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Red maple dominance and community homogenization in a disturbed forested wetland

Raymond F. Ludwig · Daniel L. McLaughlin · Frederic C. Wurster

Abstract Homogenization of forest stands with generalist species is a hallmark of past disturbance and characterizes the Great Dismal Swamp (GDS), a forested wetland in the Atlantic Coastal Plain. Once a mosaic of wetland communities, disturbances (e.g., timber harvesting and ditching) have resulted in altered hydrologic regimes and forested communities. In response, hydrologic restoration and forest management aim to enhance community composition and function. To inform these efforts, we investigated forest communities and their associations with hydrologic regimes at 79 monitoring plots across GDS, where we collected data on vegetation composition and structure, hydrologic indicators, and soil properties. Our results demonstrate that red maple (*Acer rubrum*) is the dominant species across GDS, where red maple importance is negatively correlated with stand density, richness, and diversity. A hierarchical cluster analysis revealed four distinct community types: Swamp Tupelo-Maple (ST-M), Maple-Holly (M-H), Sweetgum-Maple (SG-M), and Maple (M). Despite ubiquitous presence of red maple in these communities, significant differences in tree composition and structure were found; however, this variation rarely extended to other growth forms. Although water level estimates (via model simulations and high-water marks) failed to explain vegetation differences, soil properties indicative of wetness regimes suggest that communities exist along a hydrologic gradient. The ST-M community likely exists on wetter sites, whereas SG-M communities occur at drier locations. More maple-dominated communities (M and M-H; 68% of plots) likely occur across broader hydrologic gradients, explaining their widespread occurrence. These findings point to potential drivers of forested communities, but additional characterization of hydrology coupled with continued vegetation monitoring are needed to adaptively conduct hydrologic restoration efforts.

Keywords Hydrologic restoration · Red maple · Cluster analysis · Soil indicators

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Introduction

Described as a "most dreadful swamp [that] was ever judged impassable", Colonel William Byrd first proposed detailed plans to drain the Great Dismal

Swamp to the King of England in 1730 (Dean 1969). For the next 200 years, anthropogenic disturbance continued through ditching and logging, with substantial changes to hydrologic regimes and vegetation composition. Such impacts motivated the establishment of the Great Dismal Swamp (GDS) National Wildlife Refuge in 1974 "for the primary purpose of protecting and preserving a unique and outstanding ecosystem." (US Fish and Wildlife Service 2006). In GDS and other degraded wetlands, vegetation management and restoration of pre-disturbance hydrologic conditions are considered the best strategies for achieving such goals (King and Keim 2019; Hanberry et al. 2012). To inform these efforts, spatially extensive monitoring is required to characterize forested wetland communities and potential drivers of their variability.

Prior to ditching and logging, the GDS encompassed more than 500,000 ha, extending from the Chesapeake Bay to the Albemarle Sound in the U.S. Atlantic Coastal Plain (Lichtler and Walker 1974). Historically, this temperate peatland was characterized by a mosaic of community types, including stands variously dominated by bald cypress (*Taxodium distichum* (L.) Rich.), swamp tupelo (*Nyssa biflora* Walt.), water tupelo (*Nyssa aquatica* L.), Atlantic white cedar (*Chamaecyparis thyoides* L.), and pond pine (*Pinus serotina* Michx.) pocosins (Dabel and Day 1977). This mosaic was largely driven by spatial differences in water level and fire regimes (Carter et al. 1994; Legrand 2000). However, anthropogenic disturbance (i.e., logging, ditching, and road construction) reduced the areal extent of GDS and subsequently altered hydrologic conditions and species composition of the remaining forest communities. Constructed roads and ditch spoil banks limited overland and groundwater exchange, while ditches rapidly drained water creating drier and more homogenous water level regimes (Eggleston et al. 2018). Together with logging, these conditions reduced the spatial heterogeneity of forest communities by replacing historical stands with communities largely dominated by red maple (*Acer rubrum* L.) (Phipps et al. 1979).

Despite the significant loss of areal coverage and stand diversity, GDS remains one of the most prominent forested wetlands in the U.S. Today, GDS covers a 43,000 ha area in southeastern Virginia and northwestern North Carolina (Fig. S1). Five contemporary forested community types have previously been described at GDS: mixed hardwood, Atlantic white cedar, cypress, pocosin, and maple-gum (Dabel and Day 1977; Sleeter et al. 2017). The mixed hardwood community is located in upland locations associated with remnant sand dunes and is dominated by oak species (*Quercus* spp. L.) and sweetgum (*Liquidambar styraciflua* L.) (Levy 1991). The Atlantic white cedar community once covered over 50,000 ha and was found on seasonally saturated soils (DeBerry and Atkinson 2014). However, natural (windfall, fire) and anthropogenic disturbances (hydrologic alteration and clearcutting) have reduced its current distribution to an estimated 1600 ha, or 3% of the GDS (Levy 1991; Sleeter et al. 2017). The bald cypress-dominated community is typically found at the wettest locations with seasonal inundation and poorly drained soils. Although historical maps and vegetation surveys show that this community once dominated across large areas, extensive cypress logging in the 1850s reduced its current distribution to only ca. 10% of GDS (Kearney and Gardner 1901; Sleeter et al. 2017). Pond pine (*Pinus serotina* Michx.) dominates the pocosin community, which is estimated to currently cover more than 15% of the GDS and occurs on seasonally saturated soils (Sleeter et al. 2017). 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), which is estimated to cover over 60% of the GDS area (Sleeter et al. 2017). This community includes stands dominated by red maple, with varying densities of blackgum (*Nyssa sylvatica* Marsh.) and/or swamp tupelo and is thought to exist on a range of soil types and hydrologic regimes (Sleeter et al. 2017). We critically note, however, that the above communities and their areal extents have largely been inferred from aerial photography with minimal ground surveys for verification of mapped communities.

Reduced spatial variability of vegetation communities can homogenize ecosystem structure and processes, leading to an overall loss in functional diversity (Clavel et al. 2011). As such, primary management goals at GDS focus on recovery of historical communities together with decreases in red maple dominance. To do so, hydrologic restoration efforts (i.e., "rewetting the swamp") are being

implemented through the repair and installation of water control structures within the existing ditch network (Wurster et al. 2016). Although vegetation composition has been studied at GDS (e.g., Dabel and Day 1977; Carter et al. 1994; Drexler et al. 2017), the role of hydrology in influencing forest composition and structure requires further investigation to inform such water level management efforts. For example, Schulte et al. (2019) found that wetter sites were associated with greater stand richness and lower red maple dominance, but this study was conducted at a limited spatial-scale constraining inferences to other community types and abiotic conditions across GDS. Moreover, previous work has largely used past community characterizations (e.g., from Dabel and Day 1977) and relied on areal imagery to estimate their spatial extent. Consequently, on-the-ground work is needed to characterize vegetation communities and potential hydrologic controls across the large spatial extent of GDS.

