COMMUNITY ASSEMBLY AND VEGETATION PATTERNS ACROSS SPACE AND TIME IN THE LONGLEAF PINE ECOSYSTEM

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ABSTRACT

Kyle Ann Palmquist: Community assembly and vegetation patterns across space and time in the longleaf pine ecosystem
(Under the direction of Robert K. Peet and Alan S. Weakley)

Community assembly is the process in which species are filtered into ecological communities. Multiple processes, which often operate at different spatial and temporal scales, are thought to act synergistically to influence the number and identity of species in local communities. Thus, a key challenge in ecology is to identify those processes and determine their relative importance. Here, I document vegetation patterns in the longleaf pine ecosystem and quantify the relative importance of multiple ecological processes structuring those patterns. Chapters 2 and 3 explore how fire frequency, soil properties, and drought have influenced species richness and composition patterns across ~ 20 years in longleaf pine plant communities located in southeastern North Carolina. This work also informs land management agencies on best practices for implementing prescribed fire to maintain plant species richness. Chapter 4 uses 849 vegetation plots to determine how soil properties, climate, and biogeographic history simultaneously shape species richness across the longleaf pine range. This work reflects on where species richness is highest and identifies what processes drive differences in species richness across latitude. Chapter 5 uses species co-occurrence metrics to quantify the relative importance of stochastic processes in assembling longleaf pine plant communities by examining whether competition, environmental filtering, and stochastic processes shift in relative importance across an environmental gradient. Chapter 6 synthesizes the processes that assembly

longleaf pine communities and then extends those findings by drawing parallels to other species-rich grasslands. Local environmental filtering (e.g., soil properties) emerged as the most consistent and important factor structuring both species richness and species composition patterns across time and space. However, competition, climate, stochastic processes, fire frequency, and biogeographic history explained additional variation in species richness and composition unaccounted for by soil properties. As predicted, the relative importance of processes changed with spatial scale: environmental filtering became more important at larger spatial grains, while competition, stochasticity, and fire frequency became more important as spatial grain decreased. Thus, these results suggest vegetation patterns and their drivers are scale-dependent and community patterns in the longleaf pine ecosystem are shaped concurrently and in an often complex fashion by multiple processes.

For my parents, John and Diane Palmquist, who instilled a love of the outdoors in me at an early age and encouraged me, motivated me, and supported me ever since.

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CHAPTER 1: INTRODUCTION

A key challenge for ecologists is to identify which processes act to assemble communities to produce the patterns we see at local, regional, and global scales. Community assembly is the process in which species are filtered into ecological communities, and can be thought of as a number of sieves or filters, allowing certain species through, while excluding others (Diamond 1975, Weiher & Keddy 1995). Multiple community assembly processes (e.g., biotic interactions, environmental filtering, dispersal, disturbance, evolutionary history), often operating at different spatial and temporal scales, are thought to act simultaneously to determine both the identity and number of species that get to a site (e.g., diversity and composition; Ricklefs 2004, Harrison & Cornell 2008, Chase & Myers 2011, HilleRisLambers et al. 2012). Thus, a new goal in community ecology is to determine how the relative importance of multiple processes changes across space, time, or across communities structured along gradients (e.g., elevation, environmental stress, predator abundance; Leibold & McPeek 2006).

In this dissertation, I document vegetation patterns and identify the important processes responsible for the assembly of plant communities across space and time in the longleaf pine ecosystem. Specifically, I attempt to tease out the relative importance of fire regimes (e.g., frequency and timing), local environmental filtering (e.g., soils), regional environmental filtering (e.g., climate), biogeographic history reflected by the size of the regional species pool, stochastic processes, and competition. For several reasons, the longleaf pine ecosystem is an ideal system to explore community assembly. First, many longleaf pine plant communities are species-rich,

especially at small spatial scales (52 species in 1 m², representing the highest reported small-scale species richness in North America), which has resulted in debate amongst botanists and plant ecologists about how so many species can coexist together (Walker & Peet 1983, Myers & Harms 2011; also see Wilson et al. 2012). Second, this ecosystem is fire-dependent, occurs over a broad spatial extent, and is structured along strong regional and local environmental gradients. Thus, there is some expectation that multiple processes will be important for structuring plant species richness and composition patterns, and that the relative importance of those processes may change across space and time. Third, the longleaf pine ecosystem is of great conservation concern in the southeastern United States as less than 3% of the original, pre-settlement acreage remains, of which very little is high-quality, fire-maintained habitat. In addition, the longleaf pine ecosystem is known for its high levels of endemic and rare taxa, including several federally endangered and threatened species (Estill & Cruzan 2001, Sorrie & Weakley 2001, Sorrie &Weakley 2006, Noss 2013). Thus, a better understanding of what processes influence species richness and species composition should help guide restoration and conservation of this endangered ecosystem.

A second unifying theme across my chapters is the component of scale. Scale is a central, key concept that connects research across disciplines in ecology (Levin 1992). Over the last several decades, much attention has been focused on the scale-dependence of ecological patterns and processes (Shmida & Wilson 1985, Auerbach & Shmida 1987, Palmer & White 1994, Rosenzweig 1995, Crawley & Harral 2001, Götzenberger et al. 2012, Peet et al. 2014). More recently, time and space have been combined in a single conceptual framework for considering the scale-dependence of ecological patterns and processes, (Adler et al. 2003, Adler et al. 2005, White et al. 2010, Scheiner et al. 2011), as originally postulated in Preston's classic work in

1960. The relative importance of processes changes somewhat predictably with spatial or temporal scale, generally with processes operating at larger temporal and spatial extents becoming more important as spatial grain size increases. For instance, biotic interactions and demographic stochasticity are thought to act most strongly in structuring communities at small spatial scales (Stoll & Weiner 2000, Götzenberger et al. 2012). In contrast, environmental filtering (e.g., climate) often becomes more important at large spatial scales, since environmental heterogeneity generally increases with spatial scale (Williams 1943, Shmida & Wilson 1985, Crawley & Harral 2001, Field et al. 2009).

Examining pattern and process across multiple spatial and temporal scales is becoming increasingly important in ecology for several reasons. First, studies conducted at multiple scales are more effective in elucidating the processes that structure ecological communities. Since, ecological processes are scale-dependent, studies that do not examine community patterns at certain spatial scales, will be unlikely to find evidence of processes thought to operate primarily at those scales. For example, if climate is thought to be important in structuring species distributions across a landscape, sampling only a small portion of the landscape might lead to the conclusion that climate is not an important filter; rather, the spatial scale of sampling was not matched appropriately to the spatial scale at which climate is operating. Second, studies conducted at multiple scales that have considerable temporal or spatial breadth allow for testing the generality of ecological principles across sets of communities. Rather than simply examining ecological patterns in a spatial or temporal snap-shot, studies conducted across large spatial or temporal extents can assess whether a process is generally important. My dissertation explores the scale-dependence of ecological patterns and processes by examining vegetation patterns across spatial grain, spatial extent, and over decadal extents in the longleaf pine ecosystem.

Using this approach, I identify which processes act at particular spatial and temporal scales and how their relative importance changes with scale.

Disturbance and local environmental filtering (e.g., soil properties and site conditions) have been identified as key drivers of plant community structure, especially in fire-dependent grasslands (Walker & Peet 1983, Glitzenstein et al. 2003, Kirkman et al. 2004, Uys et al. 2004, Overbeck et al. 2005). Chapter 2 of this dissertation examines how soil properties and fire frequency have influenced species richness and beta-diversity (e.g., turnover in community composition) over 20 years in longleaf pine plant communities in eastern North Carolina. The goals of this work were threefold. First, I was interested in quantifying how dynamic longleaf pine plant communities are over decadal temporal extents and how vegetation change may proceed differently depending on fire history and environmental context. The magnitude of vegetation change is expected to vary across sites that differ in key environmental attributes (e.g., N and P availability, soil moisture) because of underlying variation in resource availability (Gibson & Hulbert 1987, Gauthier et al. 2010, Amatangelo et al. 2011). Furthermore, the effects of fire or other disturbances can change with environmental context (e.g., higher fire frequency on nutrient-rich, moist sites that produce more biomass), which has direct consequences for plant species richness and composition (Kirkman et al. 2001, Harrison et al. 2003, Collins & Calabrese 2012, Pausas & Ribeiro 2013). The second goal of this study was to investigate whether vegetation patterns and their drivers were scale dependent. To this end, I examine how species richness and beta-diversity change with spatial grain from 0.01 m² to 1000 m². Lastly, this work informs land managers about best management practices for implementing prescribed fire for biodiversity conservation. In general, most land management agencies have increased the frequency of fire in longleaf pine habitat in eastern North Carolina over the last 20 years. To

understand the outcome of this management decision and to inform land management agencies accordingly, I relate prescribed fire frequency to changes in species richness and beta-diversity patterns over time.

Chapter 3 builds on Chapter 2 and examines how changes in the fire management regime, compounded with additional stress from long-term drought have impacted plant species richness at a single site, Big Island Savanna, located in the Green Swamp Preserve, North Carolina. Chapter 2 revealed species richness at small scales had declined over time in Big Island Savanna. Recently, the fire management regime in this site changed from nearly annual fire during at least 1940-1997 (Kologiski 1977, Rome 1988) to a fire return interval of 2 to 3 years during 1997-2011. In addition, the southeastern Coastal Plain of the US has been experiencing long-term, ongoing drought for the last 25 years. To identify whether reduced fire frequency, long-term drought, or some combination of the two is responsible for the loss of biodiversity detected in Big Island Savanna, I re-sampled two sets of nested, permanent plots after ~20 and 25 years, respectively. Understanding why plant species richness has decreased over time in Big Island Savanna is critical for several reasons. First, Big Island Savanna, and more broadly the Green Swamp Preserve, is of great conservation importance in the southeastern US as it was never truly fire-suppressed in the early and mid-20th century like so many other longleaf pine sites (Kologiski 1977, McIver 1981, Rome 1988). Furthermore, the Green Swamp Preserve contains some of the best remaining examples of species-rich, mesic longleaf pine savanna on the Atlantic Coastal Plain (McIver 1981). Third, this site is famous for its high biodiversity at small spatial scales, formerly holding the North American record at 0.25 m² and 1 m² (Walker & Peet 1983). I believe this work not only has applications for land managers in the longleaf pine ecosystem, but can be generalized to species-rich grasslands elsewhere in the world, which are also sensitive to

changes in disturbance regimes and may require frequent disturbance to maintain high plant species richness.

In addition to local environmental filtering and disturbance, plant community structure at the local scale may be driven by processes that operate at larger spatial and temporal extents (e.g., climate, evolutionary history; Zobel 1997, Pärtel 2002, Harrison & Cornell 2008). Thus, an emerging goal in community ecology is to identify how local, regional, and historical processes simultaneously influence community patterns at the local scale (Carr et al. 2009, White & Hurlbert 2010, Gazol et al. 2012). In Chapter 4, I explore how processes operating at larger spatial and temporal extents (e.g., climate, biogeographic history), in addition to local processes (local environmental filtering) concurrently shape plant species richness patterns across the range of the longleaf pine ecosystem. The longleaf pine ecosystem is an excellent system in which to explore the relative importance of local, regional, and historical processes because it occurs across a broad spatial extent and along strong environmental gradients (e.g., climate, soil properties). Thus community structure in this ecosystem is likely influenced by multiple processes that vary in spatial and temporal breadth. This work builds on Chapter 2 and 3 by examining whether local environmental filtering continues to be an important filter across space in addition to time, but also expands on that work by examining the effects of climate and historical processes on longleaf pine community assembly. Variance partitioning is used to identify the unique variation in species richness explained by soil properties, climate, and species pool size (a proxy for historical processes). I then examine whether climate and species-pool size increase in relative importance as spatial grain changes from 1 m² to 100 m².

There is ongoing debate as to whether ecological communities are assembled by deterministic, niche-based processes or stochastic processes unrelated to species' differences

(Tilman 1982, van der Maarel & Sykes 1993, Chesson 2000, Hubbell 2001, Silvertown 2004). Recently these two competing hypotheses have been merged into a single conceptual framework that seeks to identify how the relative importance of deterministic versus stochastic processes changes across a set of communities (Tilman et al. 2004, Gravel et al. 2006). Where communities fall along the continuum between solely niche-based processes and solely stochastic processes depends on multiple factors, including the frequency or intensity of disturbance. One approach to quantifying the relative importance of different community assembly processes is through species co-occurrence metrics, which reveal whether community structure is more aggregated (evidence of environmental filtering), segregated (evidence of limiting similarity), or no different than random expectation (evidence of stochastic assembly). In Chapter 5, I use two different, yet complementary species-co-occurrence metrics coupled with null model analysis to explore where longleaf pine plant communities fall along the continuum of deterministic to stochastic assembly. More specifically, I examine how the relative importance of environmental filtering, competition, and stochastic processes change across a gradient of environmental stress, with spatial grain (0.01 m² to 1000 m²) and with time since fire.

Chapter 6 identifies the important community assembly processes and synthesizes their synergistic effect on plant species richness and composition patterns in the longleaf pine ecosystem over space and time. I then put my findings into context and examine similarities and differences between the drivers of vegetation patterns in the longleaf pine ecosystem and other species-rich grasslands in the world. In total, this dissertation explores how plant species richness and community composition are structured over space and time, how dynamic longleaf pine plant communities are over time, and how the relative strength of community assembly processes changes across space (e.g., grain and extent) and with environment context.

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CHAPTER 2: FIRE FREQUENCY AND ENVIRONMENTAL FILTERING DRIVE VEGETATION PATTERNS ACROSS TIME AND SPACE IN LONGLEAF PINE WOODLANDS

Abstract

Disturbance is an important factor that shapes plant community structure in fire-dependent grasslands, and alteration of disturbance regimes can have large consequences on species richness and species composition. However, the response of vegetation to disturbance may change with environmental context. I re-sampled 59 permanent vegetation plots in the longleaf pine ecosystem twenty years after they were established to determine the magnitude of vegetation change at a range of spatial scales (0.01 m² to 1000 m²). I was interested in how environmental context and fire frequency concurrently influence vegetation change over time and if those relationships change with spatial scale. I quantified the magnitude of vegetation change using two different metrics of beta-diversity (beta turnover, the proportion of species turning over and Bray-Curtis dissimilarity, an abundance-weighted metric) and by tabulating changes in species richness. The magnitude of vegetation change was highly dependent on environmental context and fire frequency. Changes in species richness, beta turnover, and Bray-Curtis dissimilarity were greatest on silty, frequently-burned sites, whereas most sandy, infrequently-burned sites remained stable. Furthermore, the amount of change detected was scale-dependent. Species richness increased at larger spatial scales over time, but decreased at the two smallest spatial scales. In contrast, beta turnover and Bray-Curtis dissimilarity decreased with increasing spatial scale, suggesting that there is greater stochasticity at small scales.

However, the magnitude of compositional change (e.g., dissimilarity of plots to themselves over time) was relatively modest, despite large amounts of beta turnover across time. I attribute this initial contradiction to the turnover of infrequent, mobile species amidst a matrix of dominant bunchgrasses. Interestingly, and in contrast to other longleaf pine studies, I found environmental site conditions to be more important in predicting the magnitude of vegetation change than fire frequency. Thus, future work addressing vegetation change in the longleaf pine ecosystem and in other species-rich grassland systems should consider not only disturbance, but environmental context as well. Since species richness and species turnover patterns were scale-dependent, I recommend sampling vegetation across multiple spatial scales to comprehensively quantify changes in community structure over time.

Introduction

Fire shapes plant community structure in many terrestrial ecosystems (Bond & Keeley 2005, Bowman et al. 2009, Turner 2010). In fire-dependent systems, particularly grasslands, fire often increases species richness through the release of resources, such as nutrients, space, and light, while preventing competitive exclusion (Walker & Peet 1983, Glitzenstein et al. 2003, Kirkman et al. 2004, Uys et al. 2004, Overbeck et al. 2005, Peet et al. 2014). However, fire regimes (including the frequency, intensity, severity, and timing of fire) are changing throughout the world (Millennium Ecosystem Assessment 2005, Westerling et al. 2006, Bowman et al. 2009), with large and lasting consequences for plant species distributions, plant species richness patterns, and plant community composition, especially where fire is necessary for the maintenance of community structure (Leach & Givnish 1996, Johnstone & Chapin 2003). For this reason, increased effort in recent years has been focused on how fire regimes affect community structure and dynamics over time (Glitzenstein et al. 2003, Burton et al. 2011).

In addition to disturbance regimes, plant communities are structured by both local and regional environmental filtering and hence vegetation change over time may be strongly dependent on the environmental context in which sites occur. Sites that differ in key environmental attributes (e.g., N and P availability, soil moisture) may have different rates of change because of underlying variation in resource availability (Gibson & Hulbert 1987, Gauthier et al. 2010, Amatangelo et al. 2011). Furthermore, the effects of fire or other disturbances can change with environmental context (e.g., increased fire frequency on nutrient-rich, moist sites that produce more biomass), which has direct consequences for plant species richness and composition (Kirkman et al. 2001, Harrison et al. 2003, Collins & Calabrese 2012, Pausas & Ribeiro 2013).

The longleaf pine (*Pinus palustris*) ecosystem is a fire-dependent woodland ecosystem located in the southeastern United States, characterized by an often species-rich herbaceous layer dominated by graminoids and forbs. Community structure in this ecosystem is strongly influenced by both fire and environmental filtering. Frequent fire (every 1-5 years) is necessary for the maintenance of plant species richness, plant species composition, and vegetation structure (Walker & Peet 1983, Frost et al. 1986, Kirkman et al. 2004). Without frequent fire, species richness declines, woody components increase, and the understory becomes dense and closed (Heyward 1939, Frost et al. 1986, Glitzenstein et al. 2003). Several studies have examined how fire frequency influences community structure across time and suggest that more frequent fire often results in increases in species richness and the abundance of herbaceous species (Lewis & Harshbarger 1976, Waldrop et al. 1992, Brockway & Lewis 1997, Glitzenstein et al. 2003).

In addition to fire frequency, plant species richness and community composition in the longleaf pine ecosystem are structured by local and regional environmental filtering (e.g., soil

properties and climate; Walker & Peet 1983, Carr et al. 2009, Peet et al. 2014). Several studies have shown that soil properties, particularly soil moisture and texture, are the most important environmental drivers of plant community structure (Drewa et al. 2002, Glitzenstein et al. 2003, Kirkman et al. 2004, Peet 2006, Carr et al. 2009, Peet et al. 2014). Although much work has investigated how fire regimes or environmental context influence species richness and composition in the longleaf pine ecosystem (Lemon 1949, Lemon 1967, Hartnett 1987, Kirkman et al. 2001, Keddy et al. 2006, Hinman & Brewer 2007), no studies have investigated how these factors concurrently affect species richness and composition over longer temporal extents.

Here I assess how prescribed fire frequency and environmental context have impacted patterns of plant species richness and community composition over time in longleaf pine communities by re-sampling 59 permanent vegetation plots nearly twenty years after they were originally installed. I quantified several aspects of community structure over time and across multiple spatial scales to pursue three main questions. First, how does the magnitude of change in community composition and species richness across time vary with spatial scale? Studies that examine how community composition (e.g., species turnover) changes simultaneously in time and space are rare (Soininen 2010) and I know of no other studies in the longleaf pine ecosystem that have documented how vegetation change proceeds across time at differential spatial grains. However, ecologists have developed a strong theoretical framework for understanding species richness and turnover in space and time, built from Preston's classic work of 1960 (Adler & Lauenroth 2003, Adler et al. 2005, White et al. 2010, Soininen 2010). Second, do the effects of fire and environmental context on the above metrics change with spatial scale? Lastly, are species composition and richness responding in similar ways over time to fire frequency and environmental context? In addition, I explore whether fire history and the past fire management

regime, relative to the current fire regime have influenced plant species richness and composition over time.

Methods

Study Area

This work was conducted on the outer Coastal Plain of North Carolina in the southeastern United States (Figure 2.1). Elevation ranges from 0 to 30 meters above sea level, with very little topographic relief. However, subtle differences in elevation (0.5 meters or less) have large consequences for hydrology, soil properties, and hence vegetation (Rome 1988, Christensen 2000). The climate is humid sub-tropical, with an average mean annual temperature of 15.5 °C and an average annual precipitation of 160 cm, most of which occurs during the growing season (Ruffner 1985, State Climate Office of North Carolina). Summer convectional storms not only provide heavy rain, but lightning and an ignition source for frequent, low-intensity fires (Christensen 2000, Frost 2006). Soils within the region derive from nutrient-poor, unconsolidated sediments of alluvial and marine origin. Several soil orders occur within the study area and soil texture is extremely important in determining water holding capacity, nutrient retention, species richness, and community composition (Peet 2006).

Sampling Design and Vegetation Data

During the summers of 1991-1993, 200 plots were sampled in the longleaf pine ecosystem of the North Carolina Coastal Plain using the Carolina Vegetation Survey protocol (CVS; Peet et al. 1998). In the summers of 2009 and 2010, I re-located and re-sampled 59 plots selected to span the compositional gradient so that vegetation change could be assessed across a variety of longleaf community types. To the extent possible, plots re-surveyed were also selected

to span a range of fire histories. Plots were not re-sampled if there were signs of human disturbance or development. The CVS sampling design consists of 1000 m² plots with several smaller sub-plots nested within (0.01 m², 0.1 m², 1 m², 10 m², 100 m², 400 m²). Each CVS plot was permanently marked with 10 pieces of steel conduit, which ensured that I re-sampled precisely the same physical location. Once a plot was re-located, presence of all vascular plant species was recorded at all six spatial scales and each species was assigned a cover class value (see Peet et al. 1998). The same sampling methodology was used during both sampling events to ensure the data collected were directly comparable. In addition, I attempted to standardize sampling effort across the two time periods by discussing effort spent (survey time) with several of the original, key participants.

Environmental and Fire History Data

In addition to vegetation data, slope, aspect, and soil samples from the A horizon were collected at the time of sampling. Soil samples were then analyzed for texture (sand, silt, clay %), nutrients (N, P, Al, B, Ca, Cu, Fe, H, K, Mg, Mn, Na, S, Zn), organic matter, base saturation, cation exchange capacity, pH, Ca/Mg ratio, and bulk density by Brookside Laboratories Inc, using Mehlich III extraction (Mehlich 1984). Elevation was determined from a digital elevation model.

Fire history data for all plots through 2008 were obtained from a GIS layer of prescribed fire events dating back to 1985, compiled from several land management agencies in southeastern North Carolina (Costanza 2010). Additional years of fire history data (2009, 2010) were obtained directly from the land management agencies. These data delineate the areas burned, but do not quantify the intensity or patchiness of fire within the burned area. Fire

frequency (the number of fires), average fire return interval (mean number of years between fires), and time since fire (number of years since fire) were determined for all plots. During the last 20 years, most land managers on government-owned lands in North Carolina have increased the frequency of prescribed burning on longleaf pine tracts.

A broad community type was also assigned to each plot, so the magnitude and direction of vegetation change could be examined with respect to vegetation types. These groups follow Peet (2006), who categorized longleaf pine vegetation into 5 community groups based on soil moisture and soil texture: silty woodlands, savannas, flatwoods, subxeric woodlands, and sandhills (Figure 2.2). These correspond relatively well to four Groups recognized within the US National Vegetation Classification: G009 Dry-Mesic Loamy Longleaf Pine Woodland, G190 Wet-Mesic Longleaf Pine Woodland, G596 Mesic Flatwoods Longleaf Pine Woodland, and for the final two G154 Xeric Longleaf Pine Woodland (http://www.usnvc.org). Silty woodlands and savannas occur on fine-textured ultisol soils. These two types are the most species-rich, with savannas being slightly wetter (Peet 2006). Flatwoods occur on spodosols with a spodic horizon below the surface where fine-textured particles and organic matter accumulates, creating a mesic to hydric growing environment, despite a mostly sandy substrate (Soil Survey Staff 2010). Subxeric woodlands, also occur on sandy substrates, but are drier than flatwoods and often contain dry-site oaks, such as *Quercus laevis* and *Quercus incana*. Sandhills occur on the driest, sandy sites, have sparse herbaceous layers, oak co-dominance in the over-story, and lower species richness.

Analysis

Prior to analysis, all taxonomic names were standardized across the two sampling periods to ensure that changes in nomenclature, taxonomic resolution, and taxonomic understanding of the flora across time did not affect the magnitude of vegetation change detected. Unknown or ambiguous species were removed from the data set, while several species were lumped into larger taxonomic complexes. As the ability to identify grasses in the genera *Andropogon*, *Dichanthelium*, and *Schizachyrium* was much more limited during the 1991-1993 sampling, all occurrences of these two genera were lumped into *Andropogon* spp., *Dichanthelium* spp. and *Schizachyrium* spp. in both data sets (1991-1993 and 2009-2010).

Several approaches were used to quantify the magnitude and direction of vegetation change over time (Table 2.1). Species richness in 1991-1993 and 2009-2010 and raw species turnover (defined here as the number of species lost and gained over time) were calculated across multiple spatial scales (0.01, 0.1, 1, 10, 100, 400, and 1000 m²) for each plot. To quantify the magnitude of compositional change over time, I used two different metrics of beta-diversity, which capture somewhat different aspects of species turnover. The first metric I used was Wilson and Shmida's (1984) beta turnover metric: $(\beta T) = (g + l) / 2\alpha$, which sums the number of species gained (g) and lost (l) over time (e.g., raw species turnover) and divides by two times the mean species richness (α; Wilson & Shmida 1984, see also Ricotta 2002, Ukmar et al. 2007). This metric describes how many species have been lost and gained over time and does not consider species abundance. The second beta-diversity metric, Bray-Curtis dissimilarity, considers how many species are shared across two sites scaled by their abundance (cover class code, see Peet et al. 1998). I calculated Bray-Curtis dissimilarity at spatial grains $\geq$ 100 m², at which I had estimates of species abundance. I used the Sørenson dissimilarity metric for spatial grains of 10

m² and below because abundance data were not available. Thus, it is not possible to directly compare dissimilarity values calculated at larger scales (> 100 m²) to those calculated at smaller scales (< 100 m²). However, it is still possible to compare differences between 100 m² and larger spatial grains (i.e. 1000 m²), and between 10 m² and smaller spatial grains (i.e. 0.01 m²). The dissimilarity of each plot to itself 20 years later was used as a quantitative estimate of the magnitude of compositional change over time.

To determine if particular groups of taxa were consistently being lost or gained over time, I assigned each species to a growth form category (caulescent herb, matrix graminoid, fern, geophyte, hemiparasite, insectivore, legume, rosette herb, shrub, single-culm graminoid, subshrub, tree, and vine; Table A.1) and then examined how the frequency of each growth form changed over time (Table 2.4). These growth form categories are modified from Raunkaier 1983 (see Table A.1 for full descriptions). I expected fire history over the last 30 years would influence the types of species turning over, with addition of woody species and loss of small-statured herbaceous species (e.g., rosette herbs) on fire-suppressed sites. In addition, I expected that certain types of species would inherently turn over more frequently than others due to life history characteristics (e.g., annual species, sparse species, species sensitive to changes in soil moisture availability). I summarized vegetation change by growth form in two ways. First, I calculated the total number of times each growth form was gained and lost over time at both 1000 and 1 m². I then calculated a ratio that reflects the number of species gained versus lost, by dividing the total number of gains for each growth form by the total number of losses. This allowed me to examine whether particular growth forms tended to be gained or lost more over time, since values > 1 indicate gains exceed losses, while values < 1 indicate losses exceed gains. Second, to examine if particular growth forms were more dynamic over time, irrespective of

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whether they were lost or gained, I re-calculated Bray-Curtis dissimilarity matrices for each growth form at 1000 m² and then calculated a mean dissimilarity value for each growth form from plots to themselves over time.

To compare dissimilarity values across spatial scales, I used null model analysis. This was necessary because I expect beta-diversity to be larger at small scales due to chance; as the size of the sample approaches the size of the pool, species composition becomes more similar. I first generated 1000 null communities using the swap-method (Gotelli and Entsminger 2003), which held row and column totals constant (e.g., species richness per site and species occupancy across all sites). I then calculated a dissimilarity matrix on each null community and extracted the dissimilarity of plots to themselves over time. To compare results across spatial grain, I calculated a standardized effect size (SES) for each scale,

SES= (I obs – I sim)/S sim,

where I obs is the observed mean dissimilarity of all plots to themselves over time, I sim is the mean simulated dissimilarity of all plots to themselves over time and, S sim is the standard deviation of the simulated indices (Gurevitch et al. 1992; Gotelli and McCabe 2002). SES values above 2 indicate dissimilarity values that are greater than expected from random chance, while SES values below 2 indicate dissimilarity values that are less than expected from random chance. Null model analysis was implemented in R version 2.15.2 using the vegan and bipartite packages (R Core Development Team 2012).

Linear models were used to quantify species richness, beta turnover, and dissimilarity over time and to evaluate how vegetation change varied with environmental context and fire

history. Model selection using AIC was utilized to identify which soil (nutrients, texture, organic matter, bulk density), site (elevation, slope, aspect), and fire (fire frequency, average fire return interval, time since fire) attributes should remain in the model for species richness and beta-diversity at 100, 400, and 1000 m² (Burnham & Anderson 2002). The influence of soil properties on vegetation change could not be examined at spatial scales below 100 m² because soil data were unavailable at those scales. Fe, Ca, Mg, and Al in parts per million (ppm) were log-transformed before analysis due to large data ranges for these variables across plots. Variance partitioning analyses were then conducted to determine the unique variance explained by each predictor in the best-fit model, along with the shared and unexplained variance in each model (Legendre and Legendre 1998).

Non-metric multi-dimensional scaling (NMS) ordination was used to examine the magnitude and direction of compositional change visually. NMS is considered the most appropriate indirect ordination technique for plant community data, as it is suited to non-normality and preserves dissimilarity values as distances in ordination space (Clarke 1993, McCune and Grace 2002). NMS displayed all plots from both sampling events in ordination space, and vectors were drawn from each plot during the 1991-1993 sampling to the same plot during 2009-2010 (Figure 2.4). Environmental overlays of soil, site, and fire variables were used to identify the environmental attributes and disturbance regimes of plots in ordination space. These graphics helped illustrate whether sites with certain fire regimes or environmental conditions had experienced more or less compositional change than other plots. Additionally, NMS ordination was used to examine whether the ordination space during 1991-1993 had expanded or contracted over time (Figure 2.5). Contraction in ordination space indicates that

plots are becoming more similar to one another in community composition over time. NMS was

performed in R v.2.15.2 using the labdsv packages (R Core Development Team 2012).

Results

Species Richness

Overall, species richness increased significantly over time at spatial scales from 1 m² to

1000 m², remained constant at 0.1 m² and decreased at the smallest spatial scale examined (0.01

m², Table 2.1). Silt % and quadratic transformed fire frequency explained the most variation in

species richness across time at 1000 m² (unique variance explained by silt %: $R^2 = 0.27$, $p <$

.001; by fire frequency: $R^2 = 0.17$, $p < .01$ for both terms; shared variance $= 0.06$, Figure 2.3).

Silt % and quadratic transformed fire frequency were also the most important predictors of

species richness patterns over time at 400 m² (unique variance explained by silt %: $R^2 = 0.32$, $p <$

.001; by fire frequency $R^2 = 0.18$, $p < .01$ for both terms) and 100 m² (unique variance explained

by silt %: $R^2 = 0.25$, $p < .001$; by fire frequency $R^2 = 0.16$, $p < .01$ for both terms). Quadratic

transformed fire frequency was a better fit to the data than untransformed fire frequency,

suggesting the most frequently burned places have not gained as many species over time as those

burned less frequently. This relationship was being driven by a single site, Big Island Savanna in

the Green Swamp Preserve, which had lost species over time (Figure 2.3). I attribute this species

loss to reduced fire frequency in recent years, compounded with ongoing, long-term drought (see

Chapter 3 for further discussion and exploration of this species loss). However, on average, silty

sites burned more frequently in the last 20 years, relative to the original fire management regime,

have gained more species over time (Figure 2.3). In contrast to silty, frequently-burned sites,

species richness on fire-suppressed sites has decreased over time, while species richness on xeric, sandy sites has remained relatively stable over time.

Species Composition

Raw species turnover, defined as the number of species lost and gained over time, was high, especially at larger spatial scales (mean = 15.7 at 100 m² and mean = 20.4 at 1000 m²; Table 2.1). Beta turnover was also high regardless of spatial scale, representing turnover of between 16 percent and 77 percent of plant species over time, but was greatest at the smallest spatial scales (< 1 m²; Table 2.1). Thus, although there are more species physically coming and going over time at larger scales, they make up a smaller portion of the total flora than the amount turning over at small scales. Community type was the only significant predictor of beta turnover (1000 m²: $R^2 = 0.25$, $p < 0.01$; 400 m²: $R^2 = 0.22$, $p < 0.01$; 100 m²: $R^2 = 0.19$, $p < 0.01$). This is in contrast to species richness, where silt percentage was a better predictor than community type. Silt percentage and community type are correlated, but not completely redundant, as silt percentage is one of two key axes that defines longleaf pine community types (Figure 2.2). Therefore, because community type also encompasses a soil moisture gradient, it appears soil texture and soil moisture are both important drivers of species turnover, with greater turnover on silty, mesic sites (e.g., silty woodlands and savannas, Table 2.2). Fire frequency was not significant in explaining variation in beta turnover at any scale.

