

# **A Vegetation Classification of Fire-Dependent Pinelands of Florida**

Authors: Carr, Susan C., Robertson, Kevin M., and Peet, Robert K.

Source: Castanea, 75(2) : 153-189

Published By: Southern Appalachian Botanical Society

URL: https://doi.org/10.2179/09-016.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your Downloaded ptannom. psi//sto Gandy of Terms of Luse, and Australia on 26 August 20 August 20 August 20 Nov 2021 Terms of Use: https://staging.bioone.org/terms-of-use

# A Vegetation Classification of Fire-Dependent Pinelands of Florida

Susan C. Carr,<sup>1</sup>\* Kevin M. Robertson,<sup>2</sup> and Robert K. Peet<sup>3</sup>

<sup>1</sup>3854 South Dayton Way  $\#307$ , Aurora, Colorado 80014 <sup>1</sup>3854 South Dayton Way  $\#307$ , Aurora, Colorado 80014<br><sup>2</sup>Tell Timbers Research Station 13093 Henry Beadel Drive, Tallahossee  $^{2}$ Tall Timbers Research Station, 13093 Henry Beadel Drive, Tallahassee, Florida 32312<br><sup>3</sup> Department of Biology, CB<sup>#</sup> 3280, University of North Carolina at Chanel Hill, Chanel B  ${}^{3}$ Department of Biology, CB $\#$  3280, University of North Carolina at Chapel Hill, Chapel Hill,

North Carolina 27599-3280

ABSTRACT Prior to European settlement, the portion of north and central Florida corresponding to the historic range of longleaf pine (Pinus palustris) was dominated by firedependent, herbaceous and open woodland plant communities. Economic development coupled with fire suppression lead to a drastic decline in the abundance, contiguity and integrity of these natural communities. We present a classification and description of natural, fire-maintained pineland communities of this highly fragmented landscape. Plot locations were stratified by region and topographic position to assure comprehensive coverage of compositional variation associated with local and regional gradients of environmental and geographic variation. Our focus was description of groundcover vegetation, which harbors most of the plant diversity. We censused all plant species within 293 vegetation plots of 1,000 m<sup>2</sup>. We then developed a comprehensive vegetation classification based on floristic similarity using K-means cluster analysis and ordination. Sixteen distinct ''communities'' are recognized, corresponding to plant assemblages that we deem readily discernable in the field. These communities were grouped into five ecological ''series'' corresponding to those of Peet: Xeric Sandy Uplands (2 communities), Subxeric Sandy Uplands (2 communities), Silty Uplands (2 communities); Flatwoods (3 communities); and Wetlands (7 communities). For each community we summarize species diversity, woody plant structure, diagnostic (indicator) species, and environmental and physiographic characteristics. Floristic variation within and between series is described relative to geographic variation and edaphic characteristics.

INTRODUCTION Vegetation classification and description play a key role in scientific research, conservation, and land management. Floristic classification systems provide a conceptual framework for understanding the ecological and evolutionary relationships among species and environment from local to regional scales. In addition, community classification systems provide essential guidance to practitioners of ecological conservation and restoration by providing appropriate goals within a given landscape and environmental context (Walker and Silletti 2006). Such a classification provides a framework for summarizing community compostion, associated environmental conditions, and species distributions.

Fire-dependent pineland communities of Florida are exceptional for their floristic richness, biodiversity, and endemism. The combination in Florida of long climatic gradients, long growing seasons, significant variation in geology and large species pools creates a prime environment for high floristic variation at both local and regional scales. More than 3,500 plant species are native to Florida (Ward 1979, Wunderlin and Hansen 2000). Plant species richness values of Florida pinelands are among the highest recorded at small scales (Walker and Peet 1983, Peet 2006) with species composition varying dramatically across subtle gradients of topography and associated moisture conditions (Bridges and Orzell 1989, Abrahamson and Hartnett 1990, Peet and Allard 1993). Over 1,600 plant taxa are endemic to the South-

\*email address: sucarr@earthlink.net Received March 18, 2009; Accepted June 22, 2009. eastern Coastal Plain, and 250 of these are endemic or nearly-endemic to Florida (Ward 1979; Sorrie and Weakley 2001, 2006). The Florida peninsula has a complex geologic history of inundation and land expansion related to sea-level change which contributes to high levels of both ''beta'' which ''gamma'' diversity (sensu Whittaker 1967).

Classification of contemporary Florida pineland communities is by necessity limited to isolated remnants of a once immense ecosystem. Open pine woodland vegetation once dominated the Southeastern Coastal Plain from southern Virginia to the southern tip of Florida and westward to eastern Texas. Frequent fires maintained the open aspect of these pinelands and their species-rich herbaceous groundcover vegetation. It is estimated that prior to European settlement fire-return intervals in pinelands of the Gulf and lower Atlantic Coastal Plain regions averaged 2–3 yr (Olson and Platt 1995, Glitzenstein et al. 2003, Frost 2006). Following European settlement native fire regimes were altered or fire was excluded altogether. Consequently, pineland communities were often colonized by fire-intolerant woody growth that outcompetes groundcover vegetation (Glitzenstein et al. 1995, Glitzenstein et al. 2003). In addition, land-use changes resulted in reduction of native pineland vegetation over most of its former range, particularly on finer-textured soils that readily support agriculture (Frost 2006, Peet 2006). Today, these native pinelands occupy less than 3% of their former range (Outcalt and Sheffield 1996). Even rarer are frequently-burned pineland communities that resemble pre-settlement conditions (Varner and Kush 2004). Although a full classification of Florida native pinelands communities is limited by what has been lost, the effort to classify existing communities provides key insights into the historic landscape diversity and places appropriate conservation value on the communities that remain.

We present a quantitative classification and description of fire-adapted pineland vegetation with herb-dominated groundcover vegetation of northern and central Florida, a region that includes the entire historic range of longleaf pine in Florida. Our objective was to describe plant community types based on floristic assemblages alone, and then characterize their geographic distribution, topographic context, and soil attributes. Community types are described by their dominant and diagnostic plant species, facilitating easy field identification. In addition, we describe edaphic and landscape features useful for field identification, such as soil attributes and landscape context.

# MATERIALS AND METHODS

#### Study Area

The study area spanned the entire Florida panhandle and northern peninsular Florida (~31 $^{\circ}$ 00' to 28 $^{\circ}$ 80'N and 87 $^{\circ}$ 30' to 80 $^{\circ}$ 00'W). This area roughly coincides with the current range of longleaf pine (Pinus palustris) in Florida and includes most of the historic range of Florida's pyrogenic pineland ecosystems (sensu Hoctor et al. 2006) dominated by longleaf and/or slash pine (P. elliottii var. elliottii, and var. densa).

Three generalized land units of Puri and Vernon (1964) subdivide the study area into regions of common geologic history: 1) the Northern Highlands, 2) the Central Highlands, and 3) the Coastal Lowlands (Figure 1). These units are further subdivided into physiographic landforms that describe major soil types, geology and prevailing landscape features: 1) Highlands; 2) Ridges, Hills, Inclines and Slopes; and 3) Lowlands, Gaps, Valleys, and Plains (Puri and Vernon 1964). These generalized land units and physiographic landforms provided a useful framework for developing our stratified design and presenting our interpretations.

The Northern Highlands land unit of the upper panhandle (Figure 1) encompasses the area lying north of an ancient Pleistocene shoreline known as the Cody Scarp, which separates this region from Pleistocene sediments along the Gulf Coast (Puri and Vernon 1964, Myers 2000). This region contains each of the three physiographic landforms described above, although the entire region is thought to have remained uninundated during periods of the highest Pleistocene sealevels (Huddlestun 1988). Included in the region are the Western and Tallahassee Highlands and the New Hope and Grand Ridges, which have dissected topography and clastic sediments of Miocene to Late Pliocene age (Puri and Vernon 1964, Huddleston 1988,



Figure 1. Physiographic landforms (shaded and unshaded areas) of the Florida study region (area north of the bold curve), modified from physiographic general types of Puri and Vernon (1964). Bold lines delineate three ''generalized landforms'': Northern Highlands (clastic sediments), Central Highlands (part of the carbonate peninsular platform) and Coastal Lowlands.

Brown et al. 1990, Myers 2000). Also included are the Marianna Lowlands (Dougherty Plain), which contain outcrops of Eocene and Oligocene carbonates (Cook 1945, Puri and Vernon 1964, Brown et al. 1990) thought to have remained above sea-level during the Miocene-Pleistocene sea rises (Puri and Vernon 1964). Soils of the Marianna Lowlands are generally well-drained owing to shallow sands overlying limestone perforated by sink holes (Brown et al. 1990). Soils in the region are primarily ultisols where Miocene-Pliocene aged sediments remain in situ, and entisols where sediments have been subsequently reworked by fluvial and aeolian processes (Huddleston 1988).

The Central Highlands land unit contains discontinuous highlands of central peninsular ridge systems amid lowland landforms (Figure 1). Along with the Northern Highlands, the Central Highlands approximate the emergent portion of the Wicomico shoreline, an early Pleistocene shoreline of an ancient high sea level. The Central Highlands region was once an integrated highland that has since been partitioned by erosion and solution (Puri and Vernon 1964). The Ridges and Uplands physiographic landforms within this land unit arose from ancient shorelines, dune systems, barrier islands, and associated terraces (Puri and Vernon 1964). Larger physiographic landforms of the Central Highlands are the Brooksville, Deland, Trail, Mount Dora and Lake Wales Ridges, and Sumter, Polk, Marion, Duval and Lake Uplands. Soils are mainly coarse, excessively drained entisols and loamy ultisols. Soils of Lowland landforms are typically spodosols formed from surfical deposited sands over limestone of the Florida peninsula platform (Brown et al. 1990).

The Coastal Lowlands land unit includes the southern portion of the panhandle south of the Cody Scarp and the coastal regions of the peninsula (Figure 1). Much of the Coastal Lowlands unit was subjected to recurrent marine inundations from late Miocene through Pleistocene (Puri and Vernon 1964, Webb 1990). The Lowlands, Gaps, Valleys, and Plains physiographic landform comprises most of this land unit. These broad plains have little relief and are characterized by poorly drained spodosols (Brown et al. 1990).

#### Site Selection

The geographic and ecologic scope of this study included all pineland and associated fire-dependent, herb-dominated communities within the natural range of longleaf pine in Florida. This scope included many types of pine woodlands and savannas, variously labeled in the local vernacular as flatwoods, scrubby flatwoods, sandhills, high pine, and piney woods. It also encompassed embedded herb-dominated communities with or without trees, including wet and dry prairies, bogs, lake margins, and seepage slopes. The later communities often represented the low end of a topographic-moisture gradient in an otherwise pine-dominated landscape. Scrub and maritime pinelands of Central Florida were outside the scope of the study because of their woody plant-dominated physiognomy and a disturbance ecology characterized by crown fires (Florida Natural Areas Inventory 1990, Myers and Ewel 1990). Pineland communities considered here included only those with historic fire regimes of frequent (1–3 yr interval) surface fires that have little immediate influence on plant species composition yet are

required for maintenance of these communities (Platt 1999).

