

Temporal patterns of ground flora response to fire in thinned *Pinus–Quercus* stands

Kevin G. Willson, Carson R. Barefoot, Justin L. Hart, Callie Jo Schweitzer, and Daniel C. Dey

Abstract: The ground flora stratum affects stand structure, resource acquisition, nutrient cycling, and taxonomic richness in forest ecosystems. Disturbances such as thinning and prescribed fire alter forest understory growing conditions that generally increase ground flora cover and richness. We studied annual changes in ground flora assemblages over three growing seasons after fire in thinned and frequently burned (3-year rotation) *Pinus–Quercus* stands. Our results corroborated trends from other studies that indicated greater ground flora richness and cover after thinning and burning compared with thin-only treatments. We also found that the stratum experienced relatively rapid succession between growing seasons that complimented the tolerance succession model. Forbs had reduced cover and richness from increasingly difficult growing conditions over time and were replaced by woody plants, shrubs, and seedlings. This likely occurred from changing competition dynamics that favored quick growth in the first growing season and long-term investment in vertical growth in the third growing season. The successful regeneration pathways also fit ground flora regeneration models and added a unique pathway to strengthen the predictive power of these models. As many stand management goals are focused towards improving biodiversity, prescribed fire and thinning may be used to increase understory richness in *Pinus–Quercus* stands.

Key words: ground flora, prescribed fire, herbs, litter, advanced reproduction.

Résumé : La strate composée de la flore du sol influence la structure du peuplement, l'acquisition des ressources, le recyclage des nutriments et la richesse taxonomique dans les écosystèmes forestiers. Les perturbations, telles que l'éclaircie et le brûlage dirigé, modifient les conditions de croissance dans le sous-bois des forêts et augmentent généralement la richesse et le couvert de la flore du sol. Nous avons étudié les variations annuelles dans les assemblages de la flore du sol pendant trois saisons de croissance après feu dans des peuplements éclaircis et fréquemment brûlés (à tous les 3 ans) de pin et de chêne (*Pinus* et *Quercus*, respectivement). Nos résultats corroborent les tendances rapportées dans d'autres études indiquant que la richesse et le couvert de la flore du sol augmentent après une éclaircie et un brûlage comparativement à une éclaircie seule. Nous avons également trouvé que la strate connaissait une succession relativement rapide entre les saisons de croissance, ce qui va dans le sens du modèle de succession basé sur la tolérance. Le couvert et la richesse des plantes herbacées non graminéoïdes ont diminué avec le temps à cause des conditions de croissance de plus en plus difficiles et elles étaient remplacées par des plantes ligneuses, des arbustes et des semis. Cela est survenu vraisemblablement à cause du changement dans la dynamique de la compétition qui a favorisé une croissance rapide durant la première saison de croissance et un investissement à long terme dans la croissance verticale durant la troisième saison de croissance. Les trajectoires qui favorisent la régénération correspondent aussi aux modèles de régénération de la flore du sol et ont ajouté une trajectoire unique pour renforcer l'efficacité prédictive de ces modèles. Étant donné que plusieurs objectifs d'aménagement des peuplements sont axés sur l'amélioration de la biodiversité, le brûlage dirigé et l'éclaircie pourraient être utilisés pour augmenter la richesse du sous-bois dans les peuplements de pin et de chêne. [Traduit par la Rédaction]

Mots-clés : flore du sol, brûlage dirigé, herbacées, litière, régénération préétablie.

1. Introduction

The ground flora stratum (herbaceous and woody plants ≤ 1 m from the forest floor) constitutes a majority of plant diversity and rare species in temperate forests (Hutchinson 2005; Gilliam 2007). A productive ground flora stratum alters stand structure and increases resource complexity and species diversity. The ground flora may change vertical stand development by increasing competition for growing space and resources. As understory competition affects tree regeneration, future overstory composition may be influenced by ground flora (Lorimer et al. 1994; Donoso and Nyland 2006; Gilliam and Roberts 2014). Herbaceous plants in the ground flora stratum have low biomass to net primary productiv-

ity ratios to rapidly cycle nutrients through annual senescence and may increase litter decomposition rates, which increases stand productivity and maintains soil fertility (Rochow 1974; Dybzinski et al. 2008; Fujii et al. 2017). Ground flora richness coincides with higher species diversity in other trophic levels of the food web by providing resources to an array of insects, birds, and mammals in forest ecosystems (Fralish 2004; Hutchinson 2005; Barrioz et al. 2013). Ground flora and associated fauna richness add complexity and diversity to stands, both of which may enhance stand resilience to disturbances (Peterson et al. 1998).

Disturbances such as thinning and prescribed surface fires are discrete events in space and time that alter stand structure and

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composition (Pickett and White 1985). Silvicultural treatments that impact stand overstory and midstory structure may also promote ground flora diversity (Waldrop et al. 2008). Thinning is an intermediate-scale tending method that increases space and resource availability to enhance desirable tree species recruitment to larger size classes, improves stand health, increases the diameter of residual trees, and creates wildlife habitat in part by increasing ground flora abundance and richness (Hutchinson 2005; Iverson et al. 2008; Nyland 2016). Thinning may also improve seedling establishment and recruitment by increasing photosynthetically active radiation near the forest floor (Lhotka and Loewenstein 2009, 2013). Increased light availability may promote rapid growth in understory strata because light is often the most limiting resource to understory plants in closed-canopy stands (Scharenbroch et al. 2012).

Managers may prescribe low-intensity surface fire to reduce unwanted competition and create site conditions that favor desired tree species. Multiple studies have indicated that ground flora richness and cover significantly increase less than 2 years after fire in hardwood and *Pinus* L. stands (Arthur et al. 1998; Hutchinson 2005; Phillips et al. 2007; Phillips and Waldrop 2008). Reduced tree density from repeated burns may increase light availability that benefits ground flora establishment (Hutchinson 2004; Arthur et al. 2012). The ground flora also positively respond to the sudden macronutrient availability of nitrogen, potassium, and phosphorus that may be released by the combustion of duff and litter layers after fire (Gray and Dighton 2009; Scharenbroch et al. 2012; Alcañiz et al. 2018). Surface fires top-kill fire-intolerant plants and temporarily clear litter to increase space and mineral soil accessibility for ground flora seed germination (Frost 1998; Hiers et al. 2007; Moghaddas et al. 2008).

Effects of combined thinning and prescribed fire on ground flora have recently been a focus of study (e.g., Schwilk et al. 2009; Willms et al. 2017). Ground flora richness and cover increased in *Pinus*- and hardwood-dominated stands that were thinned and burned compared with thinned-only stands (Waldrop et al. 2008; Phillips and Waldrop 2008). Comparisons with burned-only stands did not return conclusive results, potentially because light availability varied in the understory of burned-only stands between studies (Franklin et al. 2003; Hutchinson 2005; Phillips et al. 2007). Brewer (2016) reported significant increases in ground flora richness in tornado-disturbed *Pinus-Quercus* L. stands that were burned compared with tornado-disturbed and unburned stands. Fulé et al. (2005) and Kinkead et al. (2013) found that thinned and burned stands with a high composition of *Pinus* and *Quercus* had significantly greater understory plant cover. Kinkead et al. (2013) also reported concerns that a dense layer of woody shrubs, saplings, and vines could inhibit future herbaceous plant development and limit long-term biodiversity.

Mixed *Pinus-Quercus* stands are unique in vertical light structure compared with stands dominated by *Pinus*, *Quercus*, or other mixed hardwoods because of differences in species leaf and canopy architecture and light penetration into the understory (Canham et al. 1994; Messier et al. 1998). Because overstory composition alters light availability in light-limited forests, ground flora may differentially respond to thinning and prescribed fire in *Pinus-Quercus* stands with unique light structure compared with *Pinus*- or hardwood-dominated stands. Similarly, litter composition in *Pinus-Quercus* stands is likely different compared with other forest types, which will influence fire characteristics that are drivers of ground flora composition (Kane et al. 2008; Alexander and Arthur 2014). However, the little research that has occurred in this stand type has not been performed in light-limited *Pinus-Quercus* stands of the eastern United States (US), indicating a dearth of knowledge on ground flora responses to these disturbances. Researchers have indicated a paucity of long-term data analyzing ground flora responses to repeated prescribed fire, defining this as an important research gap (Hutchinson 2004; Arthur et al. 2012; Matlack 2013).

The ground flora stratum recovers relatively rapidly from a disturbance compared with midstory and overstory strata. Thinning immediately moves energy-exchange levels closer to the forest floor (Fahey et al. 2016), which in turn increases ground flora photosynthetic productivity (Huang et al. 2007). Surface burns generally reduce the aboveground biomass of most understory herbaceous and woody plants, thus immediately increasing resource and space availability, which provides favorable growing conditions for ground flora in subsequent growing seasons. However, midstory and overstory trees outcompete ground flora by moving the level of energy exchange to higher vertical positions, which limits ground flora photosynthetic production (Pickett and White 1985; Oliver and Larson 1996; Nyland 2016). Studies of ground flora in thinned and burned hardwood stands and *Pinus* stands of the eastern US elucidated rapid increases in ground flora cover and richness over a 1- to 3-year period (Phillips et al. 2007; Phillips and Waldrop 2008; Outcalt and Brockway 2010; Lettow et al. 2014). However, we could find no research that has quantified annual ground flora development in light-limited thinned and burned *Pinus-Quercus* stands, which indicates a lack of quantitative data on ground flora recovery at finer temporal scales in a stand type with unique light structure characteristics.

We studied the ground flora stratum over three growing seasons after prescribed fire in *Pinus-Quercus* stands 12 years after a single thinning treatment and four burns performed on a 3-year rotation. Our overarching goal was to explain how environmental variables affected ground flora in thinned and burned stands. Our specific goals were to (i) determine how annual ground flora composition and cover changed in three growing seasons (i.e., annually over the fire rotation) and (ii) determine which environmental variables best explained annual changes in composition and cover. We hypothesized that ground flora diversity would increase during the first growing season after fire and then decrease as ground flora cover, sapling density, and tree density increased. We also hypothesized that resource and space metrics such as tree and sapling density, litter depth, and (or) light availability would explain annual changes in ground flora cover over the 3-year burn cycle. Our results were used to develop recommendations for managing *Pinus-Quercus* stands for diverse ground flora assemblages.

