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HYDROLOGIC RESTORATION

Trajectories of Vegetation Response to Water Management in Taylor Slough, Everglades National Park, Florida

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Abstract Ecosystem management practices that modify the major drivers and stressors of an ecosystem often lead to changes in plant community composition. This paper examines how closely the trajectory of vegetation change in seasonally-flooded wetlands tracks management-induced alterations in hydrology and soil characteristics. We used trajectory analysis, a multivariate method designed to test hypotheses about rates and directions of community change, to examine vegetation shifts in response to changes in water management practices within the Taylor Slough basin of Everglades National Park. We summarized vegetation data by non-metric multidimensional scaling ordination, and examined the time trajectory of each site along environmental vectors representing hydrology and soil phosphorus gradients. In the Taylor Slough basin, vegetation change trajectories closely followed the hydrologic changes caused by the operation of water pumps and detention ponds adjacent to the canals. We also observed a shift in vegetation composition along a vector of increasing soil phosphorus, which suggests the need for implementing measures to avoid P-enrichment in southern Everglades marl prairies. This study indicates that shifts in vegetation composition in response to changes in hydrologic conditions and associated parameters may be detected through trajectory analysis, thereby providing feedback for adaptive management of wetland ecosystems.

Keywords Taylor Slough · Water management · Vegetation · Hydrology · Phosphorus · Trajectory analysis

Introduction

Ecosystem management practices often influence the major drivers and stressors of a system to achieve various levels of desirable ecosystem services, while maintaining natural conditions as closely as possible. Such alterations in environmental drivers often lead to directional changes in vegetation composition (Collins 2000; Chapin et al. 2006), whose time course depends on such factors as initial species composition, disturbance type and intensity, and the nature of the operative environmental factors (Eichhorn and Watts 1984; Craft et al. 2002; Armentano et al. 2006). Changes in an environmental driver may slowly erode community resilience and cause community to change in a particular direction until a threshold is reached, followed by an abrupt change in community characteristics (Folke et al. 2004; Hagerthey et al. 2008). These changes occur across the full range of ecosystem types, including wetlands where plants are often sensitive to a change in hydrology and nutrient availability, the two major drivers of wetland ecosystem

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functions (van der Valk et al. 1994; Ellison and Bedford 1995; Busch et al. 1998; Childers et al. 2003; Armentano et al. 2006; Hagerthey et al. 2008). This paper examines the trajectory of vegetation change in wetlands following management-induced alterations in hydrology and soil characteristics in seasonally-flooded marshes of the Taylor Slough basin in the southern Everglades.

In the Greater Everglades, past water management activities have negatively impacted several ecosystems, leading to the initiation of a complex group of interrelated restoration projects, the Comprehensive Everglades Restoration Plan (CERP) (USACE and SFWMD 1999). One of the severely impacted ecosystems is the wetlands of the Taylor Slough basin within Everglades National Park (ENP). Historically, the vegetation in the basin reflected natural hydrologic and fire regimes characteristic of the southern Everglades (Davis 1943; Loveless 1959; Gunderson 1994). However, in the latter half of the past century, the vegetation began to be profoundly affected by hydrologic changes caused by varying water management practices (McVoy et al. 2011). Armentano et al. (2006) provided a detailed account of a distinct vegetation shift in response to hydrologic changes in Taylor Slough. However, their study ended in 2003, and did not document the full effects of a novel water management regime, initiated in 2000. Thus, the course of vegetation shift in response to the most recent hydrologic changes has yet to be fully investigated.

In wetlands, a change in nutrient availability also can cause a regime shift in vegetation composition from one stable state to another (van der Hoek et al. 2004; Hagerthey et al. 2008). In the Greater Everglades, several researchers have investigated vegetation changes in response to increased soil-P caused by the canal water delivery, primarily in the northern part of the ecosystem (Urban et al. 1993; Doren et al. 1997; Newman et al. 1998; Childers et al. 2003; Hagerthey et al. 2008). In contrast, the southern Everglades has not received similar attention. In the northern Everglades, the expansion of southern cattail (*Typha domingensis* Pers.) has drawn the attention of researchers and managers, leading to detailed investigations into the cause of change, and ultimately a major shift in Everglades water management strategies (USACE and SFWMD 1999). In the southern Everglades, the expansion of monotypic cattail communities of similar scale has not occurred yet. However, the recent appearance of cattail in limited areas in Taylor Slough has stimulated research to determine whether its presence in this area is linked to water delivery induced soil-P enrichment (Sadle and Saha 2009; Surratt et al. 2012). At the early stage, i.e., before major shifts in vegetation composition become visible, one may expect to find changes in soil nutrients and in the competitive performance of species (Keddy et al. 2000), resulting in a change in their relative abundances and richness along nutrient gradients (Bedford et al. 1999). These subtle changes need to be thoroughly understood so they can serve as a means of early detection prior to the onset of major vegetation shifts. This information will help land managers to develop preventive strategies before undesirable and potentially irreversible changes to natural plant communities become more widespread and would require extensive restoration efforts.

In the Everglades, a general goal of recent restoration projects is to reestablish an ecological system that resembles the pre-drainage system, while providing other water-related needs of the region, including water supply and flood protection (CERP 2000). Restoration activities most likely to affect hydrologic conditions and in turn vegetation in Taylor Slough basin are those of the C-111 project, outlined in the C-111 General Reevaluation Report (GRR) and Environmental Impact Statement (USACE 1994). The objectives of the project include the restoration of historic hydrologic conditions in Taylor Slough, and the Rocky Glades. More recently, the C-111 Spreader Project, an enhancement to the GRR (USACE 1994), has been incorporated in CERP. The Spreader Project's goal is to restore the quantity, timing and distribution of water delivered to Florida Bay via Taylor Slough to levels as close as possible to pre-drainage conditions, and to improve hydroperiods and hydropatterns in wetlands adjacent to the slough in order to achieve historical vegetation (USACE and SFWMD 2011). The project goals are broad, and often lack the site specific vegetation targets. This is in part due to the difficulty in defining the pre-drainage vegetation patterns based on limited historical data and current plant community composition. Precise definition of the pre-drainage hydrologic conditions and vegetation patterns has always been a complex task, but McVoy et al. (2011) recently provided an account of the pre-drainage hydrology and landscape patterns in the greater Everglades. Apparently, beyond defining a target, restoration also requires assessing whether the ecosystem response to the restoration activities will bring about the desired changes. Thus, an analytical method that can be used to assess ecosystem response to restoration efforts and provide information for adaptive management is considered to be helpful.

In this study, we examined the trajectories of vegetation change in response to varying water management practices within the Taylor Slough basin. Using trajectory analysis (Minchin et al. 2005), we examined the time course of each surveyed site along hydrologic and soil phosphorus gradients. Trajectory analysis allows researchers to test the hypothesis that community composition is changing either toward a pre-defined target or along an environmental gradient, and that such changes are the result of a management action or disturbance event. We hypothesized that recent plant community dynamics reflects the influence of past water management activities on hydrologic conditions and soil phosphorus in the Taylor Slough basin.

Methods

Study Area

Taylor Slough, the second largest drainage basin within ENP, is comprised of a relatively narrow central channel that widens to the south, and is bordered by marl prairies which are 10–30 cm higher in elevation (Fig. 1). This basin is an important component of the wetland landscape in the southern Everglades and serves as habitat for a variety of rare species, including the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), a federally listed endangered species (Pimm et al. 2002; Ross et al. 2006). The geographical features, historical flow patterns, and baseline vegetation in Taylor Slough basin are described elsewhere (Olmsted et al. 1980; Rose et al. 1981; Van Lent et al. 1993; Armentano et al. 2006; McVoy et al. 2011). In brief, the basin includes approximately 40,900 ha of wetlands extending from the "Rocky Glades" along the eastern boundary of ENP to Florida Bay (Armentano et al. 2006). The entire region is characterized by calcareous soils underlain by the highly porous Miami oolite formation (Randazzo and Jones 1997).

