

## RESEARCH ARTICLE

# Changes in ground-layer plant species assemblages and successional patterns following a decade of oak regeneration restoration

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Open forest restoration transitions closed-canopy forests to a structure amenable to shade-intolerant species such as oak and often includes thinning or prescribed burns to promote diverse species composition. We measured how oak restoration treatments influenced ground-layer species assemblages and successional patterns in an ecologically diverse mesic hardwood forest. We tested how repeated prescribed fire, midstory herbicide applications, and the combination of shelterwood overstory harvest and prescribed fire influenced species diversity and turnover, and if species showed affinity to particular treatments throughout time. We monitored ground-layer species composition, abundance, and environmental variables for 9–11 years across manipulated forest stands. Species richness increased after roughly a decade following all treatments (+12 species following repeated fire, +9 species following shelterwood/fire, and +6 species following midstory herbicide) relative to controls (no increase), without substantial species turnover. The paired shelterwood/fire treatment increased light availability to the ground-layer 10-fold the year following overstory harvest, altering environmental parameters, species diversity, and successional patterns more than the individual midstory herbicide or repeated fire treatments. This treatment also increased *Rubus* spp. dominance, which persisted as a recalcitrant layer after 9 years. Transitioning closed-canopy forests for oak restoration simultaneously influences the diversity of the forest ecosystem, primarily following the combination of thinning and repeated fire treatments.

**Key words:** ground-layer light availability, ground-layer species diversity, oak restoration treatments, *Rubus*, species dominance patterns, species trajectory

## Implications for Practice

- Long-term monitoring of ground-layer plant species richness, turnover rates, and trajectories following oak restoration practices is vital to ecological forestry strategies that prioritize oak restoration and ecosystem function.
- Restoration practices that remove the overstory, coupled with repeated fire, increased ground-layer diversity in the degraded southern hardwood forests but also increased *Rubus* dominance for at least 9 years without favoring oaks.
- Practices that remove the midstory, such as repeated fire alone, favor ground-layer oaks without negatively influencing herbaceous diversity and may be a viable restoration option benefiting both the target species and its ecosystem.

## Introduction

In temperate forests of North America and Europe, frequent disturbances historically maintained a continuum of forest structures, including savannahs and open and closed woodlands characterized by sparse woody cover beneath the main canopy (Bobiec et al. 2018; Hanberry et al. 2018). This structural heterogeneity fostered the continuous regeneration and overstory

recruitment of *Quercus* across spatial and temporal scales (Delcourt & Delcourt 2004; Foster et al. 2004; Carrión et al. 2007). Densification of contemporary temperate *Quercus* forests (Mölder et al. 2014; Hanberry & Abrams 2018) is attributed to fire suppression policies (Abrams 1992; Hutchinson et al. 2008; Nowacki & Abrams 2008), changing climate (Pederson et al. 2014), and changing land uses, including forest clearing and agriculture (Hart & Grissino-Mayer 2008; Bobiec et al. 2018). Understory densities of shade-tolerant species are increasing in previously open *Quercus* woodlands (Fei & Steiner 2007; Woodbridge et al. 2022), and recruitment of *Quercus* into forest canopies is decreasing worldwide (Fei et al. 2011; Singh et al. 2016; Spînu et al. 2020). Loss of open forest

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conditions has negative consequences, within and among trophic levels, for bird (Hanberry & Thompson III 2019), pollinator (Hanula et al. 2015), and plant (Leach & Givnish 1999; Hedwall et al. 2013) biodiversity. The ground-layer plant community (all vascular species <1 m tall) may account for less than 1% of the total living biomass in a forested system, yet it can comprise ≥90% of the plant species richness, perform essential nutrient cycling functions (Gilliam 2007; Elliott et al. 2015), and can act as a primary biotic filter affecting tree regeneration (Royo & Carson 2006; Johnson et al. 2019).

Environmental factors associated with complex topography (elevation, slope, aspect, concavity, and convexity) influence the growth of ground-layer species by affecting temperature, moisture, and light regimes at the forest floor (Huebner et al. 1995; Hutchinson et al. 1999; Small & McCarthy 2003). Composition, productivity, and ecological functions of ground-layer plant communities are particularly sensitive to changes in environmental resource gradients associated with canopy structure (Raymond et al. 2006; Fahey & Puettmann 2007). Homogenization of the forest canopy (closure) can decrease available light and soil moisture gradients (Brudvig & Asbjornsen 2009; Grayson et al. 2012), which can reduce richness, diversity, and productivity of the ground-layer community (Kwiatkowska 1994; Jules et al. 2008; Dohn et al. 2013).

Temperate forest managers are increasingly considering the restoration of more open canopy conditions, intending to maintain/recover the diversity and productivity of the ground-layer plant community, while simultaneously favoring species-targeted tree regeneration (Moore et al. 2006; Bolton & D'Amato 2019; Vander Yacht et al. 2020). In the eastern United States, harvesting and/or prescribed fire are used to transition closed-canopied *Quercus* forests to characteristically open and closed *Quercus* woodlands (Dey et al. 2017; Vander Yacht et al. 2017; Oakman et al. 2019). Literature describing the response of *Quercus* species to restoration treatments is abundant, yet relatively less information on the short- and long-term changes in species assemblages and successional patterns of the ground-layer plant community exists (White 1983; Yantes et al. 2023). Yet, management and restoration actions focused on *Quercus* will influence other species and the ecological function of the ecosystem, underscoring the need for large-scale experimentation and long-term monitoring.

The evaluation of restoration success relies not only on tree survival, but also on how ecosystem diversity and functions benefit across time scales. Elsewhere we have reported the influence of oak-focused silvicultural treatments on the functional diversity and structure of the regeneration layer following treatment (Keyser et al. 2020; Beasley et al. 2022). In this study, we addressed how three treatments designed to restore a competitive oak regeneration layer by increasing canopy openness to varying degrees influenced microenvironmental resource gradients (including light availability to the forest floor) and diversity (species assemblages and successional patterns) of the ground-layer plant community for 9–11 years following treatments. We used a before–after control–impact design to account for inherent variability in the southern mixed hardwood forest. We used multivariate analyses to test if restoration treatments influenced (1) species diversity through turnover, abundance, and

dominance patterns, and (2) species' affinities to treatments throughout time. We hypothesized that ground-layer species composition would shift from more shade-tolerant, fire-sensitive species to more shade-intolerant, pyrophytic species following treatments that incorporated fire due to changes in light availability and soil nutrients post-fire. We further hypothesized that changes in ground-layer species assemblages and successional patterns would be most prolific following a combined harvest and fire, which most substantially increased light to the ground-layer.

