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

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Abstract

Background

In many eastern North American forests and woodlands, formerly dominant oaks (*Quercus* spp. L.) and pines (*Pinus* spp. L.) are experiencing widespread regeneration challenges and biodiversity loss. These changes are due to past land use and widespread 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 in Kentucky, USA, providing a rare opportunity to track oak-pine vegetation community recovery across a wide fire severity spectrum. 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); 0.79–3.94 in DBH) and canopy (10 + cm DBH; 3.94 + in DBH), and non-native invasive plant (NNIP) populations.

Results

After 12 years, burn severity was positively related to midstory recruitment of yellow pine (*Pinus echinata* Mill., *P. rigidia* Mill., *P. virginiana* Mill.) and unrelated to recruitment of oak and mesophytic species. Burn severity was negatively related to the relative importance of midstory mesophyte species and positively related to the relative importance of midstory pyrophyte species. Increased burn severity dramatically increased the probability of invasive species presence, particularly Chinese silvergrass (*Miscanthus sinensis* Andersson).

Conclusions

Earlier results found that up to six years post-fire, burn severity was significantly and positively related to oak sapling recruitment. Our results indicate that, 6 years later, 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 provide long-term recruitment benefits to yellow pine species and increase the competitive status of pyrophytes relative to mesophytes. To re-stimulate recruitment of oak into the midstory, it may be necessary to reintroduce fire between six and 12 years following a high-severity burn. This research demonstrates the benefits of higher-severity fire for restoring fire-adapted communities, though the proliferation of NNIPs severely undermines these benefits.

1. Background

In eastern North American forests, fire was a common occurrence until the early 20th century when fire suppression policies, such as the US Forest Service 10 AM Policy of 1935, were adopted (Delcourt and Delcourt 1997; Ryan et al. 2013). Prior to this, Native American populations maintained frequent fire regimes, with median fire return intervals of 5.4 years for 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 20th 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 (Abrams and Nowacki 1992; Nowacki and Abrams 1991). In the absence of fire, 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 (Varner et al. 2016) and facilitate forest mesophication, a process in which they cast heavy shade and limit air movement, causing understory microclimate conditions to be cooler, more humid, and less flammable. This process creates a positive feedback loop for selection 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). Now, oak species' overall importance has declined (Fei et al. 2011) and if current recruitment challenges continue, they may comprise an unprecedentedly 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 (H. D. Alexander and Arthur 2014; Heather D. Alexander and Arthur 2010), decreased compositional, structural, and spatial diversity (Hanberry et al. 2020; Nowacki and Abrams 2008), 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 (P. 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 (P. 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 at six years post-fire. This may indicate that a single higher severity fire can create long-term changes in forest conditions that allow pyrophytic oaks and pines to maintain forest dominance (Black et al. 2018).

Despite the potential benefits of higher burn severity, non-native invasive plant (NNIP) establishment and proliferation following fire complicates management. The increasingly disturbed soil, increased soil moisture availability, and greater 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) (Black et al. 2018; Miller et al. 2010). Princess tree is known to alter forest flammability 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 US (Indiana Invasive Species Council 2022; Kentucky Exotic Pest Plant Council 2015; 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 US, as wildfire events are anticipated to increase in frequency and size (Lafon and Quiring 2012; McNulty et al. 2015; 2013) 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 provided an opportunity to study changes in species composition and forest structure at varying levels of burn severity. Black et al. (2018) analyzed the vegetation response to this wildfire up to six years post-burn, and identified that further research was needed to determine whether the observed results would persist.

The 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). While this period of time is still within historic fire return intervals (Lafon et al. 2017), the results of this study are important, as repeated sampling improves our understanding of how forest communities regenerate at varying levels of burn severity, indicates future trajectories, and allows us to provide management recommendations with precise temporal resolution. 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 among 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 size classes; (H4) for trees < 2cm DBH (< 0.79 in DBH), burn severity is positively related to species diversity of small seedlings (< 50 cm height; <19.7 in height) and large seedlings (≥ 50 cm height; ≥19.7 in height); and (H5) burn severity is positively related to the presence of NNIP species.

2. Methods

2.1 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, having moderately cold winters and warm, humid summers (Wharton and Barbour 1973), with a mean annual precipitation of 136.47 cm (53.73 in) and a mean annual temperature of 13.1˚C (55.6˚F) (NOAA 2023). During winter, the average temperature was 2.3˚C (36.1˚F), whereas in summer, the average temperature was 23.1˚C (73.5˚F) (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 a myriad of 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, and the average stand age is 76 years. Prior to this, fire and management records indicate that harvesting actions were exclusive to slopes, coves, and bottomlands, with uplands and ridgetops remaining relatively undisturbed. These xeric forest communities are typically dominated by scarlet oak, chestnut oak, black oak (*Q. velutina* Lam.), white oak, and yellow pines (Black et al. 2018; Wharton and Barbour 1973). Midstories are typically composed of red maple (*Acer rubrum* L.), sourwood

(*Oxydendrum arboreum* A.P. DC.), black gum (*Nyssa sylvatica* Marshall var. *silvatica*), 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).

2.2 Fish Trap Fire

The Fish Trap Fire was ignited accidentally 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). This scale ranges from 0 to 3, spanning the possible range of severity between unburned and greatest burned effect, respectively (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 (ΔNBR) values strongly related ($r_s = 0.90$, $p = 1.19e\text{-}09$, $F_{1,25} = 87.67$, $R^2 = 0.77$). Likewise, in the absence of pre-burn vegetation data, Black et al. (2018) compared pre-burn Landsat-derived normalized differenced vegetation index (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 variability.

The burn severity of the Fish Trap Fire was highly 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% loss of vegetation within the year following the fire, and had patches where the litter layer 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).

