from fire-scarred shortleaf pine (*Pinus echinata* Mill.) and pitch pine (*Pinus rigida* Mill.) trees to describe variation in the fire regimes over time. We also made plant community measurements that spatially coincided with fire-scarred pines to assess present-day plant community structure in relation to recent fire history.

Results: Before 1970, fires at Hite Fork and Wall Fork occurred frequently and almost exclusively in the dormant season, every 7–8 years on average. The fire regimes diverged in the Post-Industrial era (1970–2020), during which there was a single fire at Wall Fork, while six major fires, scarring more than 40% of sampled trees, occurred between 1985 and 2017 at Hite Fork. Four of these dormant-season fires correspond to late fall incendiary fires in the observational record. These differences in recent fire history had large effects on plant community structure. Recent mixed-severity fires at Hite Fork likely caused mortality of pole-sized trees and opened the canopy, creating conditions favorable for pine recruitment and resulted in significantly higher species richness in the herbaceous layer compared to Wall Fork, which exhibited the effects of mesophication.

Conclusions: Our results suggest that frequent mixed-severity fire in pine-oak forests of the Cumberland Mountains can meet management objectives by reducing mesophytic tree abundance, increasing herbaceous diversity and pine recruitment, and generally promoting forest heterogeneity.

Keywords: Fire effects, Fire history, Mesophication, Oak forests, Pitch pine, Shortleaf pine

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Resumen

Antecedentes: Sin fuegos periódicos, las comunidades vegetales adaptadas al fuego en los bosques de madera dura de la Región Central (CHF) de los EEUU, han experimentado cambios significativos en estructura y composición de especies, más notablemente en una disminución de la regeneración de robles y diversidad de herbáceas y un incremento en las especies arbóreas tolerantes a la sombra y sensibles al fuego. En este estudio, realizamos un análisis comparativo de dos bosques mixtos de roble y pinos (*Pine-oak forests*) con diferentes historias de manejo en las montañas de Cumberland del sur de West Virginia donde la ecología del fuego y los efectos del fuego han sido poco estudiados. Reconstruimos la historia del fuego de ambos sitios mediante el estudio de cicatrices de fuego en árboles de pino de hoja corta (*Pinus echinata* Mill) y pino bronco (*Pinus rigida* Mill) para describir la variación, en el tiempo, de los regímenes de fuego. Hicimos también mediciones en las comunidades de plantas que coincidieron espacialmente con los pinos con cicatrices de fuego para determinar la estructura actual de las comunidades de plantas en relación con la historia reciente de los fuegos.

Resultados: Antes de 1970, los fuegos en Hite Fork y Wall Fork ocurrían frecuentemente y casi exclusivamente en la estación de dormición, cada 7-8 años en promedio. Los regímenes de fuego divergieron en la era postindustrial (1970-2020), durante la cual hubo un solo incendio en Wall Fork, mientras que cinco fuegos grandes, que dejaron cicatrices en el 40% de los árboles muestreados, ocurrieron entre 1985 y 2017 en Hite Fork. De acuerdo a los registros de observaciones, cuatro de esos fuegos ocurrieron en la estación de dormición y correspondieron a fuegos incendiarios de otoño. Esas diferencias en la historia reciente de fuegos tuvieron grandes efectos sobre la estructura de la comunidad. Fuegos recientes de severidad mixta en Hite Fork causaron probablemente la mortalidad de árboles de gran fuste y abrieron los doseles, creando condiciones favorables para el reclutamiento de pinos y resultando en un significativo incremento en la riqueza de especies herbáceas del sotobosque comparado con Wall Fork, que exhibió los efectos de una mesificación.

Conclusiones: Nuestros resultados sugieren que los fuegos de severidad mixta en los bosques mixtos de las montañas Cumberland pueden cumplir con objetivos de manejo mediante la reducción en la abundancia de árboles de especies mesófilas, incrementando la diversidad de herbáceas y el reclutamiento de los pinos y promoviendo en general la heterogeneidad del bosque.

Background

Fire is a critical biophysical process that influences the distribution of species and ecosystems on Earth (Bond et al. 2005; Bowman et al. 2009; Archibald et al. 2018). For millennia, complex interactions between climate, vegetation, and human societies (i.e., land use) have determined fire regime characteristics, including the frequency, severity, spatial extent, and seasonal timing of fire. Globally, however, fire regimes are changing rapidly, driven by climate change and by land use policies that alter fuel loads and ignition patterns or encourage fire suppression (Bowman et al. 2013; Kelley et al. 2019; Rogers et al. 2020). Understanding these changes at multiple spatial and temporal scales is particularly important for the conservation and maintenance of fire-dependent and fire-adapted species and ecosystems. In woodlands and forests, frequent fire can promote tree regeneration and enhance herbaceous diversity in fire-adapted species, stimulate seed germination, and increase resource availability, including light, growing space, and nutrients (e.g., Hutchinson et al. 2005; Izbicki et al. 2020). In the long-term absence of fire or other disturbances that create large canopy gaps, these landscapes can become homogeneous, with decreased species and structural diversity, and may experience a threshold change in ecosystem structure and function (Bond et al. 2005; Sugihara et al. 2006).

The period of fire exclusion that began in approximately 1930 in North America has had negative consequences for oak (*Quercus*) and mixed pine (*Pinus*)—oak ecosystems throughout the Central Hardwood Forest Region (CHF) (sensu Hart and Buchanan 2012; Varner et al. 2016). Without recurrent fire, the abundance of shade-tolerant, fire-sensitive tree species (e.g., red maple, *Acer rubrum* L.) has increased in historically oak and pine-dominated forests (Lorimer 1984; Cain and Shelton 1995; Abrams 1998; McEwan et al. 2011). The consequences of these shifts in tree species composition are multifold. First, increases in shade-tolerant species abundance decrease light availability in the understory and mid-story with negative consequences for more shade-intolerant species (e.g., oaks and pines) and increase competition for light between pines, oaks, and shade-tolerant species in the regeneration layer (Abrams 1992; Cain and Shelton 1995). This can result in regeneration failure for oaks (Lorimer 1984; Lorimer et al. 1994; McEwan et al.

2011) and pines (Vose et al. 1994; Cain and Shelton 1995) or prevent seedlings from recruiting into the sapling layer (Parker et al. 1985; Fei et al. 2005). Second, increases in shade-tolerant tree species and decreases in oak and pine species result in more moist, humid conditions, thereby decreasing flammability of surface fuels and reducing the occurrence of fire (Nowacki and Abrams 2008). The consequences of fire exclusion described here, along with more intense herbivory from white-tailed deer (*Odocoileus virginianus* Zimm.) and acorn foraging by wild turkey (*Meleagris gallopavo* L.) (McEwan et al. 2011) as well as a regional wetting trend (Kutta and Hubbart 2019), explain observed increases in mesic conditions over the last several decades in the CHF (i.e., "mesophication"; Nowacki and Abrams 2008, McEwan et al. 2011). Collectively, these changes in forest structure and composition have important implications for the persistence of mixed pine-oak forest ecosystems and the ecological benefits they provide.

In recent decades, prescribed fire has increasingly been used as a management tool to reduce shade-tolerant or mesophytic tree cover, promote oak and pine regeneration, diversify wildlife habitat, and manage forest fuels in oak and mixed pine-oak forests across the CHF (e.g., Brose et al. 2001; Waldrop 2014). Recent studies have shown that repeated burning (multiple fires within 10–20 years) can reduce shade-tolerant or mesophytic tree abundance (Blankenship and Arthur 2006; Izbicki et al. 2020; Borden et al. 2021) and promote oak (Hutchinson et al. 2012; Brose et al. 2013) and pine recruitment (Barden and Woods 1976; Black et al. 2018), but these effects can be variable and dependent on landscape position and pre-fire forest structure (Alexander et al. 2008; Arthur et al. 2015). Other factors, such as the timing and severity of prescribed fire, can also influence its effects. Prescribed fires conducted in the late winter-early spring before leaf out have been preferred by managers because of relatively low ambient temperatures and predictable wind patterns that reduce the risk of fire escape (Waldrop and Goodrick 2012). Recent research from the Southern Appalachians, however, suggests a potential to widen the burn window to include early growing season burns that result in greater burn coverage (Vaughan et al. 2021), a theme suggested earlier by Waldrop et al. (2016) who concluded that prescribed fire should not only be conducted more frequently, but in different seasons, otherwise management objectives may not be realized. In locations where wildfires continue to occur, such as in parts of the Southern and Central Appalachian Mountains, active management of these fires, rather than suppression, presents new opportunities for learning about fire behavior and its effects on vegetation and wildlife (Hiers et al. 2020).

Dendroecological reconstructions of fire provide an additional source of information for the implementation of prescribed fire. These high-resolution records of precisely dated scars embedded within the annual growth rings of trees can provide estimates of historical fire regime characteristics, including the frequency, severity, extent, and season of fire occurrence at multiple spatial and temporal scales (Falk et al. 2011). Networks of fire-scar data are expanding (see Margolis and Guiterman 2021), but site selection continues to be guided by the presence of pine or pine-oak stands because resinous pine species are better recorders of fire and more resistant to decomposition, especially in the CHF (Greenberg et al. 2021), with some exceptions (e.g., McEwan et al. 2007; Hutchinson et al. 2008). In the Appalachian Mountains, from eastern Tennessee to Pennsylvania, fire-scar records extend from the seventeenth century to the present, with sample depth at most sites declining rapidly in the eighteenth century (Lafon et al. 2017). These sites are concentrated in the Ridge and Valley physiographic province, the Blue Ridge Mountains, and on the western edge of the Appalachian Plateau in Ohio and Kentucky, while recent studies have addressed knowledge gaps along the Cumberland Plateau from Kentucky to Alabama (Hutchinson et al. 2019; Stambaugh et al. 2020). Mean fire intervals across the region range from approximately 2 to 12 years during the pre-exclusion era (pre-1930) and fire scars are completely or nearly absent from most site records after 1950. These fire histories provide contextual evidence for the use of fire in managing pine and pine-oak forests in the region, but there have been no relevant studies in Cumberland Mountains ecoregion (Woods et al. 1999), where regional wildfire activity has been concentrated since at least the 1980s (Fig. 1a). In this region, there are opportunities to examine uninterrupted exclusion-era fire regimes similar to those in Pennsylvania (Saladyga and Standlee 2018) and in the Red Hills Region on the Florida-Georgia border (Rother et al. 2020).

Our primary objective was to conduct a comparative analysis of the fire history and present-day plant community structure for two mixed pine-oak forests in the Cumberland Mountains ecoregion in southern West Virginia. We selected two sites with similar terrain characteristics, soil properties, overstory tree composition, and prevailing climate, but with different land management histories. Our approach integrates fire history and detailed plant community measurements to evaluate the effects of fire (or lack thereof) in mixed pine-oak forests dominated by shortleaf pine (*Pinus echinata* Mill.) and pitch pine (*P. rigida* Mill.), a vegetation type that is not well understood in West Virginia and is declining throughout its range (Oswalt 2012; South and Harper 2016). Specifically, we asked the following: (1) How do site fire histories differ

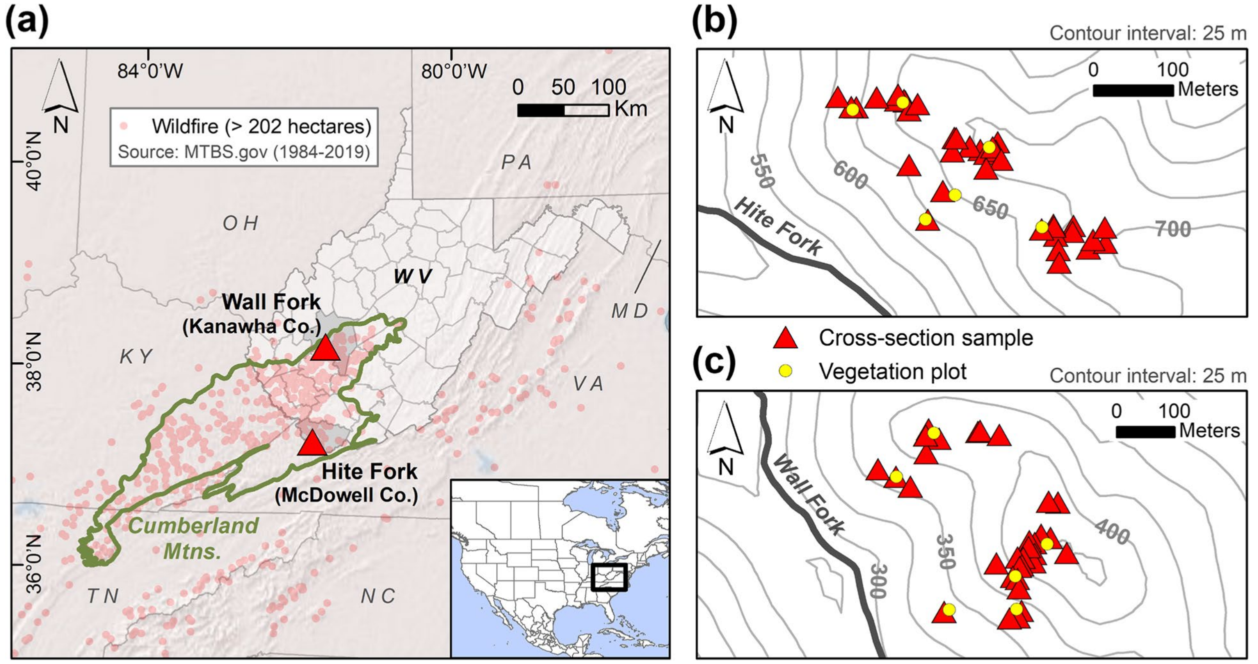

Fig. 1 Locations of fire history sites (Hite Fork and Wall Fork) within the Cumberland Mountains ecoregion. Large wildfires from the Monitoring Trends in Burn Severity (MTBS) (2020) database are shown for reference (**a**). Distribution of vegetation plots and cross-section samples cut from fire-scarred shortleaf pine (*Pinus echinata*) and pitch pine (*P. rigida*) trees at Hite Fork (**b**) and Wall Fork (**c**)

in terms of fire frequency, seasonality, and severity during the period of regional industrialization and in more recent decades? (2) Do stand and age structure differ between sites and, if so, how are these differences related to fire history? (3) How has recent fire history influenced tree regeneration? (4) How does plant species richness and composition differ between the two sites in relation to recent fire history? Answers to these questions will provide insights into the use of fire in managing similar pine-oak forests in the Cumberland Mountains and in promoting resilient forest landscapes across the CHF.

