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Effects of thinning and prescribed fire frequency on ground flora in mixed *Pinus*-hardwood stands

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ABSTRACT

Forest management is increasingly focused on enhancing native biodiversity. In temperate forests, a common goal is to increase native plant diversity of the ground flora and silvicultural treatments such as thinning and prescribed burning are often used alone or in combination to achieve this goal. These treatments often increase understory light availability, decrease litter depths, and increase nutrient availability. We examined the effects of thinning without fire and thinning with different fire frequencies (four burns on a three year return interval and two burns on a nine year return interval) to identify changes in community structure and species composition with a focus on taxonomic richness, diversity, and cover of ground flora in post-agricultural *Pinus*-hardwood stands on the Cumberland Plateau in Alabama, USA. This paper reports on one year of post-treatment data (two years post burn) within a longer-term study of thinning and repeated burns. Overstory basal area and density were lower with increased management intensity. Sapling density was substantially greater with increased management intensity; however, this did not affect ground flora richness, diversity, or cover. Ground flora richness, diversity, and cover were greatest in stands that were thinned and burned every three years, and these measures were negatively correlated with litter depth and positively correlated with exposed mineral soil in a non-metric multidimensional scaling (NMS) solution. Our results signify the need for a combination of thinning and burning in these systems. Forest managers that wish to promote native plant diversity in similar systems may consider thinning and frequent burning to increase light availability, decrease litter depth, and promote ground flora richness, diversity, and cover.

1. Introduction

Family and federal forest landowners are increasingly prioritizing amenity-oriented objectives, such as aesthetic beauty, wildlife habitat, and nature protection, over financial goals in management planning (Salwasser, 1991; Butler et al., 2016). Amenity-oriented objectives are often related to conservation of forest biodiversity (Bixler, 2014). Biodiversity is important for ecosystem function because the variety of functions that one species can perform in an ecosystem (e.g. microclimate modification, pollination, seed dispersal) is limited. Species diversity and richness are correlated with an increase in ecosystem function, or in many cases functional redundancy, which promotes the resilience of ecosystems to disturbances (Tilman et al., 1996; Peterson et al., 1998). Forest managers that wish to increase biodiversity and promote ecosystem function often focus on the ground flora (defined here as all vascular plants ≤ 1 m in height), which harbors the majority of plant diversity in temperate forest ecosystems (Gilliam, 2007).

Silvicultural treatments may be implemented to enhance ground flora richness, diversity, and cover (Puettman et al., 2009; Nagel et al., 2017). Silvicultural thinning may be used to achieve a range of objectives including to generate revenue through the harvest of economically mature trees, to increase vigor of desired trees, or to reduce the abundance of undesirable tree genera (Nyland, 2002; Cameron, 2002; Johnson et al., 2009; Schweitzer et al., 2016). Thinning operations often leave behind legacies (e.g. increased understory light and potentially increased nutrient availability) that may affect ground flora diversity (Phillips and Waldrop, 2008, Thomas et al., 1999; Duguid and Ashton, 2013). However, these effects are ephemeral and gradually decline as vegetation responds (Oliver and Larson, 1996; Nyland, 2002; Schweitzer and Dey, 2015).

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Prescribed fire is another silvicultural tool that may be used to promote ground flora richness, diversity, and cover. Prescribed fire often reduces litter accumulation and increases mineral soil exposure (Heirs et al., 2007; Schwilk et al., 2009; Arthur et al., 2017). Litter often inhibits light from reaching the seedbed and acts as a physical barrier to seed germination and early establishment (Hutchinson, 2006). Baskin and Baskin (1988) found that increased light availability resulted in increased germination for many winter and summer annual plants as well as monocarpic and polycarpic perennial plants in the temperate zone. When a seed germinates above or within the litter, the plant allocates more carbohydrates to root growth, and when a seed germinates underneath litter, the plant often exhibits less vigorous shoot growth (Facelli and Pickett, 1991; Ellsworth et al., 2004; Sydes and Grimes, 1981). Indeed, reduction of litter has been shown to significantly increase the germination and establishment of ground flora (Xiong and Nilsson, 1999). Consumption of live vegetation and litter from prescribed burning also releases nutrients into the mineral soil that may influence ground flora productivity (Hutchinson, 2006; Knoepp et al., 2009; Scharenbroch et al., 2012; Alcañiz et al., 2016, 2018). However, the effects of prescribed burning on nutrient composition and ground flora diversity are often not as pronounced when implemented without other silvicultural activities (Boerner, 2006, 2009; Phillips et al., 2007).

Thinning in combination with burning has consistently been shown to be better at increasing ground flora diversity and cover compared to either treatment implemented alone (Schwilk et al., 2009; Willms et al., 2017). However, if the site contains an abundance of hardwoods in the understory or midstory, thinning in combination with burning may increase competition from woody plants in the ground layer via prolific hardwood stump sprouts (McGuire et al., 2001; Phillips et al., 2007; Barbier et al., 2008; Schwilk et al., 2009). Frequent burning alleviated undesirable hardwood competition and maintained increased light levels in the ground layer to sustain high plant diversity in Waldrop et al. (1992), Brose and Van Lear (1998), and Hutchinson et al. (2005a).

A paucity of data is available on ground flora response to the combination of thinning and burning across different burn frequencies over extended periods and in mixed *Pinus*-hardwood systems (Hutchinson et al., 2005a). Furthermore, few studies have quantified the effects of ground flora more than a decade after overstory thinning (Thomas et al., 1999) and we know of no such studies on the response of ground flora to overstory thinning and burning in this region. Forest managers need long-term studies that analyze ground flora response years after thinning and across different burn frequencies to determine the most effective silvicultural system to promote ground flora diversity and cover (Matlack, 2013).

The overarching goal of our study was to quantify the ground flora during the growing season (one year post-treatment; two years post-burn) to three different fire frequencies in mixed *Pinus*-hardwood stands that were thinned to promote hardwood dominance and compare these results to an unthinned and unburned control. The stands we selected to sample were either untreated, thinned only, thinned and burned on a nine year return interval (two burns to date), or thinned and burned on a three year return interval (four burns to date).

The specific objectives of our study were to compare treatment-mediated differences in ground flora richness, diversity, and cover, and to analyze the environmental variables that may have influenced the ground flora response. Through the use of ordination, we examined and visually displayed ground flora composition and abundance as well as determined indicator species within each treatment. We hypothesized that the combination of thinning and burning treatments would result in greater richness, diversity, and cover of ground flora, with the greatest increases in the thinned and frequently burned treatment (burned on a three year return interval). We hypothesized that ordination would display the highest forb and grass richness, diversity, and cover in the thinned and frequently burned treatment. We also hypothesized environmental variables, specifically litter depth and understory light availability, would be key factors that influenced ground flora richness, diversity, and cover. The information synthesized in this study can be used in comparative studies to elucidate general patterns and long-term trends regarding ground flora response to different management prescriptions and aids in our ability to design silvicultural systems to promote plant richness, diversity, and cover.

2. Methods

2.1. Study site

This study took place on the William B. Bankhead National Forest (BNF), located in northern Alabama, USA. The study site is within the Central Hardwood Forest Region (Fralish, 2003). The BNF is located on the southern portion of the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman, 1938), and in the Southwestern Appalachians (level III) ecoregion (Griffith et al., 2001). The topography of the region is complex, no longer resembling a true plateau, characterized by steep slopes and narrow ridges (Smalley, 1979) that occasionally lead into steep gorges with rock bluffs (USDA Forest Service, 2004). The geology is primarily composed of the Pennsylvania Pottsville formation consisting of thick-bedded to pebbly quartzose sandstone and containing differing levels of interstratified shale, siltstone, and thin discontinuous coal (Szabo et al., 1988). The primary soil types are Enders loam, rolling phase (E_c) and Muskingum, stony fine sandy loam, steep phase (M_g) (USDA NRSC, 2017). The narrow ridges typically contain E_c and are flanked by the shallow, sandstone rich M_g (USDA SCS, 1949). The soils are strongly acidic, well drained, have moderate moisture holding capacity, and are relatively low in nutrients and organic matter (USDA SCS, 1949). The climate in the region is classified as humid mesothermal, characterized by long, hot summers and short, mild winters with no recognized dry season (Thornthwaite, 1948). Mean annual temperature is 16.0 °C with a mean monthly temperature of 4.5 °C in January and 25.6 °C in July (PRISM 2017). Mean annual precipitation from the past thirty years is 140 cm with the highest mean monthly precipitation of 14.2 cm in December and the lowest mean monthly precipitation of 9.4 cm in October (PRISM 2017). The frost-free period typically spans from March to November (Smalley, 1979).

Prior to federal acquisition in 1918, ca. 40% of the land base that now comprises the BNF was in cultivation and most ridgetops were cutover (USDA Forest Service, 2004). We explored the field notes for the three townships in which we installed plots and documented several tree species that were recorded during the land survey. The land survey was conducted in 1818 under the direction of the General Land Office and was held in the land records of the Alabama Secretary of State (2018). Field notes from several sections of each township were examined. Each treatment of this study contained similar tree species in 1818. Common trees listed by surveyors included: *Quercus* spp., *Carya* spp., *Pinus* spp., *Castanea dentata* (Marshall) Borkh., *Fraxinus americana* L., *Oxydendrum arboreum* (L.) DC., and *Sassafras albidum* (Nutt.) Nees. Stands were planted with *Pinus taeda* L. in the 1930s to re-establish forests on cutover and agricultural land and again planted with *P. taeda* in the 1960s–1980s to increase economic yield, totaling an estimated 31,970 ha of planted *P. taeda* on the national forest. Following a severe *Dendroctonus frontalis* Zimmermann (southern pine beetle) outbreak in the 1990s, which left *Pinus* spp. over approximately 7527 ha on the BNF weakened or dead, the Bankhead Forest Health and Restoration Initiative was launched (Addor and Birkhoff, 2004). Through these efforts, over 6400 ha were commercially thinned to reduce density in overstocked *Pinus* stands. Prescribed burning programs were initiated to reduce fuel loads, reduce the risk of wildfire (particularly from beetle-killed trees), and prepare the treated stands for regeneration of tree species native to the southern Cumberland Plateau region, primarily *Quercus* spp. (Addor and Birkhoff, 2004).

2.2. Treatments

In 2003, a study was initiated to analyze fuel and woody vegetation response to silvicultural thinning and prescribed burning on the BNF in association with the Bankhead Forest Health and Restoration Initiative (Clark et al., 2006; Schweitzer et al., 2008, 2016). The study was created with four replications of nine different treatments of prescribed burning and thinning. Some results from the project have been previously reported (see Clark and Schweitzer, 2009; Sutton et al., 2010; Schweitzer and Wang, 2013; Schweitzer et al., 2014, 2016; Sutton et al., 2014, 2017).

