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Prescribed fire effects on understory woody plants and fuels in *Quercus–Pinus* mixedwoods

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Abstract

To enhance forest resilience to predicted increases in forest stressors, managers increasingly desire ecologically based restoration approaches that increase ecosystem adaptation potential. Mixedwood stands, which contain a range of life history and functional traits, may be more resistant and resilient to ecosystem stressors. Management of *Quercus–Pinus* mixedwood stands includes the use of prescribed fire, which requires an understanding of vegetation-fuels-fire feedbacks in these ecosystems. However, a paucity of knowledge exists on the intra-stand spatial patterns of fire effects. We analyzed the effects of a newly initiated prescribed fire program on the intra-stand characteristics of understory woody plants and fuelbed composition and loading in a long-unburned *Quercus–Pinus* mixedwood stand in Tennessee, USA. We sampled vegetation and fuels in two plots, one that experienced two prescribed fires (burned plot), and one fire-excluded plot directly adjacent (unburned plot). On the burned plot, we recorded lower sapling and seedling densities across taxa. Spatial analysis of advance reproduction in the burned plot indicated a combination of patchy fire effects, canopy openings, and high-light understory environments. We documented significant reductions in total fuel mass. The combination of spatial analysis and ordination revealed that prescribed fires homogenized fuel loads within the burned plot.

Key words: shortleaf pine, disturbance, litter, regeneration, spatial patterns

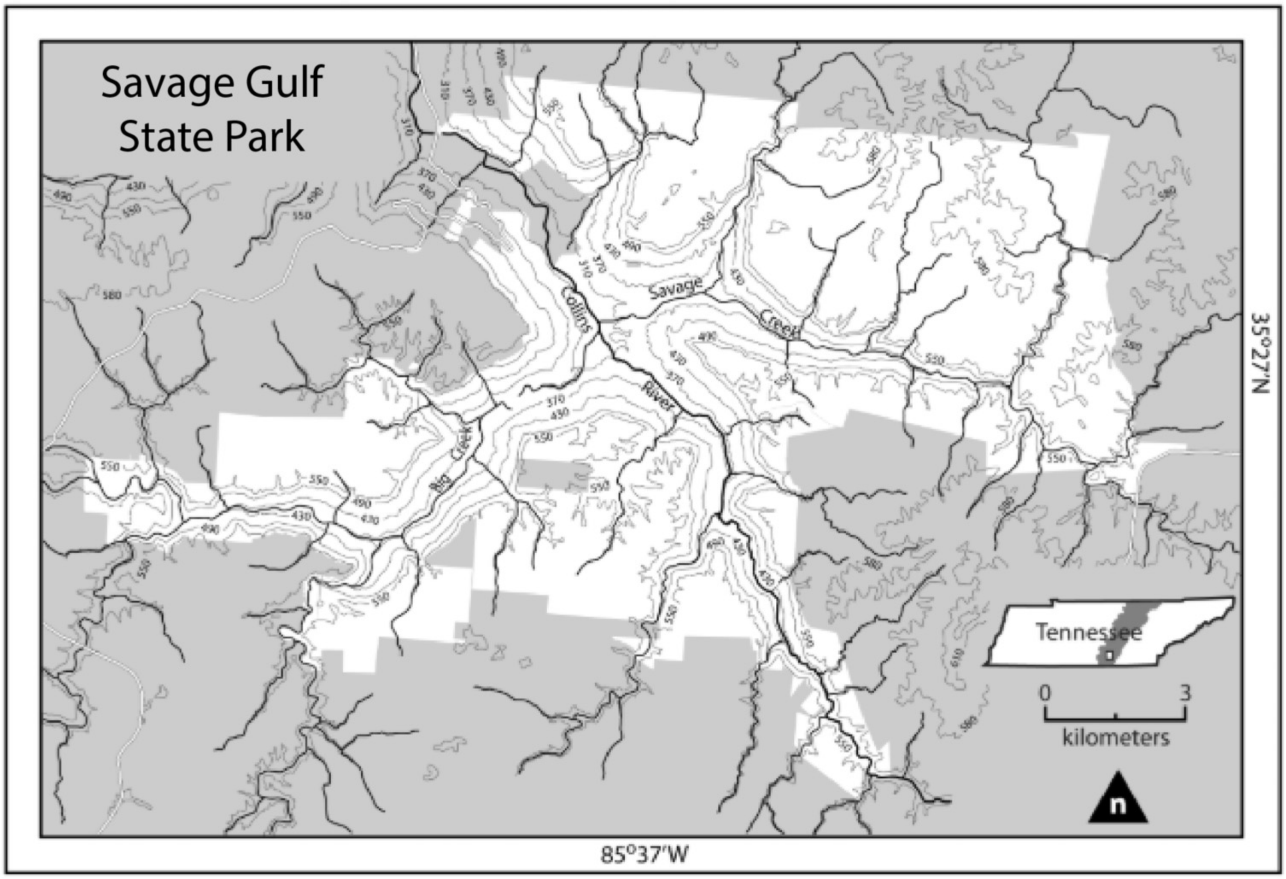
1. Introduction

Increasingly, forest managers are interested in enhancing ecosystem adaptation potential to combat future expected stresses and disturbances (Elmqvist et al. 2003; Lovett et al. 2016; D'Amato and Palik 2021). Biodiverse stands that are drought and fire adapted are hypothesized to be more resistant and resilient to future stressors by including a wider variety of functional and life history traits (growth rate, size, shade tolerance, etc.) and resource requirements that can increase biomass, carbon storage, and provide unique habitats (Kelty et al. 1992; D'Amato et al. 2011; Kabrick et al. 2017; Clark and D'Amato 2021). Mixedwood stands contain a mixture of hardwood and softwood species in which neither component constitutes more than 75%–80% of the canopy composition (Helms 1998). Recently, managers in the southeastern USA have become interested in establishing and maintaining *Quercus–Pinus* mixedwoods because these assemblages represent a wide range of structures and life history traits which should enhance ecosystem adaptation potential (Kabrick et al. 2017; Willis et al. 2019; D'Amato and Dey 2021; MacLean and Clark 2021; Hart et al. 2024).

Recurring low-to-mid severity surface fires are thought to promote *Quercus–Pinus* dominance through open-stand conditions and positive vegetation-fuels-fire feedbacks (Hart and Buchanan 2012; Stambaugh et al. 2015). Positive vegetation-fuels-fire feedbacks promote fire-adapted plant assemblages that produce fire-facilitating fuels, which in turn enhance the desired effects of low-intensity surface fire regimes (Tepley et al. 2018). If vegetation-fuels-fire feedbacks are altered, it can create lasting effects, including an increase in fire-sensitive species abundance during long periods of fire exclusion (Mitchell et al. 2009; Fill et al. 2015; Varner et al. 2015). As the number of fire-sensitive species in the midstory increases, the dense subcanopy limits light availability in the understory and creates conditions that can inhibit surface fire (e.g., a cool and moist fuel layer and greater proportion of fire-impeding fuels; Nowacki and Abrams 2008; Kane et al. 2021).

