

Restoration of low-intensity fire in *Quercus-Pinus* mixedwoods following a prolonged period of fire exclusion

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Abstract

Low-intensity surface fire is required to restore and maintain *Quercus-Pinus* mixedwood composition, structure, and function. However, historical fire exclusion has resulted in altered vegetation-fuel-fire feedbacks in long-unburned mixedwoods. Fire is now being reintroduced to reduce fire-intolerant understory and midstory stem density, consume excessive litter accumulation, eradicate the duff layer, and achieve various other goals; however, the consequences of restoring fire are poorly understood. The goal of this study was to quantify the effects of fire reintroduction on intra-stand *Pinus echinata* neighborhoods in a mixed *Quercus-P. echinata* stand following an extended period of fire exclusion. We report results from a 3-year sampling of the effects of one dormant season and one early growing season fire on woody plant dynamics, understory light, fuel conditions, and *P. echinata* basal duff-ring accumulation. The sapling assemblage was unaffected by one fire, but the second fire resulted in shoot mortality across all taxa. Understory light availability was unchanged after two fires, and litter depth was significantly reduced after the first and second fire. We found that fire seasonality was likely more important than fuel conditions to achieve desired fire effects. Our results indicated that continued fire and midstory treatment will be required to regenerate *P. echinata*.

Key words: shortleaf pine, fuels, regeneration, neighborhoods, understory light

Introduction

Increased interest in restoring low-intensity surface fire to enhance desired forest composition, structure, and function has led to the initiation of prescribed fire programs in fire-adapted forests that have experienced extended periods of fire exclusion (Gordon et al. 2020). Long fire-free periods alter vegetation-fuel-fire feedbacks, which may result in unknown fire behavior and undesirable ecological effects upon the reintroduction of fire. For example, enhanced litter and duff accumulation around the base of mature canopy trees may allow for long periods of smoldering and results in delayed tree mortality (Varner et al. 2009; Robbins et al. 2022). In some long fire-excluded forests, fire-intolerant taxa have increased in dominance resulting in a state change through a process known as mesophication, and therefore require deliberate management intervention to alter this successional trajectory (Nowacki and Abrams 2008).

The consequences of fire exclusion may be particularly exacerbated in *Quercus-Pinus echinata* mixedwood ecosystems of the southeastern USA because fire is a strong control on successional processes (Elliott and Vose 2005). In contemporary mixed *Quercus-P. echinata* stands in which the disturbance

regime has been altered, *P. echinata* is experiencing regeneration failure that can partially be attributed to fire exclusion practices that result in increased density of competing trees, low light levels in the understory, and increased litter depth (Ojha et al. 2019). In addition, there is growing concern about the loss of genetic material of the legacy *P. echinata* trees. The age of these individuals and the accumulated duff that surround the boles of these trees make them susceptible to mortality (Swezy and Agee 1991; O'Brien et al. 2010). Although *Quercus-Pinus* mixedwoods are increasingly desired by managers, we currently lack understanding of the precise use of prescribed fire to create and maintain desired species assemblages, specifically in response to altered vegetation-fuel-fire feedback and contemporary regulatory constraints to prescribed fire implementation. Thus, scientifically informed silvicultural prescriptions are needed to restore viable mixedwoods from initially novel stand composition and structure resulting from decades of fire exclusion.

Fire severity and effects may be spatially variable (i.e., patchy), which is often driven by the spatial heterogeneity of fuel loading and composition (Keane et al. 2012), microtopographic effects (Franklin et al. 1997), woody plant community

composition (Whelan et al. 2021), fire weather (Peterson and Reich 2001) and ignition patterns, among other factors. In long-unburned stands, (e.g., those that have not burned since adoption of fire exclusion policies; McEwan et al. 2007), these factors may be exacerbated by enhanced litter accumulation, duff layer formation, increased fuel moisture, and the increase in fire-impeding fuels from fire-sensitive taxa. Fire severity may range from patches of low severity fire where primarily understory and smaller midstory vegetation are affected to high severity patches of overstory mortality. In mixedwood stands, variation in severity may be attributed to differences in fire sensitivity among the dominant tree species and variations in fire behavior resulting from litter flammability differences among the species. To understand these relationships between fire and vegetation in mixedwood ecosystems, it is necessary to quantify the stand-scale impacts of fire and quantify the drivers of variability in fire severity at intra-stand scales in a holistic multi-scale approach.

Our study seeks to fill a gap in the prescribed fire literature on the variable spatiotemporal effects of reintroducing operational-scale low-intensity surface fire on woody plant assemblages and abiotic conditions in a mixed *Quercus-P. echinata* stand. Our specific objectives were to (1) document prescribed fire influence on woody plant assemblages in multiple vertical strata, (2) investigate prescribed fire impacts on abiotic conditions, and (3) quantify the patterns and drivers of variability in fire severity through space and time. We report results from a 3-year sampling of the effects of two prescribed fires in a mature, mixed *Quercus-P. echinata* stand. Our findings provide information to forest managers who intend to reintroduce fire to restore and perpetuate desired stand structure, composition, and function of *Quercus-P. echinata* ecosystems.

Methods

Study site and characteristics of two fires

Our study occurred in a complex-stage, *Quercus-P. echinata* mixedwood stand in Savage Gulf State Natural Area (SGNA) in Tennessee, USA. The SGNA is located on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938), characterized by extensive plateau remnants not yet maturely incised, situated between deep valleys. The prescribed fire program was implemented in stands on the weakly dissected plateau landtype association of the true plateau subregion (Smalley 1986), distinguished by broad undulating-to-rolling ridges and gentle-to-moderately steep-sided slopes dissected by young valleys. Soils are moderately to very deep and well-drained, and derived from sandstone, shale, siltstone, or quartzite, with loam, silt loam, and sandy loam textures (USDA NRCS 2022). The regional climate is humid mesothermal, characterized by long, moderately hot summers and short, mild winters (Thorntwaite 1948). Mean annual temperature is 13.3 °C, with the lowest monthly mean temperature of 2.3 °C in January and the highest monthly mean temperature of 23.4 °C in July (PRISM 2022). Mean monthly precipitation is 1602 mm with no wet or dry season. Forest com-

munity composition on the tablelands of the Cumberland Plateau is influenced by fine-scale topography, soil moisture content, and canopy disturbance history (Smalley 1986; Hart et al. 2012). Contemporary stand composition is dominated by *Quercus alba* (46% basal area), *P. echinata* (17% basal area), and *Acer rubrum* (16% basal area).

The Tennessee Department of Environment and Conservation implemented a prescribed fire program at SGNA in 2020. Although we were unable to implement an experimental design with replicated treatments, we support the value of monitoring fire effects at operational scales, as prescribed fire research is currently less developed than wildfire research (Hiers et al. 2020). The burn unit is 415 ha, with 48% of the unit classified as flat (<5% grade), 48% as gently sloped (5–20% grade), and 4% steeply sloped (>20% grade). The desired outcomes stated in the burn plan were to reduce litter and duff loading and top-kill 50%–60% of fire-intolerant stems in the regeneration layer and >30% of midstory stems (Murray Gheesling; TDEC SGNA Burn Plan 2020). The first prescribed fire occurred on 11 December 2020. Fire weather conditions were ca. 40% relative humidity, 10 kph winds from the west, a 4-day precipitation-free period, and Keetch-Byram Drought Severity Index (KBDI) of 4. The second prescribed fire occurred on 20 April 2022. Weather conditions were recorded at discreet times (CDT) during the second fire; 1115: temp. 18 °C, 40% RH, wind SE at 10 kph; 1200: temp. 20 °C, RH 27%–30%, wind SE at 10 kph; 1300 temp 18–21 °C, RH 24%–29%, wind S at 11 kph; 1430, temp 21 °C, RH 25%–27%, wind S at 8 kph. KBDI on the date of the second fire was 43. Both fires were ignited by a hand crew from the northeast corner and backed south into the stand from the service road (Murray Gheesling, TDEC; personal communication).