We subdivided the generalized land units of Puri and Vernon (1964) into ''ecoregions'' to guide our stratification of the study region and site selection (Figure 2). For this we used published works to identify previously recognized regions of relatively homogeneous geology, vegetation, soils, climate and physiognomy (Fenneman 1938, Puri and Vernon 1964, Davis 1967, Brooks 1982, Bailey et al. 1994, Griffith et al. 1994, United States Environmental Protection Agency 1999, Geo-Plan 2004) and consulted with experts of Florida vegetation and landscape physiognomy (B. Means, W. Platt, W. Baker, pers. comm.). Our goal was to select similar numbers of sites per ecoregion (2–4 sites), contingent on access and availability. A random sample from a pool of suitable natural areas would have been preferable, given the assumptions underpinning our numerical analyses and inference. However, a pool of suitable sites from which to randomly sample was not available a priori. Assembly of such a pool was not possible given study site limitations. In many ecoregions, few natural areas that satisfied selection criteria were available.

Ideally, a site selected for sampling contained an intact, continuous topographicmoisture gradient supporting frequently burned native vegetation. Sites that satisfied this condition were rare or absent in some ecoregions, particularly those containing only small fragments of natural communities. In these situations we pieced together a representative topographic-moisture gradient from several proximate sites. Specific criteria considered in site selection were: 1) absence of past intensive soil disturbance, 2) little to no exotic species cover, 3) presence of native canopy and midstory tree composition, 4) presence of intact and vigorous groundcover vegetation, and 5) evidence of fire within the previous five years, and preferably a history of frequent (1–3 yr interval) fires over the previous 50 yr. Soil disturbance history was evaluated using historical sources and disturbance-sensitive indicator species (Hedman et al. 2000, Dale et al. 2002, Kirkman et al. 2004, Ostertag and Robertson 2007). Small soil disturbances caused by ''natural'' factors



Figure 2. Florida ecoregions locations and labels. The 21 shaded ecoregions were used to stratify the study region for field sampling, and roughly equal numbers of plots were located in each. Individual plot locations indicated by dots, many of which overlap.

did not prompt site rejection (i.e., soil disturbance from animal burrows or tree falls). Candidate sites were identified from various sources, including the Florida Natural Areas Inventory (Florida Natural Areas Inventory 2000) and consultation with regional natural resource professionals. Three sites (12 plots) were selected in adjacent southern Georgia as these were representative of Florida pinelands of the Tallahassee Red Hills ecoregion. In total we sampled 293 vegetation plots distributed across 102 sites (Figures 2 and 3). A copy of the original plot data has been deposited with the Florida Natural Areas Inventory in Tallahassee, Florida. An appendix of plot locations (including latitudes and longitudes) is included in an earlier publication (Carr et al. 2009).

#### Field Methods

Each site was divided into three or four topographic-moisture zones based on field observations of edaphic conditions and plant species composition for the purpose of representing the range of potential species associations across the local topographic-moisture gradient. Zones were labeled 1–4 from highest to lowest elevation. In each zone, a single 1,000 m<sup>2</sup> (50 m  $\times$  20 m) rectangular plot was established within an area of relatively ho-



Figure 3. Plot locations by community type and region (Panhandle and Peninsula), superimposed on generalized landforms (adapted from Puri and Vernon 1964, as shown in Figure 1).

mogenous vegetation. Vegetation was recorded following the Carolina Vegetation Survey (CVS) protocol (Peet et al. 1998). Within each  $1,000 \text{ m}^2$  plot, all plant species were identified, and woody stems  $>1$  cm diameter at breast height (dbh) were tallied by diameter classes of 0–1 cm, 1–2.5 cm, 2.5–5 cm, and 5 cm classes from 5 to 40 cm, with stems  $>$ 40 cm dbh recorded to the closest cm. Aerial cover was estimated for all vascular plant taxa in each of four  $100\text{-m}^2$  intensive subplots using a cover-class scale  $(1 = \text{trace}, 2 = 0-1\%, 3 =$  $1-2\%$ ,  $4 = 2-5\%$ ,  $5 = 5-10\%$ ,  $6 = 10-25\%$ , 7  $=$  25–50%, 8 = 50–75%, 9 = 75–95%, 10 = .95%). Mean cover estimates among the four 100  $\text{m}^2$  subplots (calculated as means of the class midpoints) were used to estimate cover for the entire  $1,000 \text{--} m^2$  plot. Plant taxa encountered in the remaining  $600\text{-m}^2$  plot area were tallied and assigned an overall cover estimate. Plots were censused during the late growing season (August–December) over

a five-year period (2000–04). Plant taxa were identified to finest taxonomic scale possible, typically species or variety. Some taxa received lower levels of taxonomic resolution due to problems with consistent field identification. Hereafter the term ''species'' is used to indicate the finest resolution of identification, be it genus, species or variety. Taxon concepts and authorities follow Kartesz (1999) except Agalinis, Andropogon, Dichanthelium, Euthamia, Habenaria, Liatris gholsonii, L. pauciflora, L. secunda, Morella, Panicum, Rhexia, and Vaccinium staminium which follow Weakley (2008), Vaccinium corymbosum which follows Radford et al. (1968), and Carphephorus which follows Nesom (2006). We recognized Schizachyrium stoloniferum as a species separate from Schizachyrium scoparium var. stoloniferum. Voucher specimens were deposited in the University of Florida herbarium (FLAS).

A soil sample was collected from the top 10 cm of mineral soil (approximately 250 g) in each of the four 100  $m^2$  intensive modules and averaged within each  $1,000 \text{ m}^2$  plot for analysis. In addition, a single sub-soil sample from each plot was collected approximately 50 cm below ground surface. Samples were analyzed by Brookside Labs in New Knoxville, Ohio. Total cation exchange capacity (meq/ 100 g), pH, percent humic matter, estimated nitrogen release, easily extractable P, exchangeable cations (Ca, Mg, K, Na ppm), percent base saturation, extractable micronutrients (B, Fe, Mn, Cu, Zn, Al ppm), soluble sulfur and bulk density values were determined for each subsample. Extractions were carried out using the Mehlich III method (Mehlich 1984) and percent humic matter was determined by loss on ignition. Soil texture was determined for a composite of the four single-module samples, and quantified as percentage sand  $(2 \text{ mm} - 63 \text{ }\mu\text{m})$ , silt  $(63-2 \mu m)$  and clay  $(<2 \mu m)$ .

# Numerical Analysis

Our approach to vegetation classification was to apply a combination of ordination and cluster analyses to partition samples into floristically similar groups. Cover data of pine species (genus Pinus) were omitted to reduce the influence of this canopy dominant because pine abundance was affected by past land use. Species with fewer than three occurrences were deleted because rare species contribute little to calculations of inter-plot similarities (McCune and Grace 2002). We calculated a species response matrix (293 plot  $\times$  677 species) representing inter-sample similarities in species abundances among plots of Hellinger transformed Euclidean distances. Species cover values were relativized to maximum values to de-emphasize the influence of common and abundant species, following the guidelines of Legendre and Gallagher (2001) and McCune and Grace (2002).

We used non-hierarchical Euclidean-based K-means cluster analysis to partition samples in a manner that minimized within group sum of squares relative to between group differences as recommended by Legendre and Legendre (1998). We used the ''cascading Kmeans'' function of the Vegan package (Oksanen et al. 2007) to determine the optimal number of partitions for the final cluster solution. From this routine, we selected the number of partitions that maximized the "Simple Structure Index" (SSI). This index 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 cluster analysis solution presented recognizable and distinct floristic assemblages that we refer to as ''communities''. Communities are graphically displayed in a nonmetric multidimensional scaling (NMS) ordination of our response matrix of Hellinger transformed Euclidean distances. We used PC-ORD software, version 5.12 (McCune and Mefford 2006).

We compiled lists of common woody and herbaceous species typical of each community. Common woody species were restricted to those with a mean cover of  $>1 \text{ m}^2/0.1$  ha. Common herbaceous species were those that occurred in  $>75\%$  of samples and had a mean cover  $>0.2\%$ .

Diagnostic species were identified for each community as those with high constancy and fidelity. We used Indicator Species Analysis of Dufrene and Legendre (1997) and Monte Carlo randomization tests as implemented in PC-ORD (McCune and Mefford 2006). The Indicator Value (IndVal) generated from the Dufrene and Legendre (1997) algorithm quantifies species' relative frequency and abundance among communities. The null hypotheses for Monte Carlo tests (per species) were that maximum IndVal for a given species among communities is no larger than would be expected by chance. We selected species with type I error  $< 0.05$  from Monte Carlo tests as indicator species for specific communities. Indicator species were identified from species lists for each of three groups corresponding to (1) the upland Xeric, Subxeric and Silty ecological series, here combined because of the limited number of communities in each, (2) the Flatwoods series, and (3) the Wetlands series. In this manner, some species are recognized for each of two community types in different series. Some tests were performed after removal of community groups with small sample sizes due to biases introduced from unbalanced sample numbers.

Of the 677 species used in quantitative analyses, we identified those with geographically restricted distributions in Florida. A ''restricted range'' species was recognized if its Florida distribution was limited to only one of three regions (Western Panhandle, Eastern Panhandle plus North peninsula, or Central Peninsula), or if its entire range was limited to

Florida as determined from published literature. 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).

Soil and other community attributes were summarized and compared among ecological series and communities. For all communities within a specific ecological series, we compared soil variable means and standard errors. In addition, we compared species richness (number of species /0.1 ha sample) and basal area  $(m^2/ha)$  means.

RESULTS We identified 16 communities from the optimal K-means cluster solution of 293 samples (Figure 4). The 16-cluster partition yielded a high value of SSI (0.23, maximum value  $= 1.0$ ) from all partitions tested (ranging from 2 to 40). Our classification system based on the 16-cluster typology had relatively balanced number of plots per cluster  $($  > three per cluster) and presented community types which are readily distinguishable by field practitioners.

Variation in community composition reflected broad environmental gradients, which in turn corresponded to geographic areas. The first NMS axis represents most of this variation ( $r^2$  = 0.54) followed by the second NMS axis ( $r^2 = 0.29$ ) (Figure 4). The correlation between sample distances in two-dimensional NMS ordination space versus distances in original space was  $r^2 = 0.83$ . The primary gradient of variation represented by the first NMS ordination axis was strongly correlated with our *a priori* topographic zone values ( $r^2 =$ .470,  $p < 0.05$ ). Detailed interpretation of floristic gradients relative to additional environmental factors is presented elsewhere (Carr et al. 2009).