To summarize the types of species turning over across time, I assigned each species to a growth form category and calculated a ratio of gains to losses, along with Bray-Curtis dissimilarity for each growth from at 1000 m² (see Table 2.3). At 1000 m², the ratio of gained versus lost species revealed most growth forms have increased in frequency over time (i.e. gains

have exceeded losses, >1; Table 2.3). Notable exceptions include geophytes and hemiparasites, which have consistently been lost over time (ratio = 0.4, 0.5, respectively). At 1 m², insectivores (ratio = 0.3), along with geophytes (ratio = 0.4) and hemiparasites (ratio = 0.3) have been lost preferentially. Many types of species turned over across time, but species turnover (Bray-Curtis dissimilarity) was especially high for hemiparasites (0.80; e.g., *Seymeria cassioides*), geophytes (0.70; e.g., *Calopogon* spp.), single-culm graminoids (0.62; e.g., *Dichanthelium* spp., *Scleria* spp.), insectivores (0.60; e.g., *Drosera capillaris*), rosette herbs (0.49; e.g., *Eurybia paludosa*, *Liatris* spp.), and caulescent herbs (0.48; e.g., *Polygala lutea*, *Symphyotrichum dumosum*). Relatively small-statured herbaceous species and species sensitive to changes in moisture (e.g., insectivores) have been gained and lost most frequently across time. In contrast, ferns, matrix graminoids, shrubs, and subshrubs have remained relative stable over time (Table 2.3).

Dissimilarity of a plot to itself over time was largely driven by spatial scale, soil properties, and fire frequency. As with beta turnover, I expected the mean dissimilarity to increase as spatial scale decreased for the reasons described above. To examine whether the observed dissimilarity was greater or less than null expectation, I used null model analysis to calculate a mean simulated dissimilarity and standard effect size (SES). I found the observed dissimilarity was significantly lower than the simulated dissimilarity at larger spatial grains, suggesting vegetation is more stable over time at those scales (Table 2.1). In contrast, vegetation change at smaller scales (< 100 m²) was not different than random expectation (SES: -0.84 to .07). At small scales there is greater stochasticity with higher rates of local extinction and colonization owing to the smaller number of individuals present, leading to greater compositional change over time (Glen & Collins 1993).

At 1000 m², the best predictor of dissimilarity over time was community type, with moist, silty sites (e.g. savannas) experiencing the greatest compositional change over time ($R^2 = 0.31$, p < 0.001). Silt % was the best predictor of compositional change at 400 m² ($R^2 = 0.13$, p < 0.01), while both silt % and quadratic transformed fire frequency were important at 100 m² (unique R^2 for silt % = 0.07, p < 0.01, unique R^2 for fire = 0.09, p < 0.01). The shared variance explained by both silt % and fire frequency was 0.04 at 100 m². Thus, the total explained variance in dissimilarity was relatively low. The importance of fire frequency increased as spatial scale decreased and fire frequency became slightly more important in explaining compositional change than silt % at 100 m². In general, silty, frequently-burned sites have experienced greater compositional change over time, in addition to greater changes in species richness and beta turnover.

NMS confirmed that compositional change for most plots has been relatively modest across ~20 years. In Figure 2.4, vectors connect the same plot to itself over time, and the length and direction of the vectors relates to the magnitude and direction of vegetation change, respectively. Only a few plots show substantial change over time; these plots occur on fire-suppressed sandhills and subxeric woodlands (Figure 2.4). In addition, the vectors are moving in multiple directions, indicating that there is no consistency in how plots are changing over time. NMS also revealed that there has been slight homogenization of the vegetation, indicated by a small constriction in the amount of ordination space occupied by all plots over time (Figure 2.5). Thus, plots have become more similar to other plots in their community composition. I attribute this to increased burning efforts in the last 20 years by land management agencies within the study region, thus shifting the vegetation to more fire-maintained than it had previously been.

Discussion

I examined how fire frequency and environmental context have influenced vegetation structure in longleaf pine communities over ~ 20 years. Vegetation change was dependent on the environmental context of the site, fire regime, and the spatial scale of observation. In general, the magnitude of vegetation change increased as fire frequency and silt percentage increased. Thus, on average, silty, frequently-burned sites have experienced greater changes in species richness, beta turnover, and Bray-Curtis dissimilarity than sandy, infertile sites. Environmental context was the most important predictor of vegetation change, while fire frequency explained additional variation, albeit less.

Other studies in frequently-disturbed grasslands have revealed environmental filtering is an important factor structuring plant species richness and composition over time. For example, Prober et al. (2013) found that rainfall explained 31-60% of the variation in plant species richness and plant cover in a grazing experiment in Australian woodlands, while grazing frequency explained only 3-8%. This finding is consistent with my work, which suggests local environmental parameters (e.g., soil properties) are better predictors of vegetation change over time than fire history in longleaf pine woodlands. This in part reflects the fact that environmental context can influence fire frequency, intensity, and behavior itself, with generally more fire on sites that have greater fuel accumulation. In addition, vegetation change may vary with environmental context in longleaf pine woodlands due to colonization and extinction dynamics, which are generally greater in silty, wet sites due to increased competition, a larger potential species pool, along with more frequent fire.

Vegetation change was also highly dependent on the spatial scale of observation. Species richness increased at large spatial scales over time, but declined at the smallest two scales (Table 2.1). I found the expected pattern of increases in beta species turnover and Bray-Curtis dissimilarity as spatial scale decreased. Using null model analysis, I documented that there has been significantly less change in dissimilarity over time at larger spatial grains (> 100 m²), while dissimilarity at smaller scales is no different than random expectation. This suggests vegetation change is more rapid at small spatial grains (10 m² and below) than at larger scales in this ecosystem. Over time, several 0.01 and 0.1 m² plots experienced complete replacement of species. At small scales, grassland plant communities are more stochastic, with greater amounts of local colonization and extinction. Turnover at small scales occurs at a faster rate than turnover of entire subpopulations at larger scales (1000 m², Glen & Collins 1993). In addition, environmental heterogeneity generally increases with spatial scale, thus environment filters on species composition become less important at small spatial scales (Williams 1943, Shmida & Wilson 1985, Crawley & Harral 2001, Field et al. 2009). Furthermore, I found that the correlation between fire frequency and Bray-Curtis dissimilarity increased as spatial scale decreased, suggesting that the influence of fire is strongest at small spatial scales in longleaf pine communities. As the number of fire events increases, so does the likelihood of new species colonizing through re-emergence from the seed or bud bank or dispersal into the site from surrounding areas (Overbeck et al. 2005), which likely contributes to high temporal turnover at small scales. Other studies have also suggested that the effects of fire frequency may be strongest at small spatial scales (Glitzenstein et al. 2003). My finding of high species turnover at small spatial scales is consistent with results from other longleaf pine studies and studies conducted in

other species-rich grasslands (Glen & Collins 1993, Herben et al. 1993a, b, van der Maarel & Sykes 1993, Sykes et al. 1994, Overbeck et al. 2005).

In general, the magnitude of compositional change (e.g., dissimilarity) was fairly modest, as indicated by the length of vectors in Figure 2.4, however, beta turnover and changes in species richness were substantial. I believe this initial contradiction can be explained by the frequency and abundance of species in the community at each time point. Longleaf pine communities are comprised of many infrequent, low abundance species (e.g., *Asclepias pedicelata*) and a small number of frequent and abundant species (e.g., *Aristida stricta*; Figures 6.1, 6.2, see Figure 5 in Kirkman et al. 2001, see Figure 4 in Keddy et al. 2006, Clark et al. 2008). Frequent, abundant species in this ecosystem are long-lived perennials with substantial belowground storage, allowing them to persist for years or even decades in the same location. In contrast, infrequent species are typically shorter lived or susceptible to local environmental change (e.g., soil moisture, *Drosera* spp.) or changes in fire frequency (e.g., "fire-followers", Lemon 1949). Thus, community composition has been relatively stable over time because the frequent, abundant species stay constant, while there is high turnover of infrequent species, which contribute little to the abundance weighted metric of community composition (Glen & Collins 1993, Herben et al. 1993b, Overbeck et al. 2005). The constancy of some species and high mobility of others over time suggests both deterministic and stochastic processes shape longleaf pine plant communities.

Since the magnitude of vegetation change varied across spatial scales, sampling at multiple spatial scales was crucial for identifying how longleaf pine communities had changed over time. If I had only examined richness patterns over time at 1000 m², I would have missed the signal of species lost at the two smallest spatial scales. Monitoring at multiple spatial scales not only has important implications for understanding ecological pattern and process, but also for

informing management agencies about best practices and in general for conservation planning (Boyd et al. 2008). This study is unique in that I examined turnover in plant species composition simultaneously in space and time. No studies to my knowledge have documented vegetation changes over time across multiple spatial grains in the longleaf pine ecosystem. My work and this approach helps to reveal the generality of processes structuring community patterns across scales in this ecosystem.

My work helps to inform land managers on the effectiveness of their fire management regimes in maintaining plant species richness over time. In most sites, species richness has increased over time at most or all spatial scales, likely due to increased fire frequency in the last 20 years relative to the original fire regime. This recent change to more frequent fire by most managers has resulted from a realization that frequent fire is necessary to maintain the ecological integrity of longleaf pine communities and increased efforts to get fire on the ground (Costanza 2010). Thus, land managers that have implemented more frequent fire in the last 20 years relative to previous management strategies, have been effective at maintaining plant species richness over time. In addition, increased burning efforts in the last 20 years have resulted in slight homogenization of the vegetation over time, which I think reflects a state of fire-maintained vegetation. However, not all land management agencies has increased burning efforts in the last 20 years. I documented a decrease in species richness over time at small scales on one site, the Green Swamp Preserve. In the last fifteen years, the average fire-return interval changed from nearly annual fire for most of the 20th century to fire every two to three years. This change in the fire management regime has resulted in greater and more prolonger litter accumulation, which compounded with additional stress from long-term drought, is likely responsible for the

substantial loss of biodiversity at small spatial scales in the Green Swamp (see Chapter 3 for further discussion).

This work contributes to a growing pool of knowledge documenting how disturbance influences community structure in grassland ecosystems over longer temporal extents (Fuhlendorf & Smeins 1997, Glitzenstein et al. 2003, Spasojevic et al. 2010, Collins & Calabrese 2012), and reveals local environmental filtering is a key process that shapes plant diversity and composition over time. Furthermore, the magnitude of vegetation change I detected varied with spatial scale, suggesting that both ecological patterns and important processes in the longleaf pine ecosystem are scale dependent. I encourage future research to explore how fire regime and environmental context concurrently influence community structure over time in other portions of the longleaf pine ecosystem and in other fire-dependent grassland systems.

Tables

Table 2.1. Changes in species richness and beta-diversity from the 1990s to 2009 across multiple spatial grains in southeastern NC. Mean richness is the mean species richness in 2009 at each spatial scale, while Δ richness represents the mean change in richness across time. Mean turnover is the mean number of species lost and gained over time, while turnover range is the range of mean turnover. Mean β turnover is the mean turnover scaled by two times the mean species richness. Mean obs dissim is the mean Bray-Curtis or Sørenson dissimilarity of each plot to itself over time, while mean sim Dissim is the mean simulated dissimilarity of each plot to itself over time. Standard effect sizes (SES) were calculated using null model analysis to assess whether the observed dissimilarities were different than random expectation. This allowed for reflection on whether dissimilarity changed more or less than expected by random chance across scales. ** $p < 0.001$, * $p < 0.05$.

Area (m²)	Mean Richness	Δ Richness	Mean Turnover	Turnover Range	Mean β Turnover	Mean Obs Dissim	Mean Sim Dissim	SES
1000	59.1	6.3 **	20.4 **	0 to 50	0.16 **	0.21	0.36	-2.13
400	51.6	5.2 **	18.5 **	0 to 47	0.17 **	0.21	0.38	-2.20
100	36.3	4.7 **	15.7 **	0 to 45	0.20 **	0.25	0.57	-4.24
10	20.9	2.8 **	12.4 **	0 to 45	0.29 **	0.81	0.84	-0.25
1	11.9	.9 *	8.9 **	0 to 37	0.38 **	0.85	0.84	0.07
0.1	5.6	-.03	5.8 **	0 to 28	0.51 **	0.74	0.87	-0.84
0.01	2.0	-.3 *	3.3 **	0 to 14	0.77 **	0.84	0.93	-0.51

Table 2.2. Mean species richness, raw turnover (mean number of species lost and gained) and beta turnover (raw turnover/2*mean species richness) summarized by community type at 100, 400, and 1000 m² in southeastern NC. Silty, frequently burned community types (savannas, silty woodlands) have experienced more turnover than xeric, sandy community types (subxeric woodlands, sandhills).

Community Type	Area (m²)	Mean Richness	Raw Turnover	Beta Turnover
Savanna	1000	88.3	29.57	0.17
	400	80.0	28.29	0.18
	100	58.1	25.18	0.22
	10	34.8	22.41	0.33
	1	19.4	16.61	0.43
	0.1	8.8	11.42	0.66
	0.01	3.2	6.33	1.24
Silty Woodland	1000	78.5	28.63	0.18
	400	68.8	26.05	0.19
	100	48.3	22.36	0.23
	10	27.2	17.00	0.31
	1	15.5	11.37	0.36
	0.1	7.1	6.95	0.53
	0.01	2.7	3.96	0.87
Flatwood	1000	51.7	19.00	0.18
	400	44.2	16.61	0.18
	100	30.9	12.50	0.20
	10	18.7	9.88	0.26
	1	11.2	8.07	0.36
	0.1	6.3	5.49	0.44
	0.01	2.6	3.80	0.92
Subxeric Woodland	1000	33.0	7.40	0.11
	400	30.0	7.20	0.12
	100	21.1	6.67	0.16
	10	11.3	5.60	0.26
	1	6.3	4.09	0.35
	0.1	3.8	3.26	0.48
	0.01	1.9	2.55	0.77
Sandhill	1000	22.8	6.80	0.13
	400	18.4	6.00	0.16
	100	14.3	5.70	0.21
	10	6.9	4.26	0.32
	1	3.3	3.50	0.62
	0.1	2.0	2.80	0.83
	0.01	1.0	2.00	1.00

Table 2.3. Number and types of species gained and lost over time summarized by growth form at 1 and 1000 m² in southeastern NC. Gained / Lost Ratio is the total number of species in each growth form gained over time / the total number of species in each growth form lost over time. Ratios of > 1 indicate gains surpass losses, while ratios of < 1 indicate more species have been lost than gained. Dissim at 1000 m² is the mean Bray-Curtis dissimilarity of plots to themselves over time for each growth form individually. Most types of species have turned over across time, but especially small-statured herbaceous species, such as caulescent herbs, rosette herbs, and single-culm graminoids. In addition, there has been high turnover of hemiparasites, geophytes, and insectivores. Ferns, subshrubs, and matrix graminoids have been relatively stable over time.

Spatial Grain	1000 m²	1 m²	1000 m²
Growth form	Gained / Lost Ratio	Gained / Lost Ratio	Dissim
caulescent herb	1.8	1.1	0.48
clubmoss	1.7	2.2	0.43
matrix graminoid	3.3	1.5	0.20
fern	6.0	1.6	0.19
geophyte	0.4	0.4	0.70
hemiparasite	0.5	0.3	0.80
insectivore	1.6	0.3	0.60
legume	1.4	1.5	0.46
rosette herb	2.1	1.2	0.49
shrub	3.7	1.8	0.35
single-culm graminoid	1.2	1.1	0.62
subshrub	1.8	1.3	0.19
tree	2.3	1.6	0.46
vine	4.5	4.4	0.51

Figures

Figure 2.1. Study area in the outer Coastal Plain of North Carolina showing plot locations of 59 CVS plots.
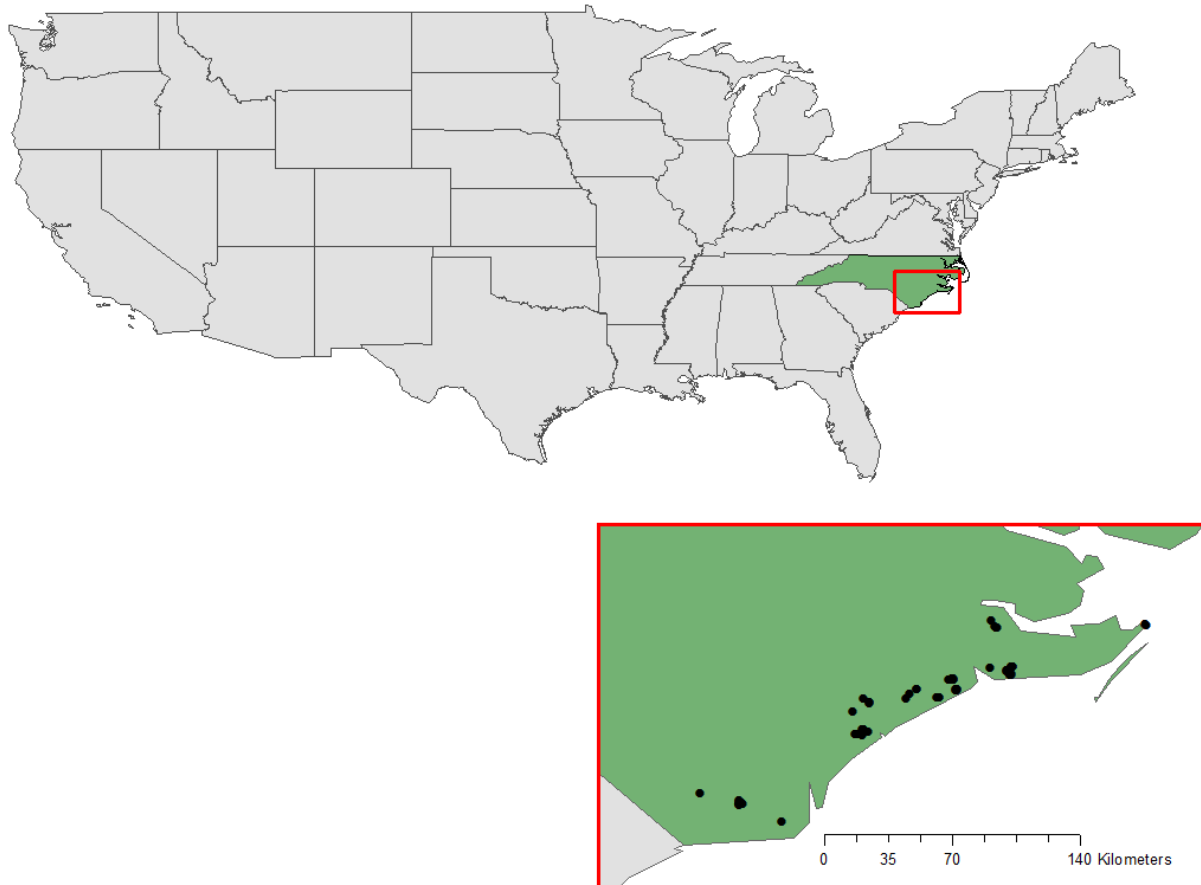
Figure 2.2. Longleaf pine vegetation partitioned into broad community types based on soil moisture and soil silt percentage (Adapted from Peet 2006). Silty woodlands and savannahs are the most species-rich and occur on fine-textured ultisol soils with relatively high silt content, although savannas are wetter. Flatwoods contain a spodic horizon below the surface, despite a mostly sandy substrate. Subxeric woodlands, also occur on sandy substrates, but are drier than flatwoods and often contain dry-site oaks. Sandhills occur on the driest, sandy sites, have sparse herbaceous layers, oak co-dominance in the over-story, and very low species richness.
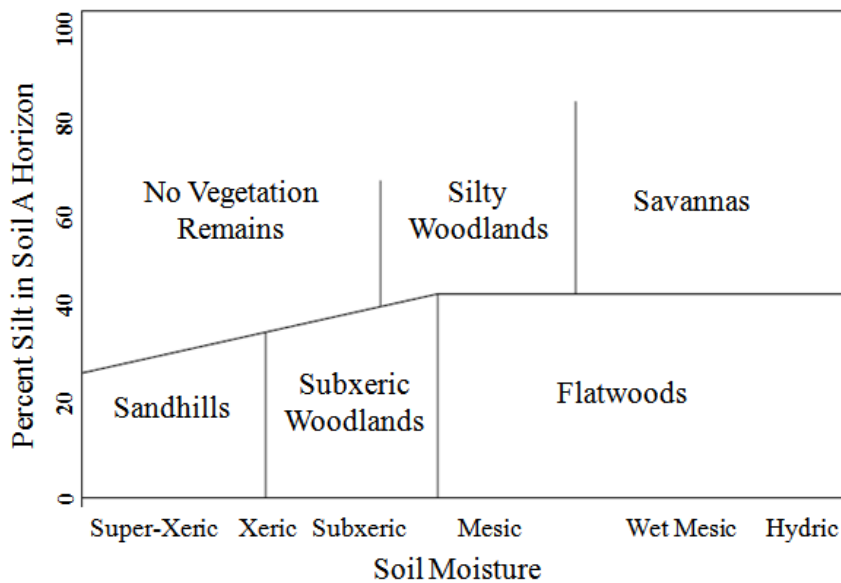
Figure 2.3. Change in species richness over time at 1000 m² versus silt percentage and fire frequency. In general, silty, frequently burned sites have gained a greater number of species over time. However, plots that have experienced the greatest fire frequency have lost species over time because of recent changes in the fire management regime on those sites. Here the R^2 values represent the variance explained by each predictor alone without additional predictors in the model.
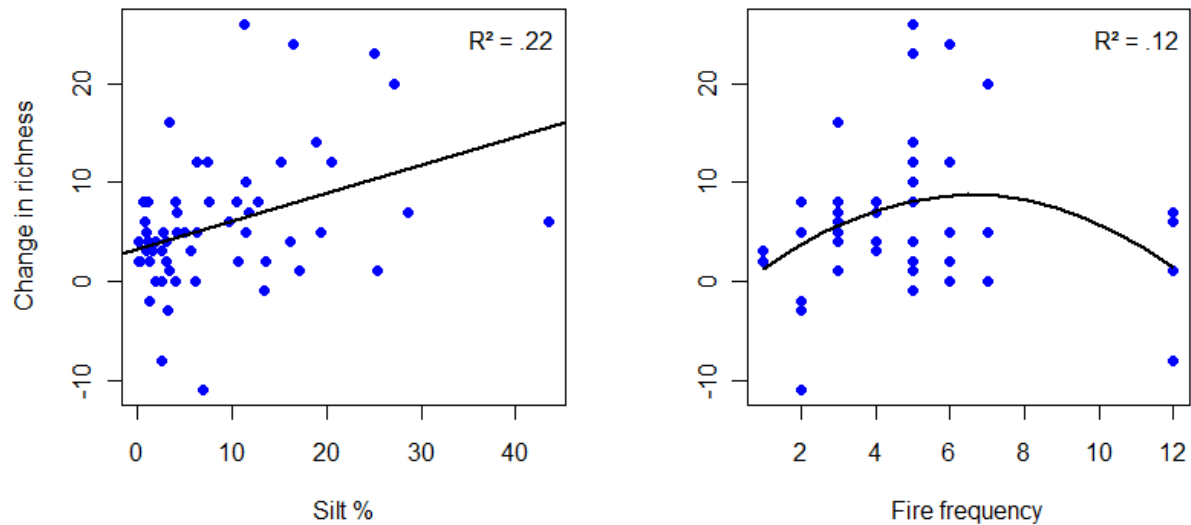
Figure 2.4. NMS ordination showing changes in community composition (Bray-Curtis dissimilarity) over time for different community types, represented by the length of vectors. Vectors connect the same plot over time. Compositional change is modest, expect for two plots in the lower left corner. Environmental vectors indicate the directions of increases in organic matter (om), silt %, sand %, fire frequency, and pH across compositional space. Compositional change over time has been greatest on sites with high sand content and high fire return intervals (e.g., infrequently burned sandhills and subxeric woodlands).
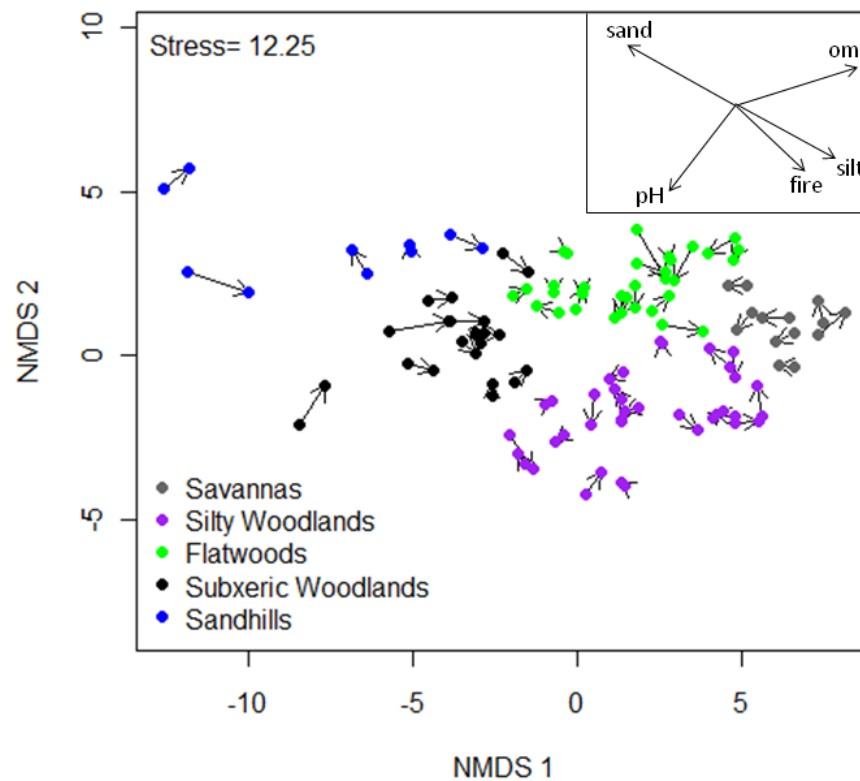
Figure 2.5. A. NMS ordination highlighting plots by sampling year (1990s, 2009). Lines outline the amount of ordination space occupied by plots in each year. The total amount of area occupied by plots in 2009 has contracted slightly from 1990. B. The average dissimilarity for each plot to all others plots in 1990 vs. the average dissimilarity of each plot to all other plots during 2009. The gray line indicates the 1-1 line. Most plots fall below the 1-1 line, indicating that there has been convergence of community composition over time.
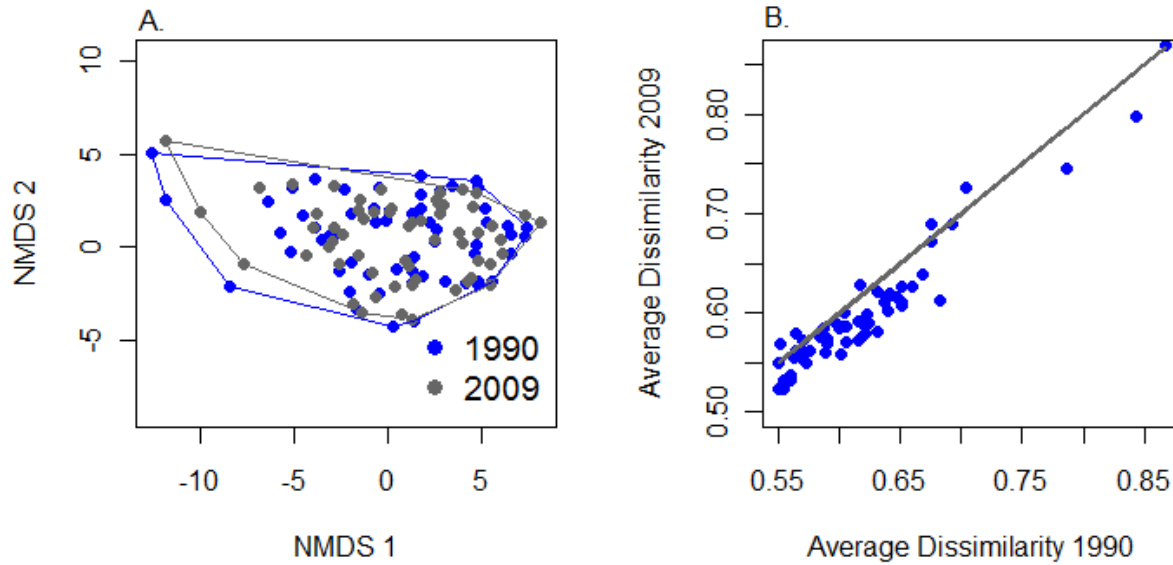
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CHAPTER 3: CHANGES IN PLANT SPECIES RICHNESS FOLLOWING REDUCED FIRE FREQUENCY AND DROUGHT IN ONE OF THE MOST SPECIES-RICH SAVANNAS IN NORTH AMERICA

Abstract

In species-rich grasslands, disturbance and environmental filtering are two key processes that shape plant species richness and composition. Alteration of disturbance regimes and environmental change can result in significant changes in community structure, often with long-lasting consequences. Here I address three issues. 1) How have plant species richness and frequency changed over two decades in one of the most species-rich savannas in North America? 2) Is an altered disturbance regime, environmental stress, or both responsible for these changes? 3) In what ways can the changes observed in this savanna inform management of other species-rich communities? In 2011-2013, I re-surveyed permanent plots established in the 1980s and 1990s in a longleaf pine (*Pinus palustris*) savanna in the Green Swamp Preserve, North Carolina to quantify changes in species richness at a range of spatial scales following 15 years of reduced fire frequency plus periodic drought. For comparison, I re-sampled other longleaf pine savannas in the region that had not experienced reduced fire frequency, but had experienced long-term drought. I identified which types of species were lost and gained, and summarized changes in species frequency by growth form, plant height, and habitat affinity. I detected substantial declines in small-scale species richness and species frequency from the 1980s to 2011, representing a loss of 33% to 41% of the flora, depending on the spatial scale. Small herbaceous species had become particularly scarce. Additional re-sampling in the wetter years of 2012 and

2013 after two consecutive years of annual fire revealed species richness had increased slightly

from 2011, but was still considerably lower than species richness in the 1980s. Other savannas

did not exhibit such dramatic declines in species richness. Reduced fire frequency and drought

appear to have contributed to species loss over time. This work suggests that nearly annual fire is

necessary for the maintenance of plant species richness in mesic longleaf pine savannas and even

a modest reduction in fire frequency can have dramatic negative impacts. This study also

suggests that drought is an important factor structuring grassland ecosystems in the southeastern

US, despite relatively high regional precipitation. I believe these findings can be generalized to

other species-rich grasslands in the world, which are also sensitive to changes in disturbance

regimes and may require frequent disturbance to maintain plant species richness.

Introduction

In species-rich grassland ecosystems, natural disturbance (e.g. fire, grazing) or processes

that mimic natural disturbance through the removal of aboveground biomass (e.g. mowing) are

essential for the maintenance of species richness, community structure, and rare species (Collins

et al. 1998, Glitzenstein et al. 2003, Fidelis 2010, Peet et al. 2014). Frequent disturbance

generally increases species richness by reducing the abundance of dominant species, increasing

resource availability in the form of light, space, and nutrients (Kirkman et al. 2004), and

resulting in a shift from asymmetric competition for light to more symmetric below-ground

competition (Peet & Christensen 1988, Wilson et al. 2012, Peet et al. 2014). In addition to

disturbance, grassland community structure is influenced by seasonal, periodic, and multi-year

drought events (Gibson & Hulbert 1987), which can have prolonged consequences (Haddad et al.

2002). At local scales, drought can result in declines in plant biomass and species richness, and

shifts in community composition (Tilman and Haddi 1992, O'Connor 1995, Haddad et al. 2002, Cheng et al. 2011).

Many species-rich grassland ecosystems are experiencing anthropogenic alterations of disturbance regimes (changes in frequency, timing, intensity, or severity of disturbance) that have long-term impacts on ecosystem structure and function. These impacts vary depending on the magnitude and direction of alteration, but may result in the loss of species richness and changes in community composition and stand structure (Heyward 1939, Belsky 1992, Glitzenstein et al. 2003). In addition, changes in disturbance regimes are often compounded with habitat destruction, fragmentation, or altered environmental conditions (e.g. nitrogen deposition, climate change), resulting in additional pressure on grassland plant communities (Leach & Givnish 1996, Stevens et al. 2011, Potts et al. 2012).

Longleaf pine (*Pinus palustris*) savannas are fire-dependent, species-rich grasslands located in the southeastern US, currently influenced by multiple stressors (e.g. fire suppression, drought, habitat destruction, and habitat fragmentation). Habitat conversion and long-term fire suppression have collectively reduced the longleaf pine ecosystem to only 2-3% of its acreage at the time of European settlement (Outcalt & Sheffield 1996, Frost 2006). Plant species richness within the herbaceous layer can be exceptionally high, and at small scales represents the highest values ever recorded in North America (52 species in 1 m², Walker & Peet 1983, Peet et al. 2012, Peet et al. 2014) and approaches world-record levels (Wilson et al. 2012). Fire is an important factor responsible for the maintenance of species richness within longleaf pine savannas, and is essential for the survival of small-statured species within the dense grass matrix (Walker & Peet 1983, Glitzenstein et al. 2003, Kirkman et al. 2004). Drought events occur periodically in longleaf pine savannas, most often in early spring (March-May, Noss 2013),

though little research has investigated how drought influences species richness in these systems (but see Myers & Harms 2011), despite recognition of the importance of drought in other grassland ecosystems (Cleland et al. 2013). In addition to periodic water stress, the southeastern Coastal Plain of the US in which these systems are embedded has been experiencing ongoing, long-term drought over the last 25 years (Figure 3.1). I believe that both periodic and multi-year drought events may be underappreciated, yet important drivers of community structure in longleaf pine savannas.