For this study, we analyzed ground flora data in the following treatments: the unmanaged control, the thinned and not burned (hereafter thin/0Rx), the thinned and burned on a nine year return interval (hereafter thin/9Rx or infrequently burned), and the thinned and burned on a three year return interval (hereafter thin/3Rx or frequently burned). At least two stands were sampled in each treatment and plots were located throughout the stands to ensure adequate spatial coverage and to be independent of other plots. Caution was taken during the stand selection process to ensure all stands were similar prior to treatments. Web Soil Survey (Soil Survey Staff, 2017) was used to select stands with the same primary soil types and data from the National Forest was used to select stands that were the same age.

All thinning operations analyzed in this study were conducted in 2006. The thinning was designed to release crop trees (i.e. free thinning) and mostly *Pinus* stems were harvested to transition stands to hardwood dominance. Target residual basal area was 11.5 $m^2 ha^{-1}$. Based on pre-treatment data, the thin for the thin/0Rx treatment reduced stem density by 28% (973 residual stems ha^{-1}), the thin for the thin/9Rx treatment reduced stem density by 29% (973 residual stems ha^{-1}), and the thin for the thin/3Rx treatment reduced stem density by 32% (842 residual stems ha^{-1}) immediately following the entry. Equipment used to harvest trees included a Hydro-Ax 511 EX wheel-mounted feller buncher and a Timbco 415-C crawler mounted feller buncher. A Fabtek 546 B forwarder with a loader bucket was also used to move felled trees to landing sites. Slash was left on site in all treatments to reduce erosion.

The initial burns for the thin/9Rx and the thin/3Rx treatments were in 2007. Every burn occurred during the dormant season months of January, February, or March. The fires were ignited in strips approximately 8 m apart as well as aerially with helicopters using potassium permanganate.

2.3. Field methods

We selected stands to sample that were in the second growing season after fire because the literature indicated that common ground flora species require more than one growing season for physiological recovery from fire, and the competition from woody plants substantially increases after two growing seasons (Phillips et al., 2007; Schwilk et al., 2009; Lettow et al., 2014; Willson et al., 2018). Shapefiles provided by the USDA Forest Service were uploaded to ArcMap version 10.3 (Environmental Systems Research Institute, 2014, Redlands, CA, U.S) to visualize stand boundaries. We installed 20 plots in each treatment. Plots were established using a fishnet overlay that was clipped to the boundaries of the USDA Forest Service stands and a random number generator was used to select plot locations. Once 20 points per treatment were determined in ArcMap, coordinates were uploaded as waypoints in a handheld GPS receiver for field navigation. During field reconnaissance, if a tentative plot was inadvertently located on a trail or influenced by an edge, plot center was moved 50 m in the cardinal direction that was most opposite from the obstruction and a new coordinate pair was recorded.

All field data were collected in June, July, and August of 2017. At each plot location, a nested design was used to measure and compare ecological variables at sampling unit sizes appropriately matched to the relative size of each variable being measured (Kleinman et al., 2017). The largest sampling unit was a 500 m^2 (0.05 ha) fixed-radius plot to measure all live stems > 1 m in height. Each ground flora taxon (vascular plants ≤ 1 m in height) and exposed mineral soil were measured in ten 1 × 1 m subplots (10 m^2) within each plot. One subplot was positioned at the center of the 0.05 ha plot and the other nine were equally spaced along 12.4 m transects at 0°, 120°, and 240° azimuths from plot center (Kleinman et al., 2017).

All ground flora individuals were identified to lowest taxonomic level possible. The percent cover of each ground flora taxon, *Pinus* litter, and broadleaf litter was estimated with different sized panels designed to cover 1% and 5% of the 1 m^2 subplot as guides. Percent cover estimations were ranked from 1 to 10 for each quadrat using the North Carolina Vegetation Survey (NCVS) protocol where 0 = none, 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). To quantify seedling (live woody stems > 1 m in height) density, the number of stems for each woody species was tallied within each 1 m^2 subplot.

Trees were defined as live stems ≥ 5 cm diameter at breast height (dbh, 1.37 m above the root collar) and saplings were defined as live woody stems < 5 cm dbh and > 1 m in height. Trees and saplings were identified to species to characterize composition and tallied to quantify density. Tree dbh was measured to quantify basal area ($m^2 ha^{-1}$) and relative dominance (species-specific basal area).

Hemispherical photographs of the canopy were taken at plot center to assess ground layer light availability. Photographs were taken with an Olympus Stylus TG-3 camera with a hemispherical lens steadied using a self-leveling mount positioned 1 m above the ground. Default settings were used for the majority of pictures, but aperture was decreased when necessary. All photographs were oriented north and taken during dusk, dawn, or overcast cloud conditions to reduce glare that may bias image analysis. Litter depth was measured to the nearest 0.25 cm at the four corners of 0.25 m^2 subplots placed 5 m from plot center in the four cardinal directions. Following litter depth measurements, all fuel (i.e. litter, dead woody material (< 10 cm in diameter), and green leaves and stems ≤ 1 m in height) was collected in the 0.25 m^2 to compare dry fuel mass across treatments. Slope was measured within each plot using a clinometer and aspect was measured at plot center using a compass. Slope and aspect were quantified to determine if differences between plots could be associated with these variables.

2.4. Analytical methods

Ground flora specimens that could not be identified to species in the field were transported to the laboratory where they were pressed, dried, and identified using Weakley (2015). A dissecting microscope was used to properly observe structures that would facilitate identification (e.g. reproductive structures). With the exception of grasses (Poaceae), vascular plants were identified to genus or species given available reproductive structures (Miller and Miller, 2005; Weakley, 2015; Keener et al., 2016). Taxonomic richness, Shannon's taxa diversity index, and total cover of ground flora were calculated using column and row summary statistics in PC-ORD v. 6.0 (McCune and Medford, 2011) to determine compositional diversity of ground flora within each treatment. Ground layer taxa richness and diversity measures considered plants that were identified to species separately from plants identified to genus. For example, *Symphiotrichum dumosum* (Linnaeus) G.L. Nesom and *Symphiotrichum patens* (Aiton) G.L. Nesom were considered individually and separately from the genus *Symphyotrichum*, which may have included *Symphyotrichum cordifolium* (Linnaeus) G.L. Nesom and *Symphyotrichum pilosum* (Willdenow) G. L. Nesom among other *Symphyotrichum* species. Thus, for the genus *Symphyotrichum* we considered there to be three separate species, which is conservative because it is possible that the unknown specimens of *Symphyotrichum* represented more than one species within that genus. Genera of specimens not always identified to species included *Desmodium*, *Eupatorium*, *Juncus*, *Prunus*, *Pycnanthemum*, *Rubus*, *Scleria*, *Solidago*, *Symphyotrichum*, and *Viola*.

To calculate average cover class per treatment, the NCVS cover class of each taxon was converted to its corresponding midpoint value, summed per plot, and reconverted to corresponding NCVS cover classes (Peet et al., 1998). Ground layer taxa were divided into growth habit and consisted of woody plants (trees or shrubs), vines, forbs (defined as a vascular plant without significant woody tissue above or at the ground), and graminoids (USDA, 2017) and compared across treatments. In the results section, the percent cover for each growth habit were reported as the range of percent cover by rounding each converted cover class to the nearest whole number. Vines were analyzed separately from forbs because of their unique ability to occupy space and capture light in forest ecosystems (Collins and Wein, 1993; Schnitzer and Bongers, 2002). Legumes were also analyzed separately from other ground flora because of their potential to be forage for wildlife, ability to make nitrogen available for other plants, and regenerative success after fire (Arianoutsou and Thanos, 1996; Sparks et al., 1998). Seedling density of all woody stems in the 10 subplots was summed and scaled to the hectare level and compared across treatments.

Canopy photographs were analyzed in WinSCANOPY v. 2014a (Regent Instruments, 2014) to determine canopy openness and ground layer light availability (Wulder, 1998) and were compared across treatments. Canopy openness was calculated by subtracting the percent of canopy cover in each hemispherical photograph from one hundred. Ground layer light availability (light levels at ≤ 1 m from the forest floor, i.e. height in which the photographs were taken) was estimated by calculating the estimated percent of full photosynthetic photon flux density reaching the ground layer (hereafter referred to as % ground layer PPFD or ground layer light availability) (calculated in WinSCANOPY v. 2014a). Dry fuel mass was calculated by drying all samples (litter and green vegetation ≤ 1 m from the forest floor) to room moisture content and weighed to the nearest 0.01 g. Litter depth was averaged per plot and compared across treatments to assess treatment-mediated differences in forest floor accumulation. Percent bare mineral soil cover was also compared across treatments to determine if treatment mediated differences in bare mineral soil exposure had an influence on ground flora.

Trees and saplings were divided into taxonomic groups based on shade tolerance and successional trends in the Central Hardwood Forest Region (e.g. Rentch et al., 2003; Cowden et al., 2014; Cox et al., 2016) and included *Pinus* spp., *Quercus-Carya*, *Acer-Fagus*, and "other spp." Live tree density (stems ha^{-1}), relative density (percent of total trees ha^{-1}), dominance (basal area), relative dominance (percent of total basal area), and relative importance (sum of relative density and relative dominance) of each taxonomic group of trees were calculated to characterize the forest overstory and assess the relative contribution of each taxonomic group across treatment categories, and were then related to ground flora measures. Density (stems ha^{-1}) and relative density (% of total saplings ha^{-1}) of saplings by taxonomic group was calculated to characterize the sapling strata and assess the relative contribution of each group across treatments.

Variables were compared across treatments using one-way analysis of variance (ANOVA) tests if variables met assumptions of normality (tested via Shapiro-Wilk Test) and homoscedasticity (tested via Levine's test) or were met after being transformed via logarithmic transformations. If ANOVA revealed significant differences, Tukey honest significance difference (HSD) post-hoc tests were utilized to detect pairwise differences. Variables that could not be transformed to meet the assumptions of normality and homoscedasticity were compared with Kruskal-Wallis and post-hoc pairwise comparison tests. Logarithmic transformed litter depth was compared to ground flora richness and diversity using correlation analysis. All logarithmic transformations, one-way ANOVA tests, Kruskal-Wallis tests, Tukey HSD post-hoc tests, post-hoc Dunn's pairwise comparisons tests, and single linear regressions were performed using SPSS 22.0 (IBM, Armonk, NY, USA). All analyses were conducted at a significance level of $p \leq 0.05$.