The 16 community types were named using existing terminology in plant community classification. Modifiers were added to distinguish landscape and regional affinities. Compositional affinities revealed in the NMS ordination along with the physical characteristics of plot locations were used to group communities into five ''ecological series'' corresponding to the ecological groups recognized by Peet (2006): These are Xeric Sandy Uplands, Subxeric Sandy Uplands, Silty Uplands, Flatwoods and Wetlands (Figure 4).



**NMS Axis 1** 

# **Xeric Sandhill Uplands**

- XU1 Peninsula Xeric Sandhills (22)
- ◆ XU2 Panhandle Xeric Sandhills (31)

#### **Subxeric Sandy Uplands**

- $\diamondsuit$  SSU1 North Florida Longleaf Woodlands (11)
- $\Box$  SSU2 North Florida Sub-xeric Sandhills (31)

# **Silty Uplands**

- \* SU1 Clayhill Longleaf Woodlands (14)
- SU2 Panhandle Silty Longleaf Woodlands (22)

#### **Flatwoods**

- O F1 Xeric Flatwoods (36)
- $\triangle$  F2 North Florida Mesic Flatwoods (30)
- F3 Central Florida Flatwoods/Prairies (22)

#### Wetlands

- $\blacklozenge$  W1 Wet Depression Prairies (11)
- $\triangle$  W2 Peninsula Savannas (16)
- $\blacktriangledown$  W3 Calcareous Savannas (4)
- W4 North Florida Wet Flatwoods (15)
- $\nabla$  W5 Upper Panhandle Savannas (7)
- O W6 Lower Panhandle Savannas (16)
- \* W7 Panhandle Seepage Savannas (5)

Figure 4. Two-dimensional NMS ordination of Sorensen's similarity metrics derived from Hellinger transformed data from 293 plot samples. Symbols indicate community type identified from K-means cluster analysis. The number of plots per community type shown in parentheses.

Individual communities are described below in terms of community structure, soil characteristics, and species composition. Throughout, tables and appendices are referenced in descriptions of communities; these are species richness/0.1 ha and total basal area (Table 1), soil and community attributes (Table 2), and frequent, abundant, indicator and characteristic species (Table 3). Text descriptions of communities follow a convention of presenting community descriptors in consistent order: soil and overstory character-

Community	Rich	BA		
Peninsula Xeric Sandhills	$68.5 \pm 3.4$	$8.1 \pm 1.0$		
Panhandle Xeric Sandhills	$75.1 \pm 2.8$	$9.5 \pm 0.9$		
North Florida Longleaf Woodlands	$106.5 \pm 4.8$	$16.1 \pm 1.4$		
North Florida Sub-xeric Sandhills	$96.2 \pm 2.8$	$11.4 \pm 0.9$		
Clayhill Longleaf Woodlands	$124.5 \pm 4.2$	$16.8 \pm 1.3$		
Panhandle Silty Longleaf Woodlands	$92.1 \pm 3.4$	$12.8 \pm 1.0$		
Xeric Flatwoods	$59.0 \pm 3.2$	$5.0 \pm 0.9$		
North Florida Mesic Flatwoods	$71.4 \pm 3.5$	$10.7 \pm 0.9$		
Central Florida Flatwoods/Prairies	$72.9 \pm 4.1$	$2.8 \pm 1.1$		
Wet Depression Prairies	$49.6 \pm 6.6$	$5.6 \pm 2.3$		
Peninsula Savannas	$69.7 \pm 6.0$	$2.4 \pm 1.9$		
Calcareous Savannas	$125.0 \pm 18.4$	$17.1 \pm 7.5$		
North Florida Wet Flatwoods	$65.7 \pm 6.3$	$15.7 \pm 2.0$		
Upper Panhandle Savannas	$126.4 \pm 7.9$	$10.9 \pm 2.9$		
Lower Panhandle Savannas	$78.3 \pm 5.4$	$4.5 \pm 2.0$		
Panhandle Seepage Savannas	$90.8 \pm 5.1$	$4.1 \pm 2.2$		

Table 1. Untransformed means and standard errors of species richness (Rich = species number / 0.1 ha) and canopy basal area (BA = Basal area  $m^2/ha$  of all stems >10 cm dbh) by community type

istics, followed by common midstory and understory species, and finally distinctive indicator species. Tree basal areas are presented as characteristic of sampled sites only, as overstory composition of most sites has been influenced by human management and should not be interpreted as ''natural'' conditions. Maps of plot locations are shown in Figures 2 and 3. Physiographic and landscape attributes for communities are described following the conventions of Figure 1.

Indicator species analysis revealed 333 species as indicators of at least one community. Of these, 106 were identified as having restricted ranges in Florida with eight taxa endemic to Florida. The remaining 98 species have provincial distributions restricted to one of three regions in Florida (Table 3). Endemic and restricted-range species characteristic of specific communities are noted in lists of indicator species (Table 3).

# Series 1: Xeric Sandhill Uplands

Xeric Sandhill Uplands are the driest of the longleaf types and are confined to sterile, poorly developed entisols (see Peet 2006) of ridgetops in the Northern Highland and Central Highland land units. Longleaf pine is joined in the canopy by the ubiquitous oaks Quercus laevis and Q. geminata. The grasses Aristida beyrichiana and Schizachyrium scoparium var. stoloniferum are consistent dominants of the herb layer.

Peninsula Xeric Sandhills (22 plots). This community is restricted to high sandy ridges of the Central Highlands and Coastal Lowlands of the northern peninsula region (Figure 3b). Coarse sandy soils contain low concentrations of clay and silt, although organic content of surface soils is relatively high compared to Panhandle Xeric Sandhills further west (Table 2). Peninsula Xeric Sandhills are species-poor compared to other communities although comparable in species richness to the Panhandle Xeric Sandhills (Table 1).

The pine canopy of the Peninsula Xeric Sandhills is sparse. Pinus elliotii and P. palustris are dominant canopy species followed by Quercus laevis (Table 3). Common shrub layer species include Quercus leavis, Q. incana, and Serenoa repens. Quercus margaretta, an oak common in other sandhill communities, is notably infrequent.

Several grass species are frequent in the ground cover of Peninsula Xeric Sandhills, including Aristida beyrichiana, Sorghastrum secundum, Schizachyrium scoparium var. stoloniferum, and Dichanthelium ovale, with A. beyrichiana by far the most abundant species in terms of cover (Table 3). Indicator species include a few grass species (Sporobolus junceus, Triplasis americana, Aristida condensata) as well as many non-grass species (Table 3). Carphephorus corymbosus and Asimina incana are indicator species with ranges restricted to the peninsula.











Downloaded From: https://staging.bioone.org/journals/Castanea on 26 Nov 2024 Terms of Use: https://staging.bioone.org/terms-of-use

Table 3. Continued

<b>Species</b>	Woody	Freq	Cover	BA	Ind Val
North Florida Subxeric Sandhills					
Desmodium floridanum		68	0.17		38.4
Palafoxia integrifolia		77	0.38		33.8
Rhynchosia reniformis		94	0.44		31.6
Physalis walteri		65	0.17		28.9
Scutellaria multiglandulosa		45	0.11		28.7
Piriqueta cistoides ssp. caroliniana		58	0.13		28.6
Asclepias verticillata		52	0.08		26.9
Eupatorium glaucescens		35	0.32		25
Lespedeza hirta		77	0.39		25
Ruellia caroliniensis ssp. ciliosa		77	0.31		23.8
Tragia urens*		97	0.42		
Helianthemum carolinianum*		94	0.3		
Croton argyranthemus*		84	0.44		
Dyschoriste oblongifolia*		84	1.17		
Gymnopogon ambiguus*		84	0.45		
Aristida beyrichiana		100	33.06		
Dichanthelium ovale var. addisonii		97	0.96		
Paspalum setaceum		97 97	0.79 3.5		
Pityopsis graminifolia	Y	97	6.72		
Quercus incana Scleria ciliata var. ciliata		97	0.65		
Pinus palustris	Y	94	11.12	15.23	
Schizachyrium scoparium var. stoloniferum		94	1.46		
Sorghastrum secundum		94	2.73		
Stillingia sylvatica		94	0.64		
Dichanthelium angustifolium		90	0.72		
Stylisma patens ssp. patens		90	0.33		
Crotalaria rotundifolia		87	0.35		
Andropogon gyrans var. gyrans		84	0.92		
Diospyros virginiana	Y	84	0.8		
Eupatorium compositifolium		84	0.59		
Quercus laevis	Y	84	6.18	2.53	
Rhus copallinum	Y	84	1.7		
Rhynchospora grayi		84	0.38		
Andropogon ternarius		81	0.63		
Lechea sessiliflora		81	0.73		
Liatris tenuifolia var. tenuifolia		81	0.4		
Sericocarpus tortifolius		81	0.44		
Sporobolus junceus		81	0.89		
Stylosanthes biflora		81	0.21		
Symphyotrichum concolor		81	0.36		
Vernonia angustifolia		81	0.55		
Aristolochia serpentaria		77	0.28		
Hieracium gronovii		77	0.26		
Smilax auriculata		77	1.44		
Quercus margaretta	Y	74	4.81	1.71	
Pinus elliottii var. elliottii	Y			3.74	
Pinus taeda	Y			7.11	
<b>Clayhill Longleaf Woodlands</b>					
Rudbeckia hirta		86	0.29		76
Acalypha gracilens		79	0.27		63.3
Malus angustifolia $1$	Y	64	0.19		55.9
Vaccinium stamineum vor. stamineum	Y	71	1.29		55.4
Galactia volubilis		71	0.32		54.4
Ceanothus americanus		57	0.25		42.7
Desmodium ciliare		86	1.12		42.7
Desmodium lineatum		93	1.04		42.7
Toxicodendron pubescens <sup>2</sup>		57	0.44		42.7