Field methods

We installed 25 permanent 0.04 ha fixed-radius plots in *P. echinata* dominated neighborhoods to sample biotic and abiotic responses to prescribed fire (Goode et al. 2021). Our sampling plots were subjectively installed in these distinct *P. echinata* neighborhoods based on greater litter accumulation that was visually evident and to monitor fire effects on *P. echinata* regeneration in these neighborhoods. To select suitable locations for sampling, we walked transects based on azimuths selected at random through the burn unit until we reached a *P. echinata* neighborhood (defined here as sampling plot that contained at least four *P. echinata* > 30 cm dbh). This process was continued until 25 neighborhoods were sampled. We report results in this study from three discreet sampling periods, all of which occurred in July in the years 2020 (before the first fire), 2021 (after the first fire), and 2022 (after the second fire).

To quantify fire effects on woody plant assemblages, we sampled trees (live woody stems \geq 5 cm dbh), saplings (live woody stems < 5 cm dbh, \geq 1 m height), and seedlings (live woody stems < 1 m height). Each tree was identified to species and measured for dbh. Saplings and seedlings were identified to the species level and tallied for abundance. Seedlings were sampled in nested 0.002 ha subplots (20 m²) located at the center of each 0.04 ha plot. Coarse woody debris (CWD; dead standing or downed woody material \geq 10 cm diameter) was

measured and identified to the lowest taxonomic level possible. Trees and CWD were sampled only before the first fire.

To quantify fire effects on abiotic conditions, we sampled litter depth, basal duff-ring depth and length, understory light availability, and ground cover dynamics. Litter depth was measured with a ruler to the nearest mm at nine locations on each plot, twice in each cardinal direction and once at plot center. Basal duff rings were defined as the enhanced accumulation of litter at the base of mature *P. echinata* in the absence of fire. Duff-ring depth and length were assessed (to the nearest cm) at the base of each *P. echinata* ≥ 20 cm dbh. Duff-ring length was measured to the point when the accumulated duff around the base of the tree was no longer visually discernable from the mean plot-level litter depth. We captured hemispherical photographs at 1 m height at plot center with a digital camera fitted with a 180° field of view fisheye lens, mounted on a self-leveling tripod, and calibrated with WinsCANOPY software (WinSCANOPY, Regent Instruments, Quebec City, Quebec, Canada) to quantify canopy gap fraction. To quantify ground cover dynamics, we visually estimated the %cover of herbaceous plants, woody plants, hardwood litter, *Pinus* litter, and bare ground on the entire plot to the nearest 5%. As a proxy for fire severity, we measured maximum bole scorch height (m) and estimated scorch percent (estimated based on a 1 m height cylinder on the bole) on each *P. echinata* ≥ 20 cm after the first and the second fire.

Analytical methods

We calculated standard descriptors of dominance (basal area; $\text{m}^2 \cdot \text{ha}^{-1}$) and relative dominance, density (stems $\cdot \text{ha}^{-1}$) and relative density, and importance (mean of relative dominance and relative density) for trees; density and relative density for saplings and seedlings; and Shannon diversity and species richness for trees, saplings, and seedlings. To test for significant differences in mean scorch height and scorch percent between the first and second fire, we used a non-parametric Mann–Whitney *U* test. We tested for significant differences pre-fire, after first fire, and after second fire between mean duff-ring depth, duff-ring length, plot litter depth, and gap fraction (abiotic response variables); and mean sapling density and seedling density (biotic response variables) with repeated measures ANOVAs. Significant differences were further assessed with Tukey HSD post-hoc pairwise comparisons. Prior to analyses, normality and homoscedasticity were assessed with Shapiro–Wilkes and Levene’s test of homogeneity of variances.

To test for significant differences in mean plot-level sapling and seedling density by functional group and sampling interval, we used repeated-measure mixed Analysis of variance (ANOVA) with taxonomic group (*A. rubrum*/*Oxydendrum arboreum*/*Nyssa sylvatica*, *Quercus*/*Carya*, and other spp.) as the between-group factors and time (pre-fire, once burned, twice burned) as the within-group factors (3×3 mixed ANOVAs). We used the same method described above to test for significant differences in ground cover classes with *Pinus* litter/hardwood litter and woody plant cover/herbaceous plant cover as between-group factors and time as within-group factors (2×3 mixed ANOVAs). If significant interaction effects

were found, post-hoc pairwise comparisons were not considered. A total of four independent, repeated-measure mixed ANOVAs were conducted.

To visualize and assess woody plant community dynamics with time since fire, we used non-metric multidimensional scaling (NMS) in PC-ORD v. 7 (McCune and Mefford 2011). Treatments were defined as pre-fire, once burned, and twice burned, with 25 plots per treatment. We conducted two separate ordination analyses, the first with seedling density data and the second with sapling density data. Ordinated woody plant assemblages were graphically assessed and statistically quantified in relation to six environmental variables: (1) bare ground cover, (2) hardwood litter cover, (3) *Pinus* litter cover, (4) CWD volume, (5) mean litter depth, and (6) gap fraction. Both NMS ordination analyses used relative Sorenson distance, were permuted 250 times with real data, and cross-checked for agreement with other solutions. A biplot overlay was added to the graphed ordinations to visualize correlation between ordination axes and environmental variables. A r^2 cutoff of 0.25 was used. To statistically confirm visual difference in woody plant assemblages by treatment, a multi-response permutation procedure (MRPP) with relative Sorenson distance and post-hoc pairwise comparison was conducted (Mielke and Berry 2001).

We used maximum bole scorch height as a proxy for fire severity. Bole scorch height was recorded after the first and second fires, but we used maximum bole scorch height recorded on trees after the second fire as the dependent variable in our modelling approach. For our model, scorch height was binned into five relative severity classes: none ($n = 18$; 0 m), low ($n = 28$; ≤ 25 cm), medium ($n = 26$; 30–60 cm), high ($n = 24$; 65–135 cm), and very high ($n = 25$; > 135 cm). To infer the drivers of variability in fire severity, we fit a multinomial logistic regression model. We used a z-score standardization of the independent variables so that the effect sizes of predictors could be directly compared. Overall model performance was assessed based on the likelihood ratio chi-squared test and measures of the areas under the receiver operator characteristic (AUROC) curves. The statistical significance of the effect of each predictor also was quantified by the likelihood-ratio chi-squared test statistic, where the null hypothesis was that the effect size was 0 for a given parameter. We selected the “none” severity category as the reference category from which to compare the low, medium, high, and very high logits. For the microscale topography predictor variable, we calculated plot-level microscale topography with the curvature tool in the Spatial Analysis toolbox in ArcGIS pro from a publicly available digital elevation model derived from LiDAR point cloud data contracted by the Tennessee State Government. Plot aspect was transformed according to Beers et al. (1966).

Results

Fire effects on woody plant assemblages

In the tree layer, *P. echinata* represented 48% of total basal area (Table 1), followed by *O. arboreum* and *A. rubrum*. However, *O. arboreum* and *A. rubrum* had the greatest stem density

Table 1. Density (stems·ha⁻¹), relative density (%), dominance (basal area; m²·ha⁻¹), relative dominance (%), and importance (average of relative dominance and importance) for all woody stems ≥5 cm dbh prior to restoring low-intensity fire in a *Quercus-Pinus echinata* mixedwood in Tennessee, USA.