To better characterize GDS-wide variability and drivers of forest community composition, we conducted a spatially distributed survey of vegetation communities along with different estimates of hydrologic conditions. This work aimed to inform hydrologic restoration and forest management at GDS by: (1) characterizing GDS-wide variation in vegetation structure and composition, (2) assessing relationships between forest communities and indicators of hydrologic regimes, and (3) using findings to propose future monitoring needs to inform water management strategies.

Materials and methods

Study site and design

The GDS is a nonriverine swamp forest located in the Atlantic Coastal Plain, USA. 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 (Fig. S1). Hereafter, we simply refer to our study site as GDS, acknowledging that the refuge (and thus our study domain) does not include the Dismal Swamp State Park, a 5805 ha protected area of the NC

Division of Parks and Recreation adjacent to the southeast corner of the refuge.

Soils at GDS are generally organic-rich, acidic, poorly drained, and nutrient poor (NRCS Web Soil Survey 2017). While GDS is often described as a peatland and Histosol soils dominate (over 80% of GDS area), Histosols are primarily classified as Terric Haplosaprists and Typic Haplosaprists in contrast to fibric (or peat) texture classes (NRCS Web Soil Survey). 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).

We established 79 survey plots (7.3 m radius) across GDS to evaluate spatial variation in vegetation composition and structure, estimated water levels, organic soil depths, and soil properties. To effectively capture ecosystem variation across GDS, we applied the space-filling curve (SFC) method following Lister and Scott (2009). This method segments a study domain into a specified number of polygons with equal area, and then randomly selects a plot location within each polygon (Bartholdi and Platzman 1988). In this way, the SFC model produces plot locations that are spatially balanced across the study domain but are also randomly selected, thereby avoiding possible spatial autocorrelation of surveyed attributes (Gregoire and Scott 2003). Plot centers were located using a Garmin eTrex Venture HC GPS, assigned a unique plot number, and marked to within 3 m of accuracy with a 1.5 m metal conduit.

Data collection

Vegetation composition

At each survey plot (n = 79), we assessed vegetation composition and structure following procedures in the USFWS Region 5 forest inventory protocol (Horan et al. 2019). 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 tree species; saplings are defined as being between 2.54 cm and 12.7 cm in diameter at midpoint height, whereas seedlings are greater than 2.54 cm in height and less than 2.54 cm in diameter at midpoint height. Shrubs and vines are combined (shrubs from here on) and defined as woody or non-

woody species not expected to reach the overstory. The herbaceous community includes species belonging to both forb and graminoid growth forms.

Using marked plot center locations, we established a 0.017 ha (7.3 m radius) fixed-radius plot to survey tree, shrub, and herbaceous growth forms. We measured tree composition and structure by recording the DBH and species of each tree. For shrub and herbaceous growth forms, we estimated total percent cover and percent cover of the four dominant species 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.

Indicators of hydrologic regime

In situ water level monitoring was not feasible in our study given the number and remote locations of our sampling plots. Consequently, we relied on water level estimates and soil properties to infer potential differences among plots in hydrologic regimes. These measurements (described below) were conducted at each study plot (n = 79), where some measurements (specifically high-water marks, and soil properties and depth) were conducted at multiple locations within each plot.

Water level estimates We used various field indicators of seasonal high-water levels as relative estimates of maximum inundation depth across survey plots. At each plot, high-water marks (n = 5 per plot, when available) were measured from ground surface to the base of lichen lines, water stains, moss collars, or the top of adventitious roots.

We also used simulated water levels from a hydrologic model recently developed by the USGS, in collaboration with the USFWS, to inform water resource management at GDS (Eggleston et al. 2018). The model is a steady-state, numerical model that combines MODFLOW-NWT (simulates groundwater flow) and the Surface-Water Routing (SWR1) Process (simulates dynamic surface water flows, water-control structure management, and groundwater/surface-water interactions) (see Eggleston et al. 2018 for model details). Model outputs are mean springtime (April-June) water levels across GDS under three scenarios: baseline conditions (WL_{base}, average springtime climatic conditions for the period 2005–2015), wet scenario (WL_{wet}, spring 2015; atypical wet season), and dry scenario (WL_{dry}, spring 2011; atypical dry season). Mean water levels (relative to ground surface, m) for these three scenarios are simulated for 500 ft^2 (152.4 m^2) grid cells, each of which are defined by one mean land elevation from a LiDAR-derived digital-elevation model (DEM). However, for this study, model outputs were adjusted to estimate mean water levels relative to the mean land elevation for each of the 79 survey plots. To do so, we overlaid each plot's area (7.3 m radius) on the DEM and then used elevation values within each plot (ca. 40/plot) to obtain a plot mean elevation, yielding a new elevation reference for each water level scenario.

Soil hydrologic indicators We measured organic soil depths 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. Measurements were recorded at five locations per plot, along a 14.6 m transect. Using a 3.6 m extendable soil probe, we located the intersection of the mineral and organic layers via resistance at the mineral layer. Organic soil depth was estimated as the depth to this area of high resistance, and the five organic soil depths were averaged to yield plot mean depth.

Additionally, we collected surface soil samples at each plot at a depth of 15 cm to explore variation in soil properties and to serve as additional indicators of hydrologic regime. Three soil samples per plot were collected along the same transect used for organic soil depths. Surface soil samples were sampled in microtopographic lows to be consistent across plots and avoid variability in soil properties associated with microtopography, the extent of which may differ among plots; although, we note that this failed to capture higher locations with potential differences in hydrologic conditions and associated influences on soil properties. To maintain field bulk density, a steel ring sampler (h = 5.02 cm, d = 7.47 cm) was inserted horizontally into a cut soil profile from which the sample was excavated using a hand trowel. Samples were bagged and transported to the lab at 4 °C.

We analyzed soil samples for bulk density and organic matter content. 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 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. Bulk density for each sample (n = 3 per plot) was determined by dividing the corrected dry mass by its corrected volume. Samples were then used for loss on ignition analysis via combustion in a muffle furnace at 500 °C for 24 h. Organic matter content was calculated as the mass difference between the original sample and remaining sample (mineral content) relative to the original sample mass. We assumed that soils with low bulk density and high organic content indicated wetter conditions (Drexler et al. 2009; Chambers et al. 2011).

