

FLORISTIC AND ENVIRONMENTAL VARIATION OF PYROGENIC PINELANDS IN THE
SOUTHEASTERN COASTAL PLAIN: DESCRIPTION, CLASSIFICATION, AND
RESTORATION

By

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To Mike, my husband and great love

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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By

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Until recent times, the landscape of north and central Florida was dominated by fire-dependent pineland savanna vegetation with sparse canopies of longleaf pine (*Pinus palustris*). Economic development coupled with fire suppression lead to the drastic decline in the distribution and integrity of these natural communities. I present a vegetation classification of natural pineland communities in this highly fragmented landscape based on data collected over large gradients of environmental and geological variation. I collected field data that quantified species composition and abundance from 293 plots (from 103 sites) distributed throughout the northern two thirds of Florida. After omission of species that occurred in < 3% of plots, a total of 677 plant species were used in numerical analyses. I developed a vegetation classification based on floristic similarity using K-means cluster and indicator species analyses. Three ecological series were described corresponding to idealized moisture conditions. These were further divided into 16 species associations. Floristic variation was related to geographic separation between the panhandle and peninsula regions of Florida. I hypothesized that the numerous plant species that have limited distributional ranges contribute to compositional

patterns. Similar geographic trends were apparent in a model of compositional variation related to environment and spatial variation. Local environmental factors, including location on a topographic/moisture gradient and soil fertility, were important correlates of local floristic variation. Regional variation was correlated with soil texture and nutrient availability. A much greater proportion of the explained variance was provided by environmental variables than by pure spatial variables. The model revealed that both regional factors (climate, edaphic, and geographic) and local factors (topographic position, soil chemistry) were correlates of with floristic variation.

In addition to spatial variation, natural pineland communities undergo temporal variation in response to periodic fires and changes in timber stand structure. Central questions regarding ecological restoration of Coastal Plain pinelands are: how resilient are these communities following anthropogenic alterations? Will ecological restoration affect vegetation succession within the range of “natural” temporal variation? I studied ground cover vegetation response to removal of woody biomass and reintroduction of natural fire regimes as it related to a program of ecological restoration in a degraded pine savanna remnant. Treatment plots were thinned for timber or else un-thinned as a control. Prescribed fire was applied at two subsequent times, and changes in species composition were monitored over an eight year period. Species richness was enhanced by mechanical woody reduction in the first two years, compared to sites that were burned only (not logged). This response largely reflected increases in detectable graminoid species. However, species richness of treatments converged within eight years, following two prescribed fires 3 years apart. Species composition responded similarly, converging between treatments over time. Succession was toward pre-settlement conditions, as suggested by comparisons to reference sites and historical data. Community composition appears to be robust

to temporary alterations in fire regime and changes in timber stand structure within the range of conditions studied. Spatial variation in species composition of pineland communities may be relatively stable over time. Woody biomass reduction via careful mechanical logging does not appear to adversely affect pineland vegetation recovery, and may expedite overall community restoration.

CHAPTER 1 INTRODUCTION

Pinelands of the Southeastern Coastal Plain are exceptional, both for their overall biodiversity and degree of biotic endemism. The combination of large climatic gradients, long growing seasons, variable geology and large species pools creates a prime environment for high local and landscape scale floristic variation. Large compositional variation has been documented both across geographic and local gradients (Peet and Allard 1993, Bridges and Orzell 1989). Such high degrees of alpha, beta and gamma diversity (*sensu* Whittaker 1967) belie the exceptional habitat specialization and regionalization of many species of the Coastal Plain. Seemingly imperceptible topographic-moisture gradients coincide with almost complete changes in plant species composition (Peet and Allard 1993). At larger scales, there is evidence of regionalization of biota concurrent with geology, physiography, soils, and historical biogeography. Accordingly, biogeographers have recognized and delineated distinct “ecoregions” in Florida based on differences in environmental conditions and vegetation patterns (Davis 1967, Brooks 1982).

In addition to biodiversity variation related to local and landscape gradients, levels of endemism are exceptionally high in the Southeastern Coastal Plain, and in Florida pinelands specifically. Sorrie and Weakley (2002) report over 1600 taxa of plants endemic to the Southeastern Coastal Plain. In addition to wide-ranging Coastal Plain endemics, many “narrow” endemic species inhabit very restricted geographic regions and/or habitats. Florida is notable both for the number of narrow endemic species it harbors, and the number of “centers of endemism” (*sensu* Sorrie and Weakley 2002) located within the State, particularly relative to plant species. In addition, Florida is home to over 2500 native plant species, many of which are restricted in range of distribution, or habitat specificity (Wunderlin 2000).

Pine savannas and woodlands native to the Southeastern Coastal Plain are among the most imperiled ecosystems in North America (Walker and Peet 1983, Croker 1987, Noss 1988, Frost 1993, Peet and Allard 1993). Although they once dominated the landscape, native pinelands now occupy less than three percent of their former range (Frost 1993, Outcalt and Sheffield 1996). Of this, an even smaller area contains vegetation composition and structure similar to that of pre-settlement conditions (Simberloff 1993). The rapid range reduction of longleaf pinelands coincided with extensive logging, agricultural land use, and expanding rural settlement in the 19th and 20th centuries (Croker 1987, Frost 1993).

Most contemporary native pinelands are small and fragmented, and are no longer subject to the natural processes under which constituent species evolved. Most notably, this precludes the natural occurrence of frequent, low intensity fires that historically swept across the landscape (Frost 1993, Simberloff 1993, Platt 1999, VanLear et al. 2005). Fire suppression of longleaf pine natural areas has contributed to large scale species replacement, as less fire tolerant pines and hardwoods invade these pyrogenic communities (Glitzenstein et al. 1995, Platt 1999, Provencher et al. 2000, VanLear et al. 2005). In the absence of frequent fire, thick growths of woody plants compete with herbaceous vegetation for light and other resources, affecting succession and community structure (Brockway and Lewis 1997, Provencher et al. 2001, VanLear et al. 2005).

Vegetation classification plays a key role in many areas of conservation, land management and scientific research. Classification of vegetation delimits the number of relevant natural communities to provide a conceptual framework for understanding the natural variation. The process of delimitation is subjective by nature. Much of this subjectivity resides in deciding which data to use, what quantitative methods to use, and how to interpret the resulting solutions.

Some vegetation classifications of large landscapes also explicitly incorporate information about geography (Peet and Allard 1993, Newell and Peet 1998, Wimberly and Spies 2001).

To date, classification systems developed specifically for Southeastern pineland communities have been quantitatively rigorous but local in scope, or wide-ranging but qualitative. Examples of the former are ecological classifications of vegetation are limited to a specific management areas, usually on the scale of several thousand hectares (Carter et al. 1999, Grace et al. 1999, Goebel et al. 2001, Abella and Shelburne 2004). Additionally, many vegetation descriptions of Southeastern plant communities only describe woody species (e.g., Harcombe et al. 1993, others), thus missing important floristic “information” residing in the ground flora (e.g. Bridges and Orzell 1989, Peet and Allard 1993, DeCoster et al. 1999, Schmitz et al. 2002, Drewa et al. 2002). Classifications that do include explicit descriptions of herbaceous vegetation are generally subjective and anecdotal in nature. The exception is the quantitative treatment of Peet and Allard (1993), which includes a regional classification of pineland vegetation of the Coastal Plain emphasizing ground cover vegetation.

Traditionally, ecologists have studied the distribution of plant species according to environmental factors (Bray and Curtis 1957, Peet 1978, Newell and Peet 1998). However, recent studies have underscored the need for spatially explicit models of environmental-composition variation (Legendre and Fortin 1989). Spatial trends are relevant in such models for three reasons: 1) failure to account for spatially auto-correlated response data leads to biased interpretations of environmental effects, 2) environmental determinants of vegetation composition may be spatially structured, and 3) spatial autocorrelation independent of environment suggests other control mechanisms of community composition (Legendre 2005).

Little is known about temporal variation in composition of pyrogenic pineland vegetation, particularly compared to spatial variation. Studies of grasslands of other regions suggest that temporal variation in species distributions is large compared to species-area relationships (Adler et al. 2005). Longitudinal studies of pineland community structure are rare and generally address successional responses to specific treatments. Natural pinelands temporarily altered by unnatural fire regimes and forest structure also provide opportunities to study the resiliency of pineland vegetation to such alterations by quantifying community responses to restoration of natural conditions (Walker and White 2006). A better understanding of temporal changes under typical and degraded conditions will contribute to the applied models of pineland restoration, as well as the models of “natural” variation used by conservationists.

I present a two-step process of vegetation classification and description of Florida pyrogenic pineland flora. First, I classify pineland communities based on vegetation data alone (primarily herbaceous ground cover vegetation). Second, I present a model of environmental-composition correlations in a spatially explicit context. Finally, I present results of an ecological restoration program of a degraded pineland remnant, and interpret vegetation responses in the context of life history traits.

The classification of pyrogenic Florida pineland vegetation is based on 293 vegetation plots (58.6 ha total) collected over a broad range of environmental conditions throughout the range of longleaf pine in panhandle and peninsular Florida. The classification, derived from floristic data alone, is presented as a system that can be used in land survey and management. Sixteen community associations are described by environmental characteristics, diagnostic and indicator species, general appearance and landscape context. I discuss floristic differences

between community association, and how range-restricted and endemic taxa influence community variation.

A spatially explicit model of environmental and historical determinants is presented with regard to the composition and diversity of pyrogenic pineland vegetation. Environmental factors included edaphic, topographic, and climate variables, presumed to be operating at different spatial and temporal scales. Variation related to pure spatial autocorrelation is hypothesized to be indicative of biotic processes (not related to environmental determinants). Biogeographic patterns were assessed by testing an “ecoregion” hypothesis of regionalization of community variation. Significant environmental-composition correlations were used to generate hypotheses regarding controls of community variation in Coastal Plain pinelands.

An experimental and longitudinal study of ecological restoration underscored the resiliency of pyrogenic pineland groundcover plant communities. Changes mediated by restoration treatments affected succession toward desired reference conditions. Furthermore, this study suggested stability in succession even in atypical conditions of long fire-free intervals. Temporal dynamics in pineland plant communities is quite variable (as are spatial trends), and it is hypothesized that life history adaptations of typical plant species buffet the community over a range of atypical environmental conditions.

As part of the restoration program, tree stand structure and frequent fire were restored in a degraded pineland savanna remnant to resemble pre-settlement conditions. I measured the effects of two restoration treatments on composition and diversity of native ground cover vegetation. Restoration was measured as changes in composition relative to that of reference sites which represented desired restored conditions. The larger question involved resiliency of a specific pineland community to temporal changes in fire regime and timber stand structure.

From that, it may be concluded that pyrogenic pineland communities in general might be relatively stable over time and over a range of conditions. Secondly, the study demonstrated resiliency of native pineland vegetation following decades of man-induced fire suppression and contributes to predictions of restoration success relative to starting conditions.

CHAPTER 2 A VEGETATION CLASSIFICATION OF FLORIDA'S PYROGENIC PINELANDS

Introduction

Fire-dependent pineland vegetation once dominated the landscape of the Southeastern Coastal Plain, ranging from southern Virginia south to the tip of Florida and westward to eastern Texas. Frequent fires perpetuated the open aspect of pine savannas and woodlands, promoting development of species-rich herbaceous ground cover vegetation. It is estimated that prior to European settlement of the Gulf and lower Atlantic Coastal Plain regions, fire return intervals in upland pinelands averaged once per 2-3 years (Martin et al. 1993, Olson and Platt 1995, Platt 1999, Glitzenstein et al. 2003). Following disruption of fire regimes, these communities are rapidly colonized by fire-intolerant woody growth, prompting drastic alteration of community composition and dynamics (Glitzenstein et al. 1995, Platt 1999, Glitzenstein et al. 2003). Economic development removed native pineland vegetation from much of its former range in the Coastal Plain, particularly from the finer-textured soils that readily support agriculture (Frost 1993, Frost 2006). Native longleaf pinelands currently occupy less than three percent of their former range (Frost 1993, Outcalt and Sheffield 1996). Even rarer are Coastal Plain pineland communities managed with fire regimes that mimic those of pre-settlement conditions (Simberloff 1993, Varner et al. 2005).

Fire-dependent pineland communities Florida are exceptional both for their overall biodiversity and the degree of biotic endemism. Over 1600 plant taxa are endemic to the Southeastern Coastal Plain, and over 250 of these are endemic or near-endemic to Florida (Ward 1979, Kautz and Cox 2001, Sorrie and Weakley 2001, Sorrie and Weakley 2006). The Florida peninsula has a complex geologic history of inundation and land expansion related to sea level change and glaciation. Ancient islands isolated during sea level rise gave rise to many endemic

species of contemporary highlands and ridge provinces and other regions served as glacial “refugia” (Webb 1990). Florida is notable for the number of “centers of endemism” (sensu Sorrie and Weakley 2002) located in the State. More than 2500 plant species are native to Florida, representing a mixture of temperate and tropical species that changes with latitude (Holdridge 1967, Ward 1979, Wunderlin 1998).

The combination of large climatic gradients, long growing seasons, variable geology and large species pools in Florida creates a prime environment for exceptional floristic variation at local and landscape scales. Florida has the third richest flora of all States (Wunderlin and Hansen 2000). Plant species richness of Florida pinelands are among the highest recorded at small scales (Walker and Peet 1983, Peet 2006). In addition, subtle topographic-moisture gradients can harbor almost complete turnover in plant species composition (Bridges and Orzell 1989, Abrahamson and Hartnett 1990, Peet and Allard 1993, Platt 1999). Such a high degree of “beta” and “gamma” diversity (sensu Whittaker 1962, 1967) belies the exceptional habitat specialization and regionalization of many pineland species. On a landscape scale, there is evidence of aggregation in floristic and community similarity associated with specific regions. Accordingly, Florida “ecoregions” have been recognized and delineated based on similarity of edaphic, geologic, physiognomic, and vegetative features (Puri and Vernon 1964, Davis 1967, Brooks 1982, Brown et al. 1990).

Floristic classification systems provide a conceptual framework for understanding natural variation across environmental and geographic gradients. Such systems are widely applied in ecological inventory, conservation, and management (1990, Grossman et al. 1998, Comer et al. 2003). To be useful in the field, a vegetation classification should provide detailed information regarding frequent and abundant species, as well as those that are diagnostic of specific

associations (i.e., “indicator species”; Defrene and Legendre 1997). Ideally, a classification would also describe relevant environmental attributes, including typical ranges of variation. A comprehensive account of floristic types and variation could aid ecological restoration programs by providing a range of reference conditions and guiding land conservation priorities (White and Walker 1997, Walker and Silletti 2006).

Vegetation classification based on quantitative data is very much dependent on sampling design, intensity, and breadth (Nekola and White 1999, Cooper et al. 2006). Random and area-proportionate sampling designs are often not practically possible in large regions containing fragmented landscapes with variable natural conditions and mixed land ownership, land use history, and degree of public access. However, subjective bias can be minimized by application of a stratified sampling design which promotes balanced sampling intensity and effort across gradients of interest (Leps and Smilauer 2007). Such a design may not yield an unbiased representation of variation of pre-settlement natural vegetation, but may facilitate a representative sample of contemporary natural vegetation in a highly modified landscape (e.g. most of Florida).

Classification systems differ in many respects, including geographic and environmental scope, and type and quality of input data. Many vegetation classifications are strictly qualitative and descriptive (FNAI 1990, Grossman et al. 1998, Comer et al. 2003), although widely used for community classification and conservation policy guidelines in Florida. These works are based on expert accounts of floristic variation over a large region. Conversely, quantitative classifications typically incorporate site specific vegetation data. Depending on program objectives, abiotic environmental attributes are either explicitly included in the classification or are presented as descriptors or explanatory factors of floristically defined types. “Ecosystem

classification” and “ecological landtype phases” typify the former approach (Cleland et al. 1993, Hix and Percy 1997, Goebel et al. 2001, Abella et al. 2003). Regional vegetation classifications that include all or part of Florida are of the latter type, based on quantitative data of species abundances collected using standardized sampling methodology (Peet and Allard 1993, Peet 2006). In the present study, abiotic variables are descriptors of community classifications, including soil properties and geology. The quantitative delineation of floristic data approach has several advantages: 1) it encourages objectivity in classification partitioning, 2) it allows *a posteriori* examination of relationships between abiotic variables and community types, which can be useful for inventory and predictive modeling; 3) it may uncover “unexplained” gradients of floristic variation, stimulating generation of hypotheses regarding determinants of biodiversity (McCune and Grace 2002, Leps and Smilauer 2003, Legendre et al. 2005, Leps and Smilauer 2007).

I present a quantitative classification of fire-adapted pineland vegetation of northern and central Florida. The study region includes the entire historic range of longleaf pine in Florida. My focus was the classification of natural communities: i.e. frequently burned (at least 2-3 times over the past two decades) vegetation of pinelands and associated communities relatively unaltered by soil disturbance or severe fire suppression. My objective was to characterize plant communities based on floristic assemblages alone, followed by descriptions of geographic distribution, topographic context, and soil characteristics. Community descriptions include identification of dominant and diagnostic plant species, facilitating easy field recognition of characteristic vegetation. My sampling design, coupled with an objective approach to cluster analysis, yielded a comprehensive yet manageable classification of 16 associations. I describe edaphic and landscape features that are useful for field identification, such as soil texture

attributes and landscape context. Furthermore, I describe geographic and environmental trends in floristic similarity among pineland associations as they relate to distribution and identification of community types.

Methods

Study Area

The study area included the entire Florida Panhandle and most of central and northern Peninsular Florida. This area extends south from the State border to a southern boundary extending from roughly 26° 70' latitude on the west coast to 28° 80' on the east coast (Figure 2-1). This area roughly coincides with the current range of longleaf pine in Florida (Figure 2-2(a)). This range is thought to represent the historic longleaf pine range in Florida (Platt 1999 and references within), although there is some evidence that historic distribution extended farther south. The southern boundary also approximates the southern extent of the “warm temperate moist forest” bioclimate zone, separating it from the “subtropical moist forest” zone (Holdridge 1967).

Three generalized land units of Puri and Vernon (1964) subdivide the Florida study region according to common geologic history. These generalized land units describe geographic regions: 1) Northern Highlands, 2) Central Highlands, and 3) Coastal Lowlands (Figure 2-1). These are further subdivided according to physiographic landforms, which describe major soil types, geology and prevailing landscape features (Puri and Vernon 1964, Myers 1990). These are 1) Highlands; 2) Ridges, Hills, Inclines and Slopes; and 3) Lowlands, Gaps, and Valleys.

The Northern Highlands of the upper panhandle lie north of a prominent ancient Pleistocene shoreline known as the Cody Scarp (Myers and Ewel 1990). This region is distinguished by broad expanses of continuous highlands. The Western and Tallahassee

Highlands, New Hope and Grand Ridges, and Marianna Lowlands landforms comprise the Northern Highlands land unit (Puri and Vernon 1964). The first two have dissected topography and clastic sediments of mainly Appalachian origin from the Miocene epoch (20 to 5 million years before present; Puri and Vernon 1964, Brown et al. 1990, Myers 2000). The Marianna Lowlands landform contains outcrops of Eocene and Oligocene carbonates in a low lying anticline (Puri and Vernon 1964, Brown et al. 1990). Although lower than the first two landforms, it is higher than the Coastal Lowlands, and is generally well-drained owing to sandy soils shallowly overlying limerock perforated by sink holes (Brown et al. 1990). Ultisols are common upland soils of Northland Highlands, although Entisols typify Citronelle Formation uplands in the Western Highland portion as well as the sandy uplands of central panhandle Ridges. The Central Highlands land unit contains discontinuous highlands of the central Peninsular ridge system amid lower and flatter landforms (Figure 2-1). The former are landforms of the Ridges, Uplands, and Slopes and Highlands types while the latter are Lowlands, Gaps, Valleys and Plains (Puri and Vernon 1964).

The Central Highlands and the Northern Highlands approximate the emergent portion of the Wicomico shoreline, an early Pleistocene shoreline of high sea level. This region was once an integrated highland that has since been partitioned by erosion and solution (Puri and Vernon 1964). The Ridges and Uplands of the peninsula arose from ancient shorelines, dune systems, barrier islands, and associated terraces (Puri and Vernon 1964). Larger ridge systems of the Central Highlands include the Brookville, Deland, Trail, Mount Dora and Lake Wales Ridge physiographic landforms, and major Uplands include Sumter, Polk, Marion, Duval and Lake landforms. Soils are mainly coarse, excessively drained Entisols and loamy Ultisols. Soils of

Lowlands landforms are typically Spodosols underlain by limestone of the Florida peninsula platform (Brown et al., 1990).

The Coastal Lowlands land unit includes the southern tier of the panhandle below the Cody Scarp, in addition to the coastal regions of the peninsula (Figure 2-1). Much of this region has been subjected several marine inundations during the Late Miocene to the Early Pliocene (Puri and Vernon 1964, Webb 1990). Most of the Coastal Lowlands region contains Lowlands, Gaps, Valleys, and Plains physiographic landforms. These are broad plains with little relief, containing poorly drained Spodosols (Brown et al. 1990).

Selection of Sample Sites

The focus of this study was fire-dependent plant communities of Florida containing herbaceous-dominated ground cover vegetation. This included many types of pine woodlands and savannas, variously labeled pine flatwoods, sandhills, high pine, piney woods, mesic flatwoods, wet flatwoods, and scrubby (or xeric) flatwoods. Also included were fire-dependent herbaceous dominated communities associated with pinelands, such as prairies, bogs, lake margins, and seepage slopes. These communities are naturally characterized by frequent, low-intensity fires in which herbaceous vegetation and litter provide the dominant fuel matrix (Platt 1999). I omitted scrub and maritime pinelands of Central Florida and coastal regions, which are typically characterized by crown fires in the shrub or tree layers and have relatively longer fire-free intervals (Myers and Ewel 1990).

Although the Florida range of longleaf pine is the large scale region of interest of this study, descriptions of pyrogenic communities were not restricted to longleaf pine dominated sites. The geographic and habitat scope of this study included all pineland and associated communities within the longleaf pine range of Florida. Sites lacking pine overstory were

included in the study based on their similarity in ecosystem processes and herbaceous ground cover structure and diversity to pine-dominated sites. Such sites often represented topographic-moisture extremes in otherwise pine-dominated landscapes.

The generalized physiographic landforms of Puri and Vernon (1964) were further subdivided into “ecoregions” to guide site selection and stratification. This ensured a representative sample of physiographic environments throughout the area of study. I delineated ecoregions based on homogeneity of geology, vegetation, soils, climate and physiography, following several published works (Fenneman 1938, Puri and Vernon 1964, Davis 1967, Fernald 1981, Brooks 1982, Bailey et al. 1994, Griffith et al. 1994). There were a total of 19 ecoregions in the study region. I present classification results relative to physiographic landforms, of which ecoregions were subsets.

I stratified sampling by ecoregions and topographic-moisture conditions. Roughly equal numbers of sites were selected per ecoregion depending on site availability and accessibility. To the best of my ability, I selected three high quality sites in different locations within each ecoregion. Ideally, each site contained an intact, continuous topographic-moisture gradient supporting frequently burned native vegetation. Unfortunately, sites that satisfy this condition are rare or absent in some regions, particularly those that lack large tracts of public land. Under these conditions, I relaxed selection criteria to include: 1) sites that contained intact topographic-moisture gradients, but lacked optimal fire history, and 2) sites with acceptable fire history but lacking intact gradients. In the latter situation, I pieced together a representative topographic-moisture gradient from several sites located in close proximity. Additional criteria were considered in site selection: 1) little or no recent man-made ground disturbance, 2) absence of invasive exotic species, 3) presence of native canopy and midstory tree composition and

structure, and 4) evidence of fire within the previous five years, and preferably a history of frequent fires during the previous 50 years. In general, the integrity of the ground cover vegetation was emphasized over structure of the tree canopy in selection evaluations. Candidate sites were identified from various sources, including the Florida Natural Areas Inventory natural community database (FNAI 2000a) and consultation with regional natural resource professionals. Three sites (12 plots) were selected in South Georgia (within 20 miles of the Florida state border). I assumed that vegetation of these sites were representative of Florida pinelands in the same ecoregion. A total of 102 sites were selected (see Appendix A)

Field Methods

Once deemed suitable for sampling, a site (or a composite site) was delineated into three or four topographic-moisture zones based on field observations. Sampling from a range of topographic-moisture conditions maximized inclusive sampling of local vegetation associations presumed to be associated with specific soil conditions. One 1000 m² rectangular plot was established in each zone such that the plot area encompassed an area of relatively homogenous vegetation. The starting point of the long plot axis was randomly assigned. Usually the main axis of the 50 x 20 m plot was oriented parallel to slope contours.

Vegetation sampling methodology followed the Carolina Vegetation Survey (CVS) sampling protocol (Peet et al. 1998). The basic sampling unit was a 1000 m² plot (dimensions 50 x 20 m). Four 100-m² “modules” were situated in each plot, each containing two sets of nested sub-plots (0.01, 0.1, 1, and 10-m²). All vascular plant taxa were recorded as they were encountered in the sequentially sampled nested sub-plots. I estimated the aerial cover of each taxon in 100-m² modules using cover classes: 1 = 0-1%, 2 = 1-2%, 3 = 2-5%, 4 = 5-10%, 5 = 10-25%, 6 = 25-50%, 7 = 50-75%, 8 = 75-95%, 9 = >95%. Mean cover estimates were

calculated from four module cover midpoints. Taxa encountered in the remaining 600-m² plot area were tallied and assigned nominal cover estimates. In the 1000-m² plots, all woody stems > 1 cm and < 40 cm diameter at breast height (dbh) were tallied by species and 5 cm diameter class. Stems > 40 cm dbh were measured and recorded individually. In plots with very sparse woody vegetation, I sampled stems in a larger area (2000-m²) to obtain better estimates of stem density and basal area.

All plots were sampled during the late summer through early winter (August-December). Sampling flora in the late growing season increased my ability to identify the copious numbers of graminoids and fall-flowering forbs typical of Southeastern pinelands. A total of 293 plots were sampled over 4 years (2000 – 2004).

The majority of sampled taxa were identified to species or variety. Some taxa received lower levels of taxonomic resolution due to problems with consistent field identification. Where variation in taxonomic resolution existed, I used the lowest resolution necessary to ensure consistency throughout the dataset. The term “species” is used to indicate the highest resolution of identification, be it genus, species or variety. Nomenclature generally follows Kartesz (1999) with a few exceptions. In field and herbarium plant identification I made frequent use of (Godfrey and Wooten 1979, Godfrey and Wooten 1981, Clewell 1985, Godfrey 1988, Wunderlin 1998, Weakley 2002). Approximately 2500 voucher specimens were deposited in the University of Florida herbarium in Gainesville, Florida.

Four surface soil samples were collected per plot. Each sample of approximately 250 g was collected to 10 cm depth. Sub-soil samples were collected from a single point approximately 50 cm below ground surface. Samples were dried and sent to Brookside Labs in New Knoxville, Ohio for nutrient and textural analyses. Texture analysis determined

compositional percentages of sand, silt, and clay particles in the surface and sub-soil samples. In addition, percent organic matter, pH, and exchangeable cations in ppm (Ca, Mg, K, Na) were measured in surface soil samples.

Numerical Analysis

A matrix of species data was assembled from the 293 census plots hereafter referred to as samples. Samples represent different topographic-moisture locations within sites. Pine species (genus *Pinus*) were omitted from the species matrix, although other woody species were retained. Species with fewer than three occurrences in were deleted from the final data matrix, as rare species contribute little to calculations of inter-plot similarities (McCune and Grace 2002). The dimensions of the final response matrix were 293 samples x 575 species.

I transformed the species response matrix prior to multivariate analyses following the guidelines of Legendre and Gallagher (2001) and McCune and Grace (2002). First, species responses were relativized to maximum species cover values which tends to de-emphasize the influence of common and abundant species. Then the species response matrix was transformed using the Hellinger distance transformation. When used in conjunction with Euclidean distance metrics this transformation improves representation of multidimensional data in low dimensional space and avoids problems inherent to sample weighting (in chi-square based ordinations) in addition to problems associated with using Euclidean distances with untransformed data (Legendre and Gallagher 2001, Legendre et al. 2005).

I used a combination of ordination and cluster analyses to partition samples into floristically similar groups. Specifically, I used non-hierarchical Euclidean-based K-means cluster analysis to partition samples into a configuration that minimized within group sum of squares relative to between group differences (Legendre and Legendre 1998). Partitions are

user-defined, so I used the “cascading K-means” function of the Vegan package (Oksanen et al. 2007) as implemented in R statistical software (R Development Core Team 2007). Cluster analysis was run multiple times using various numbers of user-defined partitions (2 to 40 groups). I selected the number of partitions that maximized an optimization index, specifically the “Simple Structure Index” (SSI). The SSI quantifies three elements of a partition model: maximum difference of each species response between clusters, the sizes of the most contrasting clusters and the deviation of species responses per cluster compared to its overall mean (Oksanen et al. 2007).

The final partition model presented clusters of samples representing recognizable and distinct floristic assemblages. I refer to these clusters as “associations”. I graphically displayed associations in a non-metric multidimensional scaling (NMS) ordination of Euclidean distances derived from the Hellinger transformed species matrix. For this I used PC-ORD software, version 5.0 (McCune and Mefford 1999).

Diagnostic species were recognized for each association, in terms of constancy and fidelity. I used Indicator Species Analysis of Dufrene and Legendre (1997) implemented in PC-ORD (McCune and Mefford 1999). The Indicator Value (IV) index quantifies a species’ relative frequency and abundance among associations. Indicator species were identified using Monte Carlo randomization tests (McCune and Mefford 1999); the null hypothesis was that the maximum IV among associations is no larger than would be expected by chance. Indicator species were considered those with type I error < 0.05 in the IV randomization test.

From the species recognized as indicators for associations, I identified those with restricted distributions in Florida. A species was identified as having “restricted range” if its Florida distribution was limited to only one of three regions (Western Panhandle, Panhandle plus

North peninsula, or Central Peninsula), or if its entire range was limited to Florida. Species' Florida distributions were categorized by visual inspection of on-line county range maps available from the Institute of Systematic Botany Atlas of Florida website (Wunderlin and Hansen 2004).

I compared soil characteristics and other community attributes among individual associations, and between three higher level groups of associations (termed ecological "series"). Within ecological series, means and pairwise comparisons of response variables among associations were analyzed with univariate ANOVA's. In addition to soil variables, I compared species richness (number of species /1000-m² sample) and basal area (m²/ha) between associations. Response variables were transformed to improve normality of residual distributions in each model. Count variables were log transformed, and logit transformations were applied to proportion response variables (Tabachnick and Fidell 1996). I maintained a Type I error of $p < 0.01$ for each pairwise comparison to reduce the overall Type I error associated with each response variable. All ANOVA and post-hoc tests were performed using SAS software, version 9 (SAS 2000).

Results

A total of 293 samples spanning the study region were included in the K-means cluster analysis of mean species cover responses (Figure 3a). I identified 16 associations from the optimal cluster solution. This partition yielded the second highest value of SSI (0.23, maximum value = 1.0) among all partitions of 2 to 40 groups. Although the 28 group partition had a higher SSI value (0.25), I chose the 16 group partition because it presented interpretable results with relatively balanced cluster sizes, with no clusters containing fewer than four samples.

The 16 associations encompass a wide range of floristic variation over environmental conditions. The primary gradient of variation, displayed by the first NMDS ordination axis, concurs with *a priori* assigned topographic-moisture conditions (Figure 2). The correlation between distances in ordination space (two dimensional NMS solution) versus distances in original space was $R^2 = 0.83$ (McCune and Mefford 1999, McCune and Grace 2002). The first axis represents most of this variation ($R^2 = 0.54$).

I categorized the 16 associations into three ecological series, which are superimposed on the ordination diagram: Dry Uplands (D), Mesic Flatwoods (M), and Wetlands (W).

Associations were named using existing vernacular in plant community descriptions: sandhills, clayhills and woodlands describe dry upland communities of varying canopy density and soil texture; mesic flatwoods refer to pine savanna communities of poorly-drained flat terrain.

Occasionally to seasonally inundated wetlands are represented by various terms depending on canopy density and moisture conditions, including wet flatwoods, wet prairies, and seepage slopes (FNAI 1990, Myers and Ewel 1990, Peet and Allard 1993). Modifiers were added to distinguish landscape and regional affinities.

One hundred and six species were categorized as having restricted ranges in Florida. Eight species are endemic to Florida. The remaining 98 species have provincial distributions, and are restricted to one of three regions in Florida: 1) Panhandle only, 2) Panhandle and north peninsular Florida, and 3) peninsula only (Tables 4 and 5).

Associations are described below in terms of community aspect, soil characteristics, and species composition. Throughout, the tables and appendix are referenced for the following: soil and community attributes (Tables 2-1 and 2-2), common canopy and midstory woody species (Table 2-3), indicator species of associations (Tables 2-4 and 2-5), and frequent and abundant

ground cover species (Appendix B). In addition, endemic and restricted-range indicator species are indicated in Tables 2-4 and 2-5. Maps of plot locations are shown in Figure 2-2.

Physiographic and landscape attributes for associations are described, and follow the conventions of Figure 2-1. Labels and cluster sizes are noted following association name. Association descriptions are grouped into three major ecological series corresponding to Figure 2-3.

SERIES 1: Dry Uplands

Dry Uplands included six associations, which were categorized as sandhills, woodlands or clayhills. The Dry Uplands associations were located within the Northern Highland and Central Highland generalized land units, primarily within the Ridges and Uplands physiographic landforms. In general, these associations occurred on ridgetops and upper slopes in areas with topographic relief exceeding several meters. Soils of Dry Uplands were sandy and low in organic content. Compared to Mesic Flatwoods and Wetlands series, Dry Uplands sand content was high in surface soils and low in sub-soils. Soil pH was intermediate compared to other series (Table 2-1).

The six Dry Upland associations exhibited geographic segregation relative to floristic composition. The Ochlochnee River basin in the eastern Panhandle distinctly separated associations of the Northern Highlands and Panhandle Coastal Lowlands from those of the Central Highlands and peninsular Coastal Lowlands. Dry Uplands of the Northern Highlands landform occurred on both Pliocene and Pleistocene deposits, including the Citronelle and Torreyia formations and the undifferentiated deposits of the lower Apalachicola basin (Puri and Vernon 1964, Brown et al. 1990). East of the Ochlochnee River, Dry Upland associations occurred primarily on Miocene and Pliocene deposits of the Central Highlands land unit, specifically within the Ridges, Uplands and Slopes physiographic landforms.

Dry Uplands soil properties reflected those of Entisols and Ultisols, which are common upland soil orders (Brown et al. 1990, Myers 1990, Myers 2000). Segregation of associations coincides with soil clay and silt content. The well-developed Ultisols of the PANHANDLE LONGLEAF PINE CLAYHILLS and PANHANDLE SILTY WOODLANDS had argillic sub-surface strata enriched with clay and silt. Soil moisture availability is typically greater in these soils (Brown et al. 1990, Brady and Weil 2000). The Dry Upland associations of the panhandle spanned a range of soil texture composition. Conversely, Dry Upland associations of the peninsula did not exhibit surface soil texture gradients, but variation was apparent in sub-soil silt and clay content and organic content. All Dry Upland soils were similar in pH, with the exception of the PANHANDLE LONGLEAF PINE CLAYHILLS association. In addition, fine-textured soil content was positively correlated with species richness and canopy density. A description of individual associations within Dry Uplands series follows.

PENINSULA XERIC SANDHILLS (22 plots, D3): This association is restricted to high sandy ridges of the Central Highlands and Coastal Lowlands of the northern peninsula region (Figure 2-2c). PENINSULA XERIC SANDHILLS soils consist of coarse sands with low concentrations clay and silt. This association is species-poor compared to other Dry Upland associations, although comparable to the PANHANDLE XERIC SANDHILLS further west.

Pine canopy of PENINSULA XERIC SANDHILLS was sparse. Longleaf pine (*Pinus palustris*) was the dominant canopy species (mean BA = 4.8 m²/ha), followed by turkey oak (*Quercus leavis*; mean BA = 1.9 m²/ha). Common midstory species included turkey oak, sand live oak (*Q. geminata*), saw palmetto (*Serenoa repens*) and bluejack oak (*Q. incana*). Sand post oak (*Q. margarettiae*), an oak common in other sandhill associations, was notably infrequent.

The most common herbaceous plants of PENINSULA XERIC SANDHILLS were grass and forb species. Frequent grasses are wiregrass (*Aristida beyrichiana*), lopsided indiagrass (*Sorghastrum secundum*), little bluestem (*Schizachyrium scoparium* var. *stoloniferum*), and eggleaf witchgrass (*Dichanthelium ovale*). The forbs silkgrass (*Pityopsis graminifolium*), pineland pinweed (*Lechea sessiliflora*) and queens delight (*Stillingia sylvatica*) were common. A few grasses were identified as indicator species, including pineywoods dropseed (*Sporobolus junceus*), perennial sandgrass (*Triplasis americana*), and big threeawn (*Aristida condensata*). The remaining indicator species were forb species common to xeric habitats: Ware's hairsedge (*Bulbostylis warei*), coastal plain honeycombhead (*Balduina angustifolia*), and pineland pinweed (*Lechea sessiliflora*). Coastal plain chaffhead (*Carphephorus corymbosus*) and wholly pawpaw (*Asimina incana*: a small shrub) are indicator species with ranges restricted to the peninsula. Two indicator species are legumes: eastern milkpea (*Galatia regularis*) and scurf hoarypea (*Tephrosia chrysophylla*). Legumes are typically common to communities of finer-textured soils (James 2000).

PANHANDLE XERIC SANDHILLS (31 plots, D4): Sites of this association were restricted to the Northern Highlands land unit (Figure 2-2b), primarily west of the Ochlochnee river basin. PANHANDLE XERIC SANDHILLS were observed in two landscape contexts: 1) on sandy ridgetops and upper slopes, and 2) as the dominant community of broad flat terrain with little apparent topographic variation. I observed the latter situation on the broad continuous uplands of the Citronelle formation in Eglin Air Force Base.

PANHANDLE XERIC SANDHILLS were similar in aspect to PENINSULA XERIC SANDHILLS. Sparse canopies consist of scattered longleaf pines (*P. palustris*: mean BA = 7.9 m²/ha) and turkey oak (*Q. leavis*: mean BA = 1.1 m²/ha). Midstory strata were dominated by turkey oaks,

bluejack oak (*Q. incana*) and sand live oak (*Q. geminata*). Unlike the PENINSULA XERIC SANDHILLS, sand post oak (*Q. margaretta*), dwarf live oak (*Q. minima*), and dwarf huckleberry (*Gaylussacia dumosa*) were common in PANHANDLE XERIC SANDHILLS.

Frequent species of PANHANDLE XERIC SANDHILLS included few grasses, most notably little bluestem (*Schizachyrium scoparium* var. *stoloniferum*) and Elliott's bluestem (*A. gyrans* var. *gyrans*) with a low frequency of wiregrass (*Aristida stricta*). Herbaceous species of xeric habitats distinguished PANHANDLE XERIC SANDHILLS ground cover. About a third of indicator species have ranges restricted to the Panhandle, including piedmont gayfeather (*Liatris pauciflora* var. *secunda*), littleleaf milkpea (*Galactia microphylla*), Morh's threeawn (*Aristida morhii*), Godfrey pineland hoarypea (*Tephrosia morhii*), royal snoutbean (*Rhynchosia cytisoides*) and greater Florida spurge (*Euphorbia floridana*). The provincial herb *Pityopsis aspera* is abundant and frequent (90% of plots). In contrast, *P. aspera* is absent from PENINSULA XERIC SANDHILLS where *P. graminifolia* is usually dominant.

NORTH FLORIDA SANDHILLS (31 plots, D2): Sites of this association occurred on various landforms of the Coastal Lowlands and Central Highlands of the eastern panhandle and northern peninsula (Figure 2-2c). NORTH FLORIDA SANDHILLS are usually found on ridgetops and upper slopes. Soils were similar in textural composition to PENINSULA XERIC SANDHILLS except they had higher silt content. In addition, they were very low in clay and organic matter.

Similar to other Dry Upland associations, NORTH FLORIDA SANDHILLS have canopies of longleaf pines (mean BA = 8.6 m²/ha) with scattered upland oaks (most abundant: turkey oak, mean BA = 1.2 m²/ha). The three common upland oaks dominate the midstory: turkey oak, bluejack oak (*Q. incana*) and sand post oak (*Q. margaretta*).

Common grasses of NORTH FLORIDA SANDHILLS are similar to those of PENINSULA XERIC SANDHILLS: wiregrass, little bluestem, lopsided indiagrass, and eggleaf witchgrass. Other frequent grasses include needleleaf witchgrass (*D. angustifolium*) and thin paspalum (*Paspalum setaceum*). Many frequent species are low growing forbs, as are 14 of the 15 indicator species. Three of these are legumes, including Florida ticktrefoil (*Desmodium floridanum*), dollarleaf (*Rhynchosia reniformis*), and hairy lespedeza (*Lespedeza hirta*). None of the NORTH FLORIDA SANDHILLS indicator species have restricted distributions. Species richness of NORTH FLORIDA SANDHILLS is notably higher compared to the xeric Dry Uplands, and likely contributed to the floristic segregation among these associations.

NORTH FLORIDA RICH WOODLANDS (11 plots, D1): This association includes longleaf pine woodlands of mid- and lower slopes in the Central Highlands and Coastal Lowlands of the northern peninsula (Figure 2-2c). These sites were usually adjacent to hardwood hammocks. All NORTH FLORIDA RICH WOODLANDS sites were in or adjacent to vegetation zones identified as “Hardwood hammocks” by Davis (1967). Most were located downslope of NORTH FLORIDA SANDHILLS. NORTH FLORIDA RICH WOODLANDS soils had physical properties similar to the three preceding Sandhills associations. However, they were distinguished by their very high organic content and sub-surface clay content. These soil attributes suggest higher water retention capacity (Brady and Weil 2000).

Canopy densities of NORTH FLORIDA RICH WOODLANDS were high relative to other Dry Uplands associations (mean BA = 16.1 m²/ha). Longleaf pine dominated canopies (mean BA = 8.5 m²/ha), but other subdominant pine species were present: slash pine (*P. elliotii* var. *elliotii*) and loblolly pine (*P. taeda*; mean BAs = 1.3 and 1.2 m²/ha respectively). Sand live oak (*Q. geminata*) and mockernut hickory (*Carya alba*) were canopy sub-dominants (mean BAs = 1.5

and 1.4 m²/ha respectively). Midstory strata were generally shrubbier compared to other Dry Upland associations, dominated by saw palmetto (*S. repens*) followed by winged sumac (*Rhus coppelinum*), mockernut hickory (*C. alba*) and two upland oaks (*Q. geminata* and *Q. margaretta*).

