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Comparative Floristic Studies of Georgian Sandhill Ecosystems Reveals a Dynamic

Composition of Endemics and Generalists

By

James M. Long

Under the mentorship of Dr. John Schenk

ABSTRACT

Sandhill habitats are characterized by sandy, xeric soils that contain a unique assemblage of plants and animals. Similar to the broader long-leaf pine (Pinus palustris) and wire grass (Aristida stricta) ecosystem that sandhills are a subset of, agriculture, development, and habitat modifications have caused sandhill ecosystems to become degraded, putting many species at risk of extinction. Previous studies have focused on diversity within individual sandhills, leaving us with an incomplete understanding of how these communities form, what species are endemic, whether endemics are widespread across sandhills, and how species have adapted to these communities. To gain a more comprehensive understanding of these ecosystems, we sampled four Georgian Coastal Plain sandhills and compared species occurrences and life history patterns. Species diversity was positively correlated with sandhill area size, however, the proportion of endemic taxa was not influenced by area, as all four sites contained approximately the same number of endemics regardless of size. Endemic species differed from generalists in that the majority of species were herbaceous perennials. Sandhill generalists were seldom widespread across sites and mostly occurred on one or two sites. Taken together, our results provide the first opportunity to observe the dynamic nature of sandhill ecosystems, which we found to differ from one another due to endemic and generalist species turnover, but were consistently inhabited by a similar subset of taxa. Continued destruction of sandhill habitats will have a negative effect on plant species diversity, which could lead to the loss of the small, but important endemic sandhill community.

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Introduction

The earth is a mosaic of unique ecosystems that all have their own specific structure and function. This diversity creates a heterogeneous landscape composed of multiple interconnected systems. Heterogeneous landscapes promote the evolution of species to specialize in very distinct habitats all the way from the ocean to the desert. Ecosystems can host various levels of biodiversity, but much of this diversity is still poorly characterized. Understanding ecosystems is especially urgent because of human population growth and increased resource demand, which has fragmented and reduced many habitats and led to the loss of rare species (Saunders et al., 2016). One such habitat that is at high risk of disappearance are sandhill habitats in the southeastern United States, and for this reason my study aims to identify the biodiversity of multiple sandhills habitats throughout southeastern Georgia.

Sandhills once covered approximately 37 million hectares, but over the last 200 years, 97% of sandhills have been destroyed by human impacts such as agriculture, logging, and development (Darracq, 2016). The biodiversity of sandhill habitats are poorly characterized and, therefore, a better understanding of the species diversity that inhabit sandhills is urgently needed in order to protect rare and endangered species that inhabit these disappearing habitats. Sandhills are upland habitats with dry, sandy soils that lack nutrients (Laessle, 1958). Biodiversity of sandhill habitats has a strong association with wildfires, as well as the wet, hot summers and cool, dry winters of the southeastern United States (Figure 1). These habitats are shaped by the resource availability as well as disturbance by fire (Meyers and White, 1987). The combination of

soil, climate, and fire has promoted the evolution and colonization of a unique plant assemblage found in sandhill habitats.

The sandhill flora is characterized by an open canopy of long-leaf pines, small, infrequent turkey oaks, and an herbaceous ground cover of wire grass (Figure 2., Meyers and White, 1987). Sandhills formed during the widespread aridification events of the Miocene caused by changing weather and marine patterns (Germain-Aubrey et al. 2014). During Pleistocene interglacial periods, winds, changing sea levels, and southward flowing long-shore currents deposited coarse, siliceous sands associated only with the deep sands of the Lakeland series and the shallower sands of the Norfolk series (Laessle, 1958). Sandhills formed at areas where those sand deposits accumulated, creating an arid upland habitat. The edaphic conditions have caused the adaptation of specialized structures, such as the deep tap roots in *Pinus palustris* and *Pinus serotina* (Ames et al., 2015).

Many plant species that occur on sandhills have unique adaptations to low soil nutrients and moisture. The sandhill endemic *Quercus laevis* (Fagaceae) was once thought to be the cause of nutrient leaching in sandhill soils and, therefore, would lead to a unique assemblage of plants that could outcompete *Quercus* for resources (Matocha, 1977). In contrast to this earlier explanation for the lack of species abundances on sandhills, we now know that sandhill plant diversity is driven by soil conditions and fire regimes (Matocha, 1977). Complex interactions between sandhill plants, the sandy soil, and fires determine species abundances in which some species are more influenced by a single factor. The distribution of *Quercus* species, for example, is driven completely by soil composition and has little to do with fire patterns; they have adapted lateral root

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systems allowing for increased survivability and water uptake (Donovan et al. 1999). While fire does not affect the distribution of *Quercus* species, it has been found to increase species recruitment and stimulate reproduction (Abrahamson and Layne, 2002).

Sandhill species respond uniquely to different fire regimes; *Astraglus michauxii* (Fabaceae) and *Pyxidanthera breviflora* (Diapensiaeae) have reduced reproductive output the year following a fire (Wall et al., 2012), whereas the reproductive output of other species, such as *Quercus* sp., *Astrida stricta* (wiregrass; Poaceae), and *Pinus palustris* (long-leaf pine, Pinaceae) benefit from fire. Frequent fires lead to habitats dominated by the fire adapted long-leaf pines, have continuous wiregrass coverage, and small and infrequent oaks (Meyers and White, 1987). Although fire does not affect the distribution of *Quercus* sp., it has been found to increase species recruitment and stimulate reproduction (Abrahamson and Layne, 2002). Fire also leads to an increased recruitment of long-leaf pines due to their persistent, fire-resistant grass stage.

The species composition of sandhill ecosystems have attracted much attention because some of them occur only on sandhills and nowhere else. Species endemism and species richness are positively correlated. Endemism is defined as species that are range restricted in a specific habitat. Endemic species are often less self-compatible, have decreased dispersal ability, lower reproductive investment, and are generally poor competitors (Ferriera and Boldrini, 2011). A subset of endemic species are edaphic endemics, in which species occur in only specific types of soil that preclude other species by being toxic or resource deficient (Ferriera and Boldrini, 2011). Although we know of several sandhill endemic species, other species that occur in these ecosystems are more widespread, and the composition of the sandhill flora remains poorly characterized.

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Furthermore, we know little about how connected the fragmented sandhill ecosystems are, and what conditions promote or filter species diversity.