I used a unique, long-term, multi-scale data set from Big Island Savanna of the Green Swamp Preserve, NC to explore how drought and fire regime have shaped plant species richness over time. Big Island Savanna has been considered one of the most species-rich and high-quality longleaf pine savannas on the Coastal Plain of the southeastern US (McIver 1981, Frost et al. 1986). This site is the source of the North American records of 42 species in 0.25 m² and 52 species in 1 m² (see Peet et al. 2012, 2014), values which rival those reported for other species-rich grasslands throughout the world (Kull & Zobel 1991, Cantero et al. 1999, Klimes et al. 2001, Dengler et al. 2009, 2012, Wilson et al. 2012). The existence of long-term plot records that span multiple spatial scales presents a unique opportunity to document changes in richness and composition. Big Island Savanna experienced a planned shift in its fire management regime from nearly annual fire from at least 1940 to 1997 (Kologiski 1977, Rome 1988) to a fire-return interval of 2 to 3 years during 1997-2011. Although fire frequency has changed only modestly, this shift may have had significant impacts on species richness as Big Island Savanna had for decades before experienced a constant fire management regime.

To explore the impact of reduced fire frequency and drought on plant species richness in Big Island Savanna, I re-sampled two sets of permanent vegetation plots established over 25 and

20 years ago. For comparative purposes and to explore the impact of drought on other longleaf pine savannas, I also re-sampled plots on other species-rich longleaf pine savannas in the region that had not experienced reduced fire frequency. Specifically, I asked:

1. Have species richness and species frequency in Big Island Savanna changed in response to reduced fire frequency and drought?

2. What is the relative importance of reduced fire frequency versus drought in driving changes in species richness and frequency in Big Island Savanna?

3. In what ways can the changes observed in this savanna inform management of other species-rich grasslands?

It is critical that I assess how changes in long-standing fire regimes, compounded with additional stress from drought have influenced plant species richness in this savanna, which, unlike most other longleaf pine sites, did not experience post-colonial fire-suppression. From a conservation perspective, Big Island Savanna is irreplaceable within the greater landscape. Moreover, this work has implications not only for fire managers in the longleaf pine ecosystem, but for managers and researchers who study other chronically disturbed, species-rich grassland ecosystems.

Methods

Study Area

The Green Swamp Preserve is located in Brunswick County, in the southeastern corner of the North Carolina Coastal Plain (34° 5' N, 78° 18' W) and covers approximately 6,700 hectares. The majority of the site consists of shrub-dominated ombrotrophic peatland (pocosin), within

which occur scattered islands of savanna on mineral soil (Kologiski 1977). Elevation ranges from 12 to 25 m above sea level, with very little topographic relief. However, small differences in elevation (> 0.2 meter) have major consequences for hydrology, soil properties, and hence vegetation (Rome 1988, Christensen 2000). The climate is humid sub-tropical, with an average mean annual temperature of 15.5 °C and an average annual precipitation of 160 cm, most of which occurs during the growing season (Ruffner 1985, State Climate Office of North Carolina). Droughts occur periodically in the region (mostly during the months of March-May) and result in at least temporary loss or dormancy of species dependent on moist soils (Kologiski 1977, Christensen 1981). Savanna soils in the Green Swamp are typically Leon series, which are derived from acidic, fine-textured, nutrient-poor, marine sediments. They are generally poorly drained, with the water table within 25 cm of the soil surface for 1 to 4 months of the year (Kologiski 1977).

This study focused primarily on a single, 30 ha savanna in the Green Swamp: Big Island Savanna. During the 18th-19th centuries, Big Island Savanna likely burned almost annually due to the flatness of the landscape, the great size of the fire compartment, and the flammability of the vegetation (Frost 2006). Written records indicate annual, late-winter fire was implemented in Big Island Savanna for much of the 20th century, from at least and likely prior to 1940 through 1997 (Kologiski 1977, Rome 1988). Thereafter, the fire management regime shifted to a mix of growing-season and dormant-season fires with a return interval of 2 to 3 years. Thus, over the 15 years prior to this study, fire-frequency was lower than had been the case with the traditional management strategy. This shift reflected an effort by managers to return to what has recently been perceived as a more "natural" fire regime with somewhat less frequent fires timed later in the growing season when natural ignition is more likely (Frost et al. 1986, Huffman 2006).

I also examined long-term changes in species richness and composition on other sites besides Big Island Savanna, including other savannas in the Green Swamp Preserve, Holly Shelter Game Lands, Croatan National Forest, and Camp Lejeune Marine Corp Base, to determine how long-term drought has impacted savanna vegetation on similar sites in the region (Figure 3.2). All of these sites have experienced long-term drought, but not reduced fire frequency. However, some sites have likely experienced somewhat more frequent fire over the last 20 years relative to the original fire management regime (e.g. Camp Lejeune, Croatan National Forest), although long-term fire history data for these sites are lacking. In contrast, fire frequency has remained relatively constant over time on other sites (other savannas in the Green Swamp Preserve, Holly Shelter Game Lands). Here, I focus on comparing changes in species richness and frequency patterns in Big Island Savanna to other environmentally similar sites that have experienced drought but not changes in fire frequency (other savannas in the Green Swamp and Holly Shelter Game Lands). I more thoroughly explore patterns of species richness and composition over time with relation to fire frequency and environmental context on these comparison sites in another study (Palmquist 2014, Chapter 2).

Sampling Design

Two different sampling protocols were used to examine changes in species richness and composition over time in Big Island Savanna, which reflect the designs of the two separate studies that I re-sampled. The first study (study 1; see Sykes at al. 1994) was based on plots established and surveyed annually during June of 1985-1989, with a sixth sample in 1994. In June 2011, I re-sampled six of the original 2.5 m² plots (see Sykes et al. 1994 for details of plot configuration), each of which contained 10 0.25 m² subplots. Three of the six plots were control plots and 3 had received sugar additions twice a year to reduce nutrient availability during 1985-

1989. The sugar additions had no noticeable impact. Each plot was permanently marked in 1985 with steel conduit and each 0.25 m² subplot was delineated with steel nails, which ensured I sampled the same physical location over time. Within each subplot, vascular plant species presence was recorded in five permanent 0.01 m² and five permanent 0.001 m² plots. This resulted in 300 observations of 0.001 m^2, 300 observations of 0.01 m^2, 60 observations of 0.25 m^2, 12 observations of 1 m^2, and 6 observations of 2.5 m^2. For consistency, plots were re-sampled in June, 4 to 5 months after fire during all sampling years. These data are archived in Dryad.

The second study (study 2) was conducted in Big Island Savanna in June of 1993 by the Carolina Vegetation Survey (CVS) using the protocol described by Peet et al. (1998, 2012). In June 2011, 4 CVS plots were re-located and re-sampled. CVS plots are 1000 m² (20 x 50m) with smaller sub-plots nested within. Similar to study 1, each CVS plot was permanently marked with 10 pieces of steel conduit. Once the plot was re-located, presence of all vascular plant species was recorded at seven spatial scales in permanent subplots (0.01 m², 0.1 m², 1 m², 10 m², 100 m², 400 m², 1000 m²; see Peet et al. 1998, 2012 for details of plot layout). All plots in Big Island Savanna were located approximately 50 to 300 m from one another. In addition, 22 1000 m² CVS plots established during 1991-1993 on other sites with similar soils and species composition were re-sampled in 2009-2010 (study 3). All 26 CVS plots are archived in VegBank (http://vegbank.org/cite/VB.ds.199852.Palmquist2014GreenSwamp).

Analysis

Prior to analysis, all taxonomic names were standardized across the sampling years to ensure that changes in nomenclature, taxonomic resolution, and taxonomic understanding of the

flora across time were not affecting the number or identity of species detected. Species richness was calculated at each spatial scale for all three data sets (study 1: 0.001 m², 0.01 m², 0.25 m², 1 m², 2.5 m², study 2 and study 3: 0.01 m², 0.1 m², 1 m², 10 m², 100 m², 400 m², 1000 m²). I used the same analytical methods for all three data sets, but analyzed them separately. Linear models and linear mixed effects models were used to detect significant changes in species richness at each spatial scale in 2011 relative to richness at each spatial scale during 1985-1994. Random intercepts models, a type of mixed effects model, were used to examine richness at all spatial scales, except the full plot size as multiple estimates of richness for these scales were drawn from the same plot. This modeling approach accounted for spatial auto-correlation caused by the nested nature of the data (Zuur et al. 2009). In each random intercept model, species richness in the 1980s was regressed against species richness in 2011-2013 using an offset function. The unique plot identifier for each subplot was set as a random effect, to account for spatial autocorrelation between subplots in the same plot. Linear models were used to examine changes in richness over time for the full plot (2.5 m² and 1000 m², respectively, for study 1 and studies 2 and 3). All statistical analyses were performed in R v.2.15.2 using the nlme package (R Core Development Team 2012). Results reported for Big Island Savanna at 2.5 m² and below were calculated from study 1, whereas results reported at scales > 2.5 m² were from study 2.

To quantify drought over the long-term and to identify individual drought years, I obtained monthly Palmer Drought Severity Index (PDSI) and monthly Palmer Z Index (PZI) data for 1970-2013 from the Southeastern Coastal Plain of North Carolina (National Climatic Data Center 2013). PDSI quantifies the duration and strength of long-term drought, whereas PZI is more sensitive to short-term pulses of water and reflects whether moisture conditions deviate from normal (short-term drought). I identified the sampling years of 1985, 1986, and 2011 as

significant drought years (Figure 3.1). To determine if changes in richness across time were due to individual drought years, I examined whether there were significant differences between richness values in drought and non-drought years. I also explored whether species richness values from 2011 were lower than richness in early drought years, which would suggest that other factors (e.g. reduced fire frequency) had influenced species richness over time.

In addition to examining changes in species richness, I investigated which species were lost and gained over time by tabulating the total number of times a species occurred at each spatial scale in every year. I summarized this information as both the mean number of species and as the percentage of subplots occupied by each species in each year. I compared the identity and frequency of species lost in earlier drought years to those lost in 2011. I expected insectivores in particular to decrease over time in response to drought, as they have been shown to be particularly sensitive to drought in other longleaf pine studies (e.g. Folkerts 1982) and became substantially less abundant during the drought years of 1985 and 1986 in my data set. I also expected 'wet' and 'mesic' species to be lost to a greater extent if drought alone was responsible for changes in species richness and identity, as 'dry' species could likely tolerate and survive drought (see Debinski et al. 2013). In addition, I expected shrubs, trees, and vines to increase over time in abundance and frequency in response to reduced fire frequency and rosette herbs, geophytes, and other small herbaceous species to decrease, as these groups have previously been shown to be sensitive to fire suppression (Glitzenstein et al. 2003, Glitzenstein et al. 2012). To identify which types of species became more or less frequent over time and whether those changes were related to drought or reduced fire frequency, I classified species in three ways. First I assigned species to one of twelve mutually exclusive growth-form categories (caulescent herb, matrix graminoid, fern, geophyte, hemiparasite, insectivore, legume, rosette

herb, shrub, single-culm graminoid, subshrub, tree, and vine, see Table B.1 for growth form

definitions) and then examined how the frequency of each growth form changed over time.

Second, I categorized species according to their maximum height (short = most plant growth

below 4dm, tall = most plant growth above 4dm) to examine whether short-statured species were

preferentially lost over time, suggestive of competitive exclusion caused by reduced fire

frequency. Third, to determine whether species with environmental optima in mesic or wet

environments were preferentially lost relative to species with optima in dry environments, I

assigned species to a categorical habitat optimum (dry, mesic, wet) based on Weakley (2012) and

my own knowledge of the 96 species in the data set.

To further disentangle the impacts of drought and reduced fire frequency on changes in

species richness and frequency over time, I used two approaches. First, I quantified changes in

richness over time at other sites on the Southeastern Coastal Plain in North Carolina that have

also recently experienced long-term drought. These sites are similar to Big Island Savanna in that

they occur on Ultisol soils and have similar hydrologic and soil properties, but differ in that they

have not experienced reduced fire frequency in the last 20 years. In contrast to Big Island

Savanna, they have generally been burned consistently or somewhat more frequently (every 2-4

years) over the last 20 years relative to the previous fire management regime. If changes in

species richness over time in other sites were similar to those in Big Island Savanna that would

suggest long-term drought had strong effects on species richness in the region. Second, I re-

sampled all plots in Big Island Savanna again in 2012 and 2013, which were wetter years than

2011 (Figure 3.1). In addition, annual fire was returned to Big Island Savanna in 2011-2013,

specifically to facilitate this study. Thus, the re-sampling events in 2012 and 2013 allowed me to

assess the extent of species richness recovery, if any, after consecutive years of fire and greater water availability.

Results

Species Richness and Frequency Patterns over Time

At all spatial scales species richness in Big Island Savanna was lower in 2011 compared to all other sampling years, and significantly lower for small spatial scales (≤ 2.5 m²; Figure 3.3, Table 3.1). These declines at small scales are exceptional and represent a loss of between 32.7% and 40.8% of the flora, depending on the spatial scale in question (Table 3.1). In contrast to small scales, richness at larger spatial scales (≥ 10 m²) declined less substantially over time, representing losses of 1.2 to 14.7% of plant species (Table 3.1).

In 2011, most species had become less frequent in subplots in Big Island Savanna, though these declines were most extreme at ≤ 1 m² (Tables B.1, B.2, B.3). In particular, small-statured, herbaceous species exhibited the greatest decrease: insectivores (1.2 of 11.5 species lost on average at 0.25 m²), single-culm graminoids (2.3 of 11.5 species lost on average), rosette herbs (4.3 of 11.5 species lost on average), and caulescent herbs (1.8 of 11.5 species lost on average; Tables 3.2, B.2). Geophytes, matrix graminoids, and hemiparasites also decreased in frequency in 2011 relative to earlier years, but less substantially (0.6, 0.8, and 0.2 species lost on average; Tables 3.2, B.2). Legumes and shrubs increased slightly in 2011, while tree species remained constant in frequency (Tables 3.2, B.1, B.2, B.3). However, *Pinus palustris* seedlings shifted from occupying 21.7% of 0.25 m² subplots in 1985 to 3.3% of subplots in 2011 (Table B.2). Both short (< 4dm) and tall (> 4dm) plant species became less frequent in 2011, but short plants became particularly scarce (8.6 short species lost on average versus 3.5 tall species lost on

average; Table 3.2). In contrast to expectation, species with their habitat optimum in wet environments decreased very little over time, whereas species with their habitat optimum in mesic and dry habitats became substantially less frequent (9.3 and 1.6 species lost, respectively; Table 3.2).

Species Richness and Frequency in Drought vs. Non-drought Years

To determine whether the loss of species across time was due to the 2011 drought, I compared patterns of species richness and frequency from 2011 to the earlier drought years of 1985 and 1986. Mean species richness was substantially lower in 2011 than in either 1985 or 1986 at small scales, 0.01 m² (5.1 versus 10), 1 m² (26.4 versus 40.8), and 2.5 m² (33.6 versus 47.2; Figures 2, 3). In fact, mean richness at small scales during 1985 and 1986 was more similar to richness in non-drought years (1987, 1988, 1989, 1994), than richness in 2011 (Figures 2, 3). The percent of subplots occupied by most species in 2011 was considerably lower than earlier drought years, especially for rosette herbs and single-culm graminoids (Tables 3.2, B.1, B.2, B.3). Species lost during the droughts of 1985 and 1986 spanned several growth form categories and included both tall shrub species (e.g. *Ilex glabra*, *Morella carolinensis*), and smaller statured herbaceous species (e.g. *Viola primulifolia, Polygala lutea*). Insectivores decreased dramatically during both the 2011 and 1985-1986 droughts, suggesting these species are more sensitive to short-term changes in moisture availability than other species in longleaf pine savannas.

Disentangling the Effects of Long-term Drought and Reduced Fire Frequency

To parse the relative effects of long-term drought and reduced fire frequency, I compared changes in species richness over time at other sites in the Southeastern Coastal Plain of North Carolina to the patterns I observed in Big Island Savanna. Species richness did not decrease at

most spatial scales in environmentally similar sites that also experienced long-term drought (Table 3.3); in fact many sites gained species. Increases in species richness were generally greater on sites that had experienced slightly more frequent fire over the last 20 years relative to the original fire management regime (Camp Lejeune Marine Corp Base, Croatan National Forest; Table 3.3). However, species richness also increased or remained constant at most spatial scales on sites with consistent fire frequency (other savannas in the Green Swamp Preserve, Holly Shelter Game Lands; Table 3.3). When species loss was detected on other sites, the magnitude of loss was substantially less than that detected at Big Island (-4.76 species lost at 0.01 m² in Big Island Savanna, versus -1.08 in Holly Shelter; Table 3.3).

I re-sampled subplots in Big Island Savanna in 2012 to determine whether species richness had recovered with two consecutive years of fire and somewhat wetter conditions (Figure 3.1). Richness in 2012 increased significantly relative to 2011 at all spatial scales except the smallest, which remained stable (Table 3.1). In addition, most species became more frequent in subplots in 2012, especially insectivores and single-culm graminoids, which increased by 15.4% and 8.8%, respectively at 0.25 m² (Tables 3.2, B.2). Very few species decreased in frequency between 2011 and 2012, except one species of club moss (*Lycopodiella appressa*, 18.3% decrease at 0.25 m²), one single-culm graminoid (*Scleria minor*, 8.3% decrease at 0.25 m²), and one rosette herb (*Aletris farinosa*, 6.7% decrease at 0.25 m²; Table B.2). Although species richness rebounded some in 2012, the increase at small spatial scales (2.5 m² and below) was not nearly great enough for recovery to 1985-1994 levels (i.e. species loss from 1994 to 2011 substantially exceeded species gain from 2011 to 2012; Table 3.2).

I observed that 2013 was a significantly wetter year than either 2011 or 2012 (Figure 3.1). In response to higher water availability and continued annual fire, species richness

increased from 2012 to 2013 at most spatial scales, although only slightly and often not significantly (Table 3.1). At the smallest spatial scale (0.001 m²), more species were gained from 2012-2013 than from 2011-2012, however at all other spatial scales the increase in species richness from 2012-2013 was substantially less than from 2011-2012 (Table 3.1, Figures 2, 3), which is surprising considering how much wetter 2013 was than 2012. Figure 3.4 shows that species richness patterns across years do not perfectly mirror changes in PZI over time. This is particularly noticeable for 2012-2013 when PZI increased dramatically, but richness did not. In contrast, richness increased substantially more from 2011-2012 despite only small increases in PZI, suggesting that species richness patterns are not solely being shaped by soil water availability and that species recovery is likely to be a slow process. Alternatively, it is possible that there is a time lag and species richness has yet to recover due to the wetter years of 2012 and 2013. A time lag may become apparent with continued monitoring of these permanent plots, if increased fire frequency is maintained. Most species increased slightly in frequency or remained constant from 2012 to 2013. However, insectivores and single-culm graminoids both increased dramatically (Tables 3.2, B.1, B.2, B.3). Despite some recovery of species richness in 2012 and 2013, species richness at small spatial scales is still far below the levels documented in the 1980s.

Discussion

The 2011 sampling event revealed large declines in species richness and species frequency in Big Island Savanna at small spatial scales (≤ 2.5 m², formerly 53 species in 2.5 m² and now 34 species, and formerly 42 in 1 m² and now 26, see Figure 3.3). Species loss was ubiquitous across most groups and extremely high for the small statured, herbaceous species that

constitute the bulk of plant species richness at this site. Despite modest recovery in 2012 and 2013, small-scale species richness remains far below the levels documented in 1985-1994.

This data suggests that both reduced fire frequency and drought have contributed to species loss in Big Island Savanna, perhaps in a complex and interactive manner. Determination of the degree to which reduced fire frequency versus long-term drought is responsible for this loss will only be fully clarified with continued monitoring of these plots and future experiments manipulating fire frequency. However, several lines of evidence suggest reduced fire frequency during the last 15 years is the primary factor driving species richness declines in Big Island Savanna. First, the declines in species richness and frequency in response to drought in 1985-1986 were substantially smaller than during the drought year of 2011, which suggests an additional factor, such as reduced fire frequency is responsible. Although individual drought events may result in small reductions in species abundance, short-term drought is unlikely to result in local extinction of species or large shifts in community composition (Grime et al. 2008). Second, the frequency of species that have a habitat optimum in wet environments has remained constant over time, which is contrary to my expectation that 'wet' species would be most sensitive to drought and would be lost preferentially if drought were the major factor influencing species richness patterns. This pattern is most likely a consequence of the 'wet' species being almost exclusively in the 'tall' group, reflecting the taller and lusher growth on wet sites. Third, reduced fire frequency in longleaf pine savannas and other fire-dependent grasslands results in the loss of small-statured species, which are competitively excluded as the abundance of woody species, ferns, and large grasses increases post-fire (Leach and Givnish 1996, Glitzenstein et al. 2003, Overbeck et al. 2005). The documented loss in 2011 of mostly small herbaceous species with dry to mesic habitat affinity is indicative of fire suppression. Finally, several species that are

known to be weak competitors, and/or highly dependent on fire (i.e. "fire-followers", Lemon 1949) decreased over time in Big Island Savanna (e.g. *Agalinis aphylla*, *Aletris farinosa*, *Aristida virgata, Calopogon* spp., *Cleistesiopsis divaricata*, *Dichanthelium strigosum*, *Drosera capillaris*, *Lycopodiella appressa*, *Pinguicula* spp., *Xyris ambigua*, Lemon 1949, Wilson & Keddy 1986, Gaudet & Keddy 1995, Brewer 1999 a, b, Keddy et al. 2006).

Further evidence suggests reduced fire frequency rather than drought is the primary cause of species loss. For example, other, environmentally similar sites within the region have experienced little if any species loss, despite having also been subjected to long-term drought. In fact, species richness at these sites has on average increased at most spatial scales, both on sites with somewhat increased fire frequency and those with consistent fire frequency (Table 3.3). Additionally, two consecutive years of fire at Big Island Savanna resulted in some recovery of species richness in 2012. Since 2012 was only slightly wetter than 2011, I attribute the increase in species richness in 2012 largely to two consecutive years of fire. However, long-term drought has likely contributed to species loss in Big Island Savanna and may explain why a few other sites in southeastern North Carolina have lost species at small spatial scales, albeit much less so than has been the case for Big Island Savanna (Table 3.3).

Species losses of the magnitude I observed at Big Island Savanna in response to alteration of disturbance regimes, compounded with additional stressors (e.g. drought, habitat fragmentation), have been reported in other species-rich grassland systems (Leach and Givnish 1996, Glitzenstein et al. 2012). Some work suggests that species richness may be slow to recover after stressful events, such as drought or fire suppression, due to a loss of local propagule sources, changes in the local environment or shifts in vegetation structure in which often woody, competitively superior species prevent the re-colonization of herbaceous species (Tilman and

Haddi 1992). Recovery following stressful events may be especially challenging in fragmented grasslands, such as Big Island Savanna, which is embedded within a matrix of ombrotrophic peatland, dominated by evergreen woody plants. For these reasons, species richness at small spatial scales on Big Island Savanna may take a significant amount of time to recover, especially in the presence of ongoing drought, and likely will not recover with continued reduced fire frequency.

The temporal and spatial breadth of this study was crucial for detecting changes in species richness in Big Island Savanna. Grasslands are structured by multiple processes that vary over space and time (e.g., fire, grazing, drought, see Collins and Smith 2006), and for this reason it is essential to quantify plant species richness patterns across multiple spatial and temporal scales. For example, previous work has suggested that fire frequency has the largest impact on species richness at small spatial scales (Glitzenstein et al. 2003, Collins & Smith 2006, Bowles & Jones 2013). Here, I document a scale-dependent response to changes in fire frequency and drought over time. Some combination of drought and reduced fire frequency have reduced the population sizes of most species in Big Island Savanna, resulting in reduced species packing at small spatial scales as there are now fewer individuals of each species present. If a nearly annual fire regime is not reinstated in Big Island Savanna, population sizes are likely to continue to decline, which may result in local extinction and declines in species richness at larger spatial scales, especially for already infrequent and rare species. This hypothesis of species loss trickling upward to larger spatial scales with continued fire suppression has been suggested previously in another longleaf pine study examining species richness patterns over time in relation to fire frequency (Glitzenstein et al. 2012). Had I examined species richness patterns only at 1000 m² in Big Island Savanna, I would have concluded that species richness had remained relatively stable

over time and that changes in the fire management regime and/or long-term drought had not affected vegetation patterns in this savanna (Table 3.1). Hence, monitoring at multiple spatial and temporal scales is critical for understanding patterns, identifying processes that drive those patterns, and informing conservation and land management agencies about best management practices.

One important finding from this study is that small changes in fire management regimes can have large and long-lasting consequences for plant species richness in longleaf pine savannas. This work suggests that very frequent to annual fire is probably necessary to maintain small-scale biodiversity and species packing in the most species-rich, moist savannas, especially in the face of additional environmental stress. I believe this work can be generalized to other species-rich grasslands that experience chronic or continuous disturbance (e.g. alvar grasslands in northern Europe, oligotrophic mowed meadows of eastern Europe, cerrado in Brazil, *Themeda triandra* grasslands in Australia, and mountain grasslands of central Argentina, Wilson et al. 2012). Some evidence from other species-rich systems also suggests that slight changes in disturbance regimes can have large impacts on plant biodiversity (Morgan 1999, Overbeck et al. 2005). In addition, this research indicates that land managers should proceed cautiously when making changes to long-standing management regimes, despite how well intentioned such changes might be, and assess impacts immediately after their implementation. Future work in other species-rich grasslands should both explore whether chronic and nearly continuous disturbance is necessary to maintain species richness and how slight alternation of disturbance regimes can affect plant species richness over time.

Both periodic and multi-year drought events are important factors that shape species richness and community composition patterns in the longleaf pine ecosystem and potentially

increase the risk of biodiversity loss with altered disturbance regime. Drought events have been recognized as important processes in many other grassland ecosystems (e.g. Tilman and Haddi 1992, Knapp et al. 2002, 2006, Anderson 2008, Evans et al. 2011, Cherwin and Knapp 2012). The severity and intensity of drought events in the southeastern US have increased in the last 25 years and are predicted to continue increasing with ongoing climate change (Klos et al. 2009). Thus, future research should explore further the relative and interactive contributions of drought and fire to changes in community structure and composition in the longleaf pine ecosystem as such knowledge will be critical for protecting these species-rich and threatened communities.

Although longleaf pine savannas, among many other grassland ecosystems, are dominated by long-lived perennial species, species richness and frequency in these ecosystems are surprisingly sensitive, both spatially and temporally, to environmental changes, alteration of disturbance regimes, and stochastic events (Sykes et al. 1994, Collins & Smith 2006). An unusually long history of detailed vegetation sampling at multiple scales in Big Island Savanna has enabled me to document complex changes in species richness in response to drought and reduced fire frequency. Additional studies in the longleaf pine ecosystem and other grass-dominated ecosystems are needed to more fully disentangle the complex and interactive effects of environmental change and altered disturbance regimes on spatial and temporal patterns of species richness. Moreover, understanding these complex relationships will be necessary to provide critical guidance to land managers responsible for conserving important biodiversity sites.

Table 3.1. Average number of species lost and gained over time at each spatial scale in Big Island Savanna from 1985 to 2013. Δ Richness 1985-1989 represents the mean change in species richness across scales between sequential observations in the original sampling. Δ Richness 1994-2011 is the change in species richness from 1994 to 2011, while Δ Richness 2011-2012 and Δ Richness 2012-2013 are the change in species richness from 2011 to 2012 and from 2012 to 2013, respectively. Double asterisks indicate $p < 0.0001$, single asterisks indicate $p < 0.05$, and single dots indicate $p < 0.10$. % Change is the percentage of species lost or gained over time relative to mean species richness.

Area (m²)	Δ Richness 1985-1994	% Change 1985-1994	Δ Richness 1994-2011	% Change 1994-2011	Δ Richness 2011-2012	% Change 2011-2012	Δ Richness 2012-2013	% Change 2012-2013
1000	--	--	-1	-1.2	5.8	6.7	1.5	1.7
400	--	--	-4.3	-5.6	7.5 *	9.4	0.5	0.6
100	--	--	-2.2	-3.9	7.4 **	12.1	0.9	1.4
10	--	--	-5.3 •	-14.7	7.6 **	19.8	-0.01	0.2
2.5	3.33	6.7	-16.3 **	-32.7	6.3 *	15.8	3.8 *	8.7
1	1.25	3.0	-15.5 **	-37	5.7 **	17.6	2.2	6.3
0.25	1.02	3.5	-11.5 **	-40.8	3.8 **	18.6	2.1 **	9.1
0.1	--	--	-5 *	-40.5	2.5 **	25.5	0.4	3.9
0.01	0.36	3.3	-4.8 **	-48.1	1.6 **	23.3	0.71 **	9.6
0.001	-0.33	-10.7	-1 **	-38.3	-0.03	0	0.24 *	13.6

Table 3.2. Mean number of species of different growth form, plant height (short < 4dm, tall > 4dm), and habitat affinity in 0.25 m² subplots in Big Island Savanna. Mean number of species in subplots is summarized for 1985-1994, for the drought years in the 1985-1994 interval (1985, 1986), non-drought years during 1985-1994, and 2011-2013. Small statured herbaceous species (e.g. rosette herbs, geophytes, caulescent herbs) have decreased in frequency from 1985-1994 to 2011-2013, while shrubs and vines have increased, suggestive of competitive exclusion caused by fire suppression.

	1985-1994	1985-1994	1985-1994	2011	2012	2013
Growth form	Mean	Drought year	Non-drought year	Mean	Mean	Mean
matrix graminoid	4.9	4.9	4.9	4.1	4.4	4.3
insectivore	2.3	2.0	2.4	1.1	1.4	2.2
single-culm graminoid	5.7	5.5	5.8	3.4	4.8	5.7
rosette herb	8.9	8.5	9.1	4.6	5.1	5.5
hemiparasite	1.4	1.3	1.4	1.2	1.4	1.4
clubmoss	1.0	1.0	1.0	1.0	1.0	1.0
subshrub	1.4	1.4	1.4	1.3	1.4	1.3
caulescent herb	3.5	3.4	3.5	1.7	1.9	2.3
geophyte	1.6	1.6	1.6	1.0	1.2	1.3
shrub	1.1	1.1	1.0	1.6	1.4	1.4
tree	1.0	1.0	1.0	1.0	1.0	1.1
legume	1.0	0.0	1.0	1.3	1.2	1.3
vine	0.0	0.0	0.0	0.0	1.0	1.0
Plant height	1985-1994	Drought year	Non-drought year	2011	2012	2013
short	15.5	15.0	15.7	6.9	9.7	12.0
tall	13.4	12.9	13.7	9.9	10.9	10.7
Habitat optimum	1985-1994	Drought year	Non-drought year	2011	2012	2013
mesic	17.9	17.3	18.2	8.6	11.0	12.9
dry	8.4	8.1	8.6	6.0	6.7	6.3
wet	2.6	2.4	2.7	2.5	3.0	3.4

Table 3.3. Mean change in richness (Δ richness) at three spatial scales from 1993 to 2009 for Ultisol savannas in the southeastern Coastal Plain of NC. Negative values indicate sites that have lost species over time, while positive values indicate sites that have gained species. Species richness has increased on Croatan National Forest and Camp LeJeune Marine Corp Base, perhaps owing to somewhat more frequent fire in the last 20 years relative to the original fire management regime. Species richness has remained constant or increased at all but the smallest spatial scale on other savannas in the Green Swamp Preserve and on Holly Shelter Game Lands, which have experienced constant fire frequency over the last several decades. Other environmentally similar sites experiencing long-term drought have not lost as many species as Big Island Savanna, suggesting long-term drought is not the primary driver of species loss in Big Island Savanna.