Common herbaceous species of NORTH FLORIDA RICH WOODLANDS included grasses typical of other upland associations, as well as some distinctive woodland forbs. Common grasses were Elliott's bluestem (*A. gyrans* var. *gyrans*), needleleaf witchgrass (*D. angustifolium*), thin paspalum (*P. setaceum*), lopsided indiangrass (*Sorghastrum secundum*), broomsedge bluestem (*A. virginicus*), and eggleaf witchgrass (*D. ovale*). Wiregrass (*A. stricta*) was present in only about 50% of the plots, and was sparse compared to other Dry Upland associations. Bracken fern (*Pteridium aquilinum*), lustral greenbriar (*Smilax laurifolia*), whitetop aster (*Sericocarpus tortifolius*), and lesser snakeroot (*Ageratina aromatica*) were ubiquitous herbaceous species. Almost all indicator species were woodland forbs and infrequent grass species, including seven grasses and five legumes. About half of the indicator species were species with restricted ranges. Species richness of North Florida Rich Woodlands was intermediate compared to other Dry Uplands (106 species/0.1 ha).

PANHANDLE LONGLEAF PINE CLAYHILLS (14 plots, D5): These sites are restricted to the Northern Highlands land unit of the panhandle. **PANHANDLE LONGLEAF PINE CLAYHILLS** inhabit the ridgetops and upper-slopes of dissected Pliocene and Miocene-aged sediments north of the Cody Scarp (Figure 2-2b). In the western panhandle, this association occupied mid-slopes in association with **PANHANDLE XERIC SANDHILLS**. The prominence of fine-textured sediments distinguishes soils of **PANHANDLE LONGLEAF PINE CLAYHILLS**. Sub surface silt and clay content

was high compared to other Dry Uplands. Similarly, soil pH was higher than all other Dry Uplands associations.

PANHANDLE LONGLEAF PINE WOODLANDS canopies were dense and dominated by longleaf pine (mean BA = 10.9 m²/ha), with minor contributions of loblolly and shortleaf pines (*P. taeda* and *P. echinata*; mean BAs = 1.2 and 0.4 m²/ha respectively). In addition to the typical Dry Uplands oak species, shrubs of more mesic habitat occupy midstory strata such as southern red oak (*Q. falcata*), running oak (*Q. pumila*), and Darrow's blueberry (*V. darrowii*).

Species richness of PANHANDLE LONGLEAF PINE CLAYHILLS is exceedingly high. The mean of 124.5 species/0.1 ha is the highest of all Dry Uplands associations. Dense herbaceous ground cover vegetation contained numerous forb and grass species. Wiregrass (*Aristida stricta*), little bluestem (*Schizachyrium scoparium* var. *stoloniferum*) and narrowleaf witchgrass (*D. angustifolium*) were ubiquitous. Indicator species included many legumes and composites (members of the *Asteraceae* family). Ten out of 25 indicator species are legume species and many of these are in the genus *Desmodium*. Eleven of the 25 indicator species have ranges that were restricted to the panhandle or northern peninsula. Several bunch grass species with restricted ranges were identified as indicators: big bluestem (*A. gerardii*), cutover muhly (*Muhlenbergia capillaris* var. *trichopodes*), Carolina fluffgrass (*T. carolinianus*), yellow indiangrass (*Sorghastrum nutans*) and shortleaf skeletongrass (*Gymnopogon brevifolius*).

PANHANDLE SILTY WOODLANDS (22 plots; D6): This association occupied Pleistocene and Miocene sediments of the Coastal Lowlands west of the Ochlochnee river basin (Figure 2-2b). Most sites were located in the Apalachicola embayment region, and many occupied Pleistocene and Holocene undifferentiated deposits of lowlands east of the Apalachicola river (Puri and Vernon 1964, Florida Department of Environmental Protection 1998). Although

included in the Dry Uplands series, PANHANDLE SILTY WOODLANDS resembled Mesic Flatwoods in landscape context. They inhabited side slopes and terraces of intermediate topography. Soils of PANHANDLE SILTY WOODLANDS were high in silt and clay content. Notably, subsurface soils had high silt and low organic content compared to other associations.

Longleaf pine dominated dense canopies of PANHANDLE SILTY WOODLANDS sites (mean BA = 11.9 m²/ha). Other canopy species were infrequent (mean BA of all other species < 0.4 m²/ha). Upland oaks and other xeric midstory hardwoods were conspicuously absent. Low growing evergreen shrub species typical of mesic habitats dominated the midstory strata, including gallberry (*Ilex glabra*), running oak (*Q. pumila*), saw palmetto (*Serenoa repens*), and dwarf live oak (*Q. minima*).

Although woody vegetation of PANHANDLE SILTY WOODLANDS resembled Mesic Flatwoods, herbaceous ground cover was floristically similar to other associations in the Dry Uplands series. Mean species richness of PANHANDLE SILTY WOODLANDS was relatively high, comparable to NORTH FLORIDA SANDHILLS and NORTH FLORIDA RICH WOODLANDS associations. Wiregrass (*A. stricta*), little bluestem (*S. scoparium* var. *stoloniferum*), narrowleaf witchgrass (*D. angustifolium*), and cypress witchgrass (*D. dicotomum* var. *tenue*) were the most common grass species. Forb species were frequent relative to grasses and shrubs. All indicator species were herbaceous species; over half were members of *Asteraceae* or *Fabaceae* plant families. Eight of 14 indicator species have ranges restricted to the panhandle or north peninsula, including two that are endemic to the Apalachicola region: pineland false sunflower (*Phoebanthus tenuifolius*) and scareweed (*Baptisia simplicifolia*).

SERIES 2: Mesic Flatwoods

This series includes three associations that can be categorized as either Mesic Flatwoods or Xeric Flatwoods according to FNAI conventions (FNAI 1990). Mesic Flatwoods associations typically inhabited flat poorly drained regions of the panhandle and peninsula Coastal Lowlands, and the peninsular Central Highlands (Figure 2-2d; Abrahamson and Hartnett 1990, FNAI 1990, Myers 2000). Mesic Flatwoods appeared to be absent from the Northern Highlands landform. Some geographic separation of Mesic Flatwoods associations was apparent, with complete separation of NORTH FLORIDA MESIC FLATWOODS and CENTRAL FLORIDA MESIC FLATWOODS/DRY PRAIRIES.

In general, Mesic Flatwoods soils are sandy and acidic. Mesic Flatwoods soils are typically Spodosols, with acidic sands underlain by clayey or organic hardpans hindering water percolation (FNAI 1990). Sub-surface clay content was consistently low in my Mesic Flatwoods sites (although sample depths may have been too shallow to detect hardpans). I did not sample sub-surface organic matter. Organic content of surface soils was high compared to Dry Uplands and similar to Wetlands associations. Variation in soil texture between Mesic Flatwoods associations was minimal, although the northern association tended to have higher surface soil clay content. Descriptions of specific associations follow.

XERIC-MESIC FLATWOODS (36 plots; M1): XERIC-MESIC FLATWOODS generally inhabited the Coastal Lowlands of the panhandle and peninsula (Figure 2-2d). They occupied upper slopes of small sandy rises embedded in large expanses of Mesic Flatwoods vegetation. In the few sites of the Central Highlands, this association occurred downslope of Dry Upland vegetation.

Soils of XERIC-MESIC FLATWOODS were coarse and contained very small concentrations of fine textured sediments. These differences distinguished XERIC-MESIC FLATWOODS soils from NORTH FLORIDA MESIC FLATWOODS. Organic content of XERIC-MESIC FLATWOODS soils is similar to other Mesic Flatwoods associations, although soil pH is relatively high.

XERIC-MESIC FLATWOODS had sparse pine canopies and dense shrubby midstory strata. Sparse longleaf pine formed the canopy (mean BA = 2.8 m²/ha). Slash pine (*P. elliottii*) was sub-dominant (mean BA = 1.0 m²/ha). Saw palmetto (*S. repens*) was by far the most abundant midstory shrub. Three upland “scrub” oaks were common in XERIC-MESIC FLATWOODS midstories: sand live oak (*Q. geminata*), Chapman’s oak (*Q. chapmanii*), and myrtle oak (*Q. myrtifolium*). Notably absent were the upland oaks of Dry Upland associations. In addition, evergreen shrub species of the heath family are common in Xeric-Mesic Flatwoods, including fetterbush, *Lyonia lucida*; dwarf huckleberry, *G. dumosa*; lowbush blueberry *V. myrsinites*).

Mean species richness of XERIC-MESIC FLATWOODS sites was low due to sparse herbaceous ground cover. Wiregrass (*A. stricta*) was by far the most common herb, followed by broomsedge bluestem (*A. virginicus*), hemlock witchgrass (*D. sabulorum* var. *thinium*) and silkgrass (*P. graminifolium*: not a grass, but a member of *Asteraceae*). Few indicator species were identified for Xeric-Mesic Flatwoods. Of these, 3 (out of 7) were shrub species, including two of the common scrub oaks and tarflower (*Befaria racemosa*). Three indicator species had restricted peninsular ranges: tarflower, Chapman’s goldenrod (*Solidago odora* var. *chapmanii*) and shortleaf gayfeather (*Liatris tenuifolia* var. *quadriflora*).

NORTH FLORIDA MESIC FLATWOODS (30 plots; M2): This association was observed in the Coastal Lowlands land unit of the panhandle and peninsula. A few sites occurred in the Central Highlands land unit of the peninsula (Figure 2-2d) where it occupied small areas

downslope of Dry Uplands. The northerly distribution of NORTH FLORIDA MESIC FLATWOODS separates it geographically from the CENTRAL FLORIDA MESIC FLATWOODS/DRY PRAIRIES. Typically, NORTH FLORIDA MESIC FLATWOODS occupied flat, poorly drained terrain of Pleistocene origin. Soil clay content and pH was low compared to other Mesic Flatwoods associations.

Overstory canopies of NORTH FLORIDA MESIC FLATWOODS were comparatively dense. Longleaf pine was the most common canopy species (mean BA = 9.3 m²/ha), and slash pine was sub-dominant (mean BA = 1.5 m²/ha). Midstory vegetation was generally low and sparse. Common shrub species were gallberry (*I. glabra*), saw palmetto (*S. repens*), and runner oak (*Q. minima*). These species formed patches of low growth in the understory, interspersed with thick herbaceous ground cover. Runner oak and another woody sub-shrub (hairy wicky, *Kalmia hirsuta*) were identified as indicator species.

NORTH FLORIDA MESIC FLATWOODS had intermediate species richness relative to other Mesic Flatwoods. Common herbaceous species resembled those of XERIC-MESIC FLATWOODS: wiregrass (*A. stricta*), broomsedge bluestem (*A. virginicus*), and silkgrass (*P. graminifolium*). Carolina yelloweyed grass (*Xyris caroliniana*) is the most frequent herbaceous species, as well as an indicator species. Only four indicator species were recognized for NORTH FLORIDA MESIC FLATWOODS. Other than those already mentioned, these include Florida dropseed (*Sporobolus floridanus*) and dwarf live oak.

CENTRAL FLORIDA MESIC FLATWOODS/DRY PRAIRIES (22 plots; M3): These sites were restricted to the Coastal Lowlands land unit of the peninsula. CENTRAL FLORIDA MESIC FLATWOODS/DRY PRAIRIES typically occupied broad flat, poorly drained terrain with sediments of Pleistocene origin (Figure 2-2d). They often surrounded XERIC-MESIC FLATWOODS

communities present on slightly higher and drier ridges. Soil characteristics of CENTRAL FLORIDA MESIC FLATWOODS/DRY PRAIRIES were similar to XERIC-MESIC FLATWOODS, although clay content was slightly higher in the sub-soil.

Canopies of CENTRAL FLORIDA MESIC FLATWOODS/DRY PRAIRIES were either sparse or absent. The latter condition distinguishes the dry prairies of Central Florida as described elsewhere (FNAI 1990, Bridges 2006, Platt et al. 2006). I did not detect floristic differences between sites with and without pine canopy. Where canopy was present, longleaf pine (*P. palustris*) was dominant and the two slash pine varieties (*P. elliotii* var. *elliotii* and *P. elliotii* var. *densa*) were infrequent (Mean BAs respectively: 2.0, 0.5, and 0.2 m²/ha). Midstory vegetation was sparse in the frequently burned CENTRAL FLORIDA MESIC FLATWOODS/DRY PRAIRIES. Woody species were relegated to the understory, where saw palmetto (*S. repens*) was abundant. Other understory shrubs included dwarf live oak (*Q. minima*), gallberry (*I. glabra*), and fetterbush (*L. lucida*).

Grass species were the most common species, such as wiregrass (*A. stricta*), hemlock witchgrass (*D. sabulorum* var. *thinium*), broomsedge bluestem (*A. virginicus*), bottlebrush threeawn (*A. spiciformis*), and cypress witchgrass (*D. chamaelonche*). The latter two grasses were indicators of CENTRAL FLORIDA MESIC FLATWOODS/DRY PRAIRIES. Two large bunchgrass species restricted to peninsular Florida were conspicuous indicators: shortspike bluestem (*A. brachystachyus*) and stoloniferous little bluestem (*Schizachyrium stoloniferum*). Graminoid species comprise about a third of the indicator species (11 out of 27). Three indicator species were shrubs and the remainder was forbs. No legumes, and only one member of *Asteraceae* were identified as indicators. Five indicator species have ranges restricted to the Florida Peninsula, including two endemics.

SERIES 3: Wetlands

Associations of the Wetlands ecological series encompassed a diverse array of floristic variation and physiognomic settings, and spanned most of the study area. Most Wetlands associations, particularly those of the Northern and Central Highlands land units, tended to occupy small areas of lower slopes in regions with relatively high relief. Two associations restricted to the Coastal Lowlands land unit (the PANHANDLE WET FLATWOODS/PRAIRIES and PENINSULA WET FLATWOODS/PRAIRIES) inhabited poorly drained areas with little topographic relief. Historically, large expanses of this vegetation extended across gradients of imperceptible elevation change (Harper 1914, Myers 2000). Geographic segregation among Wetlands associations is apparent. Three of seven associations are restricted to the panhandle and one restricted to the central peninsula (Figure 2-2e, 2-2f)

Associations of the Wetlands series show considerable variation in physical soil properties. Some associations were characterized by poorly drained and silty soils, where silt content distinguished Wetlands from Mesic Flatwoods and Dry Upland series. Texture differences were less apparent in sub-soil composition. Organic matter was high in all Wetlands associations. Fine textured soils and surface organic matter were particularly abundant in panhandle associations. Soil pH was variable among associations, ranging from 4.2 to 5.3.

Descriptions of specific associations follow.

MARGINAL PRAIRIES (11 plots; W1): This association included herbaceous dominated vegetation of depressional wetland margins in the panhandle and northern peninsula (Figure 2-2f). MARGINAL PRAIRIES occupied concentric zones surrounding shallow, seasonally inundated depressions and were seasonally inundated during periods of high rainfall. These sites occurred

on the margins of various wetland types, including dome swamps, sandhill upland lakes, and depression marshes (FNAI 1990).

MARGINAL PRAIRIES surface soils were sandy and acidic, and contained high levels of organic matter. Sub-soil silt content was low but clay content was high. This may reflect the presence of subsurface “hardpans” or “clay lens” that underlie depression marshes and dome swamps (FNAI 1990).

Canopy vegetation of MARGINAL PRAIRIES was either absent, or was comprised of young pond cypress and swamp tupelo (*Taxodium ascendens* and *Nyssa sylvatica* var. *biflora*). The latter condition may reflect “invasion” of saplings following fire suppression. Midstory vegetation was sparse or absent. A few evergreen shrubs was sporadically present, the most common were gallberry (*I. glabra*), titi (*Cyrilla racemiflora*) and sandweed (*Hypericum fasciculatum*).

Herbaceous vegetation of MARGINAL PRAIRIES was low in aspect and diversity. Mean species richness is the lowest of all Wetland associations (49.6 species/0.1 ha). Few species had high constancy across sites, reflected by the few species recognized as indicators. The most frequent herbaceous species (> 80%) were five grasses and two weedy forbs: broomsedge bluestem (*A. virginicus*), slender flattop goldenrod (*Euthamia caroliniana*), pale meadowbeauty *Rhexia mariana* var. *mariana*), and maidencane (*Panicum hemitomon*). Wiregrass (*A. stricta*) was absent from MARGINAL PRAIRIES. Maidencane, a species typical of inundated wetlands, was an indicator species. The remaining five indicators included forbs and one shrub species (buttonbush: *Cephalanthus occidentalis*).

PENINSULA WET FLATWOODS/PRAIRIES (16 plots; W2): These inhabit the flat, poorly drained regions of the Coastal Lowlands of peninsular Florida (Figure 2-2f). PENINSULA WET

FLATWOODS/PRAIRIES occupied barely perceptible lower slopes in association with NORTH FLORIDA MESIC FLATWOODS. High water tables and seasonal inundation due to rainfall contribute to wet conditions of PENINSULA WET FLATWOODS/PRAIRIES (FNAI 1990, Myers and Ewel 1990). Soils were sandy and high in organic matter compared to other Wetlands associations. Soil characteristics were particularly pronounced in sub-surface horizons, where clay and silt content was low. Soil calcium concentration and pH was high compared to other Wetlands associations.

PENINSULA WET FLATWOODS/PRAIRIES were variable in canopy structure and composition. Pine canopies were either sparse or absent. Midstory vegetation was typically low and sparse. The most common species were low growing shrubs: sandweed (*Hypericum fasciculatum*), gallberry (*I. glabra*), and pond cypress (*Taxodium ascendens*).

Floristic similarity of understory vegetation united PENINSULA WET FLATWOODS/PRAIRIES sites as this association. All common species, and 95% of indicator species were forbs and graminoids. Among frequent herbs, over 80% were recognized as indicator species. Wetland herb species, such as water cowbane (*Oxypolis filiformis*), tenangle pipewort (*Eriocaulon decangulare*), pineland rayless goldenrod (*Bigelovia nudata*), blue maidencane (*Amphicarpum muhlenbergianum*) and Elliott's yelloweyed grass (*X. elliotii*) were diagnostic in their constancy and fidelity. Wiregrass was frequent in PENINSULA WET FLATWOODS AND PRAIRIES, but was rivaled in abundance by other grass species, including longleaf threeawn (*A. palustris*). None of the 40 indicator species have restricted ranges.

CALCAREOUS WET FLATWOODS (4 plots; W3): This association was an unusual wet flatwoods assemblage that inhabited sites with shallow subsurface limestone. My small sample size precludes much generalization; however, the four plots were floristically distinct (Figure 2-

2f). The sites occurred in two situations: 1) the coastal fringe of the Big Bend region of the western peninsula, where marl is often immediately below the soil surface, and 2) as small inclusions in Coastal Lowlands, embedded in large expanses of CENTRAL FLORIDA MESIC FLATWOODS.

Soil texture characteristics of CALCAREOUS WET FLATWOODS were similar to those of PENINSULA WET FLATWOODS/PRAIRIES except that sub-surface clay content was higher. CALCAREOUS WET FLATWOODS were basic and had exceedingly high calcium concentrations relative to other Wetlands associations. This was consistent with the presence of shallow soils overlying limestone outcrops.

Three of the four CALCAREOUS WET FLATWOODS sites had dense canopies of slash pine (*P. elliottii*; mean BA = 11.15 m²/ha). Longleaf pine was absent. One plot, on Avon Park Airforce Range, had no pine overstory. Sabal palms (*Sabal palmetto*) were present in all sites, and comprised a significant canopy co-dominant (mean 1.88 m²/ha). Other hardwood species were common in the midstory, including many that are typical of swamp vegetation: wax myrtle (*Myrica cerifera*), swamp bay (*Persea palustris*), red maple (*Acer rubrum*), saw palmetto (*S. repens*), and sweetgum (*Liquidambar styraciflua*).

Mean species richness of CALCAREOUS WET FLATWOODS was exceedingly high, rivaling that of Dry Uplands on fine textured soils. Wiregrass (*A. stricta*) was infrequent. Dominant grasses were redtop panicum (*Panicum rigidulum* var. *rigidulum*), sugarcane plumegrass (*Saccharum giganteum*), cypress witchgrass (*A. dichotomum* var. *nitidum*), and switchgrass (*Panicum virgatum*). Most common species and the majority of indicator species were forbs. In addition, many graminoids were recognized as indicator species, particularly member of the

genus *Rhynchospora*. Sabal palm was the only non-herbaceous indicator species. Of 35 indicator species, only one (*R. perplexa*) has a restricted range.

NORTH FLORIDA SHRUBBY WET FLATWOODS (15 plots; W4): These sites occurred in the Northern and Central Highlands, and Coastal Lowlands of the panhandle and northern peninsula (Figure 2-2f). Most sites were east of the Ochlochnee River basin with the exception of one site in the western panhandle. NORTH FLORIDA SHRUBBY WET FLATWOODS typically occurred as small fringes along lower slopes, abutting wetland swamps. Textural composition of NORTH FLORIDA SHRUBBY WET FLATWOODS soils did not distinguish them from other Wetlands associations. However, surface soils were high in organic content and acidic.

NORTH FLORIDA SHRUBBY WET FLATWOODS have dense canopies of primarily slash pine (*P. elliotii* var. *elliotii*; mean BA = 10.93 m²/ha). Longleaf and pond pine were minor components (*P. palustris* and *P. serotina*; mean BA = 2.63 and 1.18 m²/ha respectively).

NORTH FLORIDA SHRUBBY WET FLATWOODS were floristically distinct from other wetlands associations due shrubby species abundance in the midstory and understory strata. Midstories were dominated by saw palmetto (*S. repens*), large gallberry (*I. coriacea*), and three shrub species also recognized as indicators: swamp bay (*P. palustris*), fetterbush (*L. lucida*) and coastal sweetpepperbush (*Clethra alnifolia*). The latter species is restricted in distribution to the northern peninsula. Half of all indicator species were shrubs (10 out of 20).

Herbaceous cover in NORTH FLORIDA SHRUBBY WET FLATWOODS was sparse. The most abundant herbs were purple bluestem (*Andropogon glomeratus* var. *glaucopsis*), cinnamon fern (*Osmunda cinnamomea*) and tenangle pipewort (*E. decangulare*). The few herbaceous indicators are typical of wetland habitats, including hooded pitcherplant (*Sarracenia minor*), bushy bluestem (*A. glomeratus* var. *glomeratus*, and *A. glomeratus* var. *hirsutior*), and sphagnum

moss (*Sphagneticola* spp.). Mean species richness of NORTH FLORIDA SHRUBBY WET FLATWOODS was low, likely related to the paucity of herbaceous ground cover.

It may appear that this association represents a fire suppressed variant of wet flatwoods formerly dominated by herbaceous vegetation. However, NORTH FLORIDA SHRUBBY WET FLATWOODS appear compositionally distinct, and included sample sites with histories of recent fire.

UPPER PANHANDLE WET FLATWOODS (7 plots; W5): These sites were restricted to Miocene-aged sediments of the Northern Highlands north of the Cody Scarp in the panhandle (Figure 2-2e). The number of samples comprising this association was small, which in part reflects the rarity of this association. In these sites, UPPER PANHANDLE WET FLATWOODS were situated downslope of PANHANDLE LONGLEAF PINE CLAYHILLS or PANHANDLE XERIC SANDHILLS. In general, this association occupied small areas of mid-slopes and flat terraces.

Fine-textured sediments distinguish soils of UPPER PANHANDLE WET FLATWOODS. Clay percentages of surface soils exceed that of all associations, and silt content was similarly high. These characteristics also typify sub-surface soils. Soil organic matter of UPPER PANHANDLE MESIC-WET FLATWOODS was low compared to other Wetlands associations.

UPPER PANHANDLE WET FLATWOODS have fairly sparse pine canopies comprised of three pine species: longleaf (*P. palustris*), slash (*P. elliotii*) and loblolly (*P. taeda*) pines (mean BAs: 4.55, 3.31, and 2.22 m²/ha respectively). Pond pine was a minor component (*P. serotina*: mean BA .84 m²/ha). Midstory vegetation was sparse, and shrubs were mainly relegated to the understory in my frequently burned sites. Gallberry (*I. glabra*) was by far the most abundant woody understory species, followed by running oak (*Q. pumila*), blue huckleberry (*Gaylussacia frondosa* var. *nana*) and Darrow's blueberry (*V. darrowii*).

UPPER PANHANDLE WET FLATWOODS resembled Mesic Flatwoods associations in aspect and appearance. However, they were floristically similar to Mesic Flatwoods and Wetlands associations. UPPER PANHANDLE MESIC-WET FLATWOODS were notable for their high species richness, particularly of grass and forb species. Dominant grasses included some that are typical upland species, such as little bluestem (*S. scoparium* var. *stoloniferum*), broomsedge bluestem (*A. virginicus*), and Elliott's bluestem (*A. gyrans* var. *gyrans*). Other frequent grasses included typical wetland species: toothache grass (*Ctenium aromaticum*), bushy bluestem (*A. glomeratus* var. *hirsutior*), and arrowfeather threeawn (*Aristida purpurascens* var. *virgata*). Wiregrass was absent. Two frequent grass species were also recognized as indicator species: warty panicgrass (*Panicum verrucosum*) and (*Dichanthelium consanguineum*). Most indicator species were forbs (19 out of 25). Four were members of the family *Asteraceae*, and three were legume species. A large proportion of indicator species (32%) are species with ranges restricted to panhandle or northern peninsula.

PANHANDLE WET FLATWOODS/PRAIRIES (16 plots; W6): This association occurred in the Northern Highlands and Coastal Lowlands of the panhandle, west of the Ochlochnee River basin (Figure 2-2e). Landscape and topographic context was variable; in hillier terrain PANHANDLE WET FLATWOODS/PRAIRIES occupied narrow lower slopes and was associated with Dry Upland sandhills and clayhills. In contrast, nearly treeless PANHANDLE WET FLATWOODS/PRAIRIES of the Coastal Lowlands occupied large areas associated with NORTH FLORIDA MESIC FLATWOODS. Examples of the latter are the wet prairies of the Apalachicola National Forest (Clewell 1971). PANHANDLE WET FLATWOODS AND PRAIRIES soils were low in sand and high in silt, in contrast to the PENINSULA WET PRAIRIES of Central Florida. Organic content was among the lowest of Wetlands associations.

PANHANDLE WET FLATWOODS AND PRAIRIES had sparse or no canopy. A few sites had sparse canopies of slash (*P. elliottii*) and longleaf (*P. palustris*) pines (mean BAs: 2.9 and 1.2 m²/ha respectively). Midstory vegetation was largely non-existent. Low growing gallberry (*I. glabra*) is by far the most abundant understory woody species, followed by the wetland shrub, buckwheat tree (*Cliftonia monophylla*).

Frequently burned PANHANDLE WET FLATWOODS AND PRAIRIES had well-developed, herbaceous dominated ground cover vegetation. Wiregrass (*A. stricta*) and toothache grass (*C. aromaticum*) were ubiquitous dominant grasses; the latter was also identified as an indicator species. Other common and indicator species included many forbs (27 out of 41 species), including bristleleaf chaffhead (*Carphephorus psuedoliatris*), woolly sunbonnets (*Chaptalia tomentosa*), coastalplain yelloweyed grass (*Xyris ambigua*), and savanna meadowbeauty (*Rhexia alifanus*). Pinewoods bluestem (*A. arctatus*) was a distinctive and frequent bunch grass. Twenty four (58%) of the indicator species have distributions restricted to panhandle or northern peninsula.

PANHANDLE SEEPAGE SLOPES (5 plots; W7): These few sites were located in the Northern Highlands and Coastal Lowlands of the western panhandle, situated on lower slopes where soils were usually saturated from seepage (Figure 2-2e). This condition is thought to result from water percolation through sandy soils underlain by impermeable clay or rock hardpans (FNAI 1990). In my sites, PANHANDLE SEEPAGE SLOPES occurred downslope of the drier PANHANDLE WET FLATWOODS AND PRAIRIES association, and farther downslope of Dry Uplands.

Despite the putative existence of clay lenses in the subsoil, sub-soils of PANHANDLE SEEPAGE SLOPES were very low in clay content. It is possible that my soil samples were not deep

enough to detect hardpans. Sub-soil silt was low compared to other panhandle Wetland associations. Surface soils were silty, acidic and high in organic content (although small sample size precluded statistical tests).

Sparse canopies of PANHANDLE SEEPAGE SLOPES consisted of slash (*P. elliotii*) and longleaf (*P. palustris*) pines (mean BAs: 1.9 and 1.3 m²/ha respectively). Understory shrub cover was relatively high and dominated by gallberry (*I. glabra*), evergreen bayberry (*M. caroliniensis*) and large gallberry (*I. coriacea*). The latter two species were indicator species.

Species richness and herbaceous diversity of PANHANDLE SEEPAGE SLOPES is high. Common grasses included several dominant bunch grasses: wiregrass (*A. stricta*), arrowfeather threeawn (*A. palustris*), pinewoods bluestem (*A. arctatus*) and the wetland variant of Elliott's bluestem (*A. gyrans* var. *stenophyllus*). The latter three grass species were also recognized as indicator species. Other frequent indicators of PANHANDLE SEEPAGE SLOPES included many forbs and sedges, such as Texas tickseed (*Coreopsis linifolia*), largeleaf rosegentian (*Sabatia macrophylla*), featherbristle beaksedge (*R. oligantha*), and giant whitetop (*R. latifolia*). A high proportion of indicator species have ranges restricted to North and Panhandle Florida (26 out of 31 species). A few of these are locally abundant rhizomatous species: rush featherling (*Pleea tenuifolia*), coastal false asphodel (*Tofieldia racemosa*), yellow pitcherplant (*Sarracenia flava*), large beaksedge (*R. macra*), and featherbristle beaksedge (*R. oligantha*).

Discussion

Results from this study provide the first comprehensive community classification of pyrogenic pinelands of Florida. Specifically, this classification describes variation among the remnants of natural pineland habitat following the large reduction and fragmentation of a once expansive pineland landscape. Conditions and landscape contexts of sites in this study were

dictated by the non-random distribution and management of natural areas in Florida, which is related to the timing and configuration of human settlement and economic development (Kautz and Cox 2006, Frost 2006). As such, this classification is not representative of pre-settlement conditions of pineland variation and diversity, although it represents the best approximation possible. Although most community associations fall within classifications previously suggested for southeastern U.S. pinelands (FNAI 1990, Peet 2006) this system presents a much greater refinement of recognizable species associations. The described associations are generally defined by geographic region, physiographic landform, local topography, and soil characteristics, providing additional guidance to their identification in the field.

Geographic segregation is pronounced in this floristic classification. Gradients in species composition vary with well known environmental, climatic, and geologic gradients in Florida. The Florida peninsula spans almost seven degrees in latitude, and excluding the Florida keys, spans three bioclimatic life zones including the Warm Temperate Moist Forest of North Florida and the Subtropical Moist Forest of extreme south Florida (Holdridge 1967, Myers 2000). Much of the peninsula falls into a broad “transition zone” between the two. Variation in relative proportions of temperate vs. tropical tree species with latitudinal gradient is a well-known phenomenon (Wunderlin and Hansen 2000). Florida’s complex recent geologic history also underscores panhandle and peninsula differences, which may contribute to variation in contemporary vegetation. Carbonate deposits of marine origin created the limestone platform of the peninsula between 60 to 120 MYBP. In contrast, Miocene deposits of the panhandle were mainly clastic sediments derived from Appalachian erosion and alluvial processes (Randazzo and Jones 1997, Myers 2000). Until 12 to 30 MYBP the Suwannee Strait, an elongate negative structure in southern Georgia and northeastern Florida, separated the two regions (Hull 1962,

Puri and Vernon 1964, Myers 2000). From the late Miocene to recent time, increased clastic deposition, and a series of sea level fluctuations have influenced surface geology and soil development, particularly in the peninsula (Randazzo and Jones 1997, Myers 2000). The distinct panhandle-peninsula trend in floristic variation is correlated with many of these phenomenon, including differences in geologic sedimentation, age of landforms, degree of isolation, and climate variation associated with latitude.

To varying degrees, geographic patterns are similar within the three ecological series (Dry Uplands, Mesic Flatwoods, and Wetlands). Eastern and western analogues of similar edaphic and moisture conditions are nonetheless floristically different (e.g. the xeric sandhills of peninsula vs. panhandle). The Dry Uplands associations display distinct separation east and west of the Ochlochnee River basin. Although the separations are not as pronounced, similar east-west divisions exist among the Wetlands associations. PANHANDLE WET FLATWOODS/PRAIRIES and PANHANDLE SEEPAGE SLOPES of the western panhandle are floristically distinct from other Wetlands associations. None of the Mesic Flatwoods associations is unique to the western panhandle, although there is a north-south separation between NORTH FLORIDA MESIC FLATWOODS and CENTRAL FLORIDA MESIC FLATWOODS/DRY PRAIRIES.

Geographic segregation of floristic groups is influenced by the prominence of plant taxa with distributions restricted to a particular region of the State. Nearly a fifth of all taxa (18.4% of 575) included in this analysis have restricted ranges, while a far smaller proportion (2.8 %) are endemic to Florida. Most restricted range taxa reflect the familiar segregation between panhandle and peninsula Florida, or the distinction between north (panhandle plus northern peninsula) Florida and the central peninsula. Many northerly distributed species reach their southern range limits in the north peninsula; their southern distributional limits closely

approximating the “warm temperate moist forest” bioclimate zone (Holdridge 1967, Myers 2000). Fewer species have Florida distributions either restricted to the panhandle west of the Ochlochnee River basin, or the central Florida peninsula. The large number of taxa restricted to the western panhandle (42 taxa) is consistent with other descriptions of endemism in regions within the East Gulf Coastal Plain (125 endemic taxa reported by Sorrie and Weakley 2001, Sorrie and Weakley 2006). Similarly, a large number of endemics have previously been identified in the Florida peninsula (122 taxa: Sorrie and Weakley 2001, Sorrie and Weakley 2006), where I recorded 31 restricted range taxa. Because I omitted Lake Wales Ridge from the sample region endemic species were likely under-represented in the associations of the Florida peninsula.

Restricted range taxa were frequently selected as indicator species of associations. Not surprisingly, indicator species of panhandle Dry Uplands and Wetlands associations included many restricted-range species, and many of these are endemic to the East Gulf Coastal Plain as reported by Sorrie and Weakley (2001). Taxa restricted to the Florida peninsula were prominent indicators of the XERIC-MESIC FLATWOODS and CENTRAL FLORIDA MESIC FLATWOODS/PRAIRIES. No restricted range indicator species were selected for the single Wetland association of restricted to the peninsula (PENINSULA WET FLATWOODS/PRAIRIES). In contrast, the three Wetland associations restricted to the western panhandle were characterized by numerous indicator species with restricted ranges (UPPER PANHANDLE WET FLATWOODS, PANHANDLE WET FLATWOODS/PRAIRIES, and PANHANDLE SEEPAGE SLOPES).

Comparisons to Other Classifications

This classification of fire-adapted pinelands and associated communities resembles community descriptions of the Florida Natural Areas Inventory (FNAI), both floristically and in

its description of landscape and edaphic conditions. However, my classification augments the FNAI community descriptions in recognition of geographically related floristic variation. The FNAI description of “Sandhill” corresponds to my three Dry Upland associations distinguished by region and edaphic/moisture conditions (PANHANDLE XERIC SANDHILLS vs. PENINSULA XERIC SANDHILLS and NORTH FLORIDA SANDHILLS). Likewise, three current associations (PANHANDLE LONGLEAF PINE CLAYHILLS, PANHANDLE SILTY WOODLANDS and NORTH FLORIDA RICH WOODLANDS) resemble the FNAI “Upland Pine Forest” community. FNAI reports that “Upland Pine Forests” are restricted to the Miocene-aged rolling hills of extreme northern Florida (FNAI 1990). Two of the three aforementioned associations occur outside of the FNAI geographic and landscape description, thus they lack FNAI analogues. My Mesic Flatwoods associations are similar to FNAI community descriptions. However, the two Mesic Flatwoods associations were segregated by region (NORTH FLORIDA MESIC FLATWOODS vs. CENTRAL FLORIDA MESIC FLATWOODS AND DRY PRAIRIES), whereas the FNAI distinguishes mesic flatwoods by canopy conditions (“Mesic Flatwoods” vs. “Dry Prairie”). Cross reference between this classification and FNAI types is less clear for Wetlands associations. I recognized four Wetlands associations that overlap (in whole or part) with the FNAI descriptions for “Wet Flatwoods”, “Wet Prairie” and “Marl Prairie” (the latter perhaps corresponds to CALCAREOUS WET FLATWOODS). The FNAI description of “Bogs” may partially overlap with NORTH FLORIDA SHRUBBY WET FLATWOODS. The PENINSULA WET PRAIRIES resemble FNAI’s “Wet Prairie”, although mine is regionally defined. The MARGINAL PRAIRIES association describes herbaceous vegetation associated with two FNAI lacustrine communities: “Flatwoods/Prairie/Marsh Lake” and “Sandhill Upland Lake”. The FNAI “Seepage Slopes” closely resembles my PANHANDLE SEEPAGE SLOPES association.

My classification and study area represents a subset of the regional treatment of Peet (2007). The Peet classification includes a greater breadth of environmental conditions as well as a larger geographic region. A comparison of the current community associations to associations reported by Peet as present in Florida reveals differences between the two classifications with regard to classification resolution. Geographic segregation is a primary trend in both treatments. My Dry Uplands associations variously correspond to Peet's "Xeric Sand Barrens/Uplands" and "Subxeric Sandy Uplands" groups, which include three and six associations respectively (see Table 2, Peet 2006). My PANHANDLE LONGLEAF PINE CLAYHILLS corresponds to two of Peet's "Silty Uplands" associations (types 3.4.1 and 3.4.2, Peet 2007). The Peet analogues to NORTH FLORIDA RICH WOODLANDS and PANHANDLE FLATWOODS/WOODLANDS are less obvious, perhaps corresponding to other "Silty Uplands" types. My three Mesic Flatwoods associations have 14 counterparts in the Peet treatment. Likewise, my Wetlands associations correspond to nine associations of Peet's "Savannas and Seeps".

The subjective nature of defining partitions likely contributes to differences between the classification typologies. In this study I attempted to minimize subjectivity in sampling design and numerical analysis. The distribution and management of Florida pineland natural areas is non-random and largely influenced by natural area availability (Kautz and Cox 2006, Frost 2006). However, the sampling design stratified by ecoregion and moisture gradient, coupled with large sample size, minimized bias associated with subjective sample selection (Leps and Smilauer 2007). The resulting classification describes variation in the contemporary configuration Florida pinelands in a highly fragmented landscape. This work does not explicitly describe natural variation of pre-settlement conditions. Furthermore, by using an optimization index in conjunction with cluster analysis, I minimized subjectivity associated with cluster

delineations (McCune and Grace 2002). My selection of cut-level in the cluster solution to groups > 3 samples was subjective. However, this limited proliferation of associations, which is highly dependent on sample size (Legendre and Legendre 1998, McCune and Grace 2002).

In conclusion, I developed a classification of fire-dependent pineland communities that is as comprehensive as possible while remaining applicable for management and conservation programs. The provision of indicator species, geographical distributions, and topographic contexts of associations, in addition to their full species lists, will enable identification of associations in the field. This classification system will assist in refining classifications of associations in the greater than 9.6 million acres of non-submerged conservation lands owned and/or managed by local, state, and federal agencies in Florida (over 25% of total land area; FNAI 2007). Descriptions of associations and indicator species will also guide ecological restoration efforts, by assisting the recognition of natural areas degraded from fire suppression or other reasons. Quantitative descriptions based on existing high quality natural areas provide templates for restoration goals and comparisons. Further land acquisitions via the Florida Forever Program and other conservation efforts might benefit from this classification. The present study presents a descriptive vegetation classification based on a comprehensive, systematic, and quantitative inventory of fire-dependent pineland communities as they exist today.

Table 2-1. Means and standard errors (SE) of soil and site variables by community series. Plot number indicated in parentheses. Variables are labeled as in text. Significantly different pairwise comparisons of means ($p < 0.01$) are denoted by dissimilar superscripts and different shading.

Variable	Dry Uplands (130)		Mesic Flatwoods (99)		Wetlands (64)	
	Mean	SE	Mean	SE	Mean	SE
% sand A	93.13 ^b	0.67	96.18 ^c	0.84	88.49 ^a	0.97
% sand B	88.09 ^a	1.08	95.47 ^b	1.35	88.40 ^a	1.50
% silt A	4.29 ^b	0.49	2.52 ^a	0.61	8.39 ^c	0.71
% silt B	7.54 ^b	0.70	2.89 ^a	0.88	7.12 ^b	0.97
% clay A	2.58 ^b	0.36	1.29 ^a	0.45	3.11 ^b	0.52
% clay B	4.37 ^b	0.55	1.64 ^a	0.69	4.47 ^b	0.77
% org	2.86 ^a	0.35	4.82 ^b	0.45	5.69 ^b	0.51
pH	4.75 ^b	0.03	4.53 ^a	0.04	4.52 ^a	0.05

Table 2-2. Untransformed means and standard errors (SE) of soil and site variables by community association. Dissimilar superscripts and shading indicate means that are significantly different ($p < 0.01$). Soil texture variables listed separately for surface (A horizon) and sub-surface (B horizon). Rich = species number / 1000 m²; BA = Basal area m²/ha.