Sandhills are a unique habitat that are being fragmented, altered, and destroyed by human means. Determining the biodiversity of these habitats as a whole will provide insight on how to conserve the biodiversity of the system. We measured habitat area, species composition, and distance between sandhill habitats in order to determine how habitat size and distance is related to similarities in species composition as well as if certain plant life stages, endemism, native status, and growth habit are represented more or less than expected. We ask the general question, what are the species that make up the sandhill ecosystems and what determines their presence on sandhill sites? By understanding similarities between various sandhill habitats a deeper understanding of how these habitats as a system interact can be uncovered.

Materials and Methods

Field Sites

In order to better characterize sandhill sites and understand the species diversity, we surveyed four separate sandhill habitats in southeastern Georgia (Figure 3). Charles Harrold Nature Preserve (hereafter referred to as Harrold) is managed by The Nature Conservancy, located in Candler County, GA, at 32° 25.129 N, 82° 1.960 W. The Harrold site is approximately 27.7 hectares consisting of sandhill and a wetland depression, and is associated with 15 Mile Creek. This site was not fire managed until recently and has a denser hardwood and pine canopy than the other sites. Upper Lotts Creek (hereafter referred to as Lotts) is privately owned land located in Bulloch County, GA, at 32° 28' 32.77''N, 81° 58' 21.25''W. The sandhill habitat is approximately 25.8 hectares and is located upland of Upper Lotts Creek. This site has never been managed with prescribed fire.

George L. Smith State Park (hereafter referred to as Smith) is managed by the Georgia Department of Natural Resources, and is located in Emmanuel County, GA, at 32° 32' 38.79''N, 82° 7' 2.53''W. The sandhill habitat is approximately 87.0 hectares and is managed by prescribed fires. The sandhill site is associated with 15 Mile Creek.

Fort Stewart Military Base (hereafter referred to as Stewart) is managed by the US Army, in Bryan County, GA at 31° 50' 49.03''N, 81° 40' 7.91''W. The fire managed sandhill habitat is approximately 161.8 hectares and associated with Horse Creek.

Data Collection

The sites were sampled from July 2015 to February 2017 during both growing and dormant seasons. We sampled the Lotts site five times. Data for the Harrold site was gathered during five visits and from a previous study (Mellinger, 1997). Smith was sampled three times and those results were combined with the results of three Master's theses (Jones, Jr., 1996; Perdue, 2000; and Toole, 1992). All data for the Stewart site was gathered through previous studies (Jones, 1996; Perdue, 2000) and herbarium specimens (The Nature Conservancy Ft. Stewart Inventory, housed at the GSU Herbarium).

We surveyed the entirety of the sites for all plant species present, collected, pressed, and dried the plant specimens to bring back to the Georgia Southern University Herbarium (GAS) for identification. We identified specimens using voucher specimens from GAS for reference material and with Weakley's Flora of the Southern and Mid-Atlantic States (Weakley, 2015), Flora of North America (Flora of North America, 1993), and Manual of Vascular Flora of the Carolinas (Radford et al., 1968). The habit, life history, native status, and whether species were sandhill endemics were determined using Weakley's Flora of the Southern and Mid-Atlantic States and the USDA's online Plant Database (USDA, 2017).

Data Analysis

We compiled our data into a spreadsheet and analyzed it using various statistical analyses. The number of species, families, endemics, and proportions of life histories, native status, and growth forms were evaluated with summary statistics. We standardized family occurrence using Chi-square analysis of expected and observed family occurrence with a P-value less than or equal to 0.01 in order to determine whether the represented sandhills families were more or less abundant than what we would have expected given the species diversity in the families. We used Google Earth Pro® in order to compute the area (in hectares) of each site as well as to measure the straight line distance between the four sandhill habitats. Using JMP®, we were able to generate various distributions and statistics comparing species occurrence across sites to endemism, native status, life history, and habit.

We used the Vegan package (Oksanen et al., 2015) in R

(R Development Core Team, 2005) to compare species composition to sandhill size and distance between habitats. The Jaccard Index (Corey, 1998) was used to compare species richness to sandhill size. The Jaccard similarity coefficient ranges from zero to one, with

zero indicating no similarity in species composition and one indicating that the sites have identical species occurrences. Once the Jaccard similarity coefficients were calculated, we compared them to the distance between the sites using the Mantel test in the Vegan package in R.

Results

Patterns across all sites

We identified 301 species as occurring on the surveyed sandhill sites, which belonged to 69 families. Of these species, 156 were found on a single site, 85 occurred on two sites, 33 were found on three sites, and 27 were found on all four sandhill habitats (Table 1). Applying expectations of family species diversity estimated from their current diversity, eight families were determined to be underrepresented and 16 were found to be more abundant than expected. Asteraceae (n = 42), Cyperaceae (n = 11), Euphorbiaceae (n = 13), Fabaceae (n = 37), Lamiaceae (n = 5), Orchidaceae (n = 1), Poaceae (n = 33), and Rubiaceae (n = 4) were all underrepresented on sandhill habitats while Adoxaceae (n = 2), Cistaceae (n = 6), Commelinaceae (n = 8), Cornaceae (n = 1), Cupressaceae (n = 1), Gelsemiaceae (n = 1), Gentianaceae (n = 1), Hamamelidaceae (n = 1), Hypericaceae (n = 5), Juglandaceae (n = 2), Krameriaceae (n = 3), and Smilicaceae (n = 4) were more abundant on sandhills than expected.

Eighty percent of the total species occurred on only one or two sites. Similarly, non-sandhill endemics are not widespread across sandhill sites (Figure 4). Endemic

species were found to be proportional across all sites, regardless of habitat size or distance between sandhill habitats (Figure 5). We found that within each site herbs constituted the greatest percentage of species diversity (Figure 6). Herbaceous plants also showed relatively proportional abundance across all sites (Figure 7). Of the total species collected, we found that sandhill plants are mostly perennial (Figure 8), as were the plant species that occurred across sites (Figure 9). Using the Mantel test we compared the Jaccard similarity coefficients with the distance matrix and identified no significance between species composition, sandhill size, and distance between habitats (P = 0.57).

Charles C. Harrold Nature Preserve

We identified 167 species on the 27.7 hectare sandhill. Of these species, 76.33% were herbaceous, 1.2% lianas, 11.38% shrubs, 7.78% trees, 2.4% vines (Figure 6), 83.23% were perennial (Figure 8), 97.6% were native species, and 12.58% were sandhill endemic (Figure 5). Harrold was determined to be 8.54 km from Lotts and a Jaccard similarity coefficient of 0.8117, 16.67 km from Smith with a similarity coefficient of 0.78.

