VEGETATION ECOLOGY OF AN IMPOUNDED WETLAND: INFORMATION FOR LANDSCALE-LEVEL RESTORATION

By

CHRISTA ZWEIG

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2008

To My Family

ACKNOWLEDGMENTS

I would like to thank my husband, Zach Welch, for his support through this arduous process, even though he didn't like to talk shop at home he did it anyway. I would also like to thank Wiley Kitchens for putting up with me. The list of people who contributed to my dissertation, be it data collection, reviewing papers, or just moral support, is long: Paul Wetzel, Paul Conrads, Erik Powers, Peter Frederick, Rob Fletcher, Mike Binford, Emilio Bruna, Becky Hylton-Keller, and an army of students and technicians who collected and sorted all of the plants necessary for these analyses.

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Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

VEGETATION ECOLOGY OF AN IMPOUNDED WETLAND: INFORMATION FOR LANDSCALE-LEVEL RESTORATION

By

Christa L. Zweig

December 2008

Chair: Wiley Kitchens
Major: Wildlife Ecology and Conservation

The Florida Everglades, an area of global significance, is an example of an ecosystem whose original pattern and process have been irrevocably altered and is currently the focus of a landscape level restoration effort. Projects of this scope, if they are to achieve the intended restoration, require substantial information regarding ecological mechanisms that are poorly understood. We provide critical information for the restoration of the Everglades and a methodological approach that affords the opportunity to expand knowledge of wetland vegetation pattern beyond the scope of our study area. To address the issue of the non-linear success of wetlands, we develop a general, non-spatial S&T succession conceptual model, and apply the general framework by creating annotated succession/management models as hypotheses for use in impact analysis on a portion of an imperiled wetland.

We consider the application of these theories, our S&T succession models, as a fraction of the framework for the Everglades and our understanding will only build with time. They are hypotheses for use in adaptive management as the restoration of the Everglades continues. These models represent the community response to hydrology and illustrate which hydrologic values—temporal or seasonal—are important to community structure. We also synthesize recent literature on ridge and slough landscape maintenance and suggest additional mechanisms. We

also demonstrate how these maintenance mechanisms have been disturbed, their effects on the landscape pattern, and how this creates alternate feedback loops that affect persistence of the multiple stable states of ridge and slough. We use techniques from previous analyses to assess the quality of habitat for the endangered Florida Snail Kite by tracking the dynamics of foraging communities within its reduced breeding range in the Everglades by use of multivariate analyses, and identify environmental and demographic correlates of vegetation community composition for habitat restoration purposes.

CHAPTER 1
A BRIEF OVERVIEW OF THE EVERGLADES

The Everglades is a relatively young ecosystem (Gleason et al 1984), which formed approximately 5000 YBP. The shallow basin that gave rise to the Everglades was shaped by the fluctuations of sea level over 500,000 years, depositing reef ridges as late as the Pleistocene that created a pseudo-atoll (Petuch 1987). The combination of geologic and climactic factors led to the seasonal, flooding shallow peatland that are observed today.

Pre-drainage Vegetation

The Everglades watershed extends from the Kissimmee chain of lakes (KCOL) near Orlando, FL, to Florida Bay. Water flows from the KCOL through the Kissimmee River into Lake Okeechobee, a large, extremely shallow (4.0 to 6.1 m) sub-tropical lake. Lake Okeechobee would overflow its southern bank seasonally, providing sheetflow for the Everglades (Parker 1974). Fringing the south shore of Okeechobee was a swamp dominated by *Annona glabra*. This area transitioned into a large sawgrass plain that thinned into a sawgrass mosaic further south (Davis et al 1994). This region was flanked by two large areas of sawgrass/wet prairie/slough/tree islands in Hillsborough Lake and Shark River Slough. Marl marsh formed the southern end of the Everglades, extending to mangrove communities in Florida Bay.

Drainage and Compartmentalization

Although limited draining of the Everglades occurred as early as the late 1800s, it wasn't until the Central and Southern Florida Flood Control Project for Flood Control and Other Purposes was passed by Congress in 1948 that landscape-wide drainage and compartmentalization took place. The Everglades Agriculture Area (EAA) was established in the mid-1950s (Snyder and Davidson 1994) and it encompassed the *A. glabra* swamp and the entire sawgrass plain south of Lake Okeechobee (Davis et al 1994). The Everglades peat formed by sawgrass was particularly suited for farming, unlike Loxahatchee peat whose primary component was *Nymphaea odorata* (Gleason and Stone 1994). The unsuitability of Loxahatchee peat for farming (high shrinkage when drained, highly volatile, and low mineral content) might have saved large parts of the Everglades from being incorporated into the EAA.

The Water Conservation Areas (WCA) were established in the 1960s to provide water storage and flood control (Figure 2-2). WCA1 was included in the U.S. Fish and Wildlife Refuge system in 1986 and is now known as A.R.M. Loxahatchee Wildlife Refuge. WCA 3 was bisected by Alligator Alley, later known as I-75, which created two very distinct hydrologies and vegetation community compositions. WCA 3A South is the primary source of water for Everglades National Park, which extends from Tamiami Trail to Florida Bay.

Hydrology

Seasonal flooding and sheetflow are two defining characteristics of Everglades hydrology, and have shaped the landscape over the last 5000 years. Sheetflow, the broad expanse of slowly flowing, shallow water (4 cm/s; Larsen et al 2007) has been interrupted by compartmentalization, and seasonal water fluctuations are altered by water management and pooling effects of levees.

Vegetation

The most recent comprehensive description of central Everglades vegetation on a landscape level was by Loveless in 1959, and is often cited to describe the present vegetation communities. Impoundment and water control over the intervening half century have created altered landscapes where hydrologic change has had important effects at the community level. Because each WCA is managed for different hydrologic regimes, the disturbance varies by compartment. WCA3A North has been kept relatively dry and sawgrass has encroached on sloughs, degrading the distinctive ridge and slough pattern. WCA3A South has been relatively wet, with deeper water depths, and the sawgrass strands are becoming stressed and fragmenting into sloughs (Chapter 4). Overall and individual area of tree islands has decreased since the earliest photographic records of the Everglades in 1940 both from dry conditions increasing vulnerability to fire and wet conditions drowning out less tolerant tree species (Willard et al 2006).

Most of the uplands and hardwood hammocks associated with the Everglades have been converted to the megalopolis of West Palm Beach/Ft. Lauderdale/Miami (Kranzer 2004). Approximately 10% of the rockland pine forests have been conserved, most in Everglades National Park (Gunderson 1994).

Restoration

Along with the Save our Everglades program from the Florida legislature, Congress passed the Water Resources Development Act of 2000, appropriating money to restore timing, amount, and quality of water to the Everglades. The scope is ambitious and is one of the largest restoration projects in the world. The political and scientific process of Everglades restoration will serve as a model (either positive or negative) for future large-scale restoration efforts (Sklar et al 2005). Projects of this scope require substantial information regarding ecological mechanisms that are often poorly understood. In this dissertation, I examine the vegetation ecology of WCA 3A South to provide critical information for the restoration of a large wetland landscape, and present a process that affords the opportunity to expand and contribute beyond the scope of the study area. Specifically, identifying the current communities and the specific hydrologic variables that affect them, and modeling the community/hydrologic relationships are initial steps to provide the capability of documenting and predicting the effect of restoration hydrologic alternatives on the Everglades ecosystem. I also examine the effect changing vegetation communities have as habitat to an endemic, endangered species and the consequences for its conservation

CHAPTER 2
EFFECTS OF LANDSCAPE GRADIENTS ON WETLAND VEGETATION COMMUNITIES: INFORMATION FOR LARGE-SCALE RESTORATION[1]

The Florida Everglades, an area of global significance, is an example of an ecosystem whose original pattern and process have been irrevocably altered and is currently the focus of a landscape scale restoration effort. Projects of this scope, if they are to achieve the intended restoration, require substantial information regarding ecological mechanisms that are poorly understood. Available information is often outdated, anecdotal, or insufficient to address issues at the multiple scales required. We provide critical information for the restoration of the Everglades and a methodological approach that affords the opportunity to expand knowledge of wetland vegetation pattern beyond the scope of our study area.

The Everglades was once an area characterized by its large spatial extent (1.2 million ha), habitat heterogeneity, sheetflow, and seasonally varying hydrology (Kitchens et al. 2002). Draining, compartmentalization, and agriculture have reduced the spatial extent of the Everglades by 50% (Light and Dineen 1994). Key drivers such as hydroperiod, fire frequency and intensity, water flow, seasonality, peat accretion, and nutrient inputs were altered, eliminating the wetland's original structure and function. The present hydrology of the area is highly managed and largely disconnected from the natural wet and dry seasons. Natural wet season rainfall initiates in June and extends through September with the driest months in April and May (MacPherson and Halley 1996). However, urban water needs in south Florida require maxima to extend into November and December, and minima from May to July. Conflicting water demands necessitate separate water schedules for the Water Conservation Areas (WCA) within the Everglades, causing some compartments to be overdrained while others are

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consistently flooded. This differential hydrology fragments the Everglades into a collection of wholly different landscapes that change temporally as well as spatially.

The goal of Everglades restoration is to return the area to a more natural state by reestablishing approximate historic water quantity, quality, and timing, while still providing flood control and water storage for south Florida (Science Subgroup 1994). An important indicator of restoration success will be the response of vegetation communities to the proposed hydrologic alternatives. However, this is a challenging concept because vegetation pattern is dynamic and the exact effects of hydrology and timing on Everglades vegetation community composition are poorly understood. On the short-term temporal scale (< 10 years), Everglades vegetation patterning is a function of hydrology (Davis 1943, Gunderson 1989, Armentano et al. 2006, Bazante et al. 2006) and disturbances such as fire, hurricanes, and nutrient input (Gunderson 1994). These drivers have created a highly heterogeneous mosaic of vegetation types, where the importance fine-scale gradients in community composition can supersede the control of landscape level elevation and hydrologic gradients. Small changes in elevation, and thus hydrology, at the local level create abrupt changes in vegetation communities (David 1996).

Researchers have documented the response of Everglades vegetation communities to disturbance for decades—from system-wide (Davis et al. 1994) and local levels (Gunderson 1994, Busch et al. 1998) to the response of vegetation to specific disturbances (Craft et al. 1995, Davis 1994, Childers et al. 2003). The most recent comprehensive description of central Everglades vegetation on a landscape scale was by Loveless in 1959, and is often cited to describe the present vegetation communities. Impoundment and water control over the intervening half century have created an altered paradigm (Figure 2-1) where hydrologic change has had subtle, yet important, effects at the community state level. We believe the vegetation in this region has shifted from the communities described by Loveless to deeper water communities formed by the present wet hydrology, and that identifying the current communities—and specific hydrologic variables that affect them—is the initial step in documenting the effect of restoration hydrologic alternatives on the Everglades ecosystem. We characterize the existing vegetation communities of a central, impounded Everglades remnant, describe how both present and historic hydrology affect wetland vegetation community composition, and document the change from communities described in previous studies, all to provide baseline knowledge for Everglades restoration science.

Methods

Our study area was a portion of the Everglades in the peninsular region of Florida, USA. Water Conservation Area 3A (WCA 3A) is the largest remnant of the original Everglades, approximately 200,000 ha (Figure 2-2). Our study area, the southern half of 3A (3AS), is a matrix of tree islands, sawgrass strands (*Cladium jamaicense* Crantz.), and sloughs, and is designated critical habitat for endangered species such as the Florida snail kite (*Rostrhamus sociabilis* Vieillot) (Kitchens et al. 2002). Several landscape gradients affect the ecology of 3AS, particularly the vegetation community states (herein referred to as 'communities'). There is an east-west peat depth gradient with peat shallowest on the west side and deepest on the east, and a north-south elevation gradient, with slightly higher elevations in the north, which used to maintain a natural hydrologic gradient. Due to impoundment, there is also an artificial north-south water depth gradient, with deeper depths at the south from pooling, that is currently the main driving factor of plant community structure. Water Conservation Area 3AS is the main focus of Everglades restoration for the next 30 years. The Decompartmentalization and Sheetflow Enhancement Project (DECOMP) will eliminate much of the levee and canal system that now restricts sheetflow in these areas. Approximately 70% of the eastern levees and canals in 3AS will be removed, and the highway which forms the southern barrier will be raised to restore natural flow. This is an area that will see radical hydrologic changes in the future and is a critical region for restoration monitoring.

Data Collection

Data for this analysis are taken from a vegetation monitoring project in 3AS that was initiated in 2002. Twenty 1-km^2 plots (Figure 2-2) were placed in a stratified random manner across the landscape gradients in 3AS. Plots were stratified by the landscape level gradients of peat depth and water depth. Five *a priori* physiognomic types were identified: slough, sawgrass, tree/shrub island, cattail, and wet prairie. Two or three transects in each plot were placed perpendicular to ecotones, beginning in one *a priori* type and terminating in another, e.g., slough to sawgrass. We collected 0.25 m^2 samples of all standing biomass along a belt transect, clipping the vegetation at peat level at 3 m intervals, and included any submerged aquatic plants within the sample. Shrubs were sampled in the same manner as the herbaceous vegetation; there were no trees in transects. Samples were collected from every transect in every plot during the dry (May/June) and wet season (November/December) of each year. These were sorted by species, counted, dried to a constant weight, and weighed to the nearest 0.1 g. The 0.25 m^2 samples represent pseudorepeated measures, as destructive samples were taken and we could not resample the exact location. Approximately 9,500 samples were collected and processed between 2002 and 2005. Our analysis focused on wet season data from the study period, as there were fewer issues of sampling error due to small, new growth and matted prairie vegetation than in the dry season.

Hydrologic data were provided by 17 wells installed in December 2002. On each sample date, water depths were measured with a meter stick at every quadrat and linked to water depth measurements at the nearest well (within a radius < 1 km) by subtracting the quadrat water depth from the reading at the well for that day. Historic hydrologic data for all 17 wells—from 1991 to 2002—were hindcast using an artificial neural network model (see Conrads et al. 2006).

To account for high densities of some low biomass species and high biomass of some low density species, data were relativized using an index, importance value (IV), calculated by:

IV for species i = $((R_{di} + R_{bi})/2)*100$,

where R_{di} is the relative density of species i and R_{bi} is the relative biomass of species i. Relative measures are the sum of biomass or density of species i divided by the sum of biomass or density of all species within the 1 km^2 plot. The importance values for all species in a plot sum to 100. Species that were in < 5% of the community samples were considered rare and not included in the analysis.

Combined Data Analysis

Our data were designed to be analyzed at several spatial levels—from the physiognomic community using each 0.25 m^2 sample to the landscape level by grouping samples. For this analysis, we pooled all data within a 1 km^2 plot for each *a priori* physiognomic type for each year and referred to them as community samples (n = 234). Using PC-ORD (McCune and Mefford 1999), we performed a hierarchical, agglomerative cluster analysis on the community samples from every plot and year using a relative Sorenson distance measure with a flexible beta of -0.25. We chose the optimal number of clusters with an indicator species analysis (ISA) (Dufrêne and Legendre 1997) and attempted to identify the associate species for each cluster. Communities were named according to the indicator species from the ISA and their position on the peat and water depth gradient in a non-metric multidimensional scaling ordination (NMS) (Kruskal 1964, Mather 1976). A Multi-Response Permutation Procedure (MRPP) was performed with a Sorenson distance measure to determine the separability of the clusters. MRPP

(Mielke and Berry 2001) is a non-parametric test that confirms or rejects the hypothesis of no differences between groups.

We then performed a NMS to determine the environmental factors that affect community composition in 3AS. The NMS was performed using a Sorensen distance measure, 40 runs with real data, and 50 Monte Carlo runs. Environmental variables that represented the major landscape gradients and had the greatest influence on community structure were overlain on the NMS. They included peat depth and a suite of both recent and historic hydrologic variables (Table 2-1), as they both could affect establishment of plant species (Seabloom et al. 2001). 'Recent', for this analysis, is defined as hydrology affecting the area in the past year and 'historic' is hydrology 2+ years previous to the sample event.

A Priori Physiognomic Type Analysis

Community sample data for 3 of the physiognomic types were analyzed separately (prairie (n = 47), slough (n = 72), and sawgrass (n = 80)) using the same procedures described above. These communities were the most abundant and also should exhibit rapid responses to hydrologic alteration due to their herbaceous growth structures. This afforded us the opportunity to further refine our community types and the analysis of the landscape gradients that affect them without the variation associated with data from combined physiognomic types. Stronger gradients for one physiognomic type might overwhelm the more subtle gradients for another, so we separated the data to more fully capture the variation within each physiognomic type. A MRPP analysis corroborated the separation of communities in our *a priori* groups.

Results

Combined Data Analysis

For the combined data, there were 10 plant communities evident from the cluster and indicator species analysis (ISA)—shallow peat wet prairie, shallow peat prairie, slough, longer hydroperiod slough, wet prairie, shrub island, cattail, sawgrass, strand/slough transition, and deteriorated island (Table 2-2). Results from the MRPP analysis support the separation of these clusters ($T = -87.65$, $A = 0.526$, $p < 0.0001$). The T-statistic describes the amount of separation among groups, with the more negative the T-statistic, the more the separation. The A-statistic describes how similar the samples are within each group (0 = no agreement, 1 = perfect agreement), and our data exhibit a relatively high within-group agreement. Values for A are often below 0.1 in community ecology (McCune and Grace 2002). Thus, we reject the null hypothesis of no differences among groups.

Plant species richness of the clusters was independent of both the hydrologic variables and peat depth, with a range of 14–23 species in a community cluster (Table 2-3). Average richness was 20 (± 2.6) species. Slough/strand transition and the sawgrass communities exhibited the highest richness, and the longer hydroperiod slough the lowest.

Spatially, 7 of the 10 communities were found across the entire landscape (Figure 2-3). The shallow peat wet and shallow peat prairies were found only in the western portion of the study area, while the longer hydroperiod slough community occurred only in the south and western section of our study area. The most common communities in our sites were the slough and sawgrass strands, reflecting the dominance of these communities on the landscape.

The NMS analysis yielded a 3-dimensional solution with a final stress of 10.26 and a Monte Carlo p-value of 0.0196. The three axes explained 93.4% of the variance in the data. Axis 1 explained a majority of the variation, with axes 2 and 3 having similar values. The ordination was rotated 10 degrees for ease of interpretation (Figure 2-3). Axis 1 corresponded to hydrologic gradients and axis 3 to a peat depth gradient, together explaining 73.6% of variation in the data. The variables for axis 1 with an r-squared > 0.25 were Mean1W ($r = 0.603$), Min1W

(0.589), MeanPD (0.567), Min3W (0.551), Min4W (0.537), Max1W (0.537), Mean4D (0.532), Min2W (0.529), Mean3D (0.523), and Mean1D (0.508) (see Table 2-1 to decipher codes). All but MaxPD, Max3W, Max4W, and Max5W fell above an r-squared ≥ 0.15 and were positively correlated to axis 1. Peat depth correlated to axis 3 with an r-squared of 0.391. No environmental factors from our analysis were correlated to axis 2.

A Priori Physiognomic Type Analysis

The MRPP rejected the hypothesis that community compositions of our *a priori* groups were identical, confirming their utility for further analyses (T = -76.65, A = 0.314, $p < 0.0001$). Within-group agreement was high, and between-group agreement was low. We can reject the null hypothesis of no differences among groups.

Prairie analysis

The cluster and indicator species analysis suggested 5 prairie sub-types in our study area: mixed transition prairie; wet prairie; *Eleocharis cellulosa* Torr. prairie; sparse sawgrass prairie; and *Eleocharis elongata* Chapman prairie. Spatially, the *E. elongata* prairie community was located across the whole landscape, while the wet prairie community was found only in the central and west, the *E. cellulosa* and sparse sawgrass prairie only in the west, and the mixed transition prairie only in the southeast.

The NMS suggested a 2 dimensional ordination, with a final stress of 9.57 and Monte Carlo p-value of 0.0196; 95.4% of the variance in the data was explained by the 2 axes. The ordination was rotated 140 degrees for ease of interpretation (Figure 2-4a). Axis 1, which correlated to the hydrologic variables, explained 85.3% of the variation. The vectors in Figure 2-4a represent environmental variables with r-squared ≥ 0.15. Mean2 (r = -0.412) was correlated to axis 1. Mean8 (r = 0.430), Min8 (0.401), and Max8 (0.420) were correlated to axis 2, which explains 10.1% of the variance in the data. In summary, the mean water depth of the previous wet season and the mean, minimum, and maximum of the wet season 4 years previous correlated with an axis that explained a large portion of community composition.

Slough analysis

The cluster and indicator species analysis yielded 6 slough sub-types in our study area: shallow slough invaded by sawgrass, lily slough, slough, mixed emergent slough, *Eleocharis* slough, and hurricane effects. The hurricane effect cluster only occurred at one time period, after hurricane Wilma, and the main difference in community composition was its lack of *Utricularia* spp. The high winds from Wilma deposited *Utricularia* into the strand areas, almost completely removing *Utricularia* from the sloughs (C. Zweig, pers. obs.). The shallow slough invaded by sawgrass only occurred in the northeast, while the slough and lily slough occurred across the entire study area. The mixed emergent slough community was confined to the western side, and the *Eleocharis* slough was found only in the southwest. The hurricane effects sub-type was established in all areas, but again only in 2005.

The NMS for slough community sub-types generated a 2-dimensional solution with a final stress of 11.93, a Monte Carlo p-value of 0.196, and 94.4% of the variance being explained by the 2 axes. The ordination was rotated 50 degrees for interpretation purposes (Figure 2-4b). Axis 1 correlated to both hydrologic and peat depth variables and explained 46.6% of the variation. Variables with an r-squared ≥ 0.25 include Mean4D (0.557), Peat Depth (-0.542), Min4D (0.535), Max4D (0.519), Min1W (r = 0.509), Min5W (0.503), and Mean5W (0.464). No other variable had an r-squared greater than 0.15 for axis 1. Axis 2 explained 47.8% of the variation, and was correlated to Min2W (-0.507), Min3W (-0.448), Mean1W (-0.450), Max1W (-0.435), MeanPD (-0.429), and Min1W (-0.389). In summary, a very broad temporal hydrologic range affects community composition of a slough in this area. Peat depth had a large influence on species on a landscape scale. The placement of *E. cellulosa* in the water depth gradient seems counterintuitive, however, and it highlights the importance of peat depth for species presence and density. For example, *E. cellulosa* communities were shallow peat communities, but not necessarily shallow water communities as we previously suspected, and can occur in areas of deeper water.