Species	Density (stems·ha ⁻¹)	Relative density	Dominance (m ² ·ha ⁻¹)	Relative dominance	Importance
<i>Pinus echinata</i> Mill.	131	13.9	17.9	48.2	31.0
<i>Oxydendrum arboreum</i> (L.) DC.	349	37.1	4.7	12.6	24.8
<i>Acer rubrum</i> L.	245	26.0	4.5	12.2	19.1
<i>Quercus alba</i> L.	42	4.5	3.2	8.6	6.5
<i>Nyssa sylvatica</i> Marshall	73	7.8	0.3	0.9	4.3
<i>Quercus coccinea</i> Münchh.	14	1.5	2.4	6.4	4.0
<i>Pinus virginiana</i> Mill.	24	2.6	1.1	3.0	2.8
<i>Quercus velutina</i> Lam.	14	1.5	1.1	2.9	2.2
<i>Carex tomentosa</i> L.	12	1.3	0.6	1.5	1.4
<i>Liriodendron tulipifera</i> L.	3	0.3	0.6	1.7	1.0
<i>Quercus stellata</i> Wangenh.	7	0.7	0.4	1.2	1.0
<i>Sassafras albidum</i> (Nutt.) Nees	9	1.0	0.1	0.3	0.6
<i>Ilex opaca</i> Aiton	6	0.6	0.0	0.0	0.3
<i>Quercus falcata</i> Michx.	2	0.2	0.1	0.3	0.3
<i>Carya pallida</i> (Ashe) Engl. & Graebn.	3	0.3	0.0	0.1	0.2
<i>Cornus florida</i> L.	3	0.3	0.0	0.0	0.2
<i>Fagus grandifolia</i> Ehrh.	2	0.2	0.0	0.0	0.1
<i>Liquidambar styraciflua</i> L.	1	0.1	0.0	0.1	0.1
<i>Diospyros virginiana</i> L.	1	0.1	0.0	0.0	0.1
TOTALS	941	100	37.26	100	100

Note: Species are ranked by importance.

in the tree layer. *Quercus* spp. represented 20% of total tree basal area ha⁻¹ and 8% of total stem density ha⁻¹. Tree layer species richness was 19 and Shannon diversity was 1.55. Pre-fire sapling richness was 23 and Shannon diversity was 1.19. After the first fire, sapling richness and diversity decreased to 19 and 1.10, respectively. Sapling richness and diversity experienced a more pronounced decrease after the second fire, with a recorded species richness of 9 and Shannon diversity of 0.67. Pre-fire seedling richness was 26 and Shannon diversity was 1.43. Seedling richness and diversity were reduced to 18 and 1.51 after the first fire, respectively, but increased near pre-fire levels after the second fire to a species richness of 20 and diversity of 1.47.

Sapling density marginally declined after the first fire (Table 2). The subsequent fire resulted in pronounced sapling mortality. Notably, *A. rubrum* experienced significant shoot mortality after the second fire. Generally, *Quercus* sapling density increased after the first fire but decreased to a lower density than the pre-fire density after the second fire. However, the second fire effectively top-killed *A. rubrum* and *O. arboreum* and increased the relative density of *Quercus* and other hardwood saplings. The NMS ordination visually and statistically revealed that prescribed fire altered sapling community composition (Fig. 1). Variability and ordination distance increased from pre-burn to once burned and once burned to twice burned (Fig. 1). Bare ground cover (%) was correlated with the positive range of axis one ($r = 0.49$), and litter depth ($r = -0.40$) and hardwood litter cover ($r = -0.48$) were correlated with the negative range of axis one. The MRPP results statistically confirmed the significant

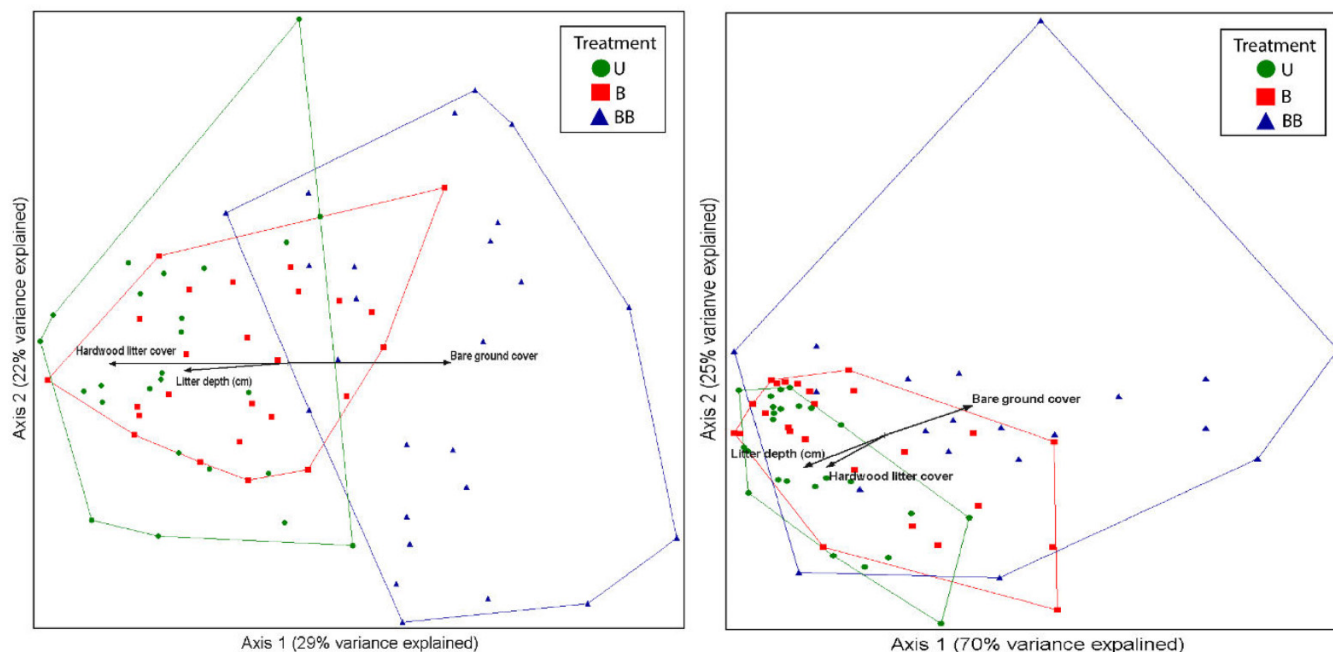
difference in sapling assemblages by treatment ($p < 0.001$). Once burned sapling assemblages were not significantly different from unburned sapling assemblages ($p = 0.14$), but unburned and twice burned ($p < 0.01$) and once burned and twice burned ($p < 0.01$) sapling assemblages were significantly different.

Total seedling density declined with additional fires (Table 2). *Acer rubrum* seedling density decreased with additional fires and *Vaccinium arboreum* seedling density increased with additional fires. We also noted a decrease of *P. echinata* seedling density with additional fire. Notably, no *P. echinata* seedlings were documented in our plots after the second fire. We also documented an initial decrease in *Liriodendron tulipifera* seedlings density after one fire, but a remarkable increase in density after the second fire. The NMS ordination visually and statistically revealed that prescribed fire altered seedling community composition (Fig. 1). Community variability decreased from the unburned to once burned treatment and increased from once burned to twice burned (Fig. 1). The seedling assemblages in unburned plots generally occurred on the negative range of axis one, the once burned treatment occurred on the midrange of axis 2, and the twice burned treatment occurred on the positive range of axis two. Bare ground cover (%) was correlated with the positive range of axis one ($r = 0.72$) and litter depth ($r = -0.57$) and hardwood litter cover ($r = -0.75$) were correlated with the negative range of axis one. The MRPP results statistically confirmed the significant difference in seedling assemblages by treatment ($p < 0.001$), and all treatments were significantly different from one another ($p < 0.001$).