To characterize and assess differences in ground layer taxa cover across treatments, non-metric multidimensional scaling (NMS) ordination, permutational multivariate analysis of variance (PerMANOVA), and indicator species analysis (ISA, Dufrêne and Legendre, 1997) were conducted using PC-ORD v. 6.0 (McCune and Medford, 2011). NMS was used to graphically interpret patterns in the composition and abundance of ground layer plant taxa in relation to eight environmental variables: (1) silvicultural treatment, (2) % ground layer PPFD (3) transformed slope aspect (Beers et al., 1966), (4) percent slope (5) sapling density (stems ha^{-1}), (6) live tree density (stems ha^{-1}), (7) litter depth (cm), and (8) bare mineral soil (%). Plot level NCVS cover classes in the main matrix were relativized by maximum class documented to account for taxa with naturally large growth forms (Peck, 2016; Kleinman et al., 2017). Additionally, taxa with only a single occurrence were eliminated from the matrix to ensure unique plant assemblages were not based on one individual (Peck, 2016). An NMS scree plot was run to determine the optimal number of axes for the final solution. NMS ordination was run using a three-axis solution with the Sørensen (Bray-Curtis) distance measure, 250 runs with real data, and random starting coordinates. The ordination was run several times to verify consistency of solutions. For genera with unknown species, species were grouped to genus for the NMS solution to ensure a conservative output for that genus rather than adding species that may or may not have been already accounted for within that same genus. However, this did not make a visual difference in the output. A biplot overlay was used to assess environmental variables and ordination axes using an $r^2 \geq 0.4$ cutoff. A one-way PerMANOVA with Sørensen distance was used to determine the statistical significance of observed differences in taxa assemblages across treatments. Indicator Species Analysis (ISA) was used to compare the average relative frequency and relative abundance (Indicator Value, IV) of each taxon per treatment to identify taxa most strongly associated with differences in ground flora across treatments detected with PerMANOVA (Dufrêne and Legendre, 1997; Peck, 2016). In addition to ISA, the ten most common (frequency of occurrence based on percentage of total plots) non-indicator taxa were added in the results to include common species encountered in the study.

3. Results

3.1. Ground flora

Ground flora taxonomic richness was the greatest ($p < 0.001$) in the thin/3Rx treatment (30 taxa ± 1 (SE) $plot^{-1}$), and greater in the thin/9Rx treatment (22 taxa ± 1 (SE) $plot^{-1}$) compared to the thin/0Rx treatment (18 taxa ± 1 (SE) $plot^{-1}$, $p < 0.05$) and the control (17 taxa ± 1 (SE) $plot^{-1}$, $p = 0.001$) (Fig. 1). The greatest number of taxa in any one 1 m^2 subplot was 18 taxa, which was in the thin/3Rx treatment. Among all treatments, 554 out of 800 subplots (69.25%) contained 5 or more taxa, and 116 out of 800 subplots (14.50%) contained 10 or more taxa. Shannon taxonomic diversity was the greatest in the thin/3Rx treatment ($p < 0.001$), and greater in the thin/9Rx treatment compared to the thin/0Rx ($p < 0.03$) treatment and the control ($p < 0.001$). Average ground flora Shannon taxonomic diversity index was 2.73 ± 0.05 (SE) per plot in the control, 2.82 ± 0.05 (SE) per plot in the thin/0Rx treatment, 2.94 ± 0.05 (SE) in the thin/9Rx treatment, and 3.30 ± 0.05 (SE) per plot in the thin/3Rx treatment.

Ground flora cover was the greatest in the thin/3Rx treatment (75–95%; at the $p < 0.03$ level relative to the thin/9Rx treatment, and at the $p < 0.001$ level relative to the thin/0Rx treatment and the control), and greater in the thin/9Rx treatment (25–50%) compared to the thin/0Rx treatment (10–25%; $p = 0.001$) and control (10–25%;

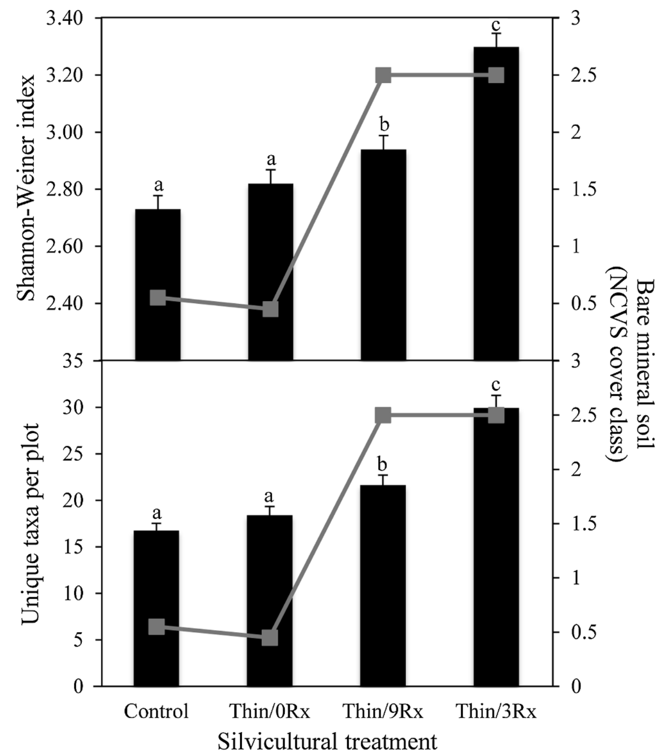

Fig. 1. Taxonomic richness (unique taxa per plot), and taxonomic diversity for ground layer flora (vascular plants ≤ 1 m height surveyed in 10-m^2 plots) in four silvicultural treatments in William B. Bankhead National Forest, Alabama, USA. Control was untreated, thin/0Rx was thinned in 2006 without burning, thin/9Rx was thinned in 2006 and burned on a nine year return interval, and thin/3Rx was thinned in 2006 and burned on a three year return interval. Lines indicate average cover class of exposed mineral soil in each 10-m^2 survey plot. Corresponding percentage ranges of cover classes were based on North Carolina Vegetation Survey (NCVS) protocol where 0 = none, 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%.

$p < 0.001$) (Fig. 2). Forb cover was statistically similar in the thin/3Rx (5–10%) and thin/9Rx treatments (2–5%; $p > 0.05$). Forb cover was greater in the thin/3Rx treatment relative to the control (0–1%; $p < 0.001$) and the thin/0Rx treatment (0–1%; $p < 0.001$). Additionally, forb cover was greater in the thin/9Rx treatment compared to the control ($p < 0.001$) and the thin/0Rx treatment ($p = 0.002$). Graminoid cover was greatest in the thin/3Rx treatment (2–5%; $p < 0.08$), similar in the thin/0Rx (0–1%) and the thin/9Rx treatments (1–2%; $p > 0.05$), and the least in the control (few; $p < 0.03$). Legume cover was significantly greater in burned and thinned treatments ($p \leq 0.05$), and significantly greater in the thin/3Rx treatments than the thin/9Rx treatments ($p = 0.03$).

A three-dimensional NMS solution revealed a difference in the composition and abundances of the 132 ground layer taxa among treatments (PerMANOVA, $p < 0.001$) (Fig. 3). Axis 1 explained 34% of the variation and was positively correlated with sapling density (r = 67%), bare mineral soil (r = 62%) and % ground layer PPFD (r = 48%, not pictured) and negatively correlated with tree density (r = −75%) and litter depth (r = −64%). Axis 2 explained 15% of the variation and was positively correlated with bare mineral soil (r = 46%). Axis 3 explained 21% of variation and was positively correlated with sapling density (r = 46%), and negatively correlated with litter depth (r = 49%) and tree density (r = 49%). The control plots (squares) were generally located in the lower left portion of the NMS output, negatively corresponding to axis 1, 2, and 3. The thin/0Rx plots (circles) were generally located in the middle lower left portion of the graph, negatively corresponding to axis 1, 2, and 3. The thin/9Rx plots

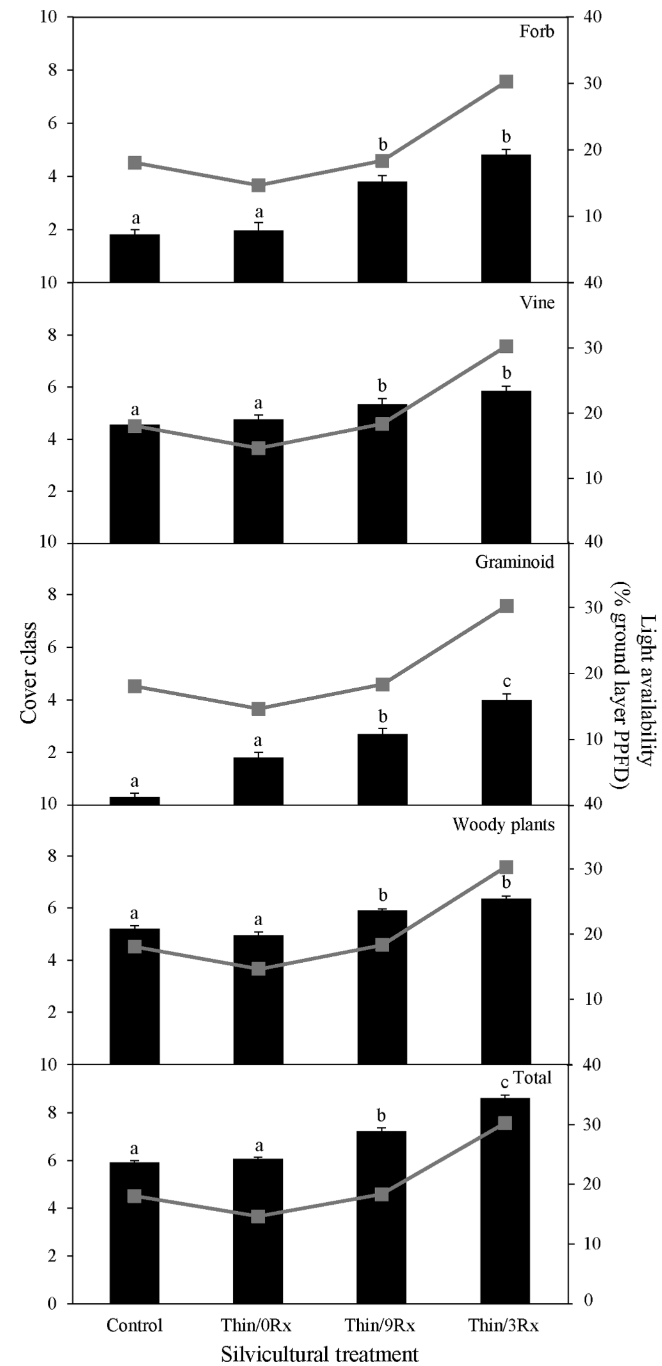

Fig. 2. Cover class based on growth habit of all vascular plants ≤ 1 m in height and light availability (% of photosynthetic photon flux density reaching 1 m above the surface) in four different silvicultural treatments in William B. Bankhead National Forest, Alabama, USA. Cover classes range from 1 to 10 where 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%. Control was untreated, thin/0Rx was thinned in 2006 without burning, thin/9Rx was thinned in 2006 and burned on a nine year return interval, and thin/3Rx was thinned in 2006 and burned on a three year return interval. Letters indicate significant differences in cover classes ($p < 0.05$).