2.3 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 one, three, six, and 12 years post-fire, respectively; results of the data collected through 2016 were published in Black et al. (2018).

At each research plot, we used 500 m^2 (0.05 ha; 0.12 acre) circular nested plots. For all stems ≥ 2 cm (0.79 in) diameter at breast height (DBH) we recorded tree species, DBH, canopy vigor, and number of basal sprouts. Additionally, within a 25 m^2 (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) height) or large (≥ 50 cm (19.7 in) height) (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).

2.4 Statistical Analysis

From the measurements described in Section 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 among years (H1), we calculated basal area (m^2/ha; ft^2/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.

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 (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 (Mary A. Arthur et al. 2021; Saladyga et al. 2022). Thus, pyrophytes are 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 (Varner et al. 2015; 2016; Hengst and Dawson 1994; Varner et al. 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; Babl et al. 2020; Kreye et al. 2018; 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. To determine the species driving the relationships observed in these groupings, we conducted analyses on genera of concern, where we specifically looked at the 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 (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 (B.A. Blankenship and Arthur 2006; M. A. Arthur et al. 1998; Beth A. 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 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 (Kassambara 2022; R Core Team 2023; Wickham 2016).

For stems < 2 cm (0.79 in) DBH, we used linear regression 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.

Table 1
Species groupings of all tree species found since 2011 at the Fish Trap Fire study site, Daniel Boone National Forest, Kentucky. Groupings are based on previous categorizations (Mary A. 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).

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

3. Results

3.1 Species Diversity and Richness

The relationships of burn severity with species diversity and richness changed over time since the Fish Trap Fire (H1). By year 12 years post-fire, midstory species richness and SHDI were positively and significantly related to burn severity (OR = 1.24, p = 0.004; R^2 = 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.

3.2 Forest Structure

The relationship between stem density and burn severity also varied by species groupings and size classes 12 years after the Fish Trap Fire (H1). Stem density trends were primarily due to changes in the midstory along the burn severity gradient. Increased burn severity yielded increased midstory stem density (R^2 = 0.293, $F_{1, 24}$ = 11.38, p = 0.003) (Sup. Figure 2A), particularly for non-oak-pine pyrophytes (R^2 = 0.392, $F_{1, 13}$ = 10.04, p = 0.007). Stem density of canopy sized trees was only related to burn severity for oak species, which had a negative relationship (R^2 = 0.600, $F_{1, 16}$ = 26.51, p < 0.001) (Sup. Figure 3B). Stem density of yellow pine, maple, non-maple mesophytes, and intermediate species had no relationship with burn severity at either size class.

Twelve years post-fire, basal area in both size classes was influenced by burn severity and varied among species groupings (H1). Among midstory trees there was a positive relationship between basal area and burn severity after 12 years (R^2 = 0.679, $F_{1, 24}$ = 16.22, p < 0.001) (Sup. Figure 4A), which was primarily the result of oaks (R^2 = 0.404, $F_{1, 24}$ = 17.97, p = 0.003) (Sup. Figure 4C) and non-oak-pine pyrophytes (R^2 = 0.358, $F_{1, 13}$ = 7.26, p = 0.018) (Sup. Figure 4B). Canopy basal area was negatively related to burn severity, particularly among oaks (R^2 = 0.500, $F_{1, 16}$ = 17.98, p < 0.001) (Sup. Figure 5B). Other species groups examined separately were not statistically related to burn severity in any size class.

3.3 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). Within the midstory size class, burn severity was negatively related to mesophytic species' IV (R^2 = 0.273, $F_{1, 24}$ = 10.4, p = 0.004) and positively related to pyrophytic species' IV (R^2 = 0.464, $F_{1, 24}$ = 22.61, p < 0.001) (Fig. 2A). Trends for mesophytic species were largely driven by non-maple mesophytes (R^2 = 0.126, $F_{1, 24}$ = 4.62, p = 0.042) (Fig. 2D) and trends for pyrophytes were driven by non-oak-pine pyrophytes (R^2 = 0.249, $F_{1, 13}$ = 5.65, p = 0.033) (Fig. 2B). For canopy size trees, burn severity was negatively related to oak IV (R^2 = 0.241, $F_{1, 16}$ = 6.39, p = 0.022) and positively related to yellow pine IV (R^2 = 0.205, $F_{1, 21}$ = 6.66, p = 0.017) (Fig. 3B).

3.4 Stem Recruitment Over Time

Recruitment of stems varied among size classes and across recruitment time (H2 and H3). There was a positive relationship between burn severity and midstory recruitment of pyrophyte stems between 2011 and 2022 (R^2 = 0.439, $F_{1, 23}$ = 19.80, p < 0.001), particularly for yellow pines (R^2 = 0.291, $F_{1, 23}$ = 10.9, p = 0.003) and non-oak-pine pyrophytes (R^2 = 0.393, $F_{1, 23}$ = 16.52, p < 0.001) (Fig. 4). Over this time span, burn severity had no influence on the recruitment of mesophytic species into the midstory (R^2 = 0.023, $F_{1, 23}$ = 0.56, p = 0.462). Conversely, canopy recruitment was significantly related to burn severity for intermediate species (R^2 = 0.144, $F_{1, 23}$ = 5.04, p = 0.034) (Fig. 5). Negative species recruitment in the canopy size class indicated stem mortality, which was observed among mesophytic species in lower severity plots (Fig. 5). As burn severity increased, there was less mortality of mesophytic stems, resulting in a significant positive relationship with burn severity (R^2 = 0.167, $F_{1, 23}$ = 5.81, p = 0.024). Recruitment of pyrophytes into the canopy had no relationship with burn severity over 12 years.