Methods

Study area

Hite Fork (37.308889, −81.785278) and Wall Fork (38.252778, −81.626667) are located within the Cumberland Mountains ecoregion in southern West Virginia (Fig. 1a). The Cumberland Mountains, or "Dissected Appalachian Plateau," is an approximately 30,000 km^2 extensively forested ecoregion stretching from northeastern Tennessee to south-central West Virginia. Its deeply dissected terrain, characterized by steep slopes and narrow valleys, is underlain by Pennsylvanian sandstone, shale, and coal of the Pottsville group (Woods et al. 1999). The latter carbon reserves, along with the region's vast timber resources, drew the attention of nineteenth century industrialists who rapidly expanded railroad networks across the rugged and remote terrain. By the early twentieth century, much of the land that was previously owned by individual families was acquired by corporate interests. The coal industry grew to dominate regional and local politics and gained control of local economies by establishing company towns. Population in many counties increased five- to tenfold between the end of the nineteenth century and 1950 (US Census Bureau 2021), but by the 1960s the coal industry was in decline and mechanization significantly reduced the need for underground mine labor. Today, with some exceptions, populations are a fraction of those seen 70 years ago, and there are perennially high rates of unemployment and poverty (Appalachian Regional Commission 2021).

Hite Fork is situated on a remote tract of land owned by the Lyme Timber Company within two miles of the Virginia border in McDowell County. Between 1890 and 1950, the population in McDowell County increased more than 1200%, but decreased by 81% between 1950 and 2020 (US Census Bureau 2021). In contrast, Wall Fork is located within Kanawha State Forest (est. 1938) less than 10 km from the state capital, Charleston—the most populous city in West Virginia—and the historically well-traveled Kanawha River Valley. Kanawha County's population increased 460% between 1890 and 1950, followed by a 25% decrease between 1950 and 2020 (US Census Bureau 2021). Recent unemployment

(2009–2019) and poverty (1990–2019) rates in McDowell County have been consistently above 9% and 30%, respectively, while rates were markedly lower in Kanawha County, where unemployment was 5–7% and poverty was 15–17% for the same time periods (Appalachian Regional Commission 2021). In recent decades (1987–2020), incendiary fires, which are common in other post-industrial landscapes in the CHF (e.g., Saladyga and Standlee 2018), burned 76,000 hectares (65% of total area burned) of forestland in McDowell County and 62,000 hectares (48% of total area burned) in Kanawha County, while fires caused by lightning accounted for less than 1% of the total area burned in both counties (West Virginia Division of Forestry, unpublished data).

We used leaf-off aerial imagery to identify and delineate multiple mixed pine-oak stands at Hite Fork and Wall Fork (Fig. 1b, c). Both sites are characterized by steep south- to southwest-facing slopes with similar rocky, well-drained, acidic soils, but Hite Fork is approximately 300 m higher in elevation (Additional file 1: Table S1, Fig. 1b, c). The plant community at both sites is classified as the imperiled (G2) Shortleaf Pine–Chestnut Oak (*Quercus montana* Willd.)–[Scarlet Oak (*Q. coccinea* Muenchh.), Black Oak (*Q. velutina* Lam.)] Forest association, which often includes other tree species, such as pitch pine, blackgum (*Nyssa sylvatica* Marsh.), and sourwood (*Oxydendrum arboreum* L.) (NatureServe Explorer 2021). Climate in the region is continental with hot, humid summers and cold winters. In McDowell County, total annual precipitation is 117.4 cm and mean annual temperature is 12.2 °C, ranging from a low of 1.0 °C in January to a high of 22.7 °C in July (1991–2020) (NOAA 2021). It is slightly wetter and warmer in Kanawha County, where total annual precipitation is 118.7 cm and mean annual temperature is 12.9 °C, with monthly temperatures ranging from 1.2 °C in January to 23.8 °C in July (1991–2020) (NOAA 2021).

Fire-scar data and analysis

We collected samples from fire-scarred shortleaf pine and pitch pine trees at Hite Fork ($n = 36$) and Wall Fork ($n = 33$) in May 2021. An individual live or standing dead tree was selected for sampling based on visual evidence of fire scarring, its geographic coordinates and elevation were recorded, and a partial cross section was cut with a chainsaw at a height of 20–50 cm above ground (Arno and Sneck 1977). No fire-scarred stumps or logs were present for sampling at either site. At Wall Fork, two increment core samples were collected from 16 living canopy-dominant shortleaf pine trees without external evidence of fire scarring for the purpose of developing a master dating chronology. No core samples were collected for this purpose at Hite Fork due to the preponderance of fire-scarred overstory pine trees.

All tree core and cross-section samples were air-dried for at least 2 weeks before surfacing with progressively finer sandpaper (up to 1200 grit) in preparation for dating (Speer 2010). We then used a large-format scanner (1200XL, Epson, Suwa, Japan) to capture a high resolution (2400 dpi) digital image of tree core and cross-section samples. Each image was uploaded into the program CooRecorder 9.4 (Larsson 2016) and annual rings were measured to the nearest 0.01 mm. We statistically crossdated all cross sections against a master chronology developed from the Wall Fork shortleaf pine tree cores using the program CDendro 9.4 (Larsson 2016). An existing tree-growth chronology was used to crossdate two cross-section samples collected at Wall Fork that predated the 1840s (Cockrell et al. 2017). All statistical crossdating was quality checked in the XDateR application (Bunn 2010) and any flagged segments were evaluated visually under a stereomicroscope to confirm dating.

We assigned fire scars identified in each cross-section sample to a calendar year and, whenever possible, the season of occurrence based on the relative position within annual growth rings (Fig. 2) (e.g., Stambaugh et al. 2020). Scars that occurred during the dormant season between annual growth rings were assigned to the calendar year after scarring. Compartmentalized injuries of other possible origins that did not correspond to a fire scar in at least one other tree in the same stand or did not contain charcoal or resin were labeled as “injury” and excluded from subsequent analyses (see Fig. 2b).

We entered all fire-scar and injury data in FHX2 format and calculated site composite fire interval statistics in Fire History Analysis and Exploration System (FHAES) software (Brewer et al. 2016). For both sites, we calculated mean fire interval (MFI) and Weibull median fire interval (WMFI) using years when at least two trees were scarred for the entirety of both records, during the full comparison period (1890–2020), and for the Boom and Bust (1890–1969) and Post-Industrial (1970–2020) eras. The comparison period begins with the first decade when sample size at both sites is at least 10 trees, while the two socioeconomic eras correspond to periods of regional social and economic volatility (“Boom and Bust”) and industrial decline and population loss (“Post-Industrial”) (Colias 2002). We used the Mann-Whitney U test to assess differences in filtered MFI and percentage of trees scarred between sites and across socioeconomic eras. For both sites, we calculated relative fire extent (RFE) for years when at least five trees and 20% of samples were scarred (hereafter “major fires”) using a convex hull polygon method (Marschall et al. 2019). The RFE is not a measure of actual area burned, but rather an estimate of fire extent in direct proportion to the area represented by recording (or live) trees in a given year. We

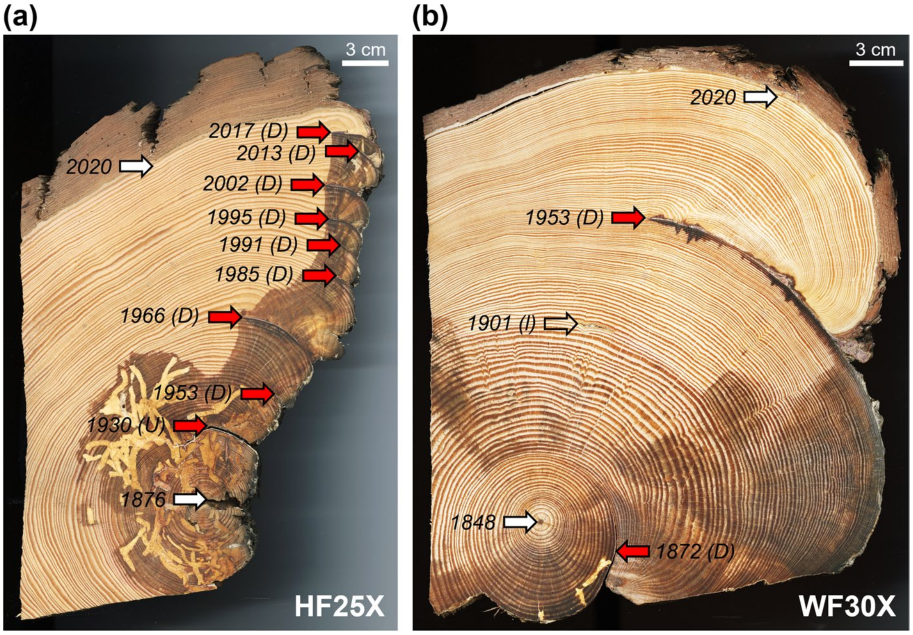

Fig. 2 Partial cross-sections cut from a fire-scarred shortleaf pine (*Pinus echinata*) at Hite Fork (**a**) and Wall Fork (**b**). Fire-scar years, including seasonality (D = dormant; U = undetermined), are highlighted by red arrows, while white arrows denote pith (1848), inner-ring (1876), and outer-ring (2020) years. The open arrow in **b** indicates an injury of unknown origin that was not included in the fire history analysis

compared these major fire years to the West Virginia Division of Forestry's unpublished county-level (1940–1986) and detailed spatial (1987–2020) databases as well as the Monitoring Trends in Burn Severity database (1984–2019) (MTBS 2020). When possible, we identified the season or date of likely occurrence and cause of fire.

Plant community sampling

We used the West Virginia Natural Heritage Program (WVNHP) vegetation plot sampling protocol (Byers et al. 2007; Vanderhorst et al. 2007) to characterize the plant community and quantify tree recruitment. This methodology was used to facilitate future comparisons to more than 4000 existing WVNHP vegetation plots, including several mixed pine-oak forest stands. Six 400 m^2 vegetation plots were established at both sites in close proximity to fire-scarred pine trees (Fig. 1b, c). The number and location of plots per site were optimized to sufficiently characterize the plant community in each stand and span the spatial extent of the mixed pine-oak stands that occurred within a greater matrix of oak-dominated or mixed mesophytic forest. Plots were chosen to meet the following criteria: (1) shortleaf pine or pitch pine overstory trees were present, (2) fire-scarred trees were located within or immediately adjacent to the plot, (3) the plot was representative of the stand and relatively homogenous throughout, and (4) stands had SW to W aspects. Plots were placed at least 50 m apart from one another and were located to run across the slope. All plots were permanently marked using four 12″ pieces of steel conduit placed in each of the four corners with 5″ exposed above the surface.

