

Variability and Drivers of Forest Communities at the Great Dismal Swamp

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Thesis submitted to the faculty of the Virginia Polytechnic Institute and State University in
partial fulfillment of the requirements for the degree of

Master of Science

in

Forest Resources and Environmental Conservation

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May 7th, 2018

Blacksburg, VA

Keywords: Great Dismal Swamp, forested wetlands, wetland vegetation, wetland hydrology,
hydrologic restoration

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ABSTRACT

The Great Dismal Swamp (GDS) is a forested peatland located in the Atlantic Coastal Plain. Once a mosaic of wetland communities, disturbances (e.g., timber harvesting and ditching) have resulted in altered hydrologic regime, homogenized forest communities, and increased peat subsidence. In response, hydrologic restoration and forest management aim to enhance community composition and function. To help inform these efforts, we investigated variability and drivers of forest communities by surveying vegetation composition and structure, hydrologic indicators, and soil properties at 79 monitoring plots across GDS. Data were augmented with modeled water levels and peat depths. Our results demonstrate red maple (*Acer rubrum*) dominance across GDS, which decreases tree density, richness, and diversity. However, hierarchical cluster analysis identified four community types: Gum (G), Maple-Gum (M-G), Sweetgum-Maple (SG-M), and Maple (M). These communities differed in tree composition and structure; differences in other growth forms (shrubs, herbaceous, and regeneration) were limited. Modeled water levels failed to explain vegetation differences, but community associations with soil properties suggest that communities exist along a hydrologic gradient. Specifically, the G community likely exists on wetter sites whereas SG-M communities occur at drier locations. Maple-dominated communities (M and M-G; 78% of plots) likely occur across broader hydrologic gradients, explaining their dominance. However, more characterization of hydrology (i.e., time-varying water levels and soil moisture) and other drivers (e.g., site history and soil hydraulics) is needed to further explain community variation. As such, we propose future strategies for long-term monitoring to inform ongoing hydrologic restoration and forest management efforts.

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GENERAL AUDIENCE ABSTRACT

The Great Dismal Swamp (GDS) is a large forested wetland located in southeastern Virginia and northeastern North Carolina. The GDS provides many ecosystem services such as wildlife habitat, biodiversity, water quality and storage, and carbon storage. Prior to disturbance, the GDS was composed of a variety of forest types, including stands dominated by cypress (*Taxodium* spp.), cedar (*Chamaecyparis* spp.), and pocosin (*Pinus* spp.) species. However, land use activities (e.g., ditching, draining, and timber harvesting) have resulted in drier conditions, forests dominated by red maple (*Acer rubrum*), land subsidence, and increased fire frequency. To restore the GDS to its pre-disturbance state, water control structures have been installed in drainage ditches to increase wetland water levels throughout the swamp. To inform those efforts, research is needed to understand how forest communities will respond to changing hydrology. In this study, we investigated forest composition throughout the GDS and found that four forested communities exist: Gum (G), Maple-Gum (M-G), Sweetgum-Maple (SG-M), and Maple (M). Our findings demonstrate that the M community is the most abundant community at GDS. Where red maple is present in large quantities, the variety of other tree species decreases. Additionally, we found that these communities exist on different degrees of wetness. The G community is located on wet sites, and the SG-M is located on dry sites. The more maple-dominated communities (M and M-G) are found across a larger range of wetness conditions. Our findings will inform future monitoring and management efforts at GDS.

ACKNOWLEDGEMENTS

I would like to express my great appreciation to the following people, whom without their help, the product of this research simply would not have been possible. First, to my advisor Daniel McLaughlin, whose guidance, expertise, and patience throughout the research process has molded me into a confident, well-rounded scientist. To my committee members, Brian Strahm and John Seiler for their assistance in the planning and execution of this project. And to the staff at the Great Dismal Swamp, Fred Wurster and Karen Balentine, for their knowledge and consistent moral support through the duration of my field work.

I would also like to extend a special thanks to my lab mates, Morgan Schulte, Jake Diamond, Nate Jones, and Gracie Erwin for their continual support inside and outside of the classroom, which has made my graduate school experience memorable. And finally, to my field partner Trevor Lawson, whose unfaltering positive attitude and motivation made conducting field work at a *truly* dismal swamp an experience of a lifetime.

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1.0 INTRODUCTION

1.1 Forested Wetlands: Extent, Functions, and Disturbance

Across the globe, forested wetlands are common landscape features that provide a suite of functions but are often vulnerable to degradation. Occupying an estimated global extent of more than 310 million ha, forested wetlands span latitudinal gradients, from tropical to boreal, and occur on a diverse range of landforms such as coastal, inland depressional, and montane (Matthews and Fung, 1987). For example, in the southeastern U.S., the term forested wetland covers a range of habitat types such as cypress domes, pocosins, bayheads, and bottomland hardwood forests (Batzer and Baldwin, 2012). Wetland ecosystems, including forested wetlands, offer a range of ecosystem functions such as providing unique habitat for flora and fauna (Russell and Beauchamp, 2017; Enge and Marion, 1986), nutrient transformations and reduction (Verhoeven et al., 2006), carbon storage (Kayranli et al., 2010), and water storage (Jones et al., 2017). Despite these valued functions, wetlands have been heavily exploited in the Anthropocene. Overall, wetland loss across the U.S. between European settlement and 1980 is estimated at 19.2 million ha or 53% of total wetland area (Dahl, 1990). In the most recent nationwide wetland monitoring report, forested wetlands accounted for the largest U.S. losses of any wetland type, with 41% of those losses occurring in the southeastern U.S. (Dahl, 2011). In addition to loss, remaining forested wetlands are often degraded, with impacts to their hydrologic regimes, biotic communities, an/or biogeochemical processes (Richardson, 1994). Both wetland loss and degradation are commonly associated with direct disturbances to vegetation (e.g., logging) and hydrologic alteration (e.g., drainage and impoundment).

Modifications to wetland hydrologic regime via ditching and draining can result in a significant loss of hydrologically driven wetland functions. Hydrologic regime (i.e., spatial and temporal changes in water level) largely determines wetland structure and processes. The depth, duration, and variability of wetland water levels are main drivers of vegetation composition and structure, selecting species based on their tolerance or preference for specific hydrologic regimes (Mitsch and Gosselink, 2007). As such, spatial variation in hydrologic regime at local to landscape scales increases habitat diversity in forested wetland environments (Semlitsch and Bodie, 1998). For example, in restored and created Delmarva Bay depressional wetlands, spatial variation in inundation depth and duration within individual wetlands increased vegetation diversity, where shallow zones supported both wetland and upland species and deep zones

supported a range of obligate wetland species (Russell and Beauchamp, 2017). Further, inundated or saturated soil conditions results in anaerobic conditions, the growth of anaerobic microorganisms, and unique biogeochemical reactions (Groffman and Tiedje, 1989). Spatial and temporal variation in such conditions often couples aerobic and anaerobic conditions, leading to important functions related to nutrient cycling and storage. For example, forested wetlands play important roles in carbon storage (Giese et al., 2000), nitrogen removal (Swanson et al., 2017), and phosphorus retention (Lane and Autrey, 2016). However, hydrologic alteration, albeit drainage or impoundment, often decreases heterogeneity in hydrologic conditions, thereby homogenizing habitat and biogeochemical conditions (Hunter et al., 2008). Moreover, most alteration seeks drier conditions (for other land uses) via ditches or subsurface tile drainage. For example, ditching is a ubiquitous landscape feature across the southeastern coastal plain and results in large reductions to wetland water storage capacity and thus duration of inundated or saturated soil conditions (Jones et al., 2017). As such, drained wetlands favor species adapted to drier conditions (Miller et al., 2015) and often experience shifts in biogeochemical functioning, including decreased nutrient retention, cation exchange capacity, and carbon storage (Holden et al., 2004).

Logging of forested wetlands for agricultural and timber provides an additional impact often with marked effects on post-harvesting vegetation composition and structure. Global estimates suggest that following European settlement, 94% of U.S. forests have been cleared at least once with nearly all southern forests having been harvested (Hurt et al., 2006). Although full recovery following land clearing has been documented in some forested wetland systems (Terwilliger and Ewel, 1986), secondary growth in many forested wetlands differs from pre-harvest communities and is a function of the existing subcanopy composition and surviving seed bank. Connor et al., 1986 documents this effect in baldcypress (*Taxodium distichum* (L.) Rich.) swamps, where regeneration is limited due to a reduction in microtopography and increased competition from existing subcanopy species not removed during logging. Any hydrologic alteration (e.g., drainage, impoundment, or logging roads) used to facilitate logging adds another determinant of post-logging communities, which may experience differing hydrologic regimes than pre-harvest conditions (Hauser et al., 1993). Moreover, altered seed dispersal patterns following hydrologic disturbance have been shown to influence future forested wetland

composition with windblown-dispersed species able to predominate over their hydrologically-dispersed counterparts (Reid et al., 2014).

Hydrologic restoration can be utilized to enhance forested wetland structure and function following disturbance. The goal of hydrologic restoration is to create a hydrologic regime that mimics pre-disturbance conditions despite remaining anthropogenic impacts (e.g., ditches, roads, and urban development). Hydrologic restoration of ditched forested wetlands occurs by two methods: (1) blocking ditches with artificial structures (i.e., dams) or (2) filling the entire volume of the ditch (Chimner et al., 2017). Both methods accomplish similar goals of reducing wetland drainage and increasing wetland water levels. However, restoring community composition and function following hydrologic disturbance remains difficult. Natural regeneration in forested wetlands is often limited by biotic (e.g., fecundity, viability, and competition) and/or abiotic (e.g., soil moisture, sunlight availability, and nutrient availability) factors making restoration difficult (Kroschel et al., 2016). Thus, to maximize long-term success, small-scale restoration of forested wetlands typically involves three-steps: (1) the removal of post-disturbance forest, (2) hydrologic restoration, and (3) replanting and treatment of target tree species (Chimner et al., 2017). However, resource constraints often limit active harvesting and replanting efforts across large scales; as such, in spatially extensive systems like the Great Dismal Swamp, the principal strategy is to restore hydrologic regime and then rely on ecosystem response (Chimner et al., 2017).

1.2 The Great Dismal Swamp: Formation, Disturbance, and Restoration

The Great Dismal Swamp (GDS) is a large expanse of forested wetlands undergoing hydrologic restoration following extensive anthropogenic disturbance. Prior to ditching and logging, the GDS encompassed more than 500,000 ha area extending from the Chesapeake Bay to the Albemarle Sound in the Atlantic Coastal Plain (Lichtler and Walker, 1974). Despite significant areal loss, the GDS remains one of the largest wetland complexes in the U.S., covering a 43,000 ha area in southeastern Virginia and northwestern North Carolina. The Great Dismal Swamp National Wildlife Refuge (GDSNWR) was established in 1973 by Congressional mandate to protect, restore, and manage the swamp's unique ecosystems. Current management efforts by the United States Fish and Wildlife Service (USFWS) aim to increase native plant diversity, decrease fire vulnerability, and increase peat accumulation at the GDS. Forest management (including active planting) is an element of such efforts; however, given the large

spatial extent, the principal strategy is hydrologic restoration to “re-wet the swamp” (Wurster et al., 2016).

The GDS is a young geologic feature with estimates of its age at approximately 12,000 years old (Whitehead, 1972). As discussed by Lichtler and Walker (1974), the hydrogeologic setting of the region combined to form the GDS and its characteristic hydrologic conditions and accumulating peat soils. In short, the GDS is bordered to the west by the Suffolk Scarp, a Pleistocene-era shoreline, and to the east by the Deep Creek Swale. The lateral and vertical movement of water throughout GDS is restricted due to low topographic relief (total net elevation change of approximately 3m) and the presence of the Sand Bridge Formation, a mineral soil layer of low permeability. The resulting hydrology has historically maintained constant saturated soil conditions fueling the accumulation of organic-rich, peat soils throughout GDS. Peat formation at GDS began approximately 9,000 years ago when erosion of the Sand Bridge formation allowed groundwater under artesian pressure to permeate clay soils and inundate the soil surface (Whitehead, 1972). Prior to disturbance, peat was estimated to accumulate at a rate of 33cm per 1,000 years and was greatest at topographic lows within wide ancient stream valleys, resulting in contemporary variation in peat thickness from a few centimeters thick to 4m (Whitehead, 1972).

Hydrologic regime has additionally driven community composition and structure at GDS since its formation. In an analysis of peat radio-carbon data and pollen analysis, Whitehead (1972) concluded that the GDS most likely began as a freshwater marsh with periods of brackish conditions and then transitioned to a forest closely resembling a contemporary boreal hardwood system. Following the last glacial period, a warming climate and peat accumulation aided in the transition to mosaic of communities that occurred prior to anthropogenic disturbance (Whitehead, 1972). Specifically, these included stands variously dominated by bald-cypress, swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walter) Sarg.), water tupelo (*Nyssa aquatic* L.), and Atlantic white cedar (*Chamaecyparis thyoides* L.), with areas of pocosin comprised of pond pine (*Pinus serotina* Michx.) and evergreen shrubs. This mosaic was largely driven by spatial differences in hydrology and fire regimes (Carter et al., 1994; Legrand Jr., 2000); however, anthropogenic disturbance (i.e., logging and ditching) has shifted historical distribution to what is seen today.

Contemporary hydrology and vegetation composition have drastically changed following more than 200 years of anthropogenic disturbance. Plans to alter GDS hydrology were crafted before the U.S. could claim itself a sovereign state, with Colonel William Byrd submitting a proposal to drain the swamp to the King of England in 1730. Describing it as a “dreadful swamp was ever judged impassable”, Byrd justifies the draining of the GDS to make the land habitable by “correcting and purifying the air, which is now infected by the malignant vapours rising continually from that large tract of mire and filthiness”. In 1736, logging began when the Dismal Swamp Land Company began work on the first drainage ditch and associated spoil bank road to facilitate timber activities (Levy, 1991). Such activities continued but were limited in scale prior to 1760. However, a rapidly growing U.S. economy and profitability of baldcypress and Atlantic White Cedar timber for construction materials resulted in increased logging activity during the 1800s. Clearcutting of the GDS continued into the 20th century with the last tract of virgin swamp land removed in 1937 (Dean, 1969). In addition to direct effects of logging on vegetation communities, the resulting 158-mile ditch and road network substantially altered hydrologic regime (Legrand Jr., 2000). Constructed roads and spoil banks now serve as dams to limit overland and groundwater exchange, while ditches rapidly drain water to locations outside of GDS creating drier and more homogenous hydrologic conditions across the GDS (Speiran et al., 2018; Figure 1).

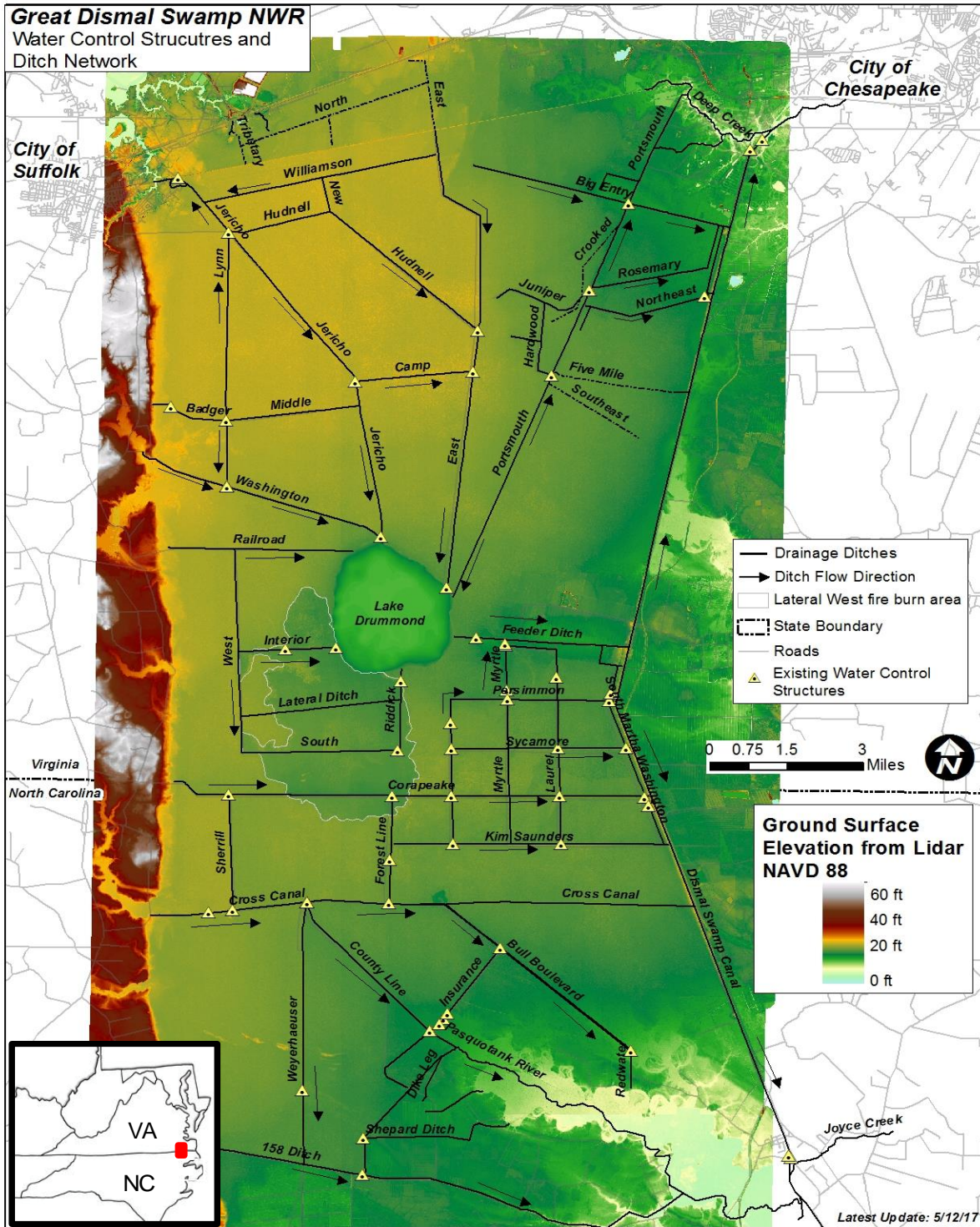


Figure 1. Land surface elevation at the Great Dismal Swamp. Ditch network (black lines) and associated water flows (black arrows) are represented (courtesy of the U.S. Fish and Wildlife Service).