Stem recruitment from year six to 12 (2016–2022) also varied among species groups and size classes (H2 and H3). Burn severity was positively related to pyrophyte species recruitment into the midstory (R^2 = 0.317, $F_{1, 23}$ = 12.12, p = 0.002), particularly for yellow pines (R^2 = 0.304, $F_{1, 23}$ = 11.47, p = 0.003) and non-oak-pine pyrophytes (R^2 = 0.471, $F_{1, 23}$ = 11.68, p < 0.001) (Fig. 4). The recruitment of pyrophytes and intermediates into the canopy was positively related to burn severity (R^2 = 0.139, $F_{1, 23}$ = 4.88, p = 0.037 and R^2 = 0.378, $F_{2, 22}$ = 8.28, p = 0.002, respectively) (Fig. 5). Pyrophyte recruitment was primarily driven by yellow pines (R^2 = 0.207, $F_{1, 23}$ = 7.25, p = 0.013), but there was a near-significant relationship for oak species as well (R^2 = 0.151, $F_{2, 22}$ = 3.14, p = 0.063) (Fig. 5). Overall, between post-fire year six and 12, there was no relationship between burn severity and mesophyte recruitment at any size class.

3.5 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 was negatively related to burn severity (R^2 = 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 = 0.3276, $F_{1, 19}$ = 10.74, p = 0.004). Conversely, the abundance of small non-maple mesophyte seedlings displayed a positive relationship with burn severity (R^2 = 0.367, $F_{1, 21}$ = 13.73, p = 0.001). Among large seedlings, yellow pine seedlings displayed a negative relationship with burn severity (R^2 = 0.204, $F_{1, 17}$ = 5.60, p = 0.030). No other species groupings were significantly related to burn severity.

3.6 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.), multiflora rose (*Rosa multiflora* Thunb. ex Murr.), and Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus), each of which were found on plots that experienced moderate to high burn severity (CBI ≥ 1.2). We recorded these latter three species only on plots that also had Chinese silvergrass, and each were present on only a single plot.

4. Discussion

Our results demonstrate that wildfire continued to have lasting effects on community assemblage and forest structure up to 12 years post-fire, and key among those effects was that greater burn severities were associated with increased competitive ability of pyrophytic species relative to the mesophytes that encroach upon upland oak-pine ecosystems (B.A. Blankenship and Arthur 2006; Palus et al. 2018). However, our results also indicate that the selective force of increased burn severity favoring pyrophytic species is starting to diminish due to midstory densification, and that to re-stimulate oak species recruitment, a natural disturbance (e.g. wind, ice, etc.), prescribed burning, or targeted management action may be needed between six and 12 years after a high-severity fire in upland landscape positions (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 there were non-significant, yet negative associations between burn severity with species diversity and richness at years one and three, but as time progressed the relationships became positive. This positive relationship by year 12 is consistent with other studies in the Southern Appalachians (Hagan et al. 2015; Wimberly and Reilly 2007; Reilly et al. 2006), 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 sassafrass, black locust (*Robinia pseudoacacia* L.), and sumacs (*Rhus* spp.), being regenerated in the moderate to high shade being cast by midstory stems, and now non-pioneer species are 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 midstory stem density and burn severity at years one and three, no relationship at year six, and our finding of a positive relationship at year 12. This indicates that increased burn severity only reduced midstory stem densities relative to lower-severity fire for up to six years, after which the regrowth that occurred in high-severity areas became denser.

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 six, 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 high-severity still exhibited increased yellow pine stem recruitment, though oak species' recruitment no longer had this relationship. Despite this lack of a relationship for oak species, it should be noted that we did see higher amounts of recruitment at greater burn severities, an improvement compared to prescribed fire sites where there is a paucity of midstory oak stems (McEwan et al. 2010; P. H. Brose et al. 2013). 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; Saladyga et al. 2022; J M Vose et al. 1993; Welch and Waldrop 2001), 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 US. The lack of oak species recruitment into the midstory at year 12 may indicate that oak seedlings and saplings are being shaded out by the now-dense midstory (Kuddes-Fischer and Arthur 2002). If so, an additional fire between year six and 12 could re-stimulate oak recruitment by culling midstory stems and increasing understory light availability (Iverson et al. 2017; Beth A. 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 (Mary A. Arthur et al. 2015) whose juvenile bark is less developed at younger ages compared to oak species (Hammond et al. 2015). Returning fire within a six to 12 year fire-free interval would be consistent with historic FRIs (Lafon et al. 2017; Guyette et al. 2012), 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 seven 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. Thus, we have reasonable evidence to suggest that yellow pine species' recruitment into midstory sizes can be stimulated for up to 12 years by higher severity fire, but such a fire can only promote oak species' recruitment for between six and 12 years. Moreover, our results are consistent with Black et al. (2018) and other research (P. H. Brose et al. 2013) in that lower-severity fire lacks the selective force needed to promote pyrophytic species' recruitment over mesophytic species after twelve years; a sought-after result of often low-severity prescribed (P. 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 six (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 increased burn severity. At lower burn severities (CBI 0.6 to 1.2), canopy recruitment of pyrophytic species between year six and 12 displayed negative recruitment, demonstrating that there was some degree of delayed canopy mortality during this 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 prompted increased canopy recruitment among yellow pine species at year 12, but no longer that of oaks. Since we observed yellow pines recruiting into the midstory at year six and then into the canopy at year 12, but did not observe the same pattern for oak species, oaks are potentially being outcompeted. To release oaks from competition and prevent them from being permanently overtopped, a thinning prescription, such as crop tree release that has been shown to directly increase diameter growth and recruitment of oak trees into dominant and codominant canopy positions (Ward 2009), should occur between 10 and 20 years post-fire (Zenner et al. 2012).