Historically, surface flow to Taylor Slough was primarily comprised of rain water with overflows from the adjacent Shark Slough during high rainfall years (Rose et al. 1981; Van Lent et al. 1993; Harvey et al. 2000; McVoy et al. 2011). However, during the past century, the hydrology of the basin was indiscriminately altered (Rose et al. 1981; Van Lent et al. 1993). Since the early 1980s, hydrologic conditions in the basin have been affected by the operations of water pumps at S332 or S332D, constructed along the L31W and L31N canals, respectively (Fig. 1). Water delivery from S332 was started in 1981 and was substantially increased in 1993

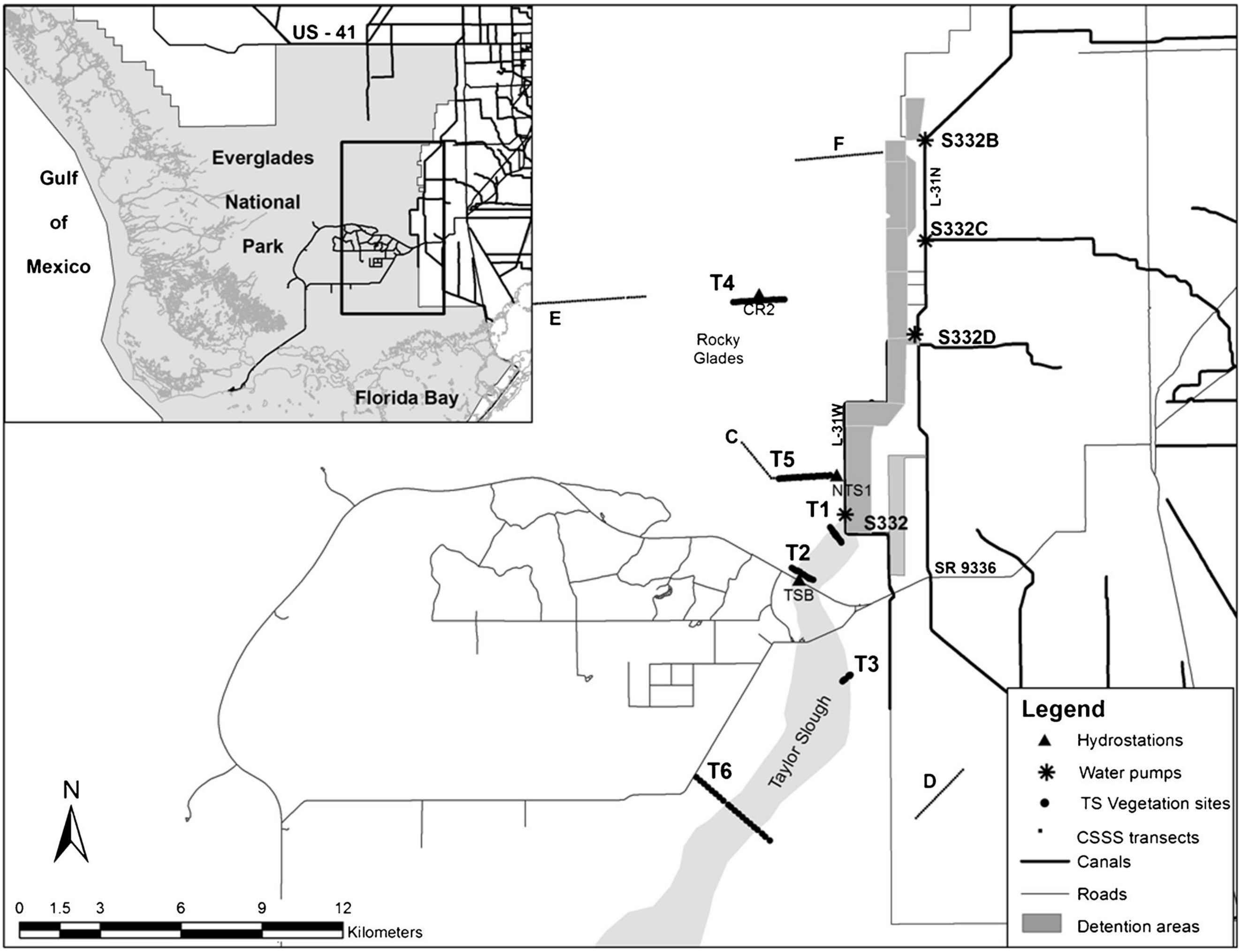


Fig. 1 Site map showing the vegetation monitoring transects in Taylor Slough basin in the Everglades National Park

Table 1 Years of transects establishment and subsequent vegetation sampling

Transect	Established year	Vegetation sampled (years)							
		1992	1995	1996	1997	1999	2003	2007	2010
T-1	1979		X			X	X	X	X
T-2	1979	X	X			X	X	X	X
T-3	1979			X		X	X	X	X
T-4	1997				X	X	X	X	X
T-5	1997				X	X	X	X	X
T-6	2007							X	X

(Kotun and Renshaw 2013). In 2000, the operation of S332 was fully replaced by S332D, with the intent of switching flow patterns from point delivery to surface flow across a broader front. Concurrent with operation of S332D, the S332B and S332C pump structures and a series of detention ponds were brought in operations with the objectives of creating hydrologic ridges along the L31N canal, reducing drainage effects of the canal, i.e. the loss of water from the marsh to the canal, and hydrating the marl prairies in Rocky Glades (Kotun and Renshaw 2013). We refer to the recent management periods affecting Taylor Slough as pre-S332 (before 1981), S332 (1981–1992), S332i (1993–1999), and S332D (2000–2010).

Vegetation in the Taylor Slough basin is primarily dominated by muhly grass (*Muhlenbergia capillaris* (Lam.) Trin. var. *filipes* (M.A. Curtis) Chapm. ex Beal), sawgrass (*Cladium mariscus* ssp. *jamaicense* (Crantz) Kük), and spikerush (*Eleocharis cellulosa* Torr.). Muhly grass is dominant in marl prairies in which hydroperiod ranges between 2 and 6 months (Olmsted et al. 1980; Ross et al. 2006). Sawgrass-dominated plant communities are the most common in the Taylor Slough basin. This species has a wide range of hydrologic tolerance, and occurs in both prairies and marshes with hydroperiod ranging from 2 to 9 months (Ross et al. 2003; Ross et al. 2006; Todd et al. 2010). In the deeper part of Taylor Slough channel, where hydroperiod ranges between 6 and 9 months, spikerush is abundant, and often co-dominates with sawgrass.

Hydrologic Models

Hydrologic changes in Taylor Slough were inferred from water levels recorded at the hydrologic station, TSB located near the Taylor Slough Bridge (Fig. 1). For the period 1961–2003, Armentano et al. (2006) developed multiple linear regression models to examine the relationship between water level in the slough and local rainfall and water delivery. In the models, mean daily water level at TSB, seasonal total rainfall at climatic station RPL (2 km southeast of TSB), and volume of water (million $m^3 s^{-1}$) pumped through S332 and S332D into the slough and detention ponds were used separately for dry (November-May) and wet (June-October) seasons. Since the models developed by Armentano et al. (2006) included only 3 years (2000–2003) of the S332D period, we extended the model to examine water level at TSB in relation to rainfall and flow through S332D for the period of 2000–2010. The stage and rainfall data were obtained from the South Florida Natural Resource Center database (Kevin Kotun *personal communication*), and flow data were obtained from DBHYDRO database (SFWMD 2012). For the dry season, the model included both rainfall and monthly mean water delivery from S332D as independent variables, whereas for the wet season, rainfall was not statistically significant, and therefore only water delivery from S332D was used in the model.

Vegetation Sampling

In Taylor Slough, vegetation was sampled periodically along six transects: two transects (T4 and T5) in the headwaters of the slough, two transects (T1 and T2) in the upper slough, and two transects (T3 and T6) in the middle slough below State Road 9336 (Fig. 1). Table 1 summarizes the sampling frequency of the sites on these transects. In 1992, only T2 was sampled. Between 1995 and 2010, the sites on five transects (T1-T5) were sampled once in 1995, 1996 or 1997, and were then re-sampled in 1999, 2003, 2007 and 2010 (Table 1). Transect 6 was sampled only in 2007 and 2010, and thus was not used in this study.