Upper Lotts Creek

The Lotts site was determined to be 25.8 hectares. We identified 56 species, 69.64% were herbs, 12.5% were shrubs, 16.07% were trees, and 1.79% were vines (Figure 6). Perennial species composed 73.21% of the species diversity (Figure 8), 98.2% of the species are native species, and 14.29% of the species collected at Lotts were endemic species (Figure 5). Lotts was determined to be 8.54 km from Harrold with a Jaccard similarity coefficient of 0.8117, 15.48 km from Smith with a similarity coefficient of 0.8073, and 75.32 km from Stewart with a Jaccard value of 0.8246.

George L. Smith State Park

We identified 179 different plant species at the George L. Smith State Park sandhill habitat, which was determined to be 87 hectares. Of these species, 70.39% were herbaceous, 2.23% lianas, 13.97% shurbs, 11.73% trees, 1.68% vines (Figure 6), 87.15% were found to be perennials (Figure 8), 96.65% were native species, and 15.08% were endemic to sandhill habitats (Figure 5). Smith was found to be 16.67 km from Harrold with a similarity coefficient of 0.6459, 15.48 km from Lotts and a Jaccard value of 0.8073, and 87.48 km from Stewart with a similarity coefficient of 0.6836.

Fort Stewart Army Preserve

Previous studies identified 128 plant species at the Fort Stewart Army Preserve sandhill habitat that we determined to be approximately 161.6 hectares. Herbaceous plants made up a 68.5% majority of the plant species identified here, whereas, vines constituted 1.58%, 11.81% shrubs, 14.17% trees, and 4.72% were vines (Figure 6). Perennials composed 84.25% of the total plant community (Figure 8), 97.64% were native species, and 14.96% were sandhill endemic plants (Figure 5). Stewart was found to be 72.86 km from Harrold and had a similarity coefficient of 0.78, 75.32 km from Lotts with a Jaccard index value of 0.8246, and 87.48 km from Smith and a similarity coefficient of 0.6836.

Discussion

Sandhills are unique habitats that are home to a diverse assemblage of plant and animal species. However, an ever-increasing human population and consumption of resources has led to the destruction of these habitats for timber, agriculture, and urban development (Saunders et al. 1990). Identifying the plant diversity across multiple sandhill habitats in southeastern Georgia gives insight into how these habitats function independently and as a connected system. Understanding the structure and function of sandhill plants ultimately can help the conservation of these unique habitats.

We determined that the majority of the sandhill plant species did not occur across all four sites, rather, they occurred on only one or two sites. Of all collected plant species, non-sandhill endemic plants also occurred mostly on one or two sites (Figure 4). Since most non-sandhill endemic species occurred on just a few sites it can be assumed that these plants are habitat generalists and colonized the sandhill sites from surrounding habitats. Stamp and Lucas (1990) proposed two hypotheses for the formation of sandhill's diverse plant assemblage. The colonization hypothesis proposed that when habitats change over time, seed dispersal increases the likelihood of suitable habitats or the escape hypothesis which posits that when the density of seed-dispersing plants is low, viable seeds will disperse farther away and settle new suitable habitats. Although these habitats have become fragmented throughout the past two centuries, we still see proportional levels of endemism across all four sites. These endemic species most likely have adapted dispersal techniques that allows them to escape disappearing sandhills while habitat generalists are able to colonize sandhills from surrounding habitats. When expected family composition was compared to observed family composition we found that 16 families were more abundant than expected while seven families were less represented than expected. Asteraceae and Poaceae were two of the most abundant families that occurred on sandhills, however, based on our Chi-Square analysis, they were underrepresented. Given that they are among the most species-diverse angiosperm families, it is unsurprising to find them abundantly represented on sandhill. These two families exhibit mostly an herbaceous growth habit and have other species that are also adapted to arid environments, which could explain why they are so well-adapted to sandhills. Poaceae, for example, has evolved C4 photosynthesis, an alternative photosynthetic pathway that conserves water, numerous times (Edwards and Smith, 2009), which might help it thrive on sandhill.

Sandhill plants are thought to have migrated either eastward from Texas or southward from the northeast. The western hypothesis states that between five and two million years ago species from the west migrated eastward and became isolated as a result of rising sea levels whereas the eastern hypothesis suggests that these communities migrated southward from eastern North America as result of increasing glacial advancement (Germain-Aubrey et al., 2014). While neither hypothesis predicted speciation of sandhills independently, it does show that sandhills acted as refugia for plant species during the changing geologic climate. A more thorough investigation into the direction of colonization is needed on the Georgian sandhills, but species, such as *Paronychia herniarioides* have relatives in western North America, while others, such as *Smilax* sp. have relatives in the east.

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Sandhill soil is subject to limited nutrients and water as well as higher rates of erosion, similar to the grasslands in Southwestern Rio Grande do Sul, Brazil (Frietas et al. 2009). Many plants in Southwestern Rio Grande du Sul are edaphic endemics and have adapted traits to thrive in these soils. Species in the Myrtaceae, for example, have developed long taproots (Freitas et al, 2009) similar to the sandhill species *Pinus palustris* (Ames et. al 2015). Sandhills have unique edaphic conditions similar to that of Southwestern Rio Grande du Sol, Brazil; however, sandhill endemic plants were found to be proportional across all four sandhill sites suggesting that sandhills are not subject to the island effect.

The majority of sandhill plant species were found to be native, perennial herbs. The biodiversity of sandhill habitats is directly correlated with the abundance of perennial herbs. Fire increases the percentage of herbaceous growth. (Gonzalez-Benecke et al, 2015). The frequency of fire is directly correlated with plant size; as frequency increases the overall size of plants decreases (Wall et al., 2012). Trees found on sandhills are found to have lower average diameter a breadth height than the same species found off of sandhills (Collins et al., 2006) and herbaceous growth is favored by shorter burn intervals (Cronan et al., 2015). Moderate burn regimes of greater than three to five years have been found to promote the highest level of vertebrate diversity and lead to an increase of long-leaf pine specialists like the flatwoods salamander (*Ambystoma cingulatum*; Darracq, 2016). In the absence of fire scrub, mesic species begin to colonize sandhill habitats without a negative effect on the composition of endemic species. Without fire, sandhill over-story composition shifts from one dominated completely by sandhill species to an over story composed of scrub species like *Magnolia* sp. and sandhill species (Meyers and

White, 1987). The absence of fire on biodiversity can be seen at the Lotts site. This site has never been burned and had the lowest abundance of perennial herbs and correspondingly also had the lowest level of biodiversity. In the absence of a fire regime sandhills are at risk of decreased biodiversity and potentially transitioning to hardwood forests, completely removing the sandhill and its unique diversity.

