TECHNICAL REPORT

Biodiversity Variation and Change on a Complex Coastal Plain Landscape:

Causes, Connections, Consequences, and Recommendations for Ecosystem Restoration and Conservation

SERDP Project RC-2245

FEBRUARY 2018

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List of Acronyms

С	unthinned control
cm	centimeter
CVS	Carolina Vegetation Survey
dbh	diameter at breast height (1.5 m)
DCERP	Defense Coastal/Estuarine Research Program
DF	degrees of freedom
DIMS	Data Information and Management System
DoD	U.S. Department of Defense
F	F ratio
ft ² /ac	square feet per acre
ha	hectare
m	meter
m^2	square meter
m²/ha	square meters per hectare
MCBCL	Marine Corps Base Camp Lejeune
NMS	non-metric multi-dimensional scaling
\mathbb{R}^2	R squared
RCW	red-cockaded woodpecker
SERDP	Strategic Environmental Research and Development Program
SOM	soil organic matter
Т	Terrestrial (Module)

Introduction

The Defense Coastal/Estuarine Research Program (DCERP) was a 10-year research and monitoring project designed to support ecosystem-based management on Marine Corps Base Camp Lejeune (MCBCL) in North Carolina, with the overarching objective to maintain MCBCL's natural resources and support the military training mission.

The goal of the Terrestrial Module monitoring activity was to provide a uniform, geographically explicit database for plant species composition and abundance that will serve as the basis for assessing regional and site-specific changes in plant communities (and associated parameters, such as fuel conditions). This activity is also intended to provide MCBCL natural resources managers with a focused set of species and site indicators to facilitate future monitoring by MCBCL that is efficient and relevant to assessing important changes in terrestrial ecosystem health. Because plant species, individually and in groups (e.g., communities or guilds) are high-fidelity indicators of variation in the physical environmental template (e.g., soils, hydrology, site fertility) and the effects of human activities that may affect that template (see Christensen [2000] for a discussion about these relationships), a network of permanent vegetation plots provides a useful barometer of habitat condition. Furthermore, data about species composition are critical to assessing potential changes in the abundance of species of interest, including threatened and endangered species and invasive, non-native species. Spatial and temporal variations in species composition and diversity not only provide important indices of ecosystem health, but they are also often diagnostic of specific environmental effects, such as soil compaction or altered fire regimes. Finally, as the ecosystems' primary producers, the community of plants in any location is the ultimate source of carbon energy and defines the structure of habitat for a diverse array of consuming and decomposing organisms. Therefore, monitoring of plant communities is key to understanding possible local- and landscape-level changes in habitat for species, such as the federally listed red-cockaded woodpecker (RCW; *Picoides borealis*). The foundation data set for such a monitoring program would involve more exhaustive sampling and will include more variables (e.g., species and site measurements) than can practically be used in an operational monitoring program. Therefore, an important objective of this effort was to identify a set of indicator species and relatively easily measured site conditions and develop sampling and analytical protocols that provide a practical and efficient monitoring tool that MCBCL staff can use.

Background

The terrestrial vegetation of North Carolina's lower coastal plain is known for its diversity across a wide range of spatial scales. MCBCL lands capture much of that variation (**Figure 1**). At the landscape scale, geomorphic variations, such as relict dune and estuarine deposits and subtle changes $(\pm 1 \text{ m})$ in elevation of the soil surface relative to the shallow water table, produce remarkable variations in ecosystem structure, composition, and processes. Within a few kilometers of the coast, vegetation composition is heavily influenced by salt aerosol and maritime climatic gradients. In pre-settlement times, inland vegetation varied along a continuum

from shrub bog (pocosin) wetlands on deep peat soils to pine-dominated flatwoods with an understory of shrubs on poorly drained mineral soils and longleaf pine (*Pinus palustris*) savannas on well-drained sands (Christensen, 2000). There was nearly complete turnover of plant species composition from one end of this gradient to the other. Some of these ecosystems display remarkable species richness and high levels of species endemism at very local scales. For example, longleaf pine savannas may support more than 60 vascular plant species per square meter and more than 120 species per hectare (Walker and Peet, 1983).