## Methods

### Study Site

This study was conducted in the Cold Mountain Game Land (CMGL; 1333 ha), Haywood County, western North Carolina, United States (35.40°N, 82.93°W). Managed by the North Carolina Wildlife Commission, CMGL is in the Pigeon River watershed, within the Southern Blue Ridge Mountains Subsection of the broader Central Appalachian Broadleaf Forest-Coniferous Forest Province (Cleland et al. 2007). Annual precipitation from 1991 to 2020 ranged from 276 mm (autumn) to 346 mm (winter), averaging 1276 mm, and annual low and high temperatures averaged 5.2 and 18.4°C, respectively (National Oceanic and Atmospheric Administration 2023). The mountainous topography includes steep slopes and associated valleys. Elevation ranged 980–1270 m, and slopes ranged from 35 to 55%. Aspect varied widely across the treatment units, including NW–NE ( $n = 7$ ), SE–SW ( $n = 6$ ), E ( $n = 2$ ), and W ( $n = 1$ ). Soils were predominantly incepticols (Typic Humudepts: Plott soil series and Typic Dystrudepts: Edneyville soil series) and ultisols (Typic Hapludults: Evard soils series, Humic Hapludults: Saunook soil series, and Humic Hapludults: Trimont soil series) (McNab & Keyser 2020).

Selected forest stands were undisturbed mature second-growth (≥80 years old) forests that originated after widespread clearcut logging and high grading that occurred around the turn of the 20th century. Species composition was typical of mesic upland Southern Appalachian mixed-*Quercus* forests. Dominant canopy species included *Quercus* (*alba*, *coccinea*, *montana*, *rubra*, and *velutina*), *Carya* (*cordiformis*, *glabra*, *ovalis*, and *tomentosa*), and *Liriodendron tulipifera* (Greenberg et al. 2012). The midstory was dominated by shade-tolerant species including *Acer rubrum*, *Cornus florida*, *Halesia tetraptera*, *Nyssa sylvatica*, and *Oxydendrum arboreum* (Keyser et al. 2012). Site index (base age 50 for *Quercus*) of experimental units ranged from 22.7 to 31.0 m, although site index in these degraded stands can be an unreliable indicator of site quality. Pre-treatment basal area (BA) of the productive mixed-*Quercus* stands ranged from 26.6 to 31.6 m<sup>2</sup>/ha (Beasley et al. 2022).

### Experimental Design and Data Collection

Sixteen experimental units in the CMGL were selected in 2008 (5 ha each; separated by ≥20 m untreated buffers) (Fig. S1). To be included, stands met the following conditions: (1) oak

comprised a substantial component of the canopy; (2) no recent (<20 years) substantial disturbance; (3) minimal ericaceous shrub cover; (4) full stocking; and (5) comprised trees that were at least 70 years old (Beasley et al. 2022). Three oak restoration treatments and an unmanipulated control (CTL) were randomly assigned to the units, each replicated four times. Within each unit, we established 3 permanent overstory vegetation plots (48 plots total) and 12 ground-layer subplots (192 plots total) that we surveyed intermittently beginning in 2008.

The objective of each oak restoration treatment was to increase light to the forest floor, in varying degrees, to promote competitive *Quercus* regeneration and recruitment. The oak shelterwood treatment (OSW; Loftis 1990) prescribed the removal of midstory stems (<25.0 cm dbh) other than *Quercus* and *Carya* via herbicide (Garlon 3A, active ingredient triclopyr, Dow Chemical Company, Indianapolis, IN, U.S.A.). Herbicide was applied using the stem injection method in September 2008, prior to leaf-fall and after pre-treatment data collection (Table S1). No canopy gaps were created. The repeated fire treatment (FIRE) prescribed conducting low-intensity fires in the dormant season, every 3–5 years. Burn applications were asynchronous due to logistics and environmental conditions. Two replicate units were burned on 25 February 2009 and 2 April 2014, and the remaining two units were burned 1 April 2010 and 18 March 2015 (Table S1). Characteristic of the region, fire intensity was low for all burns (first fires: 15–27°C and second fires: 12–23°C). Humidity ranged from 20 to 40% for all fires conducted (Beasley et al. 2022). The shelterwood harvest and fire treatment (SWF; Brose et al. 1999) began with a commercial timber harvest, leaving 9.2–11.5 m<sup>2</sup>/ha residual BA of dominant and co-dominant stems, intentionally reducing BA to levels associated with an open *Quercus* woodland (Brose et al. 2014; Hanberry & Abrams 2018). A dormant season prescribed fire was conducted 4–6 years post-harvest, with the objective of killing fire-sensitive species (e.g., *A. rubrum* and *N. sylvatica*) and favoring more pyrophytic species (*Quercus* and *Carya*) in the midstory (Keyser et al. 2020). Harvest and burn operations were asynchronous, with two replicate units harvested before the 2010 growing season and burned in March 2016, and two units harvested before the 2011 growing season and burned in March 2015 (Table S1). For all SWF burns, fire intensity was low and temperatures ranged from 7 to 16°C, with humidity ranging from 20 to 40% (Beasley et al. 2022).

Three permanent overstory plots (0.05 ha; circular) were installed within each of the 16 replicate units (Fig. S2). Species and diameter at breast height (dbh taken at 1.37 m above groundline) of all overstory stems (≥25 cm) were recorded. Within concentrically nested subplots (0.01 ha), species and dbh of all midstory stems (≥5 and <25 cm dbh) were recorded. Permanent ground-layer vegetation subplots (1 m<sup>2</sup>) were established 11 m from plot center in cardinal directions, resulting in 12 per unit (48 per treatment). Spatial data, including plot-level latitude, longitude, and elevation (m) was recorded using recreational grade global positioning system device. Plot-level terrain shape index (TSI) and landform index (LFI), which quantify landform shape from convex (low value) to concave (high

value) on a micro (TSI) or macro (LFI) scale, were calculated (McNab 1989, 1993).

Ground-layer vegetation (all herbaceous and woody vascular species, <1 m tall) surveys were conducted in each 1 m<sup>2</sup> ground-layer subplot during the summer (July–August), intermittently since 2008 (Table S1). Plants were identified to species when possible, using nomenclature and identification codes from the United States Department of Agriculture: Natural Resource Conservation Service PLANTS database (USDA NRCS 2023). Species percent cover was visually estimated and recorded in seven cover classes: 1 (<1%), 2 (1 to <5%), 3 (5 to <25%), 4 (25 to <50%), 5 (50 to <75%), 6 (75 to <95%), 7 (95–100%). Cover class midpoint values recorded for each species were averaged to plot-level species cover and used for further analyses.

Photosynthetically active radiation (PAR in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was measured at 0.3, 0.6, and 1 m above the ground surface at the center of each ground-layer subplot using an ACCUPAR LP-80 ceptometer (Decagon Devices, Pullman, WA, U.S.A.) to assess light attenuation below the canopy and midstory layers in 2019. Measurements were averaged to plot level ( $n = 4$  per plot; Fig. S2). Canopy openness was measured 8 m from plot center at 45° and 245° azimuth using a concave spherical densitometer each time the vegetation was measured and averaged to plot level ( $n = 8$  per plot; Fig. S2). Soil composition and nutrient samples were collected in each ground-layer subplot and composited to plot level ( $n = 4$  per plot; 10 cm diameter core to 15 cm deep) in the summer (July–August) of 2019. Samples were air dried and submitted to Brookside Labs (New Bremen, OH, U.S.A.) for standard texture, micro- and macro-nutrient analyses.

