EFFECTS OF THINNING AND BURNING ON GROUND FLORA IN MIXED *PINUS*-HARDWOOD STANDS

by

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ABSTRACT

Commercial thinning and prescribed fire are tools used to accomplish forest management objectives such as increased timber revenue, fuel reductions, and increased biodiversity. Silvicultural treatments can alter forest structure and nutrient flow to increase resiliency by promoting regeneration of native species, especially in the ground layer, where the majority of plant diversity is stored. Management regimes that optimize ground layer attributes in mixed *Pinus*-hardwood stands following timber monoculture are less understood. I examined the effects of thinning without fire and thinning with different fire frequencies to identify changes in community structure and species composition with a focus on taxonomic richness, evenness, diversity, and percent cover of ground flora in *Pinus*-hardwood stands on the Cumberland Plateau in northern Alabama. Overstory (live woody individuals ≥ 5 cm dbh; diameter at breast height, 1.37 m above the root collar) basal area and density decreased with increased management intensity. Sapling (live woody individuals < 5 cm dbh and > 1 m in height) density substantially increased with increased management intensity in the second growing season post-fire. Sapling density did not negatively affect light reaching the ground layer, as light availability increased with management intensity. Ground flora richness, diversity, evenness and cover were greatest in stands that were thinned, and then burned every three years, negatively correlated with litter depth and positively correlated with exposed mineral soil based on a non-metric multidimensional scaling (NMS) solution. Ground flora diversity was greater in thinned stands with fire compared to stands that were thinned and never burned, emphasizing the need of the combination of thinning and burning in these systems for native biodiversity conservation. Forest

managers who wish to promote biodiversity may consider frequent burning to promote ground flora richness, diversity, and cover.

DEDICATION

This thesis is dedicated to everyone who stood by me and believed in my grit and academic strength. In particular, I dedicate this thesis to my immediate family and my girlfriend Tyler Mathews.

LIST OF ABBREVIATIONS AND SYMBOLS

°	Degrees
%	Percent
>	Greater than
<	Less than
=	Equal to
≥	Greater than or equal to
≤	Less than or equal to
±	Plus or minus
*	Statistical significance at p < 0.05
**	Statistical significance at p < 0.01
***	Statistical significance at p < 0.001
BNF	Bankhead National Forest
C	Celsius
cm	Centimeters
dbh	Diameter at breast height
g	Gram
ha	Hectare
ISA	Indicator species Analysis
m	Meter
NCVS	North Carolina vegetation survey

NMS	Non-metric multidimensional scaling
p	Probability of occurrence under the null hypothesis of obtaining a value as extreme or more extreme than the observed value
PerMANOVA	Distance-based multivariate analysis of variances
PPFD	Photosynthetic photon flux density
r^2	Regression coefficient of determination
SE	Standard error
Thin/0Rx	Thinned in 2006 and not burned
Thin/9Rx	Thinned in 2006 and burned on a nine year return interval
Thin/3Rx	Thinned in 2006 and burned on a three year return interval
USFS	United States Forest Service

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1. INTRODUCTION

Forest owners are increasingly prioritizing amenity-oriented objectives, such as aesthetic beauty, improving wildlife habitat, and nature protection, over financial goals in management planning (Butler *et al*. 2016). Amenity-oriented objectives are often related to conservation of forest biodiversity (Bixler 2014). Biodiversity is significant because the variety of functions that one species can perform in an ecosystem (e.g. modify the physical environment, pollination, or seed dispersal) is limited. Species diversity and richness are correlated with an increase in ecosystem functions and enhanced ecosystem functions may promote 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 (all vascular plants ≤ 1 meter in height), which harbors the majority of plant diversity in temperate forest ecosystems (Gilliam 2007).

Ground flora is normally the most efficient plant stratum for enhancing nutrient and energy flows throughout the system, as they have short life spans but high productivity rates relative to co-occurring trees (Muller 2014). These plants consistently contain higher foliar concentrations of potassium and magnesium and occasionally higher foliar concentrations of nitrogen, phosphorous, and calcium compared to trees (Likens and Bormann 1970). The average ratio of net primary productivity to aboveground biomass of ground flora is 20:1 in forests of the Northern Hemisphere (Gilliam 2007). Furthermore, a diversity of ground flora may promote an abundance of wildlife by provide resources (e.g. cover and browse) that are useful to an array of insects, birds, and mammals (Martin *et al*. 1961, Fralish 2004, Barrioz *et al.* 2013). Ground flora also adds to carbon sequestration, provides erosion mitigation, and increases aesthetic value of forest ecosystems (Hutchinson 2006).

Forest managers use silvicultural treatments to promote ground flora diversity, which can be thought of as an adaptive set of tools in a changing climate (Puettman *et al*. 2009, Nagel *et al*. 2017). Silvicultural thinning of economically mature trees may be conducted to harvest timber for revenue and increase the vigor of residual trees (Nyland 2002, Cameron 2002). Thinning may also be useful to reduce the abundance of undesirable tree genera and promote the dominance of desirable genera, such as *Quercus*, which is favored for its ecological and economic values (Johnson *et al*. 2009, Schweitzer *et al.* 2016). Thinning operations often leave behind legacies that increase the availability of resources for plants, which may affect ground flora diversity (Phillips and Waldrop 2008, Thomas *et al*. 1999). Commercial thinning may increase the amount of photosynthetically active radiation (PAR) reaching the ground layer and heat up the soil, however these effects are ephemeral (Nyland 2002, Schweitzer and Dey 2015). Thinning may also increase litter depth and fine fuels, and decrease soil decomposition rates immediately following the operation, which likely have a negative influence on ground flora diversity (Thomas *et al*. 1999, Hutchinson 2006, Heirs *et al*. 2007, Schweitzer and Clark 2012).

Prescribed burning is another silvicultural tool that may be used to promote ground flora diversity (Zak *et al.* 2010). Litter acts as a physical barrier to seed germination and early establishment, and prescribed fire can be used to reduce this barrier and increase light to the seedbed, where germination occurs (Hutchinson 2006). Seeds of many herbaceous species germinate at greater rates in light vs. dark conditions (Baskin and Baskin 1988). Single prescribed fires have been shown to decrease duff accumulation by up to 50%, and repeated fires can reduce duff accumulation by more than 60% of pre-fire levels (Arthur *et al*. 2017).

Prescribed burning can also be useful to consume undesirable vegetation in lower forest strata and promote the abundance of desirable species (Dey and Hartman 2005, Brose and Van Lear 1998). Consumption of vegetation and litter from prescribed burning releases nutrients into the mineral soil that may affect ground flora productivity (Hutchinson 2006, Knoepp *et al*. 2009, Scharenbroch *et al*. 2012, Alcañiz *et al*. 2016, Alcañiz *et al*. 2018). Prescribed fire also increases mineral soil exposure, thus increasing the amount of light reaching the seedbed, which positively affects seed germination and promotes ground flora diversity (Hutchinson 2006, Phillips and Waldrop 2008, Arthur *et al.* 2017). However, the effects of prescribed burning on nutrient composition and ground flora diversity can be ambiguous when implemented without other silvicultural activities (Boerner 2006, 2009, Phillips *et al*. 2007). Further, fire may increase the abundance of hardwood saplings via prolific stump sprouting, and this response may become more pronounced when combined with thinning (Phillips and Waldrop 2008, Schweitzer *et al.* 2016).

