Patterns of Vegetation Composition and Diversity in Pine-dominated Ecosystems of the Outer Coastal Plain of North Carolina: Implications for Ecosystem Restoration

Authors:

Stephen Mitchell¹ (Corresponding)

Kyle Palmquist^{2, 3}

Susan Cohen⁴

Norman L. Christensen¹

Institutions:

¹Nicholas School of the Environment, Duke University, Durham, NC 27708

² Curriculum for the Environment and Ecology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599

³ Department of Botany, University of Wyoming, Laramie, WY 82071

⁴Naval Facilities Engineering Command, Marine Corps Base Camp Lejeune, Camp Lejeune, NC 28542

Introduction

Three pine species, longleaf (*Pinus palustris*), loblolly (*P. taeda*) and pond (*P. serotina*), are the dominant overstory trees in a variety of wetland and upland ecosystems over much of the lower coastal plain (also called the Atlantic coastal flatlands (Wear and Greis, 2002), of North and South Carolina, USA (Wells, 1932; Christensen, 2000). Longleaf pine is thought to have been the most important canopy tree across much of this landscape prior to European settlement, extending from xeric sandy sites to much moister conditions on shallow organic soil. Pond pine was most important on sites with perennially wet organic soils (Woodwell, 1958; Christensen, 1988). Loblolly pine may have been important in coastal maritime forests, along riparian corridors, and in “flatwoods” on poorly drained soils (Ashe, 1915; Wahlenberg, 1960; Christensen, 2000), but the pre-settlement abundance and distribution of this species on this landscape is not well understood. Land use and a variety of human-caused disturbances over the last 3 centuries have greatly altered the distribution and relative abundance of these species (Landers *et al.*, 1995; Owen, 2002; Wear and Greis, 2002; Frost, 2006; Noss *et al.*, 2015). Owing to a combination of timber harvest, naval stores, and clearing for agriculture, longleaf pine forests have been reduced by more than 98 percent compared to presettlement conditions (Landers *et al.*, 1995; Noss *et al.*, 1995; Schultz, 1999). Now, loblolly pine is the most abundant pine on this landscape, except on deep organic soils where

pond pine dominates, and xeric sands where longleaf pine still dominates. Roughly half of these loblolly stands were naturally seeded following land abandonment and the other half planted as plantations (Schultz, 1999; Wear and Greis, 2002).

Several studies have explored the changes in plant species richness (number of species) and community composition (identities and relative abundances of the community of species) among longleaf and pond pine dominated forests in relation to soil characteristics. Soil organic matter, bulk density and base cation availability are highly correlated with variations in species richness and composition in longleaf and pond pine stands (Walker and Peet, 1984; Christensen, 1988; Drewa *et al.*, 2002; Kirkman *et al.*, 2004; Peet, 2006; Carr *et al.*, 2009; Peet *et al.*, 2014). Species richness is highest in frequently burned longleaf stands on moist and cation-rich soils; such stands are among the most species rich temperate ecosystems in North America (Walker and Peet, 1984). However, longleaf pine is now most commonly found on sandy, well-drained soils with lower levels of species richness, perhaps because such systems were historically less attractive for agriculture or intensive silviculture.

Much change in the composition and diversity of these pine ecosystems has been caused by alteration of their fire regimes (Garren, 1943; Christensen, 1981; Frost *et al.*, 1986). Frequent fire (every one to five years) is necessary for the maintenance of plant species richness, plant species composition, and vegetation structure in longleaf pine woodlands (Walker and Peet, 1984; Frost *et al.*, 1986; Kirkman *et al.*, 2004). With fire exclusion or longer fire return intervals, species richness declines, woody components increase, and the understory becomes dense and closed (Heyward, 1939; Lewis and Harshbarger, 1976; Brockway and Lewis, 1997; Glitzenstein *et al.*, 2003). The specific location of the transition from longleaf to pond pine dominated forests along soil moisture gradients is a function of fire frequency; longer fire return intervals move that transition to wetter conditions (Kologiski, 1977; Christensen, 1981; Frost *et al.*, 1986; Frost, 2006).

Because of the high biodiversity, rarity, and endemism of the longleaf pine ecosystem and its reduced areal extent, there has been much interest in the restoration of longleaf pine stands throughout the

Southeastern US. In existing longleaf stands where short-term (≤ 10 years) fire suppression has resulted in only modest change in understory structure and composition, reestablishment of frequent, low-severity fire regimes has been, by itself, an effective restoration tool (Walker and Silletti, 2006). By contrast, the legacy of long-term (> 10 years) fire suppression presents additional challenges to the restoration of vegetation associated with fire-maintained longleaf pine woodlands. First, excessive litter and soil organic matter (SOM) accumulation associated with fire suppression decreases reproductive success of established species and prevents colonization events by new species (Nave *et al.*, 2011), as many plant species within this ecosystem, including longleaf pine, require bare, mineral soil for germination and seedling establishment. The accumulation of SOM is also a barrier to the establishment of herbaceous species characteristic of longleaf woodlands from the soil seed bank (Cohen *et al.*, 2004). Second, longleaf pine seedlings, as well as many of the associated herb-layer species native to longleaf savannas, regenerate best in an open, park-like setting (Brockway and Outcalt, 1998) and an encroachment of the forest mid-story can significantly limit recruitment via light limitation (Hiers *et al.*, 2007). Thus, in stands where decades of long-term (> 10 years) fire suppression have allowed the ingrowth of dense hardwood understories and midstories, restoration has relied on both mechanical thinning of the midstory and the restoration of appropriate fire regimes (Provencher *et al.*, 2001; Varner *et al.*, 2005; Walker and Silletti, 2006; Brockway *et al.*, 2009; Outcalt and Brockway, 2010; Steen *et al.*, 2013).

There is great interest in restoring longleaf pine to places now dominated by loblolly pine (Brockway *et al.*, 2009; Schwilk *et al.*, 2009; Knapp *et al.*, 2011). Most of these efforts involve thinning of understory and midstory woody plants, similar to methods implemented in fire-suppressed longleaf stands. Here, the short-term goal is to restore an open stand structure similar to longleaf pine savannas. Over the long-term, such treatments are combined with frequent applications of prescribed fire and may include the planting of longleaf pine and some of its associate species with the goal of eventually restoring the longleaf ecosystem (see Walker and Silletti (2006) for a detailed discussion of restoration targets and protocols). However, there are significant challenges to restoration. First, loblolly now occurs

across a wide variety of soil/site conditions, not all of which once supported longleaf. Thus, restoration will likely succeed on only a subset of sites currently supporting loblolly. Second, most areas that now support loblolly (e.g. plantations) have been altered by a long history, including over a century of agriculture and/or intensive forest management. Seed banks of longleaf pine endemics in these systems have been exhausted and few ecological legacies of longleaf pine ecosystems remain. Furthermore, areas now dominated by loblolly have not been burned for a long time, resulting in the invasion of woody species in the understory and accumulations of litter and soil organic matter, conditions that do not facilitate the establishment of longleaf pine and associated herb-layer species. Reduction of duff via prescribed fire may be effective in reducing soil organic matter but must be done with caution, as prescribed burns set in stands with an exceptionally dry duff are more likely to result in crown scorch and overstory tree mortality (Varner *et al.*, 2007; Varner *et al.*, 2009).