Data analysis

Vegetation composition

A suite of analyses was conducted to assess community composition and structure using R statistical software (R Core Team 2018). To assess occurrence of different tree species across GDS, we pooled all plots to calculate species-specific cumulative basal areas and frequencies and an overall species rank abundance curve. Rank abundance curves indicate abundance against rank order, where rank one corresponds to the species with the highest abundance (Matthews and Whittaker 2015). Then, we used several plot-level metrics to understand variation among plots. Plot tree metrics 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; values range from 0–2 and are the sum of relative basal area (species basal area/total basal area) and relative density (species density/total density). Regeneration metrics combined sapling and seedling data and included 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 each of the four dominant species observed. To assess associations between tree species dominance and overall community composition and structure, a Spearman's correlation analysis was conducted between all vegetation metrics and dominant tree species IVs.

We then used tree species abundance data from each plot and multivariate cluster analysis to determine dominant community types, classified by tree composition. Prior to this analysis, rare species were removed from the tree abundance matrix to improve the detection of significant overstory community types. Following McCune and Grace (2002), species present at 5% or fewer plots 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.). We then conducted a hierarchical, agglomerative, polythetic cluster analysis using a Bray–Curtis dissimilarity matrix (Oksanen et al. 2019). Clustering was performed with a flexible beta linkage ($\beta = -0.25$) to minimize matrix distortion (McCune and Grace 2002). The resulting dendrogram was pruned at locations yielding a variety of cluster levels (e.g., from 3 to 7 clustered groups), with an indicator species analysis used to inform the appropriate level of pruning (De Cáceres and Jansen 2016). This analysis yields an indicator value index (IVI) for each species at each clustering level and measures the association between this species and a clustered group (De Cáceres and Jansen 2016). The IVI statistic ranges from 0 to 1 and is the product of two conditional probability values: Component A (specificity value) defined as the probability that the surveyed plot belongs to the clustered group given the fact Species A is found, and Component B (sensitivity value) defined as the probability of finding Species A at plots belonging to a clustered group (McCune and Grace 2002). For each clustering level, 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 for a singular clustered group was not significantly greater than a value produced with randomized data. The final dendrogram pruning location was selected at a level where the proportion of individual community groups explained by an indicator species *and* the average Component A and Component B conditional probabilities for all significant indicator species were high.

Following cluster analysis, we analyzed differences in vegetation composition and structure among clustered community types. Rare species (i.e., those previously removed for cluster identification) were

included in the analysis of clustered community composition. We pooled plots by their identified community types and assessed significant differences among types in the suite of plot-level vegetation metrics using the non-parametric Kruskal–Wallis rank sum test, followed by a post-hoc pairwise Wilcoxon-Mann–Whitney rank sum test with a Holm *p*-adjustment for multiple comparisons (Holm 1979).

Indicators of hydrologic regimes

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), organic soil depths, and soil properties. We then evaluated plot-level correlations between these indicators and all vegetation metrics to explore associations between community composition and hydrologic regimes. We further assessed these hydrology-vegetation relationships via differences among clustered community groups using previously mentioned nonparametric statistical methods.

Results

Vegetation composition

Plot-level analysis

Red maple was the overwhelming dominant tree species, making up 48% of all trees surveyed and contributing 52% of total surveyed basal area (Fig. 1a). Swamp tupelo was the second most dominant species observed, present at 25% of plots but contributing much less to cumulative basal area and abundance as compared to red maple. The species rank-abundance curve (inset; Fig. 1a) similarly illustrates red maple and swamp tupelo dominance, as well as identifying sweetgum and American holly as the third and fourth most abundant species, respectively. However, the steep slope of the rank-abundance curve highlights overall low evenness in tree species composition across GDS. Plot-level tree IVs also demonstrated red maple dominance at most plots but clear variation across plots, where lower red maple IV was often associated with greater IV for one of the other three dominant species (Fig. 1b).

Red maple IV had significant negative correlations with both swamp tupelo IV and American holly IV (Table 1). There were also significant negative correlations between red maple IV and tree density, richness, and diversity, whereas swamp tupelo IV was positively correlated with these metrics as well as with tree basal area. Sweetgum IV did not show similar correlations with tree composition or structure metrics (with exception of tree density). However, sweetgum IV had the only significant associations with shrub and herbaceous cover. Similar to swamp tupelo, American holly IV was positively correlated with richness and diversity. No significant correlations between tree IVs and regeneration metrics were found.

Clustered community analysis

To further explore community-level variation, a cluster analysis was used to identify community types using tree abundance data. The resulting dendrogram was pruned to produce four community groupings informed by an indicator species analysis (Fig. S2). Although five community groupings produced slightly higher average Component A (0.88) and Component B (0.85) values, four community groups explained a greater proportion of community variation (75% versus 40%) with similar average conditional probability values (Component A = 0.78, Component B = 0.72) (Fig. S2). Using mean species IV values, we identified the four clustered communities based on the primary and secondary dominant species: swamp tupelo-maple (ST-M), maple-holly (M-H), sweetgum-maple (SG-M), and maple (M) (Fig. 2). Demonstrating red maple dominance, 56% (n = 44) of plots clustered within the M community. The ST-M community was the next most abundant community occurring at 20% (n = 16) of plots, with the M-H and SG-M communities consisting of 13% (n = 10) and 11% (n = 9) of plots, respectively.

Analysis of tree structure and composition demonstrated community differences among clustered communities. Tree density was highest within the ST-M community, but there were no significant differences in mean basal area among community types (Fig. 3a, b). The M community exhibited lower tree richness compared to the other three community types, but only significantly when compared to the ST-M community (Fig. 3c). Similarly, the M community had lower
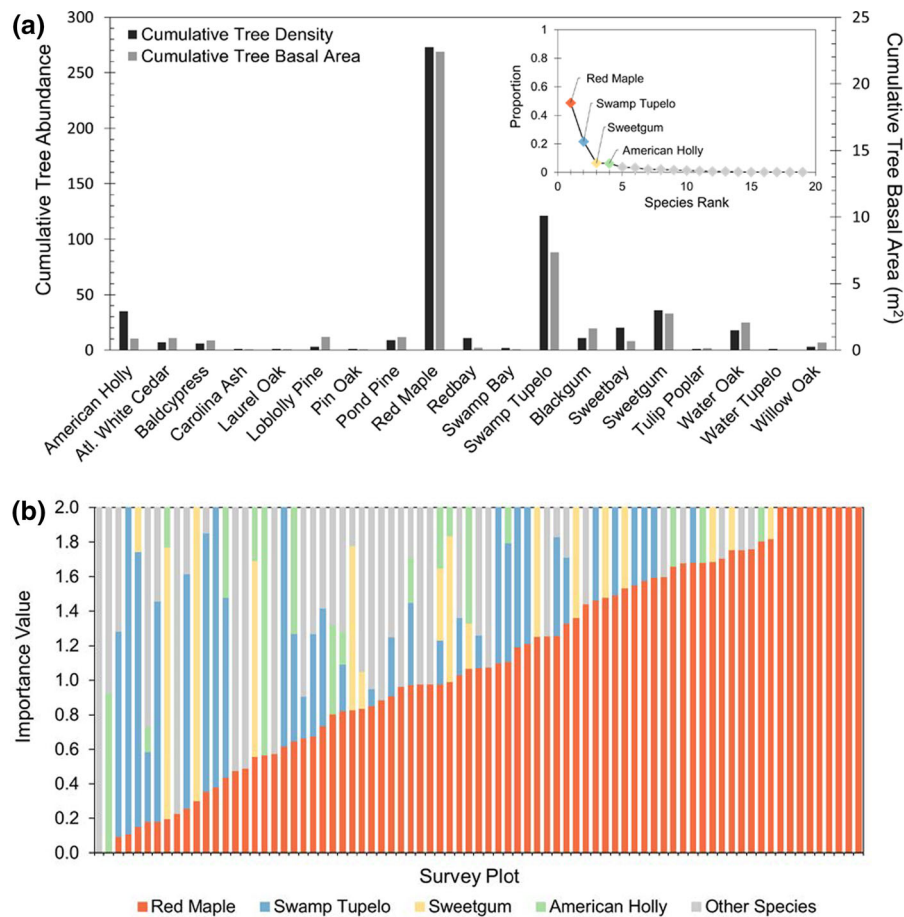
Fig. 1 **a** Cumulative tree frequency and basal area for each observed species across the 79 survey plots. Inset: Species rank-abundance curve illustrating the rank order abundance of observed species at GDS. **b** Plot-level importance values (IV; from 0–2), where bars represent plots ordered by increasing red maple IV. Red maple, swamp tupelo, sweetgum, and American holly were identified as the four most dominant species by the species rank-abundance curve. All other species are represented by "Other Species" category