Table 2. Density (stems·ha⁻¹) and relative density (%) of seedlings (woody plants <1 m height) and saplings (woody plants ≥1 m height; <5 cm dbh) before fire (unburned), after one fire (burned), and after two fires (twice burned) in a *Quercus-Pinus echinata* mixedwood in Tennessee, USA.

	Seedlings						Saplings					
	Unburned	Relative density	Burned	Relative density	Twice burned	Relative density	Unburned	Relative density	Once burned	Relative density	Twice burned	Relative density
<i>Acer rubrum</i> L.	66960	52.94	54640	56.89	17480	26.05	1302	66.06	1090	67.79	104	51.74
<i>Vaccinium arboreum</i> Marshall	12620	9.98	19900	20.72	21740	32.40	16	0.81	55	3.42	–	–
<i>Quercus alba</i> L.	11580	9.16	8320	8.66	6640	9.90	107	5.43	76	4.73	2	1.00
<i>Quercus velutina</i> Lam.	6200	4.90	3060	3.19	2940	4.38	144	7.31	104	6.47	1	0.50
<i>Oxydendrum arboreum</i> (L.) DC.	240	0.19	860	0.90	740	1.10	153	7.76	111	6.90	17	8.46
<i>Vaccinium stamineum</i> L.	7320	5.79	340	0.35	960	1.43	76	3.86	3	0.19	3	1.49
<i>Vaccinium elliotii</i> Chapm.	5820	4.60	–	–	40	0.06	–	–	–	–	–	–
<i>Quercus coccinea</i> Münchh.	4960	3.92	4820	5.02	2320	3.46	10	0.51	5	0.31	–	–
<i>Nyssa sylvatica</i> Marshall	1340	1.06	1380	1.44	960	1.43	72	3.65	99	6.16	56	27.86
<i>Sassafras albidum</i> (Nutt.) Nees	3120	2.47	500	0.52	2060	3.07	9	0.46	3	0.19	–	–
<i>Liriodendron tulipifera</i> L.	2520	1.99	1520	1.58	9920	14.78	1	0.05	1	0.06	–	–
<i>Ilex opaca</i> Aiton	340	0.27	220	0.23	140	0.21	39	1.98	40	2.49	15	7.46
<i>Ilex montana</i> Torr. & A. Gray ex A. Gray	1300	1.03	–	–	20	0.03	5	0.25	1	0.06	–	–
<i>Cornus florida</i> L.	560	0.44	–	–	–	–	14	0.71	5	0.31	–	–
<i>Fagus grandifolia</i> Ehrh.	–	0.00	–	–	–	–	8	0.41	7	0.44	1	0.50
<i>Carya tomentosa</i> L.	400	0.32	220	0.23	200	0.30	6	0.30	3	0.19	2	1.00
<i>Rhododendron periclymenoides</i> (Michx.) Shinnars	300	0.24	60	0.06	–	–	1	0.05	–	–	–	–
<i>Pinus echinata</i> Mill.	260	0.21	80	0.08	–	–	–	–	–	–	–	–
<i>Prunus serotina</i> Ehrh.	240	0.19	–	–	500	0.75	–	–	1	0.06	–	–
<i>Castanea dentata</i> (Marshall) Borkh.	60	0.05	20	0.02	–	–	3	0.15	3	0.19	–	–
<i>Amelanchier arborea</i> (Michx. f.) Fernald	100	0.08	–	–	–	–	2	0.10	–	–	–	–
<i>Quercus falcata</i> Michx.	120	0.09	80	0.08	120	0.18	–	–	–	–	–	–
<i>Viburnum acerifolium</i> L.	80	0.06	–	–	–	–	1	0.05	–	–	–	–
<i>Viburnum nudum</i> L.	20	0.02	–	–	20	0.03	1	0.05	–	–	–	–
<i>Carya pallida</i> (Ashe) Engl. & Graebn.	–	–	–	–	120	0.18	1	0.05	–	–	–	–
<i>Quercus stellata</i> Wangenh.	20	0.02	–	–	20	0.03	–	–	–	–	–	–
<i>Callicarpa americana</i> L.	–	–	20	0.02	100	0.15	–	–	–	–	–	–
<i>Liquidambar styraciflua</i> L.	–	–	–	–	60	0.09	–	–	–	–	–	–
<i>Rhododendron canadense</i> (Michx.) Sweet	–	–	–	–	–	–	–	–	1	0.06	–	–
TOTALS	126480	100	96040	100	67100	100	1971	100	1608	100	201	100

Fig. 1. Two-dimensional NMS solutions based on sapling (left; woody plants ≥ 1 m height; < 5 cm dbh) and seedling (right; woody plants < 1 m height) assemblages in three treatments: before fire (U; green circles), after one fire (B; red squares), and after two fires (BB; blue triangles). Convex hull (polygons) bound plots based on treatments and biplot overlays (arrows) indicate association with environmental variables and ordination axes.



When seedling and sapling plot-level density were compared by functional group and time (repeated-measure mixed ANOVA), we documented a significant interaction ($p < 0.001$; Table S1). Mean sapling density declined with fire across functional groups, with the *A. rubrum/O. arboreum/N. sylvatica* (AON) group experiencing the greater decline (Fig. 2a). *Quercus* and *Carya* (QC) and “other” species declined in density, but the magnitude was less than that of saplings in the AON group. Seedlings in the AON taxonomic group experienced a significant ($p < 0.001$) decrease in mean density plot⁻¹ with fire. Species in the “other” taxonomic group decreased in mean plot-level density after the first fire but increased in mean density after the second fire. After the second fire, species in the “other” group outnumbered those in the AON group (Fig. 2b).

Fire effects on abiotic conditions

Mean litter depth was significantly different among treatments ($p < 0.001$; Fig. 3a). Understory light availability was not significantly different before, after the first, or after the second prescribed fire ($p = 0.122$; Fig. 3b). We documented significant difference in *P. echinata* duff-ring depth ($p < 0.001$) and duff-ring length ($p < 0.001$). Duff-ring depth before the first fire was not significantly different than duff-ring depth after the first fire, but duff-ring depth was significantly less after the second fire when compared to depth before and after the first fire (Fig. 3c). Duff-ring length was significantly greater after the first fire compared to length before the first fire and after the second fire (Fig. 3d), but no significant difference in mean duff-ring length was documented before the first fire and after the second fire.

We documented a significant interaction effect between ground flora cover category (herbaceous vs. woody) and time ($p < 0.001$). Mean woody plant cover increased after the first fire and decreased after the second fire (Fig. 2c). Herbaceous plant cover increased after the first and second fire. We documented a significant interaction effect between ground cover category (hardwood vs. *Pinus* litter) and time ($p < 0.001$). Mean hardwood litter decreased after the first fire and after the second fire (Fig. 2d). Mean *Pinus* litter increased after the first fire, then decreased after the second fire.