Sandhill ecosystems are composed of a small proportion of species that occur only in these habitats, whereas the majority of plants come from non-specialized species opportunistically colonizing sandhill from the surrounding areas. The biodiversity of sandhills is positively correlated with the abundance of perennial herbs that occur there; however, diversity was not found to be controlled by habitat size. Our results further suggest that additional decreases in available sandhill habitats will have a negative effect on sandhill plant species diversity, which could lead to the loss of the small, but important endemic sandhill community.



Tables and Figures

Figure 1. Examples of sandhill plants. A. *Balduina angustifolia*, B. *Sabulina caroliniana*, C. *Eriogonum tomentosum*, and D. *Dicerandra odoratissima*.



Figure 2. Upper Lotts Creek sandhill ecosystem.

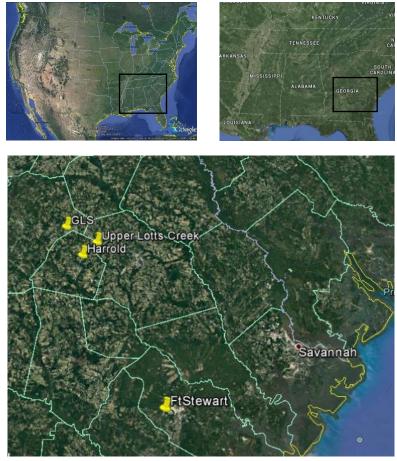
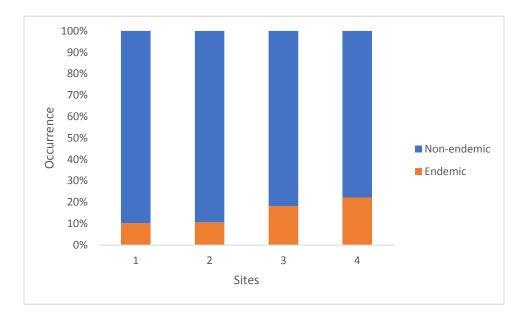
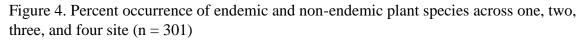


Figure 3. Map of sandhill sites in southeastern Georgia.





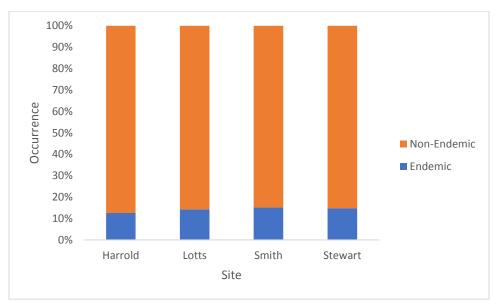


Figure 5. Percent occurrence of endemic and non-endemic plants on the Harrold, Lotts, Smith, and Stewart sites (n = 301)

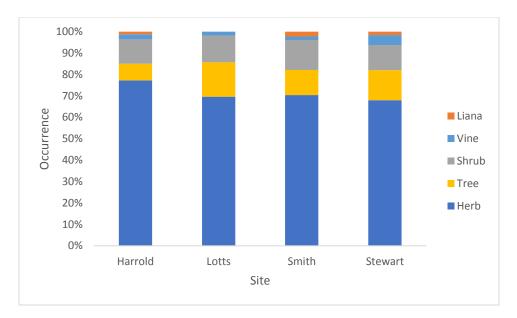


Figure 6. Percent occurrence of plant growth habit (herb, tree, shrub, vine, and liana) on the Harrold, Lotts, Smith, and Stewart sites (n = 301)

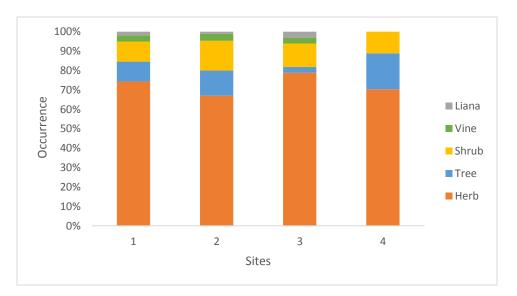


Figure 7. Percent abundance of plant growth habit (herb, tree, shrub, vine, and liana) across one, two, three, and four sites (n = 301).

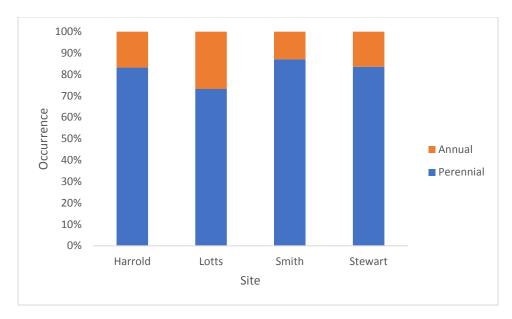


Figure 8. Percent occurrence of annual and perennial plant species on the Harrold, Lotts, Smith, and Stewart sites (n = 301)

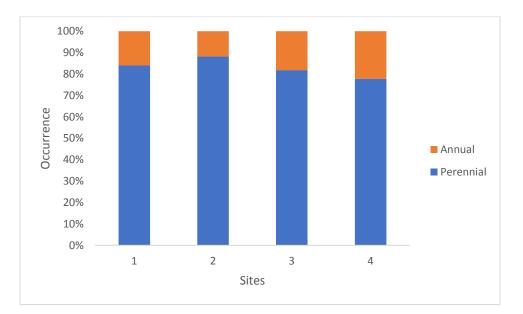


Figure 9. Percent occurrence of annual and perennial plant species across one, two, three, and four sites (n = 301)

Table 1. List of species occurrence across sandhill habitats. Total number of sites species occurred on and species occurrence on Harrold, Lotts, Smith, and Stewart sandhills independently. Values of one signify that the species is present at the site, values of zero signify they were not found.