Association	SURFACE SOILS (A)				SUBSOILS (B)																	
	rich	SE rich	BA	SE BA	% sand	SE sand	% silt	SE silt	% clay	SE clay	% sand	SE sand	% silt	SE silt	% clay	SE clay	% org	SE org	pH	SE pH	Ca	SE Ca
Peninsula Xeric Sandhills	68.5 ^a	3.4	8.1 ^a	1.01	96.9 ^b	1.58	1.68 ^a	1.07	1.38 ^a	1.04	96.97 ^a	2.76	1.66 ^a	1.73	1.36 ^a	1.52	4.01 ^b	0.56	4.62 ^a	0.07	570.57 ^b	65.58
North Florida Sandhills	96.2 ^b	2.8	11.4 ^{ab}	0.87	94.9 ^b	1.35	3.5 ^{ab}	0.92	1.53 ^a	0.89	95.16 ^a	2.36	3.28 ^a	1.48	1.54 ^a	1.30	2.96 ^a	0.48	4.76 ^a	0.07	469.17 ^b	56.16
North Florida Rich Woodlands	106.5 ^b	4.8	16.1 ^{cd}	1.44	94.7 ^b	2.34	3.63 ^b	1.59	1.68 ^a	1.54	90.25 ^{ab}	4.09	3.76 ^{ab}	2.57	5.97 ^{bc}	2.25	6.50 ^c	0.83	4.58 ^a	0.11	307.50 ^b	97.27
Panhandle Xeric Xandhills	75.1 ^a	2.8	9.5 ^a	0.85	95.6 ^b	1.33	2.70 ^a	0.90	1.67 ^a	0.88	89.98 ^b	2.45	6.75 ^b	1.53	3.26 ^{ab}	1.35	1.18 ^a	0.47	4.69 ^a	0.04	152.01 ^a	55.25
Panhandle Silty Woodlands	92.1 ^b	3.4	12.8 ^{bc}	1.01	86.8 ^a	1.58	7.40 ^b	1.07	5.8 ^b	1.04	76.67 ^c	2.76	17.00 ^c	1.73	6.32 ^c	1.52	2.02 ^a	0.56	4.78 ^a	0.06	174.38 ^a	65.58
Panhandle Longleaf Pine Clayhills	124.5 ^c	4.2	16.8 ^d	1.27	86.5 ^a	1.98	9.14 ^c	1.34	4.39 ^b	1.30	71.54 ^c	3.46	15.32 ^c	2.17	13.13 ^d	1.90	3.32 ^b	0.70	5.10 ^b	0.11	387.21 ^b	82.21
Xeric-Mesic Flatwoods	59.0 ^a	3.2	5.0 ^a	0.85	96.9 ^b	0.40	1.99 ^a	0.43	1.12 ^a	0.19	96.0 ^b	0.40	2.55 ^a	0.39	1.43 ^a	0.21	4.64 ^a	0.83	4.64 ^b	0.07	458.17 ^b	39.68
North Florida Mesic Flatwoods	71.4 ^b	3.5	10.7 ^b	0.94	95.0 ^a	0.40	3.29 ^a	0.44	1.68 ^b	0.20	94.5 ^a	0.42	3.60 ^a	0.40	1.86 ^b	0.22	5.14 ^a	0.86	4.39 ^a	0.07	247.83 ^a	41.02
Peninsula Mesic Flatwoods/Dry Prairies	72.9 ^b	4.1	2.8 ^a	1.09	96.7 ^{ab}	0.50	2.27 ^a	0.52	1.00 ^a	0.23	95.9 ^b	0.49	2.41 ^a	0.47	1.65 ^{ab}	0.26	4.65 ^a	1.01	4.55 ^{ab}	0.08	413.56 ^b	48.21
Marginal Prairies	49.6 ^a	6.6	5.6 ^a	2.32	89.2 ^{ab}	2.94	7.12 ^b	2.43	3.61 ^b	1.24	89.62 ^{bc}	3.61	3.62 ^a	2.51	6.75 ^c	1.96	7.18 ^a	1.55	4.37 ^{ab}	0.05	212.33 ^a	47.32
Calcareous Wet Flatwoods	125.0 ^{NA}	18.4	17.1 ^{NA}	7.50	96.6 ^{NA}	0.62	2.47 ^{NA}	3.74	0.88 ^{NA}	0.24	93.13 ^{NA}	5.35	3.07 ^{NA}	3.69	3.79 ^{NA}	2.93	5.97 ^{NA}	2.54	5.28 ^{NA}	0.40	1133.25 ^{NA}	563.53
Peninsula Wet Flatwoods/Prairies	69.7 ^b	6.0	2.4 ^a	1.92	95.6 ^b	2.69	3.68 ^{ab}	2.22	0.70 ^a	1.13	94.63 ^c	3.30	3.77 ^a	2.28	1.59 ^a	1.79	6.17 ^a	1.42	4.64 ^b	0.11	424.63 ^b	88.86
North Florida Shrubby Wet Flatwoods	65.7 ^{ab}	6.3	15.7 ^{bc}	1.98	87.8 ^a	2.81	8.43 ^b	2.32	3.73 ^b	1.18	91.12 ^{bc}	3.45	6.11 ^{ab}	2.39	2.76 ^{ab}	1.87	6.88 ^a	1.48	4.22 ^a	0.12	202.11 ^a	51.13
Upper Panhandle Wet Flatwoods	126.4 ^c	7.9	10.9 ^{ac}	2.90	80.9 ^a	3.52	11.05 ^b	2.90	8.08 ^c	1.48	75.50 ^a	4.32	13.52 ^c	3.00	10.97 ^c	2.34	4.23 ^a	1.85	4.62 ^b	0.09	183.25 ^a	23.67
Panhandle Wet Flatwoods/Prairies	78.3 ^b	5.4	4.5 ^a	1.98	84.5 ^a	2.40	12.76 ^{bc}	1.98	2.77 ^{ab}	1.01	82.73 ^{ab}	2.95	12.07 ^{bc}	2.05	5.18 ^{bc}	1.60	3.46 ^a	1.27	4.53 ^b	0.07	124.73 ^a	25.93
Panhandle Seepage Slopes	90.8 ^{NA}	5.1	4.1 ^{NA}	2.20	86.5 ^{NA}	5.50	12.35 ^{NA}	5.29	1.2 ^{NA}	0.36	92.00 ^{NA}	6.18	6.56 ^{NA}	4.26	1.44 ^{NA}	3.38	9.96 ^{NA}	5.92	4.28 ^{NA}	0.04	245.25 ^{NA}	59.50

Table 2-3. Common woody shrubs of midstory and understory strata, listed by association. Code in parentheses correspond to those in Figure 2-2. Mean cover in m²/100 m.

Peninsula Xeric Sandhills (D3)		
Common Name	Scientific Name	Mean cover
Turkey oak	<i>Quercus laevis</i>	14.20
Sand live oak	<i>Quercus geminata</i>	4.27
Saw palmetto	<i>Serenoa repens</i>	1.91
Bluejack oak	<i>Quercus incana</i>	1.71
Panhandle Xeric Sandhills (D4)		
Turkey oak	<i>Quercus laevis</i>	12.08
Dwarf live oak	<i>Quercus minima</i>	3.71
Sand live oak	<i>Quercus geminata</i>	3.10
Saw palmetto	<i>Serenoa repens</i>	3.00
Sand post oak	<i>Quercus margaretta</i>	2.75
Dwarf huckleberry	<i>Gaylussacia dumosa</i>	2.40
Bluejack oak	<i>Quercus incana</i>	2.11
North Florida Sandhills (D2)		
Bluejack oak	<i>Quercus incana</i>	6.72
Turkey oak	<i>Quercus laevis</i>	6.18
Sand post oak	<i>Quercus margaretta</i>	4.81
North Florida Rich Woodlands (D1)		
Saw palmetto	<i>Serenoa repens</i>	11.03
Winged sumac	<i>Rhus copallinum</i>	5.03
Mockernut hickory	<i>Carya alba</i>	4.23
Dwarf waxmyrtle	<i>Myrica cerifera</i> var. <i>pumila</i>	3.01
Sand live oak	<i>Quercus geminata</i>	2.65
Sand post oak	<i>Quercus margaretta</i>	2.43
Panhandle Longleaf Pine Clayhills (D5)		
Sand post oak	<i>Quercus margaretta</i>	5.71
Turkey oak	<i>Quercus laevis</i>	4.89
Running oak	<i>Quercus pumila</i>	4.46
Bluejack oak	<i>Quercus incana</i>	3.51
Darrow's blueberry	<i>Vaccinium darrowii</i>	3.13
Southern red oak	<i>Quercus falcata</i>	2.97
Dwarf huckleberry	<i>Gaylussacia dumosa</i>	2.60
Winged sumac	<i>Rhus copallinum</i>	2.08

Table 2-3 continued.

Panhandle Silty Woodlands (D6)		
Gallberry	<i>Ilex glabra</i>	9.01
Running oak	<i>Quercus pumila</i>	7.45
Saw palmetto	<i>Serenoa repens</i>	6.19
Dwarf live oak	<i>Quercus minima</i>	6.04
Dwarf huckleberry	<i>Gaylussacia dumosa</i>	3.27
Shiny blueberry	<i>Vaccinium myrsinites</i>	2.59
Darrow's blueberry	<i>Vaccinium darrowii</i>	2.48
Blue huckleberry	<i>Gaylussacia frondosa</i> var. <i>nana</i>	1.93
Xeric-Mesic Flatwoods (M1)		
Saw palmetto	<i>Serenoa repens</i>	26.83
Sand live oak	<i>Quercus geminata</i>	9.92
Chapman's oak	<i>Quercus chapmanii</i>	7.90
Myrtle oak	<i>Quercus myrtifolia</i>	5.35
Shiny blueberry	<i>Vaccinium myrsinites</i>	4.18
Fetterbush	<i>Lyonia lucida</i>	3.73
Dwarf live oak	<i>Quercus minima</i>	3.68
North Florida Mesic Flatwoods (M2)		
Gallberry	<i>Ilex glabra</i>	19.49
Saw palmetto	<i>Serenoa repens</i>	17.01
Dwarf live oak	<i>Quercus minima</i>	10.46
Shiny blueberry	<i>Vaccinium myrsinites</i>	6.56
Running oak	<i>Quercus pumila</i>	5.93
Dwarf huckleberry	<i>Gaylussacia dumosa</i>	2.64
Fetterbush	<i>Lyonia lucida</i>	2.45
Central Florida Mesic Flatwoods/Dry Prairies (M3)		
Saw palmetto	<i>Serenoa repens</i>	23.10
Dwarf live oak	<i>Quercus minima</i>	7.40
Gallberry	<i>Ilex glabra</i>	6.72
Fetterbush	<i>Lyonia lucida</i>	5.26
Shiny blueberry	<i>Vaccinium myrsinites</i>	3.84
Dwarf huckleberry	<i>Gaylussacia dumosa</i>	2.15

Table 2-3 continued.

Marginal Prairies (W1)		
Gallberry	<i>Ilex glabra</i>	3.55
Titi	<i>Cyrilla racemiflora</i>	3.24
Sandweed	<i>Hypericum fasciculatum</i>	3.09
Swamp tupelo	<i>Nyssa sylvatica</i> var. <i>biflora</i>	1.94
Peninsula Wet Flatwoods/Prairies (W2)		
Sandweed	<i>Hypericum fasciculatum</i>	4.30
Gallberry	<i>Ilex glabra</i>	3.48
Pond cypress	<i>Taxodium ascendens</i>	2.33
Calcareous Wet Flatwoods (W3)		
Wax myrtle	<i>Myrica cerifera</i>	5.38
Swamp bay	<i>Persea palustris</i>	2.75
Saw palmetto	<i>Serenoa repens</i>	2.28
Red maple	<i>Acer rubrum</i>	2.22
Sweetgum	<i>Liquidambar styraciflua</i>	2.06
North Florida Shrubby Wet Flatwoods (W4)		
Saw palmetto	<i>Serenoa repens</i>	6.41
Large gallberry	<i>Ilex coriacea</i>	5.73
Fetterbush	<i>Lyonia lucida</i>	4.43
Coastal sweetpepperbush	<i>Clethra alnifolia</i>	3.27
Sweetbay magnolia	<i>Magnolia virginiana</i>	3.15
Upper Panhandle Wet Flatwoods (W5)		
Gallberry	<i>Ilex glabra</i>	19.27
Running oak	<i>Quercus pumila</i>	4.52
Blue huckleberry	<i>Gaylussacia frondosa</i> var. <i>nana</i>	1.71
Darrow's blueberry	<i>Vaccinium darrowii</i>	1.61
Panhandle Wet Flatwoods/Prairies (W6)		
Gallberry	<i>Ilex glabra</i>	8.39
Buckwheat tree	<i>Cliftonia monophylla</i>	3.24
Panhandle Seepage Slopes (W7)		
Gallberry	<i>Ilex glabra</i>	13.00
Evergreen bayberry	<i>Myrica caroliniensis</i>	4.55
Large gallberry	<i>Ilex coriacea</i>	1.78

Table 2-4. Indicator species of Dry Uplands and Mesic Flatwoods associations listed in descending order of Indicator Value (IV). Superscripts indicate species with restricted distributions in Florida: ¹western Panhandle, ²north Florida, ³central Florida peninsula, ⁴Florida endemic.

Peninsula Xeric Sandhills (D3)		North Florida Sandhills con't (D2)	
Species	IV	Species	IV
<i>Bulbostylis warei</i>	41.8	<i>Helianthemum carolinianum</i>	31.9
<i>Balduina angustifolia</i>	40.3	<i>Rhynchosia reniformis</i>	31.6
<i>Aristida condensata</i>	35.0	<i>Physalis walteri</i>	28.9
<i>Lechea sessiliflora</i>	33.4	<i>Scutellaria multiglandulosa</i>	28.7
<i>Asimina incana</i> ³	33.2	<i>Piriqueta cistoides ssp. caroliniana</i>	28.6
<i>Triplasis americana</i>	31.0	<i>Dyschoriste oblongifolia</i>	28.4
<i>Opuntia humifusa</i>	29.0	<i>Asclepias verticillata</i>	26.9
<i>Callisia graminea</i>	26.8	<i>Gymnopogon ambiguus</i>	26.9
<i>Carphephorus corymbosus</i> ³	23.3	<i>Eupatorium glaucescens</i>	25.0
<i>Sporobolus junceus</i>	23.2	<i>Lespedeza hirta</i>	25.0
<i>Cnidocolus stimulosus</i>	22.9	<i>Ruellia caroliniensis ssp. ciliosa</i>	23.8
<i>Quercus laevis</i>	22.8	<i>Croton argyranthemus</i>	23.3
<i>Galactia regularis</i>	22.6	<i>Tragia urens</i>	23.3
<i>Tephrosia chrysophylla</i>	21.3		
<i>Sisyrinchium xerophyllum</i>	20.1		
		North Florida Rich Woodlands (D1)	
		Species	IV
		<i>Erythrina herbacea</i>	54.6
		<i>Dichantheium oligosanthes var. oligosanthes</i> ²	46.6
		<i>Eustachys floridana</i>	44.4
		<i>Galium hispidulum</i>	43.2
		<i>Lactuca floridana</i>	41.6
		<i>Cyperus plukenetii</i> ²	41.0
		<i>Rhynchosia cinerea</i> ^{3,4}	37.0
		<i>Aristida lanosa</i> ²	34.7
		<i>Tridens carolinianus</i> ²	34.7
		<i>Sporobolus clandestinus</i>	33.6
		<i>Ageratina aromatica</i> ²	29.6
		<i>Galium pilosum</i>	26.0
		<i>Vitis aestivalis</i>	24.1
		<i>Centrosema arenicola</i> ³	22.5
		<i>Clitoria mariana</i>	22.1
		<i>Habenaria quinqueseta</i>	22.1
		<i>Aristolochia serpentaria</i>	21.5
		<i>Dichantheium commutatum var. ashei</i>	20.4
		<i>Desmodium glabellum</i> ²	20.0
Panhandle Xeric Sandhills (D4)			
Species	IV		
<i>Galactia microphylla</i>	74.7		
<i>Euphorbia floridana</i> ¹	67.8		
<i>Liatris pauciflora var. secunda</i> ¹	35.5		
<i>Cyperus lupulinus ssp. lupulinus</i>	34.6		
<i>Rhynchosia cytisoides</i> ¹	34.2		
<i>Pityopsis aspera</i> ¹	32.1		
<i>Eriogonum tomentosum</i>	28.3		
<i>Commelina erecta</i>	26.8		
<i>Aristida mohrii</i> ²	26.6		
<i>Stylisma patens ssp. patens</i>	23.8		
<i>Liatris chapmanii</i>	23.5		
<i>Tephrosia mohrii</i> ¹	22.9		
<i>Rhynchospora grayi</i>	22.0		
<i>Bulbostylis ciliatifolia</i>	20.6		
North Florida Sandhills (D2)			
Species	IV		
<i>Desmodium floridanum</i>	38.4		
<i>Palafoxia integrifolia</i>	33.8		

Table 2-4 continued.

Panhandle Longleaf Pine Clayhills (D5)		Panhandle Longleaf Pine Clayhills con't (D5)	
Species	IV	Species	IV
<i>Rudbeckia hirta</i>	76.0	<i>Gymnopogon brevifolius</i>	24.6
<i>Acalypha gracilens</i>	63.3	<i>Eupatorium album</i>	24.3
<i>Malus angustifolia</i> ¹	55.9	<i>Dichanthelium sphaerocarpon</i> ²	24.2
<i>Vaccinium stamineum</i> var. <i>stamineum</i>	55.4	<i>Stylodon carneus</i>	24.0
<i>Galactia volubilis</i>	54.4	<i>Tridens carolinianus</i> ²	24.0
<i>Quercus falcata</i>	48.2		
<i>Carya alba</i>	47.1	Panhandle Silty Woodlands (D6)	
<i>Ceanothus americanus</i>	42.7	Species	IV
<i>Desmodium ciliare</i>	42.7	<i>Symphotrichum adnatum</i>	40.2
<i>Desmodium lineatum</i>	42.7	<i>Baptisia simplicifolia</i> ^{1,4}	38.5
<i>Toxicodendron pubescens</i> ²	42.7	<i>Angelica dentata</i> ¹	37.6
<i>Desmodium viridiflorum</i>	39.7	<i>Chrysopsis mariana</i>	32.1
<i>Prunus serotina</i>	39.0	<i>Tragia smallii</i> ²	30.7
<i>Phlox floridana</i> ²	38.2	<i>Phoebanthus tenuifolius</i> ^{1,4}	29.6
<i>Lespedeza repens</i> ²	37.0	<i>Viola septemloba</i>	29.4
<i>Rhynchosia tomentosa</i> ²	36.3	<i>Euphorbia curtisii</i> ²	28.4
<i>Euphorbia discoidalis</i> ¹	35.0	<i>Galactia erecta</i> ²	27.6
<i>Eragrostis spectabilis</i>	34.1	<i>Agalinis divaricata</i> ²	26.2
<i>Cornus florida</i>	32.2	<i>Helianthus radula</i>	25.6
<i>Strophostyles umbellata</i>	31.1	<i>Dalea carnea</i> var. <i>gracilis</i> ¹	22.5
<i>Smilax smallii</i>	30.7	<i>Crotalaria purshii</i>	21.9
<i>Desmodium strictum</i>	30.6	<i>Seymeria cassioides</i>	20.4
<i>Gaura filipes</i> ²	30.5		
<i>Sorghastrum nutans</i>	29.5	Xeric-Mesic Flatwoods (M1)	
<i>Galium pilosum</i>	29.1	Species	IV
<i>Ambrosia artemisiifolia</i>	28.6	<i>Quercus chapmanii</i>	38.1
<i>Eupatorium hyssopifolium</i> ²	28.6	<i>Solidago odora</i> var. <i>chapmanii</i> ³	32.9
<i>Clitoria mariana</i>	27.4	<i>Quercus myrtifolia</i>	26.1
<i>Lobelia puberula</i>	27.3	<i>Galactia elliotii</i>	25.6
<i>Vernonia angustifolia</i>	27.3	<i>Liatris tenuifolia</i> var. <i>quadriflora</i> ³	22.1
<i>Aristolochia serpentaria</i>	26.9	<i>Befaria racemosa</i> ³	19.5
<i>Andropogon gerardii</i> ¹	26.7	<i>Rhynchospora megalocarpa</i>	17.1
<i>Solidago odora</i> var. <i>odora</i>	26.5		
<i>Lechea minor</i>	26.1	North Florida Mesic Flatwoods (M2)	
<i>Ageratina aromatica</i> ²	26.0	Species	IV
<i>Muhlenbergia capillaris</i> var. <i>trichopodes</i> ²	25.5	<i>Xyris caroliniana</i>	23.7
<i>Tephrosia spicata</i>	25.5	<i>Sporobolus floridanus</i> ²	19.0
<i>Salvia azurea</i>	25.4	<i>Quercus minima</i>	18.4
<i>Rubus cuneifolius</i>	24.8	<i>Kalmia hirsuta</i> ²	17.5

Table 2-4 continued.

Central Florida Mesic Flatwoods/Dry Prairies (M3)	
Species	IV
<i>Hypericum reductum</i>	62.3
<i>Polygala setacea</i>	57.4
<i>Eleocharis baldwinii</i>	50.4
<i>Rhexia nuttallii</i>	43.0
<i>Fimbristylis puberula</i>	41.5
<i>Aristida spiciformis</i>	38.2
<i>Asimina reticulata</i> ^{3,4}	37.8
<i>Rhynchospora fernaldii</i>	37.5
<i>Xyris flabelliformis</i>	36.4
<i>Lyonia fruticosa</i>	34.9
<i>Lechea torreyi</i>	34.3
<i>Lachnocaulon beyrichianum</i> ³	34.0
<i>Dichantherium chamaelonche</i>	33.3
<i>Syngonanthus flavidulus</i>	32.7
<i>Xyris brevifolia</i>	32.6
<i>Polygala rugelii</i> ^{3,4}	32.2
<i>Asclepias pedicellata</i>	31.9
<i>Aristida purpurascens</i> var. <i>tenuispica</i>	30.7
<i>Oldenlandia uniflora</i>	30.7
<i>Gymnopogon chapmanianus</i> ³	29.0
<i>Gratiola hispida</i>	25.8
<i>Drosera brevifolia</i>	25.4
<i>Schizachyrium stoloniferum</i> ³	24.5
<i>Dichantherium sabulorum</i> var. <i>thinium</i>	23.8
<i>Andropogon brachystachyus</i> ³	22.6
<i>Hypericum tetrapetalum</i>	22.6
<i>Lygodesmia aphylla</i>	21.7

Table 2-5. Indicator species of Wetlands associations. Indicator values (IV) listed in descending order for each association. Superscripts same as Table 2-4.

Marginal Prairies (W1)		Peninsula Wet Flatwoods/Prairies (con't)	
Species	IV	Species	IV
<i>Eupatorium leptophyllum</i>	49.3	<i>Andropogon capillipes</i> (wetland variant)	43.9
<i>Panicum hemitomon</i>	41.1	<i>Coelorachis rugosa</i>	43.7
<i>Ludwigia suffruticosa</i>	33.5	<i>Amphicarpum muehlenbergianum</i>	43.1
<i>Cephalanthus occidentalis</i>	30.7	<i>Sabatia grandiflora</i>	42.2
<i>Rhexia mariana</i> var. <i>mariana</i>	28.8	<i>Andropogon gyrans</i> var. <i>stenophyllus</i>	40.0
<i>Xyris difformis</i> var. <i>curtissii</i> ²	28.8	<i>Fuirena scirpoidea</i>	40.0
		<i>Hyptis alata</i>	38.4
		<i>Hypericum myrtifolium</i>	37.7
North Florida Shrubby Wet Flatwoods (W4)			
Species	IV	Species	IV
<i>Persea palustris</i>	45.8	<i>Pluchea rosea</i>	36.7
<i>Osmunda cinnamomea</i>	44.3	<i>Eragrostis elliottii</i>	36.6
<i>Andropogon glomeratus</i> var. <i>hirsutior</i>	41.4	<i>Scleria baldwinii</i>	36.4
<i>Nyssa biflora</i>	37.0	<i>Bigelovia nudata</i>	36.2
<i>Vaccinium virgatum</i>	36.1	<i>Rhynchospora tracyi</i>	33.4
<i>Andropogon glaucopsis</i>	35.7	<i>Viola lanceolata</i>	32.1
<i>Andropogon glomeratus</i> var. <i>glomeratus</i>	34.8	<i>Eriocaulon decangulare</i>	31.4
<i>Viburnum nudum</i>	32.3	<i>Centella erecta</i>	30.1
<i>Photinia pyrifolia</i>	32.2	<i>Lobelia glandulosa</i>	29.7
<i>Sphagneticola</i> sp.	28.6	<i>Rhynchospora filifolia</i>	28.0
<i>Rhexia virginica</i> ²	28.1	<i>Eriocaulon compressum</i>	26.9
<i>Rhexia petiolata</i>	26.7	<i>Pluchea foetida</i>	25.8
<i>Ilex coriacea</i>	26.4	<i>Scleria muehlenbergii</i>	25.1
<i>Gordonia lasianthus</i>	25.6	<i>Ludwigia linearis</i>	25.0
<i>Sarracenia minor</i>	24.9	<i>Eupatorium mohrii</i>	24.6
<i>Vaccinium fuscatum</i>	24.3	<i>Scleria georgiana</i>	24.1
<i>Rhynchospora fascicularis</i>	24.0	<i>Xyris difformis</i> var. <i>floridana</i>	23.4
<i>Lyonia lucida</i>	22.7	<i>Rhexia mariana</i> var. <i>exalbida</i>	22.8
<i>Carex glaucescens</i>	22.2	<i>Helenium pinnatifidum</i>	22.1
<i>Clethra alnifolia</i> ²	22.0	<i>Iva microcephala</i>	21.3
		<i>Schizachyrium rhizomatum</i>	21.2
		<i>Panicum rigidulum</i> var. <i>pubescens</i>	21.1
Peninsula Wet Flatwoods/Prairies (W2)		Calcareous Wet Flatwoods (W3)	
Species	IV	Species	IV
<i>Oxypolis filiformis</i>	81.1	<i>Asclepias lanceolata</i>	100.0
<i>Dichantherium erectifolium</i>	71.4	<i>Panicum rigidulum</i> var. <i>rigidulum</i>	83.6
<i>Proserpinaca pectinata</i>	57.9	<i>Helenium pinnatifidum</i>	77.9
<i>Gratiola ramosa</i>	56.5	<i>Phyla nodiflora</i>	70.7
<i>Coreopsis floridana</i>	52.0	<i>Cirsium nuttallii</i>	67.9
<i>Ludwigia linifolia</i>	50.6	<i>Rhynchospora colorata</i>	65.6
<i>Xyris elliottii</i>	48.7	<i>Ludwigia microcarpa</i>	64.3
<i>Panicum tenerum</i>	47.4	<i>Sabal palmetto</i>	60.3
<i>Hypericum fasciculatum</i>	44.8	<i>Dichantherium dichotomum</i> var. <i>nitidum</i>	58.3
<i>Aristida palustris</i>	44.6		

Table 2-5 continued.

Calcareous Wet Flatwoods (con't)		Upper Panhandle Wet Flatwoods (con't)	
Species	IV	Species	IV
<i>Xyris jupicai</i>	55.6	<i>Diodia virginiana</i>	29.8
<i>Cyperus polystachyos</i>	54.1	<i>Polygala nana</i>	29.2
<i>Rhynchospora divergens</i>	46.8	<i>Helianthus angustifolius</i>	27.9
<i>Hyptis alata</i>	44.4	<i>Eupatorium leucolepis</i> ²	27.2
<i>Erechtites hieraciifolia</i>	42.3	<i>Andropogon glomeratus</i> var. <i>hirsutior</i>	23.8
<i>Rhynchospora perplexa</i> ²	41.2	<i>Linum medium</i>	23.6
<i>Ludwigia curtissii</i>	41.1	<i>Tephrosia spicata</i>	23.5
<i>Saccharum giganteum</i>	40.9	<i>Gratiola pilosa</i>	23.4
<i>Parthenocissus quinquefolia</i>	40.6	<i>Crotalaria purshii</i>	23.3
<i>Cyperus haspan</i>	40.4	<i>Panicum verrucosum</i>	23.1
<i>Rhynchospora globularis</i>	38.8	<i>Rhexia mariana</i> var. <i>exalbida</i>	23.1
<i>Andropogon glomeratus</i> var. <i>pumilus</i>	37.4	<i>Eupatorium rotundifolium</i>	22.1
<i>Rhynchospora microcarpa</i>	37.3	<i>Gymnopogon brevifolius</i>	21.7
<i>Setaria parviflora</i>	35.6	<i>Scutellaria integrifolia</i>	21.5
<i>Mecardonia acuminata</i>	34.9		
<i>Juncus roemerianus</i>	34.1	Panhandle Wet Flatwoods/Prairies (W6)	
<i>Sacciolepis indica</i>	34.1	Species	IV
<i>Cladium mariscus</i> ssp. <i>jamaicense</i>	31.6	<i>Coreopsis linifolia</i> ²	72.3
<i>Osmunda regalis</i>	29.8	<i>Carphephorus pseudoliatris</i> ¹	70.8
<i>Proserpinaca pectinata</i>	29.7	<i>Helianthus heterophyllus</i> ¹	61
<i>Bidens mitis</i>	29.2	<i>Drosera filiformis</i> ¹	50
<i>Hypericum cistifolium</i>	28.3	<i>Eurybia chapmanii</i> ²	50
<i>Lobelia glandulosa</i>	27.8	<i>Lophiola aurea</i>	50
<i>Muhlenbergia capillaris</i> var. <i>capillaris</i>	27	<i>Andropogon arctatus</i>	46.7
<i>Mitreola sessilifolia</i>	26.7	<i>Scleria pauciflora</i> var. <i>caroliniana</i>	45.5
<i>Iva microcephala</i>	26.1	<i>Xyris baldwiniana</i> ²	45.5
		<i>Rhexia lutea</i> ²	42.6
		<i>Ilex myrtifolia</i> ²	42.3
Upper Panhandle Wet Flatwoods (W5)		<i>Polygala cruciata</i>	41.7
Species	IV	<i>Smilax laurifolia</i>	40
<i>Hypericum setosum</i>	61.4	<i>Eryngium integrifolium</i> ²	37.5
<i>Pycnanthemum flexuosum</i> ¹	57.1	<i>Pleea tenuifolia</i> ¹	37.5
<i>Rhododendron canescens</i> ²	53.5	<i>Chaptalia tomentosa</i>	37.2
<i>Dichantheium consanguineum</i>	52.3	<i>Xyris ambigua</i>	35.3
<i>Desmodium tenuifolium</i>	39.1	<i>Sarracenia flava</i> ²	34.8
<i>Rhynchospora debilis</i> ²	38.7	<i>Eupatorium leucolepis</i> ²	34.7
<i>Hibiscus aculeatus</i> ²	35.9	<i>Pityopsis oligantha</i> ¹	34.1
<i>Elephantopus nudatus</i> ²	34.7	<i>Asclepias connivens</i>	33.4
<i>Solidago stricta</i>	32.6	<i>Gaylussacia mosieri</i> ²	32.2
<i>Agalinis georgiana</i> ¹	31.6	<i>Rhynchospora latifolia</i>	31.6
<i>Lespedeza capitata</i> ¹	30		

Table 2-5 continued

Panhandle Wet Flatwoods/Prairies (con't)		Panhandle Seepage Slopes (con't)	
Species	IV	Species	IV
<i>Rhynchospora baldwinii</i>	31.2	<i>Morella caroliniensis</i>	36.3
<i>Tofieldia racemosa</i> ²	31.2	<i>Hypericum brachyphyllum</i>	34.1
<i>Cliftonia monophylla</i> ²	31.1	<i>Tofieldia racemosa</i> ²	34.1
<i>Morella caroliniensis</i>	31.1	<i>Rhexia lutea</i> ²	33.5
<i>Dichantherium leucothrix</i>	31.0	<i>Zigadenus glaberrimus</i> ¹	33.4
<i>Rhexia alifanus</i>	30.7	<i>Dichantherium longiligulatum</i>	33.1
<i>Lobelia brevifolia</i> ¹	30.4	<i>Drosera filiformis</i> ¹	32.7
<i>Anthraenantia rufa</i> ²	30.2	<i>Oxypolis filiformis</i>	32.0
<i>Eurybia eryngiifolia</i> ¹	30.2	<i>Andropogon gyrans</i> var. <i>stenophyllus</i>	31.3
<i>Erigeron vernus</i>	30.1	<i>Eleocharis tuberculosa</i>	31.2
<i>Nyssa ursina</i> ^{1,4}	30.0	<i>Fuirena squarrosa</i> ²	31.2
<i>Rhynchospora chapmanii</i>	29.7	<i>Magnolia virginiana</i>	31.1
<i>Oxypolis ternata</i> ¹	28.2	<i>Sarracenia flava</i> ²	27.9
<i>Aletris</i> sp.	27.5	<i>Balduina uniflora</i> ²	27.5
<i>Andropogon mohrii</i> ¹	27.0	<i>Rhynchospora corniculata</i>	27.5
<i>Ctenium aromaticum</i>	27.0	<i>Anthraenantia rufa</i> ²	24.5
<i>Aristida simpliciflora</i> ²	26.5	<i>Xyris scabrifolia</i> ¹	24.5
<i>Sarracenia psittacina</i> ²	25.8	<i>Gaylussacia mosieri</i> ²	23.0
<i>Liatris spicata</i>	25.2	<i>Liatris spicata</i>	22.2
<i>Verbesina chapmanii</i> ^{1,4}	25.0		
Panhandle Seepage Slopes (W7)			
Species	IV		
<i>Sabatia macrophylla</i> ²	88.9		
<i>Rhynchospora oligantha</i> ²	81.9		
<i>Arnoglossum ovatum</i>	76.8		
<i>Juncus trigonocarpus</i> ¹	68.9		
<i>Pleea tenuifolia</i> ¹	54.5		
<i>Rhynchospora macra</i> ²	54.3		
<i>Symphyotrichum lateriflorum</i> var. <i>lateriflorum</i>	54.3		
<i>Rhynchospora latifolia</i>	50.0		
<i>Sarracenia leucophylla</i> ¹	49.4		
<i>Lophiola aurea</i>	49.2		
<i>Xyris difformis</i> var. <i>difformis</i> ²	46.2		
<i>Panicum rigidulum</i> var. <i>combsii</i>	45.5		
<i>Aristida palustris</i>	44.2		
<i>Coreopsis linifolia</i> ²	42.7		
<i>Eryngium integrifolium</i> ²	39.9		
<i>Andropogon arctatus</i>	37.0		
<i>Sarracenia psittacina</i> ²	36.8		

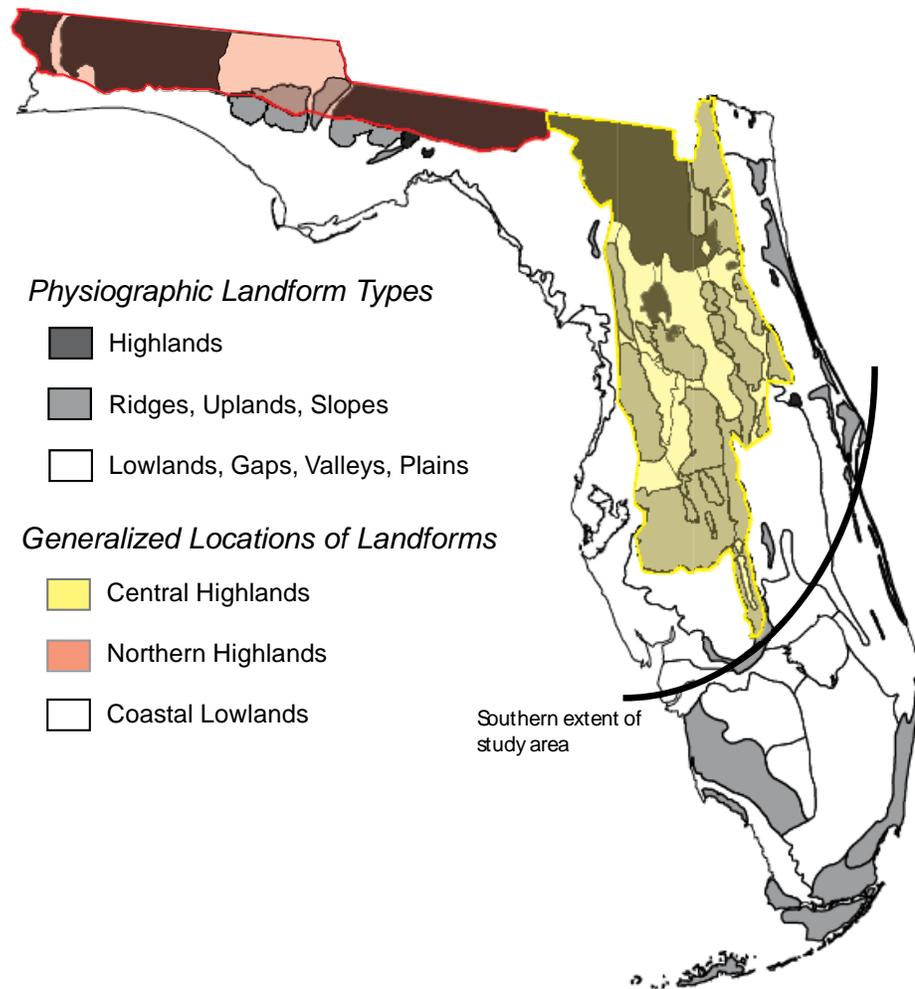


Figure 2-1. Physiographic landforms modified from Puri and Vernon (1964). Colored shading denotes three “generalized landforms” which separate Highlands from Lowlands, and Northern Highlands (Clastic sediments) from Central Highlands (part of the carbonate peninsular platform). Shaded regions indicate primary landforms denoted by landform type. Approximate southern boundary of study region is shown.

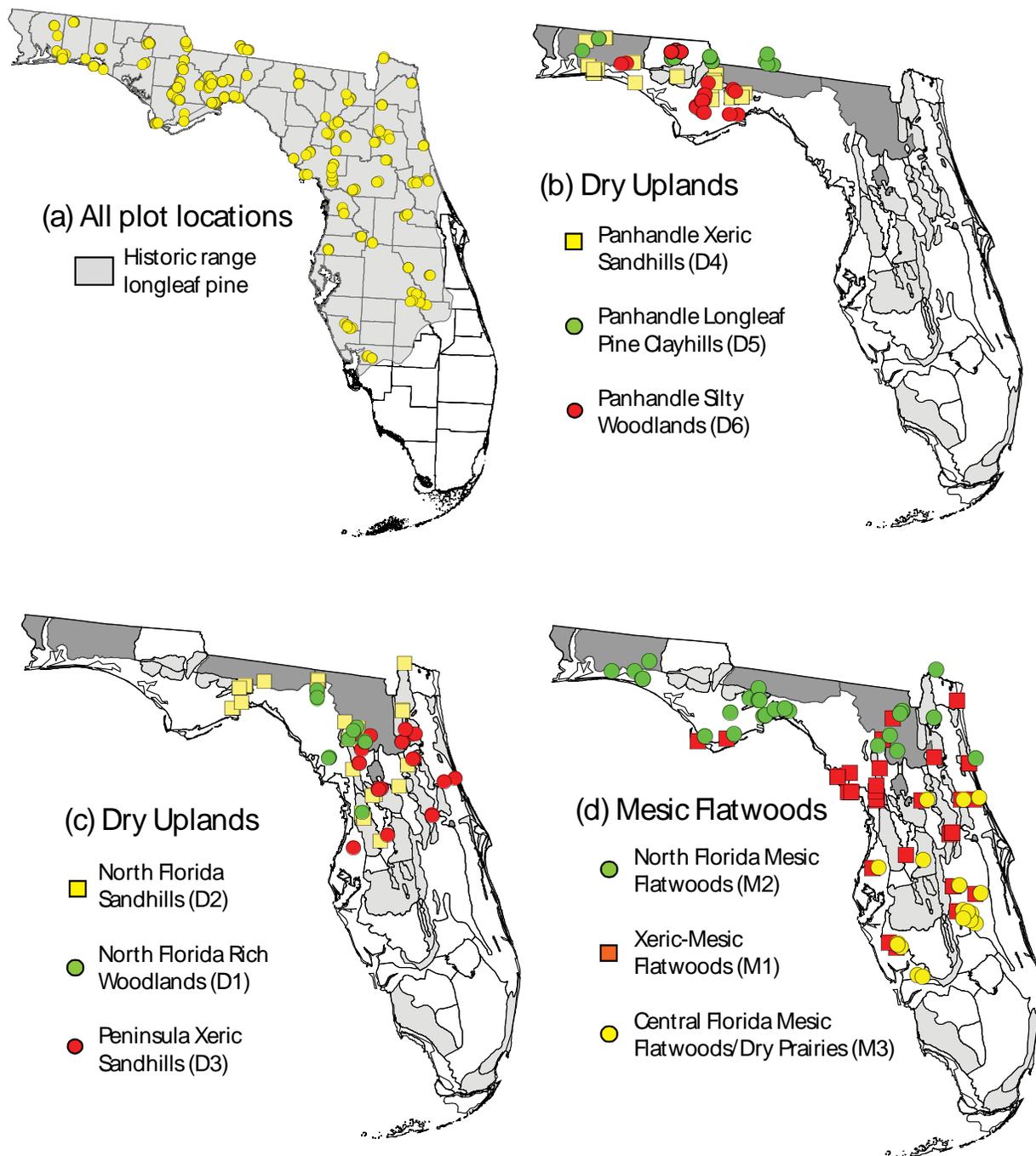


Figure 2-2. Plot locations indicated by association. (a) Historic range of longleaf pine plus all plot locations (yellow dots). Figures (b) through (f) show plot locations by community association and primary landform types (Puri and Vernon 1964). Community labels (in parentheses) correspond to Figure 2-3.

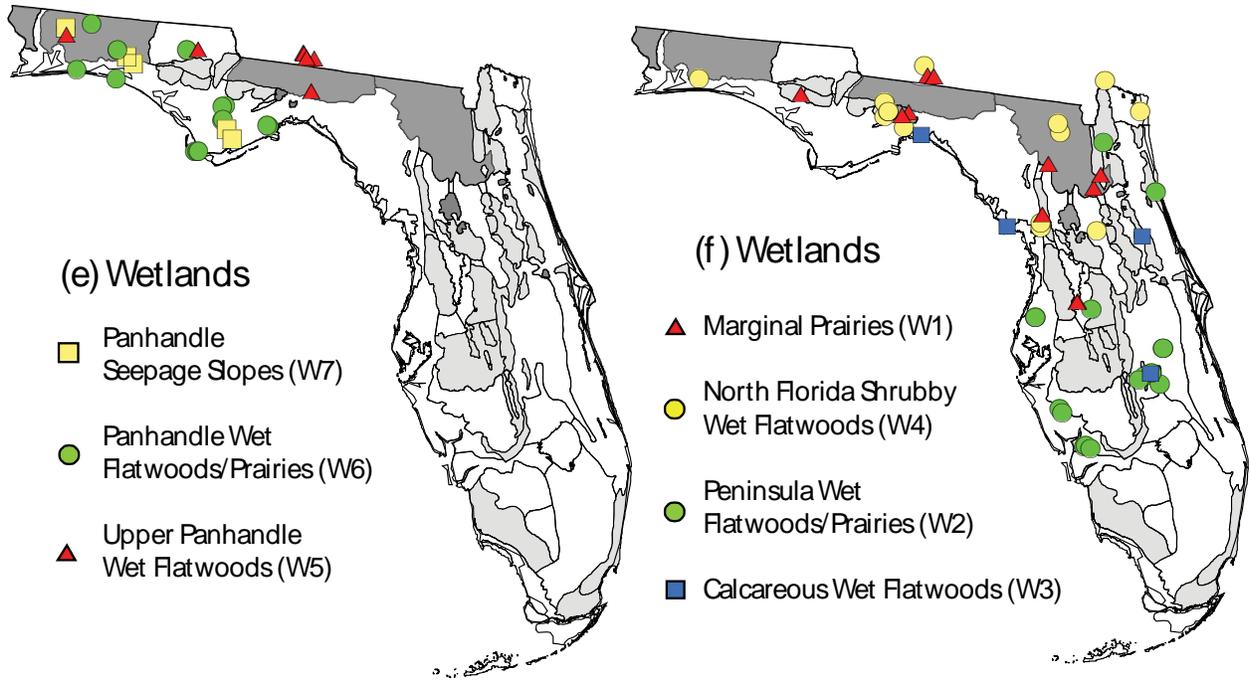
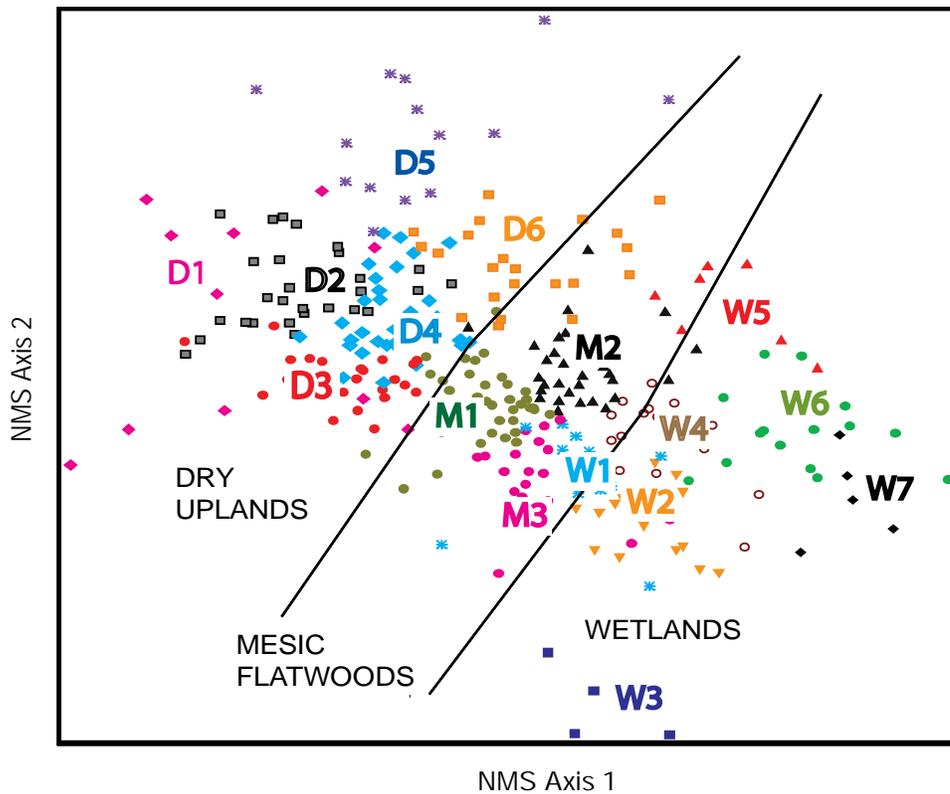


Figure 2-2 continued.