Detailed accounts of vegetation sampling protocol are given in Armentano et al. (2006). On each transect, species specific cover was recorded in 20 $5 \times 1\ m^2$ permanent plots. Each plot was divided into five $1 \times 1\ m^2$ quadrats, and a frame of $1 \times 1\ m^2$ subdivided into 4 quarters was used to estimate species specific cover. Finally, the species cover data from 20 quadrants were averaged at the plot level for further analysis.

In order to relate Taylor Slough vegetation dynamics to changes in hydrology or soil nutrients, vegetation and environmental data from the Cape Sable seaside sparrow (CSSS) habitat study were also utilized. We used vegetation and hydrology data collected in 150 $1 \times 60\ m^2$ plots along 4 transects

(C, D, E and F) established in the marl prairies within the habitat of four eastern sparrow sub-populations (Ross et al. 2006). Within each plot, plant cover was estimated by species in ten 0.25 m^2 subplots arrayed regularly at 6 m intervals. Plot level hydroperiod, the number of discrete days per year when mean water level was above the ground surface, was calculated using water level data obtained from Everglades Depth Estimation Network (EDEN) database for the nearest stage recorders (EDEN 2008), and the mean plot elevation, obtained by a topographic survey from the nearest vertical control benchmark to each plot (Ross et al. 2006).

Soil Sampling

Soil nutrient data were collected in 57 plots on Transects D and F within CSSS habitat, which served as reference sites for the Taylor Slough study. At each site, soils from the surface 10 cm were collected from 3–5 locations adjacent to the plot, bulked together, and then brought to the laboratory. Soil samples were analyzed for total carbon, inorganic carbon, total nitrogen and total phosphorus at the Soil and Water Laboratory at the Institute of Food and Agricultural Science (IFAS), University of Florida – Tropical Research and Education Center, Homestead, FL (Sah et al. 2007). In this study, we examined patterns in total soil phosphorus, which was determined using method of EPA 365.2 (Environmental Protection Agency 1979). Table 2 summarizes the environmental data from the reference sites used in the analysis.

Data Analysis

Trajectory Analysis Change in vegetation composition along hydrologic and phosphorus gradients was analyzed using trajectory analysis (Minchin et al. 2005), an ordination-based technique designed to test hypotheses about rates and directions of community change. First, we summarized the vegetation data by a non-metric multidimensional scaling (NMDS) ordination (Kruskal 1964), which has been shown to be a robust and powerful method for summarizing community data (Minchin 1987). We performed NMDS on a matrix of Bray-Curtis dissimilarities among sampling units, with cover data first standardized by species' maximum, in order to equalize the potential contributions of species to the dissimilarities (Faith et al. 1987). To avoid entrapment in local minima, we used 100 random starting configurations and to determine the required dimensionality we performed the ordination in from 1 to 6 dimensions and examined the scree plot (McCune and Grace 2002).

Table 2 Summary of environmental data from the sites on the Cape Sable seaside sparrow (CSSS) habitat study transects used as reference sites in trajectory analysis

Variable	n	Mean	Std. Dev.	Min	Max
Hydroperiod (days)	150	205	43	62	308
Total phosphorus ($\mu g\,g^{-1}$)	57	154.8	68.4	44.2	314.1

We then examined projections of the time trajectory of each site along reference vectors representing hydrologic and phosphorus gradients. In NMDS, the hydrologic and phosphorus gradient vectors were defined through a vector fitting technique in DECODA (Kantvilas and Minchin 1989; Minchin 1998). In our analysis, the vectors were defined based on the hydroperiod and total soil phosphorus data available for a subset of the sites sampled on the CSSS habitat study transects used in the ordination. In the vector-fitting method, a vector is defined in the direction through the ordination that produces the maximum correlation between the measured environmental attribute and the scores of the sampling units. The statistical significance of such correlations is tested using a Monte-Carlo permutation test with 10,000 random permutations, with values of the environmental attribute randomly shuffled among sampling units (Faith and Norris 1989). The ordination was then rotated so that the fitted vector for hydroperiod was parallel to Axis-1.

Two statistics, delta (Δ) and slope were calculated to quantify the degree and rate of change in vegetation composition along the reference vectors (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. Since NMDS ordinations were scaled in half-change units, the unit of the rate was mean half change per year. One half-change is the distance at which the mean similarity between sampling units is half of the value that would be expected for two sampling units with identical coordinates along an environmental gradient in ordination space (Whittaker 1960). In our analysis, the slope was calculated as the linear regression coefficient of projected scores on the target vector on sampling years that included all years from the last pre-intervention to the final time step. 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.

Species Response Model Change in species abundance was analyzed by fitting curves to the species cover data for species present in only the sites that showed a significant ($p<0.1$) shift in time trajectory along the hydroperiod or

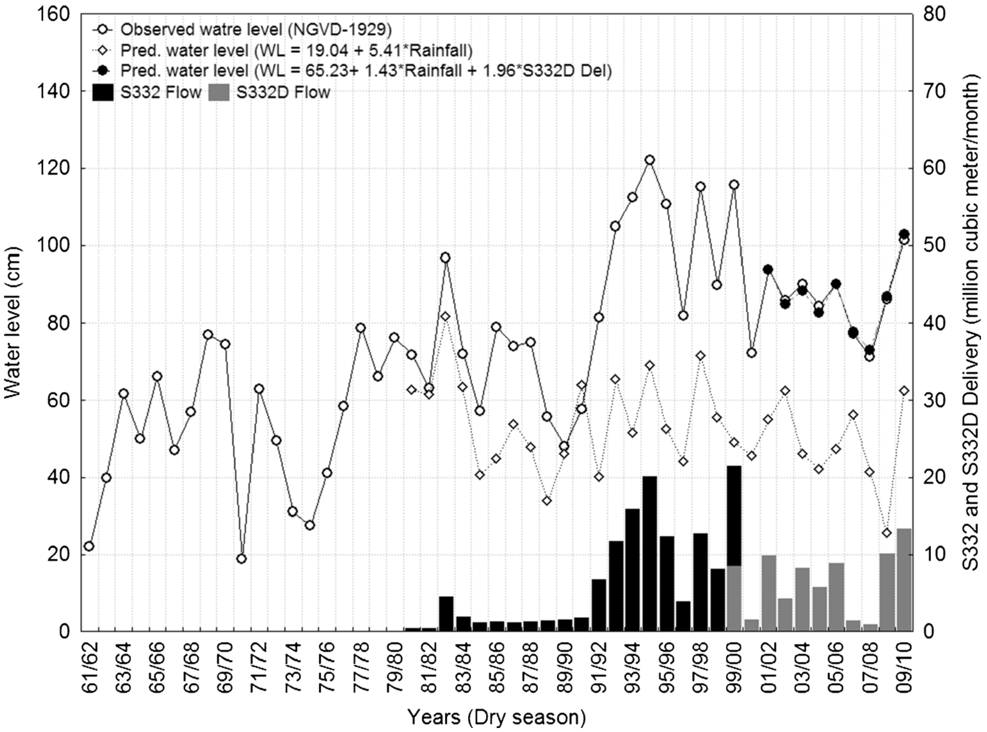


Fig. 2 Observed and predicted water level at the TSB stage recorder and water flow from L31W canal through S332 into Taylor Slough and from L31N through S332D into detention pond during the 1961–2010 dry seasons

total soil phosphorus vector. We analyzed species that were present in at least five samples from these sites, because changes in site position must have been the result of parallel changes in resident species. Species response curves were fitted using Generalized Linear Models (GLM) with quasi-Poisson error distribution and log link function (McCullagh and Nelder 1989) in the software package 'R' version 2.13.1 (R Core Team 2012). In general, the Poisson distribution assumes that the variance equals the mean. However, to deal with occurrence of over-dispersion (or under-dispersion), i.e. the variance is not equal to the mean, GLM with quasi-Poisson distribution and log link function, in which