Sawgrass analysis

The cluster and indicator species analysis suggested 5 sawgrass sub-types: deteriorated sawgrass strand; shallow peat, short sawgrass strand; shallow peat, tall sawgrass strand; sawgrass with *Peltandra*; and sawgrass with *E. cellulosa* and *Justicia*. The labels short and tall were calculated from the average biomass (g) per stem within the community (Table 2-4). Spatially, the deteriorated strand was found only in the east, while the shallow peat, short strand was found only in the southwest. The other three sub-types were established across the entire landscape.

The NMS of *a priori* sawgrass community data yielded a 3-dimensional solution (Figure 2-4c), with a final stress of 11.55 and a Monte Carlo p-value of 0.0196. The ordination was rotated 40 degrees for ease of interpretation. The 3 axes explained 91.5% of the variation in the data. Peat depth was correlated to both axis 1 ($r = 0.507$) and 3 (0.733). These two axes explained 26.8% and 47.6% of the variation, respectively. Axis 2 was correlated to Max4D and MeanPD and explained 17.2% of the variation in the data. The environmental variables with an r-squared > 0.15 were MeanPD ($r = 0.396$) and Max4D (0.416). In summary, peat depth has a strong correlation with sawgrass community composition, as do water depths in the recent and historic (up to 4 years previous) dry seasons.

Discussion

An objective of this study was to characterize the vegetation communities in WCA 3AS as baseline data for Everglades restoration monitoring. We believe the communities described previously in studies of 3AS are no longer representative due to the change in overall hydrology

(Figure 2-1). A trend toward *Nymphaea*-dominated, deep sloughs due to impoundment in the southern end of 3AS was documented by Wood and Tanner as early as 1990. In approximately 1991, the hydrology of 3AS shifted to the deeper water and extended hydroperiods of the new, wet hydrologic era, and now vegetation communities north of the impoundment effects have changed accordingly.

Hydrologic Correlations

The hydrologic correlations of each physiognomic group are quite different in regards to season (Table 2-5). The dominant species in each physiognomic type are most sensitive to hydrology during their preferred growing conditions (Edwards et al. 2003, Childers et al. 2006). Species can tolerate harsher conditions in their dormant season, but are more vulnerable to abnormal highs and lows within their growing season. *Eleocharis cellulosa's* growth improves in moderately flooded, but not high, water conditions (Macek et al. 2006). A wet season with too much or too little water would have an impact on *Eleocharis* communities, but hydrologic alterations in the dry, dormant season would not.

Temporally, the sub-types within the separate physiognomic types (slough, sawgrass, wet prairie) had correlations that all occurred within 1 to 4 years previous to the sample, which indicates a relatively short time lag between hydrologic alteration and vegetation change. Armentano et al. (2006) suggest that Everglades vegetation community response to hydrologic change is normally no more than 4 years, and our results agree that, for these physiognomic types, the communities respond within 4 years.

We are not proposing that our environmental variables are the only influences on community composition, but they are representative of the complex hydrology that affects vegetation in 3AS and provide a basis for experimentation and management. These environmental correlates do not capture all of the variability in the data, and there are probably additional hydrologic characteristics that control the composition of communities, including changes in hydrologic era (dry vs. wet periods) and other long-term hydrologic variables such as duration. Large scale changes due to restoration might alter the determinants of community composition, and thus monitoring should be continuous in order to understand the mechanisms of vegetation change.

Vegetation Communities: Past, Present, and Future

The Everglades communities we encountered were dynamic and will continue to respond to recent hydrologic alterations. Loveless (1959) described community states of Everglades vegetation that existed in a drier hydrologic era, but his observations are still frequently cited as a benchmark for vegetation restoration in the Everglades. While all of the common species identified by Loveless are still prevalent today, they have rearranged into communities that reflect the present wetter hydrologic era. *Rhynchospora* flats no longer exist in our study area, nor do extensive *Panicum hemitomon* Schult. flats (although remnants of the *P. hemitomon* flats were observed outside of our sample locations).

The concept of an Everglades wet prairie in 3AS now needs to include additional definitions. In 1959, there were 3 prairie sub-types dominated by *Rhynchospora* spp., *Panicum* spp., and *E. cellulosa*. In 1990, Wood and Tanner questioned the classification of their sites as wet prairies because they did not contain *Rhynchospora* spp. We also identified 3 prairie sub-types in our landscape analysis, but they were dominated by *E. elongata*, *Paspalidium geminatum* (Forssk.) Stapf, and *E. cellulosa*. These do not conform to the original definition of prairie, nor would they be considered sloughs as defined previously (Loveless 1959, Gunderson 1994, Busch et al 1998). *Panicum geminatum* and *E. elongata* were located deeper on the hydrologic gradient than *P. hemitomon* in our ordination, so we infer that the community sub-types from our analysis are deeper forms of prairie than those in Loveless (1959). The community sub-types delineated in the separate physiognomic analysis did not have a dominant *Panicum* or *Rhynchospora* element. *Rhynchospora* was rarely encountered, even in dry season samples. *Eleocharis* has long been considered a slough species in the Everglades (Davis 1943, Loveless 1959, Gunderson 1989, Wood and Tanner 1990), but more recently as conditions became wetter (1991-present), it has become accepted as a wet prairie species (Gunderson 1994, Daoust and Childers 1999, Armentano et al. 2006). This suggests that the perception of the Everglades wet prairie—a short-stature graminoid community interspersed among sawgrass—has changed considerably, and the extent of vegetation community transformations within 3AS is more significant than previously recognized.

The only deep water slough described from 3AS prior to our study was a *Nymphaea odorata* Ait./*Utricularia* spp. slough (Loveless 1959, Gunderson 1994). Our combined data analysis suggested two types of slough: *Utricularia* spp. slough, and a *N. odorata* slough with a longer hydroperiod. The separate physiognomic analysis indicated 6 sub-types of slough with varying amounts and species of emergents. Species of *Eleocharis* were abundant in these sloughs, underscoring their role as both slough and prairie vegetation.

The three sawgrass sub-communities that Loveless observed (*C. jamaicense/Sagittaria lancifolia* L./*P. hemitomon*, *Myrica cerifera* L./*Ilex cassine* L., and *C. jamaicense/P. hemitomon*) are not as evident in 3AS in the present water era, and *M. cerifera* and *I. cassine* were completely absent from sawgrass sub-communities in our study sites. *Cephalanthus occidentalis* L. and *Salix caroliniana* Michx. were observed within the deteriorated sawgrass strand sub-type, the only sawgrass community that contained woody species. The 5 sawgrass sub-communities indicated by the separate physiognomic analyses conform to previous designations of tall and short sawgrass communities, but not necessarily as a function of peat depth, which was thought to be the cause of difference in sawgrass heights (Gunderson 1994). Even though sawgrass is still a dominant plant after decades of impounded, stressful conditions, the sawgrass sub-communities of Loveless' time no longer exist in 3AS.

Vegetation community response depends on the nature and magnitude of the hydrologic alteration, but ecology and life history traits make some species better indicators of either short-term or long-term shifts. *Nymphaea odorata* and sawgrass are probably slower to respond to hydrologic fluctuations due to their growth structures. Sawgrass is sympodial (Snyder and Richards 2005) and can form tussocks in deeper water, climbing dead roots and culms to reach drier, more hospitable conditions. Sawgrass can maintain its canopy for some time, even while it fragments at the substrate level. Once gone it leaves areas of open water with little other vegetation due to past canopy shading (C. Zweig, pers obs). Long-term flooding will continue to degrade sawgrass strands, but will benefit *N. odorata*. David (1996) states that *N. odorata* is sensitive to dry downs and needs near optimum conditions to persist, making it an excellent indicator for sloughs. However, *N. odorata* is also a rhizomatous perennial that forms dormant root stalks and can survive extended droughts (Zaremba and Lamont 1993), so it is an indicator of both short-term and long-term slough conversion. *Eleocharis* spp. have less physical structure and respond quickly to hydrologic change, although they have specific responses to alterations in water depth. *Eleocharis cellulosa* grown in shallow water conditions (~10 cm) responds to rising water by elongating, but when grown in deeper water (~50 cm), its response to a rapid drying event is a collapse of the long, thin shoots (Macek et al. 2006), senescence, and complete regrowth (Edwards et al. 2003). It can completely recover within 9 weeks of hydrologic alteration, but recovery by plants in deep water from a precipitous drawdown is slower than that of plants in shallow water (Edwards et al. 2003). Considering species life history characteristics, wet prairie/slough species such as *Eleocharis* spp. and *N. odorata* are short-term sentinel species of community change, while sawgrass and *N. odorata* should be monitored for long-term change.

We conclude that the wetland vegetation of 3AS is influenced by both recent and historic hydrology (up to 4 years earlier), and communities of the mid-1900s no longer exist in our study area. Through a combination of time, anthropogenic activities, and past/current water management actions, the vegetation has changed to communities suited to deeper flooding, with some being eliminated completely. The vegetation communities and correlating hydrologic gradients described in this paper should be considered in future management decisions for 3AS.

Table 2-1: Hydrologic environmental variables used in NMS correlations for Water Conservation Area 3AS.

Hydrologic Characteristics	Dry Season	Wet Season
MaxPD/MinPD/MeanPD	Previous	
Max1W/Min1W /Mean1W		One year previous
Max1D/Min1D/Mean1D	One year previous	
Max2W/Min2W/Mean2W		Two years previous
Max2D/Min2D/Mean2D	Two years previous	
Max3W/Min3W/Mean3W		Three years previous
Max3D/Min3D/Mean3D	Three years previous	
Max4W/Min4W/Mean4W		Four years previous
Max4D/Min4D/Mean4D	Four years previous	
Max5W/Min5W/Mean5W		Five years previous

The number refers to the season and timing previous to the sample for which the characteristics were calculated. Max = maximum water depth, Min = minimum water depth, Mean = mean water depth.

Table 2-2: Percent Importance Value of 7 main species for landscape level communities in Water Conservation Area 3A South.

Community	CEO	CLA	ELG	ELC	NYO	PNC	UTsp
Deteriorated Island	26.7%	16.7%	0.4%	0.0%	1.5%	32.9%	2.3%
Shrub Island	53.9%	3.0%	4.9%	0.1%	3.3%	53.0%	2.9%
Sawgrass	4.2%	23.9%	15.6%	1.5%	1.5%	3.4%	1.5%
Cattail	1.0%	20.0%	0.1%	17.6%	0.9%	3.4%	1.7%
Wet Prairie	2.3%	2.8%	31.0%	2.7%	20.2%	2.6%	7.0%
Strand/Slough Transition	11.7%	18.8%	7.6%	2.8%	2.5%	3.8%	3.9%
Shallow Peat Wet Prairie	0.0%	1.4%	6.2%	24.0%	7.0%	0.1%	22.9%
Shallow Peat Prairie	0.0%	10.9%	1.0%	40.6%	2.2%	0.0%	3.4%
Slough	0.3%	0.8%	27.4%	2.1%	18.2%	0.1%	30.2%
Longer Hydroperiod Slough	0.0%	1.7%	5.9%	8.6%	42.7%	0.7%	24.2%

CEO = *Cephalanthus occidentalis*, CLA = *Cladium jamaicense*, ELG = *Eleocharis elongata*, ELC = *Eleocharis cellulosa*, NYO = *Nymphaea odorata*, PNC = *Pontideria cordata*, UTsp = *Utricularia* sp. For some communities, indicator species were not among the main species.

Table 2-3: Community summary statistics for all physiognomic types in Water Conservation Area 3A South. Water and peat depths are in cm.

	Previous wet season			Previous dry season				
Community Type	Mean	Max	Min	Mean	Max	Min	Species Richness	Peat Depth
Deteriorated Island	36.0	58.2	11.6	10.4	43.0	7.6	21	99.2
Shrub Island	46.0	70.4	19.8	13.4	52.7	6.7	19	94.7
Sawgrass	51.8	75.0	26.5	22.6	60.4	18.3	23	108.4
Cattail	57.0	78.6	32.3	27.4	64.9	25.3	21	55.3
Wet Prairie	61.6	89.9	32.3	34.4	84.4	24.4	21	90.2
Strand/Slough Transition	62.8	81.7	39.3	36.3	68.3	-3.7	23	101.0
Shallow Peat Wet Prairie	67.7	84.1	46.6	43.9	69.2	25.3	18	55.0
Shallow Peat Prairie	70.1	91.1	46.6	41.5	78.6	23.8	19	38.0
Slough	74.1	93.0	51.5	44.8	73.8	31.1	20	95.4
Longer Hydroperiod Slough	76.5	99.7	52.1	46.6	82.6	-2.7	14	83.8

Table 2-4: Biomass and density characteristics of sawgrass sub-communities in Water Conservation Area 3AS.

Community	Biomass(g)/quadrat	Stems/quadrat	Biomass(g)/stem
Deteriorated Sawgrass Strand	53.4 ± 23.51	3.1 ± 0.52	17.1 ± 5.98
Shallow Peat, Short Sawgrass Strand	69.1 ± 20.34	4.1 ± 0.80	16.5 ± 7.55
Shallow Peat, Tall Sawgrass Strand	78.9 ± 23.57	3.7 ± 1.11	22.5 ± 3.32
Sawgrass with *Peltandra*	85.4 ± 22.23	4.0 ± 0.88	22.3 ± 7.55
Sawgrass with *Justicia* and *Eleocharis*	87.7 ± 26.34	4.3 ± 1.3	20.7 ± 3.32

Table 2-5: Summary of temporal and seasonal correlations for the community compositions in 3 physiognomic groups within Water Conservation Area 3AS.

	Slough	Sawgrass	Prairie
A. Community Characteristics			
Dominant Species	*Nymphaea odorata*	*Cladium jamaicense*	*Eleocharis spp*
Conditions for Optimum Growth	Flooded (Wiersema 1988)	Requires dry season (Herndon et al 1991)	Moderately flooded (Macek et al 2006)
Response to Sub-optimal conditions	Rhizomatous tuber (Zaremba and Lamont 1993)	Vertical sympodial growth (Snyder and Richards 2005)	Elongation of stem (Edwards et al 2003)
Consequences of Sub-optimal conditions	Suspend reproduction, tuber formation (Zaremba and Lamont 1993)	Fragmentation, reduced reproduction (Wu et al 1997, Snyder and Richards 2005)	Reduced biomass, suspend reproduction (Macek et al 2006)
B. General Hydrologic Factors			
Previous Dry Season	Mean	Mean	
Wet 1 Year Previous	Max, Min, Mean		Mean
Dry 1 Year Previous			
Wet 2 Years Previous	Min		
Dry 2 Years Previous			
Wet 3 Years Previous	Min		
Dry 3 Years Previous			
Wet 4 Years Previous			Max, Min, Mean
Dry 4 Years Previous	Max, Min, Mean	Max	
Wet 5 Years Previous	Mean		

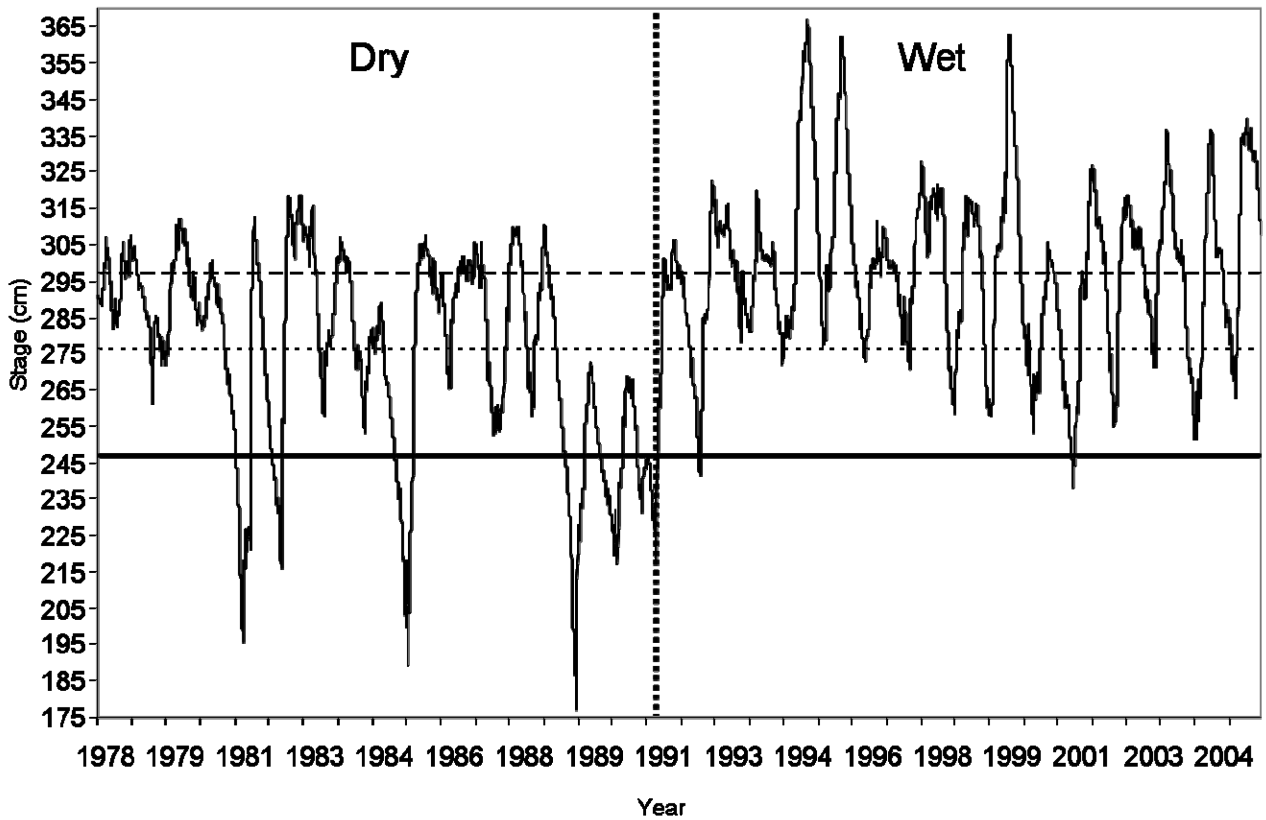


Figure 2-1: A hydrograph for Water Conservation Area 3A South from 1978–2004. The solid horizontal line indicates general ground elevation for the area and the dashed vertical lines represent the average stage in cm for the wet (— — —) and dry (- - - -) eras. The vertical dotted line indicates a transition in water eras in approximately 1991.

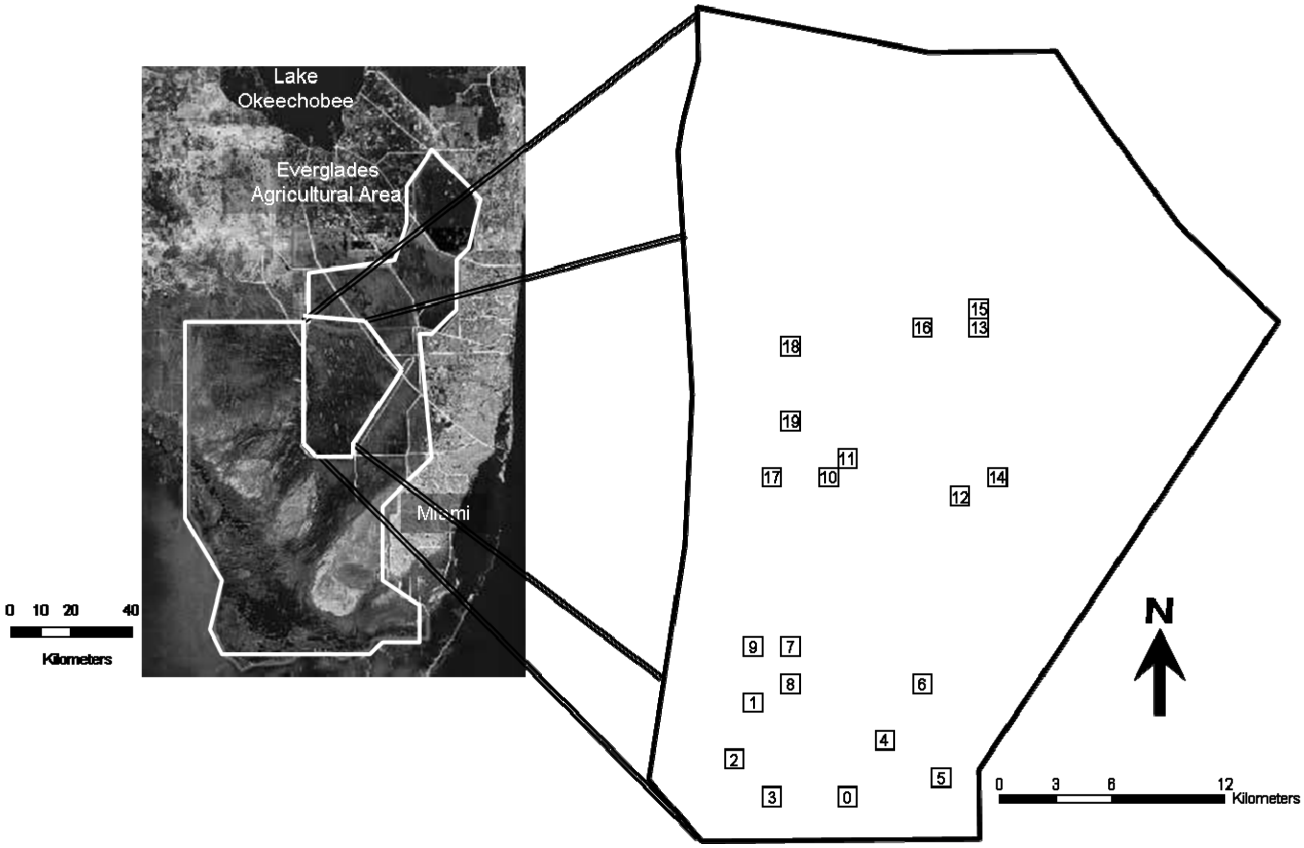


Figure 2-2: A satellite view of south Florida, USA. The white line indicates general boundaries of the Everglades and Water Conservation Area 3AS, the study site. The locations of study plots are inset.

