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Landscape Pattern – Marl Prairie/Slough Gradient: Vegetation Composition along the Gradient and Decadal Vegetation Change Pattern in Shark Slough: Annual Report 2012

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Landscape Pattern – Marl Prairie/Slough Gradient: Vegetation Composition along the Gradient and Decadal Vegetation Change Pattern in Shark Slough Annual Report - 2012 (Cooperative Agreement #: W912HZ-09-2-0018

Modification No.: P00002)

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> > April 30, 2013

Marl Prairie/Slough Gradient: Vegetation Composition along the Gradient and Decadal Vegetation Change Pattern in Shark Slough

Summary

In the southern Everglades, vegetation in both the marl prairie and ridge and slough landscapes is sensitive to large-scale restoration activities associated with the Comprehensive Everglades Restoration Plan (CERP) authorized by the Water Resources Development Act (WRDA) 2000 to restore the south Florida ecosystem. More specifically, changes in hydrologic regimes at both local and landscape scales are likely to affect vegetation composition along marl prairie-slough gradient resulting in a shift in boundary between plant communities in these landscapes. To strengthen our ability to assess how vegetation would respond to changes in underlying ecosystem drivers along the gradient, an improved understanding of reference conditions of plant community structure and function, and their responses to major stressors is important. In this regard, a study of vegetation structure and composition in relation to physical and biological processes along the marl prairie-slough gradient was initiated in 2005, and has continued through 2012 with funding from US Army Corps of Engineers (USACOE) (Cooperative Agreement # W912HZ-09-2-0018 Modification No.: P00002). This study addresses the hypothesis with respect to RECOVER-MAP monitoring item 3.1.3.5 – "Marl Prairie/Slough Gradients; patterns and trends in Shark Slough marshes and associated marl prairies".

The study design includes field sampling along five transects, namely MAP transects M1-M5, with the total length of 86.6 km. The Shark Slough portions of four MAP transects (M1-M4) overlap with the Shark Slough study transects that were established and sampled in 1998-2000, with funding from the Department of Interior's Critical Ecosystems Study Initiative (CESI). In 2012, field work was carried out on three of five transects. In the spring season, the sites on the marl prairie portions of Transects M1 and M2 were sampled, whereas in the wet season, the Shark Slough portion of Transect M3 was sampled. Data analysis focused on the characterization of vegetation composition in relation to hydrology and soil characteristics along the entire transects, and an assessment of temporal changes in vegetation composition on the Shark Slough portion of transects between 1999 and 2012. We first summarized vegetation data using nonmetric multidimensional scaling (NMDS) ordination and examined the vegetation:environment relationship by fitting environmental vectors in ordination space. To assess vegetation change at the Shark Slough sites between 1999 and 2012, we used trajectory analysis and examined the time trajectory of each site along the vector representing the hydrologic gradient.

Species composition on the transects representing the marl prairie-slough gradient was strongly influenced by hydrology at the scale of the entire study area. However, in both marl prairies and Shark Slough portions of the transects, within-landscape variation in vegetation response was also noticeable, suggesting that both local and regional scale hydrologic regimes are important in determining spatio-temporal variation in species composition. In concurrence with the overall trend in hydrologic regimes that characterized the period 1999-2012, many sites in the Shark Slough portion of the transects showed a shift towards drier vegetation. However, the direction and rate of such a shift in vegetation composition varied in space and time. While the shift towards dry vegetation on all four transects was the maximum between 1999 and 2007, the vegetation change pattern thereafter varied among transects. During 2007-2012, the drying trend

decreased from north (Transect M1) to south (Transect M4), i.e., Transect M1 had the highest percentage of sites showing a significant trajectory towards a drier condition over the period, while some portions of Transect 4 exhibited a significant change toward wetter vegetation. In general, species richness was highest on the driest sites, but on the wettest (slough) sites, the 13 year trend toward drier vegetation had little effect on species richness. In summary, hydrologic conditions had a strong influence on vegetation composition along the marl prairie-slough gradient, but vegetation response was not uniform in extent along the marsh gradient. Thus, monitoring of vegetation solely at the transition zones between marl prairie and slough landscapes may not entirely reflect changes within each zone.

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General Background

Established to track the ecological effects of Everglades restoration, the Monitoring and Assessment Program (MAP) provides the data and analytical support necessary to implement adaptive management. In the Everglades, marsh vegetation is sensitive to large-scale restoration activities associated with the Comprehensive Everglades Restoration Plan (CERP) authorized by the Water Resources Development Act (WRDA) of 2000. More specifically, changes in hydrologic regimes at both local and landscape scales are likely to affect vegetation composition especially at the marl prairie-slough ecotone, resulting in a shift in boundary between plant communities in this area. In order to track these dynamics, Florida International University (Dr Michael Ross, Project Leader) has undertaken a study of vegetation structure and composition in relation to physical and biological processes along the marl prairie-slough gradient.

Vegetation monitoring transects in the Shark Slough basin, funded by US Army Corps of Engineers (USACOE) under RECOVER-MAP, capture the full range of marl prairie and slough plant communities, and address Performance Measure (PM): GE-15 (Landscape Pattern – Marl Prairie/Slough gradient), by "... detecting spatio-temporal change in vegetation structure and composition in response to natural and restoration-induced hydrologic changes...". Monitoring of vegetation along the marl prairie/slough gradients addresses a working hypothesis that 'Spatial patterning and topographic relief of ridges and sloughs are directly related to the volume, timing and distribution of sheet flow and related water depth patterns', identified in the hypothesis cluster "Landscape Patterns of Ridge and Slough Peatlands and Adjacent Marl Prairies in Relation to Sheet Flow, Water Depth Patterns and Eutrophication" (RECOVER 2009). The study also addresses the hypothesis that resumption of historical flow and related patterns of hydroperiod, water depth, and fire with the implementation of CERP will cause a noticeable change in plant community composition and structure in the ecotonal zone between sloughs and prairies.

The third sampling cycle of the ongoing study will be completed in spring 2014. Completion will allow a comprehensive assessment of temporal change in both the ridge and slough and marl prairie landscapes. This year's annual report summarizes the vegetation:environment relationship along the whole extent of gradient, and vegetation change over the last 12 years in the Shark Slough portion of the gradient, where sites were first sampled in 1998-2000, with funding from DOI's Critical Ecosystems Study Initiative (CESI). These sites have now been resampled two to three times between 2005 and 2012.

Marl Prairie/Slough Gradient: Vegetation Composition along the Gradient and Decadal Vegetation Change Pattern in Shark Slough

1. Introduction

Plant communities arranged along environmental gradients are manifestations of ecosystem functional processes associated with underlying physico-chemical drivers that vary on both spatial and temporal scales. Along such gradients, different sets of key ecosystem processes operating at distinct spatial scales, along with a characteristic distribution of available resources, create identifiable plant communities separated by transition zones. Depending on the level of spatio-temporal variation in underlying drivers, the transition between two adjacent communities may be abrupt or gradual (Walker et al. 2003; Henneberg et al. 2005; Boughton et al. 2006). In general, the position and bio-physical attributes of a transition zone, as well as its persistence over time, depend on changes in underlying drivers, their effects on structure and function of the adjacent communities, and feedbacks between community and environment. Hence, determining the responses to spatio-temporal changes in key environmental drivers of plant assemblages along gradients, and the boundaries between them, is important for conservation and ecosystem restoration.

In the Southern Everglades, the landscape in both Shark River and Taylor Slough basins includes long hydroperiod sloughs, flanked by short hydroperiod marl prairies. Particularly in the Shark Slough basin, vegetation structure and composition change gradually along an elevation and water depth gradient from short-hydroperiod marl prairies to ridge and slough, which are characteristic features of the landscape of central Shark River Slough (Olmsted and Loope 1984; Olmsted and Armentano 1997; Ross et al. 2003). In the past century, changes in the amount and flow patterns of water, resulting from the construction and operation of a series of canals, levees and water structures (Light and Dineen 1994, McVoy et al. 2011), have altered the proportions of prairie and slough vegetation in the region. Furthermore, changes in water management associated with ongoing Comprehensive Everglades Restoration Plan (CERP 2000) are likely to affect vegetation composition in the transition zone between these ecosystems, resulting in a shift in the boundary between prairie and slough. It is therefore important to understand how restoration impacts the dynamics of prairie and slough landscapes and the boundaries therein. This study examines the changes in vegetation along the marl prairie-slough (MP-S) gradient extending across Shark River Slough and into the edges of the marl prairie to the east and west.