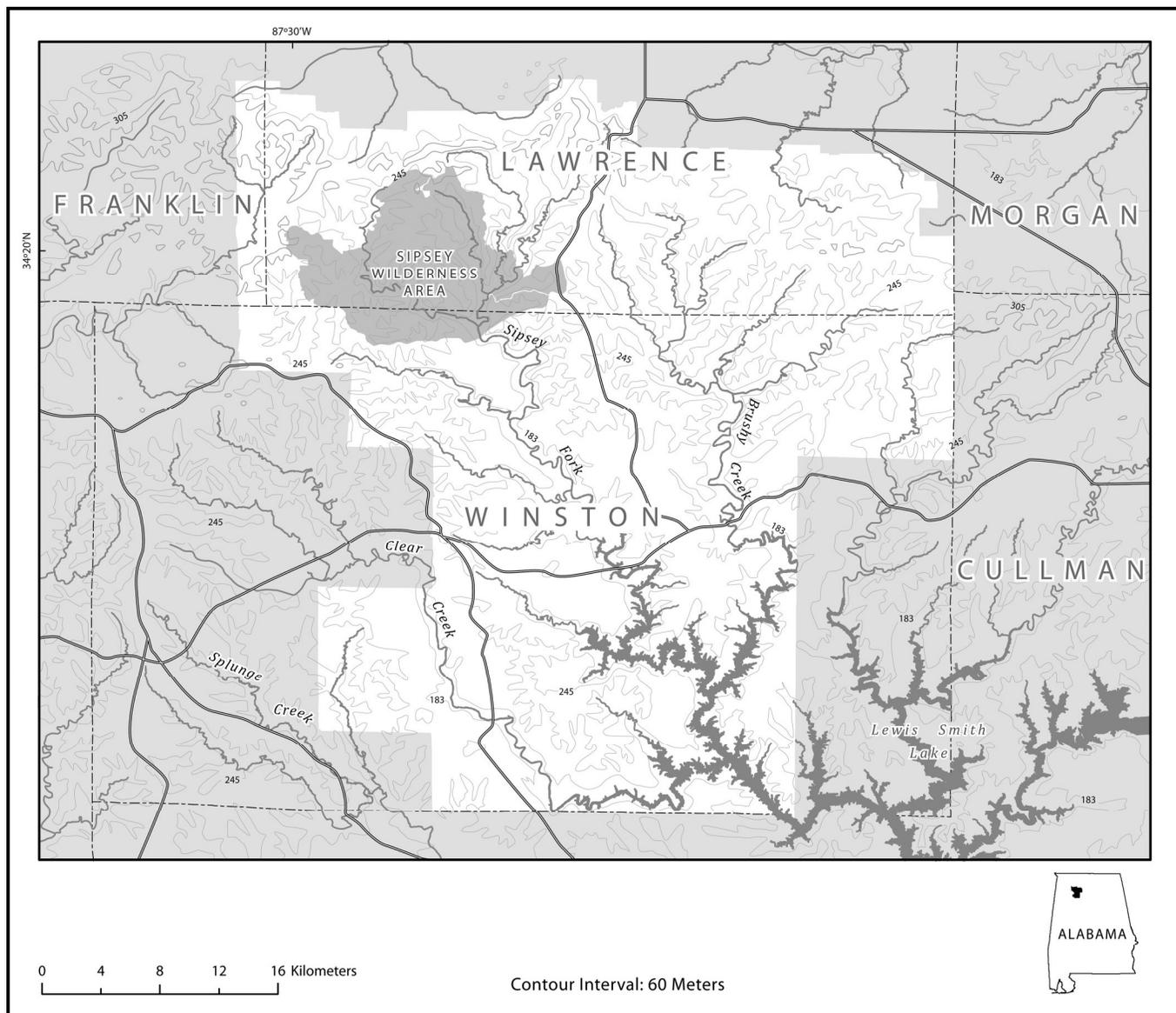
2. Materials and methods

2.1. Study area

This study was conducted on the William B. Bankhead National Forest (BNF) in northwestern Alabama, which is situated on the southern Cumberland Plateau (Fenneman 1938; Fig. 1). The Cumberland Plateau corresponds with the Southwest Appalachian level III ecoregion (Griffith et al. 2001). Braun (1950) classified the region as a transition between the mixed mesophytic forest to the north and *Pinus-Quercus* forests to the south. The underlying bedrock is the Pennsylvania Pottsville formation, which includes sandstone, stratified shale, and siltstone (Szabo et al. 1988). Soil is classified as Typic Hapludults and Dystrudepts, which are well drained, moderately deep, strongly acidic, and low in nutrients (U.S. Department of Agriculture Soil Conservation Services 1959). Regional climate is classified as humid mesothermal, consisting of long, hot summers and short, mild winters (Thornthwaite 1948). Annual precipitation averages 138 cm, with monthly means of 13.8 cm in January and 11.3 cm in July (PRISM Climate Group 2017). Annual temperature averages 15 °C, with monthly means of 26 °C in July and 5 °C in January. Smalley (1979) determined the region to have an average growing season of 220 days a year, spanning from late March to late November.

Land in BNF was previously cut over and farmed until the early 1920s (Addor and Birkhoff 2004). The USDA Forest Service (USFS) began to manage stands in Alabama national forests as *Pinus* plantations in the 1930s (USFS 2004). BNF managers planted the cur-

Fig. 1. Map of Bankhead National Forest and the Sipsey Wilderness in northwestern Alabama, U.S.A.



rent overstory *Pinus taeda* L. between 1972 and 1979, which went largely unmanaged for 30 years after establishment (Schweitzer et al. 2016).

Following a *Dendroctonus frontalis* Zimmermann outbreak that caused high mortality in *Pinus*-dominated stands on the BNF, managers decided to restore the plantations to historical mixed *Pinus-Quercus* composition (Addor and Birkhoff 2004). Managers also implemented a prescribed-burn program to reduce litter and fuel loads and prepare the *P. taeda* plantations for regeneration and transition to mixed-species stands. In 2004, a study was initiated to quantify how thinning and prescribed burning affected stand composition and structure. A randomized 3×3 factorial experiment was created to test combinations of three thinning levels (control, no thinning; low intensity, basal area reduced to $17.2 \text{ m}^2 \cdot \text{ha}^{-1}$; high intensity, basal area reduced to $11.5 \text{ m}^2 \cdot \text{ha}^{-1}$) and three fire frequencies (control: none; infrequently burned, once every 9 years; frequently burned, once every 3 years; Schweitzer et al. 2016) that were replicated four times across the landscape. Over the following 12 years, understorey *Quercus* were released into the overstorey and currently make up ca. 20% of the basal area in the frequently burned replicates studied.

Our study included replicates from the above study by Schweitzer et al. (2016) in stands that experienced a high-intensity thinning (thinned to $11.5 \text{ m}^2 \cdot \text{ha}^{-1}$) and were burned every 3 years or not burned at all. Because the Schweitzer et al. (2016) replicates were initially burned in sequential years, the replicates were at different stages of recovery after the most recent fire, which enabled a space-for-time study design to be imposed on the original project. With this, we refer to these replicates as treatments for the purposes of our study. Thinning operations were performed in 2005 as a free thinning using a wheeled feller-buncher with a hydro-axe attachment and a crawler-mounted feller-buncher to cut trees and a forwarder with a loader bucket to move felled trees to the landing. Slash was left on-site. Operators targeted trees of all merchantable size classes and removed $457 \text{ stems} \cdot \text{ha}^{-1}$ across studied areas. Study treatments have been burned four times since 2006, with fires set during the dormant months from January to March (Schweitzer et al. 2016). Temperatures were recorded 25 cm above the ground surface using 30 temperature probes (HOBO TCP6-K12 Probe Thermocouple Sensor, Onset Computer Corporation, Cape Cod, Massachusetts, USA) distributed across each treatment. Burns were ignited with hand strip fires at 8 m

intervals and aerial ignitions using potassium permanganate. Fires averaged 95.5 °C during the first burn, 123.2 °C during the second burn, 208.4 °C during the third burn, and 195.6 °C during the fourth and most recent burn (Schweitzer et al. 2016).

2.2. Field methods

To quantify litter, light availability, ground flora, sapling, and overstory tree variables, twenty 0.05 ha (500 m²) fixed-radius plots were established in three treatments identified by growing season since burn: first growing season (GS 1, burned in 2017), second growing season (GS 2, burned in 2016), and third growing season (GS 3, burned in 2015). As a control, plots were also established in replicates that experienced a high-intensity thinning but were not burned. We randomly selected plots using a fishnet overlay in ArcMap (version 10.3; Environmental Systems Research Institute, Redlands, California, USA) clipped to each treatment. A random-number generator was used to select numbers within the range of the fishnet to determine plot location. Plot selection ensured spatial coverage throughout each sampled treatment. Plots were relocated if placed within 15 m of other plots, on sites near streams or with steep slopes, or within 25 m of treatment boundaries. Field surveys and sampling occurred from June through August 2017.

On each plot, saplings (woody stems ≥ 1 m in height and < 5 cm in diameter at breast height (dbh)) were identified to species and counted for density. Trees (stems ≥ 5 cm dbh) were identified to species, measured for basal area, counted for density, and assigned a crown position. Crown positions were based on light interception compared with adjacent overstory trees and included dominant, co-dominant, intermediate, and overtopped classes (Oliver and Larson 1996). Hemispherical photos were taken at plot center using a Nikon fisheye lens attached to an Olympus Stylus TG-3 camera mounted on a self-leveling tripod using a Mid-O Mount 10MP (Regent Instruments Inc., Sainte-Foy, Quebec, Canada) at 1 m from the ground to capture light availability at the top of the ground flora stratum. Photos were oriented north and collected at dawn, dusk, or in overcast conditions to maintain consistency and reduce glare and sun fleck error during photo analysis.

On each plot, we established three 12.4 m transects at 0 degrees (north), 120 degrees (southeast), and 240 degrees (southwest), along which ten 1 × 1 m subplots (10-m²) were placed. Within subplots, all ground flora species were identified to the lowest taxonomic level possible given available reproductive structures. To ensure that all plants were properly inventoried and identified, new and (or) unidentifiable species were collected and specimens were transported to the laboratory. Plants accurately identified to species occurred in genera that also contained unidentified species. However, these species and genera were analyzed as distinct groups for taxonomic richness and nonmetric multidimensional scaling (NMS) tests. For example, *Solidago arguta* Aiton and *Solidago odora* Aiton were analyzed separately from the genus *Solidago*, in which other species were found but were unidentifiable to species. Species authorities and taxonomic classification were determined using Weakley (2015).

We estimated percent cover of ground flora using the North Carolina Vegetation Survey (NCVS) protocol: 0, absent; 1, solitary or few; 2, 0%–1%; 3, 1%–2%; 4, 2%–5%; 5, 5%–10%; 6, 10%–25%; 7, 25%–50%; 8, 50%–75%; 9, 75%–95%; and 10, 95%–100% (Peet et al. 1998). Seedlings (woody plants ≤ 1 m in height) were also identified to species, given a cover class, and counted for density within each subplot. Ground cover classes were derived from the USFS (2016) grade scale, which included bare ground, *Pinus* litter, broadleaf litter, coarse woody material (woody material ≥ 10 cm diameter), fine woody material (woody material < 10 cm not connected to coarse woody material), moss, and rock. Every category was assigned a NCVS cover class in each subplot.

Litter was defined as undecomposed or partially decomposed organic material readily identifiable, which included forest floor leaves, needles, twigs, cones, bark, flower parts, dead moss, li-

chen, and ground flora stems as demarcated by the FIA protocol (Woodall and Monleon 2008). Litter samples on each plot were collected in four 0.25 m² quadrats that were established to collect litter samples 5 m from the plot center in the four cardinal directions. The litter was then bulked by plot. Litter depth was measured to the nearest 0.1 cm at the four corners of each litter sample plot before litter was collected and averaged for each plot. Collected litter was air-dried in the laboratory for 21 days and weighed to measure litter mass. Slope and aspect were collected to determine if either variable was associated with differences between plots and treatments.

2.3. Analyses

To calculate plot-level NCVS cover classes for ground flora and ground cover, cover classes were converted to the midrange value, averaged across the 10 subplots, and converted back to the corresponding cover class (Peet et al. 1998). Ground flora were also analyzed for taxonomic richness and Shannon–Weiner diversity index measures. As ground cover was expected to total ca. 100%, the total midrange value was calculated for each plot, averaged across the treatment, and relativized to 100% before reconverting values back to NCVS classes to ensure comparable assessments of ground cover variables between treatments.