Site	Δ Richness .01 m²	Δ Richness 1 m²	Δ Richness 10 m²
Green Swamp- Big Island	-4.8	-15.8	-5.1
Green Swamp- Other Savannas	-0.8	0.3	3.1
Camp LeJeune Marine Corp Base	-0.2	3.5	5.8
Croatan National Forest	1.3	6.3	9.1
Holly Shelter Game Lands	-1.1	1.0	3.4

Figure 3.1. Mean annual Palmer Drought Severity Index (PDSI) and mean annual Palmer Z Index (PZI) from 1970-2013 for the southeastern Coastal Plain of North Carolina. PDSI and PZI values below 0 indicate drought years, whereas values above zero indicate non-drought years. PDSI quantifies long-term drought conditions, while PZI reflects short-term changes in water availability. The number of drought events has increased since 1980, as indicated by the black linear best-fit lines and a larger proportion of years below the dotted line.
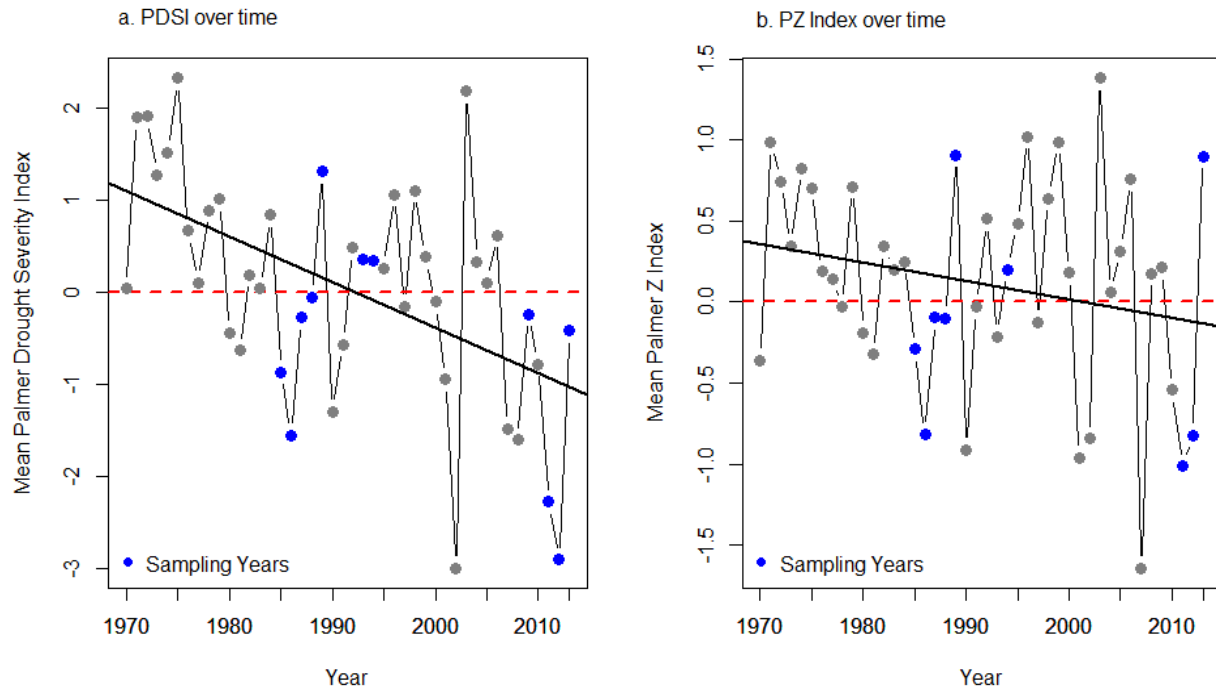
Figure 3.2. Plot locations in southeastern North Carolina, USA. Red x-marks indicate 8 plots located in the Green Swamp Preserve, which includes 4 plots in Big Island Savanna and 4 plots in other savannas. Black circles indicate 14 plots located in other environmentally similar sites.
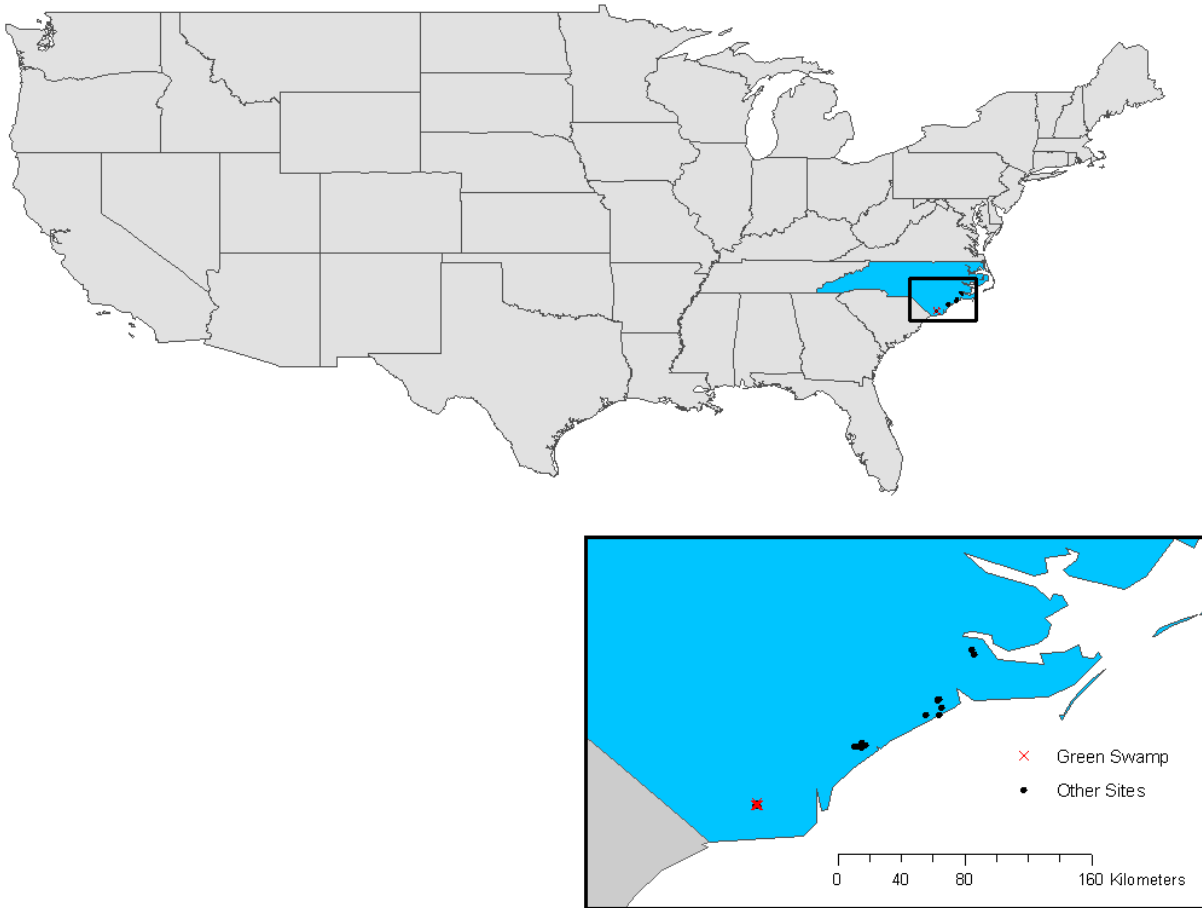
Figure 3.3. Mean species richness at each spatial scale in Big Island Savanna during 1985-1989, 1994, and 2011-2013. Richness has decreased significantly from 1994 to 2011 at all scales below 2.5 m². Although, I plot the linear trajectory between 1989 to 1994 and 1994 to 2011 (denoted with a dashed line), the variation in species richness within these intervals is unknown.
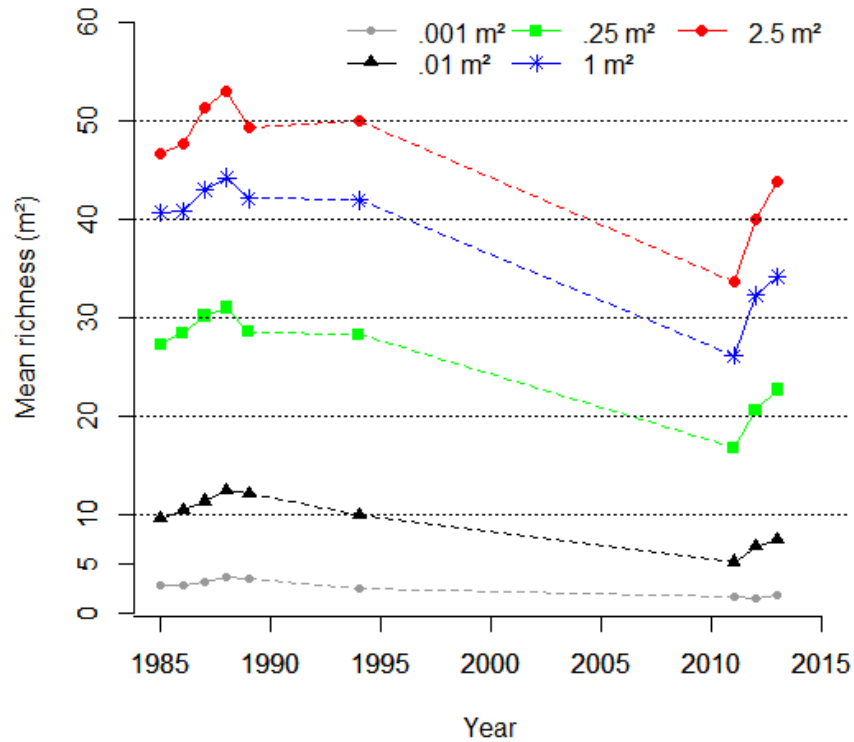
Figure 3.4. Comparison of the variation in mean species richness at 1 m² and mean annual Palmer Z Index (PZI) between 1985 and 2013. Prescribed fire events are denoted with black boxes. The trajectory of richness in the intervals 1989-1994 and 1994-2011 is indicated with a dashed line as within-interval variation in richness is unknown.
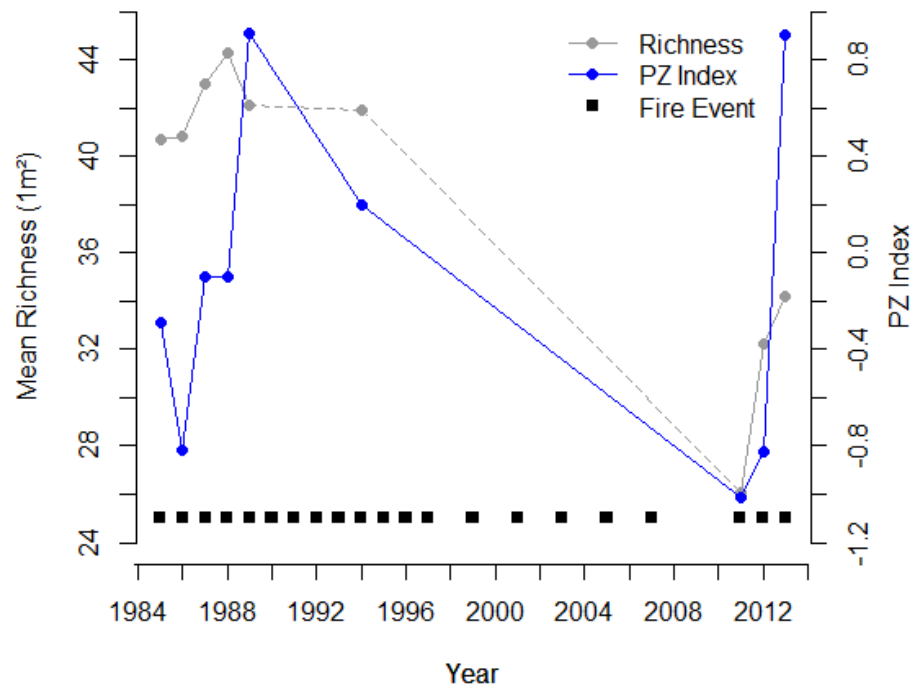
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CHAPTER 4: SPECIES RICHNESS PATTERNS ARE SHAPED BY LOCAL, REGIONAL, AND HISTORICAL PROCESSES ACROSS SPACE IN THE LONGLEAF PINE ECOSYSTEM

Abstract

Traditionally, ecologists have focused on understanding how local processes shape community structure, but have now begun to explore the influence of regional, evolutionary, and historical processes on local communities as well. Here, I examined whether multiple processes operating at different spatial and temporal extents (soil, climate, species pool size) simultaneously influence plant species richness patterns in the longleaf pine ecosystem Specifically, I ask, how does plant species richness change across the spatial extent of this ecosystem? Which processes are most important in structuring those patterns? How does the relative importance of these processes change across ecoregions and with grain size? I assembled vegetation and soil data for 849 100 m² plots from high-quality, fire-maintained longleaf pine sites located in the southeastern US and calculated species richness at 1 m² and 100 m². I used principle components analysis to extract the main axes of variation across the soil data. Climate data were obtained from the WorldClim Global Climate Database. Species pools were built using a two-step approach that accounted for dispersal limitation and environmental tolerance. Model selection using AIC and variance partitioning was used to quantify the unique variance in species richness explained by each predictor, along with the shared and unexplained variance. Soil properties collectively were the most important driver of species richness, regardless of spatial grain or ecoregion. Climate explained additional variation in species richness, although

substantially less. Surprisingly, I found that species pool size only explained variation in species richness at 1 m². These patterns remained consistent across ecoregions, yet climate and species pool size became better predictors of species richness in more southern ecoregions. These results suggest that plant species richness in the longleaf pine ecosystem is structured by multiple processes that act simultaneously. The identity and relative importance of local, regional, and historical processes change across extent and grain size in this ecosystem, indicating that the important ecological processes that structure species richness patterns are scale-dependent.

Introduction

Community assembly is the process by which species are filtered into ecological communities, and can be thought of as a series of sieves, each allowing certain species through while excluding others to ultimately determine both the number and identity of species that get to and become established at a site (e.g., species diversity and composition; Diamond 1975). Multiple ecological processes, which often operate at different spatial and temporal scales, can influence community patterns simultaneously (Auerbach & Shmida 1987, Crawley & Harral 2001, Ricklefs 2004); thus a key challenge for ecologists has been to identify which processes act to produce the patterns we see at different scales of observation. Most studies have focused on documenting ecological patterns at local scales (e.g., within a single community or small set of communities) and have suggested local, deterministic processes (e.g., environmental filtering, biotic interactions) are the key processes that shape community structure (Whittaker 1965, MacArthur & Levins 1967, Tilman 1982). More recently, ecologists have recognized that regional, evolutionary, and historical processes influence species diversity and composition patterns as well (Zobel 1997, Pärtel 2002, Harrison & Cornell 2008) and have begun to consider

how local, regional, and global processes simultaneously influence community structure (Carr et al. 2009, White & Hurlbert 2010, Gazol et al. 2012).

Identifying the important local, regional, and historical processes that drive community patterns remains challenging for several reasons. First, these processes often operate at different spatial and temporal scales, and so the processes deemed "important" depend on the spatial or temporal scale of the study (Siefert et al. 2012). Second, patterns and processes that operate at large spatial and temporal scales are hard to measure within the typical timeframe of most ecological studies, although studies at these scales have become more feasible recently due to a growing number of large, publicly available databases (e.g., Dengler et al. 2011, Kattge et al. 2011, Peet et al. 2012a). Furthermore, evolutionary and historical controls on species richness are still hard to quantify. One approach to circumvent this challenge is to use the size of regional species pools as a proxy for the strength of evolutionary and biogeographic processes (Ricklefs & Schluter 1993, Pärtel 2002), as they may reflect evolutionary rates, evolutionary time, and/or biogeographic history (e.g., evolutionary or refugial centers).

I use a large vegetation data set to identify the important local, regional, and historical processes structuring species richness patterns in longleaf pine plant communities. The longleaf pine ecosystem is located in the southeastern US and is characterized by a graminoid-dominated herbaceous layer and an open over-story of *Pinus palustris*. The high level of species richness (up to 52 species in 1 m², the record values for North America; Peet et al. 2014), endemism (Sorrie & Weakley 2006, Noss 2013), and wide-scale destruction of longleaf pine acreage (< 3% remains; Frost 2006) make the longleaf pine ecosystem a conservation priority in the United States. Plant species richness in the longleaf pine ecosystem has been observed to increase with decreasing latitude (Peet et al. 2014), which I hypothesize is due to differences in climate and

biogeographic history. At lower latitudes, there is less seasonality in temperature, a longer

growing season, and higher annual precipitation (Hijmans et al. 2005); thus, more favorable

climatic conditions may be one explanation for higher plant species richness at lower latitudes.

An alternative explanation is that biogeographic history over the last 30,000 years has shaped the

size of species pools differentially across the range of the longleaf pine ecosystem, which has

important consequences for the number of species that can filter down to local sites. In

particular, during the last glacial maxima (~18,000 years ago) species differentially persisted in

the south and likely on the now submerged portion of the Coastal Plain (Delcourt & Delcourt

1981). Since most refugial areas were likely located in the southern portion of this ecosystem,

species richness may be higher at the southern end of this ecosystem due to larger species pools

maintained by the presence of refugial centers. Since these patterns and mechanisms have not

been explored quantitatively, my first goal was to explore patterns of plant species richness

across a large spatial extent of this ecosystem. An understanding of where biodiversity is highest

in the longleaf pine ecosystem should help inform conservation planning and guide restoration

efforts in the future.

Several studies conducted in single sites or in small geographic areas have suggested that

species richness in longleaf pine plant communities is influenced by multiple ecological

processes (e.g., soil properties and fire regimes; Glitzenstein et al. 2003, Kirkman et al. 2004).

However, few studies have explored which processes act across multiple sites and/or across

broad geographic extents (but see Carr et al. 2009, Peet et al. 2014). Hence, the second goal was

to determine the important local, regional, and historical processes structuring plant species

richness across a large portion of the longleaf pine ecosystem. Specifically, I focus on local

environmental filtering (soil and site properties), regional environmental filtering (climate), and

biogeographic history (size of the regional species pool). Although soil properties, climate, and the species pool may simultaneously influence species richness patterns, I predict soil properties will explain the most variation in species richness because soil texture, nutrients, and moisture have been identified as key factors that shape community structure in other longleaf pine studies (Peet 2006, Carr et al. 2009, Peet et al. 2014).

My final aim is to determine how the relative strength of processes changed across the geographic extent of the study area (North Carolina to Florida) and across grain (i.e. plot sizes of 1 and 100 m²). Although I expected local environmental filtering would consistently be most important, I hypothesized that the relative importance of regional and historical processes would increase as spatial grain increased. Local processes (e.g., local environmental filtering), are often more important in structuring community patterns at very small spatial scales, whereas larger-scale processes generally increase in importance as spatial grain increases (Auerbach & Shmida 1987). Consequently, I expected that the signal of regional and historical processes would increase from 1 m² to 100 m². In addition, I explore whether local, regional, and historical processes change in relative importance across the spatial extent of this ecosystem by re-running analyses across the four Nature Conservancy (TNC) ecoregions in the southeastern US (i.e. Mid-Atlantic Coastal Plain, South Atlantic Coastal Plain, East Gulf Coastal Plain, Florida Peninsula; The Nature Conservancy et al. 2009).

Methods

Study Area

This project was conducted in longleaf pine plant communities across a large portion of the southeastern Coastal Plain from North Carolina south into peninsular Florida and west to the

Alabama border (Figure 4.1). The study area spans four major TNC ecoregions, listed here from north to south: Mid-Atlantic Coastal Plain, South Atlantic Coastal Plain, East Gulf Coastal Plain, and Florida Peninsula (The Nature Conservancy et al. 2009). I used these ecoregions to bin the data to examine how species richness patterns and the processes structuring those patterns change with spatial extent. The climate is humid-sub tropical with high precipitation, most of which occurs during the growing season (April-September). Annual precipitation increases with decreases in latitude and with proximity to the coast, while mean annual temperature generally increases southward (Hijmans et al. 2005). Soils within the study area are diverse, with five soil orders represented, but are generally sandy and nutrient poor (Christensen 2000).

Vegetation History

Since the beginning of the Pleistocene (2.5 mya), the southeastern US has been shaped by repeated glaciation and thaw events, despite never actually having been glaciated. Prior to and during the last glacial maxima 18,000 years ago, most species associated with the longleaf pine ecosystem likely migrated southward in response to cooling climate and remained in refugial areas in the south, along with additional refugial centers likely on the Cape Fear Arch in North Carolina, and on the now submerged continental shelf (Watts 1980, Delcourt & Delcourt 1981, Peet 1993, Christensen 2000). During this period, there was a temperature gradient across the southeastern US and the vegetation likely responded with more displacement of species in northern latitudes (Watts 1980, Jackson et al 2000 Figure 7). Although the available pollen and macrofossil data are limited, the data suggest that peninsular Florida was dominated by stands of *Pinus*, *Quercus*, and non-arboreal taxa, and that warm-temperate conifers (e.g. *Pinus palustris*) were restricted to Florida and perhaps the Gulf Coast (Jackson et al. 2000). Thereafter, as climate warmed ~10,000 years ago, some species likely migrated north and eastward out of refugial

areas, resulting in perhaps less recovery of species further north. Thus, biogeographic history in the last 30,000 years may have shaped the size of the species pool across the longleaf pine differentially due to the location of refugial centers (e.g., larger species pools in the south).

Vegetation and Environmental Data

From 1988 through 2013, the Carolina Vegetation Survey (CVS) sampled over 8000 plots across the southeastern United States (Peet et al. 2012b). The CVS sampling protocol consists of 1000 m² plots with multiple smaller sub-plots nested within (see Peet et al. 1998). Presence of all vascular plant species is recorded at multiple spatial scales within each plot (0.01 m², 0.1 m², 1 m², 10 m², 100 m², 1000 m²). I compiled CVS vegetation data for all longleaf and slash pine *(Pinus elliottii)* plots in North Carolina, South Carolina, Georgia, and Florida, resulting in a final data set of 849 plots of at least 100 m² plots (Figure 4.1). To examine how species richness patterns change with spatial grain in this system, I calculated mean species richness at 1 and 100 m² for all plots.

In addition to vegetation data, environmental data were collected at the time of sampling and included slope, aspect, and soil samples from the A and B horizons. Soil samples were analyzed for texture (sand, silt, clay %), nutrients (N, P, Al, B, Ca, Cu, Fe, H, K, Mg, Mn, Na, S, Zn), organic matter, base saturation, cation exchange capacity, pH, Ca/Mg ratio, and bulk density by Brookside Laboratories Inc. using Mehlich III extraction (Mehlich 1984). Elevation was determined from a digital elevation model. Several variables were log-transformed (Al, Ca, Cu, Fe, K, S, P, Mn, Zn, Mg, elevation, organic matter, cation exchange capacity, and Ca/Mg ratio), square-root transformed (silt %, sand %) or cubed (bulk density, sand %) prior to analysis to normalize the data. To quantify differences in soil properties across sites and to extract the major

axes of variation across the soil data, I used principal components analysis (PCA). I first

conducted PCA on all plots; the first three axes explained 99.7% of the variation in the data and

corresponded to axes of soil texture (PCA1), soil base cations (PCA2), and soil moisture

(PCA3), respectively. I interpreted PCA3 as an axis of soil moisture, as organic matter, sulfur,

and nitrogen load on this axis. Higher soil organic matter (and hence higher S and N) are

expected in soils that have higher soil moisture due to the buildup of carbon in anaerobic

conditions. To explore how the relative importance of soil properties changed across ecoregions,

I re-ran PCA within each ecoregion.

Climatic data were obtained for each plot from the WorldClim Global Climate Database

from grids with a 30 second spatial resolution ($0.93 \times 0.93 = 0.86$ km^2 at the equator). These

layers were created by interpolation of climate data from pre-existing databases and weather

stations with data from at least 10 years (Hijmans et al. 2005). Multiple temperature and

precipitation parameters, including annual, monthly, and quarterly averages were extracted for

each plot (see Hijmans et al. 2005) by intersecting the plot location and the grid in R v.2.15.2

using the raster package (R Core Development Team, 2012).

Building Regional Species Pools

I built regional species pools across the range of the data set to serve as proxies for

biogeographic and historical processes. Here, I define the species pool as the group of species

from the regional flora from which local communities are assembled (Pärtel et al. 1996, Zobel

1997). My working definition of a species pool includes both species that can disperse to a site

and tolerate the environmental conditions of that site. I built 20 different species pools across the

range of the data using a two-step approach that accounts for both dispersal limitation and

environmental tolerance. First, I assigned all plots to one of four ecoregions in the southeastern US: Mid-Atlantic CP, South Atlantic CP, East Gulf CP or Florida Peninsula (The Nature Conservancy et al. 2009). I then summarized species occurrences in plots to create a species list for each ecoregion, which was a good first approximation of the species associated with the longleaf pine ecosystem in each ecoregion. This initial data set contained 1657 taxa. However, while the plot data captured most species in each ecoregion they occur in, within any given ecoregion, a number of species were missed by plots. I filled in these missing holes for species in the plot data set using distributional data from the USDA Plants Database (USDA 2013) and Weakley 2012. In addition, many longleaf pine associated species are rare or narrowly distributed and were not captured in plots or initially included in the species pools. To overcome this, I augmented the species list for each ecoregion generated from the plot data with additional taxa (N = 123) obtained from a list of longleaf-associated species of the southeastern US (Sorrie & Weakley 2006, Weakley 2012, Weakley unpublished data).

Second, a broad community type was assigned to each plot, based on a pre-existing vegetation classification of longleaf pine communities (Peet 2006). Peet (2006) identified five broad longleaf pine community types based largely on soil moisture and soil texture: xeric sand barrens and sandy uplands (sandhills), subxeric sandy uplands (subxeric woodlands), flatwoods (flatwoods), silty uplands (silty woodlands), and savannas (savannas, see Figure 4.2 in Peet 2006). I summarized species occurrences in plots to create a species list for each broad community type, filled in geographic gaps in the data as above, and added additional species as described above. I then used these lists to create a unique regional species pool for each of the 20 ecoregion-community type combinations (e.g., Mid-Atlantic CP sandhills; Table 4.1).

Analysis

Multiple regression and model selection using AIC (Burnham & Anderson 2002) were implemented to determine the best-fit model for explaining variation in species richness across space. For soil properties I explored whether individual soil variables that are known to be important (e.g., silt %) or the PCA axes scores were better predictors of species richness. After model selection, I used variance partitioning to quantify the unique variance in species richness explained by soil properties collectively, climate, and species pool size, along with the shared variance explained by one or more predictors and the unexplained variance. I ran all analyses at both 1 m² and 100 m² to examine how patterns and the processes structuring those patterns changed with spatial grain. To determine how the relative strength of processes changed across spatial extent, I fit separate multiple regression models for each of the four ecoregions in the southeastern US. In total, I fit ten regression models, two for all plots at 1 m² and 100 m² and eight for the four ecoregions at 1 m² and 100 m².

Results

Species richness at 100 m² and 1 m² increased with decreasing latitude, albeit weakly (100 m² $R^2 = 0.06$, $p < .001$, 1 m² $R^2 = 0.02$, $p < .001$), suggesting communities in the southern portion of the longleaf pine range are on average slightly more species rich. This relationship held when constraining environmental context, as most broad community types in the East Gulf CP were more species rich than their counterparts in the Mid-Atlantic CP (Figure 4.2). Species pool size was greatest in the East Gulf CP and South Atlantic CP, regardless of community type (Table 4.1). Although species richness and species pool size increased with deceasing latitude to

the FL panhandle, species richness and species pool size decreased thereafter into the Florida peninsula (100 m² R² without peninsular FL plots = 0.08; Figure 4.2).

The explained variances I report are the unique variance components of each predictor in the final models. The best fit model for all plots at 100 m² contained all three soil PCA axes (soil texture, soil base cations, and soil moisture), annual precipitation, and temperature in the wettest quarter (Table 4.2). However, soil properties collectively explained considerably more unique variance in richness than climate (soil R² = 0.35, climate R² = 0.08; Figure 4.3). Sites with greater soil nutrient availability, higher soil moisture, and warm and wet climates had greater species richness. Species pool size was not a significant predictor in the model at 100 m² (p = .48). At 1 m², the same predictors explained differences in species richness across space, in addition to species pool size (R² = 0.01). The relative importance of soil properties versus climate was consistent at 1 m², with soil properties explaining more variation in species richness than climate (soil R² = 0.19, climate R² = 0.02; Figure 4.3). Interestingly, different soil attributes became more important predictors of species richness as spatial grain changed from 100 to 1 m²: soil base cations were the most significant predictor of species richness at 100 m², whereas soil texture was more important at 1 m² (Table 4.2). As predicted, I detected a slight increase in the amount of variance explained by climate as spatial grain increased from 1 to 100 m² (Figure 4.3).

To explore how the relative importance of local, regional, and historical processes change across space in this system, I re-ran the above analyses across the four ecoregions in the southeastern US using separate PCA analyses for each ecoregion. In the Mid-Atlantic Coastal Plain, at both 100 m² and 1 m², the best-fit model contained all three soil PCA axes and temperature seasonality (Table 4.2). Soil properties emerged again as the most important predictor of species richness (100 m² R² = 0.38, 1 m² R² = 0.32), whereas climate explained

significantly less (100 m² R² = 0.03, 1 m² R² = 0.04; Figure 4.4). In addition, species-pool size

explained additional variance in richness, but only at 1 m² (R² = 0.03). In the South Atlantic

Coastal Plain, the best fit model at 100 and 1 m² contained the first two soil PCA axes (soil

texture and soil base cations; 100 m² R² = 0.27, 1 m² R² = 0.26), along with precipitation in the

driest month (100 m² R² = .04; 1 m² R² = .03). As was the case with the Mid-Atlantic Coastal

Plain, the size of the species pool explained additional variation in species richness at 1 m² (R² =

0.03; Figure 4.4), but not at 100 m².

In the East Gulf Coastal Plain, soil base cations (PCA2), precipitation in the warmest

quarter, and temperature in the warmest quarter were the best predictors of richness at 1 m² and

100 m². Similar to other ecoregions, soil properties explained more variation in richness (100 m²

R² = 0.25, 1 m² R² = 0.24) than climate (100 m² R² = 0.15, 1 m² R² = 0.10). Species pool size

again only explained variation in species richness at 1 m² (R² = 0.10; Figure 4.4). In the East

Gulf Coastal Plain, climate and species pool size explained a greater proportion of variance in

richness compared to other ecoregions (Figure 4.4). In the Florida Peninsula, soil base cations

(PCA2) and soil moisture (PCA3), along with precipitation in the coldest quarter and

temperature in the warmest quarter, explained most of the variation in species richness at 1 m²

and 100 m². Soil properties again explained more variance in species richness than climate at

both spatial grains (soil 100 m² R² = 0.24, soil 1 m² R² = 0.14; climate 100 m² R² = 0.07, climate

1 m² R² = 0.25). In contrast to all other ecoregions, climate was a better predictor of species

richness at 1 m² than soil properties in the Florida Peninsula. In addition, species richness in the

Florida peninsula was explained by different aspects of soil properties as spatial grain changed

from 100 to 1 m²; soil base cations were more important at 100 m², whereas soil moisture was

more important at 1 m² (Table 4.2). Species pool size did not explain differences in species richness in the Florida Peninsula at either 1 m² or 100 m².

Discussion

I detected a weak latitudinal trend in species richness at both 1 m² and 100 m², with higher species richness in the South Atlantic and East Gulf Coastal Plain. Species richness increased in nutrient-rich, moist sites, with warm, wet climates, both within ecoregions and across ecoregions. Species pool size was highest in the East Gulf Coastal Plain and in sites with great nutrient and water availability (e.g. savannas and silty woodlands; Table 4.1). Soil properties consistently explained more variation in species richness than climate, regardless of ecoregion or spatial grain. Furthermore, species pool size was only a significant predictor at 1 m² in contrast to my expectation that species pool size would become a slightly more important filter on species richness at larger spatial grains.

Carr et al. (2009) found that soil properties, climate, and space explained similar proportions of variance in species composition in Florida longleaf pine communities (using a subset of the data used in this study). Soil properties explained most of the variation in community composition (48%), followed by climate (9%), and pure spatial factors (9%). My work is analogous to theirs and suggests that vegetation patterns in the longleaf pine ecosystem are shaped by multiple processes, but primarily by soil properties. In a study that investigated the relationship between soil properties and species richness, Peet et al. (2014) also found that species richness patterns in longleaf pine communities are structured by the same three axes that emerged from this analysis: soil moisture, soil texture, and soil nutrients.

I found that the relative importance of processes structuring species richness patterns changed with grain size. As predicted, the amount of variance explained by climate increased slightly as spatial grain increased, suggesting processes operating at larger spatial and temporal scales become slightly more important filters on species richness at larger scales. In addition, species richness was predicted by different attributes of soil properties as spatial grain changed: soil texture consistently became more important as spatial grain changed from 100 m² to 1 m².

The relative importance and identity of processes structuring species richness patterns also changed across ecoregions. The amount of variance in species richness explained by species pool size increased with decreases in latitude, with the exception of peninsular Florida (Figure 4.4). This suggests biogeographic history and the location of refugial centers may have direct effects on species pool size and hence the number of species that can filter down to local communities. Although soil properties were consistently the best predictors of species richness, species richness was explained by different components or axes of soil properties across space. In general, soil base cation availability explained the most variation in species richness in southern longleaf pine communities, particularly in Florida, whereas soil texture was the most important predictor of species richness in the Mid-Atlantic Coastal Plain. Soil texture became less important in the East Gulf Coastal Plain and peninsular Florida, presumably because soils are very sandy and homogenous throughout. Species richness increased on sites with greater silt %, soil moisture, and base cations, suggesting greater resource availability (nutrients, moisture), allowing more species to coexist. Unsurprisingly, base cations and topographically-influenced soil moisture, which are known to be key predictors of species richness and composition in Florida (Carr et al. 2009), emerged as important predictors of species richness in the East Gulf Coastal Plain. Lastly, the important climatic variables structuring species richness also changed

across space: temperature seasonality was more important in northern latitudes, whereas the quantity of resources (i.e. precipitation in mm) explained more variation in species richness at the southern end of this ecosystem.

Contrary to expectation, species pool size was not a good predictor of species richness at larger spatial grains (i.e. 100 m²) and only a weak predictor at 1 m². There are two possible explanations for this finding. First, my methodology for building species pools may not have been effective at approximating the actual number of species that can filter down to local communities. Although I believe the methodology for building species pools was effective at excluding species based on their environmental tolerance, it is possible that the geographic extents of the species pools (i.e. ecoregions) were too large to accurately reflect the dispersal ability of all species in the data set. Second, it is possible that species pool size is not an important determinant of species richness patterns in this system, or at least not as important as other community assembly processes. Similar to my findings, Carr et al. (2009) found that pure spatial processes explained considerably less variation in species composition in longleaf pine plant communities than soil properties or climate. Future research should explore the role of species pool size in shaping species richness in longleaf pine plant communities, especially when high-resolution range maps become available for the thousands of plant species found in this ecosystem.

In addition to soil properties, climate, and species pool size, other factors influence species richness patterns in the longleaf pine ecosystem, most notably fire regime and land-use history (Kirkman et al. 2001, Glitzenstein et al. 2003, Kirkman et al. 2004). I was unable to quantify differences in land-use history or fire regimes across the broad geographic extent of the data; however, most plots were located in sites with evidence of recent fire and lack of human

disturbance. Thus, the sites examined in this study represented the highest-quality, fire-maintained longleaf pine parcels that remain. Still, it is likely that differences in fire frequency and land-use history have influenced the species richness patterns I report here, in addition to soil properties, climate, and biogeographic history. Although I explain a significant portion of variance in species richness, especially at northern latitudes (Figure 4.4), a substantial amount of variance in species richness remains unexplained, suggesting these and other factors (e.g., environmental heterogeneity) may be influencing species richness patterns.

This work suggests that local and regional processes shape species richness patterns in the longleaf pine ecosystem simultaneously and contributes to a growing body of literature indicating community structure at local scales can be structured by processes that operate at much larger spatial and temporal scales (Carr et al. 2009, White & Hurlbert 2010). Furthermore, this work contributes to an overall understanding of the determinants and spatial patterns of species richness in longleaf pine plant communities, by documenting changes in the relative importance and identity of processes structuring richness across both grain and extent.

