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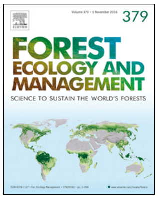

Prescribed fire and natural canopy gap disturbances: Impacts on upland oak regeneration

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ABSTRACT

Across the central and eastern U.S., decades of fire exclusion have coincided with upland oak (*Quercus* spp.) regeneration problems and a compositional shift toward shade-tolerant, fire-sensitive species like red maple (*Acer rubrum* L.) and American beech (*Fagus grandifolia* Ehrh.). Because oaks are fire-adapted and moderately shade-intolerant, prescribed fire is commonly used as a management tool to decrease competition, increase light, and promote oak regeneration. However, prescribed fire alone often fails to sufficiently open the canopy and improve oak competitive status, suggesting the combination of fire and canopy gaps may be necessary for oak success. To better understand the effects of single and multiple prescribed fires alone and combined with naturally-formed canopy gaps on tree regeneration, we measured tree densities (both seed and resprout origin) in five height size classes (small seedlings: ≤0.5 m, large seedlings (> 0.5–1.0 m), saplings (1.1–4.0 m), midstory (4.1–7.0 m), and poles (7.1–12 m)) within gaps and non-gap areas treated with no fire, single fire, or multiple fires (2–3) across six sites within the Knobs Region of Kentucky (U.S.A.) in 2017. Oaks were common as small and large seedlings without fire, especially within gaps, but they were largely absent from larger size classes. Instead, red maples and American beech dominated sapling and midstory size classes without fire, regardless of gap treatment. Single and multiple fires reduced both absolute and relative density of American beech saplings and red oaks (*Q. velutina* Lam., *Q. coccinea* Munchh. and *Q. rubra* L.) of all sizes, but single fires, both within and outside of gaps, increased red maple large seedling, sapling, and midstory dominance. Multiple fires, both within and outside of gaps, reduced red maple abundance, and this coincided with increased relative density of white (*Q. alba* L.) and chestnut oaks (*Q. montana* Willd.), but not of red oaks. Red oak small and large seedlings were the only oaks where absolute density increased in the small (~300 m^2), relatively old (20–30 yr), naturally-formed canopy gaps in this study. Our findings suggest that management techniques that include multiple prescribed fires and large canopy gaps (> 300 m^2) created relatively soon after fire will likely be necessary to reduce competing species, increase oak density, and allow oaks to reach sapling and midstory size classes.

1. Introduction

Across the central and eastern U.S., upland oak (*Quercus* spp.) regeneration failure is extensive (Fei et al., 2011; Johnson et al., 2009), and oak forests are undergoing a compositional shift toward shade-tolerant, fire-sensitive species (Fei and Steiner, 2007; Knott et al., 2019; Nowacki and Abrams, 2008). After seed germination and establishment, upland oak regeneration depends on abundant seedlings and saplings to replace overstory trees following canopy disturbance (Arthur et al., 2012; Loftis, 2004), as upland oaks are moderately shade-intolerant and require a relatively open canopy for survival and growth (Dey and Hartman, 2005). Oaks have a conservative growth strategy and allocate resources to root storage in early life stages (Johnson et al., 2009), which can lead to vigorous resprouting following a canopy-opening fire (Brose and Van Lear, 2004). Many non-oaks that are encroaching into oak landscapes, particularly red maple (*Acer rubrum* L.), possess a non-conservative shoot over root strategy and have greater shade-tolerance than oaks (Abrams, 1998; Burns et al., 1990). In the

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absence of disturbance, oaks can be out-competed by shade-tolerant species in closed-canopy forests with limited light (Lorimer et al., 1994). Although oak seedlings can be relatively abundant in closed-canopy forests, the dense canopy of shade-tolerant sapling and midstory trees leads to low-light conditions (generally $< 5\%$ direct sunlight) that impede both oak seedling growth and transition to larger size classes (Brose, 2014). As a result, species like red maple and American beech (*Fagus grandifolia* Ehrh.) are poised to replace oaks in the canopy when current overstory oaks senesce (Fei et al., 2011; Fei and Steiner, 2007; Nowacki and Abrams, 2008).

The shift of historically oak-dominated ecosystems to increased dominance of shade-tolerant species can be explained by a number of interacting ecosystem drivers (Buchanan and Hart, 2012; McEwan et al., 2011; Nowacki and Abrams, 2015). Prior to European settlement, fires were an important process in oak forests (Delcourt and Delcourt, 1997; Stambaugh et al., 2015), and evidence suggests that fire, combined with climate, land-use change, pests, and pathogens, interacted to form the oak forests that dominated at the time of settlement (Hutchinson et al., 2008; McEwan and McCarthy, 2008). Since then, changes to herbivore populations, increased moisture availability, intensive land clearing, and fire exclusion have contributed to current-day oak forests with overstory oak dominance but little understory regeneration (Abrams, 2003; McEwan et al., 2011; Nowacki and Abrams, 2008; Woodall et al., 2008).

If oaks fail to regenerate, there will be numerous ecological and economic costs. Oaks are considered a foundation genus that mediates ecosystem-level processes (Ellison et al., 2005; Hanberry and Nowacki, 2016). A compositional shift away from oaks could alter forest hydrology (Alexander and Arthur, 2010) and nutrient cycling (Alexander and Arthur, 2014; Caldwell et al., 2016), decrease biodiversity (Mitchell et al., 2019; Spetich, 2004), and reduce food and shelter for wildlife (Hamel et al., 2004; Harper et al., 2016; Mcshea et al., 2007). Oaks are also valued for their high quality timber and are used to produce a variety of products including bourbon barrels, furniture, and veneer (Brose et al., 2014; Johnson et al., 2009; Yaussy et al., 2008).

Because of oaks' importance, considerable research has focused on using prescribed fire as a management technique to promote oak regeneration (Brose, 2014; Hutchinson et al., 2012b; Keyser et al., 2017). Studies largely indicate that single prescribed fires in the absence of canopy disturbances are ineffective at promoting oak regeneration, while multiple fires are more effective in removing midstory competition, increasing understory light, and increasing oak seedling growth and density (Arthur et al., 2012; Brose et al., 2013; Green et al., 2010; Schweitzer and Dey, 2011). In general, prescribed fire is most effective at promoting oak regeneration when combined with disturbances that open the canopy (Alexander et al., 2008; Arthur et al., 2012; Brose, 2010; Hutchinson et al., 2005; Loftis, 1990). But, the number of fires, order of disturbances, size of canopy gaps, and amount of direct sunlight may also determine oak regeneration success (Albrecht and McCarthy, 2006; Waldrop et al., 2008; Iverson et al., 2017; Vander Yacht et al., 2017). For example, while single prescribed fires applied 1–2 years after the creation of relatively small canopy gaps (250-m^2) are often ineffective at increasing oak abundance or promoting oak regeneration (Albrecht and McCarthy, 2006; Van Sambeek et al., 2002; Waldrop et al., 2008), multiple prescribed fires applied ~5 years after partial overstory harvests (residual basal area $< 19\ m^2\ ha^{-1}$) with $> 30\%$ direct sunlight are beneficial to oak seedlings and sapling survival (Iverson et al., 2008, 2017; Vander Yacht et al., 2017). This work indicates that oak regeneration dynamics are fundamentally linked to the interplay between light availability and fire, which alters the understory environment and may create a competitive advantage for oaks that allows seedlings to transition into saplings.