Hydrology is one of the major drivers of species differences between marl prairie and ridge and slough landscapes of the Everglades. Hence, alterations in hydrologic conditions usually cause a shift in vegetation structure and composition within each landscape; extreme changes can lead to even dominance of hydric vegetation in marl prairie or various levels of degradation of landforms in the ridge and slough landscape. Historically, such changes in hydrologic conditions were mainly driven by annual or decadal variation in the precipitation. However, in recent years, hydrologic modifications through the operations of water structures have dramatically impacted vegetation composition in both marl prairies and Shark Slough landscapes (McVoy et al. 2011). Since the vegetation communities along the gradient are sensitive to hydrologic changes, prolonged and extreme dry or wet events may also affect the boundary between these two communities. As described for floodplains exposed to prolonged flooding (e.g., Thomaz et al.

2007), ecological processes in marl prairie and adjacent lower elevation areas may tend to be alike, resulting in an increase in similarity between plant communities. For instance, continued flooding for 3-4 years resulted in an increase in abundance of sawgrass and other hydric species in the marl prairies west of Shark River Slough (Nott et al. 1998) and in Taylor Slough basin (Armentano et al. 2006; Sah et al. 2013). Prolonged flooding of the marl prairies may also enhance peat deposition, resulting in a regime shift in vegetation community. McVoy et al. (2011) pointed out that during the pre-drainage era, large portions of the present marl prairies were covered by a shallow layer of peat that supported tall and dense sawgrass, similar to that on the ridges in the interior peatlands. Indeed, the combination of prolonged dry conditions and subsequent consumption of the shallow organic soil present over the marls in fire seem to have resulted in a large portions of the present rockland habitat (Davis 1943; Robertson 1953), and has been cited as the cause of the expansion of muhly grassdominated vegetation in rockland marl prairies (Werner 1975; Olmsted et al. 1980). Moreover, frequent and prolonged drying of ridge and slough landscape may cause the plant communities therein to follow different trajectories, thus affecting the boundaries between communities within the landscape, as well as along the boundary between Shark River Slough and adjacent marl prairies.

In 2005, we initiated a long-term study of vegetation dynamics in relation to changes in underlying environmental drivers, especially hydrology, along the MP-S gradient. The broader goal of the study is to assess the impact of Everglades restoration activities on plant communities along the gradient, and to detect any shift in position and attributes of boundaries between those communities. The study is conducted on five transects that extend across Shark River Slough into adjacent marl prairies. Shark Slough portions of the transects overlap transects that were established and sampled under different sponsorship in 1998-2000, providing the prospect to assess long-term temporal change in vegetation in those areas. The climatological records and hydrologic data from the Shark Slough region suggest that water levels during most of the last decade of the $20th$ century were well above the 30-year average. In contrast, the annual mean water level was relatively low during last 12 years (2001-2012) (**Figure 1**). Such a difference in water conditions has provided an opportunity to assess the response of vegetation to drier conditions between 1999 and 2012. In this study, our specific objectives were, i) to characterize recent vegetation composition along the marl prairie-slough gradient, and ii) to assess changes in vegetation in the Shark Slough portion of the transects over a thirteen-year period (1999-2012). Using a suite of multivariate techniques, including trajectory analysis (Minchin et al. 2005), we characterized vegetation composition along the gradient, and examined the direction and rate of shift in Shark Slough vegetation over time by quantifying the displacement of sites in relation to the hydrologic gradient in ordination space. We hypothesized that variation in vegetation composition along MP-S gradient is mainly driven by hydrology, i.e. duration and depth of flooding. We also hypothesized that Shark Slough vegetation follows the temporal trend in hydrologic regimes, and over the last thirteen years has changed in species composition toward assemblages more indicative of relatively dry conditions.

2. Methods

2.1 Study Area

The study area is located within Everglades National Park (ENP), and comprises a diverse landscape including Shark River Slough, adjacent marl prairies, and a section of coastal zone in the southeastern corner of Shark Slough (**Figure 2**). Shark Slough, the main path of the surface water drainage in ENP, is centrally located and is severely impacted by alterations in surface water flow. The construction of US Highway 41 together with the construction and operations of a network of canals and levees resulted in compartmentalization of the central Everglades north of the highway and reduction in the volume of surface water flow within the Park (Light and Dineen 1994). During the 1980s and 1990s, the goal of increasing water flow within the park was achieved by implementing several modifications in water management operations. However, a consistent pattern throughout the period was diversion of water towards the western part of the slough, i.e. away from its primary flow-way through Northeast Shark Slough (Light and Dineen 1994; McVoy et al. 2011).

Flanking both sides of Shark Slough are the elevated, short-hydroperiod marl prairies, which are characterized by thin calcitic marl soils with frequent exposures of limestone bedrock, and species-rich plant communities consisting of grasses and sedges (Olmstead and Loope 1984). Soils in the marl prairie west of Shark Slough are higher in quartz sand than those in the eastern prairies. In recent decades, the eastern marl prairies have experienced shortened hydroperiod and wet-season water-level reversals (Van Lent et al. 1999), whereas the western marl prairies have been impacted by varying water management strategies that included regulated water deliveries through the S12 structures along US 41, resulting in extended hydroperiod and drying pattern reversals (Kotun et al. 2009). Since 2000, changes have been made in water management strategies to reverse the damage done to the marl prairies on both sides of the slough. These changes in strategy included the construction and operations of a series of water retention ponds and strict regulation of water deliveries through the S12s during the dry season (Kotun et al. 2009).

2.2 Data acquisition

The study design includes field sampling along five transects, specifically MAP Transects M1 to M5, with a total length of 86.6 km. Three transects, M1, M3 and M4 extend across the Shark Slough to adjacent short-hydroperiod marl prairie habitat (**Figure 2**). M1, located in Northeastern Shark Slough (NESS), extends to the marl prairie only to the east of the slough. M3 and M4 extend to prairie on both sides of the slough. M2 covers an area restricted to Shark Slough, extending on both sides of L-67S canal. M5 covers an area in the coastal ecotone between fresh to brackish water ecosystems in the southeastern corner of Shark Slough, extending to the east into fresh water marl prairies located on both sides of the main Park road. Moreover, 29.3 km of Transects M1, M2, M3 and M4 are in slough, and overlap with Shark Slough Transects, 1, 2, 3 and 5, respectively, that were established and sampled between 1998-2000 (hereafter identified as SS transects sampled in 1999), with funding from the DOI Critical Ecosystems Study Initiative program (CESI) (Ross et al. 2001; Ross et al. 2003). The 1999 sampling event at those sites is considered as the initial sampling (E0) in the analysis reported here.

The vegetation study on the MAP transects began in the Fall 2005, and the transects were sampled every three years thereafter. On these transects, vegetation structure and composition were quantitatively studied in a set of plots at discontinuous, moderately-spaced (200-500 m) locations, whereas a qualitative but spatially fine scale characterization of plant community types was made at 5-m intervals. **Table 1** summarizes the years and numbers of sites sampled on the transects. The slough portion of the MAP transects was sampled in the wet season (July to November), accessing the sites by airboat or helicopter, depending on the Wilderness designation of the sites and the water level in the field. Marl prairie portions of the transects were sampled in the dry season (Dec. to May) and were accessed by helicopter for drop off and pickup, and on foot for sampling.

Transect	Sampling Event	Sites Sampled						
			Prairie sites	Slough sites				
		Year	Number of Sites	Year	Number of Sites			
	E1	2006	11	2005	20			
M1	E2	2009	11	2008	20			
	E ₃	2012	11	2011	20			
	E1			2005	25			
M ₂	E2			2008	26			
	E ₃			2011	25			
	E1	2007	72	2006	37			
M ₃	E2	2010	72	2009	37			
	E ₃			2012	37			
M4	E1	2008	32	2007	55			
	E2	2011	32	2010	55			
M ₅	E1	2008	31					
	E2	2011	31					

Table 1: Sites sampled on five MAP transects M1-M5 between 2005 and 2012.