- D1 North Florida Rich Woodlands (11)
- D2 North Florida Sandhills (31)
- D3 Peninsula Xeric Sandhills (22)
- D4 Panhandle Xeric Sandhills (31)
- D5 Panhandle Longleaf Pine Clayhills (14)
- D6 Panhandle Silty Woodlands (22)

- M1 Xeric-Mesic Flatwoods (36)
- M2 North Florida Mesic Flatwoods (30)
- M3 Central Florida Mesic Flatwoods/Dry Prairies (22)

- W1 Marginal Prairies (11)
- W2 Peninsula Wet Flatwoods/Prairies (16)
- W3 Calcareous Wet Flatwoods (4)
- W4 North Florida Shrubby Wet Flatwoods (15)
- W5 Upper Panhandle Wet Flatwoods (7)
- W6 Panhandle Wet Flatwoods/Prairies (16)
- W7 Panhandle Seepage Slopes (5)

Figure 2-3. Two dimensional NMS ordination of 293 samples. Lines separate samples into three community series, and colored symbols denote association from K-means cluster analysis. Plot number per association noted in parentheses. Percent variation of original distance matrix represented by NMS ordination: Axis 1 $r^2 = 0.54$, Axis 2 $r^2 = 0.29$. Stress = 14.78.

CHAPTER 3
GEOGRAPHIC, ENVIRONMENTAL AND REGIONAL VARIATION IN FLORISTIC
COMPOSITION OF FLORIDA PYROGENIC PINELANDS

Introduction

Natural variability of plant communities is shaped by complex interactions of biotic and abiotic factors. Models of “abiotic controls” (i.e. environmental control models) emphasize influences of environmental gradients, resources limitations, and niche specialization (Whittaker 1956, Bray and Curtis 1957, Hutchinson 1957, Peet and Loucks 1977, Platt and Weis 1977, Tilman 1994). In general, these models include local and regional processes which influence species coexistence and distributions (e.g. niche assembly, limited resource availability, environmental filters to species assembly, environmentally determined species pools). In addition, natural disturbances are considered environmental influences, particularly those related to density-independent processes (i.e. fire, hurricanes). Conversely, biotic control models of community structure emphasize mechanisms unrelated to environmental determinants, e.g. dispersal limitation, speciation and extinctions, competition, and herbivory. At its extreme, biotic control theory states that community structure is governed strictly by dispersal limitation and demographic stochasticity independent of local environmental influences (Hubbell and Foster 1986, Bell 2001, Hubbell 2001).

The relative importance of biotic versus abiotic factors in structuring plant communities is a subject of much recent debate (see Legendre et al. 2005). Recent models spatially explicit models of community structure have suggested the relative importance of both (Borcard and Legendre 1994, Okland et al. 2003, Tuomisto et al. 2003, Svenning et al. 2004). Spatial autocorrelation in community composition is cited as evidence of biotic control models (Hubbell and Foster 1986, Hubbell 2001, Condit et al. 2002). However, environmental variables themselves may be spatially structured, and spatial autocorrelation of community structure may

be mis-interpreted if environmental-spatial relationships are not considered (Borcard and Legendre 1994, Legendre and Legendre 1998, Legendre et al. 2005). In addition, inferred environmental-species relationships may be biased in models that fail to include spatial trends (Legendre and Fortin 1989). This underscores the need for spatially explicit models of species composition and diversity, in which spatial autocorrelation and spatially structure environmental variation can be quantified (Borcard et al. 1992, Legendre and Legendre 1998, Legendre et al. 2005). This approach allows formulation of hypotheses concerning the relative importance of underlying mechanisms that influence community structure.

The relative influence of ecological determinates varies over different spatial and temporal scales. Recent ecological theory supported by ecological observation suggests that, with regard to relative importance as determinants of species composition and diversity, regional factors and historic processes are comparable to local scale factors (Ricklefs 1987, Cornell and Lawton 1992, Collins et al. 2002). Processes related to historical biogeography, paleogeology and recent land use history have been recognized as potential influencers of contemporary community patterns (Okland et al. 2003, Graae et al. 2004, Svenning et al. 2004, Svenning and Skov 2005). Regional influences of local species diversity may be a function of distinct species pools (the “species pool effect”), in response to differential biogeographic and evolutionary histories (Zobel 1992, 1997, Grace et al. 2000).

Natural disturbance and local environmental gradients influence local-scale community structure of pyrogenic pineland vegetation of the Southeastern Coastal Plain. Studies of community composition, diversity, and species’ response underscore the influence of environmental determinants, including topography-moisture and soil properties (Kirkman et al. 2001, Drewa and Platt 2002a, Peet et al. 2003) and fire (Platt et al. 1988a, White et al. 1991, Platt

1999, Glitzenstein et al. 2003). Fire affects environmental conditions vis-à-vis regulation of limiting resources such as available soil nutrients and light (Christensen 1977, Mitchell et al. 1999, Kirkman et al. 2001). In addition, fire affects competitive dynamics, particularly that between woody and herbaceous vegetation (Streng et al. 1993). Biotic determinants of pineland species coexistence are less well known in the Coastal Plain. However, there is some evidence that dispersal limitation regulates plant diversity in temperate grasslands elsewhere.

Despite the relative wealth of research regarding local patterns and processes, little is known about regional scale environmental-community relationships in Coastal Plain pinelands and the interplay between regional and local scale relationships. Descriptions of grassland diversity usually involve meso-scale regions < 1000 ha in size (Walker and Peet 1983, Tilman 1994, Grace et al. 2000, Weiher et al. 2004). In addition to high diversity linked to local environmental gradients, Florida's pyrogenic pinelands are notable for their regional floristic diversity and high concentrations of endemic and restricted-range species (James 1961, Walker and Peet 1983, Myers 1990, Peet and Allard 1993, Myers 2000, Sorrie and Weakley 2002). These observations have led to predictions of environmental controls of community composition that include regional and local factors (Peet and Allard 1993, Grace and Pugsek 1997, Kirkman et al. 2001), as well as historical influences (Ricklefs 1987, Zobel 1992).

In this study, I present a model of variability in species composition and diversity of pyrogenic pinelands. Specifically, environment-composition variation was analyzed in a spatially explicit model, allowing quantification of environmental variation that is spatially structured and spatially independent, plus the spatial component of variation that is unrelated to measured environmental variables. This allowed formation of hypotheses concerning the mechanisms controlling landscape vegetation patterns. Furthermore, I present hypotheses

regarding scales of influence of different environmental factors and historical processes. Finally, I modified the spatially explicit model to include a generalized ecoregion model based on those presently used in conservation efforts. The ecoregion model represents of regional differences of biogeography and paleogeography. To develop these models, I used a large dataset of pineland vegetation samples collected over a broad range of geography and environmental conditions. Models based on these descriptive data were intended to generate hypotheses concerning variation of relict pineland natural areas in a highly fragmented landscape of heterogeneous land use.

Methods

Study Region

The study area includes the Florida Panhandle and most of central and northern Peninsular Florida, approximating the current range of longleaf pine. This area includes roughly nine million ha of the northern two-thirds of the state, extending approximately 480 km south from the Georgia state border (approximately 31° 00') to a southern boundary extending from approximately 26° 70' on the west coast to 28° 80' on the east coast. This southern boundary approximates southern extent of the “warm temperate moist forest” bioclimate zone (Holdridge 1967). The study region extends westward to approximately 87° 30' and eastward to the Atlantic coast (approximately 80° 00').

Florida is characterized by a humid subtropical climate. In general, mean temperature and daily radiation increase with decreasing latitude. Mean annual maximum temperatures range from 25° C in the western panhandle to 29° C in interior peninsular Florida, and minimum temperatures and shortwave radiation vary likewise southward (13 to 17 ° C, and 345 to 361 MJ/m²/day (Fernald 1981, Thornton et al. 1999). Average annual rainfall is highest in the

western panhandle (173 cm/year) and declines farther east and south, reaching its lowest point in the central peninsula (approximately 124 cm/year; Fernald 1981). The distribution of rainfall varies from northwest to southeast; winter and spring months are drier in peninsular Florida, with more pronounced rainfall during the summer months. Rainfall is more evenly distributed throughout the year in northwest Florida, with peaks during the late winter and summer months (Chen and Gerber 1990).

The study region in Florida encompasses a wide range of edaphic conditions. Soils range from droughty coarse sands to poorly drained wetland mucks with high organic content. Entisols are common in the well-drained uplands of panhandle and north Florida (Puri and Vernon 1964, Myers 1990). Older and more weathered Ultisols and Alfisols are common in these regions and are typically contain higher concentrations of fine textured sediments such as clay and silt (Myers and Ewel 1990, Myers 2000). Sandy, acidic spodosols are typical of upland woodlands in coastal and peninsular regions. These infertile mineral soils have subsurface accumulations of organic matter. Histosols with large accumulations of organic matter are common to poorly drained wetlands (Brady and Weil 2000).

Vegetation and Environmental Data

Sample site selection and field methods are described in detail in Chapter 2. In brief, the study area was stratified into 19 regions based on similarity of physiography, geology, soils, climate, and historic vegetation maps (Fenneman 1938, Puri and Vernon 1964, Davis 1967, Fernald 1981, Brooks 1982, Bailey et al. 1994, Griffith et al. 1994). Sample sites were selected across regions in roughly equal numbers. Sample sites were subjected to rigorous selection criteria which precluded those without native pineland vegetation with recent history of fire.

Sites degraded from anthropomorphic impact, fire suppression, and/or invasive species were rejected.

At each site, three or four zones were delineated relative to perceived gradients of topographic-moisture conditions and change in plant species composition. A single 1000 m² plot was randomly placed in each zone, and all vascular plant taxa were recorded as they were encountered in a series of four nested sub-plots (plot areas: 0.01, 0.1, 1, and 10 and 100 m²). Aerial cover in the 100 m² plots was estimated by cover classes and averaged (by midpoint). Species encountered in the remainder of the 1000 m² area were assigned nominal cover estimates.

All plots were sampled during the late summer through early winter (August-December) over a four year period (2000 – 2004). Taxonomic nomenclature generally follows Kartesz (1999). In field and herbarium plant identification I made frequent use of (Godfrey and Wooten 1979, Godfrey and Wooten 1981, Clewell 1985, Godfrey 1988, Wunderlin 1998, Weakley 2002). The vast majority of taxa were identified to species or variety; low resolution taxa (family or genus) were omitted from analysis unless identification was consistent throughout the dataset. The term “species” is used throughout to refer to the lowest recognized taxonomic group.

Surface and sub-surface soil samples were collected for nutrient and texture analysis. Four surface soil samples were collected from the upper 10 cm of mineral soil, and a single sub-surface sample was collected from approximately 50 cm below surface. Dried samples were analyzed at Brookside Labs in New Knoxville, Ohio. Nutrient analyses was performed via Mehlich III extractant, an analytical procedure used for routine soil testing attempts to estimate the amount of soil nutrients available to the plant during its growing season (Mehlich 1984).

Specific soil nutrient measurements were: total cation exchange capacity (meq/100g), pH, estimated nitrogen release (N, ppm), extractable phosphorous (P, ppm), exchangeable cations in ppm (Ca, Mg, K, Na), extractable micro-nutrients in ppm (B, Fe, Mn, Cu, Zn, Al), soluble sulfur (S) and bulk density. Percent organic matter was determined by loss-on-ignition. Texture analysis quantified percent sand, silt, and clay of surface and sub-soil samples.

Climate and elevation data were obtained for each geographic plot location. I downloaded extrapolated weather parameters for specific locations from the DayMet climatological model, available online (www.daymet.org). The Daymet model uses weather station and elevation data to produce smoothed parameter estimates on a 1 km gridded surface over the conterminous United States (Thornton et al. 1999). Daily parameter values were available for an eighteen year period between 1980 and 1997. I calculated annual means and standard deviations for the following: daily maximum air temperature, daily minimum air temperature, daily average air temperature, total daily precipitation, and total daily shortwave radiation. I downloaded elevation estimates for each geographic plot location from the HYDRO 1K North America DEM model webpage provided by the U.S. Geological Survey (http://edc.usgs.gov/products/elevation/gtopo30/hydro/na_dem.html). Elevation values were derived from a digital elevation model with 1 km resolution.

Numerical Data Assembly and Analysis

The response data matrix was assembled from species cover data from 270 samples. Cover values for pine species (genus *Pinus*) were omitted from this the data matrix, although other woody species cover values were retained. Species with fewer than three occurrences were deleted (McCune and Grace 2002).

Species data were relativized to maximum species values and were transformed using a Hellinger distance measure. When used in conjunction with Euclidean distance metrics and linear ordination, the Hellinger transformation affects adequate representation of complex species data without the problems associated with species weighting (i.e. chi-square distance based methods; (Legendre and Gallagher 2001, Legendre et al. 2005).

I assembled four data matrices representing groups of potential explanatory variables for statistical modeling. Collectively, these represent environmental and spatial explanatory factors. The first, referred to as the *edaphic variable matrix* (EVM), initially included 24 soil descriptors (listed above) and two variables describing local topography and elevation. Variable “topo” was a subjectively assigned descriptor of local topographic position relative to surrounding landscape (value 1 to 4). The elevation (“elev”) variable was the actual plot elevation derived from the U.S.G.S. digital elevation model.

The second matrix was the *climate variable matrix* (CVM). It included means and standard deviations calculated from the five DayMet parameter values (listed above). In addition, I calculated means and standard deviations for total precipitation and daily shortwave radiation for the growing season only (values from March 15 – October 31). A total of 14 climate variables were included as potential explanatory descriptors in the initial CVG.

When necessary, soil, topographic, and climate environmental variables were transformed to approximate normal distributions. Soil variables measured in ppm were log transformed. Logit transformations were applied to proportional data (Tabachnick and Fidell 1996). Because of the varying scales and ranges of soils and climate variables, all EVM and CVM variables were standardized to z-scores, expressed as standard deviations from the mean (Tabachnick and Fidell 1996, Legendre and Legendre 1998).

The third matrix of potential explanatory variables included descriptors of spatial patterns in the species data. The *spatial variable matrix* (SVM) described a trend surface response model of geographic locations. Geographic coordinates of plot locations (X and Y, centered by mean) were calculated from latitudes and longitudes superimposed on a geographic grid. Following Bocard et al. (1992) and others (Boccard and Legendre 1994, Okland and Eilersten 1994, Heikkinen and Birks 1996, Legendre and Legendre 1998), seven additional terms were included in the initial SVM representing nine terms of a third-order polynomial regression of X and Y coordinates:

$$Z = b_1X + b_2Y + b_3X^2 + b_4XY + b_5Y^2 + b_6X^3 + b_7X^2Y + b_8XY^2 + b_9Y^3$$

This approach allowed modeling of spatial trends that are more complex than linear gradients (Legendre and Fortin 1989, Legendre and Legendre 1998).

The final explanatory matrix was based on a simple regional model of Florida physiographic landforms. The *regional variable matrix* (RVM) categorized each plot location into one of the four regions based on the generalized physiographic landforms of Puri and Vernon (1964). In addition to the Northern and Central Highlands, the Lowlands landform was divided into the panhandle and peninsula regions (Figure 3-1). This regional delineation approximates a general regionalized model based on several widely applied models of Southeastern U.S. ecoregions (Omernik 1987, Bailey et al. 1994, Griffith et al. 1994, The Nature Conservancy 2001). This model represents presumed regional differences in geologic and evolutionary history that affect current patterns of spatial heterogeneity of pineland vegetation.

All environmental and spatial variables were individually screened for inclusion in their respective variable matrix using the forward selection procedure and associated Monte Carlo tests as implemented in CANOCO (Okland and Eilersten 1994, ter Braak and Smilauer 2002,

Leps and Smilauer 2003). Two forward selection tests were conducted. First, variables were subjected to forward selection in the context of a redundancy analysis (RDA) of a single variable group. Second, forward selection was repeated in a partial redundancy analysis (pRDA) of each variable group, with other environmental/spatial variables as covariables. Variables with $p > 0.02$ were excluded in subsequent canonical analyses corresponding to the model used for selection. In this manner, explanatory variables with highest partial correlations with species data were retained.

I applied a variation partitioning model to the species data, using the EVM, CVM, SVM as explanatory variable matrices. Variation of the species data was decomposed into components associated with pure and joint contributions of explanatory factors. Specifically, I quantified seven components of variation from six individual RDAs and pRDAs. The specific components described fractions of total variation explained (TVE). These fractions are expressed in terms of three pure factor effects and four interaction effects (following Cushman and McGarigal 2002).

Variation partitions correspond to fractions of reference diagram in Figure 3-2 as follows:

1. *Pure edaphic effects*: species variation explained by soils and topography variables, and not related to climate and space variables (fraction **a**)
2. *Pure climate effects*: variation explained by CVM but not EVM and SVM (fraction **b**)
3. *Pure spatial effects*: variation explained by SVM but not EVM and CVM (fraction **c**)
4. *Joint effects of edaphic and spatial variables*: variation jointly explained by EVM and SVM, but not related to CVM (fraction **d**)
5. *Joint effects of edaphic and climate variables*: variation jointly explained by EVM and CVM, but not related to SVM (fraction **e**)
6. *Joint effects of climate and spatial variables*: variation jointly explained by CVM and SVM, but not related to EVM (fraction **f**)

7. *Three way joint effects of edaphic, climate and spatial variables: variation jointly explained by EVM, CVM, and SVM (fraction g)*

The first variation partitioning model included EVM and CVM plus the polynomial spatial matrix (POLY SVM). In the second model, the PCNM SVM replaced the POLY SVM.

Models of variation partitioning involved application of a series of constrained and partial constrained canonical ordinations, as described by Borcard et al. 1992 and others (Borcard and Legendre 1994, Okland and Eilersten 1994, Okland 2003). Significance of terms derived from canonical ordination models were tested via Monte Carlo permutation tests (Peres-Neto et al. 2006). The null hypothesis tested was that of independence of species response data on the values of the explanatory variables (Leps and Smilauer 2003). Fractions representing two and three-way interactions and “unexplained” residual variation were calculated indirectly from simple and partial terms; therefore, they were not statistically testable (Legendre and Legendre 1998, Peres-Neto et al. 2006). Variation partitioning and statistical tests were performed using the vegan community ecology package version 1.8 for R software (Oksanen et al. 2007, R Development Core Team 2007).

The relationships between floristic variation and abiotic gradients were assessed in the context of the larger variation partition model. Constrained axes were tested via Monte Carlo permutations for each of the following canonical ordinations: 1) RDA of EVM, 2) pRDA of EVM after removal of CVM and POLY SVM effects, 3) RDA of CVM, and 4) pRDA of CVM after removal of EVM and POLY SVM effects. Higher order canonical axes were tested using pRDAs with lower order axes scores as covariables (Braak and Smilauer 2002, Leps and Smilauer 2003). Significance of marginal effects of sequential canonical axes was assessed at $p < 0.02$. Multiple simple correlations are presented as vector biplots superimposed on ordination diagrams. Angles of the vectors denote direction of the highest correlation whereas vector

lengths correspond to strength of correlation. Significant correlations between canonical axes and species richness (number species per 1000 m² plot area) are similarly presented. Canonical axes scores derived from relevant RDA and pRDA ordinations are plotted against geographic plot coordinates to visualize modeled trends in environmental and spatial variation. Individual ordinations were run using CANOCO for Windows version 4.5 (ter Braak and Smilauer 2002).

Results

A total of 1009 taxa were identified from the 270 vegetation samples used in this study, after omission of inconsistent and low resolution taxonomic identifications. After deletion of infrequent entities, a total of 670 species were retained for analysis. Species richness ranged widely in the samples, from 29 to 168 species/1000 m² area. Similarly, vegetation samples represent large variation in community composition, ranging from dry upland sandhills to seasonally inundated wetland prairies. Community types and characteristic environmental features are described in detail in preceding chapters.

About a quarter of the edaphic variables were omitted from inclusion in the EVM explanatory matrix following the forward selection procedure in CANOCO (Okland and Eilersten 1994, ter Braak and Smilauer 2002, Leps and Smilauer 2003). Of the original 26 potential explanatory variables, 14 soil property variables and two topographic variables were retained for the RDA including the EVM explanatory factor only, with no covariables (see Table 3-2 for variable list). Thirteen soils and topographic variables were selected for the pRDA of EVM, with CVM and SVM included as covariables. Three variables from the RDA set were omitted in the pRDA set (Clay A, P, and Mn), while one was added (Al).

Of the initial 12 climate variables subjected to the forward selection procedure, eight were retained in the CVM for RDA ordination. These included descriptors of temperature,

radiation, and precipitation. Forward selection for the pRDA of CVM (with EVM and SVM covariables) reduced the number of explanatory variables to only three (standard deviation and total growing season precipitation, and standard deviation of daily shortwave radiation).

Similar forward selection procedures were applied to sets of spatial explanatory variables. Of the nine terms of the initial polynomial trend regression, seven were retained for the SVM (X^2Y and Y^3 were dropped).

Variation Partitioning Models

The total variation (aka “total inertia”) of the Hellinger transformed species data set was 0.727, as expressed by the sum of all eigenvalues in an unconstrained principal component analysis (PCA). The three explanatory matrices of the first variation partitioning model accounted for 23% of the total variation (sum of all constrained eigenvalues / 0.727), leaving 77% of total inertia as “unexplained residual variation” (Figure 3-1). Although 23% is a small portion of total inertia, this “total variation explained” (TVE) value is typical of community variation studies (typically 20-50%; Okland and Eilersten 1994, Okland 1999). However, following the advice of Okland (1999), TVE as a portion of total inertia should be interpreted with extreme caution. The contribution of polynomial distortion (an artifact of eigenanalysis of numerous response variables) was estimated as 30-70% of “unexplained variation” in simulation studies of “noisy” data. The authors recommend presentation of variation fractions in terms of proportions of TVE. This convention is followed hereafter.

Edaphic variables account for the largest component of species variation in the variation partition model. Approximately 70% of TVE is related EVM, either as pure or interactions effects: fraction a includes pure edaphic effects (48%), and fraction g, the three way interaction effects (22%; Figure 3-1). The joint effects of edaphic variables with space (fraction b, 0%) and

with climate (fraction e, 0%) are too small to be included in the model. Variation attributed to climate explanatory variables (pure or joint effects) is 44% of TVE (Figure 3-1). A small percentage (9%) of TVE is pure climate effect (fraction b), and the remainder is divided between space+climate joint effects (fraction f: 13%), and the three way interaction (fraction g). Similar variation fractions are related to spatial trends with only 9% attributed to pure space effects.

Environmental Explanatory Variables

The primary complex gradient related to total edaphic variation (the EVM RDA; Figure 3-2) remains intact in the model of “pure” edaphic effects only, whereas higher order gradients are diminished (Figure 3-3). The two-dimensional pRDA of EVM represents edaphic variation after the removal of spatial structure (Figure 3-3 relative to fraction (a) of Figure 3-1). Similar to the EVM RDA, axis one separates sites of lower slopes with organic soils from sandier sites on higher topographic positions (first axis Figure 3-3 compared to Figure 3-2). Conversely, the soil texture/nutrient gradient associated with geographic region (Axis 2 Figure 3-2) largely disappeared in the pRDA (Figure 3-3), as did any evidence of regional separation of sites. The second pRDA axis appears to represent a similar gradient of soil acidity and fertility similar to the third RDA axis in Figure 3-2.

Geographic separation is dramatic in the ordination of climate variables related to species variation. The CVM RDA represents all variation fractions associated with climate explanatory factors (Figure 3-4 relative to fractions b+f+g of Figure 3-1). The first canonical RDA axis is a gradient of all eight climate variables, related to temperature, daily radiation, and precipitation (Figure 3-4). Peninsula sites are completely separated from panhandle sites along the first axes, and they are characterized by higher mean annual temperatures and daily radiation. The panhandle sites receive more annual rainfall that is more variables throughout the year and the

growing season. Species richness is also highly correlated with this climate gradient and regional separation. The CVM RDA axis 2 explains about half again as much variation in species data (Table 3-2), and is related to variation in precipitation (Table 3-1). Likewise, the third canonical axis represents a gradient in precipitation (annual, growing season and standard deviation) and radiation (daily mean and standard deviation; Table 3-1).

The influence of most climate explanatory variables disappears after removal of variation related to spatial and edaphic factors. The CVM pRDA represents the variation fraction of “pure” climate effects only, which is very small compared to total climate effects (bottom plot of Figure 3-4 relative to fraction (b) of Figure 3-1). Not surprisingly, most of the climate variables are not correlated with this small, non-spatially related variation fraction (and were eliminated in the forward selection process prior to the pRDA). Regional site separation similarly disappears in the pRDA (Figure 3-4). The first pRDA axis is related to total growing season precipitation and variation in precipitation (Table 3-1). Axis two is a gradient of variation in radiation (probably related to seasonality). Species richness is negatively correlated with pRDA axis 1, although the relationship appears non-linear (Figure 3-4).

Mapped results from the simplified variation partition model of environmental and spatial trends reveal regional patterns in species variation. The simple two part variation partition model yielded the following fractions of TVE (figure not shown): pure environmental effects (fraction a = 54%), pure spatial effects (fraction c = 9%), and joint effects of environment and space (fraction b = 37%). These fractions resemble those of the initial three part variation partition model; the spatial component (fraction c) is identical in both models. The contour map corresponding to site scores from a RDA is constrained by all environmental and spatial variables (fractions a+b+c = TVE) and displays regional distinctions (Figure 3-5). Scores from

the first and second canonical axes appear to distinguish the highlands physiographic landforms in the upper panhandle and north peninsula from the coastal lowlands (Figure 3-5a). Although it represents a small portion of TVE (9%), the canonical axis site scores for variation explained by pure space only display clear separation between panhandle and peninsula (Figure 3-5c).

Discussion

Based on the spatially explicit models of species-environment relationships, I propose several interpretations regarding determinants of understory community structure of Florida pyrogenic pinelands. First, *environmental factors influence species composition and diversity, and these controls are most prominent at local scales.* The strongest gradient in species composition is related to local topographic and edaphic features; about half of TVE is uniquely correlated with these factors and not spatially structured (presumably representing small scale gradients not captured by large scale spatial trends). Specifically, I presume that community differentiation is concurrent with gradients of soil fertility and soil moisture, represented by total N, organic matter, topographic position and soil texture\density variation. This gradient separates dry upland vegetation from herbaceous dominated flatwoods and wetlands. Previous community classification characterized vegetation along these primary gradients; sandhill vegetation inhabits infertile sands (negatively associated with Axis 1, Figures 3-2 and 3-3) while flatwoods and wetland vegetation are common in wetter, acidic sites with high nitrogen availability and organic matter. The dominance of the soil fertility/moisture gradient is demonstrated by large first axis eigenvalues, relative to those of higher order. Furthermore, this local-scale gradient is consistently prominent after removal of variation effects of spatial trends and climate.

Topographic position was the single most influential environmental variable of community composition, and the most highly correlated with the local soil moisture-fertility gradient. Understory community variation concurrent with local topographic gradients has been noted elsewhere in the Southeastern Coastal Plain, both anecdotally and quantitatively (Walker and Peet 1983, Bridges and Orzell 1989, Myers and Ewel 1990, Platt 1999, Kirkman et al. 2001, Drewa and Platt 2002). In the current study, topographic position was a subjective descriptor of position along a local topographic gradient, regardless of absolute changes in elevation or slope steepness. As revealed in the ordination models, topographic position covaries with soil texture and fertility. However, in light of the large portion of variation attributed to topographic position over and above that explained by other edaphic feature, this variable likely is a proxy for unmeasured variation related to available soil moisture. Lower slope pineland communities typically have higher perched water tables, more seasonal flooding and less soil leaching (Abrahamson and Hartnett 1990, Myers and Ewel 1990, Kirkman et al. 2001).

Available nitrogen is related to local-scale variation in species composition in the current study. In temperate grasslands elsewhere, nitrogen is a limiting resource and is related to primary productivity and diversity (Seastedt et al. 1991, but see Turner et al. 1997). Soil moisture and nitrogen availability are thought to be positively related in temperate forests (Vitousek 1982). In this model, nitrogen is highly positively correlated with soil organic matter and (presumably) soil moisture, and negatively related to soil density and coarseness. This is not unexpected, as organic matter is a major source of nitrogen (Brady and Weil 2000). However, these correlations contradict studies of nitrogen dynamics elsewhere in the Southeastern Coastal Plain where nitrogen mineralization declined with increasing soil moisture, and/or was negatively correlated with species diversity (Foster and Gross 1998, Wilson et al. 1999, Kirkman

et al. 2001). These studies involved correlation over single or few recently burned topographic-moisture gradients, whereas the current study models environmental correlations and composite gradients over a large geographic region. Available nitrogen varies with time since fire and fire frequency (Christensen 1977). Despite attempts to “control” for recent fire history in site selection, this may account for unmeasured variation in nitrogen (and other locally available resources).

The second interpretation is that *regional variation in pineland community structure is profound, and is related to variation of soil texture, soil nutrient availability, and climate.* Furthermore, *regional variation of species composition is orthogonal to local variation.* Spatial trends in compositional variation are strongly dependent on latitude and longitude (X and Y coordinates), and correspond to regional differences between the Florida panhandle and peninsula. Eighty percent of variation related to climate variables is spatially structured, reflecting distinct regional differences; the peninsula is hotter, less seasonal, and receives more growing season rainfall, whereas panhandle rainfall is more evenly distributed throughout the year (Fernald 1981, Chen and Gerber 1990). Regional differences in edaphic features represent about half of spatially structure variation in species composition, and largely reflect soil texture differences. Similar regional segregation concurrent with soil texture has been documented elsewhere in the coastal plain, at both local and regional scales (Peet and Allard 1993, Dilustro et al. 2002). Phosphorous and calcium are more abundant in soils of peninsular sites. This is not surprising considering the presence of the carbonate Florida platform that underlies most of the peninsula, and the presence of large amounts of phosphorite in some sediments of Pliestocene origin (Puri and Vernon 1964, Brown et al. 1990).

The third interpretation is that *residual spatially structured composition variation in is related to regional differentiation in phytogeographic distributions and endemism*. Furthermore, these patterns may reflect variations in biogeographic and evolutionary history, and/or recent land use patterns. The unique fraction of space in the variation partition model represents a small but inscrutable percentage of TVE (9%). This variation displays regional distinction similar to that of the joint effects of space and environmental factors (Figure 3-5). Interestingly, the divide between peninsular central Florida vs. north and panhandle Florida coincides with phytogeographic patterns. Many temperate plant species (woody and herbaceous) reach the southern limit of their distributions in north peninsular Florida (see Chapter 2). Nearly a quarter of the taxa included in the species-environment models have regionally restricted distributions in Florida, and nearly 3% are endemic to one region (Chapter 2; James 1961, Sorrie and Weakley 2002). If the contribution of “pure space” does indeed manifest phytogeographic trends, this suggests the influence of historical dynamics on contemporary patterns of species coexistence (Ricklefs 1987). Florida’s complex recent geologic history also underscores regional differences between the panhandle and peninsula, including differential sources and timing of sediment deposition and histories of sea level fluctuations (Randazzo and Jones 1997, Myers 2000). In addition, there is evidence that the two regions were physically separated by the “Suwannee Strait” for a period between 12 to 30 MRBP; an elongate negative structure extending across southern Georgia and northeastern Florida (Hull 1962, Puri and Vernon 1964, Myers 2000).

Differential land use patterns offer an alternative (but not mutually exclusive) explanation for the compositional variation concurrent with regional segregation. Unfortunately this observational study of floristic variation does not describe pre-settlement conditions, as this is no longer possible because past land use and management created non-random “selections” of

natural areas in Florida. Further subjectivity was introduced from the lack of random selection of sites from an a priori “population” of natural areas. I attempted to minimize the latter problem with a stratified sampling design and a large sample size (see Leps and Smilauer 2007). However, any described variation of community structure is inherently confounded with recent land use, particularly fire suppression and logging, as has been documented in other regions (McIntyre and Lavorel 1994, Stohlgren et al. 1999, Vandvik and Birks 2002, Svenning and Skov 2005). Because open-range ranching was common in the central peninsula until recently, large portions of this region continued to be frequently burned during the dormant season (Bridges 2006a, Bridges 2006b). Conversely, other regions of Florida suffered decades of fire suppression in the 20th century, with prescribed fire only recently introduced in selected natural areas (e.g. the Big Bend and Marianna Lowlands regions, pers. obs.). Thus, regional differences in recent fire regimes may contribute to unexplained compositional variation in the current model. Effect may be direct (fire effects on resource availability, plant delectability) and indirect (i.e. differential resource availability related to timber density and woody biomass).

A fourth interpretation is that *gradients in composition are related to gradients in species richness, and these are apparent at regional and local scales*. The variation in species richness is high among study sites, ranging from 26 to 168 species/1000 m². These herbaceous dominated pineland communities are characterized by large numbers of small-statured species present in low abundances. Community structure is influenced by the amount of “species packing” at small scales. The richness gradient is most obvious at the regional scale, where panhandle sites are consistently richer regardless of soil moisture/fertility conditions. Regional influence on local diversity is a well documented phenomenon, and is attributed to the “species pool” effect resulting from processes operating at multiple spatial and temporal scales (Zobel

1992, 1997, Collins et al. 2002). Interestingly, the richness gradient appears independent of the primary local-scale gradient of soil moisture/fertility, contrary to observations in other grassland ecosystems (Grace et al. 2000, Kirkman et al. 2001, Weiher et al. 2004).

After removal of variation associated with regional spatial trends, a richness gradient persists and is weakly associated with soil pH, available nutrients and soil texture. This secondary richness gradient is seemingly unrelated to regional segregation, and may reflect local diversity patterns. Species richness associations with soil pH and calcium have been documented in temperate grasslands and forests (Partel 2002, Palmer et al. 2003, Peet et al. 2003). Similar to Peet and Allard (2003), Florida pineland species richness is positively correlated with pH and soil calcium, suggesting either larger pools of species adapted to basic soils (regional “species pool” effect) or more favorable local conditions for plant colonization and growth (local environmental effect). Alternatively, soil reaction is merely a proxy variable for other unmeasured causative factors, such as competition for light or space. Density of woody biomass increases rapidly on more fertile sites, which affects understory species richness vis-a-vis competition for light and other resources (White et al. 1991, Streng et al. 1993, Grace and Pugsek 1997, Palmer et al. 2003, Weiher et al. 2004). Fire encourages herbaceous growth, colonization and diversity, in part, through control of woody competition (Drewa et al. 2002b). Thus, the local variation in richness likely derives from a complex gradient of soil fertility and disturbance.

The current model of community variation of Florida pineland vegetation underscores the prominence of spatially structured and spatially independent environmental factors in shaping community structure. Spatial structure in community structure and environment patterns is common in studies of local to meso-scale variation (study region scale range approximately 10 –

1000 km²; Abrahamson and Hartnett 1990, Cushman and McGarigal 2002, Dilustro et al. 2002, Graae et al. 2004, Svenning and Skov 2005, Laughlin and Abella 2007). By comparison, the extent of my study region was orders of magnitude larger (approximately 137,000 km²). Considering the relatively large region, it is somewhat surprising that the unique variation fraction explained by space is small compared to total variation explained (9%). This suggests the minor importance of biotic processes operating independently of environment. An alternative explanation is that I failed to adequately model relevant spatial trends (e.g. small scale spatial patterns). On the other hand, soils and topography appear very influential as determinants of compositional variation supporting environmental control hypotheses. I posit that the relative influence of environmental controls exceeds that of biological controls in species composition and diversity of Florida pyrogenic pineland communities.

This model of pineland floristic variation supports hypotheses of regional influences on local community structure and diversity. Regional differences in species richness and composition exist, even after removal of regional environmental effects. Species composition differs between the panhandle and peninsula sites with similar local environmental conditions. This observations suggest influences of paleogeography and evolutionary history through mediation of species pools (Ricklefs 1987, Zobel 1992, Zobel 1997), perhaps confounded with trends in recent land use history (Graae et al. 2004, Graham et al. 2005, Laughlin et al. 2005, Svenning and Skov 2005). Furthermore, the model suggests a hierarchical structure of ecological determinants relative to the focal ecosystems, and that relative influences of environmental factors are scale dependent.

Table 3-1: List of variables included in RDA and pRDA canonical ordination of variation partitioning models. Eigenvalue indicates conditional correlation of single variables (with all other variables covariables). Correlation coefficients listed for first three constrained RDA axes, and two constrained pRDA axes. Bold values indicated significant correlations $p < 0.05$.

Abbreviation	Variable	Eigen- value	RDA A1	RDA A2	RDA A3	pRDA A1	pRDA A2
<i>Edaphic Variable Matrix (EVM)</i>							
Topo	Relative position on slope (1-4)	0.08	0.79	0.05	0.06	0.82	0.03
Org	Organic matter surface soil (%)	0.03	0.37	-0.21	0.28	0.41	-0.03
Sand A	Sand in surface soil (%)	0.03	-0.25	-0.52	-0.19	-0.39	-0.18
Sand B	Sand in sub-soil (%)	0.03	-0.04	-0.63	-0.08	-0.15	-0.24
N	Estimated total extractable nitrogen (ppm)	0.03	0.42	-0.16	0.25	0.43	-0.12
Density	Bulk density (mg/m^3)	0.03	-0.41	0.09	-0.34	-0.44	-0.03
Elev	Elevation (m) from 1 km resolution DEM coverage	0.02	-0.14	0.50	0.23		
Clay A	Clay in surface soil (%)	0.02	0.04	0.50	0.04		
pH	pH surface soil	0.02	-0.25	0.26	0.25	-0.27	0.43
P	Extractable phosphorous (ppm)	0.02	-0.09	-0.36	0.42		
Ca	Calcium (ppm)	0.02	-0.12	-0.39	0.42	-0.19	0.12
B	Boron (ppm)	0.02	-0.29	0.07	0.37	-0.33	0.42
Mn	Manganese (ppm)	0.02	0.04	0.54	-0.34		
Fe	Iron (ppm)	0.01	-0.14	0.29	0.04	-0.20	0.14
Al	Aluminum (ppm)	0.01				0.22	-0.40
<i>Climate Variable Matrix (CVM)</i>							
Temp mean	Mean annual daily temperature ($^{\circ}\text{C}$)	0.05	0.79	0.08	-0.13		
Temp max	Mean annual minimum temperature ($^{\circ}\text{C}$)	0.05	0.76	0.15	-0.17		
Srad GS std	Standard deviation mean growing season shortwave radiation ($\text{MJ}/\text{m}^2/\text{day}$)	0.05	-0.78	-0.04	0.17	0.02	0.50

Table 3-1 continued.

Abbreviation	Variable	Eigen- value	RDA A1	RDA A2	RDA A3	pRDA A1	pRDA A2
Srad std	Standard deviation mean annual shortwave radiation (MJ/m ² /day)	0.04	-0.67	0.05	0.32		
Prcp_ann	Mean total annual precipitation (cm)	0.03	-0.50	-0.33	0.36		
Srad	Mean daily shortwave radiation (MJ/m ² /day)	0.02	0.38	0.16	-0.38		
Prcp GS	Mean total growing season precipitation (cm)	0.02	0.30	-0.27	0.45	0.47	0.16
Prcp std	Standard deviation of mean total growing season precipitation (cm)	0.02	-0.27	-0.36	0.36	0.48	0.33

Table 3-2: Results for Monte Carlo tests of canonical axes, for each of four ordinations. Variation attributable to explanatory constraining variables indicated by the cumulative percentage of variance (Cumulative % spp-env). F-ratio and p-value for each test of canonical axis after partialling out variation attributable to lower dimension axes.