Impaired hydrology, logging disturbance, and natural ecosystem disturbances (e.g., fire, storms) have combined to determine contemporary vegetation communities at the GDS. Dabel and Day (1977) and Sleeter et al. (2017) describe five forested community types: mixed hardwood, cedar, cypress, pond pine pocosin, and maple-gum. Current distribution of these community types is largely driven by hydrologic regime. The mixed hardwood community is a relatively undisturbed community located in upland environments associated with remnant sand dunes at the GDS. The tree strata is dominated by oak species (*Quercus* spp. L.) and sweetgum (*Liquidambar styraciflua* L.) with developed understory layers. The Atlantic white cedar (*Chamaecyparis thyoides* L.) dominated community once covered over 50,000 ha and was found on seasonally saturated soils (DeBerry and Atkinson, 2014). However, natural (severe weather, fire) and anthropogenic disturbances (hydrologic alteration and clearcutting) have reduced its current distribution to 1,600 ha, or 3% of the GDS (Levy, 1991; Sleeter et al., 2017). The understory of the cedar community is dense and current regeneration of Atlantic white cedar is low due to the exclusion of fire, which historically allowed for regeneration in pure stands. The baldcypress (*Taxodium distichum* (L.) Rich.) dominated community is typically found at the wettest locations with seasonal inundation. This community is characterized by sparse understory cover and currently encompasses 12% of the GDS following hydrologic and logging disturbances (Levy, 1991). Pond pine (*Pinus serotina* Michx.) dominates the pocosin community, which currently covers more than 15% of the GDS. This community occurs on seasonally saturated soils, and vegetation composition is largely controlled by frequency wildfire return intervals, which result in dense evergreen shrub cover and the regeneration of pond pine in pure stands. While the mixed hardwood community still dominates the limited upland locations, disturbances in the cedar, cypress, and pocosin communities have led to a drastic rise in spatial extent of the fifth community type: the maple-gum community (Levy, 1991).

As the swamp's dominant community type, the maple-gum community has been recently estimated to cover 61% of the GDS area (Sleeter et al., 2017). This community categorization includes stands dominated by red maple (*Acer rubrum* L.), with varying densities of blackgum (*Nyssa sylvatica* Marsh.) and/or swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walter) Sarg.). Notably, this community is thought to exist on a range of soil types and hydrologic regimes (Sleeter et al., 2017). Understory composition is variable, and successful regeneration of overstory species suggests this community type will perpetuate into the future (Levy, 1991). The

identification of co-occurring *Nyssa* spp. within this community is a point of confusion at GDS. Three types of *Nyssa* spp. co-exist within forest communities at GDS: blackgum, swamp tupelo, and water tupelo (*Nyssa aquatica* L.). While water tupelo is easily identified in the field by its large buttressed base and wide leaves, differentiation between swamp tupelo and blackgum is difficult. In describing forest community types at the GDS, Dabel and Day (1977) consider the maple-gum to be comprised only of swamp tupelo, whereas Sleeter et al. (2017) assume this community comprises only blackgum. This community most likely includes both blackgum and swamp tupelo, but appropriate identification of species within this genus is critical as each varies in wetland indicator status from obligate (water tupelo & swamp tupelo) to facultative (blackgum).

Hydrology and disturbance history also influence peat accumulation and soil properties at GDS. Prolonged saturation and/or flooded conditions are prerequisites for peat formation and accumulation as anoxic soil conditions slow the decomposition of organic matter. Widespread drainage at GDS has likely decreased peat accumulation rates, or even led to peat oxidation and subsidence, with important consequences for the valued carbon storage function (Drexler et al., 2017). Indeed, peat accumulation rates at GDS are lower than those of an undisturbed reference and range from 0.19 to 0.38 cm per year (Drexler et al., 2017). However, slow accumulation of peat suggests that peat depths may be a better predictor of long-term hydrology, whereas surface soil characteristics may reflect more recent changes in hydrology. In short, drier locations typically have higher soil bulk density (Drexler et al., 2009), lower organic matter content (Drzymulska, 2016), and decreased carbon to nitrogen ratios (Chambers et al., 2011). Further, a reduction in vertical peat accretion coupled with locations of increased subsidence can decrease local microtopographic variation (Day, 1982). Microtopography, or hummocks (local highs) and hollows (local lows), increase vegetation (Ehernfeld, 1995) and functional (e.g., biogeochemical processes; Bruland and Richardson, 2005) diversity within a wetland system. The loss of this habitat complexity may further lead to the homogenization of communities at the GDS.

To enhance ecosystem functioning following disturbance, the USFWS has undertaken hydrologic restoration at GDS. The primary goal of restoration is to mimic pre-disturbance hydrology and thereby protect and enhance unique forested wetland types, increase carbon storage, and decrease fire vulnerability. Given the swamp's large spatial extent, active management strategies such as the removal of secondary growth forests and replanting are

seldom utilized. As a result, passive management solutions are being implemented through the installation of water control structures within the existing ditch network. Water control structures act as dams and manipulate ditch and thus adjacent wetland water levels through use of riser boards (Wurster et al., 2016). To inform control structure installation and subsequent operation, a better understanding of hydrologic controls on ecosystem structure and function is needed.

Although vegetation composition and peat soils have been extensively investigated at GDS (e.g., Dabel and Day, 1977; Carter et al., 1994; Drexler et al., 2017), the role of hydrology in driving these ecosystem attributes has been less studied. Schulte et al. (in review) documented ecosystem structure across a hydrologic gradient at GDS using in situ water level measurements. Results showed that wetter sites were associated with greater stand richness and lower red maple dominance, while preserving peat depth and microtopography. However, this study was conducted at a limited spatial scale, thus inferences regarding these hydrologic controls cannot be extended to other community types and abiotic environments across GDS. Moreover, previous work has predominately utilized the community characterizations established by Dabel and Day (1977) more than forty years ago. Consequently, new work is needed to characterize vegetation communities, peat soils, and potential hydrologic controls across the large spatial extent of GDS. To do so requires spatially distributed surveys of vegetation communities and soil properties coupled with estimates of hydrologic regime via appropriate methods at such spatial scales, including hydrologic model outputs, field indicators, and soil properties.

In this work, we sought to inform hydrologic restoration and forest management at GDS by documenting variation in and interactions among vegetation, hydrologic regime, and soil properties. Specific objectives included:

1. Characterize swamp-wide variation in vegetation structure and composition.
2. Apply and compare methods for assessing hydrologic regime at large spatial scales.
3. Explore abiotic drivers of vegetation community variation.
4. Inform future GDS-wide management and monitoring to enhance ecosystem functions.

2.0 MATERIALS AND METHODS

2.1 Study Site and Design

The Great Dismal Swamp (GDS) is a nonriverine swamp forest located in the Atlantic Coastal Plain (Figure 2). In this study, we specifically focused on the large portion of GDS protected by the United States Fish and Wildlife Service (USFWS), which encompasses a 43,300 ha area of southeastern Virginia and northeastern North Carolina. Hereafter, we simply refer to our study site as the GDS, acknowledging that the refuge (and thus our study domain) does not include the Dismal Swamp State Natural Area, a 5,805 ha protected area of the NC Division of Parks and Recreation to the southeast corner of the refuge.

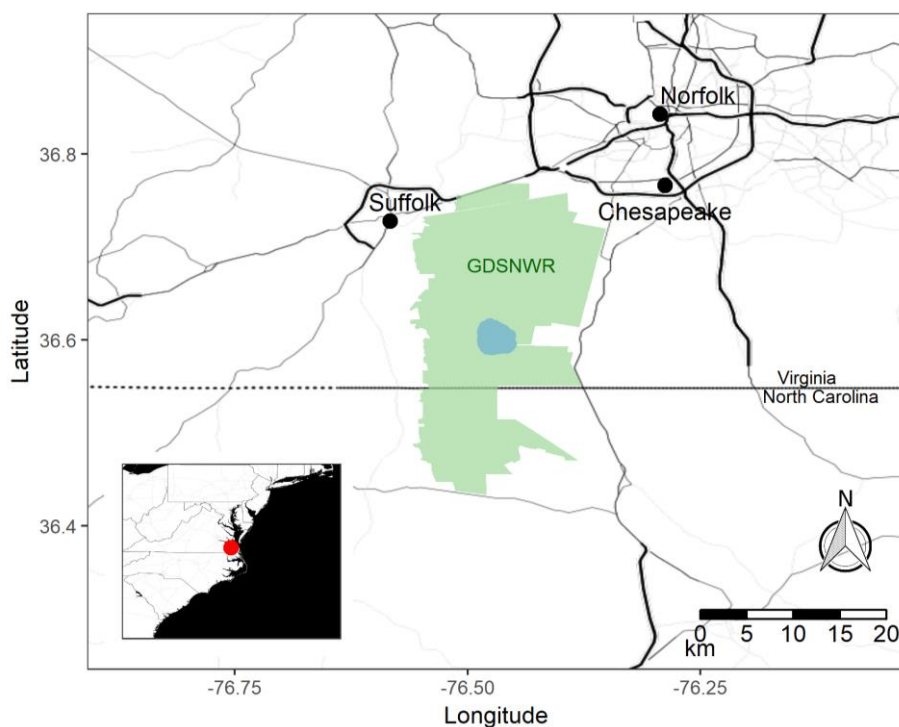


Figure 2. Location of the Great Dismal Swamp National Wildlife Refuge in southeastern Virginia and northeastern North Carolina.

Climate at GDS is considered temperate with a mean annual temperature of 15 °C and characterized by long humid summers and mild winters; mean annual precipitation is 118 cm (1981-2010; NOAA). Forest community composition is dominated by five major community types as described by Dabel and Day (1977) and Sleeter et al. (2017). The mesic hardwood is located on upland soils and is dominated by oak species (*Quercus* spp. L.) and sweetgum (*Liquidambar styracifula* L.). The cedar community is dominated by Atlantic white cedar

(*Chamaecyparis thyoides* L.) and is located on seasonally saturated soils. The baldcypress (*Taxodium distichum* (L.) Rich.) dominated community represents the wettest communities at the GDS located on seasonally inundated soils. The pond pine (*Pinus serotina* Michx.) dominated community is a pocosin environment characterized by dense evergreen shrub cover located on seasonally saturated soils. Lastly, the maple-gum community covers the largest extent at the GDS and is dominated by red maple (*Acer rubrum* L.), blackgum (*Nyssa sylvatica* Marsh.) and/or swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walter) Sarg.).

Soils at GDS are largely organic-rich, deep, and typically described as peat, leading to the common classification of GDS as a peatland. However, specific soil types vary and include Histosols (81%), Ultisols (11%), Inceptisols (2.5%), and Entisols (2.5%) with the remaining area covered by open water (3%) (NRCS Web Soil Survey). While Histosols clearly dominate, they are primarily classified as Terric Haplosaprists and Typic Haplosaprists in contrast to fibric (or peat) texture classes. Soils are generally acidic, poorly drained, and nutrient poor (NRCS Web Soil Survey).

We established 79 survey plots across GDS to evaluate the spatial variation in vegetation composition and structure, hydrologic regime, soil properties, and organic soil (hereafter peat) depths. We assessed relationships among measured parameters to explore linkages between abiotic and biotic attributes and how such linkages influence ecosystem variation across GDS.

2.1.1 Plot Selection

To effectively capture variation across GDS, the space-filling curve (SFC) method was applied following Lister and Scott (2009). A SFC is a curve or shape that encompasses a given area, where the area is segmented into a specified number of polygons with equal area (Bartholdi and Platzman, 1988). In a collaboration with the USFWS, a SFC was developed for the GDS in ArcMap (ESRI) by first creating a 30 m pixel raster and subsequently segmenting the area with a number of polygons equal to the number of desired survey locations. Within each polygon, a point was randomly projected yielding the final survey location. In this way, the SFC model produces a network of potential surveyed locations that is spatially balanced, avoiding the potential for an unequal distribution of polygons along study area boundaries and possible spatial autocorrelation (Gregoire and Scott, 2003). Using previously collected forest inventory data, 105 plots was deemed to be an acceptable sample size to capture the variation in overstory density and basal area at a 95% confidence level (J. Westfall, personal communication). Recognizing the

need for possible plot omission, 150 points were projected with this number reduced to 136 by removing plots not appropriate for the forest inventory (e.g., plots on Lake Drummond, outside the GDS NWR boundaries, on roads/ditches, or located within nonforested regions). Of these plot locations, 79 locations were surveyed (Figure 3), with survey of the remaining plots limited by site access constraints such as dense understory cover or lack of an accessible forest road. Plot centers were located using a Garmin eTrex Venture HC GPS, assigned a unique plot number, and marked to within 3m of accuracy with a 1.5m metal conduit.

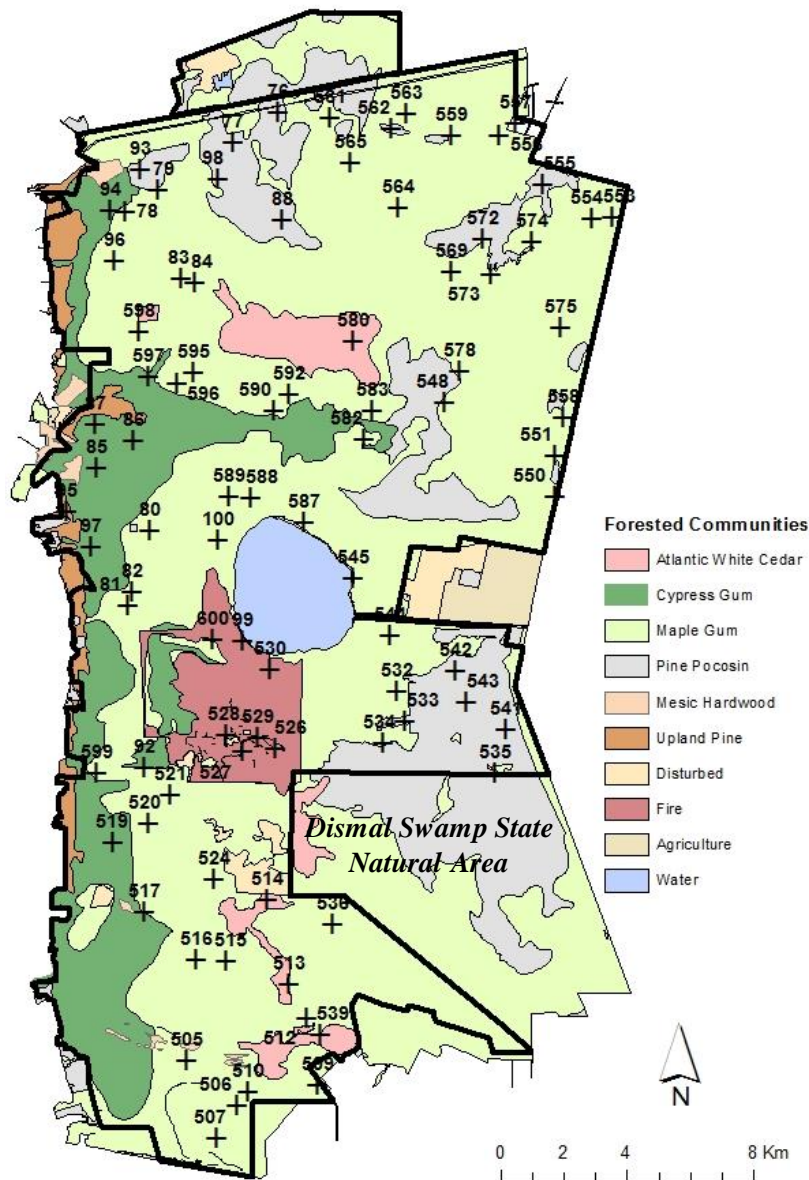


Figure 3. Forest communities at the Great Dismal Swamp and Dismal Swamp State Natural Area. Forest inventory plot locations (n=79) visited in this study are marked (+) and labeled with unique plot number. Land cover data courtesy of U.S. Fish and Wildlife Service.