An understanding of the environmental factors that control the distribution of plant species in pine forests of the Atlantic coastal plain is essential for implementing successful efforts to restore their structure, composition, and disturbance regimes. Here, using data from 75 permanent sample plots located in areas representing a wide range of soil/site conditions, we evaluated the role of environmental gradients and stand structure on plant species richness and composition among loblolly, pond, and longleaf pine stands located in the Atlantic coastal flatlands of North Carolina. We asked the following questions:

- 1). What environmental factors best explain the differences in the herb-layer composition of pond pine pocosins, loblolly pine forests, and longleaf pine woodlands?
- 2). To what extent do the herb-layer composition and trends in species richness in loblolly pine forests differ from that of longleaf pine woodlands and pond pine pocosins?
- 3). Which species are most indicative of the site conditions characterized by fire-maintained pine woodlands, and which species are most indicative of a departure from those site conditions?

- 4). What are the environmental conditions that might best facilitate restoration of the herb-layer of longleaf pine woodlands in stands that are not dominated by longleaf pine?

Of particular interest is whether there is any compositional overlap between longleaf pine woodlands and loblolly pine and/or pond pine forests. Areas of compositional overlap between loblolly and longleaf pine stands may aid in the identification of candidate restoration sites and the environmental properties for which efforts to restore the vegetation native to longleaf pine woodlands may be most promising.

Conversely, areas of compositional overlap between loblolly and pond pine stands may be indicative of stands in which efforts to restore longleaf pine vegetation are unlikely to succeed.

Methods

Study Area

We conducted our research at Marine Corps Base Camp Lejeune (MCBCL) within the Atlantic Coastal Flatlands Section of the Outer Coastal Plains Mixed Forest Province. The climate is classified as warm-humid temperate, with average annual precipitation of 1420 mm and mean annual temperature of 13°C (MCBCL, 2006). Elevation in our study area ranges from 10 to 30 m above mean sea level (AMSL). Seventy-five study sites were located in forest stands that were selected to represent a range of soil characteristics (as documented in soil series classification by Barnhill (1992)), which are determined largely by the characteristics of parent material (e.g., unconsolidated sediments and limestone) and soil moisture conditions. Longleaf pine woodlands generally occur on shallow organic and mineral soils; the depth of the water table in these ecosystems varies from a few centimeters to more than 1 m, depending on topography, creating a gradient between xeric uplands and poorly drained, lowland stands. The study area also contains high-pocosin forest-wetlands (Christensen, 2000; Harding and Walters, 2002) on poorly drained organic soils. Some plant species that are abundant in pocosins, such as *Ilex glabra* and *Persea palustris*, also occur in loblolly and longleaf forest stands on moister soils and where fires have been suppressed for long periods. Loblolly pine forests at MCBCL are largely fire-suppressed and, on

average, have higher SOM than longleaf pine stands and often contain a dense hardwood midstory with stems of sweet gum (*Liquidambar styraciflua*) and red maple (*Acer rubrum*). Historically, MCBCL was used primarily for timber production and, to a lesser extent, agriculture, but no agricultural usage has occurred since its designation as a military installation in 1941 (MCBCL, 2006).

Vegetation Sampling

Between June and September of 2009 and 2010, permanent 20-m × 50-m (0.1-ha) vegetation monitoring plots were established in each of 71 loblolly and longleaf stands, while 4 pond pine/pocosin stands were sampled in 2011. Among these, 46 were dominated by longleaf pine, 25 were dominated by loblolly pine and 4 were dominated by pond pine. Based on criteria from Schafale (2012), longleaf pine stands were divided into two groups. 23 plots were assigned to Dry Pine/Oak Savannas (DPOS), where scrub oaks (e.g., *Quercus laevis*, *Q. geminata* and *Q. hemisphaerica*) were abundant in the understory. The remaining 23 plots were assigned to a Wet Pine Savannas (WPS) group, in which the understory was dominated by graminoids and herbs. Of the loblolly plots, 16 had been subjected to hardwood mid-story removal with a Hydro-Ax® mulching device (Prentice Forestry, <http://www.prenticeforestry.com>) in the year prior to sampling. This thinning removed all stems < 20 cm dbh and created open-canopy conditions similar to those of regularly burned longleaf stands (Provencher *et al.*, 2001; Brockway *et al.*, 2009). The other 9 loblolly pine plots had a dense, untreated hardwood mid-story. Thinned loblolly, unthinned loblolly and high pocosin stands were designated as (LT), (LU) and (HPO), respectively. The 25 loblolly pine treatment plots were randomly located within compositionally homogeneous stands > 5 ha that exhibited evidence of fire exclusion. The remaining 50 monitoring points were previously located by MCBCL staff to represent gradients in soil properties, vegetation composition, and disturbance history, while avoiding any edge effects with neighboring stands. Thus, each 0.1 ha sample plot is treated as a sample universe in its own right and is not necessarily intended to be statistically representative of the entire stand within which it is contained (Peet *et al.*, 1998).

Each plot was permanently marked with heavy steel conduit, and subsequently sampled for

woody and herbaceous plant composition and cover using the Carolina Vegetation Survey (CVS) protocol (Peet *et al.*, 1998). Individual plots were located to avoid obvious vegetation transitions and represent relatively uniform soil and topographic conditions. Within each plot, all living and dead stems (greater than 1-cm dbh) were tallied by species and dbh. For the herbaceous layer, the plot was further subdivided into ten 10-m $\times$ 10-m subplots. The cover of each herb species was assessed in the intensive plots as prescribed by Peet *et al.* (1998). The cover of each herb species was assessed in the intensive plots as prescribed by Peet *et al.* 1998, as described in the methods section. For each of the four intensive modules, cover % was represented by cover class, ranging from trace coverage 1 = trace (0.25%), 2 = 0-1% (0.5%), 3 = 1-2% (1.5%), 4 = 2-5% (3.5%), 5 = 5-10% (7.5%), 6 = 10-25% (17.5%), 7 = 25-50% (37.5%), 8 = 50-75% 62.%, 9 = 75- 95% (85%), and 10 = >95% (97.5%). Final coverage % for the species matrix was calculated by the average % coverage of the four intensive modules. For “trace” species not occurring within the four intensive modules, coverage % was estimated for the entire plot area. Residual subplots were surveyed to identify all species not found in any of the four intensive subplots. Thus, species richness estimates are based on the total number of species identified in the entire plot. Species composition here refers to identities and relative abundances of the community of species. In some (11) cases, closely related species could not be reliably distinguished for estimates of percent coverage in the field, and these were lumped into genus-level complexes. *Liatris pilosa* and *Liatris virgata*, for example, were classified as simply *Liatris* [*pilosa* + *virgata*].