<b>Species</b>	Woody	Freq	Cover	BA	Ind Val
Quercus hemisphaerica Quercus nigra	Y Y			1.15 1.52	
North Florida Mesic Flatwoods					
Sporobolus floridanus <sup>2</sup>		53	6.13		19
Quercus minima	Y	87	10.46		18.4
Kalmia hirsuta <sup>2</sup>	Y	37	1.63		17.5
Ilex glabra	Y	100	19.49		
Aristida beyrichiana		97	14.93		
Serenoa repens	Y	97	17.01		
Xyris caroliniana		93	0.79		
Pinus palustris	Y	90	12.93	13.04	
Andropogon virginicus		87	1.07		
Pityopsis graminifolia		87	1.64		
Gaylussacia dumosa	Y	80	2.64		
Dichanthelium strigosum var. leucoblepharis		77	0.7		
Pterocaulon virgatum		77	0.31		
Vaccinium myrsinites	Y	77	6.56		
Pinus elliottii	Y			4.24	
<b>Central Florida Flatwoods/Prairies</b>					
Hypericum reductum	Y	86	1.07		62.3
Polygala setacea		86	0.28		57.4
Eleocharis baldwinii		77	0.67		50.4
Rhexia nuttallii		73	0.38		43
Fimbristylis puberula		82	0.3		41.5
Aristida spiciformis		91	2.06		38.2
Asimina reticulata <sup>3,4</sup>	Y	82	0.48		37.8
Rhynchospora fernaldii		45	0.09		37.5
Xyris flabelliformis Lechea torreyi		73	0.25		36.4
Lachnocaulon beyrichianum <sup>3</sup>		68 41	0.42 0.3		34.3 34
Dichanthelium chamaelonche		86	9.49		33.3
Syngonanthus flavidulus		73	0.39		32.7
Xyris brevifolia		45	0.19		32.6
Polygala rugelii <sup>3,4</sup>		45	0.27		32.2
Asclepias pedicellata		50	0.11		31.9
Aristida purpurascens var. tenuispica		68	0.34		30.7
Oldenlandia uniflora		82	0.35		30.7
Gymnopogon chapmanianus <sup>3</sup>		50	0.18		29
Gratiola hispida		77	0.33		25.8
Schizachyrium stoloniferum <sup>3</sup>		73	1.31		24.5
Andropogon brachystachyus <sup>3</sup>		55	0.25		22.6
Hypericum tetrapetalum		50	0.2		22.6
Lygodesmia aphylla		64	0.15		21.7
Eupatorium leptophyllum*		73	2.84		
Aristida beyrichiana		100	27.23		
Serenoa repens	Y	100	26.83		
Andropogon virginicus		95	1.63		
Pterocaulon virgatum		95	0.47		
Andropogon virginicus		91	10.23		
Euthamia tenuifolia var. tenuifolia		91	0.8		
Pityopsis graminifolia		91	0.82		
Drosera brevifolia		86	0.3		
Ilex glabra	Y	86	6.71		
Paspalum setaceum		86	0.32		
Quercus geminata	Y	86	9.92		
Xyris caroliniana		86	0.4		
Euthamia tenuifolia vor. tenuifolia		82	0.81		
Gaylussacia dumosa	Y	77	2.15		
Morella pumila	Y	77	1.39		









Table 3. Continued

<b>Species</b>	Woody	Freq	Cover	BA	Ind Val
Magnolia virginiana	Y	100	1.15		31.1
Balduina uniflora <sup>2</sup>		80	0.43		27.5
Rhynchospora corniculata		40	0.58		27.5
Gaylussacia mosieri <sup>2</sup>	Y	80	1.1		23
Andropogon arctatus*		100	0.7		
Andropogon gyrans vor. stenophyllus*		100	2.58		
Aristida palustris*		100	3.05		
Coreopsis linifolia $*^2$		100	0.75		
Morella caroliniensis*	Y	100	4.55		
Oxypolis filiformis*		100	0.5		
Drosera filiformis $*$ <sup>1</sup>		80	0.78		
Liatris spicata*		80	9.28		
Lophiola aurea*		80	0.6		
Rhexia petiolata*		80	0.2		
Aristida beyrichiana		100	11.15		
Bigelowia nudata		100	0.85		
Eriocaulon decangulare		100	2.33		
Ilex glabra	Y	100	13		
Rhexia alifanus		100	0.3		
Scleria muehlenbergii		100	10.05		
Smilax laurifolia		100	1.05		
Symphyotrichum dumosum var. dumosum		100	0.35		
Ctenium aromaticum		80	5.48		
Drosera brevifolia		80	0.33		
Erigeron vernus		80	0.3		
Lycopodiella appressa		80	0.43		
Morella cerifera	Y	80	0.73		
Muhlenbergia capillaris var. trichopodes <sup>2</sup>		80	6.7		
Paspalum praecox		80	0.5		
Pinus elliottii var. elliottii	Y	80	3.63	3.48	
Rubus trivialis		80	0.3		
Pinus palustris	Y			3.48	
Taxodium ascendens	Y			1.39	

An asterisk (\*) denotes species identified as either an indicator species or frequent ( $>50\%$ ) in another community type. Remaining species are listed by descending frequency. Superscripts denote indicator species with restricted distributions in Florida: <sup>1</sup>western Panhandle, <sup>2</sup>north Florida, <sup>3</sup>central Florida peninsula,<br><sup>4</sup>Elorida endemic <sup>4</sup>Florida endemic.

Panhandle Xeric Sandhills (31 plots). This community is restricted to the Northern Highlands land unit (Figure 3a) of the western Florida Panhandle and occurs in two landscape contexts: 1) on sandy ridge tops and upper slopes, and 2) as the dominant community of broad flat terrain with little apparent topographic variation on the broad uplands of the Citronelle formation (i.e., Eglin Air Force Base; Carr, pers. obs.). Surface soils of Panhandle Xeric Sandhills are coarse sands, similar to the geographically separated Peninsula Xeric Sandhills.

Panhandle Xeric Sandhills have sparse canopies of scattered Pinus palustris and Quercus laevis. Shrub strata are dominated by small oaks including Q. laevis, Q. margaretta and Q. incana. Unlike the Peninsula Xeric Sandhills, abundant understory species include low growing rhizomotous sub-shrubs Licania michauxii and Gaylussacia dumosa (Table 3); the former was identified as an indicator species.

Herbaceous species characteristic of xeric habitats distinguish Panhandle Xeric Sandhills ground cover vegetation (Table 3). Schizachyrium scoparium var. stoloniferum and Andropogon gyrans var. gyrans are common grasses. Aristida beyrichiana is somewhat less frequent, but where present tends to be the dominant grass species. Some indicator species have ranges restricted to the Panhandle,

including Liatris pauciflora var. secunda, Galactia microphylla, Aristida morhii, Tephrosia morhii, Rhynchosia cytisoides and Euphorbia floridana. Another restricted range species, Pityopsis aspera, is abundant and frequent (present in 90% of plots). In contrast, this species is absent in Peninsula Xeric Longleaf Sandhills, were P. graminifolia is common.

# Series 2: Subxeric Sandy Uplands

Longleaf pine woodland on sites with deep sandy soils but with a nearly continuous sward of grass are typically grouped as Subxeric Sandy Uplands (Peet 2006). These types are well drained with modest topographic relief, which sets them apart from the flatwood types on nearly flat terrain. Soils are predominantly entisols, setting the subseries apart from the Silty Uplands that occur primarily on ultisols, and flatwoods that occur primarily on spodosols. In addition to longleaf pine, common trees include Quercus laevis and Q. margaretta, while the groundcover is typically dominated by Aristida beyrichiana.

North Florida Longleaf Woodlands (11 plots). These sites are woodlands of middle and lower slopes in the Central Highlands and Coastal Lowlands of the northern peninsula (Figure 3b). All of our North Florida Longleaf Woodlands sites are in or adjacent to vegetation zones identified as ''Hardwood Hammocks'' by Davis (1967), and most are located downslope of North Florida Subxeric Sandhills. Soils of North Florida Longleaf Woodlands are distinguished by high organic and sub-surface clay content (Table 2), which suggests high water retention capacity (Brady and Weil 2000). Species richness of North Florida Longleaf Woodlands is relatively high, averaging 106 species/0.1 ha and second only among upland community types to Clayhill Longleaf Woodlands (Table 1).

Longleaf is abundant in our North Florida Longleaf Woodland sites although other pine species are present including P. elliottii var. elliottii and P. taeda (Table 3). Quercus geminata, Q. falcata, Q. nigra and Carya alba are canopy sub-dominants (Table 3). Midstory strata are generally shrubbier compared to other upland communities, and are dominated by Serenoa repens, Vaccinium arboreum, Liquidambar styraciflua, C. alba and two upland oak species (Q. geminata and Q. margaretta).

Common ground cover species of North Florida Longleaf Woodlands include grasses typical of upland communities, although Aristida beyrichiana is infrequent. Pteridium aquilinum, Smilax laurifolia, Andropogon gyrans var. gyrans, Dichanthelium angustifolium, Paspalum setaceum, Sorghastrum secundum, and Ageratina aromatica were ubiquitous herbaceous understory species, the latter also a range restricted indicator species. Many indicator species are woodland forbs and infrequent grass species, including four grass and four legume species. Roughly a third of the indicator species have ranges restricted to north or central Florida (Table 3).

North Florida Subxeric Sandhills (31 plots). This community occurs in the Coastal Lowlands and Central Highlands land units of the eastern panhandle and northern peninsula (Figure 3b), usually on ridge-tops and upper slopes. North Florida Subxeric Sandhills resemble the ''sandhill'' community as broadly defined by Florida Natural Areas Inventory (Florida Natural Areas Inventory 1990). Soils of this community are low in clay and organic matter (Table 2), and resemble in textural composition Peninsula Xeric Sandhills, except they are higher in surface soil silt content. Species richness of North Florida Subxeric Sandhills is relatively high, which is typical of communities of the Subxeric-Sandy Upland and the Silty Upland Series (Table 1).

North Florida Subxeric Sandhills sites have canopies of dense longleaf pines, codominated by other pine species and scattered upland oaks, particularly Quercus laevis. Oak species typical of xeric habitats dominate the midstory, including Quercus laevis, Q. incana, and Q. margaretta (Table 3).

Common understory herbaceous species of North Florida Subxeric Sandhills are similar to those of Peninsula Xeric Sandhills (Table 3). Many frequent species are grasses, including Aristida beyrichiana, D. ovale var. addisonii and Paspalum setaceum, the former by far the dominant species. Fourteen of the 15 indicator species are low-growing forbs, including the legumes Desmodium floridanum, Rhynchosia reniformis, and Lespedeza hirta. None of the indicator species had restricted ranges in Florida.

# Series 3: Silty Uplands

Silty upland communities are distinguished by relatively limited abundance of oaks and the co-dominance in the groundlayer by Aristida beyrichiana and Schizachyrium scoparium var. stoloniferum. These communities are largely confined to ultisols and have exceptionally high levels of species richness.

Clayhill Longleaf Woodlands (14 plots). This community is restricted to the Northern Highlands of the panhandle, inhabiting ridge tops and upper-slopes of dissected Pliocene and Miocene-aged terrain north of the Cody Scarp (Figure 3a). The prominence of finetextured sediments and high pH distinguishes soils of Clayhill Longleaf Woodlands from those of other upland communities (Table 2). Species richness of this community is exceedingly high, with mean species richness  $=$ 124.5 species/0.1 ha (Table 1).

Canopy vegetation of Clayhill Longleaf Woodlands is dense and dominated by longleaf pine and a minor presence of loblolly and shortleaf (P. taeda and P. echinata; Table 3). Understory vegetation includes shrubs typical of more mesic woodlands such as Quercus falcata, Q. stellata, Q. nigra, Rhus copallinum, Vaccinium stamineum var. stamineum, V. darrowii, and Cornus florida (Table 3).