## Data Analysis

Due to the asynchronous treatment schedule, data were analyzed on a “years-post-initial treatment” basis, hereafter referred to as year, or “Y” (Table S1); this allowed units that were treated in different calendar years to be analyzed together to maximize replication and focus on temporal (years-post-treatment) patterns of responses. Species richness and standard errors (SE) were calculated at the unit level ( $n = 4$  per treatment) and illustrate the sampling variability in response to treatments. Species turnover was calculated as the total number of species lost versus the total number of species gained from pre-treatment to Y9 ( $n = 4$  units/treatment) and graphed using a rank abundance curve (logarithmic scale) to visualize species richness and evenness patterns (Fig. 1). Multivariate analyses were performed at the plot-level using PC-ORD 7 (MJM Software, Corvallis, OR, U.S.A.) to evaluate changes in species composition throughout years. Multi-response permutation procedures (MRPP), with the option to make pairwise comparisons, tested the hypothesis of no differences in species occurrence (presence/absence), or abundance (percent cover), among treatments for pre-treatment through Y3, and Y9 (Peck 2016).

Nonmetric multidimensional scaling (NMS) was used to compare species composition by ordinating plots in species space and overlaying our biotic and abiotic environmental

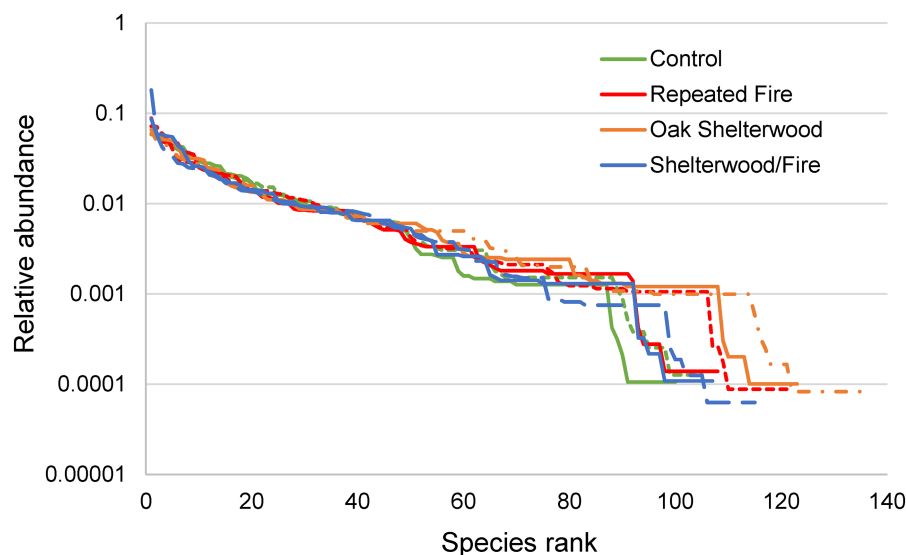


Figure 1. Rank abundance curve (log scale) with solid lines representing richness and evenness before restoration treatments (pre-treatment) and dashed lines representing conditions 9 years after treatment (treatment schedule: Table S1).

parameters to show the effects of the large-scale treatments versus microenvironmental influences on species occurrence at three separate time periods (pre-treatment, in Y1, and Y9). Environmental parameters in the secondary matrix included latitude, longitude, elevation, TSI, LFI, overstory BA (OSBA:  $\text{m}^2/\text{ha}$ ) and density (OSTph: trees/ha), midstory BA (MSBA:  $\text{m}^2/\text{ha}$ ) and density (MStph: stems/ha), and canopy openness (%). Sorensen's distance was applied to the species cover matrix and Euclidean distance was applied to the environmental variable matrix. Mantel's asymptotic approximation was used to standardize the results for randomization runs (Peck 2016). Mantel tests were performed on species abundance data using environmental parameters as the second matrix to test if the observed dissimilarities in species abundance were related to the observed dissimilarities in the environmental patterns and if this changed throughout years (pre-treatment through Y3, and Y9; Peck 2016). Soil characteristics and light availability (ceptometer) measured in 2019 were also compared with the Y9 species abundance using Mantel tests and as biplot vectors in ordinations if  $r^2$  greater than 0.3.

Indicator species analysis (Dufrene & Legendre 1997) of species abundance data used Monte Carlo procedures ( $p < 0.05$ ) to evaluate the percent affinity (indicator value-IV% based on combining the relative abundance and relative frequency) of a species to certain treatments before treatments, in Y1, and in Y9. Species present in less than 5% of surveyed plots were deleted to reduce noise in the data (Peck 2016). Sorensen's distance was applied with treatment as the grouping variable. A separate NMS was performed on combined species abundance data for pre-treatment through Y3, and Y9 to evaluate successional trajectories, or changing patterns of species abundance throughout years. Autopilot mode was used to select an appropriate number of axes for graphing ordinations and Sorensen's distance was applied to the species cover matrix.

Ceptometer measurements were normalized [ $n - \min / (\max - \min)$ ] at the subplot level to account for varying sky conditions, then averaged to plot level. We calculated the linear slope of change in PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) from 0.3 to 0.6 m and from 0.6 to 1 m ascending the forest floor and used a generalized linear model and Levene's test of homogeneity to test for differences among treatments at the different ground-layer strata. We also tested the coefficient of variation (CV) among treatments for the separate slopes to evaluate if the treatments resulted in a more or less, homogenous ground-layer light environment. Generalized linear model with a Tukey's honest significance test (HSD) was used to test for differences in canopy openness among treatments pre-treatment, in Y1, and Y9 ( $n = 12$  plots/treatment). The same model was used to test for differences in the CV of canopy openness to evaluate if treatments resulted in a more, or less, homogenous canopy cover following treatments ( $n = 4$  units/treatment). All model analyses were conducted using SAS (version 9.4; Cary, NC, U.S.A.), unless indicated otherwise.