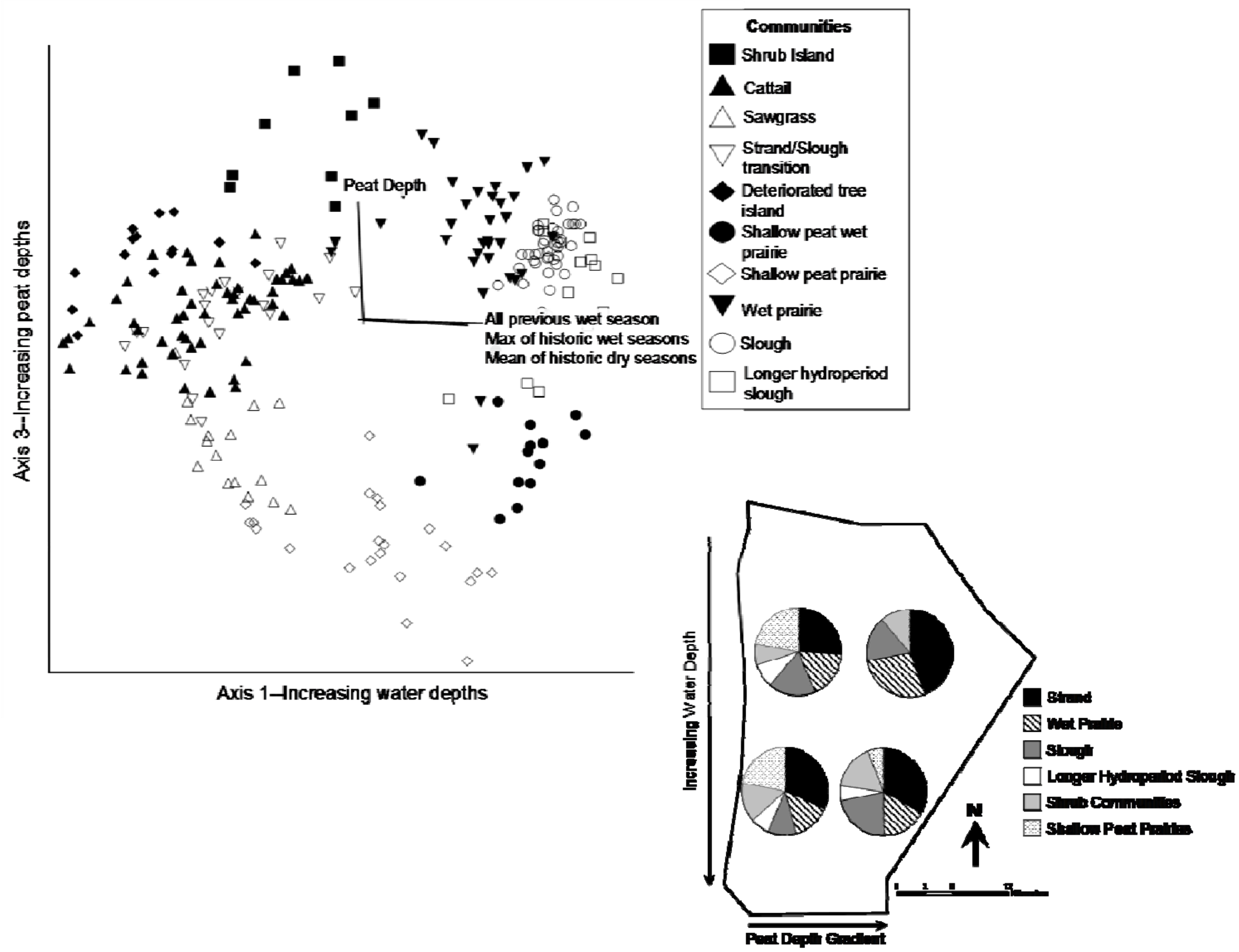


Figure 2-3: Axis 1 and 3 of the 3-dimensional NMS solution for all physiognomic types and spatial distribution of vegetation types in Water Conservation Area 3A South. Some similar communities were combined for ease of interpretation in the spatial element.

A

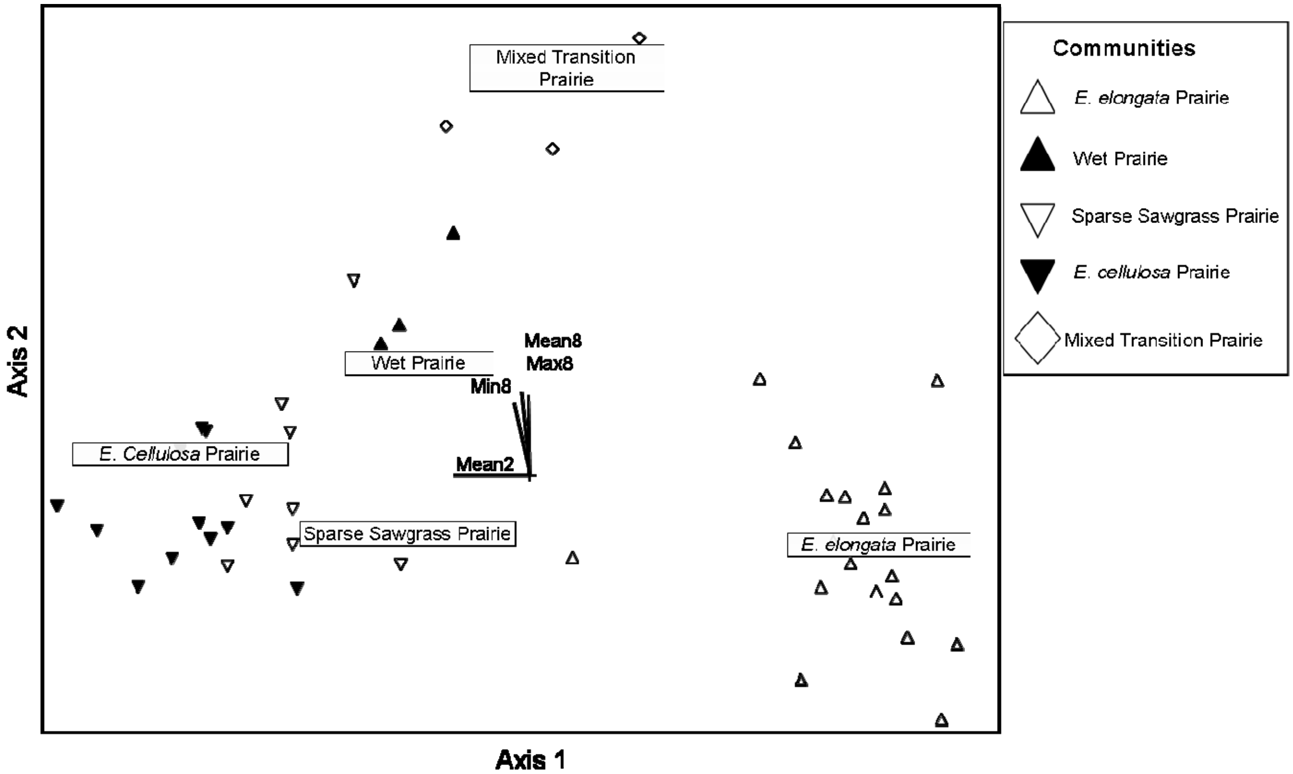


Figure 2-4: NMS graphs for the a) prairie b) slough and c) sawgrass a priori community in Water Conservation Area 3A South.

B

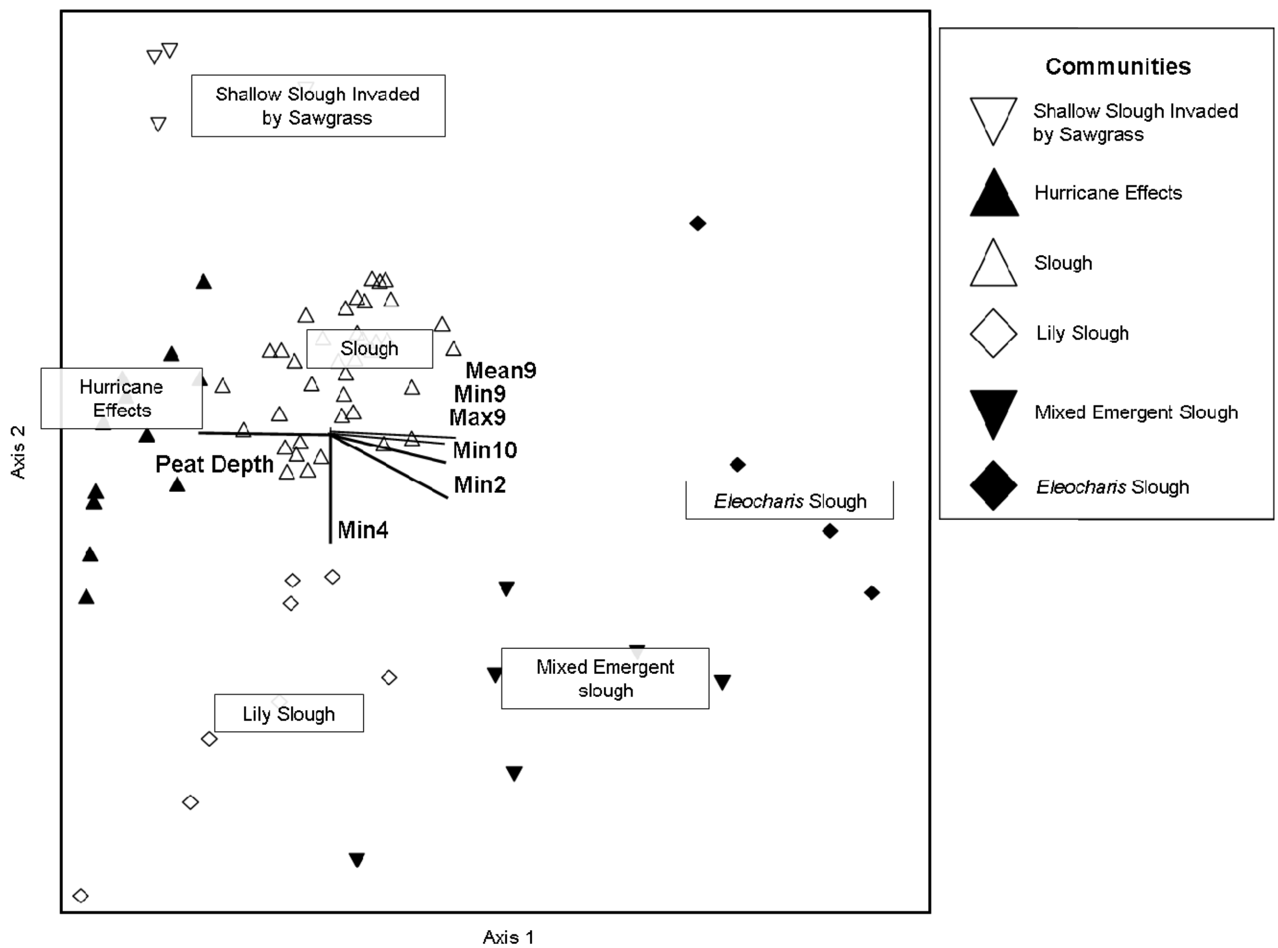


Figure 2-4. continued

C

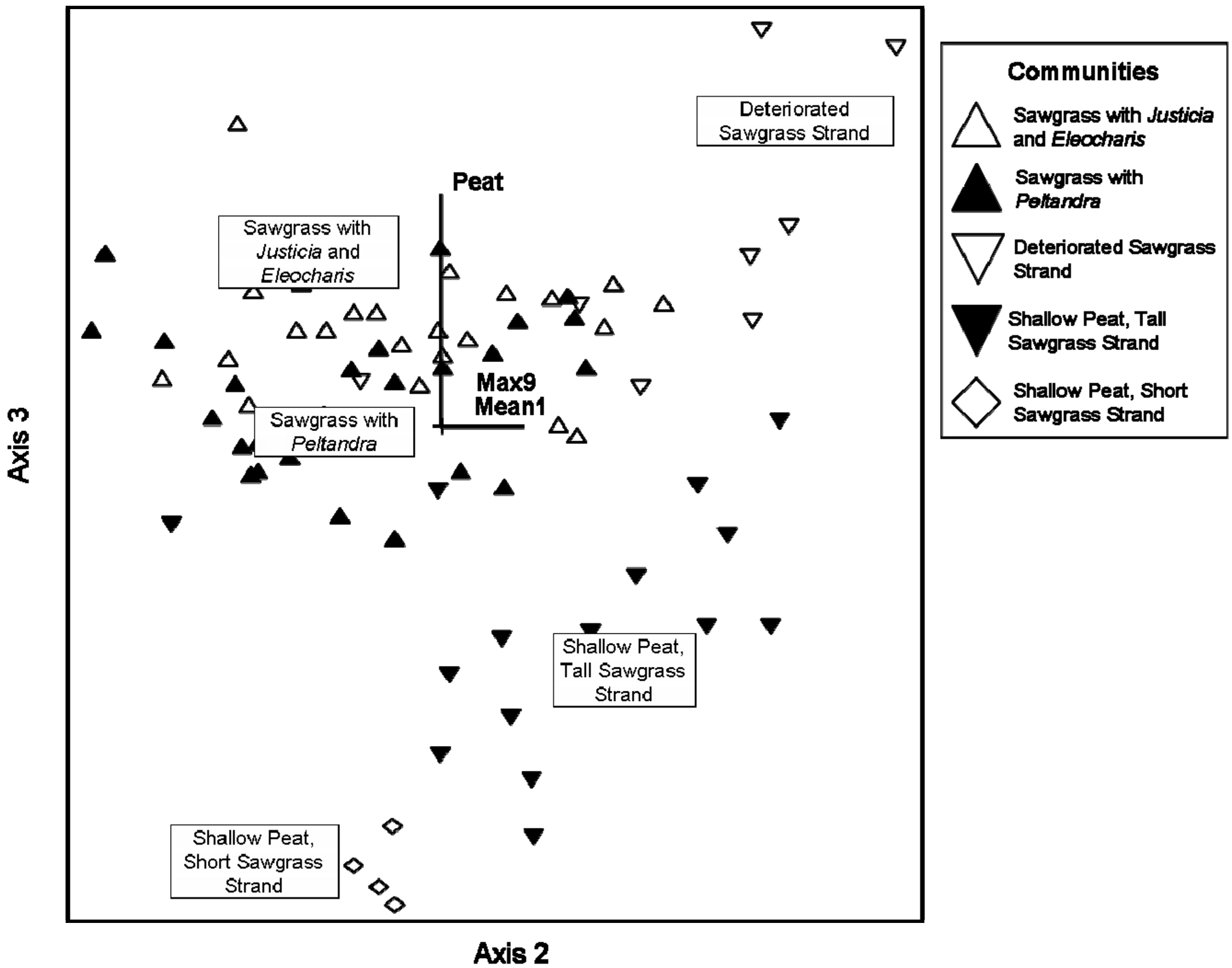


Figure 2-4. continued

CHAPTER 3
MULTI-STATE SUCCESSION IN WETLANDS: A NOVEL USE OF STATE AND TRANSITION MODELS

It is well known that the concept and application of succession theory is extremely complex (Platt and Connell 2003). Yet the complexity of ecosystems and mechanisms of succession are often simplified into linear mathematical models (Ryan et al 2007) used to understand and predict system behavior. These linear models can not incorporate multivariate, non-linear feedbacks in pattern and process that include multiple scales of organization inherent within real-world systems (Proulx 2007). It is this complexity that creates the possibility of restoration actions producing unexpected results due to reliance on traditional succession patterns that are no longer valid in a degraded system (Suding et al 2004). As wetlands are a major ecosystem type currently impacted and being restored by humans, my goal is to provide a non-linear, easily interpretable, community-based wetland vegetation change/succession model for use in restoration monitoring and management.

Wetlands have a unique pattern of succession (any vegetation change over time (Peet 1992)) due to the regular, but often inconstant, presence of water on the landscape. The vegetation exhibits both terrestrial and aquatic vegetative characteristics and is frequently considered transitional between the two (Whited et al 2007), increasing the complexity of the system. Accordingly, wetland succession has multiple trajectories and endpoints, created by hydrology, competition, edaphic factors, and other external and internal controls. Typical succession is initiated by a disturbance, partial or total (Platt and Connell 2003), in which the communities are ‘reset’. Succession progresses in a relatively directional manner (Tilman 1990, Sousa and Connell 1992) to one of many endpoints (Law and Morton 1996). Wetland reset points have two possible trajectories that are opposite each other—more aquatic or more terrestrial communities. The position of the wetlands reset point, in the middle of a bi-directional succession, is unique and is a key factor in the diversity of wetlands such as the Pantanal (Alho 2005, Junk et al 2006) and the Okavango Delta (Ellery et al 2003). The initial direction of succession, and whether the ecosystem response is continuous or discontinuous, depends on the intensity of the reset, current conditions, and vegetative and hydrologic legacies of the site. The intensity of reset determines which species are present to recolonize the affected area.

The variable position of the reset point and its multiple trajectories create the possibility of multiple stable states (Beisner et al 2003) within dynamic regimes (Mayer and Rietkerk 2004) in vegetation community succession. Transitions between stable states are typically characterized by dramatic changes, e.g. from oligotrophic to eutrophic lakes (Scheffer and Carpenter 2003), but fine-scale changes within communities are also functionally important (Arscott et al 2002), especially in areas with subtle environmental gradients (Givnish et al 2008). Here my model accounts for non-linear succession at multiple scales, including fine-scale changes from transitions within communities, defined here as state shifts, and changes between communities defined as community shifts.

State and transition (S&T) models were developed as conceptual models to address the need for flexibility (e.g. open-ended, multidirectional, and adaptive) and non-linearity in succession models for management (Westoby et al 1989). They have been widely applied in rangeland, arid, and semi-arid grasslands (Allen-Diaz and Bartolome 1998, Bestelmeyer et al 2006, Quétier et al 2007), but have had limited use in other ecosystems. They provide a simple, flexible framework for both scientists and managers and apply dynamic vegetation change theory to management models. S&T models may capture the complexity of wetland succession that is unattainable with other models and these approaches offer an excellent opportunity to build an adaptive framework for restoration/management use. This adaptability is especially useful in a time of accelerated human impacts, global climate change, and sea level rise.

An excellent system to test the S&T model's ability to capture complex, non-linear interactions for management use is one of the largest restoration projects in the world, the Florida Everglades. The Everglades is a seasonally flooded wetland in sub-tropical south Florida, USA, which is subject to extremely subtle environmental gradients (north-south elevation gradient of 2 cm/km and 1.15 cm/second flow rate (Larsen et al 2007)). Spatial and temporal variance in natural and altered hydrologic regimes maintain a highly heterogeneous landscape. Vegetation dynamics of the system have been modified along with its hydrology and represent a disturbed regime whose successional pathways are unknown. I develop a general, non-spatial S&T succession conceptual model for wetlands, and apply the general framework by creating annotated succession/management models as hypotheses for use in impact analysis on a portion of an imperiled wetland.

Methods

Study Area

The study area is Water Conservation 3A South (WCA3), one of the largest intact areas of the Everglades ridge and slough landscape in southern Florida (Figure 1). It comprises approximately 200,000 ha and the vegetation communities are subject to several key environmental gradients—an east-west peat depth gradient, north-south elevation gradient, and an artificial north-south water depth gradient due to impoundment. Hydrologic regimes in WCA3 were altered for restoration purposes beginning in 2002, an action that increased hydroperiods and water depths. Climate cycles and water control have resulted in higher maximum water depths and an increased hydrologic range from wet to dry seasons (C Zweig *unpublished data*). This is disturbance to an area already under stress from decades of sustained ponding. I monitor WCA3 to track changes in vegetation communities during this altered regime.

General Framework

The general wetlands S&T succession framework loosely follows definitions in Stringham et al (2003). I constructed my framework with multiple community states within a community and, at this four year time scale, the transitions between states tend to be dominated by hydrology (Figure 2). Each community has a finite number of states possible, but the number varies between communities. Transitions between states are considered reversible and have less distinct thresholds, defined as moving thresholds, but community shifts may require relatively more extreme disturbances to transition. State forcing functions influence state shifts and outside forcing functions influence community shifts. State and outside forcing functions share most factors: hydrologic timing, edaphic factors, autogenic effects, topography, intensity of rest, disturbance, intensity of disturbance, exotic invasion, flow, hydroperiod, nutrient cycles, seed bank, and vegetative and hydrologic legacy. Forcing functions that are considered state-only include competition and microtopography. This framework can accommodate multiple communities and states as the landscape responds to autogenic or allogenic change. I applied this general framework to the study area (Figure 3), restricted to a temporal scale of < 50 years. In my study systems, the main forcing functions consist of disturbance and long-term hydrologic variation.

Everglades Model

Delineating communities

Community state analyses were initially conducted for a previous study (Zweig and Kitchens *in press*) but are provided here in less detail, as they are input for the S&T models. Data for the Everglades analysis are taken from a vegetation monitoring project in WCA3 from

2002-2005. Five *a priori* physiognomic types were identified: slough, sawgrass, tree/shrub island, cattail, and wet prairie. Two to three transects were placed in each of 20 study plots perpendicular to ecotones, beginning in one *a priori* type and terminating in another (e.g. slough to sawgrass). I collected 0.25 m^2 quadrat samples of all above-ground standing biomass at three meter intervals along a belt transect and included any submerged aquatic plants within the sample. Samples were collected on every transect in each plot in the dry (May/June) and wet season (November/December) of each year. These were sorted by species, counted, dried to a constant weight, and weighed to the nearest 0.1 g. Approximately 9,500 samples were collected and processed between 2002 and 2005. Seventeen water wells were installed in December 2002 and historic hydrologic data—from 1991 to 2002—were hindcast using an artificial neural network model (Conrads et al 2006).

To account for high densities of low biomass species and high biomass of low density species, the data were relativized in an index called importance value (IV), calculated by:

IV for species i = $((R_{di} + R_{bi})/2)*100$,

where R_{di} is the relative density of species i and R_{bi} is the relative biomass of species i. Relative measures are the sum of biomass or density of species i divided by the sum of biomass or density of all species within the 1 km^2 plot. The importance values for all species in a plot sum to 100. Species that were in less than 5% of the community samples were considered rare and not included in the analysis.