Canonical Model	Axis	Axis eigenvalue	Cumulative % spp-env	F-ratio	p-value
RDA Edaphic variable matrix (14 vars)	1	0.095	45.1	26.67	0.002
	2	0.042	65.0	12.29	0.002
	3	0.019	73.4	5.73	0.002
	4	0.014	78.7	4.38	0.002
pRDA Edaphic variable matrix (12 vars)	1	0.081	57.6	26.06	0.002
	2	0.012	66.2	3.83	0.004
RDA Climate variable matrix (8 vars)	1	0.055	42.8	15.27	0.002
	2	0.028	64.4	7.97	0.002
	3	0.017	77.4	4.88	0.002
	4	0.010	85.2	2.93	0.006
pRDA Climate variable matrix (4 vars)	1	0.010	39.6	3.60	0.002
	2	0.005	72.7	1.87	0.016

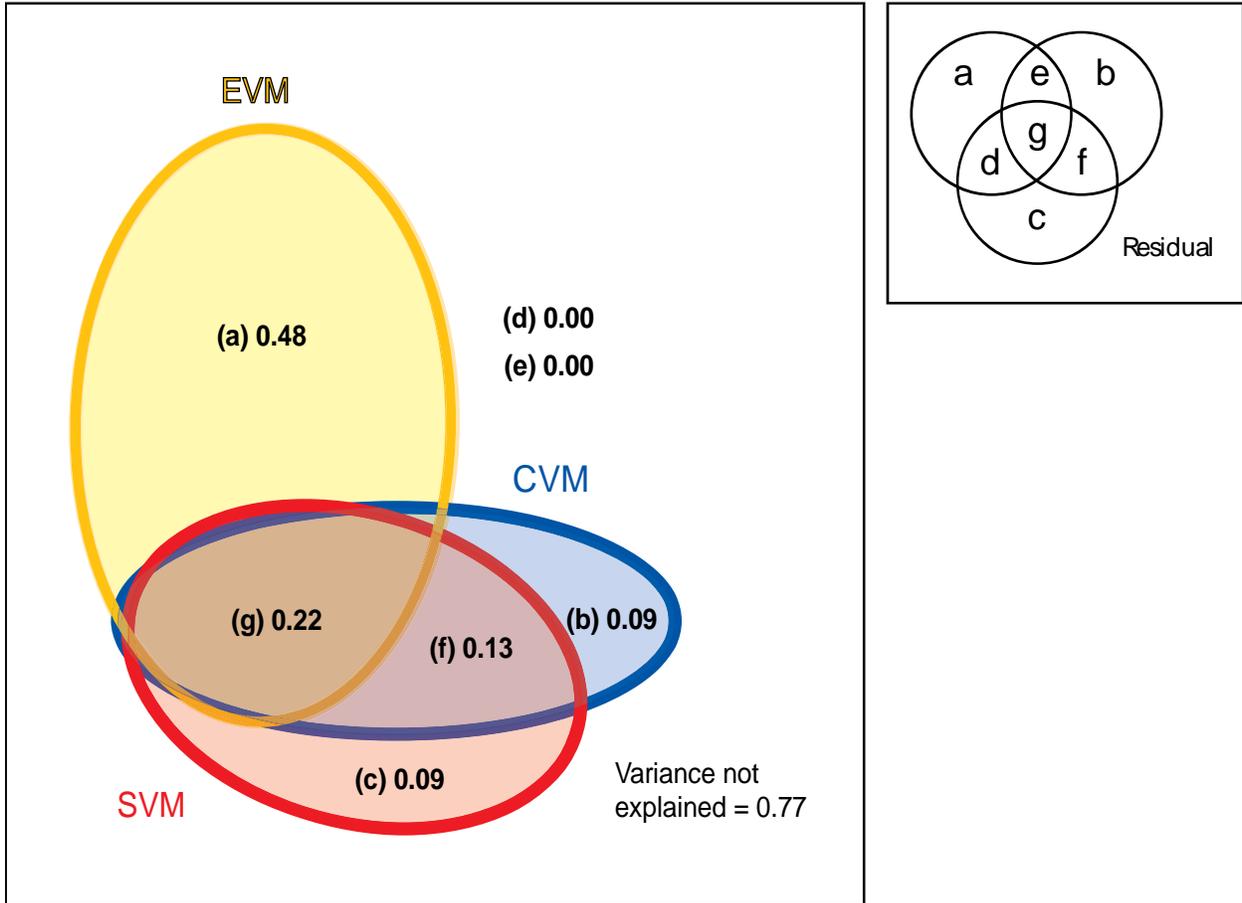


Figure 3-1: Venn diagrams of variation partition model. Ellipses represent three explanatory matrices (see text). Shaded portions labeled with letters denote variation fractions and proportion of TVE (see reference diagram top right).

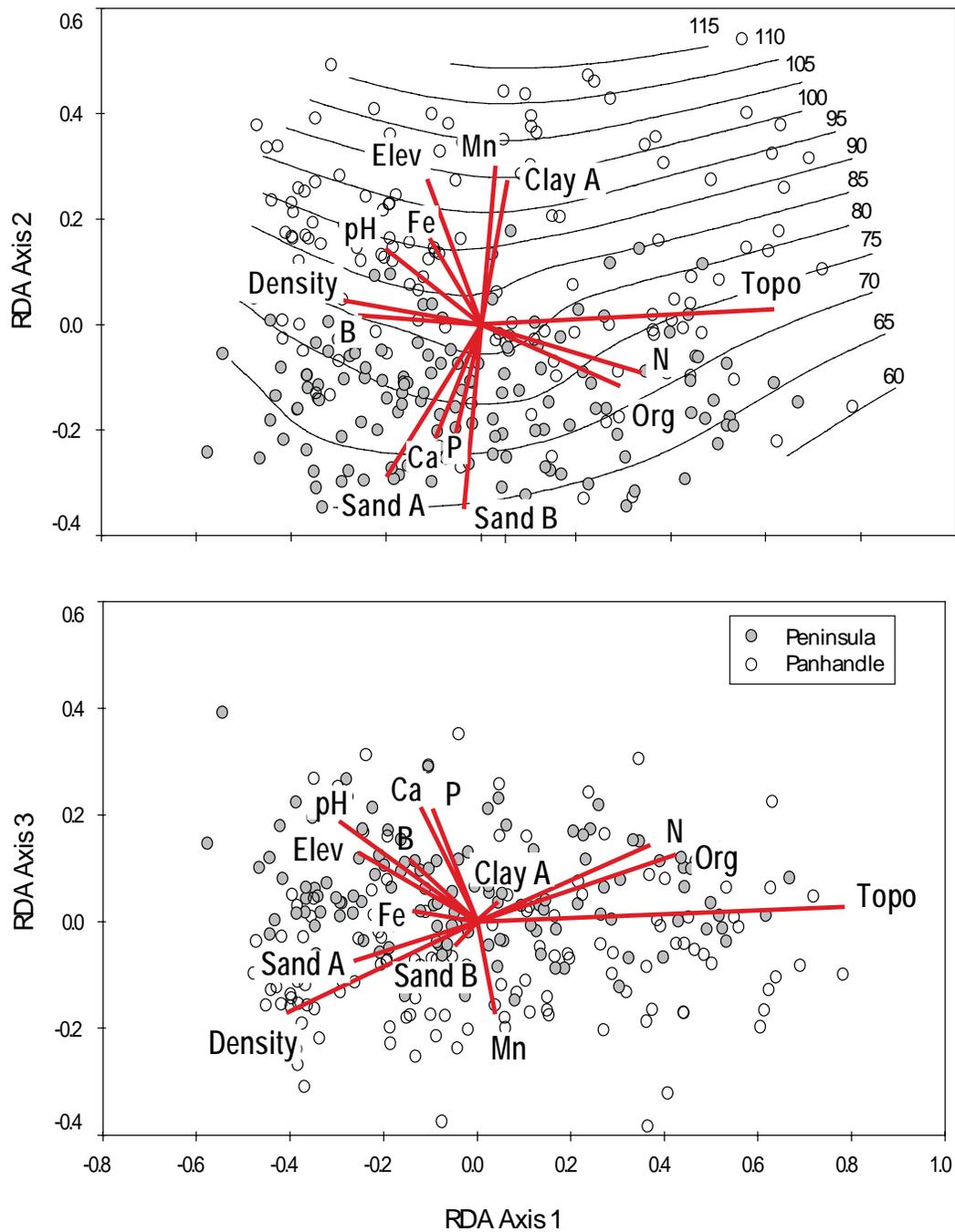


Figure 3-2: Biplots of RDA ordination, constrained by edaphic variables (EVM). Top plot = canonical axes 1 vs. 2; bottom plot = canonical axes 1 vs. 3. Vectors denote individual soils and elevation variables, scales by direction and magnitude of correlation with axes. Abbreviations same as Table 3-1. Symbols denote regional locations (panhandle vs. peninsula). Top plot contours display significant correlation of species richness with Axis 2 ($r = 0.48$).

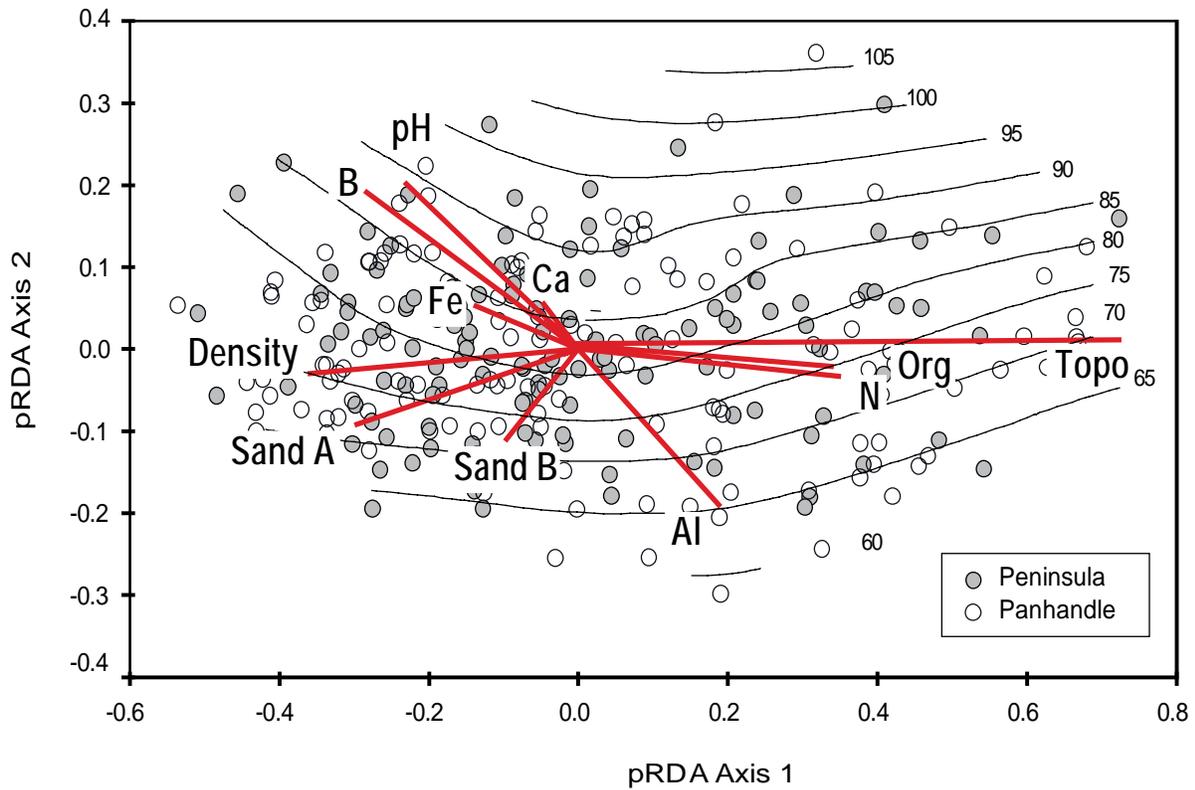


Figure 3-3: Biplot of pRDA constrained by edaphic variables (EVM) with CVM and POLY SVM covariables. Vectors show correlations of individual soils and elevation variables with the first two canonical axes. Abbreviations listed in Table 3-1. Symbols indicate regional locations (panhandle vs. peninsula). Contours display significant correlation of species richness with Axis 2 ($r = 0.59$).

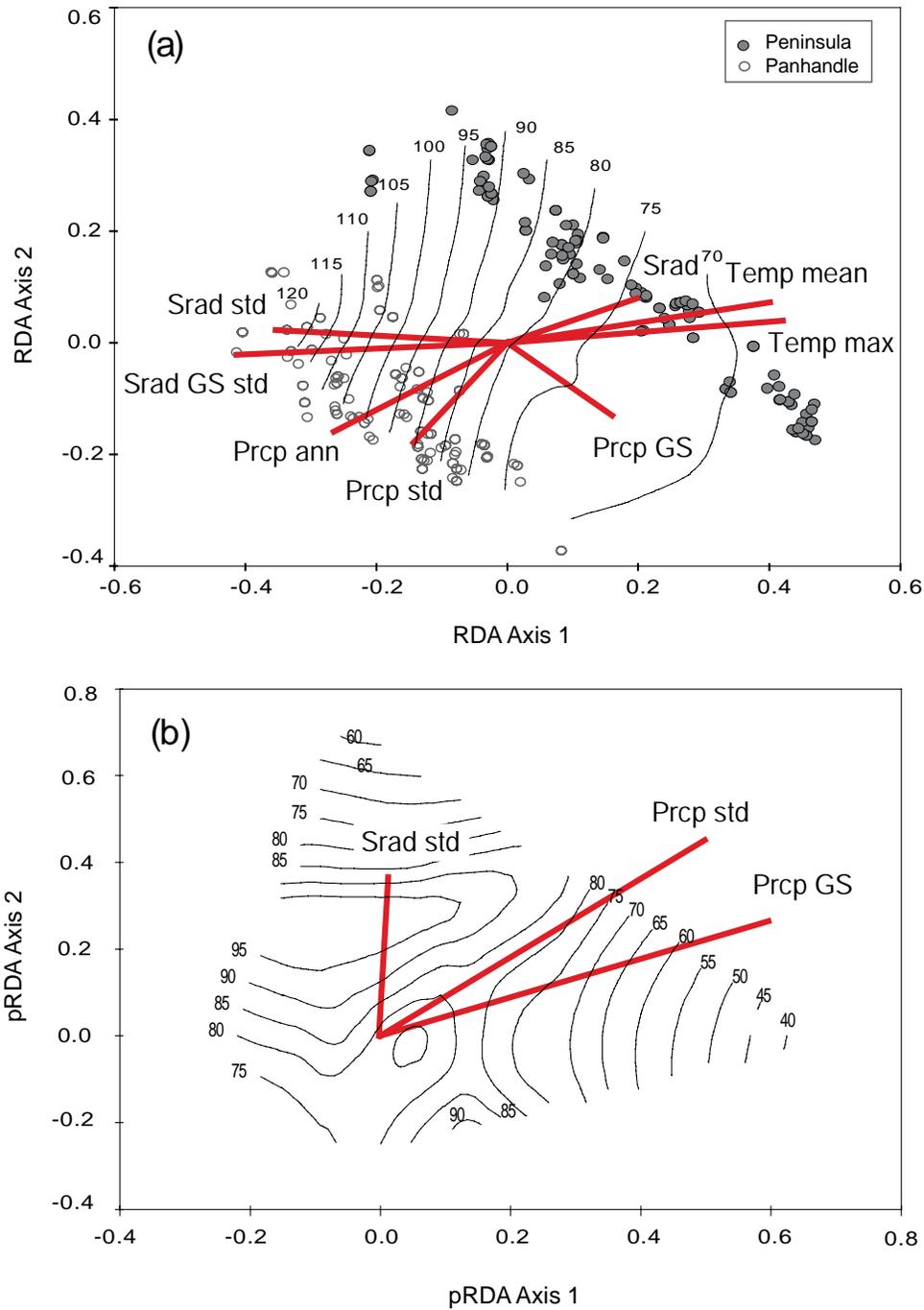


Figure 3-4: Biplots of 1) RDA constrained by climate variables (CVM; top plot) and 2) pRDA of CVM with EVM and POLY SVM covariables. Vectors show correlations of individual climate variables with the first two canonical axes. Abbreviations listed in Table 3-1. Symbols indicate regional locations (panhandle vs. peninsula). Contours display significant correlation of species richness with Axis 1 (RDA: $r = -0.593$, pRDA: $r = -0.34$). Note different scales for plots.

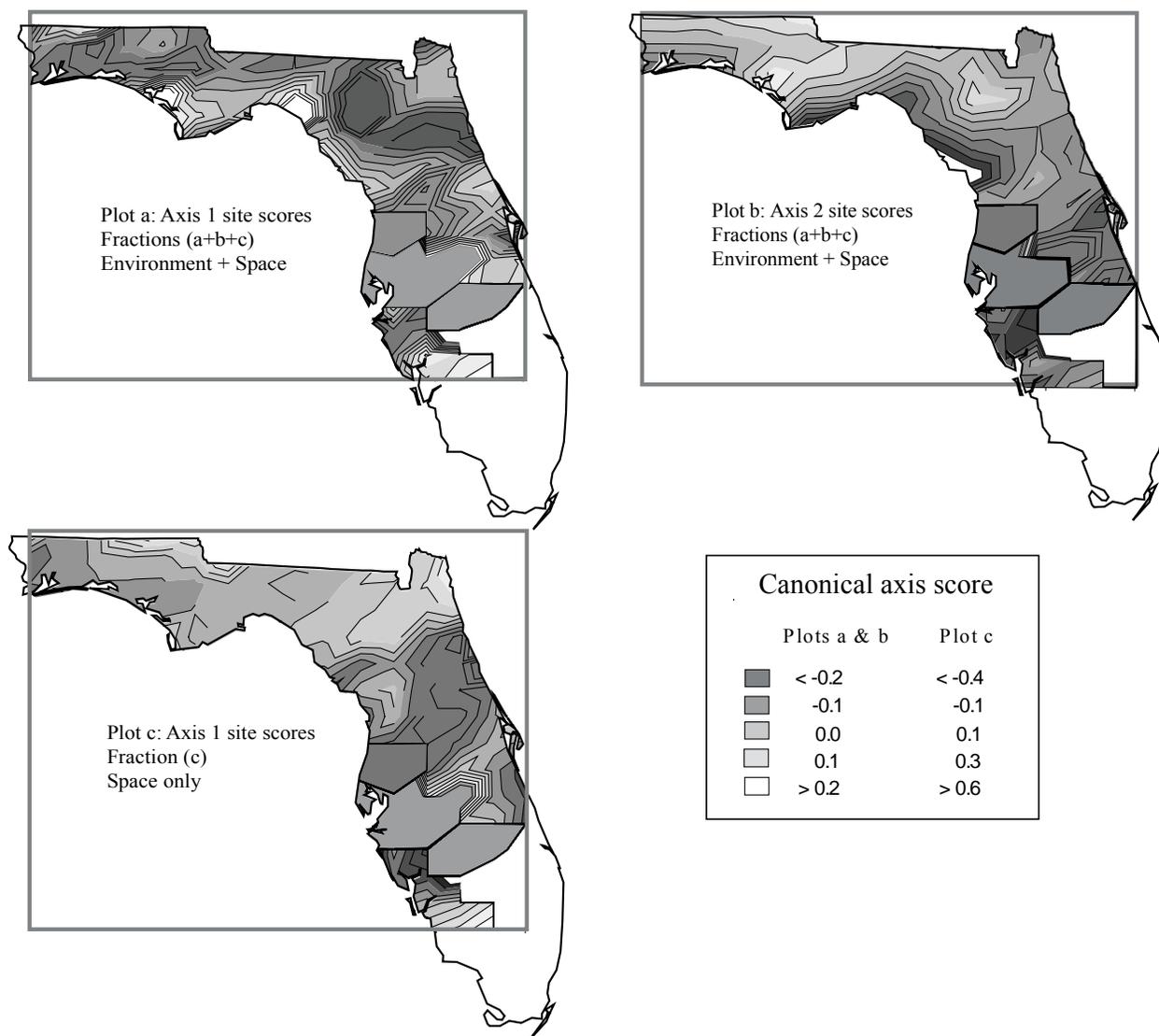


Figure 3-5: Contour maps derived from constrained ordination axis scores, displaying geographic variation in variation partitions from the model of environmental-compositional correlations. Plot (a) Axis 1 scores from RDA of all variation components (environmental and spatial factors), corresponds to fractions a+b+c in Figure 2-2. Plot (b) shows Axis 2 scores from the same RDA ordination. Plot (c) displays Axis 1 scores from pRDA of spatial trends, after removal of environmental factors (corresponds to fraction c).

CHAPTER 4
ECOLOGICAL RESTORATION OF A LONGLEAF PINE SAVANNA IN THE
SOUTHEASTERN COASTAL PLAIN

Introduction

Ecological restoration often involves rehabilitation of habitat structure to a semblance of historic or “natural” conditions. It is assumed that restoration of physical habitat structure and ecosystem function will prompt recovery or colonization of desirable native populations and restoration of native diversity and composition (Palmer et al. 1997, Walker and Silletti 2006). Community structure can be manipulated via reintroduction of natural processes (e.g., fire) and/or by “artificial” methods (mechanical or chemical treatments). Reintroduction of natural disturbance regimes can variously influence community composition through mediation of species recruitment and mortality and biotic interactions (Huston 1979, White 1979). Artificial manipulation of community structure may expedite restoration of desired conditions, particularly if remnant native populations remain on site, or if colonization is promoted (Palmer et al. 1997, Walker and Silletti 2006). It is the goal of ecological restoration to induced temporal changes in species composition and structure that resemble those of the desired conditions. Thus, it is important to quantify succession following restoration, and compare that to reference conditions.

Longleaf pine savannas and woodlands native to the Southeastern Coastal Plain are among the most imperiled ecosystems in North America (Crocker 1987, Noss 1988, Frost 1993, Means 1996, Platt 1999, Frost 2006). Native longleaf pinelands currently occupy less than 3 percent of their former range (Frost 1993, Outcalt and Sheffield 1996). Sites with vegetation composition and structure similar to that of pre-settlement conditions are even rarer (Simberloff 1993, Varner et al. 2005). The rapid range reduction of longleaf pinelands coincided with extensive logging, agricultural land use, and expanding rural settlement in the 19th and 20th

centuries (Crocker 1987, Frost 1993). Virtually all old-growth longleaf pine was logged, and much of the remaining land converted to pine plantations of slash (*Pinus elliottii*) or loblolly (*P. taeda*) pines (Frost 1993). Other sites became overgrown with second growth pine and hardwood species due to land fragmentation and suppression of natural fires (Platt 1999, Frost 2006).

Natural longleaf pine savannas of the Southeast are notable for their park-like stand structure and exceedingly diverse ground cover vegetation. Under natural fire regimes, monotypic stands of longleaf pine consist of patchily distributed cohorts of even-aged trees (Platt et al. 1988b). Other trees and shrub species are largely relegated to the midstory and understory strata and floristic diversity is concentrated in the herbaceous-dominated ground layer (Waldrop et al. 1992, Peet and Allard 1993, Glitzenstein et al. 1995, Platt 1999, Drewa and Platt 2002). At small scales, the ground cover vegetation of fire-maintained pinelands harbors exceedingly high plant species diversity (Walker and Peet 1983, Bridges and Orzell 1989, Peet and Allard 1993). Ground cover vegetation is comprised of large perennial bunch grasses, interspersed with smaller and rarer grasses and forbs (Peet and Allard 1993, Platt 1999). An estimated 95 percent of herbaceous ground cover species are perennials with adaptations for post-fire regeneration, including rapid growth and sprouting, clonal growth, and obligate post-fire seeding (Platt 1999). Post-fire growth of ground cover vegetation is rapid, with upwards of 100% biomass recovery within 1 year (Oosterheld et al. 1999). Ground cover vegetation, coupled with highly flammable longleaf pine needles, provides fine fuels necessary for ignition and spread of low intensity ground fires (Robbins and Myers 1992, Streng et al. 1993, Platt 1999).

Most contemporary native longleaf pinelands are small and fragmented, and are no longer subject to the natural processes to which constituent species are adapted. This condition

precludes the natural occurrence of frequent, low intensity fires that historically swept across the landscape (Frost 1993, Simberloff 1993, Platt 1999, VanLear et al. 2005). Fire suppression of remnant natural areas has induced shifts in species composition and community structure. Fire intolerant pine and hardwood species colonize these sites and reduce herbaceous plant abundance through shading and resource competition (Glitzenstein et al. 1995, Platt 1999, Provencher et al. 2000, VanLear et al. 2005). Fire suppressed longleaf pine communities are common in the Southeast U.S. (Mehlman 1992, Brockway and Lewis 1997, Gilliam and Platt 1998, Varner et al. 2005). These sites may harbor persistent native plant populations (in dormant and active states), but have suffered degradation of community structure in terms of shifts in species composition and abundances and physical habitat.

Reintroduction of natural fire regimes can affect recovery of community structure and species diversity in dry pinelands that have suffered moderate fire suppression (Brockway and Outcalt 2000, Provencher et al. 2001, Kirkman et al. 2004, Walker and Silletti 2006). However, little is known about restoration of pinelands that have suffered relatively long-term fire suppression (>10 years). The persistence of native vegetation (perhaps in dormant states) is the factor determining whether restoration can be accomplished by restoring natural environmental conditions versus having to re-introduce native species, which is usually prohibitively difficult and expensive (Seaman 1998, Walker and Silletti 2006, but see Cox et al. 2004).

Increases in woody biomass following fire suppression affect community structure and function of native pinelands. Thick woody growth competes with herbaceous vegetation for light and other resources, affecting succession, spatial heterogeneity, and species composition (Brockway and Lewis 1997, Provencher et al. 2001, VanLear et al. 2005). Indirectly, woody encroachment increases litter fuel loads, which may alter fire intensity and behavior to conditions

outside typical range of variability. Long periods of fire suppression and/or high intensity wildfires may affect novel shifts in species composition and succession, or extirpation of native populations (Varner et al. 2005).

Restoration success is highly dependent on initial site conditions. The degree of departure from a desired restored condition (the “reference condition”) guides the method and intensity of restoration treatments (Fule et al. 1997, White and Walker 1997, Walker and Silletti 2006). Additionally, the reference condition provides a standard by which to evaluate site restoration progress and success (White and Walker 1997). Despite problems with historic differences in environment and stochasticity, and assumed “stasis” of a target condition (Palmer et al. 1997), contemporary data from a disjunct but environmentally relevant is often the best choice for a reference site (“same time, different place” sensu Walker and Silletti 2006). Similarly, historical data may serve as reference site conditions, particularly if they are proximate in geography and environment (Fule et al. 1997, Swetnam et al. 1999, Walker and Silletti 2006).

Ecological restoration progress is often measured in terms of changes in overall species richness or shifts in members of functional groups. Dynamics of these measures are assumed to indicate changes in ecosystem production, function, and/or stability (Tilman 1996, Palmer et al. 1997). Species richness is often compared to reference sites to assess restoration progress (White and Walker 1997, Provencher et al. 2001, Kirkman et al. 2004). However, increases in species numbers do not necessarily imply congruence of successional trends or endpoints between restored and reference sites (Walker and Silletti 2006). Explicit comparison of compositional data provides more information about succession response to restoration treatments.

The purpose of this study was to evaluate the effects native stand composition and structure reconstruction have on the recovery of native ground cover vegetation. I hypothesized that woody biomass reduction via mechanical treatment would release remaining understory plant species from competition. Specifically, increased light availability from woody plant reduction will favor growth and recovery of herbaceous plants. I predicted that reduction of woody plant dominance via ecologically sensitive logging and reintroduction of native fire regime would induce recovery of native ground cover vegetation resembling reference site conditions. This prediction assumed a degree of resilience in natural temporal variability in plant community succession. I measured the immediate and long-term effects on ground cover composition following off-site pine removal (logging) and reintroduction of prescribed fire.

Methods

Study Site and Reference Sites

The Abita Creek Flatwoods Preserve (ACP) is located in the Gulf Coastal Plain region of Southeast Louisiana (The Nature Conservancy 2001). The ACP is situated on a broad flat terrace proximate to Abita Creek and its tributaries. The site encompasses Pleistocene deposits of the Prairie and Citronelle terrace formations (The Nature Conservancy 2001), and is characterized by level, poorly drained, fine silty loams dominated by the Stough soil series (Fragiaquic Paleudults; Trahan et al. 1990).

Historical accounts of the ACP area describe a landscape of longleaf pine dominated savannas and flatwoods prior to extensive logging of the early 1900's (Lockett 1870, Mohr 1898, Penfound and Watkins 1937, Penfound 1944, Wahlenberg 1946). These pyrophytic communities contained monotypic longleaf pine canopies, with trees up to 200-300 years old interspersed with patches of younger pines, and lush ground cover vegetation of grasses and

other herbaceous species (Penfound and Watkins 1937, Penfound 1944). Pine savannas were maintained by frequent (1-3 year interval) low intensity fires (Mohr 1898, Wahlenberg 1946, Glitzenstein et al. 2003).

The Louisiana Field Office of The Nature Conservancy (TNC) acquired the 312 ha ACP tract in 1996. The decision to purchase this tract was based in part on the presence of remnant native ground cover vegetation and the presumption that vegetation could be restored to approximate pre-settlement conditions. The site was never used for intensive agriculture. The original pine canopy was logged in the 1930's; early aerial photographs show the area was treeless in the early 1940's. Afterwards the site was burned infrequently, last burned circa 1980 before initiation of the current study (The Nature Conservancy 1997). As a result of fire suppression, ACP was colonized by thick growth of tree and shrub species. By 1995, slash pine (*P. elliotii*) stands comprised the dominant ACP overstory (The Nature Conservancy 1997). A few mature longleaf pines were present on site. Because regeneration of this species was hindered by the competing thick shrub vegetation, no juvenile longleaf pines were present. The midstory at ACP consisted of a nearly closed canopy of evergreen shrubs, including titi (*Cyrilla racemiflora*), sweetbay magnolia (*Magnolia virginiana*), large leaf gallberry (*Ilex coriacea*), swamp blackgum (*Nyssa biflora*), red maple (*Acer rubrum*), and gallberry (*I. glabra*). Herbaceous ground cover vegetation was sparse and patchy, interspersed within the shrub thickets.

I selected Lake Ramsey Wildlife Management Area (hereafter "Lake Ramsey") to serve as a contemporary reference site for comparisons of ground cover composition. Lake Ramsey contains native longleaf pine savanna vegetation that was frequently burned since the early 1990's and is considered a high quality example of regional native vegetation, resembling pre-

settlement conditions (Latimore Smith, pers. comm.). Lake Ramsey is approximately ten miles west of ACP and is geologically and edaphically similar to ACP. The Louisiana Department of Wildlife and Fisheries Natural Heritage Program established permanent vegetation monitoring plots at Lake Ramsey and collected vegetation data annually between 1994 and 1999. The 1999 data are used in this study.

Secondly, I used species data from Penfound and Watkins (1937; hereafter “Penfound data”) as a historical reference condition of unaltered pine savanna vegetation in southeastern Louisiana. The authors sampled ground cover vegetation of pine savannas and pine-cypress communities in the mid-1930’s, before and immediately after the original pine canopy was logged. They recorded all ground cover species present in plots of fixed dimensions comparable to that of the present study. Penfound’s “virgin longleaf pineland community” and “cutover pine” sites (the “Knott tract... located some three miles East of Mandeville”; Penfound and Watkins 1937) were within 15 kilometers of present-day ACP. Penfound’s “slash pine-pond cypress” community was also within 15 kilometers of my study area (“about 6 miles northeast of Mandeville”). I deemed the Penfound data representative of “original” natural conditions of these communities.

Restoration Treatments and Sampling Methods

My immediate goal at ACP was to restore the structure and composition of midstory and overstory strata. My model was based on historical and contemporary descriptions of old-growth longleaf pine stands. These accounts describe uneven-aged stands of longleaf pines with patches of even-aged cohorts resulting from gap regeneration. Historical accounts were anecdotal descriptions of Southeast Louisiana and surrounding regions (Lockett 1870, Mohr 1898, Penfound and Watkins 1937, Penfound 1944, Wahlenberg 1946). Contemporary descriptions of

old growth longleaf pine stand structure and dynamics came from elsewhere in the Southeastern Coastal Plain (Platt et al. 1988b, Platt et al. 1998; Platt and Rathbun 1993; Grace and Platt 1995a,b; Palik et al. 1997, 2003; Brockway and Outcalt 1998; McGuire et al. 2001).

A second goal was to restore longleaf pine canopy at ACP, and manage stands to promote older-growth characteristics. Natural seed sources for longleaf pine regeneration were unavailable. As such, I chose to remove canopy slash pine via commercial logging and plant longleaf pine seedlings. I predicted logging would reduce woody biomass and reduce competition for planted longleaf pine seedlings and recovering ground cover vegetation. In addition, I predicted faster establishment of longleaf pine canopy would provide fuel and promote fire behavior beneficial to natural community restoration (Robertson and Ostertag 2007). However, I was also concerned with potential negative impacts from soil disturbance associated with the logging process (Greenberg et al. 1995).

Two restoration treatments were applied at ACP. The first was canopy removal via commercial logging followed by prescribed fires (hereafter “logged+fire”). Five sample sites were selected for monitoring ground cover response to the logged+fire treatments. The second treatment consisted of prescribed fire only (hereafter “fire-only” treatment; four sites). Sample sites were interspersed throughout the preserve, and treatments applied following a complete randomized block design. All logged+fire sites were logged during the winter of 1997-1998 (Figure 4-1). A consulting forester worked with a small logging crew to remove trees using skidders equipped with low-psi tires. In this manner, soil disturbance and damage to surrounding trees were minimized. Logging was permitted only in dry conditions to minimize damage. All merchantable canopy pines were removed in the logged+fire sites. Mean basal areas (woody stems > 10 cm dbh) declined more than 90% after logging from 22.8 ± 5.9 m²/ha in 1997 to $2.2 \pm$

0.7 m²/ha in 1998. Over the same period, the mean basal area of the fire-only sites increased slightly from 9.6 ± 6.0 m²/ha in 1997 to 9.8 ± 5.4 m²/ha in 1998.

All treatment sites were prescribed burned twice during the study period. The first burn occurred in April, 2000, followed by the second in April 2003 (Figure 4-1). In a given year, all study sites were burned in the same day under similar conditions. Basal area of woody stems > 10 cm dbh were little affected by the burns. Mean basal area of the logged+fire treatment was already low following logging (2.2 ± 0.7 m²/ha in 1998), and declined to 1.1 ± 0.6 m²/ha in 2005. Similarly, the fire-only mean basal areas declined slightly, from 9.8 ± 5.4 m²/ha in 1998 to 8.6 ± 4.3 m²/ha in 2005.

Vegetation sampling in fixed permanent plots began in the summer-autumn of 1997, before logging. Vegetation plots were sampled annually during the autumn months prior to plant senescence after canopy removal (1998-2000). Autumn sampling facilitated plant identification given the large proportion of plant species, especially grasses, that flower in the fall. The final sample period was in the fall of 2005.

At each treatment site, I installed a single 0.1-ha rectangular permanent plot (plot dimensions: 20 m x 50 m, 1000-m² total area). All vascular plant species were recorded in each of four series of nested subplots ranging from 0.01-m² to 100-m² area. I estimated aerial cover for each species recorded in 100-m² subplots using the following cover classes: 0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95%, >95%. Additional taxa encountered in the remaining 600 m² were recorded and assigned a nominal cover estimate. Vegetation sampling approximated the field methodology described by Peet et al. (1998).

In addition, I recorded plant species' cover in four 1-m² subplots per site to obtain more accurate estimates of small scale cover. I overlaid a grid of 100 10 cm x 10 cm cells on each

subplot; each species present was assigned a value of 1-100, corresponding to the number of cells in which it occurred. In this manner, species present in the 1-m² subplots received two cover estimates: the first was the 1-m² grid count, and the second was the cover class estimate from the 100-m² sample area.

All woody stems > 2 cm diameter breast height (dbh) were tallied in the 1000-m² sample area by species and size class (2-5 cm, then 5 cm size classes up to 40 cm dbh). For trees > 40 cm dbh actual diameter was recorded. Basal area (BA) was calculated using midpoint values per size class.

I identified each plant taxon to the highest taxonomic resolution possible, which was species for the majority of identifications. However, I assigned “low-resolution” identifiers corresponding to genus or family for sterile or unidentifiable taxa. Low-resolution taxa were included in species richness estimates, but omitted from datasets used for compositional analyses.

Data Analysis

I used repeated measures models to compare trends of species richness and woody species abundance between the two restoration treatments. My experimental design resembled a Before-After Control-Impact (BACI) design, with two levels of treatment rather than one treatment versus a control (Underwood 1994). I used mixed linear models consisting of fixed and random effects, because of repeated measurements and my heterogeneous variance-covariance estimates (Littell et al. 2000). Each model included two fixed effect factors: treatment (TRT: logged+fire vs. fire-only) and time (YEAR: five levels corresponding to sample years), and their interaction (TRT*YEAR). Random effects of mixed models included between-year variances and within-year covariances of repeated measurements.

Within-subject measurements are often serially correlated in a predictable manner over time. To accommodate this, I used the first three steps of the “four stage” method of Littell et al. (2000) in determining mixed effects models for each response variable. First, I applied a “saturated” model that included TRT and YEAR effects, plus pre-treatment basal area per 1000- m^2 area as a covariable (initial BA). The variation of initial BA was large, ranging from 0.96 to 3.93 m^2/ha . Initial BA was omitted from subsequent models if it failed to explain significant variation ($p > 0.05$ in the model including “unstructured” covariance parameter estimates).

Step two involved specifying models of covariance structure for each statistical model. For this, the fixed effects portion of the model remained constant while I tested different covariance structure models using Residual Maximum Likelihood (REML) computation in PROC MIXED (SAS Version 8; Littell et al. 1996, Littell et al. 2000). I selected a covariance structure for each statistical model which most closely approximated actual data with the fewest parameter estimates. I compared the following model structures: compound symmetric (2 parameters: homogeneous variance and covariance), heterogeneous compound symmetric (6 parameters: heterogeneous variances and homogeneous covariance), Toeplitz (5 parameters: homogeneous variance and heterogeneous covariance as functions of time lag), heterogeneous Toeplitz (9 parameters: same as previous, with heterogeneous variance), first order autoregressive (2 parameters: homogeneous variance and decreasing serial covariance dependent on increasing time lag), first order heterogeneous autoregressive (6 parameters: same as previous with heterogeneous variance), and antedependence (9 parameters: heterogeneous variances and heterogeneous covariance relative to local serial autocorrelation, similar to Toeplitz structure). The latter three covariance structures typically provide good fit to repeated measures data (Kenward 1987, Littell et al. 2000). Each covariance model was compared to that of

unstructured covariance (each covariance parameter estimated independently) using Akaike's information criterion (AIC) and likelihood-ratio tests with degrees of freedom equal to the difference in number of estimated parameters (Littell et al. 1996, Littell et al. 2000). I selected the most parsimonious covariance model with least deviation from the unstructured covariance model in terms of parameter estimates and structure.

Finally, I used generalized least squares methods to test fixed effects on each of six response variables. The first response variable was small woody stems per 1000-m² (all stems > 2 cm but < 15 cm dbh). Next, I tested fixed effects on species richness, including counts by lifeform group and at different sample scales (1-m² and 1000-m²). I separately analyzed 1) total number of species, 2) number of graminoid species, which includes all true grasses (of the family *Poaceae*) and morphologically similar species of the families *Cyperaceae* and *Juncaceae*, 3) number of forb species, which include all non-graminoid herbaceous species, and 4) number of woody species, including all non-herbaceous trees and shrubs. Significance tests were evaluated using a conservative Type I error rate ($p < 0.015$) to avoid error inflation associated with multiple tests. A separate error rate of $p < 0.05$ was applied to both models of TOTAL species richness (1-m² and 1000-m²). Most dependent variables were log transformed to improve normality of residuals in the mixed linear models.

In each mixed linear model, the TRT*YEAR interaction was of primary interest because this effect represents treatment effects over time. I assessed treatment effect in individual years by using the "SLICE" option of PROC MIXED using SAS software Version 8 (SAS 2000). Significance tests evaluate treatment effects for each year separately.

Species data from two sample scales were used to assemble species response matrices. The 1000-m² species matrix included average cover class estimates from each of four years

(1997, 1998, 2000 and 2005; matrix dimensions = 36 plots x 217 species). The small scale species matrix included mean percentage cover values from the four 1-m² small plots per site (45 plots x 121 species). Data from five years were included (1997-2000 and 2005). Species with fewer than two occurrences in each dataset were deleted, as they contribute nothing to calculations of inter-plot similarities (McCune and Grace 2002).

I applied the Hellinger distance transformation to the raw species cover data. When used in conjunction with linear ordination methods, this transformation offers a better compromise between linearity and resolution than do methods based on chi-square distances. This approach avoids problems inherent to sample weighting, in addition to problems associated with using Euclidean distances with untransformed data (Legendre and Gallagher 2001, Legendre et al. 2005). The 1-m² species data were log transformed prior to Hellinger transformation, whereas the 1000-m² data were not.

I used Redundancy Analysis (RDA) as a method for direct gradient analysis of species compositional data. As a canonical ordination method, RDA directly relates species responses to environmental factors. Sample scores are “constrained” as linear combinations of explanatory variables, conceptually similar to linear (or multiple) regression. Treatment factors were explanatory variables, identical to those used in univariate analyses.

I used RDA models similar to those described by Leps and Smilauer (2003) for analysis of temporal compositional trends in a repeated measures experiment. I tested two null hypotheses per response matrix: 1) there are no directional temporal changes in species composition present in either or both restoration treatments (within subject effect), and 2) temporal trends in composition changes are independent of treatments (between subject effect). To test these, I varied constraining explanatory variables and covariables in each of two RDA's.

In the first, YEAR effect and TRT*YEAR interaction were specified as constraining variables, and Plot identity as a covariable. This corresponded to a model of YEAR effect only. The second RDA was constrained by the TRT*YEAR interaction, and YEAR and Plot identity were specified as covariables. This model corresponds to a test of interaction effects. Post-hoc “contrasts” of treatment effects between specific years were performed using the same RDA model as for hypothesis #2, with a species response data from the years of interest. Data matrices were centered by species norms prior to ordinations. Scaling focused on inter-species correlations to favor biplot interpretation (Leps and Smilauer 2003).

Significance of effects was tested with Monte Carlo permutation methods. Independence of species data relative to the explanatory (constraining) variables was tested (McCune and Grace 2002, Leps and Smilauer 2003). I used a restricted permutation configuration corresponding to a split-plot design where permutations of repeated measurements were confined within sample units (split-plots). Whole plots were permuted keeping within plot measurements intact. All ordinations and permutation tests were performed with CANOCO (version 4.5) and CanoDraw (version 4.0) software (Braak and Smilauer 2002). Small sample size and restricted block design limited number of permutation configurations. Thus, to reduce the probability of a Type II error, I selected a Type I error rate of $p < 0.10$ for omnibus tests of main and interaction effects and $p < 0.05$ for post-hoc contrasts.

Specific species most correlated with interaction effects (TRT*YEAR) were identified as those with highest “fit” to the first canonical axes in RDA ordinations. The fit value for individual species is the coefficient of determination corresponding to a regression of species responses on sample scores on the first (canonical) axis. For each RDA, I selected the top 20-30 species with highest fit using the “lower axis minimum fit” inclusion option in CanoDraw (Braak

and Smilauer 2002). Species vectors in biplots represent magnitude and direction of the first axis association.

Unconstrained ordinations were applied to species response matrices for illustrative purposes. Solutions from principal components analysis (PCA: the unconstrained analogue to RDA; Leps and Smilauer 2003) are presented to display successional trends of sample units. Each PCA ordination was based on a cross-products matrix of inter-species correlations derived from the Hellinger transformed data matrix. Compositional data were standardized by sample norm (Leps and Smilauer 2003). I present two dimensional ordination solutions and report the proportion of variance (in the species data) explained by ordination axes (McCune and Grace 2002).

Comparisons of ACP data to Reference Data

Species counts were transcribed from the Penfound data for comparison to ACP plots of similar areas. Species richness was derived from non-overlapping subplots from the Penfound data (areas = 1, 5, 10, 15, 20, 25 and 30 m²). Similarly, I tallied species from two overlapping sample scales from the Lake Ramsey reference data (1-m² and 10-m² sample areas; 11 plots). Mean species numbers by ACP treatment were calculated for increasing sample areas: 1, 2, 10, 20, and 100-m². Unlike the Penfound data, there was some overlap in ACP plot data due to the nested plots.

I compared species area relationships between ACP restoration treatments in the final sample year (2005). An ANCOVA model tested treatment effects (logged+fire vs. fire-only) on species area relationships. Pre-treatment species counts (from 1997) and log sample area were covariates in the model. Ninety-five percent confidence intervals were calculated for the two species area curves by treatment type. A species area curve derived from the Penfound data is

displayed along with restoration treatment confidence intervals (statistical comparison is not possible). Similarly, I visually compare species richness of Lake Ramsey data at two scales (1-m² and 10-m²).