In long-unburned stands (e.g., stands that have not been burned since the initiation of fire exclusion policies starting in the 1920s; McEwan et al. 2007), the effects of prescribed fire reintroduction are not well understood, especially in mixed *Quercus–Pinus* ecosystems (Hiers et al. 2020). Changes in fuelbed composition and loading, because of fire exclusion, can influence fire behavior and effects, which ultimately may alter stand composition and structure (Xiong and Nilsson 1999; Graham et al. 2004). Compounding factors during burning including seasonality, topography, fuels, and weather conditions further influence fire severity (Malanson and Trabaud 1988; Cain and Shelton 2000; Knapp

Fig. 1. Map of Savage Gulf State Park (SGSP) in Tennessee, USA. Plots were located on the northern tablelands of SGSP. Figure was digitized by the University of Alabama Cartographic Research Laboratory using Adobe Illustrator (CS6) from a quadrangle base map, courtesy of the United States Geological Survey.



et al. 2009; Vaughan et al. 2021). An understanding of prescribed fire reintroduction on vegetation-fuels-fire feedbacks is necessary to create and maintain *Quercus–Pinus* mixedwood stands. *Quercus–Pinus* mixedwoods exist in a mid-successional state and fire and local to meso-scale canopy disturbances are required to perpetuate the species assemblage (Cooper 1989). Prescribed fire as a silvicultural tool is used to expose bare mineral soil, increase understory light availability, and inhibit competition from fire-intolerant stems (Hart et al. 2024). Some *Quercus* and *Pinus* species are adapted to better survive fire through insulating bark and prolific resprouting after being topkilled. To restore or maintain *Quercus–Pinus* mixedwoods using prescribed fire, managers must be able to reinitiate positive vegetation-fuels-fire feedbacks in long-unburned *Quercus–Pinus* stands.

The intra-stand distribution of fuels, as well as species-specific characteristics of litter flammability, can influence fine-scale fire intensity (Sánchez-Pinillos et al. 2021). Currently, a paucity of data exists on the patterns of vegetation-fuels-fire feedbacks in long-unburned stands and how they influence stand structure, composition, and function. Quantitative data are needed on the effects of prescribed fire and its reintroduction to long-unburned stands (Hiers et al. 2020). Describing the patterns of vegetation-fuels-fire feedbacks can help assess prescribed fire as a tool to create and maintain desired species assemblages and stand structures, especially in long-unburned stands. Additionally, perpetuating fire-adapted species assemblages in fire-managed stands requires an understanding of the relationship between woody plant composition and fuel loading and composition. This study is a spatially explicit expansion that builds upon the work published in Goode et al. (2024). The specific goals of our study were to quantify the effects of two prescribed fires on: (1) species composition, density, and spatial patterns of understory woody plants and (2) composition, loading, and spatial patterns of fuels. We hope that our findings will help develop a deeper understanding of the spatial patterns of woody plants and fuels in *Quercus–Pinus* mixedwoods and be used to inform future management decisions.

2. Materials and methods

2.1. Study area

This study was conducted at Savage Gulf State Park (SGSP) located in Grundy County, Tennessee, USA (Fig. 1). SGSP is 6309 ha and is listed as a National Natural Landmark. Since the property was acquired by the state of Tennessee in 1973, use of the reserve has been restricted to recreation and research. SGSP is located on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938). Our study occurred on the tablelands of the Cumberland Plateau, a land type association categorized by broad rolling ridges alongside gentle to moderately steep-sided slopes, separated by young valleys (Smalley 1986). The underlying geology of SGSP is primarily composed of sandstone, conglomerate, siltstone, shale, and coal, and is in the Crab Orchard and Crooked Forked groups (Miller 1974; Smalley 1982). The study site has soils mainly belonging to the Beersheba, Jefferson, Lily, Lonewood, and Ramsey soil series (USDA NRCS 2020). These soil series are primarily derived from sandstone, shale, siltstone, or quartzite, textures are often loam, silt loam, or sandy loam, they are well-drained, and moderately deep to very deep (USDA NRCS 2020). Slopes range from 2% to 40%.

The regional climate is humid mesothermal with moderately hot, long summers and mild, short winters (Thornthwaite 1948). Mean annual temperature is 14.1 °C, with the highest monthly mean temperature in July at 24.4 °C, and the lowest monthly mean temperature in January at 3.1 °C (PRISM Climate Group 2023). Mean annual precipitation was 1545 mm, with December receiving the greatest mean precipitation (164 mm) and October receiving the lowest mean precipitation (87 mm; PRISM Climate Group 2023). The frost-free period is approximately 200 days, with the last freeze typically occurring in mid-April and the first freeze occurring in middle to late October (Smalley 1982).

Forests in this region include mixed mesophytic, mixed hardwood, and mixed *Pinus*-hardwood forest types (Hinkle 1989). The forest on the tablelands of SGSP is dominated by *Quercus alba* L., *Acer rubrum* L., and *Pinus echinata* Mill. (Hart et al. 2012). At the genus level, *Quercus* spp. (46% of basal area) are most dominant, followed by *Pinus* spp. (17% of basal area) and *Acer* spp. (16% of basal area). *Quercus* and *Pinus* spp. comprise 70% of the canopy, and *Oxydendrum arboretum* (L.) DC. and *A. rubrum* comprise most understory trees (Hart et al. 2012). The majority of the study area contained stands with multiple age classes and complex vertical structures (Hart et al. 2012; Goode et al. 2021).

The Tennessee Department of Environment and Conservation (TDEC) introduced a prescribed fire program in 2020 to help achieve their primary land management objectives of restoring and enhancing *Quercus*–*P. echinata* ecosystems and to improve native species habitats. The burn unit was 415 ha, with 48% of the unit classified as flat (<5% grade), 48% as gently sloped (<20% grade), and 4% steeply sloped (>20% grade). The unit was bounded by a two-track road, recreational hiking trails, and a bluff that drops 120–240 m to Savage Creek below. The desired outcomes 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 (TDEC SGSP Burn Plan, 2020). The burn unit has experienced two prescribed fires. Both fires were ignited by hand crews with drip torches using a 3:1 diesel to gas ratio. The first prescribed fire was conducted on 11 December 2020. Fire weather conditions onsite were a 9 °C average temperature, ca. 40% relative humidity, 10 kph winds from the west, a four-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 onsite 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 with a four-day precipitation free period. 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).

2.2. Field methods

Our study was conducted in July 2022, in a *Quercus*–*Pinus* mixedwood stand. This stand was treated as a single management unit until the initiation of the prescribed fire program in 2020, when it was divided into two stands. Thus, species composition, stand structure, and disturbance and management history for the stands were similar, save that one stand was subjected to two prescribed fires and one stand remained unburned. Basal area for the unburned and burned stands were 31.67 and 34.24 $m^2 \cdot ha^{-1}$, respectively. Quadratic mean diameter was 22.18 cm for the unburned stand and 20.87 cm for the burned stand. *Pinus* relative basal area was 33% for the unburned stand and 36% for the burned stand and *Quercus* basal area was 22% and 24%, respectively. Because of an inability to collect pre-burn data, we used a space-for-time substitution by establishing a control plot to reconstruct pre-fire conditions. Within each stand, we established a permanent 1 ha plot (hereafter referred to as the burned plot and the unburned plot). The plots were ca. 200 m from nearest edge to nearest edge of each other. The plots were subdivided into 100 quadrats, each of which was 10 m × 10 m. For both plots, the species and density of all saplings (live stems <5 cm dbh and >1 m tall) for every quadrat were recorded. Additionally, within every other quadrat in a checkboard pattern, four 1 m^2 sub-quadrats were established to quantify seedling (live stems <5 cm dbh and <1 m height) composition and density. Sub-quadrats were centered 2.5 m from quadrat center in each cardinal direction.