Light availability in the forest understory is strongly influenced by overstory canopy disturbance, including natural canopy gap formation. This ecological process is becoming increasingly important in many of the second-growth oak forests of the central and eastern U.S. As stands age, the probability of canopy gap disturbance from overstory tree mortality increases (Clinton et al., 1993; Hart and Grissino-Mayer, 2009; Rentch et al., 2003). When canopy trees die and form canopy gaps, the increase in light availability leads to changes in forest floor conditions, including temperature and moisture (Canham et al., 1989; Minckler et al., 1973). Increased light can significantly impact seedling and sapling survival in gaps, which in turn influences forest structure (Runkle and Yetter, 1987; Whitmore, 1989; Yamamoto, 2000). In addition, overstory trees adjacent to canopy openings often produce more seeds than trees in an intact forest, which can increase seed availability in gaps (Waldrop et al., 2016). While many oak forests are aging, trees are still relatively young (~80 yr old; Moser et al., 2006) compared to their life expectancy (350–400 yr); consequently, there is limited management experience with the ecological outcomes after overstory trees die and form canopy gaps (Hutchinson et al., 2012a).

The primary objective of this study was to advance understanding of the impacts of prescribed fire and naturally-formed canopy gaps on oak regeneration density. Our study system provided a unique scientific opportunity because we had access to forests treated with no fires to multiple prescribed fires, and canopy gaps of varying sizes and ages were available due to natural tree mortality. We hypothesized that multiple prescribed fires conducted in areas with naturally-formed canopy gaps would be most effective at increasing oak seedling and sapling density most likely by removing competition and increasing understory light. Our aim was to inform forest management of upland oak forests in the central and eastern U.S.

2. Methods

2.1. Study area

Research occurred at Bernheim Arboretum and Research Forest (hereafter referred to as Bernheim) located in the Knobs ecoregion of western Kentucky ~40 km south of Louisville, KY, U.S.A. (37°54′N, 85°37′W). The mean annual maximum and minimum temperatures are 24 °C and 2.5 °C, respectively (Arguez et al., 2010). Mean annual precipitation is 126 cm (Arguez et al., 2010), evenly distributed throughout the year. Soils are characterized as deep, well-drained silty loams of the Carpenter-Lenberg complex with components of the Trappist series (Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at the following link: https://websoilsurvey.sc.egov.usda.gov/. Accessed 01/28/2020).

Bernheim consists of over 6,070 ha of second growth forests (~90 years old) that established following cessation of agricultural practices and logging operations (Rhoades et al., 2004). At the time of our study, Bernheim forest structure and composition were typical of upland oak forests in the central and eastern U.S. White oak (*Q. alba* L.) and chestnut oak (*Q. montana* Willd.) dominated the overstory (~80%; stems ≥25 cm diameter at breast height (DBH)); other overstory oak species (~12% of overstory) included black oak (*Q. velutina* Lam.), northern red oak (*Q. rubra* L.), and scarlet oak (*Q. coccinea* Munchh.). Total overstory basal area ranged from 17 to 36 $m^2\ ha^{-1}$. Midstory (10.1–25.0 cm DBH) basal area ranged from 2.3 to 4.4 $m^2\ ha^{-1}$ and was comprised of primarily species from the white oak group (51%; white oak and chestnut oak) and red maple (34%). Shade-tolerant species dominated the sapling layer (5.1–10.0 cm DBH), mostly American beech (45%) and red maple (29%). In the seedling size class (stems $<$ DBH tall), oaks and non-oaks were equally represented, and most of the non-oaks were red maple (Babl et al., 2020).

Fire suppression began in Bernheim in 1929 with several wildfires occurring in subsequent years. In 1946 and 1953, major fires, burning up to 350 ha^{-1}, occurred in at least four locations with other fires likely undocumented. The earliest forest management using prescribed fire in Bernheim was in 2001 covering 140 ha^{-1}. Forest management activities in Bernheim are limited to small-scale prescribed fires

Table 1
Site and prescribed fire characteristics for six sites in Bernheim Arboretum and Research Forest, KY.

Site	Burn area (ha)	Number of burns	Years since last burn	Date of burn						
				2008	2010	2012	2013	2014	2016	2017
Yoe's	2.5	1	4				5-Apr			
Fire Tower	10.1	1	4				3-Apr			
East Road	8.5	2	1			21-Mar			21-Mar	
Salamander	5.3	2	3			27-Feb		21-Apr		
Knobs	2.8	2	5		18-Mar	20-Mar				
Fern Valley	3.3	3	0	8-Apr	1-Apr					22-Mar

(generally $< 10\ \text{ha}^{-1}$) and grazing pressure at these sites is unknown.

2.2. Study Design/Approach

In 2017, we investigated the impacts of prescribed fires and naturally-formed canopy gaps on tree regeneration density within six sites (between 2.5 and 10.1 ha; Table 1) distributed across non-contiguous ridgetops with oak-dominated overstory trees. Sites had similar composition of overstory species from the red and white oak groups with the exception of one site, Salamander, where red oak group overstory basal area was three times higher than other sites (Izbicki et al., unpublished data). Two sites (Yoe's and Fire Tower) were treated with a single prescribed fire in 2013, while the four other sites (East Road, Knobs, Salamander, and Fern Valley) were treated with multiple prescribed fires, with variable number of fires and years since fire across the sites (Table 1). Data from areas with two and three fires indicated that these sites were similar in oak and competing species seedling/sapling structure and composition when measured in 2017, so we combined them into a “multiple fire” category for analysis. All prescribed fires were ignited with a drip torch in strips during the dormant season prior to leaf expansion (February–April) under the following conditions: air temperatures 10–29 °C, relative humidity 16–45%, and wind speed 8–16 km hr^{-1}. Fire severity for all burns was low, with no crown scorch and flame heights < 1.5 m. Across sites and burn events, soil organic layer cover was reduced by $> 85\%$. Overstory trees were unaffected by prescribed fire across sites and treatments (Izbicki et al., unpublished data).

At each site, we sampled tree regeneration in both burned areas and adjacent unburned areas. Within burned areas at each site, we sampled 3–5 canopy gaps and three non-gap areas. Within unburned areas, we sampled three gaps and two non-gap areas. In total, across all sites, we sampled 20 gaps treated with no fire, eight gaps treated with a single fire, 12 gaps treated with multiple fires, and 30 non-gap plots. Canopy gaps were not measured in burned areas at one site (Salamander) due to logistical difficulties.

2.3. Canopy gaps

We defined a canopy gap as a canopy opening caused by the death of one or a few overstory trees and with regenerating tree stems no taller than two-thirds of the surrounding canopy height (Runkle, 1992). Canopy gaps consisted of all area under the canopy opening extending to the bole of surrounding canopy trees, and including areas affected by both direct and indirect light. This definition is consistent with other canopy gap studies (Brokaw and Busing, 2000; Runkle, 2013, 1982), and captures the importance of the entire gap community by measuring both true and expanded gap space (Runkle, 1982). True gap area was the area directly under the canopy opening. Expanded gap area consisted of space from the edge of the true gap area to the bole of adjacent canopy trees (Runkle, 1982).