PC-ORD version 7.0 was used to run nonmetric multidimensional scaling (NMS) to evaluate annual differences between ground flora assemblages (Peck 2016). Distance-based multivariate ANOVAs (PerMANOVAs) were used to determine if there were significant differences in species assemblages between all treatments. Species that occurred in fewer than two plots were removed from analyses to reduce extraneous error within NMS analyses and prioritize species that represented unique communities. Plot-level cover class values were relativized to each species' maximum cover class to reduce the influence of naturally large plants and increase the influence of smaller plants in ground flora assemblage analyses (Peck 2016). Eleven environmental variables were tested for correlation with ground flora composition and abundance: (1) light availability (percent photosynthetic photon flux density, % PPF), (2) tree density, (3) sapling density, (4) overstory *P. taeda* relative importance value (average of relative dominance and relative density), (5) litter depth, (6) litter mass, (7) bare ground cover, (8) broadleaf litter cover, (9) *Pinus* litter cover, (10) coarse woody cover, and (11) fine woody cover. An NMS stress plot was used to determine an optimal number of axes to use in the final solution (Peck 2016). Sørensen (Bray–Curtis) distance interpolation was used with 250 runs and was repeated with other solutions to ensure consistency of interpretation. A biplot overlay assessed correlations between axes and environmental variables, which were included on ordination plots when $r > 0.5$.

An indicator species analysis (ISA) determined the most representative species for each growing season after burn. The ISA averaged relative frequency and relative abundance to calculate an indicator value of each species per treatment (Dufrene and Legendre 1997; Peck 2016). Fourth-corner analysis (FCA) was used to quantify correspondence between ground flora assemblages by growth habit and environmental variables. To ensure that the observed differences between growth habit and environmental variables were statistically significant, randomization was performed within columns to determine how species by growth habit responded to annual environmental change.

Using the U.S. Department of Agriculture plant classification system (<https://plants.usda.gov/java/>, accessed November 2017), ground flora data were classified into four life-form groups to indirectly observe annual changes in ground flora competition dynamics after fire. Categories included forbs, graminoids, vines, and woody plants (defined as shrubs and trees). Species considered to have multiple growth habits were categorized by growth strategy observed in situ (i.e., all *Toxicodendron radicans* (L.) Kuntze were observed as forbs and not as vines). Plants identified to a

Table 1. Kruskal–Wallis results summarizing the mean values (\pm SE) of ground flora taxonomic richness by growth habit.

Growth habit	Control	GS 1	GS 2	GS 3	Significance
Forb	1.70 (\pm 0.55)a	14.40 (\pm 0.89)b	9.30 (\pm 0.94)bc	5.35 (\pm 1.05)c	$p < 0.001$
Graminoid	1.35 (\pm 0.18)a	2.05 (\pm 0.05)b	2.00 (\pm 0.00)b	1.85 (\pm 0.11)b	$p < 0.001$
Woody	11.25 (\pm 0.68)a	13.80 (\pm 0.71)ab	14.45 (\pm 0.73)b	17.90 (\pm 0.57)c	$p < 0.001$
Vine	4.50 (\pm 0.22)	4.40 (\pm 0.26)	5.10 (\pm 0.26)	5.00 (\pm 0.23)	$p = 0.105$
Total	18.85 (\pm 0.97)a	35.15 (\pm 1.14)b	31.00 (\pm 1.31)b	31.10 (\pm 1.49)b	$p < 0.001$

Note: Lowercase letters indicate significance (by Dunn's post-hoc pairwise comparison test) when $\alpha < 0.05$ within individual growing seasons and the control.

Table 2. Kruskal–Wallis results summarizing the mean values (\pm SE) of ground flora cover category by growth habit.

Growth habit	Control	GS 1	GS 2	GS 3	Significance
Forb	1.45 (\pm 0.27)a	5.85 (\pm 0.18)b	4.10 (\pm 0.24)c	3.65 (\pm 0.38)c	$p < 0.001$
Graminoid	1.70 (\pm 0.21)ac	3.40 (\pm 0.29)b	3.95 (\pm 0.23)ab	2.70 (\pm 0.22)c	$p < 0.001$
Woody	4.45 (\pm 0.17)a	6.70 (\pm 0.13)b	7.00 (\pm 0.10)b	6.75 (\pm 0.10)b	$p < 0.001$
Vine	4.50 (\pm 0.18)a	4.85 (\pm 0.20)ac	5.80 (\pm 0.22)b	5.55 (\pm 0.14)bc	$p < 0.001$
Total	5.65 (\pm 0.11)a	8.20 (\pm 0.16)b	8.20 (\pm 0.12)b	7.45 (\pm 0.11)b	$p < 0.001$

Note: Cover categories: 0, absent; 1, solitary or few; 2, 0%–1%; 3, 1%–2%; 4, 2%–5%; 5, 5%–10%; 6, 10%–25%; 7, 25%–50%; 8, 50%–75%; 9, 75%–95%; 10, 95%–100%. To remain conservative, cover values were rounded down to determine specific range. Lowercase letters indicate significance (by Dunn's post-hoc pairwise comparison test) when $\alpha < 0.05$ within individual growing seasons and the control.

family or genus that includes multiple growth habits were removed from this analysis (i.e., *Rubus*, *Fabaceae*). Average total cover for each growth habit was calculated for each plot by adding the midpoints of the cover for each species' plot average and converting the values back to the corresponding NCVS cover class to obtain an average cover class for each season.

Tree data were calculated for total density per hectare, density per hectare by crown position, total live basal area, and relative importance for each species. Seedling counts were summed across the 10 quadrats and scaled to hectare-level density. Total sapling and tree counts per plot were also scaled to hectare-level density. Hemispherical photos were analyzed using WinSCANOPY (version 2014a; Regent Instruments Inc.) to measure percent PPF in each plot.

None of the data was normally distributed when first analyzed. Kruskal–Wallis and Mann–Whitney U tests were used to determine if differences in data were significant between treatments. Post-hoc Dunn's test pairwise comparisons were used to determine significant differences of the variables between treatments. Spearman correlations were used to determine significant correlations between variables. Total ground flora cover and taxonomic richness, light availability, tree density, and bare ground cover achieved normality via Jarque–Bera tests (Jarque and Bera 1980) and homogeneity of variance via Levene's test after a logarithmic transformation. Significantly correlated ($p < 0.05$) normalized data were run for single linear and multilinear regressions. Tests for normality were performed using R (version 3.2.2; R Core Team 2015), and all other statistical analyses were performed in SPSS (version 22; IBM Corporation 2013).

We recognize that using some of the above-mentioned statistical tests violated the assumption of independence because of dependent replicates in the study caused by constraints from the larger project design. Dependent replicates caused unavoidable pseudo-replication that may have affected the significance of results and increased the chance of stochastic error. However, Schweitzer et al. (2016) selected replicates to have as similar stand conditions (stand age, stand composition, management history, soils, topography, land type, past land use, etc.) as possible, from which we subsampled and argue are representative of the broader stand type. We also used multiple lines of corroborating evidence, which included NMS statistical tests that do not require full independence within the data. Similarly, logical concerns that occur from pseudo-replication may not be a major issue in this study. Specifically, we primarily provided deductive discussion points

and conclusions, and the results from our analyses likely exceeded the background variation, points that were indicated by other researchers to avoid pseudo-replication pitfalls (Oksanen 2001; Davies and Gray 2015).

3. Results

3.1. Ground flora

We documented a total of 151 ground flora taxa across the four treatments. The control treatment had 75 taxa, GS 1 had 107 taxa, GS 2 had 98 taxa, and GS 3 had 93 taxa. Average aggregated taxonomic richness per plot was significantly higher in burned plots compared with the control ($p < 0.001$). Taxonomic richness per plot decreased from GS 1 (35 taxa) to the latter two growing seasons (31 taxa; Table 1) but were not significantly different. The Shannon–Weiner diversity index mirrored average taxonomic richness trends and did not indicate any nuanced results compared with taxonomic richness.

3.2. Growth habit

Burned treatments had significantly more forb, graminoid, and woody plant taxa per plot compared with the control ($p < 0.001$). Average forb richness was highest in GS 1 at 14 taxa per plot (Table 1). Forb richness decreased to nine forb taxa per plot in GS 2 and five forb taxa in GS 3, which was significantly lower compared with GS 1 ($p < 0.001$). Forb trends were reversed in woody taxa, with significant increases in average richness from 14 taxa per plot in GS 1 and GS 2 to 18 taxa per plot in GS 3 ($p < 0.01$). Vine ground flora richness did not significantly change between the control and any of the three growing seasons.

Ground flora cover significantly increased from an average cover range of 5%–10% in the control to 50%–75% in burned plots (Table 2). Forb, graminoid, vine, and woody cover were all significantly higher in burned treatments compared with the control. Ground flora cover did not significantly change over three growing seasons, maintaining cover ranges of either 25%–50% or 50%–75% throughout all burned plots. However, forb cover significantly decreased after GS 1 from 5%–10% to 1%–2% in GS 2 and 0%–1% in GS 3 ($p < 0.01$). Graminoid cover maintained cover of 1%–2% in GS 1 and GS 2 before significantly decreasing to 0%–1% in GS 3 ($p = 0.02$). Vine cover significantly increased from 2%–5% to 5%–10% cover by GS 2 and maintained higher cover through GS 3 ($p = 0.01$). Woody

Fig. 2. Three-dimensional nonmetric multidimensional scaling projections based on ground flora abundance in the control (squares), GS 1 (circles), GS 2 (plus signs), and GS 3 (triangles) plots. Convex hulls connect plots in the same growing season, and biplot overlays indicate the strength and direction of correlations ($r \geq 0.5$) between environmental factors and ordination axes.