To assess litter conditions across both plots, litter depth measurements were taken at quadrat center and 3.3 m from quadrat center in each cardinal direction for every quadrat. Additionally, 1 m^2 sub-quadrats were centered on the adjoining corners of every 4 quadrats to destructively sample surface fuels in both plots. Within each sub-quadrat, all dead organic material was collected to bare mineral soil, including fine woody debris (FWD) (material <10 cm in diameter; Brown 1974). Any portions of fuel extending over the sub-quadrat boundary were cut at the boundary and portions that fell outside the edges were not collected (Emery et al. 2020). All litter was collected, labeled, and transported to the laboratory for further analysis.

2.3. Fuel sorting

Collected fuels were placed in a freezer (<−10 °C) for 48 h to kill pests and diseases, and then removed and allowed to equilibrate to laboratory temperature and humidity (Varner et al. 2015; Emery et al. 2020). Fuels were sorted

Table 1. Division of identifiable litter into fire-facilitating and fire-impeding categories based on flammability characteristics recorded in other studies.

Species	Category	Citation
Acer rubrum	Fire-Imped.	Varner et al. (2021)
Castanea dentata (Marshall) Borkh.	Fire-Facil.	Varner et al. (2021)
Carya glabra (Mill.) Sweet	Fire-Facil.	Varner et al. (2021)
Carya pallida (Ashe) Engl. & Graebn.	Fire-Facil.	Based on similarities to other *Carya* spp.
Carya tomentosa (Lam.) Nutt.	Fire-Facil.	Varner et al. (2021)
Cornus florida L.	Fire-Facil.	Varner et al. (2021)
Fagus grandifolia Ehrh.	Fire-Facil.	Varner et al. (2021)
Ilex montana Torr. & A. Gray ex. A. Gray	Fire-Facil.	Based on similarities to *I. opaca*
Ilex opaca Aiton	Fire-Facil.	Mola et al. (2014)
Liquidambar styraciflua L.	Fire-Imped.	Varner et al. (2021)
Liriodendron tulipifera L.	Fire-Facil.	Varner et al. (2021)
Nyssa sylvatica Marshall	Fire-Imped.	Varner et al. (2021)
Oxydendrum arboreum	Fire-Facil.	Varner et al. (2021)
Prunus serotina Ehrh.	Fire-Facil.	Varner et al. (2021)
Quercus alba	Fire-Facil.	Varner et al. (2021)
Quercus coccinea Münchh.	Fire-Facil.	Varner et al. (2021)
Quercus falcata Michx.	Fire-Facil.	Varner et al. (2021)
Quercus montana Willd.	Fire-Facil.	Varner et al. (2021)
Quercus rubra L.	Fire-Facil.	Varner et al. (2021)
Quercus stellata Wangenh.	Fire-Facil.	Varner et al. (2021)
Quercus velutina Lam.	Fire-Facil.	Emery and Hart (2020)
Sassafras albidum (Nutt.) Nees	Fire-Imped.	Varner et al. (2021)
Vaccinium arboreum Marshall	Fire-Facil.	Emery and Hart (2020)
Vaccinium stamineum L.	Fire-Facil.	Emery and Hart (2020)

into seven categories: (1) fire-facilitating hardwood litter (including whole leaves and identifiable leaf fragments), (2) fire-impeding hardwood litter (including whole leaves and identifiable leaf fragments), (3) *Pinus* needles, (4) herbaceous plants, (5) fine woody debris (including cones, seeds, reproductive structures, and woody material), (6) duff (comprised of the Oe soil horizon—decomposing plant material with recognizable structure, and the Oa soil horizon—decomposing plant material with unrecognizable structure), and (7) unidentifiable (unidentifiable leaf fragments and whole decomposed leaves in which species could not be confidently assigned). Hardwood litter was split between fire-facilitating and fire-impeding categories based on flammability characteristics summarized by Mola et al. (2014), Emery and Hart (2020), and Varner et al. (2021); (Table 1). Not all species identified contributed to fuel loads (e.g., *Viburnum prunifolium* L. was recorded but no leaf litter was identified), and only those with litter present were classified into a flammability category.

Large and easily identifiable hardwood leaves, *Pinus* needles, FWD, and herbaceous material were sorted from the sample first. The remaining litter was then sieved through progressively finer meshes of 4.0, 2.0, and 0.5 mm (Emery and Hart 2020). Litter remaining in the 4.0 mm sieve was further sorted into the appropriate categories. The 2.0 mm sieve was used to catch and sort any fully intact, non-decomposed *Pinus* needles that may have been missed in earlier sorting. Any remaining fuel within the 2.0 and 0.5 mm sieves were combined into duff. All fuel that passed through the 0.5 mm sieve into a catchment pan was sorted into the other category, which contained materials that would have little to no effect on fire behavior (i.e., soil, insects, rocks, scat, etc.). Fuel categories were weighed to determine the percent composition for each category in a sample.

2.4. Analytical methods

To assess woody plants in the understory, we calculated density (stems ha^{-1}) and relative density (percent of total stems) for saplings and seedlings. To test for differences in sapling and seedling density, we conducted a two-sample *t*-test at a 95% confidence interval to compare mean density between plots for saplings and seedlings separately.

We conducted a two-sample *t*-test using a 95% confidence interval to explore differences in mean litter depth between burned and unburned plots. To compare differences in fuel mass between plots, we used a robust heteroscedastic mixed analysis of variance (ANOVA) within the "WRS2" package v.1.1-4 in RStudio (Mair and Wilcox 2020). The "WRS2" package computes mixed ANOVAs which analyze both within (fuel categories) and between-subjects (treatment) effects. The robust mixed ANOVAs used in this package are based on trimmed means, in which 10% each is removed from the upper and lower ends of the distribution. This makes it useful for data that may violate homoscedasticity, because of outliers, under a normal mixed ANOVA.

Table 2. Density (stems ha^{-1}) and relative density (%) for saplings (<5 cm diameter and >1 m height) in an unburned and burned 1 ha plot on the Cumberland Plateau, Tennessee, USA.

Species	Unburned density (stems ha^{-1})	Unburned relative density (%)	Burned density (stems ha^{-1})	Burned relative density (%)
Acer rubrum	1308	59.37%	190	62.09%
Asimina triloba (L.) Dunal	7	0.32%	0	0.00%
Castanea dentata	5	0.23%	0	0.00%
Carya glabra	2	0.09%	0	0.00%
Carya pallida	0	0.00%	1	0.33%
Carya tomentosa	18	0.82%	2	0.65%
Cornus florida L.	10	0.45%	0	0.00%
Fagus grandiflora	7	0.32%	1	0.33%
Ilex montana	2	0.09%	1	0.33%
Ilex opaca	59	2.68%	11	3.59%
Liquidambar styraciflua	2	0.09%	0	0.00%
Liriodendron tulipifera.	17	0.77%	0	0.00%
Nyssa sylvatica	75	3.40%	54	17.65%
Oxydendrum arboreum	87	3.95%	32	10.46%
Prunus serotina	2	0.09%	0	0.00%
Quercus alba	193	8.76%	5	1.63%
Quercus coccinea	86	3.90%	1	0.33%
Quercus falcata	14	0.64%	0	0.00%
Quercus rubra	4	0.18%	2	0.65%
Quercus velutina	263	11.94%	0	0.00%
Sassafras albidum	5	0.23%	1	0.33%
Vaccinium arboreum	28	1.27%	3	0.98%
Vaccinium stamineum	9	0.41%	2	0.65%
Total	2203	100.00%	306	100.00%

We used ArcGis Pro version 3.1.2 to identify potential spatial patterns of both understory woody plants (combined sapling and seedling density) and fuel mass. Patterns were analyzed at a 20 × 20 m resolution. We used Getis-Ord Gi* to identify clusters of similar high or low values (hereafter referred to as hot spots and cold spots) to quantify spatial distribution.