Mesophytic species' recruitment into midstory and canopy size classes was expected to be unaffected by burn severity (H3), which our results reflect. At year six, the recruitment of mesophytic competitors was uninfluenced by the effects of burn severity (Black et al. 2018), and this trend remains at year 12. 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 six. In this, at low burn severities mesophytic species were substantially more important (w/r/t IV) than pyrophytes and intermediates, but as burn severity increased, pyrophytes became more important than mesophytes. This finding contrasts assertions that wildfires in the eastern US may accelerate mesophication (Reilly et al. 2022) and is aligned with patterns observed in western US forests, where higher-severity fire shifts ecosystems toward more fire-resilient communities (Nemens et al. 2022; Cocking et al. 2014). The burn severity at which pyrophytes in our study became more important (CBI = ~ 2.0) is particularly noteworthy, 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-severity fire.

Contrary to our expectation that we would see variation in the species diversity of small (< 50 cm height; <19.7 in height) and large seedlings (> 50 cm height; >19.7 in height) 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 we did not differentiate between regeneration that came from seeds versus sprouting, these patterns are likely due to decreases in the number of sexually mature seed trees in dominant/codominant canopy positions and decreased understory light availability caused by midstory shading. In fact, small oak seedling abundance was significantly related to oak canopy basal area. This idea is consistent with oak species' life history traits, wherein it can take scarlet oak, chestnut oak, and black oak approximately twenty years to begin bearing seed (Johnson 2004; McQuilkin 2004; Sander 2004). This suggests that the oak regeneration in high-severity plots we have observed up to year 12 has primarily come from sprouting prompted by the Fish Trap Fire. The abundance of large yellow pine seedlings had a near-significant relationship with canopy yellow pine basal area. This finding is not surprising considering that the most dominant yellow pine species at the Fish Trap Fire site, pitch pine and Virginia pine, can bear mature seed at three to five years old (Carter and Snow, Jr. 2004; Little and Garrett 2004). Overall, this means that we should have observed a moderate amount of pine regeneration and little oak regeneration at year 12, which we did.

The lack of regenerating seedlings of pyrophytic species with increased burn severity, taken with our assertion that the midstory is now too dense to preferentially recruit pyrophytic oaks, provides additional justification for implementing an additional burn or targeted management action between years six and 12. These actions would minimize the competition of future seed trees, stimulate basal sprouting of seedling-sized oak stems, and create a seedbed more conducive to pine seed germination, effectively creating an additional age class of pyrophytic species to develop. Without such actions, we are already observing mesophytic seedlings becoming more abundant where midstories are denser, and this site will likely experience challenges associated with mesophication once again. Up until year 12, 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 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) contradicts 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 six 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 a 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. What is most concerning about this species' population expansion is the fire hazard it poses, as when it senesces during the fall season, it leaves densely bunched dry standing grasses that reach 1.5 to 3 m (5 to 10 ft) in height (Miller et al. 2010). These bunches are highly flammable and can increase future burn severity (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 enough, especially in areas that burned at high severity, to pose a threat to forest health. A future dormant season fire may inflate burn severity levels to a degree that undermines the compositional and structural benefits observed so far and would allow for further establishment and proliferation of NNIPs, potentially resulting in an invasional meltdown scenario (Braga et al. 2018).

To avoid the detrimental effects of NNIPs in post-fire areas, extensive control efforts should be made. At the Fish Trap Fire site, removal of princess tree stems that established immediately after the fire proved successful. In 2011, approximately one year following the fire, the USDA Forest Service conducted a ground-based survey of areas that were susceptible to NNIP establishment that revealed 2,061 princess tree stems had established following the fire (Upadhaya 2015). Immediately following this survey, these stems were targeted for removal by tree pulling in 2011, 2012, and 2013, and by stem clipping in 2014. By 2016, this method of removal for princess tree appeared to have been highly effective as no stems were observed in the year six and 12 surveys. While the survey extent in Black et al. (2018) and in our study differed from that of the USDA Forest Service, we can reasonably conclude that the proliferation of princess tree was successfully stifled by these removal efforts. In addition to early monitoring and control methods, these results 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.

5. 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). 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 up to 12 years post-fire, but pyrophytic oak species are only favored for up to six years (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 between six and 12 years following a high-severity wildfire. 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 US is increasingly important, as wildfire frequency and size are anticipated to increase from anthropogenic climate change (Lafon and Quiring 2012; McNulty et al. 2015; 2013). While changes in climate and increased wildfire activity are predicted to favor pyrophytic species like oaks (Iverson et al. 2019; James M. Vose and Elliott 2016), 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 (James M. 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.

Declarations

1. Ethics Approval and Consent to Participate

Not Applicable

2. Consent for Publication

Not Applicable

3. Availability of Data and Materials

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.

4. Competing Interests

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

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6. Author's 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.

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87.