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). Schwilk *et al.* (2009) reported the greatest increases in native herbaceous species richness between pre-treatment and the second to fourth year post-mechanical thin and burn treatments in four out of five sites in eastern USA. However, in the same review, woody stem density in the understory (e.g. saplings and seedlings) increased in three of the five eastern USA sites and saplings did not decrease at any site, and seedlings decreased at one site (Schwilk *et al.* 2009). Thinning and burning may affect the structure and composition of trees and advanced regeneration, thus altering resource availability (e.g. light, water, and soil nutrients) and influencing ground flora diversity by increasing germination and establishment of herbaceous species, but may also increase competition from woody plants in the ground layer strata (McGuire *et al*. 2001, Phillips *et al*. 2007, Barbier *et al*. 2008). Further, composition of overstory strata may influence future fire behavior because different species tend to differ in morphology and contain differential rates of drying, both of which affect flammability (Kreye *et al*. 2013).

A paucity of data is available on ground flora response to the combination of thinning and burning, especially across different burn frequencies and in mixed *Pinus*-hardwood systems (Hutchinson *et al*. 2005a). A fire regime contains several elements that all affect vegetation (e.g. intensity, severity, seasonality, frequency, size). This study examines the effects of fire frequency on ground flora in stands that have been heavily thinned to promote hardwood dominance. Further, few studies have quantified the effects of ground flora more than a decade after overstory thinning. The removal of overstory stems increases light availability immediately following the event, however light availability decreases as gaps in the canopy close from lateral branching by adjacent canopy trees or from vertical ascension by understory individuals (Oliver and Larson 1996). Forest managers are in need of long-term studies that analyze ground flora response years after thinning and across different burn frequencies to elucidate the most effective silvicultural system at promoting ground flora diversity and cover (Matlack 2013).

My study was part of a larger ongoing project implemented in 2003 by the US Forest Service, Southern Research Station, and was designed to analyze fuel and woody vegetation response to silvicultural thinning and prescribed burning in the William B. Bankhead National Forest (BNF) in northern Alabama, USA (Clark *et al.* 2006, Schweitzer *et al.* 2008, Schweitzer *et al*. 2016). The overarching goal of my study was to quantify the response of ground flora to three different fire frequencies in the same upland *Pinus*-hardwood stands in the BNF that were thinned 12 years ago to promote hardwood dominance. The stands I selected to sample in were either untreated, thinned only, thinned and burned on a nine years return interval (two burns to date), or thinned and burned on a three year return interval (four burns to date). I 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). The specific objectives of my study were to compare treatment-mediated differences in: (1) ground flora richness, diversity, evenness, and cover, and (2) environmental variables that may have influenced the ground flora. I hypothesized that the combination of thinning and burning treatments would result in greater richness, diversity, evenness, and cover of ground flora, with the greatest increases in the thinned and frequently burned treatment (burned on a three year return interval, four burns to date). I also hypothesized environment variables, specifically litter depth and understory light availability, would be key factors that influenced ground flora richness, diversity, evenness 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.

2. METHODS

2.1. Study Area

This study was located in the William B. Bankhead National Forest (BNF), located in northern Alabama (Figure 1). The study site is within the Central Hardwood Forest Region (Fralish 2003). The BNF is located in 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

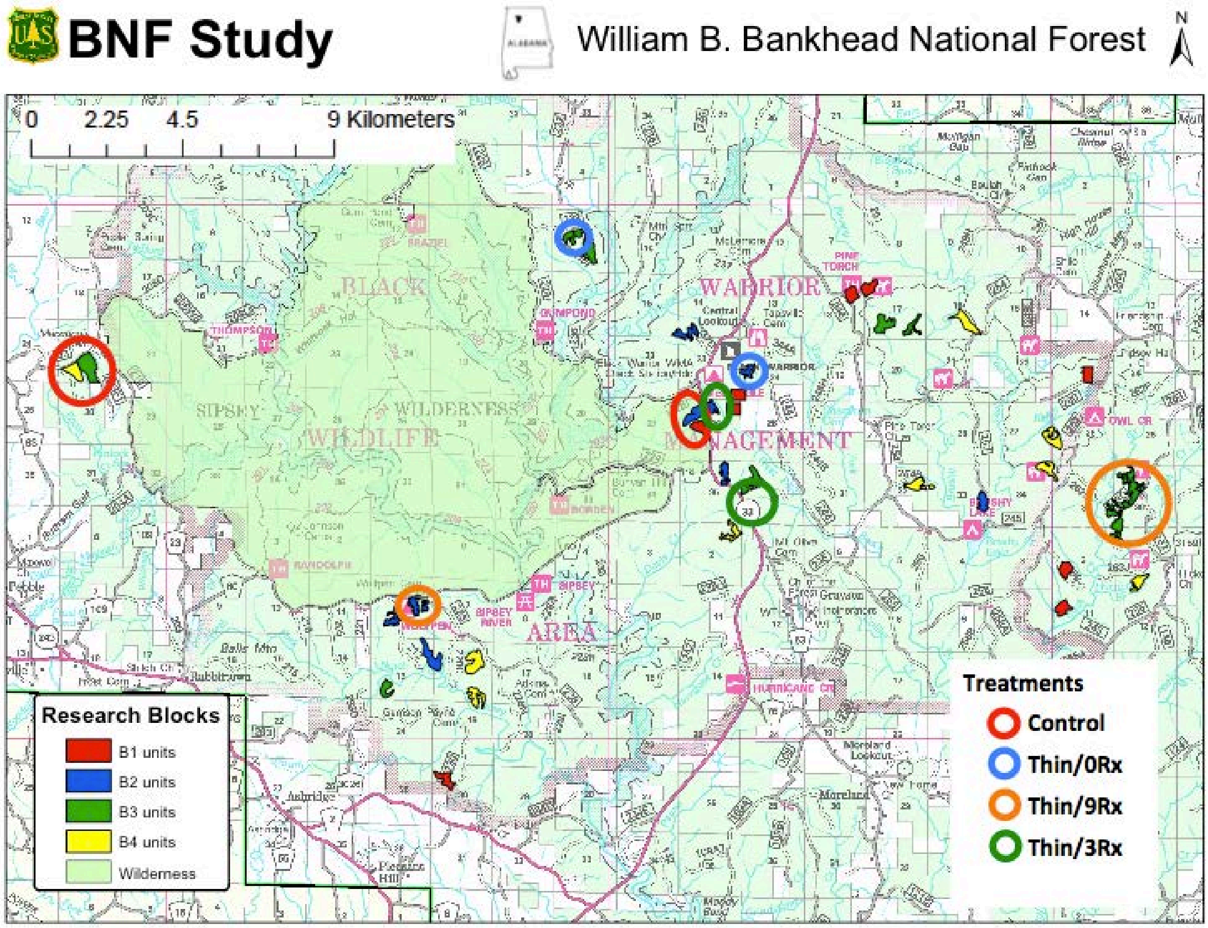

Figure 1. Map of the William B. Bankhead National Forest located in northern Alabama, USA. Research Blocks (replications) were adopted off of the study initiated in 2003 by the USFS, Southern Research Station (*sensu* Schweitzer *et al.* (2016)). Control was untreated, thin/0Rx was thinned in 2006 without 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.

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). Stands were planted with *Pinus taeda* L. in the 1930s to re-establish cutover 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 epidemic in the 1990s, which left approximately 7,527 ha of *Pinus* spp. on the BNF diseased or dead, the Bankhead Forest Health and Restoration Initiative was launched (USDA Forest Service 2003). Through these efforts, over 6,400 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 elevated fuel-loading via beetle-killed trees, and prepare the treated stands for regeneration of tree species native to the southern Cumberland Plateau region (USDA Forest Service 2003).