Tables

Table 4.1. Species pool size for each ecoregion (Florida Peninsula, East Gulf CP, South Atlantic CP, Mid-Atlantic CP; ordered from south to north), community type (savanna, flatwood, silty woodland, subxeric woodland, sandhill; order from mesic to xeric), and ecoregion-community type combination. Species pool size generally increases as latitude decreases, but drops in the Florida peninsula. Species pool size increases from sandy, xeric community types (e.g., sandhills) to silty, mesic types (e.g., savannas).

Community Type	Florida Peninsula	East Gulf CP	South Atlantic CP	Mid-Atlantic CP	Total Unique Species
Savanna	870	1120	1102	1007	1259
Flatwood	893	1083	1081	962	1221
Silty Woodland	NA	940	954	898	1039
Subxeric Woodland	740	891	902	778	1006
Sandhill	686	814	815	679	941
Total Unique Species	1106	1390	1364	1179	1657

Table 4.2. Predictors at 1 and 100 m² that explained the most variation in species richness across all plots and each of the four ecoregions in the southeastern US. Significant predictors are indicated with asterisks. Three asterisks indicate soil and climate predictors that explained the most variation in species richness in each model, while one asterisk indicates other significant predictors in the model.

Extent	Soil Texture	Soil Base Cations	Soil Moisture	Annual Precip	Precip in Driest Month	Precip in Warmest Quarter	Precip in Coldest Quarter	Temp in Wettest Quarter	Temp in Warmest Quarter	Temp Season	Species Pool Size
All regions	*	***	*	*				*			
Mid-Atlantic CP	***	*	*							*	
South Atlantic CP	*	***			*						
East Gulf CP		*				*			***		
Florida Peninsula		***	*				***		*		
1 m²											
All regions	***	*	*	***				*			*
Mid-Atlantic CP	***	*	*							*	*
South Atlantic CP	*	***			*						*
East Gulf CP		*				*			***		*
Florida Peninsula		***	*				***		*		

Figure 4.1. Southeastern Coastal Plain of the US showing locations of 849 plots and the four major ecoregions in the study area: Mid-Atlantic Coastal Plain, South Atlantic Coastal Plain, East Gulf Coastal Plain, and Florida Peninsula.
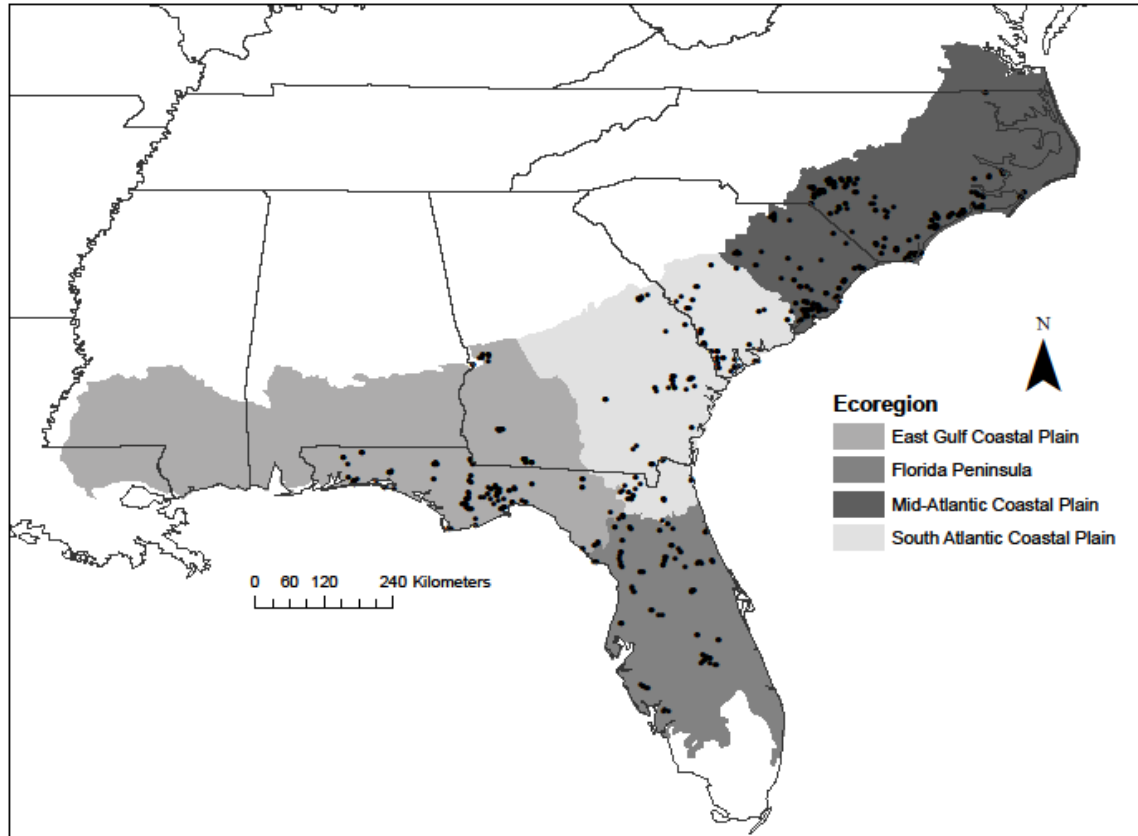
Figure 4.2. Average richness at 100m² for each ecoregion and community type. Community-type panels are ordered from dry, species-poor communities (sandhills) to mesic, species-rich communities (savannas). Ecoregions are aligned from north to south. Species richness increases generally with latitude and peaks in the Florida panhandle for most community types. The gray bars indicate the 95% confidence intervals.
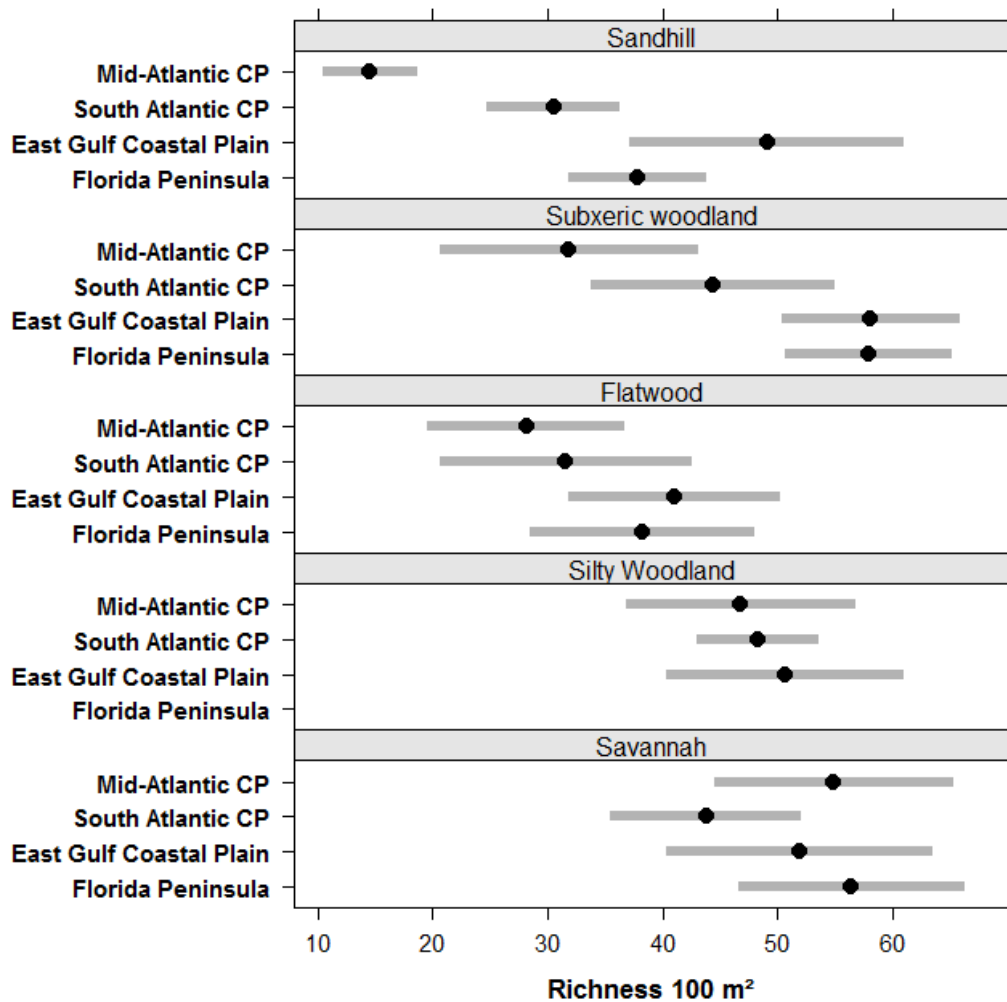
Figure 4.3. Variance partitioning results for richness at 1 m² and 100 m² for all plots. Pie charts show the unique proportion of variance explained by local predictors (soil properties), regional predictors (climate), along with shared variance explained collectively by all soil and climate parameters, and unexplained variance.
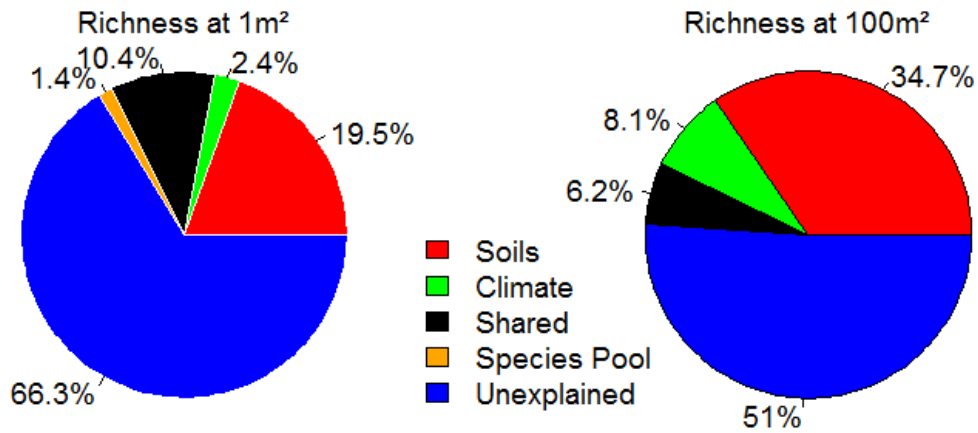
Figure 4.4. Variance partitioning results for richness at 1m² and 100 m² for the four longleaf pine ecoregions. Pie charts show the proportion of variance explained by local predictors (soils), regional predictors (climate), along with shared variance explained by multiple predictors, and unexplained variance for each ecoregion (Mid-Atlantic CP, South Atlantic CP, East Gulf CP, Florida Peninsula). Pie charts outlined in black respond to variance partitioning results at 100 m², while pie charts outlines in white correspond to 1 m².
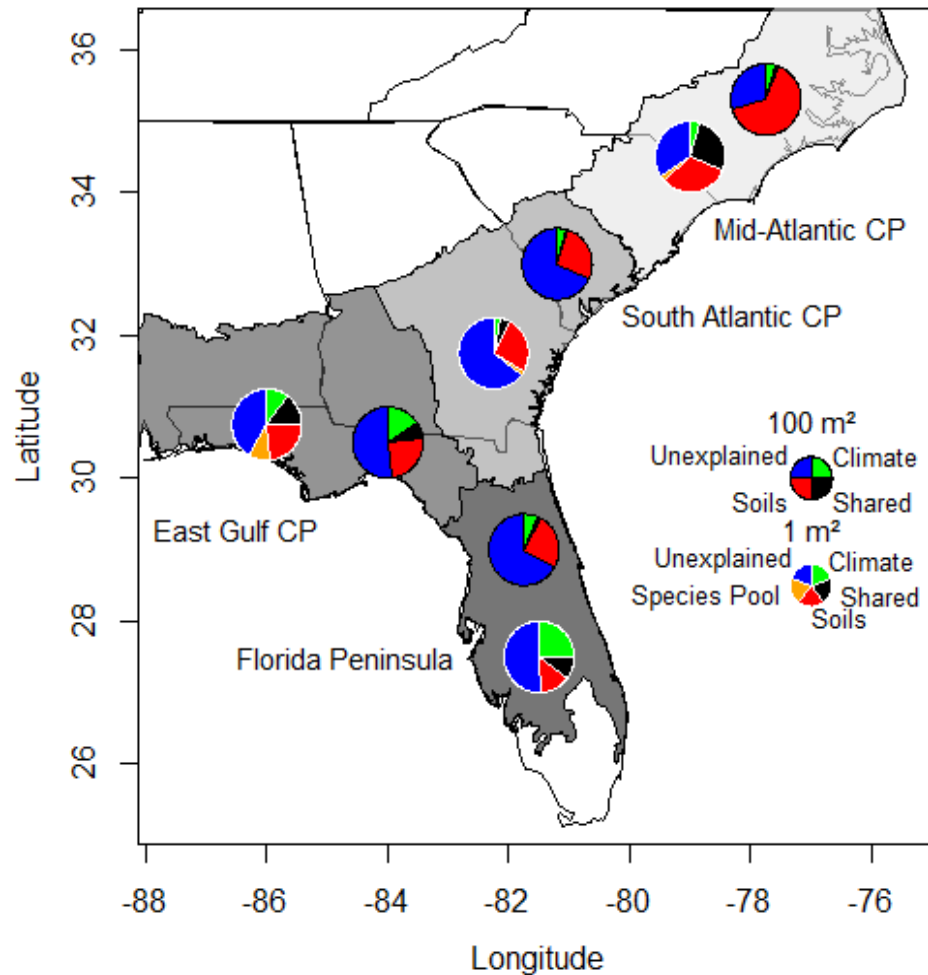
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CHAPTER 5: FIRE FREQUENCY AND SPATIAL SCALE MEDIATE THE STRENGTH OF DETERMINISTIC AND STOCHASTIC PROCESSES IN LONGLEAF PINE WOODLANDS

Abstract

There is ongoing debate on whether ecological communities are assembled by deterministic, niche-based processes or stochastic processes unrelated to species' differences. These two competing hypotheses have been merged into a single conceptual framework that seeks to identify how the relative importance of deterministic versus stochastic processes changes across a set of communities. Where communities fall along the continuum between solely niche-based processes and solely stochastic processes depends on multiple factors, such as the frequency or intensity of disturbance. One method for quantifying the relative importance of stochastic versus niche assembly is through use of species co-occurrence metrics that reveal whether community structure is more aggregated (species co-occur more frequently than expected by chance, evidence of environmental filtering), segregated (species co-occur less frequently than expected by chance, evidence of limiting similarity), or no different (evidence of stochastic assembly) than random expectation. Here, I use two different, yet complementary species co-occurrence metrics coupled with null model analysis to explore where longleaf pine plant communities fall along the continuum of deterministic to stochastic assembly. More specifically, I examine how the relative importance of environmental filtering, competition, and stochastic processes change across a gradient of environmental stress, with time since disturbance, and with spatial grain. Mean C-scores and mean modified Raup-Crick dissimilarity

metrics were calculated for five broad community types, three disturbance categories, and 15 community-disturbance categories to examine how disturbance, environmental context, and spatial scale change the relative importance of community assembly processes. I found that C-scores and mean modified Raup-Crick dissimilarity metrics changed consistently with time since fire and spatial grain, with sites becoming more dissimilar (e.g., segregated) in species co-occurrence as time since fire increased and spatial grain decreased. However, I did not detect large changes in the relative importance of community assembly processes along the environment gradient, except at the smallest spatial grain and in sites with less recent fire. These results suggest that the relative importance and identity of community assembly processes depends on the spatial scale of observation, and thus it is critical that studies using species co-occurrence data to identify ecological processes be conducted across a range of spatial scales. This work also indicates that longleaf pine plant communities are shaped by both deterministic and stochastic processes, and that disturbance changes where communities fall along the deterministic-stochastic continuum.

Introduction

Explanations for community assembly and species coexistence have been divided into two distinct theoretical models: deterministic niche-based assembly and stochastic assembly unrelated to species' differences. Deterministic models argue that species are assembled into communities through niche processes such as biotic interactions and environmental filtering (Tilman 1982, Chesson 2000, Chase & Leibold 2003, Silvertown 2004). Within this framework, species have distinct niches and species that have similar ecological roles are not able to co-exist (e.g., limiting similarity; MacArthur & Levins 1967). In contrast, stochastic assembly models postulate that species are ecologically equivalent and communities are assembled through

colonization, speciation, and extinction events (MacArthur & Wilson 1967, van der Maarel & Sykes 1993, Hubbell 1997, Bell 2000, Hubbell 2001).

These two competing hypotheses have been integrated into a single conceptual model that seeks to explore how the relative importance of deterministic and stochastic processes change across a set of ecological communities (Tilman 2004, Gravel et al. 2006, Adler et al. 2007). These approaches recognize that both niche-based and stochastic processes may be important drivers of community assembly and many natural communities lie along a continuum bounded at each end by these two conceptual models (Bell 2005, Leibold & McPeek 2006, Chase & Myers 2011). Thus, rather than identify whether communities are better fit by a neutral or niche-based model, the challenge in community ecology is to quantify the relative importance of stochastic and deterministic processes across communities (Leibold & McPeek 2006).

Multiple factors can influence the strength of stochastic versus niche assembly processes, including but not limited to dispersal limitation, habitat configuration, and the frequency and intensity of disturbance events (Chase 2007, Chase et al. 2009). For example, the stress-gradient hypothesis (SGH; Bertness & Callaway 1994, Callaway et. al 2002, Maestre et al. 2009) predicts that in harsh environments with high stress (e.g., deserts, alpine habitat), the relative importance of facilitation will increase, relative to other ecological processes. Hence, in stressful environments, deterministic processes such as facilitation, competition for limiting resources or strong environmental filtering may be more important in shaping community structure than stochastic processes. In contrast, disturbance (*sensu* Pickett & White 1985) resets the community and increases the frequency of stochastic colonization and extinction events, thereby increasing the relative importance of stochastic processes in assembling communities (Sanders et al. 2003, 2007, Myers & Harms 2009).

Species co-occurrence metrics, coupled with null model analysis, have the potential to reveal whether communities are structured primarily by deterministic or stochastic processes. If limiting similarity processes are important, communities should contain fewer species combinations than expected at random as species with identical niches and ecological strategies are unlikely to coexist (Tilman 1982, Chesson 2000, but see Scheffer & van Nes 2006). If environmental filtering is more important in assembling communities, particular pairs of species should co-occur more often relative to null expectation (e.g., species aggregation), as environment filters will assemble species with similar traits (Cornwell et al. 2006). In contrast, patterns of co-occurrence that do not differ from null expectation (i.e., species do not occur systematically with other taxa) are suggestive of stochastic community assembly (Zalewski & Ulrich 2006, Zillio & Condit 2007).

. The longleaf pine ecosystem is an ideal system to explore general predictions of how the relative importance of deterministic and stochastic processes change across communities for three reasons. First, longleaf pine woodlands are famous for their high plant species richness, particularly at small scales (52 species in 1 m²; Walker & Peet 1983) and thus present an interesting case study for exploring species co-existence mechanisms. Second, longleaf pine plant communities occur across strong environmental gradients (Peet 2006), reflecting differences in soil moisture and soil nutrients, which could have direct implications for the strength of environmental filtering and competition in communities structured on this gradient. In addition, the longleaf pine ecosystem is fire-dependent and prescribed fire is applied every 1 to 5 years to mimic natural fire regimes. Historically, sites with higher soil moisture, nutrients, and biomass production would burn more frequently than dry, nutrient-poor sites that do not generate enough fuel to carry fire on a regular basis. Thus, the relative importance of fire

frequency, environmental filtering, and competition likely change across the range of longleaf pine plant communities, with important consequences for where communities fall on the stochastic-deterministic continuum. Here, I use species co-occurrence patterns and null model analysis to examine how the relative importance of community assembly processes in longleaf pine plant communities change along a gradient of environment stress. Specifically, I ask:

1. Where do longleaf pine communities fall along the continuum between deterministic and stochastic assembly processes? What is the relative importance of stochastic events, local environmental filtering, and competition in structuring longleaf pine communities?

2. How does the relative importance of stochastic and deterministic processes vary with spatial grain and with time since disturbance?

Although I predict that both stochastic and deterministic processes are important for structuring longleaf pine plant communities, the relative strength of those processes likely varies with environmental context and fire history. More specifically, I predict that environmental filtering will be more important in xeric sites, where species physiological tolerances and strong environmental filters limit the identity and number of plant species (Bowles & Jones 2013). In contrast, I hypothesize that stochastic and/or limiting similarity processes will be most evident in wet and mesic sites that experience frequent fire (i.e., the benign end of the gradient). The relative importance of stochastic processes may increase with increasing fire frequency, as assembly processes are "restarted" following disturbance and the composition of species assemblages will largely be driven by patterns of colonization and extinction (Sanders et al. 2003, 2007). However, competition for resources may be higher at those same sites due to the presence of several dominant bunchgrasses (e.g., *Aristida stricta*, *Sporobolus pinetorum*). I

explored these alternative hypotheses by examining species-occurrence patterns across three time-since-fire categories: immediately after fire (six months), 1 to 3 years after fire, and greater than 3 years after fire. I expected to see the signature of stochastic processes immediately following fire, but also predicted that as plants become established, competitive interactions should become more important . A similar prediction was made by Chase (2007), who suggested that in benign environments, stochastic assembly should be relatively more important than in harsh environments where deterministic processes such as environmental filtering predominate.

The final issue I explore is the extent to which deterministic and stochastic processes change in relative importance with changes in the spatial grain of sampling. The scale dependence of ecological processes is a well established concept in ecology (Auerbach & Shmida 1987, Levin 1992, Crawley & Harral 2001). Previous work has shown that biotic interactions act most strongly in structuring communities at small spatial grains (Stoll & Weiner 2000, Götzenberger et al. 2012). However, demographic stochasticity is also expected to be higher at small spatial grains. Thus, I predict that both competition and stochastic processes will become more important as spatial grain decreases, regardless of environmental context. In contrast, I expected that environmental filtering would be more important at large spatial grains since environmental heterogeneity generally increases with spatial scale (Williams 1943, Shmida & Wilson 1985, Crawley & Harral 2001, Field et al. 2009). Thus, I expected to see a shift from environmental filtering to competition and/or stochastic assembly as spatial grain decreased.

Methods

Study Area

 This work was conducted using data from the outer Coastal Plain of North Carolina in the southeastern United States (using the same data set as used in Chapter 2; see Figure 2.1). Elevation ranges from 0 to 30 m above sea level, with very little topographic relief. However, subtle differences in elevation (0.5 m or less) have large consequences for hydrology, soil properties, and hence vegetation (Rome 1988, Christensen 2000). The climate is humid sub-tropical, with an average mean annual temperature of 15.5 °C and an average annual precipitation of 160 cm, most of which occurs during the growing season (Ruffner 1985, State Climate Office of North Carolina). Summer convectional storms not only provide heavy rain, but also lightning which is an ignition source for frequent, low-intensity fires (Christensen 2000). Soils within the region are predominantly derived from nutrient poor, unconsolidated sediments of alluvial and marine origin. Several soil orders occur within the study area and soil texture is extremely important in determining water holding capacity, nutrient retention, species richness, and community composition (Peet 2006).

Vegetation Data

 In 2009, I re-sampled 59 1000 m² nested vegetation plots using the Carolina Vegetation Survey (CVS) protocol (Peet et al. 1998; Peet et al. 2012). I recorded presence-absence for all vascular plant species rooted in the plot at a range of spatial scales (0.01 m², 0.1 m², 1 m², 10 m², 100 m², and 1000 m²; see Peet et al. 1998). Nomenclature follows Weakley 2012. After sampling, I assigned each plot to one of five broad community types from a pre-existing classification (Peet 2006) to assess how species co-occurrence metrics change across the

environmental gradient in the system. Peet (2006) categorized longleaf pine vegetation into 5 community groups based on soil moisture and soil texture: silty woodlands, savannas, flatwoods, subxeric woodlands, and sandhills. Silty woodlands and savannas occur on fine-textured ultisol soils, but savannas are slightly wetter (Peet 2006). Flatwoods occur on spodosols with a mesic to hydric growing environment, despite a mostly sandy substrate (Soil Survey Staff 2010). Subxeric woodlands also occur on sandy substrates, but are drier than flatwoods. Sandhills occur on the driest, sandy sites, have sparse herbaceous layers, and very low nutrient availability.

In 2010, I re-sampled 30 of the 59 CVS plots described above a second time. Plots were selected for re-sampling to span the environmental gradient and to capture variation in the number of years since a plot was last burned (time since fire). Typically plots were re-sampled in 2010 in two special cases: 1) if a plot had not experienced fire for greater than 2 years and then was reburned in 2010, or 2) if a plot had burned in 2009. Vegetation data for 2009 and 2010 were pooled to examine how time since fire influenced the relative importance of stochastic versus deterministic processes across the range of community types.

Fire History Data

Fire history data for all plots through 2008 were obtained from a GIS layer of prescribed fire events dating back to 1985, compiled from several land management agencies in southeastern North Carolina (Costanza 2010). Additional years of fire history data (2009, 2010) were obtained directly from the land management agencies. These data delineate the area burned, but do not quantify the intensity or patchiness of fire within the burned area. Time since fire (number of years since fire) was determined for all plots in both 2009 and 2010.

To examine how the relative importance of competition and stochastic processes changed with time since fire, I classified each plot into one of three time-since-fire categories: < 1 year since fire, 1 to 3 years since fire, and > 3 years since fire. I then created a community type time-since-fire category for each plot (e.g., flatwood, 1- 3 years since fire), which reflected both environmental context and fire history for each plot sampled in 2009 and 2010.

Analysis

Prior to analysis, all taxonomic names were standardized to ensure that differences in taxonomic resolution did not influence the species co-occurrence metrics. Specifically, all species varieties were lumped to the species level, all hybrid species were removed, and all genus-level taxa were removed when there were other taxa in that genus identified to species. I then compiled 5 presence-absence matrices for the five broad community types, 3 matrices for the three time-since-fire categories, and 15 separate matrices for each community type time-since-fire category. For each matrix, I calculated two complementary species co-occurrence metrics to quantify whether community structure was segregated, aggregated, or random.

First, I calculated a C-score between all species pairs (Stone & Roberts 1990, see also Gotelli 2000, Gotelli & McCabe 2002),

$$C_{ij} = (R_i - S)(R_j - S),$$

where for the species pair C_{ij}, R_i is the row total for species I, R_j is the row total for species J, and S is the total number of sites that contain both species I and J. C-scores were calculated on presence-absence data. I then calculated a mean C-score value for each matrix to assess whether

community structure of each broad community type, time since fire category, and community type-time since fire category were aggregated, segregated, or no different than null expectation. C-scores have been used extensively in community ecology as a measure of co-occurrence (Sanders et al. 2003, 2007, Pitzalis et al. 2010, Ulrich et al. 2010, Götzenberger et al. 2012) and have performed better than alternative metrics (Gotelli 2000, Gotelli & McCabe 2002). Larger C-scores are indicative of species segregation due to limiting similarity processes, while smaller C-scores are indicative of species aggregation due to environmental filtering. C-scores that do not deviate from random expectation are suggestive of stochastic processes. To assess whether observed species co-occurrence patterns differed from null expectation, I used a null model approach. First, I randomized each presence-absence matrix 1000 times using the swap-method (Gotelli & Entsminger 2003), which held row and column totals constant (e.g., species richness per site and species occupancy across all sites) and then calculated C-scores over 1000 permutations. Then I compared the frequency distribution of the simulated metrics to the observed values and calculated tail probabilities (one-tailed test) that indicate the likelihood of getting the observed metric compared to random expectation (Gotelli 2000). To compare results across broad community types and time since fire categories, I calculated a standardized effect size (SES) for each matrix,

$$SES = I_{obs} - I_{sim} / S_{sim},$$

where I_{obs} is the observed mean C-score, I_{sim} is the mean simulated C-score and, S_{sim} is the standard deviation of the simulated indices (Gurevitch et al. 1992, Gotelli & McCabe 2002). SES values above 2 reflect species segregation indicative of limiting similarity processes, whereas

values below 2 reflect species aggregation, indicative of environmental filtering. Calculation of C-scores and the corresponding null model analysis was implemented in R version 2.15.2 using the vegan and bipartite packages (R Core Development Team 2012).

Second, I calculated a modified Raup–Crick dissimilarity matrix (β_{rc}), which is a re-scaled probability metric ranging from -1 to 1 that indicates whether two communities share more species (less dissimilar) or fewer species (more dissimilar) than expected by random chance (Raup & Crick 1979, Vellend et al. 2007, Chase et al. 2011 a, b). A mean Raup-Crick dissimilarity matrix was calculated for each broad community type, time-since-fire category, and community type time-since-fire category. To quantify whether the observed dissimilarity values were more or less dissimilar than random expectation, 1000 null Raup-Crick dissimilarity matrices were generated by randomly sampling from the species pool, while holding species richness and species occupancy constant. Then, the difference between the observed dissimilarity matrix and the simulated matrices was calculated as an index of deviation (see Chase et al. 2011 b). Mean β_{rc} values were calculated at multiple spatial scales (0.01 m², 0.1 m², 1 m², 10 m², 100 m², 1000 m²) to determine how the relative strength of stochastic and deterministic processes changed with spatial grain. If environmental filtering is acting, sites with similar environmental conditions should be more similar relative to null expectation (approaching -1), while sites where competition is more important should be less similar than random expectation (approaching 1). If stochastic processes are important, communities should not differ from random expectation (approaching 0). This approach is complementary, but slightly distinct from other co-occurrence metrics (e.g., C-scores) because it considers pair wise community comparisons in contrast to most co-occurrence metrics, which are summarized over species pairs (Chase et al. 2011b). Thus, interpretation of SES values differs between these two metrics with strong effects reflected

by C-scores SES with absolute values > 2. In contrast, modified Raup-Crick values are based on quantiles, thus strong effects are reflected by absolute values of 0.95 or greater.

This null model approach (and hence the simulated values) is sensitive to the size of the regional species pool (Chase et al. 2011 b). The species pool contains all taxa detected in plots in both 2009 and 2010. I chose to use the same species pool for all broad community types and time-since-fire categories because sites are in relatively close proximity to one another and there are many shared species across community types. In addition, I had no reason to suspect that the species pool would differ significantly for sites with different time since last fire. Furthermore, if I had used different sized species pools, the simulated matrices may have changed across community types and time-since-fire categories due to those differences, resulting in incorrect inference of community assembly processes.

Results

I calculated C-scores and modified Raup-Crick dissimilarity metrics to examine whether species co-occurrence values were aggregated (suggestive of environmental filtering), segregated (suggestive of competition), or random (suggestive of stochastic processes). Mean C-scores calculated at 1000 m² for each broad community type were not different from random expectation (p > 0.2), except for the subxeric woodland community type, which was more aggregated than expectation, suggestive of environmental filtering (p = - 0.039, SES = -2.229; Figure 5.3, Table C.1). In contrast to C-scores, the mean β_{rc} at 1000 m² for most broad community types in the year 2009 was negative, although most values fell within the 25th and 75th percentiles suggesting species co-occurrence patterns in longleaf pine plant communities are not much different than random expectation (Figure 5.1). This was contrary to expectation, since I predicted that the relative importance of environmental filtering would be higher in the most

stressful community types (e.g., sandhills, subxeric woodlands) and B_{rc} and SES values would become more negative as environmental stress increased. In fact, I found that the mean β_{rc} for sandhills was closer to zero relative to all other types, suggesting that stochastic processes or multiple processes acting in opposite directions are structuring sandhill plant communities. As spatial scale decreased, the mean β_{rc} became consistently less negative for each community type, which indicates species co-occurrence in most community types became more similar to random expectation (Figure 5.1). However, the power of this metric to detect non-random patterns decreases when species richness is very low (Chase et al. 2011b). As spatial scale decreased, mean β_{rc} values changed from negative to approximately 0 for subxeric woodlands and flatwoods. In sandhills, silty woodlands, and savannas, which are the driest and wettest types, respectively, mean β_{rc} values changed from negative to slightly positive (Figure 5.1). In contrast, C-scores did not consistently become closer to zero as spatial scale decreased, except at the smallest spatial scale (0.01 m², Figure 5.3). Most C-score SES values were not significantly different than random expectation across scales, except for the sandy community types (sandhills at 0.1 to 100 m², subxeric woodlands at 100 to 1000 m², flatwoods at 0.1 and 10 m²), which were consistently more segregated than random expectation, perhaps taken as evidence of competition for limited resources in those types.

Mean C-scores at 1000 m² for each time-since-fire category were at least marginally different than simulated C-scores ($p < 0.08$), indicating non-random patterns of species co-occurrence. I detected a substantial increase in the deviation between observed C-scores and simulated C-scores as time since fire increased (SES for < 1 year since fire = 3.858, SES for > 3 years since fire = 7.988, $p < 0.001$; Table C.1). Thus, sites that have not experienced fire in three years or more have fewer shared species pairs than sites that have burned more recently. This

pattern was not as strong as spatial grain decreased; C-score SES were almost identical for plots that had not experienced fire in three or more years and for plots that had experienced fire in the last year (Figure 5.3). I also detected an increasing trend of mean β_{rc} values with increases in time since fire. At each spatial scale, mean β_{rc} values were consistently less negative as time since fire increased, suggesting sites that have experienced fire more recently are less dissimilar (more shared species) than null expectation, whereas sites that have not burned in several years are either as dissimilar or more dissimilar than random expectation (Figure 5.1).