Figures

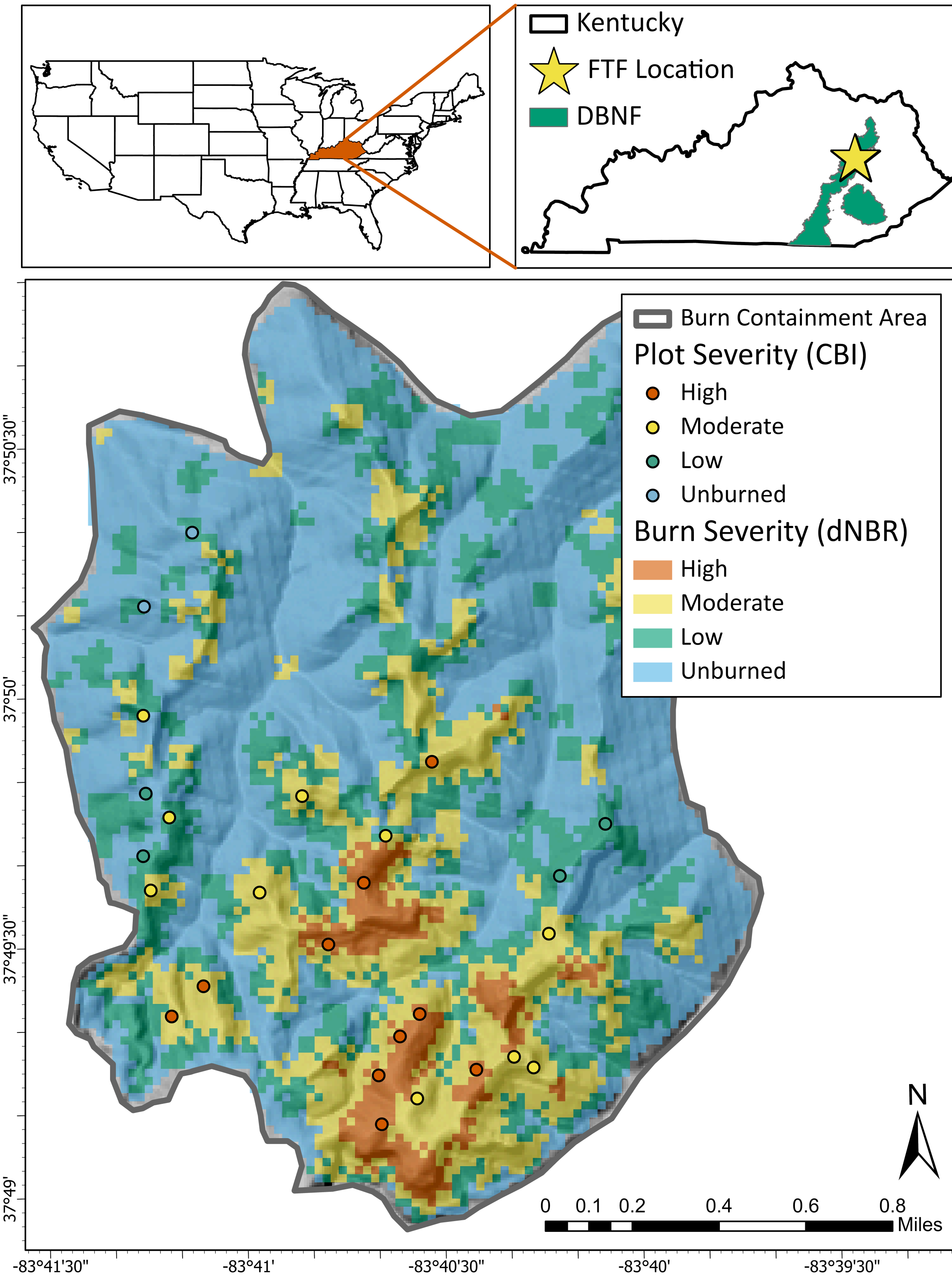

Figure 1

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.