In each plot, we recorded the presence of all vascular plant species, and estimated percentage cover for each species for multiple strata that were defined by relative height (t2: canopy, t3: subcanopy, s1: tall shrub, s2: short shrub, and h: herbaceous) (Byers et al. 2007; Vanderhorst et al. 2007). Cover by strata characterizes the general physiognomy of each stand, along with the abundance of individual species within vertical strata. For example, a woody vine could be present in the t2 layer if climbing a canopy-dominant tree. In addition, each species was assigned a total percentage cover within each plot that represented cover across all strata. Any unknown plants were collected, pressed, and later identified and deposited in the Marshall University Herbarium. Taxonomy is consistent with Weakley (2020). All trees (stems above 1.37 m tall and greater than or equal to 7 cm diameter at breast height (DBH)) were identified to species, counted according to the strata described above, and DBH was measured (Byers et al. 2007; Vanderhorst et al. 2007). All pine seedlings (individuals below 1.37 m) were counted within each 400 m^2 plot. Within 10% of each plot (40 m^2), all other tree seedlings were identified and tallied by species using a 4 m × 10 m belt transect. Although we did not count saplings (individuals above 1.37 m and less than 7 cm DBH), we characterized sapling abundance using tree species percent cover in the s1 layer, which represents all tree individuals 1 to 5 m in height, including taller seedlings.

We also collected two increment cores from eight trees of any species located closest to plot center in order to describe tree age distribution at both sites. To account for variation in diameter-age relationships, we selected four trees from the 10–20 cm DBH class, while an additional four trees greater than 20 cm DBH were cored. In some cases, it was necessary to core trees within 10 m of a plot when tree density was low or if no sound trees (lacking rot) were available. After being dried, mounted, and surfaced, samples collected from pine species were visually crossdated against the Wall Fork master chronology, while cores from hardwoods were skeleton plotted and crossdated by species (Yamaguchi 1991; Speer 2010). We estimated tree age (at coring or cutting height) based on the width and curvature of the innermost rings for all age structure cores and pine cross-section samples that did not include pith (Applequist 1958). Samples with an inner-ring year more than 10 years from estimated pith were excluded from age structure analysis. We interpreted tree establishment cohorts as evidence of mixed-severity fire in the site fire histories (e.g., Lafon et al. 2021).

A variety of other site-level variables were collected for each plot including, elevation, slope, aspect, and slope inclination. Soil samples were collected from the top 10 cm of the mineral horizon at four locations in each plot and were dried at 68 °C for 72 h and then sieved. Samples were then analyzed by Brookside Labs Inc. for soil chemical and physical properties, including percentage sand, silt, and clay, pH, and percent organic matter.

Plant community analysis

Tree species were assigned to one of five species groups (*Pinus* spp, *Quercus* spp., pyrophyte, intermediate, and mesophyte) to characterize tree compositional differences with regard to fire tolerance at Hite Fork and Wall Fork. The *Pinus* spp. group included shortleaf pine and pitch pine, while the *Quercus* spp. group included white oak (*Q. alba* L.), scarlet oak, blackjack oak (*Q. marilandica* Muenchh.), chestnut oak, northern red oak (*Q. rubra* L.), post oak (*Q. stellata* Wangenh.), and black oak. Species not included in the *Pinus* spp. and *Quercus* spp. groups were identified as either pyrophytes, intermediates, or mesophytes according to the fire tolerance classification of Arthur et al. (2021). Eight tree species documented in our sites were not included in Table 1 of Arthur et al. (2021) and were assigned to a category (pyrophyte, intermediate, or mesophyte) based on fire tolerance in the USDA PLANTS database (USDA NRCS 2021) and the US Forest Service Fire Effects Information System (FEIS; Abrahamson 2022). Trees classified as pyrophytes were pignut hickory (*Carya glabra* (Mill.) Sweet), mockernut hickory (*Carya tomentosa* (Lam.) Nutt.), American chestnut (*Castanea dentata* (Marshall) Borkh.), bigtooth aspen (*Populus grandidentata* Michx.), and black locust (*Robinia pseudoacacia* L.). Intermediate species included downy serviceberry (*Amelanchier arborea* (Michx. f.) Fernald), flowering dogwood (*Benthamidia florida* L.), white ash (*Fraxinus americana* L.), blackgum, American hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), and sassafras (*Sassafras albidum* (Nutt.) Nees). Mesophytes included red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marshall), American beech (*Fagus grandifolia* Ehrh.), tulip poplar (*Liriodendron tulipifera* L.), cucumber

Table 1 Fire history statistics for Hite Fork (HF) and Wall Fork (WF) during the full comparison period and during the "Boom and Bust" and "Post-Industrial" socioeconomic eras. Fire years and associated statistics are based on a two-scar minimum filter. *MFI* mean fire interval, *SD* standard deviation, *WMFI* Weibull median fire interval, *na* insufficient number of fire intervals to calculate statistics

	Full comparison		**Boom and Bust**		**Post-Industrial**	
	1890–2020		1890–1969		1970–2020	
Fire history statistic	HF	WF	HF	WF	HF	WF
Mean sample depth	27.3	25.3	21.8	21.1	35.9	32.0
Number of scars	184	65	57	51	127	14
Number of fire years	18	10	12	9	6	1
Earliest fire	1894	1898	1894	1898	1985	2007
Latest fire	2017	2007	1968	1965	2017	2007
MFI (years)	7.2	12.1	6.7	8.4	6.4	na
SD (years)	4.7	12.6	4.7	4.7	2.9	na
Range (years)	1–17	2–42	1–16	2–20	4–11	na
WMFI (years)	6.5	9.2	5.9	7.4	6.3	na
Mean scarred (%)	32.0	22.1	18.6	21.0	58.1	34.4

magnolia (*Magnolia acuminata* L.), sourwood, and black cherry (*Prunus serotina* Ehrh.).

To characterize differences in tree composition and stand structure, we calculated importance value (IV; Curtis and McIntosh 1951), along with stem density (individuals/ha) for the five species groups (*Pinus*, *Quercus*, pyrophyte, intermediate, and mesophyte) in each plot. We calculated IV for each species group and for each strata (s1, t3, t2) as the mean of relative frequency, relative density, and relative basal area (BA), where IV ranges between 0 and 100. Relative frequency was calculated separately for Hite Fork plots and Wall Fork plots based on the frequency of species occurrences at both sites. Thereafter, we calculated a mean IV for each species group and strata across all Hite Fork plots and all Wall Fork plots. Stem density was tabulated separately for each species group and plotted in four DBH size classes: 7–20 cm, 20–40 cm, 40–60 cm, and > 60 cm. We then calculated mean stem density by DBH size class for each species group across all Hite Fork plots and all Wall Fork plots. We also calculated total BA (m^2/ha) and total density (individuals/ha) for each plot and evaluated significant differences using a Mann-Whitney U test.

Tree recruitment was quantified in both the sapling and seedling layer. For saplings, we summarized percentage cover in the s1 layer (tall shrub) for each of the five species groups for each plot. Seedling density for each species group in each plot was calculated as the number of individuals per m^2. We used the Mann-Whitney U test to evaluate significant differences in sapling cover and seedling density between Hite Fork and Wall Fork.

Species richness was calculated for each plot. Each species was also assigned to a growth form category: tree, shrub, vine, fern, forb, and graminoid, and thereafter, richness by growth form was calculated for each plot. Graminoids included plant species in Poaceae and Cyperaceae. We used the Mann-Whitney U test to evaluate significant differences in species richness and growth form richness between Hite Fork and Wall Fork. In addition to species richness, we calculated the Shannon Index (Shannon 1948) and Pielou's species evenness (Pielou 1975) using diversity in the R package vegan (Oksanen et al. 2020).

To quantify differences in species composition between sites, we calculated Bray-Curtis dissimilarity (Bray and Curtis 1957) on square root-transformed total percentage cover, which provides a more equal balance to rare and common species. Thereafter, we evaluated significant differences in species composition between Hite Fork and Wall Fork using PERMANOVA, a non-parametric, multivariate test for differences between groups (Anderson 2001) using function *adonis* in R in the package vegan in R version 4.0.2 (Oksanen et al. 2020; R Core Development Team 2020). We then used PERMDISP2 to evaluate the multivariate homogeneity of group dispersion (Anderson 2006) using function *betadisper* in the R package vegan (Oksanen et al. 2020). Finally, we used indicator species analysis (Dufrêne and Legendre 1997) to identify indicative species at both Hite Fork and Wall Fork using function *indval* in R package labdsv (Roberts 2019).

Results

Fire history comparison

The Hite Fork fire history spans 203 years (1818–2020) with sample depth diminishing rapidly prior to the 1890s (Fig. 3a). We identified and dated a total of 186 fire scars in 36 cross-section samples cut from fire-scarred shortleaf pine ($n = 18$) and pitch pine ($n = 18$) trees. Seventeen compartmentalized injuries of unknown origin were dated, but not included in the fire history. There were 24 unfiltered fire years between 1835 and 2017 and 18 years when at least two trees recorded a fire scar between 1894 and 2017 (Fig. 3a). The MFI and WMFI for the 18 filtered fire events was 7.2 and 6.5 years, respectively. We determined the seasonality of 99% of the fire scars, of which 98% formed in the dormant season, while the remaining 2% were in earlywood positions.

Fire-scarred trees were generally older at Wall Fork, where the fire history spans 276 years (1745–2020) (Fig. 4a). Here, we dated 32 cross-section samples cut from shortleaf pine ($n = 11$) and pitch pine ($n = 21$) trees containing a total of 77 fire scars. One sample could not be dated due to substantial rot and indistinguishable growth rings. The dated fire scars represented 29 unfiltered fire years between 1794 and 2011 and 13 years when at least two trees recorded a fire scar between 1865 and 2007 (Fig. 4a). The MFI for these 13 filtered fire events was 11.8 years, while the WMFI was 8.9 years. In addition, we dated 14 injuries that were not included in subsequent analyses. We determined the seasonality of 91% of the fire scars in Wall Fork samples, of which 81% formed in the dormant season, 17% were in earlywood positions, and 1% formed in latewood.

During the full comparison period (1890–2020), filtered site composite MFI was approximately 7 years at Hite Fork and 12 years at Wall Fork (Table 1). There was no difference in MFI between sites during this period ($U = 62.5$, $p = 0.465$), although the maximum fire interval at Wall Fork (42 years) was more than twice that observed at Hite Fork (17 years). On average, a greater proportion of trees were scarred per filtered fire event at Hite Fork (32%) compared to Wall Fork (22%) during the full comparison period, but this difference was not significant ($U = 64.0$, $p = 0.221$). There was less difference in filtered site composite MFI between sites during

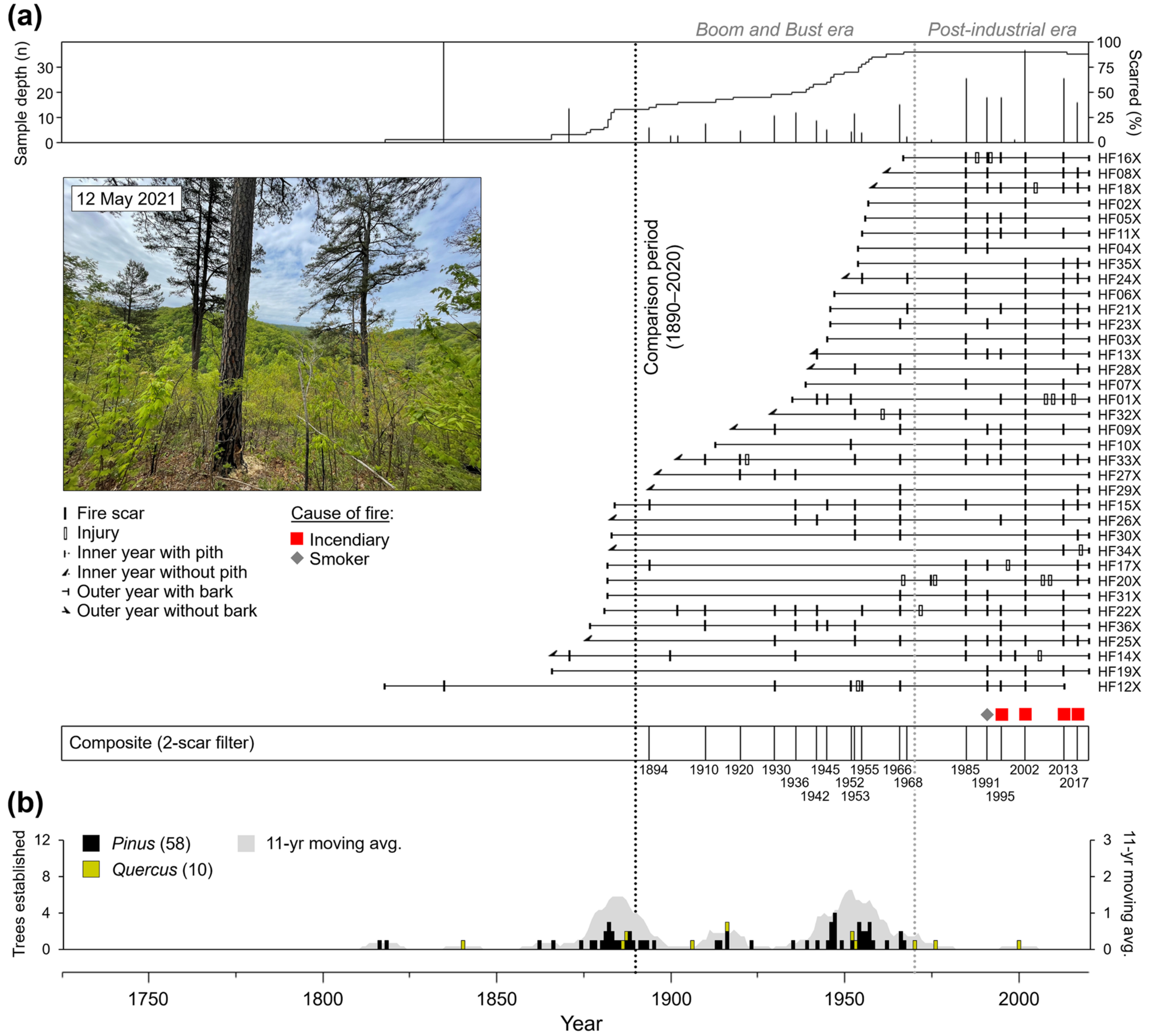

Fig. 3 Hite Fork fire history chart (**a**) and age structure for trees ≥ 10 cm DBH, including fire-scarred pine trees (**b**). In **a**, each horizontal line represents one tree, while the site composite timeline highlights years when at least two trees recorded a fire scar. The causes of corresponding fire occurrences in the West Virginia Division of Forestry's unpublished spatial database (1987–2020) are indicated