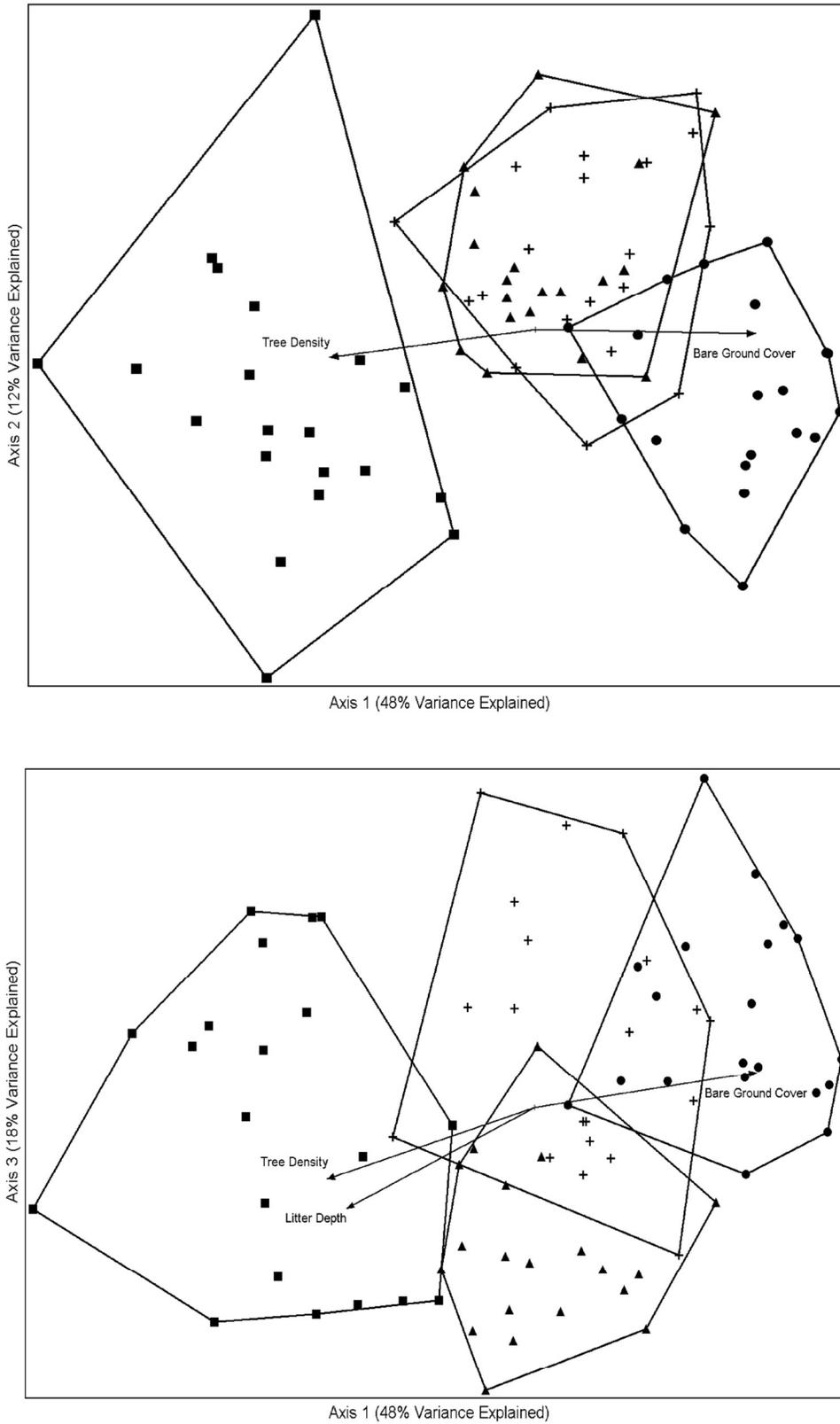


Table 3. Indicator species analysis results assessing the representative species for each growing season and the control.

Species	Growth habit	Control	GS 1	GS 2	GS 3
<i>Berchemia scandens</i> (Hill) K. Koch	Vine	*	+	+	+
<i>Bignonia capreolata</i> L.	Vine	*			+
<i>Callicarpa americana</i> L.	Woody	***			
<i>Agalinis tenuifolia</i> (Vahl) Rafinesque	Forb		*		
<i>Chamaecrista fasciculata</i> (Michaux) Greene	Forb		***	+	
<i>Chimaphila maculata</i> (L.) Pursh	Forb		*		
<i>Clitoria mariana</i> L.	Forb		***		
<i>Coreopsis major</i> Walter	Forb		**	+	+
<i>Erechtites hieracifolius</i> (L.) Rafinesque ex A.P. de Candolle	Forb		***	+	
<i>Eupatorium rotundifolium</i> L.	Forb		**	+	+
<i>Helianthus hirsutus</i> Rafinesque	Forb		*	+	+
<i>Iris verna</i> L. var. <i>smalliana</i>	Forb		***		
<i>Lespedeza hirta</i> (L.) Hornemann	Forb		***		
<i>Lespedeza procumbens</i> Michaux	Forb		***	+	+
<i>Lespedeza repens</i> (L.) W. Barton	Forb		***	+	+
<i>Lespedeza violacea</i> (L.) Persoon	Forb		***	+	+
<i>Quercus stellata</i> Wangenheim	Woody		*	+	+
<i>Rhus copallinum</i> L. var. <i>copallinum</i>	Woody		***	+	+
<i>Scleria oligantha</i> Michaux	Graminoid		***	+	
<i>Solidago odora</i> Aiton	Forb		***	+	+
<i>Symphotrichum patens</i> (Aiton) G.L. Nesom	Forb		*	+	
<i>Carya glabra</i> (P. Miller) Sweet	Woody	+	+	***	+
<i>Galactia volubilis</i> (L.) Britton	Vine	+		*	+
<i>Helianthus strumosus</i> L.	Forb			*	+
<i>Liriodendron tulipifera</i> L.	Woody	+	+	*	+
<i>Oxalis stricta</i> L.	Forb		+	**	+
<i>Prunus serotina</i> Ehrhart	Woody	+	+	*	+
<i>Solidago arguta</i> Aiton	Forb		+	*	+
<i>Styrax grandifolius</i> Aiton	Woody		+	*	
<i>Toxicodendron radicans</i> (L.) Kuntze	Forb	+	+	*	+
<i>Amelanchier arborea</i> (Michaux f.) Fernald	Woody	+			**
<i>Asimina triloba</i> (L.) Dunal	Woody	+	+	+	*
<i>Carya tomentosa</i> (Lamark) Nuttall	Woody	+	+	+	***
<i>Dioscorea villosa</i>	Graminoid		+	+	*
<i>Hydrangea quercifolia</i> Bartram	Woody		+		**
<i>Muscadinia rotundifolia</i> (Michaux) Small	Vine	+	+	+	*
<i>Nyssa sylvatica</i> Marshall	Woody	+	+	+	*
<i>Quercus alba</i> L.	Woody	+	+	+	**
<i>Quercus velutina</i> Lamarck	Woody	+	+	+	***
<i>Sassafras albidum</i> (Nuttall) Nees	Woody	+	+	+	***
<i>Vaccinium arboreum</i> Marshall	Woody	+	+	+	**
<i>Vaccinium corymbosum</i> L.	Woody				*
<i>Vaccinium pallidum</i> Aiton	Woody				***
<i>Vaccinium stamineum</i> L. var. <i>stamineum</i>	Woody	+	+	+	***
<i>Vitis aestivalis</i> Michaux var. <i>aestivalis</i>	Vine		+	+	**

Note: * indicates $\alpha < 0.05$, ** indicates $\alpha < 0.01$, and *** indicates $\alpha < 0.001$ to represent a significant increase in abundance and frequency of the species compared with the other treatments; + indicates the presence of the species in the treatment. Boldface type signifies unique indicator species that were only found in one treatment.

cover did not significantly change over the three postfire growing seasons.

3.3. NMS ordination

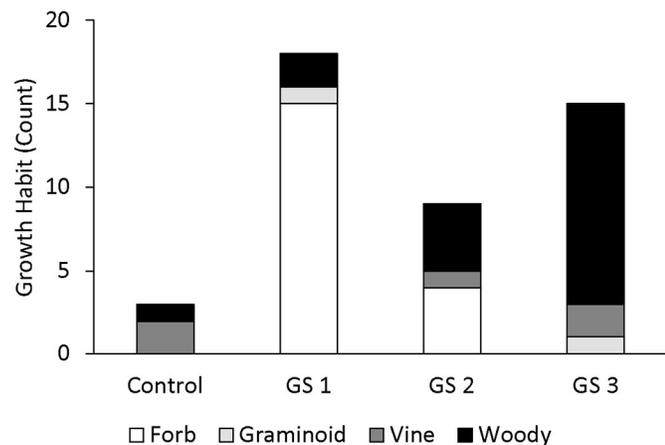
The three-dimensional NMS projections had significant differences between all four treatments (PerMANOVA, $p < 0.001$). Final stress for the three-axes solution was 17.8% and explained a cumulative 78% of variance between assemblages (NMS; McCune and Grace 2002). Both plots indicated that GS 1 was most different from the control, while GS 2 and GS 3 trended closer to control composition (Fig. 2). Axis 1 explained 48% of variance within ground flora composition and projected differences between GS 1, GS 2, and GS 3 and the control. Axis 1 was most correlated with tree density ($r = -0.717$) and bare ground cover ($r = 0.740$). Axis 2 explained 12% of the variance, but the projection with axis 1 indicated no difference between GS 2 and GS 3. Axis 3 explained 18% of

the variance and showed a difference between GS 2 and GS 3. However, no highly correlated environmental variable explained the difference.

The ISA resulted in 45 indicator species: three in the control, 18 in GS 1, nine in GS 2, and 15 in GS 3 (Table 3). When categorized by growth habit, 15 GS 1 indicator species were categorized as forbs, one as graminoid, and two as woody plants (Fig. 3). GS 2 had four woody and forb indicator species each and one vine indicator species. By GS 3, most indicator species were woody (12), with no forbs, one graminoid, and two vine indicator species. Unique indicator species followed a similar progression, with all unique indicator species categorized as forbs in GS 1, all categorized as woody plants in GS 3, and no unique indicator species in GS 2 (Table 3).

Fourth-corner analysis identified significant correlations in three of the four growth habits with the 11 environmental vari-

Fig. 3. Indicator species results categorized by growth habit for each growing season and the control. Altered competition dynamics for each growing season are indicated by the shift in indicator species assemblages from forbs in GS 1 to woody plants by GS 3.



ables used in PC-ORD. Forb assemblages were most correlated with litter depth ($r = -0.253$), light availability ($r = 0.227$), and tree density ($r = -0.223$, $p < 0.01$). Vine assemblages were most correlated with bare ground cover ($r = -0.118$) and tree density ($r = 0.114$, $p < 0.001$). Woody assemblages were most correlated with litter depth ($r = 0.178$), *P. taeda* importance ($r = -0.175$), and light availability ($r = -0.167$, $p < 0.001$). Graminoid assemblages were not significantly correlated with any variables measured.

3.4. Overstory composition and structure

All treatments averaged approximately 19 m²·ha⁻¹ and were primarily composed of *P. taeda* (67% basal area, BA), *Quercus* species (18% BA), and *Liriodendron tulipifera* L. (7% BA). *Quercus montana* Willd. (8% BA), *Quercus alba* L. (6% BA), and *Quercus coccinea* Münchh. (2% BA) had the highest basal areas of *Quercus* species. Overstory relative dominance was not significantly different between control and burned treatments within most species.

Tree density significantly decreased in burned plots compared with the control ($p < 0.001$). Tree density in burned plots significantly increased over time, from approximately 280 trees·ha⁻¹ in GS 1 and GS 2 to 600 trees·ha⁻¹ in GS 3 ($p < 0.001$). Most trees were categorized as intermediate (446 stem·ha⁻¹) or overtopped (251 stem·ha⁻¹) compared with codominant trees (190 stem·ha⁻¹) in the control treatment. In burned treatments, intermediate (125 stems·ha⁻¹) and overtopped (75 stems·ha⁻¹) tree densities were significantly lower than in the control ($p < 0.001$). However, codominant tree density (182 stems·ha⁻¹) in burn treatments was not significantly different than the control. Tree density was highly correlated with 9 of 11 variables tested and was most positively correlated with litter depth and broadleaf cover (Table 4). Tree density was most negatively correlated with ground flora cover, bare ground cover, ground flora taxonomic richness, and *P. taeda* importance values. A multiple linear regression used tree density and bare ground cover to moderately predict total annual ground flora cover ($r^2 = 0.688$, $p < 0.001$).

Pinus taeda was the most important tree, with an average importance value of 55.10 ± 2.95 standard error (SE). *Quercus* species totaled the second highest importance value at 21.75 ± 2.03 SE. *Pinus taeda* importance values significantly increased in GS 1 compared with the control ($p < 0.001$), as tree abundance and basal area of non-*P. taeda* trees decreased. However, *P. taeda* importance values significantly decreased over time with increased hardwood density and basal area ($p < 0.001$). *Pinus taeda* importance value was most positively correlated with *Pinus* litter cover, light availability, and ground flora taxonomic richness and cover, while most

negatively correlated with litter depth and broadleaf litter cover (Table 4).