The IV data for each plot were analyzed using PC-ORD (McCune and Mefford 1999), a multivariate statistics software, as I was interested in changes of community structure and not focused on one species at a time. My data were designed to be analyzed at several spatial levels—from the community state using each 0.25 m^2 sample to the landscape level by grouping samples. For this analysis, I pooled all data within a 1 km^2 plot for each *a priori* physiognomic type for each year and referred to them as community samples (n = 234).

I performed a hierarchical, agglomerative cluster analysis on the community samples from every plot and year for three of the *a priori* vegetation types (wet prairie (n=47), slough (n=72), and sawgrass (n=80)) using a relative Sorenson distance measure with a flexible beta of -0.25 in order to delineate community states present in my study area. I chose the optimal number of clusters/states with an indicator species analysis (ISA) and identified the associate species for each cluster (Dufrêne and Legendre 1997). Community states were named according to the indicator species from the ISA. I performed a non-metric multidimensional scaling (Kruskal 1964, Mather 1976) ordination (NMS) on the vegetation community data with Sorensen distance measure, 40 runs with real data, and 50 Monte Carlo. I then constructed a secondary matrix of environmental factors to determine which correlate to community state composition in WCA3. PC-ORD overlaid the secondary matrix and calculated correlation coefficients for each environmental variable, which included peat depth and a suite of both recent and historic hydrologic variables (maximum, minimum, and mean of every dry and wet season up to five years previous to the sample). 'Recent', for this analysis, is defined as hydrology affecting the area in the past year and 'historic' is hydrology 2 or more years prior to the sample event.

Classification and Regression Tree (CART)

I performed a CART analysis (Breiman et al 1984) on the three physiognomic types of interest (slough, sawgrass, and wet prairie) to provide quantitative measures of environmental variables to annotate the transitions in the S&T models, but the sample size of wet prairie was too small to provide results with acceptable error. The CART (S-plus 1993) analyses classified my community states for slough and sawgrass communities by the environmental variables used in the NMS and provided environmental thresholds that delineated community states. The

CART results were interpreted with the NMS results to supply annotated (quantitative) transitions in the S&T models, which are normally conceptual, qualitative models.

Vegetation Dynamics Development Tool (VDDT) analysis

VDDT (Beukema 2003) is an freeware program that simulates succession and disturbance, using S&T models, based on two types of user-defined transitions: probabilistic and deterministic. Probabilistic transitions are controlled by management actions or disturbance; and deterministic transitions are based on succession due to time with no disturbance or change in management. There were no probabilistic transitions defined for my simulations, as I do not consider a typical hydrarch or linear successional pathway valid here, thus the reason for my study. I identified qualitative management actions/disturbances (high and low dry season water depths, high and low wet season water depths, high winds, fire, and peat deposition and subsidence) and assigned them transition probabilities calculated from observed transitions within my S&T models, i.e. a high water wet season will have a 4% chance to changed a mixed transition prairie state to an *Eleocharis elongata* Chapman prairie state. I simulated 100 year time intervals with 50 Monte Carlo runs over 500 cells, with vegetation community configuration for 2002 as the initial conditions, for four management actions: equal, wet conditions, dry conditions, and increased hydrologic range. The equal category was added as a control to predict vegetation communities if the probability of all disturbances or management actions were equal and they occurred randomly. Wet conditions had high probability of high water depths in the wet and dry season and low probability of all other disturbances, while dry conditions had high probabilities for low water in the wet and dry season and low for all others. Increased hydrologic range included high wet seasons and low dry seasons.

Results

Delineating communities and transition probability

State transitions in the S&T model for each *a priori* group were based on my data, but transitions between communities represent extreme changes that were not present during my study period and are hypotheses only (Figure 3). The cluster/ISA suggested five prairie states, five sawgrass states, and six slough states from 2002-2005 (see Zweig and Kitchens *in press*): sparse sawgrass prairie, *E. elongata* prairie, wet prairie, mixed transition prairie, *Eleocharis cellulosa* Torr. prairie; shallow peat/short sawgrass strand, shallow peat/tall sawgrass strand, sawgrass with *Peltandra virginica* (L.) Schott & Endl, sawgrass with *Justicia alata* Vahl and *Eleocharis* spp; slough, mixed emergent slough, lily slough, shallow slough invaded by sawgrass, *Eleocharis* spp. slough, and hurricane effects. General hydrologic transitions (Figure 4) were supplied by the environmental correlates within the NMS analysis (See Zweig and Kitchens *in press*). Transitions were affected by hydrologic alteration that occurred within 4 years of the sample (Armentano 2006, Zweig and Kitchens *in press*). Community composition of prairie states were controlled by water depths in the wet season, but sawgrass and slough states were affected by water depths in both the wet and dry seasons. Overall, transitions probabilities were low within each community (Table 1), barring the hurricane effects state, but were highest in the communities not on the extreme ends of the peat or hydrologic gradients—the less extreme states are more likely to change. There was no spatial pattern in the likelihood or number of transitions and no community was more likely to change between states.

A majority of the transitions that occurred in sloughs were from the slough state to hurricane effects state in 2005. Winds from hurricane Wilma displaced the floating aquatic *Utricularia* spp. from the sloughs into the sawgrass strands. As *Utricularia* spp is the indicator species for the slough state, its absence is considered the hurricane effect state. Lesser effects were found in the mixed emergent and lily slough states. Transitions probabilities for any other *a priori* community states (sawgrass, prairie) to the hurricane effects state were small.

CART

The CART analysis augmented the number of transitions in my S&T models and supplied quantitative information to annotate existing transitions. Peat depth was a factor for both slough and sawgrass models which corresponds to NMS environmental correlations (Zweig and Kitchens *in press*). The maximum water depths of wet seasons one and two years prior to the sample were relevant to the sawgrass analysis, while the minimum of dry seasons three and four years previous to the sample were important for slough communities. The slough model classified only four of six states (CV error = 0.588, misclassification rate = 0.208), but the sawgrass model classified all 5 states (CV error = 0.647, misclassification rate = 0.238). CV error was high for both models.

VDDT Analysis

I used the VDDT program as an exploratory application to compare different management actions for the study area using S&T models constructed from 4 years of data collection and to examine the results of the models over time. For the wet conditions and increased range scenarios, there is nearly a complete disappearance of the wet prairie state and proliferation of the mixed emergent prairie, a deeper state (Table 2). The most dramatic changes occur in the slough and sawgrass communities. The slough state is greatly decreased, replaced by the deeper lily slough state in all but the dry conditions. The sawgrass with *Justicia* state decreases with the increased hydrologic range and wet conditions scenarios and is replaced by deteriorated strand. Sawgrass with *Peltandra* increases in the equal and dry conditions, replacing the sawgrass with Justicia state. Increased range is almost identical to the wet conditions management action and, as is expected, the wet conditions action is quite different than the dry conditions scenario.

Discussion

Hydrology is the primary mechanism for multi-state transitions within the study period. Water depth is a strong control of community state composition and pattern in the Everglades (Larsen et al 2007), and I show both an immediate and lagged temporal and seasonal effect on vegetation, depending on community state. More than two years of sustained depths over 61 cm in the wet season can initiate fragmentation of sawgrass communities. Drying sloughs below surface level (-2cm) for three or more years coupled with low wet season water depths allows for the encroachment of sawgrass. I do not propose that the environmental variables here are the only influences of community composition, but they are representative of the complex hydrology that affects vegetation in WCA3. The reality is these hydrologic correlates do not capture all of the variability in the data and there are additional characteristics that control the composition and transition of community states, which are likely a combination of factors that incorporate duration.

The VDDT analysis is interesting in that consistent high water conditions and increased hydrologic range (high wet season, low dry season) are very similar in their final configuration and are very different than the dry conditions management action, particularly for the sawgrass and slough communities. Drying WCA3 completely during the dry season does not seem to offset the effect of high water in the wet season to community states. This is of interest as there has been a trend of increasing wet season maximums and range within the study area since the new hydrologic schedule began in 2002 (C. Zweig *unpublished data*). According to the model, transitioning of all three community types (slough, sawgrass, wet prairie) to deeper states will continue if this trend is maintained. Predicting 100 years into the future from four years of data strains the limits of the model, but data collection is ongoing and I will continue to update the models with current data and new management scenarios.

The relationship between structure, function, and complexity is important when considering restoration alternatives and can be incorporated into S&T models to identify priorities in restoration and evaluate restoration actions (Cortina et al 2006). As hydrology is such a strong control of community composition in the Everglades, I would infer that hydrology would have a significant effect on the ecological complexity of a state, represented by structure and function (biomass and species richness (Cortina et al 2006, Ryan et al 2007)); however water depth is not a key mechanism. The deepest and shallowest states do not exhibit the highest complexity (Figure 5a-c), but they are not, as a rule, the least complex. Outside and state forcing functions, as discussed in the general wetland model, likely contribute to the structure and complexity of each state, particularly edaphic factors, vegetative legacy, and competition. Sloughs generally exhibit lower complexity than wet prairies and sawgrass states contain significantly higher biomass, which increases their complexity along the x-axis of biomass/quadrat but not the y-axis of species diversity/quadrat (Figure 5d). The most common states have the highest complexity, corresponding to Odum's (1969) ideas of ecosystem development—"maximum protection" and "maximum production". Complexity is of interest as it can indicate the stability of a community state (Pimm 1984, Jansen and Kokkoris 2003). Whether maximum state complexity in the Everglades is a desirable restoration goal remains to be seen and should be further investigated. It would provide a rare applied link between restoration ecology and diversity-stability relationships (Seabloom 2007).

Although specific to the Everglades, my approach to creating S&T models is useful in other landscapes, especially those with subtle environmental gradients such as the Okavango Delta, boreal fens, and some floodplain riparian wetlands (Larsen et al 2007) and allows scientists to address and resolve the complexity of these ecosystems. The NMS and cluster analyses can characterize states from communities that are continuous and are adaptable enough to define moving thresholds. For example, the community states in the Everglades are not characterized so much by the introduction or exclusion of a species like other systems (Connell and Slayter 1977, Platt and Connell 2003, Seabloom 2007), but by the importance (biomass and density) of that species within the state (Table 3). With this method I have defined 'successional community states' which can be categorized, as with single species, with early or late successional stages. The community states are distinct *in situ* and not ephemeral—they are temporally persistent within the landscape but change spatially, supporting a shifting mosaic steady state model (Arscott et al 2002). These states can be seen as variance within a larger-scale system, but that does not diminish their functional importance. While time and data-intensive, the ability to describe states at such a fine scale affords the opportunity to define a dynamic regime and create more realistic models than conventional linear relationships. As systems do not always respond in a predictable manner (Suding et al 2004), awareness of the mechanisms of vegetation change minimizes the possibility of less desirable states (Briske et al 2006). It also provides additional, critical information for restoration management decisions (Mayer and Rietkerk 2004) particularly as these relate to the habitat attributes for critical fauna.

These models provide a link between successional theory and the practice of ecosystem management. They represent the application of ecological models such as the shifting mosaic steady state model (Whited et al 2007), alternative stable states (Beisener et al 2003), dynamic regime (Mayer and Rietkerk 2004), and the non-equilibrium persistent model of vegetation dynamics (Suding et al 2004). The existence of multiple stable states has been debated (Schröder et al 2005), but I provide field evidence and the ability to define states that are spatially and temporally stable within a dynamic regime. Identifying the possible states and pathways of vegetation change can be used to predict restoration success or the possibility of hysteresis—systems following a different path for recovery than the initial trajectory of change (Suding et al 2004). I observed evidence of multiple pathways from one state to another within out study area, indicating potential hysteresis. Managers could also explore the possibility of transitory communities that would be necessary intermediates for a final, restored system (Connell and Slayter 1977).

The concepts of multiple steady states and shifting mosaics are key theories for understanding the dynamic nature of wetlands, including the Everglades. I consider the application of these theories, the S&T succession models, as a fraction of the framework for the Everglades and my understanding will only build with time. They are hypotheses for use in adaptive management as the restoration of the Everglades continues. These models represent the community response to hydrology and illustrate which hydrologic values—temporal or seasonal—are important to community structure. I intend for them to act as a foundation for further restoration management and experimentation. Future data will refine my current understanding of the impacts of altered hydrology on vegetation succession in the Everglades and increases the ability to apply succession theory to resolve restoration issues (Odum 1969).

Table 3-1: Transitions of community states in Water Conservation Area 3A South, FL, from 2002-2005.

Community states	Times transitioned	Percent transitioned
SG w/ *Peltandra*	1	1.7%
Shallow Peat, Tall	3	5.0%
Shallow Peat, Short	0	0.0%
SG w/ *Justicia* and *Eleocharis*	9	15.0%
Deteriorated sawgrass	2	3.3%
Sparse Sawgrass Prairie	1	3.0%
E. elongata Prairie	0	0.0%
E. cellulosa Prairie	1	3.0%
Mixed Transition Wet Prairie	1	3.0%
Wet Prairie	5	15.2%
Hurricane Effects	0*	0.0%
Lily Slough	1	1.9%
Eleocharis Slough	0	0.0%
Shallow slough invaded by Sawgrass	0	0.0%
Mixed Emergent Slough	2	3.7%
Slough	11**	20.4%

*States did not transition from the hurricane effect state to another because 2005 was the last sample date. **A majority of slough state transformations were to hurricane effects in 2005.

Table 3-2: Percent change in total area (ha) of community states for four management scenarios in Water Conservation Area 3A South, FL, run with Vegetation Dynamics Development Tool software. Parameters were set from data collected in 2002-2005. Initial conditions are equal to conditions in 2002.

Vegetation Type	Equal	Deeper Conditions	Increased Range	Dry Conditions
Sparse Sawgrass Prairie	50%	9%	44%	48%
E. elongata Prairie	22%	2%	6%	37%
Wet Prairie	-92%	-100%	-100%	-69%
Mixed Transition Prairie	36300%	48900%	56100%	11600%
E. cellulosa Prairie	-34%	-8%	-32%	-32%
Slough invaded by Sawgrass	1%	0%	1%	2%
Slough	-81%	-100%	-100%	-28%
Mixed Emergent Slough	20%	122%	5%	3%
Eleocharis Slough	0%	0%	0%	0%
Lilly Slough	1105%	1204%	1389%	378%
Deteriorated Sawgrass Strand	449%	1185%	1153%	19%
Sawgrass with Justicia	-95%	-100%	-99%	-49%
Sawgrass with Peltandra	872%	-12%	217%	798%
Shallow Peat, Tall Sawgrass	-55%	-15%	-55%	-56%
Shallow Peat, Short Sawgrass	0%	0%	0%	0%

Equal = all management actions/disturbance probabilities were set equal as a control. Deeper conditions = deep water depths in wet and dry season. Increased range = deep water depths in wet season and very low water depths in dry season. Dry conditions = low water depths in wet and dry season.

Table 3-3: Percent Importance Value (average of relative biomass and relative density) of species within community states within Water Conservation Area 3A South.

Community	Community State	BAC	CLA	ELG	Elsp	NYO	UTsp
Slough	Slough	2.6%	1.6%	49.2%	3.0%	15.5%	28.0%
	Hurricane Effects	1.5%	7.7%	46.2%	5.0%	34.3%	5.2%
	Shallow Slough Invaded by Sawgrass	3.9%	27.1%	63.4%	1.1%	3.4%	1.1%
	Mixed Emergent Slough	9.8%	3.6%	5.8%	29.7%	22.5%	28.5%
	Lily Slough	0.2%	4.2%	15.0%	5.7%	48.7%	26.2%
	Eleocharis Slough	6.3%	2.7%	23.3%	46.3%	0.0%	21.5%
Prairie	E. elongata Prairie	8.6%	2.1%	64.4%	5.0%	7.0%	12.9%
	Wet Prairie	5.3%	1.8%	19.7%	44.0%	5.2%	24.0%
	Sparse Sawgrass Prairie	11.7%	18.3%	2.8%	55.7%	4.8%	6.7%
	E. cellulosa Prairie	1.5%	16.4%	1.6%	75.6%	1.0%	3.7%
	Mixed Transition Prairie	33.9%	0.9%	3.3%	23.6%	18.5%	19.7%
Sawgrass	Sawgrass with Justicia and Eleocharis	9.4%	73.7%	13.6%	1.0%	n/a	2.4%
	Sawgrass with Peltandra	6.6%	53.7%	35.0%	3.0%	n/a	1.6%
	Deteriorated Sawgrass Strand	19.6%	38.0%	31.6%	3.9%	n/a	6.9%
	Shallow Peat, Tall Sawgrass Strand	10.8%	59.7%	0.6%	26.4%	n/a	2.5%
	Shallow Peat, Short Sawgrass Strand	0.0%	43.0%	0.0%	56.5%	n/a	0.4%

BAC = *Bacopa caroliniana*, CLA = *Cladium jamaicense*, ELG = *Eleocharis elongata*, Elsp = *Eleocharis cellulosa*, NYO = *Nymphaea odorata*, UTsp = *Utricularia* sp.

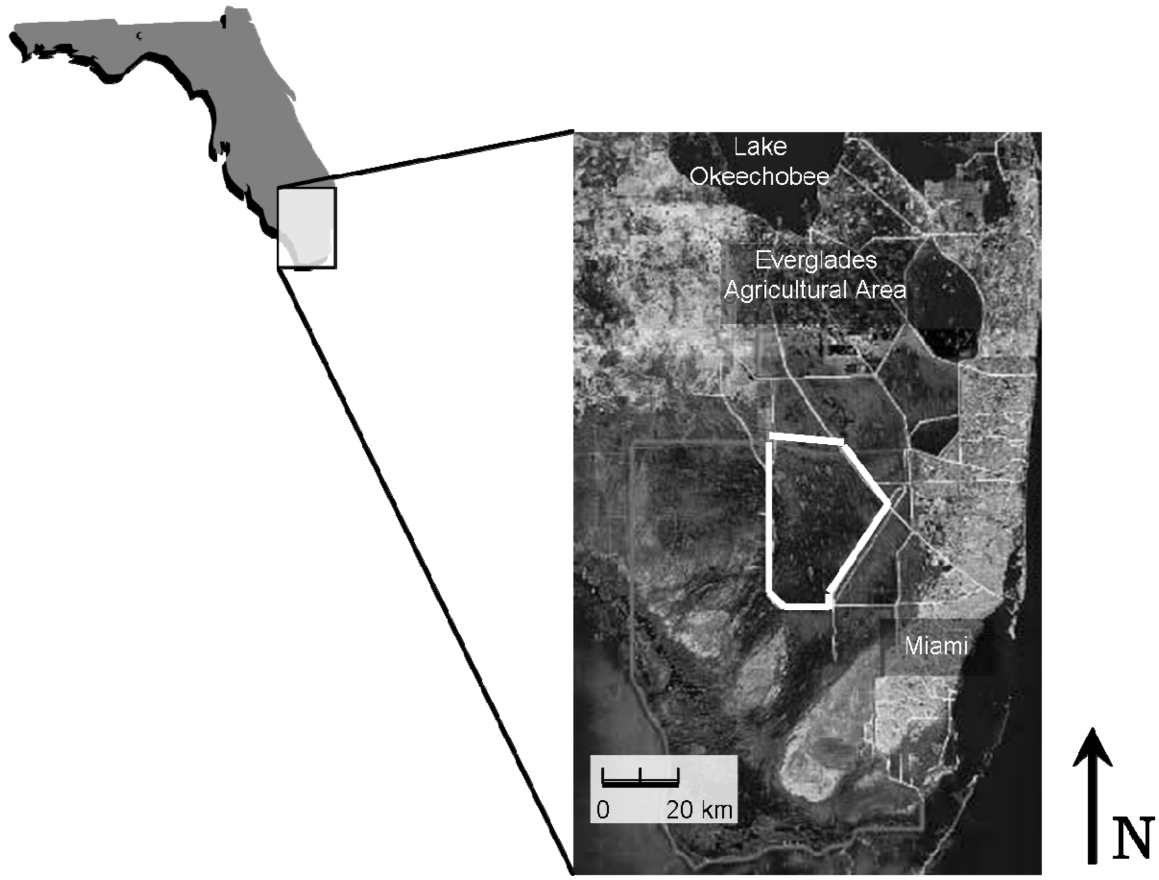


Figure 3-1: Satellite view of the Everglades in southern Florida, USA. The study site, Water Conservation Area 3A South, is outlined in white.