A variety of gap characteristics were measured to better understand potential influences of canopy cover, gap size, gap area, and gap maker basal area (basal area of trees whose death created the canopy gap; Runkle, 1982) on density of tree seedlings and saplings. To measure a range of gap sizes and ages, canopy gaps were selected using the line intercept method (Runkle, 1982). At randomly chosen starting points near a vehicle-accessible forest road, transects were set up for canopy gap selection. A gap was measured if it intersected the transect and was at least 50 m from the edge of a road or another canopy gap. Within each gap, we measured the DBH and identified the species (by distinguishing bark characteristics and branch architecture) of gap makers. Gap size was determined by measuring the length (L, the largest distance from gap edge to gap edge) and width of the gap (W, the largest distance perpendicular to the length). Because each gap was roughly the shape of an ellipse, the length and widths were then fitted into the formula of an ellipse $A = \pi LxW/4$ to calculate gap area, A (Runkle, 1982). We used a convex spherical densiometer to measure canopy cover at five positions within each gap. Once at gap center and twice along both the length and width of the gap.

We estimated gap age by collecting increment cores from a subset (3–5) of regenerating trees inside the gap area. In order to measure potential growth response to canopy gap formation, we only sampled trees that were likely present at the time of gap initiation and that were less than two-thirds of the height of the surrounding canopy. Two increment cores were collected ~30 cm above the base of each tree sampled. Samples were dried at 60 °C and sanded sequentially with finer grit sizes to obtain a smooth surface. Samples were then scanned at high-resolution, and ring widths were measured using WinDendro Basic 2012 (Regent Instruments, Canada). Tree-ring series were analyzed to detect release (a substantial increase in ring size), indicating an increase of resource availability during the gap initiation year (gap age). Release (gap initiation) was defined as 100% sustained ring width for a 10-year period, and was calculated as percent change in growth of a single ring between two 10-year increments (Nowacki and Abrams, 1997), using median rather than mean as the central tendency (Rubino and McCarthyz, 2004). When more than one release was detected, the largest was reported.

2.4. Tree regeneration

In order to understand how prescribed fire interacts with canopy gaps to affect species composition, we inventoried all regenerating stems in canopy gaps across all fire treatments in summer or fall 2017. We placed belt transects along the greatest length and width of each gap and recorded the height and species identity of each woody stem within the belt transects. Stems from both seed germination and resprout origin were combined into a single category, and in the case of resprouts, we recorded only the largest stem from each root system. The width of the belt transects varied with the size class of interest: all stems < 1 m height were measured within a 30-cm wide transect, and all stems > 1 m height were measured within a 2-m wide transect. We sought to survey approximately 10% of each gap (equal to ~2/3 of the belt transect length), regardless of gap size (Fahey and Puettmann, 2007; Runkle, 1992). To do so, we measured 2/3 of the total length of each belt transect using a series of 3–5 m segments beginning at randomly-generated starting points along the belt transect. Because 3–5 m represents the common length from the edge of the canopy opening to the bole of the adjacent canopy tree (e.g., the expanded gap space), this size of belt segment allowed us to survey both expanded and true gap space. We surveyed an equal number of 3–5 m segments in both the true and expanded gap space along each belt transect and summed the regeneration estimates across the entire gap.

To assess tree regeneration in response to prescribed fire alone, we recorded the height and species of all trees within non-gap fixed-radius plots at each of the six sites. Stems < 1 m tall were measured within 1-m radius of plot center, and stems > 1 m tall were measured within 4-m radius of plot center. We measured stems of both seed and resprout origin, and when there were clusters of resprouting stems, we measured only the largest stem of each visible root system.

2.5. Statistical analysis

To evaluate the effects of prescribed fire and canopy gaps on tree regeneration, woody stems were divided into five species groups and five height classes. Species groups of particular interest were defined as white oak (*Q alba* L.), chestnut oak (*Q. montana* Willd.), red oak group (*Q. velutina* Lam., *Q. coccinea* Munchh. and *Q. rubra* L.), red maple, and American beech. Because white, chestnut, and red oaks have different ecological traits and economic importance (Burns et al., 1990), they were analyzed separately. Both white and chestnut oak are more shade-tolerant than red oak species (Burns et al., 1990), but white oak is used exclusively for bourbon barrel production, which is of particular interest in this region. Red maple was analyzed alone because of its high abundance in the central and eastern U.S. and its “super-generalist” qualities (Abrams, 1992; Fei and Steiner, 2007; Knott et al., 2019; Lorimer et al., 1994). American beech was evaluated only in larger size classes (> 1.0 m in height) because seedlings were rare in the study area and because beech is a common competitor with oaks in the central and eastern U.S. (Abrams, 1992; Burns et al., 1990; Nowacki and Abrams, 2008). We defined five different height classes as follows: small seedlings (stems ≤ 0.5 m in height), large seedlings (stems > 0.5–1.0 m in height), saplings (stems 1.1–4.0 m in height), midstory trees (stems 4.1–7.0 m in height), and poles (stems 7.1–12.0 m in height). These size classes were chosen to maintain consistency with other prescribed fire and canopy gap studies in the region (Brokaw, 1985; Iverson et al., 2017; Keyser et al., 2017).

We used several approaches to evaluate tree regeneration density. First, we created relative density graphs that represented the proportion of the five species groups by height class in each treatment combination of prescribed fire and canopy gaps. This allowed us to qualitatively assess regeneration dynamics of oak and competing species across the study area. Second, we used regression tree analysis to model the relationship between absolute tree density of each species or species group (white oak, chestnut oak, red oak group, red maple, and American beech) and the predictor variables gap treatment (non-gap, gap) and burn treatment (no fire, single fire, and multiple fires). Regression tree analysis is an effective approach that is commonly used to assess regeneration dynamics post-fire where large numbers of plots with zero tree density and large standard errors cause separation in generalized linear mixed models (Buma and Wessman, 2011; Collins et al., 2007; Collins and Roller, 2013; Thompson and Spies, 2009). Regression tree analysis is a non-parametric technique that can evaluate non-linear relationships and high-order interactions. By partitioning data into increasingly uniform groups based on the response variable, regression trees provide decisions about the importance of predictor variables in easily interpretable figures (Moisen and Frescino, 2002). Some regression tree analyses have selection-bias and can over fit data (Hothorn et al., 2009), so we constructed conditional inference trees in R version 3.5.1 (R Core Team, 2019) statistical software package party (Hothorn et al., 2009) to minimize bias and avoid over fitting data. We constructed a regression tree for the small seedlings, large seedlings, and saplings of each species group. We did not consider the larger size classes because they represented < 1% of total stems, and we were most interested in sizes representing the regeneration pool.

A one-way analysis of variance (ANOVA) was used to test differences of gap canopy cover, size, age, and gap maker basal area between burn treatments (no fire, single fire, multiple fires). For models with evidence of a significant difference between fire treatment characteristics, we used a Tukey-Kramer HSD to test for differences between group means. Analyses were considered significant at p-values < 0.05. Model residuals were assessed and data that did not meet the assumptions of normality and homogeneity were square-root or log transformed. Statistical analyses were performed using JMP v. 13.

Linear regression models were used to test the effect of gap characteristics (canopy cover, size, age, and gap maker basal area) on tree regeneration density in small seedling, large seedling, and sapling size classes in each prescribed fire treatment. Model residuals were assessed to ensure that the assumptions of normality and homogeneity of variance were met, and we log-transformed the dependent variables where necessary to meet model assumptions. Regression analyses were performed using JMP v. 13.