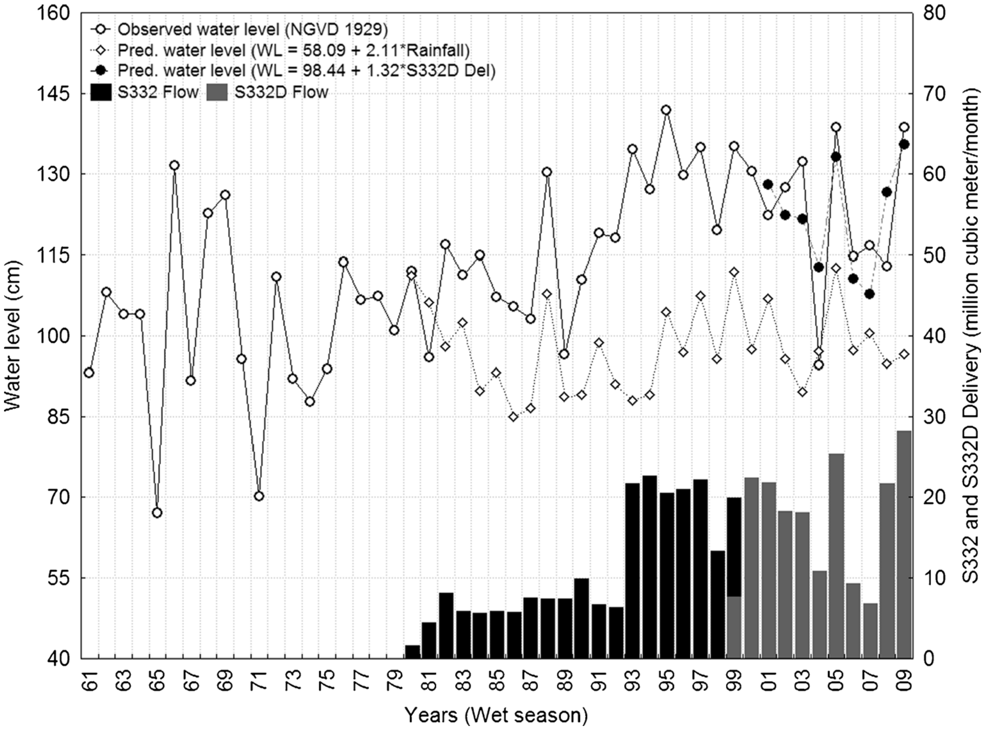


Fig. 3 Observed and predicted water level at the TSB stage recorder and water flow from L31W canal through S332 into Taylor Slough and from L31N through S332D into detention pond during the 1961–2010 wet seasons

variance is specified as proportional to the mean, was used (McCullagh and Nelder 1989).

Assuming a unimodal, symmetric or skewed, response of species to the environmental gradient, we started with a full second-order polynomial model. We developed a full model with both linear and quadratic terms, as well as reduced models with one term, linear or quadratic. We ranked the models for each species based on deviance and tested for significant differences between all pairs of models using a χ^2 test with one-degree of freedom on their residual deviance. The model that had the lowest deviance (Vincent and Haworth 1983), and differed significantly from other models was selected to represent the species response along the hydrology or phosphorus gradient vector.

Results

Hydrologic Changes in Taylor Slough

Hydrologic models developed using multiple linear regression revealed that water level in central Taylor Slough was affected by the operations of water pumps. When a precipitation-based-only hydrologic model developed from the data for the pre-S332 period was used to estimate water levels during the S332, S332i and S332D periods, observed water levels were higher than predicted. The relationship of stage level in the slough with rainfall in the basin already had started changing in 1981 when the S332 pump was brought in operation. However, the deviation in water level was much higher during the S332i period, and the trend continued to some extent through the S332D period.

Since 2000, even though water was not directly delivered into the slough, the water level in the slough was 15–40 cm higher than it would have been in a precipitation-driven system, suggesting a strong influence of the S332D pump station. The effects of this structure were particularly evident in the dry season when seasonal mean daily water level in the slough clearly tracked the amount of water delivered through S332D (Fig. 2). However, during the S332D period, the gap between observed and rain-based predicted water level was less than in the S332i period, and after showing a decreasing trend until 2008, water level had increased in the following two years. The linkage between the stage at TSB and S332D delivery was weak in the wet season (Fig. 3).

Hydrology and Vegetation Change

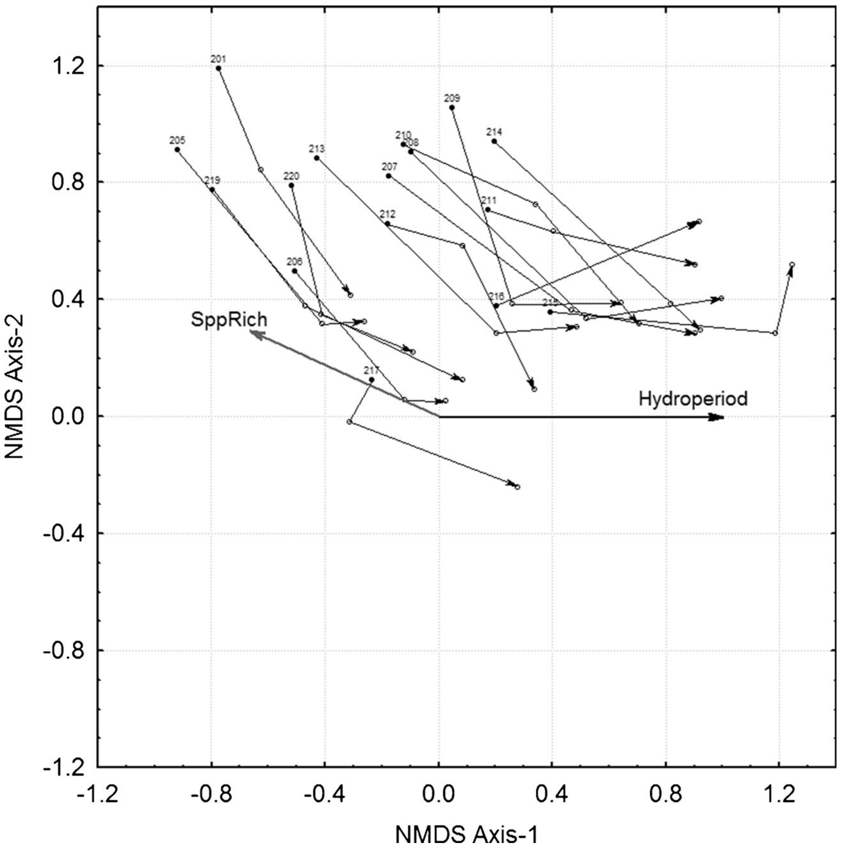
The dynamics of vegetation composition in the marl prairies of the Taylor Slough basin have in fact tracked hydrologic changes within the basin. For the Transects 1–3, located in the upper and middle Taylor Slough, trajectory analysis along the hydroperiod vector was done in two phases: one for the S332i period, and the other for S332D period. During S332i period, almost all sites on T2 followed a trajectory that roughly paralleled the hydrologic gradient from dry to wet conditions, and this compositional shift was statistically significant ($p<0.1$) at 80 % of sites (Fig. 4; Appendix 1a). Four sites on T1 also showed significant time trajectories towards increasing wetness. Species richness at these sites followed an inverse trend, and the richness decreased with hydroperiod (Fig. 4).

At the sites that showed significant vegetation trajectories towards wetter conditions, species abundances increased, decreased or showed a unimodal trend (Fig. 5; Appendix 2a). The species that significantly increased in cover along hydroperiod vector were *Bacopa caroliniana* (Walter) B.L. Rob., *E. cellulosa*, *Justicia angusta* (Chapm.) Small, *Leersia hexandra* Sw., *Panicum hemitomon* Schult., *Potamogeton illinoensis* Morong, and *Sagittaria lancifolia* L.. These species are known to be characteristic of long hydroperiod conditions in the Everglades (Busch et al. 1998; Ross et al. 2003). Cover of some species that are usually present in relatively dry conditions decreased significantly along hydroperiod vector. They were *Dichanthelium dichotomum* (L.) Gould var. *ensifolium* (Baldw. ex Elliott) Gould and C.A. Clark, *Eupatorium mikanioides* Chapm., *Ipomoea sagittata* Poir., *M. capillaris var. filipes,* and *Solidago stricta* Aiton. Several species, including *Centella asiatica* (L.) Urb., *C. mariscus* ssp. *jamaicense, Panicum tenerum* Bey. ex Trin., *Pluchea rosea* Godfrey, and *Rhynchospora microcarpa* Baldwin ex A. Gray showed unimodal response.