To examine how time since fire influenced species co-occurrence patterns along the environmental gradient, I calculated mean β_{rc} values and C-scores for each community type time-since-fire category at 1 m² and 1000 m². Time since fire had large impacts on the deviation between observed and expected dissimilarity values within community types. As time since fire increased, mean β_{rc} values increased for almost all community types at both 1 m² and 1000 m², suggesting that species co-occurrence patterns are more dissimilar than random expectation (Figure 5.2). The one exception was sandhill community types where sites that have gone longer without fire were actually closer to 0 than sites that had been burned more frequently (Figure 5.2). In addition, mean β_{rc} values consistently became less negative as spatial scale decreased from 1000 to 1 m² for most community time-since-fire categories, but particularly for plots 1 to 3 years post-fire and for the wettest, more productive sites (e.g., savannas; Figure 5.2). For all community types except silty woodlands and savannas, C-score SES values at 1 m² and 1000 m² were consistently higher and species co-occurrence more segregated as time since fire increased (Figure 5.4).

Although C-scores and β_{rc} values have both been used to examine species co-occurrence patterns, they differ in that the C-score is a pairwise species metric, whereas β_{rc} is a pairwise

community metric. I found that the two metrics captured unique information in species co-occurrence patterns (Figure 5.5). Although, the same general conclusions were reached using either metric, C-scores tended to be more positive, suggesting species aggregation, than β_{rc} values. The differences between C-scores and β_{rc} values were greater at larger spatial grains (1000 m²).

Discussion

I found that species co-occurrence patterns changed consistently with time since fire and spatial scale, with sites becoming more dissimilar (e.g., segregated) in species co-occurrence as time since fire increased and spatial scale decreased. However, I did not detect large changes in the relative importance of community assembly processes across broad community types except at the smallest spatial scale and when considering time since fire. Contrary to expectation, most community types had random species co-occurrence patterns, suggesting that perhaps both environmental filtering and limiting similarity processes influence community structure along the entire environmental gradient.

Along the environmental gradient and across broad community types, I expected to see a shift from environmental filtering in harsh sites (e.g., sandhills, subxeric woodlands) to competition or stochastic assembly in more benign environments (silty woodlands, savannas). In contrast to expectation, mean βrc values for each broad community type revealed that species co-occurrence patterns were not different than null expectation at most spatial scales (Figure 5.1). Thus, I did not detect a shift from environmental filtering to either competition or stochastic assembly along the environmental gradient, as predicted. Although mean βrc values were not significantly different from random expectation, most values tended to be negative, possibly suggesting environmental filtering was occuring along the entire environmental gradient.

However, there was no evidence of competition increasing in relative importance at the benign end of the stress gradient. There are several possible explanations for why species co-occurrence patterns were consistently negative, regardless of position along the environmental gradient. First, plots used in this study occur in relatively close proximity and hence have similar precipitation and temperature regimes, which may have resulted in species aggregation, despite differences in soil properties across sites. Second, although soil moisture, soil texture, and soil nutrient status vary across broad community types (Peet 2006), soils in this ecosystem are ancient, highly weathered and generally low in nutrients, particularly in P. Thus, low soil resource availability could be acting as an environmental filter in all sites, despite differences in soil properties across sites. Furthermore, although I predicted environmental filtering would be strongest in xeric sites, hydric sites place a different, yet perhaps equal amount of stress on plant species due to soil saturation and continued inundation (Jackson et al. 2008). However, interpretation of environmental filtering along the entire gradient needs to be done with caution, as the trends in mean βrc values were weak.

As predicted, the relative importance of community assembly processes increased with changes in time since fire and spatial scale. Both C-scores and mean β_{rc} values were more segregated (e.g., dissimilar) within a given position on the environmental gradient as time since fire increased (Table C.1, Figure 5.2, Figure 5.4). This suggests that competition becomes relatively more important in sites without recent disturbance, particularly at the wet end of the gradient (e.g., silty woodlands and savannas) where several strong competitors can limit the establishment and persistence of small-statured species in the absence of frequent fire (Heyward 1939, Frost et al. 1986, Bowles & Jones 2013). Thus, the data suggest that the relative importance of environmental filtering and competition change depending on the frequency of

disturbance. Similarly, Pitzalis et al. 2010 documented a shift from segregation in unburned arthropod communities to aggregation/randomness in arthropod communities after fire. Two other studies conducted in species-rich grasslands also detected higher species segregation in sites that had less frequent disturbance, presumably due to higher plant biomass and competitive exclusion by a few, large-statured competitive species (Reitalu et al. 2005, Mason et al. 2011).

I also detected changes in the relative importance of community assembly processes with spatial scale. Mean values consistently became less negative as spatial scale decreased across all community types and time since fire categories (Figure 5.1, Figure 5.3). This suggests a shift from environmental filtering at larger spatial scales to competition and/or stochastic assembly at smaller spatial scales. Whether stochastic assembly or competition increased in relative importance at small spatial scales depended on environmental context. For community types in the intermediate part of the environmental gradient (e.g., subxeric woodlands, flatwoods), mean βrc values changed from negative to approximately 0, as spatial scale decreased, suggesting a shift from environmental filtering to stochastic assembly. In contrast, sandhills, silty woodlands, and savannas, which are the driest and wettest types, respectively, changed from negative to slightly positive, suggesting that competitive processes become more important filters on community structure as spatial grain decreases, especially at the wet end of the environmental gradient (Figure 5.1). This suggests that competition is acting at both the harsh end of the environmental gradient where there is competition for limiting resources and at the benign end of the gradient where the presence of a few competitive dominants results in competitive exclusion. The change in species co-occurrence patterns across scales was particularly notable for savannas where plots went from being aggregated to random/slightly segregated (Figure 5.1).

Species co-occurrence patterns also changed with respect to spatial scale across sites with different fire history. Except for the smallest spatial scale (0.01 m²), mean βrc values were consistently negative in both the < 1 year and 1 to 3 years-since-fire categories, suggestive of environmental filtering. However, the mean βrc values were consistently less negative in plots that had not experienced fire for at least 3 years, perhaps due to the increased importance of competition.

Several studies have suggested that the relative importance of stochastic processes increases in benign environments with higher productivity (Chase 2010), or in frequently-disturbed sites (Sanders et al. 2003, Pitzalis et al. 2010, Santoro et al. 2012). I did not detect shifts from strong environmental filtering in harsh environments (e.g., sandhills) to stochastic processes in benign, frequently disturbed environments (e.g., savannas) at any spatial scale in the data (Figure 5.1). Although, mean βrc values were no different than random expectation at the smallest spatial scales in savannas, species co-occurrence patterns were also close to 0 for community types in harsh environments. Thus, stochastic processes did not generally increase in relative importance as environmental harshness decreased. However, as previously mentioned, the relative importance of stochastic processes did increase as spatial scale decreased across most communities and time since fire categories.

This study is unique is that it is the first to use two different, yet complementary species co-occurrence metrics simultaneously to examine the relative importance of community assembly processes along an environmental gradient. Although I reached the same general conclusions from each metric individually, unique and slightly different information resulted from the use of each metric, especially at larger spatial scales (e.g, 1000 m²). In particular, βrc

values became closer to zero as spatial grain decreased, whereas C-scores did not, except at the smallest spatial grain (0.01 m²).

One limitation of this study is that inference of community assembly processes from patterns of species co-occurrence can be challenging. Although, I assume that species aggregation indicates environmental filtering, this pattern can also result from other processes, such as facilitation (Götzenberger et al. 2012). In addition, species segregation may result from limiting similarity processes, such as competition, but also from habitat heterogeneity (Williams 1943, Reitalu et al. 2005). Furthermore, mean species co-occurrence patterns that do not differ significantly from random expectation could result from stochastic processes or from competition and environmental filtering acting in synergy. Future experimental studies are needed in this ecosystem to confirm that the interpretations of species aggregation and segregation are accurate.

This work adds to a growing pool of studies that suggest the relative importance and identity of community assembly processes depends on the spatial scale of observation (Weiher & Keddy 1995, Reitalu et al. 2005). The important assembly processes structuring communities typically change across spatial scales. Consequently future analyses of species co-occurrence patterns should be conducted across a range of spatial scales to ensure correct inference of process. This work also suggests that multiple processes, both deterministic and stochastic, shape longleaf pine plant communities and that disturbance changes the relative importance of those processes along a gradient of environmental stress.

Figures

Figure 5.1.a. Mean modified Raup-Crick dissimilarity metric at 0.01 m² to 1000 m² highlighted by community type in 2009 (sandhill, subxeric woodland, flatwood, silty woodland, savanna). b. Mean modified Raup-Crick dissimilarity metric at 0.01 m² to 1000 m² for each time since fire category in 2009 and 2010. Values approaching 1 indicated species segregation (e.g., competition), values approaching -1 indicate species aggregation (e.g., environmental filtering), while values close to 0 are suggestive of stochastic assembly.
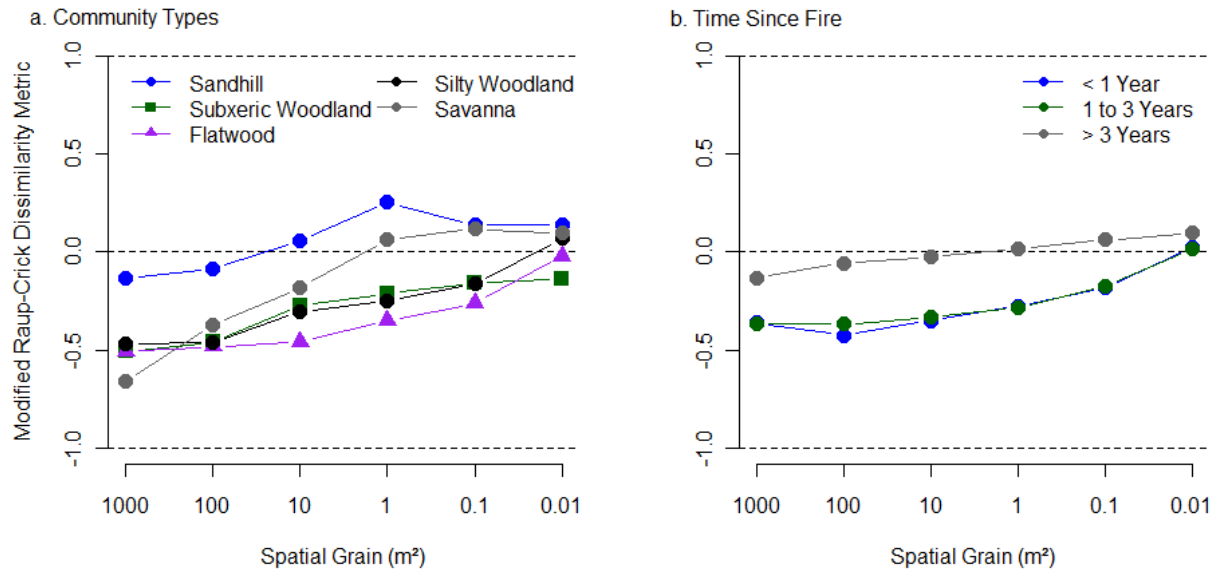
Figure 5.2. a. Mean modified Raup-Crick dissimilarity metric at 1000 m² for each time since fire category (< 1 year, 1 to 3 years, > 3 years, highlighted by community type (sandhill, subxeric woodland, flatwood, silty woodland, savanna). b. Mean modified Raup-Crick dissimilarity metric at 1 m² for each time since fire category, highlighted by each community type. Values approaching 1 indicated species segregation (e.g., competition), values approaching -1 indicate species aggregation (e.g., environmental filtering), while values close to 0 are suggestive of stochastic assembly.
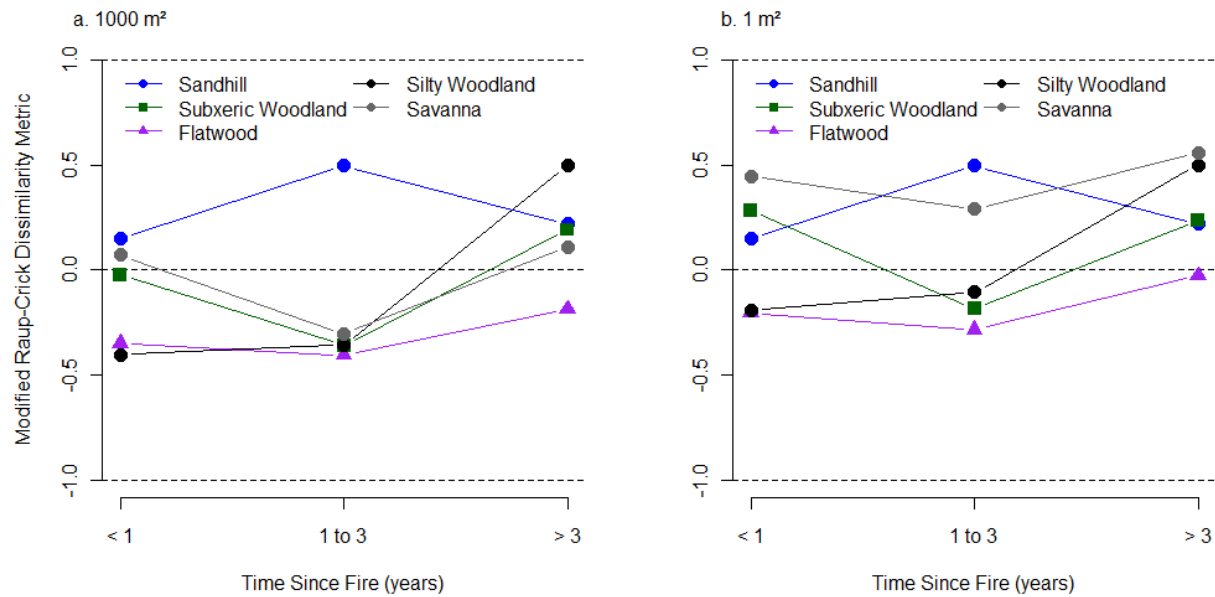
Figure 5.3.a. Mean C-score at 0.01 m² to 1000 m² highlighted by broad community type in 2009 (sandhill, subxeric woodland, flatwood, silty woodland, savanna). b. Mean C-score metric at 0.01 m² to 1000 m² for each time since fire category in 2009 and 2010. Values exceeding 2 indicated species segregation (e.g., competition), values below -2 indicate species aggregation (e.g., environmental filtering), while values close to 0 are suggestive of stochastic assembly.
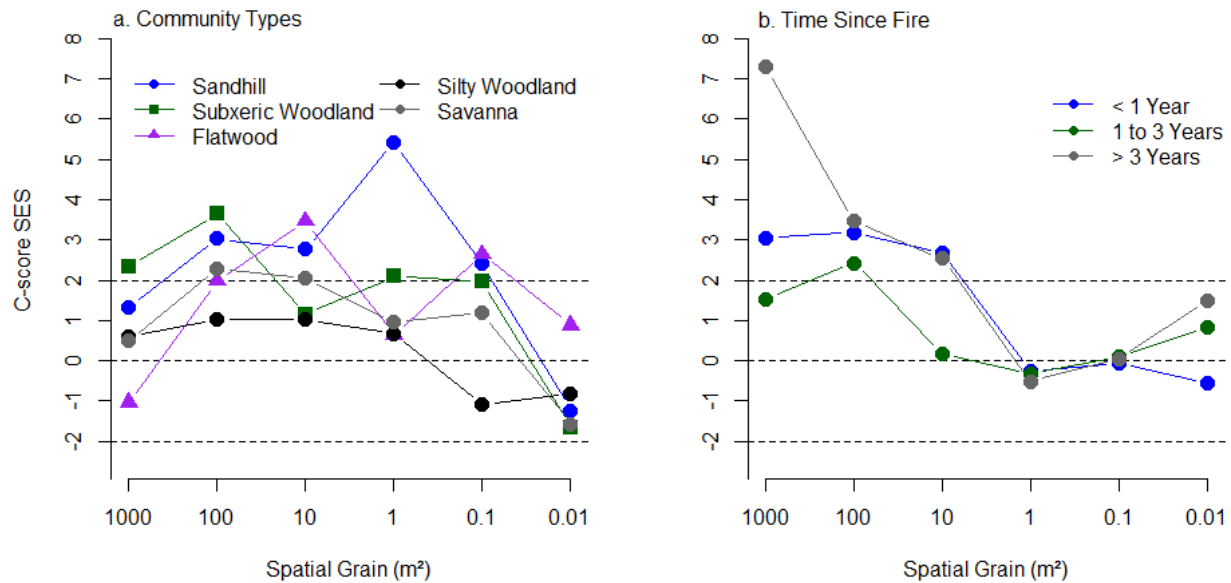
Figure 5.4. a. Mean C-score at 1000 m² for each time since fire category (< 1 year, 1 to 3 years, > 3 years) , highlighted by broad community type (sandhill, subxeric woodland, flatwood, silty woodland, savanna). b. for each time since fire category, highlighted by broad community type. Values exceeding 2 indicated species segregation (e.g., competition), values below -2 indicate species aggregation (e.g., environmental filtering), while values close to 0 are suggestive of stochastic assembly.
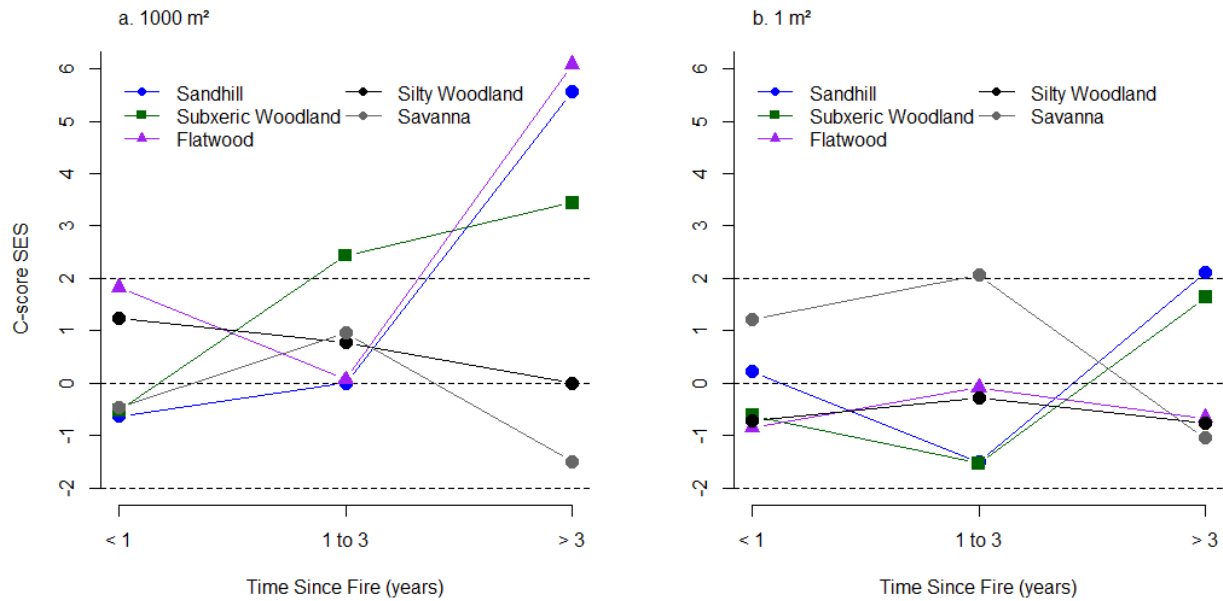
Figure 5.5. Mean C-score versus mean β_{rc} at 1000 m² for each time since fire category (< 1 year, 1 to 3 years, > 3 years).
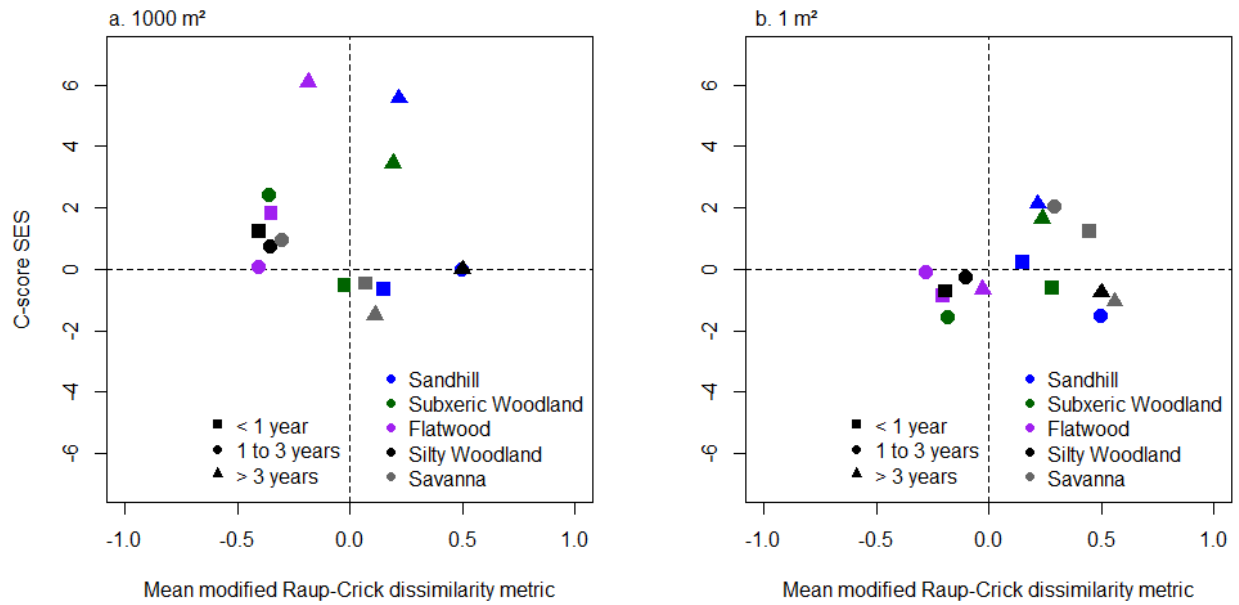
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CHAPTER 6: CONCLUSIONS AND SYNTHESIS

This dissertation explores plant species richness and composition patterns in the longleaf pine ecosystem across ~ 20 years, across the spatial extent of this system, and across spatial grain. In addition, a key goal of this work is to identify the community assembly processes that act to determine local community structure and examine how their relative importance changes with spatial scale and along the environmental gradient in this system. My work suggests that vegetation patterns in longleaf pine plant communities are driven by multiple ecological processes that vary in importance with the spatial and temporal extent at which they act. I identified local environmental filtering (e.g., soil properties) as a key driver of plant species richness and composition patterns. However, other community assembly processes explain additional variation in richness and composition unaccounted for by local environmental filtering (albeit less), including competition, climate, biogeography history, fire frequency, drought, and stochastic processes. This work also suggests ecological patterns and processes are scale-dependent, as the relative importance of environmental filtering, competition, fire frequency, biogeographic history, and stochastic processes change from small scales (≤ 1 m²) to larger scales (≥ 100 m²). I expand on these generalizations below and put them into context by synthesizing work from other species-rich grasslands in the world.

In this dissertation, local environmental filtering emerged as the most important process driving species richness and composition. In particular, soil resource availability (i.e. nutrients, moisture) explains most of the variation in vegetation patterns across space (Chapter 4 and across ~ 20 years in a smaller region of the longleaf pine range (eastern North Carolina, Chapter 2). Soil

texture, particularly silt %, emerged as the best soil predictor of species richness and composition patterns in the longleaf pine ecosystem of North Carolina (Chapter 2, Chapter 4), while base cation availability (e.g calcium) and topographically influenced soil moisture were observed to be more important in southern latitudes (Chapter 4). These findings are consistent with other studies of longleaf pine vegetation that have identified soil properties as key drivers of species richness and species composition patterns (e.g., Peet 2006, Carr et al. 2009, Peet et al. 2014). Interestingly, this work suggests that environmental context is a better predictor of the magnitude of vegetation change across 20 years than is fire frequency (Chapter 2). This is, in part, surprising, because fire frequency has previously been shown to drive patterns of species richness and composition over longer temporal extents (Lewis and Harshbarger 1976, Waldrop et al. 1992, Brockway and Lewis 1997, Glitzenstein et al. 2003, Glitzenstein et al. 2012). However, these earlier studies were confined to single sites that did not span the environmental gradient, which perhaps accounts for the discrepancy between my findings and theirs. In addition, environmental context influences fire frequency and fire behavior, with more intense and frequent fire on moist sites that generate more fuel. Thus, environmental context captures some information about fire behavior and frequency and perhaps explains, in part, why soil properties were a better predictor of vegetation change than fire frequency.

Two important filters on plant community structure that emerged in this dissertation were soil properties and drought. Although there is a gradient in soil resource availability in the longleaf pine ecosystem, most sites are relatively nutrient poor, especially in phosphorus. Low nutrient availability (namely P and N) have been attributed to the maintenance of plant biodiversity in other species-rich grasslands in the world. For example, in two separate fertilization experiments in European calcareous grasslands, fertilized sites had 30 to 50% fewer

species relative to controls (Kull & Zobel 1991, Willems et al. 1993). In addition, drought and water limitation have been identified as additional filters on grassland community structure. Water limitation, in part, helps maintains the extent of grasslands worldwide by limiting woody plant encroachment (Higgins et al. 2000, Bond 2008, Staver et al. 2011). In addition, periodic and annual drought events reduce biomass of the dominant, competitive species and result in temporary declines in species richness (Tilman & Haddi 1992, O'Connor 1995, Rosén 1995, Haddad et al. 2002, Cheng et al. 2011). However, drought also creates space for new species to colonize and may contribute over the long-term to the maintenance of species richness. Chapter 3 revealed that both periodic drought events and long-term drought are important factors that shape vegetation structure in longleaf pine savannas, despite relatively high annual precipitation. This study is one of the first to identify drought as an important filter in the longleaf pine ecosystem and I believe drought has been generally underappreciated in the southeastern US, despite its recognition as an important process in other grasslands ecosystems (Tilman and Haddi 1992, Knapp et al. 2002, Knapp et al. 2006, Anderson 2008). Future studies of how drought shapes plant biodiversity and composition in the longleaf pine ecosystem will become even more critical with ongoing climate change, which is predicted to increase the seasonality of precipitation and drought events across the southeastern United States (Klos et al. 2009).

Current fire frequency and fire history emerged as critical drivers of species richness and composition patterns in longleaf pine plant communities, especially at small spatial scales. Fire frequency was the second most important predictor of changes in species richness and composition over time in Chapter 2 with greater change on sites that had burned more frequently. Each fire event presents an opportunity for new species to emerge out of the seed or bud bank or colonize from adjacent areas; thus, an increased frequency of fire events may drive colonization

and extinction dynamics (Overbeck et al. 2005). However, frequent fire can also act as a stabilizing force. In Chapter 2, although there was more species turnover on sites with greater fire frequency, the overall magnitude of compositional change was relatively modest across all sites. It appears that the stability of plant composition over time is due to increased efforts by land managers to restore fire to longleaf pine communities over the last 20 years, which has resulted in a slight amount of convergence to fire-maintained vegetation (Figure 2.4). Frequent, low intensity disturbance is one explanation for the stability and maintenance of species richness in other species-rich grasslands (Kull & Zobel 1991, Leach and Givnish 1996, Bowles & Jones 2013). Kull & Zobel (1991) found that species density and richness declined in European calcareous grasslands with less frequent or intense mowing. Although plant species richness generally went up over time in most sites, I detected significant declines at small spatial scales in Big Island Savanna, likely driven primarily by reduced fire frequency. This work is significant because it indicates that only modest changes in the fire management regime (annual fire to fire every two to three years) may result in significant loss of biodiversity and suggests that nearly annual fire may be necessary for the maintenance of species richness in mesic longleaf pine savannas.

Processes that operate at larger spatial and temporal extents may also act as filters on local community structure. In Chapter 4, I explored whether climate and species pool size, a proxy for biogeographic history, explained variation in species richness across the longleaf pine range, in addition to local environmental filtering. Although, soil properties consistently explained more variation in species richness, climate and species pool size explained additional variation, albeit a relatively small fraction. The variance explained by soils, climate, and species pool size almost perfectly maps on to the findings of Carr et al. (2009), who explored similar

questions using plant species composition in Florida. In contrast to these findings, the relative importance of species pool size has been identified as a more important predictor of local richness in other ecosystems, including species-rich grasslands (Pärtel et al. 1996, Zobel 1997, Pärtel & Zobel 1999, Milbauer & Leach 2007).

My work suggests that longleaf pine plant communities are dynamic over both space and time, which is consistent with findings from other species-rich grasslands in the world (Herben 1993a, b, van der Maarel & Sykes 1993, Sykes et al. 1994). I detected relatively high rates of turnover across ~ 20 years, especially in silty, frequently-burned sites. At the wet, silty end of the environmental gradient (e.g., savannas), the dynamics of longleaf pine plant communities seem to fit well with the carousel model proposed for species-rich grasslands in Europe (van der Maarel & Sykes 1993, Sykes et al. 1994). The carousel model considers species to be ecologically equivalent (i.e., to have the same niche) and hypothesizes that species are riding on a carousel and given enough time, each species will colonize a given habitat patch. In savannas, many species appear to be ecologically equivalent and come and go over time in response to short-term changes in water availability, fire, and perhaps competition. To examine whether annual turnover was high in longleaf pine plant communities, I re-sampled 30 of the original 59 plots described in Chapter 2 and 5, in 2010. I detected considerable turnover over the course of a year, especially compared to the amount of turnover across ~ 20 year (Figure 6.4). Other studies in the longleaf pine ecosystem have also suggested that stochastic colonization and extinction are important drivers of plant species richness and composition (Myers & Harm 2009, Myers and Harm 2011). Furthermore, most of the species turning over across time were low in abundance. Future work should explore whether stochastic colonization and extinction events from a large

species pool of equivalent species helps to maintain the high species richness found in longleaf pine savannas.

Most plant species in the longleaf pine ecosystem occur infrequently in the landscape (Figure 6.1, Figure 6.2). The core-satellite species model categorizes species into two types: core species, which are frequent and abundance, and satellite species, which occur infrequently and in low abundance (Hanski 1982). Several studies have explored core-satellite species patterns in the longleaf pine ecosystem and found no evidence for a dichotomy between frequent, abundant species and infrequent, low-abundance species (Kirkman et al. 2001, Keddy et al. 2006, Clark et al. 2008), in contrast to other grassland ecosystems (e.g., tallgrass prairie, Collins & Glen 1990, Collins & Glen 1991; alvar grasslands, Pärtel et al. 2001). To follow up on this work, I explored core-satellite species patterns using two different data sets that vary in spatial extent: 59 plots from eastern North Carolina (Chapter 2, Chapter 5) and 849 plots spanning a large portion of the longleaf range (Chapter 4). I summarized species frequency patterns as the number of plots each species occurred in, and also examined the mean abundance of those species. Previous work, along with my analysis of core-satellite species patterns (Figure 6.1, Figure 6.2), shows that most species in the longleaf pine ecosystem are infrequent in the landscape (2.7% of species occur in $\geq 75\%$ of plots, 75.15% of species occur in $\leq 25\%$ of plots from eastern North Carolina. In fact, there appear to be very few "core" species in the longleaf pine ecosystem; the bulk of biodiversity in local sites is made up of satellite species (Figure 6.3). I suggest that the high spatial and temporal turnover in this ecosystem creates a large species pool that can filter down into local communities. In addition, the low abundance of most species in this system may contribute to the high species packing and species richness at small spatial scales for which this ecosystem is famous for (Walker & Peet 1983).

In this dissertation, I consistently detected the scale-dependence of both ecological patterns and their underlying processes. In Chapter 2, I found that the correlation between fire frequency and compositional change because more important as spatial scale decreased, consistent with the findings and suggestions of Glitzenstein et al. (2003). In addition, Chapter 2 suggested that dissimilarity over time at small scales was higher than at larger spatial scales, possibly because there is greater stochasticity at small spatial scales. I followed up on this in Chapter 5 by using species co-occurrence metrics to examine how the relative importance of deterministic and stochastic processes changes with spatial grain. Species co-occurrence patterns shifted from negative at larger grain sizes to more positive as grain size decreased. This suggests a shift in processes with a decrease in spatial scale. Thus, the spatial scale at which a study is conducted has important implications for the patterns detected and the inference of process from those patterns.

I echo other authors (e.g., Dengler et al. 2009, Wheeler et al. 2011) and argue that to understand vegetation patterns and identify the community assembly processes structuring those patterns, sampling must be conducted across a range of spatial scales. For example, the nested nature of sampling in Chapter 2 and 3 revealed declines in plant species richness in Big Island Savanna at small scales, but not at larger scales. Had I simply generated a species list for each plot across time at 100 m², I would have concluded that biodiversity had remained stable over time in Big Island Savanna. Thus, the multi-scale sampling allowed me to detect the loss of biodiversity at small scales, investigate what might be driving that loss, and communicate those findings directing to land managers implementing prescribed fire. In addition, the scale at which communities are sampled must match the goals of the project and the spatial or temporal extent of the processes being detected.

This dissertation identifies several ecological processes that act synergistically to structure vegetation patterns in the longleaf ecosystem. In addition, it explores the spatial and temporal patterns of plant species richness and species composition. My work here contributes to a growing pool of literature suggesting that multiple processes, which operate at different spatial and temporal extents, can shape ecological patterns in local communities. In addition, those processes are scale dependent and their relative importance in assembling communities changes with spatial and temporal scale.