2.2. Treatments

My study included replicates from the above study by Schweitzer *et al.* (2016) and analyzed the response of ground flora in the following treatments: the unmanaged control, the heavily thinned and not burned (hereafter thin/0Rx), the heavily thinned and burned on a nine year return interval (hereafter thin/9Rx), and the heavily thinned and burned on a three year return interval (hereafter thin/3Rx) (Table 1). Because replicates were initially burned in sequential years (Schweitzer *et al.* 2016), only two of the four replications of the thin/9Rx and the thin/3Rx were sampled to ensure time since fire stayed consistent. However, at least two stands were sampled in each treatment and each stand and sample unit was adequately spaced as to be independent of the others.

The thinning operations were conducted in 2006. The main objective of the thinning was to move the stand towards upland hardwood dominance; therefore mainly *Pinus* stems were harvested. 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. Temperatures of each burn were recorded 25 cm above the ground surface, using HOBO data recorders (HOBO U12 Series Datalogger, Onset Computer Corporation, Cape Cod, Massachusetts, USA) connected to a temperature probe (HOBO TCP6-K12 Probe Thermocouple Sensor, Onset Computer Corporation, Cape Cod, Massachusetts, USA) (Scwheitzer *et al.* 2016). A schedule of the treatments including maximum temperature for each of the burns can be found in Table 2.

2.3. Field Methods

I installed twenty plots in each treatment. 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. Plots were established randomly using a fishnet overlay

Table 1. Treatment abbreviations and descriptions for the thinning and prescribed burning study conducted in William B. Bankhead National Forest, Alabama, USA (Schweitzer *et al*. 2016). Thin/0Rx was thinned in 2006 and not burned, 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.

Treatment abbreviation	**Thinning target basal area (m^2 ha^{-1})**	**Fire return interval (yr)**	**Burns to date (*n*)**
Thin/0Rx	11.5	0	0
Thin/9Rx	11.5	9	2
Thin/3Rx	11.5	3	4

Table 2. Schedule for thinning and prescribed burning treatments including mean maximum temperatures for each recorded burn, William B. Bankhead National Forest, Alabama, USA (Schweitzer *et al*. 2016). Thin/0Rx was thinned in 2006 and not burned, 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.

Treatment abbreviation	**Thin**	**Date of burn 1 for 9Rx and 3Rx (MM/DD/YYYY) with (mean max. temp. (°C))**	**Date of burn 2 for 3Rx (MM/DD/YYYY) with (mean max. temp. (°C))**	**Date of burn 3 for 3Rx (MM/DD/YYYY) with (mean max. temp. (°C))**	**Date of burn 4 for 3Rx and burn 2 for 9Rx (MM/DD/YYYY) with (mean max. temp. (°C))**
Thin/0Rx	2006				
Thin/9Rx	2006	2007			02/10/2016 (116.9) and 03/08/2016 (221.7)
Thin/3Rx	2006	01/30/2007 (116.9)	02/25/2010 (87.9)	03/16/2013 (273.9)	03/21/2016 (145.7)

that was clipped to the boundaries of the USDA Forest Service stands and a random number generator. Once twenty 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 road 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.

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 (Figure 2). 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), *Pinus* litter, broadleaf litter, 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.

All ground flora individuals were identified to lowest taxonomic level possible. Ground flora specimens that could not be identified to species with confidence in the field were collected to be transported to the laboratory where they would be processed for identification. 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). Trees were defined as live stems ≥ 5 cm diameter at breast height (dbh, 1.37 m above the

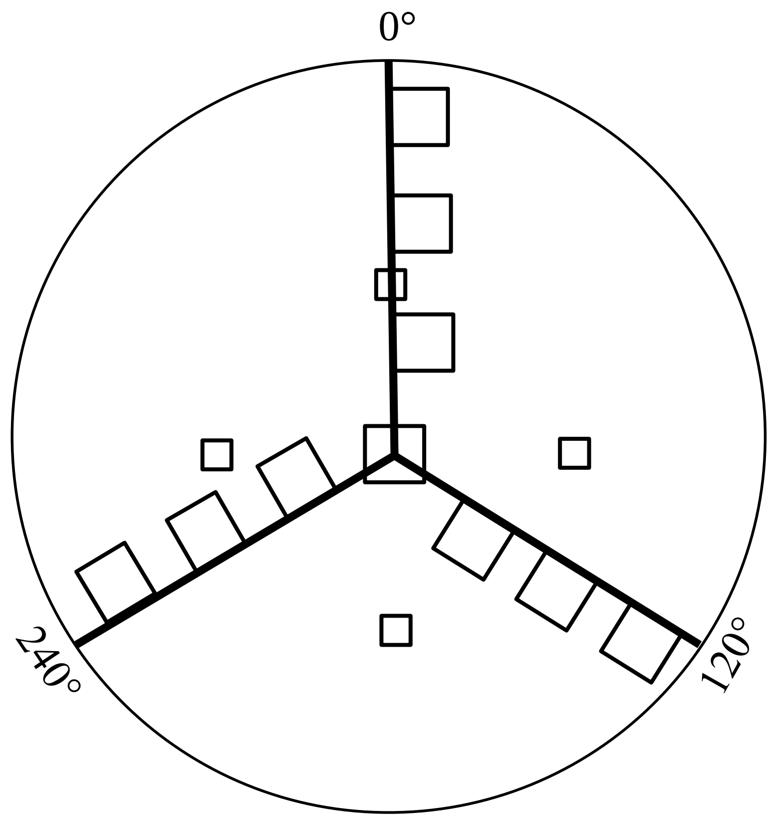

Figure 2. Schematic of vegetation sampling plots. Trees (live woody stems ≥ 5 cm dbh; diameter at breast height, 1.37 m above the root collar) and saplings (live woody stems < 5 cm dbh and > 1 m in height) were measured in the entire plot (500-m^2). Percent cover of each ground flora taxa, *Pinus* litter, broadleaf litter, and exposed bare mineral soil were visually estimated and assigned a cover class following the North Carolina Vegetation Survey (*sensu* Peet *et al.* 1998) within ten 1 × 1 m subplots (10-m^2) placed systematically along the three transects. Litter depth was measured and all fuel ≤ 1 m in height was collected in the four corners of four 0.25 m^2 subplots placed 5 m from plot center in the four cardinal directions. Hemispherical photographs of the canopy were taken at plot center.

root collar) and saplings 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 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, green leaves, and dead woody material (< 10 cm in diameter) ≤ 1 m in height) was collected in the 0.25 m^2 to compare 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, evenness, 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* I 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*, *Pycanthemum*, *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, and forbs (defined as a vascular plant without significant woody tissue above or at the ground) (USDA 2017) and compared across treatments. Vines were analyzed separately from forbs because of their unique ability to sequester space a capture light in forest ecosystems (Collins and Wein 1993, Schnitzer and Bongers 2002). Legumes were also analyzed separated from other ground flora because of their potential to be forage for wildlife, ability to make nitrogen available for plants, and regenerative success after fire (Arianoutsou and Thanos 1996, Sparks *et al*. 1998). Seedling density of all woody stems in the ten 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 reaching ≤ 1 m in height) were estimated by calculating the estimated percent of full photosynthetic photon flux density reaching the ground layer, which is referred to in my study hereafter as % ground layer PPFD, or just ground layer light availability. Litter depth was averaged per plot and compared across treatments to assess treatment-mediated differences in forest floor accumulation. Percent cover of broadleaf litter and percent cover of *Pinus* litter were compared across each treatment to assess the effects of plant litter on ground flora richness, diversity, and cover. Percent bare mineral soil cover was also compared across treatments to determine if treatment mediated differences in bare mineral soil exposure had an effect 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 “others.” 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 pair-wise 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. Variables were grouped into three categories based on whether they met the assumptions and can be seen in Table 3. Logarithmic transformed litter depth was compared to ground flora richness and diversity using single linear regression and adjusted r^2 values were reported for reduced estimator bias. 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 trends 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

Table 3. Variables that either met the assumptions of normality and homoscedasticity without transformation, met the assumptions following logarithmic transformation, or did not meet the assumptions following logarithmic or exponential transformations. Percent PPFD was percent photosynthetic flux density reaching 1 m above the ground, and cover was 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%.