(triangles) were generally located in the middle upper right portion of the graph, positively corresponding to axis 1, 2, and 3. The thin/3Rx plots (pluses) were generally located in the upper right portion of the graph, positively correlated with axis 1, axis 2, and axis 3. The thin/3Rx plots were somewhat distinct from the thin/9Rx plots. Also, there was a lack of overlap between the thin/3Rx plots and the thin/0Rx plots, but

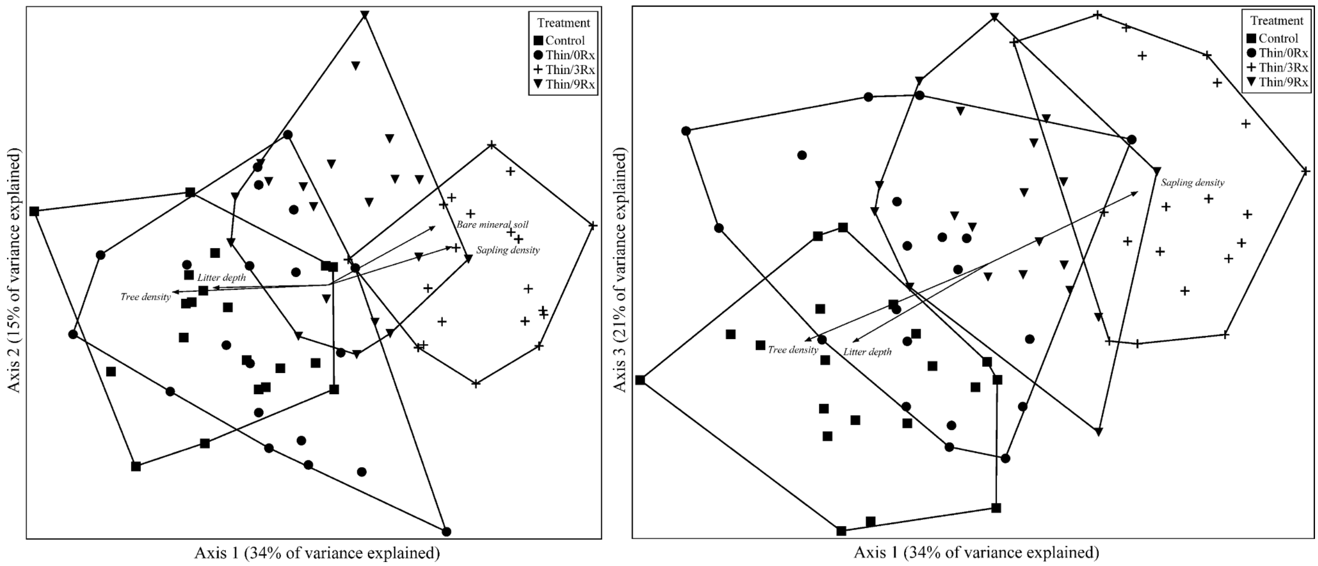

Fig. 3. Three-dimensional non-metric multidimensional scaling solution based on the abundance of ground flora (vascular plants ≤ 1 m height) in control plots (Untreated; squares), plots that were thinned in 2006 and not burned (Thin/0Rx; circles), plots that were thinned in 2006 and burned on a three year return interval (Thin/3Rx; plus signs), and plots that were thinned in 2006 and burned on a nine year return interval (Thin/9Rx; triangles) in William B. Bankhead National Forest, Alabama, USA. Polygons (convex hulls) connect plots in the same silvicultural treatment, and arrows (biplots) show the strength (length of arrow) and correlation ($r^2 \geq 0.4$) between environmental or biophysical factors and ordination axes.

some overlap between the thin/9Rx plots and the thin/0Rx plots.

We identified 32 significant indicator taxa ($p < 0.05$) (Table 1). The thin/3Rx treatment contained the majority with 22 taxa (67%), half of which were forbs. The thin/3Rx treatment was also the only treatment that contained a graminoid as an indicator taxon. Additionally, the thin/3Rx treatment contained eight woody plants and two vines as indicator taxa. Of the 11 remaining taxa, five occurred in the thin/9Rx treatment, four occurred in the control stands, and two occurred in the thin/0Rx treatment. The thin/9Rx treatment contained three woody plants, one vine, and one forb. The control plots contained three woody plant indicator taxa and one vine. The thin/0Rx treatment contained one woody plant indicator taxon and one vine taxon.

Total seedling density ha^{-1} was not significantly different ($p > 0.05$) between the control and the thin/0Rx, the thin/9Rx, or the thin/3Rx treatments ($p > 0.05$) (Table 2). However, total seedling density ha^{-1} was greater in the thin/9Rx treatment compared to the thin/0Rx treatment ($p = 0.04$). Density of seedling sized *Pinus* stems was lower than that of the hardwood groups, similar to the sapling layer. *Acer-Fagus* had the highest seedling density in all treatments except for in the thin/3Rx treatment, where it was the least abundant group ($p < 0.01$). *Quercus-Carya* had almost twice as many seedlings ha^{-1} in the thin/9Rx treatment than in the thin/3Rx treatment ($p < 0.05$).

3.2. Environmental variables

Canopy openness was higher in the thin/3Rx and the thin/9Rx treatments compared to the thin/0Rx and the control ($p < 0.03$) (Table 3). The thin/3Rx treatment contained the greatest light availability reaching the ground layer (% ground layer PPFD) ($p < 0.001$) and light availability in the ground layer was not statistically different between the control plots, the thin/0Rx treatment, and the thin/9Rx treatment ($p > 0.05$) (Fig. 2). The two burned treatments had significantly less fuel mass (i.e. litter, green leaves, and dead woody material (< 10 cm in diameter) ≤ 1 m in height) compared to the control and the thin/0Rx treatment ($p < 0.01$). However, no significant differences were found between the control and thin/0Rx ($p = 0.26$), and no significant differences were found between the thin/9Rx and thin/3Rx treatments ($p > 0.05$). Average total fuel mass was $208.56\,g\,m^{-2} \pm 12.70$ (SE) in control plots, $160.49\,g\,m^{-2} \pm 13.70$ (SE) in the thin/0Rx plots, $100.19\,g\,m^{-2} \pm 8.91$ (SE) in the thin/3Rx plots, and $97.55\,g\,m^{-2} \pm 7.0$ (SE) in the thin/9Rx plots. Logarithmic transformed litter depth was negatively associated with ground layer taxonomic Shannon diversity ($r = 0.59$, $p < 0.001$), and ground layer taxonomic richness ($r = 0.65$, $p < 0.001$). The thin/3Rx treatment contained the thinnest litter on average ($p \leq 0.01$). The thin/9Rx treatment contained thinner litter compared to the thin only treatment and the control (both $p < 0.001$). The thin/3Rx and the thin/9Rx treatments resulted in an average of 55% shallower litter compared to the thin/0Rx and the control stands. Percent cover of bare mineral soil was greater in the thin/3Rx (1–2% per plot) and the thin/9Rx (1–2% per plot) treatments compared to the thin only treatment (solitary; $p < 0.001$) and the control (0–1% per plot; $p < 0.001$) (Table 3).

3.3. Trees and saplings

Live basal area ($m^2\,ha^{-1}$) was ≥ 45% lower in the thinned treatments compared to the unmanaged control ($p < 0.001$) (Table 4). The thin/3Rx treatment contained the fewest trees ha^{-1} ($p < 0.001$), and the thin/9Rx treatment contained fewer trees ha^{-1} than the thin/0Rx treatment ($p < 0.001$) and the control ($p < 0.001$). The genus *Pinus* had the greatest density in the tree layer in all treatments except for the thin/0Rx treatment (Table 4). The *Acer-Fagus* group was the second most abundant taxonomic category in the control stands (26% relative density), but was third to the *Pinus* and *Quercus-Carya* groups in the thin/0Rx treatment and fourth behind these and the “others” group in burned treatments. The *Acer-Fagus* group contained the second greatest basal area in the control stands and the greatest in the thin/0Rx treatment. However, *Acer-Fagus* had the least basal area compared to all other taxonomic groups in burned treatments. All treated stands had high sapling density relative to the control, with the highest abundance in the thin/3Rx treatment (Table 2). Contrary to the tree stratum, *Pinus* was generally less abundant than hardwoods in the sapling stratum. The *Acer-Fagus* group had the greatest density in all treatments except for the thin/3Rx treatment, which was most occupied by the “others” group. The *Quercus-Carya* sapling group was greater than twice as abundant in the thin/3Rx treatment compared to all other treatments.

Table 1
Indicator taxa plus the ten most common non-indicator taxa ranked by frequency of occurrence (percent of total plots). Indicator taxa include the Indicator Value (based on the average of relative frequency and relative abundance) and significance (* = p < 0.05, ** = p < 0.01, *** = p < 0.001) for four silvicultural treatments in William B. Bankhead National Forest, Alabama, USA. Control was untreated, thin/0Rx was thinned in 2006 without burning, thin/9Rx was thinned in 2006 and burned on a nine year return interval, and thin/3Rx was thinned in 2006 and burned on a three year return interval. Asterisks mean only that particular treatment had a significantly different IV value than the rest of the treatments.

Taxon	Growth habit	Frequency (% of plots)	Indicator Values			
			Control	Thin/0Rx	Thin/9Rx	Thin/3Rx
Acer rubrum Linnaeus	Woody	100	18	17	33***	31
Muscadinia rotundifolia (Michaux) Small	Vine	100	20	23	29.1**	28
Smilax glauca Walter	Vine	98.75	–	–	–	–
Smilax rotundifolia Linnaeus	Vine	96.25	–	–	–	–
Poaceae	Graminoid	77.5	–	17	31	46***
Carya glabra (P. Miller) Sweet	Woody	73.75	9	16	16	42.3***
Nyssa sylvatica Marshall	Vine	65	–	–	–	–
Quercus alba Linnaeus	Woody	65	–	–	–	–
Vaccinium arboreum Marshall	Woody	63.75	–	–	–	–
Toxicodendron radicans (Linnaeus) Kuntze	Forb	61.25	9	3	26	40.4***
Carya tomentosa (Lamark) Nuttall	Woody	55	–	–	–	–
Liriodendron tulipifera Linnaeus	Woody	51.25	4	5	17	39.2***
Pinus taeda Linnaeus	Woody	50	–	–	–	–
Quercus montana Willdenow	Woody	50	–	–	–	–
Rubus spp.	Woody	48.75	1	18	12	51.7***
Quercus velutina Lamarck	Woody	47.5	37*	1	–	19
Prunus serotina Ehrhart	Woody	46.25	7	10	10	30.7*
Sassafras albidum (Nuttall) Nees	Woody	40	–	–	–	–
Parthenocissus quinquefolia (Linnaeus) Planchon	Vine	38.75	3	3	3	43.8***
Quercus falcata Michaux	Woody	38.75	1	8	23.2*	10
Berchemia scandens (Hill) K. Koch	Vine	37.5	–	–	–	–
Rhus copallinum Linnaeus	Woody	30	–	–	16	53***
Dioscorea villosa Linnaeus	Forb	25	–	–	1	17.9*
Gelsemium sempervirens (Linnaeus) St. Hilaire	Vine	25	26.7*	4	4	3
Vitis aestivalis Michaux *var. aestivalis*	Vine	23.75	–	–	1	50***
Solidago arguta Aiton	Forb	16.25	–	–	8	38.5***
Cornus florida Linnaeus	Woody	15	1	–	18.6*	1
Diospiros virginiana Linnaeus	Woody	13.75	2	3	9	24.7*
Chamaecrista fasciculata (Michaux) Greene	Forb	12.5	–	–	7	63.8***
Ilex opaca Aiton	Woody	12.5	19.6*	–	2	2
Fagus grandifolia Ehrhart	Woody	11.25	35.6***	–	1	–
Hypericum hypericoides (Linnaeus) Crantz	Woody	10	–	1	1	26.2**
Solidago odora Aiton	Forb	10	–	–	8	18.3*
Callicarpa americana Linnaeus	Woody	8.75	–	25.7**	1	–
Lespedeza violacea (Linnaeus) Persoon	Forb	8.75	–	–	–	51.1***
Bignonia capreolata Linnaeus	Vine	7.5	–	25**	–	–
Lespedeza hirta (Linnaeus) Hornemann	Forb	6.25	–	–	15*	–
Galium uniflorum Michaux	Forb	5	–	–	–	20.5**
Styrax grandifolius Aiton	Woody	3.75	–	–	2	18.7*
Helianthus hirsutus Rafinesque	Forb	2.5	–	–	–	25**
Helianthus strumosus Linnaeus	Forb	2.5	–	–	1	16.7*
Erechtites hieraciifolius (Linnaeus) Rafinesque ex A.P. de Candolle	Forb	1.25	–	1	–	20.5*