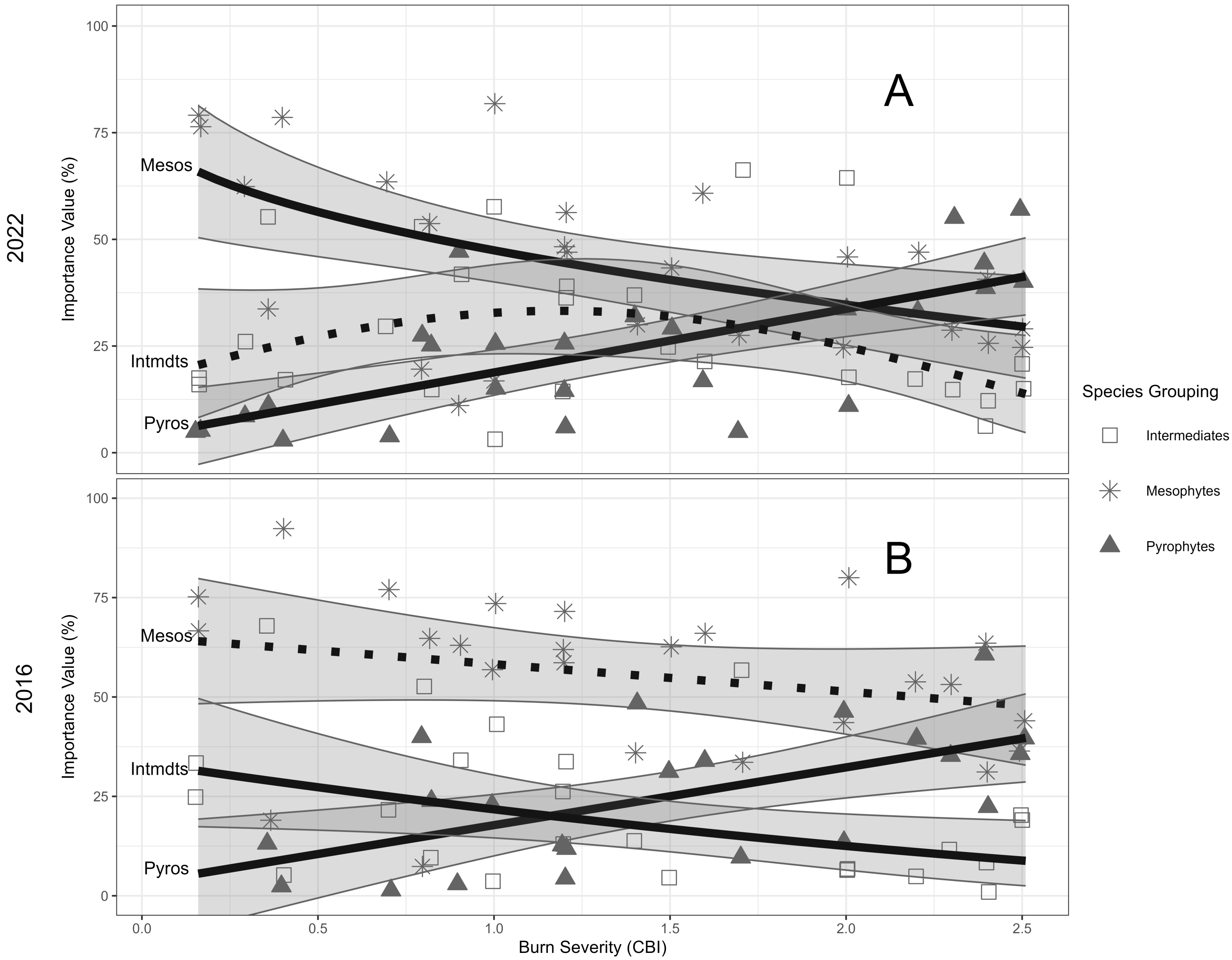

Figure 2

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 (α = 0.05) represented by a solid line and insignificant relationships represented by a dashed line.

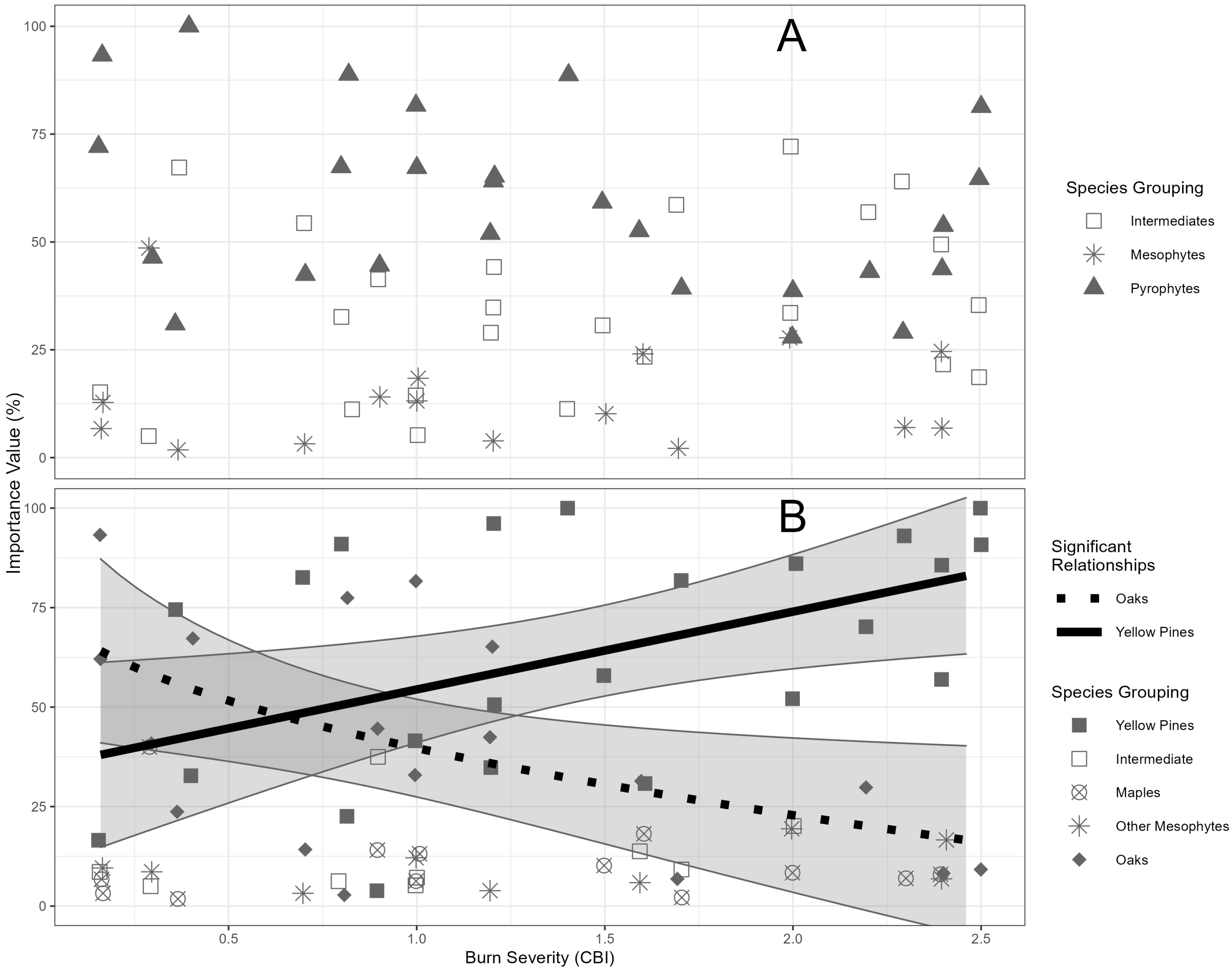

Figure 3

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 (α = 0.05).