2.2.1 Vegetation sampling

Vegetation was sampled in a nested-plot design that allowed for efficient sampling of the range of plant growth forms (herbs, shrubs and trees) present along the transects. On each of five transects, the vegetation sampling plots were established at 200 to 500 m intervals. In the marl prairie section of the transects, the plots were established at 300 m intervals, and in the Shark Slough portion of the transects, the plot density varied between 2 to 4 plots per km (250-500 meter intervals). Higher intensity sampling occurred in areas accessible by airboat, and was based on the contention that increased sampling intensity would enable us to make a more meaningful comparison of current vegetation with that present on the same transects in 1999 (Ross et al. 2001; Ross et al. 2003). In addition, eight additional plots, one each on M1 and M2, two on M3, and four on M4 were sampled, increasing density locally up to 6 plots per km. These additional sites had been sampled in 2000, when they exhibited the signature of sawgrass dieback that had occurred prior to sampling (Ross et al. 2001).

At each sampling site, a PVC tube marked the SE corner of a 10 x 10 m tree plot. Nested within each tree plot, a 5 \times 5 m herb/shrub plot was laid out, leaving a 1-m buffer strip along the southern and eastern border of the tree plot. In the 10 x 10 m tree plots, we measured the DBH and crown length and width of any woody individual \geq 5 cm DBH, then calculated species cover assuming horizontally-flattened elliptical crown form. Within each 5 x 5 m herb/shrub plot, we estimated the cover class of each species of shrub (woody stems $>1m$ height and $<$ 5cm DBH) and woody vines, using the following categories: $< 1\%$, 1-4%, 4-16%, 16-33%, 33-66%, and $> 66\%$. We estimated the cover % of herb layer species (all herbs, and woody plants $\langle 1 \text{m} \rangle$ height) in five $1-m^2$ subplots located at the four corners (NE, NW, SE and SW) and the center (CN) of the 5 x 5 m plot. Species present in the 5 x 5 m plot but not found in any of the 1 $m²$ subplots was assigned a mean cover of 0.01%. In addition, a suite of structural parameters was recorded in a 0.25 m² quadrat in the SW corner of each of the 5 subplots. Structural measurements included the following attributes: 1) The height and species of the tallest plant in the plot; 2) Canopy height, i.e., the tallest vegetation present within a cylinder of \sim 5 cm width, measured at 4 points in each 0.25 m^2 quadrat; 3) Total vegetative cover, in %, and 4) live vegetation percent cover, expressed as a % of total cover.

2.2.2 Soil and water depth measurements

Soil depth was measured in each sub-plot by driving a 1-cm diameter probe to the bedrock. Soil depth measurements were taken only during the first cycle of sampling (2005-2008). However, in the slough portion of MAP transects M1, M2 and M4 that overlap with the SS-transects, soil depth measurements were not measured during 2005-2008 sampling, as the soil depth at those sites were inferred from measurements taken during the 1998-2000 study.

On each visit, water depth was measured at the PVC, the marker of the plot, and in the center of five vegetation sub-plots in a 5 x 5 m plot. Since in the marl prairie section, vegetation was sampled in the dry season when there was no standing water, water depth measurement was a problem. At those sites, we measured water depth once in 2008. In addition, a Promark 3 GPS unit was also used to measure elevation on marl prairie sites, which helped to obtain elevations for sites with no standing water.

2.2.3 5-m vegetative community observations

Slough and marl prairie sections of transects were assigned at 5m intervals to vegetative community types that have been shown to be indicative of hydrological regime (Ross et al. 2006). In the sawgrass marsh vegetation type, we further distinguished three classes: tall sawgrass, sawgrass, and sparse sawgrass. The short hydroperiod marl prairie portions were accessed by foot, but the Slough portions required airboat access. Vegetation community data were used for temporal comparisons of plant community change in relation to similar data collected along the same transects in 1998-2000. The results from the comparison of 5-m interval data gathered during cycle one (2005-2008) with 1999 data have been described in part in previous annual reports (Ross et al. 2005, Ruiz et al. 2006; Kline et al. 2007, 2009). A further comprehensive analysis of these data for all five transects is yet to be conducted and is not included in this report.

2.3 Data Analysis

Hydroperiod and daily water depth estimation

We used field water depth-derived elevation and EDEN (Everglades Depth Estimation Network, [http://sofia.usgs.gov/eden\)](http://sofia.usgs.gov/eden) water surface elevation data to estimate the hydrologic conditions at each sampling site. We calculated the ground elevation of each plot using mean water depth for the plot and EDEN estimates of water surface elevation at that point (center of the plot) for the same sampling date. Daily water levels for each plot were estimated based on ground elevation and the time series data of water surface elevation extracted from EDEN database. We then calculated hydroperiod, the number of days per year when the location had water depth >0cm, and mean annual water depth for each plot. Previous studies have found that prairie and marsh vegetation composition are well-predicted by the previous 3-5 years of hydrologic conditions (Armentano et al. 2006; Ross et al. 2006; Zweig and Kitchens 2009). In this study, we averaged hydroperiod and mean annual water depth for the four water years (May $1st$ – April 30th) prior to each sampling event to examine the relationships between hydrologic parameters and vegetation composition.

Vegetation classification and ordination

We summarized species data by calculating the importance value (IV) of each species present in herb and shrub layers in each plot. We calculated species' importance value as: $IV = (relative$ cover + relative frequency)/2. For calculating IV of the species that did not occur in any of 5 subplots but occurred in 5 x 5 m² plot, a frequency of 4% was assigned. The assumption was that the species would have occurred in at least one subplot, had all $25 \frac{1 \times 1 \text{ m}^2}{25}$ subplots within a plot sampled. Preliminary examination of the data suggested that four sites, one on M2 and three on M3 were forested, with species assemblages very different from all other sites. Outlier analysis also distinguished these sites on the basis of average distance (Bray-Curtis) from other sites (their average distance was more than 2 standard deviations from the mean). Another two sites had <10% total vegetation cover. We eliminated these six sites and classified the remaining sites. An hierarchical agglomerative cluster analysis was used to define vegetation types at all sites that were surveyed along the five transects between 2005 and 2008. We used Bray-Curtis dissimilarity as our distance measure, and the flexible beta method to calculate relatedness among groups and/or individual sites (McCune and Grace 2002). The SIMPER (Similarity Percentage) analysis included in the PRIMER Software (Clark and Warwick 2001; Clark and Gorley 2006) was used to identify which species contribute most to within group similarities.

We used non-metric multidimensional scaling (NMDS) ordination to visualize relationships among sites based on their similarities in vegetation composition. We performed NMDS on a matrix of Bray-Curtis dissimilarities among sampling units, with species' importance value first standardized by species' maximum. We then examined the relationship between vegetation composition and environment along a reference vector representing hydrologic gradient. In NMDS, the community characteristics and environmental vectors, including one for mean annual water depth, were defined through a vector fitting technique in DECODA (Kantvilas and Minchin 1989; Minchin 1998). In the vector-fitting method, a vector is defined in the direction through the ordination that produces the maximum correlation between the measured community and environmental attribute and the scores of the sampling units. The statistical significance of such correlations was tested using a Monte-Carlo permutation test with 10,000 random permutations (Faith and Norris 1989).

Trajectory analysis

At the slough sites on Transects M1-M4, change in vegetation composition between 1999 and 2012 was analyzed using trajectory analysis (Minchin et al. 2005), an ordination-based technique designed to test hypotheses about rates and directions of community change. In this study, the direction of vegetation change was examined from the first sampling of SS sites in 1999-2000 through 2012. In the NMDS ordination performed for trajectory analysis, we included vegetation data for prairie sites collected during the first sampling cycle (2005-2008), and for SS sites the data collected between 1999 and 2012. Prairies sites were included to cover the full range of hydrologic conditions on the transects. The environmental vectors were defined in ordination space as described above.

To quantify the degree and rate of change in vegetation composition along the reference vector, two statistics, delta (∆) and slope were calculated (Minchin et al. 2005). Delta measures the total amount of change in the target direction. It was calculated as the difference between projected score at the final time step and the mean score of pre-intervention time steps. Slope measures the mean rate of change in community composition along the target vector. The statistical significance of both delta (Δ) and slope was tested using Monte Carlo simulations with 10,000 permutations of the cover scores of species among sampling times within each trajectory, with the NMDS ordination and calculation of trajectory statistics repeated on each permuted data matrix.

