



ORIGINAL RESEARCH

Open Access



Higher severity fire increases the long-term competitiveness of pyrophytes in an upland oak-pine forest, Kentucky, USA

Scott G. Culbert^{1*}, Mary A. Arthur¹, Claudia A. Cotton² and Jacob J. Muller¹

Abstract

Background In eastern North American forests and woodlands, formerly dominant oaks (*Quercus* spp. L.) and pines (*Pinus* spp. L.) are experiencing widespread regeneration challenges. These challenges are due to past land use and fire exclusion facilitating positive feedbacks that reduce the effectiveness of low-severity prescribed fire. High-severity fires (wildfires and potentially prescribed burns) offer promise to overcome these feedbacks and assist in ecosystem restoration. In 2010, a 670-ha mixed-severity wildfire burned in the Daniel Boone National Forest, Kentucky, USA, providing a rare opportunity to track oak-pine community recovery across a wide fire severity spectrum for 12 years. We examined the effects of burn severity on species diversity, forest structure, community assemblage, stem recruitment into the midstory (2–10 cm diameter at breast height [DBH]) and canopy (10+ cm DBH), and non-native invasive plant (NNIP) populations, and compared these effects to previous results published after 6 years post-fire.

Results The relative importance of midstory pyrophyte species (e.g., *Quercus* spp. and *Pinus* spp.) was positively related to field-measured burn severity, while mesophytes (e.g., *Acer rubrum*, *Betula lenta*) displayed a weaker negative relationship. After 12 years, higher burn severity yielded greater midstory recruitment of pyrophytes; however, this was only observed for yellow pines (*P. echinata* Mill., *P. rigida* Mill., *P. virginiana* Mill.) and non-oak-pine pyrophytes. Oaks and mesophytes' midstory recruitment displayed no relationship with burn severity. Increased burn severity strongly increased invasive species presence, particularly Chinese silvergrass (*Miscanthus sinensis* Andersson).

Conclusions Six years after fire, oak midstory recruitment was positively related to burn severity. By year 12, higher burn severity was no longer associated with oak midstory recruitment but was associated with increased recruitment and importance of other pyrophytic species, particularly yellow pines. Our results also suggest that a single high-severity fire can increase the long-term competitive status of pyrophytes relative to mesophytes. As such, higher-severity fire may be an important tool in restoring fire-adapted communities where low-severity fire lacks the ability to produce meaningful forest structure and community changes. However, NNIP proliferation in high-severity burn areas can undermine the restoration benefits we observed.

Keywords Burn severity, Fire management, High-severity, Invasive species, Mesophication, Recruitment, Regeneration, Wildfire

*Correspondence:

Scott G. Culbert

scott.g.culbert@gmail.com

Full list of author information is available at the end of the article

Resumen

Antecedentes En bosques y regiones forestales del este de Norteamérica, los antiguamente dominantes robles (*Quercus* spp. L.) y pinos (*Pinus* spp. L.), están experimentando grandes desafíos en su regeneración. Estos desafíos son debidos a usos de la tierra en el pasado y la exclusión del fuego, lo que facilitó retroalimentaciones positivas que reducen la efectividad de quemaduras prescritas de baja severidad. Los incendios de alta severidad (incendios naturales y potencialmente quemaduras prescritas), ofrecen la posibilidad de superar esas retroalimentaciones y asistir en la recuperación de esos ecosistemas. En 2010, un incendio de severidad mixta afectó 670 ha en el Bosque Nacional Daniel Boone, en Kentucky, EEUU. proveyendo así de una rara oportunidad para registrar la recuperación de una comunidad de roble y pino a través de un amplio espectro de diferentes severidades de fuego por 12 años. Examinamos los efectos de la severidad de los incendios en la diversidad de especies, la estructura forestal, el ensamble de la comunidad, el reclutamiento de tallos (plántulas) en el estrato medio (2 a 10 cm de DBH) y del dosel (10+ cm de DBH), y de las poblaciones de plantas invasoras no nativas (NNIP), y comparamos esos efectos con resultados de estudios previos publicados seis años luego de ese incendio.

Resultados La importancia relativa de las especies pirófitas del estrato medio (e.g., *Quercus* spp. y *Pinus* spp.) fue correlacionada positivamente con la severidad medida a campo, mientras que las mesófitas (e.g., *Acer rubrum*, *Betula lenta*, etc.) mostraron una relación negativa más débil. Luego de 12 años, la mayor severidad produjo un mayor reclutamiento de pirófitas. Sin embargo, este fue solo observado para los pinos amarillos (*P. echinata* Mill., *P. rigida* Mill., *P. virginiana* Mill.) y pirófitas que no fuesen robles. El reclutamiento de robles y mesófitas no mostraron ninguna relación con la severidad de las quemaduras. El aumento de la severidad de las quemaduras incrementó la presencia de especies invasoras, especialmente del pasto cola de zorro o pasto plateado chino (*Miscanthus sinensis* Andersson).

Conclusiones Conclusiones: Seis años luego del incendio, el reclutamiento del roble en el estrato medio fue positivamente relacionado con la severidad del incendio. En el año 12, la mayor severidad no pudo ser asociada con el reclutamiento en el estrato medio, aunque fue asociado con un incremento en el reclutamiento e importancia de otras especies pirófitas, particularmente los pinos amarillos. Nuestros resultados también sugieren que un único fuego de alta severidad puede incrementar el estatus competitivo a largo plazo de las pirófitas en relación a las mesófitas. De esa manera, una severidad de fuego más alta puede ser una herramienta importante en la restauración de comunidades adaptadas al fuego, en las cuales fuegos de baja severidad carecen de habilidad para producir una estructura forestal significativa y cambios en la comunidad. Sin embargo, la proliferación de NNIP en áreas quemadas severamente pueden minar los beneficios de la restauración observados por nosotros.

Background

In eastern North American forests, fire was a common occurrence until the early twentieth century when fire suppression policies, such as the US Forest Service 10 AM Policy of 1935, were adopted (Ryan et al. 2013; Arthur et al. 2021). Prior to this, lightning and Native American populations maintained frequent fire regimes, with median fire return intervals of 5.4 years for fire-prone ecosystems across the region (Lafon et al. 2017). The selective pressures of these fire regimes strongly shaped vegetation physiology, structure, composition, and distribution (Delcourt and Delcourt 1997; Delcourt et al. 1998; Stambaugh et al. 2015), and the cessation of fire throughout the twentieth century caused profound impacts on ecosystem dynamics, especially in oak-pine dominated forests of the eastern US (Hutchinson et al. 2008; Nowacki and Abrams 2008).

Several oak and pine species, including white oak (*Quercus alba* L.), chestnut oak (*Q. montana* Willd.), scarlet oak (*Q. coccinea* Muenchh.), and yellow pines (*Pinus echinata* Mill., *P. rigida* Mill., *P. virginiana* Mill.),

rely upon periodic fire or other disturbance to create a suite of favorable conditions that support successful understory regeneration, recruitment into larger size classes, and maintenance of canopy dominance (Nowacki and Abrams 1991; Abrams and Nowacki 1992). In the absence of fire—alongside climatic, land-use, and important biotic changes (McEwan et al. 2011)—these pyrophytic species are experiencing widespread recruitment failures (Abrams 1992) and are largely being replaced by shade-tolerant mesophytic species, including red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marshall), American beech (*Fagus grandifolia* Ehrh.), birch (*Betula* L. spp.), and yellow-poplar (*Liriodendron tulipifera* L.; Abrams 1992; Fei et al. 2011; Hutchinson et al. 2008). These species are more susceptible to being top-killed by fire (Nowacki and Abrams 2008; Arthur et al. 2021), but facilitate forest mesophication, a process in which they cast heavy shade, limit air movement, and abscise non-flammable litter, causing understory microclimate conditions to be cooler, more humid, and less flammable (Nowacki and Abrams 2008; Arthur et al. 2021). This

process creates positive selection feedback in favor of shade-tolerant mesophytic species and against pyrophytic species, resulting in ecosystem transitions to alternative stable states (Nowacki and Abrams 2008).

As a result, many eastern US forests are characterized as having canopy layers dominated by oak species that regenerated prior to fire cessation (ca. 1870–1930), whose seedlings are able to establish in the understory, but are unable to recruit into midstory sizes where mesophytic species grow densely and are more competitive (Abrams 2003; Dyer and Hutchinson 2019). Consequently, oak species' overall importance has declined (Fei et al. 2011) and if current recruitment challenges continue, these species may comprise a minor component of future forests. Such a transformation has extensive ecological implications, as oaks play a keystone role in biotic and abiotic ecosystem processes (Fralish 2004). For instance, acorn mast is essential for many wildlife (McShea 2000; McShea and Healy 2002) and insect (Tallamy 2021) populations. Decreased oak dominance is also associated with altered below-canopy precipitation and nutrient distributions (Alexander and Arthur 2010, 2014), decreased compositional, structural, and spatial diversity (Nowacki and Abrams 2008; Hanberry et al. 2020), and decreased resilience to climate change (Iverson et al. 2019).

With the aim of curtailing these forest changes, land managers have reintroduced fire primarily through prescribed burning, or burning combined with thinning treatments (Brose et al. 2001). However, there is a growing recognition of the ecological benefits of incorporating attributes of wildfire into management plans (Ryan et al. 2013), particularly for restoring fire-dependent species and alleviating oak-pine recruitment issues (Black et al. 2018; Saladyga et al. 2022). Wildfire events often create a heterogeneous mosaic of burn severity (Hutchinson et al. 2008) that prompts a greater range of ecological responses than prescribed fires, which are typically lower in severity and more spatially homogenous (Brose et al. 2001). Patches with increased burn severity are more likely to experience decreased density and basal area in the midstory and overstory initially following a fire, which increases understory light availability (Reilly et al. 2006). These changes to forest structure are essential for promoting the establishment and growth of understory pyrophytic species (Kuddes-Fischer and Arthur 2002), and have been shown to directly increase the recruitment of oak (Black et al. 2018) and pine (Black et al. 2018; Saladyga et al. 2022) saplings. At our research site in the Cumberland Plateau, Black et al. (2018) found that increased burn severity bolstered the competitive status of oaks and pines in the understory by 6 years post-fire. This may indicate that higher-severity fire can serve as a tool for creating changes in forest conditions that allow

pyrophytic oaks and pines to maintain forest dominance, though Black et al. (2018) indicated that further research was needed to determine whether their observed results would persist.

Despite the potential benefits of higher burn severity, non-native invasive plant (NNIP) establishment and proliferation following fire complicate management. The increasingly disturbed soil, increased soil moisture availability, and higher light conditions associated with high-severity fire can provide an effective pathway for NNIPs to establish in central and southern Appalachian mixed hardwood forests, especially for princess tree (*Paulownia tomentosa* [Thunb.] Siebold & Zucc. Ex. Steud) and Chinese silvergrass (*Miscanthus sinensis* Andersson) (Miller et al. 2010; Black et al. 2018). Princess tree is known to have flame retardant characteristics (Li and Oda 2007) and inhibit the germination and growth of native seedlings (Williams and Wang 2021), particularly in upland xeric ecosystems (Kuppinger et al. 2010). Chinese silvergrass dramatically increases forest litter flammability and suppresses tree growth (Stewart et al. 2009). Due to these impacts, these species have been listed as moderate to severe ecosystem threats throughout the eastern USA (Kentucky Exotic Pest Plant Council 2015, Indiana Invasive Species Council 2022, Tennessee Invasive Plant Council 2023), and can present unintended outcomes when using fire as a management tool.

Understanding the ecological implications and management utility of wildfire is becoming increasingly important in the eastern USA, as wildfire events are anticipated to increase in frequency and size (Lafon and Quiring 2012; McNulty et al. 2013, 2015) and prescribed burning windows are becoming narrower with anthropogenic climate change (Kupfer et al. 2020; Gao et al. 2021). A key difference between wildfire and prescribed fire is the range of burn severities that occur in wildfires (Hutchinson et al. 2008), so understanding ecological responses at varying levels of burn severity has the potential to inform management strategies to better meet long-term objectives. In 2010, a wildfire in the Cumberland Plateau Physiographic Region provided an opportunity to study changes in species composition and forest structure at varying levels of burn severity, the first 6 years of which were published by Black et al. (2018).