Figure 1. Vegetation variation across MCBCL is represented here in a non-metric multidimensional scaling (NMS) ordination of plant species composition in 133 permanent sample plots (the dots).

The axes of the ordination represent gradients of change in species composition that correlate with important environmental gradients. Here, the horizontal axis corresponds (left to right) with the gradient from terrestrial forests to coastal ecosystems. On the vertical axis, ecosystems vary from relatively dry (negative values) to mesic and wet soil conditions (positive values). The distance between individual points is directly related to their dissimilarity in species composition.

Ecosystem composition and structure were also heavily influenced by variations in presettlement fire regimes along this gradient. Pocosins typically experience intense, crown-killing fires at return intervals of more than 40 years, whereas longleaf pine savannas are maintained by light surface fires at intervals of 1 to 5 years (Bailey et al., 2007; Christensen, 1981, 1992, and 2000). The relative amounts and distributions of pocosin, flatwood, and savanna ecosystems on pre-settlement landscapes were heavily influenced by the frequency and behavior of fire. Repeated, low severity fires can maintain savanna on very moist soils with relatively high amounts of organic matter. Indeed, it is just these situations that support the highest plant species richness at small (square meter) spatial scales. It is also these sites that support many unique endemic species, including several insectivorous plant species. On all but very well-drained sites, the absence of fire for periods longer than 5 to 6 years results in the invasion of shrubs and a variety of understory trees. This invasion also changes the amounts and distributions of fuels such that subsequent fires are likely to be severe enough to kill and even consume canopy trees.

Post-settlement land use and disturbance have influenced the mosaic of terrestrial ecosystems on lower coastal plain landscapes such as on MCBCL. Except for the wettest and driest sites, forests on much of this landscape were cleared for agriculture during the eighteenth and nineteenth centuries (Crowley, 1996). Longleaf pine savannas that were not cut were heavily managed for naval stores (Early, 2004). Much of this farmland was abandoned in the years after the Civil War and Reconstruction up to World War II; post-abandonment succession generally produced an even-aged overstory of loblolly pine (*Pinus taeda*) with an understory dominated by shrubs and understory trees on all but the driest sites (Christensen, 2000). Fire was not only excluded from these forests, but the successional changes promoted understory vegetation and fuels that are comparatively difficult to burn (Nowacki and Abrams, 2008). From 1940 to 1960, timber companies acquired large tracts of such land and managed them to maintain loblolly pine dominance.

Across the Southeast U.S., this history of land use led to the transformation of more than 95% of the land once dominated by longleaf pine savanna to loblolly pine–dominated flatwoods. Even where longleaf pine remained, fire suppression often led to the invasion of woody understory plants and the loss of endemic plant and animal species. In many places, longleaf pine ecosystems are represented by relatively small and often isolated stands. Today, longleaf stands most commonly occur on relatively dry, well-drained sandy soils. It is important to note that these site conditions are probably a very biased subset of its historic range. Longleaf pine grows well on moister sites and heavier soils, but frequent fire is especially important for its maintenance under these conditions (Christensen, 2000; Wahlenberg, 1946).

Altered fire regimes and habitat loss and fragmentation are the major reasons for the significant number of plant and animal species found in communities dominated by longleaf pine that are currently listed as threatened or endangered under the Endangered Species Act. The RCW is probably most notable among these listed species. These listings, along with general concerns about the loss of longleaf pine habitat, have been the impetus for restoring longleaf pine savannas across its historic range. Indeed, maintenance and restoration of longleaf pine habitat and, hopefully, associated populations of RCWs have been prominent objectives of forest management over much of MCBCL's landscape.

In existing longleaf stands, where fire suppression has resulted in only modest changes in understory structure and composition, re-establishment of frequent, low-severity fire regimes has been, by itself, an effective restoration tool (Walker and Silletti, 2006). Prescribed fires at 3-year return intervals are often considered to be ideal and have historically been the goal at MCBCL.

In longleaf stands, where decades of fire suppression have allowed ingrowth of dense hardwood understories and midstories, restoration requires both mechanical thinning of the midstory and

the re-establishment of appropriate fire regimes (Brockway et al., 2009; Outcalt and Brockway, 2010; Provencher et al., 2001a and b; Steen et al., 2013; Varner et al., 2005; Walker and Silletti, 2006). Such restoration presents two important challenges. 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) because 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).