2.2 Data Collection

2.2.1 Variation in Vegetation Composition

At each survey plot, vegetation composition and structure were assessed utilizing the draft USFWS Region 5 forest inventory protocol (Horan et al., in review). The protocol characterizes the vegetation community by species growth forms. Trees are defined as woody species with diameter at breast height (DBH) greater than 12.7 cm. Saplings and seedlings are regeneration woody species; saplings are defined as being between 2.54 cm and 12.7 cm in diameter at midpoint height, and seedlings as greater than 2.54 cm in height and less than 2.54 cm in diameter at midpoint height. Shrubs and vines (shrubs from here on) are defined as woody or non-woody species not expected to reach the overstory. The herbaceous community included species belonging to both forb and graminoid growth forms.

Using marked plot center locations, a 0.017 ha (7.3 m radius) fixed radius plot was established to survey tree, shrub, and herbaceous growth forms. Tree composition and structure were assessed by recording the DBH and species of each tree. For both shrub and herbaceous growth forms, total percent cover and percent cover of the four dominant species were recorded using ocular estimates. In a smaller subplot (0.0012 ha; 1.8 m radius), tree regeneration composition and frequency were assessed by recording species and counts of all saplings and seedlings.

2.2.2 Drivers of Vegetation Composition

Water Level Indicators

Field indicators of seasonal high-water levels were recorded as relative estimates of maximum inundation depth across survey plots. When available, the height of a seasonal high-water marks (n=5) and/or cypress knees (n=5) were recorded at each plot. High-water marks were measured from ground surface to the base of lichen lines, water stains, and moss collars or the top of adventitious roots (Gilbert et al., 1995).

To further estimate hydrologic variation across plots, we used simulated water levels from a hydrologic model recently developed for GDS. The model was developed by the USGS, in collaboration with the USFWS, to inform water-resource management decisions and water control structures operation. The model is a steady-state, numerical model that combines MODFLOW-NWT (simulates groundwater flow) and the SWR1 Process (simulates dynamic surface-water flows, water-control structure management, and groundwater/surface-water

interactions) (Eggleston et al., in review). Model outputs are mean springtime (months of April-June) water levels across GDS under the three following hydrologic scenarios: baseline conditions (average springtime climatic conditions for the period 2005-2015), wet scenario (spring 2015; atypical wet season), and dry scenario (spring 2011; atypical dry season). The spatial domain of the 3-dimensional model is the entire GDS, where mean water levels (relative to ground surface) are simulated for 500 ft² (152.4 m²) grid cells, each of which are defined by one representative land elevation. Land surface elevations were calculated using three LiDAR datasets compiled into a 6.6 ft (2 m) raster grid, digital-elevation model (DEM). The DEM cell elevations were averaged within the 500 ft model grid (5,800 cells) to yield one elevation for each grid cell. However, for this study, model outputs were adjusted to estimate mean water levels relative to land elevation for each of the 88 survey plots. To do so, we refined land surface elevations to the plot area (7.3 m radius) by overlaying buffered plot locations on the land surface elevation DEM. Within each plot, DEM cell elevations (ca. 40/plot) were averaged to obtain plot mean elevations, which were then used in plot-specific water level calculations for each modeled scenario (WL_{base} , WL_{wet} , WL_{dry}).

Soil Hydrologic Indicators

Peat depths were measured at each survey plot to determine the spatial variability in organic matter accumulation and to be used as potential indicators of long-term hydrologic regime. Field measurements were recorded at five locations along a N-S transect. A 3.6 m extendable soil probe was used to locate the intersection of the mineral and organic layers via resistance at the mineral layer. Peat depth was estimated as the depth to this area of high resistance.

Peat depths values were also estimated using a raster dataset for peat depths developed by the USGS (Eggleston et al., 2017; in review). The raster was created by aggregating point measurements of peat depth from a variety of sources spanning a 42-year period (1973-2015). Previous studies, such as Oaks and Coch (1973), have mapped peat topography at the GDS, and these values were supplemented with estimations from field reconnaissance and measurement by the USFWS and USGS. Using all values of peat topography, a raster was developed by interpolating between measured values in ArcMap. The resulting raster has a 2m resolution. Survey plots were then overlaid on the raster dataset and buffered to plot extent. All raster pixels

that intersected the plot boundary were extracted ($n \geq 40$ pixels) and used to calculate plot mean peat depth.

Additionally, surface soil samples were collected at a depth of 12.6 cm to explore variation in soil composition and to serve as additional indicators of hydrologic regime. At each survey plot, three peat samples were collected along a N-S transect. Surface peat samples were consistently sampled in microtopographic lows to avoid capturing variability in soil properties associated with varying microtopography. The following method was used to maintain field bulk density. First, the root mat was cut and removed using hand tools to expose the underlying peat (Ehrenfeld, 1995). Next, a hand trowel was used to excavate a small hole (approx. diameter = 15cm) to expose the surface soil profile. A steel ring sampler ($h=5.02\text{cm}$, $d=7.47\text{cm}$) was inserted horizontally into the profile until all edges were flush with soil. The sample was then excavated using a hand trowel and excess soil was removed. The sample was bagged, labeled, and transported to the lab at 4°C.

Lab analysis of bulk density, carbon (C) content, nitrogen (N) content, and organic matter content was conducted where samples were oven-dried at 70°C to a constant weight and weighed to the nearest 0.01 g. Large root material ($d > 0.5\text{cm}$) was then removed, and its mass and volume (via water displacement) were recorded. The corrected dry mass and volume of the remaining sample were calculated by subtracting the root mass and volume, respectively. The bulk density for each sample ($n=3$ per plot) was then determined by dividing the corrected dry mass by its corrected volume. Oven-dried samples were then homogenized by grinding with mortar and pestle to pass through a 2-mm sieve. A 0.25 g subsample ($n=3$ per plot) was used for analysis of C and N content with a CN Elemental Analyzer (Elementar Analysensysteme GmbH vario Max; Langensfeld, Germany). The remaining sample was used for loss on ignition analysis. Samples ($n=3$ per plot) were combusted in a muffle furnace at 500°C for 24 hours. Organic matter content was calculated as the difference in mass between the original sample and the mass that remained (mineral fraction) relative to the original sample mass.

2.3 Data Analysis

2.3.1 Variation in Vegetation Composition

Prior to statistical analysis, the data were prepared by combining tree data for blackgum and swamp tupelo into a single “gum” field given confusion in previous studies at GDS, often

difficulty in field distinction, and similarity between the two species. However, we did attempt field distinction between the two species and retained those records for additional analysis.

A suite of vegetation metrics across growth forms were calculated to assess community variation and structure. Tree metrics calculated included cumulative and species-specific basal area and density, species richness, and diversity (Shannon-Wiener index). Plot-level importance values (IV) were also calculated for each tree species. These values range from 0-2 and are the sum of relative species basal area (sum of species basal area/sum total basal area) and relative density (sum of species density/sum of total density) of each species. Regeneration metrics were obtained by first combining sapling and seedling data followed by calculations of total count, richness, diversity (Shannon-Wiener index), and relative frequency for each species. Shrub and herbaceous metrics included cumulative percent cover by each growth form and for dominant species. To evaluate relationships among vegetation metrics across growth forms, we performed a Spearman's correlation analysis across all 79 forested plots.

Following plot-level analysis of vegetation composition and structure, multivariate statistical methods were utilized to determine significant community types, classified by tree composition. To do so, tree species abundance data were utilized to conduct a series of linked analyses, including hierarchical cluster analysis, indicator species analysis, permutational multivariate analysis of variance (permMANOVA), and nonmetric multidimensional scaling (NMDS). All statistical analyses were conducted in R (R Core Team, 2016). Prior to multivariate statistical analysis, rare species were removed from the tree abundance matrix to improve the detection of significant overstory community types. As suggested by McCune and Grace (2002), species present at 5% or fewer plots were removed. Eight species were removed: Carolina ash (*Fraxinus caroliniana* Mill.), laurel oak (*Quercus laurifolia* Michx.), loblolly pine (*Pinus taeda* L.), pin oak (*Quercus palustris* Münchh.), swamp bay (*Persea palustris* (Raf.) Sarg.), tulip-poplar (*Liriodendron tulipifera* L.), water oak (*Quercus nigra* L.), and willow oak (*Quercus phellos* L.). With the revised abundance data, we first conducted a hierarchical, agglomerative, polythetic cluster analysis using a Bray-Curtis dissimilarity matrix calculated with the 'vegdist' function in the 'vegan' package (Oksanen et al., 2007). Clustering was performed with a flexible beta linkage ($\beta = -0.25$) using the 'agnes' function in the 'cluster' package (Maechler et al., 2014) to minimize matrix distortion (McCune and Grace, 2002).

Following cluster analysis, the resulting dendrogram was pruned at locations yielding a variety of cluster levels (i.e., from 2 to 5 clustered groups), with an indicator species analysis used to inform the appropriate level of pruning. Using cluster classifications within each clustered group as categorical variables, indicator species analysis was performed using the ‘multipatt’ function in the ‘indicspecies’ package (De Cáceres et al., 2016). For each cluster level, an indicator value index (IVI) was independently generated for each species. This index measures the association between a particular species and a clustered group or combination of clustered groups (De Cáceres et al., 2016). This statistic ranges from 0 to 1 and is the product of two conditional probability values called Component A and Component B. Component A is named the *specificity* value and is defined as the probability that the surveyed plot belongs to the clustered group *given* the fact Species A was found (McCune and Grace, 2002). Component B is named the *sensitivity* value and is the probability of finding Species A at plots belonging to a clustered group (McCune and Grace, 2002). An IVI was calculated for each species within each cluster group; the maximum IVI across all clusters for a species was then assigned as its IVI at each cluster level (McCune and Grace, 2002). A *p*-value was generated for each species using 1,000 Monte Carlo simulations with randomized data to test the null hypothesis that the observed species IVI is not significantly greater than a value produced with randomized data. The number of significant indicator species and their *p* values at each cluster level were then totaled. Lastly, cluster pruning was conducted to select clustering levels that maximized the number of indicator species and minimized their total *p* value (McCune and Grace, 2002).

Two additional analyses were used to further inform clustering pruning. A permMANOVA analysis was conducted using the ‘adonis’ function in the ‘vegan’ package (Oksanen et al., 2007) to test significant differences in clustered community dissimilarities at each clustering level. Lastly, a non-metric multidimensional scaling (NMDS) analysis was performed using the ‘mds’ function in the ‘vegan’ package (Oksanen et al., 2007). Using a Bray-Curtis dissimilarity matrix for tree abundance data, the NMDS was conducted using 7 random starts for 100 iterations. A stress test was used to determine ‘goodness-of-fit’ of the ordination dimensionality in the final model. To visualize clustering in ordination space, cluster groups were used as categorical variables (via color surveyed plots).

Following cluster analysis, differences in vegetation composition and structure across clustered community types were analyzed. We pooled plots by their identified groups and

assessed significant differences among community types in the suite of vegetation metrics via nonparametric statistical methods. Specifically, a Kruskal-Wallis rank sum test was utilized followed by a post-hoc pairwise Wilcoxon-Mann-Whitney rank sum test with a Holm p -adjustment for multiple comparisons (Holm, 1979).

2.3.2 Drivers of Vegetation Composition

We first compared our indicators of hydrologic regime using Spearman's correlation analysis of our water level estimates (model outputs and high-water level indicators) and soil hydrologic properties. We then evaluated correlations between these indicators and all vegetation metrics to explore drivers of vegetation community and structure. We further assessed drivers via differences among clustered community groups using previously mentioned nonparametric statistical methods.

3.0 RESULTS

3.1 Variation in Vegetation Composition across the GDS

We quantified metrics of vegetation composition and structure across 79 forest inventory plots at the GDS. We assessed these metrics at a variety of spatial scales, include cumulatively across GDS, at the plot scale, and in a comparison of identified community types. Although we largely found homogenous vegetation composition, some variation was evident.

3.1.1 Plot-Level Variation

The surveyed forested plots characterized tree composition and structure across GDS. Across all plots, red maple was the overwhelming dominant tree species, present at 97% of plots and cumulatively contributing 148% more basal area as compared to the next most abundant species (Figure 4). Gum (i.e., combination of both blackgum and swamp tupelo) also dominated tree composition, present at 25% of plots while contributing less to cumulative basal area as compared to red maple (Figure 4). The species rank-abundance curve (inset; Figure 4) comports with tree density and basal area analysis in clearly illustrating red maple and gum dominance, as well as identifying sweetgum as the third most abundant species. The steep slope of the rank-abundance curve suggests that evenness in tree species composition is low.

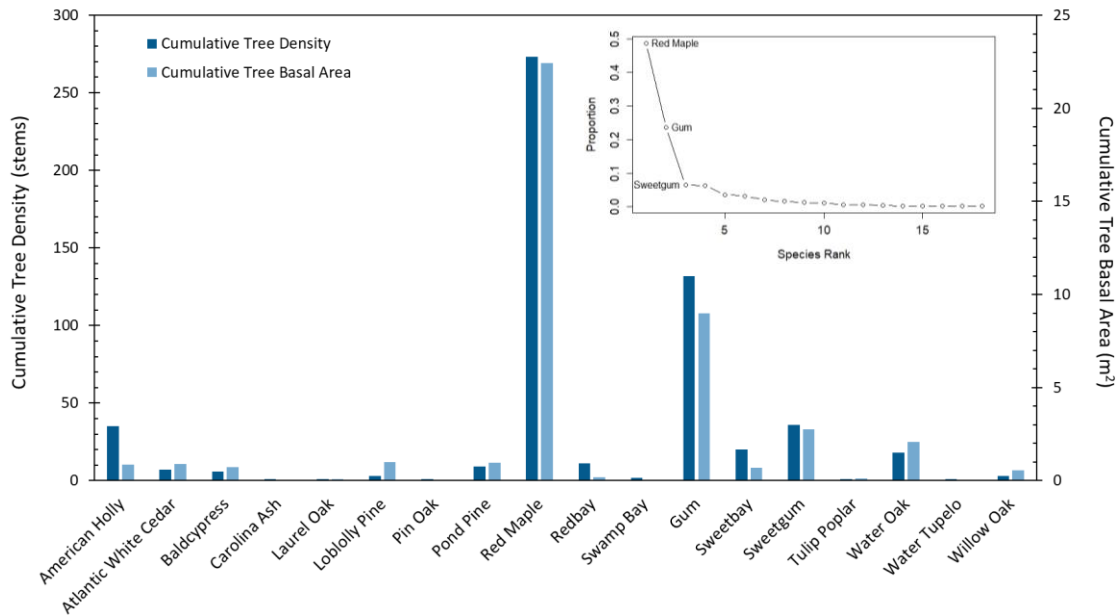


Figure 4. Cumulative tree density and basal area across 79 forest inventory plots at the Great Dismal Swamp. Inset: Species rank-abundance curve for forest inventory plots. The curve relates relative abundance (proportion) of a species to its cumulative abundance rank (species rank), where the most abundant species is ranked #1.

To investigate variation across plots, importance values (IV) were computed to assess tree species dominance. IV values range from 0-2 and sum the relative species basal area (sum of species basal area/sum total basal area) and relative density (sum of species density/sum of total density) of each species. Using IVs for the three most dominant tree species (via species rank-abundance curve), red maple dominance clearly extended to the plot-level but was variable across plots, where lower red maple IV was associated with other species, particular sweetgum and gum (Figure 5).

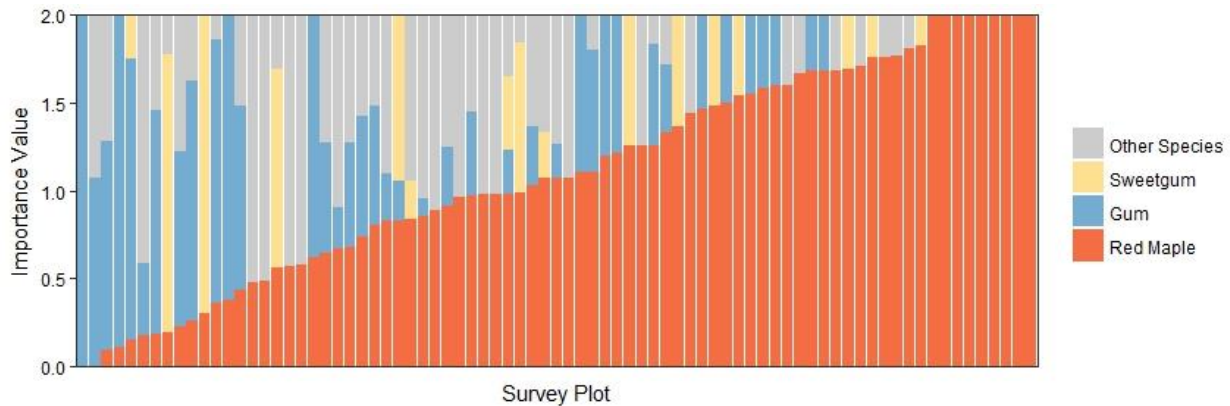


Figure 5. Plot-level importance values (IV) for 79 forest inventory plots at the Great Dismal Swamp. Bars represent forest inventory plots ordered by increasing IV (from 0-2). Red maple, gum, and sweetgum were identified as the three most dominant species by the species rank-abundance curve. All other species are represented by “Other Species” category.