The primary objective of this study was to analyze the current and long-term trends in forest stand structure and species composition at year 12 post-fire and compare them to the year 6 findings of Black et al. (2018). This repeated sampling improves our understanding of how forest communities regenerate at varying levels of burn severity, indicates future trajectories, and allows us to provide more accurate insights for future management. We hypothesized that (H1) the relationships

between species diversity, forest structure, and forest community assemblage (described by the dominance of species groups) with burn severity do not vary between or within years; (H2) burn severity is positively related to the recruitment of fire-adapted xeric species in midstory (2–10 cm DBH; 0.79–3.94 in DBH) and canopy (10+ cm DBH; 3.95+ cm DBH) size classes; (H3) burn severity has no relationship with the recruitment of shade-tolerant mesophytic species in midstory and canopy tree size classes; (H4) for trees < 2 cm DBH (< 0.79 in DBH), burn severity is positively related to species diversity of small seedlings (< 50 cm tall; < 19.7 in tall) and large seedlings (≥ 50 cm tall; ≥ 19.7 in tall); and (H5) burn severity is positively related to the presence of NNIP species.

Methods

Study area

The study was conducted on the Fish Trap Fire, described below. The study site is located within the Red River Gorge Geological Area of the Daniel Boone National Forest, in Powell County, Kentucky, which is part of the Cumberland Plateau physiographic region. The region's climate is continental, with moderately cold winters and warm, humid summers (Wharton and Barbour 1973) averaging 2.3 °C (36.1°F) and 23.1 °C (73.5°F), respectively, with mean annual precipitation of 136.47 cm (53.73 in) (NOAA 2023). The study area is characterized by highly dissected uplands and streams of the Red River watershed. The elevation ranges between 177 and 439 m (580.7–1440.3 ft). Ridgetop soils are primarily Inceptisols, with Alticrest and Ramsey soil series derived from Pennsylvanian sandstones and conglomerates and shales of the lower Breathitt formation (Soil Survey Staff 2021). This Pennsylvanian sandstone also typifies the rock outcrops and cliffs that are common to this study area. Alticrest is a well-drained sandy loam and Ramsey is an excessively drained sandy loam (Soil Survey Staff 2021). The slopes are dominated by the Helewacha soil series, consisting of parent material that is coarse loamy colluvium (Soil Survey Staff 2021). Due to the underlying geology, the Red River Gorge Geologic Area contains numerous natural sandstone arches, cliffs, rock shelters, and other geologic formations (Braun 1950). These formations, along with the area's complex topography, provide myriad site conditions that produce exceptionally high biodiversity, making the forest type here one of the most complex in North America (Braun 1950; Wharton and Barbour 1973).

This study focused on xeric uplands and ridgetops, as this was primarily where the Fish Trap Fire burned. Due to high recreation activity, forest harvesting and burning has been excluded in this area since 1993. The average stand age is 76 years. Prior to this, management records

indicate that timber harvesting actions were exclusive to slopes, coves, and bottomlands. In February 1992 and 1993, prescribed fires were conducted on the easternmost ridge of our study area (Fig. 1), burning 8 ha (20 acres) and 28 ha (70 acres), respectively. It is possible that these burns promoted mesophytic species in the understory—a common result of one or two dormant season prescribed fires in this area (Arthur et al. 1998; Kuddes-Fischer and Arthur 2002; Alexander et al. 2008)—though it is unlikely that these fires produced long-term meaningful changes in the forest community that would have altered the results we observed following the Fish Trap Fire in 2010. The only other disturbance that may have impacted this study site was a southern pine beetle (*Dendroctonus frontalis* Zimmerman) infestation that affected the Daniel Boone National Forest between 1995 and 2002 (Maingi and Luhn 2005); however, there were no recorded observations within our study site and the Red River Gorge Geological area and the northern portion of the Daniel Boone National Forest were impacted less severely than southern portions of the forest (Maingi et al. 2001).

These xeric forest communities are typically dominated by scarlet oak, chestnut oak, black oak (*Q. velutina* Lam.), white oak, and yellow pines (Wharton and Barbour 1973; Black et al. 2018). Midstories are typically composed of red maple (*Acer rubrum* L.), sourwood (*Oxydendrum arboreum* A.P. DC.), black gum (*Nyssa sylvatica* Marshall var. *sylvatica*), and sassafras (*Sassafras albidum* (Nutt.) Nees), and the understory shrub community is largely dominated by green briar (*Smilax* spp. L.), mountain-laurel (*Kalmia latifolia* L.), and *Vaccinium* spp. L. (Black et al. 2018).

Fish Trap Fire

The Fish Trap Fire was ignited accidentally during a significant drought on 24 October 2010 by campers and was not fully extinguished until 9 November 2010 having burned 673.8 ha (1665.0 acre) in the Daniel Boone National Forest, Kentucky, USA (37° 49' N, 83° 40' W). In 2011, a ground-based plot-level assessment of burn severity was conducted using composite burn index (CBI) (Key and Benson 2006) to quantify the impacts of the fire on site characteristics, such as trees, shrubs, herbs, and substrates (Key and Benson 2006). CBI ranges from 0 to 3, spanning the possible range of severity between unburned (0) and greatest burned effect (3) (Key and Benson 2006). The post hoc use of CBI was determined to be an accurate measure of burn severity (Upadhaya 2015), with CBI and post-fire differenced normalized burn ratio (Δ NBR) values strongly related ($r_s = 0.90$, $p = 1.19 \times 10^{-9}$, $F_{1,25} = 87.67$, $R^2_{adj} = 0.77$). In the absence of pre-burn vegetation data,

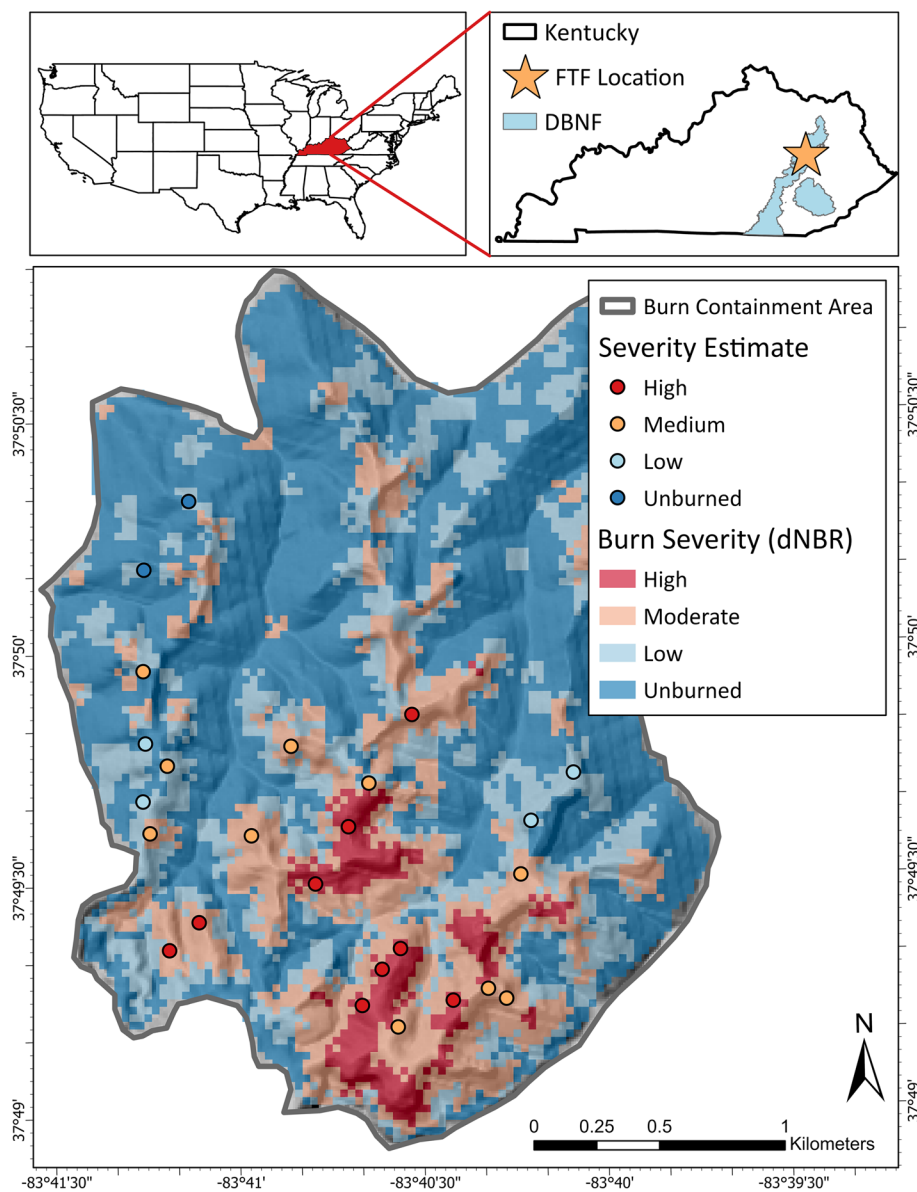


Fig. 1 Locations of the 26 permanent field plots at the location of the Fish Trap Fire (FTF), a wildfire that burned within the Daniel Boone National Forest (DBNF) in 2010 on the Cumberland Plateau, Kentucky, USA

Upadhaya (2015) compared pre- and post-burn Landsat-derived normalized difference vegetation index (NDVI) to a reference site and found pre-burn NDVI of the Fish Trap Fire site to exhibit no significant differences in canopy cover compared to the reference site, but after the fire, NDVI varied significantly with detectable differences in burn severity, meaning that variation in NDVI was directly a result of the Fish Trap Fire. Black et al. (2018) compared pre-burn NDVI values with field-based CBI measurements to determine if pre-burn vegetation was associated with fire severity.

They also tested for the effects of any pre-existing moisture variation across the study plots using topographic wetness index (TWI), and tested whether burn severity (CBI) was associated with TWI. Overall, they found that TWI had no significant effect on the study site, meaning these plots were similar in moisture as measured by topographic position and that there was no relationship between CBI and pre-burn NDVI and TWI, meaning that CBI variation was a function of the effects of the fire, rather than pre-fire landform and vegetation variability.

The burn severity of the Fish Trap Fire was heterogeneous, ranging from high-severity stand-replacing fire to unburned areas (Black et al. 2018). The most severely burned areas, which occupied < 10% of total area burned, experienced nearly 100% topkill of vegetation within the year following the fire, and had patches where the forest floor burned down to mineral soil (Black et al. 2018). In areas where there was substantial mortality of large trees, the soil was much wetter for several years following the fire allowing for the successful establishment of species not commonly found on xeric uplands (David Taylor, Daniel Boone National Forest Botanist, Winchester, Kentucky USA, personal communication).

Data collection

In August of 2011, we established 30 permanent research plots across the Fish Trap Fire containment boundary, which were monumented with rebar and referenced with GPS coordinates (Fig. 1). We removed four plots from analysis, yielding 26 total plots that were all upland sites and were distributed across the gradient of burn severity relatively evenly, with 26% of plots being unburned to low burn severity (CBI 0 to 1), 38% moderate (CBI 1 to 2), and 38% high (CBI 2 to 3) severity. Data collection occurred in 2011, 2013, 2016, and 2022, yielding measurements for 1, 3, 6, and 12 years post-fire, respectively; results of the data collected through 2016 (6 years) were published in Black et al. (2018).

At each plot, we used 500 m² (0.05 ha; 0.12 acre) circular nested plots. For all stems ≥ 2 cm (0.79 in) diameter at breast height (DBH), we visually estimated canopy vigor and recorded tree species, DBH, and number of basal sprouts. Additionally, within a 25 m² (0.006 acre) circular microplot sharing the same plot center, we counted and identified to species stems < 2 cm (0.79 in) DBH, and recorded them as small (< 50 cm (19.7 in) tall) or large (≥ 50 cm (19.7 in) tall) (H4). To accompany these data, we recorded ground cover type as mineral soil, rock, moss, litter, vegetation, or woody debris every 10 cm (3.9 in) along two 25.2 m (82.7 ft) transects oriented N to S and E to W. Lastly, we recorded the presence of any non-native invasive woody or non-woody plant species occurring within the entire plot (H5).