3. Results

3.1. General regeneration trends

Mean total woody regeneration density was 46,237 stems ha^{-1} across treatments, species, and size classes (Table 2). Total stem density was marginally different between fire treatments (p = 0.056). In areas with no fire, stem density was 56,569 stems ha^{-1}, while density was 40,023 and 36,087 stems ha^{-1} for single and multiple fires, respectively. Across fire treatments, canopy gaps had 2.4 times higher stem density (61,901 stems ha^{-1}) than non-gaps (25,351 stems ha^{-1}; p < 0.001). Small seedlings represented an overwhelming majority of the regeneration across fire and gap treatments, accounting for 87% of the total stems. Across all treatments, small and large seedlings combined were dominated by red maple (39%), chestnut oak (29%), white oak (25%), and species from the red oak group (11%). Red maple represented a majority (55%) of the saplings across treatments.

Table 2
Mean (± SE) density (stems ha^{-1}) of small seedlings (≤0.5 m height), large seedlings (> 0.5–1.0 m height), and saplings (1.1–4.0 m height) by species across fire and gap treatments within Bernheim Arboretum and Research Forest, KY sampled in 2017.

Species	Small seedlings	Large seedlings	Saplings	Total
Red maple	16,635 (3,096)	1,338 (338)	514 (153)	18,487 (3,181)
American beech	202 (149)	78 (50)	71 (15)	351 (162)
White oak	9,116 (1,156)	1,256 (321)	127 (43)	10,498 (1,248)
Chestnut oak	10,767 (1,560)	1,030 (360)	92 (35)	11,889 (1,697)
Red oak group	4,158 (745)	1,009 (220)	196 (36)	5,364 (869)
Total	40,878 (499)	4,710 (726)	1,000 (170)	46,237 (463)

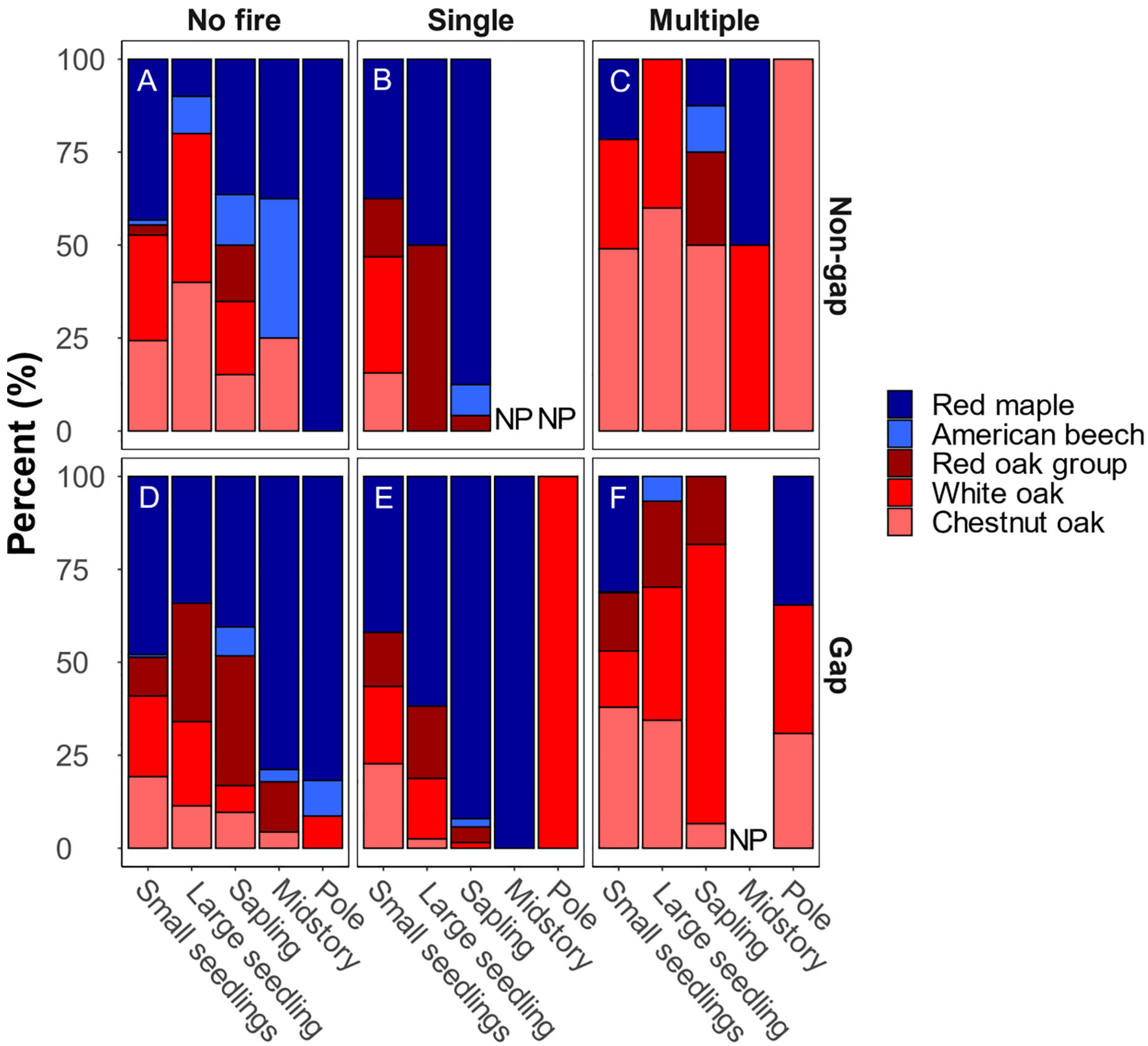

Fig. 1. Relative density of the five tree species and species groups examined in this study, organized by height class: small seedlings (≤ 0.5 m height), large seedlings (> 0.5–1.0 m height), saplings (1.1–4.0 m height), midstory (4.1–7.0 m height); and pole (7.1–12.0 m in height). There were six possible treatments measured within Bernheim Arboretum and Research Forest, KY in 2017: non-gap, no fire (A); non-gap, single fire (B); non-gap, multiple (2–3 times) fires (C); gap, no fire (D); gap, single fire (E); and gap, multiple fires (F). All size classes and species were measured in each treatment. Not Present (NP) means that no stems of these species were recorded in a height class.

3.2. *Changes in relative stem density following gaps and fire*

In the absence of fire, species' relative density varied with size class and gap treatment (Fig. 1A and D). Without fire or canopy gaps, white and chestnut oaks comprised 52% and 80% of small and large seedlings, respectively (Fig. 1A). White, chestnut, and red oak group stems represented 50% of saplings, and 25% of midstory stems, while red maple and American beech comprised 50% of saplings and 75% of midstory stems. Without fire, but with canopy gaps, oaks were relatively abundant as small (~50%) and large (60%) seedlings, and the red oak group increased in gaps compared to non-gaps in all but the pole size class. In the midstory of gaps without fire, red maple and American beech were almost 5 times more abundant than oaks, and in the pole-sized class red maple and American beech were 9.4 times more abundant than oaks (Fig. 1D).

Following a single fire, the relative density of large seedling, sapling, and midstory size classes shifted toward red maple dominance in both gap and non-gap areas (Fig. 1B and E). After a single fire in non-gaps, the relative density of red maple stems was higher than other species in the sapling size class (88%). American beech represented only a small fraction (8%) of sapling relative density (Fig. 1B). In gap areas following single fires, red maples represented 62% of large seedlings, 92% of saplings, and 100% of midstory stems, while American beech was scarce, comprising only 2% of sapling relative density. White, chestnut, and red oaks were rare in the sapling and midstory size classes following a single fire, even though these species represented 38% and 58% of the large and small seedling size classes, respectively (Fig. 1B and E).