Figures

Figure 6.1. A. Frequency of plant species in 1000 m² plots in eastern North Carolina (Chapter 2, 5). B. The frequency of plant species in 1000 m² across the southeastern US (Chapter 4). Most species are infrequent and occur in fewer than 10% of sites. More notably, there is no second mode, suggesting the absence of "core" species (i.e. species that are frequent and abundant) in the longleaf pine ecosystem. This pattern remains constant when constraining environmental context and looking with each broad longleaf pine community type as well.
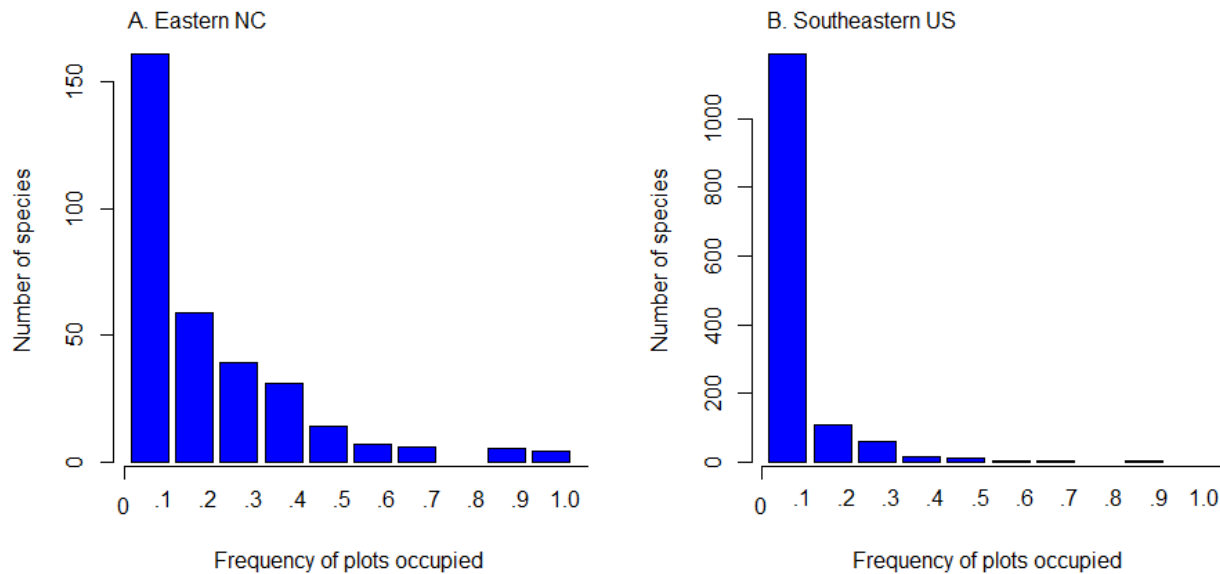
Figure 6.2. A. Number of plots occupied by each species versus abundance for that species (log mean cover %). Points represent each species in the data set (326) from eastern NC (Chapter 2, Chapter 5). B. Number of plots occupied by each species versus abundance across the longleaf range (Chapter 4). Species in the upper right corner of the graph are considered "core", as they are abundant and occur frequently in plots. Species in the lower left corner are satellite species, which are infrequent and low in abundance. There are very few core species in longleaf pine communities.
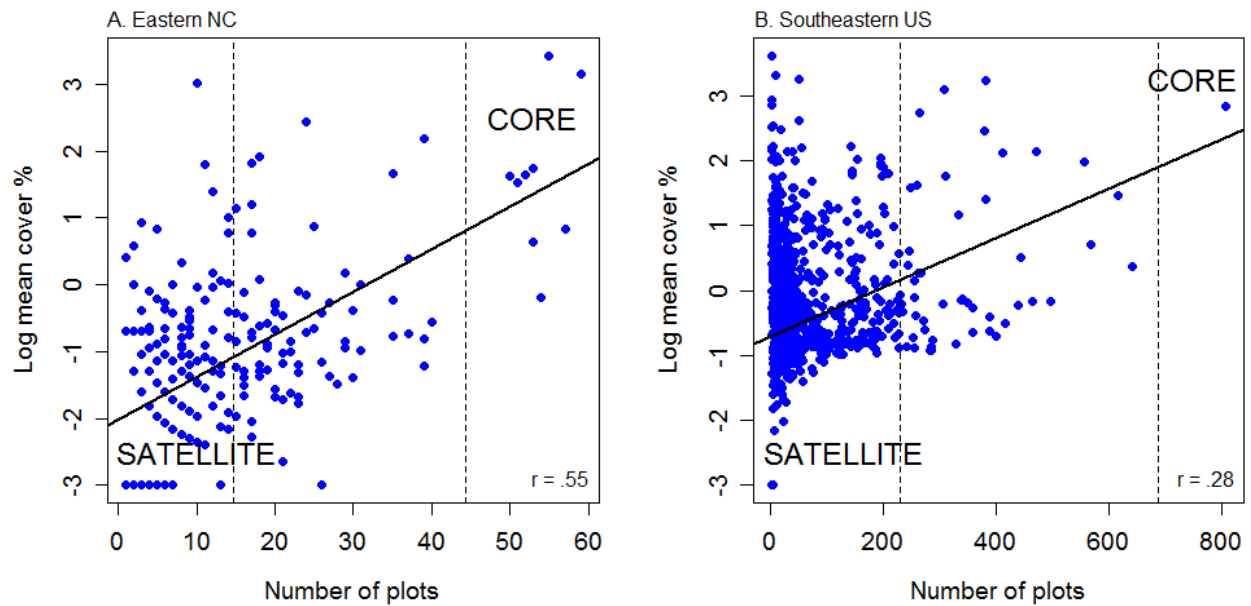
Figure 6.3. Number of satellite species versus species richness at 1000 m² for the 59 plots located in eastern North Carolina. Here, satellite species are species which occur in 25% or less of plots and have low abundance when they occur. Satellite species number and species richness are strongly correlated, suggesting most species in plots in longleaf pine plant communities are satellite species.
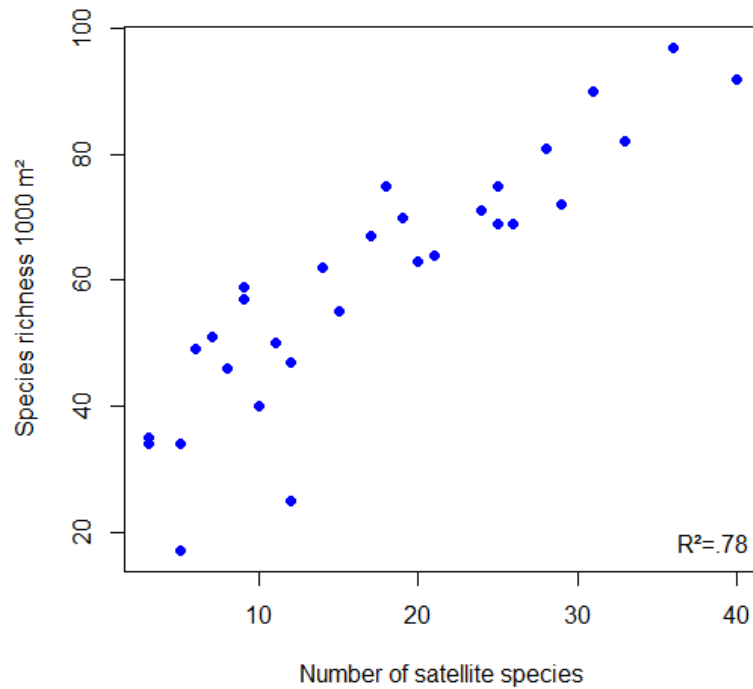
Figure 6.4. Mean species turnover (defined here as the number of species gained and lost across time) from 1990 to 2009 and from 2009 to 2010 for 30 plots in eastern North Carolina. The magnitude of species turning over on an annual basis is considerable, especially compared to the magnitude across ~20 years.
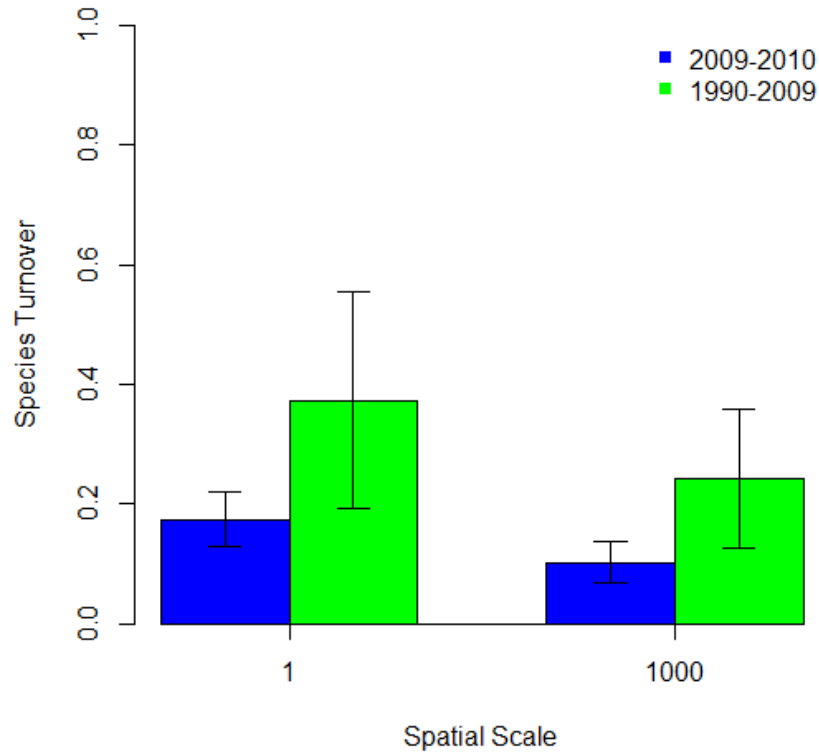
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APPENDIX A. GROWTH FORM ASSIGNMENTS FOR CHAPTER 2 SPECIES

Table A.1. Growth form assignments to all 398 taxa in the data set for Chapter 2. Composite and standardized taxonomic names are not shown here.

Taxon	Growth Form
Acer rubrum	tree
Agalinis aphylla	hemiparasite
Agalinis fasciculata	hemiparasite
Agalinis linifolia	hemiparasite
Agalinis obtusifolia	hemiparasite
Agalinis purpurea	hemiparasite
Agalinis setacea	hemiparasite
Agalinis virgata	hemiparasite
Aletris [*farinosa* + *lutea*]	rosette herb
Amorpha confusa	legume
Amorpha herbacea	legume
Amphicarpum amphicarpon	single-culm graminoid
Andropogon capillipes	matrix graminoid
Andropogon elliottii	matrix graminoid
Andropogon glaucopsis	matrix graminoid
Andropogon glomeratus var. glomeratus	matrix graminoid
Andropogon glomeratus var. hirsutior	matrix graminoid
Andropogon mohrii	matrix graminoid
Andropogon ternarius	matrix graminoid
Andropogon virginicus var. virginicus	matrix graminoid
Antennaria [*parlinii* + *plantaginifolia*]	rosette herb
Anthenantia rufa	single-culm graminoid
Anthenantia villosa	single-culm graminoid
Aristida purpurascens	single-culm graminoid
Aristida stricta	matrix graminoid
Aristida virgata	single-culm graminoid
Arnica acaulis	rosette herb
Aronia arbutifolia	shrub
Arundinaria tecta	shrub
Asclepias amplexicaulis	caulescent herb
Asclepias humistrata	caulescent herb
Asclepias longifolia	caulescent herb
Asclepias pedicellata	caulescent herb
Balduina uniflora	rosette herb
Bartonia virginica	caulescent herb
Bigelowia nudata var. nudata	rosette herb
Bulbostylis [*ciliatifolia* + *coarctata*]	single-culm graminoid

Table A.1 (cont). Growth form assignments to all 398 taxa in the data set for Chapter 2. Composite and standardized taxonomic names are not shown here.

Taxon	Growth Form
Bulbostylis capillaris	single-culm graminoid
Calamagrostis cinnoides	single-culm graminoid
Calamovilfa brevipilis	single-culm graminoid
Callicarpa americana	shrub
Calopogon barbatus	geophyte
Calopogon pallidus	geophyte
Calopogon tuberosus var. tuberosus	geophyte
Carex striata var. brevis	matrix graminoid
Carphephorus bellidifolius	rosette herb
Carphephorus odoratissimus var. odoratissimus	rosette herb
Carphephorus paniculatus	rosette herb
Carphephorus tomentosus	rosette herb
Carya alba	tree
Centella erecta	rosette herb
Chamaecrista [*nictitans + fasciculata*]	caulescent herb
Chamaecyparis thyoides	tree
Chamaesyce sp.	caulescent herb
Chaptalia tomentosa	rosette herb
Chasmanthium laxum	single-culm graminoid
Chrysopsis gossypina	rosette herb
Chrysopsis mariana	rosette herb
Cirsium horridulum	rosette herb
Cirsium lecontei	rosette herb
Cirsium repandum	rosette herb
Cirsium virginianum	rosette herb
Cleistesiopsis divaricata	geophyte
Clethra alnifolia	shrub
Cnidoscolus stimulosus	caulescent herb
Commelina erecta	caulescent herb
Coreopsis falcata	rosette herb
Coreopsis linifolia	rosette herb
Cornus florida	tree
Cornus stricta	shrub
Crataegus aprica	tree
Crocanthemum carolinianum	rosette herb
Crotalaria purshii	legume
Ctenium aromaticum	matrix graminoid
Cuscuta sp.	vine

Table A.1 (cont). Growth form assignments to all 398 taxa in the data set for Chapter 2. Composite and standardized taxonomic names are not shown here.

Taxon	Growth Form
Cuthbertia graminea	rosette herb
Cyperus grayi	single-culm graminoid
Cyperus retrorsus	single-culm graminoid
Cyrilla racemiflora	tree
Danthonia sericea	matrix graminoid
Desmodium [*obtusum + tortuosum*]	legume
Desmodium [*tenuifolium + strictum*]	legume
Desmodium ciliare	legume
Desmodium lineatum	legume
Desmodium marilandicum	legume
Desmodium obtusum	legume
Desmodium paniculatum	legume
Desmodium perplexum	legume
Desmodium rotundifolium	legume
Desmodium tenuifolium	legume
Dichanthelium aciculare	single-culm graminoid
Dichanthelium angustifolium	single-culm graminoid
Dichanthelium arenicoloides	single-culm graminoid
Dichanthelium commutatum var. ashei	single-culm graminoid
Dichanthelium consanguineum	single-culm graminoid
Dichanthelium ensifolium	single-culm graminoid
Dichanthelium leucothrix	single-culm graminoid
Dichanthelium longiligulatum	single-culm graminoid
Dichanthelium mattamuskeetense	single-culm graminoid
Dichanthelium ovale var. addisonii	single-culm graminoid
Dichanthelium ovale var. ovale	single-culm graminoid
Dichanthelium portoricense ssp. patulum	single-culm graminoid
Dichanthelium portoricense ssp. portoricense	single-culm graminoid
Dichanthelium strigosum var. glabrescens	single-culm graminoid
Dichanthelium strigosum var. leucoblepharis	single-culm graminoid
Dichanthelium strigosum var. strigosum	single-culm graminoid
Dichanthelium tenue	single-culm graminoid
Dichanthelium villosissimum var. villosissimum	single-culm graminoid
Diodia virginiana	caulescent herb
Dionaea muscipula	insectivore
Dioscorea villosa	vine
Diospyros virginiana	tree
Drosera brevifolia	insectivore

Table A.1 (cont). Growth form assignments to all 398 taxa in the data set for Chapter 2. Composite and standardized taxonomic names are not shown here.

Taxon	Growth Form
Drosera capillaris	insectivore
Elephantopus nudatus	rosette herb
Epigaea repens	subshrub
Erechtites hieracifolia var. hieracifolia	rosette herb
Erigeron strigosus var. strigosus	rosette herb
Erigeron vernus	rosette herb
Eriocaulon compressum	rosette herb
Eryngium integrifolium	rosette herb
Eubotrys racemosa	shrub
Eupatorium [*mohrii + recurvans*]	caulescent herb
Eupatorium album	caulescent herb
Eupatorium capillifolium	caulescent herb
Eupatorium leucolepis	caulescent herb
Eupatorium linearifolium	caulescent herb
Eupatorium mohrii	caulescent herb
Eupatorium pilosum	caulescent herb
Eupatorium rotundifolium	caulescent herb
Euphorbia curtisii	caulescent herb
Euphorbia ipecacuanhae	caulescent herb
Euphorbia pubentissima	caulescent herb
Eurybia compacta	rosette herb
Eurybia paludosa	rosette herb
Euthamia caroliniana	caulescent herb
Fimbristylis annua	single-culm graminoid
Fimbristylis puberula var. puberula	single-culm graminoid
Galactia [*regularis + volubilis var. volubilis*]	legume
Galactia erecta	legume
Galactia volubilis var. volubilis	legume
Galium pilosum	caulescent herb
Gamochaeta purpurea	rosette herb
Gaultheria procumbens	subshrub
Gaylussacia dumosa	subshrub
Gaylussacia frondosa	shrub
Gelsemium sempervirens	vine
Gentiana autumnalis	caulescent herb
Gymnopogon ambiguus	single-culm graminoid
Gymnopogon brevifolius	single-culm graminoid
Helianthus angustifolius	rosette herb

Table A.1 (cont). Growth form assignments to all 398 taxa in the data set for Chapter 2. Composite and standardized taxonomic names are not shown here.

Taxon	Growth Form
Helianthus atrorubens	rosette herb
Helianthus heterophyllus	rosette herb
Hieracium gronovii	rosette herb
Hieracium marianum	rosette herb
Hypericum cistifolium	caulescent herb
Hypericum crux-andreae	caulescent herb
Hypericum hypericoides	caulescent herb
Hypericum setosum	caulescent herb
Hypericum tenuifolium	caulescent herb
Hypoxis [*hirsuta + wrightii*]	single-culm graminoid
Hypoxis juncea	single-culm graminoid
Hypoxis sessilis	single-culm graminoid
Hypoxis wrightii	single-culm graminoid
Ilex coriacea	tree
Ilex glabra	shrub
Ilex myrtifolia	shrub
Ilex opaca var. opaca	tree
Ionactis linariifolia	caulescent herb
Iris verna var. verna	rosette herb
Juncus biflorus	single-culm graminoid
Juncus canadensis	single-culm graminoid
Juncus scirpoides	single-culm graminoid
Lachnanthes caroliniana	rosette herb
Lachnocaulon anceps	rosette herb
Lactuca sp.	rosette herb
Lechea minor	caulescent herb
Lechea pulchella var. ramosissima	caulescent herb
Lechea torreyi var. congesta	caulescent herb
Lespedeza angustifolia	legume
Lespedeza capitata	legume
Lespedeza cuneata	legume
Lespedeza hirta var. curtissii	legume
Lespedeza hirta var. hirta	legume
Lespedeza virginica	legume
Liatris [*pilosa + virgata*]	rosette herb
Liatris pilosa	rosette herb
Liatris spicata	rosette herb
Lilium catesbaei	geophyte

Table A.1 (cont). Growth form assignments to all 398 taxa in the data set for Chapter 2. Composite and standardized taxonomic names are not shown here.

Taxon	Growth Form
Linum floridanum	caulescent herb
Linum striatum	caulescent herb
Liquidambar styraciflua	tree
Lobelia nuttallii	caulescent herb
Ludwigia virgata	caulescent herb
Lycopodiella alopecuroides	clubmoss
Lycopodiella appressa	clubmoss
Lyonia ligustrina var. foliosiflora	shrub
Lyonia lucida	shrub
Lyonia mariana	shrub
Lysimachia asperulifolia	caulescent herb
Lysimachia loomisii	caulescent herb
Magnolia virginiana	tree
Marshallia graminifolia	rosette herb
Minuartia caroliniana	caulescent herb
Monotropa uniflora	caulescent herb
Morella caroliniensis	shrub
Morella cerifera	shrub
Morella pumila	shrub
Muhlenbergia expansa	matrix graminoid
Nyssa sylvatica	tree
Opuntia humifusa	cactus
Orbexilum pedunculatum var. psoralioides	caulescent herb
Osmanthus americanus	tree
Osmunda cinnamomea var. cinnamomea	fern
Oxalis dillenii	caulescent herb
Oxypolis denticulata	caulescent herb
Panicum anceps var. rhizomatum	single-culm graminoid
Panicum virgatum	single-culm graminoid
Parthenium integrifolium	rosette herb
Parthenocissus quinquefolia	vine
Paspalum praecox	single-culm graminoid
Paspalum setaceum var. ciliatifolium	single-culm graminoid
Persea palustris	tree
Phoradendron serotinum ssp. serotinum	subshrub
Pinguicula caerulea	insectivore
Pinguicula lutea	insectivore
Pinguicula pumila	insectivore

Table A.1 (cont). Growth form assignments to all 398 taxa in the data set for Chapter 2. Composite and standardized taxonomic names are not shown here.

Taxon	Growth Form
Pinus palustris	tree
Pinus serotina	tree
Pinus taeda	tree
Pityopsis graminifolia	caulescent herb
Platanthera ciliaris	geophyte
Platanthera cristata	geophyte
Pleea tenuifolia	rosette herb
Pluchea foetida var. foetida	caulescent herb
Pogonia ophioglossoides	geophyte
Polygala brevifolia	caulescent herb
Polygala cruciata	caulescent herb
Polygala hookeri	caulescent herb
Polygala lutea	caulescent herb
Polygala ramosa	caulescent herb
Polygonella polygama	subshrub
Prenanthes autumnalis	rosette herb
Prunus caroliniana	tree
Prunus serotina	tree
Pseudolycopodiella caroliniana	clubmoss
Pteridium aquilinum var. pseudocaudatum	fern
Pterocaulon pycnostachyum	caulescent herb
Pycnanthemum flexuosum	caulescent herb
Pyxidanthera barbulata	caulescent herb
Quercus falcata	tree
Quercus geminata	tree
Quercus hemisphaerica	tree
Quercus incana	tree
Quercus incana x marilandica	tree
Quercus laevis	tree
Quercus laevis x marilandica	tree
Quercus margaretta	tree
Quercus marilandica var. marilandica	tree
Quercus nigra	tree
Quercus phellos	tree
Quercus stellata	tree
Quercus velutina	tree
Quercus virginiana	tree
Quercus xashei	tree

Table A.1 (cont). Growth form assignments to all 398 taxa in the data set for Chapter 2. Composite and standardized taxonomic names are not shown here.

Taxon	Growth Form
Quercus xblufftonensis	tree
Quercus xincomita	tree
Quercus xsubintegra	tree
Rhexia [*nashii + mariana var. mariana*]	caulescent herb
Rhexia alifanus	caulescent herb
Rhexia lutea	caulescent herb
Rhexia mariana var. mariana	caulescent herb
Rhexia petiolata	caulescent herb
Rhododendron atlanticum	shrub
Rhus copallinum	shrub
Rhynchosia reniformis	legume
Rhynchosia tomentosa var. tomentosa	legume
Rhynchospora baldwinii	single-culm graminoid
Rhynchospora breviseta	single-culm graminoid
Rhynchospora chapmanii	single-culm graminoid
Rhynchospora ciliaris	single-culm graminoid
Rhynchospora fascicularis var. fascicularis	single-culm graminoid
Rhynchospora filifolia	single-culm graminoid
Rhynchospora glomerata	single-culm graminoid
Rhynchospora harveyi	single-culm graminoid
Rhynchospora inexpansa	single-culm graminoid
Rhynchospora latifolia	single-culm graminoid
Rhynchospora plumosa	single-culm graminoid
Rhynchospora rariflora	single-culm graminoid
Rhynchospora wrightiana	single-culm graminoid
Robinia nana	shrub
Rubus [*enslenii + flagellaris*]	subshrub
Rubus cuneifolius	subshrub
Rubus trivialis	subshrub
Sabatia difformis	caulescent herb
Saccharum sp.	matrix graminoid
Sarracenia flava	insectivore
Sarracenia purpurea var. venosa	insectivore
Sarracenia rubra	insectivore
Sassafras albidum	tree
Schizachyrium scoparium	matrix graminoid
Scleria ciliata var. ciliata	single-culm graminoid
Scleria ciliata var. glabra	single-culm graminoid

Table A.1 (cont). Growth form assignments to all 398 taxa in the data set for Chapter 2. Composite and standardized taxonomic names are not shown here.

Taxon	Growth Form
Scleria elliottii	single-culm graminoid
Scleria minor	single-culm graminoid
Scleria nitida	single-culm graminoid
Scleria pauciflora var. caroliniana	single-culm graminoid
Scleria pauciflora var. pauciflora	single-culm graminoid
Scleria triglomerata	single-culm graminoid
Scutellaria integrifolia	caulescent herb
Selaginella acanthonota	caulescent herb
Sericocarpus asteroides	rosette herb
Sericocarpus linifolius	rosette herb
Sericocarpus tortifolius	rosette herb
Seymeria cassioides	hemiparasite
Silphium compositum	rosette herb
Sisyrinchium capillare	rosette herb
Smilax auriculata	vine
Smilax bona-nox	vine
Smilax glauca	vine
Smilax laurifolia	vine
Smilax rotundifolia	vine
Solidago arguta	rosette herb
Solidago gracillima	rosette herb
Solidago odora var. odora	rosette herb
Solidago pulchra	rosette herb
Solidago stricta	rosette herb
Sophronanthe pilosa	caulescent herb
Sorghastrum nutans	matrix graminoid
Spiranthes [*praecox + sylvatica*]	geophyte
Spiranthes lacera var. gracilis	geophyte
Spiranthes praecox	geophyte
Spiranthes vernalis	geophyte
Sporobolus pinetorum	matrix graminoid
Stenanthium densum	rosette herb
Stipulicida setacea var. setacea	caulescent herb
Stylisma patens ssp. angustifolia	caulescent herb
Stylisma patens ssp. patens	caulescent herb
Stylosanthes biflora	legume
Symphyotrichum concolor var. concolor	caulescent herb
Symphyotrichum dumosum var. dumosum	caulescent herb

Table A.1 (cont). Growth form assignments to all 398 taxa in the data set for Chapter 2. Composite and standardized taxonomic names are not shown here.

Taxon	Growth Form
Symphyotrichum walteri	caulescent herb
Symplocos tinctoria	tree
Tephrosia florida	legume
Tephrosia hispidula	legume
Tephrosia spicata	legume
Tephrosia virginiana	legume
Tillandsia usneoides	caulescent herb
Toxicodendron pubescens	vine
Toxicodendron radicans var. radicans	vine
Tragia urens	caulescent herb
Triantha racemosa	rosette herb
Triplasis purpurea var. purpurea	single-culm graminoid
Utricularia subulata	insectivore
Vaccinium arboreum	shrub
Vaccinium crassifolium	subshrub
Vaccinium formosum	shrub
Vaccinium fuscatum	shrub
Vaccinium stamineum	shrub
Vaccinium tenellum	subshrub
Vernonia acaulis	rosette herb
Viburnum nudum	shrub
Viola primulifolia	rosette herb
Viola septemloba	rosette herb
Vitis rotundifolia var. rotundifolia	vine
Woodwardia areolata	fern
Woodwardia virginica	fern
Xyris ambigua	rosette herb
Xyris baldwiniana	rosette herb
Xyris caroliniana	rosette herb
Xyris platylepis	rosette herb
Yucca filamentosa	subshrub
Zenobia pulverulenta	shrub
Zigadenus glaberrimus	rosette herb

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[1] Growth form classifications modified and expanded from Raunkaier 1937. Club mosses are spore-bearing vascular plants. Caulescent herbs are hemicryptophytes with a leafy stem. Geophytes are plants with subterranean organs, from which stems emerge. Insectivores are

hemicryptophytes that obtain additional N and P from insects. Legumes are nitrogen-fixing hemicryptophytes. Matrix graminoids are hemicryptophytes with many flowering culms and a bunch-grass habit. In contrast, single-culm graminoids have a single flowering culm. Rosette herbs are hemicryptophytes with leaves restricted to a basal rosette and a stem that only supports flowers. Trees are phanerophytes with a main stem, while -shrubs are phanerophytes with multiple stems. Subshrubs are chamaephytes, whose shoots are produced very close to the ground. Vines are trailing chamaephytes.

APPENDIX B. PERCENTAGE OF SUBPLOTS OCCUPIED BY SPECIES FROM 1985-2013

Table B.1. Percentage of 0.01 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Eupatorium leucolepis	caulescent herb	mesic	tall	8.0	7.7	7.7	8.3	6.3	8.3	6.7	5.0	6.7
Eupatorium rotundifolium	caulescent herb	dry	tall	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euphorbia curtisii	caulescent herb	dry	short	17.3	19.0	20.7	19.0	10.3	22.7	15.3	18.0	19.7
Lactuca sp.	caulescent herb	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
Linum sp.	caulescent herb	mesic	short	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Lobelia nuttalli	caulescent herb	mesic	tall	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.7	1.7
Ludwigia virgata	caulescent herb	wet	tall	0.0	0.0	0.0	0.0	0.3	0.7	0.3	0.3	0.3
Oxypolis ternata	caulescent herb	wet	tall	2.3	1.0	3.3	2.3	0.0	1.7	0.3	1.3	0.7
Pityopsis graminifolia	caulescent herb	dry	short	17.3	22.0	22.7	23.3	19.0	21.0	0.7	2.3	4.0
Polygala hookeri	caulescent herb	mesic	short	43.7	41.7	35.0	36.7	36.0	16.3	0.0	0.3	0.3
Polygala lutea	caulescent herb	mesic	short	7.0	1.7	7.7	8.7	12.0	9.7	0.3	0.3	5.3
Pteridium aquilinum	caulescent herb	dry	tall	0.0	0.0	0.0	0.0	0.3	4.0	7.0	8.0	7.7
Rhexia alifanus	caulescent herb	dry	tall	23.3	23.3	24.0	23.7	20.0	18.0	10.0	10.0	7.7
Rhexia lutea	caulescent herb	mesic	tall	0.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Rhexia petiolata	caulescent herb	wet	tall	2.7	7.0	8.0	6.7	7.3	9.7	1.0	2.7	2.0
Sabatia difformis	caulescent herb	wet	tall	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.7
Sabatia gentianoides	caulescent herb	wet	tall	0.0	1.0	1.3	0.7	0.0	1.0	0.0	0.0	0.7
Symphyotrichum dumosum	caulescent herb	dry	tall	7.0	9.0	8.3	8.0	7.7	6.0	0.7	1.3	2.0
Lycopodiella alopecuroides	clubmoss	mesic	short	0.0	0.0	0.0	0.0	0.0	0.7	0.0	4.0	3.7
Lycopodiella appressa	clubmoss	mesic	short	24.0	16.3	21.3	21.7	23.7	8.0	11.3	3.3	5.0
Calopogon pallidus	geophyte	mesic	short	14.3	26.7	32.3	31.7	28.0	19.3	1.0	0.3	0.7
Calopogon tuberosus	geophyte	mesic	short	0.7	0.7	1.0	0.3	0.0	0.7	0.0	0.0	0.0
Cleistesiopsis divaricata	geophyte	mesic	short	1.7	4.7	8.0	5.3	1.3	3.7	0.0	2.3	1.7
Lilium catesbaei	geophyte	mesic	short	3.0	1.7	0.7	0.7	0.0	1.7	0.0	2.0	1.0
Platanthera sp.	geophyte	mesic	tall	9.0	9.7	10.0	10.7	8.3	5.0	0.0	3.7	2.3
Pogonia ophioglossoides	geophyte	mesic	short	0.3	0.3	1.7	3.0	2.3	0.3	0.0	0.0	0.7
Spiranthes sp.	geophyte	mesic	tall	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Agalinis aphylla	hemiparasite	mesic	tall	3.0	3.3	3.3	3.7	3.7	1.7	2.0	1.3	0.7

Table B.1 (cont). Percentage of 0.01 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Agalinis obtusifolia	hemiparasite	dry	tall	2.3	17.0	37.0	49.7	36.3	20.0	6.0	19.0	32.0
Seymeria cassioides	hemiparasite	dry	tall	9.7	10.0	6.7	3.7	12.7	13.3	36.3	34.7	8.7
Dionaea muscipula	insectivore	mesic	short	67.0	68.3	68.0	69.7	70.7	36.0	30.7	47.7	44.7
Drosera capillaris	insectivore	mesic	short	36.3	15.0	56.7	68.3	55.0	14.0	4.3	12.7	40.7
Pinguicula sp.	insectivore	mesic	short	20.3	17.0	19.7	27.0	28.7	13.0	0.0	4.3	10.7
Utricularia subulata	insectivore	wet	short	0.0	0.7	12.3	5.3	4.7	0.0	0.0	0.0	0.3
Desmodium lineatum	legume	dry	short	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
Desmodium tenuifolium	legume	mesic	tall	0.0	0.0	1.7	1.3	1.7	1.3	1.0	1.3	1.0
Tephrosia hispidula	legume	dry	short	0.0	0.0	0.0	0.3	0.0	2.7	3.0	2.3	3.7
Andropogon sp.	matrix graminoid	dry	tall	54.0	61.0	66.7	68.7	65.3	66.3	62.0	66.7	69.7
Andropogon sp. 2	matrix graminoid	dry	tall	26.7	28.7	27.0	26.3	21.0	26.7	0.7	0.0	0.0
Aristida stricta	matrix graminoid	dry	tall	43.3	46.0	44.7	44.7	41.7	46.7	31.7	39.3	37.3
Carex striata var. brevis	matrix graminoid	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	4.3	4.3	3.3
Ctenium aromaticum	matrix graminoid	mesic	tall	22.3	22.0	24.0	25.0	24.7	27.3	17.0	20.7	21.3
Muhlenbergia expansa	matrix graminoid	mesic	tall	41.7	42.7	44.0	47.0	44.3	47.7	40.3	39.3	37.7
Sporobolus pinetorum	matrix graminoid	mesic	tall	50.0	55.3	54.3	56.0	57.7	59.3	66.3	53.3	54.0
Aletris farinosa	rosette herb	mesic	short	9.3	9.7	10.3	10.0	8.7	6.3	2.7	1.3	1.0
Bigelowia nudata	rosette herb	dry	short	71.3	76.0	77.7	79.0	76.3	67.7	23.3	24.3	23.3
Carphephorus paniculatus	rosette herb	dry	tall	3.3	4.0	3.3	4.0	4.3	5.0	4.3	5.0	3.7
Carphephorus tomentosus	rosette herb	dry	tall	16.3	20.3	26.7	25.3	25.7	25.0	5.3	6.0	6.3
Chaptalia tomentosa	rosette herb	mesic	short	0.0	0.0	0.0	0.7	0.3	0.3	0.0	0.0	0.0
Coreopsis linifolia	rosette herb	mesic	short	90.7	90.0	95.0	93.3	93.7	94.3	13.0	20.3	23.3
Erigeron vernus	rosette herb	mesic	short	7.7	8.3	8.7	8.7	6.7	8.7	7.0	9.3	5.7
Eryngium integrifolium	rosette herb	mesic	short	19.0	18.0	16.7	16.3	14.7	10.0	0.7	4.3	7.7
Eurybia paludosa	rosette herb	mesic	tall	12.0	11.3	15.0	18.0	16.7	19.3	25.0	28.3	27.0
Helianthus angustifolius	rosette herb	mesic	tall	2.0	0.3	2.0	1.7	3.0	3.7	0.7	1.0	1.0
Helianthus heterophyllus	rosette herb	mesic	tall	15.0	17.3	20.7	19.0	16.0	13.0	6.7	7.3	7.7
Lachnanthes caroliniana	rosette herb	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Lachnocaulon anceps	rosette herb	wet	short	13.3	13.3	14.0	13.0	12.7	12.3	9.7	11.7	12.7