Statistical analysis

From the measurements described in Sect. 2.3, we calculated several metrics to provide information on the vegetation response to the Fish Trap Fire. To evaluate how the relationships between burn severity and diversity, community assemblage, and structure vary between or within years (H1), we calculated basal area (m²/ha; ft²/acre), stem density (stems/ha; stems/acre), relative importance values, Shannon's Diversity Index (SHDI), and species

richness for stems ≥ 2 cm (0.79 in) DBH, and compared those calculations to previous measurement years. The formula used for calculating relative importance values was:

$$\frac{R_{ba} + R_{sd}}{2} * 100$$

where R_{ba} and R_{sd} are the basal area and stem density of a given species relative to all species measured in a given plot. Respectively, these represent relative dominance and density metrics and constitute an IV scale of 200.

To analyze community assemblage (H1) and stem recruitment over time of fire-adapted xeric species (H2) and shade-tolerant mesophytic species (H3), we grouped species into one of four categories: pyrophytes, mesophytes, intermediates, and no relationship to fire (Table 1). We determined categorizations based on species' fire tolerances, adaptive traits, response to fire events, and ecological impacts on post-fire environments, as well as similar categorizations in recent literature (Arthur et al. 2021; Saladyga et al. 2022). We defined pyrophytes as species that have physiological tolerances to fire, have evolved characteristics to promote fire events, and are known to be more successful in frequent fire regimes (Hengst and Dawson 1994; Varner et al. 2015, 2016, 2021). Mesophytes are species that are known to facilitate the process of mesophication through having branch architecture and leaf morphology that casts heavy shade and limits understory air movement and whose litter is notably fire-inhibiting (Nowacki and Abrams 2008; Kreye et al. 2018; Babl et al. 2020; Varner et al. 2021). Intermediate species are those that do not have traits associated with fire tolerance, but are also not known to facilitate mesophication, and species categorized as no relationship are those that have a relative dearth of published literature related to a species pyrophilicity. Some species' categories were relatively ambiguous. For instance, *P. virginiana* has low litter flammability and low bark allometry (Sullivan 1993; Arthur et al. 2021) but requires mineral soil for seed germination and frequent fire maintains their populations (Sullivan 1993)—resulting in us categorizing it as an intermediate, despite it being a yellow pine that is more prevalent in frequent fire regimes (Sullivan 1993) and also having mesophytic characteristics (Arthur et al. 2021). While there may not be a scientific consensus for categorizing some of the species we observed, this approach still serves as an effective heuristic for considering how an upland forest community may be comprised in relation to how much fire is occurring within it.

To determine the species driving the relationships observed in these groupings, we conducted analyses on genera of concern, where we specifically looked at the

Table 1 Species groupings of all tree species found since 2011 at the Fish Trap Fire study site, Daniel Boone National Forest, Kentucky

Pyrophytes	Mesophytes	Intermediates	No relationship
<i>Carya glabra</i> (Mill.)	<i>Acer rubrum</i> L	<i>Amelanchier arborea</i> (Michx. F.) Fernald	<i>Aralia spinosa</i> L
<i>Carya tomentosa</i> (Poir.) Nutt	<i>Acer saccharum</i> Marshall	<i>Cornus florida</i> L	<i>Hamamelis virginiana</i> L
<i>Castanea dentata</i> (Marshall) Borkh	<i>Betula lenta</i> L	<i>Fraxinus americana</i> L	<i>Ilex opaca</i> Ait
<i>Kalmia latifolia</i> L	<i>Fagus grandifolia</i> Ehrh	<i>Nyssa sylvatica</i> var. <i>sylvatica</i>	<i>Magnolia macrophylla</i> Michx
<i>Pinus echinata</i> Mill	<i>Liriodendron tulipifera</i> L	<i>Ostrya virginiana</i> (Mill.) K. Koch	<i>Malus</i> sp. Mill
<i>Pinus rigida</i> Mill	<i>Magnolia acuminata</i> L	<i>Pinus virginiana</i> Mill	<i>Platanus occidentalis</i> L
<i>Populus grandidentata</i> Michx	<i>Oxydendrum arboreum</i> A.P. DC	<i>Sassafras albidum</i> (Nutt.) Nees	<i>Rhus copallinum</i> L
<i>Quercus alba</i> L	<i>Pinus strobus</i> L		<i>Rhus glabra</i> L
<i>Quercus coccinea</i> Muenchh			<i>Viburnum dentatum</i> L
<i>Quercus montana</i> Willd			
<i>Quercus rubra</i> L			
<i>Quercus velutina</i> Lam			
<i>Robinia pseudoacacia</i> L			

Groupings are based on previous categorizations (Arthur et al. 2021; Saladyga et al. 2022) and species' fire tolerances, adaptive traits, response to fire events, and ecosystem impacts (i.e., if they facilitate mesophication or not)

effects on oaks, yellow pines, non-oak-pine pyrophytes, maples, and non-maple mesophytes. For each of these species' groupings, we calculated recruitment as the difference in number of stems per area between year 12 and previous measurement years (years 1 and 6) at a given size class. Size classes were midstory (2–10 cm DBH; 0.79–3.94 in DBH) and canopy trees (10+ cm DBH; 3.94+ in DBH), which were based on size classes used by Black et al. (2018) and those common in the literature from the area (Arthur et al. 1998; Blankenship and Arthur 2006; Blankenship et al. 2023). We calculated recruitment from 2011 to 2022 and from 2016 to 2022.

We used linear regression analyses to assess the hypothesized relationships between fire severity and forest vegetation measurements. Prior to any regression modeling, we assessed statistical assumptions of data independence and normality for all variables being analyzed. After model generation, we assessed statistical assumptions (homoscedasticity, outliers, and normally distributed residuals) for each model. We corrected any violations of these assumptions by transforming the data with a square-root or natural log transformation. We generated linear regression models using R (R Core Team 2023), and for each calculated metric, linear, square-root, and 2nd, 3rd, and 4th degree polynomial models were generated, though we often removed high-degree polynomials to avoid overfitting and only considered them if they followed a hypothesized pattern associated with H1–H5 and there was a reasonable explanation for the phenomena they were describing. From these models, we used Akaike's Information Criteria (AIC) to determine which model best described the metric's relationship with burn severity. We then plotted the resulting

best-fit model using the ggplot2 and ggpubr packages in R (Wickham 2016; Kassambara 2022; R Core Team 2023;).

For stems < 2 cm (0.79 in) DBH, we used linear regression to assess the relationships of species abundance and species diversity with burn severity (H4), and generalized linear models (GLM) with a Poisson distribution to model species richness in R (R Core Team 2023). Similarly, we used GLM with a binomial distribution to predict the presence of NNIPs in year 12 post-fire, based on burn severity and groundcover (H5). For all statistical analyses conducted, we used an α level of 0.05.

Results

Species diversity and richness

The relationships between burn severity and woody plant species diversity and richness changed over time since the Fish Trap Fire (H1). By 12 years post-fire, mid-story species richness and SHDI were positively and significantly related to burn severity (OR=1.24, $p=0.004$; $R^2_{\text{adj}}=0.330$, $F_{1, 24}=13.30$, $p=0.001$, respectively) (Sup. Figure 1). Prior to this and within the canopy size class, there were no significant relationships between burn severity and species diversity and richness.

Forest structure

Twelve years post-fire, basal area in both tree size classes was influenced by burn severity and varied among species groupings (H1) (Table 2). Midstory basal area had a strong ($R^2_{\text{adj}}=0.679$) positive relationship and canopy basal area had a strong ($R^2_{\text{adj}}=0.662$) negative relationship with burn severity. Pyrophytes in the midstory had a moderate ($R^2_{\text{adj}}=0.553$) positive relationship

Table 2 *P*-values indicating the statistical significance of linear regression tests analyzing the relationship between forest structural measurements and burn severity among various species groups and size classes observed at the Fish Trap Fire study site, Daniel Boone National Forest, Kentucky, 12 years post-fire

	Species Group	All		Midstory		Canopy	
Basal Area	All	(-) < 0.001	(R ² = 0.599)	(+) < 0.001	(R ² = 0.679)	(-) < 0.001	(R ² = 0.662)
	Pyrophytes	(-) < 0.001	(R ² = 0.485)	(+) < 0.001	(R ² = 0.553)	(-) < 0.001	(R ² = 0.664)
	Mesophytes	0.857		0.158		0.126	
	Intermediates	0.370		0.087		0.213	
	Oak	(-) < 0.001	(R ² = 0.502)	(+) < 0.001	(R ² = 0.404)	(-) < 0.001	(R ² = 0.500)
	Yellow Pine	0.327		0.127		0.070	
	Non-oak-pine Pyro	0.070		(+) 0.018	(R ² = 0.358)	NA	
	Maple	0.742		0.782		0.070	
	Non-maple Meso	0.633		0.252		0.054	
	Intermediates	0.081		0.782		0.585	
Stem Density	All	(+) 0.003	(R ² = 0.280)	(+) 0.003	(R ² = 0.293)	(-) 0.039	(R ² = 0.130)
	Pyrophytes	(+) < 0.001	(R ² = 0.382)	(+) < 0.001	(R ² = 0.479)	(-) 0.002	(R ² = 0.317)
	Mesophytes	0.387		0.356		0.052	
	Intermediates	0.185		0.182		0.356	
	Oak	0.678		0.085		(-) < 0.001	(R ² = 0.600)
	Yellow Pine	0.123		0.385		0.716	
	Non-oak-pine Pyro	(+) 0.013	(R ² = 0.345)	(+) 0.007	(R ² = 0.392)	NA	
	Maple	0.858		0.773		0.382	
	Non-maple Meso	0.205		0.193		0.141	
	Intermediates	0.873		0.797		0.993	
Importance Value	Pyrophytes	0.546		(+) < 0.001	(R ² = 0.464)	0.074	
	Mesophytes	0.503		(-) 0.004	(R ² = 0.273)	0.719	
	Intermediates	0.954		0.123		0.186	
	Oak	(-) < 0.001	(R ² = 0.385)	0.321		(-) 0.022	(R ² = 0.241)
	Yellow Pine	0.528		0.818		(+) 0.017	(R ² = 0.205)
	Non-oak-pine Pyro	(+) 0.030	(R ² = 0.261)	(+) 0.033	(R ² = 0.294)	NA	
	Maple	0.130		0.900		0.900	
	Non-maple Meso	0.771		(-) 0.042	(R ² = 0.126)	0.287	
	Intermediates	0.363		(-) 0.018	(R ² = 0.180)	0.255	

Significant relationships are represented in bold font and the direction of a significant relationship is shown by a (+) or (-) sign, where (+) indicates that as burn severity increased, there was a significant increase in a given forest structural measurement and vice versa for a (-) sign

with burn severity, which was primarily the result of oaks ($R^2_{\text{adj}}=0.404$) and non-oak-pine pyrophytes ($R^2_{\text{adj}}=0.358$) (Sup. Figure 4). Pyrophytes in the canopy had a strong ($R^2_{\text{adj}}=0.664$) negative relationship with burn severity, particularly among oaks ($R^2_{\text{adj}}=0.500$) (Sup. Figure 5B). Basal area of yellow pines, mesophytes, and intermediate species was unrelated to burn severity in any size class.

The relationship between tree stem density and burn severity also varied by species groupings and tree size classes 12 years after the Fish Trap Fire (H1) (Table 2). Midstory

stem density had a weak ($R^2_{\text{adj}}=0.293$) positive relationship with burn severity and canopy stem density had a very weak ($R^2_{\text{adj}}=0.13$) negative relationship with burn severity (Sup. Figure 2, 3). Increased burn severity yielded moderate increases in midstory pyrophyte density ($R^2_{\text{adj}}=0.479$), particularly for non-oak-pine pyrophytes ($R^2_{\text{adj}}=0.392$). Stem density of canopy sized trees was only related to burn severity for oak species, which had a strong negative relationship ($R^2_{\text{adj}}=0.600$) (Sup. Figure 3B). Stem density of yellow pines, mesophytes, and intermediate species had no relationship with burn severity at either size class.