Status	Variables
Assumptions met	Ground flora diversity, evenness, light availability (% PPFD)
Logarithmic transformation	Ground flora richness, litter depth (cm), basal area (m^2 ha^{-1}), sapling density (stems ha^{-1})
Assumptions not met	Total cover, forb cover, graminoid cover, woody plant cover, vine cover, exposed mineral soil cover, Pinus litter cover, broadleaf litter cover

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 (Peck 2016). 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 so that independent species did not reduce the weight of that 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 analyses 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 detected with PerMANOVA (Dufrêne and Legendre 1997, Peck 2016).

3. RESULTS

3.1. Ground flora

Ground flora taxonomic richness was the greatest in the thin/3Rx treatment ($p < 0.001$), and greater in the thin/9Rx treatment compared to the thin/0Rx treatment ($p < 0.05$) and the control stands ($p = 0.001$) (Figure 3). Average ground layer taxonomic richness was 16.75 taxa ± 0.78 (SE) per plot in the control stands, 18.40 taxa ± 0.94 (SE) per plot in the thin/0Rx treatment, 21.65 taxa ± 1.08 (SE) per plot in the thin/9Rx treatment, and 29.95 taxa ± 1.33 (SE) per plot in the thin/3Rx treatment. Ground flora 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 stands ($p < 0.001$). Average ground flora Shannon taxonomic diversity index was 2.73 ± 0.05 (SE) per plot in the control stands, 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 taxonomic evenness was greater in the thin/0Rx treatment compared to the thin/9Rx and the thin/3Rx treatments ($p = 0.002$ and $p = 0.005$ respectively). Additionally, ground flora taxonomic evenness was greater in the control stands compared to the thin/9Rx and thin/3Rx treatments ($p < 0.001$). Average ground flora taxonomic evenness was 0.980 ± 0.002 (SE) per plot in the control stands, 0.980 ± 0.003 (SE) in the thin/0Rx treatment, and 0.970 ± 0.002 (SE) in both the thin/9Rx and the thin/3Rx treatments.

Ground flora cover was the greatest in the thin/3Rx treatment (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 stands), and greater in the thin/9Rx treatment compared to the thin/0Rx treatment

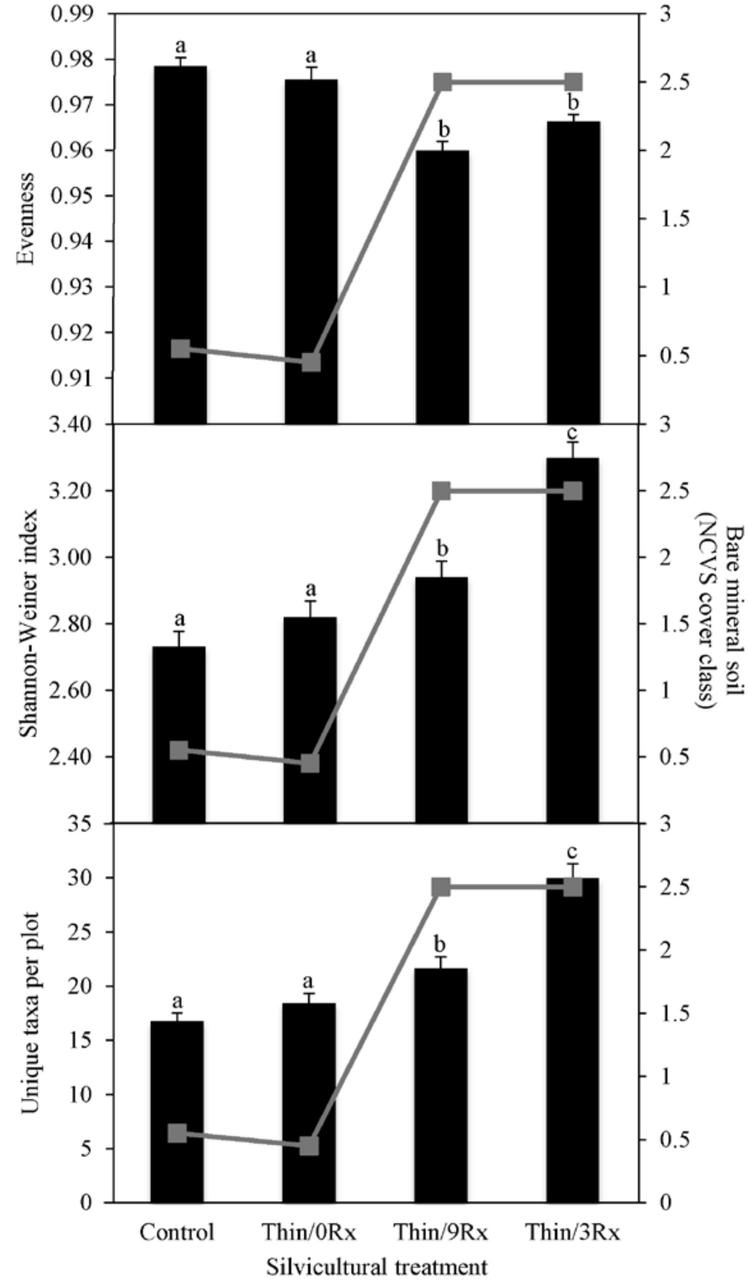

Figure 3. Taxonomic richness (unique taxa per plot), taxonomic diversity and percent cover for ground layer flora (vascular plants ≤ 1 m height surveyed in 10-m^2 plots) in four silvicultural treatments in William B. Bankhead National Forest located in northern Alabama, USA. Control was untreated, thin/0Rx 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. 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%.

($p = 0.001$) and control stands ($p < 0.001$) (Figure 4). Average NCVS cover class of all ground flora combined was 5.90 ± 0.10 (SE) in the control stands, 6.05 ± 0.09 (SE) in the thin/0Rx treatment, 7.20 ± 0.16 (SE) in the thin/9Rx treatment, and 8.60 ± 0.13 (SE) in the thin/3Rx treatment. Forb cover was similar in the thin/3Rx and thin/9Rx treatments ($p > 0.05$). Forb cover was greater in the thin/3Rx treatment relative to the control ($p < 0.001$) and the thin/0Rx treatment ($p < 0.001$). Additionally, forb cover was greater in the thin/9Rx treatment compared to the control stands ($p < 0.001$) and the thin/0Rx treatment ($p = 0.002$). Graminoid cover was greatest in the thin/3Rx treatment ($p < 0.08$), similar in the thin/0Rx and the thin/9Rx treatments ($p > 0.05$), and the least in the control stands ($p < 0.03$). 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 ($p = 0.03$). Average cover class of legumes was 0.1 ± 0.1 (SE) in the control stands, 0.45 ± 0.22 (SE) in the thin/0Rx treatment, 1.7 ± 0.31 (SE) in the thin/9Rx treatment, and 3.0 ± 0.21 (SE) in the thin/3Rx treatment. Exotic species were only found in the thin/0Rx the thin/3Rx treatments, with a significantly greater average cover class in the thin/3Rx treatment (0.6 ± 0.26 (SE)) than the thin/0Rx treatment (0.3 ± 0.22 (SE); $p = 0.04$).