At MCBCL and other locations across the Southeastern United States, there is great interest in restoring longleaf pine to places now dominated by loblolly pine (Brockway et al., 2009; Knapp et al., 2011; Schwilk et al., 2009). In some areas, restoration has taken the form of clear-cutting, followed by planting of longleaf pine and the eventual reestablishment of an appropriate prescribed fire regime (**Figure 2**). Restoration of mature longleaf pine habitat by using this approach will, of course, require many decades. As an alternative strategy to accelerate habitat restoration, MCBCL staff have implemented



Figure 2. (A). A 50- to 60-year old loblolly stand with typical ingrowth of understory and midstory hardwoods. (B) A former loblolly stand that has been clear-cut and planted with longleaf pine. (C) A 50- to 60-year old loblolly stand shortly after mechanical thinning.

mechanical thinning treatments (HydroAxing) to remove understory and midstory hardwoods (generally stems less than 20 cm in dbh). Here, the short-term goal is to restore an open stand structure and understory fuels similar to longleaf pine savannas. In the longer term, it is hoped that application of frequent prescribed fire, perhaps with planting of longleaf pine and some of its associate species, will eventually restore the longleaf pine ecosystem (for a detailed discussion about restoration targets and protocols, see Walker and Silletti, 2006).

Restoration treatments of this sort are being applied to hundreds of MCBCL acres each year. Variations on this management theme include different seasons (growing and dormant) of mechanical control of the woody understory. Restoration of low-severity, high-frequency fire regimes is a key objective; therefore, the goal is that all thinned areas should receive a late winter or early spring prescribed burn in the following year.

There are, however, several significant challenges to such restoration efforts. First, it is not always clear whether a site is suitable for longleaf pine restoration; loblolly pine now grows across a wide variety of soil site conditions, not all of which once supported longleaf pine. Responses to mechanical thinning across the soil-site gradient have not been studied. Determining site suitability is even more challenging because little is known about the variations in plant species composition among loblolly pine stands and their relationship to such variations among longleaf pine stands on the Atlantic coastal flatlands. Second, most areas that now support loblolly pine have been altered by a long history that includes more than a century of agriculture and/or intensive forest management. Soils have been altered, seedbanks of longleaf pine endemics have been exhausted, and few ecological legacies of longleaf pine ecosystems remain. Third, most areas now dominated by loblolly pine have not been burned for a long time, if at all. The absence of fire has resulted in especially heavy invasion of woody species in the understory and accumulations of litter and SOM.

Conservation and restoration are important goals at MCBCL, but military training is the most important priority for MCBCL terrestrial ecosystems. It is inevitable that anthropogenic disturbance regimes are superimposed on natural regimes that occur across the MCBCL (Demarais et al., 1999). The urbanized areas, and training and testing areas are a mix of heavily disturbed areas with little natural vegetation. Terrestrial training ranges tend to be cleared areas whose vegetative cover differs significantly from the historical cover. However, over most of the installation, the military's mission is consistent with and even depends on the conservation of natural ecosystems and their key ecological processes. Such ecosystems often are important for training because they provide training realism, as well as resilience at landscape scales and critical ecosystem services to the military and its ability to sustainably use these landscapes (Demarais et al., 1999).

Vegetation Composition and Diversity in MCBCL Pine Ecosystems

There are several reasons why assessing the variations in composition and diversity of plants in MCBCL forests was an important priority early in the DCERP project. First, although the compositional variation of undisturbed longleaf forests is well studied, little is known about

the vegetation variation among the disturbed pine forests that are so common at MCBCL and the landscape that surrounds it. Second, a study of forest vegetation provided an opportunity to resample 18 mature longleaf pine stands that were sampled nearly two decades earlier during the Carolina Vegetation Survey (CVS; Peet et al., 1998). This study provided an opportunity to assess changes that might be occurring in these stands that are being managed primarily for RCW conservation. Third, this vegetation assessment provided the opportunity to establish a network of permanent, georeferenced sample sites that provided baseline data for evaluation of future landscape change.