Disturbance History

Since 1995, MCBCL has maintained a GIS database of all known fires. Perimeters and dates of each fire were mapped with a GIS data recorder and stored as a shape file in a geodatabase maintained by base personnel. We used these data to calculate the time since most recent fire, as well as fire frequencies from 1995 until the sampling date. Both categories of longleaf pine stands (DPOS and WPS) had a fire frequency commensurate with the historical mean fire return intervals for longleaf pine of ~3 years (Table 1). As expected, longleaf pine stands were also burned fairly recently, ~2 years for prior to sampling for

both DPOS and WPS (Table 1). By contrast, thinned (LT) and unthinned loblolly pine (LU) stands had fire frequencies of ~9 and ~8 years, respectively. Loblolly pine stands had been burned, on average, 2 years prior to sampling for both LU plots and LT plots. Pocosin plots were limited in number, and all had a fire frequency of ~4 years, with all fires occurring ~1-2 years prior to sampling. These fire return intervals are considerably shorter than those of historical pocosin fire regimes (40-60 year return intervals, Christensen, 1981; Christensen, 2000). Thus, recent fire regimes in pocosin systems may be driven by an impetus for fuels and fire hazard management.

Soil Sampling

A uniform sample of the top 0–10 cm of mineral soil (soil beneath layers of litter and duff) was collected using a 5-cm diameter piston corer at each of four points located 10 m from the center point of each 0.1 ha plot. Each soil sample was subsequently analyzed by Brookside Laboratories (New Knoxville, OH). Soil pH was measured using a glass electrode in a 1:1 slurry of soil and distilled water (McLean, 1982). Percent soil organic matter (SOM) was determined by weight loss after ignition at 360°C. Aluminum (Al), boron (B), calcium (Ca), copper (Cu), iron (Fe), phosphorus (P), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), sulfur (S), and zinc (Zn) were extracted according to (Mehlich, 1984) and concentrations were determined using plasma-emission spectroscopy. P concentrations in the Mehlich extract were measured colorimetrically. Cation exchange capacity (CEC) was measured by summation of all cations as mEq/100 grams of soil (Ross, 1995). Percent hydrogen (%H) was estimated based on the fraction of total CEC not occupied by the metallic cations listed above. Thus, %H is inversely correlated with percent exchangeable bases.

Statistical Analyses

We tested for significant differences in herb-layer plant composition among these five stand types using a Multi-Response Permutation Procedure (MRPP, see Mielke and Berry (2007)). MRPP is a nonparametric procedure for testing the hypothesis of no difference between two or more groups of

entities. As such, MRPP was used to examine the magnitude of the differences in community composition between these five stand types. MRPP calculates the statistic A, a descriptor of within-group homogeneity compared to the random expectation. This is known as chance-corrected within-group agreement. Values for A are commonly below 0.1, even when the observed delta differs significantly from the expected, while an $A > 0.3$ is considered rather high (McCune and Grace, 2002). Of particular interest to our study were differences between longleaf pine stands and loblolly pine stands with mid-story removal treatments.

Non-metric multidimensional scaling (NMS) ordination (Kruskal, 1964) was used to analyze trends in species composition among plots. NMS analyses were carried out using the Sørensen dissimilarity metric for 1,000 iterations and a stability criterion of 0.00001. Only species occurring in 3 or more of our 0.1 ha study sites were included in the ordinations. To account for covariation among soil properties, we conducted a Principle Components Analysis (PCA) of soil organic matter, soil bulk density, and soil nutrient concentrations (Peet *et al.*, 2014). To ensure that the soil data conformed to a multivariate normal distribution prior to PCA, we conducted a Mardia test (Mardia, 1970) for multivariate normality using the MVN statistical package (Korkmaz *et al.*, 2014) in R software. Bulk density and pH did not require any data transformation to meet assumptions for multivariate normality, while soil nutrient data needed log transformations for P, Ca, K, Na, and B. Other soil nutrients were not amenable the assumptions of multivariate normality following log transformation and were thus excluded from the PCA. We regressed NMS axes against the PCA axes to ascertain the relationship between soil properties and the composition of herb-layer vegetation. Additionally, to separate the respective contributions of soil properties and disturbance history (i.e. fire frequency, and time since most recent fire), we utilized the variance partitioning function from the vegan statistical package in R software (Dixon and Palmer, 2003) to ascertain the unique contributions of soil properties (PCA Axes 1 and 2) vs. those of disturbance history in determining plant composition as represented by NMS analysis.

Finally, upon confirming statistically significant differences in our five stand types through the MRPP analysis, we performed an Indicator Species Analysis (ISA, Dufrêne and Legendre (1997)). ISA

generates an indicator value for species ranging from 0 to 100. A maximum value of 100 is achieved when all individuals of a taxon occur at all sites of a single pre-defined group and no other sites. The significance of the indicator value for each species was generated with a Monte Carlo randomization procedure with 9999 permutations. Of particular interest is whether more species showed an apparent preference for treated over untreated loblolly pine stands and how indicative species vary between loblolly stands and fire-maintained longleaf pine stands, as well as how soil properties are associated with the fidelity of certain species. Thus, ISA was conducted for two types of grouping variables. First, we used our five stand types [Dry Pine/Oak Savanna (DPOS), Wet Pine Savanna (WPS), Loblolly Unthinned (LU), Loblolly Thinned (LT), and High Pocosin (HPO)] as categorical variables. Additionally, we conducted ISA on soil PCA scores for PCA axes 1 and 2. Scores were grouped into positive (+) and negative (-) PCA score values for both axes. All analyses (MRPP, NMS, and ISA) were performed using PC-ORD software version 6.247 Beta (McCune and Mefford, 2002).