3.5. Advanced reproduction

Seedling density significantly increased from 34 400 ± 3390 seedlings·ha⁻¹ (mean ± SE) in the control treatment to 57 830 ± 3310 seedlings·ha⁻¹ in burned treatments ($p < 0.001$). Seedling density decreased in GS 2 but increased back to comparable GS 1 density by GS 3. Seedling density was positively correlated with total ground flora cover and bare ground cover (Table 4). Sapling density was not statistically different from the control to GS 1. Sapling density significantly increased from 3750 saplings·ha⁻¹ in GS 1 to 7111 saplings·ha⁻¹ in GS 2 ($p < 0.001$), but significantly decreased to 4806 saplings·ha⁻¹ in GS 3 ($p = 0.031$). Sapling density was positively correlated with ground flora richness and cover and negatively correlated with tree density (Table 4).

3.6. Litter

Litter depth decreased by 3.6 cm from the control to GS 1 ($p < 0.001$; Table 5). Litter depth significantly increased 2 years after fire to an average depth of 3.7 cm by GS 3 ($p < 0.01$). Corresponding litter mass followed depth trends, with an average litter mass of 1611 g in the control, 479 g in GS 1, and 1400 g by GS 3 (Table 5). Ground cover also reflected changes in litter depth and mass, as litter depth was negatively correlated with bare ground cover (Table 4). Bare ground cover was highest in GS 1 at an average cover of 5%–10%, which decreased to 0%–1% by GS 2, was solitary by GS 3, and was generally absent in the control. Ground cover changed from mostly *Pinus* litter to mostly broadleaf litter in three growing seasons. *Pinus* litter covered 50%–75% of the ground in GS 1, but decreased to 5%–10% cover in GS 3. Conversely, broadleaf cover increased from 1%–2% cover in GS 1 to 50%–75% cover by GS 3 (Table 5).

3.7. Light availability

Light availability increased from 15% ± 2% (mean ± SE) in the control to 32% ± 2% in burned treatments ($p < 0.001$). Percent PPFD was greatest in GS 1 at 45% and decreased to 30% and 20% by GS 2 and GS 3, respectively (Fig. 4; $p < 0.001$). Light availability was most positively correlated with bare ground cover and *Pinus* litter and negatively correlated with litter depth and broadleaf cover (Table 4). Light availability explained 23% of variability in taxonomic richness throughout all four treatments ($p < 0.001$). Decreases in PPFD were most strongly explained by increased tree density ($r^2 = 0.431$, $p < 0.001$).

4. Discussion

4.1. Ground flora and rapid succession

Ground flora richness and cover were higher in our burned and thinned *Pinus-Quercus* treatments than in the thin-only treatment, which is consistent with other results in *Pinus*- and hardwood-dominated stands across the US (Phillips et al. 2007; Phillips and Waldrop 2008; Outcalt and Brockway 2010; Willms et al. 2017). Although Phillips and Waldrop (2008) reported that taxonomic richness continuously increased in mixed *Pinus* stands on the South Carolina Piedmont, our taxa totals peaked in GS 1 and decreased in GS 2 and GS 3. Differences in taxonomic richness patterns may be attributed to different stand types and ecoregions between the studies, as the South Carolina *Pinus*-dominated stands likely had different canopy-specific leaf area and structure compared with the mixed *Pinus-Quercus* stands. Increased richness was partially explained by increased light availability after fire, as past studies in other forest types had found (Phillips et al. 2007; Phillips and Waldrop 2008; Barrioz et al. 2013; Bowles et al. 2017). As light availability is generally considered a limiting resource for ground flora in closed-canopy stands, we hypothesize that increased light availability caused by thinning and maintained by frequent burning provided adequate conditions for ground flora

Table 4. Results of a Spearman correlation analysis that determined the strength and significance of correlations between light availability, tree, sapling, and seedling density, overstory *P. taeda* importance value, ground flora taxonomic richness and cover, litter depth, bare ground cover, broadleaf litter cover, and *Pinus* litter cover.

	1	2	3	4	5	6	7	8	9	10
1. Light availability	—									
2. Tree density	-0.669***	—								
3. <i>P. taeda</i> importance value	0.633***	-0.679***	—							
4. Sapling density	0.097	-0.366**	0.021	—						
5. Seedling density	0.106	-0.165	-0.001	0.115	—					
6. Ground flora richness	0.512***	-0.583***	0.293**	0.255*	0.157	—				
7. Ground flora cover	0.573***	-0.831***	0.497***	0.415***	0.239*	0.609***	—			
8. Litter depth	-0.663***	0.737***	-0.638***	-0.059	-0.195	-0.541***	-0.621***	—		
9. Bare ground cover	0.642***	-0.677***	0.503***	0.102	0.252*	0.528***	0.617***	-0.836***	—	
10. Broadleaf litter cover	-0.561***	0.546***	-0.824***	0.132	-0.113	-0.361**	-0.379**	0.673***	-0.573***	—
11. <i>Pinus</i> litter cover	0.448***	-0.495***	0.816***	-0.021	-0.033	0.301**	0.374**	-0.522***	0.407***	-0.811***

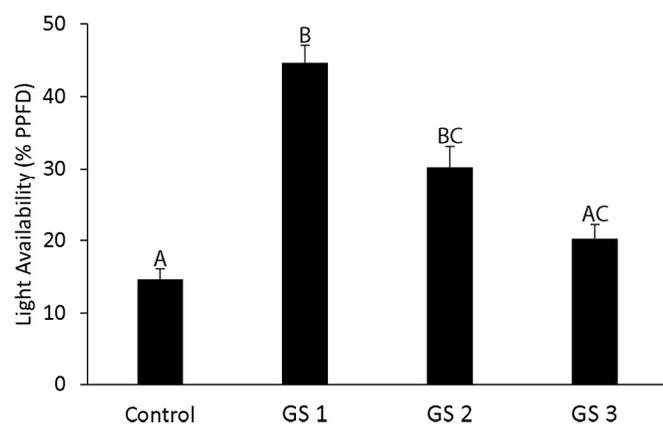
Note: * indicates $\alpha < 0.05$, ** indicates $\alpha < 0.01$, and *** indicates $\alpha < 0.001$.

Table 5. Kruskal–Wallis results summarizing the mean values (\pm SE) of litter depth and mass, bare ground cover, *Pinus* litter cover, and broadleaf litter cover by growing season and the control.

Variable	Control	GS 1	GS 2	GS 3	Significance
Litter depth (cm)	4.2 (\pm 0.3)a	0.5 (\pm 0.0)b	2.1 (\pm 0.1)c	3.7 (\pm 0.2)a	$p < 0.001$
Litter mass (g)	1611 (\pm 111)a	479 (\pm 50)b	768 (\pm 85)b	1400 (\pm 82)a	$p < 0.001$
Bare ground cover	0.55 (\pm 0.22)a	5.05 (\pm 0.23)b	2.65 (\pm 0.21)c	1.10 (\pm 0.23)a	$p < 0.001$
<i>Pinus</i> litter cover	6.55 (\pm 0.26)ac	8.35 (\pm 0.25)b	7.15 (\pm 0.22)ab	5.80 (\pm 0.32)c	$p < 0.001$
Broadleaf litter cover	7.90 (\pm 0.14)a	3.85 (\pm 0.25)b	7.40 (\pm 0.20)a	8.30 (\pm 0.18)a	$p < 0.001$

Note: Cover categories: 0, absent; 1, solitary or few; 2, 0%–1%; 3, 1%–2%; 4, 2%–5%; 5, 5%–10%; 6, 10%–25%; 7, 25%–50%; 8, 50%–75%; 9, 75%–95%; 10, 95%–100%. To remain conservative, cover values were rounded down to determine specific range. Lowercase letters indicate significance (by Dunn's post-hoc pairwise comparison test) when $\alpha < 0.05$ within individual growing seasons and the control.

Fig. 4. Light availability, measured in percent photosynthetic photon flux density (PPFD), of each growing season and the control. Error bars indicate standard error for each treatment. Dunn's post-hoc pairwise comparison test letters indicate significance when $\alpha < 0.05$ within individual growing seasons and the control.



germination (Scharenbroch et al. 2012; Waldrop et al. 2016). Fire-induced increases in richness and cover also indicated a greater ground flora response to forest disturbances such as thinning followed by frequent prescribed fire, which altered stand functions in ways that thinning alone could not emulate (Kinkead et al. 2013; Waldrop et al. 2016).

Changes in taxonomic richness and cover by growth habit were indicative of relatively rapid succession in ground flora. Total forb cover and richness were highest in GS 1 and decreased with waning light availability, which was similar to other studies (Phillips and Waldrop 2008; Waldrop et al. 2008; Lettow et al. 2014) and indicative of high light requirements that forbs need to persist. Similar trends in forb indicator species and unique indicator species suggested that competition dynamics favored quick growth and resource acquisition in the growing season directly after fire. This trend indicates that fire is an important driver that promotes

herbaceous cover and richness in *Pinus–Quercus* stands, as found in other studies that have a *Pinus* and (or) *Quercus* component across North American forests (Fulé et al. 2005; Phillips and Waldrop 2008; Outcalt and Brockway 2010; Kinkead et al. 2013; Lettow et al. 2014).

Although woody cover did not statistically change in three growing seasons, woody biomass likely increased, as woody plants had grown above the 1 m delineation of ground flora by GS 3. Competition dynamics changed by GS 3 to favor growth habits that invested energy and resources into long-term vertical growth, exhibited in the shift of ISA species to woody indicator species by GS 3. Increased woody competition for space and resources correlated with decreased forb and graminoid cover and richness, which was a concern stated by Kinkead et al. (2013) for maintaining future herb diversity. Phillips et al. (2007) and Phillips and Waldrop (2008) recorded similar increases in high woody cover several years after treatment that may indicate an analogous succession to woody dominant cover in the ground flora stratum after thinning and fire disturbance. Many of these woody plants were saplings that re-sprouted in GS 1 and blocked light from reaching ground flora by GS 2. Continued re-sprouting in our study supported results from Knapp et al. (2015), who found that saplings re-sprouted more successfully in stands burned in the dormant season every 4 years compared with saplings in stands burned annually.

Vine cover was the only growth form to have peak cover in GS 2. Vines may have taken longer to grow because many taxa observed in situ depended on taller shrubs and trees. This was corroborated by positive correlations between vines and tree density in FCA results. Once woody plants grew above the ground flora stratum, vines could grow up stems and outcompete other ground flora for light. Graminoid cover was comparable with results from Phillips and Waldrop (2008) in mixed *Pinus* stands, with significantly higher cover and richness in plots that were thinned and burned compared with thinned-only plots. However, graminoid cover decreased by GS 3, likely from greater competition by woody plants and vines for light capture. Specifically, lower graminoid cover may have occurred because of reduced levels of light availability,

which usually needs to remain high for many graminoids to persist. In general, total ground flora cover did not change until light availability decreased below 30% PPF, although the change in total cover did not statistically change in the latter two growing seasons.