3. Results

3.1 Marl Prairie-Slough gradient

3.1.1 Physical environments: Hydrology and Soil depth

Hydrology: Marl prairie-slough gradient transects represented a wide range of hydrologic conditions present in the prairies and marshes in Everglades National Park. **Table 2** summarizes long-term hydroperiod and mean annual water depth averaged over 21 years (1991-2011), the period for which the daily EDEN water surface elevation data were available.

Transect M3, the longest transect (35.8 km) extending from marl prairie near the eastern border of the ENP to the west of Shark Slough, had the widest range of hydrologic conditions (**Figure 3**). On this transect, mean hydroperiod ranged from 83 to 364 days, and mean annual water depth from -25.6 to 54.2 cm (**Table 2**). The variation in hydroperiod (Coefficient of variation, CV = 0.243) on M3 was greatest among all transects. Transect M2, which has the sites only within Shark Slough landscape, had the longest mean hydroperiod $(347 \pm 17 \text{ days})$ with minimum variation (CV = 0.05). In contrast, Transect M5 had the sites that were relatively dry. This transect had the shortest mean hydroperiod (255 \pm 27 days) and the lowest mean annual water depth (4.1 \pm 5.7 cm). Transects M1 and M4 both had short-hydroperiod prairie as well as longhydroperiod slough sites. Though only a small portion of Transect M1 (7 sites in 3.5 km) was

within the MP landscape. M1 and M4 had moderate variation (CV) in hydrologic conditions (**Table 2**).

Table 2: Summary of hydrologic conditions, hydroperiod (days) and annual water depth (cm), averaged over 21 years (1991-2011) at sites on five marl prairie-slough gradient transects in Everglades National Park. * = Hydrologic parameters for two sites on M4 and 6 sites on M5 were not calculated.

N Transect		Hydroperiod (days)						Annual Water Depth (cm)				
		Mean	SD	Min	Max	CV	Mean	SD	Min	Max	CV	
M1	32	307	39	202	347	0.125	22.7	11.4	-3.3	37.9	0.502	
M ₂	26	342	17	288	359	0.050	34.4	8.6	14.2	49.8	0.249	
M ₃	109	269	65	83	364	0.243	13.0	17.5	-25.6	54.2	1.338	
M4	$85*$	316	46	181	363	0.146	26.1	13.4	-3.6	46.3	0.515	
M ₅	$25*$	255	27	208	303	0.104	4.1	5.7	-4.7	15.4	1.410	

Soil depth: Soil depth varied greatly among and within MAP transects. Mean (\pm SD) soil depth was lower on M3 and M5 (30.8 \pm 22.1 and 31.0 \pm 11.3 cm, respectively) than on other transects. However, these two transects differed notably in within-transect variability (**Table 3**). M3 had much greater variation in soil depth than M5, which had the lowest variation ($CV = 0.364$) among all transects. Mean soil depth was highest on Transect M2 (74.9 \pm 50.6 cm), primarily because the transect does not include any sites in the marl prairie landscape, where soils are relatively shallow. On this transect, however, soil depth varied greatly $(CV = 0.675)$, and the soils were deeper in the central portion than the distal portions of the transect (**Figure 4**). Transects M1 and M4 also had great variation in soil depth $(CV = 0.617$ and 0.636, respectively), ranging from 0.4 cm to 150 cm (**Table 3; Figure 4**).

Table 3: Summary of soil depth measured on five marl prairie-slough gradient transects in southern Everglades.

Transect	N	Mean	SD	Min	Max	CV
M1	32	37.8	23.3	1.4	85.4	0.617
$\bf M2$	26	74.9	50.6	9.8	170.1	0.675
$\mathbf{M}3$	109	30.8	22.1	4.2	105.1	0.717
$\mathbf{M}4$	87	49.1	31.2	0.4	150.0	0.636
$\overline{\mathbf{M}}$ 5	31	31.0	11.3	10.7	53.2	0.364

3.1.2 Vegetation Composition

Plant communities arranged along the MP-S gradient varied in species composition. The single most dominant species was sawgrass (*Cladium mariscus* ssp. *jamaicense*). Within a data set that included the first-cycle (2005-2008) sampling of a full set of sites on all five transects, 14 vegetation types were identified through the classification procedure (**Appendix 1**). The distinctive composition of 12 vegetation types is evident in **Table 4**, which summarizes the mean importance value (IV) of the 25 plant species that were identified in the SIMPER analysis as characteristic (cumulative contribution of \geq 95% to the group similarity) of one or more vegetation assemblages. These characteristic species represented a range of hydrologic conditions along which the vegetation types were differentiated, as evident in the increasing importance of species, arranged by their optimum water depth, from the upper-left to lower-right side of the table. Species composition of three vegetation types, *Schizachyrium* WP, *Muhlenbergia* WP and *Cladium* WP overlapped somewhat. However, they were distinguished based on the differences in species that had highest relative dominance in each group. Two vegetation types, *Schoenus* WP and *Paspalum-Cladium* WP, each of which had only one site, were not included in the SIMPER analysis or in Table 4.

Table 4; Mean importance value (IV) of species identified as the characteristic species (cumulative contribution to \geq 95% to mean group similarity) within each vegetation types. The vegetation types with at least two sites are included. Species (except *Rhizophora mangle*) are sorted by their optimum water depth and vegetation types (except RHIMAN) by mean annual water depth for four years prior to vegetation sampling. SCWP =*Schizachyrim* Wet Prairie (WP); MWP = *Muhlenbergia* WP; CWP = *Cladium* WP; RCM = *Rhynchospora-Cladium* Marsh: CMM = *Cladium* Mixed Marsh; CM = *Cladium* Marsh; CEM = *Cladium-Eleocharis* Marsh; ECM = *Eleocharis-Cladium* Marsh, EM = *Eleocharis* Marsh; TCM = *Typha-Cladium* Marsh*; Nymphaea* Open Marsh; RHIMAN = Red mangrove. The IV values of species identified as the characteristic species of the vegetation type in SIMPER analysis are in bold.

The spatial distribution of vegetation types along transects provides a view of the status of vegetation composition along the MP-S gradient. While Marl Wet Prairie (WP) types are dominant within marl prairie landscape, long-hydroperiod Marsh vegetation types were common in Shark Slough portion of transects. However, some sites with relatively wet vegetation types were also present throughout the marl prairie portion of the transects (**Figure 5; Appendix 1**). The most dominant vegetation type in prairie and slough portions of transects were *Cladium* Wet Prairie and *Cladium* Marsh, respectively. Spikerush Marsh was most dominant on Transect M4 (**Figure 5**). In the transition zones of Transects M1, M3 and M4, the vegetation composition was of mixed types, i.e. species composition at those sites were dominated by sawgrass, but also included a number of species that were characteristic in both WP and Marsh vegetation groups. Red mangroves were present at sites in the western portion of Transect 5, which occupies the transition between brackish and fresh water vegetation.

Variation in species composition in relation to environmental gradients was effectively summarized by a NMDS ordination $(3-D)$: stress = 0.15) that was rotated to align with the hydrologic gradient (**Figure 6**). The first axis, which was aligned to parallel the fitted vector of mean annual water depth in rotated ordination space, separates the SS sites from most of the MP sites, suggesting that species composition along the gradient is influenced by hydrology (hydroperiod - r = 0.88, p < 0.001; mean annual water depth r = 0.87, p < 0.001) (**Table 5**). However, the overlap between prairie and slough sites in ordination space is noticeable. Some sites within the MP landscape had species composition similar to that at long-hydroperiod SS sites, as previously noted for the spatial distribution of vegetation types along transects (**Figure 5**). The distribution of species along the gradient is shown in **Figure 7**. The characteristic species of short hydroperiod marl prairie sites are confined to the left side in the ordination space. These include muhly grass (*Muhlenbergia capillaris* ssp. *filipes*), little bluestem (*Schizachyrium rhizomatum*), back-top sedge (*Schoenus nigricans*), spadeleaf (*Centella asiatica*)*,* rosy camphorweed (*Pluchea rosea*), among others. The characteristic species of long hydroperiod sites, in both MP and SS landscapes, included spikerush (*Eleocharis* sp.), bladderwort (*Utricularia* sp.), arrowhead (*Sagittaria lancifolia*), maidencane (*Panicum hemitomon*), pickerelweed (*Pontederia cordata*), and others (**Figure 7**). Sawgrass (*Cladium*), which has the most ubiquitous distribution in Everglades due to its wide range of hydrologic tolerance, occupied an intermediate position in the ordination.