Species	Family	Sites	Harrold	Lotts	Smith	Stewart
Dyschoriste oblongifolia	Acanthaceae	2	1	0	1	0
Viburnum prunifolium	Adoxaceae	1	0	0	1	0
Viburnum rufidulum	Adoxaceae	1	0	0	0	1
Froelichia floridana	Amaranthaceae	2	1	0	1	0
Rhus aromatica	Anacaridaceae	1	1	0	0	0
Rhus copallinum	Anacaridaceae	3	0	1	1	1
Rhus michauxii	Anacaridaceae	1	0	0	1	0
Rhus pubescens	Anacaridaceae	2	0	0	1	1
Toxicodendron radicans	Anacaridaceae	1	1	0	0	0
Thaspium barbiNode	Apiaceae	1	0	0	1	0
Amsonia ciliata	Apocynaceae	3	1	0	1	1
Apocynum cannabinum	Apocynaceae	1	0	0	1	0
Asclepias amplexicaulis	Apocynaceae	1	0	0	1	0
Asclepias cinerea	Apocynaceae	1	1	0	0	0
Asclepias humistrata	Apocynaceae	3	1	0	1	1
Asclepias syriaca	Apocynaceae	2	0	0	1	1
Asclepias tuberosa	Apocynaceae	3	1	0	1	1
Asclepias verticillata	Apocynaceae	2	1	0	1	0
Ilex glabra	Aquifoliaceae	2	1	0	1	0
Ilex myrtifolia	Aquifoliaceae	1	0	0	1	0
Ilex vomitoria	Aquifoliaceae	1	0	0	1	0
Manfreda virginica	Asparagaceae	1	1	0	0	0
Nolina georgiana	Asparagaceae	1	0	0	1	0
Yucca filamentosa	Asparagaceae	3	1	1	1	0
Yucca flaccida	Asparagaceae	1	0	0	1	0
Balduina angustifolia	Asteraceae	4	1	1	1	1
Croptilon divaricatum	Asteraceae	3	1	0	1	1
Heterotheca subaxillaris	Asteraceae	1	0	0	1	0
Krigia virginica	Asteraceae	2	1	0	1	0
Pseudognaphalium obtusifolium	Asteraceae	4	1	1	1	1
Hymenopappus scabiosaeus	Asteraceae	1	0	0	0	1
Ageratina aromatica	Asteraceae	1	0	0	1	0
Bigelowia nudata	Asteraceae	1	0	0	0	1

Brickellia eupatorioides	Asteraceae	2	1	0	1	0
Chrysopsis gossypina	Asteraceae	2	1	1	0	0
Cirsium repandum	Asteraceae	1	0	0	1	0
Elephantopus nudatus	Asteraceae	1	1	0	0	0
Eupatorium capillifolium	Asteraceae	4	1	1	1	1
Eupatorium glaucescens	Asteraceae	2	1	0	1	0
Eupatorium leucolepis	Asteraceae	1	1	0	0	0
Euthamia caroliniana	Asteraceae	2	0	0	1	0
Helianthus radula	Asteraceae	1	1	0	0	0
Hieracium gronovii	Asteraceae	2	1	0	1	0
Ionactis linariifolius	Asteraceae	1	0	0	0	1
Lactuca graminifolia	Asteraceae	2	1	0	1	0
Liatris gracilis	Asteraceae	3	1	0	1	1
Liatris secunda	Asteraceae	1	1	0	0	0
Liatris tenuifolia	Asteraceae	4	1	1	1	1
Pityopsis graminifolia	Asteraceae	3	1	1	1	0
Pityopsis pinifolia	Asteraceae	2	0	0	1	1
Pterocaulon pycnostachyum	Asteraceae	1	1	0	0	0
Rudbeckia hirta	Asteraceae	2	1	0	0	1
Sericocarpus tortifolius	Asteraceae	3	1	1	1	0
Silphium compositum	Asteraceae	2	1	0	1	0
Solidago canadensis	Asteraceae	1	0	0	1	0
Solidago erecta	Asteraceae	1	0	1	0	0
Solidago odora	Asteraceae	3	1	1	1	0
Solidago petiolaris	Asteraceae	1	0	0	1	0
Solidago tortifolia	Asteraceae	1	1	0	0	0
Symphyotrichum concolor	Asteraceae	2	1	0	1	0
Symphyotrichum walteri	Asteraceae	1	1	0	0	0
Trilisa odoratissima	Asteraceae	1	0	0	1	0
Vernonia acaulis	Asteraceae	1	1	0	0	0
Vernonia angustifolia	Asteraceae	1	0	0	1	0
Erigeron strigosus	Asteraceae	2	1	0	1	0
Eupatorium compositifolium	Asteraceae	4	1	1	1	1
Eupatorium hyssopifolium	Asteraceae	1	0	0	1	0
Heliotropium amplexicaule	Boraginaceae	1	0	0	0	1
Lithospermum virginianum	Boraginaceae	1	0	0	0	1
Warea cuneifolia	Brassicaceae	1	0	0	0	1
Tillandsia usneoides	Bromeliaceae	4	1	1	1	1

Polypremum procumbens	Buddlejaceae	1	1	0	0	0
Opuntia humifusa	Cactaceae	4	1	1	1	1
Wahlenbergia marginata	Campanulaceae	1	1	0	0	0
Polanisia tenuifolia	Capparaceae	2	1	0	0	1
Lonicera japonica	Caprifoliaceae	1	0	0	1	0
Paronychia herniarioides	Caryophyllaceae	4	1	1	1	1
Sabulina caroliniana	Caryophyllaceae	4	1	1	1	1
Stipulicida setacea	Caryophyllaceae	2	0	0	1	1
Crocanthemum carolinianum	Cistaceae	1	0	0	0	1
Crocanthemum rosmarinifolium	Cistaceae	1	1	0	0	0
Lechea minor	Cistaceae	2	0	0	1	1
Lechea mucronata	Cistaceae	1	1	0	0	0
Lechea pulchella	Cistaceae	1	0	0	0	1
Lechea sessiliflora	Cistaceae	1	1	0	0	0
Callisia graminea	Commelinaceae	1	1	0	0	0
Commelina communis	Commelinaceae	1	0	0	0	1
Commelina diffusa	Commelinaceae	1	1	0	0	0
Tradescantia rosea var. graminea	Commelinaceae	2	1	0	1	0
Commelina erecta	Commelinaceae	2	1	0	1	0
Cuthbertia rosea	Commelinaceae	1	0	0	1	0
Tradescantia hirsutiflora	Commelinaceae	2	0	0	1	1
Tradescantia roseolens	Commelinaceae	1	1	0	0	0
Ipomoea pandurata	Convolvulaceae	2	0	0	1	1
Stylisma humistrata	Convolvulaceae	1	1	0	0	0
Stylisma patens	Convolvulaceae	3	1	1	1	0
Cornus florida	Cornaceae	1	0	0	1	0
Citrullus lanatus	Cucurbitaceae	1	0	0	0	1
Juniperus virginiana	Cupressaceae	1	1	0	0	0
Bulbostylis stenophylla	Cyperaceae	3	1	0	1	1
Bulbostylis warei	Cyperaceae	4	1	1	1	1
Carex tenax	Cyperaceae	1	0	0	0	1
Cyperus croceus	Cyperaceae	1	0	0	1	0
Cyperus filliculmus	Cyperaceae	1	1	0	0	0
Cyperus rotundus	Cyperaceae	2	1	0	1	0
Rhynchospora grayi	Cyperaceae	1	1	0	0	0
Rhynchospora megalocarpa	Cyperaceae	3	1	0	1	1
Scleria oligantha	Cyperaceae	1	1	0	0	0
Scleria triglomerata	Cyperaceae	1	0	0	1	0
Bulbostylis capillaris	Cyperaceae	3	1	1	1	0