To explore differences in fuelbed composition and loading, we used non-metric multidimensional scaling (NMS) in PC-ORD v.7 (McCune and Mefford 2011). The main matrix was constructed using plot-level categorical fuel mass by treatment. A scree plot was used to determine the appropriate number of axes, data were simulated 250 times with relative Euclidean distance, and the final solution was cross-checked for conformity with other solutions. A two-axis solution was recommended for ordination. A multi-response permutation procedure (MRPP) was used to test for significant differences ($p < 0.05$) in fuel composition between plots. Correlation with axes were reported for fuel categories that had a correlation coefficient greater than or equal to 0.4, or less than or equal to −0.4 (Peck 2016).

To visualize and assess differences in understory woody plant assemblages by treatments, we conducted NMS. The main matrix was constructed with total combined seedling and sapling density (considered understory woody plants) at the 20 × 20 m scale because of differences in sampling design used to inventory seedlings and saplings. Thus, each treatment contained 25 quadrats. A scree plot was used to determine the appropriate number of axes, data were simulated 250 times with relative Sørenson distance, and the final solution was cross-checked for conformity with other solutions. A two-axis solution was recommended for the final ordination. A MRPP was used to test for significant differences ($p < 0.05$) in woody plant assemblages between treatments. To quantify differences in understory woody plant assemblage variability between treatments, we calculated average dispersion (i.e., variability) between plots within each treatment with NMS dissimilarity matrices.

3. Results

3.1. Understory woody plants

The unburned plot had a sapling density of 2203 stems ha^{-1} (Table 2). The sapling species assemblage of the unburned plot was dominated by *A. rubrum*, which accounted for almost 60% of all sapling sized stems. Seedling density on the unburned plot was 354,650 stems ha^{-1} (Table 3). Similar to the sapling layer, the seedling species assemblage was dominated by *A. rubrum*, which represented almost 65% of all seedlings.

Sapling density on the burned plot was 306 stems ha^{-1}. Similar to the sapling layer of the unburned plot, *A. rubrum* represented ca. 63% of all sapling sized stems on the burned plot. Seedling density on the burned plot was 161,250 stems

Table 3. Density (stems ha^{-1}) and relative density (%) for seedlings (<5 cm diameter and <1 m height) in an unburned and burned 1 ha plot on the Cumberland Plateau, Tennessee, USA.

Species	Unburned density (stems ha^{-1})	Unburned relative density (%)	Burned density (stems ha^{-1})	Burned relative density (%)
Acer rubrum	230 000	64.85%	38 700	24.00%
Asimina triloba (L.) Dunal	300	0.08%	0	0.00%
Carya glabra	50	0.01%	0	0.00%
Carya pallida	100	0.03%	200	0.12%
Carya tomentosa	450	0.13%	200	0.12%
Cornus florida L.	150	0.04%	0	0.00%
Ilex montana	550	0.16%	500	0.31%
Ilex opaca	600	0.17%	5350	3.32%
Liquidambar styraciflua	100	0.03%	0	0.00%
Liriodendron tulipifera.	11 150	3.14%	30 600	18.98%
Nyssa sylvatica	2750	0.78%	2100	1.30%
Oxydendrum arboreum	1000	0.28%	1100	0.68%
Pinus echinata	600	0.17%	50	0.03%
Quercus alba	19 850	5.60%	6150	3.81%
Quercus coccinea	7150	2.02%	13 050	8.09%
Quercus falcata	200	0.06%	0	0.00%
Quercus rubra	750	0.21%	0	0.00%
Quercus velutina	6250	1.76%	5150	3.19%
Sassafras albidum	6900	1.95%	22 000	13.64%
Vaccinium arboreum	63 550	17.92%	34 050	21.12%
Vaccinium stamineum	2200	0.62%	2050	1.27%
Total	354 650	100.00%	161 250	100.00%

ha^{-1}. Although *A. rubrum* was the most abundant species in the seedling layer of the burned plot, the relative density of the species was much lower than on the unburned plot and *Liriodendron tulipifera* and *Vaccinium arboreum* were more abundant than in the seedling layer of the unburned plot.

Sapling density was significantly different ($p < 0.001$) between plots. The unburned plot had a mean of 22 (±1; standard error) saplings per quadrat, and the burned plot had a mean of 3 (±1) saplings per quadrat. Seedling density was also significantly different ($p < 0.001$) between plots, with a mean of 36 (±1) seedlings per sub-quadrat in the unburned plot and a mean value of 16 (±1) seedlings per sub-quadrat in the burned plot.

Getis-Ord Gi* analysis of understory woody plant density indicated several hot and cold spots across both plots (Fig. 2). The unburned plot had three significant cold spots ($p = 0.06$, 0.08, and 0.05), two of which were contiguous, and one significant hot spot ($p = 0.05$). Conversely, within the burned plot there were three significant hot spots ($p = 0.09$, 0.07, and 0.06), two of which were contiguous, and one significant cold spot ($p = 0.05$).

The final two-dimensional NMS solution of the understory woody plant assemblages had a non-metric r^2 of 0.97 and a final stress of 11.1. Quadrats in the burned treatment were completely segregated from quadrats in the unburned treatment in ordination space (Fig. 3), and the MRPP statistically confirmed these visual differences in woody plant assemblages between treatments ($p < 0.001$). The unburned quadrats were associated with the positive range of axis one, and the burned quadrats were associated with the negative range of axis one. Mean dispersion was greater in the burned quadrats (0.38 ± 0.01 SE) than in the unburned quadrats (0.22 ± 0.02 SE). Visual interpretation of the final ordination graph revealed that ca. four burned quadrats occurred adjacent to unburned plots in ordination space, which provided evidence for variable fire effects on woody plant assemblages.

3.2. Fuels

Mean mass of unburned fuel samples was 1273.7 $g{\cdot}m^{-2}$ with a maximum of 4285.2 $g{\cdot}m^{-2}$ and a minimum of 500.7 $g{\cdot}m^{-2}$ (Fig. 4). The mean percent of total fuel mass was 6.0% for fire-facilitating leaves, 3.5% for fire-impeding, 4.5% for needles, 51.9% for FWD, 0.2% for herbaceous plants, 7.8% for unidentifiable leaves, and 26.1% for duff. Comparatively, the mean mass of fuel samples from the burned plot was 1022.9 $g{\cdot}m^{-2}$ with a maximum of 2929.5 $g{\cdot}m^{-2}$ and a minimum of 290.8 $g{\cdot}m^{-2}$. On the burned plot, the mean percentage of total fuel mass was 0.7% for fire-facilitating leaves, 0.6% for fire-impeding leaves, 3.0% for needles, 67.8% for FWD, 0.1% for herbaceous plants, 3.0% for unidentifiable leaves, and 24.8% for duff. Mean litter depth across the unburned plot was 59.7 mm (±1.3). On the burned plot, mean litter depth was 58.6 mm (±2.0). Mean litter depth was not significantly different ($p = 0.65$) between the burned and unburned plots.