During the 2009 and 2010 growing seasons, 133 permanent vegetation monitoring plots were established in terrestrial ecosystems across MCBCL (Figure 3). Each site was located by geographic information systems, was permanently marked with heavy steel posts, and was subsequently sampled for fuel load, woody and herbaceous vegetation, and soil characteristics. The CVS protocol (Peet et al., 1998) was used at all sites to estimate the relative abundance of all plant species with the 0.1-ha plots. Soil samples (0-10 cm of mineral soil) were also collected and subsequently analyzed for an array of physical and chemical properties, including organic matter content, bulk density, pH, calcium and phosphate. The details of both vegetation and soil sampling and analysis are described by Mitchell et al. (2015). We measured species diversity in terms of richness (the total number of species present in a sample). Species composition refers to identities and relative abundances of the community of species. Of these 133 plots, 93 were dominated by longleaf, loblolly, and/or pond (Pinus serotina) pines, and they are the focus of this section. In these pine-dominated plots, in addition to assessing vegetation and soils, fuels such as logs and woody debris, were measured by size class by using line intercept transects across the plot (e.g., Harmon and Sexton, 1986). Plot locations and all associated data can be retrieved from the DCERP Data Information and Management System (DIMS).



Figure 3. The locations of 133 permanent sample plots across Marine Corps Base Camp Lejeune (MCBCL).

Variation plant species composition among the 93 pine-dominated stands is shown in **Figure 4**. Two different species composition gradients were apparent. The first (NMS Axis 1) was a range related to variations in SOM and bulk density represented by the horizontal (*x*) axis of this ordination. Sites with low Axis 1 scores had organic soils and were dominated by pond pine; sites with high Axis 1 scores had sandy, well-drained soils and were dominated by longleaf pine. The very strong correlation between Axis 1 and SOM can be observed in **Figure 5**. Soil organic matter and bulk density are correlated negatively; when soil organic matter is high, bulk density is low.





The axes of the ordination represent gradients of change in species composition that correlate with important environmental gradients. Here, the horizontal axis corresponds (left to right) with the gradient from moist pond pine–dominated sites with high soil organic matter through mesic sites to longleaf pine stands on well-drained sandy soils. On the vertical axis, ecosystems vary from disturbed (negative values) to undisturbed conditions (positive values). The distances between individual points are directly related to their dissimilarity in species composition.



Figure 5. NMS Axis 1 ordination scores compared with soil organic matter for 93 pinedominated plots.

The vertical (y) axis of this ordination (NMS Axis 2) was correlated with the extent of disturbance. Loblolly pine–dominated stands that had been in various ways disturbed had low y-axis scores; undisturbed stands had high y-axis scores. This difference is probably best illustrated by the relationship between Axis 2 and stand basal area (in square meters per hectare, **Figure 6**). Stands with low NMS Axis 2 scores (<0) had uniformly low pine basal areas (<25 m²/ha, 109 ft²/ac). These stands were also characterized by the presence of weedy herbs and grasses and abundant vines (see below). There was considerable variability in basal area among stands with high Axis 2 scores (>0). The stands with basal areas >40 m²/ha were the most mature longleaf pine stands that also had the highest diversity of plant species (see below).



Figure 6. NMS Axis 2 ordination scores compared with stand basal area for 93 pine-dominated plots.

The plant species that were typical of the extremes of these two NMS axes gradients are presented in **Table 1**. Among these, *Lyonia lucida*, *Gordonia lasianthus*, and *Persea palustris* were most indicative of high organic matter, wet soil conditions (low *x*-axis values). Sites where these species are prevalent are likely poor candidates for longleaf pine restoration. The longer list of species indicative of high *x*-axis values reflects the higher diversity of plants at this end of the gradient. The list of species typical of disturbed sites (low *y*-axis scores) includes several roadside weeds (e.g., *Eupatorium capillifolium*, *Dicanthelium* spp.) and an abundance of vines (e.g., *Vitis*, *Smilax*, *Gelsemium*, *Parthenocissus*). Stands where these species were dominant had relatively few of the indicator species for undisturbed longleaf pine–dominated stands. Restoration of the longleaf pine ecosystem flora on such sites will likely need to include seeding or planting of native species.