## Results

### Ground-Layer Species Richness and Turnover

More than 250 ground-layer plant species were identified during vegetation surveys. Species richness increased in Y1 following the SWF (overstory harvest only; +15 species) and FIRE (single fire; +13 species) and decreased in Y1 following OSW herbicide (−4 species; Table 1). By Y9, species richness had increased in all treatments (+12 in FIRE, +8 in SWF, and +6 in OSW), with no change observed in the CTL. Variability (SE) in species richness was greatest among SWF units pre-treatment, yet decreased following treatments, despite an increase in total richness (pre-treatment:  $49.8 \pm 7$ ; Y1:

**Table 1.** Species richness (with standard errors below) and turnover of ground-layer vegetation by treatment throughout treatment years. Mean richness represents variability in occurrence among 16 experimental units (measured in 48, 1 m<sup>2</sup> subplots per unit). Turnover represents the number of species lost or gained at the plot level between pre-treatment and Y9. Asterisks indicate years when only two (of four) shelterwood/fire treatment units were measured.

| Treatment        | Species richness by treatment and year-post-treatment |             |             |             |             |              |             |             | Turnover   |             |
|------------------|-------------------------------------------------------|-------------|-------------|-------------|-------------|--------------|-------------|-------------|------------|-------------|
|                  | Pre                                                   | 1           | 2           | 3           | 6           | 7            | 8           | 9           | Loss       | Gain        |
| Control          | 50.3<br>4.9                                           | 54.3<br>4   | 54.8<br>4.3 | 53<br>5.1   | —           | 49.5<br>3.5  | —           | 50<br>4.4   | 6.4<br>0.9 | 9.3<br>0.6  |
| Oak shelterwood  | 52.3<br>4.3                                           | 48.3<br>7.9 | 57.8<br>8.2 | 56.5<br>5.3 | —           | —            | —           | 58.3<br>4.2 | 7.3<br>1.2 | 12.8<br>1.6 |
| Repeated fire    | 43<br>4.9                                             | 55.8<br>5.6 | 54.3<br>5.9 | 52<br>4.1   | 56.3<br>8.5 | 52.8<br>7.1  | 55.3<br>5.9 | 55.3<br>5.8 | 5.2<br>0.4 | 11.4<br>0.8 |
| Shelterwood/fire | 49.8<br>7                                             | 65<br>6.4   | 62<br>4.6   | 60.3<br>4.2 | —           | *46.5<br>7.5 | *60<br>10   | 58<br>5.5   | 3.8<br>1.7 | 16.5<br>1.1 |

65 ± 6.4; Y9: 58 ± 5.5). Plot-level species turnover was similar for all treatments, with the number of species lost between pre-treatment and Y9 being less than the number gained, supporting increasing richness patterns (Table 1).

### Ground-Layer Species Composition

Species occurrence (presence/absence; Table S2) and abundance (percent cover) differed significantly among treatments throughout the years (overall MRPP,  $p < 0.001$ ; Table 2). Species occurrence was similar between FIRE and OSW for all years ( $p \geq 0.07$ ), and between CTL and FIRE in Y9 ( $p = 0.07$ ). Species abundance revealed fewer significant pre-treatment differences, and all treatment combinations were significantly different by Y9 ( $p \leq 0.046$ ). Species evenness among treatments was relatively similar between pre-treatment and Y9 for common species (ranked <60), but less similar for more rare species (ranked >90; Fig. 1). The relative abundance of more rare species increased by Y9 for all treatments, chiefly in FIRE. Inspection of the Y9 species abundance data suggests that *Rubus*

*allegheniensis* (high shade- and fire-tolerance) was primarily responsible for the higher dominance pattern evident in SWF.

Differences in species abundance among treatments were evident in the distribution of plots in the NMS ordination space for pre-treatment (final stress = 16.6, instability = 0), Y1 (final stress = 15.9, instability = 0), and Y9 (final stress = 16.3, instability = 0) (Fig. 2). Most of the variation in species abundance was explained by axis 1, with axes 2 and 3 explaining less, but nearly equal variance throughout years (cumulatively representing 69–72% of the variation explained in ordinations). Pre-treatment, plots were not organized into discrete clusters in the ordination space. Axis 1 had the most associated species ( $r^2 > 0.2$ ), including seven species that remained associated into Y1 (Table S3).

Before silvicultural manipulations, each treatment had a unique set of significant indicator species, ranging from one in the FIRE to seven in the SWF (Table S4). *Carya cordiformis*, a shade-intolerant species associated with axis 3 in pre-treatment ordinations, was a pre-treatment indicator of the SWF (as were five herbaceous species and another shade-

**Table 2.** Results from multi-response permutation procedures (MRPP) performed on species occurrence (presence/absence), and species abundance (cover) data showing statistically significant (bolded if  $p < 0.05$ ) overall and pairwise differences in response by treatment year. Treatments include: controls (CONT), shelterwood/fire (SWF), oak shelterwood (OSW), and repeated fire (FIRE).

| Year                     | Overall |                  | CONT<br>versus SWF |                  | CONT<br>versus OSW |              | CONT<br>versus FIRE |             | FIRE<br>versus SWF |                  | FIRE<br>versus OSW |              | OSW<br>versus SWF |                  |
|--------------------------|---------|------------------|--------------------|------------------|--------------------|--------------|---------------------|-------------|--------------------|------------------|--------------------|--------------|-------------------|------------------|
|                          | A       | p=               | A                  | p=               | A                  | p=           | A                   | p=          | A                  | p=               | A                  | p=           | A                 | p=               |
| Species presence/absence |         |                  |                    |                  |                    |              |                     |             |                    |                  |                    |              |                   |                  |
| Pre                      | 0.048   | <b>&lt;0.001</b> | 0.081              | <b>&lt;0.001</b> | 0.026              | <b>0.02</b>  | 0.026               | <b>0.03</b> | 0.034              | <b>0.02</b>      | 0.013              | 0.131        | 0.02              | <b>0.04</b>      |
| Y1                       | 0.064   | <b>&lt;0.001</b> | 0.089              | <b>&lt;0.001</b> | 0.036              | <b>0.01</b>  | 0.03                | <b>0.01</b> | 0.056              | <b>0.001</b>     | 0.014              | 0.141        | 0.036             | <b>0.005</b>     |
| Y2                       | 0.062   | <b>&lt;0.001</b> | 0.086              | <b>&lt;0.001</b> | 0.028              | <b>0.02</b>  | 0.026               | <b>0.02</b> | 0.065              | <b>0.001</b>     | 0.014              | 0.128        | 0.041             | <b>0.003</b>     |
| Y3                       | 0.057   | <b>&lt;0.001</b> | 0.071              | <b>&lt;0.001</b> | 0.025              | <b>0.03</b>  | 0.024               | <b>0.03</b> | 0.068              | <b>&lt;0.001</b> | 0.013              | 0.114        | 0.037             | <b>0.006</b>     |
| Y9                       | 0.062   | <b>&lt;0.001</b> | 0.085              | <b>&lt;0.001</b> | 0.025              | <b>0.02</b>  | 0.017               | 0.07        | 0.07               | <b>&lt;0.001</b> | 0.022              | 0.068        | 0.042             | <b>0.001</b>     |
| Species cover            |         |                  |                    |                  |                    |              |                     |             |                    |                  |                    |              |                   |                  |
| Pre                      | 0.026   | <b>&lt;0.001</b> | 0.041              | <b>&lt;0.001</b> | 0.017              | <b>0.008</b> | 0.01                | 0.08        | 0.02               | <b>0.02</b>      | 0.009              | 0.1          | 0.008             | 0.1              |
| Y1                       | 0.055   | <b>&lt;0.001</b> | 0.056              | <b>&lt;0.001</b> | 0.024              | <b>0.005</b> | 0.013               | <b>0.04</b> | 0.066              | <b>&lt;0.001</b> | 0.013              | 0.09         | 0.054             | <b>&lt;0.001</b> |
| Y2                       | 0.061   | <b>&lt;0.001</b> | 0.061              | <b>&lt;0.001</b> | 0.012              | 0.07         | 0.013               | 0.06        | 0.084              | <b>&lt;0.001</b> | 0.012              | 0.1          | 0.075             | <b>&lt;0.001</b> |
| Y3                       | 0.061   | <b>&lt;0.001</b> | 0.067              | <b>&lt;0.001</b> | 0.005              | 0.22         | 0.01                | 0.08        | 0.096              | <b>&lt;0.001</b> | 0.009              | 0.1          | 0.07              | <b>&lt;0.001</b> |
| Y9                       | 0.066   | <b>&lt;0.001</b> | 0.074              | <b>&lt;0.001</b> | 0.025              | <b>0.006</b> | 0.023               | <b>0.01</b> | 0.071              | <b>&lt;0.001</b> | 0.019              | <b>0.046</b> | 0.064             | <b>&lt;0.001</b> |