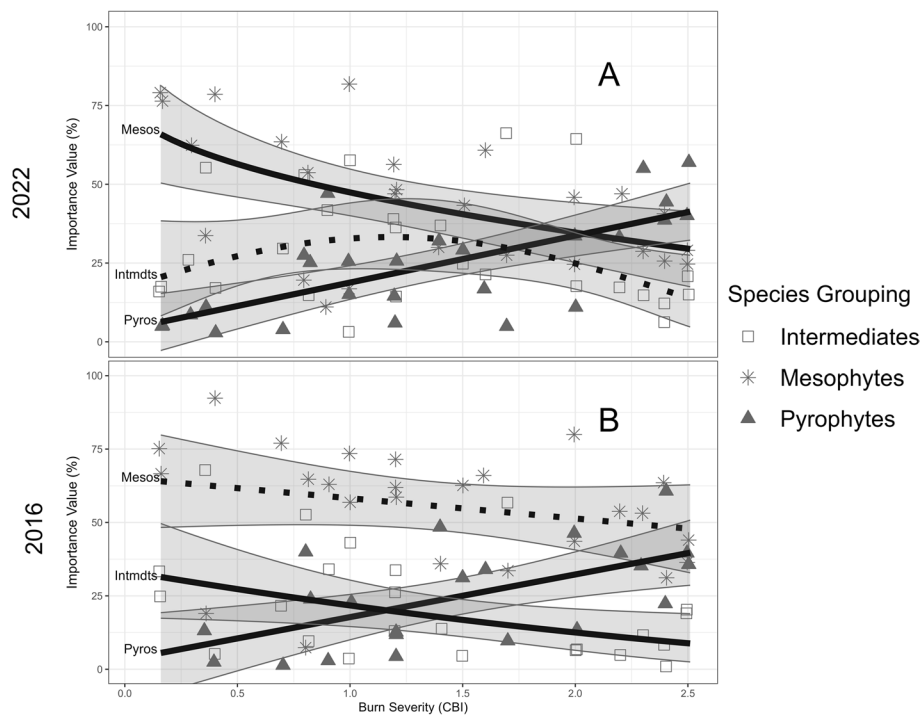


Fig. 2 Relationship between burn severity, measured as CBI, with midstory (2–10 cm [0.79–3.94 in] DBH) species' importance values after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Species were grouped based on their fire ecology characteristics and importance values were calculated as the average of relative stem density and relative basal area. Relationships are displayed for post-fire year 12 (**A**) and post-fire year 6 (**B**), with significant relationships ($\alpha=0.05$) represented by a solid line and insignificant relationships represented by a dashed line

Community assemblage

Twelve years post-fire, there were significant differences between the relative importance values (IV) of different species groupings, which varied among size classes (H1) (Table 2). Within the midstory, burn severity had a moderate positive relationship with pyrophyte IV ($R^2_{\text{adj}}=0.464$) and a weak negative relationship with mesophyte IV ($R^2_{\text{adj}}=0.273$) (Fig. 2A). Trends for mesophytic species were largely driven by non-maple mesophytes, albeit a very weak relationship ($R^2_{\text{adj}}=0.126$), and trends for pyrophytes were driven by non-oak-pine pyrophytes ($R^2_{\text{adj}}=0.249$). For canopy trees, burn severity had a weak negative relationship with oak IV ($R^2_{\text{adj}}=0.241$) and positive relationship with yellow pine IV ($R^2_{\text{adj}}=0.205$) (Fig. 3B).

Stem recruitment over time

Post-fire tree recruitment varied among size classes and across recruitment time (H2 and H3) (Table 3). Burn severity had a weak positive ($R^2_{\text{adj}}=0.317$) relationship with pyrophyte stem recruitment into the midstory between 2016 and 2022, particularly for yellow pines ($R^2_{\text{adj}}=0.304$) and non-oak-pine pyrophytes ($R^2_{\text{adj}}=0.471$) (Fig. 4). The recruitment of pyrophytes and intermediates into the canopy was positively

related to burn severity (Fig. 5), though intermediates ($R^2_{\text{adj}}=0.378$) displayed a stronger relationship than pyrophytes ($R^2_{\text{adj}}=0.139$). Pyrophyte recruitment was primarily driven by yellow pines ($R^2_{\text{adj}}=0.207$), but there was a near-significant relationship for oak species as well (Fig. 5; Table 3). Overall, between post-fire year 6 and 12, there was no relationship between burn severity and mesophyte recruitment at any size class.

Stem recruitment since the Fish Trap Fire (2011–2022) varied among species groups and size classes (H2 and H3) (Table 3). There was a moderate ($R^2_{\text{adj}}=0.439$) positive relationship between burn severity and recruitment of midstory pyrophyte stems between 2011 and 2022, particularly for yellow pines ($R^2_{\text{adj}}=0.291$) and non-oak-pine pyrophytes ($R^2_{\text{adj}}=0.393$) (Fig. 4). Over this time span, burn severity had no influence on the recruitment of mesophytic species into the midstory. Conversely, canopy recruitment was significantly, though very weakly, related to burn severity for intermediate species ($R^2_{\text{adj}}=0.144$) (Fig. 5). Negative species recruitment values indicate fewer stems in the canopy size class at year 12 than were observed in previous years. Since these canopy stems are not growing into a larger size class, the only reason for a negative recruitment value is stem mortality, which we observed among mesophytic species in lower

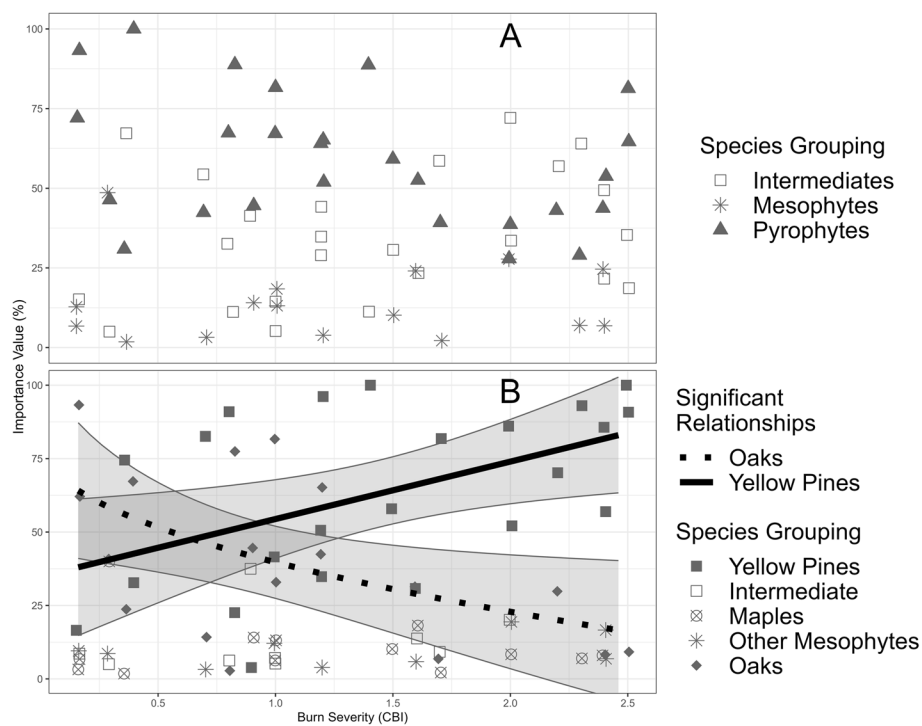


Fig. 3 Relationship of burn severity, measured as CBI, with canopy (10+ cm (3.94+ in) DBH) species' importance values 12 years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Importance values were calculated as the average of relative stem density and relative basal area. **A** represents species grouped based on their fire ecological characteristics and **B** distinguishes which genera are driving the relationships in **A**. Regression lines are shown only for relationships that are significant ($\alpha=0.05$)

severity plots (Fig. 5). As burn severity increased, there was less mortality of canopy sized mesophytic stems over 12 years, which resulted in a significant positive relationship (Table 3), although this relationship was very weak ($R^2_{adj}=0.167$). Recruitment of pyrophytes into the canopy had no relationship with burn severity over 12 years.

Seedlings

For trees < 2 cm (0.79 cm) DBH, species diversity was not related to burn severity in either the small (< 50 cm; < 19.7 in) or large (≥ 50 cm; ≥ 19.7 in) height class, though stem abundance varied with burn severity (H4). The abundance of small seedling pyrophytes had a very weak negative relationship with burn severity ($R^2_{adj}=0.132$, $F_{1,24}=4.816$, $p=0.038$), which was driven by a decrease in small oak seedlings as burn severity increased ($R^2_{adj}=0.3276$, $F_{1,19}=10.74$, $p=0.004$). Conversely, the abundance of small non-maple mesophyte seedlings displayed a weak positive relationship with burn severity ($R^2_{adj}=0.367$, $F_{1,21}=13.73$, $p=0.001$). Among large seedlings, yellow pine seedlings displayed a weak negative relationship with burn severity ($R^2_{adj}=0.204$, $F_{1,17}=5.60$, $p=0.030$). No other species groupings were significantly related to burn severity.

Non-native invasive species

The presence of NNIPs was strongly related to burn severity 12 years post-burn (H5). For all NNIPs species, burn severity was a significant predictor of invasive species presence (OR = 34.58, $p < 0.001$) (Fig. 6), meaning that for every increase in CBI of 1.0, there was a 34.58 times increase in the probability of detecting an invasive species. NNIP presence was not related to percent mineral soil (OR = 2.07e-11, $p=0.134$). The most prevalent NNIP was Chinese silvergrass, which was found on 73% of research plots. The other NNIPs were autumn olive (*Elaeagnus umbellata* Thunb.) (Presence = 3.8%), multiflora rose (*Rosa multiflora* Thunb. ex Murr.) (Presence = 3.8%), and Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus) (Presence = 3.8%), each of which were found on plots that experienced moderate to high burn severity ($CBI \geq 1.2$). These latter three species were only present on plots that also had Chinese silvergrass.

Discussion

Our results demonstrate that mixed-severity wildfire in an eastern Kentucky forest continued to have lasting effects on community assemblage and forest structure up to 12 years post-fire, and key among those effects was that

Table 3 *P*-values indicating the statistical significance between stem recruitment and burn severity among various species groups and size classes observed at the Fish Trap Fire study site, Daniel Boone National Forest, Kentucky, 12 years post-fire

Species group	Size class		Size class		
	Midstory	Canopy	Midstory	Canopy	
Recruitment: Years 6–12	Pyrophytes	(+) 0.002 (R ² = 0.317)	(+) 0.002 (R ² = 0.378)	(+) < 0.001 (R ² = 0.439)	0.184 (+) 0.024 (R ² = 0.167)
	Mesophytes	0.358	0.072	0.462	
	Intermediates	(+) 0.039 (R ² = 0.188)	(+) 0.038 (R ² = 0.139)	0.197	(+) 0.035 (R ² = 0.144)
	Oak	0.220	0.063	0.099	0.125
	Yellow Pine	(+) 0.003 (R ² = 0.304)	(+) 0.013 (R ² = 0.207)	(+) 0.003 (R ² = 0.291)	0.075
	Non-oak-pine Pyro	(+) < 0.001 (R ² = 0.471)	NA	(+) < 0.001 (R ² = 0.393)	NA
	Maple	0.556	0.247	0.932	0.174
	Non-maple Meso	0.088	NA	0.223	(+) 0.040 (R ² = 0.185)
	Intermediates	0.693	NA	0.902	NA

Significant relationships are represented in bold font and the direction of a significant relationship is shown by a (+) or (–) sign, where (+) indicates that as burn severity increased, there was a significant increase in the recruitment of a given species group into a given size class and vice versa for a (–) sign