To assess the role of tree species dominance in driving community composition and structure, a Spearman’s correlation analysis was conducted among vegetation metrics and dominant tree species IVs (Table 1). The correlation matrix confirms trends observed in plot-level analysis, and highlights influences of variable tree dominance on tree density and diversity. Red maple IV had significant negative correlations with both sweetgum IV and gum IV. Further, red maple IV significantly decreased tree density, richness, and diversity, while gum IV was positively correlated with these metrics. Sweetgum IV did not exhibit similar controls on tree structure (with exception of tree density); however, cover of understory growth forms may differ at sites where this species is dominant (Table 1).

Table 1. Spearman’s correlation matrix of dominant species importance values (IV) vs. calculated vegetation metrics. Bold values are significant at p-values < 0.05.

	Red Maple IV	Gum IV	Sweetgum IV
Red Maple IV	1	–	–
Gum IV	-0.55	1	–
Sweetgum IV	-0.07	-0.31	1
Tree Basal Area	-0.17	0.29	-0.14
Tree Density	-0.42	0.24	0.23
Tree Richness	-0.61	0.36	0.11
Tree Diversity	-0.60	0.34	0.04
Shrub % Cover	0.21	-0.05	-0.25
Herbaceous % Cover	-0.16	-0.03	0.28
Regeneration Density	-0.11	0.14	-0.01
Regeneration Richness	-0.19	0.11	0.12
Regeneration Diversity	-0.18	0.09	0.13

3.1.2 Clustered Forest Communities

Analysis of plot-level tree composition and structure revealed rather homogenous tree composition across GDS with red maple as the dominant species. However, some variation in tree dominance was evident and resulted in significant vegetation by vegetation interactions (Table 1). To further explore possible community-level variation, a hierarchical, polythetic, agglomerative cluster analysis was used to identify significant community types at the GDS. The clustering scheme using plot-level tree abundance values produced the dendrogram represented in Figure 6.

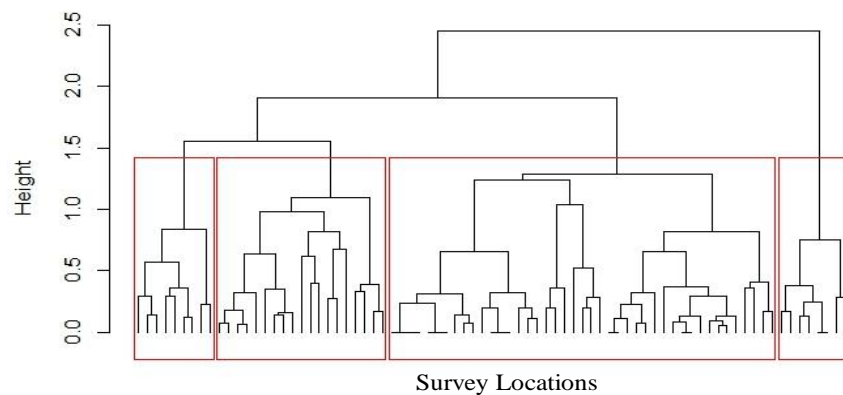


Figure 6. Dendrogram produced following hierarchical cluster analysis of tree abundance data of 10 species. Survey locations represent 79 forest inventory plots at the Great Dismal Swamp. Red boxes represent location of dendrogram pruning based on subsequent indicator species analysis and visualization with non-metric multidimensional scaling (NMDS).

The dendrogram was pruned using an indicator species analysis to identify the number of significant communities (red boxes; Figure 6). Cumulative p -values for each species ($n=10$; solid line in Figure 7) and the number of significant indicator species ($p<0.05$; dotted line) were plotted against the number of clusters (Figure 7). Locations resulting in four and five clusters corresponding with both low total p and a high number of significant indicator species; for parsimony, the clustering level producing four clusters was chosen for subsequent analysis. A permutation MANOVA with post-hoc pairwise comparisons resulted in significant differences in tree community composition ($p<0.05$) across these four clusters.

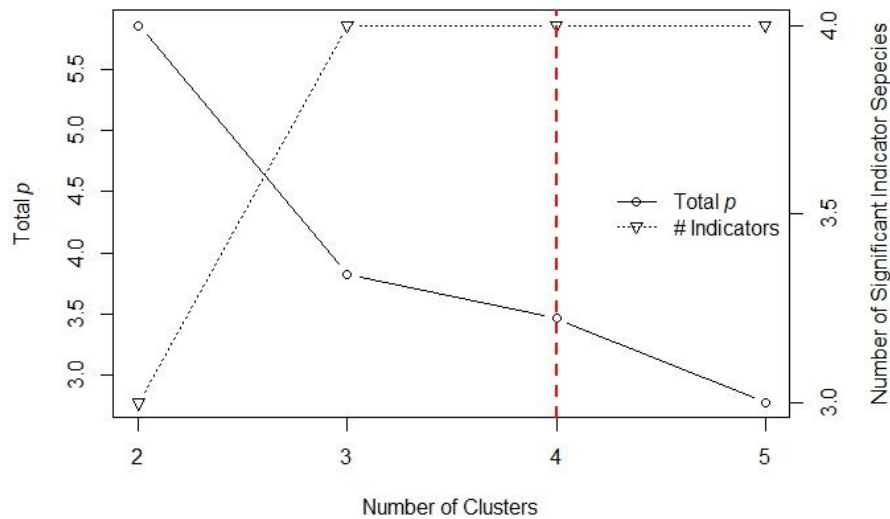


Figure 7. Indicator species analysis for 10 tree species at the Great Dismal Swamp. Hierarchical cluster analysis was used to separate forest inventory plots ($n=79$) into 2-5 clusters. Using cluster numbers as categorical variables, an indicator value index (IVI) was assigned to each species within a cluster to assess its utility as an indicator species. A p value was individually generated for each species within a cluster using 1,000 Monte Carlo simulations with randomized data to test the null hypothesis that the observed IVI is not significantly greater than a value produced by random chance. A p -value less than 0.05 represents a significant indicator species for a respective cluster. Location of dendrogram pruning (dashed red line) was determined at a location where low total p corresponded with a high number of significant indicator species.

To visualize community types and variation, a non-metric multidimensional scaling (NMDS) was used to plot communities in ordination space. A three-dimensional model was selected for analysis with a final stress value of 0.17 for 100 iterations. However, only MDS axes 1 and 2 were used for visualization of community clustering (Figure 8). To assess how tree species covary with community types in ordination space, vectors for red maple and indicator species (gum, sweetgum, sweetbay, baldcypress, and American holly) were overlaid on the

NMDS. Tree species vectors illustrate that the most dominant species (red maple, gum, and sweetgum) covary with three community clusters in the NMDS. Specifically, vectors for gum, sweetgum, and red maple covaried with communities 1, 3, and 4, respectively. Community 2 was not readily differentiated using ordination analyses, suggesting this community may represent an intermediary between communities 1 and 4.

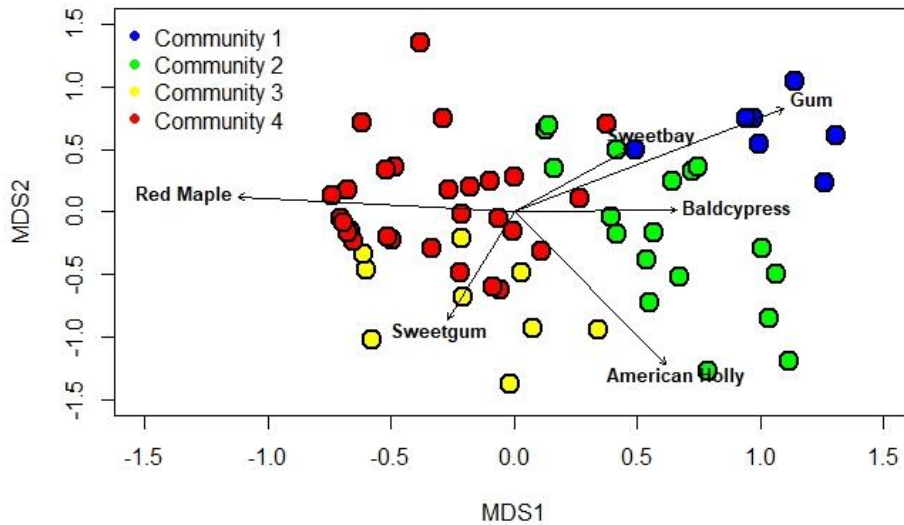


Figure 8. Two-dimensional representation of a three-dimensional NMDS ordination of tree abundance for 79 forest inventory plots at the Great Dismal Swamp. Forest inventory plots are colored by community type as determined by cluster analysis, indicator species analysis, and permMANOVA. Vectors of indicator species (sweetgum, American holly, baldcypress, sweetbay, gum) and the most abundant tree species (red maple) are overlaid to examine covariance in ordination space. The direction and length of vectors represents the strength of covariance in the ordination.

Following cluster analysis, distinct community types were named as distinguished by the NMDS analysis and further differentiated through differences in vegetation metrics. Specifically, we identified communities as G (gum; community 1), M-G (maple-gum; community 2), SG-M (sweetgum-maple, community 3), and M (maple, community 4). Analysis of tree IV across these communities supports this naming convention, showing significant differences in red maple IV, gum IV, and sweetgum IV across community types (Figure 9; Table 2). Further demonstrating red maple dominance, 54% (n=43) of plots clustered within the M community. The M-G community was the next most abundant community with 24% (n=19) of plots, with the SG-M and G communities consisting of 12% (n=9) and 10% (n=8) of plots, respectively.

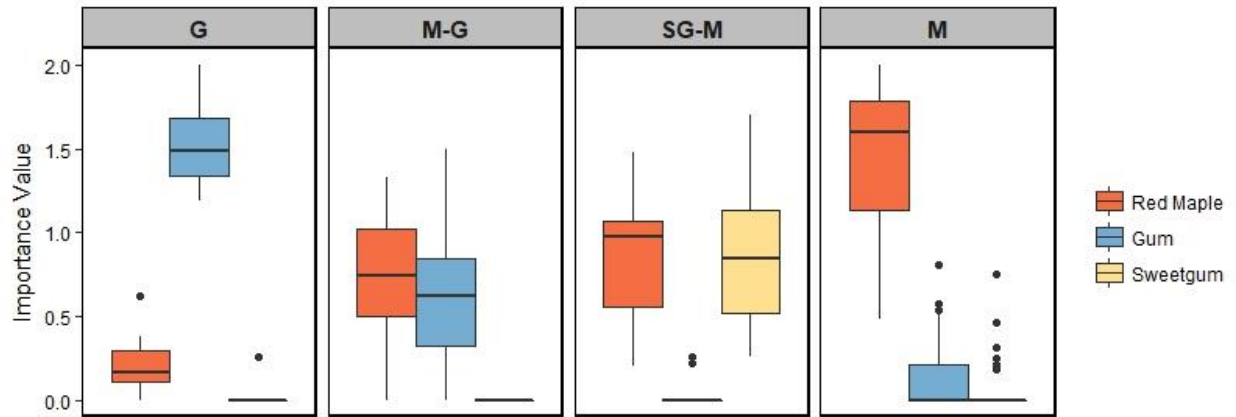


Figure 9. Importance values (IV) for dominant tree species across clustered community types at the Great Dismal Swamp ordered by increasing red maple IV. IVs range from 0-2 and represent species dominance within a community type; see Table 2 for results from statistical comparisons.

Table 2. Results of a Kruskal-Wallis test for significant differences in tree species importance values (IV) across communities. Pairwise comparisons conducted using a Mann-Whitney U test with p-adjustment. Communities with different letters were significantly different ($p < 0.05$) with respect to species IVs.

	G	M-G	SG-M	M
Red Maple IV	A	B	B	C
Gum IV	A	B	C	C
Sweetgum IV	A	A	B	A

Species rank-abundance curves were calculated to further illustrate community differences in tree composition (Figure 10). The dominance of red maple and gum in their respective communities decreased overall tree richness, as indicated by their steep relative abundance slopes and thus low evenness in tree composition.

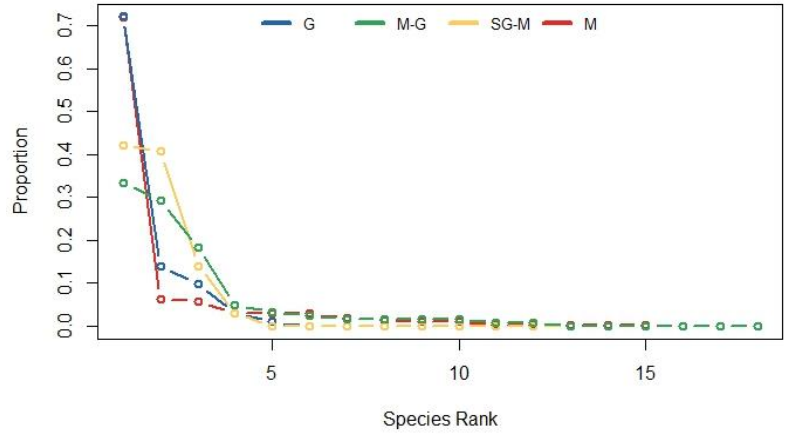


Figure 10. Community-level species rank-abundance curves. Within each distinct community (G, M-G, SG-M, M), identified species are ranked by their cumulative abundance and then plotted against their relative abundance. The slope of the rank-abundance curve represents species evenness within a community type with steeper slopes indicating low evenness in tree composition.

Comparisons of tree richness and diversity further demonstrated community differences. With the exception of G, increasing red maple IV across communities (in increasing order: M-G, SG-M, and M) lowers overstory richness (Figure 11a) and diversity (Figure 11b). Low richness in the G community, despite low red maple IV, suggests dominance of gum exhibits similar controls on tree composition as red maple. However, this contradicts plot-level correlations, which found increased gum IV associated with higher richness and diversity (Table 1).

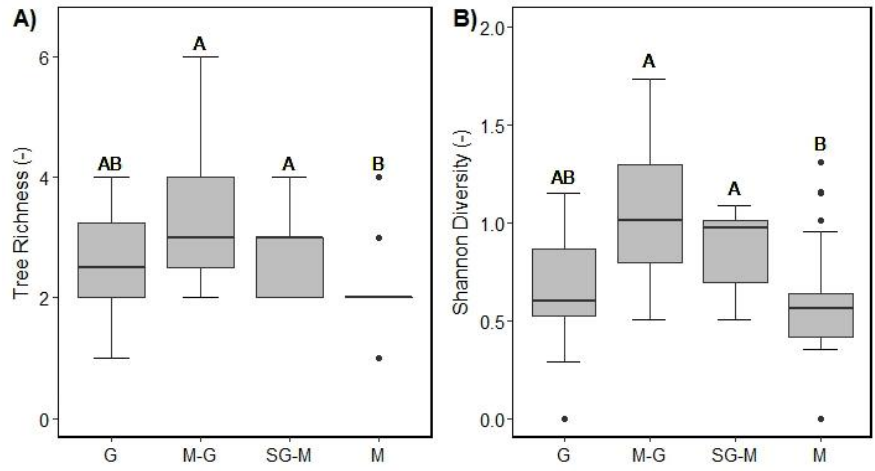


Figure 11. A) Mean tree richness across community types at the Great Dismal Swamp. B) Mean tree diversity (H) across community types using the Shannon index. Significant differences ($p < 0.05$) were determined through Kruskal-Wallis test with a pairwise Mann-Whitney U test and p-adjustment. Letters denote significant differences if found. Communities that share a letter were not significantly different.

Analysis of tree density and basal area demonstrated that communities also differ with respect to tree structure. Tree density significantly differed between community types ($p < 0.05$), with the highest densities within G community (Figure 12A). Additionally, a negative relationship between red maple density (red in Figure 12A) and total tree density was found, which comports with results of plot-level correlation analysis showing a negative correlation between these two attributes. However, mean basal area was not significantly different across community types, suggesting that a greater number of smaller trees exists where gum dominates tree composition (Figure 12B).

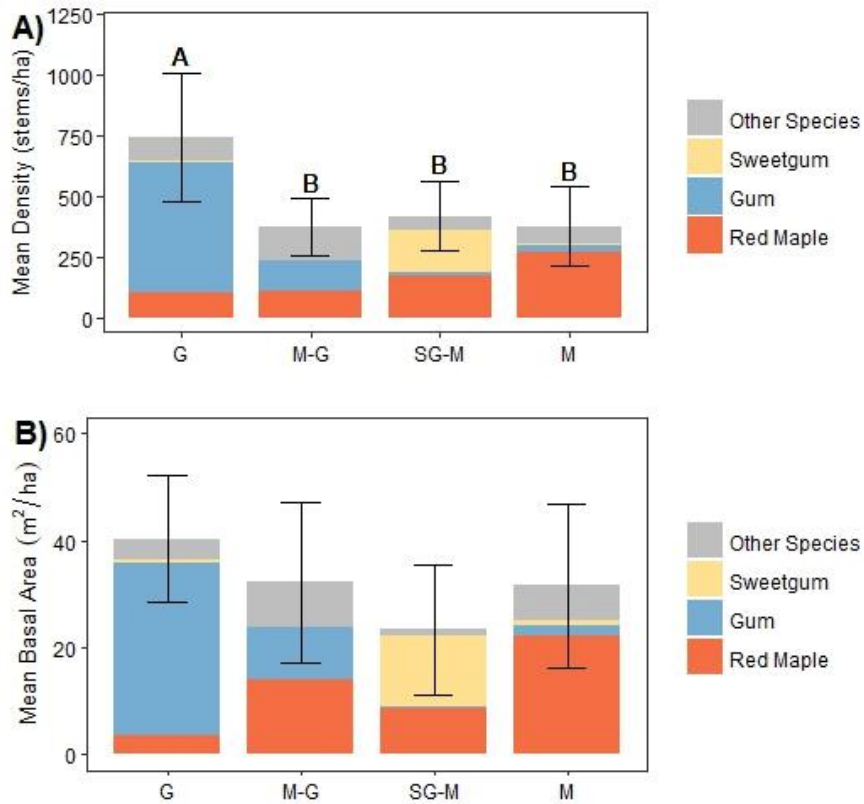


Figure 12. A) Mean tree density (cumulative and by species) across communities. B) Mean tree basal area (cumulative and by species) across communities. Significant differences ($p < 0.05$) were determined through Kruskal-Wallis test with a pairwise Mann-Whitney U test and p-adjustment. Letters denote significant differences if found. Communities that share a letter were not significantly different.