Spatiotemporal variability and drivers of fire severity

Of the 121 *P. echinata* sampled, we documented 27 (22%) scorched stems after the first fire and 104 (87%) scorched stems after the second fire. We documented a significantly greater mean scorch height after the second fire when compared to mean scorch height after the first fire ($p < 0.001$; Fig. 4). We documented a similar significantly greater scorch percent after the second fire compared to mean scorch percent after the first fire ($p < 0.001$; Fig. 4). The majority of tree scorch (33%) occurred on the north aspect of trees, followed by the northwest (20%) and west (14%; Fig. S1). Fire effects were patchy after the first fire as documented by sapling mortality (Fig. 5). We recorded an increase in sapling density plot⁻¹ after the first fire on 10 of the 25 plots. After the second fire, saplings density plot⁻¹ was reduced to levels less than pre-fire sapling density values on each of the 25 plots.

Our final model contained all possible predictors hypothesized to influence bole scorch height. The likelihood ratio

Fig. 2. Interaction plots from repeated-measures mixed ANOVAs for mean sapling (a) and seedling (b) density-plot⁻¹ by taxonomic group (A/O/N: *A. rubrum*/*O. arboreum*/*N. sylvatica*, Q/C: *Quercus*/*Carya*, and other spp.), and plant cover (c) and litter cover (d) with standard error by treatment (unburned, once burned, twice burned) in a *Quercus-Pinus echinata* mixedwood in Tennessee, USA.

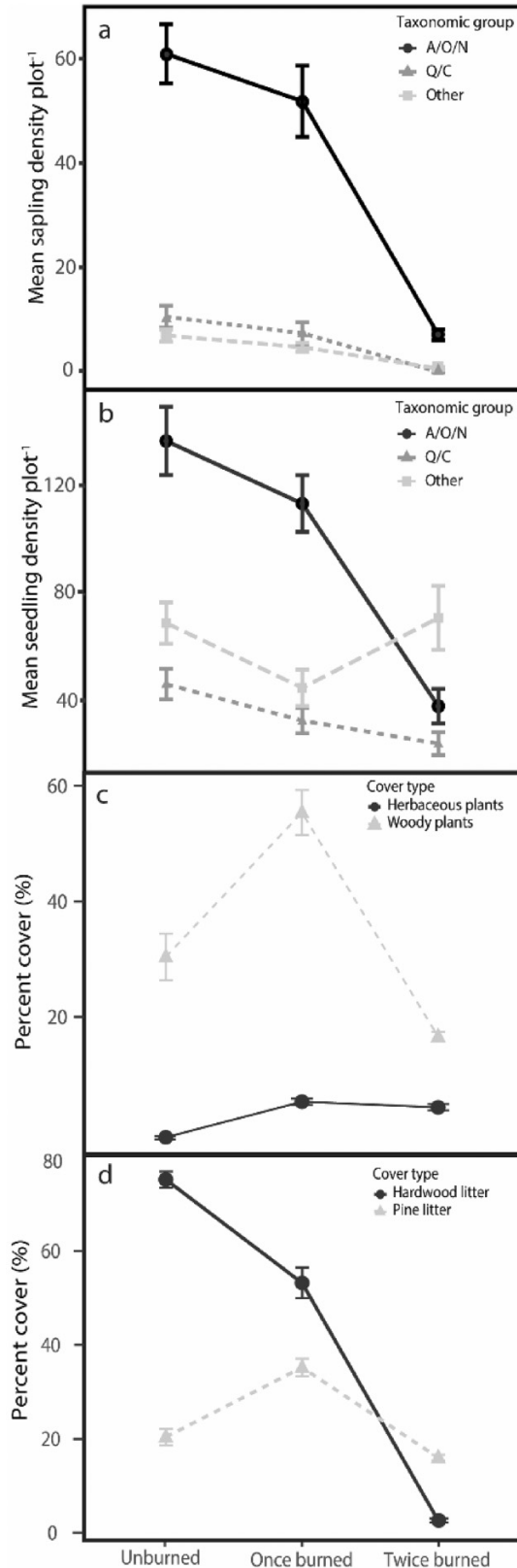
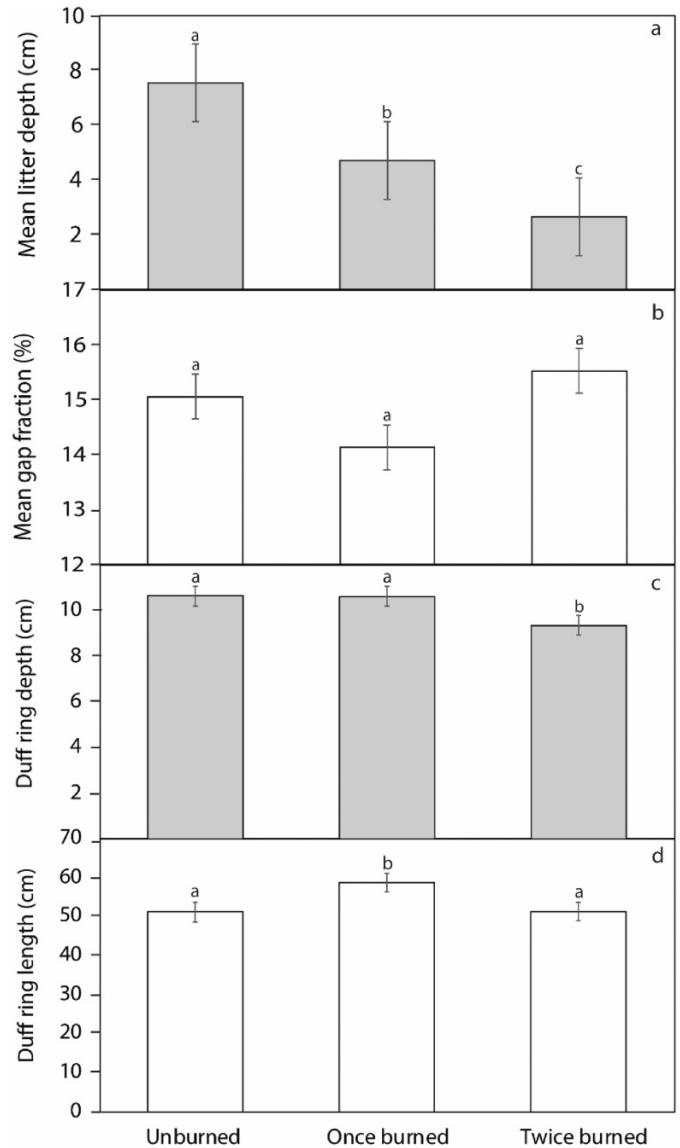


Fig. 3. Mean litter depth (a) gap fraction (b), duff ring depth, (c) and duff ring length (d) with standard error by treatment (unburned, once burned, twice burned) in a *Quercus-Pinus echinata* mixedwood at Savage Gulf State Natural Area, TN, USA. Bars with different lowercase letter indicate significant difference ($p < 0.05$) among treatments.



chi-square test indicated the model was statistically significant (87.69, $p = 0.004$) and fit better than a null model. Area under the receiver operating curve values also indicated the model performed well, correctly classifying the very low, low, medium, high, and very high scorch severity classes at rates of 0.86, 0.77, 0.74, 0.78, and 0.81%, respectively. Likelihood ratio chi-square effect test revealed that 7/14 predictors were significant in the model. The seven significant predictors were aggregated plot-level predictors, which included plot litter depth before the first fire, plot litter depth before the second fire, sapling density before the first fire, sapling density before the second fire, *Pinus* relative basal area plot⁻¹, microscale topography, and transformed aspect (Table S2).