diversity values, which were significantly lower than those for all other community types (Fig. 3d).

Despite the importance of red maple, swamp tupelo, sweetgum, and American holly abundance in community differentiation, other tree species were observed (i.e., "Other Species" in Fig. 1b). However, species often associated with the GDS (e.g., baldcy-press, Atlantic white cedar, and pond pine) were rarely observed (Table 2). Baldcypress IV, an obligate wetland species, was significantly higher in ST-M community and absent in the M-H and SG-M communities. Blackgum IV was significantly higher in the M-H community; however, its overall abundance was far lower than swamp tupelo, a closely related species.

Variation among communities in tree composition was not associated with community variation in other growth forms (shrubs, herbaceous, regeneration), with some exceptions (Table 2). For example, community differences in sweet pepperbush cover, a well-documented dominant shrub species at GDS, approached significance (p = 0.06), with the SG-M having lower percent cover than all other communities. In the herbaceous growth form, marsh fern (*Thelypteris palustris*) was significantly higher in the ST-M community when compared to the M community, and Virginia chain fern (*Woodwardia virginica*) cover was significantly higher in the SG-M community when compared to the ST-M and M communities. Mean herbaceous cover was highest in the SG-M

Table 1 Spearman's correlation matrix of dominant tree species importance values (IV) versus plot-level vegetation metrics

	Red maple IV	Swamp Tupelo IV	Sweetgum IV	American holly IV
Red maple IV	1	–	–	–
Swamp tupelo IV	− **0.4**	1	–	–
Sweetgum IV	− 0.07	− **0.29**	1	–
American holly IV	− **0.23**	− 0.04	0.13	1
Tree basal area	− 0.17	**0.29**	− 0.14	− 0.06
Tree density	− **0.42**	**0.35**	**0.23**	0.09
Tree richness	− **0.61**	**0.39**	0.11	**0.29**
Tree diversity	− **0.6**	**0.36**	0.04	**0.29**
Shrub % cover	0.21	− 0.02	− **0.25**	− 0.14
Herbaceous % cover	− 0.16	− 0.01	**0.28**	− 0.03
Regeneration density	− 0.11	0.12	− 0.01	− 0.02
Regeneration richness	− 0.19	0.04	0.12	0.12
Regeneration diversity	− 0.18	0.02	0.13	0.11

Bold values are significant at p-values < 0.05
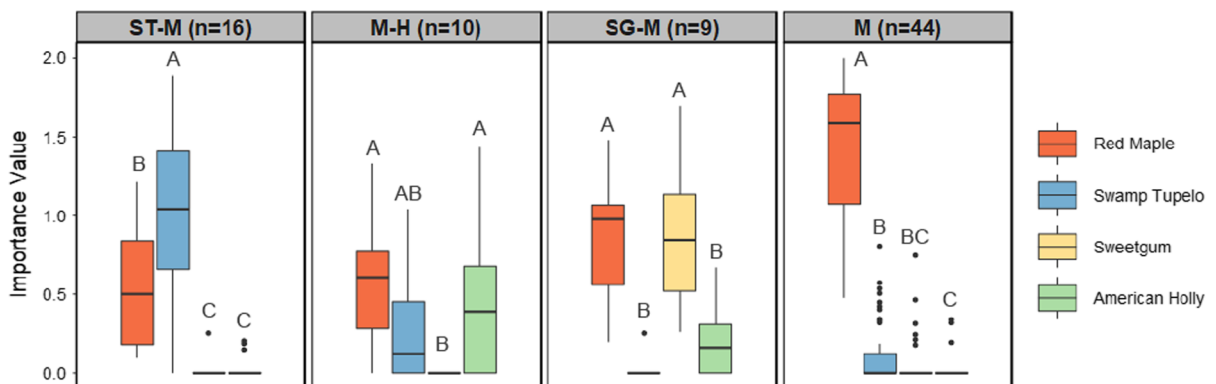
Fig. 2 Importance values (IV) of dominant tree species for clustered community types, where community types are ordered by increasing red maple IV. Letters denote significant differences (p < 0.05) in species IV within each community type

community, largely driven by the abundance of giant cane. Of note, tree dominance of red maple and sweetgum was not reflected in their regeneration frequencies, which were more similar across communities. Further, redbay was the dominant regeneration species across all communities, which was in contrast to much lower presence in the tree strata.

Indicators of hydrologic regimes

Plot-level analysis

No significant associations were found between modeled water levels and measured high-water marks (data not shown). Further, these water level estimates were poor predictors of measured plot soil characteristics (Table S1). In contrast, strong negative correlations were found between bulk density and both organic matter content and organic soil depth values, which themselves had significant positive correlations (Table S2).