Mean fuel mass was significantly different ($p < 0.0001$) among fuel categories in both burned and unburned

Fig. 2. Map of understory woody plant (≥1 m height, <5 cm dbh) density and significantly ($p \leq 0.10$) hot and cold spots by 20 m^2 quadrats in burned and unburned 1 ha plots in a *Quercus*–*Pinus* mixedwood.

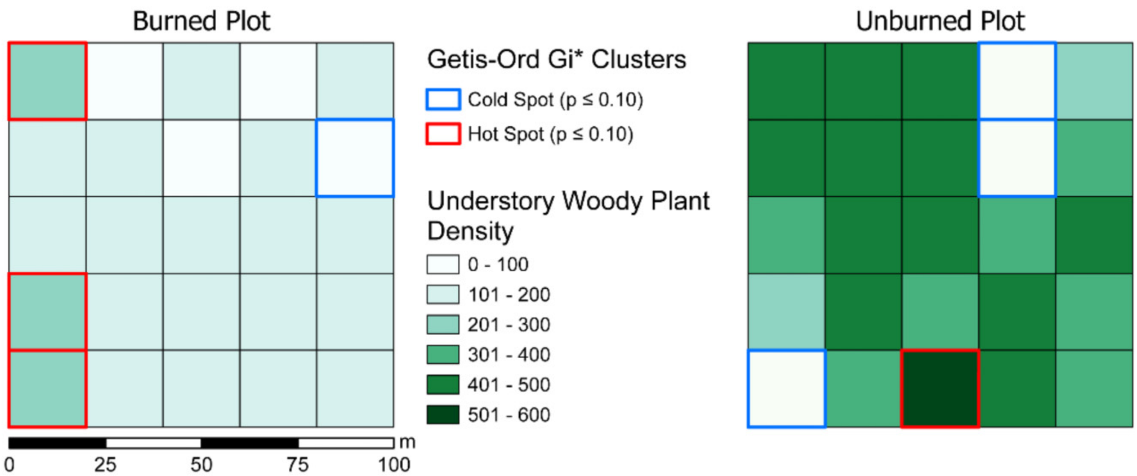
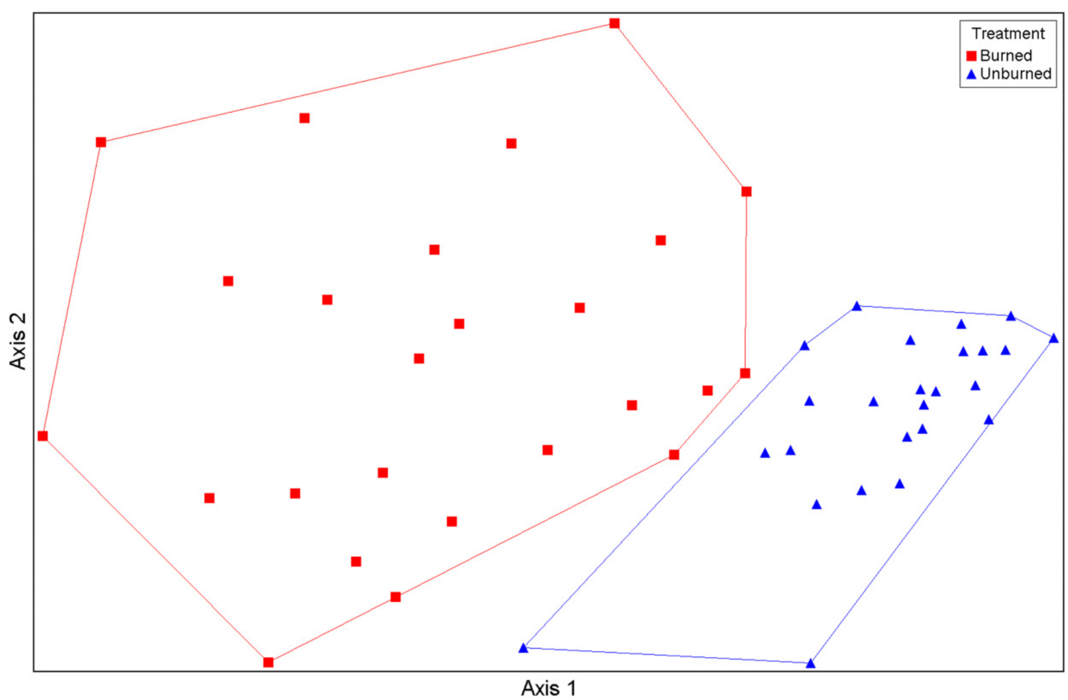


Fig. 3. Non-metric multidimensional scaling ordination of the understory woody plant (≥1 m height, <5 cm dbh) density (final stress = 11.1). Squares represent burned plot understory woody plant quadrats and triangles represent unburned plot understory woody plant quadrats.