Diospyros virginiana	Ebenaceae	2	0	0	1	1
Ceratiola ericoides	Ericaceae	1	0	0	1	0
Gaylussacia dumosa	Ericaceae	2	1	0	1	0
Gaylussacia frondosa	Ericaceae	2	1	0	1	0
Lyonia lucida	Ericaceae	2	0	0	1	1
Lyonia mariana	Ericaceae	3	1	1	1	0
Rhododendron atlanticum	Ericaceae	2	1	0	1	0
Vaccinium arboreum	Ericaceae	4	1	1	1	1
Vaccinium corymbosum	Ericaceae	2	0	0	1	1
Vaccinium elliottii	Ericaceae	1	0	0	0	1
Vaccinium fuscatum	Ericaceae	1	1	0	0	0
Vaccinium myrsinites	Ericaceae	2	0	0	1	1
Vaccinium stamineum	Ericaceae	2	0	1	1	0
Acalypha gracilens	Euphorbiaceae	1	0	1	0	0
Croton capitatus	Euphorbiaceae	1	1	0	0	0
Croton michauxii var. elliptica	Euphorbiaceae	1	1	0	0	0
Euphorbia cordifolia	Euphorbiaceae	1	1	0	0	0
Euphorbia supina	Euphorbiaceae	1	1	0	0	0
Cnidoscolus stimulosus	Euphorbiaceae	4	1	1	1	1
Croton argyranthemus	Euphorbiaceae	1	0	0	1	0
Croton punctatus	Euphorbiaceae	1	0	0	1	0
Euphorbia gracilior	Euphorbiaceae	2	1	0	1	0
Euphorbia ipecacuanhae	Euphorbiaceae	1	1	0	0	0
Stillingia aquatica	Euphorbiaceae	1	0	0	0	1
Stillingia sylvatica	Euphorbiaceae	1	0	0	1	0
Tragia urens	Euphorbiaceae	1	0	0	0	1
Astragalus villosus	Fabaceae	1	0	0	0	1
Chamaecrista fasciculata	Fabaceae	3	1	1	1	0
Amorpha herbacea	Fabaceae	1	0	0	1	0
Astragalus michauxii	Fabaceae	1	0	0	1	0
Baptisia perfoliata	Fabaceae	4	1	1	1	1
Centrosema virginianum	Fabaceae	2	1	0	1	0
Chamaecrista nictitans	Fabaceae	2	1	0	0	1
Clitoria mariana	Fabaceae	3	1	0	1	1
Crotalaria angulata	Fabaceae	1	1	0	0	0
Crotalaria sagittalis	Fabaceae	1	1	0	0	0
Dalea pinnata	Fabaceae	3	1	0	1	1
Desmodium ciliare	Fabaceae	1	0	0	0	1

Desmodium floridanum	Fabaceae	1	1	0	0	0
Desmodium lineatum	Fabaceae	1	1	0	0	0
Desmodium strictum	Fabaceae	1	1	0	0	0
Galactia minor	Fabaceae	2	0	0	1	1
Galactia regularis	Fabaceae	3	1	1	1	0
Galactia volubilis	Fabaceae	2	1	0	0	1
Hylodesmum glutinosum	Fabaceae	1	0	0	1	0
Indigofera caroliniana	Fabaceae	3	1	0	1	1
Lespedeza hirta	Fabaceae	4	1	1	1	1
Lespedeza repens	Fabaceae	2	1	0	1	0
Lespedeza violacea	Fabaceae	2	0	0	1	1
Lupinus diffusus	Fabaceae	2	0	0	1	1
Lupinus perennis	Fabaceae	2	0	0	1	1
Lupinus villosus	Fabaceae	1	0	0	0	1
Mimosa microphylla	Fabaceae	2	1	0	1	0
Orbexilum lupinellus	Fabaceae	3	1	0	1	1
Pediomelum canescens	Fabaceae	2	0	0	1	1
Rhynchosia reniformis	Fabaceae	2	1	0	1	0
Rhynchosia simplicifolius	Fabaceae	1	1	0	0	0
Stylosanthes biflora	Fabaceae	3	1	0	1	1
Tephrosia floridia	Fabaceae	2	1	0	1	0
Tephrosia hispidula	Fabaceae	1	0	0	0	1
Tephrosia spicata	Fabaceae	1	1	0	0	0
Tephrosia virginiana	Fabaceae	3	1	0	1	1
Wisteria sinensis	Fabaceae	1	0	0	1	0
Castanea pumila	Fagaceae	1	1	0	0	0
Quercus austrina	Fagaceae	2	0	0	1	1
Quercus chapmanii	Fagaceae	1	0	0	1	0
Quercus falcata	Fagaceae	1	0	0	0	1
Quercus geminata	Fagaceae	1	0	0	0	1
Quercus hemisphaerica	Fagaceae	2	0	0	1	1
Quercus incana	Fagaceae	4	1	1	1	1
Quercus laevis	Fagaceae	4	1	1	1	1
Quercus laurifolia	Fagaceae	2	0	0	1	1
Quercus margarettae	Fagaceae	4	1	1	1	1
Quercus nigra	Fagaceae	2	0	1	0	1
Quercus oglethorpensis	Fagaceae	1	0	0	1	0
Quercus palustris	Fagaceae	1	0	0	1	0