4. Discussion

4.1. Ground flora

Thinning without prescribed fire altered the stand structure and the light regime enough to elicit a greater percentage of graminoid cover compared to the control that was detectable 12 years after the event. Because we did not measure the initial response of the thin only treatment, we can only infer that light and likely ground flora richness, diversity, and cover were increased for several years following the thinning event, or until growth of residual and new individuals filled the growing space (Oliver and Larson, 1996). Increased light has been documented in other studies that quantified the response of ground flora richness and diversity immediately following thinning (Thomas et al., 1999; Phillips and Waldrop, 2008; Bowles et al., 2011; Brewer, 2016). Brewer (2016) found greater herbaceous species richness subsequent to an EF4 tornado that reduced canopy cover to an average of 40% in upland *Quercus-Pinus* forests compared to undamaged plots. Bowles et al. (2011) found an up to 100% increase in ground flora richness after a ≤50% reduction in canopy cover in a *Quercus* stand. Phillips and Waldrop (2008) recorded increased understory plant richness in *P. taeda/P. echinata* stands that were thinned from below to $18\,m^2\,ha^{-1}$ compared to unthinned stands in the Piedmont of South Carolina, USA. Thomas et al. (1999) found significant positive responses to understory plant diversity and cover after a thin that resulted in a final stem density of 494 trees ha^{-1} in a *Pseudotsuga menziesii* (Mirb.) Franco stand. However, the thinned plots contained litter depths ca. 50% greater than the unthinned plots in the study (Thomas et al., 1999).

Although thinning alone may increase ground flora cover, richness, and diversity immediately following the treatment, the results of our study indicate that repeated prescribed burning subsequent to thinning will help perpetuate increases in ground flora richness, diversity, and cover compared to thinning alone. Fire is a unique disturbance that releases a quick pulse of nutrients within the system, consumes litter, and topkills many smaller stems, all of which are alterations to forest systems that are different from those achieved by thinning (Boerner, 2006; Phillips et al., 2007; Lettow et al., 2014; Brewer, 2016). In our study, thinning coupled with frequent burning (the thin/3Rx treatment) resulted in significantly greater values for ground flora richness,

Table 2
Density (stems ha^{-1}) and relatively density (%) of saplings (live woody stems > 1 m in height and < 5 cm dbh) and seedlings (live woody stems ≤ 1 m in height) divided into four taxonomic groups in four different silvicultural in William B. Bankhead National Forest, Alabama, USA. Control was untreated, thin/0Rx was thinned in 2006 without burning, thin/9Rx was thinned in 2006 and burned on a nine year return interval, and thin/3Rx was thinned in 2006 and burned on a three year return interval. Letters on total density indicate significant differences ($p < 0.02$).

Saplings	Sapling Density (stems ha^{-1})				Relative Sapling Density (%)			
	Control	Thin/0Rx	Thin/9Rx	Thin/3Rx	Control	Thin/0Rx	Thin/9Rx	Thin/3Rx
Acer-Fagus	665	1378	1403	2570	43.44	43.91	35.6	36.14
Other spp.*	462	725	1173	3054	30.18	23.1	29.76	42.95
Quercus-Carya	404	731	547	1480	26.39	23.3	13.88	20.81
Pinus spp.	–	304	818	7	–	9.69	20.76	0.1
Total	1531[a]	3138[b]	3941[b]	7111[c]	100.00	100.00	100.00	100.00
Seedlings	**Seedling Density (stems ha^{-1})**				**Relative Seedling Density (%)**			
Acer-Fagus	21,200	15,400	8700	23,800	49.82	44.77	20.62	44.20
Other spp.	15,400	14,250	19,750	23,150	36.19	41.42	46.80	42.99
Quercus-Carya	5950	4750	12,900	6550	13.98	13.81	30.57	12.16
Pinus spp.	–	–	850	350	–	–	2.01	0.65
Total	42,550[a]	34,400[a]	42,200[a]	53,850[a]	100.00	100.00	100.00	100.00

* The top 10 "other" sapling species: *Nyssa sylvatica* Marshall, *Ilex opaca* Aiton, *Frangula caroliniana* (Walter) A. Gray, *Vaccinium arboreum* Marshall, *Oxydendrum arboreum* (L.) DC., *Liriodendron tulipifera* L., *Viburnum acerifolium* L., *Asimina triloba* (L.) Dunal, *Amelanchier arborea* (Michx. f.) Fernald, and *Cornus florida* L.

diversity, and cover compared to thinning and infrequent burning. Others have also found that more frequent burning favors ground flora diversity. For example, Peterson and Reich (2008) found that understory species richness was highest on sites burned five times in a decade and plateaued with increased fire in *Quercus* systems in Minnesota, USA. After four decades of dormant season burning in a *Pinus palustris* Mill. community, Brockway and Lewis (1997) found the highest richness (39 species) following biennial burns, the second highest richness (34 species) following annual burns, the third highest richness (31 species) following triennial burns, and the lowest richness (17 species) in the unburned plots. Brockway and Lewis (1997) also reported the greatest understory diversity and cover following biennial burns. The studies conducted by Peterson and Reich (2008) and Brockway and Lewis (1997) both found an intermediate level of disturbance to promote the greatest species richness (consistent with the intermediate-scale disturbance hypothesis). However, after 43 years of burning in a coastal *P. taeda* stand, Waldrop et al. (1992) found the greatest increases in grass, forb, and legume diversity occurred following annual burns, the most frequent fire regime tested. The results from these studies indicate the significance of fire frequency on ground flora change through time. However, the increases in ground flora diversity documented by Waldrop et al. (1992) were found without the combination of a thinning treatment. Peterson and Reich (2008) found the greatest increases in understory diversity in stands that had less canopy cover (20–70%). The results from our study are consistent with these and others (e.g. Willms et al., 2017; Schwilk et al., 2009; Brewer, 2016) that indicate ground flora diversity is higher in stands that are burned frequently and that have reduced canopy cover.

Frequently burning increased the abundance of legumes; especially for the two species with the greatest indicator values for the thin/3Rx treatment (*Chamaecrista fasciculata* and *Lespedeza violacea*). This was similar to a finding in *P. echinata* Mill. grassland communities in Arkansas, USA, where multiple dormant season prescribed burns favored the abundance of legumes (Sparks et al., 1998). Legumes tend to persist in the seedbed and in post-fire environments, and if nitrogen has combusted with the organic matter (Raison et al., 1985; DeBano, 1990), legumes gain a competitive advantage because of their ability to fix nitrogen (Arianoutsou and Thanos, 1996).

Of the 22 indicator species in the thin/3Rx treatment, 11 species were listed in Brewer (2016) for a site that was impacted by an EF4 tornado and had biennial prescribed fires in Mississippi, USA. Of those 22 indicator species in our study, five were described as forest indicators, six were described as indicators of severe anthropogenic disturbance, and none were described as open habitat, fire-maintained indicators (*sensu* Brewer, 2016). The presence of forest indicator species was not surprising because these sites have been forested for half of a century. These species likely persisted in small patches during the 19th and 20th century land clearing and may have increased in abundance with the contemporary management regime. The increased abundance of disturbance indicator species and the lack of fire-maintained indicator species may be attributed to multiple causes. Perhaps there has never been abundant populations of fire-tolerant ground flora species in our study area, or that the exclusion of fire in the 20th century eliminated these species (Matlack, 2013; Brewer, 2016). Much of the land within the study site was at one time cutover agricultural land, which has been found to reduce species richness by reducing resource availability and increasing tree density in *P. palustris* stands (Veldman et al., 2014; Walker and Silletti, 2007). Perhaps species composition of the ground flora will shift toward more open habitat, fire-maintained species with the continuation of the prescribed fire program. Taxa such as

Table 3
One-way analysis of variance tests summarizing mean values (± standard error) of canopy openness, light availability (% of full photosynthetic photon flux density reaching 1 m above the surface), cover of bare mineral soil (cover classes based on North Carolina Vegetation Survey), and litter depth (cm) across four different silvicultural treatments in the William B. Bankhead National Forest, Alabama, USA. Control was untreated, thin/0Rx was thinned in 2006 without burning, thin/9Rx was thinned in 2006 and burned on a nine year return interval, and thin/3Rx was thinned in 2006 and burned on a three year return interval. NCVS cover classes range from 1 to 10 where 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%. Different letters indicate significant differences ($p \leq 0.01$).

Variable	Control	Thin/0Rx	Thin/9Rx	Thin/3Rx
Canopy openness	10.26 ± 0.93[a]	7.57 ± 0.41[a]	10.36 ± 1.22[b]	15.02 ± 0.86[b]
Light availability (% ground PPFD)	18.05 ± 1.78[a]	14.63 ± 1.48[a]	18.34 ± 2.18[a]	30.25 ± 2.91[b]
Cover of bare mineral soil (NCVS)	0.55 ± 0.20[a]	0.45 ± 0.18[a]	2.5 ± 0.17[b]	2.5 ± 0.15[b]
Litter depth (cm)	4.7 ± 0.4[a]	4.2 ± 0.3[a]	2.8 ± 0.2[b]	2.1 ± 0.1[c]

Table 4
Relative importance (relative density + relative dominance) table for trees (stems ≥ 5 cm dbh) divided into four taxonomic groups in four different silvicultural treatments in William B. Bankhead National Forest located in northern Alabama, USA. Control was untreated, thin/0Rx was thinned in 2006 without burning, thin/9Rx was thinned in 2006 and burned on a nine year return interval, and thin/3Rx was thinned in 2006 and burned on a three year return interval. Different letters on total densities indicate significant differences ($p < 0.05$).