A three-dimensional NMS solution revealed a difference in the composition and abundances of the 132 ground layer taxa (PerMANOVA, $p < 0.001$) (Figure 5). 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

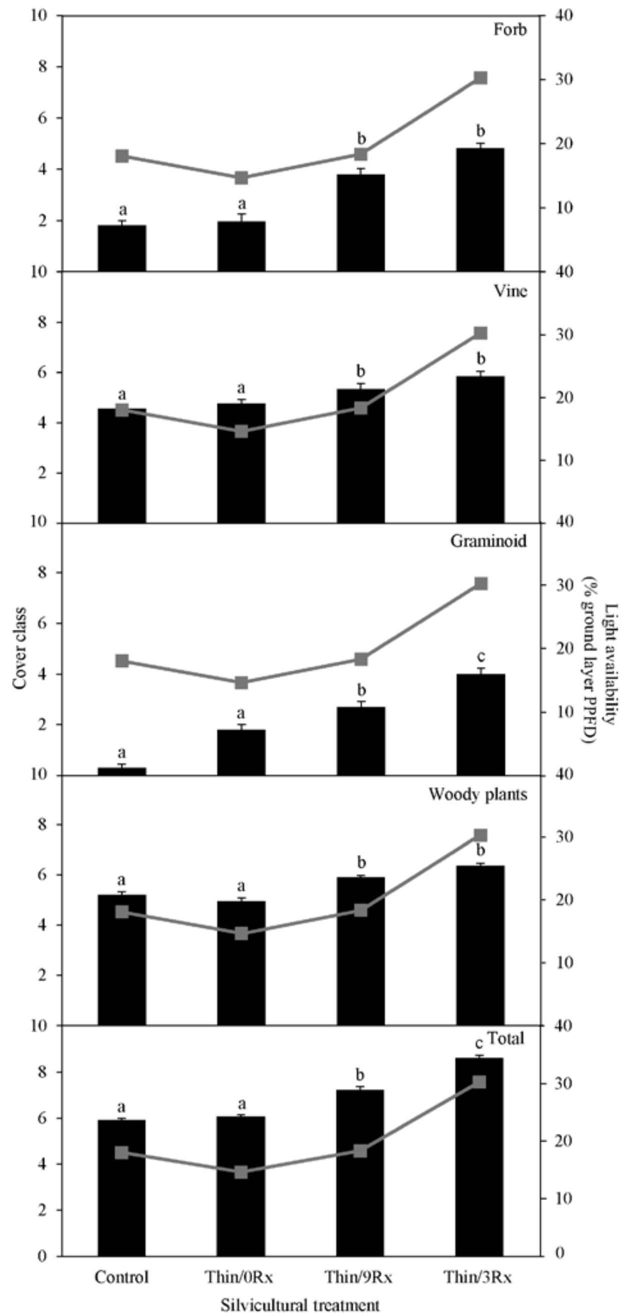

Figure 4. Cover class based on growth habit of all vascular plants ≤ 1 m in height and light availability (% of photosynthetic photon flux density reaching 1 m above the surface) in four different silvicultural treatments in William B. Bankhead National Forest located in northern Alabama, USA. Cover 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 ($p < 0.05$).

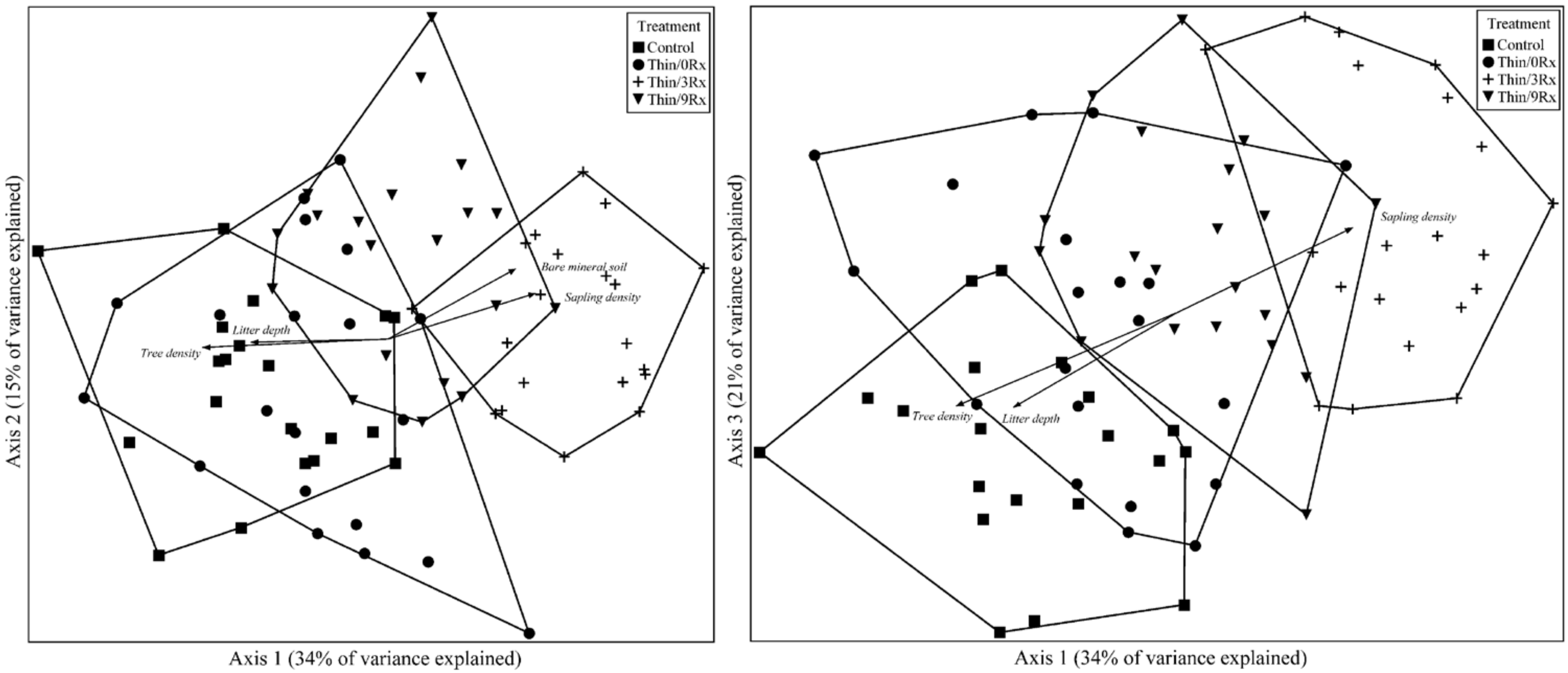

Figure 5. Three-dimensional non-metric multidimensional scaling solution based on the abundance of ground flora (vascular plants ≤ 1 m height) in control plots (Untreated; squares), plots that were thinned in 2006 and not burned (Thin/0Rx; circles), plots that were thinned in 2006 and burned on a three 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 located in northern 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.

the far reach of 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 (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 study area contained 33 significant indicator taxa ($p < 0.05$) (Table 4). The thin/3Rx treatment contained the majority with 22 taxa (67%), half of which were forbs (Figure 6). 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 stands contained three woody plant indicator taxa and one vine. The thin/0Rx treatment contained one woody plant and one vine.