Results and Discussion

Soil Variability and Plant Composition

MRPP pairwise comparisons indicated that each stand type (DPOS, WPS, LU, LT, and HP) was significantly different from all other groups. Within group agreement values (A) for most comparisons were > 0.1 , indicative of significant differences between most groups (Table 2). Lower values of A for DPOS vs HP, LU vs LT, and LT vs HPO are probably due to the smaller sample sizes of the LU and HPO groups (McCune and Grace 2002). Differences among our community groups/stand types can be seen in the 2-D plot of our NMS ordination (stress = 16.41, instability < 0.00001 after 67 iterations), even though variation within community groups and overlap among groups is generally high (Figure 1). However, much of this variation can be explained by soil properties. Means and ranges for soil variables in each community group are displayed in Table 3, with soil variable eigenvectors for PCA axes 1 and 2 shown in Table 4. Soil PCA Axis 1 explained 40.8% of the variation in the soil data matrix, while soil PCA Axis 2 explained an additional 24.2%. PCA Axis 1 was highly correlated with bulk density (BD), K, and Na.

While there was considerable overlap in group ranges (Table 3), the high correlation of bulk density with PCA axis 1 was very clearly related to the gradient of soil moisture conditions from sandy, well drained DPOS sites to moister, more poorly drained WPS sites, to very wet HPO sites. Thus, soil properties related to soil moisture conditions were strongly correlated with vegetation composition, evidenced by a very strong relationship between soil PCA Axis 1 and NMS Axis 1 ($R^2 = 0.57$, $p < 0.01$, Figure 2). In general, Dry Pine-Oak Savanna (DPOS) stands had the highest NMS Axis 1 scores, followed by Wet Pine Savannas (WPS), while High Pocosin (HPO) stands had the lowest NMS Axis 1 scores; mean Axis 1 scores for Loblolly-Unthinned (LU) and Loblolly-Thinned (LT) fell between those for WPS and HPO (Table 5).

PCA axis 2 was highly correlated with $\text{PO}_4\text{-P}$, pH, and B, and was moderately correlated with Ca (Table 4). We found a moderately strong relationship between PCA Axis 2 and NMS Axis 2 ($R^2 = 0.30$, $p < 0.01$, Figure 2). One potential explanation for the relationship between PCA axis 2 and NMS Axis 2 is the variation in soil properties that often results from historic applications of phosphate fertilizer and lime on former agricultural lands, many of which later transition to loblolly pine stands. The effects of such additions can persist for years. Richter *et al.* (2006) examined the long-term soil chemistry of a loblolly pine forest with a history of fertilization and found evidence for a resupplying of the most labile fractions of soil P from release of organic and inorganic P associated with Fe and Al oxides and Ca compounds. Our findings are somewhat consistent with a scenario in which the previous fertilization and liming of agricultural land may have facilitated a slow release of P associated with Ca. Stands with high values for the 2nd PCA Axis were strongly dominated by the LU and LT groups, which had mean $\text{PO}_4\text{-P}$ values of 7.01 and 6.38 $\mu\text{g/g}$ compared to 3.80, 2.88, and 3.40 $\mu\text{g/g}$ for DPOS, WPS, and HPO. LU and LT groups had higher Ca as well, at 229.21 and 288.64 $\mu\text{g/g}$, compared to 186.86, 143.54, and 157.00 $\mu\text{g/g}$ for DPOS, WPS, and HPO (Table 3). However, we cannot confirm a legacy effect of fertilization without long-term soil records.

To ascertain the relative contributions of soil properties and disturbance history on the first NMS axis of plant composition, we conducted a variance partitioning of soil PCA Axis 1, fire frequency, and time since most recent fire. Soil PCA Axis 1 was highly correlated with NMS Axis 1 (discussed above, and see Figure 2) and our variance partitioning found that soil PCA Axis 1 uniquely explained 43% of the variation in NMS Axis 1, while fire frequency uniquely explained only 2% and time since most recent fire uniquely explained 0%. Thus, fire frequency, while correlated with the 1st NMS axis of plant composition ($R^2 = 0.17$, $p < 0.01$), did not uniquely explain a significant proportion of the variation of it, suggesting that soil properties have a much stronger relationship with plant community composition than fire frequency. Similarly, for NMS Axis 2, we conducted a variance partitioning of soil PCA Axis 2, fire frequency, and time since most recent fire. PCA Axis 2 uniquely explained 30% of the variation in NMS Axis 2, while both fire frequency and time since most recent fire uniquely explained 0%. However, it would be highly premature to suggest that fire frequency does not have a significant influence on plant community composition. Instead, the relationship between fire frequency and vegetation may be manifested, in part, through the relationship of fire frequency on soil properties, whereby frequent fires reduce the accumulation of soil organic matter. Fire frequency did have a slightly positive correlation to PCA Axis 1 ($R^2 = 0.12$, $p < 0.01$) of soil properties. However, such a relationship may also reflect a propensity by forest managers to conduct prescribed fires more frequently in stands that are low in soil organic matter accumulation to begin with.

Indicator Species Analysis by Stand Type

Indicator Species Analysis using five stand types as categorical variables revealed 53 species with a statistically significant association ($p < 0.05$) with a particular group (Table 6). Of these, 23 were significant indicators for the DPOS group (e.g. *Aristida stricta*, *Vaccinium tenellum*), 16 for the WPS group (e.g. *Rhexia alifanus*, *Pteridium aquilinum*), 4 for the LT group (e.g. *Acer rubrum*, *Liquidambar styraciflua*), and 9 for the HPO group (e.g. *Gordonia laisianthus*, *Lyonia lucida*). No species was a significant indicator for the LU group by itself. It should be noted that 3 of the 4 LT indicators were

seedlings of *Acer rubrum*, *Pinus taeda*, and *Liquidambar styraciflua*. All three are shade intolerant, and their importance in these thinned stands undoubtedly reflects higher irradiance at the forest floor. Thus, species that are indicative of loblolly pine are all indicators of disturbance via midstory removal. By contrast, several herbaceous layer species were associated with the HPO group (e.g. *Rhychospora plumosa*, *Desmodium spp*, *Rhexia mariana*, and *Carphephorus paniculatus*).

Indicator Species Analysis by Soil Properties

The Indicator Species Analysis using positive (+) and negative (-) PCA axis score groups from the 1st and 2nd PCA axes found 54 species that exhibited a statistically significant association ($p < 0.05$) for at least 1 soil PCA axis group, with 19 species showing a statistically significant association for both the 1st and 2nd soil PCA axis groups. Our ISA found 28 species with that were significantly associated with the positive soil PCA Axis 1 group, which were primarily soils with high bulk density and low soil organic matter generally associated with longleaf pine stands (Table 7). Conversely, we found 10 species associated with the negative PCA Axis 1 group, which were primarily soils with low bulk density and high soil organic matter, typical of loblolly pine stands. Soil PCA Axis 2 values were associated with a PO₄-P gradient more than anything else (Table 4), with positive values associated with high PO₄-P availability, and negative values associated with low PO₄-P availability. We found 17 species that were significantly associated with the positive soil PCA axis 2 value group, and 18 species that were significantly associated with the negative soil PCA axis 2 value group (Table 7). Thus, soil properties can exert considerable influence on species associations in these ecosystems.