Water level estimates (modeled and via field high-water mark indicators) had few associations with plot-level vegetation attributes (Table 3). Analysis of soil hydrologic indicators, however, resulted in stronger correlations. Bulk density had significant correlations with several vegetation metrics, including positive associations with sweetgum IV and herbaceous cover
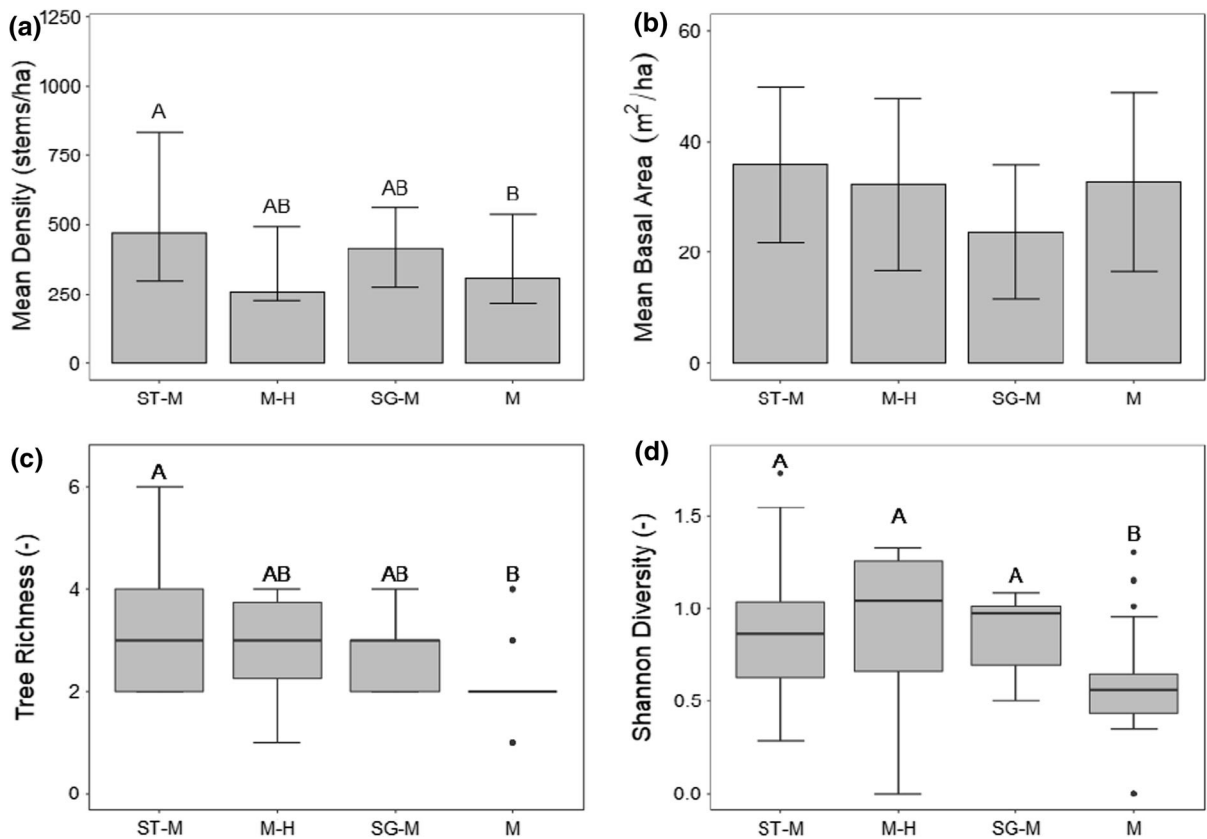
Fig. 3 Tree structure and composition for the four clustered community types: **a** tree density, **b** tree basal area, **c** tree richness, and **d** tree Shannon diversity. Letters denote significant differences among community types ($p < 0.05$)

and negative correlations with swamp tupelo IV and shrub cover. Opposite relationships were found between these same metrics and organic matter content, with the exception of swamp tupelo IV. Organic soil depth values exhibited similar relationships with vegetation metrics with the addition of a negative relationship with tree density.

Clustered community analysis

Following plot-scale analysis, water level indicators and soil characteristics were examined for variation among the clustered community types (Fig. 4). Modeled base-scenario water level (Fig. 4a) and measured highwater marks (Fig. 4b) failed to significantly differentiate community types. However, the M community exhibited the largest variation for both metrics. Additionally, mean modeled water levels were near ground surface elevations across all communities.

In contrast to water level indicators, differences were found across community types with respect to measured soil characteristics. Bulk density was significantly higher in the SG-M community and lowest in the ST-M community, with M-H and M communities serving as intermediaries (Fig. 4c). Differences in organic matter content (Fig. 4d) and organic soil depth (data not shown) approached significance (p values = 0.054 and 0.078, respectively), with lower and more variable values in the SG-M community.

Discussion

Through a spatially extensive survey across 79 plots, we assessed ecosystem variation and sought to understand associations between vegetation communities and hydrologic regimes across GDS. Notably, our surveyed plots attempted to cover the full extent of GDS and were often located in remote areas rarely