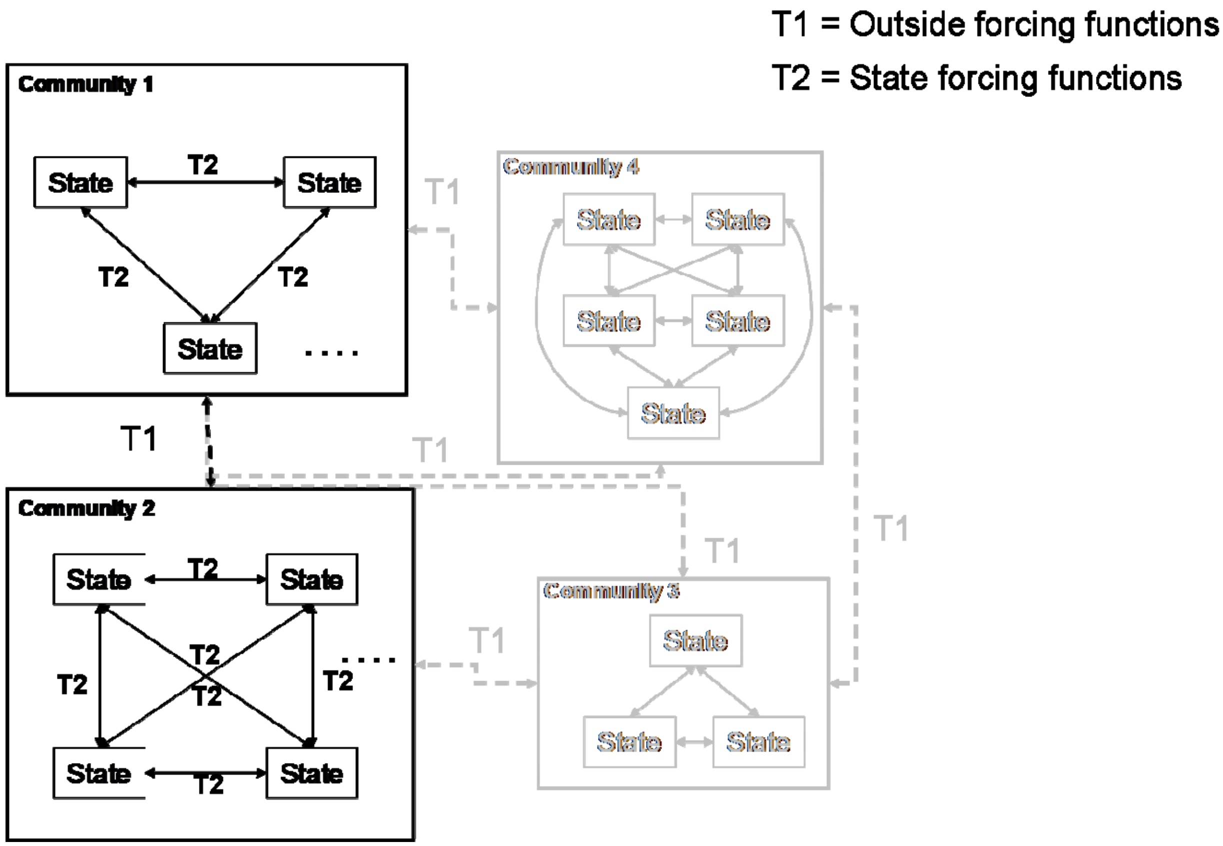


Figure 3-2: General state and transition model for wetlands

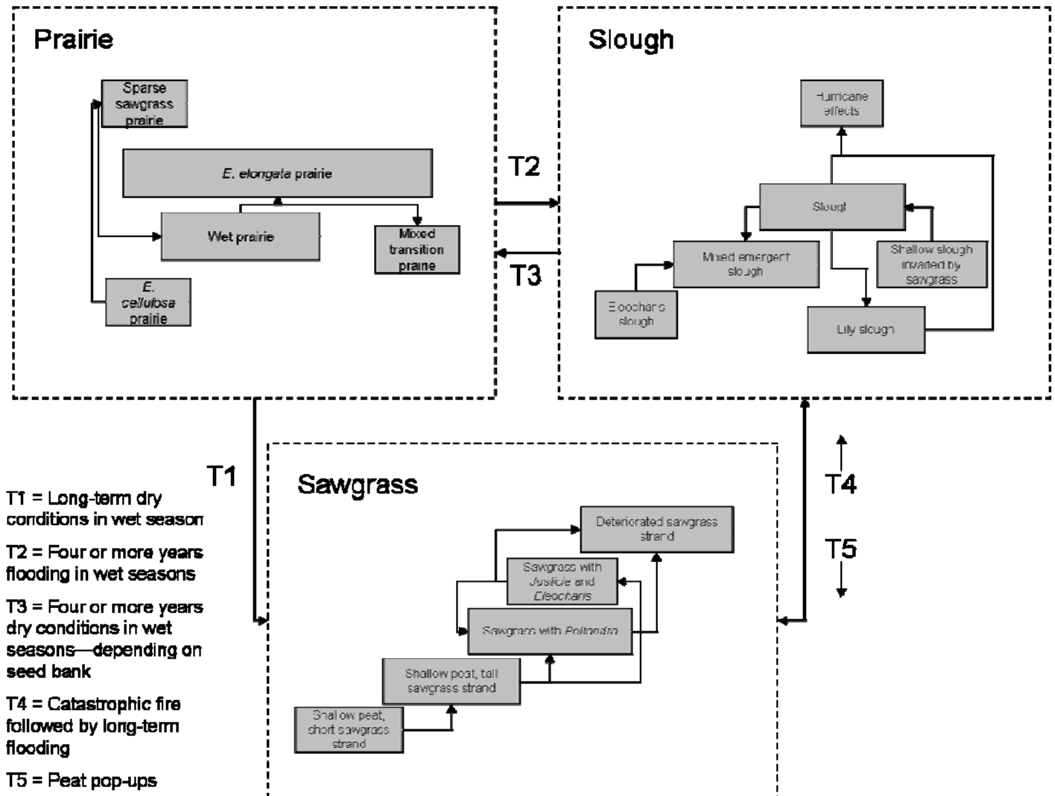
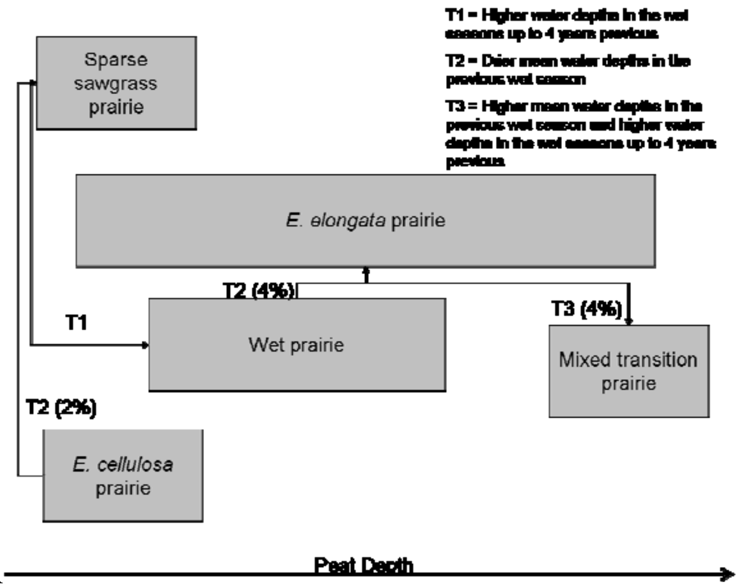
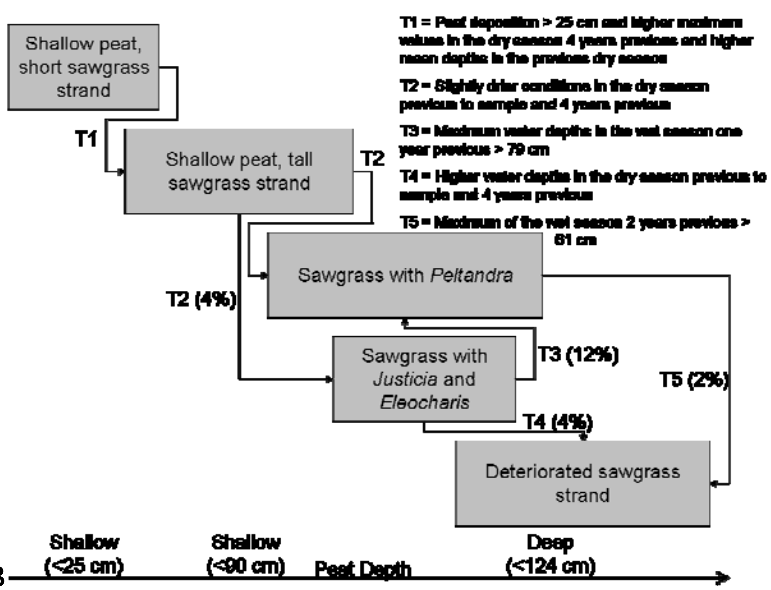


Figure 3-3: Landscape level state and transition model for Water Conservation Area 3A South in the Everglades, Florida, USA.



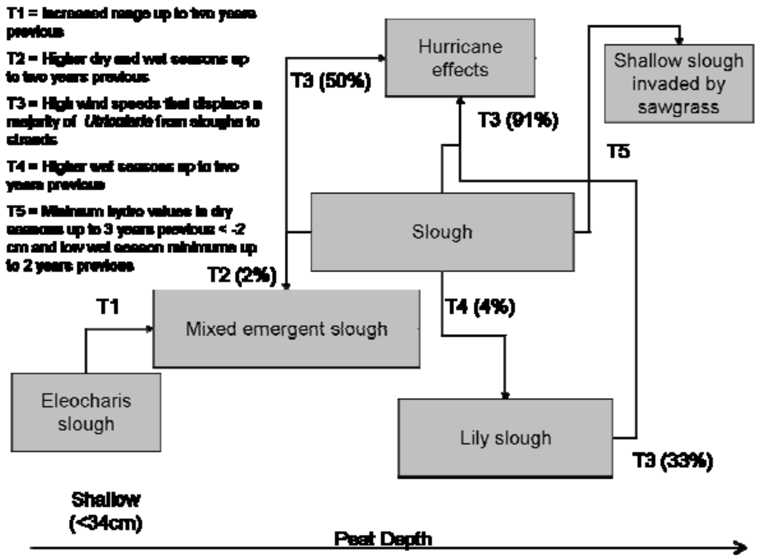
A

Figure 3-4: State and transition model for the a) wet prairie b) sawgrass and c) slough communities in Water Conservation Area 3A South. Community states are arranged on a general hydrologic gradient with drier communities at the top and deepest communities at the bottom. Percentages (times transitioned/total number of possible transitions) represent the how often transitions occurred during the study period (2002-2005).



B

Figure 3-4. continued



C
Figure 3-4. continued

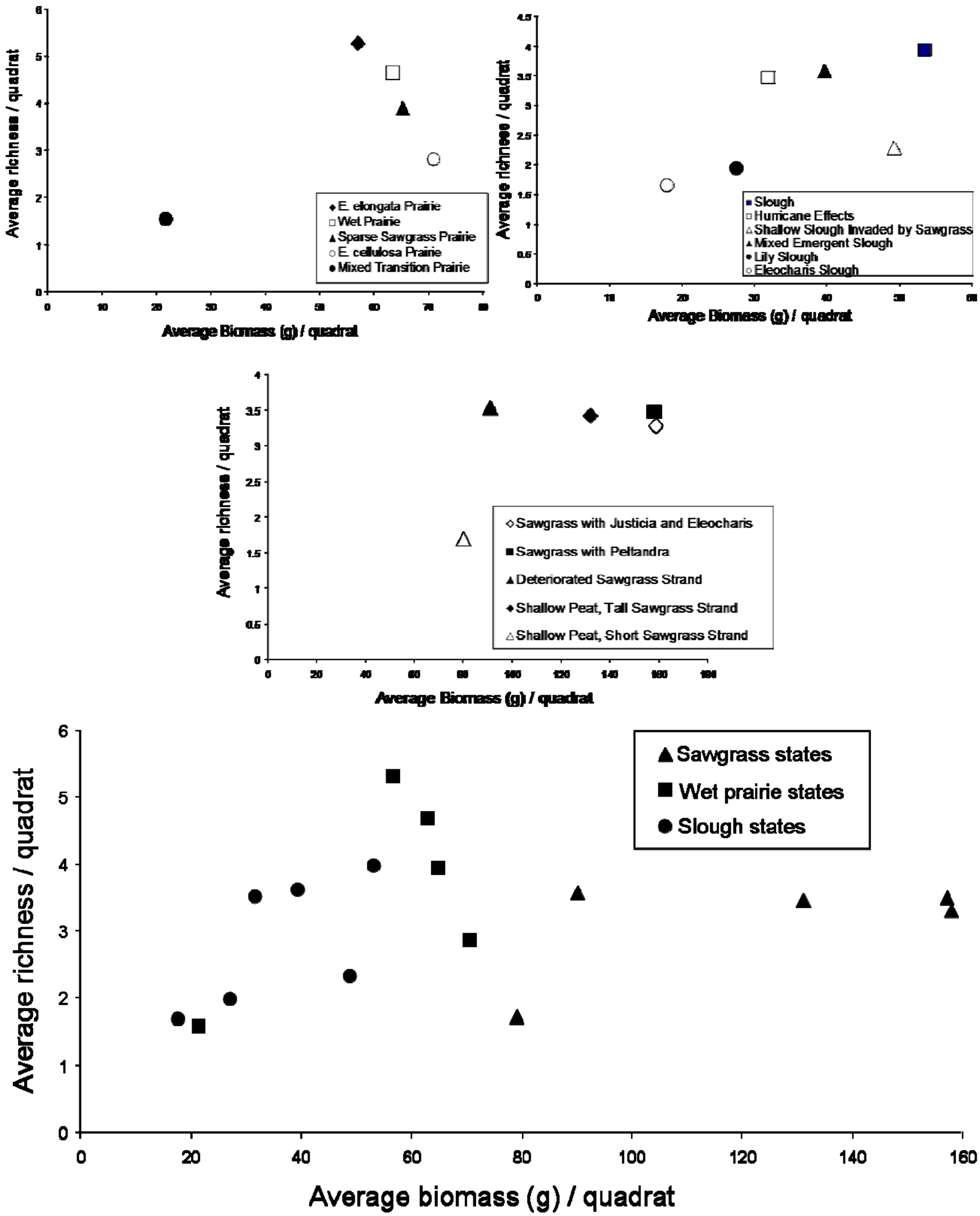


Figure 3-5: Ecological complexity graphs for three communities in Water Conservation Area 3A South—(a) wet prairie, (b) slough, (c) sawgrass, (d) all communities. Complexity is represented by species richness and biomass per 0.25 m2 quadrat.

CHAPTER 4
A SYNTHESIS OF PATTERN AND PROCESS FEEDBACK CYCLES AND THEIR EFFECT ON A STEPPED WETLAND LANDSCAPE

Large wetlands all over the world face the possibility of degradation, not only by complete conversion, but by subtle changes in their structure and function (Dobson et al 1997, Arscott et al 2002). Human activities such as drainage, impoundment, and increased nutrients have fragmented wetlands, leaving few completely intact. Wetlands are often considered landscape components, but rarely an entire landscape themselves. Fragmentation of wetlands within a landscape is important, but the disruption of spatial patterns and fragmentation particularly within large, patterned wetlands is just as significant. How fragmentation within wetland landscapes affects and is affected by the resulting alteration of maintenance processes, such as peat deposition and natural disturbance regimes, is of great interest (Turner 1989, Bürgi et al 2004), particularly in regard to two pertinent topics in ecology today: restoration and global climate change (Zedler 2002, Opdam and Wascher 2004). Degraded wetland systems do not always respond to landscape changes in a linear, predictable manner (Zedler 2000, Suding et al 2004). A greater understanding of pattern/process relationships (e.g. how flow/peat deposition/disturbance/nutrient cycles affect patterning in wetlands and vice versa) and what occurs when they are altered could help avoid undesirable consequences of restoration actions (Briske et al 2006, Alvarez-Cobelas et al 2008). This is critical as wetland complexes such as the Pantanal and Okavango Delta are currently being impacted by human activities on a landscape level (Ellery et al 2003, Junk et al 2006), and one such wetland, the Everglades, is the focus of the world's largest restoration effort.

These large wetlands are subject to subtle gradients that, in concert with fluvial dynamics, create extremely heterogeneous systems with distinct patterning (Ward et al 1999). Subtle should not be confused with continuous, especially regarding elevation. Disturbances will have differential effects across the landscape in response to abrupt gradient changes, such as stepped elevation (Williams et al 1999). There is a very tight feedback loop between pattern and processes for the creation and maintenance of the patterned landscape (Larsen et al 2007). Natural or anthropogenic changes to either may modify the feedback loop in a way that is not readily apparent but ecologically important (Sklar et al 2005).

The Everglades is an example of how human disturbance can alter the patterns and processes within a wetland ecosystem, creating a feedback cycle that changes both the pattern and processes of the landscape, while it continues to function superficially as a wetland (Sklar et al 2005). The Everglades was once characterized by its large spatial extent, sheetflow, habitat heterogeneity, and ridge and slough landscape (Davis et al 1994). Due to human activities, the Everglades ecosystem has been developed and compartmentalized, losing over 50% of its spatial extent (Leonard et al 2006) and over 80% of its upland habitats. Sheetflow has been disrupted by agriculture and compartmentalization, and hydrology has become highly regulated. Nutrient inputs from surrounding agriculture have caused fragmentation of the landscape by invasion of Typha sp. (Wu et al 1997) and by alternating loss of slough and sawgrass (Cladium jamaicense Crantz.) strands with different hydrologic regimes (Ogden 2005).

This fragmentation is particularly important in the characteristic ridge and slough landscape (RSL) within the Everglades. The RSL was a dominant landscape type of the southern portion of the Everglades and has been highly affected by compartmentalization and reduced flows (Ogden 2005). The RSL consisted of long, linear strands of sawgrass interspersed with deeper hydroperiod sloughs and occasional tree islands oriented parallel with the slow-moving flow of water from north to south. The RSL provided refugia for aquatic organisms during the dry season, provided a large amount of water storage potential, and was the primary area for primary and secondary production (Ogden 2005). This area is now of particular interest in the restoration (Science Coordination Team 2003) and understanding the maintenance processes for the RSL is a focal target of the Everglades restoration (Sklar et al 2005). There have been numerous hypotheses, especially regarding the role of flow, on the creation and maintenance of the RSL and I synthesize recent literature and suggest additional mechanisms. I also demonstrate using remote sensing and landscape indices how these maintenance mechanisms have been disturbed, their effects on the landscape pattern, and how this creates alternate feedback loops that affect persistence of the multiple stable states of ridge and slough.

Methods

Study Site

The study site, Water Conservation Area 3A South (WCA3AS), is the largest intact remnant of the RSL in the Everglades, FL (Figure 4-1). It is subject to several key environmental gradients—an east-west peat depth gradient, north-south elevation gradient, and an artificial north-south water depth gradient created by impoundment. When examining the hydrology of the sites, I realized that the elevation gradient is not continuous as previously thought, and divided the study site into north and south sections along an elevation break. The break, visible on satellite imagery, was delineated using the 2.0 m contour line on a digital elevation map provided by the Everglades Depth Estimation Network (http://sofia.usgs.gov/eden/models/groundelevmod.php). This contour corresponded closely to the visual break and follows the general boundary between the underlying Miami and Fort Thompson formations (Gleason and Stone 1994).

The northern section of the study area is considered over-drained and cut off from sheetflow by Alligator Alley (Interstate 75), which is the north boundary of WCA3AS. Construction on Alligator Alley to create culverts for wildlife crossings began in the late 1980's and was completed by 1992. This produced improved flow for the northern section of WCA3AS (Gunderson et al 1995).

An era of increased water depths and hydroperiods also began circa 1991, changing conditions within WCA3AS (Zweig and Kitchens *in press*). This had the greatest impact on the southern section due to the influence of the levee and the resultant increased ponding. WCA3AS was already managed as the wettest compartment within the water conservation areas (Childers et al 2003) and higher water levels exacerbated the increase of sloughs and disappearance of ridges within the system.

Classification and FRAGSTATS Analysis

Two cloud-free satellite images (Figure 4-3a) were obtained of the study area from approximately the same season (dry season). The images obtained were from 1988 and 2002—2002 approximating present conditions and 1988 representing the drier hydrologic era. The images—March 5, 1988 (Landsat TM) and February 5, 2002 (Landsat ETM+)—were geometrically and radiometrically corrected. Both images were classified, using non-parametric, supervised classification in ERDAS Imagine^{TM}, into three vegetation classes: slough, sawgrass, and tree island (Figure 4-3b).

The 1988 and 2002 classified images were split into north and south sections (Figure 4-4) along the elevation break and were input into FRAGSTATS. FRAGSTATS (McGarigal et al 2002) is public domain software that computes landscape metrics on spatial categorical data. There are dozens of metrics on three different scales—landscape, class, or patch. These metrics have been widely used in ecology, especially landscape ecology. I chose the following class metrics for the main types of vegetation communities in WCA3AS (slough, sawgrass, tree island) to quantify the total area of communities and degree of fragmentation over time (McGarigal and Marks 1995):

- Total Class Area: total class area in hectares in the landscape
- Percentage of Landscape: total area of a class divided by the total area of the landscape
- Number of Patches: sum of patches that belong to a certain class
- Patch Density: the number of class patches per 100 hectares
- Largest Patch Index: a percentage calculated by the area of the largest patch divided by the total landscape, multiplied by 100
- Contiguity: contiguity or spatial connectedness of cells. 0 = one cell patch and increases to a limit of 1.
- Related circumscribing circle: describes linearity of patches. 0 = circular patch and 1 = linear patch one cell wide.

Results

Classification and FRAGSTATS Analysis

The 1988 and 2002 images were classified with an accuracy of 88.76% and 95.51% respectively (Table 4-1), using field test points obtained in January 2007. The decrease in accuracy could be explained by the time lag between the image and the field data and the obvious vegetation community changes that have occurred. Visually, WCA3AS still has remnants of the characteristic linear landscape pattern that was formed by historic sheetflow which generated tear-drop shaped tree islands and the RSL pattern oriented north/south. Much of the sawgrass loss occurs along the south and east levees. The tree islands in the south also shrink considerably. There are areas of higher loss in the northern and eastern sides. In the southern end, there is a pattern of sawgrass disappearing from the fringes of tree islands.

The landscape metrics are reported only for sawgrass and slough and illustrate a decline in the area of sawgrass and increased fragmentation (Table 4-2). Total sawgrass area in 3AS declined by 21% from 1988 to 2002, and the density and number of patches increased—a 33% increase in the number of patches. Conversely, slough communities increased in total area and decreased in number and density of patches. The contiguity and circle metrics indicate that sawgrass and slough in the north section were slightly more linear in 2002 but decreased slightly in contiguity. Sawgrass in the southern section was much less contiguous in 2002 and more linear, likely reflecting the fragmentation and shrinking of sawgrass strands.

Discussion

Synthesis

The Everglades' distinctive ridge and slough pattern originated approximately 2700 years BP (Larsen et al 2007), and is believed to be maintained by both autogenic and allogenic factors (Figure 6) (Leonard et al 2006, Wu et al 2006). This RSL is a product of long-term (geology, soils, and climate) and short-term maintenance processes (hydrology, flow, nutrient cycles, microtopography, variations in rainfall, and disturbance regimes) (Gunderson 1994). The short-term processes, particularly hydrology and fire, are extremely variable in their temporal and spatial extent, and maintain the patterns of the heterogeneous landscape. Flow and hydrology have become highly regulated by an extensive canal/levee system and the RSL pattern is degrading (Science Coordination Team 2003, Sklar et al 2005). I found relatively little published literature on the maintenance of the RSL considering the Everglades is a target of a $10 billion restoration effort.