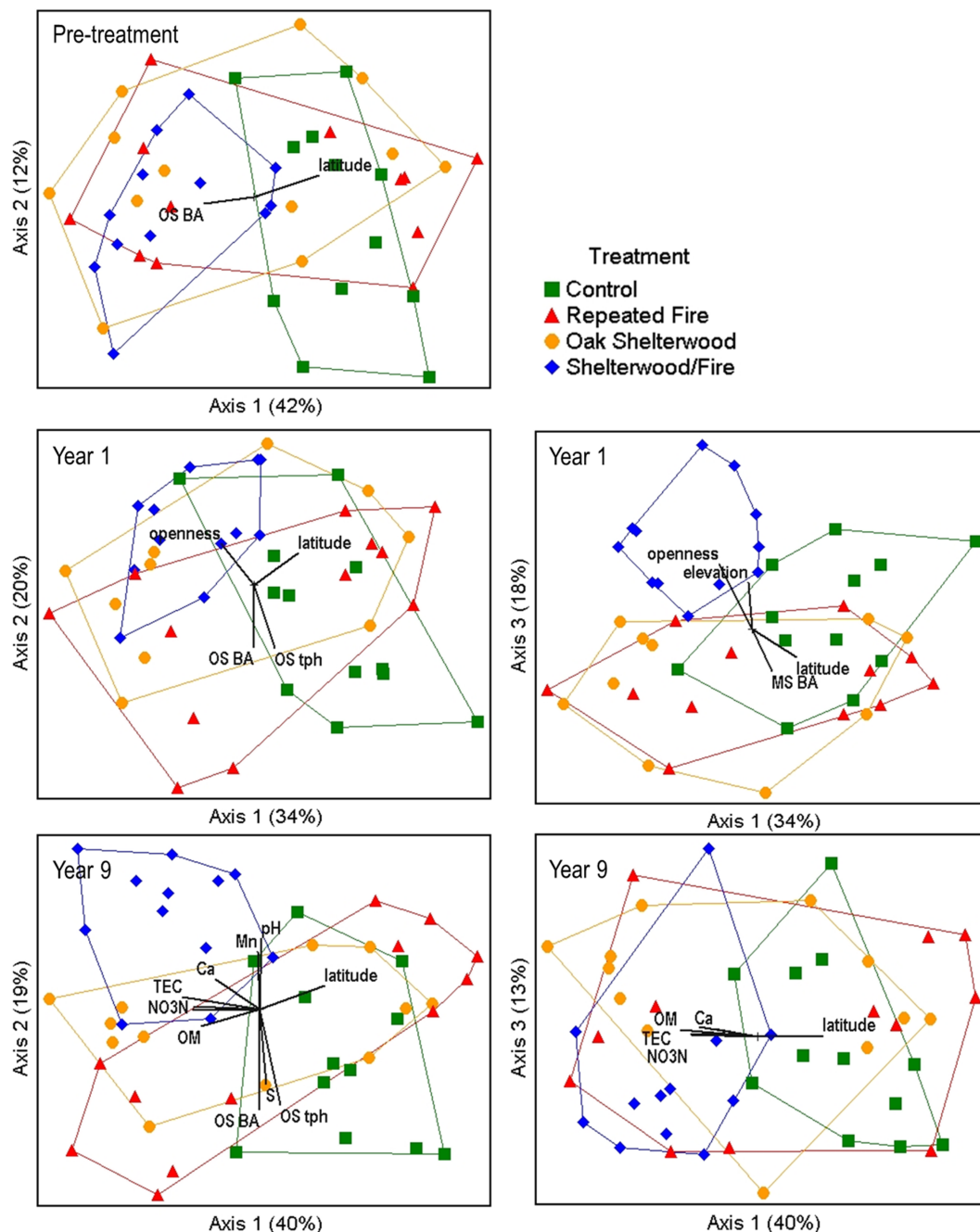


Figure 2. Nonmetric multidimensional scaling ordinations of plots (colored symbols) in species space comparing changes to species abundance patterns pre-treatment, Y1, and Y9. Environmental joint biplot vectors ( $r^2 > 0.2$ ) display changes to environmental parameters throughout treatment years (solid black lines). Three axes cumulatively account for 69–72% of the variation explained in ordinations (axis 1 representing the most variance for all ordinations/years). Axis 3 in the pre-treatment NMS is supplemented in Figure S3. Soil nutrient variables ( $r^2 > 0.3$ ; measured in 2019) are displayed in the Y9 ordination.

intolerant woody species, *Fraxinus americana*). Five pre-treatment CTL indicators included four woody species (notably shade-tolerant *A. rubrum*, shade-intolerant *Liriodendron tulipifera*, and *Quercus montana*) and one herbaceous species. The OSW had two pre-treatment indicator species: *Symphotrichum cordifolium* (switched affinities to SWF in Y9) and *Parthenocissus quinquefolia* (intermediate shade-tolerance and low fire tolerance; increasing IV through Y9).

*Quercus coccinea* (medium fire-, low shade-tolerance), the only pre-treatment FIRE indicator and a species with remained significant through Y9.

In Y1, SWF plots shifted higher along axis 2, shifting from other treatments (Fig. 2). A complete separation of the SWF relative to other treatments occurred along axis 3. Some FIRE plots shifted and spread wider along axis 2, while others shifted only slightly. In addition to the seven previously mentioned species,

three more were associated ( $r^2 > 0.20$ ) with axis 1. Species associated with axis 3 included several vines: two species with high fire tolerance (*Rubus allegheniensis* and *R. odoratus*) and two with low fire tolerance (*P. quinquefolia* and *Vitis aestivalis*), all indicators of the OSW (*P. quinquefolia*) or SWF (all others) in Y1. No species were associated with axis 2.

Nine more indicator species showed affinity to the SWF than any other treatment in Y1, including several that were associated with axis 2 in ordinations (Tables S3 & S4). Additional Y1 SWF indicators included three early-successional/disturbance species with high fire tolerance: *Erechtites hieracifolius*, *Robinia pseudoacacia*, and *Phytolacca americana*. In Y1, four additional herbaceous species and *P. quinquefolia* became indicators of OSW, and three new indicators showed affinity to FIRE, including *Q. coccinea*. Indicators of CTL in Y1 included the retention of two fire-intolerant woody species, shade-tolerant *A. rubrum* and *Q. montana*, and the addition of one new herbaceous species.