The NMDS ordination also revealed within landscape variation in species composition. In both MP and SS landscapes, the species composition varied among sites along the second axis that was aligned to soil depth vector in rotated ordination space (**Figure 6**). When considering only MP landscapes from both sides of the Shark Slough, species composition differed between eastern and western sites. This difference was significant (ANOSIM: $R = 0.475$, $p = 0.01$), particularly on Transect M3. The location (UTM Easting coordinate) of MP sites on this transect was also strongly correlated ($r = 0.66$, $p < 0.01$) with the second axis (**Figure 8**), suggesting that regional differences in species composition are driven by differences in underlying environmental drivers between the two regions. The vegetation east of Shark Slough was mostly dominated by muhly grass and sawgrass, whereas muhly grass had very low cover west of the Shark Slough. On the west side of Shark Slough, *S. rhizomatum*, *S. nigricans* and *Paspalum monostachyum* were more common than muhly. The vegetation composition within the SS landscape also varied from relatively open vegetation dominated by spikerush and bladderworts to denser, sawgrass vegetation to mixed vegetation with some woody components. Across both landscapes, sawgrass cover was strongly correlated ($r = 0.74$, $p < 0.001$) with the second axis that was also aligned with soil depth.

Species richness: Species richness ranged between 1 and 27 species/plot, and differed significantly (ANOVA: F4,280 = 9.8, p < 0.001) among transects (**Table 6**). Transects M1 and M2 that included all or mostly SS sites had significantly lower species richness than other transects. M3 had the highest mean species richness (11.7 species/plot). Across all transects, species richness was negatively correlated ($r = -0.70$; p <0.001) with hydroperiod. On each of three transects that included substantial areas of both marl prairie and slough, short hydroperiod MP sites had higher number of species than SS sites (**Figure 9**).

Table 6: Plant species richness on five marl prairie-slough gradient transects in southern Everglades.

3.2 Decadal Vegetation Change Pattern in Shark Slough

Shark River Slough hydrology (1999-2012)

In concurrence with a general trend in hydrologic conditions during the late 1990s and 2000s, the mean hydroperiod and annual water depth averaged over four years prior to vegetation sampling in Shark Slough showed a decreasing trend (**Figure 10**). In the late 1990s, i.e. before the 1999/2000 vegetation sampling, mean hydroperiod on all four transects were >360 days, and mean annual water depths were >40 cm at all transects except Transect M1. During that period, sites on Transect M1 were drier than sites on the other transects. During each of the subsequent sampling events, mean hydroperiod and annual water depth were lower than before 1999. The

differences in mean hydroperiod and water depth between two successive sampling periods was significant (Paired t-Test) on almost all transects. In the late 2000s, i.e. before 2011-2012, hydroperiod was 30-60 days shorter and mean water depth 17-18 cm less than before the 1999 sampling. The drying trend observed at sites in Shark Slough was not uniform through the region. The decrease in water level on Transects M2 and M4 was less than on M1 and M3.

Shark River Slough vegetation change (1999-2012)

Between 1999 and 2012, marsh vegetation showed a shift in relative abundance of species, and the trend was somewhat consistent with the increasing dryness in Shark Slough during the period. In general, trajectory analysis results revealed that in the slough portion of the four MAP transects (M1-M4), sampled repeatedly at 3-6 year intervals between 1999 and 2012, species composition primarily shifted towards drier vegetation types (**Figures 11-14; Appendix 2**). However, the percent of sites that showed a drying trend varied among four transects. The percent of sites with a significant shift towards dry vegetation was highest (56.6%) on M1, located in NESS (**Table 7**). In the far south, on M4 that runs across Shark Slough and was sampled only three times (**Table 1**), the percent of sites showing a shift towards dry vegetation (22.9%) was much less than on the other three transects. On this transect, many sites even showed a wetting trend (**Figure 14**). On M2 and M3, the percent of sites with significant time trajectories indicating a shift towards dry vegetation were 39% and 44%, respectively.

On the Shark Slough portion of the transects, direction and rate of vegetation change varied at both temporal and spatial scale. On all four transects, the shift towards drier vegetation was the maximum between first two sampling events, E0 and E1. However, during the following sampling periods, the vegetation change pattern was spatially differentiated. Between E1 and E2, the shift towards dry vegetation continued on only two transects, M1 and M3 (**Figures 11, 13**). In contrast, on M2 and M4, sites showed a slight shift towards wet vegetation during that period (**Figures 12, 14**). A shift in vegetation composition towards a relatively wet type was also observed at many sites on M1 and M3 during the last sampling period, between 2008 and 2012.

Table 7: Proportion of Shark Slough (SS) sites (%) on four transects showing a progressive shift in vegetation composition indicative of increasingly wet or dry conditions. The number in parenthesis is the percent of sites at which the shift was statistically significant $(p < 0.1)$ in trajectory analysis.

The sites showing a significant shift in vegetation composition along hydrology vector in ordination spaces were not uniformly distributed on individual transects (**Figure 15**). For instance, while a drying trend was observed at most of sites on M2 and M3, the shift in vegetation composition was significant mostly in the western portion of the transects. In contrast, eastern sites on Transect M4 showed a shift towards dry vegetation, but many sites on the western portion of the transect showed a shift towards wet vegetation.

The change in vegetation composition observed over thirteen years on four transects also resulted in changes in species richness. Since all transects were not sampled four times, a pair- wise t-test was performed for individual transects rather than a repeated measures analysis of variance. While mean species richness was significantly higher on Transects M3 and M4 in later sampling events than in 1999, the mean richness on M2 did not differ among sampling years (**Figure 16**). Contrary to expectation, species richness on Transect M1was significantly lower in the last sampling event (2011) than in the previous three sampling events.

Between 1999 and 2012, total plant cover did not differ among years. However, among the most abundant (Importance Value > 2.0) species, the relative abundance of sawgrass (*C. mariscus* ssp. *jamaicense*) and spikerush (*E. cellulosa*), averaged over all transects, increased significantly after 1999 (**Figure 17**). In contrast, abundance of the bladderworts (*Utricularia* sp.), which are indicator species of relatively wet condition and are commonly found in *Nymphaea odorata*, *E. cellulosa*, and/or *P. hemitomon*-dominated sloughs, significantly decreased in Shark Slough. The mean abundance of two other species, *Bacopa caroliniana* and *P. hemitomon* did not show a significant change over the years. However, several other species, that were locally confined at certain sites on transects, increased in abundance over the years. In general, temporal changes in abundance of species varied among and within transects depending on whether the sites were getting drier or wetter (**Appendix 3**).

4. **Discussion**

Marl prairie-slough gradient

In the southern Everglades, a strong relationship between species composition and hydrologic conditions observed along marl prairie-slough gradient reiterates that hydrology is a primary driver of the ecological processes that define the structure and composition of plant communities. Species composition in the Shark Slough portion of the gradient sharply differs from those at the majority of marl prairies sites. However, within-landscape variation as well as some overlap in species composition between these two distinct landscapes were also evident, suggesting that both local and regional scale hydrologic regimes are important in determining spatial and temporal variation in species composition.