Quercus pumila	Fagaceae	3	1	0	1	1
Quercus stellata	Fagaceae	2	1	0	1	0
Quercus virginiana	Fagaceae	1	0	0	0	1
Gelsemium sempervirens	Gelsemiaceae	3	1	0	1	1
Gentiana villosa	Gentianaceae	1	0	0	1	0
Geranium carolinianum	Geraniaceae	1	1	0	0	0
Hamamelis virginiana	Hamamelidaceae	1	0	0	1	0
Hypericum gentianoides	Hypericaceae	4	1	1	1	1
Hypericum brachyphyllum	Hypericaceae	1	0	0	0	1
Hypericum harperi	Hypericaceae	1	0	0	0	1
Hypericum hypericoides	Hypericaceae	4	1	1	1	1
Hypericum tenuifolium	Hypericaceae	2	1	0	1	0
Sisyrinchium albidum	Iridaceae	1	1	0	0	0
Sisyrinchium nashii	Iridaceae	1	0	0	1	0
Carya pallida	Juglandaceae	1	1	0	0	0
Carya tomentosa	Juglandaceae	2	1	0	0	1
Juncus dichotomus	Juncaceae	2	0	0	1	1
Juncus scirpoides	Juncaceae	1	0	0	1	0
Krameria lanceolata	Krameriaceae	1	0	0	1	0
Dicerandra odoratissima	Lamiaceae	1	0	1	0	0
Trichostema dichotomum	Lamiaceae	1	1	0	0	0
Trichostema setaceum	Lamiaceae	2	0	1	1	0
Clinopodium coccineum	Lamiaceae	1	0	0	1	0
Salvia azurea	Lamiaceae	2	1	0	1	0
Sassafras albidum	Lauraceae	1	0	1	0	0
Rotala ramosior	Lythraceae	1	0	0	0	1
Mollugo verticillata	Molluginaceae	1	1	0	0	0
Morella cerifera	Myricaceae	1	0	0	1	0
Chionanthus virginicus	Oleaceae	1	1	0	0	0
Oenothera filipes	Onagraceae	1	0	0	1	0
Spiranthes lacera var. gracilis	Orchidaceae	1	0	0	0	1
Agalinis obtusifolia	Orobancaceae	1	0	0	0	1
Agalinis purpurea	Orobancaceae	2	1	1	0	0
Agalinis setacea	Orobancaceae	3	1	1	1	0
Aureolaria pectinate	Orobancaceae	2	0	0	1	1
Aureolaria pedicularia	Orobancaceae	2	0	0	1	1
Seymeria pectinate	Orobancaceae	3	1	0	1	1
Phytolacca americana	Phytolaccaceae	1	1	0	0	0

Pinus elliottii	Pinaceae	2	0	0	1	1
Pinus palustris	Pinaceae	4	1	1	1	1
Pinus taeda	Pinaceae	2	0	1	1	0
Veronica arvensis	Plantaginaceae	1	0	1	0	0
Aristida oligantha	Poaceae	2	1	1	0	0
Setaria corrugata	Poaceae	1	0	0	0	1
Triplasis purpurea	Poaceae	1	0	0	1	0
Andropogon brachystachyus	Poaceae	3	1	0	1	1
Andropogon gyrans	Poaceae	4	1	1	1	1
Andropogon ternarius	Poaceae	2	1	0	1	0
Andropogon virginicus var. glaucus	Poaceae	2	1	0	1	0
Andropogon virginicus var. virginicus	Poaceae	2	1	0	1	0
Anthaenantia villosa	Poaceae	1	0	0	1	0
Aristida purpurascens	Poaceae	4	1	1	1	1
Aristida stricta	Poaceae	4	1	1	1	1
Dichanthelium aciculare	Poaceae	3	1	0	1	1
Dichanthelium acuminatum	Poaceae	2	1	0	0	1
Dichanthelium commutatum	Poaceae	1	1	0	0	0
Dichanthelium consanguineum	Poaceae	2	0	1	1	0
Dichanthelium dichotomum	Poaceae	2	0	1	1	0
Dichanthelium laxiflorum	Poaceae	2	1	0	0	1
Dichanthelium ravenelii	Poaceae	1	0	0	0	1
Dichanthelium scoparium	Poaceae	1	0	0	1	0
Dichanthelium villosissimum	Poaceae	1	1	0	0	0
Digitaria cognata	Poaceae	1	0	0	1	0
Eragrostis curvula	Poaceae	1	1	0	0	0
Eragrostis elliottii	Poaceae	1	0	0	0	1
Eragrostis spectabilis	Poaceae	1	1	0	0	0
Muhlenbergia capillaris	Poaceae	1	1	0	0	0
Paspalum notatum	Poaceae	1	0	0	0	1
Piptochaetium avenaceum	Poaceae	1	1	0	0	0
Schizachyrium scoparium	Poaceae	2	1	0	1	0
Sorghastrum elliotti	Poaceae	2	1	1	0	0
Sorghastrum secundum	Poaceae	2	1	0	1	0
Sporobolus junceus	Poaceae	1	0	0	0	1
Tridens flavus	Poaceae	1	0	0	1	0
Triplasis americana	Poaceae	3	1	1	1	0
Phlox nivalis	Polemoniaceae	1	1	0	0	0

Polygonum articulatum	Polygonaceae	2	1	0	1	0
Polygonum erectum	Polygonaceae	1	0	0	1	0
Polygonum fimbriata	Polygonaceae	2	1	0	1	0
Polygonum pinicola	Polygonaceae	4	1	1	1	1
Polygonum tomentosum	Polygonaceae	1	0	1	0	0
Eriogonum tomentosum	Polygonaceae	4	1	0	1	1
Rumex acetosella	Polygonaceae	1	1	0	0	0
Pteridium latiusculum	Polypodiaceae	2	0	0	1	1
Ceanothus microphyllus	Rhamnaceae	1	1	0	0	0
Crataegus uniflora	Rosaceae	1	1	0	0	0
Licania michauxii	Rosaceae	4	1	1	1	1
Prunus angustifolia	Rosaceae	2	1	0	1	0
Prunus umbellata	Rosaceae	2	0	1	0	1
Rubus argutus	Rosaceae	1	1	0	0	0
Rubus cuneifolius	Rosaceae	3	1	0	1	1
Rubus flagellaris	Rosaceae	2	0	0	1	1
Rubus illecebrosus	Rosaceae	1	0	0	1	0
Diodella teres	Rubiaceae	4	1	1	0	1
Galium pilosum	Rubiaceae	3	0	1	1	1
Houstonia longifolia	Rubiaceae	1	0	0	0	1
Houstonia procumbens	Rubiaceae	1	1	0	0	0
Sideroxylon lanuginosum	Sapotaceae	1	0	0	0	1
Bryodesma arenicola	Selaginellacaea	2	0	0	1	1
Smilax auriculata	Smilicaceae	1	0	0	0	1
Smilax bona-nox	Smilicaceae	1	0	0	0	1
Smilax rotundifolia	Smilicaceae	1	0	0	0	1
Smilax smalli	Smilicaceae	1	0	0	0	1
Solanum sarrachoides	Solanaceae	1	0	0	1	0
Physalis virginiana	Solanaceae	1	0	0	0	1
Melochia corchorifolia	Sterculiaceae	1	0	0	0	1
Symplocos tinctoria	Symplocaceae	2	0	0	1	1
Piriqueta caroliniana	Turneraceae	2	1	0	0	1
Urtica dioica	Urticaceae	2	0	0	1	1
Verbena carnea	Verbenaceae	2	1	0	1	0
Nuttallanthus canadensis	Plantaginaceae	3	1	0	1	1
Penstemon australis	Plantaginaceae	1	1	0	0	0
Viola villosa	Violaceae	1	1	0	0	0
Viola walteri	Violaceae	1	1	0	0	0
Muscadinia rotundifolia	Vitaceae	2	0	0	1	1