Despite the importance of red maple, gum, and sweetgum abundance in driving community differentiation, other tree species were observed (i.e., “Other Species” in Figures 12). American holly IV was significantly greater in the M-G and SG-M communities as compared to the M community (Table 3). In contrast, sweetbay was more dominant (although not

significantly as IV) in the G community. Notably, other species often associated with the GDS (e.g., baldcypress, Atlantic white cedar, and pond pine) were rarely observed. Lastly, despite confusion regarding the identification of gum species (blackgum and swamp tupelo), differentiation between the species was possible with the overwhelming majority (93%) of species identified as swamp tupelo.

Variation among communities in tree composition was not associated with community variation in other growth forms (shrubs, herbaceous, regeneration), with some notable exceptions (Table 3). For example, community differences in sweet pepperbush cover approached significance ($p=0.054$), with the SG-M having lower percent cover than all other communities. A similar trend was seen in muscadine cover, with the M and M-G having higher cover. In the herbaceous growth form, Virginia chain fern abundance was significantly higher in the SG-M community. Further, mean herbaceous cover was highest in the SG-M community, largely driven by the abundance of giant cane. Of note, tree dominance of red maple and sweetgum was not reflected in their regeneration, which was similar across all communities. However, swamp tupelo regeneration density was significantly higher in the G community. Last, red bay was the dominant regeneration species across all communities, which was in contrast to much lower presence in the tree strata.

Table 3 (below). List of observed species at the Great Dismal Swamp. Species are organized by their growth forms and ordered by prevalence in a wetland environment as indicated by the Atlantic and Gulf Coastal Plain (AGCP) Regional Wetland Plant List Classification: (OBL) obligate wetland, (FACW) facultative wetland, (FAC) facultative, (FACU) facultative upland, and upland (UPL). Bolded values denote significant differences ($p<0.05$) in community composition as determined through a global Kruskal-Wallis test. Superscripts denote pairwise differences following Mann-Whitney U test and p-adjustment. Communities which share a letter were not significantly different from each other.

			Community			
<i>Tree</i>			G	M-G	SG-M	M
Common Name	Scientific Name	AGCP	Importance Value (SD)			
Atlantic W. Cedar	<i>Chamaecyparis thyoides</i>	OBL	0.00	0.08 (0.25)	0.00	0.01 (0.08)
Baldcypress	<i>Taxodium distichum</i>	OBL	0.07 (0.14)	0.07 (0.26)	0.00	0.01 (0.04)
Gum	–	–	1.54^A (0.29)	0.57^B (0.42)	0.05^C (0.11)	0.12^C (0.21)
Blackgum	<i>Nyssa sylvatica</i>	FAC	0.25 (0.71)	0.09 (0.28)	0.02 (0.07)	0.01 (0.05)
Swamp tupelo	<i>Nyssa sylvatica</i> var. <i>biflora</i>	OBL	1.28^A (0.57)	0.48^B (0.44)	0.03^C (0.08)	0.11^C (0.21)
Water tupelo	<i>Nyssa aquatica</i>	OBL	0.00	0.02 (0.10)	0.00	0.09 (0.32)
Pond pine	<i>Pinus serotina</i>	FACW	0.00	0.03 (0.13)	0.00	0.08 (0.30)
Redbay	<i>Persea borbonia</i>	FACW	0.00	0.06 (0.12)	0.00	0.02 (0.06)
Sweetbay	<i>Magnolia virginiana</i>	FACW	0.13 (0.20)	0.02 (0.08)	0.00	0.05 (0.17)
American Holly	<i>Ilex opaca</i>	FAC	0.00^{AB}	0.26^A (0.40)	0.19^A (0.22)	0.02^B (0.08)
Red Maple	<i>Acer rubrum</i>	FAC	0.22^A (0.20)	0.73^B (0.37)	0.86^B (0.44)	1.47^C (0.45)
Sweetgum	<i>Liquidambar styracifula</i>	FAC	0.03^A (0.09)	0.00^A	0.89^B (0.50)	0.05^A (0.15)
Shrubs						
Common Name	Scientific Name	AGCP	Percent Cover (SD)			
Sweet Pepperbush	<i>Clethra alnifolia</i>	FACW	21.88 (27.12)	30.05 (27.16)	3.89 (5.46)	28.21 (27.79)
Inkberry	<i>Ilex glabra</i>	FACW	1.0 (2.83)	0.79 (1.87)	0.00	1.47 (5.16)
Shinyleaf	<i>Lyonia lucida</i>	FACW	3.75 (10.61)	0.53 (2.29)	1.11 (3.33)	1.47 (5.27)
Laurel Greenbrier	<i>Smilax lauiifolia</i>	FACW	0.75 (1.39)	4.11 (6.21)	2.22 (5.07)	2.56 (9.54)
High. Blueberry	<i>Vaccinium corymbosum</i>	FACW	8.00 (6.95)	6.32 (10.91)	13.33 (18.87)	8.02 (10.94)
Virginia Creeper	<i>Parthenocissus quinquefolia</i>	FACU	0.63 (1.77)	0.95 (1.93)	0.00	0.33 (1.21)
Poison Ivy	<i>Toxicodendron radicans</i>	FAC	3.75 (5.18)	1.95 (3.57)	7.22 (12.28)	7.77 (11.89)
Cat Greenbrier	<i>Smilax glauca</i>	FAC	1.25 (3.54)	2.37 (5.86)	6.67 (14.79)	3.49 (7.36)
Horsebrier	<i>Smilax rotundifolia</i>	FAC	2.75 (4.37)	6.37 (9.67)	3.89 (8.21)	8.53 (15.00)
Muscadine	<i>Vitis rotundifolia</i>	FAC	1.63 (3.11)	14.00 (22.44)	5.56 (8.82)	11.16 (18.35)
Total Cover	–	–	35.38 (26.40)	50.87 (29.21)	31.67 (17.14)	47.70 (29.23)
Herbaceous						
Common Name	Scientific Name	AGCP	Percent Cover (SD)			
Lizard Tail	<i>Saururus cernuus</i>	OBL	0.00	0.42 (1.84)	0.00	1.51 (4.44)
Marsh Fern	<i>Thelypteris palustris</i>	OBL	1 (1.93)	1.21 (3.59)	0.00	0.23 (1.52)
Netted Chain Fern	<i>Woodwardia areolata</i>	OBL	1.38 (2.88)	0.84 (2.52)	1.67 (3.54)	2.1 (6.39)
VA Chain Fern	<i>Woodwardia virginica</i>	OBL	0.00^{AB}	0.47^{AB} (1.12)	5.33^A (6.95)	1.00^B (4.13)
Giant Cane	<i>Arundinaria gigantea</i>	FACW	9.25 (11.56)	3.32 (6.58)	16.44 (23.85)	8.49 (19.04)
New York Fern	<i>Thelypteris noveboracensis</i>	FAC	0.00	0.52 (1.26)	3.89 (11.67)	0.12 (0.76)
Sedge spp.	<i>Carex</i> spp.	–	0.63 (1.77)	3.16 (13.76)	0.89 (2.67)	0.53 (1.52)
Total Cover	–	–	11.00 (10.66)	10.47 (24.23)	29.22 (35.78)	16.26 (26.76)
Regeneration						
Common Name	Scientific Name	AGCP	Mean Frequency (SD)			
Swamp Tupelo	<i>Nyssa biflora</i>	OBL	1.38^A (1.60)	0.32^{AB} (1.00)	0.33^{AB} (1.00)	0.14^B (0.47)
Redbay	<i>Persea borbonia</i>	FACW	3.25 (4.50)	3.89 (5.15)	4.11 (7.47)	4.40 (6.81)
Sweetgum	<i>Liquidambar styracifula</i>	FAC	0.63 (1.77)	0.32 (1.38)	0.67 (2.00)	0.81 (2.57)
Red Maple	<i>Acer rubrum</i>	FAC	2.50 (3.33)	0.84 (1.50)	2.00 (2.29)	1.23 (2.55)
Pawpaw	<i>Asimina triloba</i>	FAC	0.88 (2.48)	0.47 (1.22)	0.11 (0.33)	1.33 (3.29)
American holly	<i>Ilex opaca</i>	FAC	0.75 (1.34)	0.95 (1.72)	0.55 (1.33)	0.23 (0.72)

3.2 Drivers of Vegetation Composition across the GDS

To understand drivers of community variation (albeit it rather limited), plot-level metrics describing hydrologic regime and soil properties were calculated. Variation in these metrics were investigated at both plot and clustered community levels and then used as predictors for calculated metrics of vegetation structure and composition.

3.2.1 Plot-Level Analysis of Abiotic Drivers

From hydrologic model outputs, mean springtime water levels were estimated at surveyed locations (Figure 13). Under the base-wetness hydrologic scenario, predicted plot water levels were drier than the distribution of predictions across the entire GDS domain, with a mean water level of -0.26 m ($\pm 0.45\text{ m}$) (i.e., 0.26 m below ground surface) across our plots compared to the GDS-wide mean of -0.01 m ($\pm 0.43\text{ m}$) (Figure 13).

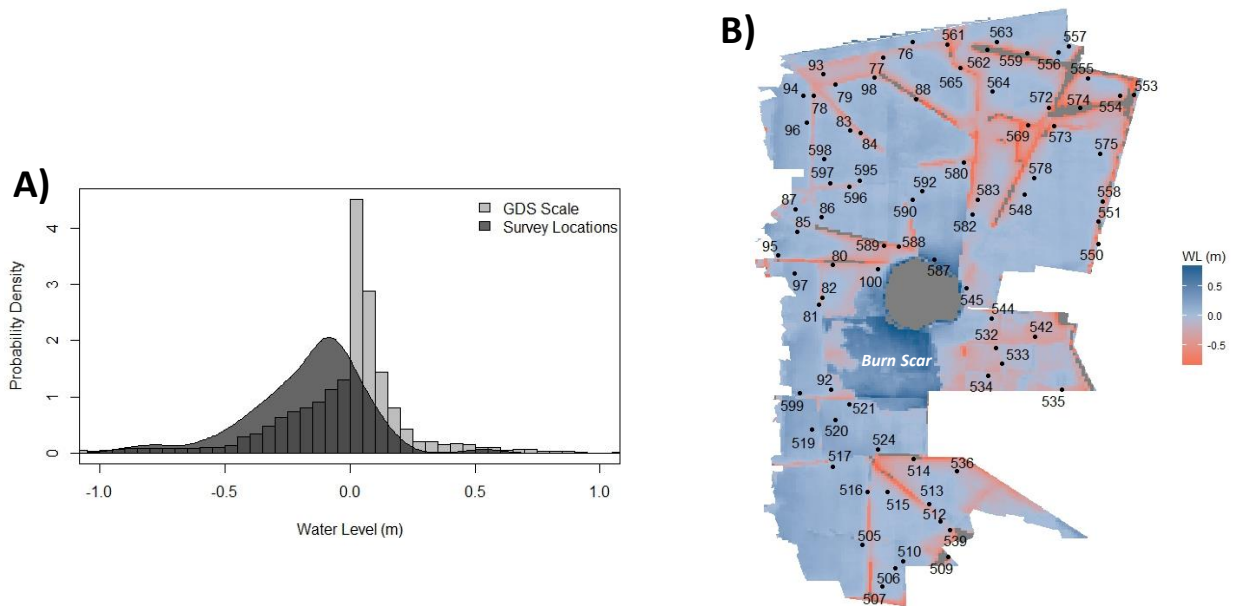


Figure 13. A) Probability density distributions of simulated (base case scenario) mean springtime water levels for both surveyed plots and across the Great Dismal Swamp via a steady-state MODFLOW-NWT hydrology model. B) Spatial representation of mean springtime water level predictions across the Great Dismal Swamp in the baseline hydrologic scenario. Inventoried plot locations ($n=79$) are marked and labeled.

A range of modeled raster peat depths were also captured at surveyed locations (Figure 14). Modeled plot-level peat depths had a mean of 1.15 m (± 0.66) and followed the distribution across GDS (mean depth of 1.22 m ± 0.63).

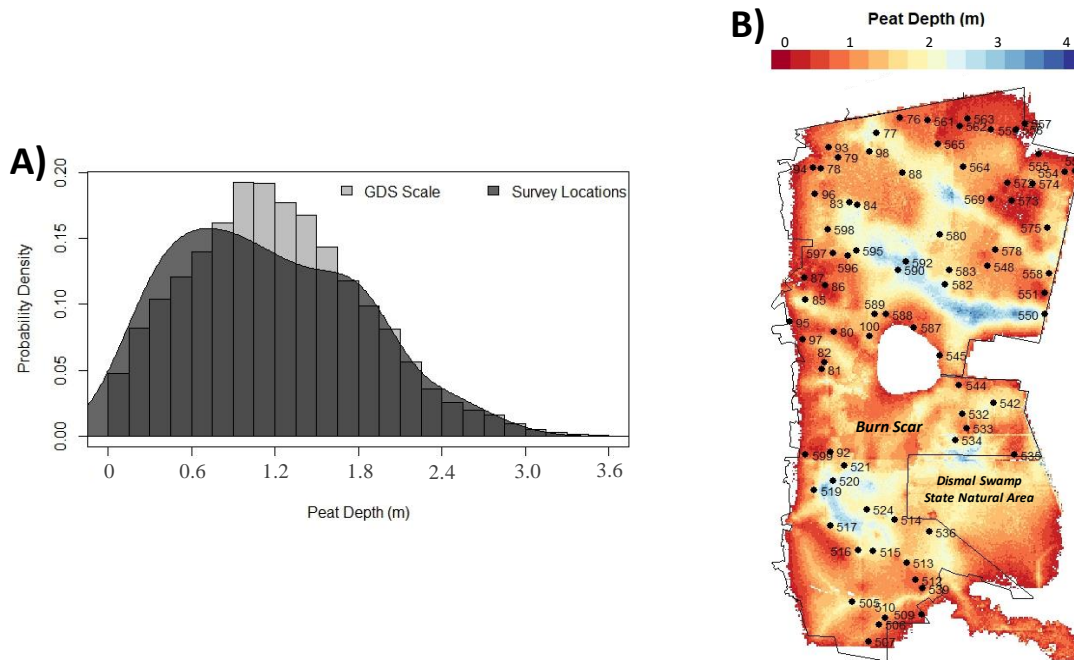


Figure 14. A) Probability density distributions of peat depths at both surveyed plots and across the Great Dismal Swamp via from a raster dataset developed by the USGS. B) Raster representation of peat depth variation across the Great Dismal Swamp. Invented plot locations (n=79) are marked and labeled.

We also assessed variation in measured soil characteristics across plot locations (Figure 15). Bulk density and organic matter fraction values followed non-normal distributions with right and left skews, respectively (Figure 15 A, B). Low bulk density values were similar to expected values in wetland soils with a mean of $0.23 \text{ (g/cm}^3\text{)} (\pm 0.19)$. Concordantly, organic matter fraction was high (mean = 0.75 ± 0.27) across most plots (Figure 15B). However, organic matter fraction exhibited a bi-modal distribution with peaks at higher and lower fractions, suggesting that surveyed plots occurred on both mineral and organic soils. C/N ratios and measured peat depths exhibited normal distributions (Figure 15 C & D). The distribution of field measured peat depths were similar to that of modeled depths (Figure 14); however, measured values had a higher mean ($1.68 \text{ m} \pm 0.76$).