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. *Pinus* had 0 seedlings ha^{-1} in the control and the thin/0Rx treatment, and comprised < 1% of total seedlings ha^{-1} in the thin/9Rx treatment and < 2% of total seedlings ha^{-1} in the thin/3Rx treatment. *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

Table 4. Indicator taxa ranked by Indicator Value (based on the average of relative frequency and relative abundance) and significance (* = p < 0.05, ** = p < 0.01, *** = p < 0.001) in four silvicultural treatments in William B. Bankhead National Forest 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.

Taxon	Indicator Value	Control	Thin/0Rx	Thin/9Rx	Thin/3Rx
Chamaecrista fasciculata (Michaux) Greene	63.8			7	***
Rhus copallinum Linnaeus var. *copallinum*	53			16	***
Rubus spp.	51.7	1	18	12	***
Lespedeza violacea (Linnaeus) Persoon	51.1				***
Vitis aestivalis Michaux var. *aestivalis*	50			1	***
Poaceae	46		17	31	***
Parthenocissus quinquefolia (Linnaeus) Planchon	43.8	3	3	3	***
Carya glabra (P. Miller) Sweet	42.3	9	16	16	***
Toxicodendron radicans (Linnaeus) Kuntze	40.4	9	3	26	***
Liriodendron tulipifera Linnaeus	39.2	4	5	17	***
Solidago arguta Aiton	38.5			8	***
Quercus velutina Lamarck	37	*	1		19
Fagus grandifolia Ehrhart	35.6	***		1	
Acer rubrum Linnaeus	33	18	17	***	31
Prunus serotina Ehrhart	30.7	7	10	10	*
Muscadinia rotundifolia (Michaux) Small	29.1	20	23	**	28
Gelsemium sempervirens (Linnaeus) St. Hilaire	26.7	*	4	4	3
Hypericum hypericoides (Linnaeus) Crantz	26.2		1	1	**
Callicarpa americana Linnaeus	25.7		**	1	
Bignonia capreolata Linnaeus	25		**		
Helianthus hirsutus Rafinesque	25				**
Diospiros virginiana Linnaeus	24.7	2	3	9	*
Quercus falcata Michaux	23.2	1	8	*	10
Erechtites hieraciifolius (L.) Raf. ex DC.	20.5		1		*
Galium uniflorum Michaux	20.5				**
Rudbeckia hirta Linnaeus	20				*
Ilex opaca Aiton	19.6	*		2	2
Styrax grandifolius Aiton	18.7			2	*
Cornus florida Linnaeus	18.6	1		*	1
Solidago odora Aiton	18.3			8	*
Dioscorea villosa Linnaeus	17.9			1	*
Helianthus strumosus Linnaeus	16.7			1	*
Lespedeza hirta (Linnaeus) Hornemann var. *hirta*	15			*	

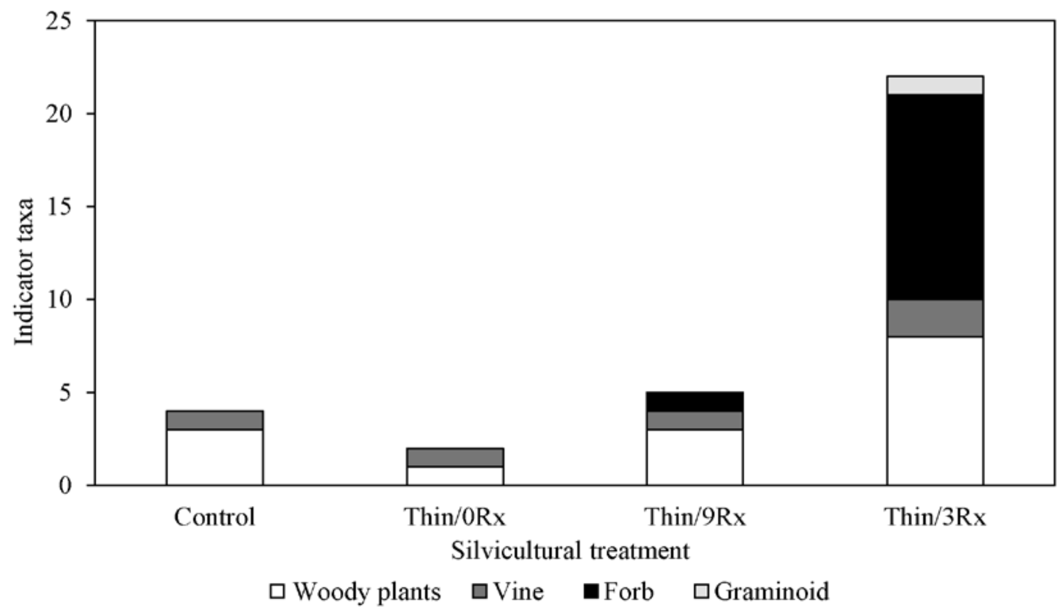

Figure 6. Indicator taxa based on growth habit in four different silvicultural treatments in William B. Bankhead National Forest located in northern Alabama, USA. Control was untreated, thin/0Rx was thinned in 2006 without burning, thin/9Rx was thinned in 2006 and burned on a nine year return interval, and thin/3Rx was thinned in 2006 and burned on a three year return interval.

treatment ($p < 0.05$).

3.2. Environmental variables

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 for the control stands, the thin/0Rx treatment, and the thin/9Rx treatment ($p > 0.05$) (Figure 4). The control stands contained 18.13 % ground layer PPFD ± 1.78 (SE), the thin/0Rx treatment contained 14.63% ± ground layer PPFD 1.48 (SE), the thin/9Rx treatment contained 18.34 % ground layer PPFD ± 2.18 (SE), and the thin/3Rx treatment contained 30.25 % ground layer PPFD ± 2.91 (SE).

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} ± 12.70 (SE) in control plots, 160.49 g m^{-2} ± 13.70 (SE) in the thin/0Rx plots, 100.19 g m^{-2} ± 8.91 (SE) in the thin/3Rx plots, and 97.55 g m^{-2} ± 7.0 (SE) in the thin/9Rx plots.

Logarithmic transformed litter depth was negatively associated with ground layer taxonomic Shannon diversity (adjusted $r^2 = 0.348$, $p < 0.001$), and ground layer taxonomic richness (adjusted $r^2 = 0.420$, $p < 0.001$) (Table 5). The thin/3Rx treatment contained the thinnest average litter depth (at the $p = 0.01$ level compared to the thin/9Rx treatment and at the $p < 0.001$ level compared to the thin/0Rx treatment and the control stands) (Table 6). The thin/9Rx treatment contained a thinnest litter depth compared to the thin only treatment ($p < 0.001$) and the control stands ($p < 0.001$). 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. Average litter depth was 4.6 cm ± 0.2 (SE) in the control stands, 4.2 cm ± 0.3 (SE) in the thin/0Rx treatment, 2.8 cm ± 0.2 (SE) in the thin/9Rx treatment, and 2.1 cm ± 0.1 (SE) in the thin/3Rx treatment. Percent cover of broadleaf litter was significantly less in the thin/3Rx treatment compared to all other treatments ($p < 0.001$). Average NCVS cover class of broadleaf litter was 7.05 ± 0.15 (SE) in the thin/3Rx treatment, 7.5 ± 0.17 (SE) in the control stands, 7.8 ± 0.14 (SE) in the thin/0Rx treatment, and 7.15 ± 0.22 (SE) in the thin/9Rx treatment. Percent cover of *Pinus* litter was similar across all treatments ($p > 0.05$).