Herb-Layer Coverage and Species Richness

Mean values for species richness (#/0.1ha, min-max) for both DPOS (44.5, 24-72) and WPS (57.4, 25-118) groups were significantly higher than the LU (22.5, 7-48), LT (26.1, 13-41), and HPO (18.2, 9-29) groups based on ANOVA and multiple range comparisons ($p < 0.01$). Hedman *et al.* (2000) compared longleaf and loblolly pine stands and likewise found higher levels of species richness among (35, 25-95) longleaf pine. Although mean species richness was higher in the WPS than the DPOS

community group, the difference was not statistically significant ($p > 0.074$). Nevertheless, 7 WPS stands supported more than 75 species/0.1ha, whereas no DPOS stands had more than 72 species. There were no significant differences in species richness among the LU, LT and HPO groups. Species richness was positively correlated with both PCA axis 1 and NMS axis 1 (Figure 3). However, species richness in stands with the very highest scores was generally lower than would be predicted by a simple linear regression line, and the highest species richness scores were observed in stands with high-intermediate PCA and NMS axis 1 scores (i.e., WPS).

Mean herb-layer cover (% , min-max) was about two times higher in the DPOS (89.2%, 30.9-170.6), WPS (90.0%, 27.5-148.7), and HPO (116.8%, 99.1-133.6) groups compared to the LU (33.9%, 7.1-67.1) and LT (45.2%, 11.2-84.5) groups ($p < 0.01$). Others have also found noted higher herb-layer coverage among longleaf pine stands compared to loblolly pine stands, with longleaf pine stands exhibiting 45% more coverage (Hedman *et al.*, 2000). The herb layer in the HPO stands was predominantly low woody shrubs, whereas herbaceous species comprised the majority of DPOS and WPS group herb layer cover. No significant difference in herb layer cover between LU and LT groups was evident 12-18 months after thinning treatments.

Restoration Implications

Overall, our results suggest that a utilization of loblolly pine stands as surrogate sites for the restoration of longleaf pine vegetation remains an uncertain endeavor that will be highly constrained by site characteristics and disturbance history. Soil properties, particularly bulk density (BD), were highly correlated with plant community composition, whereby high SOM and low BD were not characteristic soil conditions of fire-maintained longleaf pine woodlands (Cohen *et al.*, 2004; Walker and Silletti, 2006). While other studies have examined the relationship between soil properties and herb-layer species composition, our work is in contrast to many previous case studies of longleaf pine restoration focused on the restoration of longleaf stands in which SOM content is already low. Studies of restoration in fire-suppressed longleaf pine stands in northern Florida, USA (Eglin Air Force Base) are primarily

concentrated on longleaf stands on xeric soils with high bulk density and low SOM (<0.9%). Kirkman *et al.* (2013) examined the long-term (15 year) response of herb-layer vegetation in fire-suppressed longleaf pine to midstory treatments with frequent (every 3 year) post-treatment prescribed fires and found that treated stands showed a positive restoration trajectory of the herbaceous layer toward that of longleaf pine woodlands (Rodgers and Provencher, 1999; Kirkman *et al.*, 2013).

The restoration of longleaf pine woodlands has not been limited to mature longleaf stands; conversion of abandoned agricultural land to longleaf pine woodlands has also taken place in sites that likewise have low (~1%) SOM (Markewitz *et al.*, 2002). Furthermore, the vegetation associated with fire-maintained longleaf pine stands is not limited to soils with high bulk density and low (~1%) SOM content. Other sites occurring in a more mesic environment, such as longleaf pine-depressional wetland landscapes, have higher (~6%) SOM in the upper portion of the soil profile (Craft and Chiang, 2002). Higher SOM content can also be found in mixed loblolly-longleaf pine forests, with as much as 8-11% SOM in the upper (0-10 cm) portion of the soil profile (Binkley *et al.*, 1992). Median SOM content among longleaf pine stands was rather low at ~4%, although it was considerably higher in some stands. Sites with 10-18% SOM still contained many of the species that are highly correlative of fire-maintained longleaf pine woodlands, including (*Aristida stricta*), creeping blueberry (*Vaccinium crassifolium*), and dwarf huckleberry (*Gaylussacia dumosa*, Table 6). Thus, while it appears that efforts to restore the herb-layer of longleaf pine woodlands are more likely to succeed on sites in which there is minimal SOM accumulation (<15%), a successful restoration of vegetation in our study sites remains uncertain and many require many years of monitoring before the effectiveness of restoration treatments can be fully ascertained.

Re-introduction of fire to the landscape is essential to ongoing restoration efforts, and the effects of a re-introduction of fire can take many years to become apparent. Frequent burning (every 2-3 years) can discourage the post-treatment sprouting and growth of trees and shrubs (Brockway *et al.*, 2009; Outcalt and Brockway, 2010) while reducing the risks of high severity fire propagation via mid-story ladder fuels (Agee and Skinner, 2005; Brockway *et al.*, 2009). Frequent burning can also facilitate the

recolonization of the vegetation found in longleaf pine woodlands. Grasses such as *Aristida stricta* and *Andropogon spp.* are sensitive to duff accumulation and can increase in coverage following the combustion of duff materials (Hiers *et al.*, 2007), but their post-fire recovery is not immediate. Outcalt and Brockway (2010) examined a xeric longleaf pine forest in Alabama with a history of fire suppression to ascertain the response of herb-layer vegetation to burning and thinning treatments. While grass species cover shortly after prescribed fire was minimal, after 3 years they observed an increase in grass species on the burned, thinned, and burned + thinned plots, with the largest gains in the burned + thinned plots. After 6 years following the initial restoration treatments, the thinning without burning treatment had 14% grass coverage, while all of the treatments that included burning had approximately 30% more grass coverage than when the study sites were first treated. Thus, some of the more tangible effects of restoration treatments may require several years to become apparent.

Summary

On the lower coastal plain of North Carolina, loblolly pine grows on a wide variety of soil moisture conditions. Attempts to restore understory composition and species richness typical of longleaf pine savannas should be focused on the subset of loblolly pine stands on the mesic to xeric portion of that soil moisture gradient. Historical legacies of past agriculture such as higher concentrations of calcium and phosphate are evident in some loblolly soils and their potential effect on restoration should also be evaluated (Brudvig *et al.*, 2013). As might be expected from the apparent habitat preferences exhibited by many plant species, all five of our stand types (DPOS, WPS, LT, LU, and HPO) exhibited statistically significant differences from each other as indicated by the MRPP analysis. However, there was some apparent overlap between longleaf and loblolly pine stands with similar levels of SOM. An overlap in herb-layer composition of longleaf and loblolly pine stands may suggest some potential for restoring longleaf pine vegetation in loblolly pine stands.