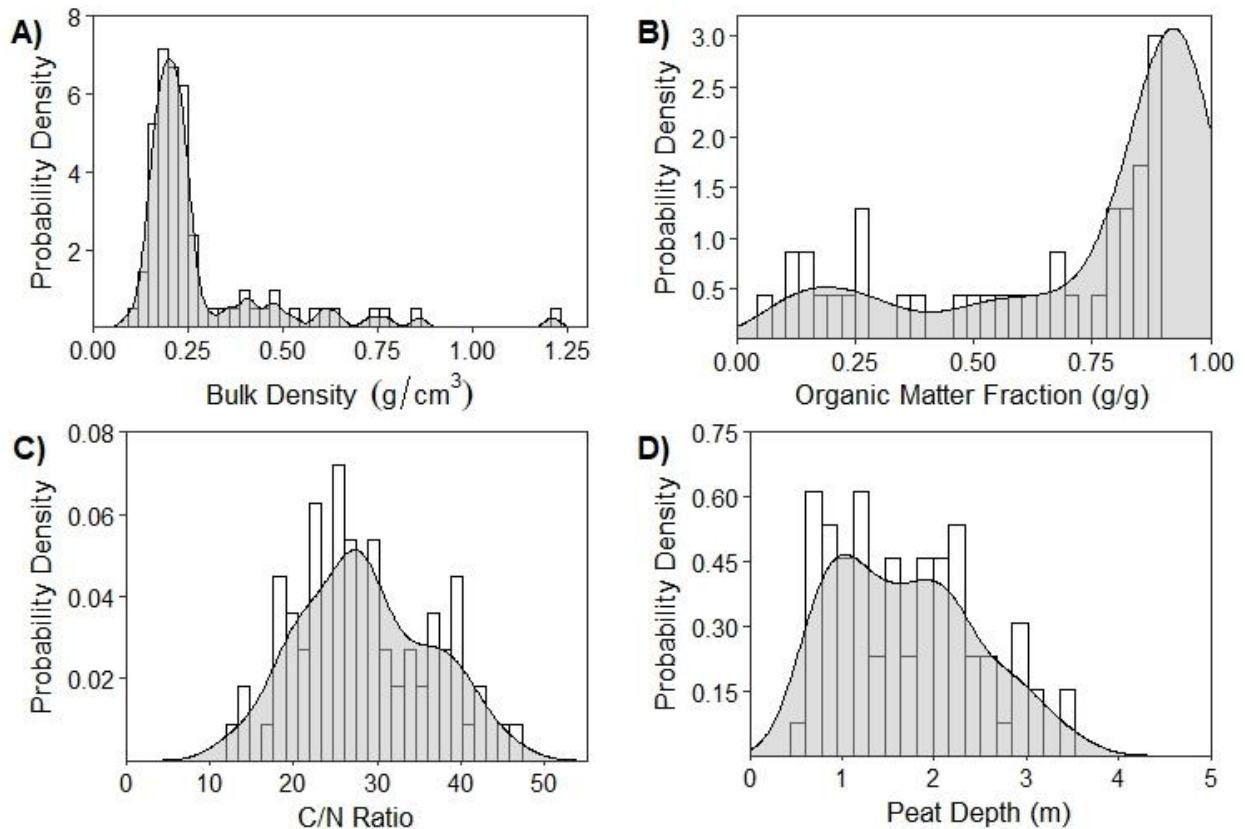


Figure 15. Probability density distributions of collected soil properties across 79 forest inventory plots at the Great Dismal Swamp. Metrics include: A) bulk density; B) organic matter fraction; C) C/N ratio; and D) measured peat depth.

We next assessed relationships among abiotic metrics via Spearman's correlation analysis (Tables 4 and 5). No significant associations were found between modeled water level predictions and measured high-water marks (data not reported). Further, these water level indicators were poor predictors of measured soil characteristics (Table 4). Negative correlations found between water level indicators and specific soil hydrologic indicators (OM fraction, C:N ratio, and % C) contradict expected relationships in a wetland environment. Moreover, water level indicators were not associated with bulk density or peat depths. However, modeled water level predictions were strongly correlated with plot distance to ditch, an input parameter in the model structure.

Table 4. Spearman’s correlation matrix of hydrologic metrics vs. soil properties. Hydrologic metrics include simulated mean springtime water levels across three hydrologic scenarios (base case; WL base, wet season; WL Wet, & dry season; WL Dry) obtained via a steady-state MODFLOW-NWT model developed by the USGS, and field-collected high water mark indicators (HWM). Bold values are significant at p-values <0.05.

	WL Base	WL Wet	WL Dry	HWM
Bulk Density	-0.01	-0.17	-0.01	0.04
Organic Matter Fraction	-0.05	0.08	-0.03	-0.35
C/N Ratio	-0.29	-0.26	-0.3	-0.41
% Carbon	-0.06	0.05	-0.04	-0.42
% Nitrogen	0.28	0.33	0.24	0.24
Peat Depth (raster)	0.06	0.14	0.09	0.02
Peat Depth (meas)	0.09	0.18	0.06	-0.05
Distance to Ditch	0.6	0.37	0.59	0.11

In contrast, correlations between measured soil characteristics revealed expected relationships in a wetland environment (Table 5). A strong negative correlation was found between bulk density and organic matter fraction, C content, N content, C/N ratio, and peat depth values. Moreover, a positive correlation was found between organic matter fraction and measured and modeled peat depth values. These two peat depth estimates were positively correlated.

Table 5. Spearman’s correlation matrix of soil properties vs soil properties. Collected metrics include: bulk density (BD), organic matter fraction (OM), C/N ratio (C/N), percent Carbon content (%C), percent Nitrogen content (%N), and peat depths collected via raster data set (raster) and measured in the field (meas). Bold values are significant at p-values <0.05.

	BD	OM	C/N	% C	% N	Peat Depth (raster)	Peat Depth (meas)
Bulk Density (BD)	1	–	–	–	–	–	–
Organic Matter Fraction (OM)	-0.61	1	–	–	–	–	–
C/N Ratio (C/N)	-0.24	0.68	1	–	–	–	–
% Carbon (%C)	-0.57	0.96	0.73	1	–	–	–
% Nitrogen (%N)	-0.6	0.32	-0.2	0.29	1	–	–
Peat Depth (raster)	-0.53	0.42	0.16	0.32	0.32	1	–
Peat Depth (meas)	-0.42	0.62	0.28	0.58	0.48	0.57	1

Following correlations with abiotic metrics, plot-level relationships between abiotic and vegetation metrics were investigated. Water level predictions were poor indicators of vegetation attributes (Table 6), with only a weak negative correlation found between red maple IV and water level in the wet scenario. Analysis of soil hydrologic indicators resulted in stronger

correlations (Table 7). Bulk density was correlated with vegetation metrics across growth forms, with positive associations with sweetgum IV and herbaceous cover and negative correlations with gum IV and shrub cover. Opposite relationships were found between these same metrics and organic matter fraction (and carbon content), with the exception of sweetgum IV. N content was positively correlated with gum IV and shrub cover, and negatively correlated with sweetgum IV and herbaceous cover. Extracted and measured peat depth values exhibited similar relationships as expected following soil by soil correlations (Table 7).

Table 6. Spearman’s correlation matrix of water level indicators vs. vegetation metrics. Hydrologic metrics include simulated mean springtime water levels across three hydrologic scenarios (base case; WL base, wet season; WL Wet, & dry season; WL Dry) obtained via a steady-state MODFLOW-NWT model developed by the USGS, and field-collected high water mark indicators (HWM). Bold values are significant at p-values<0.05.

	WL Base	WL Wet	WL Dry	HWM
Red Maple IV	-0.23	-0.24	-0.2	-0.09
Gum IV	0.14	0.2	0.16	0.01
Sweetgum IV	-0.03	-0.13	-0.1	-0.06
Tree Basal Area	-0.12	-0.08	-0.15	-0.17
Tree Density	-0.02	0.01	-0.06	-0.13
Tree Richness	0.07	0.08	0.04	-0.12
Tree Diversity	0.05	0.03	0.01	-0.09
Shrub % Cover	-0.05	0.11	-0.08	-0.07
Herbaceous % Cover	0.09	-0.07	0.15	0.11
Regeneration Density	0.08	0.08	0.07	0.1
Regeneration Richness	0.1	0.08	0.09	0.11
Regeneration Diversity	0.19	0.17	0.17	0.12

Table 7. Spearman’s correlation matrix of soil properties vs. vegetation metrics. Collected metrics include: bulk density (BD), organic matter fraction (OM), C/N ratio (C/N), percent Carbon content (%C), percent Nitrogen content (%N), and peat depths collected via raster data set (raster) and measured in the field (meas). Bold values are significant at p-values<0.05.

	BD	OM	C/N	% C	% N	Peat Depth (raster)	Peat Depth (meas)
Red Maple IV	0.19	0.18	0.22	0.19	-0.08	-0.06	0.23
Gum IV	-0.37	0.06	-0.03	0.04	0.25	0.22	0.02
Sweetgum IV	0.49	-0.39	-0.18	-0.39	-0.37	-0.34	-0.42
Tree Basal Area	-0.13	-0.07	-0.03	-0.04	0.09	-0.01	-0.05
Tree Density	0.02	-0.15	-0.13	-0.17	-0.15	-0.06	-0.27
Tree Richness	-0.08	-0.05	-0.06	-0.07	-0.06	-0.14	-0.21
Tree Diversity	-0.1	-0.02	-0.01	-0.04	-0.05	-0.01	-0.12
Shrub % Cover	-0.32	0.41	0.21	0.37	0.27	0.23	0.32
Herbaceous % Cover	0.3	-0.57	-0.49	-0.57	-0.27	-0.3	-0.49
Regeneration Density	-0.14	0.05	-0.12	0.01	0.07	0.01	-0.01
Regeneration Richness	-0.16	-0.05	-0.25	-0.1	0.1	0.09	-0.03
Regeneration Diversity	-0.17	-0.07	-0.33	-0.13	0.17	0.11	-0.03

3.2.2 Community Analysis of Abiotic Drivers

Differences in abiotic metrics among clustered communities were also assessed. Similar to correlation analysis at the plot scale, modeled and measured water level indicators failed to differentiate community types (Figure 16), except that the M community exhibited the largest interquartile range across modeled scenarios (Figure 16A-C). Additionally, mean modeled water levels were near ground surface elevations across all communities and most model scenarios.

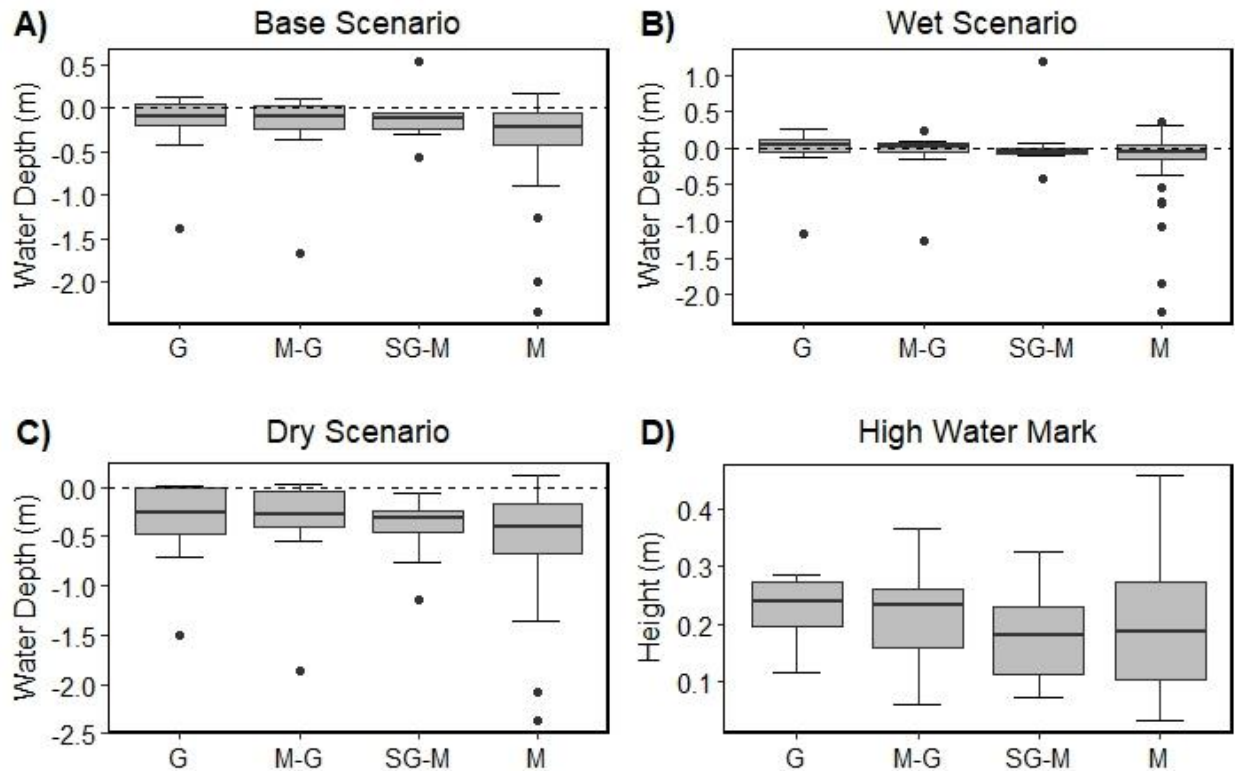


Figure 16. Water level indicators across communities at the Great Dismal Swamp. Panels A-C): represent modeled mean springtime water level as determined by a steady-state MODFLOW-NWT hydrology model. D) Field collected high-water mark indicators. No significant differences via Kruskal-Wallis tests were found.

In contrast to water level indicators, significant differences were found across community types with respect to measured soil characteristics (Figure 17). Bulk density was highest in the SG-M community and lowest in the G community, with M-G and M communities serving as intermediaries (Figure 17A). Differences in organic matter content approached significance ($p = 0.054$), with lower and more variable values in the SG-M community. Community variation in percent C content matched that of organic matter fraction, and no significant differences were found for C/N ratios (not shown). However, significant differences were found in percent N content, which was highest in the G community (Figure 17C). Measured peat depth also approached significance ($p=0.051$), where SG-M community had lower values (Figure 17D).

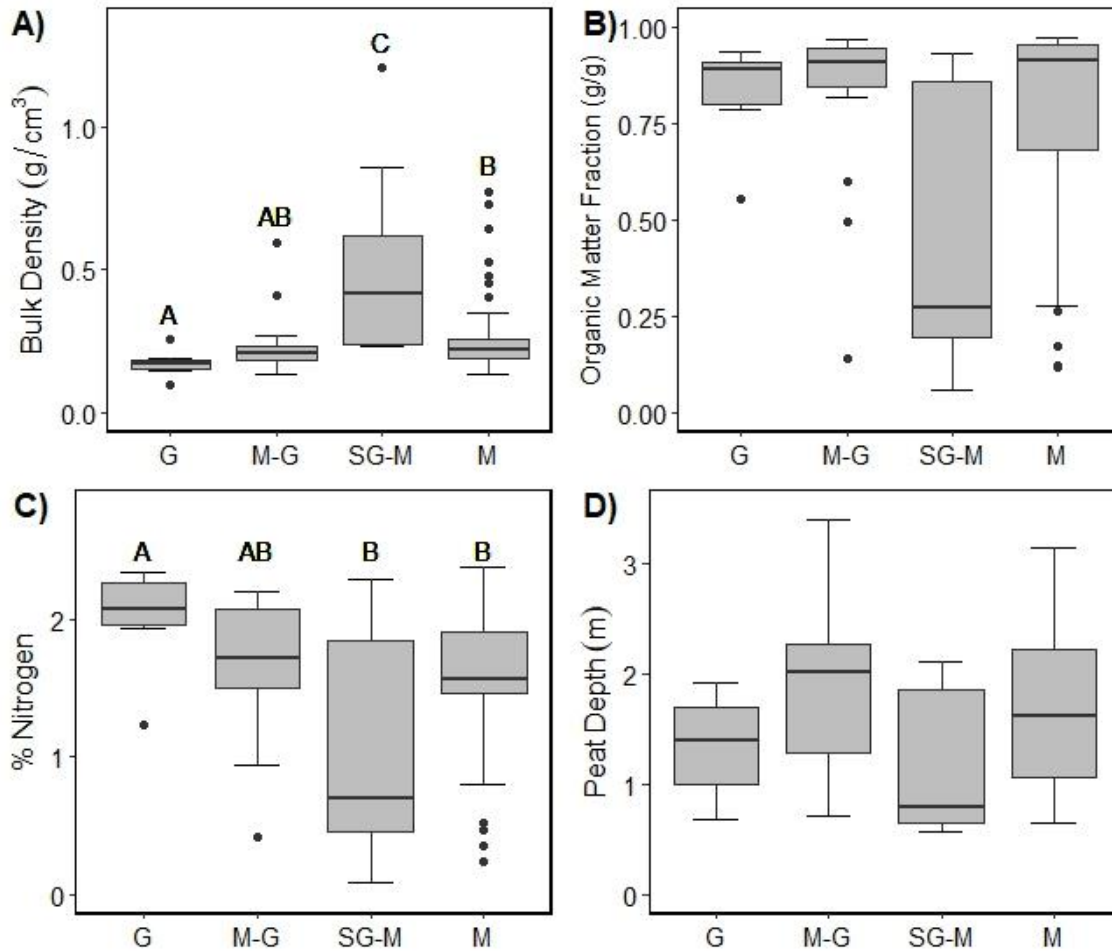


Figure 17. Measured soil properties across community types: A) bulk density; B) organic matter; fraction; C) percent nitrogen content; and D) field measured peat depth. Significant differences ($p < 0.05$) were determined through Kruskal-Wallis test with a pairwise Mann-Whitney U test and p-adjustment. Letters denote significant differences if found. Communities that share a letter were not significantly different.