Table 1. Species Showing Significant Correlations with Specific Portions of the Pine Stand Ordination (cf. **Figure 4**). Although Site Conditions Cannot Be Inferred Based on a Single Species, Several Species Together Can Be Reliable Indicators of Site Conditions.

Typical Low Axis 1 Score Species (Wet Sites)	Typical High Axis 1 Score Species (Mesic Dry Sites)	Typical Low Axis 2 Score Species (Disturbed Sites)	Typical High Axis 2 Score Species (Undisturbed Sites)
Acer rubrum	Aristida stricta	Acer rubrum	Aristida stricta
Desmodium spp.	Cnidoscolus stimulosus	Carex spp	Asclepias pedicullata
Gordonia lasianthus	Diospyros virginiana	Dicanthelium spr.	Carphephorus bellidifolius
Ilex coriacea	Morella pumila	Eupatorium capillifolium	Carphephorus odoratus
Lvonia lucida	Pinus palustris	Gelsemium sempervirens	Cnidoscolus stimulosus
Nyssa sylvatica	Pityopsis graminifolia	Liquidambar styraciflua	Desmodium tenuifolium
Persea palustris	Quercus hemispherica	Nyssa sylvatica	Dicanthelium ovale
Pinus taeda	Quercus laevis	Osmunda cinnamomea	Euphorbia ipecacuanhae
Rhyncospora plumosa	Quercus marilandica	Panicum virgatum	Gaylusacia dumosa
Smilax laurifolia	Rhus copalina	Parthenocissus quinquefolia	Gentiana autumnalis
Zenobia pulverulenta	Sassafras albida	Rubus spp.	Gymnopodium brevifolius
	Seriocarpus tortifolius	Smilax bona nox	Hieraceum gronovii
	Toxicodendron radicans	Smilax glabra	Ilex glabra
	Tragia urens	Smilax laurifolia	Ionactis linariifolia
	Vaccinium tenellum	Solidago odora	Iris verna
		Vitis rotundifolia	Lespediza virginica
			Liatris pilosa
			Lvonia mariana
			Morella pumila
			Pinus palustris
			Pterocaulon pycnostachyum
			Quercus geminata
			Quercus hemispherica
	8		Quercus laevis
			Scleria nitida
			Seriocarpus tortifolius
			Stylosanthes biflora
			Symphotrichium dumosum
			Symphotrichium walteri
			Tragia urens
			Vaccinium crassifolium
			Vaccinium stamineum
			Vaccinium tenellum
			Xvris caroliniana

Across all 93 pine-dominated plots, vascular plant species richness varies from as few as seven to as many as 118 species per 0.1–ha plot. In general, plant species richness increases with increasing NMS Axis 1 plot scores or lower SOM (**Figure 7**). However, the sites with the highest richness (>60 species/0.1 ha) have NMS Axis 1 scores that are in the upper intermediate range. These sites are also the least disturbed among the longleaf pine stands, occurring in somewhat moister conditions than the plots with the highest NMS Axis 1 scores. Many of these

stands have flourishing RCW colonies, and they receive priority management attention. All sites have been regularly prescribe burned at 3-year intervals over the past two decades. The plots with the highest NMS Axis 1 (lowest SOM) occur on the sandiest, driest sites and are typified by a sparse understory of wiregrass (*Aristida stricta*), turkey oak (*Quercus laevis*), and open areas of bare sand.



Figure 7. NMS Axis 1 ordination scores compared with plant species richness for 93 pinedominated plots.

The relationship between vascular plant species richness and SOM is shown in **Figure 8**. The richest sites occur where SOM is less than 10%. However, within that range of 1% to 10% SOM, there is considerable variation in richness; plots with the lowest richness in this range are mostly dominated by loblolly pine with a dense hardwood understory, have a history of past disturbance, and have not been burned for more than a decade.