Works Cited

- Abrahamson, W.G. and Layne, J.N. 2002. Post-fire recovery of acorn production by four oak species in southern ridge sandhill association in south-central Florida. American Journal of Botany 89(1):119-123.
- Ames, G.M., Vineyard, D.L., Anderson, S.M., Wright, J.P. 2015. Annual growth in longleaf (*Pinus palustris*) and pond pine (*P. serotina*) in the sandhills of North Carolina is driven by interactions between fire and climate. Forest Ecology and Management 340:1-8.
- Collins, B., Sharitz, R., Madden, K., and Dilustro, J. 2006. Comparison of sandhills and mixed pine-hardwood communities at Fort Benning, Georgia. Southeastern Naturalist 5(1): 92-102.
- Corey, D.T., Stout, I.J., Edwards, G.B. 1998. Ground surface spider fauna in Florida sandhill communities. The Journal of Arachnology 26:303-316.
- Cronan, J.B., Wright, C.S., Petrova, M. 2015. Effects of dormant and growing season burning on surface fuels and potential fire behavior in northern Florida longleaf pine (*Pinus palustris*) flatwoods. Forest Ecology and Management 354:318-333.
- Darracq, A.K., Boone IV, W.W., McCleery, R.A. 2016. Burn regime matters: A review of the effects of prescribed fire on vertebrates in longleaf pine ecosystem. Forest Ecology and Management 378:214-221.
- Donovan, L.A, West, J.B, and McLeod, K.W. 1999. *Quercus* species differ in water and nutrient characteristics in a resource-limited fall-line sandhill habitat. Tree Physiology 20:929-936.
- Edwards, E.J. and Smith, S.A. 2009. Phylogenetic analyses reveal the shady history of C4 grasses. PNAS 107(6): 2532-2537.
- Ferreira, P.M.A., and Boldrini, I.I. 2011. Potential Reflection of Distinct Ecological Units in Plant Endemism Categories. Conservation Biology 25(4):672-679.
- Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 20+ vols. New York and Oxford.
- Freitas, E.M., Trevisan, R., Schneider, A.A., Boldrin, I.I. 2009. Floristic diversity in areas of sandy soil grasslands in Southwestern Rio Grande do Sul, Brazil. Brazilian Journal of Biosciences.
- Germain-Aubrey, C.C., Soltis, P.S., Neubig, K.M., Thurston, T., Soltis, D.E., and Gitzendanner, M.A. 2014. Using comparative biogeography to retrace the origins of an ecosystem: the case of four plants endemic to the central Florida scrub. International Journal of Plant Sciences 175(4):418-431.

- Gonzalez-Benecke, C.A., Samuelson, L.J., Stokes, T.A., Cropper, W.P., Jr., Martin, T.A., Johnsen, K.H. 2015. Understory plant biomass dynamics of prescribed burned *Pinus palustris* stands. Forest Ecology and Management 344:84-94.
- Jones, D.N., Jr. 1996. Population biology of the Gopher Tortoise, *Gopherus polyphemus*, in Southeastern Georgia (Master's thesis). Georgia Southern University, Statesboro, Georgia, USA.
- Laessle, A.M. 1958. The Origin and Successional Relationship of Sandhill Vegetation and Sand-Pine Scrub. Ecological Monographs 28(4):361-387.
- Matocha K.G. 1977. Turkey Oak Ecology on a Georgia Sandhill. The American Midland Naturalist 98(2):487-491.
- Mellinger, M.B. 1977. The Nature Conservancy Stewardship master plan for Charles C. Harrold Nature Preserve. The Nature Conservancy, Metter, Georgia, USA.
- Meyers, R.L. and White, D.L. 1987. Landscape history and changes in sandhill vegetation in north-central and south-central Florida. Bulletin of the Torrey Botanical Club 114(1):21-32.
- Perdue, V.K. 2000. The effect of forage quality on reproduction and growth of the Gopher Tortoise, *Gopherus polyphemus*, in Southeast Georgia (Master's thesis). Georgia Southern University, Statesboro, Georgia, USA.
- Radford, A.E., Ahles, H.E., Bell, C.R. 1968. *Manual of the vascular flora of the Carolinas*. Chapel Hill: University of North Carolina Press
- Saunders, D.A., Hobbs, R.J., and Margules, C.R. 1990. Biological Consequences of Ecosystem Fragmentation: A Review. Conservation Biology 5(1): 18-32.
- Shappell, L.J. and Koontz, S.M. 2015. Fire reintroduction increased longleaf pine (*Pinus paulstris L.*) recruitment and shifted pine demographics in a long-unburned xeric sandhill assemblage. Forest Ecology and Management 354:344-352.
- Stamp, N.E. and Lucas, J.R. 1990. Spatial patterns and dispersal distances of explosively dispersing plants in Florida sandhill vegetation. Journal of Ecology 78:589-600.
- Toole, M.A., Jr. 1992. A floristic study of vegetation analysis of the southern portion of George L. Smith State Park in Emanuel County, GA, USA (Master's thesis). Georgia Southern University, Statesboro, Georgia, USA.
- USDA, NRCS. 2017. The PLANTS Database (<u>http://plants.usda.gov</u>, 3 April 2017). National Plant Data Team, Greensboro, NC 27401-4901 USA.
- Wall, W.A. Hoffman, W.A, Wentworth, R.T., Gray, J.B., and Hohmann. 2012. Demographic effects of fire on two endemic plant species in the longleaf pinewiregrass ecosystem. Plant Ecology 213:1093-1104.

Weakley, A.S. 2015. Flora of the Southern and Mid-Atlantic States. University of North Carolina, Chapel Hill, N.C.