A lack of unique indicator species in GS 2 was also symptomatic of rapid succession in ground flora assemblages. We interpreted GS 2 as a transition from herbaceous to woody dominance, with a mix of species found in either GS 1 or GS 3 and an even split of four indicator species for each growth habit. Transitions from forb to woody cover could have effects on species in other trophic levels of the food web. As ground flora provides insects, birds, and mammals with habitat and food supply, changes in ground flora assemblages towards woody plants will likely affect animals that eat specific forbs, grasses, vines, and woody plants (Fralish 2004; Hutchinson 2005; Barrioz et al. 2013).

This type of succession complimented the tolerance succession model whereby succession is determined through dispersal type and differences in physiology. Peet et al. (2014) reported similar results in the herbaceous layer in North Carolina Piedmont regions converting back from forests after long-term human intervention ended. Our results also uniquely fit a model created by Roberts (2004) that introduced a three-dimensional representation of ground flora regeneration pathways based on three disturbance severity metrics: percent forest canopy removed; percent understory vegetation removed; and percent forest floor and soil removed or disrupted. The initial thinning treatment removed more than 20% but less than 80% of the overstory, while the prescribed fire removed close to 100% of the understory and moderately disrupted ground litter and soil. Thus, the combined disturbance would be placed in the front center of the Roberts (2004) model. The three growing seasons followed the expectations of the successful regeneration pathways, which accurately identified seedbank and deep-seeded vegetation as the most prominent regeneration methods 12 years after a single thinning and four fires. Many of the indicator species from GS 1 were seed-obligate reproducers that could quickly grow after the fire because of the removal of most competing understory vegetation. However, GS 2 and GS 3 indicator species were dominated by species that could regenerate via rhizomes and root sprouts, indicative of tolerance succession and moderate soil disruption that occurred a year earlier. Because fire has maintained a relatively open canopy (greater than 40% in GS 1), our results indicate that a one-time thinning and frequent burn regime would maintain a place in the front-middle part of the Roberts (2004) model. However, the plant response was dynamic over time and would have to shift from a lower-front-center position during GS 1 to an upper-front-center position during GS 2 and GS 3 to properly represent changes in successful plant reproduction strategies.

Only 16 of our 80 plots contained an invasive plant, and all invasive species occurred at low cover. After 12 years, our thinned and burned stands had three invasive species (*Lespedeza bicolor* Turcz., *Lespedeza cuneata* (Dum. Cours.) G. Don, and *Lonicera japonica* Thunb.). Both *Lespedeza* species are capable of surviving fire and may benefit from low-intensity surface burns over time. However, neither species occurred at covers above 0%–1% across a plot or indicated any capability to increase dominance or abundance with the current silvicultural prescription. The highest average cover class of *L. japonica* occurred in the control treatment near old rock walls indicative of a homestead that was abandoned when the land came into federal ownership, at which time it began converting back to forest. Invasive plants did not significantly contribute to the cover in any treatment or indicate signs of future dominance within the ground flora stratum. Though not specified, differences in land uses may have also impacted ground flora composition, abundance, and invasive species cover over time that could have altered results across all compared studies (Gilliam 2007). The long-term perspective inherent in this study

may alleviate concerns of invasive plant intrusion into this stand type in the eastern US. Unlike areas that experience chronic disturbance with relatively quick return intervals (i.e., roadways, agricultural landscapes, highly used waterways, etc.), periodic tree removal and prescribed fire disturbances do not seem to create niches suitable for invasive species to dominate the ground flora layer of *Pinus-Quercus* stands in the eastern US. However, we also acknowledge that propagule pressure for the study site may be relatively low compared with forests nearer urbanized areas.

4.2. Biotic and abiotic effects on ground flora

Greater tree density was indicative of increased competition for space and resources, explaining annual decreases in light availability and ground flora cover. Fewer canopy trees created a relatively open overstory that increased light availability and growing space at the forest floor for smaller plants. Increased tree density in the understory with time since fire decreased resources and space available for ground flora as the hardwood trees in higher strata outcompeted smaller plants for light. Because light availability partially explained changes in ground flora richness ($r^2 = 0.22$), tree density also indirectly affected ground flora richness. As prescribed fire removed vegetation in understory strata, ground flora likely had enhanced photosynthetic productivity and performance (Huang et al. 2007) that caused increased cover. Fire also affected litter accumulation that likely influenced ground flora germination and growth, as litter depth correlated with ground flora cover and taxonomic richness (Table 4). However, our results did not align with those of Phillips et al. (2007), who reported a delayed response in cover in stands of the central Appalachian Plateau in Ohio and southern Appalachian Mountains in North Carolina that were thinned and burned compared with the thin-only treatment. Method collection differences could have caused the variation in results, as Phillips et al. (2007) collected their data directly after the disturbances, while we collected data 4 months after fire. Variations in stand type, site quality, and past land use history may have also affected postdisturbance ground flora recovery and caused difference between the two studies. If stands continue to transition from *P. taeda-Quercus* stands to mixed hardwood stands, decreased light transmission into the understory may cause a decline in ground flora cover.

Dominant litter cover was also symptomatic of annual changes in ground flora growing conditions that affected competition over time. Annual shifts from *Pinus* to broadleaf litter cover correlated to increasingly difficult growing conditions for smaller plants. Greater *Pinus* litter cover correlated with low litter depth and greater bare mineral soil accessibility, both of which are favorable for ground flora germination (Hiers et al. 2007; Moghaddas et al. 2008). Increases in broadleaf cover correlated with increased litter depth and diminished bare mineral soil accessibility, both of which correlated with reduced ground flora establishment. GS 3 had litter depths and masses that, if extrapolated to GS 4, would likely return to preburn depths and weights (i.e., the control treatment).

Postfire litter recovery time seemed to be quicker than suggested in Stambaugh et al. (2006), who reported that litter depths recovered to 75% accumulation after 4 years and took 12 years to return to comparable litter depths in mixed hardwood stands in the Missouri Ozarks. However, accumulation was slower than reported by Arthur et al. (2017), who determined that litter recovered to comparable preburn masses within one growing season in mixed hardwood stands in the Cumberland Plateau of eastern Kentucky. In southern Appalachian mixed *Quercus* stands, Waldrop et al. (2016) reported deeper litter depths, on average, but found concurring results that litter in thinned and burned treatments approached thin-only litter levels after three growing seasons before the next burn in the fourth dormant season. Differences in litter recovery and depth may be attributed to regional differ-

ences in productivity (e.g., more trees or leaves in more highly productive stands) and stand type (e.g., *Pinus* species do not drop leaves every year like many hardwoods). As changes in average litter depth and mass correlated with ground flora richness and cover over three growing seasons in our study, differences in litter may also help explain variability in ground flora assemblages and succession rates between our study and other studies in the eastern US.

Of similar interest, litter composition may have affected ground flora competition dynamics because of the influence that litter has on fire characteristics and ground moisture (Kane et al. 2008; Alexander and Arthur 2014). For example, needles of *Pinus* species burn at high temperatures with quick rates of spread because of lower moisture levels, relatively fast litter drying rates after precipitation events, and long decomposition rates (Williamson and Black 1981; Fonda 2001). In comparison, mesic species such as *Acer rubrum* L. drop litter that decomposes relatively quickly, holds moisture for longer periods, requires more energy to ignite, and does not burn as intensely as *Pinus* or *Quercus* litter (Kreye et al. 2013; Alexander and Arthur 2014). Some *Quercus* species have litter that has combustion comparable with fire-tolerant *Pinus palustris* Mill. but generally have traits that indicate moderate fire tolerance with lobed leaves, moderate decomposition rates, and moderate moisture retention compared with *Pinus* and *A. rubrum* litter (Kane et al. 2008). Alterations in fire severity, intensity, and duration and soil moisture retention affect tree seedling and re-sprouting capabilities and likely affect herbaceous ground flora response, composition, and cover. These differences may have also caused unique burning and environmental conditions that could account for variability in our *Pinus-Quercus* ground flora assemblages compared with other stand types that were thinned and burned. However, this study did not analyze litter composition by functional burning characteristics. Circumstantial evidence indicates that litter depth and (or) composition affect soil moisture, which, in turn, affect ground flora growth (Sydes and Grime 1981; North et al. 2005; Albrecht and McCarthy 2009). However, we could not find research that has attempted to directly relate ground flora assemblages with litter, moisture, and fuels composition, a literature gap that should be addressed to better elucidate ground flora response to prescribed fire.

4.3. Advanced reproduction

Our thinned and burned plots had significantly higher seedling and sapling densities than thinned-only plots, as found in other studies within BNF (Schweitzer et al. 2016) and eastern US stand types (Albrecht and McCarthy 2006; Phillips and Waldrop 2008; Waldrop et al. 2008; Iverson et al. 2008). Our seedling data revealed incongruities in trends between treatments, decreasing in density from GS 1 to GS 2 and recovering by GS 3. This trend may have occurred from seedlings growing into sapling size classes in favorable growing conditions. Sapling density may have decreased by GS 3 because of decreased light availability in the lower midstory that occurred with greater small-tree density, as sapling density was positively correlated with light availability. A second possible reason for declined sapling density was recruitment into larger size classes, as sapling density was negatively correlated with tree density. These reasons may explain why our seedling and sapling densities did not significantly increase between GS 1 and GS 3 as has been observed in other studies (Albrecht and McCarthy 2006; Phillips and Waldrop 2008).

After four fire rotations in these treatments, we did not observe a decrease in *A. rubrum* re-sprouts as was described in Albrecht and McCarthy (2006). *Acer rubrum* likely maintained high density in the understory because the 3-year fire return interval allowed for re-sprouts that quickly grew into saplings in the relatively high light environment of thinned *Pinus-Quercus* stands. Arthur et al. (1998), Blankenship and Arthur (2006), and Knapp et al. (2015) reported

similar trends across *A. rubrum* and other species, with higher re-sprouting in stands with longer fire return intervals compared with stands burned on shorter fire rotations. *Quercus* seedlings outnumbered *A. rubrum* seedlings but failed to recruit to the sapling class, possibly because *A. rubrum* saplings were preventing enough light from reaching the ground flora. However, few *A. rubrum* re-sprouts successfully recruited into tree size classes, which we suspect occurred because most saplings were top-killed from the fire, with only 40 *A. rubrum* trees recorded in burned plots and only eight greater than 20 cm dbh. Burns during the growing season may return different results when species with different resource allocation strategies have varied levels of carbon stores above- and below-ground (Brose et al. 2013). However, burning at a 3-year return interval for 12 years has caused clumps of *A. rubrum* to possibly have enough stems to insulate the inner stems from being damaged by fire, regardless of when a fire is introduced to the stand. Managers may want to consider the long-term response of mesic re-sprouts to frequent prescribed fire for long periods when determining stand management methods.

4.4. Management implications

Managers have become interested in promoting stand biodiversity (Lindenmayer et al. 2000; USFS 2000), which can be accomplished in many stand types by managing for a diverse ground flora stratum. Thinning and prescribed burning are methods to increase ground flora taxonomic richness and understory cover in *Pinus-Quercus* stands. Our results were comparable with thinned and burned stands with large *Pinus* and (or) *Quercus* components in other regions of North America, which may indicate a general trend across *Pinus-Quercus* stands on the continent. Fire seemed to perpetuate herbaceous plant richness and cover that a one-time thin could not continue to maintain, which likely affected resource availability for herbivores and omnivores (Fralish 2004; Barrioz et al. 2013). Succession from herbs to woody plants occurs quickly, and fire would have to occur annually or biannually to maintain long-term herb richness and cover for plant and animal biodiversity. If stands are burned annually, sapling re-sprouting may cease to occur (Knapp et al. 2015) and could allow continual forb availability. However, annual burning may not be possible in these stand types because fuel loading may not be great enough to carry fires every dormant season. To increase ground flora richness while meeting long-term management goals, managers may want to consider maintaining a portion of stands in the stand initiation or understory re-initiation stages across the landscape to conserve beta and gamma diversity that is indicative of ecosystem resilience (Peterson et al. 1998). Managers may also be able to use annual successional changes in ground flora assemblages to describe stand characteristics after a disturbance, as small plants are sensitive to stand-scale disturbances (Onaindia et al. 2004).