the Boom and Bust era ($U = 37.5$, $p = 0.618$), when fire occurred on average every 7 years at Hite Fork and 8 years at Wall Fork (Table 1). No statistically significant difference in the percentage of trees scarred exists between sites during the Boom and Bust era ($U = 48.0$, $p = 0.700$). A statistical comparison between sites during the Post-Industrial era was not possible due to there being only one fire event at Wall Fork. Notably, there was no difference in Hite Fork filtered site composite MFI when comparing socioeconomic eras ($U = 26.0$, $p = 0.910$), but the percentage of trees scarred during the Post-Industrial era was, on average, approximately three times greater than during the Boom and Bust era ($U = 0.0$, $p < 0.001$) (Table 1).

There were 11 major fires in the Hite Fork fire history during the comparison period, including 6 that occurred during the Post-Industrial era (Table 2). The four most recent of these fires are each associated with a late fall incendiary wildfire, including a nearly 2000-ha wildfire in early November 2001 that was recorded by nearly all trees across the site. In comparison, there were three major fires in the Wall Fork fire history, with only one occurring in the Post-Industrial era (Table 2). All but two of the growing season scars in the Wall Fork fire history

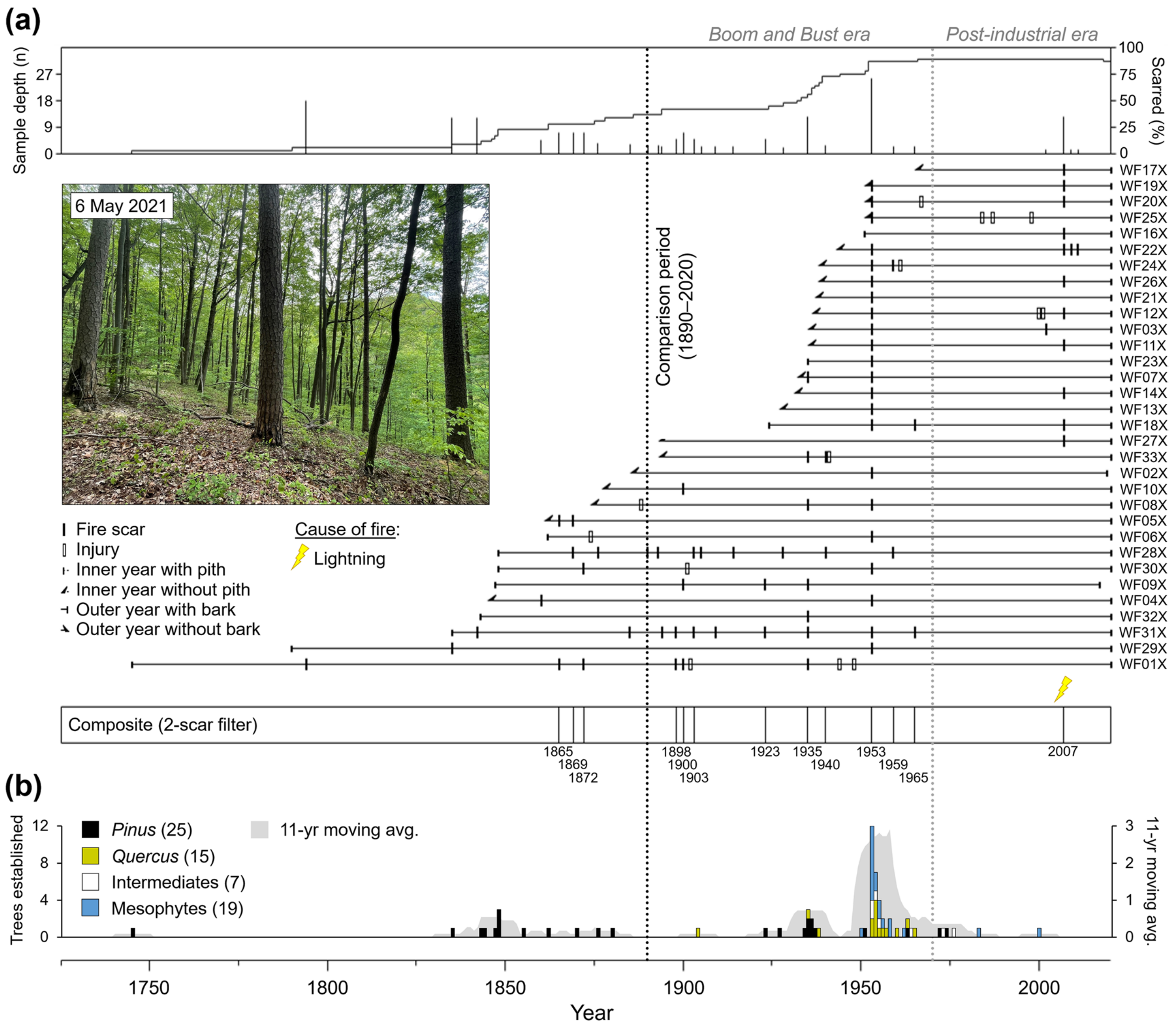

Fig. 4 Wall Fork fire history chart (**a**) and age structure for trees ≥ 10 cm DBH, including fire-scarred pine trees (**b**). In **a**, each horizontal line represents one tree, while the site composite timeline highlights years when at least two trees recorded a fire scar. The cause of a corresponding fire occurrence in the West Virginia Division of Forestry's unpublished spatial database (1987–2020) is indicated. In **b**, tree species in the intermediate fire tolerance group include blackgum (*Nyssa sylvatica*; $n = 5$) and sassafras (*Sassafras albidum*; $n = 2$), while mesophytes include red maple (*Acer rubrum*; $n = 14$) and sourwood (*Oxydendrum arboreum*; $n = 5$)

were recorded in 2007, which was the least extensive major fire (RFE = 6.6) and the only major fire linked to lightning in either fire history. The 1953 dormant season (likely fall 1952) fire was the only year when a major fire, or any fire in general, was recorded by trees at both sites (Table 2).

Forest structure and patterns of tree establishment

Tree basal area (m^2/ha) did not significantly differ between Hite Fork (mean = 35.1) and Wall Fork (mean = 35.2) ($U = 17$, $p = 0.94$). However, the relative importance of pine, oak, pyrophyte, intermediate, and mesophyte tree species diverged between the two sites. Mesophytic and intermediate trees greater than or equal to 7 cm DBH were notably absent from Hite Fork in all strata, but were present in all strata at Wall Fork and were dominant in both the tall shrub (s1) and subcanopy (t3) layers (Fig. 5). The most abundant mesophytic tree species in Wall Fork plots was red maple (IV in t3: 26.4, IV in t2: 13.3, absent in s1). Pines were considerably more abundant in the subcanopy layer and pyrophytes were more abundant in the tall shrub layer at Hite Fork,

Table 2 "Major fires" at Hite Fork and Wall Fork with the percentage of trees scarred, relative fire extent (RFE), fire-scar seasonality, and likely fire occurrence(s), including cause and area burned. Fire-scar seasonality: *D* dormant, *E* early earlywood, *M* middle earlywood, *L* late earlywood, *A* latewood

Dated fire year	Hite Fork			Wall Fork			Likely fire occurrence(s)	Cause of fire	Hectares burned
	%Trees scarred	RFE	Season	%Trees scarred	RFE	Season			
1930	26.3	53.6	D/E	-	-	-	Unknown	Unknown	Unknown
1935	-	-	-	35.0	31.9	D	Unknown	Unknown	Unknown
1936	30.0	25.0	D	-	-	-	Unknown	Unknown	Unknown
1942	21.7	73.3	D	-	-	-	Unknown	Unknown	Unknown
1953	28.6	40.0	D	71.0	79.7	D	Late fall 1952[a]	Unknown	Unknown
1966	37.1	81.3	D	-	-	-	Unknown	Unknown	Unknown
1985	64.0	71.9	D	-	-	-	Unknown	Unknown	Unknown
1991	44.4	71.9	D	-	-	-	Apr. 2, 1991[a]	Smoker	61
1995	44.4	84.4	D	-	-	-	Oct. 30, 1994[a]	Incendiary	30
							Oct. 31, 1994[a]	Incendiary	20
							Nov. 4, 1994[a]	Incendiary	30
2002	91.7	97.0	D	-	-	-	Nov. 1, 2001[a,b]	Incendiary	1963
2007	-	-	-	34.4	6.6	M/L/A	Jul. 3, 2007[a]	Lightning	18
2013	64.0	91.0	D	-	-	-	Nov. 18, 2012[a]	Incendiary	40
2017	40.0	55.0	D	-	-	-	Oct. 30, 2016[a]	Incendiary	19

Source: [a]West Virginia Division of Forestry, [b]Monitoring Trends in Burn Severity (www.MTBS.gov)

relative to Wall Fork (Fig. 5). The canopy layer (t2) was co-dominated by pine and oak at both sites, but pine was slightly more important at Hite Fork (Fig. 5).

Total tree density was significantly lower at Hite Fork (mean = 263 individuals/ha) than at Wall Fork (mean = 733 individuals/ha) ($U = 0.0$, $p < 0.01$), indicating more open conditions at Hite Fork. Differences in tree density between Hite Fork and Wall Fork were most apparent in the smaller size classes (7–20 cm and 20–40 cm), due to higher densities of intermediates and mesophytes, especially for the 7–20 cm size class (Fig. 5). Pole-sized trees were notably absent from Hite Fork. Pine stem density was slightly higher at Hite Fork for all but the largest size class, while oak stem density was higher at Wall Fork for all but the largest size class. Stem density for the largest pine and oak trees was similar at the two sites (Fig. 5).

Age structure at Hite Fork was based on the pith or estimated pith year of 68 trees, including 37 trees within or near vegetation plots and 31 additional fire-scarred pine trees (Fig. 3b). Here, it was not possible to collect cores from the target number of 8 trees per plot due to the relatively low density of trees $\geq$ 10 cm DBH. Pine establishment at Hite Fork occurred in all but one decade between the 1860s and 1960s, while oaks established in five different decades during the record (Fig. 3b). At Wall Fork, age structure was based on the pith or estimated pith year of 66 trees, including 45 trees within vegetation plots (heart rot prevented estimation of pith year in 3 trees) and 21 additional fire-scarred pine trees. Most notable here was the pulse of oak and mesophytic tree establishment in the 1950s and relatively low rate of pine establishment across the entire record, except for small cohorts in the 1840s and 1930s (Fig. 4b).

Regeneration

Pine sapling percentage cover was significantly higher at Hite Fork (mean = 2.8%) than at Wall Fork (mean = 0.17%) ($U = 31.5$, $p = 0.03$) (Fig. 6a, b). At Hite Fork, sapling percentage cover was also higher for oaks (mean = 17%) ($U = 36$, $p < 0.01$) and pyrophytes (mean = 11%) ($U = 36$, $p < 0.01$), relative to Wall Fork (oak mean cover = 0.6%, pyrophyte mean cover = 0.3%). Intermediate and mesophyte sapling percentage cover was also slightly higher at Hite Fork (intermediate mean = 7.8%, mesophyte mean = 12.8%) compared to Wall Fork (intermediate mean = 2.8%, mesophyte mean = 6.0%) ($U = 30$, $p = 0.06$) (Fig. 6a, b). Pine seedling density (m^2) was not significantly different between the two sites ($U = 29$, $p = 0.09$), although mean density was higher at Hite Fork (Fig. 6c, d). There were also no significant differences in oak ($U = 8$, $p = 0.13$), pyrophyte ($U = 26.5$, $p = 0.19$), and intermediate ($U = 8$, $p = 0.13$) seedling density across the two sites. In contrast, seedling density for mesophytes was higher at Wall Fork (mean = 7.3) relative to Hite Fork (mean = 0.6) ($U = 3$, $p = 0.015$) (Fig. 6c, d).