Between 1999 and 2010, the trajectory of 45 % of the sample sites on T2 moved significantly in a negative direction along the hydroperiod vector (Fig. 6), showing a shift towards vegetation composition indicative of drier conditions. Another 25 % also shifted in composition towards drier conditions, but the change was not statistically significant (Appendix 1a). On T1 and T3, 55 % of prairie sites showed a trajectory towards drier conditions. However, the shift in vegetation composition on these transects was significant on only 3 and 2 sites, respectively. At the sites that showed significant shift in trajectory towards drier conditions, the change in species composition was marked by a significant decrease in cover of hydric species including *B. caroliniana, E. cellulosa,* and *P. hemitomon*. In contrast, the cover of *M. capillaris var. filipes*, *P. rosea*, *R. microcarpa*, *Sabatia stellaris* Pursh., and *Setaria parviflora* (Poir.) Kerguélen significantly increased. Ten species, including *C. mariscus* ssp. *jamaicense, L. hexandra,* and *Rhynchospora tracyi* Britton showed a unimodal trend (Appendix 1a).

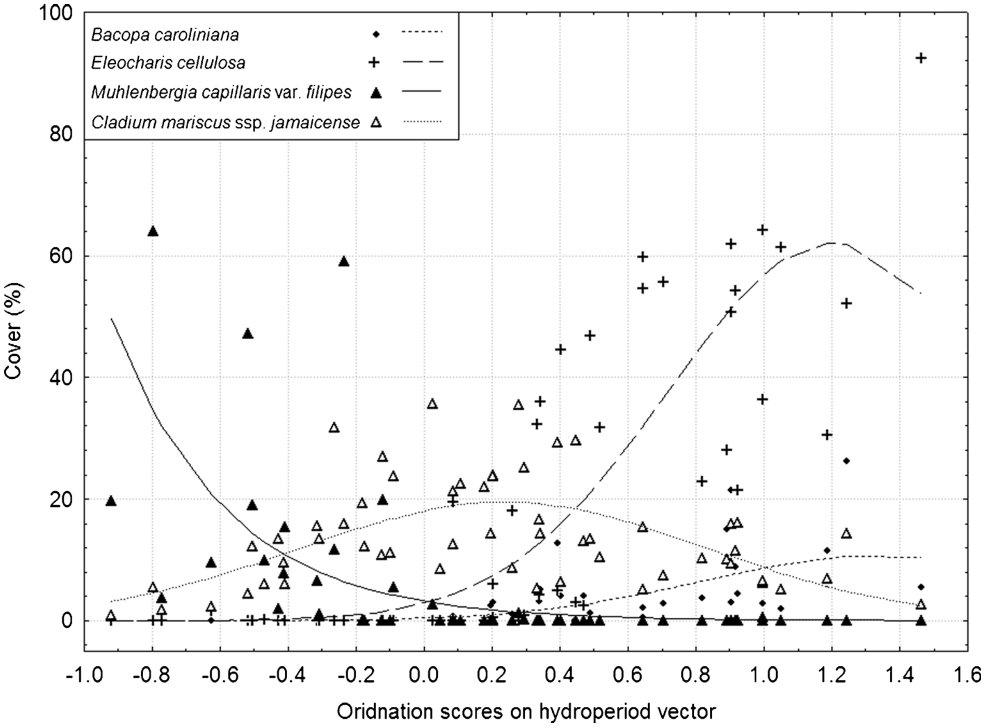
For the Transects 4 and 5, located in the Taylor Slough headwaters, 1997 and 1999 were considered base years and the trajectory analysis examined the vegetation change between 1999 and 2010. During the test period, 75 % of the sites on these transects showed a significant trajectories

Fig. 4 The NMDS ordination showing the trajectory of sites from Transect 2 sampled in 1992, 1995 and 1999. Only the sites that showed significant ($p \leq 0.1$) rate of change in species composition along the hydrology gradient are shown. Initial point and the end of arrows on each site trajectory represent the 1992 and 1999 sampling event, respectively



toward increasing hydroperiod (Fig. 7; Appendix 1b). At these sites, 40 species showed significant change in cover along the hydrology vector (Appendix 2a). The species that showed significant increase in cover included *C. mariscus* ssp. *jamaicense, B. caroliniana, P. hemitomon, Proserpinaca palustris* L.*, S. lancifolia*, among others (Fig. 8). Interestingly,

Fig. 5 Species response curve of major species (average maximum cover >25 %) modeled on hydroperiod vector in the ordination space. The species were present at least five samples of Transect 2 sites that showed significant time trajectory between 1992 and 1999



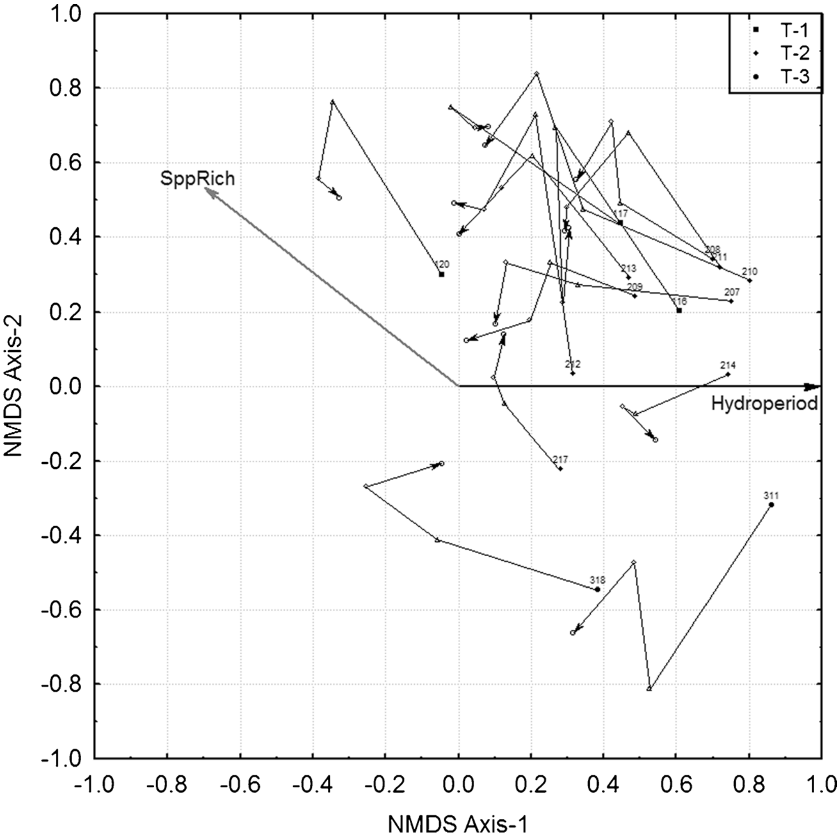


Fig. 6 The NMDS ordination showing the trajectory of sites from Transects 1–3 sampled in 1999, 2003, 2007 and 2010. Only the sites that showed a significant ($p \leq 0.1$) rate of change in species composition along the hydrology gradient are shown. Initial point and the end of arrows on each site trajectory represent the 1999 and 2010 sampling event, respectively

M. capillaris var. *filipes*, the characteristic species of short-hydroperiod marl prairie (Ross et al. 2006), showed a skewed unimodal pattern (Fig. 8).