Multiple fires altered the relative density of all size classes, and in general, led to a higher relative density of oaks (Fig. 1C and F). After multiple fires in non-gaps, white and chestnut oaks dominated small and large seedlings classes, accounting for a combined 78% of small seedlings and 100% of the large seedlings. The red oak group comprised 25% of saplings, and chestnut oak was the only species present as pole-sized stems (100%). After multiple fires, red maple and American beech combined relative density was 0% of large seedlings and 26% of saplings (Fig. 1C). With multiple fires and canopy gaps (Fig. 1F), all oak species were well represented in a majority of the size classes. Combined, the red oak group, white oak, and chestnut oak accounted for most of the small seedlings (69%), large seedlings (93%), saplings

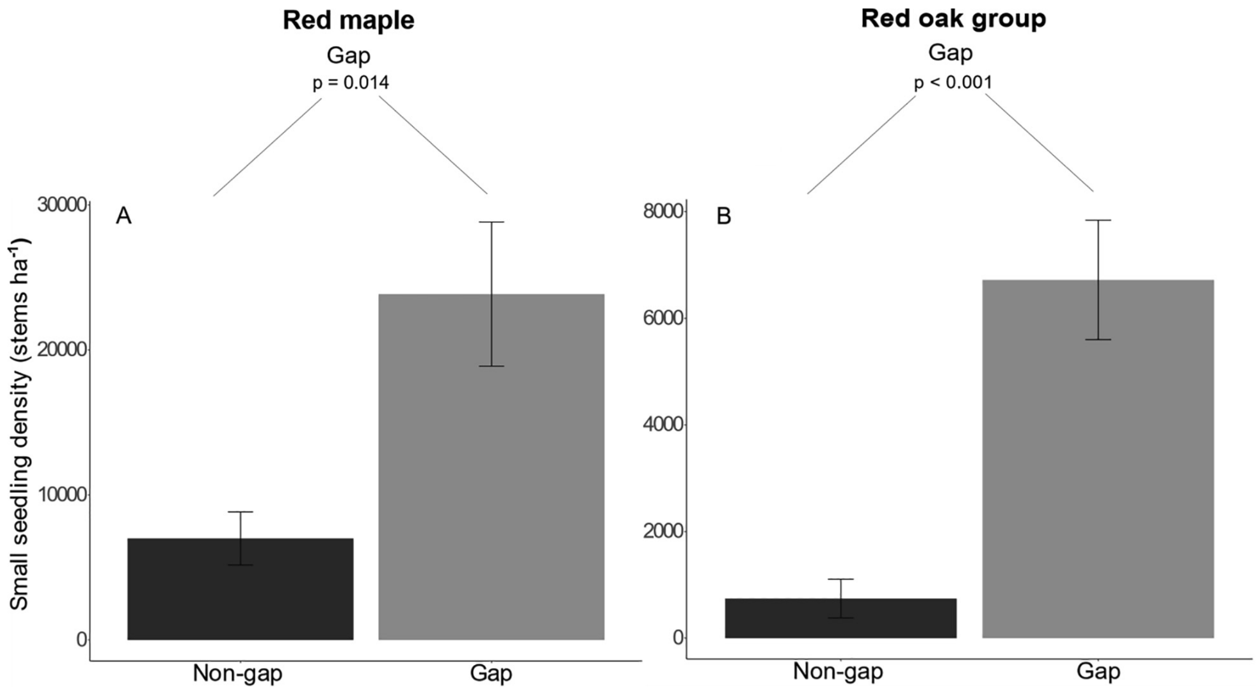

Fig. 2. Regression trees of red maple (A) and red oak group (B) small seedlings (≤ 0.5 m height) explaining absolute density (stems ha^{-1}) patterns between non-gap and gap treatments within Bernheim Arboretum and Research Forest, KY sampled in 2017. Note that there were no fire effects and density scales differ between species groups.

(100%), and pole (65%) size classes. Red maple comprised a smaller portion of seedlings (31%), and of pole sized stems (35%), and American beech was only present as large seedlings (7%).

3.3. *Absolute density of small seedlings*

Gaps, independent of fire, were the most important treatment influencing the absolute density of small seedlings of red maple and the red oak group (Fig. 2). Red maple small seedlings were 3.4-fold more abundant in canopy gaps (23,856 ± 4,970 stems ha^{-1}) compared to non-gaps (7,006 ± 1,820 stems ha^{-1}; $p = 0.014$; Fig. 2A). The absolute density of small seedlings in the red oak group was ~9-fold higher in gaps (6,719 ± 1,120 stems ha^{-1}) compared to non-gaps (743 ± 369 stems ha^{-1}, $p < 0.001$; Fig. 2B). In contrast to red maple and the red oak group, the absolute density of both white oak (9,116 ± 1,160 stems ha^{-1}) and chestnut oak (10,767 ± 1,560 stems ha^{-1}) small seedlings were statistically indistinguishable across all fire and gap treatment combinations.

3.4. *Absolute density of large seedlings*

Similar to small seedling regeneration, the absolute density of the red oak group ($p < 0.001$) and red maple ($p = 0.008$) large seedlings was higher in gaps compared to non-gaps, but within gaps, burn treatment also influenced the absolute density of large red maple seedlings ($p = 0.029$; Fig. 3). Inside canopy gaps, the red oak group large seedling density (1,686 ± 341 stems ha^{-1}) was 16 times higher than under a closed canopy (106 ± 106 stems ha^{-1}; Fig. 3B). Red maple large seedling density was 10 times higher in gaps (2,182 ± 546 stems ha^{-1}) than non-gaps (212 ± 148 stems ha^{-1}). Unburned and single fire treatments had higher red maple large seedling density (3,117 ± 713 stems ha^{-1}), compared to multiple fires, where red maple seedlings were absent from the regeneration pool (0 ± 0 stems ha^{-1}; Fig. 3A). As with small seedlings, the absolute densities of large white and chestnut oak seedlings were unaffected by burn and canopy gap treatments (white oak, 1,256 ± 321; chestnut oak, 1,030 ± 360 stems ha^{-1}).

3.5. *Absolute density of saplings*

Burn treatment had a strong effect on sapling regeneration for several species, independent of gap treatment (Fig. 4). The absolute density of red maple saplings was 5 times higher on sites with single fires (1,450 ± 592 stems ha^{-1}) compared with no fire or multiple burn treatments (279 ± 103; $p = 0.007$; Fig. 4A). The absolute density of red oak group saplings was higher in unburned areas (344 ± 64 stems ha^{-1}) compared to single and multiple fires (72 ± 25 stems ha^{-1}; $p = 0.002$; Fig. 4B). Similarly, the absolute density of American beech saplings was reduced by ~75% following single and multiple fires (31 ± 14 stems ha^{-1}) compared to unburned areas (119 ± 26 stems ha^{-1}; $p = 0.016$; Fig. 4C). The absolute densities of both white and chestnut oak saplings were unaffected by burn and gap treatment combinations (white oak, 127 ± 43; chestnut oak, 92 ± 35 stems ha^{-1}).

3.6. *Gap characteristics*

Canopy gap characteristics were similar across treatments and showed no obvious relationships to regeneration density. Gap canopy cover, size, age, and gap maker basal area did not differ between fire treatments (no fire, single fire, multiple fires, Table 3). Oak and red maple density did not have a significant relationship with any gap characteristic (all *p*-values > 0.05; no data shown).