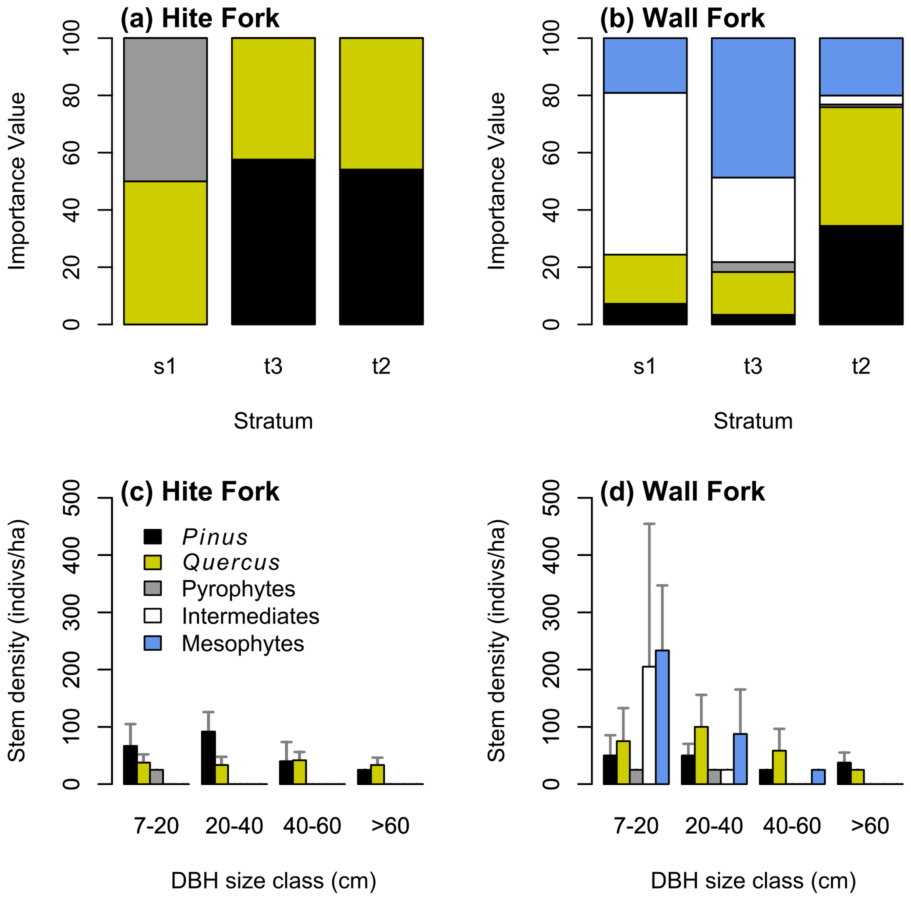

Fig. 5 Importance values for each stratum (**a**, **b**) and mean stem density (individuals/ha) by DBH size class (cm) (**c**, **d**) for *Pinus* spp., *Quercus* spp., pyrophytes, intermediates, and mesophytes at Hite Fork and Wall Fork. Only trees (>7 cm DBH) are shown here. Strata correspond to tall shrub (s1), tree subcanopy (t3), and tree canopy (t2). Importance values range between 0 and 100 and were calculated as the mean of relative basal area, relative density, and relative frequency. Error bars represent 1 standard deviation

Species richness and composition

Collectively across both sites, we documented 105 species: 87 in Hite Fork plots and 56 in Wall Fork plots (Additional file 2: Table S2). Of those 105 species, only two were non-native; oriental bittersweet (*Celastrus orbiculatus* Thunb.) was documented in three Wall Fork plots with 0.01% cover and multiflora rose (*Rosa multiflora* Thunb.) was documented in two Hite Forks plots with 1% cover (see Additional file 2: Table S2). Plot-level species richness was higher at Hite Fork (mean = 47) relative to Wall Fork (mean = 24) ($U = 36$, $p < 0.01$) (Fig. 7a). Differences in species richness between the two sites were driven primarily by forbs and shrubs, due to higher forb and shrub richness at Hite Fork (Fig. 7b). Fern, graminoid, tree, and vine richness were similar across the two sites (Fig. 7b). Across all plots, species richness was negatively related to tree stem density (Pearson's $r = -0.87$). Species diversity as measured by the Shannon Index was higher at Hite Fork (mean = 2.81, range = 2.62 to 2.93), relative to Wall Fork (mean = 2.18, range = 1.86 to 2.47). Pielou's evenness was also higher at Hite Fork (mean = 0.73, range = 0.69 to 0.77), relative to Wall Fork (mean = 0.69, range = 0.63 to 0.77).

To characterize differences in species composition between the two sites, we used indicator species analysis to identify diagnostic species of each site. Unsurprisingly, many of the indicator species for Hite Fork were forbs including four species with very high indicator values: woodland coreopsis (*Coreopsis major* Walter), hairy lespedeza (*Lespedeza hirta var. hirta* Hornem), running five-fingers (*Potentilla canadensis* L.), and forest goldenrod (*Solidago arguta var. arguta* Aiton) (Table 3). Several shrub species also emerged as indicators at Hite Fork, along with two graminoid species, and *Vitis* sp. (a vine) (Table 3). Indicative trees at Hite Fork included downy

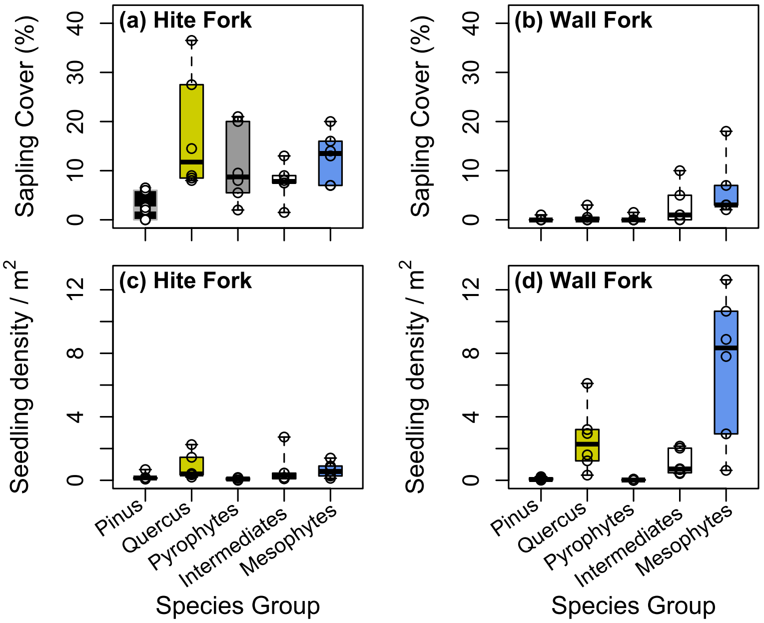

Fig. 6 Sapling percentage cover (**a**, **b**) and seedling density per m^2 (**c**, **d**) for *Pinus* spp., *Quercus* spp., pyrophytes, intermediates, and mesophytes at Hite Fork and Wall Fork. Boxplots show the median and range of sapling cover and seedling density across plots at each site

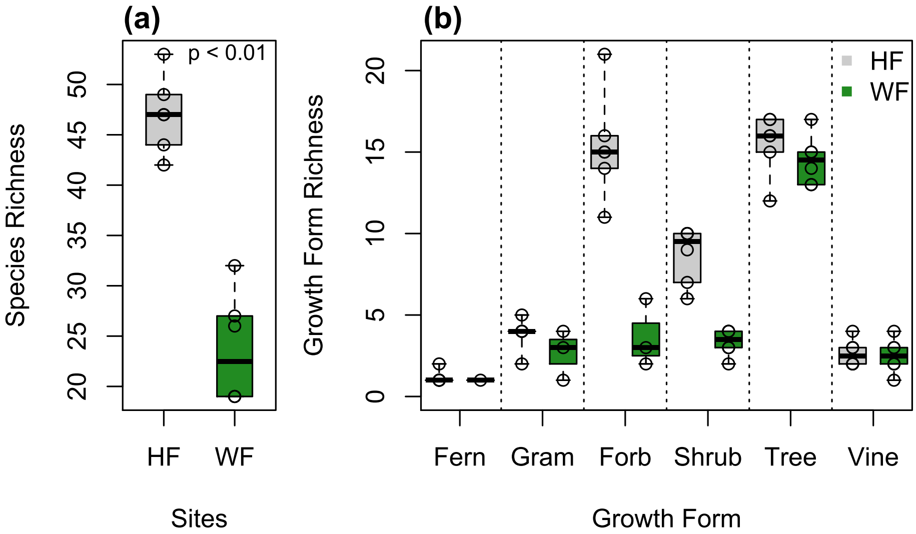

Fig. 7 Species richness (**a**) and richness by growth form (**b**) in Hite Fork (HF) and Wall Fork (WF) plots. Gram = graminoid and includes Poaceae and Cyperaceae. Boxplots show the median and range of richness across plots at each site

serviceberry, black locust, and shortleaf pine (which was a weak indicator). In contrast, there were no indicative forbs, shrubs, graminoids, or vines at Wall Fork. American beech, a mesophyte, was the only indicator at Wall Fork. PERMANOVA and PERMDISP2 confirmed significant differences in species composition between the two sites ($p < 0.01$).

Discussion

The integration of dendroecological data and plant community measurements in our study provided multiple points of comparison, both historical and contemporary, that indicate a late-twentieth century divergence in fire regimes and associated forest structure and composition at two mixed pine-oak sites in the Cumberland

Table 3 Dufrene-Legendre indicator species analysis for Hite Fork vs. Wall Fork plots

Growth form	Hite Fork		Wall Fork	
	Species	IV	Species	IV
Tree	*Amelanchier arborea*	100‡	*Fagus grandifolia*	100 ‡
	Robinia pseudoacacia	95‡		
	Pinus echinata	65*		
Shrub	*Vaccinium stamineum*	93‡	n/a	
	Rubus sp.	91‡		
	Kalmia latifolia	88‡		
	Rhus glabra	83*		
Vine	*Vitis* sp.	71*	n/a	
Forb	*Coreopsis major*	100‡	n/a	
	Lespedeza hirta var. hirta	100‡		
	Potentilla canadensis	100‡		
	Solidago arguta var. arguta	100‡		
	Erigeron pulchellus	83*		
	Hieracium venosum	83*		
	Aureolaria flava	71*		
Graminoid	*Danthonia spicata*	91‡	n/a	
	Dichanthelium commutatum ssp. commutatum	83*		

Statistical significance based on Monte Carlo test: $^{*}p < 0.05$, $^{\ddagger}p < 0.01$

Mountains ecoregion. We documented the effects of "mesophication" (Nowacki and Abrams 2008) at Wall Fork, where there has been a near absence of fire since the 1950s. Here, the fire history is similar to that observed in other regional fire-scar records sourced from public lands where fire was excluded from the landscape by the mid-twentieth century (Lafon et al. 2017; Stambaugh et al. 2020). Conversely, we observed significantly more pine recruitment and herbaceous diversity (i.e., no evidence of mesophication) at Hite Fork, where multiple fires have burned since the 1980s. Our data suggest these late twentieth-century fires on privately owned and managed timberland were the driver of significantly different vegetation development compared to the average mixed pine-oak forest in the CHF during the last few decades (Alexander et al. 2021) and that frequent mixed-severity fire may provide ecological benefits in these forest ecosystems.

Before 1970, the Hite Fork and Wall Fork fire regimes were similarly characterized by frequent fire, occurring almost exclusively during the dormant season. Filtered MFI was approximately 7–8 years during the Boom and Bust era (1890–1969), which is slightly longer than the approximately 5-year MFI observed at two mixed pine-oak sites at the New River Gorge in nearby Fayette County, West Virginia during a similar time period (Maxwell and Hicks 2010; Saladyga 2017). The majority of pine or mixed pine-oak sites in the CHF have a comparable pre-fire exclusion or industrial era MFI of less than 12 years (e.g., Hessl et al. 2011; Aldrich et al. 2014; Howard et al. 2021), with some shorter intervals (3–4 years) on the Appalachian (Hutchinson et al. 2019), Cumberland (Stambaugh et al. 2020), and Ozark (Guyette et al. 2006) Plateaus. The general correspondence of MFI among these sites as well as the preponderance of dormant season fire scars in each record suggest these fire regimes were driven primarily by human ignitions. Fires that occurred in the dormant season are unlikely to have been caused by lightning, which is more commonly associated with low-pressure thunderstorms during the growing season (Lafon 2010).