Table 2 List of observed species across all surveyed plots

Tree			Community			
			ST-M	M-H	SG-M	M
Common name	Scientific name	AGCP	Importance value (SD)			
Atlantic W. Cedar	*Chamaecyparis thyoides*	OBL	0.00	0.09 (0.28)	0.00	0.03 (0.14)
Baldcypress	*Taxodium distichum*	OBL	**0.12^A (0.29)**	0.00	0.00	**0.01^B (0.04)**
Swamp Tupelo	*Nyssa biflora*	OBL	**1.01^A (0.55)**	**0.27^B (0.36)**	**0.03^B (0.08)**	**0.11^B (0.21)**
Blackgum	*Nyssa sylvatica*	FAC	0.00	**0.47^A (0.69)**	**0.02^{AB} (0.07)**	**0.01^B (0.05)**
Water tupelo	*Nyssa aquatica*	OBL	0.04 (0.18)	0.00	0.00	0.09 (0.32)
Pond pine	*Pinus serotina*	FACW	0.04 (0.15)	0.00	0.00	0.08 (0.30)
Redbay	*Persea borbonia*	FACW	0.04 (0.10)	0.05 (0.11)	0.00	0.02 (0.07)
Sweetbay	*Magnolia virginiana*	FACW	0.09 (0.17)	0.00	0.00	0.05 (0.17)
American Holly	*Ilex opaca*	FAC	**0.03^{BC} (0.07)**	**0.44^A (0.49)**	**0.19^{AB} (0.23)**	**0.02^C (0.07)**
Red Maple	*Acer rubrum*	FAC	**0.56^B (0.39)**	**0.57^B (0.42)**	**0.86^B (0.44)**	**1.47^A (0.45)**
Sweetgum	*Liquidambar styracifula*	FAC	**0.02^B (0.06)**	0.00	**0.89^A (0.50)**	**0.05^B (0.14)**
Shrubs						
			Percent cover (SD)			
Sweet Pepperbush	*Clethera alnifolia*	FACW	29.68 (30.25)	24.10 (23.29)	3.89 (5.46)	28.25 (27.47)
Inkberry	*Ilex glabra*	FACW	0.81 (2.29)	0.50 (1.58)	0.00	1.55 (5.12)
Shinyleaf	*Lyonia lucida*	FACW	2.50 (7.75)	0.00	1.11 (3.33)	1.43 (5.21)
Laurel Greenbrier	*Smilax lauifolia*	FACW	2.56 (5.40)	3.50 (5.80)	2.22 (5.07)	2.68 (9.45)
High. Blueberry	*Vaccinium corymbosum*	FACW	6.50 (7.41)	6.50 (13.34)	13.33 (18.87)	8.18 (10.86)
Virginia Creeper	*Parthenocissus quinquefolia*	FACU	0.63 (1.71)	1.30 (2.16)	0.00	0.32 (1.20)
Poison Ivy	*Toxicodendron radicans*	FAC	2.25 (2.79)	3.10 (5.84)	7.22 (12.28)	7.59 (11.81)
Cat Greenbrier	*Smilax glauca*	FAC	3.44 (6.51)	0.00	6.67 (14.79)	3.41 (7.30)
Horsebrier	*Smilax rotundifolia*	FAC	4.63 (9.04)	6.90 (8.17)	3.89 (8.21)	8.34 (14.88)
Muscadine	*Vitis rotundifolia*	FAC	7.06 (17.68)	16.60 (22.68)	5.56 (8.82)	10.91 (18.21)
Total cover		–	63.19 (36.68)	62.50 (45.93)	49.44 (32.92)	74.09 (41.05)
Herbaceous						
			Percent cover (SD)			
Lizard Tail	*Saururus cernuus*	OBL	0.50 (2.00)	0.00	0.00	1.48 (4.39)
Marsh Fern	*Thelypteris palustris*	OBL	**1.75^A (3.96)**	**0.3^{AB} (0.95)**	0.00	**0.23^B (1.51)**
Netted Chain Fern	*Woodwardia areolata*	OBL	1.19 (2.76)	0.80 (2.53)	1.67 (3.54)	2.05 (6.32)
VA Chain Fern	*Woodwardia virginica*	OBL	**0.19^B (0.75)**	**0.60^{AB} (1.26)**	**5.33^A (6.95)**	**0.98^B (4.08)**
Giant Cane	*Arundinaria gigantea*	FACW	7.00 (9.66)	2.50 (6.35)	16.44 (23.85)	8.29 (18.86)
New York Fern	*Thelypteris noveboracensis*	FAC	0.19 (0.75)	0.70 (1.50)	3.89 (11.67)	0.11 (0.75)
Sedge spp.	*Carex spp.*	–	4.06 (14.97)	0.00	0.89 (2.67)	0.52 (1.50)
Total cover		–	15.56 (26.37)	5.20 (8.38)	28.56 (34.33)	16.36 (26.68)
Regeneration						
			Mean frequency (SD)			
Swamp Tupelo	*Nyssa biflora*	OBL	0.69 (1.30)	0.00	0.33 (1.00)	0.14 (0.47)
Redbay	*Persea borbonia*	FACW	5.00 (5.72)	1.20 (1.62)	4.11 (7.47)	4.48 (6.77)
Sweetgum	*Liquidambar styracifula*	FAC	0.69 (1.89)	0.00	0.67 (2.00)	0.80 (2.54)

Table 2 continued

Regeneration

			Mean frequency (SD)			
Red Maple	*Acer rubrum*	FAC	1.81 (2.79)	0.50 (0.85)	2.00 (2.29)	1.25 (2.53)
Pawpaw	*Asimina triloba*	FAC	0.13 (0.50)	1.40 (2.50)	0.11 (0.33)	1.30 (3.25)
American holly	*Ilex opaca*	FAC	**0.31**[B] **(0.87)**	**1.90**[A] **(2.08)**	**0.55**[AB] **(1.33)**	**0.23**[AB] **(0.71)**

Species are organized by their growth forms and categorized 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)

Significant differences in community composition were determined through a global Kruskal–Wallis test. Pairwise differences were calculated only for communities that contained the particular species using a Mann–Whitney U test and p-adjustment. Bolded values denote significant differences ($p < 0.05$) with superscripts denoting pairwise differences if applicable

Table 3 Spearman's correlation of water level and soil hydrologic indicators versus vegetation metrics

	WL_{Base}	HWM	BD	OM	Organic soil depth
Red maple IV	**− 0.23**	− 0.09	0.19	0.18	**0.23**
Swamp tupelo IV	0.05	− 0.14	**− 0.31**	0.09	− 0.03
Sweetgum IV	− 0.03	− 0.06	**0.49**	**− 0.39**	**− 0.42**
American holly IV	0.19	− 0.04	0.11	− 0.03	0.07
Tree basal area	− 0.12	− 0.17	− 0.13	− 0.07	− 0.05
Tree density	− 0.02	− 0.13	0.02	− 0.15	**− 0.27**
Tree richness	0.07	− 0.12	− 0.08	− 0.05	− 0.21
Tree diversity	0.05	− 0.09	− 0.1	− 0.02	− 0.12
Shrub % cover	− 0.05	− 0.07	**− 0.32**	**0.41**	**0.32**
Herbaceous % cover	0.09	0.11	**0.3**	**− 0.57**	**− 0.49**
Regeneration density	0.08	0.1	− 0.14	0.05	− 0.01
Regeneration richness	0.1	0.11	− 0.16	− 0.05	− 0.03
Regeneration diversity	0.19	0.12	− 0.17	− 0.07	− 0.03

Water level indicators shown are mean springtime water levels in the base-case water level scenario (WL_{Base}) and field-collected high-water mark indicators (HWM). Soil properties shown are bulk density (BD), organic matter content (OM), and organic soil depth

The other two modeled water level scenarios (WL_{Wet} and Wet_{Dry}) are not shown due to poor correlations with vegetation metrics, with a weak (− 0.24) negative correlation between WL_{Wet} with Red Maple IV as the strongest correlation

Bold values are significant at p-values < 0.05

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.