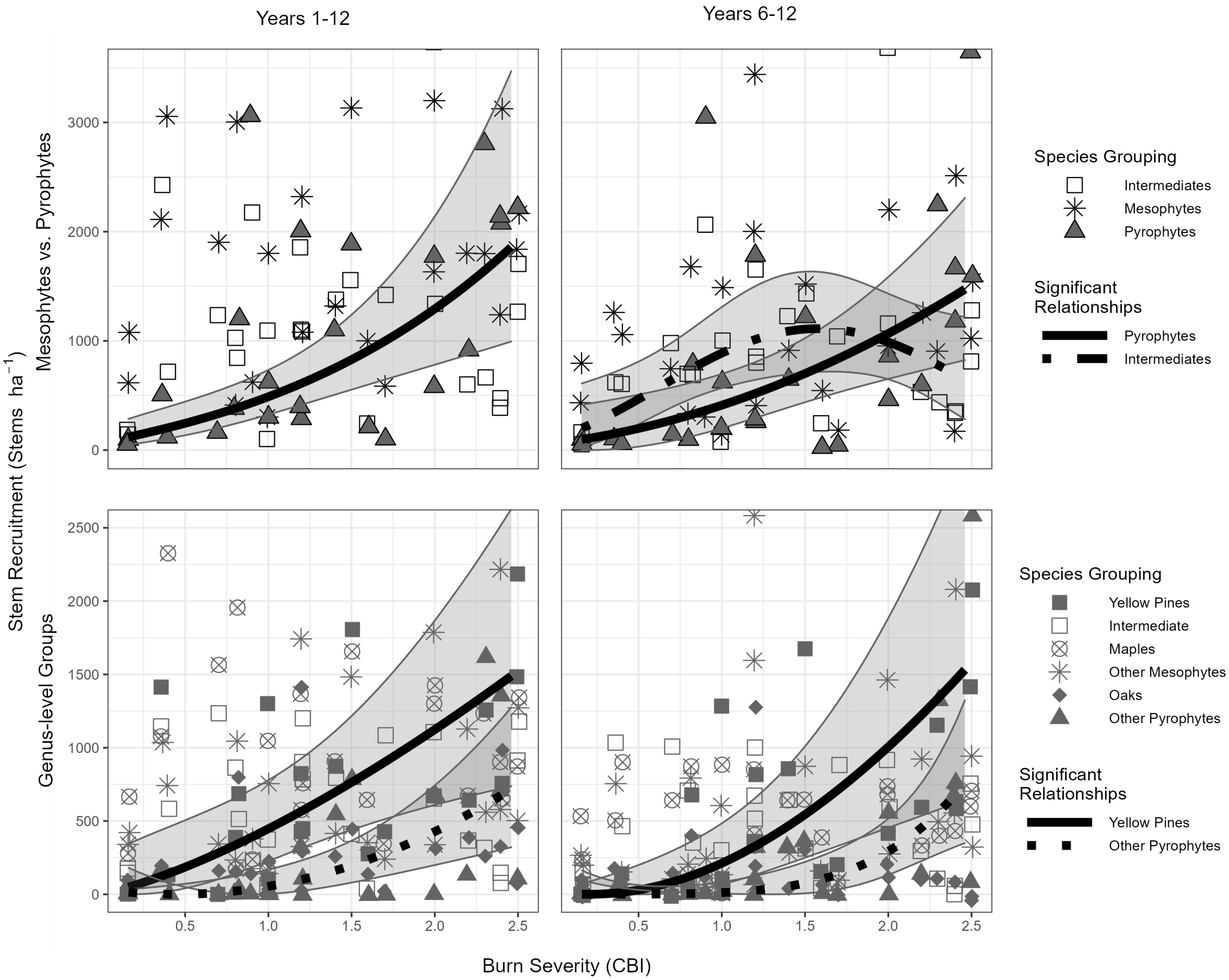

Figure 4

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 (α = 0.05).