The presence of numerous fire-scarred survivors at our study sites suggests most fires were low-severity events during the Boom and Bust era. Tree establishment cohorts that correspond to major fire events in the 1940s and 1950s at Hite Fork, and in the 1930s and 1950s at Wall Fork, however, provide evidence of mixed-severity fire. The 1953 dormant season fire was the last relatively extensive fire that scarred a large proportion of trees (> 70%) at Wall Fork. This fire likely occurred in the late fall of 1952 and corresponds to a multi-scar dormant season event in the Hite Fork fire history and in two fire histories from the New River Gorge (Maxwell and Hicks 2010; Saladyga 2017). The fall of 1952 was the most extensive fall fire season on record in West Virginia when at least 580,000 hectares burned across the state (West Virginia Division of Forestry, unpublished data). Vigorous resprouting of oaks and other hardwoods occurred at Wall Fork following this fire event and these advanced into the mid- and upper-canopy over subsequent decades in the near absence of fire (see Figs. 4 and 5). Our estimates of fire severity before the twentieth century are limited by sample depth at both sites, but we can infer from pine establishment cohorts that significant canopy disturbances likely occurred in the 1880s–1890s at Hite Fork and in the 1840s at Wall Fork. These inferences are similar to the mixed-severity fire regime documented by Lafon et al. (2021) in pine-oak stands in Virginia. The timing of disturbance at Hite Fork is associated with the completion of the Norfolk and Western Railroad and influx of extractive industries in McDowell County (ca. 1891), but the driver of disturbance early in the Wall Fork record is less clear since much of the nearby Kanawha River Valley was already cleared and settled by the beginning of the nineteenth century (Brooks 1910). The narrow creek drainages in present-day Kanawha State Forest, however, were traversed by Civil War-era hog drovers who may have used fire to open the forest understory and promote

American chestnut (*Castanea dentata* (Marshall) Borkh.) as a food source (Callahan 1923).

We identified a divergence in the Hite Fork and Wall Fork fire regimes that began in the 1980s following a nearly fire-free period at both sites in the 1970s. Six fires, five associated with known human ignitions, that scarred at least 40% of the sampled trees occurred between 1985 and 2017 at Hite Fork, while only one localized fire caused by lightning was observed in the Wall Fork record during the same time period. Not only does the Hite Fork fire regime diverge from Wall Fork, it departs from most other mixed pine-oak forests in the CHF where fire has been excluded since the early- to mid-twentieth century (e.g., Aldrich et al. 2014; Stambaugh et al. 2018; Hutchinson et al. 2019; Howard et al. 2021; Lafon et al. 2021). Exclusion-era fire-scar records that document frequent and sometimes extensive fires in the CHF are rare because most fire history studies are conducted on public land where human ignition sources have been excluded and fire has been actively suppressed by federal and state land management agencies (e.g., Wall Fork). The Post-Industrial era fire regime at Hite Fork, however, is similar to that observed in the Pennsylvania Anthracite (Coal) Region where a mosaic of early- to late-successional pine and hardwood forest types are maintained by frequent burning (Saladyga and Standlee 2018). In this region of Pennsylvania, increases in fire activity on unmanaged lands were associated with mine closures and related economic downturns, particularly in the mid-twentieth century. Similar to southern West Virginia, debris burning and incendiary fires account for the majority of area burned in the last three decades, while lightning-ignited fires make up approximately 1% of area burned. In both coal-producing regions, the legacy of dependence on a single extractive industry persists in the twenty-first century in the form of high rates of unemployment, low median incomes, and underfunded services (e.g., trash disposal) (Keil and Keil 2014; Appalachian Regional Commission 2021). Relationships between these socioeconomic stressors, incendiary ignitions, and informal land management in southern West Virginia and in the Cumberland Mountains in general deserve further investigation (e.g., Diaz et al. 2016; Coughlan 2016).

Although we lack vegetation data prior to the Post-Industrial era, the similarity of our sites in terms of topography, soil properties, and climate suggests that differences in forest structure and composition likely resulted from the recent divergence in fire history at Hite Fork and Wall Fork. Pine saplings were more abundant at Hite Fork due to more open, high-light conditions likely resulting from overstory tree mortality caused by more frequent severe fire in the Post-Industrial era. Similar to our findings, Barden and Woods (1976) and Vose et al. (1994) provide evidence that pine recruitment in the southern Appalachians was substantially higher after high-severity fire due to increased mortality of competing, shade-tolerant or mesophytic tree species, relative to sites with no fire or low-severity surface fires. Black et al. (2018) also documented higher shortleaf pine sapling recruitment at sites that burned more intensely in the Cumberland Mountains of eastern Kentucky. In contrast to Hite Fork, less frequent fire over the last 40 years at Wall Fork promoted recruitment of mesophytic tree species at the expense of pines, providing evidence for ongoing “mesophication” (Nowacki and Abrams 2008). The absence of pine saplings at Wall Fork highlights the importance of mixed-severity fire that is frequent enough to enhance pine seedling regeneration, but not so frequent as to repeatedly top-kill and inhibit pine seedlings from advancing into the sapling layer. This is especially critical for shortleaf pine as seedling survival is greatly diminished under more closed canopy conditions (stand basal area > 17 m^2/ha, Shelton and Cain 2000; Cain 1993) and because the removal of litter is critical for seedling establishment (Shelton 1995). Similar to pines, oak and pyrophyte sapling abundance was also higher at Hite Fork, which is consistent with multiple studies that have documented recruitment of shade-intolerant, pyrophytic tree seedlings into the sapling layer in response to canopy gaps created through recurrent fire and/or mechanical thinning (Hutchinson et al. 2012; Brose et al. 2013; Iverson et al. 2017; Izbicki et al. 2020). However, mesophytic tree species cover was also slightly higher in the sapling layer at Hite Fork, presumably due to rapid re-sprouting post-fire. Collectively, these results suggest that frequent mixed-severity may be necessary to promote both pine and oak recruitment in the CHF.

Species richness in the herbaceous layer was considerably higher at Hite Fork, especially for forbs and shrubs, which we also attribute to more frequent mixed-severity fire. This is consistent with ecological theory (i.e., the Intermediate Disturbance Hypothesis, Connell 1978) and with many studies that documented a positive relationship between either fire frequency or fire severity and diversity in oak and pine-oak forest understories (Glasgow and Matlack 2007; Jenkins et al. 2011; Hagan et al. 2015; Knapp et al. 2015; Black et al. 2018; Borden et al. 2021). In addition, we documented significant differences in species composition between Hite Fork and Wall Fork, likely driven by gradients in species richness and the divergent fire histories of our sites. Fire generally promotes colonization or re-emergence of graminoids, forbs, and shrubs by reducing litter, decreasing competition with tree seedlings and saplings, and increasing forest understory light availability (Reilly et al. 2006; Black et al. 2018; Vander Yacht et al. 2020). Higher species richness at Hite Fork likely resulted from increased light availability after severe fire due to a significant reduction in the density of mid-story and pole-sized trees. We did not document a greater non-native species abundance or richness at Hite Fork that has been demonstrated by other studies and attributed to increased light availability after high-severity fire (Hagan et al. 2015; Black et al. 2018). Forbs and shrubs in particular benefited from more frequent fire due to life-history traits that promote rapid post-fire growth and recovery (i.e., perennating meristems at or below the soil surface and associated re-sprouting and belowground allocation) (Raunkiaer 1934; Whigham 2004). In addition, several of the species identified as indicators at Hite Fork (*Vitis* sp.; smooth sumac, *Rhus glabra* L.) are known to respond positively to high-severity fire via enhanced seed germination due to increases in solar radiation and soil temperature (Glasgow and Matlack 2007) or via rapid re-sprouting (variable panicgrass, *Dichanthelium commutatum ssp. commutatum* Gould*;* hairy lespedeza) (Hutchinson et al. 2005). In contrast, an almost complete lack of fire at Wall Fork in the Post-Industrial era resulted in more closed canopy conditions, which along with higher densities of mesophytic seedlings, likely reduced opportunities for establishment and persistence of forbs and shrubs. Interestingly, graminoid species richness was not considerably higher at Hite Fork, even though fire often increases graminoid diversity and cover (Hutchinson et al. 2005; Glasgow and Matlack 2007; Vander Yacht et al. 2020). This is likely due to the xeric conditions of our sites where the graminoid layer is relatively species-poor and graminoid cover is relatively low compared to more mesic oak-dominated stands (i.e, Hutchinson et al. 2005), but could also indicate a lack of graminoid seed sources on or near our sites. Some studies have found no changes in herbaceous layer richness after a single fire event (Kuddes-Fischer and Arthur 2002; Elliott and Vose 2005), while others have found little effect of repeated low-severity fire on herbaceous species richness (Hutchinson et al. 2005; Jenkins et al. 2011). These results suggest that repeated prescribed fire occasionally of higher severity may be necessary to increase herbaceous cover and diversity (Arthur et al. 2012; Hutchinson et al. 2012; Brose et al. 2013).

In addition to repeated application of prescribed fire to meet management objectives, it may also be necessary to vary the burn season to promote the benefits of mixed-severity fire (Waldrop et al. 2016). At Hite Fork, at least five fall fires within the last 40 years likely produced the observed open canopy, minimal mesophytic tree cover, higher species richness, and conditions favorable for pine regeneration. While fall burning is not typically favored by fire managers in the CHF because of increased risk of fire escape or potential impacts on wildlife (Austin et al. 2018; Jacobsen et al. 2020), an occasional fall burn when weather and fuel conditions are conducive to more intense prescribed fire may be appropriate for some landscapes. Furthermore, there is potential to leverage local ecological knowledge to promote greater pyrodiversity (i.e., season, severity), particularly in areas where fires have continued to burn in the twenty-first century, such as the Cumberland Mountains. In the absence of fire and mechanical thinning that opens the canopy and increases light availability to the forest floor, declines in oak and pine abundance and associated wildlife habitat and food resources will likely continue (Vander Yacht et al. 2020; Alexander et al. 2021). As suggested elsewhere, sites with continuously documented fire like Hite Fork have the potential to serve as reference sites in forest restoration or fire management plans (Rother et al. 2020).

Conclusions

This study provides news insights into the fire history and present-day plant community structure of mixed pine-oak forests in the Cumberland Mountains ecoregion within the CHF. The fire regimes at Hite Fork and Wall Fork during the Boom and Bust era (1890–1969) were similar to other pine or mixed pine-oak sites across the CHF during the pre-fire exclusion or industrial era. Notably, we documented a divergence in fire regimes that began in the 1980s with six major fires recorded at Hite Fork between 1985 and 2017 and an almost complete lack of fire at Wall Fork. The resulting impacts for plant community structure were substantial. Repeated mixed-severity fires at Hite Fork decreased the abundance of mesophytic tree species and opened the canopy resulting in greater pine recruitment and herbaceous diversity. In contrast, vegetation development at Wall Fork appears to have followed a path similar to most mixed pine-oak forests across the CHF (i.e., "mesophication"). Our results indicate the potential benefits of incorporating more intense prescribed fire to meet management objectives in similar landscapes when appropriate. While much of the literature has focused on the "demise of oak" in the CHF (Lorimer 1984; Abrams 1992; McEwan et al. 2011), future research should address the effects of fire exclusion on fire-adapted pine species and associated vegetation types that are facing multiple threats and are declining throughout their range.

Abbreviations

BA: Relative Basal Area; CHF: Central Hardwood Forest Region; DBH: Diameter at breast height; FHAES: Fire History Analysis and Exploration System Software; IV: Importance Value; MFI: Mean Fire Interval; RFE: Relative Fire Extent; WMFI: Weibull Median Fire Interval; WVNHP: West Virginia Natural Heritage Program.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-022-00143-6.

Additional file 1: Table S1. Site information for Hite Fork (McDowell County, WV) and Wall Fork (Kanawha County, WV).

Additional file 2: Table S2. 105 species

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Authors' contributions

TS and KAP contributed equally to study design, data collection and analysis, and writing the manuscript. CMB contributed to data collection and analysis and manuscript editing. The authors read and approved the final manuscript.

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Availability of data and materials

After acceptance for publication, the fire history data will be made publicly available in the International Multiproxy Paleofire Database (IMPD) and the plant community data will be deposited in VegBank, a publicly available repository for vegetation plot data within the USA (http://vegbank.org/).

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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References

Abrahamson, I. 2022. Fire Effects Information System (FEIS). https://www.feis-crs.org/feis/

Abrams, M.D. 1992. Fire and the development of oak forests: In eastern North America, oak distribution reflects a variety of ecological paths and disturbance conditions. *BioScience* 42: 346–353. https://doi.org/10.2307/1311781.

Abrams, M.D. 1998. The Red Maple Paradox: What explains the widespread expansion of red maple in eastern forests? *BioScience* 48: 355–364. https://doi.org/10.2307/1313374.

Aldrich, S.R., C.W. Lafon, H.D. Grissino-Mayer, and G.G. DeWeese. 2014. Fire history and its relations with land use and climate over three centuries in the central Appalachian Mountains, USA. *Journal of Biogeography* 41: 2093–2104. https://doi.org/10.1111/jbi.12373.