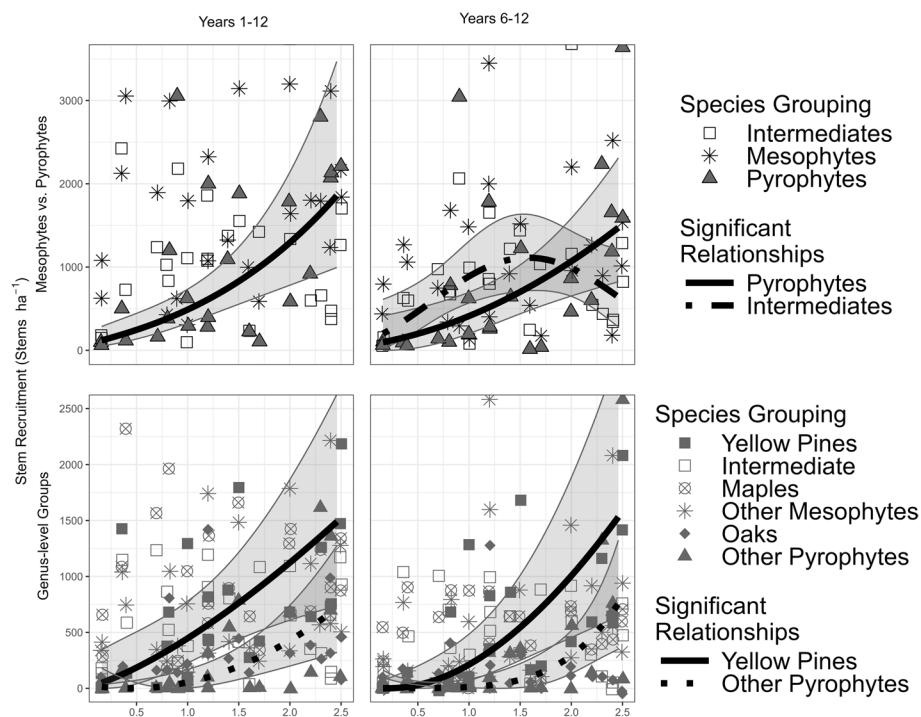


Fig. 4 Relationship between burn severity, measured as CBI, with midstory (2–10 cm (0.79–3.94 in) DBH) stem recruitment after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Recruitment was calculated as the difference in number of stems between measurement years, where the left column indicates recruitment since the fire and the right column indicates recruitment since year 6 measurements (Black et al. 2018). Top row represents species grouped on their fire ecology characteristics and the bottom row distinguishes which genera are driving the relationships in the first row. Regression lines are shown only for relationships that are significant ($\alpha = 0.05$)

greater burn severities were associated with increased competitive ability of pyrophytic species relative to the mesophytes that encroach upon upland oak-pine ecosystems (Blankenship and Arthur 2006; Palus et al. 2018). However, our results also indicate that the selective force of higher burn severity favoring pyrophytic species is beginning to diminish due to midstory densification, and that to restore oak dominance, future disturbances (e.g., wind, prescribed fire, wildfire, mechanical treatments) will be required (Cannon and Brewer 2013). However, this should only be considered if NNIP monitoring and eradication measures were successful following the fire and can be implemented subsequent to additional disturbance, as our results highlight how increased burn severity can facilitate the establishment and proliferation of NNIPs.

We observed variations in species diversity and richness through time (H1), where by year 12, the regenerating forest community was more diverse at higher burn severity—a pattern which had not been observed previously at this site. This positive relationship is consistent with studies in the Southern Appalachians (Reilly et al. 2006; Wimberly and Reilly 2007; Hagan et al. 2015) and is the result of large increases in resources and colonization

opportunities for new species which occur as burn severity increases (Wimberly and Reilly 2007). At the Fish Trap Fire site, there was an atypical increase in soil moisture in some of the most severely burned areas—due to a combination of reduced transpiration, the resinous discharge of *Pinus* species, and shallow clay lenses (personal observation), resulting in the emergence of wetland plants, large bryophyte mats, and seeps in typically xeric uplands (Black et al. 2018). These conditions in areas of high-severity fire likely allowed for more mesic tree species to establish following the fire than might be observed at other upland sites, causing increased diversity and richness. Additionally, at year 12, we were no longer observing early post-fire pioneer species, such as sassafras, black locust (*Robinia pseudoacacia* L.), and sumacs (*Rhus* spp.), being regenerated in the moderate to high shade being cast by midstory stems. Instead, non-pioneer species were regenerating and growing into the midstory size class, causing an increase in diversity and richness.

Forest structure varied among years, contrary to our expectations (H1). Much of this variation was within the midstory at areas of higher burn severity which grew increasingly dense through time. This is exemplified by Black et al. (2018) finding a negative relationship between

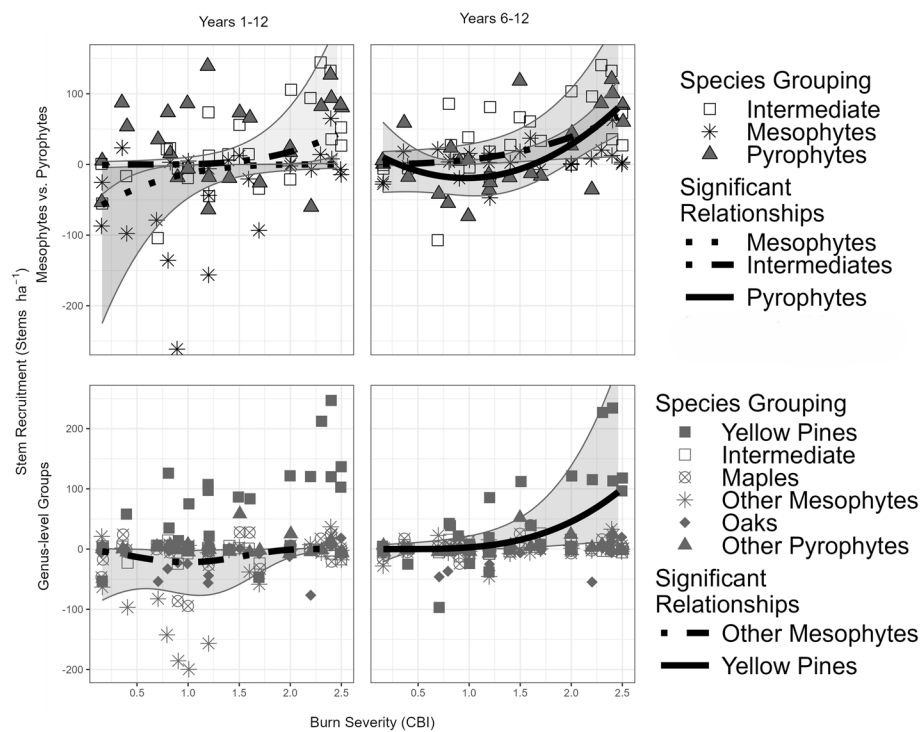


Fig. 5 Relationship between burn severity, measured as CBI, with canopy (10 + cm (03.94 + in) DBH) stem recruitment after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Recruitment was calculated as the difference in number of stems between measurement years, where the left column indicates recruitment since the fire and the right column indicates recruitment since year 6 measurements (Black et al. 2018). Top row represents species grouped on their fire ecology characteristics and the bottom row distinguishes which genera are driving the relationships in the first row. Regression lines are shown only for relationships that are significant ($\alpha = 0.05$)

midstory stem density and burn severity at years 1 and 3, no relationship at year 6, and our finding of a positive relationship at year 12. In other words, increased burn severity only reduced midstory stem densities relative to lower-severity fire for 6 years, after which the regrowth that occurred in high-severity areas became denser. Stem density within forest midstories and canopies has profound effects on the regenerating community (Dey and Parker 1997), and the changes we have observed in species composition since the Fish Trap Fire are highly aligned with the stem density patterns within these size classes. That is, greater burn severities initially caused greater stem mortality in all size classes, which created higher light environments that were more conducive to regenerating pyrophytic species' growth compared to lower light conditions found in low-severity burn areas. Over time, these greater burn severity areas regenerated more densely than lower severity areas (Table 2), and now pyrophytic seedlings are no longer more successful in the lower understory light conditions.

We predicted burn severity to be positively related to the recruitment of fire-adapted xeric seedlings and saplings into the midstory size class, as it was in previous data collection years (H2), but these expectations

were only partially supported by our results. At year 6, Black et al. (2018) found burn severity to be significantly related to the recruitment of oak and pine stems into the midstory size class. Six years later, plots that burned at higher-severity still exhibited higher yellow pine stem recruitment, though oak species' recruitment no longer had this relationship (Fig. 4; Table 3). Despite this, it should be noted that we did see higher oak recruitment at greater burn severities, an improvement compared to prescribed fire sites where there is a paucity of midstory oak stems (Brose et al. 2013; McEwan et al. 2011). The strongest recruitment relationship we observed was that of non-oak-pine pyrophytes, though, on average, greater numbers of yellow pines were recruited into the midstory as burn severity increased. High-severity disturbance is known to be integral to restoring early seral yellow pine communities in areas that have undergone successional changes associated with fire cessation (Barden and Woods 1976; Vose et al. 1993; Welch and Waldrop 2001; Saladyga et al. 2022), but few studies other than Black et al. (2018) have found such clear effects of a single high-severity fire on oak recruitment in the eastern USA. The lack of oak species recruitment into the midstory at year 12 may indicate

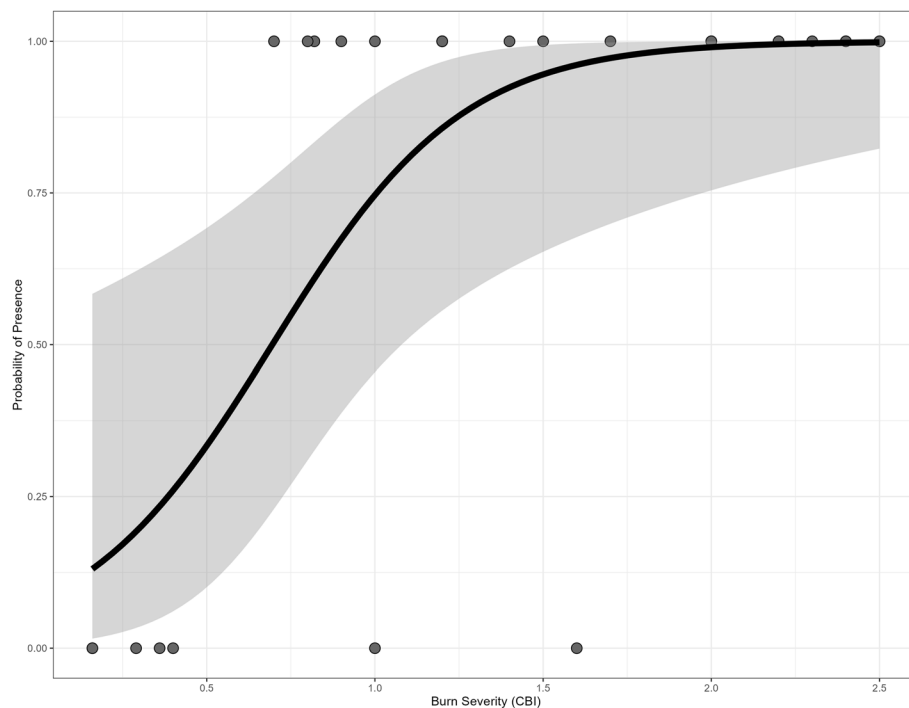


Fig. 6 Relationship between burn severity, as described by CBI, and the presence/absence of non-native invasive plant (NNIP) species 12 years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. The line indicates that burn severity significantly predicts the presence/absence of NNIPs ($\alpha=0.05$)

that oak seedlings and saplings are being shaded out by the now-dense midstory (Kuddes-Fischer and Arthur 2002). If so, an additional fire could re-stimulate oak recruitment by culling midstory stems and increasing understory light availability (Iverson et al. 2017, Blankenship et al. 2023). While this may negatively impact oak stems currently in the midstory, an additional fire would disproportionately affect competing mesophytic and intermediate species (Arthur et al. 2015) whose juvenile bark is less developed at younger ages compared to oak species (Hammond et al. 2015). Returning fire after a 6- to 12-year fire-free interval would be consistent with historic FRIs (Guyette et al. 2012; Lafon et al. 2017), and recent research has directly linked mixed-severity fire at a mean FRI of 7–8 years to oak and pine recruitment (Saladyga et al. 2022). Hagan et al. (2015) observed that 7 years following a wildfire, a second burn prompted increases in the relative number of oak stems in xeric communities, suggesting that oak species would particularly benefit from an additional burn. Overall, the midstory recruitment patterns we have observed indicate that greater severity fire can effectively promote the growth of fire-adapted trees into larger size classes, particularly for yellow pines and non-oak-pine pyrophytes. Moreover, our results are

consistent with Black et al. (2018) and other research (Brose et al. 2013) in that lower-severity fire lacks the selective force needed to promote the recruitment of pyrophytic species' over mesophytic species over time, a sought-after result of often low-severity prescribed fire (Brose et al. 2001).