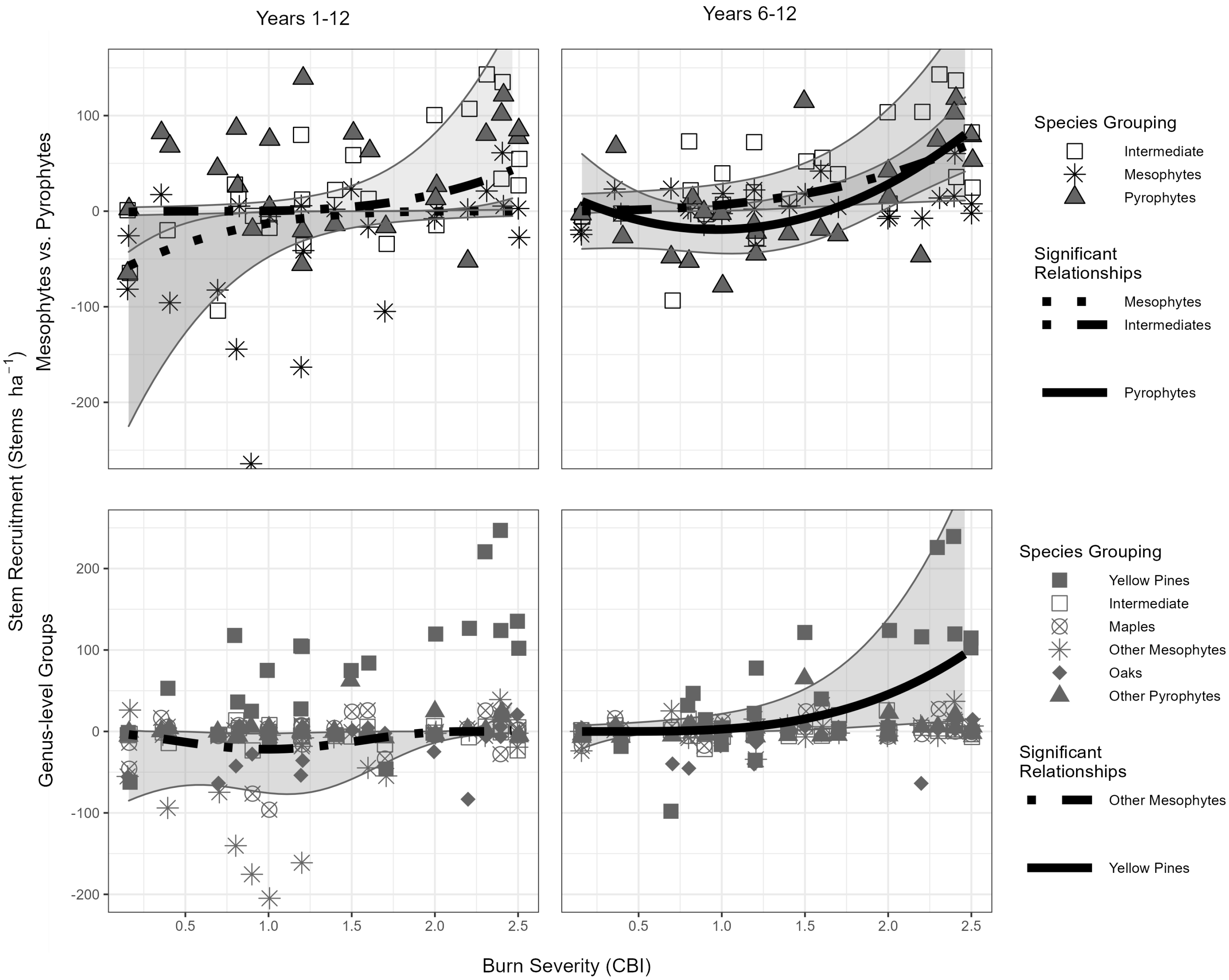

Figure 5

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 (α = 0.05).

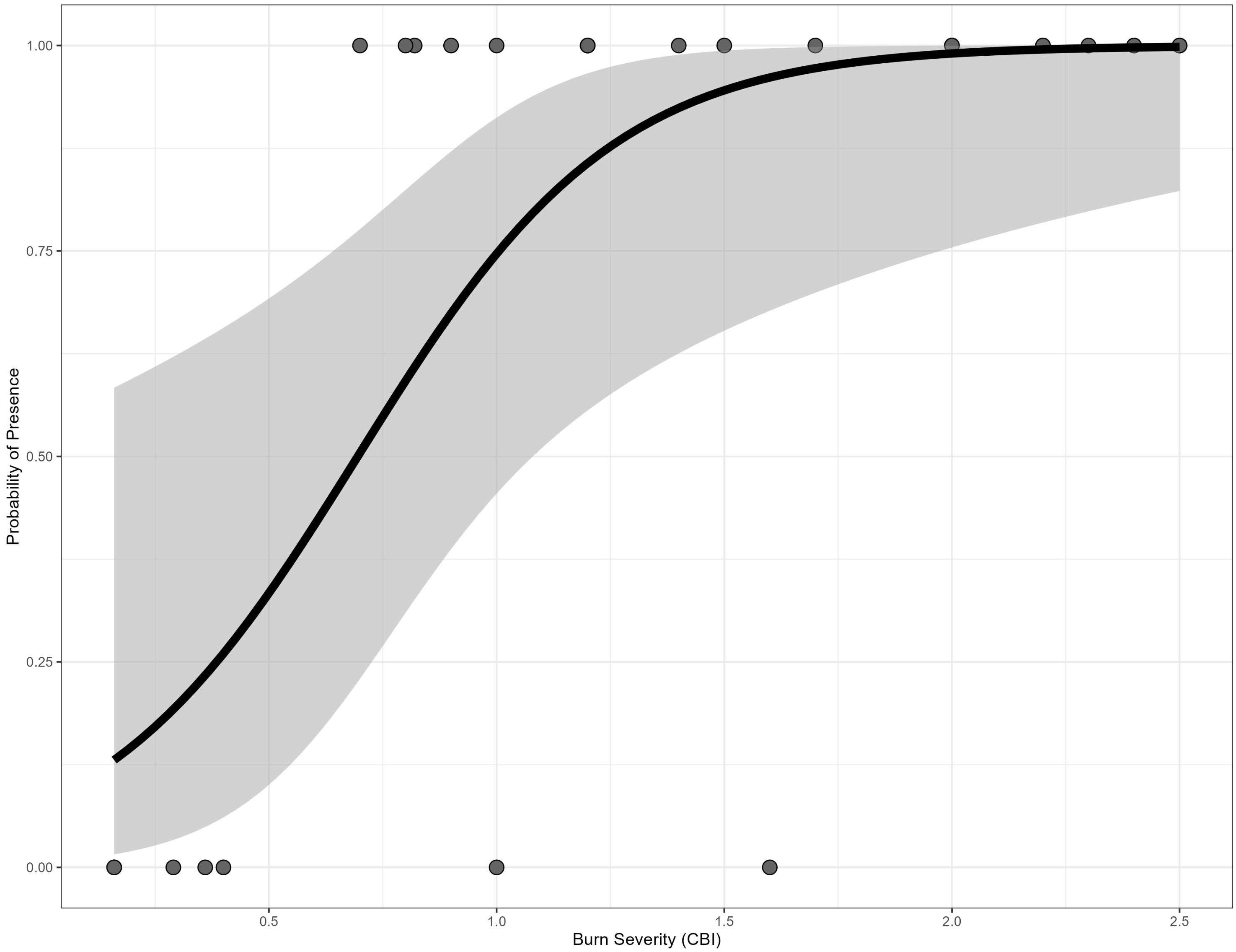

Figure 6

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 (α = 0.05).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupFig1MidstoryDIV.tiff
- SupFig2MidstoryDEN.tiff
- SupFig3CanopyDEN.tiff
- SupFig4MidstoryBA.tiff
- SupFig5CanopyBA.tiff