Fig. 4. Mean scorch height (left) and %bole scorch (right) with standard errors by treatment (once burned, twice burned) in a *Quercus-Pinus echinata* mixedwood at Savage Gulf State Natural Area, TN, USA. Bars with different lowercase letter indicate significant difference ($p < 0.05$) between treatments.

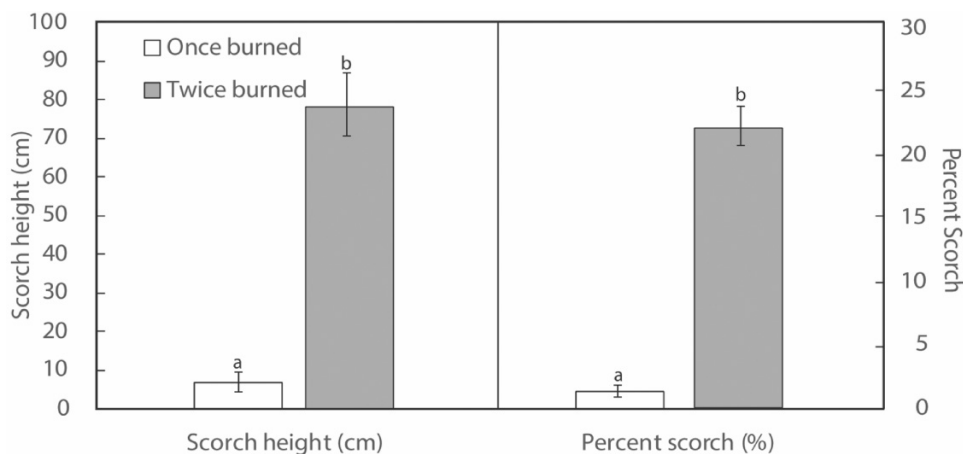
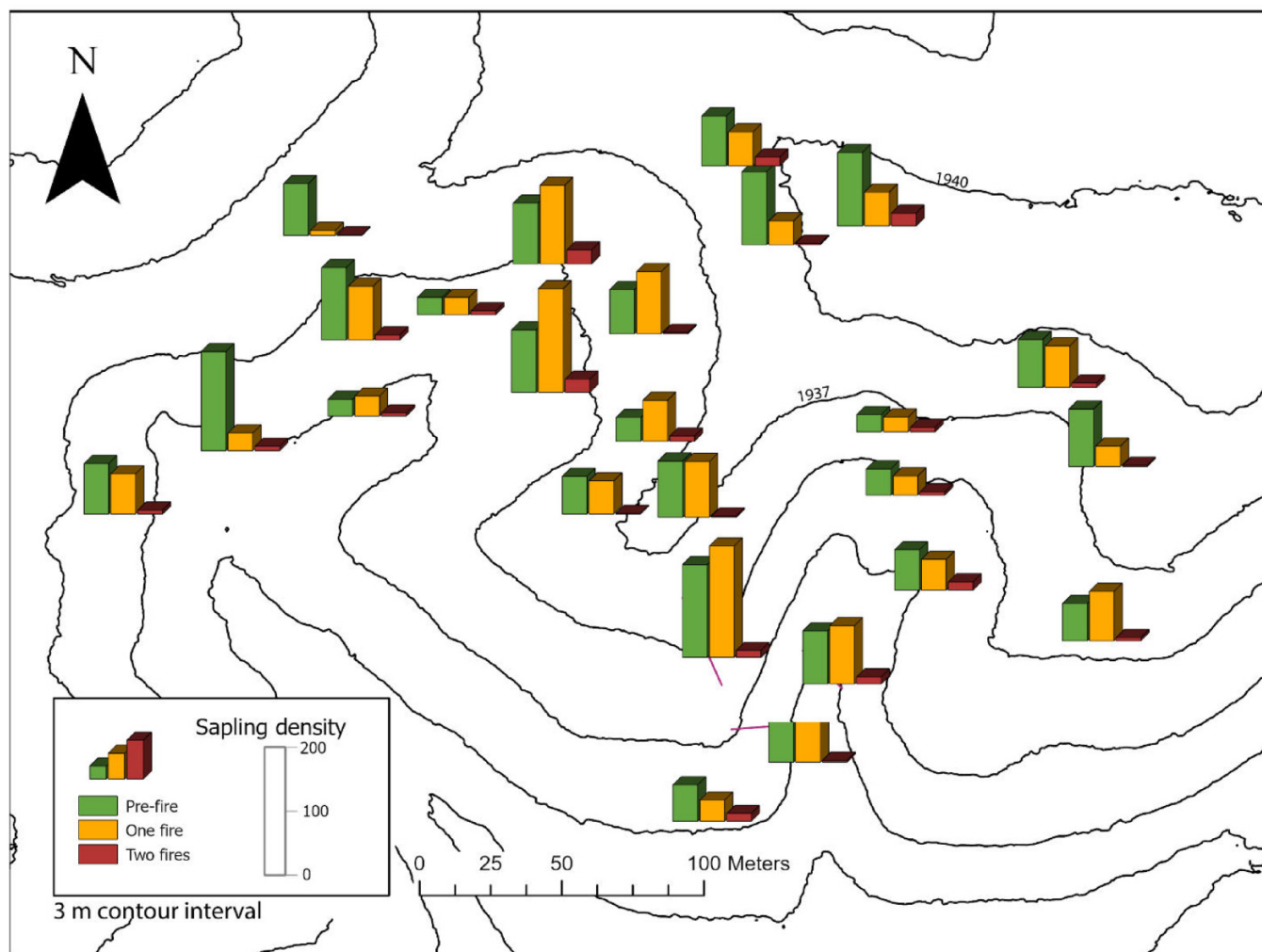
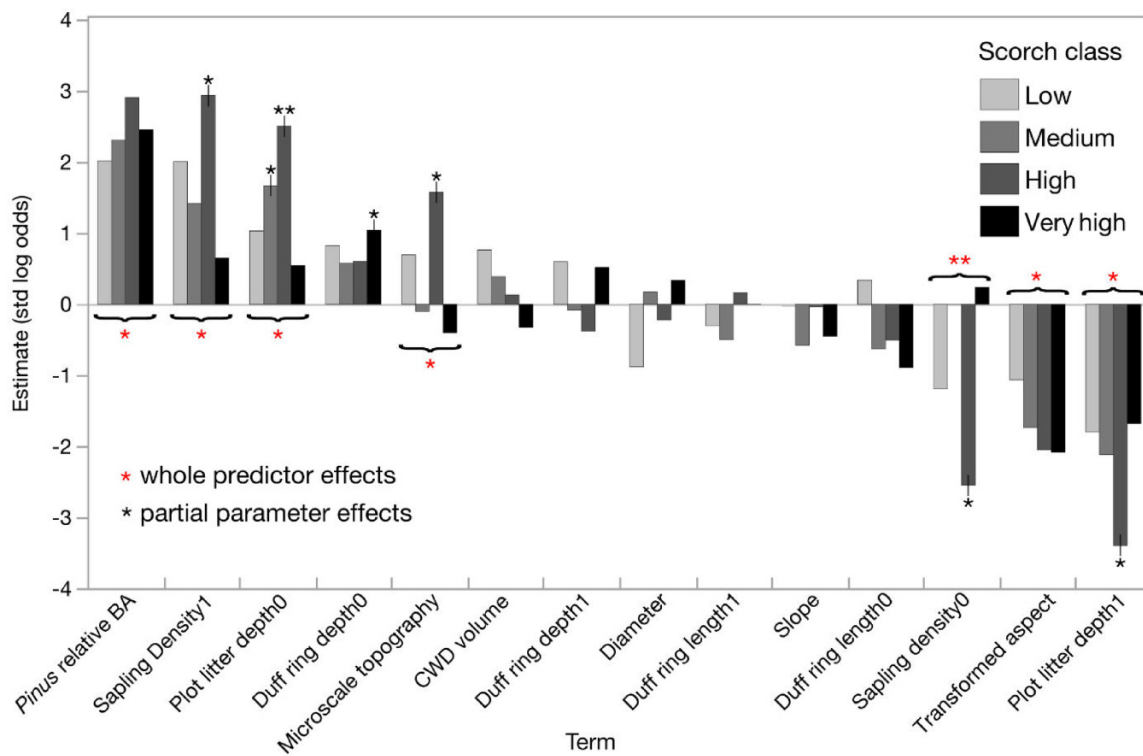


Fig. 5. Spatially referenced bar graphs (overlayed on sampling plot locations) of raw sapling density by treatment (pre-fire, once burned, twice burned) in a *Quercus-Pinus echinata* mixedwood in Tennessee, USA.