Hydrology, Phosphorus and Vegetation

Vegetation at several sites, mostly in T1, T4 and T5, showed a change in species composition indicative of a response to increasing soil phosphorus. In the NMDS ordination space, 22 sites showed a significant time trajectories parallel to the phosphorus vector (Fig. 9; Appendix 1c). Such trajectories in the direction of increasing phosphorus were more obvious after 1999. At those sites, 32 species showed a significant change in their cover along the phosphorus gradient (Appendix 2b). Among them, 44 % species (14) species showed a unimodal trend. Major species (mean cover≥1 %) that showed a unimodal trend were *C. mariscus* ssp. *jamaicense, M. capillaris var. filipes,* and *R. trayci,* (Fig. 10). Thirteen species, including *C. asiatica, Coleorachis rugosa* (Nutt.) Nash*, J. angusta, Paspalum monostachyum* Vasey*, P. rosea, R. microcarpa,* and *Saccharum giganteum* (Walter) Pers. showed an increasing trend in cover along the phosphorus gradient vector (Appendix 2b). Only a few species significantly decreased in cover. Those were *Hyptis alata* (Raf.)Shinners*, Rhynchospora divergens* Chapm. Ex M.A. Curtis, and *Utricularia cornuta* Michx.

Discussion

Vegetation trajectories associated with environmental drivers are often governed by the strength and duration of management practices. In the Taylor Slough basin, the direction and rate of vegetation change was closely linked to the strength of hydrologic shifts resulting from water management activities, as well as associated change in soil chemistry.

The pattern of vegetation change observed in this study suggests that a shift in water management strategies implemented to ameliorate the harmful effects of previous drainage, and thereby to restore historic hydrologic conditions to Taylor Slough basin, had noticeable influence on vegetation composition in the region. During the S332i period, when mean water level near the Taylor Slough Bridge was 30–40 cm higher than during the pre-S332 and S332 periods (Fig. 2, see also Armentano et al. 2006), the vegetation composition began to resemble that of long hydroperiod marshes, dominated by spikerush and other hydric species. Concurrently, the characteristic species of the short hydroperiod marl prairie, especially muhly grass, sharply declined. The trend was reversed in the S332D period, when surface water flow replaced point deliveries from the canal, resulting in reduced hydroperiod and mean water level in the slough (Kotun and Renshaw 2013). For instance, the mean hydroperiod at stage recorder TSB was

8.2 and 5.8 months during S332i and S332D periods, respectively. In response to the shift in water delivery pattern, vegetation change trajectories also tracked the hydrologic conditions in slough.

In the Everglades, the restoration of historical hydrologic conditions in Taylor Slough and the Rocky Glades has been one of restoration goals linked to C111 projects (USACE 1994). Our study suggests that the operation of water structures and adjacent detention ponds in these projects has affected both the hydrology and vegetation in the Rocky Glades. In the Taylor Slough basin north of S332, the water-mediated changes in species composition were not detected in the late 1990s or early 2000s (Armentano et al. 2006). However, in this study which included two additional surveys after 2003, a shift in vegetation composition towards wetter types on T4 and T5 in the Taylor Slough headwaters suggests an increase in hydroperiod in the marsh. During the S332D period, both the hydroperiod and mean wet season water level at stage recorder NTS1 (e.g. T5) was higher than during the S332i period, primarily because the removal of the pump station at S332 reduced the drainage of water from marsh to the canal (Kotun and Renshaw 2013). In addition, during this period, water from the detention ponds along L31W in the Frog Pond area also seeped into the canal from where water entered as surface and sub-surface flows into ENP (Gaiser et al. 2008; Kotun and Renshaw 2013). Vegetation further north (e.g., T4) seemed to track changes in hydrologic regime influenced by the detention ponds, which received water from S332B and S332C. In this region, while surface flow from the ponds to the marsh could occur over a fixed-crest weir in the levee, the hydrologic ridge created at the detention ponds reduces the drainage effects of the adjacent canal and alters the ground

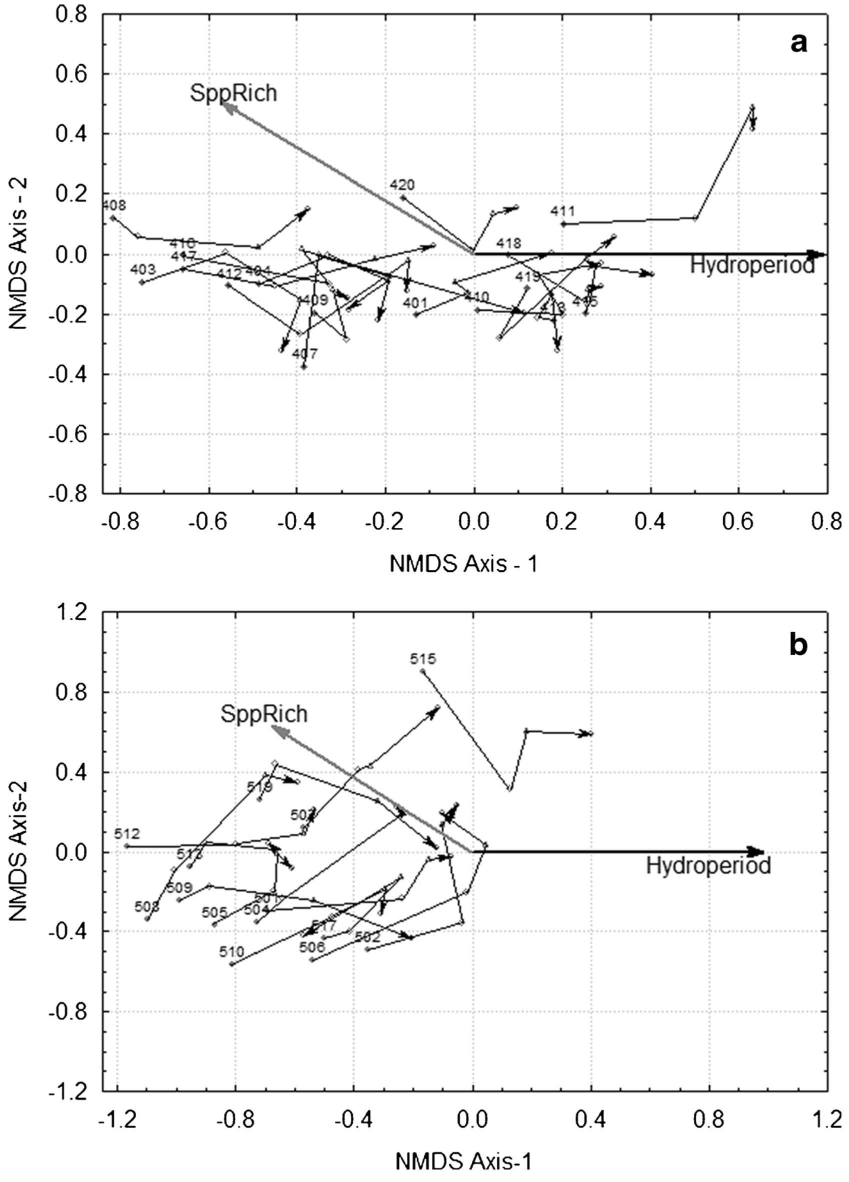


Fig. 7 The NMDS ordination showing the trajectory of sites from Transect 4 and 5 sampled in 1997, 1999, 2003, 2007 and 2010. Only the sites that showed significant ($p \leq 0.1$) rate of change in species composition along the hydrology gradient are shown. Initial point and the end of arrows on each site trajectory represent the 1999 and 2010 sampling event, respectively