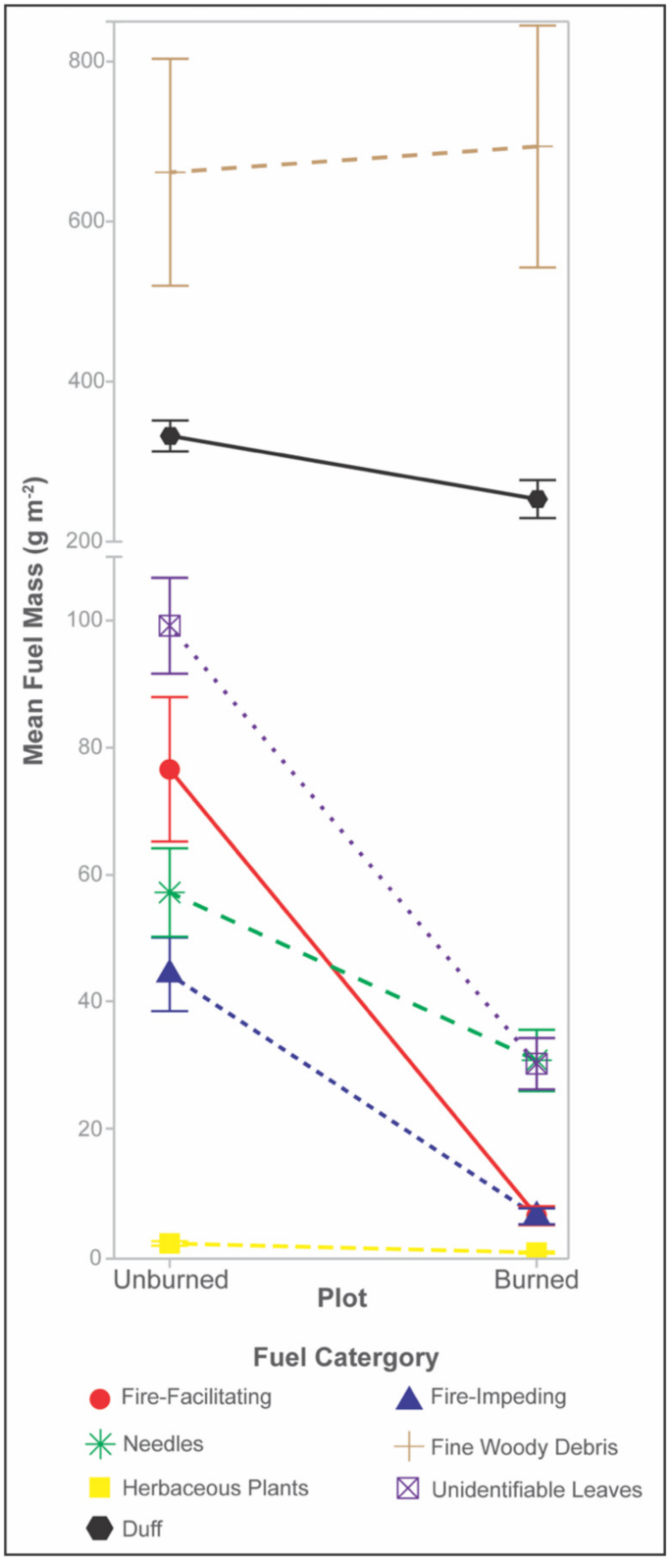


treatments. Additionally, mean categorical fuel mass between unburned and burned treatments was significantly different ($p < 0.01$). The mean mass of each fuel category, as well as percent contribution to mean mass, was lower in the burned plot compared to the unburned plot, except for FWD, which was slightly higher in the burned plot relative to the unburned plot.

Getis-Ord Gi* analysis indicated several hot spots of fuel mass across both the burned and unburned plots (Fig. 5). The unburned plot contained one significant fuel mass hot spot ($p < 0.01$). The burned plot had three significant hot spots ($p = 0.01$, 0.04, and 0.01) and two of the three hot spot quadrats were contiguous.

Using NMS within PC-ORD, fuelbed composition and loading were segregated by plot (final stress = 2.99; Fig. 6). Both plots had fuel samples ranging from the positive to negative ends of axis one. Burned fuels were clustered towards the negative range of axis two; however, unburned fuels exhibited wider variation in ordination space. Results from MRPP indicated that fuel assemblages were significantly different ($p < 0.01$) between the burned plot and the unburned plot. Fire-facilitating and fire-impeding fuels were positively

Fig. 4. 2 × 7 robust heteroscedastic mixed analysis of variance with 10% trimmed means showing mean fuel mass (g·m^{-2}) by category for burned and unburned 1 ha plots.



correlated ($r = 0.790$ and $r = 0.670$) with axis two. Additionally, unidentifiable leaves were positively correlated with axis two ($r = 0.738$). Fine woody debris was positively correlated with axis one ($r = 0.713$).

4. Discussion

4.1. Woody plant composition

The burned plot had fewer understory woody plants than the unburned plot. The difference was greater for sapling sized stems (86% less) compared to seedling sized stems (55% less). The difference in the sapling layer was noteworthy since some stems were almost 5 cm dbh. We acknowledge that our study was conducted during the first growing season after the latest fire, and that the distribution of seedling and sapling sized stems would be different if we had sampled two growing seasons post-fire as more stems would have recruited to the sapling size class.

A goal of the prescribed fire program was to promote regeneration of *P. echinata*. Despite the presence of sexually mature *P. echinata* trees across the burned plot, two prescribed fires alone did not appear to have altered *P. echinata* regeneration dynamics. We documented no *P. echinata* saplings post-fire and noted ca. 90% fewer *P. echinata* seedlings in the burned plot compared to the unburned plot. Initial reductions in *P. echinata* reproduction density post-burn have been recorded in other studies (Arthur et al. 1998; Dey and Hartman 2005; Elliott and Vose 2005; Clabo and Clatterbuck 2020; Goode et al. 2024). Although *P. echinata* advance reproduction in the seedling layer is often topkilled by fire, early allocation of resources to the root system and dormant buds on the basal crook enable individuals to resprout after topkill (Mattoon 1915). We propose two explanations for the low abundance of *P. echinata* seedlings. First, fire conditions may have been intense enough to kill *P. echinata* saplings and seedlings, as found in Lilly et al. (2012). Alternatively, decades-long accumulation of litter and duff development from historical fire suppression was not conducive substrate for *P. echinata* germination. In turn, all identified *P. echinata* seedlings in the burned plot could be resprouts of the already low density of individuals that had been present prior to the prescribed fires.

We observed a lower abundance of *Quercus* spp. advance reproduction in the seedling and sapling layer on the burned plot compared to the unburned plot. Alexander et al. (2008) found that *Quercus* spp. seedling survival decreased after a singular and three prescribed fires when compared to *Quercus* seedlings not subjected to prescribed fire. Other studies have also reported increased mortality of *Quercus* saplings and seedlings following single and repeated burns (Ferguson 1957; Brose and Van Lear 1998; Dey and Hartman 2005; Willson et al. 2018; Izbicki et al. 2020). It should be noted that recording abundance 3 months post-fire should allow time for initial resprouting of surviving stems (Alexander et al. 2008; Lilly et al. 2012). It is possible that accumulation of fuels from altered vegetation-fuels-fire feedbacks, combined with relatively intense fire behavior caused by weather conditions (Goode et al. 2024), adversely impacted *Quercus* spp. density in the regeneration layer.

Density of shade-tolerant understory woody plants was lower in the burned plot, which was consistent with other studies (Blankenship and Arthur 2006; Green et al. 2010; Arthur et al. 2015; Izbicki et al. 2020). Understory layer *A. rubrum*, *Nyssa sylvatica*, and *Oxydendrum arboreum* stems of-

Fig. 5. Map of fuel loading (g) and significantly ($p \leq 0.10$) hot and cold spots by 20 m^2 quadrats in burned and unburned 1 ha plots in a *Quercus–Pinus* mixedwood.