4. Discussion

In the absence of fire and canopy disturbances, Bernheim stands were similar to other upland oak forests in the region (Arthur et al., 2015; Hutchinson et al., 2012b; Keyser et al., 2017; Schweitzer et al., 2016a,b). Oaks dominated the overstory, and small oak seedlings, especially white oak and chestnut oak, were abundant in the understory. However, red maple and American beech comprised a majority of the sapling and midstory trees. This trend indicates a bottleneck between the seedling and sapling phase (Abrams, 2003; Nowacki and Abrams, 2008), which suggests overstory oaks will likely be replaced by

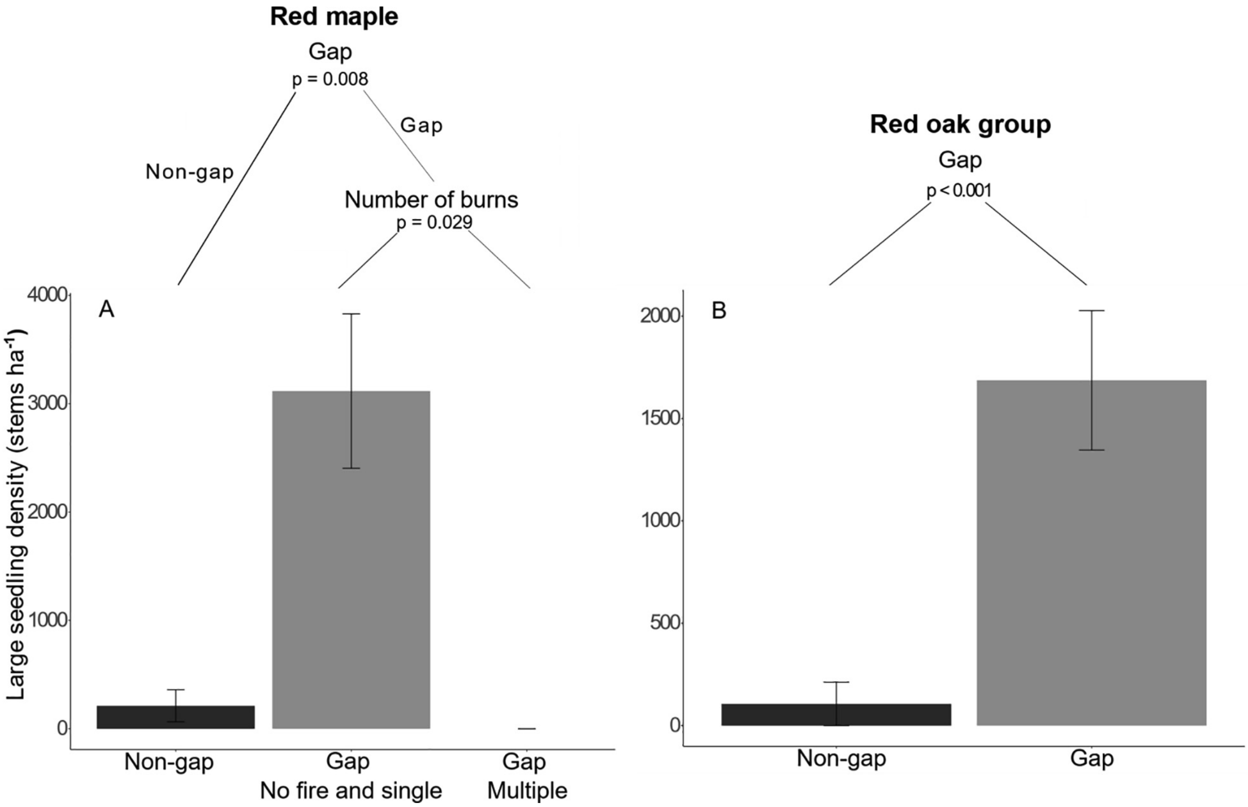

Fig. 3. Regression trees of red maple (A) and red oak group (B) large seedlings (> 0.5–1.0 m height) explaining absolute density (stems ha^{-1}) patterns between gap and burn treatments within Bernheim Arboretum and Research Forest, KY sampled in 2017. Note that density scales differ between species groups.

shade-tolerant species in the continued absence of canopy-opening disturbances and fire. Our findings suggest single and multiple fires reduced both absolute and relative density of American beech saplings and the red oak group of all sizes, but single fires, regardless of gap presence, increased red maple large seedling, sapling, and midstory dominance. Multiple fires, both within and outside of gaps, reduced red maple abundance, and coincided with increased relative density of white and chestnut, but not red oaks. Small and large seedling red oaks were the only oaks where absolute density increased in the small (~300 m^2), relatively old (20–30 yr), naturally-formed canopy gaps in this study.

For both small and large seedlings, canopy gaps had a higher absolute and relative density of red oaks and red maples than non-gaps. Although the majority (65%) of the gap area in our study was occluded by tree branches adjacent to the canopy opening, the small decline in canopy cover in gaps (91% canopy cover in non-gaps versus 87% canopy cover in gaps) likely contributed to increases in these species. Red oaks are relatively shade-intolerant and respond positively (increased growth and survival) to silvicultural treatments that decrease canopy cover, particularly as seedlings (Anning and McCarthy, 2013; Knapp et al., 2015). While red maples are more shade-tolerant than oaks, red maple seedling survival increases with increased light availability when moisture is not limiting, after canopy gap formation (Hutchinson et al., 2016). For red oaks and red maple, canopy gaps were the most important factor determining small and large seedling density, but prescribed fire treatments also played a significant role in red maple large seedling density.

Multiple prescribed fires reduced the relative density of red maple large seedlings, and the absolute density of red maple large seedlings decreased within canopy gaps after multiple fires. Red maple large seedling density was zero on sites that were treated with two or three fires, which may be due to red maple resource allocation. Red maples allocate resources to leaf area and shoot elongation, whereas upland oaks tend to allocate more resources to belowground structures (Canham et al., 1999; Dillaway et al., 2007; Wang et al., 2005). Because resources are allocated to aboveground structures, root storage and resprouting ability are depleted with increased number of fires, which results in decreased survival (Kruger and Reich, 1997). Other studies in the central and eastern U.S. have also documented a similar decrease in red maple density after multiple fires (Fan et al., 2012; Hutchinson et al., 2012a; Kruger and Reich, 1997). In our plots, multiple fires eliminated red maple large seedlings, leading the relative density of all oak species to increase. Thus, the use of multiple fires could be a practical technique to reduce the absolute and relative density of large red maple seedlings, potentially releasing oaks from competition.