Aristida beyrichiana, Schizachyrium scoparium var. stoloniferum and Dichanthelium angustifolium were ubiquitous grass species of Clayhill Longleaf Woodland understory vegetation, the first two being aspect dominants. Other frequent grass species include Dichanthelium angustifolium, Aristida purpurascens var. purpurascens, Gymnopogon ambiguus, and Schizachyrium tenerum. Abundant forbs included Pteridium aquilinum, Solidago odora var. odora, and Pityopsis graminifolia. Herbaceous species of Fabaceae and Asteraceae were the most frequent species encountered. Similarly, many legumes and composites comprise most of the indicator species (Table 3). Ten out of 37 indicator species are legume species and several of these are in the genus Desmodium. Eleven of the 37 indicator species have ranges restricted to the panhandle or northern peninsula, including several bunchgrass species identified as indicators: Andropogon gerardii, Eragrostis spectabilis, Sorghastrum nutans and Gymnopogon brevifolius (Table 3).

Panhandle Silty Longleaf Woodlands (22 plots). This community occupies Pleistocene and Miocene sediments of the Coastal Lowlands west of the Ochlockonee River basin, with the exception of sites on Saint Marks National Wildlife Refuge (Figure 3a). Most of our plots were situated in the Apalachicola embayment region on Pleistocene and Holocene undifferentiated lowlands east of the Apalachicola river (Puri and Vernon 1964, Florida Department of Environmental Protection 1998). Although included in the Silty Uplands series, Panhandle Silty Longleaf Woodlands resemble Flatwoods communities in landscape context in that they inhabit side slopes and terraces. Surface soils are high in silt and clay content, whereas subsurface soils also have high silt but low organic content (Table 2). Species richness of Panhandle Silty Longleaf Woodlands is moderately high, comparable to the North Florida Longleaf Woodlands and North Florida Subxeric Sandhills communities, but not approaching the extreme richness of the Clayhill Longleaf Woodlands (Table 1).

Longleaf pine dominates the somewhat dense canopies of Panhandle Silty Longleaf Woodland sites, whereas other canopy species are uncommon (Table 3). Notably absent are upland oaks and other xeric hardwoods. In contrast, low-growing evergreen shrub species dominate the ground cover, including Ilex glabra, Gaylussacia dumosa, Morella pumila, and Serenoa repens (Table 3). Vaccinium darrowii and Quercus pumila are also abundant (not shown in Table 3, frequency  $\langle 75\% \rangle$ .

Herbaceous vegetation of Panhandle Silty Longleaf Woodlands is similar to other Subxeric and Silty uplands communities. Aristida beyrichiana, Schizachyrium scoparium var. stoloniferum, Dichanthelium angustifolium, and Dichanthelium dicotomum var. tenue are the most frequent grass species with Aristida beyrichiana by far the dominant species. As in the Clayhill Longleaf Woodlands, Pteridium aquilinum is the most abundant forb-layer species (not the most frequent). In general, frequent forb species are similar to those of other upland communities, although species of Fabaceae and Asteraceae are better represented (Table 3). All indicator species of Panhandle Silty Longleaf Woodlands are herbs, and over half are legume or composite

species. Eight of 13 indicator species have ranges restricted to the panhandle or north peninsula, including two that are endemic to the Apalachicola region: Phoebanthus tenuifolius and Baptisia simplicifolia (Table 3).

#### Series 4: Flatwoods

Communities of the Flatwoods series typically inhabit flat, poorly-drained regions of the panhandle and peninsula Coastal Lowlands and the peninsular Central Highlands, and are notably absent from the better drained, rolling topography of the Northern Highlands region (Abrahamson and Hartnett 1990, Florida Natural Areas Inventory 1990). Soils are generally sandy and acidic, as is typical of Spodosols (Florida Natural Areas Inventory 1990, Peet 2006). Organic content of surface soils is higher than that of Xeric, Subxeric and Silty Uplands, although similar to that of Wetlands communities.

Xeric Flatwoods (36 plots). Xeric Flatwoods of the panhandle and peninsula Coastal Lowlands typically occur on upper slopes of small sandy rises embedded in large flat expanses (Figure 3c). In the Central Highlands, Xeric Flatwoods occupy small areas down-slope of Panhandle Xeric Sandhills and North Florida Subxeric Sandhills. Soils of Xeric Flatwoods are coarser, with less finetextured sediments, compared to all communities other than Peninsula Xeric Sandhhills. These textural attributes distinguish Xeric Flatwoods soils from North Florida Mesic Flatwoods (Table 2).

Xeric Flatwoods sites have sparse canopies of longleaf and slash pine. In contrast, midstory vegetation is dense. Serenoa repens is by far the most abundant species in the midstory and shrub layer, followed by three upland ''scrub'' oaks: Quercus geminata, Q. chapmanii, and Q. myrtifolia. Notably absent are the oaks of Xeric and Subxeric Upland communities (Q. laevis, Q. incana, Q. margaretta; Table 3). Evergreen shrub species of the heath family are common in Xeric Flatwoods, including Lyonia lucida, Gaylussacia dumosa and Vaccinium myrsinites, in addition to Quercus minima, and Befaria racemosa (Table 3).

The herbaceous understory of Xeric Flatwoods is sparse and species-poor. The grass Aristida beyrichiana is ubiquitous and by far the most abundant herb. Also frequent are Andropogon virginicus, Dichanthelium sabulorum, and Pityopsis graminifolia. Relatively few frequent species are recognized for Xeric Flatwoods compared to other communities (Table 3), perhaps reflecting the general paucity of herbaceous species. Of the seven indicator species identified, three are shrub species, and three species have ranges restricted to the peninsula: Befaria racemosa, Solidago odora var. chapmanii and Liatris tenuifolia var. quadriflora.

North Florida Mesic Flatwoods (30 plots). This community occurs in the Coastal Lowlands and the Central Highlands of the panhandle and peninsula (Figure 3c), in flat and poorly drained terrain of Pleistocene origin. In the latter landscape, North Florida Mesic Flatwoods often occupy large areas interspersed with Xeric Flatwoods on low ridges. The northerly distribution of North Florida Mesic Flatwoods geographically separates it from the Central Florida Flatwoods/ Prairies.

Canopies of North Florida Mesic Flatwoods contain dense longleaf and/or slash pine (Table 3). Shrub vegetation forms patchy growth interspersed with thick herbaceous ground cover. Common shrub species include Ilex glabra, Gaylussacia dumosa, Serenoa repens, Vaccinium myrsinites and Quercus minima (Table 3).

Common herbaceous species of North Florida Mesic Flatwoods resemble those of Xeric Flatwoods. Frequent grass species are similar, with the exception of Dichanthelium strigosum var. leucoblepharis (Table 3). Only three indicator species were recognized for North Florida Mesic Flatwoods, perhaps reflecting the large geographic and floristic range of this community. These include two small statured rhizomatous shrub species: Quercus minima and Kalmia hirsuta. In addition the grass Sporobolus floridanus is the sole herbaceous indicator species. This species of wetter habitats is largely restricted to the north peninsula and panhandle regions.

Central Florida Flatwoods/Prairies (22 plots). This community is restricted to the Coastal Lowlands of the peninsula on broad, flat, poorly-drained terrain of Pleistocene origin. Central Florida Flatwoods/Prairies are the southerly counterpart to North Florida Mesic Flatwoods. Soils of this community are similar to those of Xeric Flatwoods and North Florida Mesic Flatwoods (Table 2).

Central Florida Flatwoods/Prairies have sparse to absent tree canopies. Absence of pine overstory distinguishes dry prairies of Central Florida as described elsewhere (Florida Natural Areas Inventory 1990, Bridges 2006). We did not detect floristic differences between plots with and without a pine canopy. When present, the overstory consists of longleaf pine and one of the two varieties of slash pine (Pinus elliottii var. elliotii and P. elliottii var. densa; Table 3). Midstory vegetation is sparse in frequently-burned sites, and shrubs are relegated to the understory, where Serenoa repens is ubiquitous and abundant. Other understory shrubs include Ilex glabra, Lyonia lucida, Quercus geminata, Gaylussacia dumosa, Morella pumila, Hypericum reductum, and Vaccinium myrsinites (Table 3).

Grasses are among the most frequent groundcover species of Central Florida Flatwoods/Prairies, in particular Aristida beyrichiana, Andropogon virginicus, Aristida spiciformis, Schizachyrium stoloniferum and Dichanthelium chamaelonche. Similarly, grasses comprise six of the 25 indicator species, including the frequent species Aristida spiciformis, and Dichanthelium chamaelonche (Table 3). Two large bunchgrass species restricted to peninsular Florida are conspicuous indicators: Andropogon brachystachyus and Schizachyrium stoloniferum. Six indicator species have ranges restricted to the peninsula, including two Florida endemics (Table 3).

# Series 5: Wetlands

Communities of the Wetlands series occupy diverse physiognomic settings. Many occur on lower-slopes in regions with relatively high relief, particularly in the Northern and Central Highlands. Two communities restricted to the Coastal Lowlands, the Lower Panhandle Savannas and Peninsula Savannas, inhabit poorly drained lowlands with little topographic relief. Historically, large expanses of these vegetation types extended across gradients of imperceptible elevation change (Harper 1914, Myers 2000).

Most Wetlands communities have poorlydrained, silty, acidic soils. High content of silt and organic matter, coupled with low pH, distinguishes these soils from those of the Flatwoods and Dry Upland communities (see

Table 2). These soil characteristics were particularly pronounced in Wetland communities of the panhandle.

Wet Depression Prairies (11 plots). This community is restricted to the margins of depressional wetlands of the panhandle and northern peninsula (Figure 3e), including cypress swamps, sandhill upland lakes, and depression marshes (sensu Florida Natural Areas Inventory 1990). Surface soils are sandy, acidic and high in organic content. Sub-soil silt content is low and clay content is high (Table 2). This may reflect the presence of subsurface ''hardpans'' or ''clay lens'' described as underlying depression marshes and dome swamps (Florida Natural Areas Inventory 1990). Mean species richness (49.6/ 0.1 ha) was the lowest of any of the communities examined, perhaps reflecting the irregular hydroperiod common to these communities.

Canopy vegetation of Wet Depression Prairies is absent. Similarly, midstory vegetation is sparse or absent. A few evergreen shrubs are sporadically present, including Ilex glabra, I. myrtifolia, Cyrilla racemiflora and Hypericum fasciculatum (all less frequent than 75%, not listed in Table 3).

Herbaceous vegetation of Wet Depression Prairies is low in aspect and diversity. Few species have high constancy across sites, as seen by the paucity of frequent species in Table 3. Frequent grasses include Andropogon virginicus and Panicum hemitomon: Aristida beyrichiana is notably absent. Similarly, few species are recognized as indicator species. The four indicators include three forbs typical of wetlands (United States Department of Agriculture, Natural Resource Conservation Service 2007) and the wetland grass Panicum hemitomon. One species, Xyris difformis var. curtissii, is restricted in range to North Florida (Table 3).