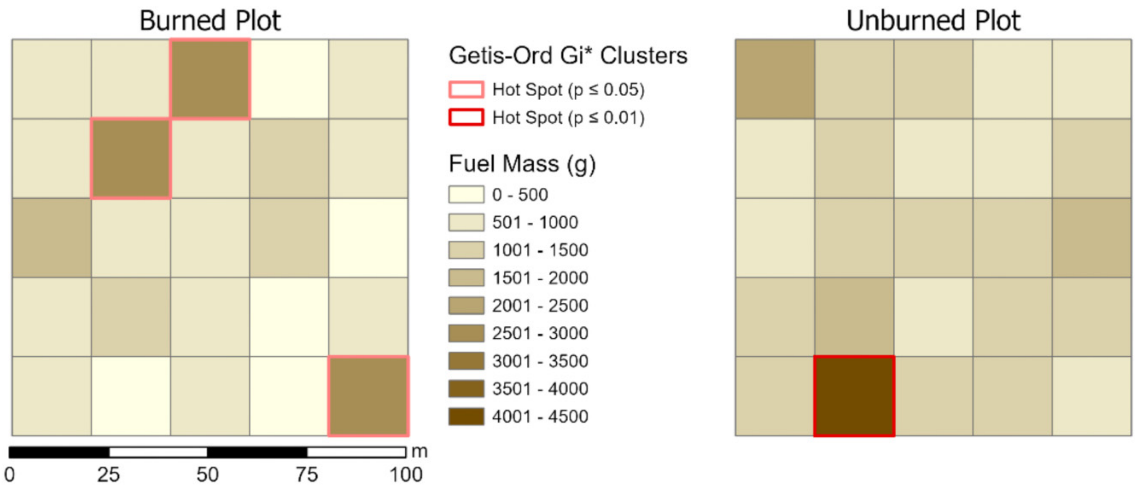
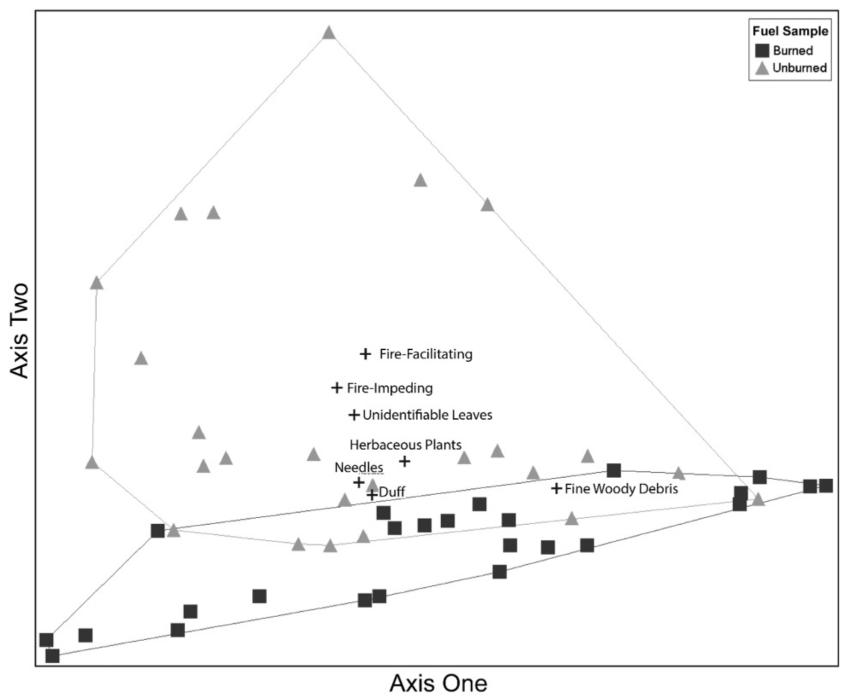


Fig. 6. Non-metric multidimensional scaling ordination summarizing variation in fuelbed loading by plot (final stress = 2.99). Squares represent burned plot fuel samples and triangles represent unburned plot fuel samples. Plus symbols are centroids of different fuel categories.



ten sprout prolifically after being topkilled, which can result in higher stem densities in the growing seasons following fire (Arthur et al. 1998; Willson et al. 2018). Although two prescribed fires may have reduced shade-tolerant saplings and seedlings, repeated fire and additional management strategies will likely be needed to further control shade-tolerant species prevalence and meet management goals.

Densities of *L. tulipifera* and *Sassafras albidum* seedlings within the burned plot were almost three times higher than their densities within the unburned plot. Dey and Hartman (2005) found that over 90% of *S. albidum* saplings and seedlings survived after three to four prescribed fires. *Sassafras albidum* advance reproduction also showed a relatively low mortality rate over 10 years of prescribed fire treatments of varying frequency (Fan et al. 2012). Beck and Sims (1983) and Hutchinson et al. (2005) found an increase in *L. tulipifera* germination and seedling density after fire. Seeds of *L. tulipifera* are able to remain viable in the seed bank for up to eight years (Beck and Sims 1983), which may explain the increased density of seedlings we observed. However, density of opportunistic species should not increase over time because prescribed fire alone may not increase understory photosynthetically active radiation (Chiang et al. 2005; Barefoot et al. 2019; Bassett et al. 2020). Opportunistic species such as *L. tulipifera* and *S. albidum* may germinate in abundance after prescribed fire, but recurring treatment (e.g., prescribed fire, mechanical or chemical removal) is often effective at inhibiting these species from recruiting to larger size classes.

Our spatial analyses indicated three significant hot spots of high understory woody plant density in the burned plot. This significant pattern was likely attributed to variability of fire intensity and resultant patchy effects on the understory woody plant assemblage. Other studies have documented a similar pattern of patchy fire effects on understory woody plant assemblages in upland *Quercus* and *Quercus*–*Pinus* stands (Franklin et al. 1997; Hutchinson et al. 2005; Goode et al. 2024). The final ordination solution of collected fuel samples also provided support for patchy fire effects. The three significant hot spots of high understory woody plant density corresponded to outlying plots in the fuels ordination. Fuels collected from these three hotpots had a greater mass than the remaining 22 fuel samples in the burned plot. Although sprouting could potentially explain greater understory woody plant density in these observed hot spots, the woody plants in the three significant hot spots would have likely had to experience a greater sprouting response than the woody plant communities in the remaining 22 quadrats that likely experienced more uniform fire effects. However, the woody plant density in the identified hot spots on the burned plot was only slightly lower than the cold spots on the unburned plots. The three 400 m^2 woody plant hot spots in the burned plot had a density of 204, 204, and 206 stems. Spatial analyses of the unburned plot indicated three significant cold spots and one significant hot spot of understory woody plant density. These significant 400 m^2 cold spots had a woody plant density of 232, 250, and 227 stems. Based on these results, we posit that the fire uniformly topkilled understory woody plants in the 22 insignificant quadrats, but also had a marginal effect on woody plant density in the hot spots. We suspect, based on the findings reported in Goode et al. (2024), that the significant cold spots of understory woody plant density occurred in intra-plot neighborhoods in which understory light availability was minimal, and the significant hot spot of understory woody plant density occurred in canopy gaps or similar high-light environments.

Understory woody plant assemblages were significantly different between burned and unburned plots. The burned plot exhibited greater variability in the understory woody plant assemblages relative to the unburned plot. We suspect that this was because some shade-tolerant species quickly resprouted after fire, as well as the addition of more shade-intolerant species like *L. tulipifera* that responded to fire. We can acknowledge *L. tulipifera* and other shade-intolerant species are likely ephemeral since understory light would not be sufficient without additional intervention. Furthermore, microsite variability was greater after the prescribed fire, as some intra-plot neighborhoods experienced minimal fire effects, so woody plant assemblages in the burned plot were composed of species that persisted through the fires as well as species that responded to variable microsites influenced by the fire effects. Although seedling and sapling density was significantly lower in the burned plot, woody plants with a variety of life history strategies and functional traits persisted or colonized after the prescribed fire, resulting in greater variability of the woody plant assemblages in the burned plot.

4.2. Fuels

Litter depth in the burned plot was not significantly different than in the unburned plot. In mixed *Pinus*–*Quercus* stands on the Cumberland Plateau in Alabama, Barefoot et al. (2019) found that litter depth varied from 2.1 cm in a stand burned on a three-year rotation to 4.7 cm in a fire excluded stand; and in an upland *Quercus* stand on the Cumberland Plateau in Kentucky, Arthur et al. (2017) found a singular fire had no significant effect on litter depth, but multiple fires significantly reduced litter depth. Although litter depth was similar, re-introduction of fire altered fuelbed composition, as fuelbed mass was significantly different between burned and unburned plots, which is consistent with prior findings (Waldrop et al. 2010; Arthur et al. 2017). For all fuel categories except FWD, mean fuelbed loading was lower in the burned plot. Additionally, the percent contribution to total fuel mass of all fuel categories, other than FWD, was lower in the burned plot relative to the unburned plot. Loucks et al. (2008) similarly found no reduction in 1 and 10 h fuels after a single prescribed fire in Appalachian hardwood stands. Similarities in mean FWD mass between plots could be the result of dead saplings and seedlings post-fire. Although the fire likely consumed FWD already present, it may have killed but not consumed saplings and seedlings thereby contributing FWD fuels to the fuelbed. In eastern USA *Quercus* stands, fuelbed loading has been found to increase to pre-burn levels within a few years after fire (Loucks et al. 2008; Waldrop et al. 2010; Arthur et al. 2017; Willson et al. 2018). We hypothesize that a fire return interval of five years or less would be needed to further reduce the fuelbed and expose bare mineral soil.