I assembled species matrices from the Penfound and Lake Ramsey data in a manner compatible with ACP taxonomy and sample scales. First, a presence-absence matrix of ACP and Penfound species data was assembled from 30 m² sample areas (38 samples x 163 species). This matrix contained data from four ACP sample years plus one sample from each of two Penfound habitats sampled in late summer 1936 (the “cut-over pineland” and “pine-cypress community” Penfound sites). Both habitats were described by the authors as open, herb-dominated communities that burned frequently. Second, a similar presence-absence matrix was constructed from ACP and Lake Ramsey species data from 10-m² sample areas. For this I used two 10-m² sample areas per ACP (over 4 sample years; 72 total ACP samples), plus data from eleven 10-m² Lake Ramsey plots sampled in October 1999.

I used unconstrained ordination to display temporal trends of ACP samples relative to the Penfound and Lake Ramsey reference data. I applied non-metric multidimensional scaling (NMS) ordination with an inter-sample distance matrix of Bray-Curtis coefficients derived from the presence-absence species matrices. This method displays geographically disparate data without constraints of explanatory factors (McCune and Grace 2002). Successional vectors depict temporal trends in composition of the two restoration treatments relative to reference data.

Results

Trends in Species Richness and Woody Stems

Following logging, abundance of small woody stems (< 10 cm dbh) declined precipitously (nearly 86%, from 192.4 ± 67.9 stems / 0.1 ha in 1997 to 27.2 ± 9.7 stems in 1998)

and remained low in the logged+fire treatment throughout the study (Figure 4-2). Declines in fire-only small stem counts occurred following the 2000 prescribed burn (dropping from a high of 349.2 ± 151.1 to 49.7 ± 15.1 per 0.1 ha). Repeated measures ANOVA of log transformed small stem counts indicated significant YEAR and TRT*YEAR effects (Table 4-1). Treatment differences are significant in the first two post-logging years (1998 and 1999) but disappear after the first prescribed fire in 2000 (Figure 4-2).

Post-logging species richness increased in the logged+fire plots relative to the fire-only plots (Figure 4-2). The main effect of YEAR was significant in an ANOVA of species richness per 1000-m² (Table 4-1). The TRT*YEAR interaction was significant ($p = 0.047$), indicating different temporal changes in species richness by treatment. Treatment differences were greatest in 1999 (two years post-logging), then diminished after prescribed burning in 2000 and 2005. Similar trends were not apparent in the 1-m² sample data (Table 4-1).

Changes in numbers of graminoid species are responsible for treatment differences in species richness. Individual ANOVA models showed significant temporal effects in graminoids species richness (per 1000-m²) only. The YEAR and TRT*YEAR effects were significant (Table 4-1). Similar to overall trends, treatment differences in graminoid richness were significant only in the second year post-logging (1999) and dissipated following prescribed fire (Figure 4-3). Similar trends were not apparent in forb and woody species richness.

Trends in Species Composition

Initial changes in species composition were pronounced in the logged+fire relative to the fire-only treatment. Successional trajectories from 1997 to 1998 are greater in magnitude and more uniform in direction for the logged+fire treatment, compared to the fire-only treatment. Trends are more pronounced at the 1000-m² than the 1-m² scale (Figure 4-4; PCA of 1-m² data

not shown). The 1000-m² PCA explained 36.3 percent of species variation in the first two dimensions (first four eigenvalues = 0.22, 0.13, 0.10, 0.08). Permutation tests of treatment and temporal effects support successional trends observed in PCA ordinations. The RDA of the pre- and post-logging 1000-m² species data (1997 vs. 1998), constrained by TRT*YEAR interaction effect, indicated differential species responses between treatments (Table 4-2; Figure 4-5). Similarly, this contrast was significant in constrained ordination of the 1-m² species data (Table 4-2).

The magnitude and direction of species composition shifts became increasingly similar between treatments over time. Successional trajectories between 1997 and 2005, represented by the PCA of 1000-m² species data, are similar between logged+fire and fire-only treatments (Figure 4-4). Permutation tests of YEAR and TRT*YEAR effects in RDA ordinations support the observed pattern in succession. The constrained ordination of 1000-m² species data from all years revealed significant YEAR effect, and TRT*YEAR interaction effects were marginally significant ($p = 0.07$; Table 4-2 and Figure 4-6). These effects were similarly significant in constrained ordinations of the 1-m² species data. Contrasts between first and last study years only (1997 vs. 2005) showed no TRT*YEAR interaction effect in either the 1-m² or 1000-m² species data (Table 4-2). As illustrated by the PCA of species data, successional trends from 1997 to 2005 were similar between treatments. Initial post-logging differences appear to have diminished at the end of the study.

Initial response of herbaceous species to logging was pronounced. Logging triggered increases in presence and abundance of many graminoid species and annual herbs. These species were identified as those with highest correlations (of abundance data) with the first constrained axis of the RDA of 1997 and 1998 data only. The first axis was constrained by

TRT*YEAR interaction (Figure 4-6; see Appendix A for species code legend). In RDA solutions of 1-m² and 1000-m² species data, there were more grasses, sedges, and forbs associated with the logged+fire treatment plots. Eight logging responders are sedges (member of the family *Cyperaceae*) and most of these are in the genus *Rhynchospora*. In addition, depending on observation scale, there are 6 or 10 forbs and several grass species that responded to logging. Many species that initially responded to logging were annuals, such as *Scleria muhlenbergia*, *Rhynchospora chapmanii*, *Eupatorium cappillifolium*, *Bidens mitis*, *Bartonia paniculata*, *Drosera brevifolia*, and *Diodia teres*. The response of an annual grass species, *Panicum verrecosum*, was particularly pronounced at both sample scales. A few sub-dominant perennial grasses responded quickly to woody removal, including *Panicum rigidulum*, *Paspalum floridanum*, and *Anthraenantia rufa*. In contrast, the few species associated with fire-only treatment in the first post-logging year are mainly shrubs and vines.

Compositional differences between treatments persisted over most of the study period. However, species associated with the logged+fire treatment over the study duration differed from the initial responders. None of the longer-term responders were annuals. Most long-term species associated with the logged+fire treatment were grasses, forbs, and a few sedges (at the 1000-m² scale: Figure 4-7). None were woody species. At the 1-m² scale, abundances of bluestem grasses (*Andropogon virginicus* and *A. cappilipes*) increased in response to the logged+fire treatment (Figure 4-7). Similarly, perennial sedges of the genus *Rhynchospora* (*R. elliotii*, *R. cephalanthus*, *R. oligantha*, and *R. gracilis*) increased in presence and abundance in the logged+fire treatment. The latter species was the dominant non-grass monocot of ACP pine savannas. Other post-logging responders included small statured perennial forbs, most having over-wintering rosettes and member of the families *Asteraceae* and *Xyridaceae*. Few species

were associated with the fire-only treatment over the study period at either sample scale, and these were mainly shrubs, vines, and forbs.

ACP Treatment Responses vs. Reference Conditions

Species-area relationships differed between restoration treatments at the end of the study period (Figure 4-8). An ANCOVA of the 2005 sample data revealed a significant treatment effect with initial BA included as a covariable in the model (TRT: $F_{1,40} = 6.1$, $p = 0.018$; initial BA: $F_{1,40} = 132.9$, $p < 0.0001$). Area was significant ($F_{1,40} = 47.39$, $p < 0.0001$) but the TRT*AREA interaction was not ($F_{1,40} = 0.49$, $p = 0.487$).

Species richness of the logged+fire ACP plots (in 2005) exceeded that of Lake Ramsey plots at the 10-m² sample area, although they were similar at the 1-m² scale. At the 10-m² scale, mean and standard error of Lake Ramsey species counts falls below the 95 percent confidence interval of the ACP logged+fire treatment (Figure 4-8). In contrast, species richness of the Penfound data exceeds that of both ACP treatment sites at areas $\geq 10\text{-m}^2$, exceeding ACP 95% confidence intervals. I was unable to formally test differences in species richness between Penfound and ACP data due to lack of replication and differences in sampling methods (overlapping vs. non-overlapping plot layouts). However, the species-area pattern of the ACP logged+fire treatment suggests recovery of ground cover richness approaching that of my historic reference site.

Both of the ACP restoration treatments prompted species composition changes that resembled reference site conditions. Compositional shifts were similar in direction but apparently differed in magnitude between treatments. The largest temporal changes were in plots with higher initial BA (Figures 3-8 and 3-9). The NMS ordination in Figure 4-8 compares presence-absence species data from Lake Ramsey and ACP successional vectors (10-m² plot

size). Most ACP trajectories indicate directional shifts toward the reference composition. Similar patterns were apparent in the NMS ordination of Penfound reference data plus ACP successional vectors (Figure 3-9). Compositional shifts of the high initial BA plots appear most pronounced along the first NMS axis, toward the Penfound data points. Smaller shifts of the “Low initial BA” plots are directed toward the “pine-cypress” Penfound data point specifically (Figure 3-9). In general, ACP treatments promoted compositional changes toward reference site composition.

Discussion

The current study demonstrates dramatic recovery of an ecologically degraded pineland plant community following restoration of natural forest structure and ecosystem processes. These results underscore the historical importance of forest structure and fire regime in maintaining this natural ecosystem, and the importance of timber management and prescribed burning for restoration of similarly degraded pinelands. The recovery of understory herbaceous vegetation was rapid, and resembled the quality of reference sites. Changes in ground cover species composition were pronounced following reduction of midstory shrubby vegetation in both ACP treatments, as the open aspect of pre-settlement conditions was restored. Although direction of change appeared similar between logging treatments, rates of change appeared to be accelerated by timber removal.

In this case, fire appeared to ultimately have a greater effect on ground cover species composition than mechanical tree harvest. Following two prescribed burns, trends in species richness and composition suggest convergence between mechanical restoration treatments, despite persistent differences in canopy densities. The mechanical activity of logging immediately reduced shrubby biomass, which prompted a flush of herbaceous growth and

diversity, which was subsequently sustained by prescribed fire. However, the initial tree basal area of fire-only sites was less than that of the logged+fire treatment. Within the range of my overstory tree basal area among treatments following logging (1-10-m²/ha), competitive interaction between canopy and understory vegetation was probably minimal compared to that of midstory and understory interactions. Thus, it should be noted that the positive restorative effects of fire might be limited at higher levels of tree basal area. In the logged+fire treatment, fire invoked woody biomass decline, subsequently resembling that of the fire-only treatment. The trend toward similarity in woody biomass roughly coincided with convergence in herbaceous plant richness and composition between treatments.

Fire mediated effects are most pronounced in the ground layer. Streng et al. (1993) suggested that frequent fire promotes establishment of rarer species in an environment dominated by long-lived perennials by freeing up space and resources available for colonization, and by reducing competition from dominant grasses and woody species. Fire likely decreases competition between understory woody and herbaceous plants for light and space (Platt et al. 1988a, Streng et al. 1993, Glitzenstein et al. 2003, Walker and Silletti 2006). Other restoration studies report herbaceous vegetation recovery in response to fire plus hardwood reduction that exceeded that expected from the chemical and mechanical treatments alone (Brockway and Outcalt 2000, Provencher et al. 2001). In the latter, fire alone prompted greater herbaceous ground cover response than mechanical hardwood reduction in Florida longleaf pine sandhill restoration (Provencher et al. 2001). Similar to my results, fire effects on ground cover vegetation extend beyond reduction of canopy density (Platt et al. 1988a, Robbins and Myers 1992, Waldrop et al. 1992, Streng et al. 1993, Provencher et al. 2001).

The restoration treatments preferentially prompted responses of species that are characteristic of pine savanna natural areas. All species that responded to restoration treatments were native, and with few exceptions, were not ruderal generalists. Species that initially responded to logging were characteristic savanna herbaceous species. The flush of “new” species included many grasses (plant family *Poaceae*) and sedges (family *Cyperaceae*), particularly small statured, rhizomatous species of the genus *Rhynchospora*. Longer-term species responders were primarily sedges and perennial forbs. Plant populations likely persisted at ACP during the period of fire suppression, either in the seed bank or in dormant vegetative states. The initial flush of rhizomatous sedges and clonal grasses suggests long term persistence in vegetative states followed by rapid growth in response to increased light and space. These dormant lifeforms may not have been detected in pre-treatment sampling. Increases in species richness and abundance have been noted in other studies of woody removal by mechanical and chemical means (Greenberg et al. 1995, Harrington and Edwards 1999, Brockway and Outcalt 2000, Provencher et al. 2000, Provencher et al. 2001). In these studies, increased richness and cover were attributed to soil disturbance as a direct effect of mechanical manipulations (Greenberg et al. 1995, Harrington and Edwards 1999, Cox et al. 2004), in addition to indirect effects of increased light, moisture, and space availability (Harrington and Edwards 1999, Brockway and Outcalt 2000, Provencher et al. 2000, Provencher et al. 2001). Most studies indicate eventual increases in native species typical of the focal habitat, rather than increases in exotic or ruderal species (but see Greenberg et al. 1995, Harrington and Edwards 1999).

The absence of ruderal additions to the local species pool affirms predictions that ecologically sensitive logging would not cause novel trends in post-logging succession. The number and abundance of non-ruderal annual species increased in response to logging, but

declined after the first year. Similarly, restoration of Florida xeric pinelands via mechanical methods prompted an initial insurgence of native ruderal species (Greenberg et al. 1995, Provencher et al. 2000), although the short duration of these studies precluded eventual detection of decline. Similar to my findings, these studies documented no invasions of non-native species that invoked novel succession.

Response of pine savanna herbaceous vegetation to woody reduction apparently differs by life form type across moisture conditions. Restoration of xeric pineland communities of the Gulf and Atlantic Coastal Plain regions (via mechanical, chemical, and prescribed burning treatments) prompted greatest increases in forb richness and abundance (Brockway and Outcalt 2000, Provencher et al. 2000, Provencher et al. 2001, Platt et al. 2006), whereas prescribed burning of wet-mesic Atlantic coastal pine savannas simulated increases in grasses and sedges (Walker and Peet 1983, Glitzenstein et al. 2003). Although I documented increases in all herbaceous life form types following restoration treatments, grass and sedge increases were most pronounced in my mesic to wet pine savanna site. These observations suggest similar restoration treatments in different moisture conditions may trigger different compositional responses, relative to the composition of the residual species pool and the differential loss of species groups (Walker and Silletti 2006).

ACP Restoration Compared to Reference Model

Ground cover vegetation of ACP ultimately resembled that of my reference sites following restoration of stand structure. Successional endpoints of ACP treatments were similar to both the historic (Penfound) and contemporary (Lake Ramsey) reference data. Congruence may be attributable to shifts in composition (constituent species and relative abundances) rather than changes in species richness (species presence). Species richness increases were sustained in

the logged+fire treatment only, and these numbers approached those of the historic (Penfound) reference condition. Similarly, species richness of fire suppressed Florida longleaf pine sandhills increased following mechanical hardwood reduction coupled with fire, approaching and in some cases exceeding that of the reference site (Provencher et al. 2001). The authors credit fire as the dominant cause of increases in species richness and densities.

Succession in response to restoration of stand conditions and ecosystem function depended largely on starting conditions. Compositional shifts were qualitatively similar between treatments and over varying initial of canopy and midstory densities. However, the magnitude of ground cover response depended on initial canopy and midstory densities, which ranged considerably (approximately 10 – 22 m²/ha basal area and 24 – 756 stems (< 10 cm dbh) per 0.1 ha). Restoration responses relative to starting condition have been observed by others (White and Walker 1997, Walker and Silletti 2006), with densely wooded sites having largest vegetation responses to woody biomass reductions.

Although studies of pineland restoration document significant changes in ground cover vegetation (Greenberg et al. 1995, Harrington and Edwards 1999, Brockway and Outcalt 2000, Provencher et al. 2000, Provencher et al. 2001, Walker and Silletti 2006), most do not include explicit and quantitative comparisons to reference models. Changes in species composition or richness alone do not necessarily indicate restoration success, if the goal is to mimic some historical or contemporary “natural” condition. It is possible to trigger novel or unintended succession that may be difficult to detect without reference comparisons (Fule et al. 1997, White and Walker 1997). Comparison of treatment responses to proximate and quantitative reference data allowed me to assess progress and conclude that efforts have promoted vegetation recovery

approximating that of desired conditions. Furthermore, undesirable non-native or weedy species were not introduced nor was undesirable succession invoked.

Management and Conservation Implications

Success of pineland restoration depends in large part on starting conditions and ecological resiliency of the treatment site. To date, few studies in the Southeastern Coastal Plain indicate the potential of plant community recovery, in terms of species composition and diversity, resembling a desired condition (Harrington and Edwards 1999, Brockway and Outcalt 2000, Hedman et al. 2000, Provencher et al. 2001, Glitzenstein et al. 2003, Platt et al. 2006). These studies indicate ground cover vegetation recovery following reduction of woody biomass via various means, including mechanical and chemical methods, and prescribed burning (Harrington and Edwards 1999, Brockway and Outcalt 2000, Provencher et al. 2001). It is important to examine ecological starting conditions represented in these restoration studies, and compare these to the current study. Where available, approximate mean starting (or control) densities of mechanically or chemically treated sites (in longitudinal or retrospective studies) were as follows: 10.4 m²/ha basal area (Harrington and Edwards 1999), ~124 (oak) stems/0.1 ha (Provencher et al. 2001), and ~14-18 m²/ha basal area and ~53-130 stems/0.1 ha (Hedman et al. 2000). Canopy and midstory densities of the aforementioned studies appear to approximate densities of typical second growth pine stands not subjected to industrial plantation management (basal areas < 20 m²/ha; see Robertson and Ostertag 2007). By comparison, my starting basal areas of roughly 10-22 m²/ha were similar to those of Harrington and Edwards (1999) and Hedman et al. (2000). However, initial stem densities of my treatment sites were high in comparison to those reported, and my initial variance was also large (overall mean and standard error is 241.4 ± 81.7; range 47-781 stems/0.1 ha). My higher stem density mean and variance

may be attributable to differences in moisture conditions and community type. Other restoration study sites were upland woodlands or dry upland sandhills, whereas mine contained mesic and wet pine savanna communities.

These results contribute to an overall model of restoration potential for Southeastern Coastal Plain pinelands. Similar to other studies, mine indicates that ground cover recovery is possible on degraded pineland site that has suffered fire suppression and/or fire regime alteration over a period of 10-20 years, and the associated dense woody growth. Recovery is possible in the absence of previous extensive soil disturbance associated with past agricultural or silvicultural land uses. Little is known about the resiliency of pineland ground cover following ground tilling, although Hedman et al. (1999) and Ostertag and Robertson (2006) found evidence of persistent changes in succession in second growth pinelands on fallow fields. Furthermore, the current study shows plant community recovery is possible in a wetter site, with a species pool adapted to different moisture and edaphic conditions than those previously examined.

Although reintroduction of native fire regime was arguably the most important management prescription for ecological restoration, there were benefits to canopy removal via commercial logging at ACP. Over time, it is likely that frequent fire alone would eventually reduce woody vegetation in fire suppressed pinelands such as ACP. However, reduction of woody vegetation in this manner may require decades of frequent and intense burning (Waldrop et al. 1992, Glitzenstein et al. 1995, Olson and Platt 1995, Drewa et al. 2002). This may exceed the time in which remnant populations of ground cover species are available for re-colonization (Hedman et al. 2000, Walker and Silletti 2006). For this reason, expediting restoration of stand structure using mechanical methods may enhance ecological restoration. In addition, financial

returns from commercial timber sale may offset restoration costs without introducing detrimental effects.

These results, along with other restoration studies, demonstrate that ground cover vegetation recovery is possible in degraded pine savannas over a range of starting conditions, without resorting to artificial species reintroductions. Furthermore, results highlight the innate resiliency of pineland groundcover plant communities. Life history adaptations of plant species for dormancy may buffer populations in periods of atypical environmental conditions (i.e. fire suppression). Temporal rebounds of plant community composition suggest some degree of successional “stability” within a range of fire regime and stand structure variability.

However, succession in former pinelands that have been severely altered (ground tilling, agricultural land uses, and fire suppression exceeding several decades) may exceed that range of resiliency and require more intensive restoration treatments to achieve reference conditions (Walker and Silletti 2006). Although re-seeding efforts were successful in former longleaf pine sandhills (Seaman 1998, Cox et al. 2004), it is costly which limits its application to small areas (Walker and Silletti 2006). Because of this, treatments of lower intensity and cost are desirable, and appropriate for ecological restoration of large areas (Provencher et al. 2001). Fortunately, restoration of Southeastern Coastal Plain pineland stands with mechanical woody reduction can be labor and cost efficient, and yield favorable results if coupled with appropriate fire management.

Table 4-1. ANOVA tables for models of species richness and stem numbers. Main, interaction, and covariable effects listed in “Effect” column. “Slice” effects (treatment effects in individual YEARS) indicated for first three models. The covariance structure and number of parameters selected for each model are listed. P-values less than critical values are shown in bold type.

Model	Cov structure	Effect	Num df	Den df	F-value	p-value
Number stems (1000 m ²)	Hetero toeplitz (9 cov parameters)	Treatment	1	7.01	3.57	0.101
		Year	4	7.89	10.54	0.003
		Trt*Year	4	7.89	13.88	0.001
		1997: Trt effect	1	8.31	0.01	0.923
		1998: Trt effect	1	7.87	9.37	0.016
		1999: Trt effect	1	7.13	7.51	0.02
		2000: Trt effect	1	7.45	1.97	0.2
		2005: Trt effect	1	7.33	1.61	0.243
Total species (1000 m ²)	Antedependence (9 cov parameters)	Treatment	1	7.1	2.98	0.13
		Year	4	9.5	4.81	0.022
		Trt*Year	4	9.5	3.64	0.047
		1997: Trt effect	1	7	0.23	0.644
		1998: Trt effect	1	7	3.89	0.089
		1999: Trt effect	1	7	8.96	0.02
		2000: Trt effect	1	7	6.18	0.042
		2005: Trt effect	1	7	4.59	0.069
Gram species (1000 m ²)	Autoregressive (2 cov parameters)	Treatment	1	7.95	2.56	0.149
		Year	4	27.3	3.79	0.014
		Trt*Year	4	27.3	7.82	0.001
		1997: Trt effect	1	16	4.73	0.045
		1998: Trt effect	1	16	3.82	0.068
		1999: Trt effect	1	16	8.81	0.009
		2000: Trt effect	1	16	3.99	0.063
		2005: Trt effect	1	16	1.99	0.178
Forb species (1000 m ²)	Antedependence (9 cov parameters)	Treatment	1	7.03	0.39	0.551
		Year	4	8.71	2.23	0.148
		Trt*Year	4	8.71	1.4	0.311
Woody species (1000 m ²)	Autoregressive (2 cov parameters)	Treatment	1	7.22	0.62	0.458
		Year	4	27.8	3.08	0.032
		Trt*Year	4	27.8	1.99	0.124
Total species (1 m ²)	Autoregressive (2 cov parameters)	Initial BA	1	5.7	31.19	0.002
		Treatment	1	5.84	6.7	0.042
		Year	4	26.7	3.42	0.022
		Trt*Year	4	26.7	1.8	0.159

Table 4-2. Results of Monte Carlo permutation tests from RDA constrained ordinations. Specific datasets subjected to ordinations and permutation tests are listed in left column (1000 and 1-m² species data), along with data matrix dimensions. The null hypothesis tested is listed in the Model column. Significant p-values highlighted in bold text.

Dataset	Matrix dimension	Model	Sum all eigenvalues	First canonical eigenvalue	F-ratio	p-value
1000 m ² 4 years	36 plots x 217 spp	No YEAR effect	0.369	0.057	4.62	0.05
		No YEAR*TRT effect	0.341	0.022	1.71	0.07
1000 m ² '97 vs. '98	18 plots x 190 spp	No YEAR*TRT effect	0.141	0.044	3.2	0.02
1000 m ² '97 vs. '05	18 plots x 193 spp	No YEAR*TRT effect	0.204	0.037	1.53	0.17
1 m ² 5 years	45 plots x 121 spp	No YEAR effect	0.308	0.034	4.22	0.01
		No YEAR*TRT effect	0.279	0.016	2.09	0.02
1 m ² '97 vs. '98	18 plots x 98 spp	No YEAR*TRT effect	0.123	0.026	1.85	0.03
1 m ² '97 vs. '99	18 plots x 96 spp	No YEAR*TRT effect	0.138	0.065	1.62	0.05
1 m ² '97 vs. '05	18 plots x 99 spp	No YEAR*TRT effect	0.209	0.032	1.26	0.17

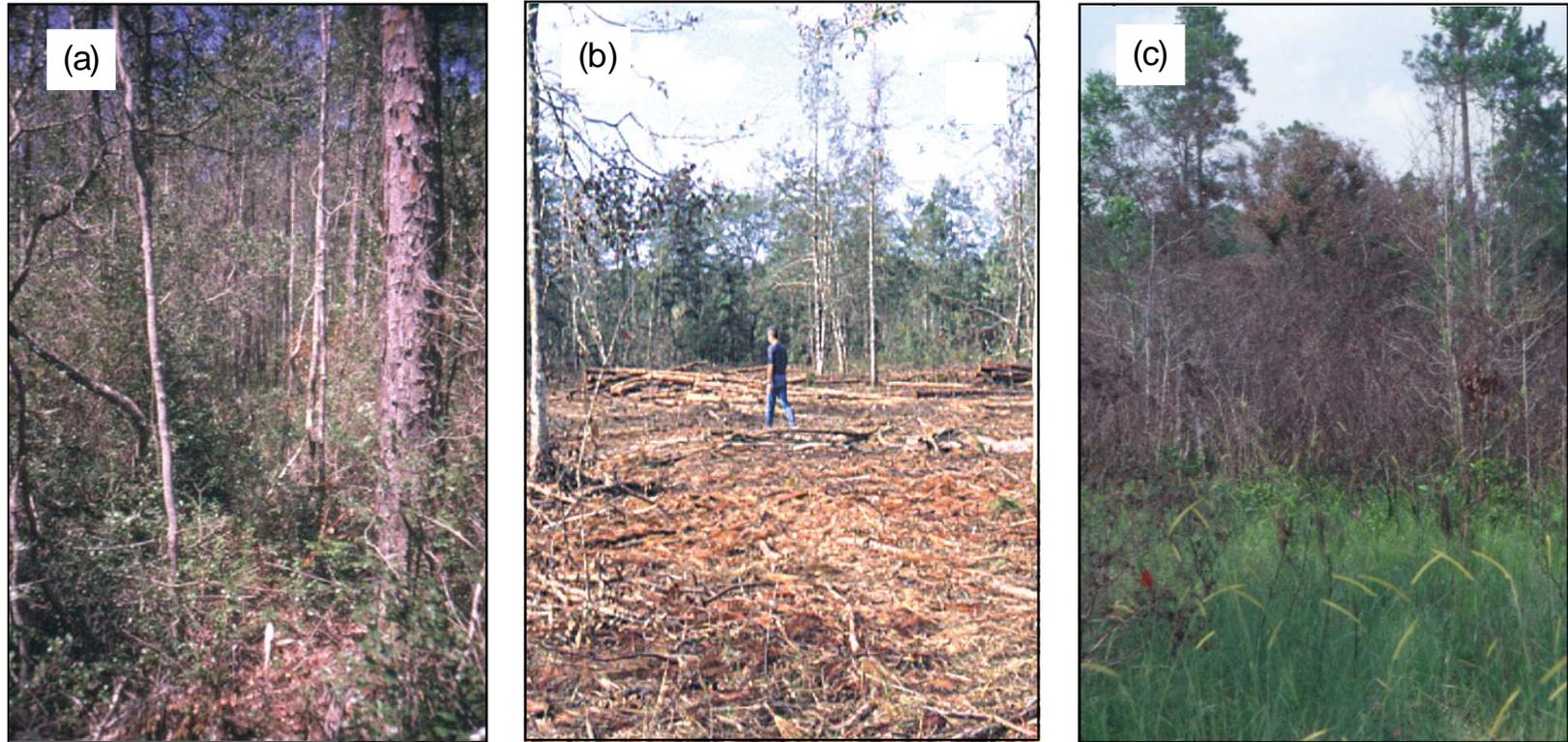


Figure 4-1. ACP pictures: (a) pre-treatment in 1997, (b) immediately after logging in 1998, and (c) after logging and first prescribed fire in 2000.

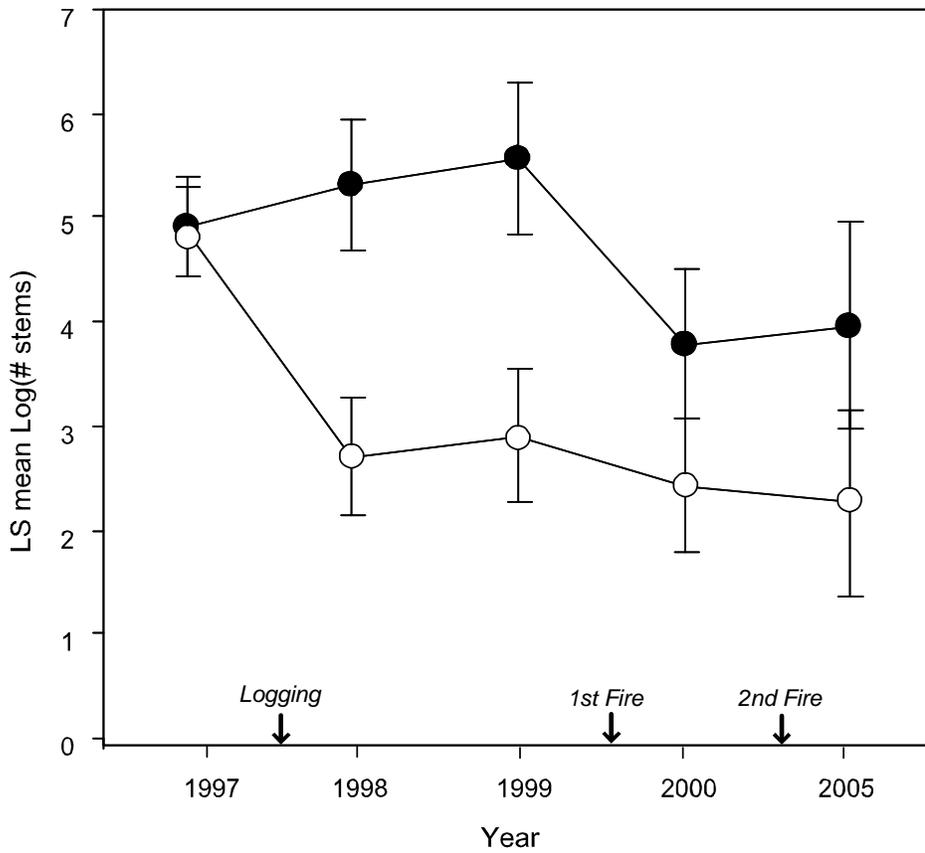


Figure 4-2. Least squares means (LS means) and standard errors of the number of small stems (< 15 cm dbh) per 1000-m² sample. Closed circles = fire-only plots, open circles = logged+fire plots. Arrows indicate timing of specific restoration treatments.

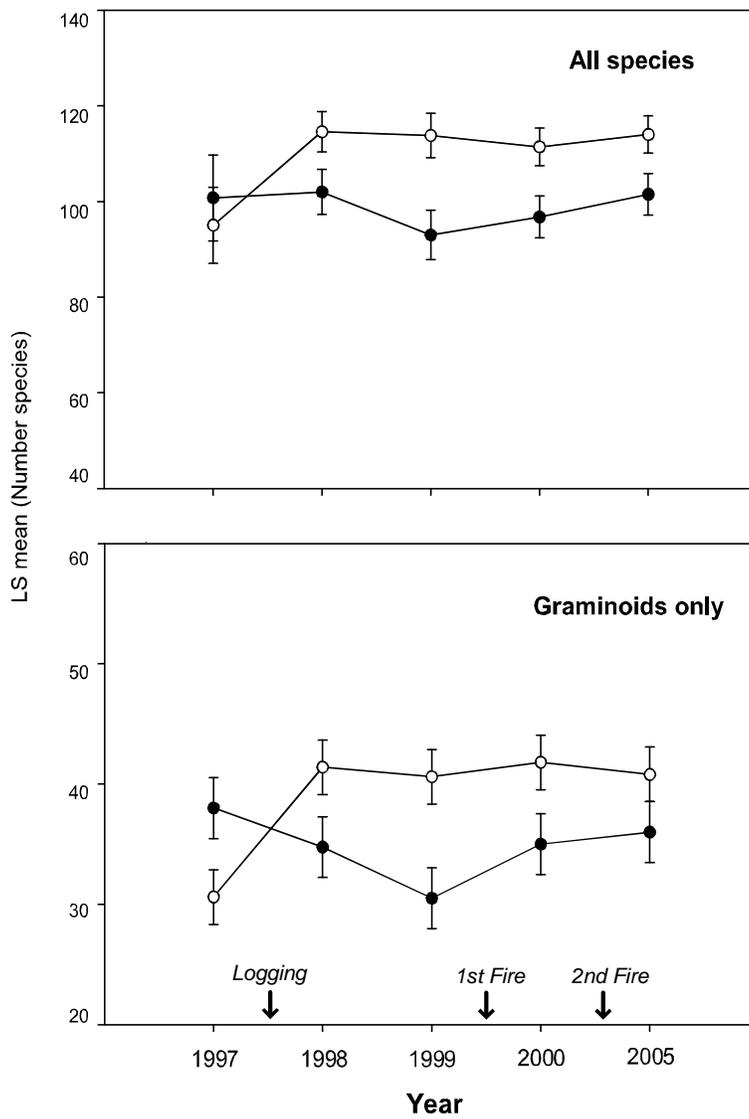


Figure 4-3. Least square means (LS means) and standard errors of species richness by treatment and year. Open circles = logged+fire treatment; closed circles = fire-only treatment. Top plot shows total species richness 1000-m² sample area; bottom plot shows means of graminoid species only. Timing of treatments indicated by arrows.

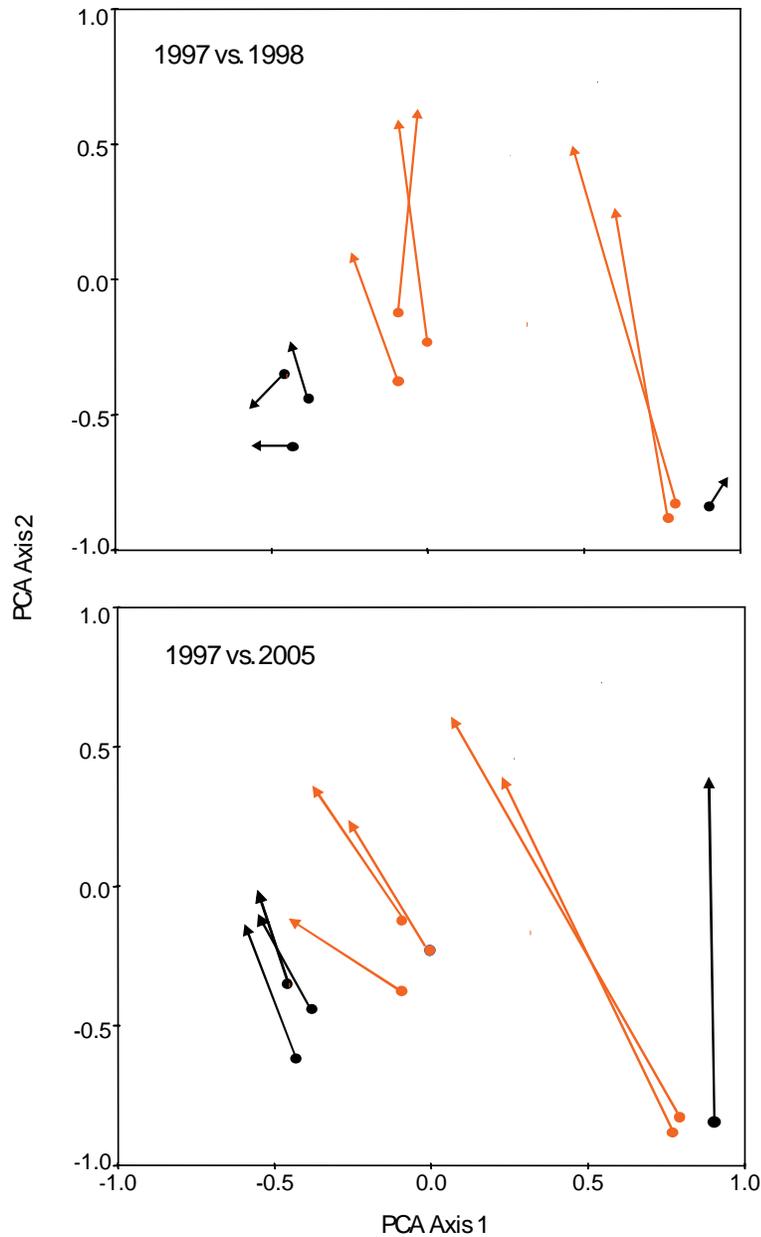


Figure 4-4. PCA ordination of ACP species data (1000-m² scale); first two ordination axes displayed. Dots indicate 1997 pre-treatment compositional data in ordination space. Successional trajectories correspond to compositional shifts of data from individual plots: red = logged+fire treatment, black = fire-only treatment. Top plot shows changes between pre-treatment and first post-logged years (1997 vs. 1998). Bottom plot shows shifts from pre-treatment (1997) and after logging and fire (2005).

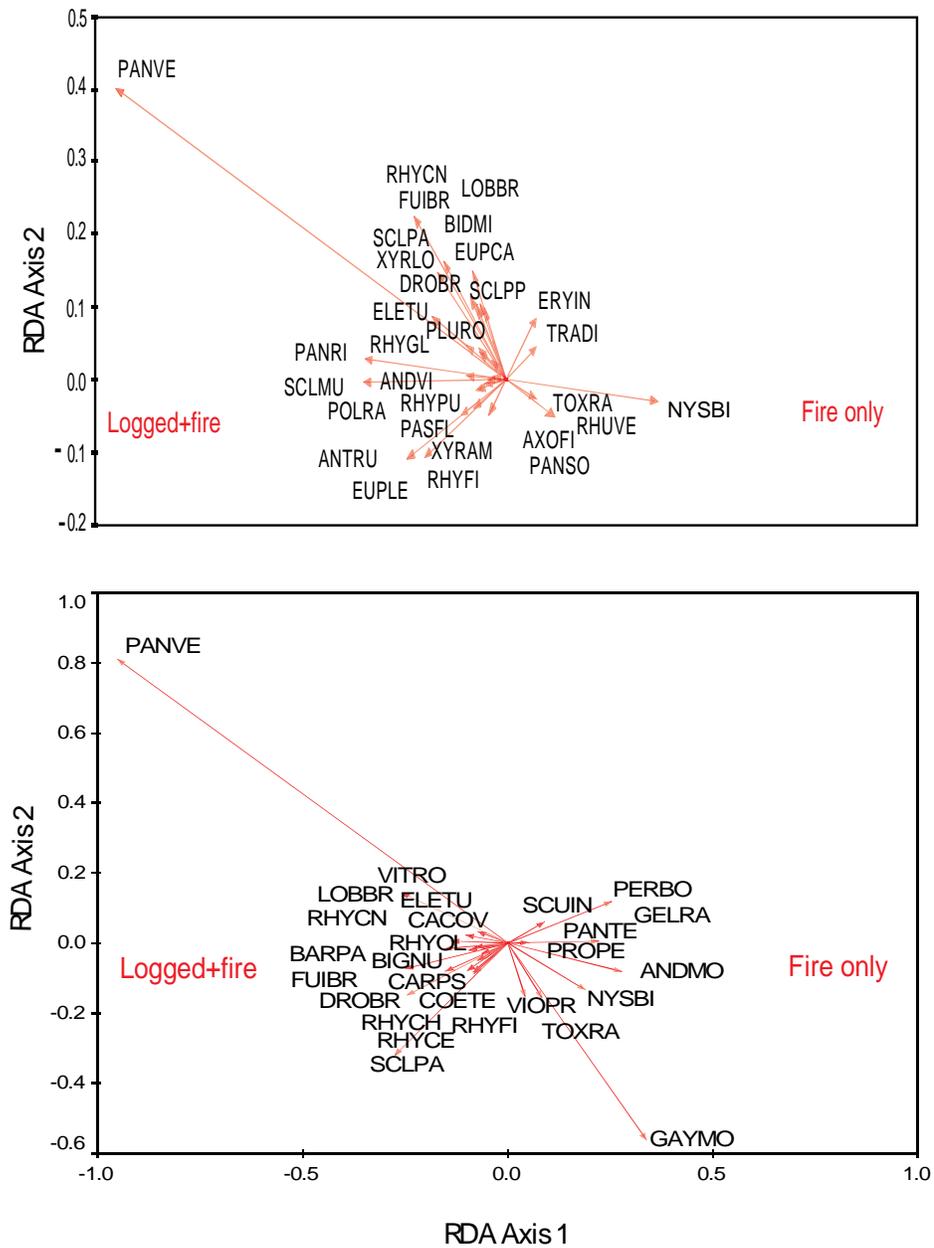


Figure 4-5. Constrained RDA ordinations of pre-logged (1997) and first post-year (1998) species data. First canonical axes are constrained by TRT*YEAR interaction. Species highly correlated with first canonical axes are displayed by vectors and codes (see Appendix C for species names). Top plot displays RDA of 1000-m² species data; bottom plot shows 1-m² species data. Note different scales of Axis 2.

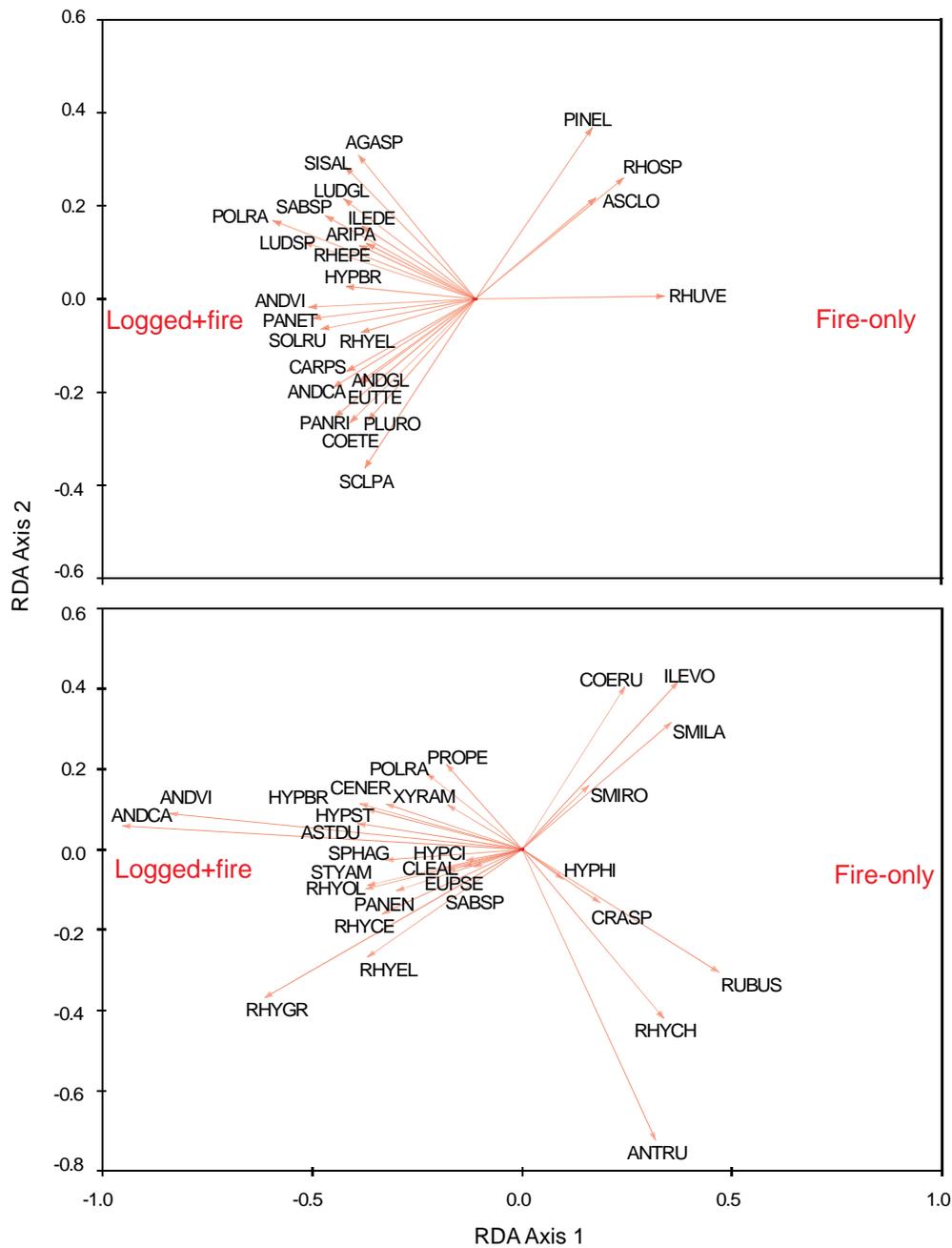


Figure 4-6. Constrained RDA ordinations of ACP species data including 1997 pre-treatment data. Top plot = 1000-m² data (excluding 1999 data), bottom plot = 1-m² species data (all years). First canonical axes are constrained by TRT*YEAR interaction indicated by treatment label in red text. Species most highly correlated with first canonical axes are displayed by red vectors and codes (see Appendix C). Vector length and angles indicate strength and direction of correlation.