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Fig. 6. Standardized effect sizes (γ) with standard error of 14 predictor variables (x) used to fit a multinomial logistic regression model with five fire severity classes. Parameter names followed by a “0” (e.g., duff length 0) indicate data collected prior to the first fire and effect names followed by a “1” indicate data collected after the first fire in a *Quercus-Pinus echinata* mixedwood in Tennessee, USA. An asterisk above or below a bar indicates a whole predictor or partial parameter effect ($*p < 0.05$; $**p < 0.01$) on scorch severity.



Notably, none of the individual tree predictors significantly affected any scorch severity class. The standardized effect sizes were both positive and negative and differentially influential on scorch severity classes (Fig. 6). Sapling density after the first fire, plot litter depth before the first fire, and microscale topography had significantly positive effects ($p < 0.05$) on the likelihood of high scorch severity; and sapling density before the first fire and plot litter depth after the first fire had significantly negative effects ($p < 0.05$) on the likelihood of high scorch severity (Fig. 6). Plot litter depth before the first fire and duff-ring depth before the first fire had a significantly positive effect ($p < 0.05$) on the likelihood of medium and very high scorch severities, respectively.

Discussion

Effects of fire seasonality on the woody plant community

In fire-adapted stands, fire frequency is often the primary filter on woody plant community composition and structure (Mason and Lashley 2021). The seasonality of these two fires differentially impacted woody plant assemblages, which was attributed to differences in fire weather; fuel moisture, composition, and loading; and atmospheric conditions (a function of seasonality). During the December 2020 fire, which

consumed a negligible amount of fuel on approximately half of the plots, temperature, and wind speeds were lower, and relative humidity and fuel moisture were higher compared to atmospheric and fuel conditions of the April 2022 fire. Further evidence of patchy fire effects was the documented increase in mean duff ring length, which likely occurred because *P. echinata* needle cast prior to the first fire exceeded fuel consumption during the first fire. Because the December 2020 fire intensity was relatively low at the stand scale, and patchy at the neighborhood scale, we noted an increase in sapling density in approximately half of our plots (i.e., half the plots experienced negligible fire effects). However, after the April 2022 fire, we documented a significant reduction in sapling density across all plots to levels lower than pre-fire sapling density. Atmospheric and fuel conditions for the April 2022 fire were more suitable for more intense fire behavior and desired fire effects (i.e., hotter temperature and longer flame residence time; Pausas et al. 2017). Although the December 2020 fire significantly reduced fine-surface fuels, residual fuels that remained after the December fire were adequate to sustain the April 2022 fire. We note that we cannot definitively separate the effects of seasonality from the effects of repeated burning.

Woody plant taxa in the sapling layer were differentially impacted across space and among fires. Sapling density decreased across all taxa after the second fire, but was most

pronounced in fire-intolerant saplings such as *A. rubrum*, *O. arboreum*, and *N. sylvatica*, and moderately fire-tolerant *Quercus* spp. Among these species, *A. rubrum* is the least fire-tolerant in sapling and small-diameter size classes. Although some studies have documented no effects of prescribed fire on *A. rubrum* sapling shoot mortality (e.g., Clark and Schweitzer 2013), fire has been found to be effective in top-killing *A. rubrum* saplings and small trees (Abella et al. 2021). *Quercus* sapling spp. also experienced fire-induced mortality, with a similar magnitude as fire-intolerant species particularly after the second fire. *Quercus* saplings and small-diameter trees may also be sensitive to shoot mortality after low-intensity fire (Fan et al. 2012). However, Arthur et al. (1998) reported that hardwood stems <10 cm dbh have a high probability of shoot mortality regardless of taxa. The timing of the second fire coincided with leaf expansion for many taxa. High-intensity spring burning has been found to reduce the re-sprouting ability in *A. rubrum*, *L. tulipifera*, and other fire-intolerant species (Brose 2010; Abella et al. 2021). During early growing-season fires, these species expend carbohydrates during initial bud-break, which are subsequently depleted and limit post-fire sprouting ability (Robertson and Hmielowski 2014) and physiologically active tissue is more susceptible to high fire temperature (O'Brien et al. 2010). We documented no tree-layer mortality, which indicated that 5 cm dbh is a sufficient size to resist immediate fire-induced mortality after two prescribed fires. However, we acknowledge that delayed mortality is still possible, especially after the second prescribed fire.

Although prescribed fire indiscriminately top-killed saplings regardless of taxa, the impact of prescribed fire on the seedling community was more variable. *Acer rubrum* seedling survival has been found to be low after repeated fires (Alexander et al. 2008; Green et al. 2010), which is similar to *A. rubrum* seedling dynamics documented in our study. Similarly, *Quercus* seedling survival was negatively affected by two prescribed fires, but the magnitude of mortality was significantly less than *A. rubrum* and other fire-sensitive species. Notably, we documented an increase in *L. tulipifera* seedlings with additional fire. *Liriodenron tulipifera* seeds remain viable in litter for up to 8 years, and fire has been found to increase germination and seedling density of this species (Beck and Sims 1983). Hutchinson et al. (2005) documented a similar initial increase in *L. tulipifera* seedling density after fire, but this initial increase did not persist with time likely because prescribed fire did not increase understory light availability. Although the first fire did not alter the sapling community, it significantly altered the seedling community, which was largely driven by litter depth and hardwood litter cover. We posit that this was a function of stem size and taxa-specific fire sensitivity (Dey and Hartman 2005). After the second fire, we documented no *P. echinata* in the seedling or sapling layer. Elliott and Vose (2005) also found no *P. echinata* advance reproduction after one prescribed fire. We suspect residual litter and low understory light availability prevented germination of *P. echinata*. Thus, additional management will be required to enhance the regeneration potential, establishment, and recruitment of *P. echinata*.