Vegetation and Avian Species Composition

Do the composition and diversity of plant species correlate with the composition and diversity of bird species? This is an important question for two reasons. First, if particular groups of plant species correlate with the distribution of important bird species, they may be useful habitat indicators. Second, it is important to establish whether management focused on a particular taxon is detrimental to or supportive of other taxa. Work at MCBCL and elsewhere has firmly established that the healthiest and most robust RCW populations occur in open, savanna-like stands of longleaf pine (e.g., Garcia, 2014; Walters, 1991). Walters also found that site conditions that favor RCWs also support the populations of most avian species. Thus, the RCW is, in the jargon of conservation biology, an excellent umbrella species. Does this same relationship extend to the community of plant species?

Breeding bird censuses were conducted in 45 out of the 93 MCBCL permanent pine plots in spring and early summer 2010 and 2011. Among these plots, there was a very strong and positive correlation between plant and avian species richness (**Figure 9**). This result was similar to that observed by Provencher et al. (2002) in Florida sandhill vegetation. There was also a remarkable similarity in the variation in plant species composition and bird species composition among plots (**Figure 10**), so much so that the soil factors (e.g., SOM, bulk density) that are predictive of plant species composition are equally well correlated with variation in the composition of the bird community. The mechanisms underlying the relationships among soil characteristics and plant and avian species diversity and composition are not well understood. Nevertheless, these results provide strong assurance that management strategies focused on either plants or birds are likely to have favorable outcomes for the entire ecosystem. Certainly, management aimed at restoration of longleaf pine will have favorable consequences for a great variety of plant and bird species.



Figure 9. Plant species richness compared with bird species richness for 45 pine-dominated plots.



Figure 10. Variations in plant and bird species composition among pine-dominated sample plots are represented here in a non-metric multi-dimensional scaling (NMS) ordination of plant species composition in 45 permanent sample plots (the dots).

The axes of the ordination represent gradients of change in species composition that correlate with important environmental gradients. Here, the horizontal axis corresponds (left to right) to the gradient from moist pond pine–dominated sites with high soil organic matter through mesic sites to longleaf pine stands on well drained sandy soils. The distances between individual points are directly related to their dissimilarity in species composition.

Understory and Midstory Thinning in Loblolly Pine Stands

Over the past decade, longleaf pine restoration at MCBCL has focused on the use of understory and midstory thinning (HydroAxing) to produce savanna-like conditions and allow for restoration of historical fire regimes by using prescribed burning. As previously discussed,

such thinning is effective in creating savanna-like conditions in loblolly pine stands. Before this study, however, it had not been determined whether these changes result in changes in species composition similar to that of longleaf pine savannas (the restoration target). Furthermore, it was unclear whether there were any differences between thinning treatments applied during the dormant season and those applied during the growing season. Therefore, a key goal of the DCERP terrestrial studies was to assess the effects of understory and midstory thinning treatments applied during the dormant and growing seasons and prescribed burning in loblolly pine stands aged between 50 and 60 years and located on plant and avifaunal communities. This goal was pursued by using a randomized block design field experiment consisting of eight blocks with three treatments in each block. Individual blocks were located on MCBCL to represent a range of soil site conditions previously described (Figure 11). Treatments included an unthinned control (C), dormant season thinning (D), and growing season thinning (G). All experimental plots (including controls) received a prescribed burning application 6 to 18 months after treatment. It was intended that these plots would receive a prescribed burning application again in 2014 or 2015, but weather and air quality conditions did not meet prescription standards during either year.



Figure 11. The names and location of experimental blocks and treatment plots for Research Project T-1 on MCBCL.

Pre-treatment density of 1–20 cm dbh woody stems averaged 24,440 per hectare and varied from 5,500 to 57,000 per hectare across all treatment blocks (**Table 2**). There was significant within-block variation in pre-treatment stem density, and there was no apparent relationship between pre-treatment stem density and block site characteristics (such as soil wetness conditions). Thinning and prescribed fire reduced the density of 1–20 cm dbh stems by

more than 90% in most plots. This finding was true even for control plots because they had been prescribe burned in either 2010 or 2011 along with the thinned plots. One year after treatment, there were no significant differences in 1–20 cm dbh stem density among blocks (F=0.98, DF=7, P>0.48) due to the differences in their site conditions. However, there were significant differences among treatments (F=47.56, DF=2, P<0.00001). Specifically, stem density was uniformly highest in control plots, lower in dormant season thinning plots, and lowest in growing season thinned plots (**Figure 12**). However, after 5 or 6 years without regular prescribed burning, there were no differences among controls and thinning treatments. The ingrowth of woody stems during this interval was visually obvious (**Figure 13**). These results indicate that, in the short term, growing season thinning may be more effective than dormant season thinning in reducing understory hardwood density, but if thinning treatments are not followed by regular prescribed fire, then the benefits of thinning are quickly lost.