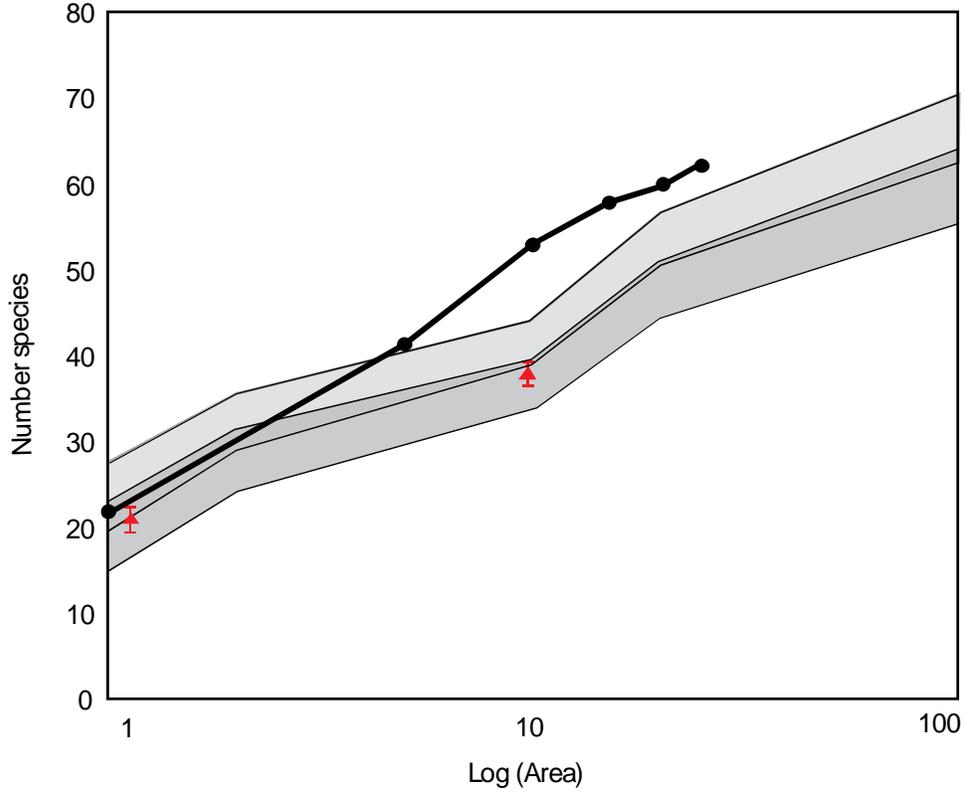


Figure 4-7. Number species per log sample area (m^2): mean species counts from ACP treatments vs. Penfound and Lake Ramsey species richness. Shaded regions show 95% confidence intervals of ACP treatment means from 2005 samples; areas = 1, 2, 10, 20, and 100- m^2 . Light shading = logged+fire; dark shading = fire-only. Dark line denotes species numbers from Penfound "cut-over pineland" at areas = 1, 5, 10, 15, 20, and 25 m^2 . Red triangles show means and standard errors of Lake Ramsey species richness ($n = 11$) at areas = 1 and 10- m^2 .

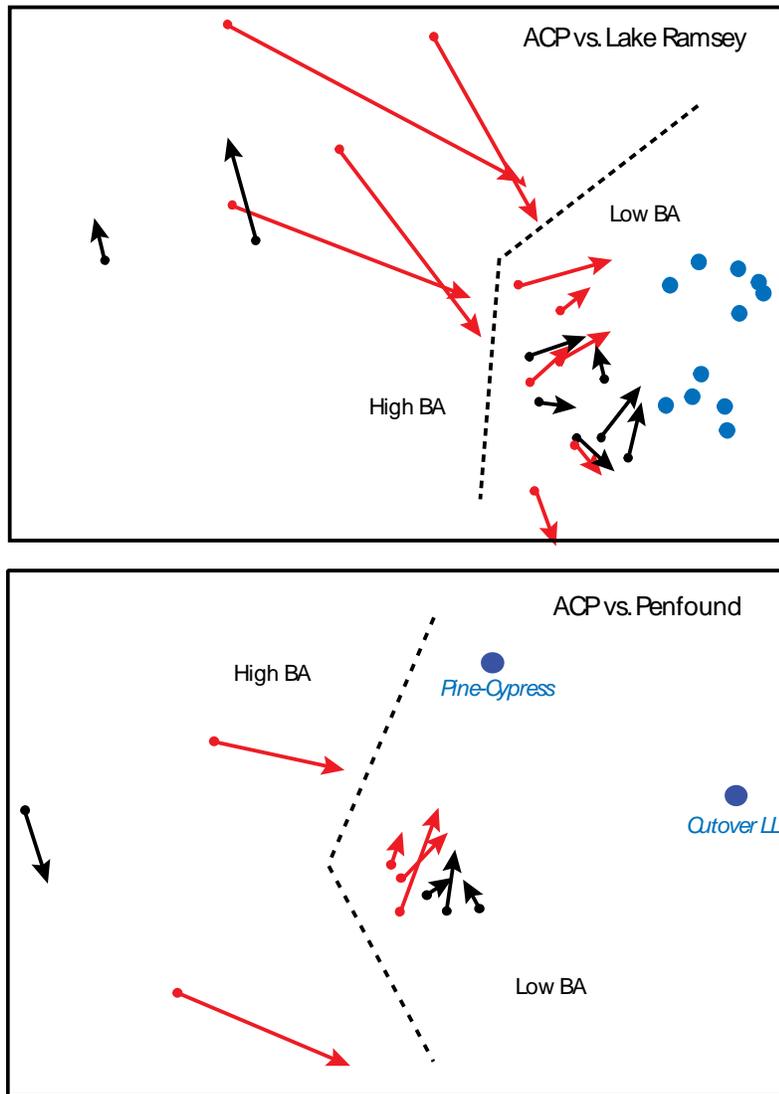


Figure 4-8. Successional trends of ACP species data compared to Penfound and Lake Ramsey reference data (NMS ordination of presence-absence data of comparable sample sizes – see text). Red vectors depict compositional shifts in the logged+fire treatment between 1997 and 2005; black vectors depicts shifts in fire-only treatment. Blue symbols show relative positions of reference data in ordination space. Bold dashed lines separate ACP samples with High and Low initial BA.

CHAPTER 5 CONCLUSION

My dissertation presents a vegetation classification of pineland communities in Florida, a model of the relationships between species composition and physical and spatial factors, and description of temporal variation of pineland species composition in response to restoration of fire regime and forest structure. The research revealed predictable spatial patterns of species composition at both local and regional scales, and suggests resiliency of community composition to temporary alterations to fire regime and timber density. Furthermore, the study of ecological restoration suggests the resiliency of pineland vegetation, in that recovery approximating natural conditions followed re-introduction of native fire regimes after a long period of fire suppression.

I presented a comprehensive vegetation classification based on floristic similarity, using K-means cluster analysis and ordination methods. I recognized three ecological series corresponding to idealized moisture conditions. These were further divided into 16 associations. The series included Dry Uplands (6 associations), Mesic Flatwoods (3 associations), and Wetlands (7 associations). Summary information described each community association relative to species diversity, woody plant structure, diagnostic species, and environmental and physiographic features. Floristic variation varied greatly with geographic segregation and edaphic characteristics, particularly between the panhandle and peninsula regions of Florida. Distinctions between community associations were related to the prominence of species with restricted distributions, and to a lesser degree, endemic species. The floristic classification presented here is comprehensive but applicable in the field, compared to other classification based on regional flora.

The spatially explicit model of environmental-composition relationship revealed many of the same patterns seen in the floristic classification. Most notably, the effects of geographic

separation were prominent in community structure, particularly the floristic distinctions between the panhandle and peninsula. However, the effects of local environmental factors dominated vegetation gradients, particularly variables related to topography and soil moisture. In the context of all environmental factors, both regional and local environmental effects appear to influence vegetation patterns. Effects of pure spatial structure were also evident, although these made up a much smaller proportion of explained variance than environmental effects. Variation associated with recent fire regime and timber stand structure may have contributed to unexplained variance. I interpret the data as demonstrating a relatively strong control of environmental factors on the distribution of pineland species, with biotic control mechanisms and historical biogeography playing a lesser role.

The study of ground cover vegetation recovery following fire and stand structure restoration suggests the resiliency of pineland community composition to atypical environmental alterations. Temporal variation in pineland community structure is poorly understood relative to spatial variation. However, longitudinal studies following restoration treatments shed light on succession that is within the range of “natural” community stability. The study of ecological restoration following a relatively long period of suppression of native fire regime demonstrates that there is a certain degree of successional “stability” in pineland community structure.

Ecological restoration of a degraded Coastal Plain pineland remnant was successful in terms of ground cover vegetation recovery that resembled reference site conditions. These results suggest that recovery is possible on sites that have suffered moderate to severe fire suppression but minimal ground disturbance (from cultivation). Ground cover species richness was enhanced by overstory and midstory woody biomass reduction, mainly as increases in detectable graminoid species. Furthermore, species richness and composition of restoration

treatments converged following two prescribed fires suggesting both the relative importance of fire in ecological restoration and minimal adverse effects from mechanical logging. Pine removal via carefully supervised mechanical logging does not appear to adversely affect savanna vegetation recovery, and may expedite overall community restoration.

In sum, results of this observational and experimental research are relevant to conservation and management of pyrogenic pineland communities of the Southeastern Coastal Plain. The classification of Florida pineland communities based on compositional similarities can be applied to inventory and restoration efforts in the State and surrounding regions. In addition, the classification provides useful reference conditions for restoration, a basis for quantifying regional variation in community variation, and specific diagnostic indicators for community identification. The model of environmental-composition relationships contributes to the overall understanding of environmental determinants of pineland vegetation, in addition to quantifying ranges of environmental conditions correlated to compositional variation. The final restoration study showed that pine savanna vegetation is resilient to moderate degradation related to fire suppression, and can rebound following reconstruction of native stand structure. These results add to the regional model of ecological restoration in the Southeast, specifically by showing that restoration is achievable in wet pineland sites with increased alteration from fire suppression.

APPENDIX A
LOCATIONS OF SAMPLE PLOTS AND SITES

Table A-1: Vegetation sample plots listed by code (“Plot”). Site code indicates Site containing plots. The assigned community association (“Assoc”) is indicated by code (see Figure 2-3). Latitude and Longitude indicated in decimal degrees. Some specific plot locations are not reported as per landowner request (“NR”). “Region” indicates ecoregion delineation used for site stratification (see text). “Management Area” indicates public land unit; private lands are noted. Abbreviations indicate management unit types: SF = State Forest, AFB = Air Force Base, AFR = Air Force Range, SP = State Park, WMA = Wildlife Management Area, NF = National Forest, ARD = Apalachicola Ranger District, WRD = Wakulla Ranger District, NFWMD = Northwest Florida Water Management District, SWFWMD = Southwest Florida Water Management District, DEP = Florida State Department of Environmental Protection, NWR = National Wildlife Refuge, CA = Conservation Area (State), SRA = State Recreation Area, TNC = The Nature Conservancy preserve.

Region	Management Area	Site	Plot	Assoc	Latitude	Longitude
Northwest Uplands	Blackwater River SF	BW01	FL092	D4	8639.023	3054.668
Northwest Uplands	Blackwater River SF	BW01	FL093	W6	8638.869	3054.435
Northwest Uplands	Blackwater River SF	BW01	FL094	D6	8638.835	3054.417
Northwest Uplands	Blackwater River SF	BW02	FL098	D5	8652.411	3043.187
Northwest Uplands	Blackwater River SF	BW03	FL099	D4	8656.497	3050.387
Northwest Uplands	Blackwater River SF	BW03	FL100	W6	8656.545	3050.399
Northwest Uplands	Blackwater River SF	BW03	FL275	W7	8656.577	3050.434
Northwest Uplands	Blackwater River SF	BW03	FL276	W5	8656.378	3050.381
Northwest Uplands	Blackwater River SF	BW01	FL284	D5	8639.132	3054.441
Northwest Uplands	Blackwater River SF	BW01	FL285	D4	8639.738	3054.574
W Panhandle Gulf Coast	Eglin AFB	EG08	FL058	M2	8625.442	3027.510
W Panhandle Gulf Coast	Eglin AFB	EG02	FL304	M2	8645.831	3025.537
W Panhandle Gulf Coast	Eglin AFB	EG02	FL041	D4	8645.827	3025.486
W Panhandle Gulf Coast	Eglin AFB	EG02	FL042	W6	8645.905	3025.583
W Panhandle Gulf Coast	Eglin AFB	EG02	FL046	D4	8646.216	3025.085
W Panhandle Gulf Coast	Pt. Washington SF	PT01	FL280	D4	8608.742	3020.642
W Panhandle Gulf Coast	St. Joe Bufferlands (DEP)	SJ01	FL022	M2	8517.839	2942.753
W Panhandle Gulf Coast	St. Joe Bufferlands (DEP)	SJ01	FL163	W6	8517.886	2942.757
W Panhandle Gulf Coast	St. Joe Bufferlands (DEP)	SJB01	FL255	M1	8517.558	2942.183
W Panhandle Gulf Coast	St. Joe Bufferlands (DEP)	SJ01	FL257	W6	8516.240	2942.836
W Panhandle Gulf Coast	St. Joe Bufferlands (DEP)	SJ01	FL258	W6	8515.401	2943.102
W Panhandle Gulf Coast	Topsail SP	TP01	FL077	M2	8617.644	3022.437
W Panhandle Gulf Coast	Topsail SP	TP01	FL078	W6	8617.739	3022.383
W Panhandle Gulf Coast	Topsail SP	TP01	FL079	M2	8618.011	3022.380
W Panhandle Gulf Coast	Topsail SP	TP01	FL293	M2	8617.609	3022.307
West Panhandle Sandhills	Eglin AFB	EG01	FL040	D4	8643.830	3029.049
West Panhandle Sandhills	Eglin AFB	EG03	FL043	D4	8647.440	3027.046

Table A-1 continued

Region	Management Area	Site	Plot	Assoc	Latitude	Longitude
West Panhandle Sandhills	Eglin AFB	EG03	FL044	D4	8646.915	3027.165
West Panhandle Sandhills	Eglin AFB	EG03	FL045	W4	8646.786	3027.083
West Panhandle Sandhills	Eglin AFB	EG04	FL047	D4	8613.336	3036.250
West Panhandle Sandhills	Eglin AFB	EG05	FL048	D4	8611.709	3037.040
West Panhandle Sandhills	Eglin AFB	EG05	FL049	D6	8611.971	3036.542
West Panhandle Sandhills	Eglin AFB	EG06	FL050	D4	8651.788	3030.834
West Panhandle Sandhills	Eglin AFB	EG07	FL051	D4	8646.726	3027.923
West Panhandle Sandhills	Eglin AFB	EG07	FL052	D4	8646.742	3028.417
West Panhandle Sandhills	Eglin AFB	EG07	FL053	D4	8646.616	3028.509
West Panhandle Sandhills	Eglin AFB	EG04	FL054	M2	8613.419	3036.190
West Panhandle Sandhills	Eglin AFB	EG04	FL055	D6	8612.760	3035.829
West Panhandle Sandhills	Eglin AFB	EG06	FL056	D4	8651.927	3031.046
West Panhandle Sandhills	Eglin AFB	EG07	FL057	D4	8646.748	3028.740
West Panhandle Sandhills	Eglin AFB	EG04	FL095	W6	8613.417	3036.402
West Panhandle Sandhills	Eglin AFB	EG05	FL096	W7	8611.918	3036.500
West Panhandle Sandhills	Eglin AFB	EG04	FL097	W7	8613.460	3036.581
Marianna Lowlands	Apalachee WMA	AP01	FL076	D5	8457.250	3047.156
Marianna Lowlands	Apalachee WMA	AP01	FL090	D5	8457.504	3048.523
Marianna Lowlands	Apalachee WMA	AP01	FL091	D5	8457.343	3048.404
Marianna Lowlands	Falling Waters SP	FW01	FL074	D6	8531.682	3043.656
Marianna Lowlands	Falling Waters SP	FW01	FL075	D6	8531.796	3043.587
Marianna Lowlands	Falling Waters SP	FW01	FL085	D5	8531.530	3043.739
Marianna Lowlands	Rock Hill TNC	RH01	FL060	D6	8529.065	3044.275
Marianna Lowlands	Rock Hill TNC	RH01	FL065	W6	8529.151	3044.134
Marianna Lowlands	Rock Hill TNC	RH01	FL089	D6	8529.375	3044.358
Marianna Lowlands	Rock Hill TNC	RH01	FL287	W5	8530.054	3044.665
Marianna Lowlands	Rock Hill TNC	RH01	FL288	W6	8530.190	3044.662
Marianna Lowlands	Rock Hill TNC	RH01	FL292	D5	8529.503	3044.369
Marianna Lowlands	Three Rivers SP	TR01	FL070	D5	8455.295	3044.163
Marianna Lowlands	Three Rivers SP	TR01	FL071	D5	8455.173	3044.162
East Panhandle Sandhills	Apalachicola Bluffs TNC	AB01	FL059	D4	8458.419	3027.440
East Panhandle Sandhills	Apalachicola Bluffs TNC	AB02	FL061	D4	8458.438	3028.383
East Panhandle Sandhills	Apalachicola Bluffs TNC	AB02	FL066	D4	8458.303	3028.538
East Panhandle Sandhills	Apalachicola NF: WRD	WD01	FL011	D2	8415.779	3021.186
East Panhandle Sandhills	Apalachicola NF: WRD	WD01	FL012	D2	8415.845	3021.163
East Panhandle Sandhills	Apalachicola NF: WRD	WD03	FL018	D2	8420.988	3019.288
East Panhandle Sandhills	Apalachicola NF: WRD	WD03	FL019	D2	8421.027	3019.361
East Panhandle Sandhills	Apalachicola NF: WRD	WD01	FL229	W1	8416.194	3021.513
East Panhandle Sandhills	Apalachicola NF: WRD	WD03	FL230	W1	8421.040	3019.371
East Panhandle Sandhills	Apalachicola NF: WRD	WD01	FL259	D2	8416.217	3021.525
East Panhandle Sandhills	Apalachicola NF: WRD	WD03	FL260	D2	8420.988	3019.333
East Panhandle Sandhills	Econfina River NFWMD	ER01	FL269	D4	8532.023	3029.139

Table A-1 continued

Region	Management Area	Site	Plot	Assoc	Latitude	Longitude
East Panhandle Sandhills	Econfina River NFWMD	ER01	FL270	D4	8531.764	3028.899
East Panhandle Sandhills	Econfina River NFWMD	ER01	FL294	W1	8534.151	3027.401
East Panhandle Sandhills	Private land	DY01	FL072	D4	8457.033	3026.435
East Panhandle Sandhills	Private land	DY01	FL073	D6	8457.070	3026.424
Apalachicola Lowlands	Apalachicola NF: ARD	AD01	FL062	W6	8500.932	3003.534
Apalachicola Lowlands	Apalachicola NF: ARD	AD02	FL063	D4	8459.533	3016.618
Apalachicola Lowlands	Apalachicola NF: ARD	AD02	FL064	D6	8459.107	3016.757
Apalachicola Lowlands	Apalachicola NF: ARD	AD01	FL067	D6	8500.818	3003.595
Apalachicola Lowlands	Apalachicola NF: ARD	AD03	FL068	D4	8458.989	3012.292
Apalachicola Lowlands	Apalachicola NF: ARD	AD03	FL069	D6	8459.224	3012.360
Apalachicola Lowlands	Apalachicola NF: ARD	AD04	FL080	D6	8505.324	3006.344
Apalachicola Lowlands	Apalachicola NF: ARD	AD04	FL081	D6	8505.157	3006.033
Apalachicola Lowlands	Apalachicola NF: ARD	AD03	FL082	W6	8459.254	3012.255
Apalachicola Lowlands	Apalachicola NF: ARD	AD02	FL083	D6	8458.749	3016.388
Apalachicola Lowlands	Apalachicola NF: ARD	AD05	FL084	D6	8501.290	3011.725
Apalachicola Lowlands	Apalachicola NF: ARD	AD05	FL086	W6	8501.305	3011.662
Apalachicola Lowlands	Apalachicola NF: ARD	AD05	FL087	D6	8500.861	3011.980
Apalachicola Lowlands	Apalachicola NF: ARD	AD01	FL088	W6	8500.194	3003.788
Apalachicola Lowlands	Apalachicola NF: ARD	AP06	FL162	W7	8457.638	3002.444
Apalachicola Lowlands	Apalachicola NF: ARD	AP06	FL164	M2	8457.496	3002.541
Apalachicola Lowlands	Apalachicola NF: ARD	AP06	FL265	D6	8458.099	3002.054
Apalachicola Lowlands	Apalachicola NF: ARD	AD01	FL266	D6	8500.904	3003.299
Tallahassee Red Hills	Pebble Hill (Private land)	PH01	FL227	W1	8405.221	3045.918
Tallahassee Red Hills	Pebble Hill (Private land)	PH01	FL228	W5	8405.213	3045.904
Tallahassee Red Hills	Pebble Hill (Private land)	PH01	FL289	D5	8405.342	3045.849
Tallahassee Red Hills	Pebble Hill (Private land)	PH01	FL290	D5	8405.508	3046.390
Tallahassee Red Hills	Private land	AV01	FL028	D2	NR	NR
Tallahassee Red Hills	Private land	AV01	FL029	W5	NR	NR
Tallahassee Red Hills	Private land	BE01	FL031	W5	NR	NR
Tallahassee Red Hills	Private land	BE02	FL037	D5	NR	NR
Tallahassee Red Hills	Private land	BE02	FL038	W5	NR	NR
Tallahassee Red Hills	Private land	BE01	FL039	W4	NR	NR
Tallahassee Red Hills	Torreya SP	TY01	FL030	D4	8457.027	3033.462
Tallahassee Red Hills	Torreya SP	TY01	FL036	D4	8457.129	3033.376
Tallahassee Red Hills	Wade Tract (Private land)	WT01	FL224	D5	8359.851	3045.724
Tallahassee Red Hills	Wade Tract (Private land)	WT01	FL226	W5	8359.742	3045.752
Tallahassee Red Hills	Wade Tract (Private land)	WT01	FL286	D5	8359.978	3045.688
Tallahassee Red Hills	Wade Tract (Private land)	WT01	FL291	W1	8400.672	3045.552
Wakulla Lowlands	Apalachicola NF: WRD	WD02	FL017	D4	8429.542	3020.029
Wakulla Lowlands	Apalachicola NF: WRD	WD04	FL020	D4	8441.153	3015.381
Wakulla Lowlands	Apalachicola NF: WRD	WD04	FL021	M2	8441.207	3015.161
Wakulla Lowlands	Apalachicola NF: WRD	WD05	FL025	D4	8432.368	3016.952

Table A-1 continued

Region	Management Area	Site	Plot	Assoc	Latitude	Longitude
Wakulla Lowlands	Apalachicola NF: WRD	WD05	FL026	D4	8432.287	3016.911
Wakulla Lowlands	Apalachicola NF: WRD	WD06	FL027	W4	8433.080	3013.853
Wakulla Lowlands	Apalachicola NF: WRD	WD07	FL032	D6	8433.938	3022.967
Wakulla Lowlands	Apalachicola NF: WRD	WD07	FL033	M2	8434.031	3023.016
Wakulla Lowlands	Apalachicola NF: WRD	WD06	FL034	M2	8433.130	3013.746
Wakulla Lowlands	Apalachicola NF: WRD	WD05	FL035	M2	8432.176	3013.861
Wakulla Lowlands	Apalachicola NF: WRD	WD07	FL261	W4	8433.715	3022.721
Wakulla Lowlands	Apalachicola NF: WRD	WD07	FL262	W4	8433.898	3022.858
Wakulla Lowlands	Apalachicola NF: WRD	WD07	FL263	D6	8431.724	3021.255
Wakulla Lowlands	Apalachicola NF: WRD	WD05	FL267	W4	8430.400	3017.106
Wakulla Lowlands	Apalachicola NF: WRD	WD05	FL268	W4	8430.493	3017.197
E Panhandle Gulf Coast	St. Joe Bufferlands (DEP)	SJ02	FL165	M1	8452.457	2946.138
E Panhandle Gulf Coast	St. Joe Bufferlands (DEP)	SJ02	FL166	W7	8452.460	2946.223
E Panhandle Gulf Coast	St. Joe Bufferlands (DEP)	SJ02	FL167	M2	8452.525	2946.190
E Panhandle Gulf Coast	St. Marks NWR: Panacea	SM01	FL001	D2	8425.094	3002.987
E Panhandle Gulf Coast	St. Marks NWR: Panacea	SM01	FL002	D6	8427.700	3002.281
E Panhandle Gulf Coast	St. Marks NWR: Panacea	SM01	FL003	M2	8427.739	3002.233
E Panhandle Gulf Coast	St. Marks NWR: Panacea	SM01	FL004	W6	8427.761	3002.230
E Panhandle Gulf Coast	St. Marks NWR: Panacea	SM01	FL005	D2	8425.101	3002.886
E Panhandle Gulf Coast	St. Marks NWR: Panacea	SM03	FL006	D2	8426.210	3002.846
E Panhandle Gulf Coast	St. Marks NWR: Panacea	SM03	FL007	M2	8426.161	3002.904
E Panhandle Gulf Coast	St. Marks NWR: Panacea	SM03	FL008	M2	8426.110	3002.889
E Panhandle Gulf Coast	St. Marks NWR: Panacea	SM04	FL009	D6	8429.020	3002.591
E Panhandle Gulf Coast	St. Marks NWR: Panacea	SM04	FL305	W6	8429.047	3002.529
Big Bend Coast	Cedar Key Scrub SP	CK01	FL199	M1	8259.824	2912.314
Big Bend Coast	Cedar Key Scrub SP	CK01	FL200	W3	8259.754	2912.307
Big Bend Coast	Cedar Key Scrub SP	CK01	FL201	M1	8259.680	2912.317
Big Bend Coast	Cedar Key Scrub SP	CK01	FL212	M1	8301.709	2912.251
Big Bend Coast	Cedar Key Scrub SP	CK01	FL295	M1	8258.871	2912.365
Big Bend Coast	Lower Suwannee NWR	LS01	FL238	M2	8301.263	2927.417
Big Bend Coast	Lower Suwannee NWR	LS01	FL239	M1	8301.153	2927.433
Big Bend Coast	Lower Suwannee NWR	LS02	FL240	M1	8311.944	2923.701
Big Bend Coast	Lower Suwannee NWR	LS02	FL241	M1	8311.969	2923.713
Big Bend Coast	St. Marks NWR: St. Marks	SM06	FL023	M2	8405.373	3007.873
Big Bend Coast	St. Marks NWR: St. Marks	SM06	FL024	W3	8405.479	3007.913
Big Bend Coast	St. Marks NWR: St. Marks	SM06	FL283	M2	8409.138	3009.513
Big Bend Interior Lowlands	Goethe SF	GO04	FL299	M1	8237.265	2918.862
Big Bend Interior Lowlands	Goethe SF	GO02	FL119	M1	8235.430	2907.339
Big Bend Interior Lowlands	Goethe SF	GO02	FL120	M1	8236.329	2908.709
Big Bend Interior Lowlands	Goethe SF	GO02	FL121	W4	8236.277	2908.756
Big Bend Interior Lowlands	Goethe SF	GO03	FL122	W4	8236.443	2911.963
Big Bend Interior Lowlands	Goethe SF	GO03	FL123	M1	8237.461	2914.514

Table A-1 continued

Region	Management Area	Site	Plot	Assoc	Latitude	Longitude
Big Bend Interior Lowlands	St. Marks NWR: Wakulla	SM05	FL014	D2	8418.119	3007.903
Big Bend Interior Lowlands	St. Marks NWR: Wakulla	SM05	FL015	M2	8418.126	3007.803
Big Bend Interior Lowlands	St. Marks NWR: Wakulla	SM05	FL016	W4	8418.356	3007.606
North Central Highlands	Ichetucknee SP	IC01	FL168	D2	8246.013	2958.323
North Central Highlands	Manatee SP	MA01	FL185	D1	8257.606	2929.961
North Central Highlands	Manatee SP	MA01	FL186	D1	8257.919	2929.953
North Central Highlands	Manatee SP	MA01	FL187	D1	8257.910	2929.422
North Central Highlands	Oleno SP	OL01	FL148	D2	8234.150	2954.866
North Central Highlands	Oleno SP	OL01	FL149	M1	8234.195	2954.837
North Central Highlands	Oleno SP	OL02	FL150	M1	8234.493	2954.978
North Central Highlands	Oleno SP	OL02	FL151	D1	8235.095	2955.080
North Central Highlands	Oleno SP	OL01	FL235	M2	8234.198	2954.432
North Central Highlands	Oleno SP	OL01	FL236	W1	8234.215	2954.623
North Central Highlands	River Rise SP	RR01	FL161	D1	8238.055	2952.208
North Central Highlands	Twin Rivers SF	TR01	FL126	D2	8311.814	3029.308
North Central Highlands	Twin Rivers SF	TR01	FL127	D2	8312.048	3029.460
North Central Highlands	Twin Rivers SF	TR01	FL128	D2	8312.734	3030.330
North Central Highlands	Twin Rivers SF	TR01	FL129	D2	8312.458	3030.175
North Central Highlands	Twin Rivers SF	TR02	FL252	D2	8312.337	3022.682
North Central Highlands	Twin Rivers SF	TR02	FL253	D1	8312.452	3022.386
North Central Highlands	Twin Rivers SF	TR02	FL254	D1	8312.361	3022.399
Interior Northeast Lowlands	Jennings SF	JE01	FL177	M2	8156.067	3010.410
Interior Northeast Lowlands	Jennings SF	JE01	FL178	W2	8156.087	3010.380
Interior Northeast Lowlands	Jennings SF	JE01	FL179	D2	8156.160	3010.816
Interior Northeast Lowlands	Osceola NF	OS01	FL101	M2	8224.710	3014.328
Interior Northeast Lowlands	Osceola NF	OS01	FL102	M2	8224.582	3014.134
Interior Northeast Lowlands	Osceola NF	OS01	FL103	M2	8224.743	3014.261
Interior Northeast Lowlands	Osceola NF	OS02	FL242	W4	8226.883	3011.485
Interior Northeast Lowlands	Osceola NF	OS02	FL244	M2	8226.528	3011.540
Interior Northeast Lowlands	Osceola NF	OS02	FL245	M1	8226.420	3011.883
Interior Northeast Lowlands	Osceola NF	OS03	FL247	W4	8229.095	3017.087
North Atlantic Coast	Favor Dykes SP	FD01	FL309	M1	8116.487	2940.420
North Atlantic Coast	Favor Dykes SP	FD01	FL310	M1	8115.807	2940.653
North Atlantic Coast	Favor Dykes SP	FD01	FL313	W2	8116.588	2940.331
North Atlantic Coast	Heart Island CA	HI01	FL296	M1	8121.280	2911.812
North Atlantic Coast	Heart Island CA	HI01	FL297	W3	8123.827	2911.175
North Atlantic Coast	Heart Island CA	HI01	FL298	M3	8124.455	2910.867
North Atlantic Coast	private land	HI01	FL301	D3	NR	NR
North Atlantic Coast	Pumpkin Hill SP	PP01	FL311	M2	8116.559	2940.512
North Atlantic Coast	Pumpkin Hill SP	PP01	FL312	M1	8130.126	3028.824
North Atlantic Coast	Pumpkin Hill SP	PP01	FL315	W4	8130.536	3028.344
North Atlantic Coast	Tigar Bay SF	TB01	FL300	D3	8111.349	2914.129

Table A-1 continued

Region	Management Area	Site	Plot	Assoc	Latitude	Longitude
North Atlantic Coast	Tigar Bay SF	TB01	FL302	M3	8110.758	2913.184
North Atlantic Coast	Tigar Bay SF	TB01	FL303	M1	8110.287	2912.531
Coastal Northeast Lowlands	Jennings SF	JE02	FL180	M2	8155.906	3010.360
Coastal Northeast Lowlands	Jennings SF	JE02	FL181	D2	8155.888	3009.956
Coastal Northeast Lowlands	Simmons SF	SI01	FL182	M2	8156.597	3047.671
Coastal Northeast Lowlands	Simmons SF	SI01	FL183	D2	8156.999	3047.972
Coastal Northeast Lowlands	Simmons SF	SI01	FL184	W4	8157.434	3046.913
West Central Highlands	Ashton (Private land)	AS01	FL124	M1	8235.041	2932.284
West Central Highlands	Ashton (Private land)	AS01	FL125	D3	8234.781	2932.527
West Central Highlands	Cross Florida Greenway SRA	GW01	FL112	D3	8215.520	2903.090
West Central Highlands	Cross Florida Greenway SRA	GW01	FL113	D2	8215.197	2902.864
West Central Highlands	Davidson Ranch TNC	DR01	FL106	D3	8241.860	2944.586
West Central Highlands	Davidson Ranch TNC	DR01	FL107	D2	8241.710	2945.139
West Central Highlands	Davidson Ranch TNC	DR01	FL116	D1	8241.925	2944.969
West Central Highlands	Goethe SF	GO01	FL104	D3	8236.197	2921.450
West Central Highlands	Goethe SF	GO01	FL105	D2	8236.187	2921.480
West Central Highlands	Goethe SF	GO01	FL233	D3	8236.138	2921.452
West Central Highlands	Goethe SF	GO01	FL234	W1	8236.017	2921.580
West Central Highlands	Ross Prairie SF	RP01	FL114	D3	8217.955	2901.933
West Central Highlands	Ross Prairie SF	RP01	FL115	D2	8217.802	2901.821
West Central Highlands	Ross Prairie SF	RP01	FL232	D3	8217.527	2902.185
West Central Highlands	San Felasco SP	SF01	FL130	D3	8228.090	2944.222
West Central Highlands	San Felasco SP	SF01	FL131	D1	8227.762	2944.601
West Central Highlands	San Felasco SP	SF01	FL132	D1	8226.901	2943.903
West Central Highlands	San Felasco SP	SF02	FL133	M2	8226.743	2942.961
East Central Highlands	Etoniah Creek SF	ET01	FL117	D3	8152.401	2947.222
East Central Highlands	Etoniah Creek SF	ET01	FL118	D3	8152.077	2947.064
East Central Highlands	Etoniah Creek SF	ET02	FL306	M1	8147.309	2943.782
East Central Highlands	Etoniah Creek SF	ET02	FL314	W2	8120.974	2737.601
East Central Highlands	Goldhead SP	GH01	FL175	D3	8157.421	2950.975
East Central Highlands	Goldhead SP	GH01	FL176	W1	8156.427	2949.631
East Central Highlands	Ocala NF	OC01	FL139	D3	8148.342	2927.505
East Central Highlands	Ocala NF	OC01	FL142	D2	8148.587	2927.381
East Central Highlands	Ocala NF	OC01	FL144	D3	8148.596	2947.468
East Central Highlands	Ocala NF	OC01	FL145	D3	8149.589	2927.472
East Central Highlands	Ocala NF	OC02	FL146	W4	8156.602	2909.451
East Central Highlands	Ocala NF	OC02	FL147	M1	8156.316	2909.687
East Central Highlands	Ocala NF	OK01	FL307	D2	8154.813	2910.331
East Central Highlands	Ocala NF	OK01	FL308	M3	8156.729	2909.302
East Central Highlands	Rock Springs SP	RS01	FL206	M1	8127.770	2845.729
East Central Highlands	Rock Springs SP	RS01	FL207	M1	8127.623	2845.946
East Central Highlands	Swisher-Ordway: Univ of FL	OR01	FL152	D3	8159.907	2940.846

Table A-1 continued

Region	Management Area	Site	Plot	Assoc	Latitude	Longitude
East Central Highlands	Swisher-Ordway: Univ of FL	OR01	FL153	D3	8159.764	2940.761
East Central Highlands	Swisher-Ordway: Univ of FL	OR01	FL154	W1	8200.641	2940.532
East Central Highlands	Wekiwa Springs SP	WE01	FL135	D3	8129.779	2844.307
East Central Highlands	Wekiwa Springs SP	WE01	FL137	M1	8129.866	2844.789
East Central Highlands	Wekiwa Springs SP	WE01	FL141	D3	8129.604	2843.923
East Central Highlands	Wekiwa Springs SP	WE01	FL143	M1	8129.792	2844.467
West Central Lowlands	Green Swamp WMA	GS01	FL155	M3	8457.196	2822.252
West Central Lowlands	Green Swamp WMA	GS02	FL156	D2	8208.258	2826.337
West Central Lowlands	Green Swamp WMA	GS02	FL157	M1	8207.163	2826.372
West Central Lowlands	Green Swamp WMA	GS02	FL158	W1	8207.115	2826.402
West Central Lowlands	Green Swamp WMA	GS02	FL159	W1	8207.274	2826.118
West Central Lowlands	Green Swamp WMA	GS02	FL160	D3	8207.151	2826.273
West Central Lowlands	Green Swamp WMA	GS01	FL174	W2	8157.163	2821.828
West Central Lowlands	Starkey Wilderness SWFWMD	SW01	FL169	M1	8235.709	2814.806
West Central Lowlands	Starkey Wilderness SWFWMD	SW01	FL170	W2	8235.867	2814.418
West Central Lowlands	Starkey Wilderness SWFWMD	SW01	FL171	M3	8235.840	2814.531
West Central Lowlands	Starkey Wilderness SWFWMD	SW02	FL172	D3	8236.488	2815.010
West Central Lowlands	Starkey Wilderness SWFWMD	SW01	FL173	W2	8235.853	2814.422
Kissimmee Basin	Avon Park AFR	AV01	FL188	M3	8117.614	2740.173
Kissimmee Basin	Avon Park AFR	AV01	FL189	W2	8117.347	2940.170
Kissimmee Basin	Avon Park AFR	AV01	FL190	M3	8117.231	2740.268
Kissimmee Basin	Avon Park AFR	AV01	FL191	M3	8117.292	2740.290
Kissimmee Basin	Avon Park AFR	AV02	FL192	M1	8119.719	2744.531
Kissimmee Basin	Avon Park AFR	AV03	FL193	W3	8112.519	2742.114
Kissimmee Basin	Avon Park AFR	AV02	FL196	M3	8119.757	2744.752
Kissimmee Basin	Avon Park AFR	AV03	FL197	W2	8112.691	2742.545
Kissimmee Basin	Avon Park AFR	AV03	FL198	M3	8112.664	2742.536
Kissimmee Basin	Avon Park AFR	AV04	FL219	M3	8112.629	2737.055
Kissimmee Basin	Avon Park AFR	AV05	FL220	M3	8115.758	2743.773
Kissimmee Basin	Avon Park AFR	AV06	FL221	M3	8119.176	2738.357
Kissimmee Basin	Disney Wilderness TNC	DW01	FL134	M1	8124.340	2804.012
Kissimmee Basin	Disney Wilderness TNC	DW01	FL136	M3	8124.281	2804.050
Kissimmee Basin	Disney Wilderness TNC	DW01	FL138	M3	8124.302	2804.020
Kissimmee Basin	Disney Wilderness TNC	DW01	FL140	M1	8124.378	2804.009
Kissimmee Basin	Kississimee Prairie Preserve SP	KI01	FL194	M3	8108.116	2735.082
Kissimmee Basin	Kississimee Prairie Preserve SP	KI01	FL195	W2	8106.414	2735.298
Kissimmee Basin	Three Lakes WMA	TL01	FL202	M3	8105.123	2758.670
Kissimmee Basin	Three Lakes WMA	TL01	FL203	W2	8105.205	2758.715
Kissimmee Basin	Three Lakes WMA	TL01	FL204	W2	8105.241	2758.735
Kissimmee Basin	Three Lakes WMA	TL01	FL205	M1	8104.352	2758.957
Southwest Central Lowlands	Myakka River SP	MY01	FL208	M1	8210.671	2714.092
Southwest Central Lowlands	Myakka River SP	MY02	FL209	M1	8217.429	2717.423

Table A-1 continued

Region	Management Area	Site	Plot	Assoc	Latitude	Longitude
Southwest Central Lowlands	Myakka River SP	MY03	FL210	M3	8214.965	2716.027
Southwest Central Lowlands	Myakka River SP	MY03	FL211	W2	8214.926	2716.119
Southwest Central Lowlands	Myakka River SP	MY04	FL213	W2	8213.196	2713.914
Southwest Central Lowlands	Myakka River SP	MY04	FL214	M3	8212.229	2713.572
Southwest Central Lowlands	Myakka River SP	MY03	FL215	M3	8215.152	2715.225
Southwest Highlands	Withlacoochee SF	WF01	FL108	D2	8225.963	2847.513
Southwest Highlands	Withlacoochee SF	WF01	FL109	D1	8225.653	2848.063
Southwest Highlands	Withlacoochee SF	WF02	FL110	D2	8224.071	2843.674
Southwest Highlands	Withlacoochee SF	WF02	FL111	D2	8223.958	2843.519
Caloosahatchie Lowlands	Cecil Webb WMA	CW01	FL216	M3	8156.349	2652.335
Caloosahatchie Lowlands	Cecil Webb WMA	CW01	FL217	W2	8156.456	2652.301
Caloosahatchie Lowlands	Cecil Webb WMA	CW01	FL218	W2	8155.595	2653.341
Caloosahatchie Lowlands	Cecil Webb WMA	CW02	FL222	M3	8151.861	2651.547
Caloosahatchie Lowlands	Cecil Webb WMA	CW02	FL223	W2	8151.948	2651.597