Fire effects on abiotic conditions

Litter depth was significantly reduced by both fires, which we expected based on the enhanced litter accumulation over the extended period of fire exclusion. Our initial litter depth values prior to prescribed fire were slightly greater than those reported by other studies in fire-excluded upland stands in the eastern US. Kreye et al. (2018) found that litterbed depths ranged from 3.6 to 8.3 cm in a long-unburned *Quercus-Carya* stand undergoing mesophication. Barefoot et al. (2019) reported mean litter depth of 4.7 cm in fire-excluded mixed *Pinus*-hardwood stands on the Cumberland Plateau, Royse et al. (2010) reported mean litter depth values of 3.2 cm in fire-excluded *Quercus* stands on the Cumberland Plateau, and Burton et al. (2011) reported a litter depth of approximately 2.0 cm in an upland *Quercus* forest after 20 years of fire exclusion. However, in fire-excluded *Pinus palustris* Mill. stands, litter has been found to accumulate to depths >25 cm (Kush et al. 2004). Although the litter depth on approximately half of the plots remained the same or slightly increased after the first fire, the first fire did consume a significant amount of litter on the plots that did burn. Comparatively, the second fire indiscriminately consumed a significant amount of litter across all 25 sampling plots. If mineral soil exposure is desired, prescribed fire on a short interval will be necessary, as litter rapidly accumulates in fire-free periods (Burton et al. 2011). We also documented significant interactions in fuel cover categories. Herbaceous and woody plant cover increased after the first fire, followed by a sharp decrease in woody plant cover and no change in herbaceous cover after the second fire. The increase in herbaceous cover after the first fire could have increased fire intensity, which may have resulted in the sharp decline in woody plant cover. In mixed *Quercus-Pinus* stands on the Cumberland Plateau, Arthur et al. (1998) found that herbaceous and shrub cover increased after one fire, and shrub cover decreased after a second fire. The increase in *Pinus* litter after the first fire could have increased the intensity of the second fire, as *Pinus* litter has been found to burn at a higher intensity than most hardwood litter (Varner et al. 2015). Our results indicated that two prescribed fires had no significant effect on understory light availability at 1 m above the ground. Although sapling density was significantly reduced after the second prescribed fire, the mid-story was largely unaffected. We documented no mortality of trees in the mid-story (>5 cm dbh but not in canopy positions), which was largely composed of *O. arboreum* and *A. rubrum*. Our results were consistent with findings from other studies on the short-term effects of prescribed fire on understory light availability (Hutchinson et al. 2005; Alexander et al. 2008).

Pinus fine roots grow in basal duff rings and near the surface of mineral soil (O'Brien et al. 2010; Varner et al. 2009). We measured the depth and length of basal duff rings out of concern that fire smoldering in basal duff rings would cause delayed mortality of mature *P. echinata* upon the reintroduction of fire. Our results indicated that the first prescribed fire did not consume the litter and duff around the base of canopy *P. echinata*. The duff-ring depth and length were not significantly different after the first fire, but the second fire significantly reduced the depth of *P. echinata* duff

rings. The lack of consumption during the first fire may be explained by the fuel moisture in the duff rings. The first fire occurred after a 4-day precipitation-free period, which is a relatively short amount of time for this region. Furthermore, the month of December receives the greatest mean precipitation in Grundy County, Tennessee, USA at 168.5 mm (PRISM 2022). Varner et al. (2009) found that fire exceeded lethal temperatures (>60 °C) for over an hour duration in basal duff rings and mineral soil of *P. palustris* Mill. stands in Florida USA, and the excessive heating was best explained by lower moisture of the *Oe* horizon. Swezy and Agee (1991) found that enhanced litter accumulation in old-growth *Pinus ponderosa* stands in the western USA resulted in lethal fire temperatures and subsequent delayed mortality even when the bases of trees were raked. These studies occurred in woodlands in which fuel moisture loss likely occurred at a greater magnitude than in our study. Although not measured, we suspect that the moisture retained in basal duff rings around *P. echinata* in our study precluded fires from reaching lethal temperatures. The dense midstory of the stand studied here likely reduced fuel moisture evaporation and litter drying.

Spatiotemporal variability and drivers of fire severity

Data collected after the first fire indicated that approximately half of the neighborhoods sampled experienced little-to-no fire effects. On these plots, some stems in the seedling layer recruited to sapling height (1 m), which accounted for the increase in sapling density in these plots that were largely unburned during the first fire. The fire-weather conditions and intensity of the second fire led to the spread of fire through these previously unburned plots. We hypothesized that the first fire may have limited the subsequent severity of the second fire by consuming excess fuels, while still providing sufficient residual fuels to sustain the second fire.

Although bole scorch height may not be the best indicator of fire line intensity (Alexander and Cruz 2011), we considered scorch height to be the best fire severity proxy of all response variables collected. Our final fire severity model revealed that aggregated plot-level predictors better explained the variability in scorch height than did individual-tree predictors. The effect sizes for plot-level predictors (e.g., plot litter depth) were significantly larger (both positively and negatively) than individual-tree predictors (e.g., *P. echinata* duff-ring depth). Since fire smolders in *Pinus* duff rings, we did not expect duff-ring depth to have a positive effect on fire severity (Varner et al. 2009), and this was supported by our findings. Plot-level *Pinus* basal area had a significantly positive effect on fire severity, which is likely a function of increased flammability of *Pinus* litter compared to hardwood litter (Varner et al. 2015). Sapling density after the first fire and mean litter depth prior to the first fire also had significantly positive effects on fire severity. Saplings that were unaffected by the first fire or seedlings that recruited to sapling size may have marginally contributed fuels to increase the severity of the second fire. For plots that did burn during the first fire, we

suspect fuelbed composition was modified, resulting in fuel loads that potentially enhanced fire effects during the second fire. Deeper fuelbeds have been found to retain more moisture (Zhao et al. 2021), therefore fuel partially consumed by the first fire may have enhanced combustion of litter during the second fire. Notably, for the significant whole predictor effects, we documented diminishing partial parameter effects after the high scorch class (i.e., no significant partial effects were documented on the very high scorch class), which indicated that modeled predictor effects had an upper threshold of influence on scorch severity that peaked at the high severity scorch class. In other words, the biophysical predictors of the model (primarily fuels and microsite conditions) had no significant influence on the likelihood of very high scorch severity, but other factors that were not directly measured influenced the likelihood of the very high scorch severity class. These factors likely included fine-scale atmospheric conditions during the second fire. Therefore, we suggest that fuels and microsite conditions limited fire severity to the high severity scorch class during the second fire, and fine-scale atmospheric conditions (unmeasured) influenced the likelihood of very high scorch severity during the second fire. Furthermore, although our model identified significant partial parameter effects of pre-fire conditions (e.g., litter depth prior to the first fire, sapling density prior to the first fire) on likelihood of scorch severity after the second fire, the seasonality of the second fire likely had the greatest effect on the spatial uniformity of this fire. Specifically, although parameters recorded prior to, and after, the first fire did have a significant effect on scorch height after the second fire, we hypothesize that the seasonality of the second fire was the most influential driver of uniform reductions in fuel, sapling density, and seedling density regardless of stand conditions prior to the first fire.

Fire effects on *Pinus Echinata*

Common barriers to *P. echinata* germination and seedling establishment are litter and duff accumulation (Grano 1949) and understory light availability (Bower and Ferguson 1968). In long-unburned mixedwood stands in which vegetation-fuel-fire feedbacks are altered, these barriers to regeneration are particularly exacerbated. Our results indicated that two prescribed fires were not sufficient to secure adequate *P. echinata* natural regeneration. The dense midstory of the long-unburned stand was not significantly impacted by either prescribed fire and understory light availability was not altered. Although both fires did consume a significant amount of forest-floor litter, our results indicated that subsequent fire(s) will be required to expose bare mineral soil. The second prescribed fire top-killed the majority of saplings but had no immediate effect on small-diameter trees. In addition to prescribed fire, mechanical or chemical midstory removal will be necessary to increase understory light availability. In long-unburned stands in which vegetation-fire-fuel feedbacks are altered, we urge managers to continue monitoring prescribed fire effects and adapt silvicultural prescriptions based on desired management objectives and regeneration niches of desired species.

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Data availability

Data provided by corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfr-2023-0116>.

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