I present two types of RSL maintenance: constant and pulse maintenance processes. One hypothesis for the constant maintenance of the RSL is differential sediment accumulation due to flow velocities in vegetated and open areas, or ridge and slough (Leonard et al 2006). This phenomenon is well documented in other wetlands (Christiansen et al 2000, Neumeier and Ciavola 2004), and there are several published mechanism hypotheses for sediment accumulations within the Everglades. The literature suggests that flow velocity—higher in sloughs which scours floc (unconsolidated peat) and reduced in ridges by stem density and biomass—allows for greater settling of suspended solids (Leonard 2006) in ridges, stem-generated turbulence needed to settle particulates out of the water column does not occur at current flow rates (1.15 cm/sec, Larsen et al 2007). Stem-generated turbulence in *Eleocharis* stands could be high enough to cause settling if flow rates were 3-5 cm/sec (Leonard 2006). Pre-drainage flow rates for the Everglades were approximately 4 cm/sec (Larsen et al 2007) and could have historically contributed to the processes that maintained the RSL.

Another hypothesized process is the differential decay of vegetation in slough and sawgrass (Foster and Fritz 19897. Peat forms in the sloughs primarily from rhizomes and roots of *Nymphaea odorata* Ait., the white water lily (Gleason and Stone 1994). Above-ground slough biomass is extremely labile, as opposed to the refractory characteristics of sawgrass (Godshalk and Wetzel 1978, Davis 1991), increasing the microtopological differences in peat accretion. Sawgrass-dominated Everglades peat is most common within the Everglades basin, indicating persistence, and lily-dominated Loxahatchee peat is second in abundance (Jones and Bennett 1948). The differential topography might be offset by the oxidation of peat when the higher sawgrass strands are exposed during the dry season (Fleming et al 1994), except for the significantly greater amount of vegetation biomass available for decomposition in the sawgrass strands (Lockwood et al 2003) as opposed to the sloughs (modeled estimates from data provided by Zweig and Kitchens *in press*: sawgrass biomass per $0.25m^2$ quadrat = 150.2g (SE = 3.0849) and slough biomass per $0.25m^2$ quadrat = 48.0g (SE = 0.867), $p < 0.0001$). This difference could very well compensate for the sawgrass strands' periodic exposure to air and subsequent peat oxidation. Loxahatchee slough peat demonstrates a high rate of shrinkage when dried (Gleason and Stone 1994), a mechanism to further reduce the elevation of sloughs when they are exposed during dry downs. Sloughs are rarely dry, so the increased exposure and oxidation of ridges could be the reason that, in the presence of differential peat accretion in the ridges, the RSL still retains a very low microtopographic gradient.

The maintenance of the RSL could also be attributed to processes that occur as pulses instead of constant influences. Data indicates that organic particulates in the water column are attracted to periphyton growing on emergent stems and submerged aquatic vegetation (Lee et al 2004, Harvey et al 2005). Organic matter is added to the sediment layer when the plant dies or settles to the ground during low water events (Leonard 2006). However, sediment-laden submerged aquatics such as *Utricularia* sp. are deposited in sawgrass strands during high wind events, transporting sediment that would have originally settled in sloughs onto strands. This was witnessed in 2005 with Hurricane Wilma (Larsen et al 2007, Zweig and Kitchens *in press*) and to a lesser degree in 2006 with Hurricane Ernesto (C. Zweig pers. comm.). Virtually all *Utricularia* sp. was removed from the sloughs, displacing a large amount of organic matter to ridges. Wind events also distribute peat islands that are dislodged from sloughs onto ridges, greatly increasing topography and heterogeneity of the pattern (Gleason and Stone 1994).

Fire is a pulsed phenomenon that maintains the heterogeneity of the RSL (Gunderson and Snyder 1994). In wet conditions it burns through the sawgrass, removing wrack and releasing nutrients back into the strand for regrowth, while sloughs are relatively resistant to burning (Gunderson and Snyder 1994). Ridges can recover quickly from moderate fires, returning to pre-fire conditions after two years (Loveless 1959). An intense fire during drier conditions will burn peat, lower the elevation of the ridge, and kill the vegetation (Herndon et al 1991), and subsequent flooding will convert the burned area into slough (Craighead 1971, Herndon et al 1991).

It is likely that differential sediment transport in all its variations was responsible for a large part of maintaining the RSL, as well as the sheer biomass available for the strands to convert to substrate. Reduced flows and altered hydroperiods have had varied effects on the landscape pattern—over-drained sections lose sloughs due to sawgrass encroachment (Craft and Richardson 1993) and under-drained sections slowly convert to slough (Wood and Tanner 1990). When landscapes change, the processes change with the landscape (Bürgi et al 2004), creating a feedback loop that alters the system's response to structuring variables, especially disturbance (Nowacki and Abrams 2008).

Pattern/process feedback loops in the Everglades

Draining of the Everglades began as early as 1881, but the Central and Southern Florida Project for Flood Control in 1948 created large-scale fragmentation with a canal/levee system and water conservation areas (Light and Dineen 1994). Restoring the RSL pattern is of particular interest for the entire ecosystem restoration (Science Subcommittee 2003) and I quantify the current amount of fragmentation and loss of sawgrass ridges as baseline information. Most literature concerned with fragmentation of the RSL include *Typha* sp. invasion (Wu et al 1997, Childers et al 2003) or tree island disappearance (Willard et al 2006), but do not address the loss of pattern by the effects of deep water. The data show the general replacement of sawgrass strands by more aquatic sloughs, presumably due to higher water depths in the wet era circa 1991 or improvements to Alligator Alley around the same time period.

An important distinction is the differential effect altered hydrology has on WCA3AS, particularly the north and south sections due to the elevation break. I can state that the study area is losing sawgrass strands, but the manner in which they are being lost and fragmented is important to the understanding of the pattern/process feedback loops. The northern area of the study site was over-drained and dry, allowing sawgrass to encroach into the sloughs. The 1988 image shows solid areas of sawgrass that become fragmented in 2002. This fragmentation appears to be a restoration, not degradation, of the RSL pattern and is supported by the increase of linearity of both slough and sawgrass in 2002. The southern section has lost a considerable amount of sawgrass to slough, but the fragmentation appears to be degradation of the RSL pattern and drowning of the sawgrass strands from high water and levee effects. Linearity of sawgrass increased slightly and contiguity decreased. Slough area increased, decreased in number of patches, and became less linear and less contiguous. This suggests the thinning and fragmentation of ridges and consolidation of sloughs, but not a total disappearance of sawgrass. The sympodial growth form of sawgrass allows it to persist in less than ideal conditions for an extended period (Snyder and Richards 2005) by growing up instead of out, forming tussocks—or fragmenting—instead of growing in continuous strands (Figure 7).

The disruption of one process or pattern, here the pattern of the RSL and a process that maintains it, will affect others in a system (Turner 1989), reinforcing degraded feedback loops. If water depths were deep enough and of long enough duration to stress enough sawgrass to form tussocks, stem density and biomass of the ridge could be greatly reduced, further decreasing peat accretion in the ridges by reducing the stem-turbulence from flow and the subsequent deposition of suspended sediments, and by the simple reduction of biomass from the ridges available to create peat. Increased flow velocities from reduced stem densities within the strands will increase scouring of unconsolidated material, also slowing peat accretion. Sawgrass fragmented by tussock growth will also affect the ability of fire to travel through the RSL by reduced biomass and increased fuel moisture content (Lockwood et al 2003), reducing nutrient availability and reducing its role as a maintenance process. Disruption of sheetflow by impoundment has already reduced flow velocities to a level that does not support the pre-drainage maintenance processes (< 3 cm/sec), which would also reduce the microtopographic differences in the RSL.

It is likely, based on the synthesis of available literature, that suspended sediment deposition due to differential flow velocities was once a RSL maintenance process in the pre-drainage Everglades, and that natural water depths and hydrologic duration also contributed to microtopographic differences in the landscape (Craft and Richardson 1993). WCA3AS, especially the southern section, is now experiencing degraded forms of these processes (high water and slow/no flow) and the landscape is responding. I demonstrated how the RSL pattern has fragmented—that the characteristic linear sawgrass strands are being drowned out and replaced by sloughs—reinforcing a degraded feedback loop of altered maintenance processes. I hypothesize that the mechanisms of this fragmentation are prolonged ponding and the reduction of flow by compartmentalization and deeper water. There is an attempt to restore flow and natural hydrologic regimes to WCA3AS within Everglades restoration, but more direct evidence of the pattern/process linkages, consideration of the stepped nature of WCA3AS, and monitoring of the RSL pattern are critical to the success of the complete Everglades ecosystem.

Table 4-1: Producer and user’s accuracy for non-parametric, supervised classification of LANDSAT TM and ETM+ satellite images from 1988 and 2002 of Water Conservation Area 3A South, FL, USA. The Kappa statistic is a measure of agreement and is used as a measure of accuracy (0 < Kappa > 1).

Class	Producer's Accuracy	User's Accuracy
1988		
Slough	96.77%	88.24%
TreeIsland	80.00%	100.00%
Sawgrass	89.29%	80.65%
Overall Classification Accuracy =		88.76%
Overall Kappa Statistics = 0.8314		
2002		
Slough	100.00%	93.94%
TreeIsland	93.33%	100.00%
Sawgrass	96.43%	96.43%
Overall Classification Accuracy =		96.63%
Overall Kappa Statistics = 0.9494		

Table 4-2: FRAGSTATS indices calculated for slough and sawgrass communities in Water Conservation Area 3A South, FL, USA. Data is from classified LANDSAT TM and ETM+ satellite images from 1988 and 2002.

	Total Area in Landscape	Percent of Area in Landscape	Number of Patches	Patch Density	Related Circumscribing Circle	Contiguity
North Section						
Slough 1988	19692.72	37.5387	3066	5.8445	0.7678	0.7745
Slough 2002	22197.87	42.3141	3086	5.8826	0.7873	0.754
Difference	2505.15	4.7754	20	0.0381	0.0195	-0.0205
Sawgrass 1988	31147.47	59.374	3099	5.9074	0.6363	0.849
Sawgrass 2002	26811.63	51.109	4361	8.313	0.6776	0.7642
Difference	-4335.84	-8.265	1262	2.4056	0.0413	-0.0848
South Section						
Slough 1988	34883.91	72.0399	1174	2.4245	0.7476	0.9014
Slough 2002	37353.51	77.1399	911	1.8813	0.7332	0.8922
Difference	2469.6	5.1	-263	-0.5432	-0.0144	-0.0092
Sawgrass 1988	11387.88	23.5175	6522	13.469	0.7254	0.7023
Sawgrass 2002	9703.89	20.0398	8627	17.816	0.7504	0.602
Difference	-1683.99	-3.4777	2105	4.347	0.025	-0.1003

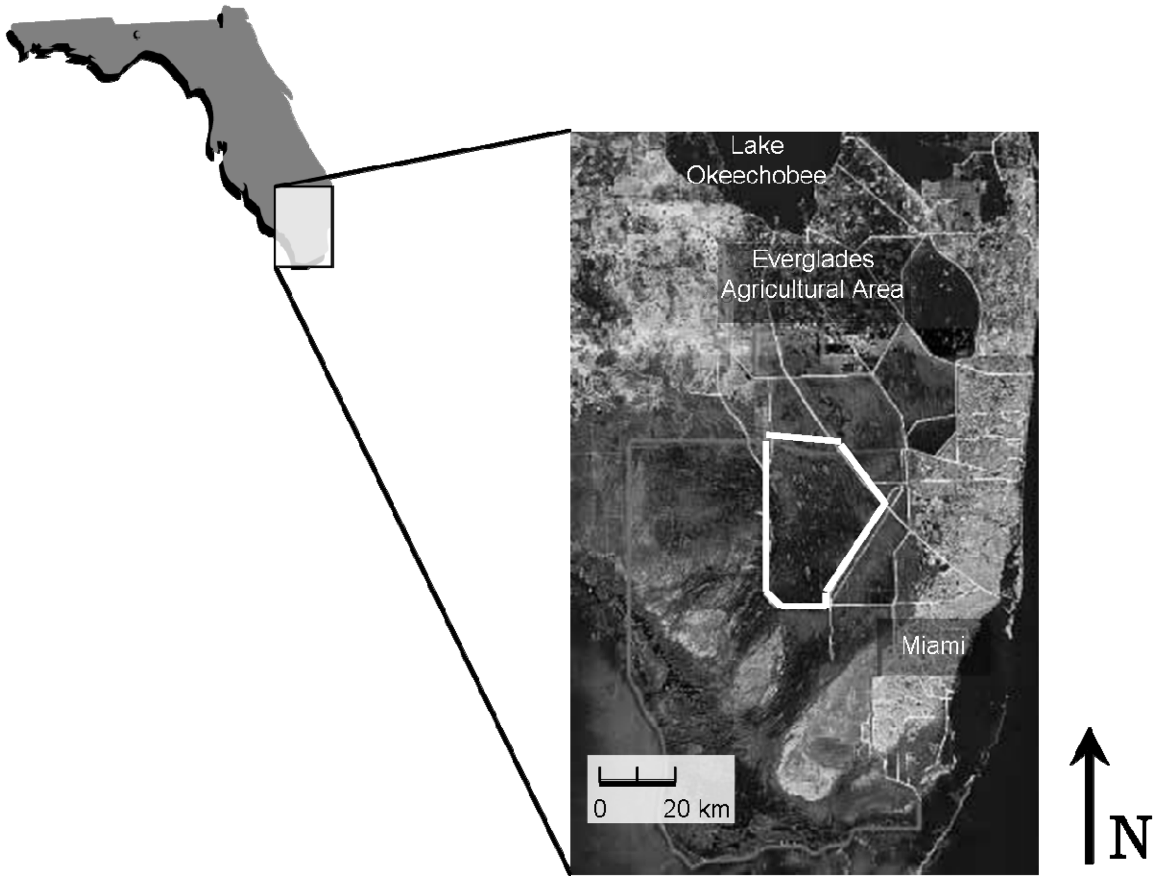


Figure 4-1: The study area, Water Conservation Area 3A South in the Everglades, FL, USA, is outlined in white.

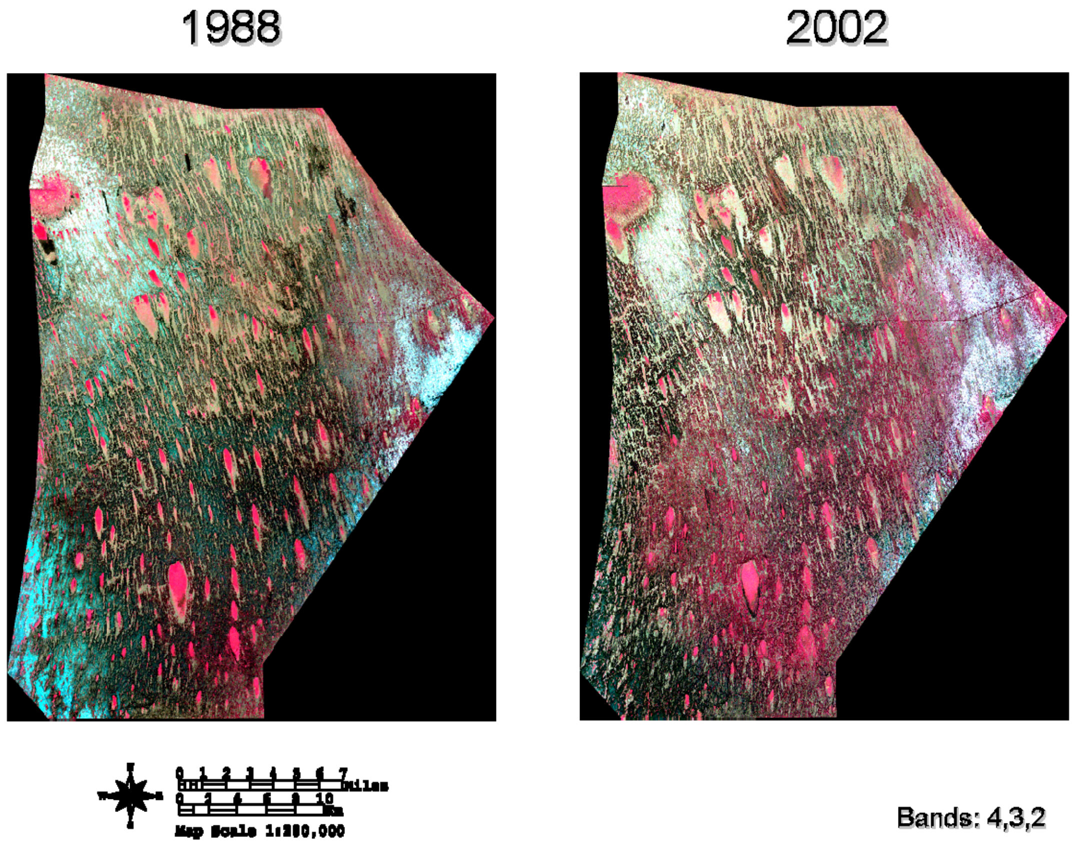


Figure 4-2: LANDSAT TM and ETM+ satellite images from 1988 and 2002 of Water Conservation Area 3A South, FL, USA. Bands shown are 4,3,2.

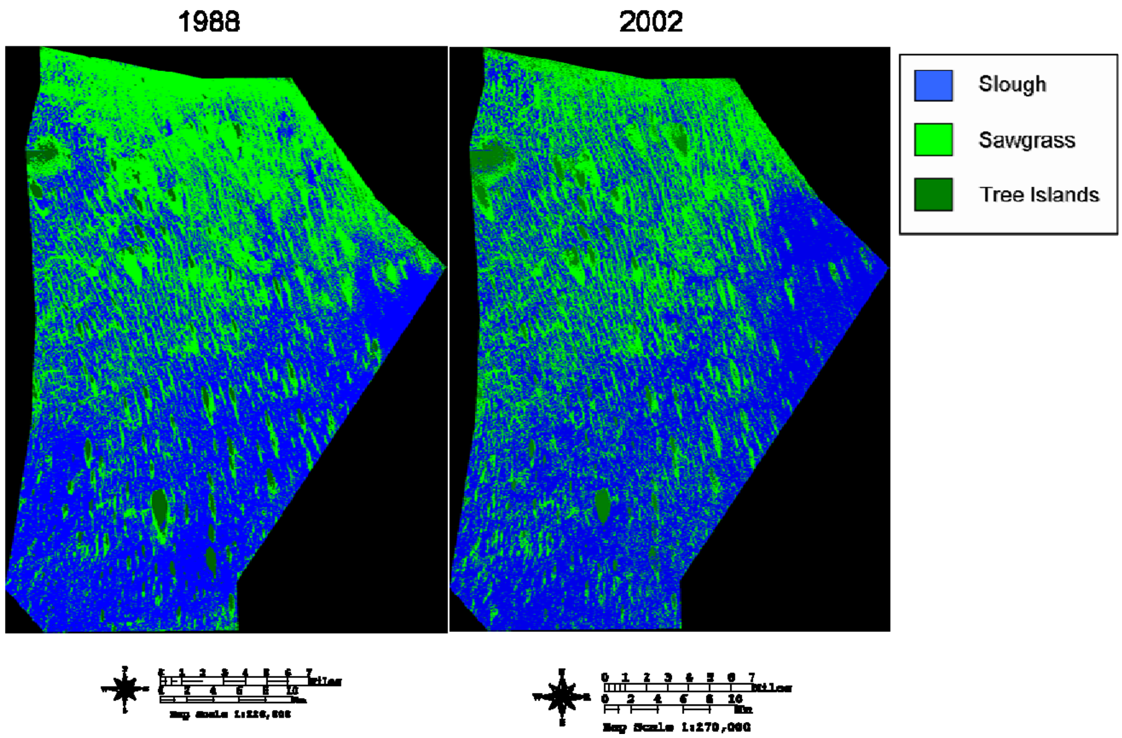


Figure 4-3: Non-parametric, supervised classification of 1988 and 2002 images of Water Conservation Area 3A South, FL, USA.

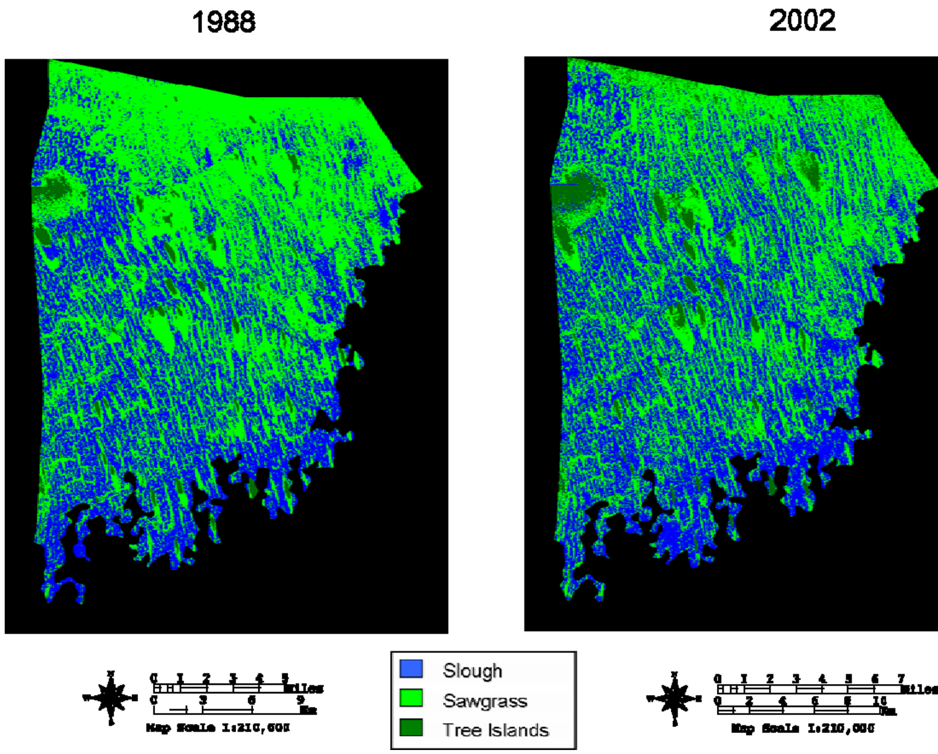


Figure 4-4: Non-parametric, supervised classification of 1988 and 2002 images of Water Conservation Area 3A South, FL, USA from the 2 meter elevation contour and higher.