Table 2. Summary of Pre-treatment and Post-treatment 1–20 cm dbh Stem Data for Experimental Plots. Blocks Are Ordered Top to Bottom as High Pocosin (FGE, FGW, and IES), wet mesic (IEN, HA, and MF), and mesic (RBE and RBW).

	Age (year)		Post-treatment	Post-treatment
Block-Treatment	in 2010	Pre-treatment	2010-2011	2016
FGE-C	50	Not applicable	2,660	2,880
FGE-D	50	11,020	920	2,690
FGE-G	50	21,440	150	1,910
FGW-C	50	Not applicable	2,170	2430
FGW-D	50	11,520	790	2,690
FGW-G	50	22,370	160	2,160
IES-C	60	47,260	380	250
IES-D	60	7,390	770	2,160
IES-G	60	11,880	620	7,410
IEN-C	50	57,120	2,070	2,875
IEN-D	50	11,520	1,000	2,440
IEN-G	50	16,670	220	2,980
HA-C	53	28,360	1,430	1,220
HA-D	53	17,100	90	1,490
HA-G	53	9,340	380	1,370
MF-C	63	34,980	2,770	2,140
MF-D	65	73,320	350	2,790
MF-G	65	11,760	570	3,310
RBE-C	60	13,330	2,710	2,550
RBE-D	64	6,830	1,080	1,970
RBE-G	64	10,800	200	2,320
RBW-C	56	11,880	1,280	2,550
RBW-D	56	6,650	1,020	2,920
RBW-G	56	9,710	190	2,320



Figure 12. Post-treatment density of stems 1–20 cm dbh in 2010–2011 (blue) and 2016 (orange). Significant differences (*P*<0.05, Duncan's Multiple Range Test) by the letter in each bar. Bars sharing the same letter are statistically homogeneous.



Figure 13. (A) A typical treatment plot immediately after thinning. (B) The appearance of the same plot in 2016 without prescribed burning for 6 years.

The differences in understory stem density in the absence of prescribed burning have several important ecosystem consequences. For instance, woody sprouts compete with understory herbs for light and other resources, and they change the physical structure of the understory in ways that influence feeding and nesting habitat for birds. Woody sprouts also result in a general increase in the quantity of understory fuel and potentially increase the severity of future fires.

One year after treatment, total plant species richness (number of species per 0.1 ha) ranged from as low as 7 in FGW-C (a pocosin plot), to as high as 52 in RBW-G (a wet-mesic plot). Richness was highest in thinned plots immediately after treatment, although the season when thinning occurred had no significant effect (**Figure 14**). This increase in plant species richness in thinned treatment plots during the growing season after treatment applications and prescribed burning is very likely a consequence of increased light to the understory owing to diminished canopy cover, reduced amounts of litter, and diminished competition from understory shrubs. There were no significant differences among treatments in 2016. Species richness in the thinned plots had returned to levels similar to the unthinned controls, which is also likely a consequence of the absence of a second fire.



Figure 14. Post-treatment understory plant diversity (number of taxa per 0.1 ha) in 2010–2011 (blue) and 2016 (orange).

Significant differences (P<0.05, Duncan's Multiple Range Test) are indicated by the letter in each bar. Bars sharing the same letter are statistically homogeneous. Vertical red lines indicate ±1 standard deviation.

There were no significant differences among treatments in avian species diversity in either 2010–2011 or 2016 (**Figure 15**) However, bird species richness was significantly lower across all treatments and blocks in 2016 compared with 2010–2011. This finding is very likely a direct consequence of changes in plant species composition and vegetation structure such as the increased density of woody stems in the understory caused by the absence of prescribed burns. As observed in our monitoring plots, there was a significant and positive correlation between plant species richness and bird species richness in the year after thinning and prescribed burning; however, without subsequent prescribed fire, that relationship virtually disappeared in the 2016 sample (**Figure 16**).