The variation in fuel flammability across intra-stand neighborhoods may create fine-scale differences in fire behavior and effects. The spatial analysis of total fuel mass by treatment provided marginal support for the effect of fine-scale fuelbed compositional differences. Although hot spots of understory woody plant density and fuel mass were few, a patchy distribution of fuels has been found to influence survival and mortality of woody plants following fire (Dunn and Bailey 2016; Robertson et al. 2019). We suggest that the hot spots of fuel mass indicated that either the fire did not consume a significant amount of fuel in the 400 m^2 hot spots, or that pre-fire fuel loading was greater in these hot spots than the surrounding neighborhoods. When these patterns were analyzed by fuel flammability categories, we found that fuel hot spots had a greater mass of fine woody debris. This increased FWD mass was attributed to sapling shoot mortality and lack of consumption of the resultant woody material, or the increased snag abundance in these hot spots, which contributed woody debris. We acknowledge that without pre-fire fuel loading, our spatial analyses of fuel loading in the burned plots lack important context.

The ordination of fuel mass indicated that fuel assemblages were significantly different by treatment. The fuel assemblage of the burned plot exhibited less variability in ordination space than the fuel assemblage of the unburned plot. We posit that the prescribed fire homogenized fuel loads, and this was supported by our Getis-Ord Gi* analysis of fuel mass. In 22 of the 25 fuel quadrats, no significant hotpots were documented, which indicated relatively uniform fuel consumption across these plots. Insufficient time elapsed between the prescribed fire and the fuel sample collection for significant litterfall to occur. Thus, the reduced fuel mass and decreased variability in the fuel assemblage in ordination space was likely attributed to fuel consumption by the prescribed fire. In long-unburned *Quercus*–*Pinus* mixedwoods, the intra-stand spatial variability of *Quercus*, *Pinus*, and mesophytic taxa differentially contribute to fuelbed composition and loading. Furthermore, we posit that if fuels were sampled after the growing season, fuel assemblages in the burned and unburned plots would have likely converged, because of fuel inputs from trees in the burned plot. Other fuel studies in mixedwoods and upland hardwoods have reported that fuel loads return to pre-burn levels often less than 5 years after a burn (Loucks et al. 2008; Waldrop et al. 2010; Arthur et al. 2017).

Despite differences in flammability and burning characteristics of fire-facilitating and fire-impeding litter, weather conditions during the fire may be more influential than fuelbed composition in determining fuel consumption. We found both fire-facilitating and fire-impeding fuel mass had strong positive correlation with axis two, but clustering of burned samples occurred in the negative range of axis two. Combined with the nearly identical mean mass of fire-impeding and fire-facilitating fuels, this indicates that fire-impeding litter was consumed at similar rates as fire-facilitating litter. Goode et al. (2024) analyzed prescribed fire effects located within the same *Quercus*–*P. echinata* stand and found that ca. half of their plots experienced fire effects after the first fire (i.e., the fire was patchy), and all plots experienced fire effects after the second fire. They found that after the second fire, all plots had a similar reduction in litter depth, despite some having only been burned by the second prescribed fire. The second fire occurred during a period of relatively warmer temperatures, low relative humidity, and steady wind through the day. We suggest that weather conditions, like those exhibited in the growing season fire studied here, contributed to more intense fire behavior. Thus, we contend that this fire reached an intensity threshold in which fuel flammability characteristics had minimal to no impact on fire behavior. We argue that more research is required to fully understand this proposed threshold in which weather conditions override the effects of individual fuel flammability characteristics on fire behavior.

4.3. Management implications

As has been shown repeatedly in other studies (Schwilk et al. 2009; Schweitzer et al. 2016; Barefoot et al. 2019), prescribed fire alone is not sufficient to restore and maintain *Quercus*–*Pinus* mixedwoods in forests that have not been managed for decades. Silvicultural prescriptions designed to reduce the fuelbed, increase understory light availability, and create microsite variability may be most suited for *Pinus* regeneration. Retention of the intact overstory during fire reintroduction should be prioritized, which will ensure a continued source of surface fuels that in turn promote desired fire effects, such as hardwood competition control and preparation of the seedbed. In our study, these desired effects had not yet fully manifested after two prescribed fires. Although continued use of fire may adversely impact seedling and sapling layer *P. echinata*, reducing hardwood competition and exposing bare mineral soil may be advantageous, especially if *P. echinata* advance reproduction density is low. Canopy openings created through harvests should increase available light while simultaneously removing fuel sources, creating more variability in fuel distribution. Utilizing patch shelterwood harvests or patch seedtree harvests with reserves, depending on *P. echinata* advance reproduction, should increase light availability in the regeneration layer and facilitate *P. echinata* regeneration (Hart et al. 2024). Artificial regeneration of *P. echinata* may be necessary in areas where no mature *Pinus* individuals exist to serve as a seed source, or where *Pinus* advance reproduction is lacking.

In *Quercus*–*Pinus* systems, recurring prescribed fire is necessary to create stand conditions suitable for *Pinus* regeneration, including creating bare mineral soil. After two prescribed fires, fuel mass was lower in the burned plot, but there was no significant difference in litter depth between burned and unburned plots. A slow reduction in fuel layer depth through repeated prescribed fires may be best to avoid stress and mortality among overstory trees. Additionally, based on a combination of Getis-Ord Gi* analysis and ordination, the prescribed fires appeared to homogenize fuel loads within the burned plot. We suggest that species-specific flammability characteristics are less influential to fire behavior and effects when weather conditions are conducive to burning. That is to say, burning under weather conditions similar to the growing season fire studied here may override litter flammability characteristics and homogenize the fuelbed.

Although we did document homogenized effects on fuel composition and understory woody plant communities, continued use of fire in *Quercus*–*Pinus* mixedwoods can lead to variability in plant and fuel assemblages. Additionally, burning under different weather conditions can further compound variability in fire behavior and effects. Thus, we recommend that managers forgo strict adherence to predetermined prescribed fire intervals. Frequent fire intervals of 1–4 years may enhance *Quercus* and *Pinus* reproduction potential. When desired stocking of *Quercus* and *Pinus* advance reproduction has been met, extending the fire return interval to 8–15 years may help improve survival and overstory recruitment of *Quercus* and *Pinus* individuals (Stambaugh et al. 2006). Thus, we encourage an adaptive fire management approach that can be altered to correspond with sporadic *P. echinata* seed production, and enhance germination potential and survival of advance reproduction. Embracing variability within *Quercus*–*Pinus* mixedwoods would be consistent with the natural patterns of disturbance that create neighborhood-scale differences in species assemblages and stand structure (Hart et al. 2024).

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

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