Litter is another important consideration for ground flora assemblages and fuels management, a concern for managers of fire-influenced forests across the world (Waldrop et al. 2016). We found that burning every 3 years maintained reduced litter depths that kept fuel loads below control levels over all three growing seasons. Litter also became more mesic as time since burn increased, changing from *Pinus* in GS 1 to hardwood (specifically *A. rubrum* litter, personal observation) by GS 3 (Nowacki and Abrams 2008). This may affect fire characteristics (i.e., fire line intensity and rate of spread) in these stands that managers should be aware of for the future (Kreye et al. 2013; Alexander and Arthur 2014), as fire characteristics could have long-term effects on ground flora assemblages and regeneration.

Restoring stands from uniform structure and composition (e.g., plantations) to historical composition depends on advanced reproduction to create and maintain desired stand conditions that maintain important ground flora diversity. Although thinning and fire treatments released *Quercus* stems to create general *Pinus-Quercus* overstory composition, advanced reproduction surveyed

in frequently burn treatments had few *Pinus* seedlings, no *Pinus* saplings, few *Quercus* saplings, and an abundance of *A. rubrum* saplings that will likely maintain dominance in smaller size classes. As *A. rubrum* canopy structure reduces the amount of light reaching the ground flora stratum, the change in overstory composition could be detrimental to future understory diversity. If composition of advanced reproduction is dominated by mesic taxa, we would recommend performing at least one growing-season burn (Arthur et al. 2012) and a second burn within 2 years to reduce species such as *A. rubrum* in the understory and change competition dynamics to favor *Pinus* and *Quercus* advanced reproduction. Note that managers should be aware of the initial reduction of ground flora diversity that may occur from a growing-season burn compared with a dormant season burn for up to 3 years, as evidenced by Gilliam and Christensen (1986). Managers should also consider potential issues that can arise while attempting prescribed growing-season fires in regions that experience high humidity during the growing season. However, by including a focus on herbaceous and woody ground flora assemblages, managers can use prescribed fire after thinning to increase understory richness and stand resilience, while recruiting desired advanced reproduction that can accomplish multiple management goals across many stand types.

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References

- Addor, M.L., and Birkhoff, J. 2004. Bankhead National Forest Health and Restoration Initiative: final report. USDA Forest Service, National Forests in Alabama, Bankhead National Forest.
- Albrecht, M.A., and McCarthy, B.C. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. *For. Ecol. Manage.* **226**: 88–103. doi:10.1016/j.foreco.2005.12.061.
- Albrecht, M.A., and McCarthy, B.C. 2009. Seedling establishment shapes the distribution of shade-adapted forest herbs across a topographical moisture gradient. *J. Ecol.* **97**(5): 1037–1049. doi:10.1111/j.1365-2745.2009.01527.x.
- Alcañiz, M., Outeiro, L., Francos, M., and Úbeda, X. 2018. Effects of prescribed fires on soil properties: a review. *Sci. Total Environ.* **613–614**: 944–957. doi:10.1016/j.scitotenv.2017.09.144. PMID:28946382.
- Alexander, H.D., and Arthur, M.A. 2014. Increasing red maple leaf litter alters decomposition rates and nitrogen cycling in historically oak-dominated forests of the eastern U.S. *ecosystems*, **17**(8): 1371–1383. doi:10.1007/s10021-014-9802-4.
- Arthur, M.A., Paratley, R.D., and Blankenship, B.A. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak–pine forest. *J. Torrey Bot. Soc.* **125**(3): 225. doi:10.2307/2997220.
- Arthur, M.A., Alexander, H.D., Dey, D.C., Schweitzer, C.J., and Loftis, D.L. 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *J. For.* **110**(5): 257–266. doi:10.5849/jof.11-080.
- Arthur, M.A., Blankenship, B.A., Schörgendorfer, A., and Alexander, H.D. 2017. Alterations to the fuel bed after single and repeated prescribed fires in an Appalachian hardwood forest. *For. Ecol. Manage.* **403**: 126–136. doi:10.1016/j.foreco.2017.08.011.
- Barrioz, S., Keyser, P., Buckley, D., Buehler, D., and Harper, C. 2013. Vegetation and avian response to oak savanna restoration in the mid-south USA. *Am. Midl. Nat.* **169**(1): 194–213. doi:10.1674/0003-0031-169.1.194.
- Blankenship, B.A., and Arthur, M.A. 2006. Stand structure over 9 years in burned and fire-excluded oak stands on the Cumberland Plateau, Kentucky. *For. Ecol. Manage.* **225**: 134–145. doi:10.1016/j.foreco.2005.12.032.
- Bowles, M.L., Lawrence, B.A., and Antlitz, D.J. 2017. Thinning effects on canopy structure and ground layer diversity in a burned mesic oak savanna. *J. Torrey Bot. Soc.* **144**(2): 191–205. doi:10.3159/TORREY-D-16-00015R1.
- Braun, E.L. 1950. Eastern deciduous forests of North America. Blakiston, Philadelphia.
- Brewer, J.S. 2016. Natural canopy damage and the ecological restoration of fire-indicative groundcover vegetation in an oak–pine forest. *Fire Ecol.* **12**(2): 105–126. doi:10.4996/fireecology.1202105.
- Brose, P.H., Dey, D.C., Phillips, R.J., and Waldrop, T.A. 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America? *For. Sci.* **59**(3): 322–334. doi:10.5849/forsci.12-039.
- Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* **24**(2): 337–349. doi:10.1139/x94-046.
- Davies, G.M., and Gray, A. 2015. Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). *Ecol. Evol.* **5**: 5295–5304. doi:10.1002/ece3.1782.
- Donoso, P.J., and Nyland, R.D. 2006. Interference to hardwood regeneration in northeastern North America: the effects of raspberries (*Rubus* spp.) following clearcutting and shelterwood methods. *North. J. Appl. For.* **23**: 288–296.
- Dufrière, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* **67**(3): 345. doi:10.1890/0012-9615(1997)067[0345:SAAI]2.0.CO;2.
- Dybzinski, R., Fargione, J.E., Zak, D.R., Fornara, D., and Tilman, D. 2008. Soil fertility increases with plant species diversity in a long-term biodiversity experiment. *Oecologia*, **158**(1): 85–93. doi:10.1007/s00442-008-1123-x. PMID:18690478.
- Fahey, R.T., Stuart-Haëntjens, E.J., Gough, C.M., De, La, Cruz, A., Stockton, E., Vogel, C.S., and Curtis, P.S. 2016. Evaluating forest subcanopy response to moderate severity disturbance and contribution to ecosystem-level productivity and resilience. *For. Ecol. Manage.* **376**: 135–147. doi:10.1016/j.foreco.2016.06.001.
- Fenneman, N.M. 1938. Physiography of eastern United States. McGraw-Hill, New York.
- Fonda, R.W. 2001. Burning characteristics of needles from eight pine species. *For. Sci.* **47**: 390–396.
- Fralish, J.S. 2004. The keystone role of oak and hickory in the central hardwood forest. USDA Forest Service, Southern Research Station, Asheville, N.C., Gen. Tech. Rep. SRS-73. pp. 78–87.
- Franklin, S.B., Robertson, P.A., and Fralish, J.S. 2003. Prescribed burning effects on upland *Quercus* forest structure and function. *For. Ecol. Manage.* **184**: 315–335. doi:10.1016/S0378-1127(03)00153-1.
- Frost, C.C. 1998. Presettlement fire frequency regimes of the United States: a first approximation [online]. In *Proceedings of Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription*, Boise, Idaho, 7–10 May 1996. Edited by T. Pruden and L. Brennan. Tall Timbers Research Station, Tallahassee, Fla. pp. 70–81. Available from <http://is.muni.cz/el/1423/jaro2006/ENS220/um/PresettlementFire.pdf> [accessed 13 February 2017].
- Fujii, S., Mori, A.S., Koide, D., Makoto, K., Matsuoka, S., Osono, T., and Isbell, F. 2017. Disentangling relationships between plant diversity and decomposition processes under forest restoration. *J. Appl. Ecol.* **54**(1): 80–90. doi:10.1111/1365-2664.12733.
- Fulé, P.Z., Laughlin, D.C., and Covington, W.W. 2005. Pine–oak forest dynamics five years after ecological restoration treatments, Arizona, USA. *For. Ecol. Manage.* **218**: 129–145. doi:10.1016/j.foreco.2005.07.005.
- Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *AIBS Bull.* **57**(10): 845–858.
- Gilliam, F.S., and Christensen, N.L. 1986. Herb-layer response to burning in pine flatwoods of the lower Coastal Plain of South Carolina. *Bull. Torrey Bot. Club.* **113**: 42–45. doi:10.2307/2996233.
- Gilliam, F.S., and Roberts, M.R. 2014. Interactions between the herbaceous layer and overstory canopy of eastern forests. In *The herbaceous layer in forests of eastern North America*. 2nd ed. Edited by F. Gilliam. Oxford University Press, Oxford, U.K. pp. 233–254.
- Gray, D.M., and Dighton, J. 2009. Nutrient utilization by pine seedlings and soil microbes in oligotrophic pine barrens forest soils subjected to prescribed fire treatment. *Soil Biol. Biochem.* **41**(9): 1957–1965. doi:10.1016/j.soilbio.2009.06.021.
- Griffith, G.E., Omernik, J.M., Comstock, J.A., Lawrence, S., Martin, G., Goddard, A., Hulcher, V.J., and Foster, T. 2001. Ecoregions of Alabama and Georgia. U.S. Geological Survey, Reston, Va.
- Hiers, J.K., O'Brien, J.J., Will, R.E., and Mitchell, R.J. 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. *Ecol. Appl.* **17**(3): 806–814. doi:10.1890/06-1015. PMID:17494398.
- Huang, J., Boerner, R.E., and Rebbeck, J. 2007. Ecophysiological responses of two herbaceous species to prescribed burning, alone or in combination with overstory thinning. *Am. J. Bot.* **94**(5): 755–763. doi:10.3732/ajb.94.5.755. PMID:21636444.
- Hutchinson, T.F. 2004. Prescribed fire effects on understory vegetation across a topographic moisture gradient in oak forests. Ph.D. dissertation, Ohio State University, Columbus, Ohio.
- Hutchinson, T. 2005. Fire and the herbaceous layer of eastern oak forests. In *Proceedings of Fire in Eastern Oak Forests: Delivering Science to Land Managers*, Columbus, Ohio, 15–17 November 2005. Edited by M.B. Dickinson. USDA Forest Service, Northern Research Station, Newtown Square, Penn., Gen. Tech. Rep. NRS-P-1. pp. 136–149.
- IBM Corporation. 2013. IBM SPSS Statistics for Windows. Version 22.0. IBM Corp., Armonk, New York, USA.
- Iverson, L.R., Hutchinson, T.F., Prasad, A.M., and Peters, M.P. 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. *For. Ecol. Manage.* **255**(7): 3035–3050. doi:10.1016/j.foreco.2007.09.088.