Peninsula Savannas (16 plots). This community inhabits flat, poorly-drained terrain of the Coastal Lowlands (Figure 3e), often on lower slopes proximate to North Florida Mesic Flatwoods where high water tables and seasonal inundation are common (Florida Natural Areas Inventory 1990, Myers and Ewel 1990). Soils of Peninsula Savannas are sandier and higher in organic matter in comparison to other Wetlands communities. Sub-soil

differences are particularly distinct, with low clay and silt content (Table 2).

Peninsula Savannas have pine canopies that are either sparse or absent. Similarly, midstory vegetation is typically sparse, and when present is dominated by Taxodium ascendens (Table 3). Common understory woody species are the low-growing shrubs Hypericum fasciculatum, and H. myrtifolium.

Ground cover vegetation of Peninsula Savannas is distinctive for its abundance and diversity of herbaceous species. All frequent species and 95% of indicator species are herbaceous (Table 3). These include typical wetland species, such as Oxypolis filiformis, Eriocaulon decangulare, Bigelowia nudata, Amphicarpum muhlenbergianum and Xyris elliottii. Aristida beyrichiana is frequent in Peninsula Savannas, but is rivaled in abundance by various wetland grass species, particularly Aristida palustris, Andropogon capillipes, Dichanthelium erectifolium, and Panicum rigidulum var. pubescens. None of the 31 indicator species have restricted ranges in Florida.

Calcareous Savannas (4 samples; W3). This community is an unusual floristic assemblage that inhabits wetlands overlying shallow subsurface limestone. Although our small sample size precludes much generalization, floristic composition of our sites were highly distinct compared to other communities (Table 3, Figure 4). Calcareous Savannas occur in two physiographic settings: 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 the Coastal Lowlands embedded in large expanses of Central Florida Flatwoods/Prairies (Figure 3e). Soil texture is similar to that of Peninsula Savannas, despite higher sub-surface clay content. Calcareous Savannas soils are basic and have exceedingly high calcium concentrations, consistent with the presence of shallow soils overlying limestone outcrops (Table 2). Mean species richness of Calcareous Savannas is exceedingly high (125 species / 0.1 ha), rivaling that of Clayhill Longleaf Woodlands and Upper Panhandle Savannas (Table 1).

Three of the four Calcareous Savannas vegetation plots had dense canopies of slash pine but no longleaf pine (Table 3). A single plot on Avon Park Air Force Range had no overstory at all. Sabal palmetto is a significant canopy co-dominant at all plots, and is selected as an indicator species. Other hardwood species typical of swamp vegetation are common in the midstory such as Morella cerifera, Acer rubrum, Cornus foemina and Ilex glabra (Table 3).

Understory vegetation of Calcareous Savannas is dense and diverse. Aristida beyrichiana is uncommon. Rather, the dominant grasses include Panicum rigidulum var. rigidulum, Andropogon glomeratus var. glomeratus, Dichanthelium dichotomum var. nitidum, and Axonopus furcatus. All but one indicator species are forbs, grasses and sedges, notably members of the genus Rhynchospora (Table 3; indicator species with frequency  $<$ 75% not shown due to large numbers and small sample size). One indicator species (Rhynchospora perplexa) has a range restricted to North Florida.

North Florida Wet Flatwoods (15 plots). This community occurs in the panhandle and northern peninsula, usually in Highlands and Ridge physiographic landforms in narrow fringes along lower slopes adjacent to wetland swamps (Figure 3d). Most of our sites are east of the Ochlockonnee River basin, though one site is in the western panhandle. Soil texture of North Florida Wet Flatwoods soils is not distinct from other Wetlands communities, although surface soils are higher in organic content and are more acidic (Table 2).

Dense canopy and midstory vegetation distinguishes North Florida Wet Flatwoods from other Wetlands communities. Slash pine is the most abundant canopy species, followed by longleaf pine, whereas Persea palustris, Nyssa sylvatica var. biflora and Prunus serotina are minor components (Table 3). Abundant shrub cover includes many species such as Serenoa repens, Persea palustris, Lyonia lucida, Nyssa sylvatica var. biflora, Ilex coriacea and I. glabra (Table 3). Total cover of shrub species is second only to the North Florida Mesic Flatwoods.

Understory vegetation of North Florida Wet Flatwoods is sparse and patchy, consisting of herbaceous growth interspersed with patchy shrubs, such as Andropogon glaucopsis, Osmunda cinnamomea, Xyris ambigua and Eriocaulon decangulare (Table 3). Eight of the 17 indicator species are shrubs, reflecting the preva-

lence of woody vegetation that distinguishes North Florida Wet Flatwoods. Most of the shrub indicators are typical of wetland swamps, such as Persea palustris, Lyonia lucida, Nyssa biflora, and Clethra alnifolia (Table 3). The latter species is restricted in distribution to the northern peninsula. The few herbaceous indicators are typical of wetland habitats, including Sarracenia minor, Andropogon glomeratus var. glomeratus, A. glaucopsis, Carex glaucescens, and Sphagneticola spp.

Upper Panhandle Savannas (7 plots). This community is restricted to Pliocene and Miocene-aged sediments of the panhandle Northern Highlands north of the Cody Scarp (Figure 3d). Our sample size for this community is small, in part because of the rarity of this community in the landscape. Our sites occupy mid-slopes and flat river terraces that are down-slope of Clayhill Longleaf Woodlands or Panhandle Xeric Sandhills. Finetextured soils distinguish soils of Upper Panhandle Savannas, with higher combined clay and silt content than any other community examined in this study and low organic matter compared to other Wetland communities (Table 2).

Upper Panhandle Savanna sites have sparse pine canopies comprised of longleaf, slash and loblolly pines. Pinus serotina is a minor component (Table 3). Midstory vegetation is sparse, as shrub species are relegated to the understory of these frequently burned sites. Ilex glabra, Diospyros virginiana and Rhus copallinum are the most frequent woody understory species, followed by Quercus pumila, and Gaylussacia frondosa var. nana (Table 3).

Understory vegetation of Upper Panhandle Savannas is particularly rich in grass and forb species. Species richness (126 species / 0.1 ha) is the highest of any of the communites examined in this study. Some dominant grasses are typical of xeric-mesic habitats, such as Schizachyrium scoparium var. stoloniferum, Andropogon gyrans var. gyrans, and Dichanthelium dichotomum var. tenue. Similarly, upland forbs are frequent, such as Pityopsis graminifolia. Other frequent herbs include characteristic wetland species, such as Ctenium aromaticum, Panicum verrucosum, Andropogon glomeratus var. hirsutior, and Aristida purpurascens var. virgata (Table 3). Of the 20 species selected as indicators of Upper Panhandle Savannas, all but one are herbaceous. Six indicator species have ranges restricted to panhandle or northern peninsula (Table 3).

Lower Panhandle Savannas (16 plots). This community is restricted to the Northern Highlands and Coastal Lowlands of the panhandle, west of the Ochlocknee River (Figure 3d). In hillier terrain, Lower Panhandle Savannas occupy narrow lower-slopes, in association with Xeric or Subxeric Upland communities. In contrast, Lower Panhandle Savannas in the Coastal Lowlands inhabit large lowlands proximate to North Florida Mesic Flatwoods and are nearly treeless. Examples of the latter condition are the 'wet prairies' of the Apalachicola National Forest (Clewell 1971). Soils are relatively low in sand and organic matter, and high in silt, in contrast to soils of the Peninsula Savannas (Table 2).

Lower Panhandle Savanna sites have sparse canopies of slash and longleaf pines (Table 3), although the canopy is absent in some sites. Midstory vegetation is largely absent although low growing shrubs are present in the understory. Ilex glabra is the most abundant understory woody species. Other frequent shrubs include Ilex myrtifolia, Nyssa ursina and Cliftonia monophylla.

Lower Panhandle Savannas have well-developed, herb-dominated ground cover vegetation. Aristida beyrichiana and Ctenium aromaticum are dominant grasses. Andropogon arctatus and A. morhii are distinctive savanna grasses that are identified as indicators and are restricted in range to north Florida. Twenty five of 27 indicator species are forbs, some of the most frequent including Carphephorus pseudoliatris, Chaptalia tomentosa, Xyris ambigua, Helianthus heterophyllus, and Rhexia alifanus. Over half of the indicator species have distributions restricted to panhandle or northern peninsula (Table 3).

Panhandle Seepage Savannas (5 plots). This community occurs in the Northern Highlands and Coastal Lowlands of the western panhandle and is situated on lower slopes with soils usually saturated by ground seepage (Figure 3d). This condition is thought to result from water percolation through sandy soils underlain by impermeable clay or rock hardpans, as elsewhere described for seepage slope communities (Florida Natural

Areas Inventory 1990). Despite the putative existence of clay lenses in the subsoil, subsoils from our Panhandle Seepage Savannas are low in clay content, although it is possible that our soil samples were not sufficiently deep to detect hardpans. Sub-soil silt of Panhandle Seepage Savannas is low compared to other panhandle Wetland communities (Table 2). Surface soils are silty, acidic and high in organic content, although small sample size precluded statistical tests.

The sparse canopies of Panhandle Seepage Savannas consist of longleaf and slash pine (Table 3). Shrub cover is relatively dense and dominated by Ilex glabra, Morella caroliniensis, Magnolia virginiana, Gaylussacia mosieri, and Hypericum brachyphyllum (Table 3).

Species richness and understory vegetation density of Panhandle Seepage Savannas is high compared to other Wetlands communities (Table 1). Abundant grasses and sedges include Aristida beyrichiana, Scleria muehlenbergii, Rhynchospora oligantha, Muhlenbergia capillaris var. tricopodes, Ctenium aromaticum, Rhynchospora oligantha, R. latifolia, Aristida palustris, A. gyrans var. stenophyllus, and Andropogon arctatus (Table 3). Indicator species include the grasses Aristida palustris, Andropogon arctatus and A. gyrans var. stenophyllus, as well as many forbs such as Coreopsis linifolia, Sabatia macrophylla. Most indicator species have ranges restricted to north and panhandle Florida (Table 3). A few of these are locally abundant species (e.g., Pleea tenuifolia, Triantha racemosa, Sarracenia flava, Rhynchospora macra, and R. oligantha).

**DISCUSSION** This study provides a comprehensive classification and description of pyrogenic pineland plant communities of Florida. The use of detailed, quantitative vascular plant data from relatively large scale (0.1 ha) samples allows partitioning of community types based on vegetation data alone, and a comprehensive assessment of distinctive community characteristics. The resultant descriptions of communities in terms of geographic region, physiographic landform, local topography, and soil characteristics should assist field identification of communities.

Our approach contrasts with many previous classifications of Coastal Plain pineland communities, which are based on quantitative data but have been limited in geographic scope, are geographically broad but qualitative, or are based only on woody species composition. Conservation workers and land managers require a classification system that is relevant to the geographic scope and variation of their region, yet that is manageable in terms of ease of community recognition and the number of units recognized. The vegetation classification of the Florida Natural Areas Inventory (FNAI) has heretofore provided such a classification, albeit a subjective one based on qualitative observation rather than quantitative field data (e.g., Florida Natural Areas Inventory 1990). The FNAI classification presents broad descriptions of natural communities that emphasize conspicuous and common plant species. We have attempted to provide a solid foundation for such a classification based on quantitative field data.