The SWF moved even higher along axis 2 by Y9 and was more distinctly separated from all other treatments (Fig. 2). Two species associated with axis 1 in Y1 persisted (*Aristolochia macrophylla* and *Desmodium nudiflorum*), and three species associated with axis 1 since pre-treatment remained significant (*Dichanthelium boschii*, *Sanguinaria canadensis*, and *Smilax glauca*; Table S3). Three new species became associated with axis 1 in Y9, and axis 2 associations included one shrub and two vines, notably *R. allegheniensis*. Axis 3 had no strong species associations. By Y9, only the SWF retained a high number of indicators (16), and indicators associated with the CTL had vanished (Table S4). Five new indicators of the SWF included several herbaceous and one woody species (shade-intolerant *L. tulipifera*). Persistent SWF indicators included two vines (*R. allegheniensis* and *V. aestivalis*; associated with axis 2), a shrub, a graminoid, and three additional herbaceous species.

#### Ground-Layer Composition Relative to Other Biotic and Abiotic Conditions

Although not apparent pre-treatment (Mantel,  $p = 0.5$ ), species abundance was highly correlated with environmental parameters following treatments (Mantel,  $p < 0.001$ ) and strong relationships remained apparent into Y9. Differences in the spatial patterns of species abundance were evident in ordinations throughout years (latitude was included as a proxy), explaining some of the variation described by axis 1 (Table S3; Fig. 2). Overstory BA was highly correlated with species abundance in pre-treatment NMS ordinations, decreasing along axis 1. The SWF had the lowest midstory density (185 stems/ha fewer) and midstory BA (2–4 m<sup>2</sup>/ha less; Table S5) among treatments throughout years. Pre-treatment canopy openness was approximately 5% and did not differ among treatments ( $F_{[3,44]} = 0.68$ ,  $p = 0.57$ ); yet variability (CV) among plots within the FIRE was 29–45 higher than in any other treatment (CV:  $F_{[3,12]} = 5.14$ ,  $p = 0.016$ ).

Species compositional responses to decreasing overstory BA and density, and increasing canopy openness, both direct effects of heavy overstory reductions in the SWF, were evident in Y1

ordinations and explained some of the separation of SWF plots (Fig. 2). Axis 3 correlated with decreasing midstory BA and elevation in Y1 ordinations. Midstory density declined throughout the years in all treatments, yet the immediate effects of silvicultural manipulations (Y1) were most similar between the OSW and the SWF with decreases of 200 and 175 midstory stems/ha, respectively, compared to the FIRE and CTL with decreases of 16 and 50 midstory stems/ha, respectively (Table S5). Following overstory harvest in the SWF (Y1), the reductions in overstory BA (–24 m<sup>2</sup>/ha) and density (–163 trees/ha), and midstory density (–175 stems/ha) resulted in a tenfold increase in canopy openness from 5 to 51.2% (39–49% greater than other treatments), leading to significant differences in canopy openness among treatments for that year ( $F_{[3,38]} = 68.4$ ,  $p < 0.001$ ). Canopy openness in the OSW increased 16.5% the year following herbicide treatments (Y1), but quickly decreased 14.3% by the following year. In FIRE, canopy openness increased 10.2% following the second prescribed fires (Y6) but was largely unchanged by fires conducted prior to Y1.

Only the influence of latitude, overstory BA, and density was still evident in Y9 ordinations. Patterns of change in overstory BA and density following FIRE (OSBA: 0, OSth: –21 trees/ha) and OSW (OSBA: –1 m<sup>2</sup>/ha, OSth: –20 trees/ha) were similar to patterns of natural change seen in the CTL (OSBA: –2 m<sup>2</sup>/ha, OSth: –17 trees/ha; Table 3). Midstory density was relatively similar between OSW and SWF, with  $75 \pm 25$  and  $33 \pm 19$  stems/ha, respectively, and between FIRE and CTL with  $300 \pm 66$  and  $383 \pm 53$  stems/ha, respectively (Table S5). Differences between the SWF and other treatments were still evident by Y9, with the lowest overstory BA (17 m<sup>2</sup>/ha less) and density (145 trees/ha fewer; Table S5). The SWF also had 5% greater canopy openness than other treatments in Y9 ( $F_{[3,44]} = 13.02$ ,  $p < 0.001$ ), yet treatments reduced within-treatment variations in canopy openness, which did not differ among treatments in Y1 (CV:  $F_{[3,10]} = 0.21$ ,  $p = 0.89$ ) or in Y9 (CV:  $F_{[3,12]} = 0.28$ ,  $p = 0.84$ ).

Although not significantly different, the vertical percent change in PAR (dPAR  $\pm \mu\text{mol m}^{-2} \text{s}^{-1}$ ) in 2019 was most pronounced in SWF (–32%), the most open canopy treatment, and least pronounced in FIRE (–12%; Fig. 3), both resulting in a more variable light profile relative to CTL. The FIRE had greater PAR values, although less open due to a denser midstory and overstory. Extensive testing of differences in the linear slope of change of normalized PAR measurements ascending the forest floor failed to reveal statistically significant differences among treatments (all  $p > 0.3$ ). Several soil characteristics significantly varied among plots in species abundance ordinations, with TEC (total exchange capacity) and nitrogen being associated with axis 1, and sulfur and pH being associated with axis 2 (biplot cutoff  $r^2 > 0.3$ ; Table S6; Fig. 2). Organic matter and nitrogen were higher in sites that were treated relative to the controls (Table 3).

#### Do Treatments Change Ground-Layer Trajectories?

Ordinations of plots pre-treatment through Y3 and Y9 illustrated successional trajectories or changes in redundant patterns of species abundance throughout the years. A three-axis solution

**Table 3.** Summary of descriptive variables averaged for each treatment ( $\pm$  standard error). The variables describe the location, overstory and midstory structure (volume (m<sup>2</sup>/ha) and density (TPH= trees per hectare) approximately 9–11 years following treatment, and soil properties in 2019.

