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Patterns of vegetation composition and diversity in pine-dominated ecosystems of the Outer Coastal Plain of North Carolina: Implications for ecosystem restoration

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ABSTRACT

Terrestrial ecosystems of the Atlantic coastal plain have experienced considerable change over the past two centuries, largely due to agricultural activities and fire suppression and exclusion. Many areas that were once dominated by open longleaf pine (*Pinus palustris*) woodlands now support closed canopy stands of loblolly pine (*Pinus taeda*) with a dense midstory of broadleaved shrubs and trees. In recent years, efforts to restore the herbaceous plant communities typically found in fire-maintained longleaf pine woodlands have focused on the use of midstory thinning to produce savanna-like conditions and to facilitate the restoration of historical fire regimes through prescribed burning. Previous efforts to restore longleaf pine stands have focused on the potential of fire-suppressed longleaf pine woodlands, which have been met with some success. However, it is unclear what the potential is for loblolly pine stands to act as a 'surrogate' environment for the restoration of the often species-rich herbaceous layer of longleaf pine woodlands. To assess the effectiveness of longleaf pine restoration treatments in existing loblolly pine stands, we analyzed the drivers of plant community composition in loblolly pine stands with mechanical midstory removal treatments, untreated loblolly pine stands, longleaf pine stands, and pond pine dominated high-pocosin systems. We sampled 75 plots, from which more than 200 individual plant taxa were identified, with species richness (number of species per 0.1 ha) ranging from 9 in pond pine pocosins to 118 in longleaf pine woodlands. Plant species richness and composition varied in response to soil properties, with the first NMS ordination axis correlated with soil properties related to soil moisture and organic matter content (SOM), and the second NMS ordination axis correlated to the concentration of certain soil nutrients (P, Ca), the variability of which may be due, in part, to historic fertilizer applications. While stand types were largely distinct from each other in their vegetation composition, there was nevertheless some compositional overlap among some longleaf and loblolly pine stands. Areas of compositional overlap appear to have somewhat similar soil properties, whereby the soils found in overlapping loblolly pine stands were closer to those found in longleaf pine stands (i.e. low SOM content). Thus, an assessment of the soil properties of loblolly pine stands may allow for an identification of candidate sites for which longleaf pine restoration treatments may be most effective.

1. 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;

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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 (Walker and Silletti, 2006), 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 layer are more likely to result in crown scorch and overstory tree mortality (Varner et al., 2007, 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?