Shark Slough and adjoining marl prairies are hydrologically connected. Vegetation composition and dynamics observed along the Everglades gradient are perhaps most analogous to those occurring in shallow river channels and floodplains. As such, marl prairies are the floodplain in both the Shark River and Taylor Slough basins in the southern Everglades. As in many other river floodplains, variation in plant community structure and composition on the marl prairie portions of the gradient could conceivably be the results of ecological processes linked to the dry and wet phases of the systems described in the flood pulse concept, first proposed for Amazon floodplain by Junk et al. (1989), and applied to other floodplains (Bayley 1995; Benke et al. 2000; Toth and van der Valk 201). In the Shark Slough basin, when surface water recedes into the slough during the dry season, and water level in the prairies drops below the ground, many terrestrial plants grow well in the prairies. Luxuriant growth of long hydroperiod-adapted wetland species is confined to depressions and sinkholes. With the onset of rising water in the slough in the wet season, resulting from natural rainfall and/or water management activities, water gradually spread over the adjoining marl prairies. The dry season terrestrial species die and decompose releasing nutrients into the water, where they are rapidly taken up by growing aquatic species, more so by rehydrating periphyton that are abundant and highly productive in marl prairie habitat (Thomas et al. 2006; Ewe et al. 2006). Variation in vegetation composition observed in this study is probably due to physiological adaptations to these fluctuations in water level by species occupying different positions along the gradient. For instance, the relative proportion of C_4 and C_3 species varies from prairie to slough gradient. While C_4 graminoids, such as muhly grass and bluestem, are dominant in the drier end of the prairies, their proportions decrease toward wetter environments (Sah et al. *manuscript in preparation*). Moreover, floodplain behavior in the marl prairie has changed in the last century, mainly due to anthropogenic interventions, and vegetation patterns of the present day reflect recent hydrologic connections between slough and its floodplain. For instance, in the pre-drainage era, hydrologic differences between Shark Slough covered with deep peat and the marl prairies covered with shallow peat was much less than it is in recent years (McVoy et al. 2011). Past presence of organic soils would imply that surface water flowing through the region as sheet flow covered a larger portion of the marl prairies for more extended periods than in recent decades of acute regional water management activities. As a result, the differences in plant community composition along the gradient are probably now more distinct than during the pre-drainage period.

Regional differences in vegetation composition observed in this study in similar landscapes, e.g. in marl prairies on both sides of the slough, are driven by both topographic differences and the effects of water management. For instance, shortened hydroperiod and increased drought severity that are prevalent on eastern marl prairies (Van Lent et al 1999) have resulted in vegetation dominated by short hydroperiod-adapted species. In contrast, in the mid-1990s, marl prairies west of Shark Slough experienced high water conditions and extended flooding due to water deliveries from the Water Conservation Area north of Tamiami Trail, coupled with high precipitation during the period (Kotun et al. 2009). These high water conditions resulted in sawgrassdominated vegetation in most areas (Nott et al. 1998). Muhly grass-dominated community that was once common in 1980s and early 1990s (Ross et al. 2004) was practically absent during the three-year extensive survey of vegetation in mid 2000s in those areas (Ross et al. 2006). In subsequent years, in concurrence with the restrictions on water deliveries through the S12 structures at Tamiami Trail practiced since 2000, a drying trend was observed in some western marl prairies (Sah et al. 2011). However, the vegetation has not returned to what was present in that region before the mid-1990s, and which currently characterizes the eastern marl prairies. Differences in fire frequency over the 25 year period 1980-2005, with eastern prairies burning much more frequently than western prairies (Ross et al. 2006, Sah et al. 2007), also might have contributed to the differences in vegetation composition observed in this study.

Within individual regions, vegetation composition is affected by small scale variation in major environmental drivers. Topography is very uneven, and depressions and sinkholes are widespread within the marl prairie landscape. Even though the shallow peat layer laid down over marl soils has disappeared from a large portion of marl prairies east and west of Shark Slough, peat is still found in depressions and solution holes occupied by dense sawgrass and occasionally spikerush communities similar to those found in Shark Slough (McVoy et al. 2011). Moreover, marl prairie landscape is traversed by numerous longitudinal shallow drainages that also influence the spatial

continuity of vegetation in the area. The nature and origin of such drainages have not so far been described in detail. In other floodplains, researchers have associated the floodplain geomorphic features to sources of flood water, stage and frequency of floods, and associated fluvial processes (Hupp and Osterkamp 1985; Hupp 2000). In addition to geological processes, the role of regular flood pulses as well as extreme flooding events is also important. In the pre-drainage era, when there was gradual deposition of peat in the main channel of the Everglades, the extent of flooding and duration of water retention on the adjoining floodplains might have progressively increased. In such circumstances, flash floods would have been more likely to cause erosion and gully formation on the floodplains. However, only a focused research effort could ascertain the processes of formation and/or maintenance of those drainages.

Within the Shark Slough portion of the marl-prairie slough gradient, the variations in vegetation composition observed in this study are due to differences in both local and regional processes. In general, the marsh landscape in Shark Slough consists of elevated ridges with tall sawgrassdominated vegetation and sloughs with more open water and/or spikerush dominated vegetation (Ross et al. 2003). In a healthy ridge and slough landscape, a sharp distinction in elevation and hydrologic regimes, represented in their bimodal distribution (Watts et al. 2010), exist between ridge and slough. However, in Shark Slough the ridge and slough landscape might have been degraded by early 20th-century drainage and subsequent water management activities discussed above. Although hydrologic differences among different communities within the landscape still exist, these differences become fuzzy when considered across the region. For instance, Ross et al. (2003) pointed out that while a difference in hydrology existed between tall sawgrass and spikerush communities in the same region, tall sawgrass had a longer hydroperiod in northern Shark Slough than spikerush-dominated vegetation in any other region of the Park. This explains why slough communities were not well separated on NMDS Axis 1 that represented the water depth along marl prairie slough gradient (**Figure 6a**).

The marl prairie portions of the transects had much higher species richness than the sloughs. Local species richness varies along disturbance and environmental stress gradients (Grime 1973; Connell 1978), and the mechanisms involved are often described as competitive exclusion (Grime 1973) and/or facilitation among species (Michalet et al. 2006). Whether it is through competition, positive interactions, or both, the role of spatial heterogeneity in available resources is important, though the relationship between habitat heterogeneity and species richness also depends on the scale considered (Auerbach and Shmida 1987). Marl prairies with high variability in topography and soil characteristics are likely to have high heterogeneity in water and soil nutrient availability, resulting in relatively high species richness. Fire is also known to create habitat heterogeneity in forests as well as grasslands (Collins 1992; Turner et al. 1994). In this study, we have not analyzed the fire data yet. However researchers have reported that fire frequency is relatively high in dry portions of the marl prairies, and thus may have enhanced habitat heterogeneity resulting in higher species richness in prairies than marshes. Moreover, within the relatively wet conditions, highly productive environment with dense canopy of tall sawgrass had low species richness probably due to limitation posed by light resources, whereas the relatively low species richness in thewettest environment dominated by spikerush community could be due to flooding stress that limited the regeneration and growth of many species.

Shark Slough vegetation change (1999-2012)

In the Greater Everglades, the relationship between hydrologic regime and vegetation distribution

is dynamic. In Shark Slough, spatial variation in vegetation composition dynamics observed in this study is not surprising. The reason for such variation probably involves the fact that the water is not evenly distributed in the slough mainly due to spatial differences in water flow from Water Conservation Areas north of the Park. Northeast Shark Slough, a pathway for the historic northeast-southwest flow of water, has been kept relatively dry throughout the 1980s and 1990s (Van Lent et al. 1999). Even though the partial filling of L67S extension to homogenize the water distribution by reconnecting NESS to the rest of Shark Slough was completed during the last decade, the effects of this structure continued in the 2000s. NESS was therefore drier than it was in the mid to late 1990s when the water levels were relatively high throughout the region due to unusually high rainfall, resulting in a shift in vegetation composition on Transect M1 located in northeast Shark Slough. In the Northern Shark Slough (NSS), the region west of the L-67 levee, the drying trend was also obvious, due to both lower precipitation and regulated deliveries through the S12s connecting ENP to the Water Conservation Area. In contrast, in the south where there may be less impact of spatial variation in water delivery, the vegetation change pattern might have reflected natural variation in water regime.

Vegetation dynamics in the ridge and slough landscape, including Shark Slough, is also affected by the events of 'sawgrass die-off', a pronounced, spatially extensive, and episodic decadence. Such areas were observed in mono-dominant stands of sawgrass at several sites in 1999-2000 on Shark Slough transects (Ross et al. 2001). In the present study, we have not thoroughly investigated the cause of sawgrass die-off. However, a mixture of factors, including the reduced fire frequency, nutritional imbalance, fungal infection, a boring larva (*Scirpophaga perstrialis*), and hurricane caused periphyton deposition (Hofstetter and Parson 1975; Wade et al. 1980; Alexander and Cook 1984; Clark et al. 2009) and extreme flooding in the mid-1990s (Olmsted and Armentano 1997) may be involved. In areas of sawgrass die-off, plant succession may start within months (Alexander 1967), but years may pass before full vegetation recovery is achieved. In parts of our study transects where open water sites due to sawgrass die-off prevailed in 1999- 2000, sawgrass was still sparse \langle <50 %) after 10 to 12 years. While these areas of sawgrass dieoff seem to have recovered to some extent, periodic sawgrass die-off events within the ridgeslough landscape have important implications, including the diminished viability of the ridgeslough mosaic through shrinkage of the elevation difference between these two important features (Clark et al. 2009).