Our classification expands and refines the classifications of Peet and Allard (1993) and Peet (2006). These classifications of coastal plain fire-maintained pineland communities include parts of Florida and are currently the only large-scale classifications of Southeastern pinelands based on quantitative and complete floristic data. In general, our series reflect the major ecological groups of longleaf pine dominated vegetation recognized by Peet (2006). Our detailed descriptions emphasize characteristic and diagnostic plant taxa and community attributes to facilitate field identifications of communities. Furthermore, by using an optimization index in conjunction with cluster analysis, we minimized subjectivity associated with cluster partitioning (McCune and Grace 2002). Our restriction of cut-levels in the cluster solution to groups  $>3$ samples was subjective but limited delineation of communities with little documentation (Legendre and Legendre 1998, McCune and Grace 2002).

Although our results are compatible with the United States National Vegetation Classification (NVC; Anderson et al. 1998, Grossman et al. 1998, Jennings et al. 2003), our classification is more coarsely grained to facilitate application. The NVC classification spans the full United States, is derived from quantitative data and qualitative information, and aims at more narrowly defined and

homogeneous units (associations) with a goal of providing a framework for precise documentation of ecological context and biodiversity significance (see Federal Geographic Data Committee 2008, Jennings et al. 2009). Communities of the present study span more floristic variation than NVC associations, but are more practical and identifiable for the typical user.

To facilitate crosswalks between classifications, we identified NVC associations that correspond to or cluster within community types of the present study. As supporting plot data is limited for NVC associations, we used careful inspection of supporting documentation to assign each NVC association to the most closely approximated community type. Because NVC associations generally circumscribe less variation than our communities, we encountered relatively little ambiguity (see Appendix 1). We anticipate that the data collected in this study will be used to refine or define the narrower vegetation associations of the NVC following the United States Federal Geographic Data Committee standards (Federal Geographic Data Committee 2008) and the Ecological Society of America guidelines (Jennings et al. 2009).

By necessity, our vegetation classification describes pineland community variation from a highly fragmented landscape of remaining natural areas. The distribution of intact pineland communities reflects the non-random distribution and management of natural areas in Florida and has been influenced by the timing and pattern of economic development (Kautz and Cox 2001, Frost 2006). Thus, our classification describes natural communities that resemble present ''natural'' conditions rather than the potentially wider range of historical communities. Given these limitations, we strived to achieve a balanced representation of extant conditions via a sampling design stratified by ecoregion and moisture gradient. This approach, coupled with our large study size, minimized bias in incorporating the remaining fragments of natural pineland vegetation (Lepš and Smilauer 2007).

Geographic and edaphic differentiation among floristically-defined communities is pronounced in our classification. Regionalization of Coastal Plain pineland community vegetation was noted by Peet and Allard (1993) in addition to floristic variation coincident with soil texture. Our results using a larger and more densely arrayed set of vegetation samples reinforce these observations. In particular, soil texture distinguishes sites at the series level. Furthermore, soil texture variation is generally predictable among communities and between geographic regions. Peninsula soils are typically coarser than panhandle soils, and conversely, panhandle soils typically have finer sub-soil texture. Distinct regionalization of physiognomically similar communities often coincides with regional soil texture differences. For example, although representatives of the two Xeric Upland communities (Peninsula Xeric Sandhills vs. Panhandle Xeric Sandhills) are similar in landscape position and surface soil attributes, they differ in sub-soil clay and organic content, consistent with observed regional edaphic trends. Similar regional soil texture variation was apparent among physiognomic analogs of the Wetlands series (e.g., Peninsula Savannas vs. Upper and Lower Panhandle Savannas). Conversely, soil texture variation between regionally distinct communities of the Flatwoods series is not obvious (e.g., North Florida Mesic Flatwoods vs. Central Florida Flatwoods/Prairies).

Geographic regionalization of species composition varies with latitudinal gradients of environmental, climate, and geologic conditions. The Florida peninsula spans almost seven degrees in latitude including the transition between the Warm Temperate Moist Forest of North Florida and the Subtropical Moist Forest of extreme south Florida (Holdridge 1967, Myers 2000) with much of the peninsula falling into a broad ''transition zone'' between the two. Florida's complex recent geologic history contributes to panhandle and peninsula differences. Carbonate deposits of marine origin created the limestone platform of the peninsula 60–120 ma. Following the late Miocene, increased clastic deposition and sea level fluctuation influenced surface geology and soil development in the peninsula. In contrast, Pliocene and Miocene deposits of the panhandle are predominantly clastic sediments derived from Appalachian erosion and alluvial processes (Randazzo and Jones 1997, Myers 2000). The

2010 CARR ET AL.: CLASSIFICATION OF FLORIDA PINELAND COMMUNITIES 183

Suwannee Strait, an elongate depressed feature in southern Georgia and northeastern Florida, separated the two regions by water 12–30 ma (Hull 1962, Puri and Vernon 1964, Myers 2000). The familiar panhandle-peninsula distinction in floristic variation tracks these phenomena, including differences in geologic sedimentation, age of landforms, degree of isolation, and climate variation associated with latitude.

Plant taxa with restricted ranges contribute to regional partitioning among communities, despite similarities in physiognomic setting. Nearly a fifth of taxa retained for numerical analysis (18.4%) have restricted ranges within Florida, as do a third of identified indicator species (106 of 333). Most restricted-range taxa reflect the familiar segregation between panhandle and peninsula Florida (i.e., those restricted to the western panhandle or the peninsula east of the Ochlocknee River basin). The large number of taxa restricted to the western panhandle (42 taxa) is consistent with other descriptions of endemism in the East Gulf Coastal Plain (e.g., 125 endemic taxa reported by Sorrie and Weakley 2001, 2006). In addition, many taxa reach their southern limits of distribution in the northern peninsula, closely approximating the ''warm temperate moist forest'' bioclimate zone (Holdridge 1967). Numerous endemics are restricted to the Florida peninsula (122 taxa: Sorrie and Weakley 2001), and we recorded in our plots 31 taxa endemic or near-endemic to the peninsula. This pattern reinforces the segregation of communities between north and central Florida (e.g., North Florida Mesic Flatwoods vs. Central Florida Flatwoods/Prairies). Similarly, the three wetland communities restricted to the western panhandle (Upper Panhandle Savannas, Lower Panhandle Savannas, and Panhandle Seepage Savannas) have numerous indicator species with restricted range.

**CONCLUSIONS** We present a vegetation classification and description of extant firedependent pineland communities based on a geographically broad, systematic, and quantitative inventory. Our classification is as comprehensive as possible while remaining broadly applicable for management and conservation programs. The provision of indicator species, geographical distributions, and physiographic context of communities should facilitate field identification of the identified communities and series. Recognition of the breadth of Florida pineland communities along with assessment of their rarity should guide prioritization of land acquisition with the goal of preserving the full range of native plant biodiversity. Quantitative community descriptions should also provide a geographically specific guide for ecological restoration projects. The present study provides a glimpse into the exceptional floristic diversity of the historic Florida landscape, presenting the challenge of both understanding and preserving the full range of remaining pineland plant community diversity.

ACKNOWLEDGMENTS For help with site selection, ecoregion delineation and sampling design, we thank Bruce Means, Bill Platt, Wilson Baker, Ann Johnson, Carolyn Kindell, Louis Provencher, Doria Gordon, Brenda Herring and numerous employees of state, federal, and private land management agencies in Florida. For help with data collection, entry, management and analysis we thank John Brubaker, Christine Carlson, Deb Cupples, Jeff Glitzenstein, Joel Gramling, Maynard Hiss, Jean Huffman, Jessica Kaplan, Patrick McMillan, Brian Mealor, Donna Streng and Brian Strom. We are grateful to the faculty and staff of the University of Florida Herbarium for use of facilities and taxonomic assistance, especially Walter Judd, Trudy Lindler, Kent Perkins and Norris Williams. We thank Richard Abbott, Richard LeBlond, and Brenda Herring for their help with plant identification. The manuscript benefited from critical review by Ann Johnson, Doria Gordon, George Tanner, Wiley Kitchens, Debrah Miller, and an anonymous reviewer. This study was funded by the nongame program of the Florida Fish and Wildlife Conservation Commission.







# Appendix 1. Continued.

# LITERATURE CITED

- Abrahamson, W.G. and D.C. Hartnett. 1990. Pine flatwoods and dry prairies. p. 103–149. In: Myers, R.L. and J.J. Ewel (eds.). Ecosystems of Florida. The University of Central Florida Press, Orlando, Florida.
- Anderson, M., P. Bourgeron, M.T. Bryer, R. Crawford, L. Engelking, D. Faber-Langendoen, M. Gallyoun, K. Goodin, D.H. Grossman, S. Landaal, K. Metzler, K.D. Patterson, M. Pyne, M. Reid, L. Sneddon, and A.S. Weakley. 1998. International classification of ecological communities: terrestrial vegetation of the United States. Volume II. The National Vegetation Classification System: list of types. The Nature Conservancy, Arlington, Virginia, USA.
- Bailey, R.G., P.E. Avers, T. King, and W.H. McNab (eds.). 1994. Ecoregions and subregions of the United States (map). Supplementary table of map unit descriptions. United States Department of Agriculture, Washington, D.C. 1:7,500,000.
- Brady, N.C. and R.R. Weil. 2000. Elements of the nature and properties of soils, 12th ed. Prentice-Hall Inc., Upper Saddle River, New Jersey.
- Bridges, E.L. 2006. Landscape ecology of Florida dry prairie in the Kissimmee River region. p. 14–42. In: Noss, R. (ed.). Land of fire and water: proceedings of the Florida Dry Prairie Conference. University of Central Florida, Painter, DeLeon Springs, Florida.
- Bridges, E.L. and S.L. Orzell. 1989. Longleaf pine communities of the West Gulf Coastal Plain. Nat. Areas J. 9:246–263.
- Brooks, H.K. 1982. Guide to the Physiographic Divisions of Florida. Institute of Food and Agricultural Sciences, Florida Cooperative Extension Services. University of Florida, Gainesville, Florida.
- Brown, R.B., E.L. Stone, and V.W. Carlisle. 1990. Soils. p. 35–69. In: Myers, R.L. and J.J. Ewel (eds.). Ecosystems of Florida. University of Central Florida Press, Orlando, Florida.
- Carr, S.C., K.M. Robertson, W.J. Platt, and R.K. Peet. 2009. A model of geographic, environmental and regional variation in vegetation composition of pyrogenic grasslands of Florida. J. Biogeogr. 36:1600–1612.
- Clewell, A.F. 1971. The vegetation of the Apalachicola National Forest: an ecological perspective. United States Department of Agriculture Forest Service, Atlanta, Georgia.
- Cook, C.W. 1945. Geology of Florida. Florida Geological Survey Bulletin No. 29. Florida Department of Conservation, Florida Geological Survey, Tallahassee, Florida.
- Dale, V.H., S.C. Beyler, and B. Jackson. 2002. Understory vegetation indicators of anthropogenic disturbance in longleaf pine forests at Fort Benning, Georgia. Ecological Indicators 1:155–170.
- Davis, J.H. 1967. General map of natural vegetation of Florida, circular S-178. Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Florida.
- Dufrene, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67:345–366.
- Federal Geographic Data Committee. 2008. National Vegetation Classification Standard, Version 2. FGDC Document number FGDC-STD-005-2008.http://www.fgdc.gov/standards/ projects/FGDC-standards-projects/vegetation/ NVCS\_V2\_FINAL\_2008-02.pdf
- Fenneman, N.M. 1938. Physiography of eastern United States. McGraw-Hill Book Co., New York, New York.
- Fernald, E.A. 1981. Atlas of Florida. Florida State University Foundation, Tallahassee, Florida.
- Florida Department of Environmental Protection. 1998. Surficial geology of Florida. Florida Geographic Data Library, Gainesville, Florida.
- Florida Natural Areas Inventory. 1990. Guide to the natural communities of Florida. Florida Department of Natural Resources, Tallahassee, Florida.
- Florida Natural Areas Inventory. 2000. Unpublished element occurrence data. Florida Department of Natural Resources, Tallahassee, Florida.
- Frost, C. 2006. History and future of the longleaf pine ecosystem. p. 297–326. In: Jose, S., E.J. Jokela, and D.L. Miller (eds.). The longleaf pine ecosystem: ecology, silvi-