Alexander, H.D., M.A. Arthur, D.L. Loftis, and S.R. Green. 2008. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. *Forest Ecology and Management* 256: 1021–1030. https://doi.org/10.1016/j.foreco.2008.06.004.

Alexander, H.D., C. Siegert, J.S. Brewer, J. Kreye, M.A. Lashley, J.K. McDaniel, A.K. Paulson, H.J. Renninger, and J.M. Varner. 2021. Mesophication of oak landscapes: evidence, knowledge gaps, and future research. *BioScience* 71: 531–542. https://doi.org/10.1093/biosci/biaa169.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Anderson, M.J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62: 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x.

Appalachian Regional Commission. 2021. Socioeconomic data profile by county. https://data.arc.gov/data. Accessed 4 Aug 2021.

Applequist, M.B. 1958. A simple pith locator for use with off-center increment cores. *Journal of Forestry* 56: 141. https://doi.org/10.1093/jof/56.2.138.

Archibald, S., C.E.R. Lehmann, C.M. Belcher, W.J. Bond, R.A. Bradstock, A.-L. Daniau, K.G. Dexter, E.J. Forrestel, M. Greve, T. He, S.I. Higgins, W.A. Hoffmann, B.B. Lamont, D.J. McGlinn, G.R. Moncrieff, C.P. Osborne, J.G. Pausas, O. Price, B.S. Ripley, B.M. Rogers, D.W. Schwilk, M.F. Simon, M.R. Turetsky, G.R. Van der Werf, and A.E. Zanne. 2018. Biological and geophysical feedbacks with fire in the Earth system. *Environmental Research Letters* 13: 033003. https://doi.org/10.1088/1748-9326/aa9ead.

Arno, S.F., and K.M. Sneck. 1977. *A method for determining fire history in coniferous forests of the Mountain West. Gen. Tech. Rep. INT-GTR-42*, 28. Ogden: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

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

Arthur, M.A., H.D. Alexander, D.C. Dey, C.J. Schweitzer, and D.L. Loftis. 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *Journal of Forestry* 110: 257–266. https://doi.org/10.5849/jof.11-080.

Arthur, M.A., B.A. Blankenship, A. Schörgendorfer, D.L. Loftis, and H.D. Alexander. 2015. Changes in stand structure and tree vigor with repeated prescribed fire in an Appalachian hardwood forest. *Forest Ecology and Management* 340: 46–61. https://doi.org/10.1016/j.foreco.2014.12.025.

Austin, L.V., A. Silvis, W.M. Ford, M. Muthersbaugh, and K.E. Powers. 2018. Bat activity following restoration prescribed burning in the central Appalachian upland and riparian habitats. *Natural Areas Journal* 38: 183–195. https://doi.org/10.3375/043.038.0208.

Barden, L .S. and F.W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the southern Appalachians. *Forest Science* 22: 399–403.

Black, D.E., Z.W. Poynter, C.A. Cotton, S. Upadhaya, D.D. Taylor, W. Leuenberger, B.A. Blankenship, and M.A. Arthur. 2018. Post-wildfire recovery of an upland oak—pine forest on the Cumberland Plateau, Kentucky, USA. *Fire Ecology* 14: 14. https://doi.org/10.1186/s42408-018-0013-9.

Blankenship, B.A., and M.A. Arthur. 2006. Stand structure over 9 years in burned and fire-excluded oak stands on the Cumberland Plateau, Kentucky. *Forest Ecology and Management* 225: 134–145. https://doi.org/10.1016/j.foreco.2005.12.032.

Bond, W.J., F.I. Woodward, and G.F. Midgley. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525–538. https://doi.org/10.1111/j.1469-8137.2004.01252.x.

Borden, C.G., M.C. Duguid, and M.S. Ashton. 2021. The legacy of fire: Long-term changes to the forest understory from periodic burns in a New England oak-hickory forest. *Fire Ecology* 17: 24. https://doi.org/10.1186/s42408-021-00115-2.

Bowman, D.M.J.S., J.K. Balch, P. Artaxo, W.J. Bond, J.M. Carlson, M.A. Cochrane, C.M. D'Antonio, R.S. DeFries, J.C. Doyle, S.P. Harrison, F.H. Johnston, J.E. Keeley, M.A. Krawchuk, C.A. Kull, J.B. Marston, M.A. Moritz, I.C. Prentice, C.I. Roos, A.C. Scott, T.W. Swetnam, G.R. van der Werf, and S.J. Pyne. 2009. Fire in the earth system. *Science* 324: 481–484. https://doi.org/10.1126/science.1163886.

Bowman, D.M.J.S., J.A. O'Brien, and J.G. Goldammer. 2013. Pyrogeography and the global quest for sustainable fire management. *Annual Review of*

Environment and Resources 38: 57–80. https://doi.org/10.1146/annurev-environ-082212-134049.

Bray, J.R., and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349. https://doi.org/10.2307/1942268.

Brewer, P. W., M. E. Velásquez, E. K. Sutherland, and D. A. Falk. 2016. Fire History Analysis and Exploration System (FHAES) version 2.0.2.

Brooks, A.B. 1910. *Forestry and wood industries. West Virginia Geological Survey*. Morgantown: Acme Publishing Co.

Brose, P., T. Schuler, D. van Lear, and J. Berst. 2001. Bringing fire back: The changing regimes of the Appalachian mixed-oak forests. *Journal of Forestry* 99: 30–35. https://doi.org/10.1093/jof/99.11.30.

Brose, P.H., D.C. Dey, R.J. Phillips, and T.A. Waldrop. 2013. A meta-analysis of the fire-oak hypothesis: Does prescribed burning promote oak reproduction in Eastern North America? *Forest Science* 59: 322–334. https://doi.org/10.5849/forsci.12-039.

Bunn, A.G. 2010. Statistical and visual crossdating in R using the dplR library. *Dendrochronologia* 28: 251–258. https://doi.org/10.1016/j.dendro.2009.12.001.

Byers, E.A., J.P. Vanderhorst, and B.P. Streets. 2007. Classification and conservation assessment of high elevation wetland communities in the Allegheny Mountains of West Virginia. W. Va. Division of Natural Resources, Wildlife Resources Section.

Cain, M.D. 1993. A 10-year evaluation of prescribed winter burns in uneven-aged stands of *Pinus taeda* L and *P. echinata* Mill-woody understorey vegetation response. *International Journal of Wildland Fire* 3: 13–20. https://doi.org/10.1071/WF9930013.

Cain, M.D., and M.G. Shelton. 1995. Thirty-eight years of autogenic, woody understory dynamics in a mature, temperate pine–oak forest. *Canadian Journal of Forest Research* 25: 1997–2009. https://doi.org/10.1139/x95-216.

Callahan, J.M. 1923. *History of West Virginia, old and new*. Vol. 1. Chicago and New York: The American Historical Society, Inc..

Cockrell, S.W., K.K. de Graauw, A.M. Ziegler, and A.E. Hessl. 2017. Precision dating of Cook's Mill, a Civil War era structure in West Virginia. *Dendroarchaeology* 43: 20–26. https://doi.org/10.1016/j.dendro.2017.01.009.

Colias, C. 2002. Almost heaven still? Post-industrial development and local response in Fayette County, West Virginia. *Journal of Appalachian Studies* 8: 91–119 http://www.jstor.org/stable/41446517.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a nonequilibrium state. *Science* 199: 1302–1310 https://www.science.org/doi/10.1126/science.199.4335.1302.

Coughlan, M.R. 2016. Wildland arson as clandestine resource management: A space–time permutation analysis and classification of informal fire management regimes in Georgia, USA. *Environmental Management* 57: 1077–1087. https://doi.org/10.1007/s00267-016-0669-3.

Curtis, J.T., and R.P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32: 476–496. https://doi.org/10.2307/1931725.

Diaz, J.M., T. Steelman, and B. Nowell. 2016. Local ecological knowledge and fire management: What does the public understand? *Journal of Forestry* 114: 58–65. https://doi.org/10.5849/jof.14-026.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366. https://doi.org/https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Elliott, K.J., and J.M. Vose. 2005. Effects of understory prescribed burning on shortleaf pine (*Pinus echinata* Mill.)/mixed-hardwood forests. *The Journal of the Torrey Botanical Society* 132: 236–251. https://doi.org/10.3159/1095-5674(2005)132[236:EOUPBO]2.0.CO;2.

Falk, D.A., E.K. Heyerdahl, P.M. Brown, C. Farris, P.Z. Fulé, D. McKenzie, T.W. Swetnam, A.H. Taylor, and M.L. Van Horne. 2011. Multi-scale controls of historical forest-fire regimes: New insights from fire-scar networks. *Frontiers in Ecology and the Environment* 9: 446–454. https://doi.org/10.1890/100052.

Fei, S., P.J. Gould, K.C. Steiner, J.C. Finley, and M.E. McDill. 2005. Forest regeneration composition and development in upland, mixed-oak forests. *Tree Physiology* 25: 1495–1500. https://doi.org/10.1093/treephys/25.12.1495.

Glasgow, L.S., and G.R. Matlack. 2007. Prescribed burning and understory composition in a temperate deciduous forest, Ohio, USA. *Forest Ecology and Management* 238: 54–64. https://doi.org/10.1016/j.foreco.2006.08.344.

Greenberg, C.H., B.S. Collins, S. Goodrick, M.C. Stambaugh, and G.R. Wein. 2021. Introduction to fire ecology across USA forested ecosystems: Past, present, and future. In *Fire ecology and management: Past, present, and future of US forested ecosystems*, ed. C.H. Greenberg and B. Collins, 1–30. New York: Springer International Publishing.

Guyette, R.P., M.A. Spetich, and M.C. Stambaugh. 2006. Historic fire regime dynamics and forcing factors in the Boston Mountains, Arkansas, USA. *Forest Ecology and Management* 234: 293–304. https://doi.org/10.1016/j.foreco.2006.07.016.

Hagan, D.L., T.A. Waldrop, M. Reilly, and T.M. Shearman. 2015. Impacts of repeated wildfire on long-unburned plant communities of the southern Appalachian Mountains. *International Journal of Wildland Fire* 24: 911–920. https://doi.org/10.1071/WF14143.

Hart, J.L., and M.L. Buchanan. 2012. History of fire in eastern oak forests and implications for restoration. In *Proceedings of the 4th fire in eastern oak forests conference*, Gen. Tech. Rep. NRS-P-102, ed. D.C. Dey, M.C. Stambaugh, S.L. Clark, and C.J. Schweitzer, 34–51. Newtown Square: US Department of Agriculture, Forest Service, Northern Research Station.

Hessl, A.E., T. Saladyga, T. Schuler, P. Clark, and J. Wixom. 2011. Fire history from three species on a central Appalachian ridgetop. *Canadian Journal of Forest Research* 41: 2031–2039. https://doi.org/10.1139/x11-125.

Hiers, J.K., J.J. O'Brien, J.M. Varner, B.W. Butler, M. Dickinson, J. Furman, M. Gallagher, D. Godwin, S.L. Goodrick, S.M. Hood, A. Hudak, L.N. Kobziar, R. Linn, E.L. Loudermilk, S. McCaffrey, K. Robertson, E.M. Rowell, N. Skowronski, A.C. Watts, and K.M. Yedinak. 2020. Prescribed fire science: The case for a refined research agenda. *Fire Ecology* 16: 11. https://doi.org/10.1186/s42408-020-0070-8.

Howard, L.F., G.D. Cahalan, K. Ehleben, B.A. Muhammad El, H. Halza, and S. DeLeon. 2021. Fire history and dendroecology of Catoctin Mountain, Maryland, USA, with newspaper corroboration. *Fire Ecology* 17: 8. https://doi.org/10.1186/s42408-021-00096-2.

Hutchinson, T.F., R.E. Boerner, S. Sutherland, E.K. Sutherland, M. Ortt, and L.R. Iverson. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. *Canadian Journal of Forest Research* 35: 877–890. https://doi.org/10.1139/x04-189.

Hutchinson, T.F., R.P. Long, R.D. Ford, and E.K. Sutherland. 2008. Fire history and the establishment of oaks and maples in second-growth forests. *Canadian Journal of Forest Research* 38: 1184–1198. https://doi.org/10.1139/X07-216.

Hutchinson, T.F., D.A. Yaussy, R.P. Long, J. Rebbeck, and E.K. Sutherland. 2012. Long-term (13-year) effects of repeated prescribed fires on stand structure and tree regeneration in mixed-oak forests. *Forest Ecology and Management* 286: 87–100. https://doi.org/10.1016/j.foreco.2012.08.036.

Hutchinson, T.F., M.C. Stambaugh, J.M. Marschall, and R.P. Guyette. 2019. Historical fire in the Appalachian Plateau of Ohio and Kentucky, USA, from remnant yellow pines. *Fire Ecology* 15: 33. https://doi.org/10.1186/s42408-019-0052-x.