In Everglades peatlands, surface microtopography that affects the hydrologic conditions of an area is the result of a balance between soil accretion and degradation. Fire is another important factor affecting surface microtopography. Fires that occur in peat-dominated wetlands, i.e. *peat fires*, may consume a substantial amount of the organic soils, thereby altering the microtopography and ultimately affecting the hydrology and vegetation of the peatland (Loveless 1959; McVoy et al. 2011). In Shark Slough, historical fires have probably affected the distribution of plant communities directly by consuming biomass, and indirectly by destroying upper, dry peat layers, lowering the ground surface, and altering hydrologic regimes. However, the extent to which fires burn peat layers depends on the depth of the water table below the surface and the moisture of the surface peat. Within the study area, the Mustang Corner fire that occurred in May 2008, following almost two years of drought and at the time when water level was 65 cm below the surface (Ruiz et al. 2013), may have burned significant amount of peat on Shark Slough portions of Transect 1. The vegetation at five burned sites on Transect M1, where the mean cover was 66% in 1999, is currently very sparse (cover 17.5%) and comprised mostly of hydric species. A change in hydrologic condition due to fire- induced elevation loss may also have contributed to a change in vegetation at some sites to wetter types after 2008 (**Figure 11**).

An overall increase in sawgrass and spikerush cover in response to relatively dry conditions in last thirteen years in Shark Slough reiterates the phenomenon described for the post-drainage era in the Everglade (Bernhardt and Willard, 2009). Other researchers also have reported an expansion of sawgrass and other emergent species, such as spikerush, in the ridge and slough landscape, primarily due to decreased water levels (Busch et al., 1998; Zweig and Kitchens, 2008 2009, Nungesser 2011) and flow velocities (Larsen et al. 2011). Such expansion may occur within 3-4 years, especially when a minimum water level is maintained in the sloughs beneath the peat surface for three consecutive dry seasons (Zweig and Kitchens 2009). During this study, sites experienced a severe drought in 2001, and again for three years from 2006 to 2009. While the extensive expansion of sawgrass could be a step towards succession toward woody vegetation, especially when it occurs on elevated ground that experiences prolonged dry conditions, the extended wet seasons that occur intermittently in some years or a severe fire that burns the peat layer would reverse the process.

In summary, at the broader scale, vegetation composition varies along the environmental gradient from short hydroperiod marl prairie to the sloughs that remain inundated for longer periods annually. This variation in species composition is evident at both local and regional scales. Regional differences in hydrologic regimes resulting from alternative management strategies have caused variation in species composition within individual landscapes, and have also brought on temporal change in vegetation composition in Shark River Slough. The occurrence of these changes coincided with changes in the hydrologic regimes during the past thirteen years. The temporal changes in vegetation composition across the gradient are likely to have affected the position and attributes of transition zones in ways yet to be fully understood. A more comprehensive analysis of the data for assessing temporal change in vegetation across the whole gradient, and any shift in position and attributes of the transition between prairie and slough, is scheduled to be conducted after the completion of third cycle of vegetation sampling on all transects, which will be completed in spring 2014. The results from such an analysis are expected to provide feedback for the adaptive management of Everglades wetland ecosystems along the marl prairie-slough gradient.

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Figure 1: Mean (± S.E.) annual and 30-Yr (1981-2010) average water level at the stage recorder P-33 located in Shark River Slough within Everglades National Park.

Figure 2: Location map of Marl prairie-Slough Gradient Study plots on Transects M1-M5. Slough plots represent long hydroperiod and marl prairie plots represent short hydroperiod plots.

Figure 3: Long-term hydroperiod (days) averaged over 21 years (1991-2011) at the vegetation sampling sites on Transects M1-M5 along marl-prairie slough gradient.

Figure 4: Soil depth (cm) at the vegetation sampling sites on Transects M1-M5.

Figure 5: Vegetation types at the vegetation sampling sites on Transects M1-M5 (*See also Appendix 1*). SCWP =*Schizachyrium* Wet Prairie (WP); MWP = *Muhlenbergia* WP; CWP = *Cladium* WP; SOWP = *Schoenus* WP; PCWP = *Paspalum-Cladium* WP; RCM = *Rhynchospora-Cladium* Marsh: CMM = *Cladium* Mixed Marsh; CM = *Cladium* Marsh; CEM = *Cladium-Eleocharis* Marsh; ECM = *Eleocharis-Cladium* Marsh, EM = *Eleocharis* Marsh; TCM = *Typha-Cladium* Marsh*; Nymphaea* Open Marsh; RHIMAN = Red mangrove.

Figure 6: Bi-plots of site from three-dimensional non-metric multidimensional scaling (NMDS) ordination based on species abundance data collected at sites in both marl prairie (MP) and Shark Slough (SS) portions of five transects during the 2005-2008 period. Environmental and community characteristic vectors fitted in the ordination spaces represent the direction of their maximum correlation with ordination configuration. Codes for vector variables are as in Table 5. Sites are grouped by (A) Transects, and (B) Vegetation types. Codes for the vegetation types are as in Figure 5.

Figure 7: Bi-plots of major species' axis scores from three-dimensional non-metric multidimensional scaling (NMDS) ordination based on species abundance data collected at the sites on five marl prairie-slough gradient Full name of species are given in Table 4 Environmental and community characteristic vectors fitted in the ordination spaces represent the direction of their maximum correlation with ordination configuration.

Figure 8: Scatter plot showing the relationship between location of sites in the marl prairie portions of the Transect M3 and Axis scores from three-dimensional non-metric multidimensional scaling (NMDS) ordination based on species abundance data collected at the sites on Transects M1-M5 during the 2005-2008 period.

Figure 9: Box Plots showing species richness in marl prairie and slough portions of MAP transects sampled between 2005 and 2008. Different letters represent significant difference in mean species richness between marl prairie and slough sites on individual transects. Different letters indicate significant difference (ANOVA: p <0.05) in mean species richness between two landscapes on the same transect.

Figure 10: Box Plots showing hydroperiod averaged over four years prior to vegetation sampling in the Shark Slough portions of MAP transects sampled between 1999 and 2012.

Figure 11: NMDS ordination bi-plots of site scores, the environmental vectors fitted in the ordination space, and the trajectory of centroid. The ordination is based on species abundance data collected four times between 1999 and 2012 in the Shark Slough portion of the Transect M1. Only the sites that showed significant (p≤0.1) rate of change in species composition along the hydrology gradient are shown. Initial point and the end of the trajectory represent the 1999 and 2011 sampling event, respectively.

Figure 12: NMDS ordination bi-plots of site scores, the environmental vectors fitted in the ordination space, and the trajectory of centroid. The ordination is based on species abundance data collected four times between 1999 and 2012 in the Shark Slough portion of the Transect M2. Only the sites that showed significant (p≤0.1) rate of change in species composition along the hydrology gradient are shown. Initial point and the end of the trajectory represent the 1999 and 2011 sampling event, respectively.

Figure 13: NMDS ordination bi-plots of site scores, the environmental vectors fitted in the ordination space, and the trajectory of centroid. The ordination is based on species abundance data collected four times between 1999 and 2012 in the Shark Slough portion of the Transect M3. Only the sites that showed significant ($p \le 0.1$) rate of change in species composition along the hydrology gradient are shown. Initial point and the end of the trajectory represent the 1999 and 2012 sampling event, respectively.

Figure 14: NMDS ordination bi-plots of site scores, the environmental vectors fitted in the ordination space, and the trajectory of centroid. The ordination is based on species abundance data collected three times between 1999 and 2012 in the Shark Slough portion of the Transect M4. Only the sites that showed significant ($p \le 0.1$) rate of change in species composition along the hydrology gradient are shown. Initial point and the end of the trajectory represent the 1999 and 2010 sampling event, respectively.

Figure 15: Sites in the Shark Slough portion of four transects showing the vegetation trajectory trend that was determined using trajectory analysis on vegetation data collected four times between 1999 and 2012. ns – not significant; sig = significant.