While the long-term success of implementing restoration treatments in loblolly pine stands remains uncertain, our analysis suggests that the application of mid-story thinning restoration treatments

to loblolly stands is more likely to shift the composition of herbaceous plant communities toward that of longleaf pine woodlands when performed on sites with low (i.e. < 15%) amounts of SOM. Forests that have only recently accumulated marginal amounts of SOM as a direct result of fire suppression may be potential candidates for the restoration of the plant communities native to longleaf pine woodlands (Kirkman *et al.*, 2013), as many such forests may still have viable seed banks. Stands that are in close proximity to high-quality longleaf pine stands may also warrant additional consideration for having the additional benefit of seed availability. With midstory thinning and the reintroduction of fire, herb composition and diversity in longleaf stands with a history of fire suppression show definite restoration progress in 5-10 years (Outcalt and Brockway 2010, Kirkman *et al.* 2013). Given the legacy of land use that has removed much of the presettlement flora and its seedbank, and the buildup of duff and soil organic matter associated with fire suppression, restoration in loblolly pine stands will likely take much longer.

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Table 1. Mean values of fire frequency and time since most recent fire for each community group. Ranges are shown in parentheses. Values of 0.5 are given for all fires occurring during the year of sampling, but prior to the actual sampling.

	Mixed Pine/Oak Savanna	Wet Pine Savanna	Loblolly Unthinned	Loblolly Thinned	High Pocosin
Abbreviation	DPOS	WPS	LU	LT	HPO
Number of Sites	N=23	N=23	N=9	N=16	N=4
MFRI (1995-2010)	3.12 (1.36-14)	3.53 (1.56-20)	8.30 (1.36-20)	9.43 (3-20)	4 (4)
Time since most recent fire	2.43 (0.5-8.5)	2.15 (0.5-8.5)	1.89 (0.5-8.5)	1.81 (0.5-8.5)	2.25 (1.5-2.5)

Table 2. Results of pairwise comparisons from MRPP analysis. Values for A are commonly below 0.1, even when the observed delta differs significantly from the expected (McCune and Grace, 2002). An A > 0.3 is fairly high.

Pairwise Comparisons	T-Value	A	p <
DPOS vs WPS	-11.823	0.156	0.00001
DPOS vs LU	-19.184	0.153	0.00001
DPOS vs LT	-13.097	0.127	0.00001
DPOS vs HPO	-4.031	0.022	0.004
WPS vs LU	-8.258	0.127	0.00001
WPS vs LT	-3.294	0.109	0.02
WPS vs HPO	-10.201	0.118	0.00001
LU vs LT	-2.620	0.029	0.02
LU vs HPO	-15.314	0.103	0.00001
LT vs HPO	-10.847	0.091	0.00001

Table 3. Mean values of soil variables for each community group. Ranges are shown in parentheses. Statistically significant differences ($P < 0.05$) among groups (as determined by ANOVA and Duncan's Multiple Range Tests) are indicated by letter superscripts.

	Dry Pine/Oak Savanna	Wet Pine Savanna	Loblolly Unthinned	Loblolly Thinned	High Pocosin
Abbreviation	DPOS	WPS	LU	LT	HPO
Number of Sites	N=23	N=23	N=9	N=16	N=4
BD (g/cm ³)	1.16 (0.63-1.40) ^a	1.16 (0.81-1.40) ^a	0.63 (0.18-1.09) ^b	0.63 (0.31-0.98) ^b	0.70 (0.30-1.10) ^{ab}
pH	4.39 (3.8-4.9)	4.14 (3.8-4.6)	4.12 (3.63-4.55)	4.05 (3.83-4.68)	4.50 (3.9-5.1)
CEC (mEq/100g)	4.24 (2.0-6.1) ^a	4.09 (2.3-9.5) ^a	6.86 (3.26-10.42) ^b	8.11 (5.69-11.48) ^b	4.37 (2.4-6.3) ^a
SOM (%)	3.52 (1.45-12.7) ^a	4.17 (0.97-10.6) ^a	30.40 (2.85-85.45) ^b	25.04 (5.92-68.34) ^b	18.66 (2.7-55.8) ^b
PO ₄ -P (μg/g)	3.8 (1.0-8.0) ^a	2.88 (1.0-7.0) ^a	7.01 (3.0-13.0) ^b	6.38 (2.5-11.5) ^b	3.40 (2.8-3.8) ^a
Ca (μg/g)	186.86 (117.7-286.8) ^a	143.54 (54.9-276.3) ^a	229.21 (54.9-595.0) ^b	288.64 (170.5-518.3) ^b	157.00 (103.3-190.5) ^a
Mg (μg/g)	34.27 (16.3-65.5)	30.45 (15.0-65.8) ^a	59.78 (24.0-114.0)	61.63 (42.3-94.0)	63.95 (38.8-127.0)
K (μg/g)	21.82 (11.5-54.8)	20.06 (9.0-37.8)	41.97 (18.25-87.75)	37.27 (23.5-63.0)	21.50 (15.3-31.5)
Na (μg/g)	25.39 (15.5-38.3)	25.40 (17.8-46.3)	37.22 (20.25-67.75)	31.66 (21.3-52.5)	32.55 (26.5-37.0)
B (μg/g)	0.17 (0.1-0.37)	0.17 (0.1-0.49)	0.26 (0.15-0.38)	0.24 (0.15-0.35)	0.14 (0.1-0.30)
Fe (μg/g)	53.75 (27.0-188.3)	119.04 (21.8-382.5)	107.83 (38.0-204.3)	114.41 (29.3-232.8)	46.40 (22.3-82.3)
Mn (μg/g)	4.88 (0.8-11.3)	2.06 (0.8-6.8)	1.76 (0.9-4.0)	2.35 (1.1-4.5)	1.82 (0.8-3.5)
Cu (μg/g)	0.48 (0.16-0.91)	0.77 (0.27-1.72)	0.72 (0.41-1.22)	0.67 (0.35-1.93)	0.37 (0.28-0.56)
Zn (μg/g)	1.03(0.58-1.93)	1.26 (0.46-4.49)	1.29 (0.66-2.90)	2.16 (0.62-12.12)	0.69 (0.51-0.92)
Al (μg/g)	151.07 (69.5-401.5) ^a	298.50 (52.5-798.0) ^a	568.27 (121.5-1211.5) ^b	483.77 (113.75-1003.5) ^a	185.25 (110.0-274.5) ^b

Table 4. Soil variable eigenvectors for PCA axes 1 and 2, each scaled to its standard deviation. Scaled in this manner, eigenvectors are equivalent to the correlation coefficients between stand PCA scores and the values for each soil variable for each sample area. PCA axes 1 and 2 account for 40.8% and 24.2% of the total multivariate variance. Shaded values are significant at the $P < 0.001$ level.