Iverson, L.R., T.F. Hutchinson, M.P. Peters, and D.A. Yaussy. 2017. Long-term response of oak-hickory regeneration to partial harvest and repeated fires: Influence of light and moisture. *Ecosphere* 8: e01642. https://doi.org/10.1002/ecs2.1642.

Izbicki, B.J., H.D. Alexander, A.K. Paulson, B.R. Frey, R.W. McEwan, and A.I. Berry. 2020. Prescribed fire and natural canopy gap disturbances: Impacts on upland oak regeneration. *Forest Ecology and Management* 465: 118107. https://doi.org/10.1016/j.foreco.2020.118107.

Jacobsen, C.D., D.J. Brown, W.D. Flint, J.L. Schuler, and T.M. Schuler. 2020. Influence of prescribed fire and forest structure on woodland salamander abundance in the central Appalachians, USA. *Forest Ecology and Management* 468: 118185. https://doi.org/10.1016/j.foreco.2020.118185.

Jenkins, M.A., R.N. Klein, and V.L. McDaniel. 2011. Yellow pine regeneration as a function of fire severity and post-burn stand structure in the southern Appalachian Mountains. *Forest Ecology and Management* 262: 681–691. https://doi.org/10.1016/j.foreco.2011.05.001.

Keil, T., and J.M. Keil. 2014. *Anthracite's demise and the post-coal economy of northeastern Pennsylvania*. Washington D.C.: Rowman and Littlefield.

Kelley, D.I., I. Bistinas, R. Whitley, C. Burton, T.R. Marthews, and N. Dong. 2019. How contemporary bioclimatic and human controls change global fire regimes. *Nature Climate Change* 9: 690–696. https://doi.org/10.1038/s41558-019-0540-7.

Knapp, B.O., K. Stephan, and J.A. Hubbart. 2015. Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. *Forest Ecology and Management* 344: 95–109. https://doi.org/10.1016/j.foreco.2015.02.009.

Kuddes-Fischer, L.M., and M.A. Arthur. 2002. Response of understory vegetation and tree regeneration to a single prescribed fire in oak-pine forests. *Natural Areas Journal* 22: 43–52.

Kutta, E., and J. Hubbart. 2019. Climatic trends of West Virginia: A representative Appalachian microcosm. *Water* 11 (6): 1117. https://doi.org/10.3390/w11061117.

Lafon, C.W. 2010. Fire in the American South: Vegetation impacts, history, and climatic relations. *Geography Compass* 4: 919–944. https://doi.org/10.1111/j.1749-8198.2010.00363.x.

Lafon, C.W., A.T. Naito, H.D. Grissino-Mayer, S.P. Horn, and T.A. Waldrop. 2017. *Fire history of the Appalachian region: a review and synthesis. Gen. Tech. Rep. SRS-219*, 1–97. Asheville: US Department of Agriculture, Forest Service, Southern Research Station 219.

Lafon, C.W., G.G. DeWeese, W.T. Flatley, S.R. Aldrich, and A.T. Naito. 2021. Historical fire regimes and stand dynamics of xerophytic pine–oak stands in the southern Appalachian Mountains, Virginia, USA. *Annals of the American Association of Geographers*: 1–23. https://doi.org/10.1080/24694452.2021.1935206.

Larsson, L.Å., 2016. CDendro & CooRecorder Program Package, Version 9.4. Available online: https://www.cybis.se/forfun/dendro.

Lorimer, C.G. 1984. Development of the red maple understory in northeastern oak forests. *Forest Science*: 3–22. https://doi.org/10.1093/forestscience/30.1.3.

Lorimer, C.G., J.W. Chapman, and W.D. Lambert. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology* 82: 227–237. https://doi.org/10.2307/2261291.

Margolis, E.Q., and C.H. Guiterman. 2021. *NOAA/WDS Paleoclimatology - North American Tree-ring Fire Scar Synthesis (NAFSS)*. NOAA National Centers for Environmental Information. https://doi.org/10.25921/pef0-zz47 Accessed 14 May 2022.

Marschall, J.M., M.C. Stambaugh, B.C. Jones, and E. Abadir. 2019. Spatial variability of historical fires across a red pine–oak landscape, Pennsylvania, USA. *Ecosphere* 10: e02978. https://doi.org/10.1002/ecs2.2978.

Maxwell, R.S., and R.R. Hicks. 2010. Fire history of a rimrock pine forest at New River Gorge National River, West Virginia. *Natural Areas Journal* 30: 305–311. https://doi.org/10.3375/043.030.0311.

McEwan, R.W., T.F. Hutchinson, R.P. Long, D.R. Ford, and B.C. McCarthy. 2007. Temporal and spatial patterns in fire occurrence during the establishment of mixed-oak forests in eastern North America. *Journal of Vegetation Science* 18: 655–664. https://doi.org/10.1111/j.1654-1103.2007.tb02579.x.

McEwan, R.W., J.M. Dyer, and N. Pederson. 2011. Multiple interacting ecosystem drivers: Toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography* 34: 244–256. https://doi.org/10.1111/j.1600-0587.2010.06390.x.

Monitoring Trends in Burn Severity (MTBS). 2020. https://mtbs.gov/.

National Oceanic and Atmospheric Administration (NOAA). 2021. Climate at a Glance—County Time Series. https://www.ncdc.noaa.gov/cag/county/time-series. Accessed 3 Sept 2021.

NatureServe Explorer. 2021. https://explorer.natureserve.org/. Accessed 17 Aug 2021.

Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. *BioScience* 58: 123–138. https://doi.org/10.1641/B580207.

Oksanen J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs, and H. Wagner. 2020. vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Oswalt, C.M. 2012. *Spatial and temporal trends of the shortleaf pine resource in the eastern United States*. In Proceedings of the Shortleaf pine conference: East meets West, eds., J. Kush, R.J. Barlow, and J.C. Gilbert. Spec. Rep. No. 11. Alabama Agricultural Experiment Station, Auburn, AL, 33–37.

Parker, G.R., D.J. Leopold, and J.K. Eichenberger. 1985. Tree dynamics in an old-growth, deciduous forest. *Forest Ecology and Management* 11: 31–57. https://doi.org/10.1016/0378-1127(85)90057-X.

Pielou, E.C. 1975. *Ecological diversity*. New York: Wiley.

R Development Core Team. 2020. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Raunkiaer, C. 1934. *The life forms of plants and statistical plant geography*. Oxford: Clarendon Press.

Reilly, M.J., M.C. Wimberly, and C.L. Newell. 2006. Wildfire effects on plant species richness at multiple spatial scales in forest communities of the southern Appalachians. *Journal of Ecology* 94: 118–130. https://doi.org/10.1111/j.1365-2745.2005.01055.x.

Roberts, D.W. 2019. labdsv: Ordination and Multivariate Analysis for Ecology. R package version 2.0-1. https://CRAN.R-project.org/package=labdsv.

Rogers, B.M., J.K. Balch, S.J. Goetz, C.E.R. Lehmann, and M. Turetsky. 2020. Focus on changing fire regimes: interactions with climate, ecosystems, and society. *Environmental Research Letters* 15: 030201. https://doi.org/10.1088/1748-9326/ab6d3a.

Rother, M.T., J.M. Huffman, C.H. Guiterman, K.M. Robertson, and N. Jones. 2020. A history of recurrent, low-severity fire without fire exclusion in southeastern pine savannas, USA. *Forest Ecology and Management* 475: 118406. https://doi.org/10.1016/j.foreco.2020.118406.

Saladyga, T. 2017. Forest disturbance history from 'legacy' pitch pine (*Pinus rigida*) at the New River Gorge, West Virginia. *Natural Areas Journal* 37: 49–57. https://doi.org/10.3375/043.037.0108.

Saladyga, T., and A. Standlee. 2018. Historical drivers and contemporary perceptions of wildfire in a post-industrial rural landscape. *Fire* 1: 33. https://doi.org/10.3390/fire1020033.

Shannon, C.E. 1948. A mathematical theory of communication. *The Bell System Technical Journal* 27: 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x.

Shelton, M.G. 1995. *Effects of seed production, seedbed condition, and overstory basal area on the establishment of shortleaf pine seedlings in the Ouachita Mountains*. USDA Forest Service., Southern Forest Experiment Station, Res. Pap. SO-293, 13 pp.

Shelton, M.G., and M.D. Cain. 2000. Regenerating uneven-aged stands of loblolly and shortleaf pines: the current state of knowledge. *Forest Ecology and Management* 129: 177–193. https://doi.org/10.1016/S0378-1127(99)00161-9.

South, D.B., and R.A. Harper. 2016. A decline in timberland continues for several southern yellow pines. *Journal of Forestry* 114: 116–124. https://doi.org/10.5849/jof.15-006.

Speer, J.H. 2010. *Fundamentals of tree-ring research*. Tucson: University of Arizona Press.

Stambaugh, M.C., J.M. Marschall, E.R. Abadir, B.C. Jones, P.H. Brose, D.C. Dey, and R.P. Guyette. 2018. Wave of fire: An anthropogenic signal in historical fire regimes across central Pennsylvania, USA. *Ecosphere* 9: e02222. https://doi.org/10.1002/ecs2.2222.

Stambaugh, M.C., J.M. Marschall, and E.R. Abadir. 2020. Revealing historical fire regimes of the Cumberland Plateau, USA, through remnant fire-scarred shortleaf pines (*Pinus echinata* Mill.). *Fire Ecology* 16: 24. https://doi.org/10.1186/s42408-020-00084-y.

Sugihara, N.G., J.W. Van Wagtendonk, and J. Fites-Kaufman. 2006. Fire as an ecological process. In *Fire in California's ecosystems*, ed. N.G. Sugihara, J.W. van Wagtendonk, J. Fites-Kaufman, K.E. Shaffer, and A.E. Thode, 58–74. Oakland: University of California Press.

United States Census Bureau. Decennial Census Data (1890–2020). 2021. https://www.census.gov/library/publications.html. Accessed 6 Aug 2021.

USDA, NRCS. 2021. The PLANTS Database. http://plants.usda.gov.

Vander Yacht, A.L., P.D. Keyser, S.A. Barrioz, C. Kwit, M.C. Stambaugh, W.K. Clatterbuck, and R. Jacobs. 2020. Litter to glitter: Promoting herbaceous groundcover and diversity in mid-southern USA oak forests using canopy disturbance and fire. *Fire Ecology* 16: 17. https://doi.org/10.1186/s42408-020-00072-2.

Vanderhorst, J., J. Jeuck, J. and S. Gawler. 2007. Vegetation classification and mapping of New River Gorge National River, West Virginia. US Dept. of the Interior, National Park Service. Northeast Region, Philadelphia, Pennsylvania.

Varner, J.M., M.A. Arthur, S.L. Clark, D.C. Dey, J.L. Hart, and C.J. Schweitzer. 2016. Fire in eastern North American oak ecosystems: Filling the gaps. *Fire Ecology* 12: 1–6. https://doi.org/10.4996/fireecology.1202001.

Vaughan, M.C., D.L. Hagan, W.C. Bridges, M.B. Dickinson, and T.A. Coates. 2021. How do fire behavior and fuel consumption vary between dormant and early growing season prescribed burns in the southern Appalachian Mountains? *Fire Ecology* 17: 27. https://doi.org/10.1186/s42408-021-00108-1.

Vose, J.M., B.D. Clinton, and W.T. Swank. 1994. Fire, drought, and forest management influences on pine/hardwood ecosystems in the southern Appalachians. In *A paper presented at the 12th Conference on Fire and Forest Meteorology, October 26-28, 1993, at Jekyll Island, GA*.

Waldrop, T.A. 2014. *Wildland fire in the Appalachians: Discussions among managers and scientists*, 8–10. Roanoke: Oct 2013.

Waldrop, T.A., and S.L. Goodrick. 2012. Introduction to prescribed fires in Southern ecosystems. Science Update SRS-054. Asheville, NC: US Department of Agriculture Forest Service. *Southern Research Station* 54: 1–80.

Waldrop, T.A., D.L. Hagan, and D.M. Simon. 2016. Repeated application of fuel reduction treatments in the southern Appalachian Mountains, USA: Implications for achieving management goals. *Fire Ecology* 12: 28–47. https://doi.org/10.4996/fireecology.1202028.

Weakley, A.S. 2020. *Flora of the southeastern United States*. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC.

Whigham, D.F. 2004. Ecology of woodland herbs in temperate deciduous forests. *Annual Review of Ecology, Evolution, and Systematics* 35: 583–621. https://doi.org/10.1146/annurev.ecolsys.35.021103.105708.

Woods, A. J., J. M. Omernik, and D. D. Brown. 1999. Level III and IV ecoregions of Delaware, Maryland, Pennsylvania, Virginia, and West Virginia. US Environmental Protection Agency, National Health and Environmental Effects Research Laboratory, Corvallis, Oregon. Report with map supplement, Scale 1:1,000,000.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* 21: 414–416. https://doi.org/10.1139/x91-053.

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