4.0 DISCUSSION

The goal of this study was to inform long-term forest and hydrologic management strategies at the GDS through the following objectives:

1. Characterize swamp-wide variation in vegetation structure and composition.
2. Apply and compare methods for assessing hydrologic regime at large spatial scales.
3. Explore abiotic drivers of vegetation community variation.
4. Inform future GDS-wide management and monitoring to enhance ecosystem functions.

Through a GDS-wide survey across ca. 80 plots, we assessed ecosystem variation and sought to understand the drivers of vegetation structure and composition across GDS. Notably, our surveyed plots attempted to cover the full extent of GDS and were often located in remote areas rarely visited and even less studied. Our findings highlight that red maple dominates tree composition across GDS, which in turn reduces local and GDS-wide forest community variation. However, other communities exist, albeit to a much lesser extent, and we suggest that variability in community composition may be partially explained through differences in hydrologic regime. Community differences in soil properties support this conclusion but also point to future monitoring needs. As such, our findings have direct implications for future monitoring and management aimed at enhancing forest community composition at GDS.

4.1 Maple Dominance and Ecosystem Homogenization

Analysis of tree composition clearly demonstrated that red maple is the dominant species across GDS (Figure 4; inset). Red maple was identified at 97% of our plots and was the major basal area and density contributor at 54% and 52% of plots, respectively (Figure 4). Multiple studies investigating vegetation structure and composition at GDS have documented similar results (Dabel and Day, 1977, Carter et al., 1994, Schulte et al., in review). Our work extends this general conclusion across GDS, where pervasive red maple dominance severely limits spatial richness in tree species (Figure 18). That is, when sampling across the GDS, a survey of approximately 40 plots would have resulted in maximum site-scale richness. Understanding the drivers and consequences of such low spatial richness is critical to guide future management actions.

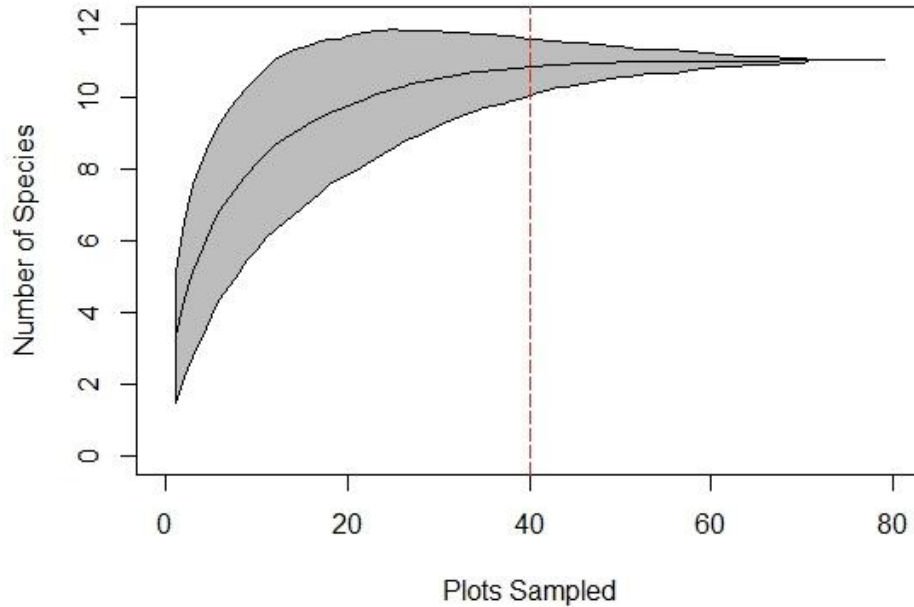


Figure 18. Species accumulation curve across 79 forest inventory plots at the Great Dismal Swamp. Shaded region represents 95% confidence interval of mean richness as determined by 1,000 permutations of random sampling with replacement.

From both plot-level and cluster analysis, it is clear that red maple dominance exerts strong controls on tree composition and structure. We found that increasing red maple IV decreases tree density; however, a similar influence on plot-level basal area was not found, suggesting lower maple dominance is associated with greater number of smaller trees, consistent with previous studies (Table 1; Schulte et al., in review). Red maple dominance also exhibits controls on tree composition, with significant reductions in both tree richness and diversity (Table 1). However, we did not observe marked influences of red maple dominance on other growth forms. Moreover, our sampling design precluded estimates of overall stand richness as abundance of all shrub and herbaceous species were not recorded. However, low stand richness in maple-dominated communities at GDS has been observed in smaller scale studies (Schulte et al., in review). Our work helps to further demonstrate potential influences of red maple on community composition across the full extent of GDS.

Wetland disturbances, such as ditching and clearcutting, can result in overall ecosystem homogenization through rapid expansion of generalist species (e.g., red maple) taking advantage of newly available resources and often drier conditions (Miller et al., 2015). The ability of red maple to outcompete other species within disturbed wetland environments has been attributed to its low resource requirements (Abrams, 1998), high post-disturbance seedling recruitment

window (Warren et al., 2004), and ability to adapt to a range of hydrologic regimes (Will et al. 1995). While forested wetland water levels often increase following clearcutting via reduced transpiration (i.e., watering-up; Dubé et al., 1995), subsequent ditching mitigates this effect particularly at sites in close proximity to drainage ditches (Marcotte et al., 2008). As a result, facultative wetland (as opposed to obligate) species such as red maple can increase in abundance following clearcutting in drained wetlands without post-disturbance management (Roy et al., 2000). Accordingly, historical logging and ditching at GDS are widely thought responsible for widespread red maple dominance and the reduced extent of other wetland communities (e.g., Atlantic white cedar, baldcypress, pond pine pocosin; Whitehead, 1972; Musselman, 1977; Levy, 1991).

Red maple dominance following disturbance can also occur in upland systems, further supporting its ability to respond and across a broad range of hydrologic conditions. For example, in forests surrounding the Great Lakes region, maple species (red and sugar) abundance has more than doubled at the expense of historic forested communities (i.e., hemlock, beech, birch, and pine) following post-colonization clearcutting (Schulte et al., 2007). Moreover, in forests throughout Ohio, anthropogenic disturbance has been found to exhibit stronger controls on ecosystem structure than natural processes (e.g., dispersal and competition) resulting in the spread of homogeneous communities of maple and oak dominated forests and a loss of spatial complexity (Deines et al., 2016).

Across ecosystem types, reduction in vegetation diversity can lead to a decrease in functional diversity, loss of important ecosystem services, and overall homogenization of ecosystem structure and processes (Clavel et al., 2011). For example, in northern Great Lakes coastal wetlands, species invasion of hybrid cattail (*Typha X glauca*) has decreased vegetation richness and altered soil carbon and nutrient cycling following both natural (e.g., flooding and ice flow) and anthropogenic (e.g., land clearing and drainage) disturbance (Frieswyk et al., 2007; Lishawa et al. 2010). Moreover, homogenization of herbaceous composition in wetland ecosystems can cascade to reduce taxonomic variation throughout higher trophic levels (e.g., macroinvertebrates; Loughheed et al., 2008). In upland forests, disturbances affecting seedling distribution and survival such as herbivory, forest fragmentation, and pollinator disruption can result in a decrease vegetation complexity and associated functions (Rooney et al., 2004). Critically, homogenization and the loss of structural and compositional diversity at varying

spatial scales can decrease ecosystem resilience to future disturbance (Foley et al., 2005). Mitigating the impacts of ecosystem homogenization is a challenge for land managers; however, a better understanding of the environmental drivers of heterogeneous communities can inform adaptive management strategies.

4.2 Forest Community Variation

Despite the dominance of red maple across the GDS, variation in forest structure and composition does occur. The results of the indicator species analysis revealed four distinct forest community types at the GDS driven by variation in red maple, gum, and sweetgum species dominance (Figure 9). Although distinct community types exist, over half (55%) of surveyed plots clustered within the maple (M) community with the remaining plots distributed within the maple-gum (M-G) (24%), sweetgum-maple (SG-M) (11%), and gum (G) (10%) communities. These community types are related, but not identical, to those found in previous studies at GDS. Our M-G community included plots with co-occurring red maple and gum species (largely swamp tupelo) and with higher richness compared to most other plots (Figure 11). This community type seems closely related to the maple-gum community described by Dabel and Day (1977). However, dominance of water tupelo in the aforementioned study suggests this community may be a wetter variant than that described here. Dabel and Day (1977) also describe a mixed hardwood community, which is similar to that of the SG-M community. Occurring on drier, mineral soils this community is described as having relatively high species richness, which is in line with our results (Figure 11). However, our M community has not previously been quantitatively delineated. Despite encompassing 55% of plots, literature reviewing GDS vegetation have only qualitatively described this community (Musselman, 1977; Levy, 1991). Existing as stands of almost purely red maple with low tree richness and diversity (Figure 11), this community most likely exists on a gradient of red maple abundance within the broader maple-gum community described by Dabel and Day (1977) and Sleeter et al., (2017). Similar conclusions can be drawn for the G community, which is a relatively pure stand of gum species (largely swamp tupelos) that has not been previously described. This community likely exists along a gradient of gum abundance in broader community classes provided by previous studies. Plots within the G community had significantly higher tree density (Figure 9) but low tree richness (Figure 12).

Notably, our study does not describe historical community types that existed in greater abundance at the GDS prior to anthropogenic disturbance. The cypress-gum community described by Dabel and Day (1977) and Sleeter et al. (2017) is estimated to cover only 12% of the GDS and was not identified in our study. Cypress IV was low across all communities, with higher values in the G and M-G communities (Table 3). Similarly, the Atlantic white cedar and pond pine pocosin communities previously described by Dabel and Day (1977) and Sleeter et al. (2017) were also not found. Interestingly, cedar and pond pine were only present within the maple dominated communities (M & M-G), supporting the conclusions of previous studies for red maple expansion in historical wetland communities (DeBerry and Atkinson, 2014; Sleeter et al., 2017).

Despite clear differences in tree composition, variation in composition of other growth forms (shrubs, herbaceous, and regeneration) was limited across our clustered community types. This lack of variation suggests limited influence of both environmental conditions and overstory composition and structure on other growth forms. Exceptions include Virginia chain fern (*Woodwardia virginica*), which was most abundant in the SG-M community, as well as sweet pepperbush (*Clethra alnifolia*), which approaches significance ($p=0.054$) and was least abundant in this same community (Table 3). For regeneration, swamp tupelo regeneration was significantly highest in the G community, suggesting it will persist in the future (Table 3). In contrast, red maple and sweetgum regeneration were more similar across community types (Figure 3), suggesting either potential stand conversion (Dabel and Day, 1977) or more likely that environmental conditions limit future growth (Vann and Megonigal, 2002).

An analysis of wetland indicator status of dominant tree species suggests hydrologic differences across our community types. Red maple and sweetgum are facultative wetland species, suggesting the M, M-G, and SG-M communities may exist on drier sites; yet, we again note common observations of red maple occurrence across wide hydrologic gradients (Carter et al., 1994; DeBerry and Atkinson, 2014). While our statistical analysis combined swamp tupelo (*Nyssa sylvatic* var. *biflora* (Walter) Sarg.) and blackgum (*Nyssa sylvatica* L.) as “gum”, we did attempt field differentiation and found that 93% were swamp tupelo. In previous work at the GDS, Dabel and Day (1977) characterized “blackgum” as swamp tupelo, whereas Sleeter et al. (2017) appropriately distinguishes between swamp tupelo and blackgum but never allows for coexistence within a community type. However, this distinction is important as these species

differ in their wetland indicator status, with swamp tupelo listed an obligate species and blackgum a facultative species. This suggests that the G community, and possibly to a lesser extent M-G, may occur at wetter sites. The lack of significant differences in other growth forms across communities limits further indication of possible hydrologic differences. Across all plots, we did not observe any obligate wetland shrub species; however, evident (although not significantly) lower sweet pepperbush in the SG-M community may further indicate that this community typically occurs on drier sites. However, a significant increase in abundance of the obligate species Virginia chain fern in the SG-M community seems to contradict this trend. However, all community types likely encompass sites with wetland hydrologic conditions, making interpretations of hydrologic differences via species wetland classes difficult (Carter et al., 1994) and highlighting the need for additional information to fully explore possible hydrologic controls on vegetation community composition.

4.3 Abiotic Drivers

In forested wetlands, hydrologic regime exerts primary controls on vegetation species composition, structure, and distribution (Duberstein and Kitchens, 2007, Burke et al., 2003). At the GDS, spatial variation in past hydrology selected for specific forested communities (e.g., cypress-gum at seasonally inundated sites, Atlantic white cedar at seasonally saturated sites, maple-gum at variable hydrologic regimes, and mixed hardwood at upland sites; Dabel and Day, 1977; Day, 1985; DeBerry and Atkinson, 2014). However, drier and more spatially homogenous hydrologic conditions have likely reduced variation in forested communities and possibly increased red maple dominance (Levy, 1991). Indeed, recent work at GDS has highlighted potential decreases in red maple abundance, and associated higher stand richness, with increased wetness (Schulte et al., in review). However, detection of hydrologic controls on vegetation composition is complexed by other environmental drivers (e.g., stand history, soil types), microtopographic variation, and the rate at which different species respond to hydrologic change (Russell and Beauchamp, 2017). Consequently, assessing hydrologic controls across the full array of GDS forest communities and environmental conditions requires linked observations of hydrologic regime and ecosystem response at the GDS scale. Resource constraints that limit in situ monitoring at high spatial resolutions and across large spatial extents present challenges to such investigations.

Various methods can be used to assess hydrologic regime at large spatial scales. For example, remotely sensed data can be used to evaluate inundated area and soil moisture in wetland environments, but are limited in temporal resolution (Kim et al., 2017). Process-based hydrologic models can simulate hydrologic regimes at varying time (from days to years) and spatial scales but are often limited by requisite input and calibration datasets (e.g., Evenson et al., 2016). Field based indicators, such as water-marks, are in situ indicators of seasonal high-water levels and are commonly used to determine wetland extent (Lichvar et al., 2012). However, they may fail to characterize variation in water level and soil moisture dynamics important in many wetland environments (Lichvar et al., 2012). Lastly, soil properties are often considered longer term integrators of hydrologic regime, with variable water levels altering biogeochemical processing and its influence on soil physical and chemical properties (Reddy and Patrick, 1975). The selection of an appropriate method for evaluating wetland hydrologic regime is largely determined by project goals and available resources. Here, we took advantage of multiple methods (water level estimates and soil hydrologic indicators) to assess hydrologic regime across our plots.

We estimated water level regimes in two ways. First, high-water mark indicators (i.e., water stains, adventitious roots, and lichen lines) were measured in multiple locations at each plot to estimate seasonal high-water levels (relative to ground surface). However, we observed little variation in these metrics across community types (Figure 16D), and no correlations were found with specific vegetation metrics (Table 6). Further, correlations with other hydrologic indicators were either not significant (with model outputs; data not shown) or contradictory (soil metrics) to what is expected in wetland environments (e.g., decreased bulk density with higher water levels; Drexler et al., 2017). However, water marks simply document maximum water levels, which may be transient, and fail to characterize the duration and variation of inundation and/or soil saturation (Carter et al., 1994). Temporary surface flooding depths have been suggested to be poor indicators of hydrologic controls at the GDS (Day et al., 1988), where, similar to other wetland systems, the duration of inundation or soil saturation can have stronger controls on species regeneration (Connor et al., 1986) and soil properties (Ehrenfeld, 1995).

We also estimated water level regimes using a steady-state hydrology model developed by the USGS. The model predicts mean springtime water levels at 500ft² pixels, but we refined model outputs to be relative to land elevations of our smaller plot domains. Overall, the model

failed to detect expected relationships between vegetation metrics and hydrology at both the plot and community levels. Correlation analysis revealed only one weakly significant negative trend between red maple IV and water level in the wet scenario (Table 6). Moreover, no significant differences were found between simulated mean water levels across community types (Figure 16). These results fail to support our hypothesis that a hydrologic gradient exists across community types and suggests water stress is ubiquitous at GDS (note similar mean water levels centered on ground surface in Figure 16). However, the poor predictive capacity of the model may be explained by specific model limitations. For example, the model fails to capture temporal variation in water levels and soil saturation, which can exert stronger influences on vegetation composition and soil processes (Day et al., 1988). Indeed, sites at GDS can have similar mean water levels but quite different temporal water level variation (Schulte et al., in prep). Moreover, the spatial distribution of water level predictions at both survey locations and across the entire GDS demonstrate very small ranges, making more nuanced differences and seasonal variation in water levels difficult to detect (Figure 13). Further, the spatial resolution of the original model (500ft²) is coarse as compared to plot area, microtopographic variation, and, importantly, the scale at which hydrologic controls may act. Last, water level predictions are acutely sensitive to the distance between survey locations and ditch structures (Table 4). However, we note that the model may sufficiently predict larger spatial variation in mean water levels, which indeed may be limited at GDS (see Figure 13), and thus serve as a useful tool to explore outcomes of future ditch management to increase both wetness and spatial heterogeneity in water level regimes.