While the presence of a gap appeared to influence the absolute density of small and large seedlings of red oaks and red maple, gap characteristics (canopy cover, size, age, and gap maker basal area) were not significant predictors of absolute density, likely because these characteristics showed little variation across the gaps or because we failed to measure the gap attribute(s) that most impacts density. In our study, canopy gaps were relatively small (~300 m^2) with high canopy cover (~87%) and little variation in size or canopy cover between gaps, possibly because of the age of the gaps (20–30 yr. old). Lateral branch extension increases with gap age and occurs when overstory trees adjacent to the gap expand their lateral branches into the newly-available growing space, thereby decreasing understory light within the gap (Runkle, 1981; Yamamoto, 2000). Across burn treatments, a majority (65%) of the total gap area was occluded by tree branches adjacent to the canopy opening (expanded gap area) and may have led to substantial decreases in understory light. As such, there was likely little differentiation between light regimes and/or growing conditions to lead to pronounced differences in regeneration density across our gaps. If our gaps were more variable in their conditions, we may have been able to detect a relationship between gap characteristics and tree regeneration density. It is likely that gap characteristics would be better

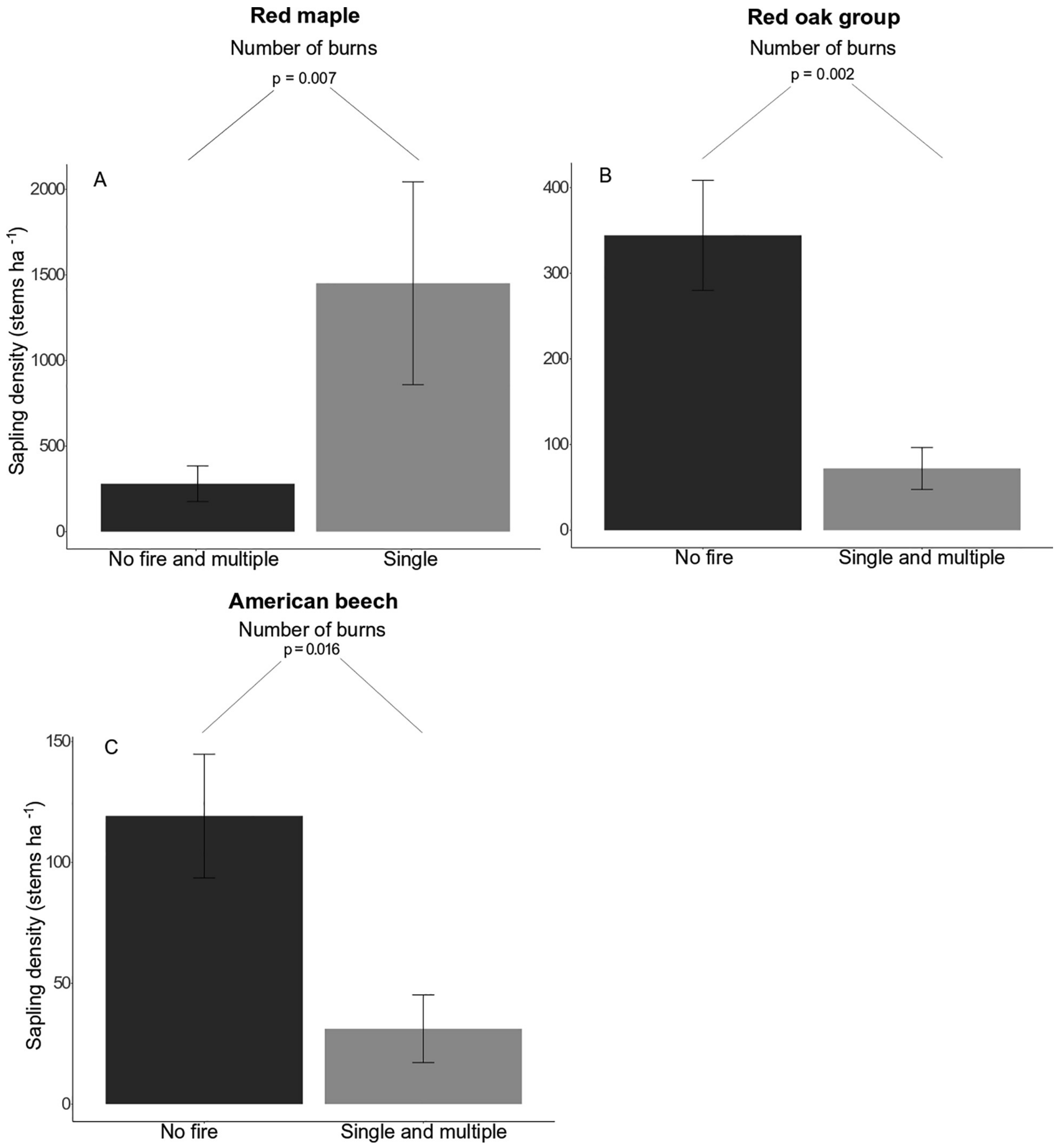

Fig. 4. Regression trees of red maple (A), red oak group (B), and American beech (C) saplings (1.1–4.0 m height) explaining absolute density (stems ha^{-1}) patterns between burn treatments within Bernheim Arboretum and Research Forest, KY sampled in 2017. Note that density scales differ between species groups.

predictors of regeneration density if they were measured soon after gap formation, rather than 20–30 years later, as this is when conditions would have been most different from the intact forest and most representative of the conditions at the time of regeneration establishment. Alternatively, we may have failed to measure the gap characteristics that predict regeneration density, such as location within the gap or soil moisture. For example, in central and eastern temperate forests like those studied here, most light within canopy gaps is concentrated at the center and northern edge of the gap, which can influence seedling and sapling density (Canham et al., 1989; Greenler and Saunders, 2019). Several studies also noted that differences in gap soil moisture can impact oak regeneration density (Hutchinson et al., 2012a; Iverson et al., 2008, 2017). While the presence of canopy gaps clearly influenced tree regeneration density, the gap characteristics we measured, which exhibited little variation across our gaps, did not predict absolute density.

Prescribed fire treatments had a strong effect on both the absolute and relative density of red maple saplings at each plot. Red maple sapling absolute and relative density was highest after single fires compared with unburned areas and areas with multiple fires. Elsewhere in the region, single prescribed fire treatments also led to increased red maple sapling density (Elliott and Vose, 2010; Van Sambeek et al., 2002; Vander Yacht et al., 2017). Most prescribed fires in the region are conducted during the dormant season and tend to be low severity because of high litter moisture and relatively low fuel loads (Brose, 2010). These low severity fires can increase the likelihood of post-fire

Table 3
Mean (± SE) gap canopy cover, size, age, and gap maker basal area (BA) in non-gap and gap areas in unburned, single burn, and multiple burn (2–3 times) treatments within Bernheim Arboretum and Research Forest, KY sampled in 2017.

	Characteristic	Treatment		
		Unburned	Single burn	Multiple burn
Non-gap	Canopy Cover (%)	92.6 (0.4)	91.3 (0.5)	90.3 (0.6)
Gap	Canopy Cover (%)	85.3 (2.5)	87.3 (2.3)	85.1 (2.5)
	Gap maker BA (m^2/ha)	1.1 (0.1)	0.92 (0.1)	1.26 (0.2)
	Oak gap maker BA (%)	96 (1.0)	100 (0.0)	95 (2.0)
	Size (m^2)	303.4 (23.1)	298.9 (49.0)	300.5 (22.5)
	True gap (m^2)	83.5 (13.1)	64.4 (24.3)	86.2 (13.0)
	Expanded gap (m^2)	186.4 (12.2)	145.5 (19.8)	168.2 (14.2)
	True: Expanded area ratio	0.5 (0.1)	0.4 (0.1)	0.5 (0.1)
	Age (year)	29.0 (3.1)	19.7 (4.8)	22.4 (2.3)

resprouting because fire may top-kill seedlings and saplings, but does not necessarily remove the epigeal bud (Hutchinson et al., 2005; Waldrop et al., 2008), leading to increased red maple sapling density after single fires. In our study area, many red maple resprouts were located at the base of top-killed trees 10–30 cm DBH (where we counted one stem per bunch) and these resprouts were tall (1.5–4 m in height), suggesting a response to ample belowground resources necessary for resprouting four years after a single fire. In contrast to single fires, multiple fires reduced the relative density of red maple saplings. Again, this is likely because red maple allocates resources to aboveground structures, expending root stores and decreasing resprout ability after multiple fires, which in turn decreases survival. Our results suggest that single fires increase red maple sapling absolute and relative density, which is likely detrimental to upland oak saplings in a critical life-stage for oak canopy accession, and that multiple fires are likely an effective management technique to decrease red maple sapling abundance.