Table 5. One-way analysis of variance tests summarizing mean values (± standard error) of 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 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. 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
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}

Percent cover of bare mineral soil was greater in the thin/3Rx and the thin/9Rx treatments compared to the thin only treatment ($p < 0.001$) and the control stands ($p < 0.001$). Average NCVS cover class was 0.55 ± 0.20 (SE) in the control stands, 0.45 ± 0.18 (SE) in the thin/0Rx treatment, 2.5 ± 0.17 (SE) in the thin/9Rx treatment, and 2.5 ± 0.15 (SE) in the thin/3Rx treatment.

3.3. Trees and saplings

Live basal area (m^2 ha^{-1}) was reduced in the thinned treatments by ≥ 45% ($p < 0.001$) (Table 6). 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 stands ($p < 0.001$). The genus *Pinus* had the greatest density in the tree layer in all treatments except for the thin/0Rx treatment (Table 6). The *Acer-Fagus* group was the second most abundant taxonomic category in the control stands (26% relative density), but was third to the

Table 6. 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 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	49.30	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	0.60	0.21	6.25	64.43	3.31	1.23
Quercus-Carya	236	256	126	84	20.68	28.73	21.80	29.37	3.77	2.40	3.12	3.26	10.12	11.66	17.10	18.87
Other	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

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 7). 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 7. 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 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. Letters on total density indicate significant difference (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	1,378	1,403	2,570	43.44	43.91	35.60	36.14
Other spp.	462	725	1,173	3,054	30.18	23.10	29.76	42.95
Quercus-Carya	404	731	547	1,480	26.39	23.30	13.88	20.81
Pinus spp.	-	304	818	7	-	9.69	20.76	0.10
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	8,700	23,800	49.82	44.77	47.18	19.08
Other spp.	15,400	14,250	19,750	23,150	36.19	41.42	39.15	50.77
Quercus-Carya	5,950	4,750	12,900	6,550	13.98	13.81	12.98	28.29
Pinus spp.	-	-	850	350	-	-	0.69	1.86
Total	42550[a]	34400[a]	50450[a]	45600[a]	100.00	100.00	100.00	100.00

4. DISCUSSION

4.1. Ground flora

Thinning without prescribed fire altered the stand structure and the light regime enough to elicit a slight increase in ground flora taxonomic richness (although not significant) and graminoid cover compared to the control that was detectable 12 years after the event. Basal area on the thinned treatments was reduced by ~ 50% 12 years after the operation, which allowed enough light to penetrate the canopy and increase the germination and growth of grasses (Abella and Springer 2015). Because I did not measure the initial response of the thin only treatment, I can only infer that light and likely ground flora richness, diversity, and cover were increased for several years following the thinning event, or until residual and new vegetation filled the space (Oliver and Larson 1996). This is consistent with other studies that showed an overall increase in understory vegetation with increased overstory removal (Thomas *et al*. 1999, Decocq *et al*. 2004). Brewer (2016) found an increase in 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) showed an up to 100% increase in ground flora richness after a ≤ 50% reduction in canopy cover in a remnant *Quercus* savanna that had experienced increased tree density subsequent to fire suppression. Phillips and Waldrop (2008) recorded increased understory plant richness in stands that were thinned from below to 18 m^2 ha^{-1} compared to unthinned stands. Thomas *et al*. (1999) found significantly 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* stand. However, the thinned plots contained litter depths ~ 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 thinning, the results of my study indicate that repeatedly prescribed burning subsequent to thinning will ensure enduring increases in ground flora richness, diversity, and cover of ground flora compared to thinning only and control stands. Fire is a unique disturbance that likely increases the cycling of nutrients within the system, and alteration of the ecosystem that cannot be mimicked through structural alteration alone (Boerner 2006, Phillips *et al*. 2007, Lettow *et al*. 2014, Brewer 2016). Taxa such as fireweed (*Erechtites hieraciifolius*), species of the Poaceae family, and species of the *Lespedeza* genus are all dependent upon fire for increased growth and survival (Sparks *et al.* 1988, Hutchinson 2005a, Phillips and Waldrop 2008). Several species in the Asteraceae family were indicative of stands that were thinned and repeatedly burned in my study (e.g. *S. arguta*, *S. odora*, *H. hirsuta*, and *R. hirta*), which is consistent with Weakley (2015) who reported that these species are commonly found in open, disturbed sites. The increased ground flora richness, diversity, and cover (including the cover of forbs and graminoids) in the treatments with a combination of thinning and burning corroborated a study in upland *Pinus* stands in South Carolina, USA done by Phillips and Waldrop (2008).

In my study, frequently burning (the thin/3Rx treatment) resulted in significantly greater values for ground flora taxonomic richness, ground flora taxonomic diversity, and cover of ground flora compared to infrequently burning (the thin/9Rx treatment). Peterson and Reich (2008) examined understory species richness response to fire frequency in *Quercus* savannas, woodlands, and grassland communities in eastern Minnesota. Sites were burned 0–26 times from 1962–1995 and the greatest increases in understory species richness, including forbs and graminoids, were following five burns in a decade, which leveled off with greater frequency. Brockway and Lewis (1997) found a similar result in a *P. palustris* wiregrass community. After four decades of dormant season burning, they 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 least richness (17 species) in the control plots. Brockway and Lewis (1997) also reported the greatest understory diversity and cover following the 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 (Waldrop *et al.* 1992) were found without the combination of a thinning treatment as is in my study, although Peterson and Reich (2008) found the greatest increases in understory diversity in stands that had less canopy cover (20–70%). The results from my study (as well as Willms *et al.* 2017, Schwilk *et al.* 2009, and Brewer 2016) indicate the greatest increases in ground flora diversity following the combination of thinning and prescribed burning, which increased the germination and establishment of ground flora by increasing light availability in the ground layer and removing physical barriers (Hutchinson *et al.* 2006)

Frequently burning increased the abundance of legumes, and two of the greatest indicators of the thin/3Rx treatment were *Chamaecrista fasciculata*, which had the highest indicator value, and *L. violacea*. This was similar to a finding in 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 some have the ability to make atmospheric nitrogen available, giving them an advantage for germination and establishment in post-fire environments (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 biennial prescribed fires in Mississippi, USA. Of those 22 indicator species in my 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 increased abundance of forest indicator species indicates that these may have once been closed canopy stands, although it is difficult to discern whether these species persisted from before agricultural land clearing or recently migrated upon re-forestation. The increased abundance of disturbance indicator species and the lack of fire-maintained indicator species may be attributed to multiple causes. This could indicate that there have never been abundant populations of fire-tolerant ground floral species in my study area, or that the exclusion of fire in the 20th century eliminated these species (Matlack 2013, Brewer 2016). It will be interesting to see if species composition of the ground flora shifts towards more open habitat, fire-maintained species with the continuation of the Bankhead Forest Health and Restoration Initiative (i.e. open canopy and periodic–frequent fire return intervals). The increased abundance (i.e. disturbance-mediated abundance) of ruderal species (e.g. Poaceae) in the thin/9Rx and the thin/3Rx treatments were likely caused by the thinning and repeated prescribed fire in these stands, which opened the canopy, consumed understory vegetation, and allowed for more r-selection species to migrate and rapidly colonize within the system. These indicator species may suggest that the anthropogenic disturbance these sites experienced mimicked the natural disturbance regimes (i.e. catastrophic tornadoes similar to Brewer 2016). However, the information these results offer for a historic fire regime is less evident. Nevertheless, the increased taxonomic richness and diversity in treated stands indicated that silvicultural treatments (thinning and prescribed fire) are worthwhile operations for managers that desire to increase stand-level plant diversity (Nowacki and Abrams 2008, Puettman *et al*. 2009, Matlack 2013, 2015, Stambaugh *et al*. 2015).