BD	-0.856	0.0748
pH	-0.4382	0.6167
PO ₄ -P	0.4247	0.7527
Ca	0.4625	0.473
K	0.8705	-0.1414
Na	0.808	-0.3654
B	0.354	0.6051

Table 5. Mean NMS Axis 1 and Axis 2 scores for five community groups. Ranges are indicated in parentheses.

	Dry Pine/Oak Savanna	Wet Pine Savanna	Loblolly Unthinned	Loblolly Thinned	High Pocosin
Abbreviation	DPOS	WPS	LU	LT	HPO
Number of Sites	N=23	N=23	N=9	N=16	N=4
NMS axis 1 score	0.733 (-0.633 – 1.235)	0.378 (-0.719 – 1.049)	-0.902 (-1.532 – -0.0736)	-0.8214 (-1.39 – -0.190)	-1.073 (-1.455 – -0.628)
NMS axis 2 score	0.011 (-0.500 – 0.665)	0.247 (-0.334 – 0.968)	-0.407 (-1.534 – 0.642)	-0.369 (-1.214 – 0.400)	0.911 (0.711 – 1.101)

Table 6. Results from indicator species analysis with stand as the categorical variables. Species are listed in order of decreasing indicator value (% of perfect indication). No species was found to exhibit preference for Loblolly--Unthinned.

Species	ISA Value	p
Dry Pine/Oak Savanna		
<i>Quercus laevis</i>	66	0.002
<i>Quercus incana</i>	60.4	0.0026
<i>Aristida stricta</i>	59	0.0002
<i>Gaylussacia dumosa</i>	59	0.0068
<i>Pinus palustris</i>	47.4	0.0068
<i>Vaccinium tenellum</i>	46.9	0.0112
<i>Toxicodendron pubescens</i>	46.7	0.0056
<i>Liatris [pilosa + virgata]</i>	46.6	0.0144
<i>Cnidoscolus stimulosus</i>	42.9	0.013
<i>Andropogon spp</i>	42.7	0.0264
<i>Pityopsis graminifolia</i>	41.4	0.0304
<i>Sericocarpus tortifolius</i>	40.1	0.0112
<i>Carphephorus bellidifolius</i>	39.6	0.0214
<i>Diospyros virginiana</i>	38.5	0.0298
<i>Rhus copallina</i>	38.5	0.0338
<i>Ionactis linariifolius</i>	35.4	0.0292
<i>Tragia urens</i>	31.7	0.0466
<i>Morella pumila</i>	31.5	0.0436
<i>Quercus hemisphaerica</i>	29.7	0.0372
<i>Euphorbia ipecacuanhae</i>	29	0.0404
<i>Scleria nitida</i>	27.1	0.0412
<i>Chrysopsis gossypina</i>	24.5	0.0344
<i>Cirsium vulgare</i>	17.4	0.0332
Wet Pine Savanna		
<i>Rhexia alifanus</i>	56.8	0.0096
<i>Pteridium aquilinum</i>	56.2	0.0172
<i>Xyris caroliniana</i>	48	0.0108
<i>Lachnocaulon anceps</i>	45.9	0.0092
<i>Lyonia mariana</i>	45.6	0.0132
<i>Carphephorus odoratissimus</i>	43.7	0.0138
<i>Pinus serotina</i>	40.5	0.0386
<i>Lobelia nuttallii</i>	36	0.0242
<i>Pterocaulon pycnostachyum</i>	33.4	0.0494
<i>Gymnopogon brevifolius</i>	30.4	0.0326
<i>Hypericum crux-andreae</i>	26.4	0.0416

Table 6 (Continued)

<i>Species</i>	ISA Value	p-value
Wet Pine Savanna (cont.)		
<i>Woodwardia virginica</i>	26	0.0348
<i>Desmodium tenuifolium</i>	25.5	0.0464
<i>Eupatorium pilosum</i>	25.3	0.043
<i>Carphephorus tomentosus</i>	23	0.0482
<i>Ludwigia virgata</i>	21.7	0.0374
High Pocosin		
<i>Rhynchospora plumosa</i>	94.2	0.0002
<i>Gordonia lasianthus</i>	91	0.0002
<i>Desmodium spp.</i>	90.8	0.0002
<i>Zenobia pulverulenta</i>	75	0.0006
<i>Ilex coriacea</i>	70.1	0.003
<i>Lyonia lucida</i>	66.1	0.0006
<i>Magnolia virginiana</i>	62	0.0062
<i>Rhexia mariana</i>	61	0.0006
<i>Carphephorus paniculatus</i>	21.2	0.0398
Successional Loblolly-Thinned		
<i>Acer rubrum</i>	72.4	0.0006
<i>Pinus taeda</i>	60.1	0.0014
<i>Smilax laurifolia</i>	41.9	0.0376
<i>Liquidambar styraciflua</i>	41.8	0.0344

Table 7. [See attachments]**Figures 1-3** [See attachments]