|                           | Control        | Repeated fire  | Oak shelterwood | Shelterwood/fire |
|---------------------------|----------------|----------------|-----------------|------------------|
| Latitude                  | 35.402         | 35.407         | 35.397          | 35.394           |
| Elevation (m)             | 1096           | 1094           | 1074            | 1141             |
| TSI                       | 3.5 $\pm$ 1.7  | 0.5 $\pm$ 0.3  | -0.3 $\pm$ 1.3  | -0.8 $\pm$ 1.0   |
| LFI                       | 31 $\pm$ 3     | 26 $\pm$ 1     | 27 $\pm$ 1      | 24 $\pm$ 2       |
| OSBA (m <sup>2</sup> /ha) | 25 $\pm$ 2     | 29 $\pm$ 3     | 29 $\pm$ 3      | 8 $\pm$ 2        |
| OS density (TPH)          | 185 $\pm$ 19   | 195 $\pm$ 19   | 200 $\pm$ 13    | 40 $\pm$ 9       |
| MSBA (m <sup>2</sup> /ha) | 5 $\pm$ 1      | 6 $\pm$ 1      | 2 $\pm$ 1       | 1 $\pm$ 1        |
| MS density (TPH)          | 383 $\pm$ 53   | 300 $\pm$ 66   | 75 $\pm$ 25     | 33 $\pm$ 19      |
| %Openness                 | 3.5 $\pm$ 0.6  | 7.5 $\pm$ 0.8  | 5.4 $\pm$ 0.7   | 12.4 $\pm$ 1.7   |
| TEC (meq/100 g)           | 6.4 $\pm$ 1.2  | 6.1 $\pm$ 1.1  | 7.3 $\pm$ 0.4   | 6.6 $\pm$ 0.9    |
| pH                        | 5.3 $\pm$ 0.0  | 5.1 $\pm$ 0.0  | 5.3 $\pm$ 0.1   | 5.2 $\pm$ 0.1    |
| Organic Matter (%)        | 11.5 $\pm$ 1.4 | 13.4 $\pm$ 1.6 | 11.1 $\pm$ 1.5  | 13.8 $\pm$ 1.6   |
| Ca (ppm)                  | 35.5 $\pm$ 1.7 | 33.0 $\pm$ 1.2 | 38.7 $\pm$ 2.4  | 34.8 $\pm$ 1.8   |
| NO <sub>3</sub> (ppm)     | 1.6 $\pm$ 0.5  | 5.3 $\pm$ 1.9  | 5.6 $\pm$ 1.8   | 4.1 $\pm$ 1.3    |
| NH <sub>4</sub> (ppm)     | 12.6 $\pm$ 2.5 | 10.8 $\pm$ 1.4 | 13.6 $\pm$ 0.8  | 13.0 $\pm$ 1.6   |

cumulatively explained 64% of the variation in the ordinations. Several species that were associated ( $r^2 > 0.2$ ) with axis 1 in individual year ordinations were again associated with axis 1 here. These included one fern, four herbaceous species, and two vines (Table S3). Only *R. allegheniensis* was associated with axis 2, and axis 3 had no associated species. The SWF resulted in the most pronounced successional trajectories, gaged by the length of vector lines joining plots chronologically, with the longest vector lines joining pre-treatment plots to Y1 plots (Fig. S4). Temporal changes in species composition for all other treatments were similar to those in CTL, with less movement of plots along ordination axes and less distance from pre-treatment conditions by Y9.

## Discussion

### Changes to Species Assemblages

Ground-layer species richness often increases following treatments that reduce woody plant cover and increase light to the forest floor. Yet, richness often declines quickly in the absence of repeated disturbance (Elliott et al. 1999; Glasgow & Matlack 2007). Combined overstory thinning and fire can reduce leaf litter, expose mineral soil, and increase nutrient availability to the ground-layer, amplifying changes to resource availability (Barefoot et al. 2019). Our results indicated an increase in ground-layer species richness after a decade in all

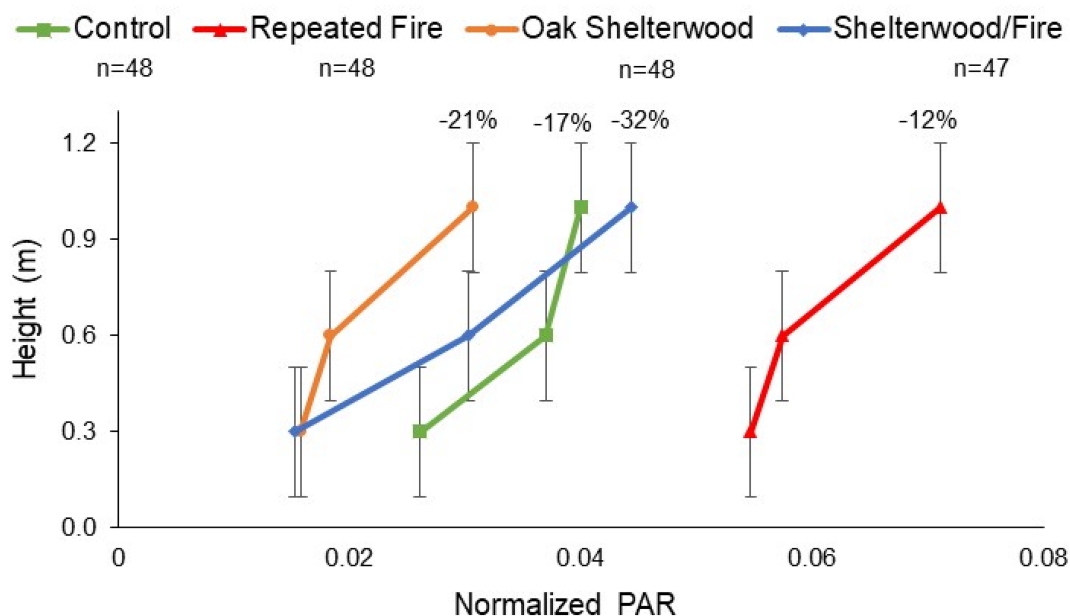


Figure 3. Vertical PAR slope intensity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; normalized to 1) descending ground-layer subplots, by treatment. Error bars represent the  $\pm$  SE. Labels above treatment groups indicate the percent change in the vertical light profile descending from 1 to 0.3 m above the forest floor (mean dPAR  $\pm \mu\text{mol m}^{-2} \text{s}^{-1}$ ). For all treatments  $n = 48$ , except for shelterwood/fire  $n = 47$ .

three treatments compared to the CTL, particularly following the SWF. Changes to species trajectories were most pronounced following the SWF, and minor in other treatments. These results supported our hypothesis that the SWF would lead to the most notable changes in species dominance patterns. Species turnover was similar between all treatments and in CTL; more species were gained than lost after 9–11 years. Several ruderal species became more abundant following SWF. Notably, the increased relative abundance of *Rubus* that persisted for at least 9 years after SWF could be influencing midstory oak regeneration in these forests. Nevertheless, Keyser et al. (2020) found that SWF in this study did not negatively impact taxonomic diversity of the regeneration layer (woody stems <5 cm dbh) in the first decade following treatment.

We hypothesized that ground-layer species composition would shift from shade-tolerant, fire-sensitive species to shade-intolerant, pyrophytic species following SWF and FIRE. Results showed the most changes to indicator species following overstory reduction in the SWF (Y1). This pulse of species that increased in importance included several shade-intolerant or intermediate vines (*Vitis aestivalis*, *Rubus allegheniensis*, and *R. odoratus*), one shrub (*Hydrangea arborescens*), and at least one disturbance-tolerant species (*Erechtites hieracifolius*), and all except *E. hieracifolius* persisted as indicator species into Y9. Only four indicator species were found following the FIRE (Y1), and none were considered shade-intolerant or pyrophytic.