Group	Density (stems ha^{-1})				Relative Tree Density (%)				Dominance (m^2 ha^{-1})				Relative Dominance (%)			
	Control	Thin/0Rx	Thin/9Rx	Thin/3Rx	Control	Thin/0Rx	Thin/9Rx	Thin/3Rx	Control	Thin/0Rx	Thin/9Rx	Thin/3Rx	Control	Thin/0Rx	Thin/9Rx	Thin/3Rx
Pinus spp.	408	179	188	141	35.76	20.09	32.53	49.3	28.08	0.89	12.19	12.61	75.35	4.34	66.87	72.89
Acer-Fagus	301	218	68	11	26.38	24.47	11.76	3.85	2.33	13.25	0.6	0.21	6.25	64.43	3.31	1.23
Quercus-Carya	236	256	126	84	20.68	28.73	21.8	29.37	3.77	2.4	3.12	3.26	10.12	11.66	17.1	18.87
Other spp.*	196	238	196	50	17.18	26.71	33.91	17.48	3.08	4.02	2.32	1.21	8.28	19.57	12.72	7.02
Total	1141[a]	891[a]	578[b]	286[c]	100.00	100.00	100.00	100.00	37.26[a]	20.57[b]	18.23[b]	17.30[b]	100.00	100.00	100.00	100.00

* The top 10 "other spp.": *Liriodendron tulipifera* L., *Prunus serotina* Ehrhart, *Nyssa sylvatica* Marshall, *Oxydendrum arboreum* (L.) A.P. de Candolle, *Cornus florida* L., *Magnolia macrophylla* Michaux, *Frangula caroliniana* (Walter) A. Gray, *Sassafras albidum* (Nuttall) Nees, *Amelanchier arborea* (Michaux f.) Fernald, and *Fraxinus pennsylvanica* Marshall.

Erechtites hieraciifolius, *Chamaecrista fasciculata*, Poaceae, and *Lespedeza* spp. all respond positively to fire and canopy removal because of adaptions such as the ability to persist in the seedbed or rapidly colonize disturbed sites (Sparks et al., 1998; Hutchinson et al., 2005a; Phillips and Waldrop, 2008). Several species in the Asteraceae family were indicative of stands that were thinned and repeatedly burned in our study (e.g. *Solidago arguta*, *Solidago odora*, *Helianthus hirsuta*, and *Rudbeckia hirta*), which is consistent with Weakley (2015) who reported that these species are commonly found in open, disturbed sites. The frequency of occurrence was consistent with the response to a natural disturbance event (e.g. a tornado similar to Brewer, 2016). The increased taxonomic richness and diversity in treated stands indicated that thinning and prescribed fire are worthwhile operations for managers that desire to increase stand-level plant diversity (Brose et al., 2001; Nowacki and Abrams, 2008; Puettman et al., 2009; Stambaugh et al., 2015).

The combination of thinning and burning contained a greater abundance of *Quercus* seedlings compared to the control, which was consistent with Phillips and Waldrop (2008), and the density was greatest in infrequently burned stands. This greater density may be attributed to the increased light availability associated with thinning and decreased soil moisture associated with burning (because fire consumes soil organic matter, which is where plant available moisture is often stored) (Hutchinson, 2006; Nyland, 2002), which tends to favor the establishment of drought-tolerant genera such as *Quercus* in the seedling layer rather than mesophytic genera such as *Acer* (Brose and Van Lear, 1998). It should be noted that we did not sample soil moisture and therefore we can only speculate. The greater abundance of *Quercus* seedlings in the infrequently burned treatment compared to the frequently burned treatment was likely because they need fire to outcompete other hardwoods, but the longer period between fires probably allowed them to reach a more fire-tolerant size before the next burn (Brose et al., 2014). Further, the seedlings had more time to accumulate carbohydrates in the root system, which increased the vigor of resprouting after a fire (Brose et al., 2014).

4.2. Effects of environmental variables on ground flora

An interesting finding of our study was that ground flora richness, diversity, and cover increased in the thin/9Rx treatment compared to the thin/0Rx treatment and the control stands, even without increases in ground layer light availability (measured at 1 m above the forest floor). The combination of thinning and burning resulted in reductions in litter depth compared to the thinned only and control stands (by over half in the thinned and frequently burned treatment), which was reiterated by the NMS solution (associations between litter depth and ground flora composition in the thinned only and control plots). Although the accumulation of litter in the control stands was relatively low compared to other long unburned forest systems (e.g. *P. palustris* stands where litter can accumulate to depths > 25 cm, Varner et al., 2000; Kush et al., 2004), the reductions of litter from repeatedly burning seem to have had a positive impact on the germination and establishment of ground flora. The output from correlation analysis of light availability and ground flora richness and diversity was not statistically significant, however litter depth was negatively correlated with ground flora richness and diversity ($p < 0.001$). Hutchinson et al. (2005a) found that reduced litter mass from 466 $g\,m^{-2}$ to 216 $g\,m^{-2}$ (54%) after one fire was enough to elicit a positive response in herbaceous plant diversity in southern Ohio, USA. This reduction was similar to the fuel mass reductions in the thinned and burned treatments compared to the thinned only and control stands in our study, if we assume all stands had similar fuel loads prior to implementation of the silvicultural treatments (those data are not available). In a *P. palustris* dominated system in the southeastern USA, the development of litter was found to be the biggest factor contributing to decreased plant diversity (Heirs et al., 2007). Further, in a review of 36 studies from around the globe in both field and laboratory settings, Xiong and Nilsson (1999) reported on the effects of litter on the germination and establishment (seedlings that survived between one month and two years) of forest plants. Xiong and Nilsson (1999) stated that germination was significantly negatively correlated with litter depth (from 0 to 4 cm, with 1.5 cm deep litter most favorable for seed germination), and establishment was significantly negatively correlated with litter depth and litter mass (from 0 to 4000 $g\,m^{-2}$, with < 200 $g\,m^{-2}$ favoring the highest plant establishment). Litter acts as a mechanical barrier to seeds reaching the mineral soil, thus the reduction of litter likely facilitates the establishment of a diverse and rich ground flora stratum (Hamrick and Lee, 1987; Hutchinson, 2006; Heirs et al., 2007). Newly germinated seeds on top of the litter expend more carbohydrates to lengthen roots to the mineral soil (Facelli and Pickett, 1991; Ellsworth et al., 2004). Sydes and Grimes (1981) reported a negative relationship between shoot biomass of herbaceous vegetation and dry litter weight under an *Acer-Quercus* canopy.

Although we did not examine annual changes in litter accumulation, we found that stands burned on a three year return interval had lower fuel loads than stands burned on a nine year interval during the second growing season post-fire, and that ground flora in the stands burned more frequently was more species rich, diverse, and had greater coverage. The repeated consumption of fuel from frequent fire, the ephemeral dieback of understory woody plants (a reduction in vegetation before the re-sprouting process began), and a reduction of midstory stems (Schweitzer et al., 2016) increased the amount of light reaching the ground layer and the seedbed, which we contend promoted the germination and establishment of ground flora (also reported in Hutchinson et al., 2005a). The decreases in fuel mass and litter depth measured in this study were enough to increase germination of seeds adapted to germination in high light environments (e.g. Poaceae). Litter and fuel may return to pre-burn levels rather quickly; for example, after two fire free years in Hutchinson et al. (2005a). Several studies reported decreased litter depths after fire, but the majority of these sites returned to pre-burn depths 3–5 years post-fire (Fernandes and Botelho, 2003; Schwilk et al., 2009). Burning at a shorter return interval may maintain the increases in ground flora diversity, richness, and cover by maintaining reduced litter. The NMS solution also revealed a positive association between ground flora frequency and abundance in the thin/9Rx and the thin/3Rx stands and percent bare mineral soil. This finding was consistent with Arthur et al. (2017), who reported that the increased exposure of bare mineral soil likely had a positive effect on species diversity, because of the increased light reaching the seedbed and the increased available space to grow. However, it should be noted that the area of bare mineral soil in the burned treatments was small. We speculate that bare mineral soil was greater the first year post fire compared to the second, which may have been important in seed germination and establishment.

The ephemeral yet more frequent influx of nutrients was likely also a factor in promoting greater ground flora abundance and diversity in the frequently burned treatments compared to the infrequently burned treatments. The sites in this study were relatively nutrient poor (hence the conversion to forests from row cropping), thus we speculate soil chemistry was altered upon nutrient release via prescribed fire (Gilliam and Christensen, 1986; Boerner, 2006). Christensen (1977) found green leaf tissue in burned plots to be higher in N, P, K, Ca, and Mg compared to unburned plots in a *Pinus* savanna in South Carolina, USA. However, these nutrients decreased to pre-burn levels within six months post-burn. Thus, dormant season burning may have a greater impact on nutrient availability for ground flora compared to growing season burns because of the timing and duration of enhanced nutrient availability. Black char (which decreases albedo) and increased insolation immediately following fire, likely temporarily elevated soil temperature, and may have also influenced ground flora germination and growth rates (Iverson and Hutchinson, 2002). Increased cover of the regeneration layer following frequent fire may also retain ground layer heat and moisture (Deardorff, 1978).

4.3. Effects of trees and saplings on ground flora

The thinning changed the stand structure of trees ≥ 5 cm dbh and altered the species composition across all treatments (Schweitzer et al., 2016). In prior research in these stands, Schweitzer et al. (2016) found decreased tree density immediately following the thinning, however stem density substantially increased by 2013 in the thinned only stands compared to thinned and burned stands. Our study showed a similar trend with no significant reductions in tree density in the thinned only stands 12 years following the harvest. The greater tree densities in the thinned only plots likely contributed to the lack of light availability in the ground layer, thus reducing ground flora richness, diversity, and cover compared to thinned and burned stands. However, basal area on the thinned treatments was reduced by ca. 45% 12 years after the operation, which allowed enough light to penetrate the canopy and increase the germination and growth of some grasses, but no other ground flora life-forms were affected (Abella and Springer, 2015).

Burning on a three year return interval reduced the stem density of smaller sized trees (stems 5–10 cm dbh) in our study, which is consistent with Schweitzer et al. (2016), who found the greatest reduction in stems ≥ 3.8 cm dbh and < 10.3 cm dbh after a high intensity thin (target residual BA of 11.5 $m^2\,ha^{-1}$) and three burns over nine years. Smaller sized trees were likely the most susceptible to fire-induced mortality because of less developed (i.e. thinner) bark to keep the cambium insulated and the closer proximity of their leaves and buds to flames compared to taller individuals (Wade and Johansen, 1986; Peterson and Reich, 2001; Dey and Hartman, 2005). The thin/3Rx treatment had the lowest basal area and the fewest trees ha^{-1}, which was also reported in similar studies comparing stands throughout the southeastern USA that were repeatedly burned (Schwilk et al., 2009; Arthur et al., 2015; Schweitzer et al., 2016). All of the National Fire and Fire Surrogate study sites in the eastern USA found increased understory diversity with decreased basal area from thinning and burning, a finding consistent with our study (Schwilk et al., 2009).

The increase in small sized stems (< 5 cm dbh) may not influence light availability in the ground layer or ground flora richness, diversity, or cover, which has been reported in other studies (Heirs et al., 2007; Lettow et al., 2014). However, undesirable hardwoods may outcompete desirable hardwoods (e.g. *Quercus* spp.) if not managed properly throughout the recruitment phase of the stand. If a management goal is to decrease or eliminate undesirable hardwoods, repeated annual burns may be needed. Waldrop et al. (1992) found that repeated annual burns were the only treatment in the study that completely eliminated hardwood competition in a *P. taeda* stand.