Figure 16: Box Plots showing species richness in Shark Slough portion of MAP transects sampled multiple times between 1999 and 2012. Different letters represent significant (pair-wise t-test; $p < 0.05$) difference in mean species richness among years on individual transects. Different letters indicate significant difference (pair-wise 't'-test: $p \le 0.05$) in mean species richness between two landscapes on the same transect.

Figure 17: Box-plots of major species' importance value (IV) averaged across all transects for each sampling period.

Appendices

Appendix 1: Vegetation types at the vegetation sampling sites on Transects M1-M5. Vegetation types at the sites that were surveyed along the five transects between 2005 and 2008 were identified using an hierarchical agglomerative cluster analysis with Bray-Curtis dissimilarity as distance measure and flexible beta as linkage method.

Site_ID	Transect	Plot	EASTNAD83	NORTHNAD83	Vegetation type
M1-00000	M1	$\mathbf{0}$	545528	2837755	Cladium Wet Prairie
M1-00300	M1	300	545251	2837899	Typha Marsh
M1-00600	M1	600	545007	2838042	Cladium-Eleocharis Marsh
M1-00900	M1	900	544745	2838187	Cladium Wet Prairie
M1-01200	M1	1200	544482	2838330	Open Prairie
M1-01500	M1	1500	544220	2838476	Cladium-mixed Marsh
M1-01800	M1	1800	543954	2838617	Cladium Marsh
M1-02100	M1	2100	543691	2838766	Cladium-mixed Marsh
M1-02400	M1	2400	543428	2838908	Eleocharis Marsh
M1-02700	M1	2700	543164	2839051	Eleocharis-Cladium Marsh
M1-03000	M1	3000	542904	2839204	Cladium-mixed Marsh
M1-03500	M1	3500	542466	2839440	Eleocharis Marsh
M1-04000	M1	4000	542029	2839683	Cladium Marsh
M1-04500	M1	4500	541588	2839923	Cladium Marsh
M1-05000	M1	5000	541150	2840169	Cladium Marsh
M1-05300	M1	5300	540886	2840314	Cladium-Eleocharis Marsh
M1-05500	M1	5500	540711	2840411	Eleocharis Marsh
M1-05800	M1	5800	540448	2840557	Eleocharis Marsh
M1-06000	M1	6000	540274	2840652	Cladium Marsh
M1-06300	M1	6300	540011	2840798	Eleocharis Marsh
M1-06500	M1	6500	539836	2840894	Eleocharis Marsh
M1-06900	M1	6900	539487	2841088	Cladium-Eleocharis Marsh
M1-07000	M1	7000	539398	2841136	Cladium Marsh
M1-07300	M1	7300	539136	2841282	Cladium Marsh
M1-07500	M1	7500	538961	2841379	Cladium-Eleocharis Marsh
M1-07800	M1	7800	538699	2841524	Cladium Marsh
M1-08000	M1	8000	538523	2841620	Cladium Marsh
M1-08260	M1	8260	538297	2841747	Cladium Marsh
M1-08300	M1	8300	538262	2841767	<i>Cladium</i> Marsh
M1-08500	M1	8500	538087	2841863	Cladium Marsh
M1-08800	M1	8800	537824	2842008	Cladium Marsh
M1-09000	M1	9000	537647	2842105	Cladium Marsh
M2-00000	M ₂	$\mathbf{0}$	537477	2838897	Cladium Marsh
M2-00500	M ₂	500	537030	2839126	Eleocharis Marsh
M2-01000	M ₂	1000	536584	2839356	Cladium Marsh
M2-01500	M ₂	1500	536142	2839586	Cladium Marsh

Shark Slough Transect -ID	MAP Transect	Plot	N1	N2	Delta	p-value	Slope	p-value
$T1_0$	M1	5000	$\mathbf{1}$	3	-0.416	0.145	-0.041	0.100
T1 300	M1	5300	$\mathbf{1}$	\overline{c}	-0.634	0.056	-0.064	0.085
T1 500	M1	5500	$\mathbf{1}$	3	-0.698	0.093	-0.067	0.047
$T1_800$	M1	5800	$\mathbf{1}$	$\sqrt{2}$	-0.784	0.048	-0.065	0.048
$T1_1000$	M1	6000	$\mathbf{1}$	3	-0.842	0.027	-0.072	0.024
$T1_1300$	M1	6300	$\mathbf{1}$	3	-0.516	0.060	-0.046	0.047
T1 1500	M1	6500	$\mathbf{1}$	3	-0.769	0.079	-0.079	0.032
T1 1900	M1	6900	$\mathbf{1}$	3	-0.418	0.149	-0.031	0.179
$T1_2000$	M1	7000	$\mathbf{1}$	3	-0.176	0.173	-0.013	0.224
$T1_2300$	M1	7300	$\mathbf{1}$	3	-0.060	0.397	-0.008	0.338
$T1_2500$	M1	7500	$\mathbf{1}$	3	-0.452	0.089	-0.042	0.079
T1_2800	M1	7800	$\mathbf{1}$	3	-0.189	0.115	-0.016	0.103
T1_3000	M1	8000	$\mathbf{1}$	3	-0.843	0.018	-0.077	0.005
$T1_3260$	M1	8260	$\mathbf{1}$	3	-0.060	0.397	-0.006	0.332
T1_3300	M1	8300	$\mathbf{1}$	3	-0.348	0.105	-0.031	0.071
T1 3500	M1	8500	$\mathbf{1}$	3	0.153	0.903	0.010	0.832
T1_3800	M1	8800	$\mathbf{1}$	3	-0.300	0.059	-0.020	0.078
T1_4000	M1	9000	$\mathbf{1}$	3	-0.380	0.124	-0.031	0.130
$T2_0$	M ₂	3500	1	3	-0.330	0.283	-0.035	0.232
$T2_300$	M ₂	3800	$\mathbf{1}$	3	-0.134	0.337	-0.014	0.329
T _{2_500}	M ₂	4000	$\mathbf{1}$	3	-0.836	0.059	-0.067	0.083
T _{2_800}	M ₂	4300	$\mathbf{1}$	3	-0.415	0.090	-0.040	0.067
$T2_1000$	M ₂	4500	1	3	-0.268	0.189	-0.032	0.116
$T2_1300$	M ₂	4800	$\mathbf{1}$	3	-0.096	0.320	0.001	0.489
T _{2_2000}	M ₂	5500	$\mathbf{1}$	3	-0.558	0.070	-0.041	0.100
T _{2_2260}	M ₂	5760	$\mathbf{1}$	3	-0.056	0.368	-0.003	0.425
T _{2_2500}	M ₂	6000	$\mathbf{1}$	3	-0.378	0.213	-0.026	0.275
T _{2_3000}	M ₂	6500	$\mathbf{1}$	3	-0.204	0.210	-0.016	0.245
T _{2_3500}	M ₂	7000	1	3	-0.645	0.018	-0.039	0.108
T ₂ _4000	M ₂	7500	$\mathbf{1}$	3	-0.520	0.049	-0.036	0.089
T _{2_4500}	M ₂	8000	$\mathbf{1}$	3	-0.619	0.012	-0.051	0.028
T ₂ _5000	M ₂	8500	$\mathbf{1}$	3	-0.427	0.044	-0.035	0.060
T ₂ _5500	M ₂	9000	1	3	-0.673	0.046	-0.053	0.064
T ₂ _6000	M ₂	9500	1	3	-0.297	0.195	-0.019	0.264
T ₂ _6500	M ₂	10000	$\mathbf{1}$	3	-0.103	0.158	-0.011	0.108
T ₂ _7000	M ₂	10500	$\mathbf{1}$	3	-0.121	0.046	-0.011	0.030
$T3_0$	M ₃	15500	1	3	-0.413	0.047	-0.040	0.020

Appendix 2: Results (delta and slope values) of trajectory analysis for sites on Shark Slough portions of transects M1, M2, M3 and M4 along hydroperiod vector for 1999-2012 period. N1 and N2 are the number of sampling years during Shark Slough transect and Marl prairie-Slough gradient study, respectively. P-values <0.1 are in bold.

Appendix 3: Importance value index (IV) of species present at the Shark Slough sites that were first sampled in 1998-2000, and then multiple times between 2005 and 2012