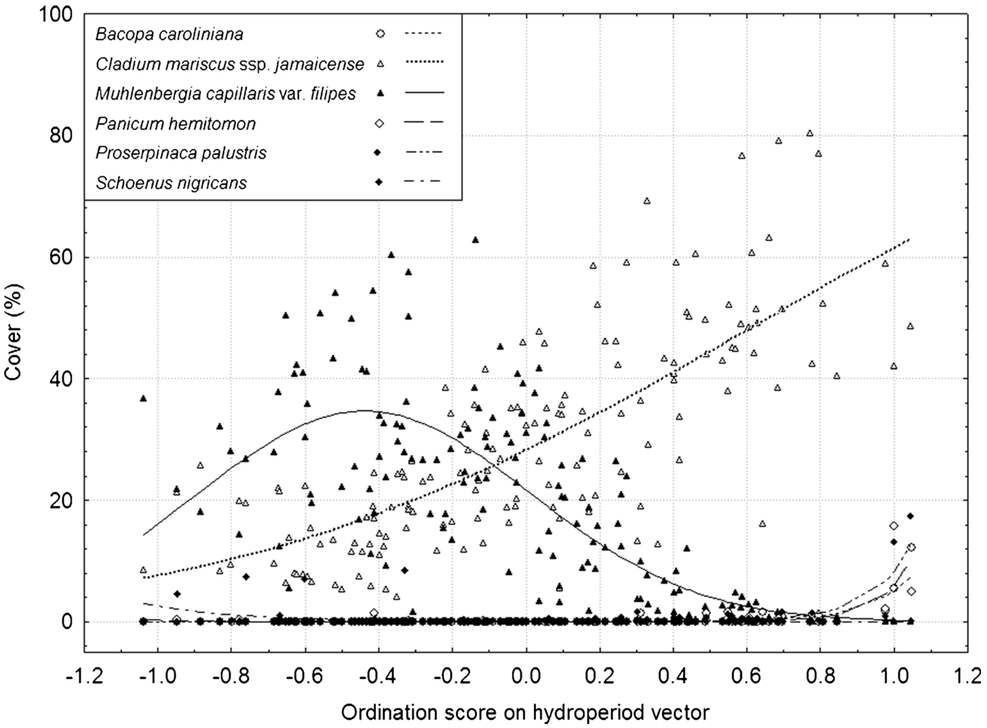


Fig. 8 Species response curve of major species modeled on hydroperiod vector in the ordination space. The species were present at least five samples of Transect 4 and 5 sites that were sampled between 1997 and 2010, and showed significant time trajectory paralleled to the hydroperiod vector in the NMDS ordination

water flow resulting in high water level in marsh (Kotun and Renshaw 2013). For instance, mean annual (water year) hydroperiod at stage recorder CR2 was higher during 2003–2010 (184 days) than 1996–2002 (172 days) period, and it was much higher during 4 year period between 2002 and 2006 (201 days). Vegetation dynamics on T4 and T5 that occurred subsequent to Armentano et al's (2006) study were concurrent with the construction and operation of the detention basins associated with the S332B, S332C, and S332D pump stations. Thus, shifts in plant community along a hydrologic gradient

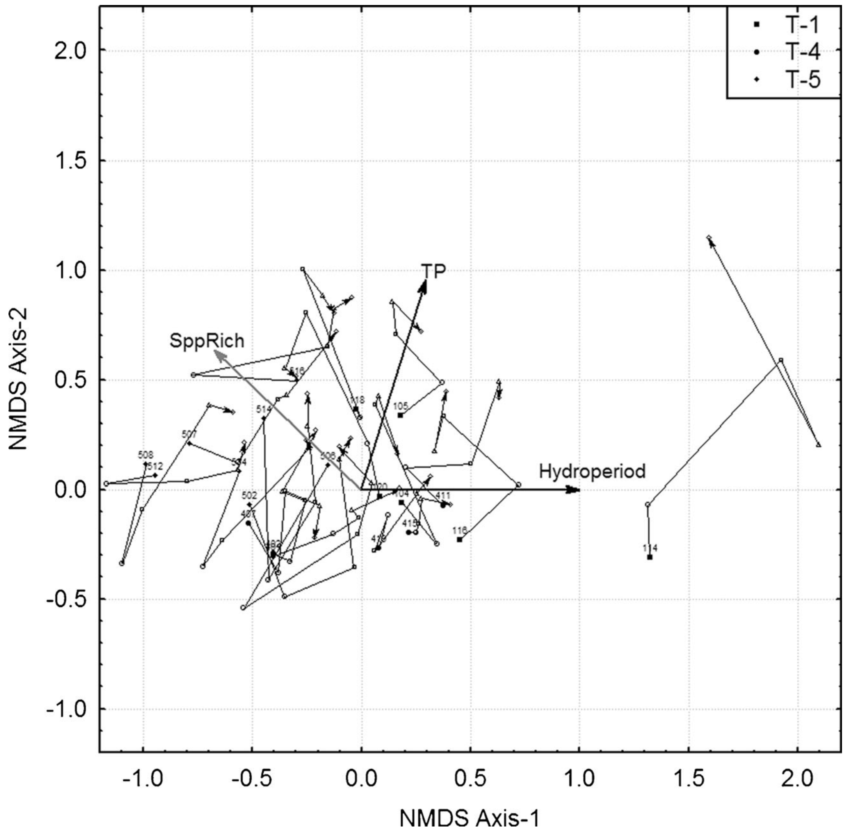


Fig. 9 The NMDS ordination showing the trajectory of sites from Transect 1–5, sampled between 1992 and 2010. Only the sites which showed significant ($p \leq 0.1$) rate of change in species composition along phosphorus (TP) gradient are shown. Ordination axes were rotated to perfectly align the hydroperiod vector with the first axis. Initial point on each site trajectory represents the 1995 or 1997 sampling and the end of arrows represents the 2007 sampling

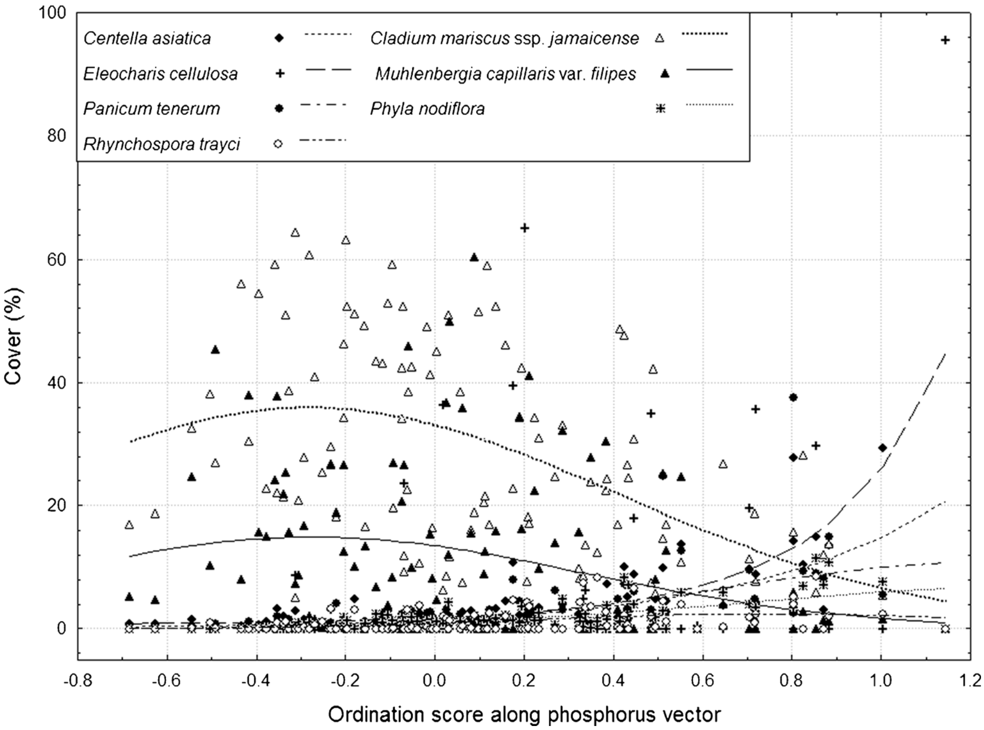


Fig. 10 Species response curve of major species along the phosphorus gradient vector in the ordination space. The species were present at least five samples of sites from Transects 1–5 that were sampled between 1992 and 2010, and showed significant time trajectory paralleled to the phosphorus vector in the NMDS ordination

towards wetter types on these transects suggest that use of these features is leading to increased hydroperiod in the marsh. The high water level in marshes in Taylor Slough headwaters is likely to enhance the sheet flow within the basin (Van Lent et al. 1993), contributing to the restoration of historic flow in Taylor Slough.