Seedling density did not significantly increase with any of the treatments, which is contrary to several other thinning and prescribed fire studies in the USA (Schwilk *et al*. 2009, Schweitzer *et al.* 2016). Schweitzer *et al.* (2016) found increased seedling density in thinned and frequently burned treatments. However, she measured seedlings as all stems ≥ 3.8 cm dbh, which differed from this study. It is possible that the seedlings that were in the stands may have re-sprouted to > 1 m in height after two growing seasons, causing these stems to be counted in the sapling category for this study. The combination of thinning and burning increased the abundance of *Quercus* seedlings, which was consistent with Phillips and Waldrop (2008), although the increase was more profound in infrequently burned stands. This increase may be attributed to the increased light availability associated with thinning and decreased soil moisture associated with burning (because fire consumed soil organic matter, which is where moisture is usually stored) (Hutchinson 2006, Nyland 2002), which tends to favor the establishment of earlier successional genera such as *Quercus* in the seedling layer rather than later successional genera such as *Acer* (Brose and Van Lear 1998).

4.2. Environmental variables effects on ground flora

An interesting find of my 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, 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 small compared to other long unburned forest systems (e.g. *P. palustris* Mill. 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 regression 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 (2005a) found that reducing litter mass by 54% (from 466 g m^{-2} to 216 g m^{-2}) after two fires in four years and by 46% (from 419 g m^{-2} to 226 g m^{-2}) was enough to elicit a positive response in herbaceous plant diversity in southern Ohio, USA, which was similar to the fuel mass reductions in the thinned and burned treatments compared to the thinned only and control stands from this study. In another *Pinus* 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 (of seeds) and establishment (seedlings that survived between one month and two years) of forest plants. The review stated that germination was significantly negatively correlated with litter depth (from 0–4 cm, with 1.5 cm deep litter most favorable of seed germination), and establishment was significantly negatively correlated with litter depth and litter mass (from 0–4000 g m^{-2}, with < 200 g m^{-2} favoring the most vegetation 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 strata (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 Grime (1981) reported a negative relationship between shoot biomass of herbaceous vegetation and dry litter weight under an *Acer-Quercus* canopy.

Burning on a three year return interval compared to burning on a nine year return interval resulted in even greater reductions in litter depth and even greater increases in ground flora richness, diversity, and cover. The repeated consumption of fuel from frequent fire, coupled with the ephemeral dieback of understory woody plants and a reduction of midstory stems (Schweitzer *et al.* 2016), increased the amount of light reaching the ground layer and entering the seedbed, which promoted the germination and establishment of ground flora (also reported in Hutchinson 2005a). The decreases in fuel mass and litter depth measured in this study were enough to increase germination of seeds adapting to germination in high light environments (e.g. Poaceae). Baskin and Baskin (1988) investigated environmental factors influencing seed dormancy break and germination requirements and found that temperature of the soil was the primary factor influencing germination phenology in 56 winter annual and 32 summer annual herbaceous species native to temperate regions. However, litter and fuel returns to pre-burn levels rather quickly (after two fire free years in Hutchinson 2005a), thus burning at a shorter return interval shall maintain the increases in ground flora diversity, richness, and cover.

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 overall seed germination, which is because of the increased light reaching the seedbed and the increased available space to grow. Several studies report decreased litter depths after fire, but the majority of these sites return to pre-burn depths after 3–5 years (Fernandes and Botelho 2003, Schwilk *et al.* 2009). The increased ground flora diversity, richness, and cover reported in this study was mostly because of the frequency of fire.

The ephemeral yet more frequent influx of nutrients likely also was 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 agriculture), thus soil chemistry was greatly altered upon nutrient release via prescribed fire (Gilliam and Christensen 1986, Boerner 2006). Christensin (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*-wiregrass 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 nutrients will be readily available to ground flora in the growing season post-burn when burned in the dormant season, however nutrient availability will reach pre-burn levels by the following spring when burned in the prior growing season. Black char in the ground layer (i.e. decreased albedo) and increased insolation immediately following fire may have also influenced ground flora germination and growth rates (Hutchinson 2006). Increased cover of the regeneration layer following frequent fire may also retain ground layer heat and moisture

(Deardorff 1978). I should note that other factors, such as soil texture, depth to water table, distribution of species assemblages across the site, intensity of belowground competition, etc. may also affect ground flora growth.

4.3. Trees and saplings effects on ground flora

The increases in sapling (stems < 5 cm dbh and > 1 m in height) density in the thinned and frequently burned stands did not seem to decrease ground layer light availability, or ground flora richness, diversity, or cover, which has been reported in other studies. Phillips and Waldrop (2008) found thinning to 18 m^2 ha^{-1} in combination with dormant season fire substantially increased the density of woody plants > 1.4 m in height and < 10 cm dbh three years post treatment. Understory light availability and diversity were the greatest in this treatment as well. However, the thinning treatments conducted in Phillips and Waldrop (2008) differed from the thinning in my study in that Phillips and Waldrop (2008) thinned from below removing small merchantable, diseased, or insect-infested trees primarily, whereas this study was a commercial thin primarily targeting *P. taeda* to promote hardwoods. Heirs *et al.* (2007) found no reductions in understory diversity with a dense midstory layer (stems < 10 cm dbh) in a *P. palustris* stand. Also, Lettow *et al.* (2014) found no increase in light availability in the understory following the removal of stems < 10 cm dbh in a remnant *Quercus* savanna that has accumulated a dense hardwood canopy following cessation of the historical burning and grazing disturbance regime.

However, the way the treatments affected trees ≥ 5 cm dbh did seem to affect the ground flora in this study. The thinning changed the stand structure and altered the species composition across all treatments (Schweitzer *et al.* 2016). 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 (personal communication, Callie Schweitzer, Research Forester, 730 D Cook Avenue, Huntsville, AL 35801). Schweitzer *et al.* (2016) found decreases in stem densities immediately following the thinning, however stem density substantially increased by 2013 in the thinned only stands compared to thinned and burned stands. My 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.

The increased ground flora richness, diversity, and cover, found in the stands that were thinned and burned on a three year return interval were partly attributed to the reductions in tree density and basal area that increased growing space and light availability in the ground layer. Burning on a three year return interval seemed to reduce stem density of smaller sized trees in my 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 heavy thin (target residual BA of 11.5 m^2 ha^{-1}) and three burns in 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 (Peterson and Reich 2001, Schwilk *et al*. 2009, Arthur *et al*. 2015, Schweitzer *et al.* 2016). All of the studies in the review by Schwilk et al. (2009) that were conducted in the eastern USA found increased understory diversity with decreased basal area from thinning, a finding consistent with my study.

5. MANAGEMENT IMPLICATIONS

Overstory thinning of planted *Pinus* stands that were once dominated by mid-successional hardwoods 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. Thinning coupled with prescribed burning resulted in the greatest increases in ground flora richness, diversity, and cover, which may increase ecosystem productivity and may improve resiliency to future perturbations (Tillman *et al*. 1996, Peterson *et al*. 1998). Fire frequency is one of the most important factors related to 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, I recommend burning at least every three years in addition to partially removing the overstory, or as frequently as fuels will allow to control competing fire-sensitive hardwoods and favor fire-adapted ground flora growth forms (e.g. forbs and graminoids). Litter accumulation is a concern because of the risk of losing plant diversity (Heirs *et al.* 2007) and creating conducing conditions for severe fire (Varner 2007). Although litter accumulation is relatively slow in the BNF, 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.

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