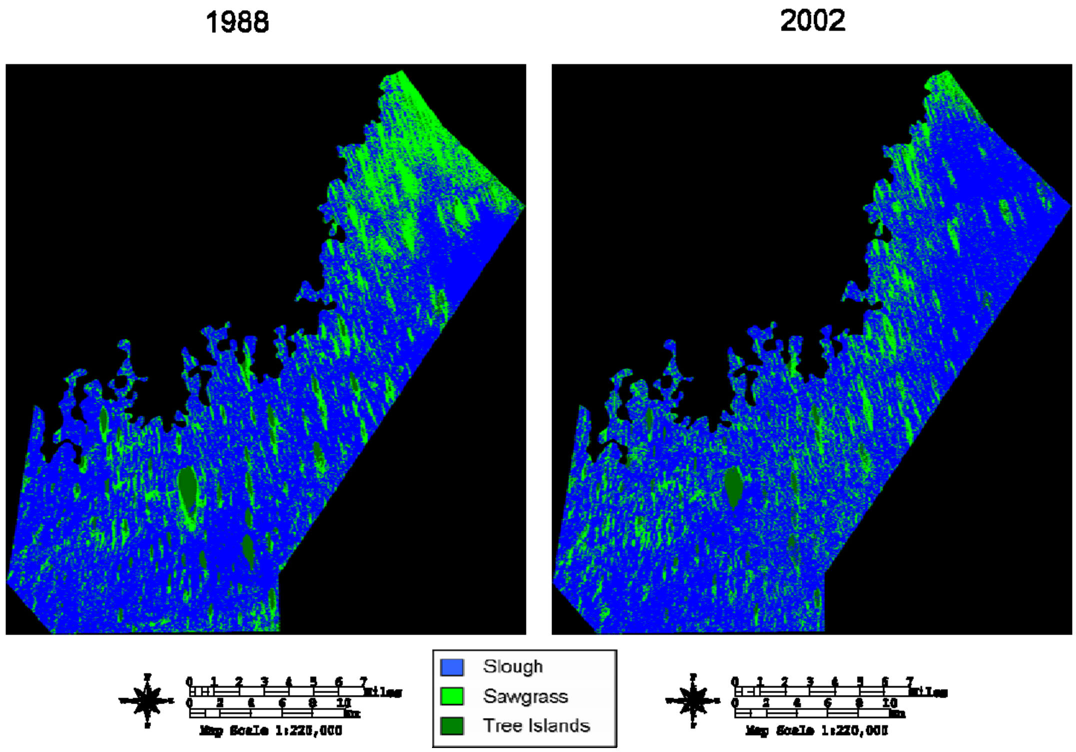


Figure 4-5: Non-parametric, supervised classification of 1988 and 2002 images of Water Conservation Area 3A South, FL, USA from the 2 meter elevation contour and lower.

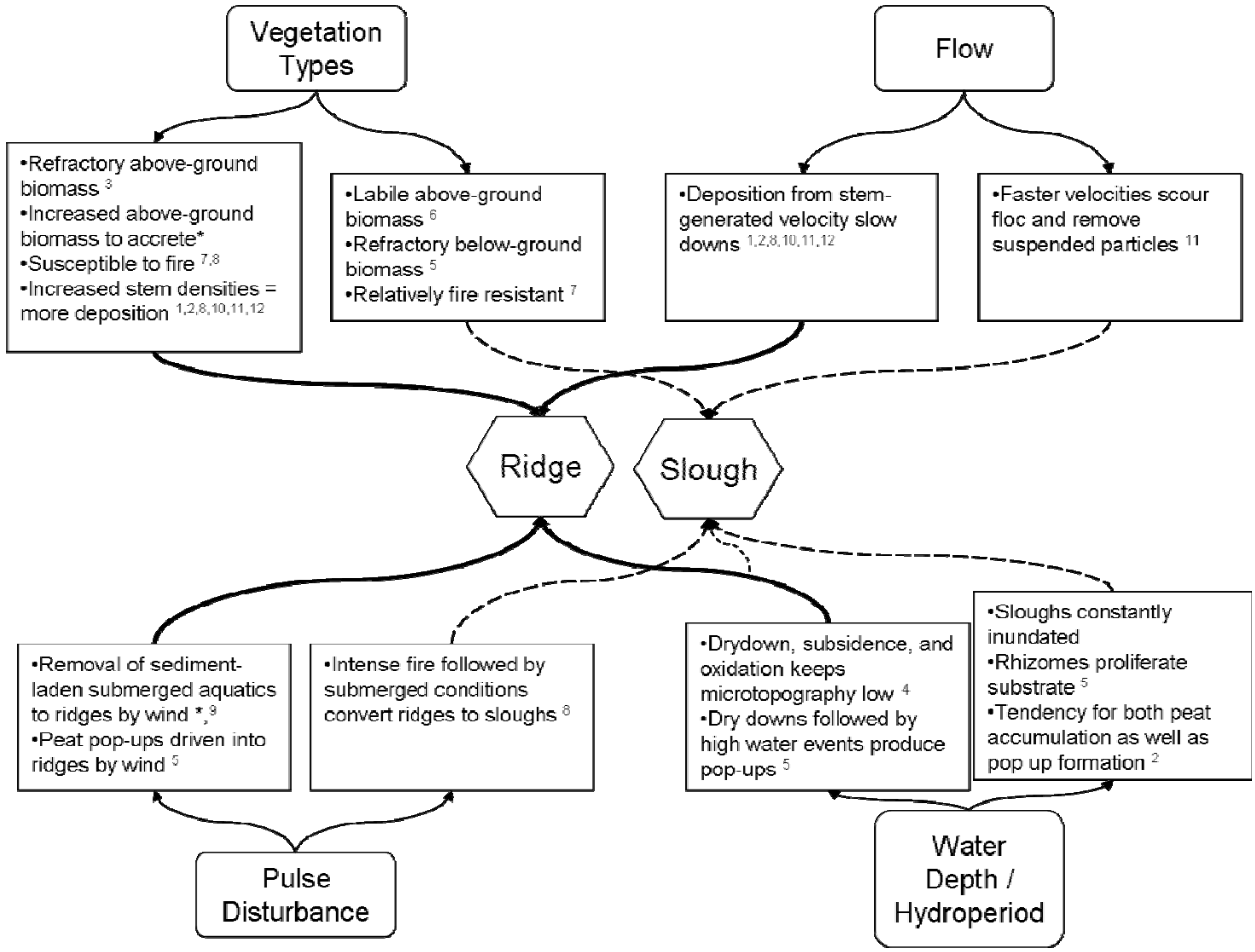


Figure 4-6: Conceptual model of ridge and slough maintenance mechanisms in the Everglades, FL, USA. * indicates this paper. Numbers indicate cites labeled in references.

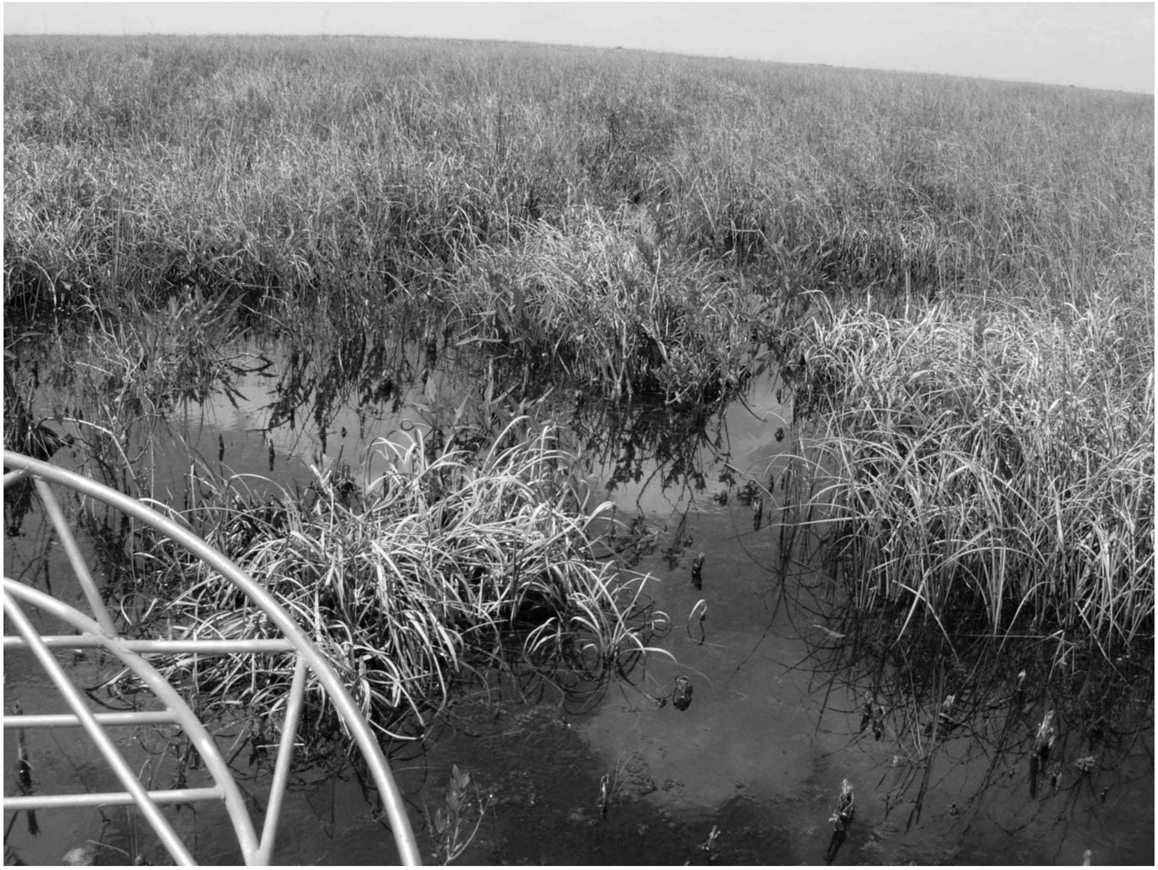


Figure 4-7: Example of fragmented sawgrass ridges in Water Conservation Area 3A South, FL, USA.

CHAPTER 5
HABITAT, HYDROLOGY, AND REPRODUCTION RELATIONSHIPS FOR AN ENDANGERED SPECIES—THE FLORIDA SNAIL KITE

The Florida Snail Kite (*Rostrhamus sociabilis*) is a wetland-dependant endangered species adapted to a unique and extremely dynamic system, the Everglades. The Snail Kite's range encompasses the entire Everglades watershed, a mosaic of wetland habitat types that are highly impacted by anthropogenic activities (Davis et al 1994). Alterations in water depths, hydroperiods and habitat degradation have short and long-term impacts on Snail Kite demography, principally nest success (Beissinger and Snyder 2002, Bennetts et al 2002, Kitchens et al 2002). Especially in this time of Everglades restoration, understanding the effect that environmental processes can have on habitat, what changes will occur with alteration of those processes, and how it affects Snail Kite reproduction potential is essential to a sound conservation strategy (Bennetts et al 1998). This is especially important as the declining Snail Kite population has halved in the last two years and is reaching critical lows (W.M. Kitchens, pers. comm.).

The Snail Kite is a dietary specialist and its primary prey is the apple snail (*Pomacea paludosa*), whose population levels and availability as prey are also controlled by hydrology and habitat (Darby et al. 2002). Apple snail availability has decreased (P. Darby, pers. comm.) and is a suspected contributor to Snail Kite decline. However, even with sufficient prey available, habitat structure is critical in enabling Snail Kites to find food resources (Bennets et al 2006). I believe that not only is the rate at which Snail Kites encounter apple snails important, but just as critical is the rate at which Snail Kites encounter apple snails on emergent vegetation, particularly during the breeding season. Simply studying constraints on the apple snail would not explain changes in Snail Kite demography (Bennetts et al. 2006), but incorporating constraints on availability of foraging habitat, especially in breeding regions, would contribute significantly to the entire conservation perspective.

Water Conservation Area 3A (Figure 5-1) was the largest and most consistently used component of the habitat designated critical to the Snail Kite (Kitchens et al. 2002, Mooij et al. 2002). Its historic contribution to kite reproduction is significant (Kitchens et al. 2002). The current negative population trends of the Snail Kite may reflect the degradation of foraging and nesting habitat quality in Water Conservation Area 3A South (WCA3A) alone (Martin 2007, Martin et al. 2007), particularly the decline of the two habitats in proximity to each other. Shifts of Snail Kite nesting density up the slight, but significant elevation gradient in WCA3A have been documented over the past two decades (Bennetts and Kitchens 1997). This is presumably in response to degradation of nesting or foraging habitat as a result of sustained high water levels from impoundment and water management (Kitchens et al 2002). Nesting activity has shifted up the elevation gradient to the west, and has also moved south in response to recent increased drying rates, restricting current nesting to the southwest corner of WCA3A (Figure 5-2). Reproduction in this critical breeding area has waned significantly (Table 5-1). No birds were produced in WCA3A in 2005, and only 9 of 81 nests were successful in 2006. In 2007 there were no nesting attempts.

In WCA3A, kites forage mainly in wet prairies and emergent sloughs where their primary prey, the apple snail, are most visible and abundant (Bennetts et al. 2006, Karunarante et al. 2006). Although apple snails are found in varied wetland habitats, abundances tend to be higher in sparse prairies and emergent sloughs and very low in *Nymphaea odorata* Ait. dominated sloughs (Karunarante et al. 2006). Previous studies in this region (Wood and Tanner 1990, David 1996) indirectly documented the conversion of wet prairies to aquatic sloughs, which constitutes a loss of quality Snail Kite foraging habitat (Kitchens et al. 2002). None of these studies were designed to provide inference beyond the isolated sites in which they were conducted, and unfortunately occurred largely outside kite foraging and nesting areas. There is concern that conversion of wet prairie/emergent slough habitats to deeper, less desirable sloughs will lower kite reproduction, primarily through lower prey base availability in those communities (Karunarante et al 2006).

To address the issue of habitat degradation within breeding areas and its effect on snail kite reproduction success, a vegetation study was initiated in 2002 to monitor critical kite foraging habitat in WCA3A. It is now particularly vital to monitor kite habitat given their critical state and a continuing trend towards higher maximum water levels and a more extreme hydrologic range (Table 5-2) within WCA3AS. In this study, we hypothesize that there is a link between vegetation community composition and environmental and demographic factors for the snail kite.

Methods

To monitor foraging habitat, I used data in the breeding area described in Figure 5-2 from a large scale vegetation study in WCA3A (Zweig and Kitchens 2008), plots 7, 8, and 9. Twenty 1-km^2 plots (Figure 5-1) were placed in a stratified random manner across the landscape gradients in WCA3A South. Plots were stratified by the landscape level gradients of peat depth, water depth and snail kite nesting activity. Five *a priori* physiognomic types were identified: slough, sawgrass, tree/shrub island, cattail, and wet prairie. Two or three transects in each plot were placed perpendicular to ecotones, beginning in one *a priori* type and terminating in another, e.g., slough to sawgrass. I collected 0.25 m^2 samples of all standing biomass along a belt transect, clipping the vegetation at peat level at 3 m intervals, and included any submerged aquatic plants within the sample. Shrubs were sampled in the same manner as the herbaceous vegetation; there were no trees in transects. Samples were collected from every transect in every plot during the dry (May/June) and wet season (November/December) of each year. These were sorted by species, counted, dried to a constant weight, and weighed to the nearest 0.1 g. Approximately 10,000 samples were collected and processed between 2002 and 2006.

Our analysis focused on the slough samples in the core Snail Kite nesting area, plots 7,8 and 9, and only the wet season data and as there were fewer issues of sampling error due to small, new growth and matted prairie vegetation than in the dry season. I used only the *a priori* slough samples within this area as the area contained no *a priori* wet prairie communities. The *a priori* labels were general and sloughs also contained emergent vegetation.

Hydrologic data were provided by 17 wells installed in December 2002 within plots that did not already have permanent water wells. On each sample date, water depths were measured with a meter stick at every quadrat and linked to water depth measurements at the nearest well (within a radius < 1 km) by subtracting the quadrat water depth from the reading at the well for that day. Historic hydrologic data for all 17 wells—from 1991 to 2002—were hindcast using an artificial neural network model (see Conrads et al. 2006). These wells are currently in place and six have become permanent, real-time wells for the Everglades Depth Estimation Network (EDEN).

Multivariate Analysis

To account for high densities of low biomass species and high biomass of low density species, the data were relativized in an index, importance value (IV), calculated by:

IV for species i = $((R_{di} + R_{bi})/2)*100$,

where R_{di} is the relative density of species i and R_{bi} is the relative biomass of species i. Relative measures are the sum of biomass or density of species i divided by the sum of biomass or density of all species within each sample.

I combined the *a priori* slough 0.25 m^2 samples on each transect that contained sloughs (Transects 7-1, 7-3, 8-1, 8-2, 9-1, and 9-3) into one point (n = 35) and performed a hierarchical cluster analysis on the IV data with a Sorenson distance measure and flexible beta of -0.25 in PC-ORD (McCune and Mefford 1999). To choose how many clusters were present during the study period, I ran an indicator species analysis (ISA) (Dufrêne and Legendre 1997) to prune the cluster dendrogram. I used a non-metric multidimensional scaling (NMS) (Mather 1976, Kruskal 1964) ordination on the same IV data with a Sorenson distance measure to identify the strongest environmental and demographic correlates with species composition. Environmental variables in the analysis included maximum, mean, and minimum water depths for each wet and dry season up to five years previous to the sample; the mode (referred to as frequency) of water depths for each season up to two years previous; annual water depth ranges (max – min); and average stem density/0.25 m^2 of four slough/prairie species for each year. The hydrologic variables were calculated with the modeled well data (Conrads et al 2006) by a custom Excel application and tailored to each transect by water depths collected at the samples.

Univariate Analysis

I ran an analysis of variance (ANOVA) (PROC GLM, SAS Institute 1989) on density data of dominant wet prairie and slough species (*Eleocharis cellulosa* Torr., *Eleocharis elongata* Chapman, *Panicum hemitomon* Schult., *Paspalidium geminatum* (Forssk.) Stapf, *Bacopa caroliniana* Walt., *Nymphaea odorata* Ait., and *Utricularia* spp.) to determine significant changes over time. I did not combine samples as in the multivariate analysis, but used the 0.25 m^2 samples separately for the ANOVA to provide a more precise estimate of local density.

Demographic analyses

Adult survival tends to be constant for Snail Kites in the recent past (Dreitz et al. 2002), excepting drought events, and fertility has currently emerged as more important than survival (Martin 2007), so I only included reproductive variables in the analyses.

Our nest success data was provided by a database maintained by W.M. Kitchens at the Florida Cooperative Fish and Wildlife Research Unit. Snail Kite nesting and survival data has been collected at the Cooperative Unit, range-wide, since the late 1990's. Nests are located by quasi-systematic searches (Dreitz et al 2001) during the breeding season in all known active and recently reported areas. Crews revisit nests during the season to assess survival and to band chicks.

I used the nest survival model in Program MARK (White and Burnham 1999) on nests located within WCA3AS to estimate nest success by year from 2002–2006. Only nests with complete data were used in the analysis (n = 79), and sample size per year was 21, 14, 6, 2, and 36, respectively. I provided the day each nest was found, the last day the active nest was checked, the last day the nest was checked, the fate of the nest, and used nest success estimates in the NMS secondary matrix to explore correlations between success, environmental variables, and habitat community composition. I ran MARK with two pre-defined models: dot, which assumes no difference between years; and group, which assumes a difference between years.

Results

Multivariate analysis

The cluster and ISA suggested five clusters, or vegetation sub-communities within the sloughs, which were named according to their indicator species and placement on the ordination axes: transitional to sawgrass, emergent slough, emergent/lily slough, slough, and longer hydroperiod slough. Spatially, the transitional to sawgrass community only occurred in plot 8 and temporally only in 2006, but no other communities exhibited spatial or temporal trends. Average densities of species of interest were calculated for each cluster to further describe the sub-community (Figure 5-3).

The NMS analysis yielded a two-dimensional solution, with 40 runs of real data and 50 Monte Carlo runs (stress = 11.6, $p = 0.02$). The axes explained 92.6% of the variation in the model, 55.7% and 36.9% respectively. Environmental vectors were overlain on the ordination, with the angle and length of the line indicating the direction and strength of the correlation (Figure 4). Hydrologically, axis 1 was positively correlated ($r^2 = 0.15–0.257$, $r = |0.401–0.507|$, $p < 0.001$) with the minimum of the previous dry season, the minimum of the dry season four years previous, and the frequency for the wet season two years previous. Axis 2 was positively correlated ($r^2 = 0.193–0.470$, $r = |0.439–0.686|$, $p < 0.001$) with the maximum water depth of entire previous water year; the dry seasons two, three, and four years previous; and all variables in the wet season two years previous. Densities of *E. elongata*, *P. geminatum, and P. hemitomon* were negatively correlated with axis 2, as was nest success ($r = -0.529$, $p < 0.001$). *N. odorata* was positively correlated with axis 2 ($r=0.606$, $p < 0.001$).

I also traced the progression of the sloughs through time in the NMS (Figure 5-5). Temporally, transects tend to move up both axes towards deeper communities (Figure 5-5). The ordination points for 2006 were spread in a wider pattern across both axes. A majority of transects transitioned from emergent slough to slough over time, indicating a loss of emergent species.

Univariate Analysis

The density data exhibited significant ($p < 0.05$) decreases of the emergents *E. elongata, P. geminatum, B. caroliniana,* and *P. hemitomon* and a significant increase in the longer hydroperiod species *N. odorata* (Figure 5-6). This trend of decreasing emergent species corresponded to the species response across the whole WCA3A landscape. Density over time was also analyzed for all 20 plots in the expanded study area, and there was a significant ($p < 0.05$) decrease in density of all the major wet prairie species: *E. elongata*, *P. geminatum, E. cellulosa,* and *P. hemitomon.* There was no significant change across the landscape in *N. odorata*. This decline in emergent species density supports the movements of slough sub-communities in the study area to deeper communities in the multivariate analysis.

Demographic analysis

Program MARK modeled nest success within WCA3AS and the most parsimonious model was the group model (AICc = 102.3251, ΔAICc = 0.00, AICc weight = 1.0, number of parameters = 5). Yearly nest success estimates for 2002–2006 were 53.6% (SE = 0.00613), 100% (SE = 0.000), 100% (SE = 0.000), 0.941% (SE = 0.0601), and 8.67% (SE = 0.00820), respectively. The dot model was for comparison only and AICc = 129.7933, ΔAICc = 27.4682, AICc weight = 0, and number of parameters = 1.