Species	PCA Axis 1 Group	ISA Value	Mean	StDev	<i>p</i>	PCA Axis 2 Group	ISA Value	Mean	StDev	<i>p</i>
<i>Acer rubrum</i>	-	74.6	27.4	5.83	0.0001	-	36.5	27.2	5.73	0.0797
<i>Andropogon spp</i>	+	65	43.4	5.24	0.0013	+	37.4	43.4	5.13	0.9212
<i>Aristida stricta</i>	+	70.7	34.9	4.56	0.0001	+	45.5	34.9	4.47	0.0277
<i>Arundinaria tecta</i>	+	18.9	26.6	6.69	0.9054	-	55.3	26.4	6.58	0.0001
<i>Aster spp.</i>	+	3.1	5.9	2.44	0.9096	-	12.1	6	2.46	0.0363
<i>Cnidoscolus stimulosus</i>	+	36.3	20.3	4.61	0.0054	+	24	20.1	4.42	0.1852
<i>Carphephorus bellidifolius</i>	+	37.2	20.2	4.59	0.0046	+	35	20.1	4.46	0.0075
<i>Carphephorus odoratissimus</i>	+	63.5	32.9	5.08	0.0002	+	47.6	32.8	5	0.013
<i>Carphephorus tomentosus</i>	+	17.4	9.8	3.38	0.0376	-	9.8	9.7	3.43	0.4609
<i>Carex spp.</i>	-	8.5	5.6	2.24	0.2965	-	12.1	5.5	2.3	0.0332
<i>Dichanthelium mattamuskeetense</i>	+	3.5	8.3	3.07	0.9709	-	15	8.3	3.08	0.0316
<i>Dichanthelium portoricense</i>	+	14.5	10.9	3.59	0.1764	+	23.8	10.8	3.48	0.003
<i>Dichanthelium spp.</i>	-	26.3	24.3	5.07	0.2941	-	56.6	24.2	4.94	0.0001
<i>Diospyros virginiana</i>	+	47.4	28.4	5.23	0.0036	+	34.9	28.2	5.05	0.1148
<i>Eupatorium capillifolium</i>	-	16.1	12.9	4.14	0.212	-	21.6	12.9	4.06	0.0441
<i>Euphorbia ipecacuanhae</i>	+	13.1	10.8	3.54	0.2333	+	21	10.6	3.41	0.0122
<i>Gaylussacia dumosa</i>	+	73.8	35.7	6.01	0.0001	+	52.1	35.6	5.93	0.0134
<i>Gaylussacia frondosa</i>	+	62.7	48.2	5.24	0.013	-	49.5	48	5.19	0.3264
<i>Gentiana autumnalis</i>	+	23.9	12.2	3.98	0.0115	+	16.6	12.2	3.9	0.1712
<i>Hypericum tenuifolium</i>	+	41.4	21	4.72	0.0025	-	15.7	20.9	4.64	0.9441
<i>Ilex opaca</i>	-	32.6	24.3	5.16	0.081	-	39.2	24.1	5.06	0.0131
<i>Iris verna</i>	+	52.7	31	4.66	0.0009	+	54.2	31	4.66	0.0007
<i>Kalmia carolina</i>	+	29.3	15.5	4.54	0.0102	-	21.3	15.4	4.36	0.1081
<i>Liatris [pilosa + virgata]</i>	+	51.8	27.3	5.26	0.001	+	41.6	27.2	5.12	0.0128
<i>Liquidambar styraciflua</i>	-	45.1	30.1	5.99	0.0212	-	52.6	29.8	5.82	0.0013
<i>Lyonia lucida</i>	-	54.5	32.2	5.63	0.0021	+	37.3	32.1	5.55	0.17
<i>Lyonia mariana</i>	+	36.4	21.2	4.88	0.0088	+	17	21.2	4.8	0.7969
<i>Morella pumila</i>	+	21.1	14.3	4.25	0.0862	+	27.9	14.2	4.13	0.0083

<i>Nyssa sylvatica</i>	-	41.9	27.2	5.68	0.0159	-	49.8	27.1	5.56	0.0007
<i>Osmunda cinnamomea</i>	-	83.5	41.4	8.63	0.0001	-	67.5	41.1	8.71	0.0014
<i>Osmunda regalis</i>	-	15.8	9	3.22	0.0539	-	17.3	8.9	3.23	0.0234
<i>Panicum virgatum</i>	-	21.4	10.2	3.53	0.0081	-	19.3	10.1	3.42	0.0213
<i>Persea palustris</i>	-	77.9	51	6.48	0.0002	-	62.1	50.7	6.32	0.0586
<i>Pinus serotina</i>	+	38.5	27.2	5.67	0.0456	+	39.1	27	5.56	0.0381
<i>Pinus palustris</i>	+	70	36.2	5	0.0001	+	51.6	36.1	4.83	0.0072
<i>Pinus taeda</i>	-	59.5	33.9	5.35	0.0004	-	38.4	33.7	5.17	0.173
<i>Pityopsis graminifolia</i>	+	58	30.2	5.5	0.0005	+	28.3	30.1	5.4	0.548
<i>Pterocaulon pycnostachyum</i>	+	34.5	16.9	4.54	0.0015	+	26.8	16.9	4.44	0.0343
<i>Quercus incana</i>	+	27.4	16.2	4.56	0.0292	+	21.2	16	4.38	0.1341
<i>Quercus laevis</i>	+	43.1	22.2	5.61	0.0013	+	33.9	22.1	5.51	0.0317
<i>Quercus marilandica</i>	+	21	12.6	3.82	0.0455	+	21.2	12.5	3.79	0.0366
<i>Rhynchospora plumosa</i>	+	16.3	14.1	4.37	0.2887	+	28	14.1	4.28	0.0053
<i>Rubus spp.</i>	+	5.8	6	2.42	0.7036	-	12.1	6	2.42	0.0332
<i>Sassafras albidum</i>	+	41.1	26.9	6	0.0207	-	20	26.8	5.96	0.883
<i>Sericocarpus tortifolius</i>	+	48.1	25	4.67	0.0003	+	31.1	24.9	4.57	0.1094
<i>Smilax laurifolia</i>	-	70.8	31	5.6	0.0001	-	47.7	31	5.58	0.0101
<i>Toxicodendron radicans</i>	-	13.5	7.5	2.94	0.0248	-	14.8	7.5	2.94	0.0315
<i>Vaccinium crassifolium</i>	+	59.4	35.2	6.37	0.0019	+	55.9	35.2	6.31	0.004
<i>Vaccinium formosum</i>	+	22.8	33.3	6.67	0.9814	-	46.5	33.2	6.5	0.0315
<i>Vaccinium fuscatum</i>	+	30.8	28	5.27	0.266	-	41.9	27.8	5.17	0.0141
<i>Vaccinium stamineum</i>	+	22.6	13.6	4.16	0.0404	+	28.5	13.5	4.02	0.0038
<i>Vaccinium tenellum</i>	+	68.7	41.5	5.32	0.0002	+	47.5	41.3	5.28	0.1324
<i>Vitis rotundifolia</i>	-	26.9	20.7	5.16	0.1301	-	33.3	20.8	5.01	0.0145
<i>Xyris caroliniana</i>	+	35.2	20.6	4.87	0.0118	+	16.6	20.5	4.81	0.7543

Table 7. Indicator species analysis results for species with a statistically significant association with at least one soil PCA Axis group.

Figure 1

Figure 1. NMS ordination results showing longleaf pine stands tightly clustered on the right side of ordination space. Loblolly pine stands, with and without midstory removal, exhibited a much higher range of compositional variation in ordination space. Our 2-D NMS ordination of plant community composition had a final stress of 16.41 and an instability < 0.00001 after 67 iterations.

Figure 2. NMS axes 1 and 2 plotted against soil PCA Axes 1 and 2, respectively. Points are highlighted by their respective stand type. The soil variables indicative of the PCA axes are displayed in Table 3.

Figure 3. Herb-layer species richness plotted against soil PCA Axis 1 and NMS Axis 1. High pocosin (HPO) study sites had the lowest levels of species richness, while wet pine savanna (WPS) sites had the highest species richness. Some longleaf pine stands had exceptionally high levels of species richness (> 60 species) that weakened the strength of the linear correlation between species richness and PCA Axis 1 and NMS Axis 1.