Soil properties may be better indicators of more local and time-varying hydrologic regimes and thus their control on local ecosystem properties (Reddy and Patrick, 1975). Spatial and temporal variation in hydrology can lead to differences in decomposition rate, organic matter accumulation, and biogeochemical cycling with consequent effects to specific soil properties, including bulk density (Drexler et al., 2009), organic matter fraction (Drzymulska, 2016), and carbon to nitrogen ratios (Chambers et al., 2011). Compared to peat depth, which may be a better indicator of historical hydrology (i.e., ca. accumulation rates of 0.33 mm/yr at GDS; Whitehead, 1972), surface soil physical and chemical properties are more dynamic and likely more representative of contemporary hydrologic regime (Beylea and Baird, 2006). Plot-level correlations between specific soil properties comport with expected relationships in a wetland environment. For example, a negative relationship was found between bulk density and organic

matter fraction, C/N ratio and peat depth, while organic matter content was positively correlated with C content and peat depth (Table 5), supporting use of soil properties as predictors of hydrologic regime and resultant vegetation communities. However, correlations between soil properties and modeled hydrologic outputs failed to reveal expected trends, further highlighting possible limitations of the hydrologic model to represent the temporal and spatial hydrologic variation that influences local soil properties (Table 4).

Linkages between soil properties and our vegetation metrics highlight potential hydrologic controls on GDS forest communities. Variation in soil properties was limited, with plots mostly characterized by low bulk density, high organic matter soils consistent with other GDS studies (Drexler et al., 2017; Figure 15). However, a proportion of plots clearly represent more mineral-rich sites. This variation partially explained differences in vegetation communities. Bulk density was positively correlated with sweetgum IV and negatively correlated with gum IV (Table 7). This trend was also represented at the community level, where the G and SG-M communities had significantly lower and higher bulk densities than all other communities, respectively (Figure 17). Further, organic matter was lowest ($p=0.054$) for plots in in the SG-M community and, together with peat depths, had significant negative correlation with sweetgum IV. Taken together with differences in wetland species indicator status (Table 3), these soil differences suggest that SG-M communities may largely occur on drier sites whereas G occur on the wettest. Nitrogen content also had opposing associations with SG-M and G communities (and significantly with sweet gum and gum IVs), with lower values for SG-M and higher for G communities (Table 7, Figure 17). One possible explanation is provided by Reddy and Patrick (1975). In short, slow decomposition in wetter environments (e.g., G community) results in stable organic-N content, whereas regular aerobic-anaerobic cycles in drier wetland communities (SG-M community) drives coupled nitrogen mineralization and denitrification. Moreover, litter production in wetter communities at GDS is higher, which can result in higher N concentrations when compared to drier communities (Gomez and Day, 1982).

No correlation was found between red maple IV and soil metrics, and community analysis suggests M and M-G communities may be intermediaries with respect to both bulk density and nitrogen. As such, these communities may span a larger and more common hydrologic gradient at GDS, helping to explain their dominance. Relative probability distributions of bulk density (as an indicator of hydrologic regime) for each community type

illustrates this conclusion. Probability density in the G community peaks at low bulk densities, while SG-M community increases with increasing bulk density. The M and M-G communities are found at more intermediate bulk densities values, which dominate the frequency of our bulk density observations (bars in Figure 19). By using bulk density as an indicator of local hydrologic regime, we suggest that communities exist along a hydrologic gradient at GDS, but that limited spatial variation in hydrologic regimes favors M and M-G community types and reduces spatial distributions of other communities.

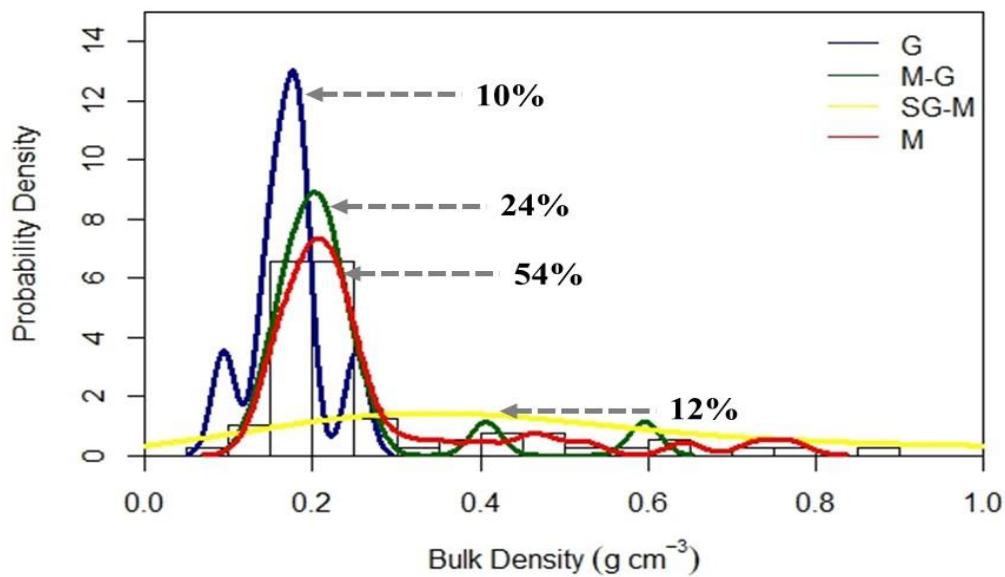


Figure 19. Probability density distribution for bulk density across community types. Colored lines represent the distribution of plots within each community type along the gradient of observed bulk density values (bars). Proportion of all plots in each community type is denoted.

Our conclusion regarding hydrologic controls on community variation assumes that surface soil properties reflect contemporary hydrologic regimes. Local factors such as surface water drainage patterns, site history, and tree litter quality can also influence organic matter decomposition and associated soil properties (Megonigal and Day, 1988). Moreover, historical hydrologic regimes largely determined today's spatial distribution of peat deposits (Whitehead, 1972), and the location of survey plots on versus off these historical peat deposits may introduce additional variation in soil properties. The GDS is not uniformly covered by peat (Figure 14B), and according to the NRCS Web Soil Survey, 14 of our surveyed plots exist on mineral soils.

Figure 20 supports this classification, where plots occurring off peat deposits have significantly lower organic matter fractions and modeled peat depths. However, these 14 plots could experience similar water level regimes as sites on historical peat deposits despite observed differences in soil properties. Previous work at GDS observed such a possibility, where some mineral soils sites (with high bulk density and low organic matter fractions) experienced relatively wet regimes (Gile 2017, unpublished data). Such wet but mineral-rich soil sites could support our suggested wet communities and confound linkages between soil metrics and vegetation measures. Indeed, two of our hypothesized wet (G) community plots existed on mineral soils. However, removal of all mineral soil plots (and thus examination of only on-peat deposit plots) did not significantly change correlations between bulk density and vegetation metrics. Moreover, more than half of the plots on mineral soils were represented by maple-dominated communities (M and M-G), comporting with the conclusion that red maple inhabits a range of conditions. The remaining four plots were represented by proposed dry communities (SG-M), which is consistent with the results of Dabel and Day (1977).

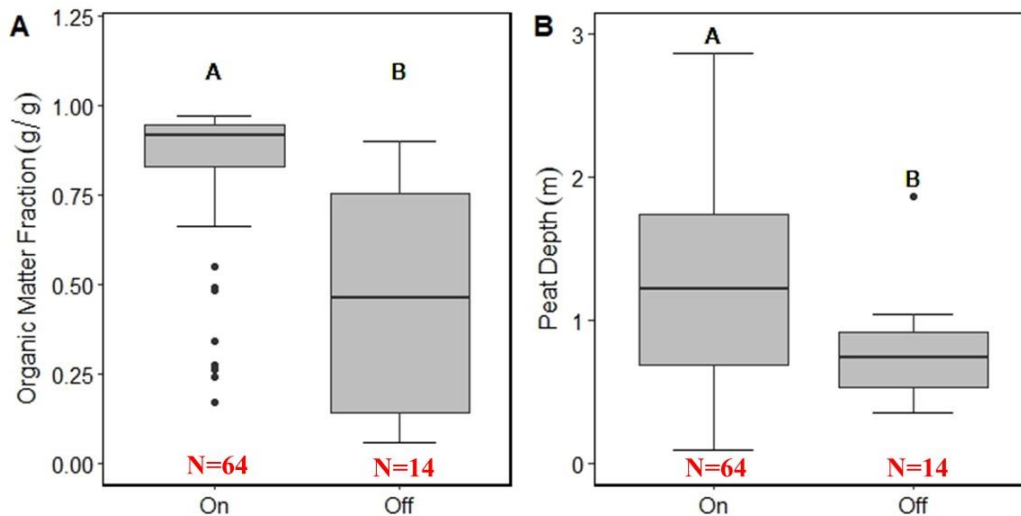


Figure 20. Comparison of soil properties for plots located on and off peat deposits (as determined by NRCS Web Soil Survey): A) organic matter fraction and B) peat depths extracted from raster dataset. Significant differences were determined via Kruskal-Wallis test. Pairwise comparisons conducted using a Mann-Whitney U test with p-adjustment. Communities with different letters were significantly different from each other.

Lastly, differences in soil physical properties exert reciprocal influences on hydrologic conditions. Soils with different moisture holding capacities but equivalent water table depths (water tensions) can experience different soil moistures (Verry et al., 2011), associated redox

potentials (Reddy and DeLaune, 2008), and thus influences on vegetation composition and soil properties. Moisture holding capacity varies with soil properties, particularly bulk density, where increased bulk density decreases moisture holding capacity (Boelter, 1968; Verry et al., 2011). As such, increased bulk density in mineral soils may decrease soil saturation (and thus anaerobic stress) for equivalent water table fluctuations as compared to organic-rich soils. This soil-hydrology interaction may select for different species and suggests more work is needed to understand effects of soil type and associated hydraulic properties at GDS.

4.4 Monitoring and Management Implication

Our fourth objective was to inform future management and monitoring at GDS, particularly recent efforts to initiate long-term monitoring plots using new protocols. The results of this work suggest that hydrologic regime may drive community composition and structure at GDS. However, improved characterization of both hydrologic conditions (e.g., temporal variability and soil moisture regimes) and other potential drivers is needed to inform long-term management aimed at enhancing community variation. While soil properties proved to be the best metric for assessing hydrologic regime in this study, they remain a proxy for in-situ water level (and soil moisture) measurements and may be somewhat confounded by historical variation in peat accumulation. Moreover, additional drivers of ecosystem structure exist such as fire regime, disturbance history, soil hydraulic properties, and microtopography (Dabel and Day, 1977; Levy, 1991; Carter et al., 1994; Sleeter et al., 2017). While we addressed some of these drivers using metrics such as distance to ditch, qualitative (and rather coarse) estimates of clearcut area, and plot-level variation in peat depth, these were poor predictors of our vegetation metrics (not reported). More detailed data for disturbance histories (e.g., fire, logging, and hurricanes), prescribed management actions, stand age, and past hydrologic change is needed to couple with long-term monitoring to help inform and monitor future management actions.

Appropriate selection of long-term monitoring plots is critical to assess drivers of ecosystem structure and effects of specific management actions. Through the investigation of swamp-wide variation in forest structure and composition, our study provides four distinct community types that merit further investigation. However, biotic and abiotic variation exists both across and within these community types. For example, in maple dominated (M) communities, variation in understory composition (note standard deviations in Table 3) and soil properties (Figure 17) exist, which may be used for finer community differentiation and

association with more specific hydrologic regimes. Therefore, selection of long-term monitoring plots should represent the major community types present but also the within-community gradients in biotic and abiotic variables to further document variability and drivers of vegetation communities.

Long-term monitoring protocols should include a suite of abiotic and biotic measurements to assess current ecosystem variation and potential response to hydrologic restoration and other management actions (e.g., prescribed fire, planting). First, high frequency, in situ monitoring of plot-level water levels is critical to characterize baseline and post-restoration hydrologic regimes. Moreover, hydrologic monitoring efforts should also account for interactions between soil properties and water levels that drive important soil moisture regimes. Moisture release curves can be developed for soil samples at each plot to predict soil moistures as a function of water level variation. Alternatively, direct monitoring of in situ soil moisture regimes could be conducted. With either option, accounting for soil moisture regimes (and possibly resultant redox conditions) could better characterize hydrologic controls on vegetation composition and soil processes. Further, soil moisture is the dominant driver of smoldering fire vulnerability (Reardon et al., 2007), further justifying including soil moisture monitoring at long-term plots. Additionally, soil sampling should explore variability in soil physical and chemical properties with depth, and how such profiles may indicate both contemporary and historical hydrologic regimes. Drexler et al. (2017) concluded that bulk density and C content decreases with depth as a function of drainage-induced subsidence at GDS. Future studies could conduct similar assessments and well as investigate site and depth variation in other parameters (organic matter lability, C/N ratio, N isotopes, pollen records) that may help to describe chronologies of hydrologic regimes and vegetation communities. As hydrologic restoration shifts the degree of soil saturation, a long-term record of peat accumulation will also be needed. Although this response is expected to be slow, surveyed sediment rods at monitoring plots can provide a record of soil accumulation. Moreover, soil variation in soil accumulation can impact plot-level microtopography, requiring topographic surveys along transects to assess local elevation variation at each plot. Alternatively, although costlier, repeated terrestrial based light detection and ranging surveys (TLS) could be conducted, representing a novel use of emerging technology (Stovall et al., 2017). Such information would also be valuable in explaining variation of and linkages among soil elevations and vegetation structure.

Lastly, metrics of plot-level abiotic conditions should be coupled with more quantitative assessments of vegetation communities across growth forms. For example, metrics of stand age can be collected via tree cores to better document disturbance histories. Additionally, replacing our ocular estimates of percent cover for understory and shrub species with stem counts would allow for clustering and richness calculations including all growth forms. Further, canopy conditions are likely to be the first structural component to respond to changes in hydrologic conditions (Morrissey et al., 1994), highlighting the potential utility of leaf area index (LAI) measurements over time. Ultimately, long-term monitoring should seek predictive relationships among hydrologic regimes, soil properties, and forest community characteristics, and in doing so, inform future management efforts across other GDS locations.

5.0 CONCLUSION

On-going hydrologic and forest management efforts at the GDS focus on restoring natural hydrologic regime to enhance forest community composition. As such, research is needed to better understand current variation in and drivers of forest structure and composition. In response, we surveyed ca. 80 forest monitoring plots throughout the GDS and explored linkages among forest composition, hydrologic indicators, and soil properties. Findings suggest hydrologic influences on forest communities and point to future monitoring needs.

Through our GDS-wide survey, we found a relatively homogenous forest composition. Red maple (*Acer rubrum* L.) is overwhelmingly the dominant tree species with implications for community composition and structure. Red maple importance value (IV) significantly decreased plot-level tree density, richness, and diversity (Table 1). Additionally, pervasive red maple dominance severely limits the spatial scale in tree richness across GDS (Figure 18). However, variation in tree community composition exists and is also largely driven by abundance of swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walter) Sarg.) and sweetgum (*Liquidambar styraciflua* L.) (Figure 5). Indeed, hierarchical cluster analysis revealed four distinct community types at the GDS. Our survey locations clustered in the following way: 54% represented in the Maple (M) community, 24% in the Maple-Gum (M-G), 12% in the Sweetgum-Maple (SG-M) community, and 10% in the Gum (G) community. These communities differed in their community composition and structure. For example, species dominance in the M and G communities decreased species evenness, richness, and diversity (Figures 10 & 11). Additionally, tree density was higher in the G community, but did not translate to greater basal area, suggesting a greater number of smaller trees exist where gum species dominate. Notably, variation in composition and structure was limited in other growth forms (shrubs, herbaceous, and regeneration). An analysis of wetland indicator statuses suggests that a hydrologic gradient exists between communities, with the G community existing on wetter sites and the SG-M community on drier locations.

To explore abiotic drivers of community variation, we assessed plot-level hydrologic regime in three ways: high-water mark indicators, modeled water levels, and soil physical and chemical properties. We found that high-water mark indicators and hydrologic modeling failed to explain variation in vegetation composition and structure (Table 6, Figure 16) or measured soil properties (Table 7). These metrics are limited by their spatial scale, as well as their ability

to represent dynamic temporal changes in water levels (and soil moisture regimes) that most likely drive community variation and soil processes. In contrast, soil properties were found to vary in predictable ways in a wetland environment (Table 5). Bulk density significantly differed between community types, with the lowest bulk density in the G community and highest in the SG-M community (Figure 17A). These soil differences indicate a potential hydrologic gradient among community types (Figure 19). Probability density in the G community peaked at low bulk densities, while the SG-M community increased with increasing bulk density. The M and M-G communities were found at more intermediate bulk densities values, which dominated the frequency of our bulk density observations (bars in Figure 19). Community differences in other soil properties (C content, organic matter fraction, N content, and peat depths) further support the general conclusion that communities exist along a hydrologic gradient at GDS. However, limited spatial variation in hydrologic regimes favors M and M-G community types, thereby reducing extents of other communities and overall spatial complexity in forest communities.

Our findings suggest that hydrologic regime drives community variation, but also highlights some future monitoring needs. In situ water level and soil moisture monitoring would better represent dynamic hydrologic conditions and attendant influences on forest communities and soil properties. The effect of soil type on soil-hydrology interactions also merits future investigation at the GDS. Further, soil property variation with depth may provide new insights into past linkages among hydrology, peat accumulation, and vegetation composition. Last, fine-scale elevation monitoring over time would document potential change in peat accumulation, as well as explore influences of microtopography on forest communities. Through findings and proposed future monitoring strategies, our work can be directly used to inform future forest monitoring and on-going management efforts at the GDS.

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