Figure 15. Post-treatment bird diversity (number of species per plot) in 2010–2011 (blue) and 2016 (orange).

Significant differences (P < 0.05, Duncan's Multiple Range Test) by the letter in each bar. Bars sharing the same letter are statistically homogeneous. Vertical red lines indicate ± 1 standard deviation.





Blue points represent 2010–2011 samples; orange dots represent 2016 samples.

Compositional variation in the community of plants among treatment plots, based on NMS ordination, is presented in **Figure 17**. Each arrow in this ordination represents a change from 2010 to 2016 in a single treatment plot. Treatment blocks are arrayed as a continuum from high pocosin with low Axes 1 and 2 scores to wet mesic with intermediate Axes 1 and 2 scores and mesic plots with high Axes 1 and 2 scores. This gradient also correlates with plant species richness, which increases from high pocosin stands to mesic stands ($R^2=0.65$, P<0.0001, multiple regression species richness versus Axes 1 and 2). Based on NMS scores, understory composition of thinned stands is generally more similar to that of high diversity longleaf pine savannas than their respective controls. However, there were no obvious differences between plots that were thinned in the dormant season versus the growing season. These trends are absent among 2016 NMS scores. Indeed, high pocosin and wet mesic plot 2016 NMS scores are uniformly less similar to the longleaf pine restoration target when compared with 2010. It is very likely that this shift in understory plant species composition away from restoration goals is a direct consequence of the absence of prescribed fire and the rapid ingrowth of woody stems.



Figure 17. NMS ordination of plant species composition in 24 experimental plots.

The point at the base of each arrow represents the 2010–2011 sample, and the point at the tip of each arrow is that same plot sampled in 2016. The green arrow indicates the general direction of change in species composition toward the restoration target of longleaf pine savanna.

Compositional variations in the community of birds among treatment plots based on NMS ordination are presented in **Figure 18**. Although **Figure 18** is oriented a bit differently from Figure 17, the general arrangement of plots relative to one another is remarkably similar, particularly among the 2010 samples. High pocosin blocks have low NMS Axis 2 scores, and mesic plots have high NMS Axis 2 scores. There is a very clear separation of the 2010 samples from the 2016 samples along Axis 1, indicating a very consistent change in the composition of the bird communities in these plots over this time interval. This finding is because of notable increases in the prevalence of eastern bluebirds (Sialia sialis), Connecticut warblers (Oporornis agilis), gray catbirds (Dumetella calolinensis), Acadian flycatchers (Empidonax virescens), and brown thrashers (Toxostoma rufum) in 2016 and because of diminished importance of blue-gray gnatcatchers (*Polioptila caerulea*), Bachman's sparrows (*Aimophila aestivalis*), eastern kingbirds (Tyrannus tyrannus), and white-eved vireo (Vireo griseus). It is not possible to assign a single cause to these changes. This finding is almost certainly due in part to normal year-to-year variation in population sizes that occur in many bird species. This finding is also likely because of changes in the vegetation structure (e.g., increased density of understory woody stems) and plant species composition of these plots that has occurred in the absence of prescribed fire.



Figure 18. NMS ordination of bird species composition in 24 experimental plots.

The point at the base of each arrow represents the 2010–2011 sample, and the point at the tip of each arrow is that same plot sampled in 2016.

In summary, although short-term results indicated significant benefits of both dormant season and growing season thinning for restoration plant diversity and composition of 50- to 60-year-old loblolly pine-dominated forests to conditions similar to those of longleaf pine savannas, those benefits were lost in the absence of subsequent prescribed burning. Without prescribed burning, differences in the density of understory woody stems between thinned treatments and unthinned controls quickly disappeared. This ingrowth resulted in an increase in understory fuels and may increase the severity of future fires. Finally, the lack of prescribed burning was very likely a contributing factor to significant changes in bird species diversity and composition over the duration of this study. Probably the most important conclusion of this study is that mechanical restoration treatments, such as understory thinning, must be accompanied by a regular prescribed burning to be effective.

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