Even though oaks are generally fire-tolerant (Burns et al., 1990; Johnson et al., 2009), the absolute and relative density of saplings in the red oak group decreased in response to both single and multiple prescribed fire treatments with the exception of the non-gap multiple fire treatment where relative density increased slightly (3%). This trend may be related to the relationship between time since fire and oak resprout post top-kill. Oaks generally survive prescribed fires when they reach sufficient size ($>$ 1.3 cm basal diameter). In order for oaks to reach that size, a fire-free period of 10–30 years is commonly necessary (Brose et al., 2013; Dey, 2014). If the fire-free period is too short ($<$ 10 years in our study area), then oaks are rarely able to ascend to the sapling/midstory size classes, and instead remain in the seedling size class between fires (Schweitzer et al., 2016a,b). Other research in the region reports similar findings to our study where red oak group sapling density decreased after single and multiple fires (Anning and McCarthy, 2013; Miller et al., 2017), and suggests that sufficient time after fire is important for successful regeneration of saplings in the red oak group.

Single and multiple fires reduced the absolute and relative density of American beech saplings. American beech has relatively thin bark, which can be vulnerable to cambial damage during fire and can lead to post-fire mortality (Bova and Dickinson, 2005). Also, American beech typically resprouts only from relatively small trees ($<$ 10 cm DBH) and sprouts generally do not attain tree structure (Burns et al., 1990). American beech does develop large quantities of root sprouts when injured, but root sprout survival is limited when the stem is removed (Burns et al., 1990). Most American beech saplings in our study area were $>$ 10 cm DBH and were likely too large to produce resprouts following prescribed fire. Red maples also have relatively thin bark, which can lead to post-fire mortality (Babl et al., 2020; Bova and Dickinson, 2005), but are able to resprout from much larger trees ($\sim$30 cm DBH) than American beech (Burns et al., 1990). After single fires, red maple often increase in density when the epigeal bud is not removed by fire (Hutchinson et al., 2005; Albrecht and McCarthy, 2006). If the reduction of American beech saplings is a primary goal, our results suggest that prescribed fire could be an effective management technique.

While most species of interest were impacted by natural canopy gaps and/or prescribed fire, neither treatment influenced absolute white or chestnut oak density in any size class. However, multiple fires increased their relative densities in small/large seedling and sapling size classes. White and chestnut oak absolute densities were likely unchanged due to the physiological and morphological adaptations of species from the white oak group. In contrast to more shade-intolerant red oaks, white oak species can persist in the understory for long periods of time as seedlings ($>$ 90 years; Rentch et al., 2003). As a result, when light availability increases due to canopy gap formation or by removal of competing species with prescribed fire, white oaks are often unable to immediately respond to disturbance because their resources are depleted following these long periods in relatively low-light conditions. It's likely that in our study area, the white oak group individuals in the understory were resource limited after survival in the understory for several decades, and unable to respond to the increased growing space following treatments. Even though prescribed fire and canopy gaps did not directly affect the absolute density of the white oak group, the relative abundance of white and chestnut oak increased in most size classes following multiple fires. Multiple fires likely depleted red maple belowground resources, decreased their survival, and increased the white oak group relative density. Thus, if the objective is to maintain white oaks on the landscape, successful management practices should include multiple fires and canopy opening disturbances that perpetuate increased light for longer periods of time (10–30 yr).

We expected that multiple prescribed fires combined with naturally-formed canopy gaps would be most effective at increasing oak seedling and sapling absolute density by removing competition and increasing understory light. In our study, the 'multiple' prescribed fires category included areas with variable time after fire and number of fires (2–3). Variable time after fire likely contributed to different seedling and sapling size class distributions that had no clear effect on absolute oak density. That said, previous research demonstrated that two and three prescribed fires combined with canopy gaps can increase oak absolute density more than multiple prescribed fires alone (Hutchinson et al., 2012a; Iverson et al., 2008, 2017). Our results differ from these studies because our gaps had higher canopy cover and a longer length of time between gap formation and implementation of prescribed fires. For example, in Ohio, Iverson et al. (2017) reported increased oak sapling density when canopy cover was $\sim$70% in gaps burned repeatedly (3–5 times). Within Bernheim, canopy cover in gaps with multiple fires was much higher ($\sim$85%). Additionally, some research suggests that in order for canopy gaps and prescribed fires to increase oak absolute density, prescribed fires must occur several years (4–7) prior to gap formation (Brose and Van Lear, 1998; Hutchinson et al., 2012a). If prescribed fire is implemented prior to canopy gap formation, and reduces density of competing species, oak survival may increase with additional light available upon gap creation. In our stands, canopy gap formation often occurred well before prescribed fire implementation ($>$ 20 yr). Our findings further emphasize the importance of light availability in gaps and the sequence of prescribed fires and gap formation to increase the absolute density of oak species.

5. Conclusions

This study provided a unique opportunity to investigate how single and repeated prescribed fires interact with naturally-occurring canopy gaps to influence regeneration in upland oak forests. Many upland oak forests in the central and eastern U.S. are second-growth and are experiencing increased canopy gap formation as stands age. Prescribed fire is a commonly used tool among managers in this region to manipulate forest composition and midstory structure to promote oak regeneration. As such, gap formation along with fire disturbances could be important processes contributing to future stand dynamics in this region. Our findings suggest natural canopy gap formation influences seedling regeneration demographics, and the number of fires is an important factor for sapling regeneration density in upland oak forests. Regardless of canopy gap presence, single and multiple fires decreased red oak group and American beech sapling density, and single fires often increased red maple sapling density because of prolific resprouting from the base of top-killed trees. Although canopy gaps increased red oak group seedling density, the addition of a naturally-formed canopy gap into the disturbance regime did not increase red oak group sapling or white oak species absolute density in any size class. This is likely because the naturally-formed gaps in this study were too small (~300 m^2) to have an impact on the light environment (canopy cover remained > 87%), or because they occurred too many years (> 20 years) prior to fire treatment. Even though the treatments in our study did not increase absolute oak density, multiple fires often increased the relative density of the white oak group by reducing red maple abundance. This suggests management techniques that include larger canopy gaps created by silvicultural treatments (mechanical or chemical) and additional prescribed fires conducted several years following the initial burn will likely be necessary to reduce competition density and create open canopies sufficient to improve upland oak regeneration in the region.

6. Availability of data and materials

The data sets used and analyzed during the current study are available from the corresponding author upon request.

CRediT authorship contribution statement

Brian J. Izbicki: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing - original draft. **Heather D. Alexander:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing - review & editing. **Alison K. Paulson:** Data curation, Formal analysis, Software, Validation, Visualization, Writing - review & editing. **Brent R. Frey:** Writing - review & editing. **Ryan W. McEwan:** Writing - review & editing. **Andrew I. Berry:** Resources, Writing - review & editing.

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