Recruitment of pyrophytic species into the canopy size class at year 12 followed a pattern similar to pyrophytic recruitment in the midstory size class at year 6 (H2), indicating that the post-fire regenerating cohort of pyrophytes observed by Black et al. (2018) are moving into overtopped canopy positions and do so increasingly with higher burn severity. At lower burn severities (CBI 0.6 to 1.2), we observed delayed canopy mortality of pyrophytic species between years 6 and 12 (as indicated by negative recruitment values; see section "Stem recruitment over time"), particularly among oak species. This delayed mortality conforms to model predictions (Robbins et al. 2022) that found old (> 100 years) fire-resistant oak trees are likely to experience delayed mortality following fire events due to fine-root growth in organic matter that is consumed by fire (Carpenter et al. 2021). Higher burn severity was associated with greater canopy recruitment among yellow pine species at year 12, but no longer that of oaks

(Fig. 5). Since we observed yellow pines recruiting into the midstory at year 6 and then into the canopy at year 12, but did not observe the same pattern for oak species, oaks are potentially being outcompeted and may become permanently overtopped if there is no disturbance to release them from competition. Intermediate species' recruitment into the canopy displayed substantially stronger relationships with burn severity than that of pyrophytes, and we observed greater recruitment at of intermediate species at moderate burn severity between years 6 and 12 (Fig. 5). This indicates that the intermediate species are those which are primarily competing with pyrophytes growing into overtopped canopy positions.

Mesophytic species' recruitment into midstory and canopy size classes was expected to be unaffected by burn severity (H3), which our results reflect. At year 6, the recruitment of mesophytic competitors was uninfluenced by the effects of burn severity (Black et al. 2018), and this trend remains at year 12 (Table 3). This is likely due to the generalist nature of the most prevalent mesophytic competitors (i.e., red maple) that can thrive on a wide variety of sites with broad ranges of light, moisture, and nutrient availability (Abrams 1998). Relative to other species groupings, mesophytic competitors exhibited decreased importance with increased burn severity at year 12, which was not the case at year 6. In other words, at low burn severities, mesophytic species were substantially more important (with respect to IV) than pyrophytes and intermediates, but as burn severity increased, pyrophytes became more important than mesophytes (Fig. 2). Similar results have been observed in higher-quality oak-hickory communities (Brose 2010), but few studies have evaluated community changes as the result of variable burn severity. Pyrophytic species' importance was also more strongly related to burn severity, suggesting that increased burn severity produces more consistent positive responses in pyrophyte importance than that of the decreases in mesophyte importance.

These findings conform to assertions that low-severity fire in the eastern USA may accelerate mesophication (Reilly et al. 2022) by bolstering mesophytic species importance (Brose et al. 1999; Brose 2010), and are aligned with patterns observed in some western US forests, where higher-severity fire shifts ecosystems toward more fire-resilient communities (Cocking et al. 2014; Nemens et al. 2022). The burn severity at which pyrophytes in our study became more important ($CBI > 2.0$) is particularly noteworthy (Fig. 2), because prescribed fires in this area rarely exceed a CBI of 1.5 (Winkenbach 2020). This means that a typical prescribed fire's severity is inadequate to alter forest community assemblages and site conditions in ways that allow for pyrophytic species

to maintain a competitive advantage over mesophytic species. As such, management objectives of restoring and maintaining fire-adapted communities may be facilitated by widening burn prescription parameters or suppression policies to allow for areas of higher-intensity prescribed fire and high-severity fire effects.

Contrary to our expectation that we would see variation in the species diversity of small (< 50 cm tall; < 19.7 in tall) and large seedlings (> 50 cm tall; > 19.7 in tall) along our gradient of burn severity (H4), we saw none. However, we did observe variation among species groupings, in that small oak seedling and large yellow pine seedling abundances were negatively related to burn severity, while small non-maple mesophyte seedlings were positively related. Despite these relationships being weak, at low burn severities ($CBI < 1.0$), oaks had significantly greater abundances of small seedlings compared to non-maple mesophytes, and vice versa at high severities. These patterns, taken with our assertion that the midstory is now too dense to preferentially recruit pyrophytic oaks in higher severity areas, indicate that this site will likely experience challenges associated with mesophication once again. Despite this, we have reasonable evidence to suggest increased burn severity mitigated or potentially reversed some of the effects of mesophication to a point that additional management could effectively restore pyrophytic communities in upland oak-pine forests. Further, our evidence suggests that over the course of 12 years, low-severity fire has caused few changes in forest structure and species composition, and these areas are continuing to experience mesophication and pyrophytic species' recruitment challenges.

The strong relationship between NNIP presence and burn severity we observed (H5) is a major tradeoff to the ecosystem benefits stemming from high-severity fire and highlights the responsibility land managers have to engage in monitoring and eradication efforts following a fire, especially in high-use areas. Six years post-fire, Black et al. (2018) found only two NNIP species—multiflora rose and Chinese silvergrass—occupying a total of 23% of research plots. Six years later, NNIPs were found in 73% of research plots with two additional species present: autumn olive and Japanese stiltgrass. Chinese silvergrass had the greatest recent population expansion, having occupied 19% of plots at year 6 and occupying 73% at year 12. This change can be reasonably attributed to the Fish Trap Fire providing a seed bed and habitat conducive for NNIP establishment (Taylor 2010) combined with high amounts of propagule pressure coming from abundant Chinese silvergrass populations lining the roads near the Fish Trap Fire site and the Red River Gorge Geologic Area being a high-use outdoor recreation area. This species poses a potential fire hazard, as it leaves densely

bunched dry standing grasses that reach 1.5 to 3 m (5 to 10 ft) tall when senesced (Miller et al. 2010), and which are highly flammable (Stewart et al. 2009). While we only obtained presence/absence data, our personal observations of Chinese silvergrass at this site are that it is sufficiently dense—especially in areas that burned at high severity—to pose a threat to forest health and undermine the forest compositional and structural benefits of higher burn severity fire we observed.

To avoid the detrimental effects of NNIPs in post-fire areas, extensive control efforts should be made. At the Fish Trap Fire site, substantial removal efforts by the USDA Forest Service of princess tree stems that established immediately after the fire proved successful, as no stems were observed in the year 6 and 12 surveys (Black et al. 2018). While the survey extent was different between our study and that of the USDA Forest Service's, we can reasonably conclude that the proliferation of princess tree was successfully stifled by these removal efforts. These results highlight the value of early post-disturbance monitoring and control efforts and call attention to the importance of continual monitoring of post-disturbance environments for NNIP establishment, as Chinese silvergrass was not detected in initial surveys and it is possible that this site could have been safeguarded from this impending threat if it had been detected and controlled early in the invasion process.

Conclusion

Fire-adapted ecosystems are declining in range and quality due in part to historical fire exclusion policies facilitating mesophication, and the restoration of these communities is a primary goal of forest management in the southern Appalachians (Dey 2014; Arthur et al. 2021). A central issue in restoring these communities is the inability of regenerating oak and pine seedlings and saplings to recruit into larger size classes (Abrams 2003). Our results demonstrate that higher levels of burn severity following a single wildfire can substantially favor pyrophytic pine species recruitment into midstory and canopy positions for several years post-fire, but pyrophytic oak species are only favored for a short period of time before they begin to be outcompeted (Black et al. 2018). Recruitment of mesophytic species was unresponsive to variation in burn severity, and as time progressed, they became less important than pyrophytes at higher levels of burn severity. To further stimulate oak species recruitment and to safeguard the ecosystem benefits of increased burn severity, we recommend that additional management, such as prescribed fire or midstory thinning, occur soon after high-severity wildfire. If done, pyrophytic species at this site may continue to predominate the regenerating cohort and reach intermediate

or codominant canopy positions. However, following any severe fire and prior to any additional management actions, comprehensive NNIP monitoring and eradication efforts must be made, as our study indicates that post-fire environments are highly conducive to their establishment and spread, but eradication efforts can sometimes be successful.

Understanding the impacts of wildfire on forest ecosystems in the eastern USA is increasingly important, as wildfire frequency and size are anticipated to increase from anthropogenic climate change (Lafon and Quiring 2012; McNulty et al. 2013, 2015). While changes in climate and increased wildfire activity are predicted to favor pyrophytic species like oaks (Vose and Elliott 2016; Iversen et al. 2019), active forest management that is focused on facilitating a more rapid transition to restored oak dominance is needed to avoid degraded forest health, decreased ecosystem services, and undesirable future conditions (Vose and Elliott 2016). To this end, our study provides evidence that incorporating characteristics of wildfires, such as increased burn severity, combined with other silvicultural tools or natural disturbances may be an effective tool in quickly restoring fire-adapted ecosystems.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-024-00340-5>.

Supplementary Material 1: Supplemental Fig. 1. Relationship of burn severity, measured as CBI, with midstory (2–10 cm [0.79–3.94 in] DBH) species' diversity and richness 12 years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. A displays Shannon's Diversity Index (SHDI) and B displays species richness. Regression lines indicates relationships that are significant ($\alpha=0.05$).

Supplementary Material 2: Supplemental Fig. 2. Relationship of burn severity, measured as CBI, with midstory (2–10 cm [0.79–3.94 in] DBH) species' stem density 12 years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. A represents species grouped based on their fire ecological characteristics and B distinguishes which genera are driving the relationships in A. Regression lines are shown only for relationships that are significant ($\alpha=0.05$).

Supplementary Material 3: Supplemental Fig. 3. Relationship of burn severity, measured as CBI, with canopy (10 + cm [3.94 + in] DBH) species' stem density 12 years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. A represents species grouped based on their fire ecological characteristics and B distinguishes which genera are driving the relationships in A. Regression lines are shown only for relationships that are significant ($\alpha=0.05$).

Supplementary Material 4: Supplemental Fig. 4. Relationship of burn severity, measured as CBI, with midstory (2–10 cm [0.79–3.94 in] DBH) species' basal area 12 years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. A represents species grouped based on their fire ecological characteristics and the bottom row displays the only genera that are driving the relationships in A, where B represents non-oak-pine pyrophytes and C represents oaks species. Regression lines are shown only for relationships that are significant ($\alpha=0.05$).

Supplementary Material 5: Supplemental Fig. 5. Relationship of burn severity, measured as CBI, with canopy (10 + cm [3.94 + in] DBH) species'

basal area 12 years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. A represents species grouped based on their fire ecological characteristics and B distinguishes which genera are driving the relationships in A. Regression lines are shown only for relationships that are significant ($\alpha = 0.05$).

Acknowledgements

We thank our USDA Forest Service collaborators from the Cumberland District of the Daniel Boone National Forest (DBNF), especially E.J. Bunzendahl, former DBNF Fire Management Officer, and D. Taylor, DBNF Botanist, for providing background information and other pertinent details of the Fish Trap Fire, and for guiding project design, implementation, and logistical support. We also thank the University of Kentucky Department of Forestry and Natural Resources' senior laboratory technician M. Hamilton, research analyst Z. Hackworth, and several field technicians for their assistance and commitment to research in the service of this project. We also express gratitude to D. Black for her previous work on this project and providing background information.

Authors' contributions

SC was the primary writer of this manuscript, collected all field data in 2022, and conducted statistical analyses. MA and CC designed and implemented the study following the Fish Trap Fire in 2010, and were involved in data collection during all study years. JM and MA acquired funding and supervised study implementation, methodology, data analysis, and writing in 2022. All authors contributed to revisions, and approved the final draft.

Funding

This work was supported by the National Institute of Food and Agriculture, US Department of Agriculture, McIntire-Stennis project KY0009032. This study was partially funded through a participating agreement with the DBNF (agreement number 15-PA-11080226-005).

Data availability

The datasets generated or analyzed during this study are not publicly available due to privacy concerns for study plot locations in close proximity to a popular public recreation area, but are available from the corresponding author on reasonable request.

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.

Author details

¹Department of Forestry and Natural Resources, Thomas Poe Cooper Building, University of Kentucky, Lexington, KY 40546, USA. ²USDA Forest Service, Daniel Boone National Forest, 1700 Bypass Road, Winchester, KY 40391, USA.