Maple dominance and ecosystem homogenization

Analysis of tree composition clearly demonstrated that red maple is the dominant species across GDS (Fig. 1).
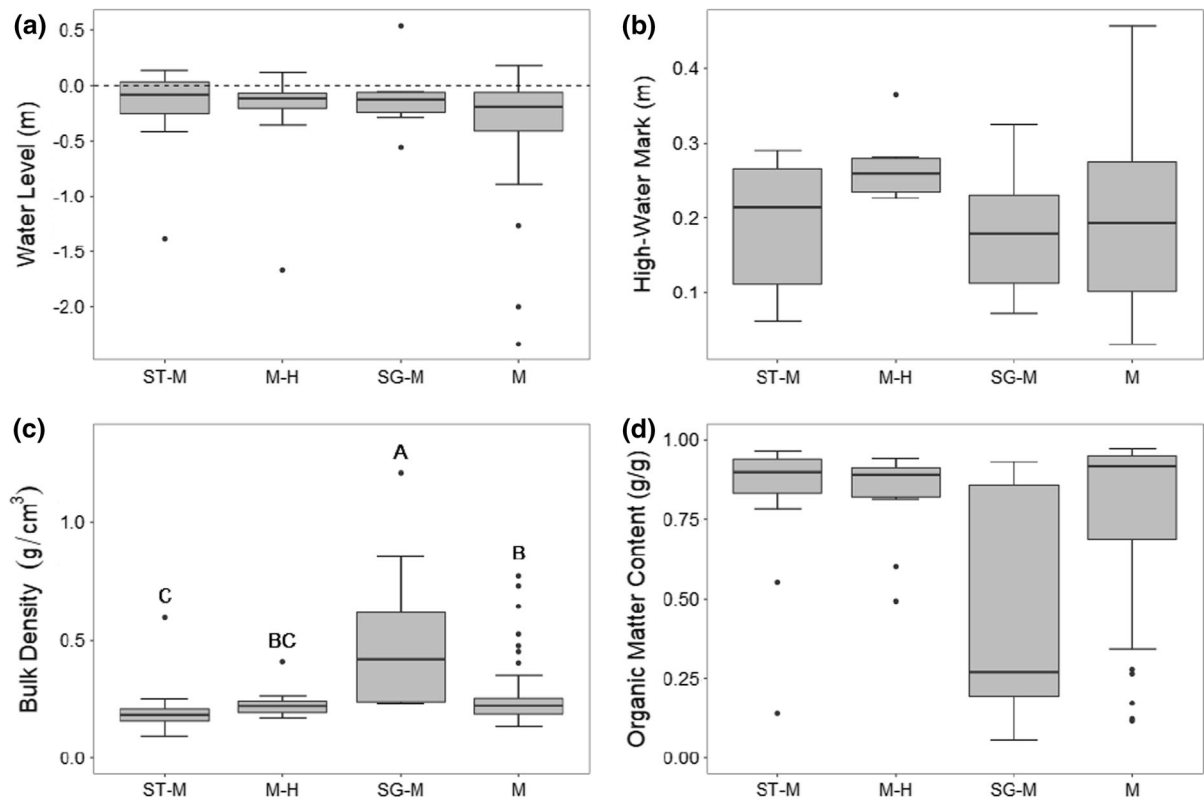
Fig. 4 Water level and soil hydrologic indicators for the four community types: **a** modeled mean springtime water level in the base-case scenario, **b** height of high-water marks (e.g., water stains, adventitious roots, and lichen lines), **c** bulk density, and **d** organic matter content. Letters denote significant differences if found (p < 0.05)

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. Multiple studies investigating vegetation structure and composition at GDS have documented similar results (Dabel and Day 1977; Carter et al. 1994; Schulte et al. 2019). Our work extends this general conclusion across GDS, where pervasive red maple dominance severely limits spatial richness in tree species. Understanding the drivers and consequences of such low spatial richness is critical to guide future management actions.

From both plot-level and cluster analysis, we found that red maple dominance was associated with lower tree density, richness, and diversity. For example, there was a negative correlation between red maple IV and 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; Fig. 3; Schulte et al. 2019). Red maple IV

was also negatively correlated with tree richness and diversity (Table 1); concordantly, the M community had significantly lower tree richness and diversity values (Fig. 3). However, our sampling design precluded estimates of overall stand richness as abundance of all shrub and herbaceous species were not recorded. Yet, low stand richness in maple-dominated communities at GDS was observed by Schulte et al. (2019), albeit over much smaller spatial scales. Our work helps to further demonstrate relationships between red maple dominance and community composition across the full extent of GDS.

Wetland disturbances (e.g., ditching and clearcutting) can result in ecosystem homogenization through rapid expansion of generalist species, such as red maple, taking advantage of newly available resources and often drier conditions (Miller et al. 2015). The ability of red maple to establish and dominate 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), ditching mitigates this effect particularly at sites in close proximity to drainage ditches (Marcotte et al. 2008). As a result, facultative wetland 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). This decrease in forest stand richness and diversity motivates efforts at GDS and other disturbed systems to enhance community variation.

Forest community variation

Despite the dominance of red maple across GDS, some variation in forest structure and composition does exist. Cluster analysis revealed four distinct forest community types (Fig. 2), which are similar, but not identical, to those described in previous studies at GDS. For example, community types at our plot locations are inconsistent with community maps defined through aerial surveys (see Fig. S1), underscoring the importance of on-the-ground surveys. Notably, our M community, representing almost pure stands of maple, has not been previously characterized at GDS. Occurring at 56% of our plots, this community largely influences GDS-wide tree composition as shown when comparing rank abundance curves for each community with the GDS-scale curve (all plots pooled) (Fig. 5). With median red maple IV over 1.5 (Fig. 2), the M community is associated with low tree richness and diversity (Fig. 3c, d) and likely occurs within the broader maple-gum community described by Dabel and Day (1977) and Sleeter et al. (2017). Further, our ST-M community may also largely occur within the previously described maple-gum community. However, Dabel and Day (1977) identified blackgum, a facultative species, as the dominant gum species within their maple-gum category. In contrast, we observed very little occurrence of
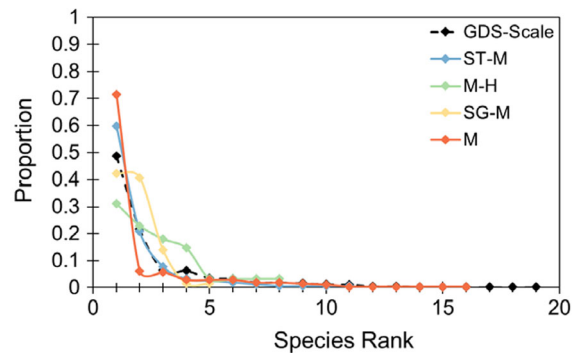

Fig. 5 Species rank abundance curves across all plots (dotted line) and clustered community types (solid lines). Tree species within each community are ranked by their total abundance and plotted against their relative contribution to total community abundance. Rank abundance curve slope is indicative of species evenness with steeper slopes representing low evenness

blackgum and much higher occurrence of swamp tupelo, which dominated our ST-M community. Dominance of this obligate wetland species suggests this community exists at wetter sites at GDS, which may occur in areas previously characterized as maple-gum and others described as cypress-gum. Indeed, we observed some, albeit limited, occurrence of cypress within some ST-M plots (Table 2). Our M-H community may also occur within the broader maple-gum community, where the exclusion of American holly in past community characterization was likely due to its inability to reach main canopy height at GDS (often 20–25 m). Last, our SG-M community likely exists in areas previously characterized as either maple-gum or the mixed hardwood community by Dabel and Day (1977), which occurs on drier mineral soils. We critically note, however, that all of our four community types included red maple as the dominant or co-dominant species (Fig. 2). The relative importance of maple dominance for tree richness and diversity (Fig. 3) underscores the importance of distinguishing between otherwise maple-dominated communities at GDS.