Two *Rubus* species (*R. allegheniensis* and *R. odoratus*) known to colonize disturbed areas became indicator species following the SWF. Furthermore, *R. allegheniensis* had the highest IV of any species, across treatments, throughout years and remained as a dense, recalcitrant understory layer through Y9 (Royo & Carson 2006; Johnson et al. 2019). Other studies show increasing dominance and IVs for *Rubus* following a shelterwood harvest (Elliott & Knoepf 2005) or two prescribed fires (Elliott & Vose 2010). Although the SWF resulted in the greatest percent canopy openness in Y9, a sharp decrease in vertical percent change in PAR (dPAR) at ground layer was likely due to the high relative abundance of *R. allegheniensis*. *Rubus* spp. are common competitors throughout the southeastern United States, as they produce prolific quantities of seeds, which persist in the seed bank and are widely dispersed by animals (Cain & Shelton 2003). *Rubus* are also nitrophilic, known for their ability to hinder regeneration of other ground-layer species by efficiently using nitrogen for rapid growth, quickly outshading competing vegetation (Faillace et al. 2018; Gilliam 2019). This recalcitrant *Rubus* layer could affect light and nutrient availability, altering species composition of woody seedlings able to grow into midstory layers. *Rubus* may also facilitate growth and establishment of tree seedlings by providing protection from browsing animals, though the seeds of some species, such as oak, are favored food of smaller mammals that benefit from the thickets (Williams et al. 2006; Harmer et al. 2010).

Shade-intolerant *Liriodendron tulipifera* was a pre-treatment CTL indicator but became a SWF indicator by Y9, likely due to increased light availability following harvest. Schuler and Miller (1995) reported increased *L. tulipifera* abundance following a

60% residual harvest and herbicide treatment, with little advantage to *Quercus* regeneration. Positive relationships of seedling density and IVs for *L. tulipifera* with increasing gap size illustrate the importance of light availability in relation to competitive interactions among ground-layer species following overstory disturbance events (Lhotka 2013). Shade-intolerant, early successional species *Symphyotrichum cordifolium* was a pre-treatment OSW indicator but showed an increased affinity to SWF following the second prescribed fire.

Three *Quercus* species showed affinity to treatments. *Quercus montana* was a CTL indicator through Y2. *Q. coccinea* was a consistent FIRE indicator, with increasing IVs throughout years (33–44); *Q. alba* (IV: 31) also showed affinity to FIRE in Y3. Repeated fire is a tool used to favor *Quercus* regeneration, and our indicator analysis results suggest it was the best candidate for maintaining ground-layer *Quercus*. Holzmüller et al. (2009) reported that *Q. alba* and *Q. rubra* seedlings (but not other *Quercus* species) showed affinity to repeated fire over that of a single fire, even after 15 years without fire. Barefoot et al. (2019) also reported an affinity of *Q. alba* seedlings to a combination of thinning and repeated fire. Conceivably, adding repeated fire to the OSW prescription could further promote ground-layer oak regeneration.

### Ground-Layer Light Regime

The vertical percent reduction in PAR descending ground-layer subplots varied 20% among treatments in Y9 but was not significant. Despite initial heavy overstory reduction, the SWF resulted in the greatest dPAR descending ground-layer subplots after roughly a decade. Keyser et al. (2020) found greater height (average 3.3 m taller by Y9) of the regeneration layer (stems <5 cm dbh) in the SWF than in other treatments. This rapid height growth likely contributed to the high dPAR rates in Y9. Conversely, FIRE resulted in the lowest dPAR among treatments after two low intensity fires, corresponding with the shortest height of the regeneration layer (Keyser et al. 2020). Johnson et al. (2019) found repeated, low intensity, dormant season fires reduced midstory tree density and increased light availability to the ground-layer by 10–20%, but effects lasted only 3–5 years. Tsai et al. (2018) reported that light availability to the ground-layer did not differ 9 years following variable retention overstory thinning, but variation in the light environment remained twice as high in thinned plots relative to controls. Increasing light heterogeneity at the ground-layer can increase species diversity by creating different microhabitats, which favor species with varying light requirements.

Heavy overstory removal from SWF greatly reduced overstory BA and density, which substantially increased canopy openness and light availability. Other studies evaluating the effects of timber harvesting in the Appalachian region show shifts in plant dominance patterns and increased species diversity following silvicultural disturbances with heavy BA reduction and associated increases in light availability, with effects lasting for at least 10 years (Belote et al. 2012; Vander Yacht et al. 2017). In this study, the effects of SWF on species dominance patterns were still evident, and species assemblages did

not revert to pre-treatment patterns within our 9- to 11-year study period.

We sought to evaluate whether treatments developed to restore a dominant midstory *Quercus* regeneration layer can meet traditional management objectives, but also effectively maintain and promote a diverse ground-layer plant community. The ground-layer community responds quickly to disturbance and can be a timely indicator of tree and shrub species assemblages which could eventually compose midstory layers, with some species ultimately developing into the mature forest canopy (Gilliam 2007; Johnson et al. 2019). Species richness increased the most by Y9 following FIRE, with certain oak species showing affinity to this treatment throughout years. The second greatest gain in species richness was seen by Y9 in SWF, with species more adapted to disturbance showing affinity to this treatment. In contrast to FIRE and SWF, the OSW resulted in the fewest changes in ground-layer resource availability and the fewest changes to species assemblages and successional patterns. We found comparable species turnover in all treatments, highlighting the resiliency of the ground-layer community to different types, intensities, and frequencies of silvicultural disturbances. However, these results are short-term and will require continued monitoring of the ground-layer species to evaluate the long-term effects of these oak restoration treatments on successional patterns and trajectories.

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## Supporting Information

The following information may be found in the online version of this article:

**Table S1.** Oak restoration treatment and ground-layer vegetation measurement schedule.

**Table S2.** Species present (*P*) before (Pre), 1 year (Y1), and 9 years following (Y9) treatments, sorted by lifeform, alphabetically.

**Table S3.** (A) Axis correlations for the nonmetric multidimensional scaling of ground-layer species abundance prior to (Pre), the year after (Y1), and 9 years (Y9) following treatments (see Table S1); and (B) axis correlations for species influencing trajectories through time.

**Table S4.** Significant ( $p \geq 0.5$ ) results from Indicator Species Analysis (ISA) performed on species abundance (cover) data by treatment and treatment year ( $P$  = pre-treatment).

**Table S5.** Environmental metrics ( $\pm$  standard error;  $n = 12$  plots/treatment) influenced by treatments throughout treatment years.

**Table S6.** Nonmetric multidimensional scaling axis correlations for long-term environmental parameters.

**Figure S1.** Experimental unit map for the Regional Oak Study.

**Figure S2.** Nested experimental design of overstory, midstory, and ground-layer subplots developed for the Regional Oak Study.

**Figure S3.** Supplemental to Figure 2 in main text.

**Figure S4.** Vertical PAR slope intensity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; normalized to 1) descending ground-layer subplots, by treatment.

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