Received: 3 December 2023 Accepted: 2 December 2024

Published online: 02 January 2025

References

- Abrams, Marc D. 1992. Fire and the Development of Oak Forests. *BioScience* 42 (5): 346–353. <https://doi.org/10.2307/1311781>.
- Abrams, Marc D. 2003. Where has all the white oak gone? *BioScience* 53 (10): 927–939. [https://doi.org/10.1641/0006-3568\(2003\)053\[0927:WHATWO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0927:WHATWO]2.0.CO;2).
- Abrams, Marc D., and Gregory J. Nowacki. 1992. Historical Variation in Fire, Oak Recruitment, and Post-Logging Accelerated Succession in Central Pennsylvania. *Bulletin of the Torrey Botanical Club* 119 (1): 19. <https://doi.org/10.2307/2996916>.
- Alexander, Heather D., and Mary A. Arthur. 2010. Implications of a Predicted Shift from Upland Oaks to Red Maple on Forest Hydrology and Nutrient Availability. *Canadian Journal of Forest Research* 40 (4): 716–726. <https://doi.org/10.1139/X10-029>.
- Alexander, Heather D., and Mary A. Arthur. 2014. Increasing Red Maple Leaf Litter Alters Decomposition Rates and Nitrogen Cycling in Historically Oak-Dominated Forests of the Eastern U.S. *Ecosystems* 17 (8): 1371–1383. <https://doi.org/10.1007/s10021-014-9802-4>.
- Alexander, Heather D., Mary A. Arthur, David L. Loftis, and Stephanie 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 (5): 1021–1030. <https://doi.org/10.1016/j.foreco.2008.06.004>.
- Arthur, Mary A., Robert D. Paratley, and Beth A. Blankenship. 1998. Single and Repeated Fires Affect Survival and Regeneration of Woody and Herbaceous Species in an Oak-Pine Forest. *Journal of the Torrey Botanical Society* 125 (3): 225–236. <https://doi.org/10.2307/2997220>.
- Arthur, Mary A., Beth A. Blankenship, Angela Schörgendorfer, David L. Loftis, and Heather D. Alexander. 2015. Changes in Stand Structure and Tree Vigor with Repeated Prescribed Fire in an Appalachian Hardwood Forest. *Forest Ecology and Management* 340 (March): 46–61. <https://doi.org/10.1016/j.foreco.2014.12.025>.
- Arthur, Mary A., J. Morgan Varner, Charles W. Lafon, Heather D. Alexander, Daniel C. Dey, Craig A. Harper, Sally P. Horn, et al. 2021. "Fire Ecology and Management in Eastern Broadleaf and Appalachian Forests." In *Fire Ecology and Management: Past, Present, and Future of US Forested Ecosystems*, 105–47. Managing Forest Ecosystems. https://doi.org/10.1007/978-3-030-73267-7_4.
- Babl, Emily, Heather D. Alexander, Courtney M. Siegert, and John L. Willis. 2020. Could Canopy, Bark, and Leaf Litter Traits of Encroaching Non-Oak Species Influence Future Flammability of Upland Oak Forests? *Forest Ecology and Management* 458 (February): 117731. <https://doi.org/10.1016/j.foreco.2019.117731>.
- Barden, Lawrence S., and Frank W. Woods. 1976. Effects of Fire on Pine and Pine-Hardwood Forests in the Southern Appalachians. *Forest Science* 22 (4): 399–403.
- Black, Devin E., Zachary W. Poynter, Claudia A. Cotton, Suraj Upadhyaya, David D. Taylor, Wendy Leuenberger, Beth A. Blankenship, and Mary A. Arthur. 2018. Post-Wildfire Recovery of an Upland Oak–pine Forest on the Cumberland Plateau, Kentucky, USA. *Fire Ecology* 14 (14): 1–12. <https://doi.org/10.1186/s42408-018-0013-9>.
- Blankenship, Beth A., and Mary 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 (1–3): 134–145. <https://doi.org/10.1016/j.foreco.2005.12.032>.
- Blankenship, Beth A., Zachary W. Poynter, and Mary A. Arthur. 2023. Fire Exclusion vs. a Fire-Free Interval Following Repeated Prescribed Fire: Consequences for Forest Stand Structure and Species Composition in an Upland Oak Forest. *Forest Ecology and Management* 546 (October): 121367. <https://doi.org/10.1016/j.foreco.2023.121367>.
- Braun, E. Lucy. 1950. *Deciduous Forests of Eastern North America*. Vol. 71. 2 vols. Philadelphia: The Blakiston Company.
- Brose, Patrick H. 2010. Long-term effects of single prescribed fire on hardwood regeneration in oak shelterwood stands. *Forest Ecology and Management* 260: 1516–1524. <https://doi.org/10.1016/j.foreco.2010.07.050>.
- Brose, Patrick H., David Van Lear, and Roderick Cooper. 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. *Forest Ecology and Management* 113: 125–141. [https://doi.org/10.1016/S0378-1127\(98\)00423-X](https://doi.org/10.1016/S0378-1127(98)00423-X).
- Brose, Patrick H., Thomas Schuler, David Van Lear, and John Berst. 2001. Bringing Fire Back-The Changing Regimes of the Appalachian Mixed-Oak Forests. *Journal of Forestry* 99 (11): 30–35. <https://doi.org/10.1093/jof/99.11.30>.
- Brose, Patrick H., Daniel C. Dey, Ross J. Phillips, and Thomas A. Waldrop. 2013. A Meta-Analysis of the Fire-Oak Hypothesis: Does Prescribed Burning Promote Oak Reproduction in Eastern North America? *Forest Science* 59 (3): 322–334. <https://doi.org/10.5849/forsci.12-039>.
- Cannon, Jeffery B., and J. Stephen Brewer. 2013. Effects of Tornado Damage, Prescribed Fire, and Salvage Logging on Natural Oak (*Quercus* Spp.)

- Regeneration in a Xeric Southern USA Coastal Plain Oak and Pine Forest. *Natural Areas Journal* 33 (1): 39–49. <https://doi.org/10.3375/043.033.0105>.
- Carpenter, Dana O., Melanie K. Taylor, Mac A. Callahan, J. Kevin Hiers, E. Louise Loudermilk, Joseph J. O'Brien, and Nina Wurzbarger. 2021. Benefit or Liability? The Ectomycorrhizal Association May Undermine Tree Adaptations to Fire After Long-Term Fire Exclusion. *Ecosystems* 24 (5): 1059–1074. <https://doi.org/10.1007/s10021-020-00568-7>.
- Cocking, Matthew I., J. Morgan Varner, and Eric E. Knapp. 2014. Long-Term Effects of Fire Severity on Oak-Conifer Dynamics in the Southern Cascades. *Ecological Applications* 24 (1): 94–107. <https://doi.org/10.1890/13-0473.1>.
- Indiana Invasive Species Council. 2022. "Official IISC Invasive Plant List." 2022. <https://www.entm.purdue.edu/iisc/invasiveplants.html>.
- Tennessee Invasive Plant Council. 2023. "Tennessee Pest Plant List." 2023. <https://www.tnipc.org/invasive-plants/>.
- Delcourt, Hazel R., and Paul A. Delcourt. 1997. Pre-Columbian Native American Use of Fire on Southern Appalachian Landscapes. *Conservation Biology* 11 (4): 1010–1014. <https://doi.org/10.1046/j.1523-1739.1997.96338.x>.
- Delcourt, Paul A., Hazel R. Delcourt, Cecil R. Ison, William E. Sharp, and Kristen J. Gremillion. 1998. Prehistoric Human Use of Fire, the Eastern Agricultural Complex, and Appalachian Oak-Chestnut Forests: Paleoecology of Cliff Palace Pond, Kentucky. *American Antiquity* 63 (2): 263–278. <https://doi.org/10.2307/2694697>.
- Dey, Daniel C. 2014. Sustaining Oak Forests in Eastern North America: Regeneration and Recruitment, the Pillars of Sustainability. *Forest Science* 60 (5): 926–942. [https://doi.org/10.5849/forsci.ID="EN24">13-114](https://doi.org/10.5849/forsci.ID=).
- Dey, Daniel C., and William C. Parker. 1997. Overstory Density Affects Field Performance of Underplanted Red Oak (*Quercus rubra* L.) in Ontario. *National Journal of Applied Forestry* 14 (3): 120–125. <https://doi.org/10.1093/njaf/14.3.120>.
- Dyer, James M., and Todd F. Hutchinson. 2019. Topography and Soils-Based Mapping Reveals Fine-Scale Compositional Shifts over Two Centuries within a Central Appalachian Landscape. *Forest Ecology and Management* 433 (February): 33–42. <https://doi.org/10.1016/j.foreco.2018.10.052>.
- Fei, Songlin, Ningning Kong, Kim C. Steiner, W. Keith Moser, and Erik B. Steiner. 2011. Change in Oak Abundance in the Eastern United States from 1980 to 2008. *Forest Ecology and Management* 262 (8): 1370–1377. <https://doi.org/10.1016/j.foreco.2011.06.030>.
- Fralish, James S. 2004. *The Keystone Role of Oak and Hickory in the Central Hardwood Forest*. General Technical Report, SRS-73. Asheville, NC: USDA Forest Service-Southern Research Station.
- Gao, Peng, Adam J. Terando, John A. Kupfer, J. Morgan Varner, Michael C. Stambaugh, Ting L. Lei, and J. Kevin Hiers. 2021. "Robust Projections of Future Fire Probability for the Conterminous United States." *Science of The Total Environment*, 147872, 789 (October). <https://doi.org/10.1016/j.scitotenv.2021.147872>.
- Guyette, Richard P., Michael C. Stambaugh, Daniel C. Dey, and Rose-Marie Muzika. 2012. Predicting Fire Frequency with Chemistry and Climate. *Ecosystems* 15 (2): 322–335. <https://doi.org/10.1007/s10021-011-9512-0>.
- Hagan, Donald L., Thomas A. Waldrop, Matthew Reilly, and Timothy M. Shearman. 2015. Impacts of Repeated Wildfire on Long-Unburned Plant Communities of the Southern Appalachian Mountains. *International Journal of Wildland Fire* 24 (7): 911. <https://doi.org/10.1071/WF14143>.
- Hammond, Darcy H., J. Morgan Varner, John S. Kush, and Zhaoifei Fan. 2015. Contrasting Sapling Bark Allocation of Five Southeastern USA Hardwood Tree Species in a Fire Prone Ecosystem. *Ecosphere* 6 (7): 1–13. <https://doi.org/10.1890/ES15-00065.1>.
- Hanberry, Brice B., Don C. Bragg, and Heather D. Alexander. 2020. Open Forest Ecosystems: An Excluded State. *Forest Ecology and Management* 472 (September): 118256. <https://doi.org/10.1016/j.foreco.2020.118256>.
- Hengst, Gretel E., and Jeffrey O. Dawson. 1994. Bark Properties and Fire Resistance of Selected Tree Species from the Central Hardwood Region of North America. *Canadian Journal of Forest Research* 24 (4): 688–696.
- Hutchinson, Todd F., Robert P. Long, Robert D. Ford, and Elaine Kennedy Sutherland. 2008. Fire History and the Establishment of Oaks and Maples in Second-Growth Forests. *Canadian Journal of Forest Research* 38 (5): 1184–1198. <https://doi.org/10.1139/X07-216>.
- Iverson, Louis R., Todd F. Hutchinson, Matthew P. Peters, and Daniel A. Yaussy. 2017. "Long-term Response of Oak-hickory Regeneration to Partial Harvest and Repeated Fires: Influence of Light and Moisture." *Ecosphere* 8 (1): 1–24. e01642. <https://doi.org/10.1002/ecs2.1642>.
- Iverson, Louis R., Matthew P. Peters, Stephen N. Matthews, Anantha Prasad, Todd F. Hutchinson, Jarel Bartig, Joanne Rebbeck, Dan Yaussy, Susan Stout, and Gregory J. Nowacki. 2019. "Adapting Oak Management in an Age of Ongoing Mesophication but Warming Climate." In , SRS-237:35–45. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. <https://doi.org/10.2737/SRS-GTR-237>.
- Kassambara, Alboukadel. 2022. "Ggpubr: 'ggplot2' Based Publication Ready Plots." R. <https://rpkgs.datanovia.com/ggpubr/>.
- Kentucky Exotic Pest Plant Council. 2015. "Kentucky Pest Plant List." 2015. <https://www.se-eppc.org/ky/list.htm>.
- Key, Carl H., and Nathan C. Benson. 2006. "Landscape Assessment: Ground Measure of Severity, the Composite Burn Index, and Remote Sensing of Severity, the Normalized Burn Index." RMRS-GTR-164-CD. FIREMON: Fire Effects Monitoring and Inventory System. USDA Forest Service General Technical Report.
- Kreye, Jesse K., J. Morgan Varner, Gregory W. Hamby, and Jeffrey M. Kane. 2018. Mesophytic Litter Dampens Flammability in Fire-excluded Pyrophytic Oak-Hickory Woodlands. *Ecosphere* 9 (1): e02078. <https://doi.org/10.1002/ecs2.2078>.
- Kuddes-Fischer, Linda M., and Mary A. Arthur. 2002. Response of Understory Vegetation and Tree Regeneration to a Single Prescribed Fire in Oak-Pine Forests. *Natural Areas Journal* 22 (1): 43–52.
- Kupfer, John A., Adam J. Terando, Peng Gao, Casey Teske, and J. Kevin Hiers. 2020. Climate Change Projected to Reduce Prescribed Burning Opportunities in the South-Eastern United States. *International Journal of Wildland Fire* 29 (9): 764–778. <https://doi.org/10.1071/WF19198>.
- Kuppinger, Dane M., Michael A. Jenkins, and Peter S. White. 2010. Predicting the Post-Fire Establishment and Persistence of an Invasive Tree Species across a Complex Landscape. *Biological Invasions* 12 (10): 3473–3484. <https://doi.org/10.1007/s10530-010-9745-4>.
- Lafon, Charles W., and Steven M. Quiring. 2012. Relationships of Fire and Precipitation Regimes in Temperate Forests of the Eastern United States. *Earth Interactions* 16 (11): 1–15. <https://doi.org/10.1175/2012EIO00442.1>.
- Lafon, Charles W., Adam T. Naito, Henri D. Grissino-Mayer, Sally P. Horn, and Thomas A. Waldrop. 2017. *Fire History of the Appalachian Region: A Review and Synthesis*. General Technical Report, SRS-219. USDA Forest Service.
- Li, Peng, and Juhachi Oda. 2007. Flame retardancy of paulownia wood and its mechanism. *Journal of Materials Science* 42: 8544–8550. <https://doi.org/10.1007/s10853-007-1781-9>.
- Maingi, John K., and William M. Luhn. 2005. Mapping Insect-Induced Pine Mortality in the Daniel Boone National Forest, Kentucky Using Landsat TM and ETM+ Data. *GIScience & Remote Sensing* 42 (3): 224–2450. <https://doi.org/10.2747/1548-1603.42.3.224>.
- Maingi, John K., Marc C. Henry, and William M. Luhn. 2001. Assessing forest damage by the southern pine beetle in the Daniel Boone National Forest, Kentucky. *Papers and Proceedings of Applied Geography Conferences* 24: 27–34.
- McEwan, Ryan W., James M. Dyer, and Neil Pederson. 2011. Multiple Interacting Ecosystem Drivers: Toward an Encompassing Hypothesis of Oak Forest Dynamics across Eastern North America. *Ecography* 34 (2): 244–256. <https://doi.org/10.1111/j.1600-0587.2010.06390.x>.
- McNulty, Steven, Peter Caldwell, Thomas W. Doyle, Kurt Johnsen, Yongqiang Liu, Jacqueline Mohan, Jeffrey Prestemon, and Ge Sun. 2013. "Forests and Climate Change in the Southeast USA." In *Climate of the Southeast United States: Variability, Change, Impacts, and Vulnerability*, 165–89. USDA Forest Service-Southern Research Station. https://doi.org/10.5822/978-1-61091-509-0_8.
- McNulty, Steven, Sarah Wiener, Emrys Treasure, Jennifer Moore Myers, Hamid Farahani, Lisa Fouladbash, David Marshall, and Rachel F. Steele. 2015. "Southeast Regional Climate Hub Assessment of Climate Change Vulnerability and Adaptation and Mitigation Strategies." United States Department of Agriculture. <https://doi.org/10.32747/2015.7279978.ch>.
- McShea, William J. 2000. "The Influence of Acorn Crops on Annual Variation in Rodent and Bird Populations" 81 (1): 228–38.
- McShea, William J., and William M. Healy. 2002. *Oak Forest Ecosystems: Ecology and Management for Wildlife*. Johns Hopkins University Press.
- Miller, James H., Erwin B. Chambliss, and Nancy J. Loewenstein. 2010. *A Field Guide for the Identification of Invasive Plants in Southern Forests*. General Technical Report, SRS-119. USDA Forest Service-Southern Research Station.