5. Management implications

Overstory thinning of planted *Pinus* stands in temperate regions has the potential to increase ground flora richness, diversity, and cover. However, thinning alone may not result in the greatest possible increases in these measures. We found thinning coupled with prescribed burning resulted in the greatest increases in ground flora richness, diversity, and cover, which may increase ecosystem productivity and improve resiliency to future perturbations (Tilman et al., 1996; Peterson et al., 1998). Light and therefore, treatments that influence light such as thinning and fire frequency, is one of the most important drivers of ground flora richness, cover, and diversity (Brockway and Lewis, 1997; Heirs et al., 2007). If an objective is to increase ground flora richness, diversity, and cover in *Pinus*-hardwood systems, we recommend reducing overstory cover and burning at least every three years or as frequently as fuels will allow to control competing, fire-sensitive hardwoods and favor fire-adapted ground flora growth forms (e.g. many forbs and graminoids). If fire frequency is low, the competition from hardwood resprouts may have a negative affect on ground flora species richness (Veldman et al., 2014). Litter accumulation may be a concern for managers because it negatively impacts plant diversity by inhibiting germination and establishment (Heirs et al., 2007) and may create conditions for severe fire during droughts (Varner et al., 2007). The continuation of periodic burning (in this study every three or nine years) can reduce litter depths enough to promote the germination and establishment of a species rich and diverse ground flora. It should be noted that prescribed burning without a thinning operation might also increase species richness, diversity, and cover in mixed *Pinus*-hardwood systems (Waldrop et al., 1992; Knapp et al., 2015; Hutchinson et al., 2005). However, we do think that the increased light levels from thinning in combination with the burning in this study likely yielded higher species richness, diversity, and cover than if these sites were burned but never thinned.

Declarations of interest

None.

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References

Abella, S.R., Springer, J.D., 2015. Effects of tree cutting and fire on understory vegetation in mixed conifer forests. For. Ecol. Manage. 335, 281–299.
Addor, M.L., Birkhoff, J., 2004. Bankhead National Forest health & restoration initiative: final report. For the USDA Forest Service, National Forests in Alabama, Bankhead National Forest Bankhead National Forest Liaison Panel and Community U.S. Institute for Environmental Conflict Resolution. Available from: https://www.researchgate.net/publication/228771344_Bankhead_National_Forest_health_and_restoration_initiative_final_report [accessed Oct 08 2018].
Alabama Secretary of State. Land Records. Available online at arc-sos.state.al.us/CGI/LANDTOWN.MBR/INPUT. Accessed [09/16/2018].
Alcañiz, M., Outeiro, L., Francos, M., Farguell, J., Úbeda, X., 2016. Long-term dynamics of soil chemical properties after a prescribed fire in a Mediterranean forest (Montgrí Massif, Catalonia, Spain). Sci. Total Environ. 572, 1329–1335.
Alcañiz, M., Outeiro, L., Francos, M., Úbeda, X., 2018. Effects of prescribed fires on soil properties: a review. Sci. Total Environ. 613–614, 944–957.
Arianoutsou, M., Thanos, C.A., 1996. Legumes in the fire-prone mediterranean regions: an example from Greece. Int. J. Wildland Fire 6 (2), 77–82.
Arthur, M.A., Blankenship, B.A., Schörgendorfer, A., 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.
Arthur, M.A., Blankenship, B.A., Schörgendorfer, A., Loftis, D.L., Alexander, H.D., 2015. Changes in stand structure and tree vigor with repeated prescribed fire in an Appalachian hardwood forest. For. Ecol. Manage. 340, 46–61.
Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved—a critical review for temperate and boreal forests. For. Ecol. Manage. 254, 1–15.
Baskin, C.C., Baskin, J.M., 1988. Germination ecophysiology of herbaceous plant species in a temperate region. Am. J. Bot. 75, 286–305.
Beers, T.W., Dress, P.E., Wensel, L.C., 1966. Aspect transformation in site productivity research. J. Forest. 64, 691–692.
Brose, P., Schuler, T., Van Lear, D., Berst, J., 2001. Bringing fire back: the changing regimes of the Appalachian mixed-oak forests. J. For. 99 (11), 30–36.
Bixler, R.P., 2014. Biodiversity conservation and wildlife management in the Anthropocene. Pinchot Lett. 17 (4), 1–17.
Boerner, R.E.J., 2006. Soil, fire, water, and wind: how the elements conspire in the forest context. In: Dickinson, Matthew B. (Ed.), Fire in Eastern Oak Forests: Delivering Science to Land Managers, Proceedings of a Conference; 2005 November 15–17; Columbus, OH. General Technical Report NRS-P-1. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 104–112.
Boerner, R.E., Huang, J., Hart, S.C., 2009. Impacts of fire and fire surrogate treatments on forest soil properties: a meta-analytical approach. Ecol. Appl. 19 (2), 338–358.
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.
Brockway, D.G., Lewis, C.E., 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. For. Ecol. Manage. 96, 67–183.
Brose, P.H., Dey, D.C., Waldrop, T.C., 2014. The fire-oak literature of eastern North America: synthesis and guidelines. USDA Forest Service General Technical Report NRS-135.
Brose, P.H., Van Lear, D.H., 1998. Responses of hardwood advanced regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Can. J. For. Res. 28, 331–339.
Bowles, M., Apfelbaum, S., Haney, A., Lehnhardt, S., Post, T., 2011. Canopy cover and groundlayer vegetation dynamics in a fire managed Eastern sand savanna. For. Ecol. Manage. 262, 1972–1982.
Butler, B.J., Hewes, J.H., Dickinson, B.J., Andrejczyk, K., Butler, S.M., Markowski-Lindsay, M., 2016. Family forest ownerships of the United States, 2013: findings from the USDA Forest Service's national woodland owner survey. J. Forest. 114 (6), 638–647.
Cameron, A.D., 2002. Importance of early selective thinning in the development of long-term stand stability and improved log quality: a review. Forestry 75 (1), 25–35.
Christensen, N.L., 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the Coastal Plain of North Carolina. Oecologia 31, 27–44.
Clark, S., Schweitzer, C., 2009. Red maple (*Acer rubrum*) response to prescribed burning on the William B. Bankhead National Forest, Alabama. In: Hutchinson, Todd F. (Ed.), Proceedings of the 3rd Fire in Eastern Oak Forests Conference; 2008 May 20–22; Carbondale, IL. Gen. Tech. Rep. NRS-P-46. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 147.
Clark, S., Schweitzer, C., Dimov, L., 2006. Effectiveness of thinning and prescribed burning on fuel reduction and residual oak tree health on the Bankhead National Forest, Alabama. Third International Fire Ecology and Management Congress, November 13–17, 2006, San Diego, CA.
Collins, B.S., Wein, G.R., 1993. Understory vines: distribution and relation to environment on a southern mixed hardwood site. Bull. Torrey Bot. Club 120 (1), 38–44.
Cowden, M.M., Hart, J.L., Schweitzer, C.J., Dey, D.C., 2014. Effects of intermediate-scale wind disturbance on composition, structure, and succession in Quercus stands: implications for natural disturbance-based silviculture. For. Ecol. Manage. 330, 240–251.
Cox, L.E., Hart, J.L., Dey, D.C., Schweitzer, C.J., 2016. Composition, structure, and intra-stand spatial patterns along a disturbance severity gradient in a Quercus stand. For. Ecol. Manage. 381, 305–317.
Deardorff, D.W., 1978. Efficient prediction of ground surface temperature and moisture, with inclusion of a layer of vegetation. J. Geophys. Res. 83 (C4), 1889–1903.
DeBano, L.F., 1990. The effect of fire on soil properties. Symposium on Management and Productivity of Western-Montane Forest Soils, Boise, ID, April 10–12, 1990.
Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetric approach. Ecol. Monogr. 67 (3), 345–366.
Dey, D.C., Hartman, G., 2005. Returning fire to Ozark Highland forest ecosystems: effects on advance regeneration. For. Ecol. Manage. 217, 37–53.
Duguid, M.C., Ashton, M.S., 2013. A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. For. Ecol. Manage. 303, 81–90.
Ellsworth, J., Harrington, R., Fownes, J., 2004. Seedling emergence, growth, and allocation of oriental bittersweet: effects of seed input, seed bank, and forest floor litter. For. Ecol. Manage. 190 (2–3), 255–264.
Environmental Systems Research Institute, 2014. Redlands, CA, US.
Facelli, J.M., Pickett, S.T.A., 1991. Plant litter: light interception and effects on an oldfield plant community. Ecology 72, 1024–1031.
Fernandes, P.M., Botelho, H.S., 2003. A review of prescribed burning effectiveness in fire hazard reduction. Int. J. Wildland Fire 12, 117–128.
Fenneman, N.M., 1938. Physiography of Eastern United States. McGraw-Hill, New York, USA.
Fralish, J.S., 2003. The central hardwood forest: its boundaries and physiographic provinces. In: Van Sambeek, J.W., Dawson, J.O., Ponder, F., Loewenstein, E.F., Fralish, J.S. (Eds.), Proceedings, 13th Central Hardwood Forest conference; 2002 April 1–3; Urbana, IL. Gen. Tech. Rep. NC-234. U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, MN 565p.
Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57 (10), 845–858.
Gilliam, F.S., 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.
Griffith, G.E., Omernik, J.M., Comstock, J.A., Lawrence, S., Martin, G., Goddard, A., Hulcher, V.J., Foster, T., 2001. Ecoregions of Alabama and Georgia. US Geological Survey, Reston, Virginia, USA.
Hamrick, J.L., Lee, J.M., 1987. Effect of soil surface topography and litter cover on the germination, survival and growth of musk thistle (Carduus nutans). Am. J. Bot. 74 (3), 451–457.
Heirs, J.K., O'Brien, J.J., Will, R.E., Mitchell, R.J., 2007. Forest floor depth mediates understory vigor in xeric Pinus palustris ecosystems. Ecol. Appl. 17 (3), 806–814.
Hutchinson, T.F., 2006. Fire and the herbaceous layer of eastern oak forests. In: Dickinson, Matthew B. (Ed.), Fire in Eastern Oak Forests: Delivering Science to Land Managers, Proceedings of a Conference; 2005 November 15-17; Columbus, OH. Gen. Tech. Rep. NRS-P-1. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 136–149.
Hutchinson, T.F., Boerner, R.E.J., Sutherland, S., Sutherland, E.K., Ortt, M., Iverson, L.R., 2005a. Prescribed fire effects on the herbaceous layer of mixed-oak forests. Can. J. For. Res. 35 (4), 877–890.
Hutchinson, T.F., Sutherland, E.K., Yaussy, D.A., 2005b. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. For. Ecol. Manage. 218, 210–228.
Iverson, L.R., Hutchinson, T.F., 2002. Soil temperature and moisture fluctuations during and after prescribed fire in mixed-oak forests, USA. Nat. Areas J. 22 (4), 296–304.
Johnson, P.S., Shifley, S.R., Rogers, R., 2009. The Ecology and Silviculture of Oaks, 2nd ed. CAB International.
Keener, B.R., Diamond, A.R., Davenport, L.J., Davison, P.G., Ginzbarg, S.L., Hansen, C.J.,