culture, and restoration. Springer, New York, New York.

- GeoPlan. 2004. Physiographic provinces of Florida. Derived from (Puri and Vernon 1964). http://www.fgdl.org/metadata/fgdl\_ html/phprov.htm.
- Glitzenstein, J.S., D.R. Streng, and D.D. Wade. 2003. Fire frequency effects on longleaf pine (Pinus palustris) vegetation in South Carolina and Northeast Florida, USA. Natural Areas J. 23:22–37.
- Glitzenstein, J.S., W.J. Platt, and D.R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in North Florida longleaf pine savannas. Ecol. Monogr. 65:441–476.
- Griffith, G.E., J.M. Omernic, C.M. Rohm, and S.M. Pierson. 1994. Florida Regionalization Project. EPA/Q-95/002. United States Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon.
- Grossman, D.H., D. Faber-Langendoen, A.S. Weakley, M. Anderson, P. Bourgeron, R. Crawford, K. Goodin, S. Landaal, K. Metzler, K.D. Patterson, M. Pyne, M. Reid, and L. Sneddon. 1998. International classification of ecological communities: terrestrial vegetation of the United States. Volume I, The National Vegetation Classification System: development, status, and applications. The Nature Conservancy: Arlington, VA.
- Harper, R.M. 1914. Geography and vegetation of north Florida. Florida State Geological Survey Annual Report, Tallahassee, Florida.
- Hedman, C.W., S.L. Grace, and S.E. King. 2000. Vegetation composition and structure of southern Coastal Plain forests: an ecological comparison. For. Ecol. Manage. 134:233–247.
- Hoctor, T.S., R.F. Noss, L.D. Harris, and K.A. Whitney. 2006. Spatial ecology and restoration of the longleaf pine ecosystem. p. 377–402. In: Jose, S., E. Jokela, and D. Miller (eds.). Longleaf pine ecosystems: ecology, management, and restoration. Springer, New York, New York.
- Holdridge, L. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.
- Huddlestun, P.F. 1988. A revision of the lithostratigraphic units of the Coastal Plain

of Georgia: the Miocene through Holocene. Georgia Geol. Surv. Bull. 104.

- Hull, J.P. 1962. Cretaceous Suwannee strait, Georgia and Florida. Amer. Assoc. Petroleum Geologists Bull. 46:118–122.
- Jennings, M., O. Loucks, D. Glenn-Lewin, R. Peet, D. Faber-Langendoen, D. Grossman, A. Damman, M. Barbour, R. Pfister, M. Walker, S. Talbot, J. Walker, G. Hartshorn, G. Waggoner, M. Abrams, A. Hill, D. Roberts, and D. Tart. 2003. Guidelines for describing associations and alliances of the United States National Vegetation Classification. The Ecological Society of America, Vegetation Classification Panel, Version 3.0 November 2003.
- Jennings, M.D., D. Faber-Langendoen, O.L. Loucks, R.K. Peet, and D. Roberts. 2009. Characterizing associations and alliances of the United States National Vegetation Classification. Ecol. Monogr. 79:173–199.
- Kartesz, J.T. 1999. A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland, 1st ed. Synthesis of the North American Flora, version 1. North Carolina Botanical Garden, Chapel Hill, North Carolina.
- Kautz, R.S. and J.A. Cox. 2001. Strategic habitats for biodiversity conservation in Florida. Conserv. Biol. 15:55–77.
- Kirkman, L.K., K.L. Coffey, R.J. Mitchell, and E.B. Moser. 2004. Ground cover recovery patterns and life-history traits: implications for restoration obstacles and opportunities in a species-rich savanna. J. Ecol. 92:409–421.
- Legendre, P. and E.D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271–280.
- Legendre, P. and L. Legendre. 1998. Numerical ecology, 2nd ed. Elsevier Science, Amsterdam, Netherlands.
- Lepš, J. and P. Smilauer. 2007. Subjectively sampled vegetation data: don't throw out the baby with the bath water. Folia Geobotanica 42:169–178.
- McCune, B. and J. Grace. 2002. Multivariate analysis of ecological communities. MjM Software, Gleneden Beach, Oregon.
- McCune, B. and M.J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data version 5.12. MjM Software, Gleneden Beach, Oregon.
- Mehlich, A. 1984. Mehlich 3 soil test extraction modification of Mehlich 2 extractant. Comm. Soil Sci. Plant Anal. 15:1409–1416.
- Myers, R.L. 2000. Physical setting. p. 10–19. In: Wunderlin, R.P. and B.F. Hansen (eds.). Flora of Florida: pteridophytes and gymnosperms. The University Press of Florida, Gainesville, Florida.
- Myers, R.L. and J.J. Ewel, (eds.). 1990. Ecosystems of Florida. University Press of Florida, Gainesville, Florida.
- Nesom, G.L. 2006. Carphephorus. p. 535–538. In: Flora of North America Editorial Committee (eds.). Flora of North America north of Mexico. Volume 21. Asteraceae, part 3. Oxford University Press, New York, New York.
- Oksanen, J., R. Kindt, P. Legendre, and R.B. O'Hara. 2007. Vegan: community ecology package version 1.8-6 (http://cran.r-project. org).
- Olson, M.S. and W.J. Platt. 1995. Effects of habitat and growing season fires on resprouting of shrubs in longleaf pine savannas. Vegetatio 119:101–118.
- Ostertag, T.E. and K.M. Robertson. 2007. A comparison of native versus old-field vegetation in upland pinelands managed with frequent fire, south Georgia, USA. Tall Timbers Fire Ecology Conference Proceedings 23:109–120.
- Outcalt, K.W. and R.M. Sheffield. 1996. The longleaf pine forest: trends and current conditions. United States Department of Agriculture, Forest Service Resource Bulletin SRS-9. Southern Research Station, Asheville, North Carolina.
- Peet, R.K. 2006. Ecological classification of the longleaf pine woodlands. p. 51-94. In: Jose, S., E.J. Jokela, and D.L. Miller (eds.). The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, New York.
- Peet, R.K. and D.J. Allard. 1993. Longleaf pine vegetation of the Southern Atlantic and eastern Gulf Coast regions: a preliminary classification. Proc. Tall Timbers Fire Ecol. Conf. 18:45–81.
- Peet, R.K., T.R. Wentworth, and P.S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63:262–274.
- Platt, W.J. 1999. Southeastern pine savannas. p. 23–51. In: Anderson, R.C., J.S. Fralish, and J.M. Baskin (eds.). Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, New York, New York.
- Puri, H.S. and R.O. Vernon. 1964. Summary of the geology of Florida and a guidebook to the classic exposures. Florida Geological Survey Special Publication 5, Gainesville, Florida.
- Radford, A.E., C.R. Bell, and H. Ahles. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill, North Carolina.
- Randazzo, A.F. and D.S. Jones (eds.). 1997. The geology of Florida. University Press of Florida, Gainesville, Florida.
- Sorrie, B.A. and A.S. Weakley. 2001. Coastal plain vascular plant endemics: phytogeographic patterns. Castanea 66:50–82.
- Sorrie, B.A. and A.S. Weakley. 2006. Conservation of the endangered Pinus palustris ecosystem based on Coastal Plain centers of plant endemism. Appl. Veg. Sci. 9:59–66.
- United States Department of Agriculture, Natural Resources Conservation Service. 2007. The PLANTS database (http://plants. usda.gov, 15 July 2007). National Plant Data Center, Baton Rouge, Louisiana.
- United States Environmental Protection Agency. 1999. Florida ecoregion map. St. Johns River Water Management District. Palatka, Florida.
- Varner, J.M. and J.S. Kush. 2004. Remnant old-growth longleaf pine savannas and forests of the Southeastern USA: status and threats. Nat. Areas J. 24:141–149.
- Walker, J. and R.K. Peet. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. Vegetatio 55:163–179.
- Walker, J.L. and A.M. Silletti. 2006. Restoring the ground layer of longleaf pine ecosystems. p. 297–326. In: Jose, S., E.J. Jokela,

and D.L. Miller (eds.). The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, New York.

- Ward, D. (ed.). 1979. Rare and endangered biota of Florida. Volume 5. Plants. University Press of Florida, Gainesville, Florida.
- Weakley, A.S. 2008. Flora of the Carolinas, Virginia, and Georgia, northern Florida, and surrounding areas. http://www.herbarium. unc.edu/flora.htm/. University of North Carolina at Chapel Hill Herbarium, Chapel Hill, North Carolina. Version of April 7, 2008.
- Webb, S.D. 1990. Historical biogeography. p. 70–102. In: Myers, R.L. and J.J. Ewel

(eds.). Ecosystems of Florida. University of Central Florida Press, Orlando, Florida.

- Whittaker, R.H. 1967. Gradient analysis of vegetation. Biol. Reviews 42:207–264.
- Wunderlin, R.P. and B.F. Hansen (eds.). 2000. Flora of Florida. The University Press of Florida, Gainesville, Florida.
- Wunderlin, R.P. and B.F. Hansen. 2004. Atlas of Florida vascular plants http://www. plantatlas.usf.edu [S. M. Landry and K. N. Campbell (application development), Florida Center for Community Design and Research.] Institute for Systematic Botany, University of South Florida, Tampa, Florida. Accessed June 16, 2007.