- Nemens, Deborah G., Kathryn R. Kidd, J. Morgan Varner, and Brian Wing. 2022. Recurring Wildfires Provoke Type Conversion in Dry Western Forests. *Ecosphere* 13 (8): 1–16. <https://doi.org/10.1002/ecs2.4184>.
- NOAA. 2023. "National Oceanic and Atmospheric Administration Climate Data." <https://www.ncei.noaa.gov/access/us-climate-normals/#dataset=normals-annualseasonal&timeframe=15&location=KY&station=USC00150483>.
- Nowacki, Gregory J., and Marc D. Abrams. 1991. "Community and Edaphic Analysis of Mixed Oak Forests in the Ridge and Valley Province of Central Pennsylvania." *8th Central Hardwood Forest Conference*.
- Nowacki, Gregory J., and Marc D. Abrams. 2008. The Demise of Fire and 'Mesophication' of Forests in the Eastern United States. *BioScience* 58 (2): 123–138. <https://doi.org/10.1641/B580207>.
- Palus, James D., P. Charles Goebel, David M. Hix, and Stephen N. Matthews. 2018. Structural and Compositional Shifts in Forests Undergoing Mesophication in the Wayne National Forest, Southeastern Ohio. *Forest Ecology and Management* 430 (December): 413–420. <https://doi.org/10.1016/j.foreco.2018.08.030>.
- R Core Team. 2023. "R: A Language and Environment for Statistical Computing." Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Reilly, Matthew J., Michael C. Wimberly, and Claire L. Newell. 2006. Wildfire Effects on Plant Species Richness at Multiple Spatial Scales in Forest Communities of the Southern Appalachians. *Journal of Ecology* 94 (1): 118–130. <https://doi.org/10.1111/j.1365-2745.2005.01055.x>.
- Reilly, Matthew J., Steven P. Norman, Joseph J. O'Brien, and E. Louise Loudermilk. 2022. Drivers and Ecological Impacts of a Wildfire Outbreak in the Southern Appalachian Mountains after Decades of Fire Exclusion. *Forest Ecology and Management* 524 (November): 120500. <https://doi.org/10.1016/j.foreco.2022.120500>.
- Robbins, Zachary J., E. Louise Loudermilk, Matthew J. Reilly, Joseph J. O'Brien, Kate Jones, Christopher T. Gerstle, and Robert M. Scheller. 2022. Delayed Fire Mortality Has Long-term Ecological Effects across the Southern Appalachian Landscape. *Ecosphere* 13 (6): 1–11. <https://doi.org/10.1002/ecs2.4153>.
- Ryan, Kevin C., Eric E. Knapp, and J. Morgan Varner. 2013. Prescribed Fire in North American Forests and Woodlands: History, Current Practice, and Challenges. *Frontiers in Ecology and the Environment* 11 (s1): e15-24. <https://doi.org/10.1890/120329>.
- Saladyga, Thomas, Kyle A. Palmquist, and Cassie M. Bacon. 2022. Fire History and Vegetation Data Reveal Ecological Benefits of Recent Mixed-Severity Fires in the Cumberland Mountains, West Virginia, USA. *Fire Ecology* 18 (19): 1–20. <https://doi.org/10.1186/s42408-022-00143-6>.
- Soil Survey Staff. 2021. "Web Soil Survey." Natural Resources Conservation Service, United States Department of Agriculture.
- Stambaugh, Michael C., J. Morgan Varner, Reed F. Noss, Daniel C. Dey, Norman L. Christensen, Robert F. Baldwin, Richard P. Guyette, et al. 2015. Clarifying the Role of Fire in the Deciduous Forests of Eastern North America: Reply to Matlack: Fire in Deciduous Forests. *Conservation Biology* 29 (3): 942–946. <https://doi.org/10.1111/cobi.12473>.
- Stewart, J. Ryan., Yo. Toma, Fabián G. Fernández, Aya Nishiwaki, Toshihiko Yamada, and Germán Bollero. 2009. The Ecology and Agronomy of Miscanthus Sinensis, a Species Important to Bioenergy Crop Development, in Its Native Range in Japan: A Review. *GCB Bioenergy* 1 (2): 126–153. <https://doi.org/10.1111/j.1757-1707.2009.01010.x>.
- Sullivan, Janet. 1993. "Pinus virginiana". Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. <https://www.fs.usda.gov/database/feis/plants/tree/pinvir/all.html>
- Tallamy, Douglas W. 2021. *The Nature of Oaks: The Rich Ecology of Our Most Essential Native Trees*. Timber Press.
- Taylor, David. 2010. *Fish Trap Fire Non-Native Invasive Plant Species Assessment for BAER-Daniel Boone National Forest*. USDA Forest Service.
- Upadhyaya, Suraj. 2015. "Use of Landsat Data to Characterize Burn Severity, Forest Structure and Invasion by Paulownia (Paulownia Tomentosa) in an Eastern Deciduous Forest, Kentucky." M.S. Thesis, Department of Forestry and Natural Resources: University of Kentucky. https://uknowledge.uky.edu/forestry_etds/23/.
- Varner, J. Morgan, Jeffrey M. Kane, Erin M. Banwell, and Jesse K. Kreye. 2015. "Flammability of Litter from Southeastern Trees: A Preliminary Assessment." In *Proceedings of the 17th Biennial Southern Silvicultural Research Conference*, 183–87. General Technical Report, GTR-SRS-203. Asheville, NC: USDA Forest Service.
- Varner, J. Morgan., Jeffrey M. Kane, J. Kevin Hiers, Jesse K. Kreye, and Joseph W. Veldman. 2016. Suites of Fire-Adapted Traits of Oaks in the Southeastern USA: Multiple Strategies for Persistence. *Fire Ecology* 12 (2): 48–64. <https://doi.org/10.4996/fireecology.1202048>.
- Varner, J. Morgan., Jeffrey M. Kane, Jesse K. Kreye, and Timothy M. Shearman. 2021. Litter Flammability of 50 Southeastern North American Tree Species: Evidence for Mesophication Gradients Across Multiple Ecosystems. *Frontiers in Forests and Global Change* 4 (October): 727042. <https://doi.org/10.3389/ffgc.2021.727042>.
- Vose, James M., and Katherine J. Elliott. 2016. Oak, Fire, and Global Change in the Eastern USA: What Might the Future Hold? *Fire Ecology* 12 (2): 160–179. <https://doi.org/10.4996/fireecology.1202160>.
- Vose, James M., Barton D. Clinton, and Wayne T. Swank. 1993. "Fire, Drought, and Forest Management Influences on Pine/Hardwood Ecosystems in the Southern Appalachians." *A Paper Presented at the 12th Conference on Fire and Forest Meteorology*.
- Welch, Nicole Turrill, and Thomas A. Waldrop. 2001. Restoring Table Mountain Pine (Pinus pungens Lamb.) Communities with Prescribed Fire: An Overview of Current Research. *Castanea* 66 (1–2): 42–49.
- Wharton, Mary E., and Roger W. Barbour. 1973. *Trees and Shrubs of Kentucky*. The University Press of Kentucky.
- Wickham, Hadley. 2016. "Ggplot2: Elegant Graphics for Data Analysis." R. Springer-Verlag, New York. <https://ggplot2.tidyverse.org>.
- Williams, Roger, and Haibin Wang. 2021. Effects of Wildfire and the Presence of the Invasive Paulownia Tomentosa on the Regeneration of Native Tree Species in North-Central Appalachia. *Fire* 4 (60): 1–14. <https://doi.org/10.3390/fire4030060>.
- Wimberly, Michael C., and Matthew J. Reilly. 2007. Assessment of Fire Severity and Species Diversity in the Southern Appalachians Using Landsat TM and ETM+ Imagery. *Remote Sensing of Environment* 108 (May): 189–197. <https://doi.org/10.1016/j.rse.2006.03.019>.
- Winkenbach, Jordan. 2020. "The Role of Fire and a Fire-Free Interval in the Restoration of Upland Oak Communities on the Cumberland Plateau." M.S. Thesis, Department of Forestry and Natural Resources: University of Kentucky. https://uknowledge.uky.edu/forestry_etds/52/.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.