Studies in the Everglades have shown that vegetation shifts in response to hydrologic change may occur as rapidly as within 3–5 years (Nott et al. 1998; Armentano et al. 2006; Zweig and Kitchens 2008). In this study, while we observed changes occurring in 3–4 years, the number of sites showing a significant drying trend in the S332D period was fewer than those showing a wetting trend in the S332i period (Figs. 4 and 6). The results demonstrate that the rate and degree of vegetation change depends on the strength of natural and management-induced hydrologic changes. Mean water level decreased between the S332i and S332D periods. However, this decrease was less dramatic than the increase in mean water level between S332 and S332i periods (Figs. 2 and 3), probably due to continued flow of water from the canal through adjacent marshes to the slough in the S332D period. Moreover, the degree of change in plant community composition in response to external drivers also depends on community resilience, i.e. its ability to absorb disturbances (Gunderson 2000). For instance, when muhly grass-dominated prairie is exposed to increased hydroperiod, several species characteristic of short hydroperiod conditions are less likely to thrive, and the communities show relatively low resilience to increasing wetness. In contrast, once established, species characteristic of long hydroperiod conditions, such as sawgrass and *R. tracyi* may take longer to be replaced by prairie species. These species have wide range of hydrologic tolerances and often flourish in organic soils resulted from long hydroperiod, as was present in the slough during S332i period. But, prairie species, such as muhly grass, usually get established on only marl soils, and are often favored by fire (Olmsted et al. 1980). For instance, the combination of prolonged dry conditions and consumption by fires of shallow organic soil in sawgrass-dominated landscape has been cited as the major cause of the expansion of muhly grass-dominated prairie vegetation in marl prairies (Werner 1975; Olmsted et al. 1980; McVoy et al. 2011).

The unimodal response exhibited by several species including sawgrass suggests that a change from a typical short to long-hydroperiod vegetation and vice versa occurred with several transitional vegetation assemblages. For instance, with an increase in hydroperiod, sawgrass cover increased in muhly-dominated short hydroperiod prairies, remained dominant in plots with intermediate hydroperiod, but decreased in slough plots leading to spikerush-dominated vegetation (Armentano et al. 2006). In the Taylor Slough headwaters, where sawgrass showed an increasing trend (Fig. 8), the unimodal response of muhly grass to the hydrologic gradient was also surprising, but indicated the severity of dryness in the glades in the previous management periods (Rose et al. 1981; Van Lent et al. 1993). While the results suggest that some degree of hydration of the glades may be helpful to create the optimum condition for muhly-dominated prairies, continued hydration of the prairies will shift the vegetation toward sawgrass marsh.

In the Everglades, fire and phosphorus availability, combined with water management practices influence marl prairie and slough vegetation composition (Newman et al. 1998; Lockwood et al. 2003; Ponzio et al. 2004). In the Taylor Slough basin, fire regime also has had a strong impact on vegetation (Pimm et al. 2002; Sah et al. 2011). However, ENP fire records indicate that only 6 of the 100 plots along Transects 1–5 have burned since 1999. Thus, fire seems to have had little influence on the changes in vegetation composition observed in this study. However, the lack of fire for a relatively long period might have caused an increase in total cover, while also impacting species composition by suppression of species that grow well in frequently burned, open marl prairies.

Currently, soil phosphorus content is unknown for the Taylor Slough vegetation survey sites themselves, and thus was inferred from vegetation patterns observed in similar locations elsewhere in the southern Everglades. A significant trajectory parallel to the soil phosphorus vector was observed at several sites, suggesting that vegetation change was probably influenced by increasing soil phosphorus content over time. Since those sites were also impacted by management-induced changes in water regime, a link between hydrologic change, soil phosphorus and vegetation is likely. Elsewhere in the Everglades, researchers have demonstrated relationships among canal water delivery, elevated soil phosphorus and an expansion of southern cattail (Newman et al. 1998; Childers et al. 2003; Boers and Zedler 2008; Hagerthey et al. 2008). In Taylor Slough, southern cattail was observed for the first time in 2007 at 5 sites along T1, the transect closest to S332D, and in 2010 this species was recorded at two additional sites. The trajectory analysis also identified six sites on T1, including one with cattail, whose composition shifted significantly in a positive direction along the phosphorus gradient (Fig. 9). Not all sites with cattail showed significant trajectories, probably because the TP gradient derived from our reference sites did not include sites whose soil phosphorus content was as high as those typically associated with cattail expansion. However, our results suggest that soil P-enrichment has occurred to some extent at sites on T1. In a recent study also, soils along the entire 6.5 km length of the central flow way in Taylor Slough were found P-enriched with values exceeding an enrichment threshold of >500 mg kg^{-1} (Osborne et al. 2013). In the Taylor Slough basin, surface water entering ENP typically has low average phosphorus content (10 μgl^{-1}) (Sutula et al. 2001), i.e. within the range considered to be protective of oligotrophic Everglades habitats. However, the cumulative effects of phosphorus loading in outflows from the canal seem to have enriched adjacent soils in Taylor Slough (Surratt et al. 2012), resulting in a change in plant species composition.

In the Taylor Slough headwaters, where sites were not as impacted by direct delivery of canal water as sites further south in the drainage, a significant shift in species composition along a gradient of increasing phosphorus was observed at 35 % of the sampled sites. This surprising shift in species composition is within the range of vegetation assemblages present in non-impacted areas of southern Everglades. However, the change pattern could represent an early sign of increasing soil phosphorus, probably due to the influence of direct or passive water movement into the marsh. As with vegetation, the phosphorus content in periphyton mats is an excellent indicator of P-enrichment (Gaiser et al. 2004). Several studies showed elevated phosphorus content in periphyton near the L31 canals in comparison to adjacent marl prairie sites to the west, suggesting an increase in P-loading due to long-term exposure of the canal-side sites to seepage (Gaiser 2006; Gaiser et al. 2008). However, a time lag in P-enrichment in the soil is inevitable, delaying any plant response by species that flourish in high soil phosphorus conditions. Therefore, before phosphorus content in the soil passes a threshold that brings on regime shift in the plant community to another stable state adapted to P-enriched soil (van der Hoek et al. 2004; Hagerthey et al. 2008), it is important to minimize phosphorus loading in water directly entering the Park from the canal. Minimization of P-loading is of course linked to the effectiveness of the detention ponds in functioning as storm water treatment areas (STAs).

In summary, long-term monitoring of vegetation and other indicators of change in hydrologic conditions and associated drivers is essential to provide feedback for the adaptive management of Everglades ecosystems. Effective implementation of these monitoring efforts, however, requires an analytical tool capable of extracting broad level patterns and assessing site-specific responses of biological communities to changes in physico-chemical drivers and stressors. The results of this study indicate that trajectory analysis is an effective analytical technique in extracting the underlying pattern in community data, and is also appropriate for testing the extent and direction of change in community composition with reference to restoration targets. In the main channel of Taylor Slough which historically was more open type slough with water lily-dominated vegetation (McVoy et al. 2011), the trajectory of vegetation change over the period of this study indicated varying hydrologic conditions in response to alternating water management activities. During the period when S332D was in full operation with the objective of raising the water level in the slough, a shift in vegetation towards drier types was concurrent with relatively dry condition in the slough. However, the reduced hydroperiod during the S332D period was due in part to lower annual and dry season rainfall, and the construction and operation of additional detention ponds by 2012 are expected to enhance hydrologic conditions in Taylor Slough (Kotun and Renshaw 2013). Similarly, the operation of water pumps and associated detention ponds affecting hydrologic conditions in the Taylor Slough headwaters has led to plant communities indicative of wetter conditions in recent years, and the trend seems to be consistent with the goal of restoring historic hydrologic conditions in this landscape.

In addition, the trajectory analysis method used in this study made it possible to detect a shift in vegetation composition along a vector representative of increasing soil phosphorus. Previously, only major plant community changes that involved a shift in alternative stable states from sawgrass marsh vegetation to southern cattail monoculture were required before an underlying eutrophication problem was recognized and addressed. This work demonstrated that a more sensitive tool based on plant assemblages is available for tracking the outcome of management decisions. With a long-term vegetation and environmental monitoring data from a number of habitats for which restoration targets are well defined, this type of analysis could be useful for a wide variety of restoration projects that may impact vegetation in the southern Everglades and other ecosystems.

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