- Jarque, C.M., and Bera, A.K. 1980. Efficient tests for normality, homoscedasticity and serial independence of regression residuals. *Econ. Lett.* **6**(3): 255–259. doi:10.1016/0165-1765(80)90024-5.
- Kane, J.M., Varner, J.M., and Hiers, J.K. 2008. The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeters. *For. Ecol. Manage.* **256**(12): 2039–2045. doi:10.1016/j.foreco.2008.07.039.
- Kinkead, C.O., Kabrick, J.M., Stambaugh, M.C., and Grabner, K.W. 2013. Changes to oak woodland stand structure and ground flora composition caused by thinning and burning. *In Proceedings of the 18th Central Hardwood Forest Conference, Morgantown, W. Va., 26–28 March 2012. Edited by G.W. Miller, T.M. Schuler, K.W. Gottschalk, J.R. Brooks, S.T. Grushecky, B.D. Spong, and J.S. Rentch. USDA Forest Service, Northern Research Station, Newtown Square, Penn., Gen. Tech. Rep. NRS-P-117. pp. 373–383.*
- Knapp, B.O., Stephan, K., and Hubbart, J.A. 2015. Structure and composition of an oak–hickory forest after over 60 years of repeated prescribed burning in Missouri, U.S.A. *For. Ecol. Manage.* **344**: 95–109. doi:10.1016/j.foreco.2015.02.009.
- Kreye, J.K., Varner, J.M., Hiers, J.K., and Mola, J. 2013. Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. *Ecol. Appl.* **23**: 1976–1986. doi:10.1890/13-0503.1. PMID: 24555322.
- Lettow, M.C., Brudvig, L.A., Bahlai, C.A., and Landis, D.A. 2014. Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. *For. Ecol. Manage.* **329**: 89–98. doi:10.1016/j.foreco.2014.06.019.
- Lhotka, J.M., and Loewenstein, E.F. 2009. Effect of midstory removal on understory light availability and the 2-year response of underplanted cherrybark oak seedlings. *South. J. Appl. For.* **33**(4): 171–177.
- Lhotka, J.M., and Loewenstein, E.F. 2013. Development of three underplanted hardwood species 7 years following midstory removal. *South. J. Appl. For.* **37**(2): 81–90. doi:10.5849/sjaf.12-001.
- Lindenmayer, D.B., Margules, C.R., and Botkin, D.B. 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conserv. Biol.* **14**: 941–950. doi:10.1046/j.1523-1739.2000.98533.x.
- Lorimer, C.G., Chapman, J.W., and Lambert, W.D. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* **82**(2): 227. doi:10.2307/2261291.
- Matlack, G.R. 2013. Reassessment of the use of fire as a management tool in deciduous forests of eastern North America: fire in deciduous forest. *Conserv. Biol.* **27**(5): 916–926. doi:10.1111/cobi.12121. PMID:24073811.
- McCune, B., and Grace, J. 2002. MRPP (Multi-response Permutation Procedures) and related techniques. Analysis of Ecological Communities, MjM Software Design, Glenden Beach, Oregon, U.S.A. pp. 188–197.
- Messier, C., Parent, S., and Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *J. Veg. Sci.* **9**(4): 511. doi:10.2307/3237266.
- Moghaddas, J.J., York, R.A., and Stephens, S.L. 2008. Initial response of conifer and California black oak seedlings following fuel reduction activities in a Sierra Nevada mixed conifer forest. *For. Ecol. Manage.* **255**: 3141–3150. doi:10.1016/j.foreco.2007.11.009.
- North, M., Oakley, B., Fiegner, R., Gray, A., and Barbour, M. 2005. Influence of light and soil moisture on Sierran mixed-conifer understory communities. *Plant Ecol.* **177**(1): 13–24. doi:10.1007/s11258-005-2270-3.
- Nowacki, G.J., and Abrams, M.D. 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience*, **58**(2): 123–138. doi:10.1641/B580207.
- Nyland, R.D. 2016. *Silviculture: concepts and applications*. Waveland Press, Long Grove, Ill.
- Oksanen, L. 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos*, **94**: 27–38. doi:10.1034/j.1600-0706.2001.11311.x.
- Oliver, C.D., and Larson, B.C. 1996. *Forest stand dynamics*. John Wiley & Sons, New York.
- Onaindia, M., Dominguez, I., Albizu, I., Garbisu, C., and Amezaga, I. 2004. Vegetation diversity and vertical structure as indicators of forest disturbance. *For. Ecol. Manage.* **195**: 341–354. doi:10.1016/j.foreco.2004.02.059.
- Outcalt, K.W., and Brockway, D.G. 2010. Structure and composition changes following restoration treatments of longleaf pine forests on the Gulf Coastal Plain of Alabama. *For. Ecol. Manage.* **259**: 1615–1623. doi:10.1016/j.foreco.2010.01.039.
- Peck, J.E. 2016. *Multivariate analysis for ecologists: step-by-step using PC-ORD*. MjM Software Design, Glenden Beach, Ore.
- Peet, R.K., Wentworth, T.R., and White, P.S. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea*, **63**: 262–274.
- Peet, R.K., Christensen, N.L., and Gilliam, F.S. 2014. Temporal patterns in herbaceous layer communities of the North Carolina Piedmont. *In The herbaceous layer in forests of eastern North America*. 2nd ed. Edited by F. Gilliam. Oxford University Press, Oxford, U.K.
- Peterson, G., Allen, C.R., and Holling, C.S. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems*, **1**(1): 6–18. doi:10.1007/s100219900002.
- Phillips, R.J., and Waldrop, T.A. 2008. Changes in vegetation structure and composition in response to fuel reduction treatments in the South Carolina Piedmont. *For. Ecol. Manage.* **255**: 3107–3116. doi:10.1016/j.foreco.2007.09.037.
- Phillips, R., Hutchinson, T., Brudnak, L., and Waldrop, T. 2007. Fire and fire surrogate treatments in mixed-oak forests: effects on herbaceous layer vegetation. *In Proceedings of the Fire Environment — Innovations, Management and Policy*, Destin, Fla., 26–30 March 2007. Compiled by B.W. Butler and W. Cook. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colo., Proc. RMRS-P-46CD. pp. 475–485.
- Pickett, S.T., and White, P.S. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Fla.
- PRISM Climate Group. 2017. PRISM climate data [online]. Available from <http://www.prism.oregonstate.edu/> [accessed 10 November 2017].
- R Core Team. 2015. R: a language and environment for statistical Computing. Version 3.2.2. R Core Team, Vienna, Austria. Available at <https://www.R-project.org>.
- Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Can. J. Bot.* **82**(9): 1273–1283. doi:10.1139/b04-091.
- Rochow, J.J. 1974. Estimates of above-ground biomass and primary productivity in a Missouri forest. *J. Ecol.* **62**(2): 567. doi:10.2307/2258999.
- Scharenbroch, B.C., Nix, B., Jacobs, K.A., and Bowles, M.L. 2012. Two decades of low-severity prescribed fire increases soil nutrient availability in a Midwestern, USA oak (*Quercus*) forest. *Geoderma*, **183–184**: 80–91. doi:10.1016/j.geoderma.2012.03.010.
- Schweitzer, C.J., Dey, D.C., and Wang, Y. 2016. Hardwood–pine mixedwoods stand dynamics following thinning and prescribed burning. *Fire Ecol.* **12**(2): 85–104. doi:10.4996/fireecology.1202085.
- Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J., Bailey, J.D., Fetting, C.J., Fiedler, C.E., Harrod, R.J., Moghaddas, J.J., Outcalt, K.W., Skinner, C.N., Stephens, S.L., Waldrop, T.A., Yaussy, D.A., and Youngblood, A. 2009. The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. *Ecol. Appl.* **19**(2): 285–304. doi:10.1890/07-1747.1. PMID:19323191.
- Smalley, G.W. 1979. Classification and evaluation for forest sites on the southern Cumberland Plateau. USDA Forest Service, Southern Forest Experiment Station, New Orleans, La., Gen. Tech. Rep. SO-23.
- Stambaugh, M.C., Guyette, R.P., Grabner, K.W., and Kolaks, J. 2006. Understanding Ozark forest litter variability through a synthesis of accumulation rates and fire events. *In Proceedings of Fuels Management: How to Measure Success*, Portland, Ore., 28–30 March 2006. Compiled by P.L. Andrews and B.W. Butler. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colo., Proc. RMRS-P-41. pp. 321–332.
- Sydes, C., and Grime, J.P. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland: II. An experimental investigation. *J. Ecol.* **69**(1): 249–262. doi:10.2307/2259829.
- Szabo, M.W., Osborne, E.W., and Neathery, T.L. 1988. Geologic map of Alabama, scale 1:250,000. Geological Survey of Alabama Special Map 220.
- Thorntwaite, C.W. 1948. An approach toward a rational classification of climate. *Geogr. Rev.* **38**: 55–94. doi:10.2307/210739.
- USDA Forest Service (USFS). 2000. Forest biodiversity guidelines [online]. Available from <https://www.agriculture.gov/ie/media/migration/forestry/publications/biodiversity.pdf> [accessed 5 April 2018].
- USDA Forest Service (USFS). 2004. Revised Land and Resource Management Plan: national forests in Alabama [online]. Available from https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_002528.pdf [accessed 5 April 2018].
- USDA Forest Service (USFS). 2016. Forest Inventory and Analysis National Core Field Guide. Volume 1: Field Data Collection Procedures for Phase 2 Plots. Version 7.1. Available from https://www.fia.fs.fed.us/library/field-guides-methods-proc/docs/2016/core_ver7-1_10_2016-opt.pdf.
- USDA Soil Conservation Service. 1959. Soil survey: Lawrence County, Alabama. Series 1949, No. 10. USDA Soil Conservation Service, Washington, D.C., U.S.A.
- Waldrop, T.A., Yaussy, D.A., Phillips, R.J., Hutchinson, T.A., Brudnak, L., and Boerner, R.E.J. 2008. Fuel reduction treatments affect stand structure of hardwood forests in Western North Carolina and Southern Ohio, USA. *For. Ecol. Manage.* **255**: 3117–3129. doi:10.1016/j.foreco.2007.11.010.
- Waldrop, T.A., Hagan, D.L., and Simon, D.M. 2016. Repeated application of fuel reduction treatments in the Southern Appalachian Mountains, USA: implications for achieving management goals. *Fire Ecol.* **12**(2): 28–47. doi:10.4996/fireecology.1202028.
- Weakley, A.S. 2015. Flora of the southern and mid-Atlantic states. Working draft of 21 May 2015. University of North Carolina Herbarium (NCU), Chapel Hill, N.C.
- Williamson, G.B., and Black, E.M. 1981. High temperature of forest fires under pines as a selective advantage over oaks. *Nature*, **293**: 643–644. doi:10.1038/293643a0.
- Willms, J., Bartuszevige, A., Schwilk, D.W., and Kennedy, P.L. 2017. The effects of thinning and burning on understory vegetation in North America: a meta-analysis. *For. Ecol. Manage.* **392**: 184–194. doi:10.1016/j.foreco.2017.03.010.
- Woodall, C.W., and Monleon, V.J. 2008. Sampling protocol, estimation, and analysis procedures for the down woody materials indicator of the FIA program. USDA Forest Service, Northern Research Station, Newtown Square, Penn., Gen. Tech. Rep. NRS-22.