An analysis of wetland indicator status of dominant tree species suggests hydrologic differences across our community types. Red maple and sweetgum are facultative species, suggesting the M, M-H, 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). In contrast, swamp

tupelo dominance indicates that the ST-M likely occurs at wetter sites. However, the lack of significant differences in other growth forms among communities limits further indication of possible hydrologic differences. Across all plots, we did not observe any obligate wetland shrub species; however, evident lower sweet pepperbush, a facultative wetland species, in the SG-M community may further suggest that this community typically occurs on drier sites (Table 2). A significant increase in abundance of the obligate species Virginia chain fern in the SG-M community seems to contradict this trend. Yet, all community types likely encompass microsites with wetter conditions, making interpretations of hydrologic differences via understory species wetland classes difficult (Carter et al. 1994).

Notably, our study did not observe several historical community types that have been documented by others to still occur but at reduced spatial extent compared to pre-disturbance conditions. For example, a cypress-dominated community was not identified in our study in contrast to previous studies (Dabel and Day 1977; Sleeter et al. 2017). Similarly, the Atlantic white cedar and pond pine pocosin-dominated communities previously described by Dabel and Day (1977) and Sleeter et al. (2017) were also not found. When observed, all three species (cypress, cedar, and pond pine) had low IV values (Table 2), supporting the conclusions of previous studies for red maple expansion in historical wetland communities (DeBerry and Atkinson 2014; Sleeter et al. 2017).

Forest communities and hydrologic regimes

Evaluating hydrologic controls across the full array of GDS forest communities and environmental conditions requires linked observations of hydrologic regime and community attributes. However, resource constraints limit in situ water level monitoring across such large spatial extents as the GDS. As such, we took advantage of multiple methods (water level estimates and soil hydrologic indicators) to assess hydrologic regime across our 79 plots.

We estimated water levels at each plot in two ways. First, high-water mark indicators were measured to estimate seasonal high-water levels. Yet, we observed little variation in these metrics across community types (Fig. 4b), and no correlations were found with soil properties and specific vegetation metrics

(Table 3). High-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), which can have stronger controls on species regeneration (Conner et al. 1986) and soil properties (Ehrenfeld 1995). We also estimated water level regimes by refining previously simulated mean water levels to better represent our plot-scale surface elevations. Correlation analysis revealed only one (but weak) significant negative trend between red maple IV and water level in the base wetness scenario (Table 3), and no significant differences were found between simulated mean water levels across community types (Fig. 4a). Indeed, results suggest similar water stress across GDS communities, where mean water levels were generally near ground surface (Fig. 4a). However, variability in simulated mean water levels was highest within the M community, suggesting this community may exist across the widest range of hydrologic regimes at GDS. Nonetheless, and similar to high water marks, modeled mean water levels do not indicate temporal variation in water levels and soil saturation. Further, the spatial resolution of the original model is coarse as compared to plot area, microtopographic variation, and the scale at which hydrologic controls may act. Yet, the model may sufficiently predict larger spatial variation in mean water levels, and thus serve as a useful tool to explore outcomes of future water control to increase both wetness and spatial heterogeneity in water level regimes.

Soil properties may be better indicators of more local and time-varying water level regimes (Reddy and Patrick 1975), where low bulk density (Drexler et al. 2009) and high organic matter content (Drzymulska 2016) are indicative of wetter conditions. Overall variation in these soil properties was limited, with plots mostly characterized by low bulk density, high organic matter soils consistent with other GDS studies (Fig. 4c, d) (Drexler et al. 2017; Schulte et al. 2019). We note, however, that we consistently sampled microtopographic lows (or "hollows") to avoid possible influences from microtopography that may differ among plots but, in doing so, failed to capture high locations with potentially different hydrologic regimes and thus soil properties to relate with plot-level vegetation metrics. Nonetheless, some observed variation helps to explain differences in vegetation communities. For example, bulk density was

positively correlated with sweetgum IV and negatively correlated with swamp tupelo IV (Table 3). This trend was also represented in the clustered-community analysis, where the ST-M and SG-M communities had significantly lower and higher bulk densities, respectively, than all other communities (Fig. 4c). Further, organic matter content and organic soil depth were lowest for plots in in the SG-M community and had significant negative correlations with sweetgum IV. Taken together with differences in wetland species indicator status (Table 2), these soil differences suggest that SG-M communities may largely occur on drier sites whereas ST-M occur on the wettest. For red maple IV, there was only one weak correlation (organic soil depth) with soil metrics (Table 3), and community analysis suggests M and M-H communities may be intermediaries with respect to both bulk density and organic matter (Fig. 4c, d). As such, these communities may span a larger and more common hydrologic gradient at GDS, helping to explain their dominance.

Monitoring and management implications

Our final objective was to inform future monitoring and management strategies at GDS. This analysis is timely as the USFWS is currently developing a refuge-wide Habitat Management Plan, defining management strategies for the next 15 years. Our results suggest that the dominant community across GDS is almost a pure maple stand (M community) with low richness and diversity, but that this system may be limited in the wettest locations where swamp tupelo (and higher tree richness) occurs. This finding comports with those from Schulte et al. (2019), supporting current efforts to "re-wet the swamp" for reduction of maple dominance and recovery of other forested communities. By necessity, restoring forest stand diversity at GDS will be an adaptive process that requires coupled monitoring and management actions to identify successful strategies. Indeed, such monitoring is underway in some hydrologically restored GDS locations, and our study highlights key community types and additional measures to include in expanded monitoring of management effects. For example, the current study was limited in its ability to quantify associations between maple dominance and other growth forms due to the lack of richness data across all strata, warranting its collection in future vegetation

monitoring. Further, our results suggest that hydrologic regime at least partially explains variation in GDS communities, but improved characterization of water level and soil moisture dynamics is needed. While soil properties provided the best metric for assessing hydrologic regime in our study, they remain a poor proxy for in-situ water level (and soil moisture) measurements and may be somewhat confounded by within-plot microtopography. Therefore, long-term monitoring should include water level measurements of sufficient frequency to relate hydrologic regimes and forest community characteristics and thus to inform ongoing and future water management efforts. Beyond the direct importance of our work to such efforts at GDS, our approach and general findings are broadly relevant to other disturbed forested wetlands where ecosystem homogenization has occurred.

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