Major, C.S., Spaulding, D.D., Triplett, J.K., Woods, M., 2016. Alabama Plant Atlas. http://www.floraofalabama.org.
Kleinman, J.S., Ford, S.A., Hart, J.L., 2017. Catastrophic wind and salvage harvesting effects on woodland plants. For. Ecol. Manage. 403, 112–125.
Knapp, B.O., Stephen, K., Hubbart, J.A., 2015. Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, USA. For. Ecol. Manage. 344, 95–109.
Knoepp, J.D., Elliott, K.J., Clinton, B.D., Vose, J.M., 2009. Effects of prescribed fire in mixed oak forests of the Southern Appalachians: forest floor, soil, and soil solution nitrogen responses. J. Torrey Bot. Soc. 136 (3), 380–391.
Kush, J.S., Meldahl, R.S., Avery, C., 2004. A restoration success: longleaf pine seedlings established in a fire-suppressed, old-growth stand. Ecol. Restorat. 22, 6–10.
Lettow, M.C., Brudvig, L.A., Bahlai, C.A., 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.
Matlack, G.R., 2013. Reassessment of the use of fire as a management tool in deciduous forests of eastern North America. Conserv. Biol. 27 (5), 916–926.
McCune, B., Medford, M., 2011. PC-ORD Version 6: Multivariate Analysis of Ecological Data. MjM Software, Gleneden Beach, OR.
McGuire, J.P., Mitchell, R.J., Moser, E.B., Pecot, S.D., Gjerstad, D.H., Hedman, C.W., 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. Can. J. For. Res. 31, 765–778.
Miller, J.H., Miller, K.V., 2005. Forest Plants of the Southeast and Their Wildlife Uses, revised ed. University of Georgia Press, Athens, GA, pp. 454.
Nagel, L.M., Palik, B.J., Battaglia, M.A., D'Amato, A.W., Guldin, J.M., Swanston, C.W., Janowiak, M.K., Powers, M.P., Joyce, L.A., Millar, C.I., Peterson, D.L., Ganio, L.M., Kirschbaum, C., Roske, M.R., 2017. Adaptive silviculture for climate change: a national experiment in manager-scientist partnerships to apply an adaption framework. J. Forest. 115, 1–12.
Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58, 123–138.
Nyland, R.D., 2002. Silviculture: Concepts and Applications. Waveland Press Inc., Long Grove, Illinois.
Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics, Update ed. John Wiley and Sons, New York, NY, pp. 520.
Peck, J.E., 2016. Multivariate Analysis for Ecologists: Step-by-Step using PC-ORD. MjM Software Design, Gleneden Beach, OR, pp. 192.
Peet, R.K., Wentworth, T.R., White, P.S., 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63, 262–274.
Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1, 6–18.
Peterson, D.W., Reich, P.B., 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecol. Appl. 11 (3), 914–927.
Peterson, D.W., Reich, P.B., 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. Plant Ecol. 191 (1), 5–16.
Phillips, R., Hutchinson, T., Brudnak, L., Waldrop, T., 2007. Fire and fire surrogate treatments in mixed-oak forests: effects on herbaceous layer vegetation. In: Butler, Bret W., Cook, Wayne, comps (Eds.), The fire environment—innovations, management, and policy; conference proceedings. 26-30 March 2007; Destin, FL. Proceedings RMRS-P-46CD. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO pp. 662 CD-ROM.
Phillips, R.J., 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.
Puettman, K.J., Coates, D.K., Messier, C., 2009. A Critique of Silviculture: Managing for Complexity. Island press, Washington, D.C.
Raison, R.J., Khanna, P.K., Woods, P.V., 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. Can. J. For. Res. 15 (1), 132–140.
Regent Instruments, 2014. WinSCANOPY 2014a for Canopy Analysis. Canada Incorporated.
Rentch, J.S., Fajvan, M.A., Hicks II, R.R., 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. For. Ecol. Manage. 184 (1–3), 285–297.
Salwasser, H., 1991. New perspectives for sustaining diversity in U.S. National Forest ecosystems. Conserv. Biol. 5 (4), 567–569.
Scharenbroch, B.C., Nix, B., Jacobs, K.A., Bowles, M.L., 2012. Two decades of low-severity prescribed fire increases soil nutrient availability in Midwestern, USA oak (Quercus) forest. Geoderma 183–184, 89–91.
Schnitzer, S.A., Bongers, F., 2002. The ecology of lianas and their role in forests. Trends Ecol. Evol. 17 (5), 223–230.
Schweitzer, C.J., Clark, S.L., Gaines, G., Finke, P., Gottschalk, K., Loftis, D., 2008. Integrating Land and Resource Management Plans and Applied Large-Scale Research on Two National Forests. Gen. Tech. Rep. PNW-GTR-733. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 127–134.
Schweitzer, C.J., Dey, D.C., 2015. The Conundrum of Creating Understory Light Conditions Conducive to Promoting Oak Regeneration: Midstory Herbicide Treatment Versus Prescribed Fire. In: Holley, G., Haywood, D., Connor, K. (Eds.), Proceedings of the 17th Biennial Southern Silvicultural Conference. e-Gen. Tech. Rep. SRS-203. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 45–56.
Schweitzer, C.J., Dey, D.C., Wang, Y., 2016. Hardwood–pine mixedwoods stand dynamics following thinning and prescribed burning. Fire Ecol. 12 (2), 85–104.
Schweitzer, C.J., Dey, D., Yong, W., 2014. Thinning and prescribed fire alters hardwood seedling sprouting and competitive dynamics on the William B. Bankhead National Forest, AL. In: Groniner, J.W., Holzmueller, R.J., Nielsen, C.K., Dey, D.C. (Eds.), Proceedings, 19th Central Hardwood Forest Conference. Gen. Tech. Rep. NRS-P-142. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 137–138.
Schweitzer, C.J., Wang, Y., 2013. Overstory tree status following thinning and burning treatments in mixed pine-hardwood stands on the William B. Bankhead National Forest, Alabama. In: Guldin, J. (Ed.), Proceedings, 15th Biennial Southern Silvicultural Conference; 2009 November 17-20, 2009; Hot Springs, AR. Gen. Tech. Rep. SRS-175. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 57–63.
Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J., Bailey, J.D., Fettig, 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., Youngblood, A., 2009. The National Fire and Fire Surrogate Study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecol. Appl. 19, 285–304.
Smalley, G.W., 1979. Classification and Evaluation for Forest Sites on the Southern Cumberland Plateau. USDA Forest Service, Southern Forest Research Station, GTR SO-23, New Orleans, LA.
Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at the following link: https://websoilsurvey.sc.egov.usda.gov/. Accessed [04/15/2017].
Sparks, J.C., Masters, R.E., Engle, D.M., Palmer, M.W., Bukenhofer, G.A., 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. J. Veg. Sci. 9 (1), 133–142.
Stambaugh, M.C., Varner, J.M., Noss, R.F., Dey, D.C., Christensen, N.L., Baldwin, R.F., Guyette, R.P., Hanberry, B.B., Harper, C.A., Lindblom, S.G., Waldrop, T.A., 2015. Clarifying the role of fire in the deciduous forests of eastern North America: reply to Matlack. Conserv. Biol. 29, 942–946.
Sutton, W., Wang, Y., McClure, C., Schweitzer, C., 2017. Spatial ecology and multi-scale habitat selection of the copperhead (Agkistrodon contortrix) in a managed forest landscape. For. Ecol. Manage. 391, 469–481.
Sutton, W., Wang, Y., Schweitzer, C., 2010. Habitat relationships of reptiles in pine beetle disturbed forests of alabama, U.S.A., with guidelines for a modified drift-fence sampling method. Curr. Zool. 56 (4), 411–420.
Sutton, W.B., Wang, Y., Schweitzer, C.J., Steen, D.A., 2014. Lizard microhabitat and microclimate relationships in southeastern pine-hardwood forests managed with prescribed burning and thinning. For. Sci. 60 (1), 180–190.
Sydes, C., Grimes, J.P., 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland: I. Field investigations. J. Ecol. 69 (1), 237–248.
Szabo, M.W., Osborne, E.W., Neatherly, T.L., 1988. Geologic map of Alabama. Geological Survey of Alabama Special Map 220, Scale 1:250,000. Geological Survey of Alabama, Tuscaloosa, AL.
Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., Austin, K.A., 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. Ecol. Appl. 9, 864–879.
Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grasslands ecosystems. Nature 379, 718–720.
Thornthwaite, C.W., 1948. An approach toward rational classification of climate. Geogr. Rev. 38, 55–94.
USDA, 2017. Plant database for life-forms. www.plants.usda.gov.
USDA Forest Service, 2004. Revised land and resource management plan: National Forests in Alabama. Management Bulletin R8-MB 112A.
USDA SRC, 1949. Soil Survey of Lawrence County, Alabama. Soil Survey Series 10, 35–48.
Varner III, J.M., Hiers, J.K., Ottmar, R.D., Gordon, D.R., Putz, F.E., Wade, D.D., 2007. Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. Can. J. For. Res. 37 (8), 1349–1358.
Varner, J.M. III. Kush, J.S., Meldahl, R.S., 2000. Ecological restoration of an old-growth longleaf pine stand utilizing prescribed fire. In: Proceedings from Tall Timbers Fire Ecology Conference, vol. 21, pp. 216–219.
Veldman, J.W., Brudvig, L.A., Damschen, E.I., Orrock, J.L., Mattingly, W.B., Walker, J.L., 2014. Fire frequency, agricultural history and the multivariate control of pine savanna understory plant diversity. J. Veg. Sci. 25 (6), 1438–1449.
Waldrop, T.A., White, D.L., Jones, S.M., 1992. Fire regimes for pine-grassland communities in the southeastern United States. For. Ecol. Manage. 47 (1–4), 195–210.
Walker, J.L., Silletti, A.M., 2007. Restoring the ground layer of longleaf pine ecosystems. In: The Longleaf Pine Ecosystem. Springer, New York, NY, pp. 297–333.
Wade, D.D., Johansen, R.W., 1986. Effects of fire on southern pine: observations and recommendations. USDA Forest Service General Technical Report SE-41.
Weakley, A., 2015. Flora of the Southern and mid-Atlantic States. University of North Carolina Herbarium.
Willms, J., Bartuszevige, A., Schwilk, D.W., 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.
Willson, K.G., Barefoot, C.R., Hart, J.L., Schweitzer, C.J., Dey, D.C., 2018. Temporal patterns of ground flora response to fire in thinned Pinus-Quercus stands. Can. J. For. Res.
Wulder, M., 1998. Optical remote-sensing techniques for the assessment of forest inventory and biophysical parameters. Prog. Phys. Geogr. 22, 449–476.
Xiong, S., Nilsson, C., 1999. The effects of plant litter on vegetation: a meta-analysis. J. Ecol. 87, 984–994.