Table B.1 (cont). Percentage of 0.01 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Liatris [*pilosa + virgata*]	rosette herb	dry	tall	0.7	0.0	0.0	0.7	0.3	1.0	1.0	1.3	0.0
Marshallia graminifolia	rosette herb	mesic	short	10.0	6.3	9.3	11.7	10.3	7.0	2.7	1.3	4.3
Sisyrinchium capillare	rosette herb	mesic	short	18.7	26.7	27.7	35.0	35.7	37.0	5.0	9.0	4.7
Sisyrinchium sp.	rosette herb	mesic	short	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Solidago [*stricta + pulchra*]	rosette herb	mesic	tall	23.7	24.0	24.0	26.7	24.0	25.7	18.7	18.0	17.7
Solidago sp.	rosette herb	mesic	short	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Triantha racemosa	rosette herb	mesic	short	28.3	32.7	34.7	38.7	37.0	33.7	15.7	15.7	18.3
Viola primulifolia	rosette herb	mesic	short	12.0	18.3	15.3	18.3	18.3	9.7	4.3	6.0	7.3
Viola septemloba	rosette herb	mesic	short	0.0	0.0	1.3	0.7	0.7	1.0	0.0	0.0	1.3
Xyris ambigua	rosette herb	wet	tall	16.3	16.7	17.0	17.0	17.0	16.0	6.3	4.3	6.3
Xyris caroliniana	rosette herb	dry	tall	12.0	20.3	17.3	18.7	22.7	23.0	8.0	11.0	7.7
Aronia arbutifolia	shrub	wet	tall	3.7	4.7	5.3	6.0	4.3	3.7	8.3	8.3	9.3
Arundinaria tecta	shrub	wet	tall	2.0	2.0	2.0	1.7	1.0	0.7	0.0	0.0	0.0
Gaylussacia frondosa	shrub	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.3
Ilex glabra	shrub	wet	tall	0.7	0.7	1.3	2.0	0.0	2.0	0.0	0.3	1.7
Lyonia mariana	shrub	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0
Morella carolinensis	shrub	wet	tall	0.3	0.3	1.0	0.3	0.0	0.0	5.3	5.3	6.0
Aristida virgata	single culm graminoid	mesic	tall	8.0	12.0	9.7	10.3	5.3	12.0	0.0	1.0	0.0
Dichanthelium ensifolium	single culm graminoid	mesic	tall	79.0	83.7	85.3	85.3	85.0	76.7	72.0	81.7	86.0
Dichanthelium strigosum	single culm graminoid	mesic	tall	13.0	15.3	13.0	13.7	12.3	11.7	0.3	0.3	0.7
Fimbristylis sp.	single culm graminoid	wet	tall	0.0	0.7	2.0	1.7	2.7	3.3	0.7	2.0	2.0
Gymnopogon brevifolius	single culm graminoid	dry	tall	0.0	2.0	2.0	2.0	2.0	2.7	0.0	0.7	0.7
Hypoxis micrantha	single culm graminoid	mesic	short	7.0	15.7	15.3	18.7	26.3	22.0	12.3	18.7	28.0
Rhynchospora baldwinii	single culm graminoid	mesic	tall	4.7	4.0	2.3	3.3	3.0	3.7	1.3	0.7	2.3
Rhynchospora breviseta	single culm graminoid	wet	short	83.0	94.0	94.3	94.3	96.0	80.3	52.7	66.0	73.3
Rhynchospora chapmanii	single culm graminoid	mesic	short	51.0	66.0	77.3	82.7	83.0	67.7	34.3	68.3	72.7
Rhynchospora ciliaris	single culm graminoid	mesic	short	31.0	32.3	31.0	34.7	33.0	24.7	0.3	10.0	20.0
Scleria minor	single culm graminoid	wet	tall	0.0	0.0	2.7	1.0	1.7	1.0	4.0	0.0	4.0
Scleria pauciflora	single culm graminoid	mesic	short	52.0	53.3	56.0	56.3	55.7	50.7	15.3	22.7	34.0

Table B.1 (cont). Percentage of 0.01 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Scleria reticularis	single culm graminoid	mesic	tall	3.7	2.0	1.3	3.3	3.7	2.7	0.0	0.0	0.0
Gaylussacia dumosa	subshrub	dry	short	11.0	11.7	13.0	15.0	14.0	14.7	5.3	4.0	4.3
Hypericum crux-andreae	subshrub	mesic	tall	3.7	4.3	3.3	3.7	2.0	5.3	1.0	2.0	0.7
Vaccinium crassifolium	subshrub	dry	short	14.7	11.3	11.3	18.3	12.7	12.3	5.3	5.3	5.0
Vaccinium tenellum	subshrub	dry	short	0.0	0.0	0.0	0.0	0.0	0.0	5.3	5.3	6.0
Acer rubrum	tree	wet	tall	0.0	0.0	0.0	0.7	0.0	0.0	1.0	0.3	1.0
Persea palustris	tree	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.3
Pinus palustris	tree	dry	tall	5.7	4.0	2.3	2.0	1.7	0.3	0.7	0.7	0.7
Pinus taeda	tree	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.7
Smilax laurifolia	vine	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	2.0

Table B.2. Percentage of 0.25 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Eupatorium leucolepis	caulescent herb	mesic	tall	23.3	26.7	25.0	28.3	23.3	31.7	23.3	21.7	26.7
Eupatorium rotundifolium	caulescent herb	dry	tall	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euphorbia curtisii	caulescent herb	dry	short	58.3	68.3	71.7	68.3	36.7	71.7	56.7	60.0	61.7
Lactuca sp.	caulescent herb	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7
Linum sp.	caulescent herb	mesic	short	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0
Lobelia nuttalli	caulescent herb	mesic	tall	0.0	0.0	0.0	0.0	0.0	0.0	3.3	3.3	6.7
Ludwigia virgata	caulescent herb	wet	tall	0.0	0.0	0.0	0.0	0.0	1.7	1.7	1.7	1.7
Oxypolis ternata	caulescent herb	wet	tall	6.7	3.3	10.0	6.7	0.0	5.0	1.7	5.0	3.3
Pityopsis graminifolia	caulescent herb	dry	short	40.0	45.0	41.7	43.3	33.3	43.3	3.3	10.0	15.0
Polygala hookeri	caulescent herb	mesic	short	95.0	81.7	86.7	85.0	73.3	51.7	0.0	1.7	1.7
Polygala lutea	caulescent herb	mesic	short	20.0	6.7	20.0	26.7	35.0	28.3	1.7	1.7	18.3
Pteridium aquilinum	caulescent herb	dry	tall	0.0	0.0	0.0	0.0	0.0	15.0	15.0	16.7	16.7
Rhexia alifanus	caulescent herb	dry	tall	66.7	61.7	68.3	70.0	60.0	55.0	40.0	40.0	31.7
Rhexia lutea	caulescent herb	mesic	tall	1.7	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0
Rhexia petiolata	caulescent herb	wet	tall	6.7	18.3	16.7	18.3	18.3	18.3	1.7	6.7	6.7
Sabatia difformis	caulescent herb	wet	tall	0.0	0.0	0.0	0.0	0.0	6.7	0.0	0.0	3.3
Sabatia gentianoides	caulescent herb	wet	tall	0.0	3.3	3.3	1.7	0.0	3.3	0.0	0.0	1.7
Symphyotrichum dumosum	caulescent herb	dry	tall	21.7	23.3	18.3	18.3	18.3	18.3	3.3	5.0	8.3
Lycopodiella alopecuroides	clubmoss	mesic	short	0.0	0.0	0.0	0.0	0.0	1.7	0.0	8.3	8.3
Lycopodiella appressa	clubmoss	mesic	short	56.7	40.0	48.3	45.0	41.7	20.0	28.3	10.0	11.7
Calopogon pallidus	geophyte	mesic	short	36.7	61.7	66.7	61.7	48.3	46.7	3.3	1.7	1.7
Calopogon tuberosus	geophyte	mesic	short	1.7	3.3	5.0	1.7	0.0	1.7	0.0	0.0	0.0
Cleistesiopsis divaricata	geophyte	mesic	short	8.3	15.0	26.7	21.7	5.0	13.3	0.0	10.0	6.7
Lilium catesbaei	geophyte	mesic	short	10.0	5.0	1.7	1.7	0.0	5.0	0.0	6.7	5.0
Platanthera sp.	geophyte	mesic	tall	40.0	41.7	43.3	45.0	35.0	20.0	0.0	11.7	10.0
Pogonia ophioglossoides	geophyte	mesic	short	1.7	1.7	5.0	6.7	1.7	1.7	0.0	0.0	1.7
Spiranthes sp.	geophyte	mesic	tall	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Agalinis aphylla	hemiparasite	mesic	tall	11.7	10.0	10.0	10.0	8.3	5.0	5.0	3.3	1.7
Agalinis obtusifolia	hemiparasite	dry	tall	8.3	48.3	65.0	75.0	63.3	51.7	16.7	46.7	70.0

Table B.2 (cont). Percentage of 0.25 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Seymeria cassioides	hemiparasite	dry	tall	33.3	33.3	21.7	13.3	38.3	43.3	90.0	85.0	28.3
Dionaea muscipula	insectivore	mesic	short	98.3	96.7	95.0	96.7	96.7	76.7	60.0	85.0	86.7
Drosera capillaris	insectivore	mesic	short	80.0	30.0	90.0	96.7	83.3	33.3	11.7	35.0	91.7
Pinguicula sp.	insectivore	mesic	short	51.7	45.0	50.0	63.3	63.3	45.0	0.0	13.3	41.7
Utricularia subulata	insectivore	wet	short	0.0	1.7	26.7	13.3	11.7	0.0	0.0	0.0	1.7
Desmodium lineatum	legume	dry	short	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0
Desmodium tenuifolium	legume	mesic	tall	0.0	0.0	5.0	5.0	5.0	5.0	3.3	3.3	3.3
Tephrosia hispidula	legume	dry	short	0.0	0.0	0.0	1.7	0.0	10.0	10.0	8.3	13.3
Andropogon sp.	matrix graminoid	dry	tall	88.3	93.3	95.0	91.7	96.7	98.3	91.7	95.0	93.3
Andropogon sp. 2	matrix graminoid	dry	tall	68.3	73.3	65.0	70.0	53.3	65.0	1.7	0.0	0.0
Aristida stricta	matrix graminoid	dry	tall	85.0	88.3	83.3	83.3	73.3	88.3	66.7	83.3	76.7
Carex striata var. brevis	matrix graminoid	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	15.0	16.7	13.3
Ctenium aromaticum	matrix graminoid	mesic	tall	50.0	53.3	60.0	60.0	53.3	65.0	45.0	60.0	63.3
Muhlenbergia expansa	matrix graminoid	mesic	tall	93.3	95.0	95.0	95.0	93.3	96.7	91.7	91.7	83.3
Sporobolus pinetorum	matrix graminoid	mesic	tall	90.0	93.3	98.3	95.0	88.3	100.0	98.3	96.7	96.7
Aletris farinosa	rosette herb	mesic	short	31.7	35.0	35.0	35.0	30.0	20.0	11.7	5.0	5.0
Bigelowia nudata	rosette herb	dry	short	100.0	100.0	100.0	100.0	96.7	100.0	73.3	76.7	81.7
Carphephorus paniculatus	rosette herb	dry	tall	13.3	15.0	13.3	16.7	18.3	20.0	16.7	18.3	16.7
Carphephorus tomentosus	rosette herb	dry	tall	46.7	65.0	66.7	61.7	68.3	70.0	20.0	23.3	25.0
Chaptalia tomentosa	rosette herb	mesic	short	0.0	0.0	0.0	1.7	0.0	1.7	0.0	0.0	0.0
Coreopsis linifolia	rosette herb	mesic	short	98.3	100.0	100.0	100.0	100.0	100.0	35.0	40.0	48.3
Erigeron vernus	rosette herb	mesic	short	26.7	25.0	30.0	26.7	23.3	30.0	25.0	28.3	18.3
Eryngium integrifolium	rosette herb	mesic	short	48.3	50.0	45.0	41.7	41.7	33.3	1.7	15.0	28.3
Eurybia paludosa	rosette herb	mesic	tall	31.7	25.0	38.3	41.7	41.7	43.3	55.0	55.0	53.3
Helianthus angustifolius	rosette herb	mesic	tall	8.3	1.7	6.7	5.0	6.7	10.0	3.3	5.0	5.0
Helianthus heterophyllus	rosette herb	mesic	tall	45.0	50.0	56.7	58.3	46.7	45.0	16.7	16.7	18.3
Lachnanthes caroliniana	rosette herb	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0
Lachnocaulon anceps	rosette herb	wet	short	36.7	35.0	36.7	33.3	30.0	35.0	30.0	41.7	40.0
Liatris [*pilosa + virgata*]	rosette herb	dry	tall	1.7	0.0	0.0	1.7	1.7	3.3	5.0	3.3	0.0

Table B.2 (cont). Percentage of 0.25 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Marshallia graminifolia	rosette herb	mesic	short	36.7	25.0	31.7	41.7	31.7	28.3	6.7	5.0	13.3
Sisyrinchium capillare	rosette herb	mesic	short	48.3	70.0	73.3	80.0	75.0	78.3	16.7	26.7	20.0
Sisyrinchium sp.	rosette herb	mesic	short	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Solidago [*stricta + pulchra*]	rosette herb	mesic	tall	43.3	48.3	45.0	51.7	43.3	45.0	35.0	36.7	35.0
Solidago sp.	rosette herb	mesic	short	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Triantha racemosa	rosette herb	mesic	short	61.7	68.3	71.7	81.7	76.7	66.7	40.0	38.3	46.7
Viola primulifolia	rosette herb	mesic	short	35.0	46.7	41.7	45.0	48.3	26.7	11.7	21.7	30.0
Viola septemloba	rosette herb	mesic	short	0.0	0.0	5.0	3.3	1.7	3.3	0.0	0.0	5.0
Xyris ambigua	rosette herb	wet	tall	58.3	61.7	61.7	61.7	61.7	58.3	23.3	18.3	28.3
Xyris caroliniana	rosette herb	dry	tall	36.7	58.3	48.3	56.7	71.7	73.3	31.7	38.3	26.7
Aronia arbutifolia	shrub	wet	tall	10.0	11.7	13.3	13.3	11.7	10.0	25.0	26.7	25.0
Arundinaria tecta	shrub	wet	tall	10.0	10.0	10.0	8.3	5.0	3.3	0.0	0.0	0.0
Gaylussacia frondosa	shrub	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	1.7	1.7	1.7
Ilex glabra	shrub	wet	tall	3.3	3.3	5.0	6.7	0.0	6.7	0.0	1.7	8.3
Lyonia mariana	shrub	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0
Morella carolinensis	shrub	wet	tall	1.7	1.7	5.0	1.7	0.0	0.0	18.3	20.0	23.3
Aristida virgata	single culm graminoid	mesic	tall	20.0	28.3	26.7	26.7	16.7	31.7	0.0	3.3	0.0
Dichanthelium ensifolium	single culm graminoid	mesic	tall	100.0	100.0	98.3	100.0	98.3	98.3	93.3	96.7	98.3
Dichanthelium strigosum	single culm graminoid	mesic	tall	36.7	41.7	33.3	38.3	33.3	35.0	1.7	1.7	3.3
Fimbristylis sp.	single culm graminoid	wet	tall	0.0	1.7	6.7	6.7	10.0	11.7	1.7	6.7	6.7
Gymnopogon brevifolius	single culm graminoid	dry	tall	0.0	6.7	8.3	8.3	10.0	11.7	0.0	3.3	3.3
Hypoxis micrantha	single culm graminoid	mesic	short	20.0	43.3	40.0	50.0	58.3	48.3	31.7	43.3	61.7
Rhynchospora baldwinii	single culm graminoid	mesic	tall	18.3	15.0	10.0	11.7	11.7	15.0	3.3	1.7	6.7
Rhynchospora breviseta	single culm graminoid	wet	short	100.0	100.0	100.0	100.0	100.0	100.0	86.7	90.0	85.0
Rhynchospora chapmanii	single culm graminoid	mesic	short	93.3	100.0	98.3	100.0	98.3	91.7	50.0	98.3	95.0
Rhynchospora ciliaris	single culm graminoid	mesic	short	60.0	56.7	58.3	63.3	56.7	55.0	1.7	31.7	55.0
Scleria minor	single culm graminoid	wet	tall	0.0	0.0	8.3	3.3	6.7	3.3	8.3	0.0	10.0
Scleria pauciflora	single culm graminoid	mesic	short	71.7	75.0	76.7	80.0	78.3	76.7	40.0	56.7	76.7
Scleria reticularis	single culm graminoid	mesic	tall	11.7	5.0	5.0	8.3	5.0	6.7	0.0	0.0	0.0

Table B.2 (cont). Percentage of 0.25 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Gaylussacia dumosa	subshrub	dry	short	28.3	28.3	30.0	31.7	26.7	30.0	11.7	10.0	13.3
Hypericum crux-andreae	subshrub	mesic	tall	13.3	16.7	11.7	10.0	6.7	18.3	1.7	6.7	1.7
Vaccinium crassifolium	subshrub	dry	short	40.0	33.3	31.7	48.3	35.0	38.3	20.0	21.7	21.7
Vaccinium tenellum	subshrub	dry	short	0.0	0.0	0.0	0.0	0.0	0.0	15.0	16.7	18.3
Acer rubrum	tree	wet	tall	0.0	0.0	0.0	3.3	0.0	0.0	5.0	1.7	5.0
Persea palustris	tree	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	1.7	1.7	1.7
Pinus palustris	tree	dry	tall	21.7	15.0	10.0	10.0	8.3	1.7	3.3	3.3	3.3
Pinus taeda	tree	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	3.3
Smilax laurifolia	vine	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	10.0

Table B.3. Percentage of 1 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Eupatorium leucolepis	caulescent herb	mesic	tall	66.7	50.0	50.0	58.3	50.0	58.3	58.3	66.7	58.3
Eupatorium rotundifolium	caulescent herb	dry	tall	16.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euphorbia curtisii	caulescent herb	dry	short	83.3	83.3	83.3	83.3	66.7	83.3	83.3	83.3	83.3
Lactuca sp.	caulescent herb	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.3
Linum sp.	caulescent herb	mesic	short	0.0	0.0	0.0	0.0	0.0	0.0	8.3	0.0	0.0
Lobelia nuttalli	caulescent herb	mesic	tall	0.0	0.0	0.0	0.0	0.0	0.0	16.7	8.3	25.0
Ludwigia virgata	caulescent herb	wet	tall	0.0	0.0	0.0	0.0	8.3	8.3	8.3	8.3	8.3
Oxypolis ternata	caulescent herb	wet	tall	25.0	8.3	25.0	16.7	0.0	8.3	0.0	25.0	8.3
Pityopsis graminifolia	caulescent herb	dry	short	66.7	66.7	66.7	75.0	66.7	66.7	16.7	25.0	50.0
Polygala hookeri	caulescent herb	mesic	short	100.0	100.0	100.0	100.0	100.0	91.7	0.0	8.3	0.0
Polygala lutea	caulescent herb	mesic	short	50.0	16.7	41.7	75.0	83.3	58.3	8.3	0.0	41.7
Pteridium aquilinum	caulescent herb	dry	tall	0.0	0.0	0.0	0.0	0.0	16.7	16.7	16.7	25.0
Rhexia alifanus	caulescent herb	dry	tall	100.0	91.7	100.0	100.0	100.0	91.7	75.0	75.0	66.7
Rhexia lutea	caulescent herb	mesic	tall	8.3	0.0	0.0	8.3	0.0	0.0	0.0	0.0	0.0
Rhexia petiolata	caulescent herb	wet	tall	16.7	33.3	25.0	25.0	25.0	25.0	8.3	16.7	16.7
Sabatia difformis	caulescent herb	wet	tall	0.0	0.0	0.0	0.0	0.0	8.3	0.0	0.0	8.3
Sabatia gentianoides	caulescent herb	wet	tall	0.0	16.7	16.7	8.3	0.0	8.3	0.0	0.0	8.3
Symphyotrichum dumosum	caulescent herb	dry	tall	33.3	50.0	50.0	41.7	41.7	41.7	8.3	25.0	25.0
Lycopodiella alopecuroides	clubmoss	mesic	short	0.0	0.0	0.0	0.0	0.0	8.3	0.0	16.7	16.7
Lycopodiella appressa	clubmoss	mesic	short	83.3	66.7	58.3	58.3	58.3	33.3	33.3	33.3	33.3
Calopogon pallidus	geophyte	mesic	short	75.0	83.3	83.3	83.3	83.3	66.7	16.7	8.3	8.3
Calopogon tuberosus	geophyte	mesic	short	0.0	16.7	25.0	8.3	0.0	8.3	0.0	0.0	0.0
Cleistesiopsis divaricata	geophyte	mesic	short	25.0	33.3	41.7	41.7	16.7	25.0	0.0	33.3	8.3
Lilium catesbaei	geophyte	mesic	short	41.7	16.7	8.3	8.3	0.0	16.7	0.0	16.7	25.0
Platanthera sp.	geophyte	mesic	tall	83.3	75.0	91.7	83.3	83.3	75.0	0.0	41.7	41.7
Pogonia ophioglossoides	geophyte	mesic	short	8.3	8.3	8.3	16.7	16.7	8.3	0.0	0.0	8.3
Spiranthes sp.	geophyte	mesic	tall	0.0	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Agalinis aphylla	hemiparasite	mesic	tall	50.0	41.7	33.3	41.7	33.3	16.7	25.0	16.7	0.0
Agalinis obtusifolia	hemiparasite	dry	tall	16.7	66.7	91.7	100.0	100.0	75.0	33.3	66.7	83.3

Table B.3 (cont). Percentage of 1 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Seymeria cassioides	hemiparasite	dry	tall	66.7	66.7	33.3	66.7	83.3	91.7	100.0	100.0	50.0
Dionaea muscipula	insectivore	mesic	short	100.0	100.0	100.0	100.0	100.0	100.0	83.3	91.7	91.7
Drosera capillaris	insectivore	mesic	short	100.0	50.0	100.0	100.0	100.0	66.7	25.0	75.0	100.0
Pinguicula sp.	insectivore	mesic	short	83.3	83.3	91.7	91.7	91.7	66.7	0.0	25.0	75.0
Utricularia subulata	insectivore	wet	short	0.0	8.3	41.7	25.0	25.0	8.3	0.0	0.0	0.0
Desmodium lineatum	legume	dry	short	0.0	0.0	0.0	0.0	8.3	0.0	0.0	0.0	0.0
Desmodium tenuifolium	legume	mesic	tall	0.0	0.0	16.7	16.7	25.0	8.3	8.3	16.7	8.3
Tephrosia hispidula	legume	dry	short	0.0	0.0	0.0	8.3	0.0	33.3	25.0	25.0	25.0
Andropogon sp.	matrix graminoid	dry	tall	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Andropogon sp. 2	matrix graminoid	dry	tall	100.0	100.0	91.7	83.3	83.3	91.7	8.3	0.0	0.0
Aristida stricta	matrix graminoid	dry	tall	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Carex striata var. brevis	matrix graminoid	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	25.0	33.3	25.0
Ctenium aromaticum	matrix graminoid	mesic	tall	66.7	66.7	75.0	66.7	66.7	66.7	66.7	66.7	66.7
Muhlenbergia expansa	matrix graminoid	mesic	tall	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	91.7
Sporobolus pinetorum	matrix graminoid	mesic	tall	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Aletris farinosa	rosette herb	mesic	short	50.0	66.7	66.7	75.0	75.0	41.7	16.7	16.7	16.7
Bigelowia nudata	rosette herb	dry	short	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Carphephorus paniculatus	rosette herb	dry	tall	25.0	33.3	33.3	33.3	33.3	33.3	41.7	41.7	41.7
Carphephorus tomentosus	rosette herb	dry	tall	83.3	100.0	100.0	100.0	91.7	91.7	41.7	50.0	50.0
Chaptalia tomentosa	rosette herb	mesic	short	0.0	0.0	0.0	8.3	8.3	8.3	0.0	0.0	0.0
Coreopsis linifolia	rosette herb	mesic	short	100.0	100.0	100.0	100.0	100.0	100.0	50.0	58.3	66.7
Erigeron vernus	rosette herb	mesic	short	66.7	66.7	66.7	58.3	58.3	66.7	50.0	58.3	50.0
Eryngium integrifolium	rosette herb	mesic	short	50.0	58.3	50.0	50.0	58.3	58.3	8.3	33.3	58.3
Eurybia paludosa	rosette herb	mesic	tall	58.3	58.3	50.0	58.3	58.3	58.3	58.3	75.0	66.7
Helianthus angustifolius	rosette herb	mesic	tall	33.3	8.3	8.3	8.3	8.3	8.3	8.3	16.7	8.3
Helianthus heterophyllus	rosette herb	mesic	tall	75.0	75.0	83.3	91.7	75.0	83.3	50.0	41.7	50.0
Lachnanthes caroliniana	rosette herb	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	8.3	0.0	0.0
Lachnocaulon anceps	rosette herb	wet	short	66.7	58.3	50.0	50.0	50.0	58.3	50.0	66.7	66.7
Liatris [*pilosa + virgata*]	rosette herb	dry	tall	8.3	0.0	0.0	8.3	8.3	8.3	16.7	8.3	0.0

Table B.3 (cont). Percentage of 1 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Marshallia graminifolia	rosette herb	mesic	short	75.0	58.3	83.3	75.0	66.7	66.7	33.3	25.0	41.7
Sisyrinchium capillare	rosette herb	mesic	short	75.0	91.7	100.0	100.0	100.0	100.0	58.3	66.7	50.0
Sisyrinchium sp.	rosette herb	mesic	short	0.0	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Solidago [*stricta + pulchra*]	rosette herb	mesic	tall	58.3	58.3	66.7	58.3	58.3	66.7	50.0	58.3	50.0
Solidago sp.	rosette herb	mesic	short	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Triantha racemosa	rosette herb	mesic	short	100.0	100.0	100.0	100.0	100.0	91.7	50.0	75.0	66.7
Viola primulifolia	rosette herb	mesic	short	66.7	66.7	66.7	83.3	66.7	66.7	16.7	41.7	66.7
Viola septemloba	rosette herb	mesic	short	0.0	0.0	16.7	16.7	0.0	8.3	0.0	0.0	8.3
Xyris ambigua	rosette herb	wet	tall	83.3	83.3	91.7	83.3	83.3	83.3	50.0	50.0	66.7
Xyris caroliniana	rosette herb	dry	tall	75.0	100.0	91.7	91.7	100.0	100.0	58.3	91.7	50.0
Aronia arbutifolia	shrub	wet	tall	16.7	16.7	33.3	33.3	16.7	16.7	33.3	41.7	33.3
Arundinaria tecta	shrub	wet	tall	25.0	25.0	25.0	16.7	16.7	16.7	0.0	0.0	0.0
Gaylussacia frondosa	shrub	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	8.3	8.3	8.3
Ilex glabra	shrub	wet	tall	16.7	8.3	25.0	16.7	0.0	16.7	0.0	0.0	25.0
Lyonia mariana	shrub	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	8.3	0.0	0.0
Morella carolinensis	shrub	wet	tall	8.3	8.3	16.7	8.3	0.0	0.0	33.3	41.7	41.7
Aristida virgata	single culm graminoid	mesic	tall	50.0	75.0	50.0	41.7	58.3	83.3	0.0	16.7	0.0
Dichanthelium ensifolium	single culm graminoid	mesic	tall	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Dichanthelium strigosum	single culm graminoid	mesic	tall	58.3	66.7	58.3	66.7	58.3	58.3	8.3	8.3	16.7
Fimbristylis sp.	single culm graminoid	wet	tall	0.0	8.3	25.0	25.0	33.3	41.7	8.3	33.3	25.0
Gymnopogon brevifolius	single culm graminoid	dry	tall	0.0	16.7	25.0	33.3	33.3	33.3	0.0	16.7	16.7
Hypoxis micrantha	single culm graminoid	mesic	short	50.0	75.0	75.0	75.0	91.7	75.0	66.7	75.0	83.3
Rhynchospora baldwinii	single culm graminoid	mesic	tall	41.7	41.7	33.3	25.0	33.3	50.0	8.3	0.0	16.7
Rhynchospora breviseta	single culm graminoid	wet	short	100.0	100.0	100.0	100.0	100.0	100.0	91.7	100.0	100.0
Rhynchospora chapmanii	single culm graminoid	mesic	short	100.0	100.0	100.0	100.0	100.0	100.0	58.3	100.0	100.0
Rhynchospora ciliaris	single culm graminoid	mesic	short	66.7	66.7	58.3	66.7	75.0	75.0	8.3	66.7	83.3
Scleria minor	single culm graminoid	wet	tall	0.0	0.0	8.3	8.3	8.3	8.3	16.7	0.0	16.7
Scleria pauciflora	single culm graminoid	mesic	short	91.7	91.7	91.7	91.7	100.0	91.7	75.0	83.3	100.0

Table B.3 (cont). Percentage of 1 m² subplots occupied by all species from 1985-2013.

Species	Growth Form	Habitat	Height	1985	1986	1987	1988	1989	1994	2011	2012	2013
Scleria reticularis	single culm graminoid	mesic	tall	16.7	8.3	8.3	33.3	25.0	33.3	0.0	0.0	0.0
Gaylussacia dumosa	subshrub	dry	short	33.3	33.3	41.7	50.0	41.7	33.3	16.7	16.7	25.0
Hypericum crux-andreae	subshrub	mesic	tall	41.7	58.3	41.7	41.7	25.0	50.0	0.0	25.0	8.3
Vaccinium crassifolium	subshrub	dry	short	66.7	50.0	41.7	91.7	50.0	58.3	41.7	50.0	50.0
Vaccinium tenellum	subshrub	dry	short	0.0	0.0	0.0	0.0	0.0	0.0	16.7	16.7	25.0
Acer rubrum	tree	wet	tall	0.0	0.0	0.0	16.7	0.0	0.0	25.0	0.0	16.7
Persea palustris	tree	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	8.3	8.3	8.3
Pinus palustris	tree	dry	tall	58.3	41.7	25.0	33.3	25.0	16.7	8.3	8.3	8.3
Pinus taeda	tree	dry	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.7
Smilax laurifolia	vine	wet	tall	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.7	33.3

APPENDIX C. OBSERVED AND SIMULATED C-SCORES FOR CHAPTER 5

Table C.1. Observed and simulated C-score values for each broad community type (sandhill, subxeric woodland, flatwood, silty woodland, savanna) and time since fire category (< 1 year, 1 to 3 years, > 3 years). P-values indicate whether the observed value is significantly different from random expectation (simulated C-scores). SES values above 0 indicate species segregation (e.g., limiting similarity), while values below 0 indicate species aggregation (e.g., environmental filtering).

	Obs C-score	Sim C-score	*p*-value	SES
Community type				
Sandhill	0.393	0.387	0.285	1.036
Subxeric Woodland	0.372	0.360	0.039 *	2.229
Flatwood	0.537	0.542	0.207	-1.254
Silty Woodland	0.498	0.497	0.660	0.304
Savanna	0.240	0.237	0.353	0.925
Time since fire				
<1 year	0.582	0.571	0.001 *	3.858
1 to 3 years	0.586	0.581	0.081 *	1.856
>3 years	0.578	0.546	0.001 *	7.988
Community type - Time since fire				
Sandhill <1 year	0.188	0.189	0.754	-0.540
Sandhill 1 to 3 years	0.100	0.100	1.000	0.219
Sandhill >3 years	0.199	0.118	0.001 *	5.732
Subxeric Woodland <1 year	0.136	0.138	0.523	-0.577
Subxeric Woodland 1 to 3 years	0.283	0.268	0.019 *	2.740
Subxeric Woodland >3 years	0.291	0.276	0.009 *	3.395
Flatwood <1 year	0.441	0.435	0.133	1.559
Flatwood 1 to 3 years	0.484	0.484	0.862	0.148
Flatwood >3 years	0.395	0.369	0.001 *	6.270
Silty Woodland <1 year	0.463	0.457	0.121	1.718
Silty Woodland 1 to 3 years	0.438	0.434	0.205	1.096
Silty Woodland >3 years	0.252	0.252	0.748	-0.698
Savanna <1 year	0.115	0.115	0.976	-0.153
Savanna 1 to 3 years	0.194	0.192	0.285	0.999
Savanna >3 years	0.112	0.114	0.071 *	-1.415