APPENDIX B
LIST OF FREQUENT AND ABUNDANT SPECIES BY COMMUNITY ASSOCIATION

Table B-1: Species included that present in > 70-75 % of plots within an association, and > 0.2 m² mean cover. Freq = percent frequency of occurrence, cover = mean cover in m². Number of plots per association indicated in parentheses

Peninsula Xeric Sandhills (22)	Freq	Cover
<i>Aristida beyrichiana</i>	100	39.80
<i>Sorghastrum secundum</i>	100	2.99
<i>Pityopsis graminifolia</i>	100	2.52
<i>Lechea sessiliflora</i>	100	0.44
<i>Schizachyrium scoparium</i> var. <i>stoloniferum</i>	95	1.28
<i>Dichantherium ovale</i> var. <i>addisonii</i>	95	0.80
<i>Stillingia sylvatica</i>	95	0.72
<i>Sporobolus junceus</i>	91	1.14
<i>Paspalum setaceum</i>	91	0.51
<i>Cnidoscolus stimulosus</i>	91	0.28
<i>Bulbostylis ciliatifolia</i>	86	0.84
<i>Andropogon ternarius</i>	86	0.76
<i>Smilax auriculata</i>	86	0.59
<i>Rhynchospora grayi</i>	86	0.33
<i>Tragia urens</i>	86	0.33
<i>Crotalaria rotundifolia</i>	86	0.30
<i>Balduina angustifolia</i>	82	0.50
<i>Andropogon gyrans</i> var. <i>gyrans</i>	82	0.36
<i>Tephrosia chrysophylla</i>	77	1.11
<i>Croton argyranthemus</i>	77	0.48
<i>Liatris tenuifolia</i> var. <i>tenuifolia</i>	77	0.40
<i>Scleria ciliata</i> var. <i>ciliata</i>	77	0.30
Panhandle Xeric Sandhills (31)	Freq	Cover
<i>Schizachyrium scoparium</i> var. <i>stoloniferum</i>	100	4.38
<i>Smilax auriculata</i>	100	1.66
<i>Andropogon gyrans</i> var. <i>gyrans</i>	100	1.26
<i>Stylisma patens</i> ssp. <i>patens</i>	100	0.45
<i>Stylosanthes biflora</i>	94	0.31
<i>Pityopsis aspera</i>	90	3.29
<i>Bulbostylis ciliatifolia</i>	90	1.16
<i>Cyperus lupulinus</i> ssp. <i>lupulinus</i>	90	0.38
<i>Galactia microphylla</i>	87	2.38
<i>Sorghastrum secundum</i>	87	1.91
<i>Eriogonum tomentosum</i>	87	1.04
<i>Rhynchospora grayi</i>	87	0.58
<i>Dichantherium angustifolium</i>	87	0.52
<i>Andropogon virginicus</i>	84	2.23
<i>Solidago odora</i> var. <i>odora</i>	84	1.56
<i>Scleria ciliata</i> var. <i>ciliata</i>	84	0.54
<i>Commelina erecta</i>	84	0.35

Table B-1 continued

Panhandle Xeric Sandhills (continued)	Freq	Cover
<i>Dichantherium ovale</i> var. <i>addisonii</i>	81	0.88
<i>Sporobolus junceus</i>	81	0.77
<i>Aristida beyrichiana</i>	77	19.06
<i>Schizachyrium tenerum</i>	77	1.19
<i>Tragia urens</i>	77	0.28
<i>Croton argyranthemus</i>	74	0.75
<i>Liatris tenuifolia</i> var. <i>tenuifolia</i>	74	0.36
North Florida Sandhills (31)	Freq	Cover
<i>Aristida beyrichiana</i>	100	33.06
<i>Pityopsis graminifolia</i>	97	3.50
<i>Dichantherium ovale</i> var. <i>addisonii</i>	97	0.96
<i>Paspalum setaceum</i>	97	0.79
<i>Scleria ciliata</i> var. <i>ciliata</i>	97	0.65
<i>Tragia urens</i>	97	0.42
<i>Sorghastrum secundum</i>	94	2.73
<i>Schizachyrium scoparium</i> var. <i>stoloniferum</i>	94	1.46
<i>Stillingia sylvatica</i>	94	0.64
<i>Rhynchosia reniformis</i>	94	0.44
<i>Helianthemum carolinianum</i>	94	0.30
<i>Dichantherium angustifolium</i>	90	0.72
<i>Stylisma patens</i> ssp. <i>patens</i>	90	0.33
<i>Crotalaria rotundifolia</i>	87	0.35
<i>Dyschoriste oblongifolia</i>	84	1.17
<i>Andropogon gyrans</i> var. <i>gyrans</i>	84	0.92
<i>Eupatorium compositifolium</i>	84	0.59
<i>Gymnopogon ambiguus</i>	84	0.45
<i>Croton argyranthemus</i>	84	0.44
<i>Rhynchospora grayi</i>	84	0.38
<i>Sporobolus junceus</i>	81	0.89
<i>Lechea sessiliflora</i>	81	0.73
<i>Andropogon ternarius</i>	81	0.63
<i>Vernonia angustifolia</i>	81	0.55
<i>Sericocarpus tortifolius</i>	81	0.44
<i>Liatris tenuifolia</i> var. <i>tenuifolia</i>	81	0.40
<i>Symphyotrichum concolor</i>	81	0.36
<i>Stylosanthes biflora</i>	81	0.21
<i>Smilax auriculata</i>	77	1.44
<i>Lespedeza hirta</i>	77	0.39
<i>Palafoxia integrifolia</i>	77	0.38
<i>Ruellia caroliniensis</i> ssp. <i>ciliosa</i>	77	0.31
<i>Aristolochia serpentaria</i>	77	0.28
<i>Hieracium gronovii</i>	77	0.26
<i>Elephantopus elatus</i>	74	2.04
<i>Solidago odora</i> var. <i>odora</i>	74	0.50

Table B-1 continued

North Florida Sandhills (continued)	Freq	Cover
<i>Aristida purpurascens</i> var. <i>purpurascens</i>	74	0.37
<i>Andropogon virginicus</i>	74	0.29
<i>Ageratina aromatica</i>	74	0.29
North Florida Rich Woodlands (11)	Freq	Cover
<i>Pteridium aquilinum</i>	100	4.72
<i>Sorghastrum secundum</i>	100	4.00
<i>Ageratina aromatica</i>	100	1.24
<i>Dichantherium angustifolium</i>	100	0.97
<i>Paspalum setaceum</i>	100	0.75
<i>Andropogon gyrans</i> var. <i>gyrans</i>	100	0.39
<i>Smilax auriculata</i>	100	0.36
<i>Dichantherium ovale</i> var. <i>addisonii</i>	91	1.11
<i>Scleria ciliata</i> var. <i>ciliata</i>	91	0.77
<i>Sericocarpus tortifolius</i>	91	0.75
<i>Houstonia procumbens</i>	91	0.48
<i>Andropogon virginicus</i>	91	0.40
<i>Aristolochia serpentaria</i>	82	0.31
<i>Galium pilosum</i>	82	0.31
<i>Cyperus plukenetii</i>	82	0.27
<i>Hypericum hypericoides</i>	82	0.18
<i>Dyschoriste oblongifolia</i>	73	1.61
<i>Eupatorium compositifolium</i>	73	1.49
<i>Dichantherium oligosanthes</i> var. <i>oligosanthes</i>	73	1.09
<i>Dichantherium aciculare</i>	73	0.98
<i>Pityopsis graminifolia</i>	73	0.93
<i>Stillingia sylvatica</i>	73	0.47
<i>Aristida purpurascens</i> var. <i>purpurascens</i>	73	0.42
<i>Andropogon ternarius</i>	73	0.39
<i>Helianthemum carolinianum</i>	73	0.38
<i>Cyperus retrorsus</i>	73	0.31
<i>Rhynchosia reniformis</i>	73	0.31
<i>Crotalaria rotundifolia</i>	73	0.26
<i>Hieracium gronovii</i>	73	0.24
Panhandle Longleaf Pine Clayhills (14)	Freq	Cover
<i>Aristida beyrichiana</i>	100	22.72
<i>Schizachyrium scoparium</i> var. <i>stoloniferum</i>	100	8.75
<i>Solidago odora</i> var. <i>odora</i>	100	4.46
<i>Dichantherium angustifolium</i>	100	1.65
<i>Elephantopus elatus</i>	100	1.59
<i>Vernonia angustifolia</i>	100	0.82
<i>Stylosanthes biflora</i>	100	0.50
<i>Sericocarpus tortifolius</i>	93	1.66
<i>Andropogon gyrans</i> var. <i>gyrans</i>	93	1.13
<i>Symphytotrichum dumosum</i> var. <i>dumosum</i>	93	1.09
<i>Desmodium lineatum</i>	93	1.04

Table B-1 continued

Panhandle Longleaf Pine Clayhills (continued)	Freq	Cover
<i>Lespedeza repens</i>	93	0.38
<i>Hieracium gronovii</i>	93	0.29
<i>Pteridium aquilinum</i>	86	5.65
<i>Rubus cuneifolius</i>	86	1.19
<i>Desmodium ciliare</i>	86	1.12
<i>Dichantherium ovale</i> var. <i>addisonii</i>	86	1.05
<i>Muhlenbergia capillaris</i> var. <i>trichopodes</i>	86	1.00
<i>Scleria ciliata</i> var. <i>ciliata</i>	86	0.86
<i>Aristida purpurascens</i> var. <i>purpurascens</i>	86	0.73
<i>Andropogon virginicus</i>	86	0.52
<i>Symphyotrichum adnatum</i>	86	0.47
<i>Symphyotrichum concolor</i>	86	0.44
<i>Mimosa microphylla</i>	86	0.40
<i>Eupatorium compositifolium</i>	86	0.38
<i>Liatris gracilis</i>	86	0.34
<i>Rudbeckia hirta</i>	86	0.29
<i>Pityopsis graminifolia</i>	79	4.64
<i>Schizachyrium tenerum</i>	79	2.27
<i>Pityopsis aspera</i>	79	1.37
<i>Ageratina aromatica</i>	79	0.95
<i>Chamaecrista nictitans</i>	79	0.78
<i>Euphorbia discoidalis</i>	79	0.58
<i>Chrysopsis mariana</i>	79	0.46
<i>Smilax glauca</i>	79	0.40
<i>Acalypha gracilens</i>	79	0.27
<i>Aristolochia serpentaria</i>	79	0.27
<i>Houstonia procumbens</i>	79	0.26
<i>Gymnopogon ambiguus</i>	79	0.23
Panhandle Silty Woodlands (22)	Freq	Cover
<i>Aristida beyrichiana</i>	100	33.64
<i>Schizachyrium scoparium</i> var. <i>stoloniferum</i>	100	3.28
<i>Dichantherium dichotomum</i> var. <i>tenue</i>	100	1.15
<i>Scleria ciliata</i> var. <i>ciliata</i>	100	0.75
<i>Symphyotrichum adnatum</i>	100	0.65
<i>Dichantherium angustifolium</i>	95	1.79
<i>Tragia smallii</i>	95	0.47
<i>Pityopsis graminifolia</i>	91	5.36
<i>Andropogon gyrans</i> var. <i>gyrans</i>	91	1.07
<i>Sericocarpus tortifolius</i>	91	0.73
<i>Stylosanthes biflora</i>	91	0.3
<i>Chrysopsis mariana</i>	86	0.52
<i>Andropogon virginicus</i>	86	0.41
<i>Smilax auriculata</i>	82	1.38
<i>Lespedeza repens</i>	82	0.27
<i>Viola septemloba</i>	82	0.25
<i>Pteridium aquilinum</i>	77	8.8

Table B-1 continued

Panhandle Silty Woodlands (continued)	Freq	Cover
<i>Helianthus radula</i>	77	3.11
<i>Carphephorus odoratissimus</i>	77	1.01
<i>Galactia erecta</i>	77	0.27
Xeric Mesic Flatwoods (36)	Freq	Cover
<i>Aristida beyrichiana</i>	92	18.24
<i>Dichanthelium sabulorum</i> var. <i>thinium</i>	86	0.75
<i>Andropogon virginicus</i>	86	0.69
<i>Pityopsis graminifolia</i>	83	0.85
<i>Smilax auriculata</i>	81	0.51
<i>Pterocaulon virgatum</i>	78	0.42
<i>Bulbostylis ciliatifolia</i>	75	0.67
<i>Gratiola hispida</i>	72	0.43
North Florida Mesic Flatwoods (30)	Freq	Cover
<i>Aristida beyrichiana</i>	97	14.93
<i>Xyris caroliniana</i>	93	0.79
<i>Pityopsis graminifolia</i>	87	1.64
<i>Andropogon virginicus</i>	87	1.07
<i>Dichanthelium strigosum</i> var. <i>leucoblepharis</i>	77	0.70
<i>Pterocaulon virgatum</i>	77	0.31
<i>Pteridium aquilinum</i>	73	3.05
<i>Sericocarpus tortifolius</i>	73	0.21
<i>Dichanthelium sabulorum</i> var. <i>thinium</i>	73	0.70
Central Florida Mesic Flatwoods/Dry Prairies (22)	Freq	Cover
<i>Aristida beyrichiana</i>	100	27.23
<i>Dichanthelium sabulorum</i> var. <i>thinium</i>	100	0.85
<i>Andropogon virginicus</i>	95	1.63
<i>Pterocaulon virgatum</i>	95	0.47
<i>Aristida spiciformis</i>	91	2.06
<i>Pityopsis graminifolia</i>	91	0.82
<i>Dichanthelium chamaelonche</i>	86	9.49
<i>Xyris caroliniana</i>	86	0.40
<i>Paspalum setaceum</i>	86	0.32
<i>Drosera brevifolia</i>	86	0.30
<i>Polygala setacea</i>	86	0.28
<i>Euthamia tenuifolia</i> var. <i>tenuifolia</i>	82	0.81
<i>Oldenlandia uniflora</i>	82	0.35
<i>Fimbristylis puberula</i>	82	0.30
<i>Eleocharis baldwinii</i>	77	0.67
<i>Gratiola hispida</i>	77	0.33
Marginal Prairies (11)	Freq	Cover
<i>Andropogon virginicus</i>	91	10.23
<i>Euthamia tenuifolia</i> var. <i>tenuifolia</i>	91	0.80
<i>Panicum hemitomon</i>	82	12.35

Table B-1 continued

Marginal Prairies (continued)	Freq	Cover
<i>Rhexia mariana</i> var. <i>mariana</i>	82	0.75
<i>Axonopus furcatus</i>	73	15.27
<i>Eupatorium leptophyllum</i>	73	2.84
<i>Centella erecta</i>	73	2.72
<i>Andropogon capillipes</i> (wetland variant)	73	1.23
<i>Aristida purpurascens</i> var. <i>virgata</i>	73	0.60
Peninsula Wet Flatwoods/Prairies (16)	Freq	Cover
<i>Oxypolis filiformis</i>	100	1.73
<i>Eriocaulon decangulare</i>	94	5.87
<i>Bigelowia nudata</i>	94	2.16
<i>Eragrostis elliotii</i>	94	1.11
<i>Amphicarpum muehlenbergianum</i>	88	5.95
<i>Xyris elliotii</i>	88	3.68
<i>Andropogon gyrans</i> var. <i>stenophyllus</i>	88	0.66
<i>Aristida beyrichiana</i>	81	15.24
<i>Dichantherium erectifolium</i>	81	2.84
<i>Centella erecta</i>	81	1.41
<i>Drosera brevifolia</i>	81	0.40
<i>Eupatorium mohrii</i>	81	0.32
Peninsula Wet Flatwoods/Prairies (16)	Freq	Cover
<i>Aristida palustris</i>	75	6.44
<i>Scleria muehlenbergii</i>	75	5.38
<i>Andropogon capillipes</i> (wetland variant)	75	4.86
<i>Fuirena scirpoidea</i>	75	2.63
<i>Panicum tenerum</i>	75	1.98
Calcareous Wet Flatwoods (4)	Freq	Cover
<i>Sabal palmetto</i>	100	4.75
<i>Centella erecta</i>	100	2.09
<i>Hyptis alata</i>	100	1.50
<i>Saccharum giganteum</i>	100	0.63
<i>Helenium pinnatifidum</i>	100	0.34
<i>Lobelia glandulosa</i>	100	0.34
<i>Panicum rigidulum</i> var. <i>rigidulum</i>	100	0.34
<i>Rhynchospora globularis</i>	100	0.28
<i>Cirsium nuttallii</i>	100	0.22
<i>Asclepias lanceolata</i>	100	0.09
<i>Dichantherium dichotomum</i> var. <i>nitidum</i>	75	5.31
<i>Panicum virgatum</i> var. <i>virgatum</i>	75	3.31
<i>Rhynchospora divergens</i>	75	2.44
<i>Dichantherium caeruleascens</i>	75	2.13
<i>Pluchea rosea</i>	75	2.00
<i>Ludwigia microcarpa</i>	75	1.75
<i>Rhynchospora colorata</i>	75	1.13
<i>Fuirena breviseta</i>	75	1.00

Table B-1 continued

Calcareous Wet Flatwoods (continued)	Freq	Cover
<i>Mikania scandens</i>	75	0.97
<i>Rubus trivialis</i>	75	0.88
<i>Scleria muehlenbergii</i>	75	0.78
<i>Hypericum cistifolium</i>	75	0.75
<i>Diodia virginiana</i>	75	0.72
<i>Rhynchospora perplexa</i>	75	0.59
<i>Dichantherium strigosum</i> var. <i>glabrescens</i>	75	0.53
<i>Hypericum hypericoides</i>	75	0.53
<i>Andropogon capillipes</i> (upland variant)	75	0.50
<i>Berchemia scandens</i>	75	0.50
<i>Eustachys glauca</i>	75	0.44
<i>Scleria pauciflora</i>	75	0.44
<i>Phyla nodiflora</i>	75	0.41
<i>Cyperus polystachyos</i>	75	0.38
<i>Oxypolis filiformis</i>	75	0.31
<i>Proserpinaca pectinata</i>	75	0.31
<i>Smilax laurifolia</i>	75	0.31
<i>Andropogon glomeratus</i> var. <i>glomeratus</i>	75	0.28
<i>Mitreola petiolata</i>	75	0.28
<i>Toxicodendron radicans</i>	75	0.28
<i>Axonopus furcatus</i>	75	0.25
<i>Eleocharis flavescens</i>	75	0.25
<i>Mitreola sessilifolia</i>	75	0.25
<i>Vitis rotundifolia</i>	75	0.25
<i>Xyris jupicai</i>	75	0.25
North Florida Shrubby Wet Flatwoods (15)	Freq	Cover
<i>Andropogon glaucopsis</i>	87	5.20
<i>Osmunda cinnamomea</i>	87	4.38
<i>Eriocaulon decangulare</i>	80	7.57
<i>Smilax laurifolia</i>	80	0.66
<i>Xyris ambigua</i>	80	0.39
<i>Photinia pyrifolia</i>	80	0.34
<i>Andropogon glomeratus</i> var. <i>hirsutior</i>	73	2.27
<i>Rhynchospora fascicularis</i>	73	2.09
<i>Andropogon capillipes</i> (upland variant)	73	0.43
<i>Rhexia petiolata</i>	73	0.23
Upper Panhandle Wet Flatwoods (7)	Freq	Cover
<i>Schizachyrium scoparium</i> var. <i>stoloniferum</i>	100	5.32
<i>Pityopsis graminifolia</i>	100	5.11
<i>Pteridium aquilinum</i>	100	4.68
<i>Eupatorium rotundifolium</i>	100	4.21
<i>Andropogon virginicus</i>	100	4.14
<i>Panicum verrucosum</i>	100	3.52
<i>Rhexia alifanus</i>	100	2.43
<i>Helianthus angustifolius</i>	100	1.64

Table B-1 continued

Upper Panhandle Wet Flatwoods (continued)	Freq	Cover
<i>Euthamia tenuifolia</i> var. <i>tenuifolia</i>	100	1.32
<i>Symphyotrichum dumosum</i> var. <i>dumosum</i>	100	1.09
<i>Smilax glauca</i>	100	0.95
<i>Solidago stricta</i>	100	0.93
<i>Diodia virginiana</i>	100	0.50
<i>Xyris caroliniana</i>	100	0.48
<i>Chamaecrista nictitans</i>	100	0.34
<i>Ctenium aromaticum</i>	86	10.54
<i>Dichantherium dichotomum</i> var. <i>tenue</i>	86	3.11
<i>Andropogon glomeratus</i> var. <i>hirsutior</i>	86	2.82
<i>Aristida purpurascens</i> var. <i>virgata</i>	86	2.32
Upper Panhandle Wet Flatwoods (7)	Freq	Cover
<i>Panicum anceps</i> var. <i>rhizomatum</i>	86	1.88
<i>Chaptalia tomentosa</i>	86	1.73
<i>Dichantherium strigosum</i> var. <i>leucoblepharis</i>	86	1.59
<i>Panicum virgatum</i> var. <i>virgatum</i>	86	0.70
<i>Desmodium tenuifolium</i>	86	0.64
<i>Bigelovia nudata</i>	86	0.55
<i>Hypericum crux-andreae</i>	86	0.48
<i>Andropogon gyrans</i> var. <i>gyrans</i>	86	0.41
<i>Dichantherium consanguineum</i>	86	0.38
<i>Hypericum setosum</i>	86	0.27
<i>Gymnopogon brevifolius</i>	86	0.25
<i>Crotalaria purshii</i>	86	0.23
<i>Polygala nana</i>	86	0.20
<i>Rubus trivialis</i>	86	0.20
Panhandle Wet Flatwoods/Prairies (16)	Freq	Cover
<i>Aristida beyrichiana</i>	100	50.51
<i>Xyris ambigua</i>	100	2.00
<i>Rhexia alifanus</i>	100	1.79
<i>Smilax laurifolia</i>	100	0.95
<i>Ctenium aromaticum</i>	94	9.88
<i>Carphephorus pseudoliatris</i>	94	1.38
<i>Eriocaulon decangulare</i>	88	4.75
<i>Chaptalia tomentosa</i>	88	1.21
<i>Andropogon arctatus</i>	81	5.31
<i>Helianthus heterophyllus</i>	81	2.47
<i>Andropogon gyrans</i> var. <i>stenophyllus</i>	81	1.43
<i>Erigeron vernus</i>	81	0.96
<i>Coreopsis linifolia</i>	81	0.74
<i>Rhynchospora chapmanii</i>	75	10.92
<i>Bigelovia nudata</i>	75	1.66
<i>Muhlenbergia capillaris</i> var. <i>trichopodes</i>	75	1.48
<i>Rhynchospora plumosa</i>	75	1.23
<i>Rhynchospora baldwinii</i>	75	0.95

Table B-1 continued

Panhandle Seepage Slopes (5)	Freq	Cover
<i>Aristida beyrichiana</i>	100	11.15
<i>Scleria muehlenbergii</i>	100	10.05
<i>Rhynchospora oligantha</i>	100	6.03
<i>Aristida palustris</i>	100	3.05
<i>Andropogon gyrans</i> var. <i>stenophyllus</i>	100	2.58
<i>Eriocaulon decangulare</i>	100	2.33
<i>Smilax laurifolia</i>	100	1.05
<i>Bigelowia nudata</i>	100	0.85
<i>Coreopsis linifolia</i>	100	0.75
<i>Andropogon arctatus</i>	100	0.70
<i>Lobelia glandulosa</i>	100	0.60
<i>Rhynchospora latifolia</i>	100	0.58
<i>Oxypolis filiformis</i>	100	0.50
<i>Symphyotrichum dumosum</i> var. <i>dumosum</i>	100	0.35
<i>Rhexia alifanus</i>	100	0.30
<i>Sabatia macrophylla</i>	100	0.15
<i>Liatris spicata</i>	80	9.28
<i>Muhlenbergia capillaris</i> var. <i>trichopodes</i>	80	6.70
<i>Ctenium aromaticum</i>	80	5.48
<i>Pleea tenuifolia</i>	80	1.03
<i>Arnoglossum ovatum</i>	80	0.73
<i>Dichantherium longiligulatum</i>	80	0.65
<i>Lophiola aurea</i>	80	0.60
<i>Paspalum praecox</i>	80	0.50
<i>Balduina uniflora</i>	80	0.43
<i>Lycopodiella appressa</i>	80	0.43
<i>Rhexia lutea</i>	80	0.35
<i>Drosera brevifolia</i>	80	0.33
<i>Erigeron vernus</i>	80	0.30
<i>Rubus trivialis</i>	80	0.30
<i>Juncus trigonocarpus</i>	80	0.23
<i>Rhexia petiolata</i>	80	0.20
<i>Eryngium integrifolium</i>	80	0.20

APPENDIX C
MASTER LIST OF ABITA CREEK PRESERVE PLANT SPECIES.

Table C-1: All vascular plant species (and varieties) recorded at Abita Creek Preserve during sample period 1997-2005. Code corresponds to labels on Figure 4-5 and 4-6. “Type” indicates woody (W) or herbaceous (H). “Lifeform” indicates forb (F), graminoid (G), and woody (W).

Code	Species	Type	Lifeform
ACERU	<i>Acer rubrum</i>	W	W
AGAOB	<i>Agalinus obtusifolia</i>	H	F
AGASP	<i>Agalinus sp.</i>	H	F
AGRPE	<i>Agrostis perennans</i>	H	G
ALESP	<i>Aletris sp.</i>	H	F
AMBAR	<i>Ambrosia artemisiifolia</i>	H	F
AMOSP	<i>Amorpha sp.</i>	H	F
ANDCA	<i>Andropogon capillipes</i>	H	G
ANDGL	<i>Andropogon glomeratus</i>	H	G
ANDGY	<i>Andropogon gyrans</i> var. <i>gyrans</i>	H	G
ANDMO	<i>Andropogon mohrii</i>	H	G
ANDPE	<i>Andropogon perangustatus</i>	H	G
ANDSP	<i>Andropogon sp.</i>	H	G
ANDVI	<i>Andropogon virginicus</i>	H	G
ANTRU	<i>Anthraenantia rufa</i>	H	G
ANTVI	<i>Anthraenantia villosa</i>	H	G
ARIPA	<i>Aristida palustris</i>	H	G
ARIVI	<i>Aristida virgata</i>	H	G
ARUTE	<i>Arundinaria gigantea</i> ssp. <i>tecta</i>	H	G
ASCLO	<i>Asclepias sp.</i>	H	F
ASCLO	<i>Asclepias longifolia</i>	H	F
ASTAD	<i>Symphyotrichum adnatum</i>	H	F
ASTDU	<i>Symphyotrichum dumosum</i> var. <i>dumosum</i>	H	F
AXOFI	<i>Axonopus fissifolius</i>	H	G
BACHA	<i>Baccharis halimifolia</i>	W	W
BALUN	<i>Balduwiana uniflora</i>	H	F
BARPA	<i>Bartonia paniculata</i>	H	F
BIDMI	<i>Bidens mitis</i>	H	F
BIGCA	<i>Bignonia capreolata</i>	H	F
BIGNU	<i>Bigelovia nudata</i>	H	F
BOLSP	<i>Boltonia sp.</i>	H	F
BURSP	<i>Burmannia sp.</i>	H	F
CACOV	<i>Cacalia ovata</i>	H	F
CALAM	<i>Callicarpa americana</i>	W	W
CARGL	<i>Carex glaucescens</i>	H	C
CARPS	<i>Carphephorus pseudoliatris</i>	H	F

Table C-1 continued

Code	Species	Type	Lifeform
CENER	<i>Centella erecta</i>	H	F
CEPOC	<i>Cephalanthus occidentalis</i>	W	W
CHALA	<i>Chasmanthium laxum</i>	H	G
CHAOR	<i>Chasmanthium ornithorhynchum</i>	H	G
CHATO	<i>Chaptalia tomentosa</i>	H	F
CHIVI	<i>Chionanthus virginicus</i>	W	W
CLEAL	<i>Clethra alnifolia</i>	W	W
CLEDI	<i>Cleistes divaricata</i>	H	F
COERU	<i>Coelorachis rugosa</i>	H	G
COETE	<i>Coelorachis tessellata</i>	H	G
CORLI	<i>Coreopsis linifolia</i>	H	F
CRASP	<i>Crataegus</i> sp.	W	W
CROTO	<i>Croton</i> sp.	H	F
CTEAR	<i>Ctenium aromaticum</i>	H	G
CYPSP	<i>Cyperus compressus</i>	H	C
CYRRA	<i>Cyrilla racemiflora</i>	W	W
DICDI	<i>Dichantherium dichotomum</i>	H	G
DICLA	<i>Rhynchospora latifolia</i>	H	C
DIOTE	<i>Diodia virginiana</i>	H	F
DIOTE	<i>Diodia teres</i>	H	F
DIOVI	<i>Diospyros virginiana</i>	W	W
DROBR	<i>Drosera</i> sp.	H	F
ELEMI	<i>Eleocharis minima</i>	H	C
ELETU	<i>Eleocharis tuberculosa</i>	H	C
ERARE	<i>Eragrostis refracta</i>	H	G
ERARE	<i>Eragrostis elliotii</i>	H	G
EREHI	<i>Erechtites hieraciifolia</i>	H	F
ERICO	<i>Eriocaulon compressum</i>	H	F
ERIDE	<i>Eriocaulon decangulare</i>	H	F
ERIGI	<i>Saccharum giganteum</i>	H	G
ERIST	<i>Saccharum strictus</i>	H	G
ERIVE	<i>Erigeron vernus</i>	H	F
ERYIN	<i>Eryngium integrifolium</i>	H	F
EUPCA	<i>Eupatorium capillifolium</i>	H	F
EUPLE	<i>Eupatorium leucolepis</i>	H	F
EUPRO	<i>Eupatorium rotundifolium</i>	H	F
EUPSE	<i>Eupatorium semiserratum</i>	H	F
EUTLE	<i>Euthamia leptcephala</i>	H	F
EUTTE	<i>Euthamia tenuifolia</i> var. <i>tenuifolia</i>	H	F
FRAPE	<i>Fraxinus caroliniana</i>	W	W
FUIBR	<i>Fuirena breviseta</i>	H	G
FUISP	<i>Fuirena</i> sp.	H	G

Table C-1 continued

Code	Species	Type	Lifeform
GALMO	<i>Gaylussacia mosieri</i>	W	W
GAYMO	<i>Gaylussacia dumosa</i>	W	W
GELRA	<i>Gelsemium rankinii</i>	H	F
GENSA	<i>Gentiana saponaria</i>	H	F
GRAPI	<i>Gratiola pilosa</i>	H	F
GRAPI	<i>Gratiola brevifolia</i>	H	F
GRASP	<i>Gratiola</i> sp.	H	F
GYMBR	<i>Gymnopogon brevifolius</i>	H	G
HELAN	<i>Helianthus angustifolius</i>	H	F
HELHE	<i>Helianthus heterophyllus</i>	H	F
HELVE	<i>Helenium vernale</i>	H	F
HIBAC	<i>Hibiscus asculenta</i>	H	F
HYPAL	<i>Hyptis alata</i>	H	F
HYPBR	<i>Hypericum brachyphyllum</i>	W	W
HYPCL	<i>Hypericum cistifolium</i>	H	F
HYPHI	<i>Hypoxis</i> sp.	H	F
HYPHY	<i>Hypericum hypericoides</i>	H	F
HYPMU	<i>Hypericum multilum</i>	H	F
HYPSE	<i>Hypericum setosum</i>	H	F
HYPST	<i>Hypericum crux-andreae</i>	H	F
HYPWA	<i>Triadenum virginicum</i>	W	W
ILECO	<i>Ilex coriacea</i>	W	W
ILEDE	<i>Ilex decidua</i>	W	W
ILEGL	<i>Ilex glabra</i>	W	W
ILEMY	<i>Ilex myrtifolia</i>	W	W
ILEOP	<i>Ilex opaca</i>	W	W
ILEVO	<i>Ilex vomitoria</i>	W	W
IRIVI	<i>Iris virginica</i>	H	F
ITEVI	<i>Itea virginica</i>	W	W
JUNMA	<i>Juncus marginatus</i>	H	C
JUNTR	<i>Juncus trigonocarpus</i>	H	C
LACCA	<i>Lachnanthes caroliana</i>	H	F
LECSP	<i>Lechea</i> sp.	H	F
LIASP	<i>Liatris spicata</i>	H	F
LIGSI	<i>Ligustrum sinense</i>	W	W
LINME	<i>Linum medium</i>	H	F
LINME	<i>Linum floridanum</i>	H	F
LIQST	<i>Liquidambar styraciflua</i>	W	W
LIRTU	<i>Liriodendron tulipifera</i>	W	W
LOBBR	<i>Lobelia brevifolia</i>	H	F
LOBFL	<i>Lobelia floridana</i>	H	F
LOBPU	<i>Lobelia puberula</i>	H	F

Table C-1 continued

Code	Species	Type	Lifeform
LOPAU	<i>Lophiola aurea</i>	H	F
LUDGL	<i>Ludwigia glandulosa</i>	H	F
LUDHI	<i>Ludwigia pilosa</i>	H	F
LUDHI	<i>Ludwigia hirtella</i>	H	F
LUDLI	<i>Ludwigia linearis</i>	H	F
LUDSP	<i>Ludwigia</i> sp.	H	F
LUDVI	<i>Ludwigia virgata</i>	H	F
LYCAL	<i>Lycopodiella</i> sp.	H	F
LYCVI	<i>Lycopus virginicus</i>	H	F
LYCVI	<i>Lycopus rubellus</i> var. <i>angustifolius</i>	H	F
LYGJA	<i>Lygodium japonicum</i>	H	F
LYOLU	<i>Lyonia lucida</i>	W	W
MAGGR	<i>Magnolia grandiflora</i>	W	W
MAGVI	<i>Magnolia virginiana</i>	W	W
MALAN	<i>Malus angustifolia</i>	W	W
MECAC	<i>Mecardonia acuminata</i>	H	F
MITSE	<i>Mitreola sessilifolia</i>	H	F
MUHEX	<i>Muhlenbergia cappillaris</i> var. <i>tricopodes</i>	H	G
MYRCE	<i>Morella cerifera</i>	W	W
MYRHE	<i>Morella heterophylla</i>	W	W
NYSBI	<i>Nyssa biflora</i>	W	W
OSMAM	<i>Osmanthus americanus</i>	W	W
OSMCI	<i>Osmunda cinnamomea</i>	H	F
OSMRE	<i>Osmunda regalis</i>	H	F
OXYFI	<i>Oxypolis filiformis</i>	H	F
PANAC	<i>Dichantherium acuminatum</i>	H	G
PANAN	<i>Panicum anceps</i>	H	G
PANAN	<i>Panicum hians</i>	H	G
PANCO	<i>Dichantherium consanguineum</i>	H	G
PANEN	<i>Dichantherium ensifolium</i>	H	G
PANER	<i>Dichantherium erectifolium</i>	H	G
PANET	<i>Dichantherium ensifolium</i> var. <i>tenua</i>	H	G
PANLE	<i>Dichantherium leucothrix</i>	H	G
PANLO	<i>Dichantherium longiligulatum</i>	H	G
PANRI	<i>Panicum rigidulum</i>	H	G
PANSC	<i>Dichantherium scabriusculum</i>	H	G
PANSO	<i>Dichantherium scoparium</i>	H	G
PANSP	<i>Dichantherium</i> sp.	H	G
PANST	<i>Dichantherium strigosum</i>	H	G
PANTE	<i>Panicum tenerum</i>	H	G
PANVE	<i>Panicum verrucosum</i>	H	G
PANVI	<i>Panicum virgatum</i>	H	G

Table C-1 continued

Code	Species	Type	Lifeform
PARQU	<i>Parthenocissus quinquefolia</i>	W	W
PASFL	<i>Paspalum floridanum</i>	H	G
PASPR	<i>Paspalum praecox</i>	H	G
PASSE	<i>Paspalum setaceum</i>	H	G
PENSP	<i>Penstemon</i> sp.	H	F
PERBO	<i>Persea borbonia</i>	W	W
PINEL	<i>Pinus elliottii</i>	W	W
PINPA	<i>Pinus palustris</i>	W	W
PINTA	<i>Pinus taeda</i>	W	W
PITGR	<i>Pityopsis graminifolia</i>	H	F
PLURO	<i>Pluchea rosea</i>	H	F
PLURO	<i>Pluchea foetida</i>	H	F
POLLU	<i>Polygala lutea</i>	H	F
POLRA	<i>Polygala ramosa</i>	H	F
PROPE	<i>Proserpinaca pectinata</i>	H	F
PRUSE	<i>Prunus serotina</i>	W	W
PTEAQ	<i>Pteridium aquilinum</i>	H	F
PYRAR	<i>Photinia pyrifolia</i>	W	W
QUEFA	<i>Quercus falcata</i>	W	W
QUELA	<i>Quercus laurifolia</i>	W	W
QUENI	<i>Quercus nigra</i>	W	W
QUENI	<i>Quercus laurifolia</i>	W	W
QUEVI	<i>Quercus virginiana</i>	W	W
RHEAL	<i>Rhexia alifanus</i>	H	F
RHELU	<i>Rhexia lutea</i>	H	F
RHEMA	<i>Rhexia mariana</i> var. <i>mariana</i>	H	F
RHEPE	<i>Rhexia petiolata</i>	H	F
RHESP	<i>Rhexia</i> sp.	H	F
RHEVI	<i>Rhexia virginiana</i>	H	F
RHOSP	<i>Rhododendron</i> sp.	W	W
RHUCO	<i>Rhus copallinum</i>	W	W
RHUVE	<i>Toxicodendron vernix</i>	W	W
RHYCA	<i>Rhynchospora chalarocephala</i>	H	C
RHYCE	<i>Rhynchospora cephalantha</i>	H	C
RHYCH	<i>Rhynchospora chapmanii</i>	H	C
RHYCN	<i>Rhynchospora corniculata</i>	H	C
RHYCO	<i>Rhynchospora compressa</i>	H	C
RHYDE	<i>Rhynchospora debilis</i>	H	C
RHYEL	<i>Rhynchospora elliottii</i>	H	C
RHYFI	<i>Rhynchospora filifolia</i>	H	C
RHYGB	<i>Rhynchospora globularis</i>	H	C
RHYGL	<i>Rhynchospora glomerata</i>	H	C

Table C-1 continued

Code	Species	Type	Lifeform
RHYGR	<i>Rhynchospora gracilentia</i>	H	C
RHYIN	<i>Rhynchospora inexpansa</i>	H	C
RHYOL	<i>Rhynchospora oligantha</i>	H	C
RHYPL	<i>Rhynchospora plumosa</i>	H	C
RHYPU	<i>Rhynchospora pusilla</i>	H	C
RHYRA	<i>Rhynchospora rariflora</i>	H	C
RHYSP	<i>Rhynchospora</i> sp.	H	C
RUBUS	<i>Rubus</i> sp.	H	F
RUENO	<i>Ruellia noctiflora</i>	H	F
SABSP	<i>Sabatia</i> sp.	H	F
SABSP	<i>Sabatia difformis</i>	H	F
SABSP	<i>Sabatia campanulata</i>	H	F
SAGLA	<i>Sagittaria lanceolata</i>	H	F
SALAZ	<i>Salvia azurea</i>	H	F
SAPSI	<i>Sapium sebiferum</i>	W	W
SARAL	<i>Sarracenia alata</i>	H	F
SARPS	<i>Sarracenia psittacina</i>	H	F
SCHSC	<i>Schizachyrium scoparium</i>	H	G
SCHTE	<i>Schizachyrium tenerum</i>	H	G
SCLCI	<i>Scleria ciliata</i> var. <i>ciliata</i>	H	C
SCLGE	<i>Scleria georgiana</i>	H	C
SCLHI	<i>Scleria hirtella</i>	H	C
SCLMU	<i>Scleria muhlenbergia</i>	H	C
SCLPA	<i>Scleria pauciflora</i> var. <i>caroliniana</i>	H	C
SCLPP	<i>Scleria pauciflora</i> var. <i>pauciflora</i>	H	C
SCLTR	<i>Scleria triglomerata</i>	H	C
SCUIN	<i>Scutellaria integrifolia</i>	H	F
SETSP	<i>Setaria</i> sp.	H	G
SISAL	<i>Sisyrinchium atlanticum</i>	H	F
SMIBO	<i>Smilax bona-nox</i>	H	F
SMIGL	<i>Smilax glauca</i>	H	F
SMILA	<i>Smilax laurifolia</i>	H	F
SMIRO	<i>Smilax rotundifolia</i>	H	F
SMISM	<i>Smilax smallii</i>	H	F
SOLOD	<i>Solidago odora</i>	H	F
SOLRU	<i>Solidago rugosa</i>	H	F
STOLA	<i>Stokesia laevis</i>	H	F
STYAM	<i>Styrax americanus</i>	W	W
SYMTI	<i>Symplocos tinctoria</i>	W	W
TEPON	<i>Tephrosia onobrachooides</i>	H	F
TILUS	<i>Tillandsia usneoides</i>	H	F
TOFRA	<i>Tofieldia racemosa</i>	H	F

Table C-1 continued

Code	Species	Type	Lifeform
TOXRA	<i>Toxicodendron radicans</i>	W	W
TRADI	<i>Trachelospermum difforme</i>	H	F
TRIAM	<i>Tridens ambiguus</i>	H	G
TRIVI	<i>Triadenum virginicum</i>	W	W
UTRIC	<i>Utricularia juncea</i>	H	F
VACAR	<i>Vaccinium arboreum</i>	W	W
VACEL	<i>Vaccinium elliottii</i>	W	W
VIBDE	<i>Viburnum dentatum</i>	W	W
VIBNU	<i>Viburnum nudum</i>	W	W
VIOLA	<i>Viola lanceolata</i>	H	F
VIOPR	<i>Viola primulifolia</i>	H	F
VITRO	<i>Vitis rotundifolia</i>	W	W
WOOAR	<i>Woodwardia areolata</i>	H	F
XYRAM	<i>Xyris ambigua</i>	H	F
XYRBA	<i>Xyris baldwiniana</i>	H	F
XYRCA	<i>Xyris caroliniana</i>	H	F
XYRDI	<i>Xyris difformis</i>	H	F
XYRLO	<i>Xyris louisianica</i>	H	F
XYRSM	<i>Xyris smalliana</i>	H	F
XYRSP	<i>Xyris</i> sp.	H	F
XYRST	<i>Xyris iridifolia</i>	H	F
XYRST	<i>Xyris sticta</i>	H	F
ZIGSP	<i>Zigadenus</i> sp.	H	F

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BIOGRAPHICAL SKETCH

Susan Carr was born and raised in Gainesville, Florida. She graduated from the University of Florida in 1982 with a Bachelor of Science degree in botany. After college, Susan worked in the fields of land management and conservation, including employment with the Florida Natural Areas Inventory, U.S. Forest Service and The Nature Conservancy. She returned to graduate school in the mid-1990s and earned a Master of Science in plant ecology from Louisiana State University. Following a long period of field data collection in Florida and employment with the University of North Carolina in Chapel Hill, Susan joined the Department of Wildlife Ecology and Conservation at the University of Florida in 2005.