Discussion

Snail Kites were once thought to be highly nomadic and resistant to localized disturbances (Bennetts and Kitchens 2002), but a recent study (Martin et al. 2006) suggests they exhibit more site fidelity than previously considered, especially juveniles. From the kites' perspective, the Everglades watershed can be considered a network of discrete habitats or regions (Kitchens and Bennetts 2002). Theoretically, this network continues to function properly (i.e. net gain in kite population) even if regions are offline (Figure 5-7), but there is a threshold at which the viability of the network is compromised (Bennetts and Kitchens 1997). The Snail Kites' network seems to have exceeded this threshold and the population is responding negatively with reduced reproductive success (Kitchens et al 2006). Offline regions could have more of an effect on the Snail Kite population than simply forcing migration to an online region as previously believed—

they could trap birds with high natal philopatry and decrease juvenile survival and recruitment. This underscores the importance of maintaining multiple online regions of quality habitat, especially those considered critical to the Snail Kites.

WCA3A has been the most critical habitat unit within the Snail Kites' range, providing both the largest extent of quality nesting and foraging habitats and the highest juvenile production (Kitchens et al 2006). Given the importance of WCA3A within the Snail Kites' habitat network (Kitchens et al. 2002, Martin 2007), the vegetation community transformations documented in this study are particularly pertinent and may help explain why WCA3A appears to be offline for reproduction and recruitment. Four out of seven transects in the study transitioned or remained in a deeper, less desirable Snail Kite foraging habitat, while two transitioned to light sawgrass. Many transects made abrupt changes in community composition in 2005 due to hurricane Wilma, but returned to more normal community compositions in 2006. I demonstrated that even in a relatively short period of four years, wet prairie/emergent sloughs are converting to deeper, less desirable Snail Kite habitats in response to hydrologic factors, with a strong temporal trend (Figure 5-5). Important emergent species, such as *E. elongata*, *P. geminatum,* and *P. hemitomon* declined significantly in a relatively short amount of time. Emergents were replaced by *N. odorata*, a species that has less value as foraging habitat to the Snail Kite and its prey base (Bennetts et al. 2006, Karunarante et al. 2006).

Both *Eleocharis* species used in the study are perennials that grow best in shallowly flooded conditions (Macek et al. 2006). According to the results, if the minimum and maximum water levels of the recent and historic (>1 year previous) dry seasons are too low, the area transitions to light sawgrass. However, if dry seasons are too wet, emergent vegetation is reduced and results in a *N. odorata*-dominated community. Once *N. odorata* and sawgrass are established, their life history characteristics allow them to persist in non-ideal conditions. Once established, they could shade out *Eleocharis spp* which are less tolerant to harsh conditions (Edwards et al. 2003), slowing the return to an emergent slough community when favorable hydrologic conditions return, resulting in a long-term loss of foraging habitat.

Connecting foraging and nesting habitat availability and breeding performance is the key to a sound conservation strategy for the Florida Snail Kite. Variation in habitat quality and water levels influence breeding success of birds (Johnson 2007), particularly the Snail Kite that is adapted to dynamic wetlands (Beissinger and Snyder 2002, Bennetts et al 2006). While there is not a solid link between nest success and vegetation community composition, the correlations demonstrated here suggest that nest success could be associated to the structure of slough communities in WCA3A and the hydrology that shapes those communities. Nest success is also associated with the density of *P. geminatum* and negatively associated with the density of *N. odorata*, similar to the abundance of the Snail Kite's main prey, the apple snail (Karunarante et al. 2006). This suggests that the decline of emergent species and increase in *N. odorata* could have an effect on nest success. I demonstrate that foraging habitats respond relatively quickly to altered hydrology, especially maximum and minimum water depths in the dry seasons, which encompass a large part of the Snail Kite's breeding season. Restoring and maintaining quality foraging habitat for reproduction of Snail Kites in WCA3A, using the provided hydrologic variables as input, might be completed quickly and should be a primary consideration in water management decisions for the future.

One point of note was that only nest success, not number of nests, was associated with habitat community composition. Nest success was used as the primary demographic variable because it is a sensitive indicator of Snail Kite population stability (Donovan and Thompson

2001) that responds quickly to subtle environmental perturbations, and reproductive success, not the previously considered adult survival, is vital to this critically endangered population (Martin 2007). Our conclusions are supported by the fact that hydrology has previously been associated with Snail Kite reproductive success. Higher maximum water depths prior to the breeding season are linked to poor Snail Kite nest success, and increased drying event frequencies are linked to lower juvenile survival, population growth, and nest success (Beissinger and Snyder 2002, Martin et al. 2006).

The time period in which community and species density changes occurred is similar to previous studies of Everglades vegetation (Armentano et al. 2006, Childers et al. 2006), but I provide specific hydrologic factors that can be used as inputs in adaptive management decisions to improve Snail Kite habitat in WCA3A. This is not to say that hydrologic variables computed for this study are the only environmental factors correlated with community composition in Snail Kite foraging habitat of WCA3A. They are, however, a starting point—a foundation for adaptive management decisions to increase reproductive success by restoring a critically endangered species' habitat.

Table 5-1: Number of nests and nest success from 2002–2006 within Water Conservation Area 3A South, FL, USA.

Year	Total Nests	Percent Nest Success
2002	22	0.5366
2003	22	1
2004	8	1
2005	2	0.941
2006	76	8.67

Table 5-2: Increasing maximum water levels and hydrologic range in cm within the core breeding area (Plots 7, 8, and 9) of Water Area 3A South, FL, USA. Linear regression and R^2 values of depth and range are shown below each section of the table.

Maximum Water Depths	Year					
	2000	2001	2002	2003	2004	2005
Well 7	55.9	73.5	76.2	89.8	93.5	95.6
Well 8	70.0	86.7	89.4	103.1	107.1	111.2
Well 9	60.9	77.3	79.9	94.5	98.8	89.8
$y = 7.7683x + 53.575$	$R^2 = 0.9155$					

Hydrologic Range	Year					
	2000	2001	2002	2003	2004	2005
Well 7	38.2	34.9	62.9	61.1	76.4	74.2
Well 8	47.5	33.3	76.4	61.1	87.3	80.3
Well 9	47.0	34.6	71.3	66.7	86.0	80.1
$y = 8.6574x + 27.631$	R2 = 0.8395					

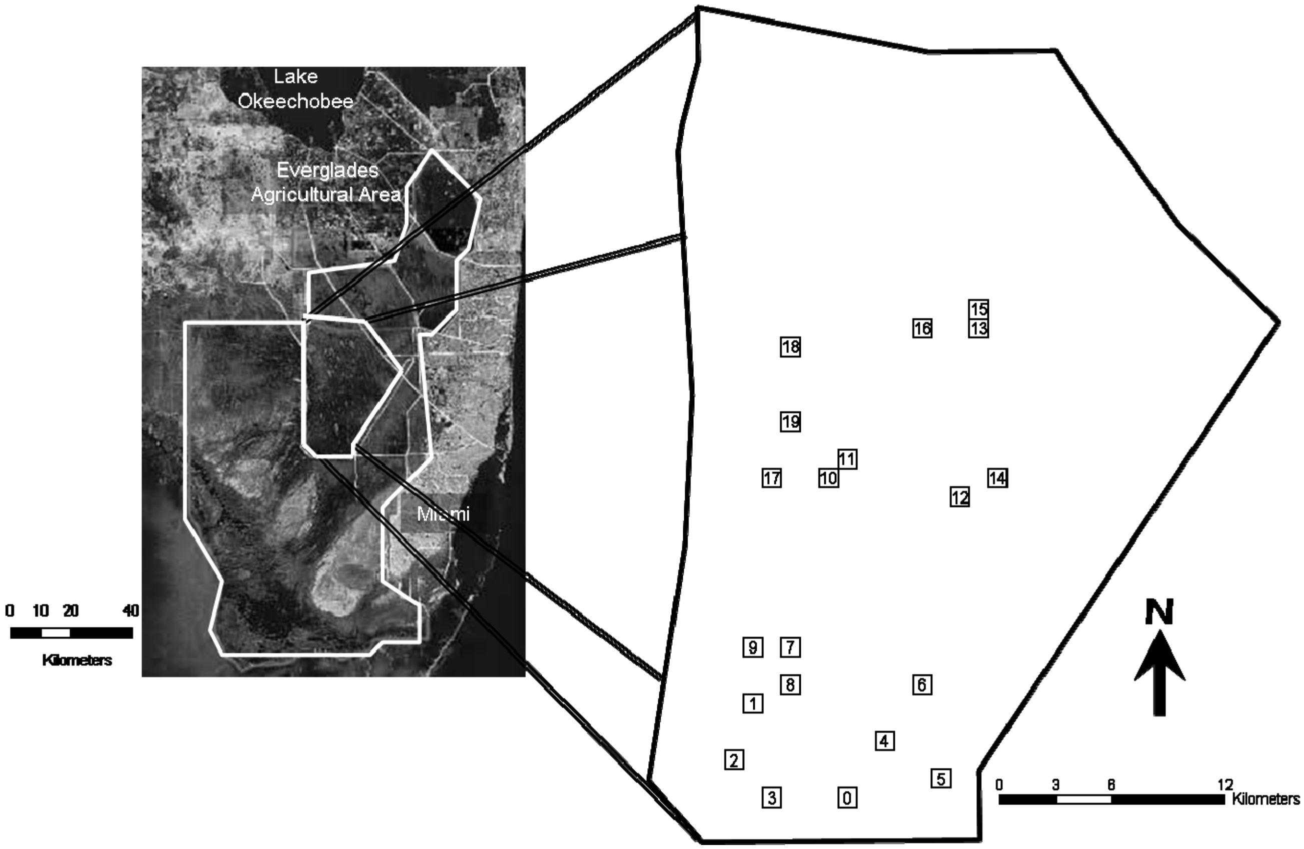


Figure 5-1: Expanded study sites in Water Conservation Area 3A South, FL, USA

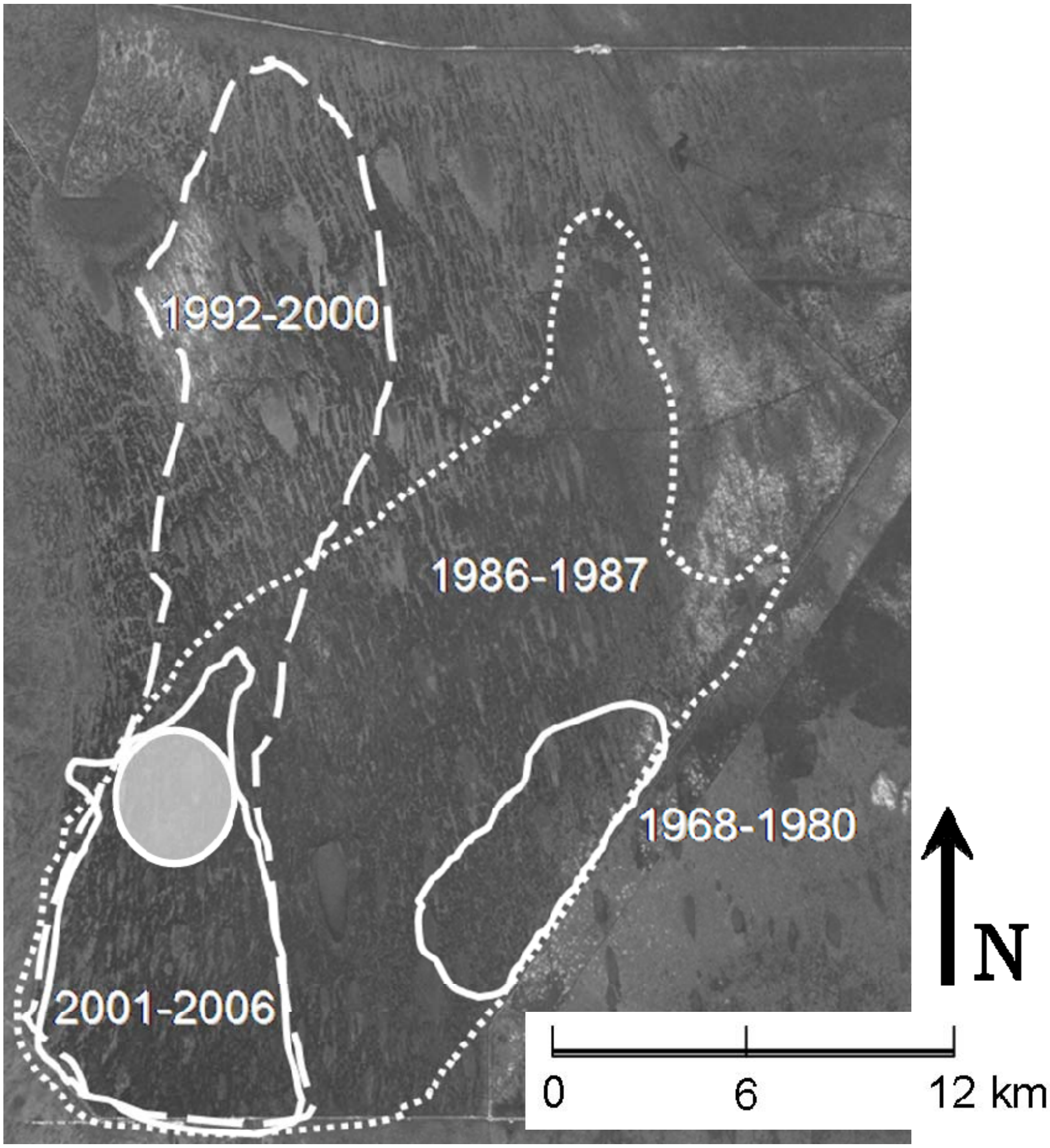
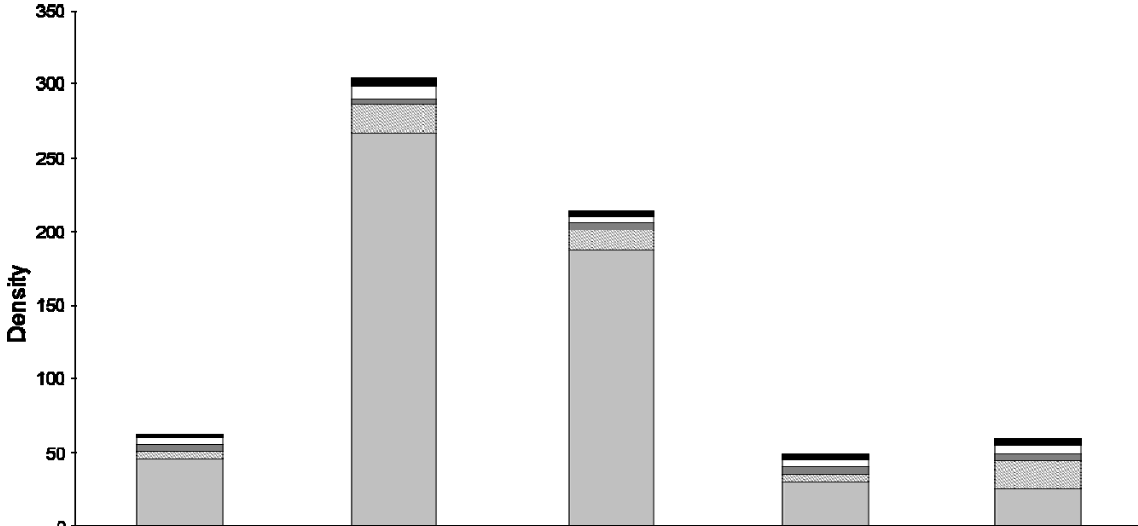


Figure 5-2: Movement of nesting concentration in Water Conservation Area 3A, FL, USA. White circle indicates critical breeding area and focus of study. Adapted from Bennetts et al 1998.



	Transitional to sawgrass	Emergent slough	Emergent/lily slough	Slough	Longer hydroperiod slough
PDG	2.5	5.3	3.4	4.0	3.7
PAH	4.5	8.4	4.1	4.6	6.3
NYO	5.6	4.4	5.5	5.5	5.3
ELsp	5.0	19.0	13.1	5.0	18.7
ELG	45.3	266.6	187.2	29.9	24.9

Community

Figure 5-3: Densities of key emergent slough species by community in Water Conservation Area 3A. PDG = P. geminatum, PAH = P. hemitomon, NYO = N. odorata, ELsp = E. cellulosa, and ELG = E. elongata.

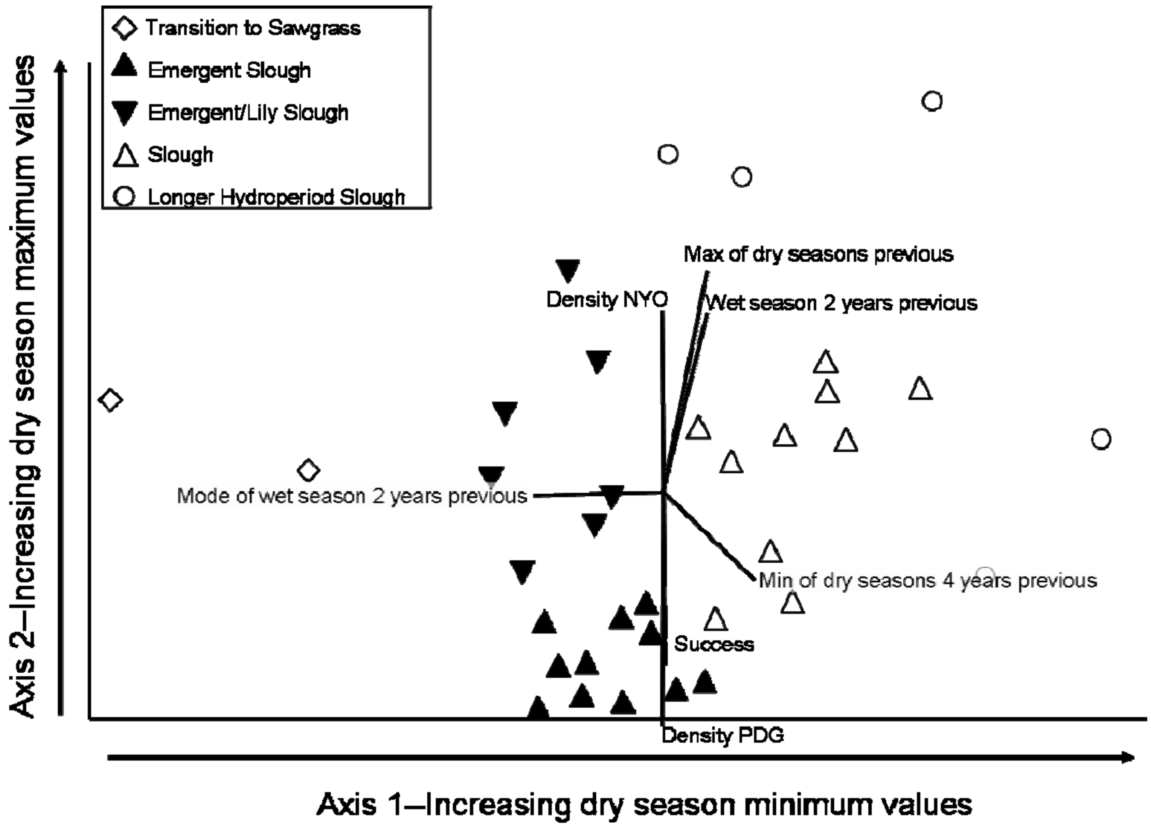


Figure 5-4: Non-metric multidimensional scaling ordination of Snail Kite habitat communities in Water Conservation Area 3A. Vectors represent key environmental correlates with r2 ≥ 0.15 ($p < 0.009$). NYO = N. odorata, PDG = P. geminatum, Success = nest success.

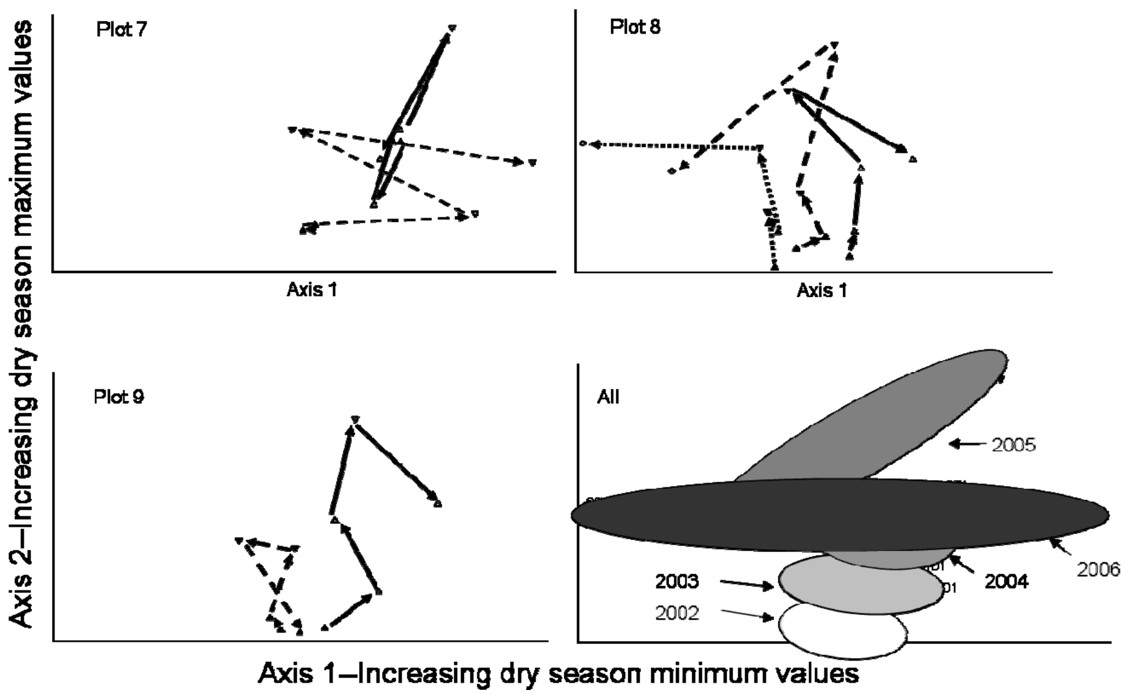


Figure 5-5: Temporal movement of Snail Kite habitat communities in Water Conservation Area 3A from 2002-2006. Dotted and solid lines represent different transects within a plot moving through time. Bubbles on All graph encompass a majority of points from that year and show trends of communities over time.

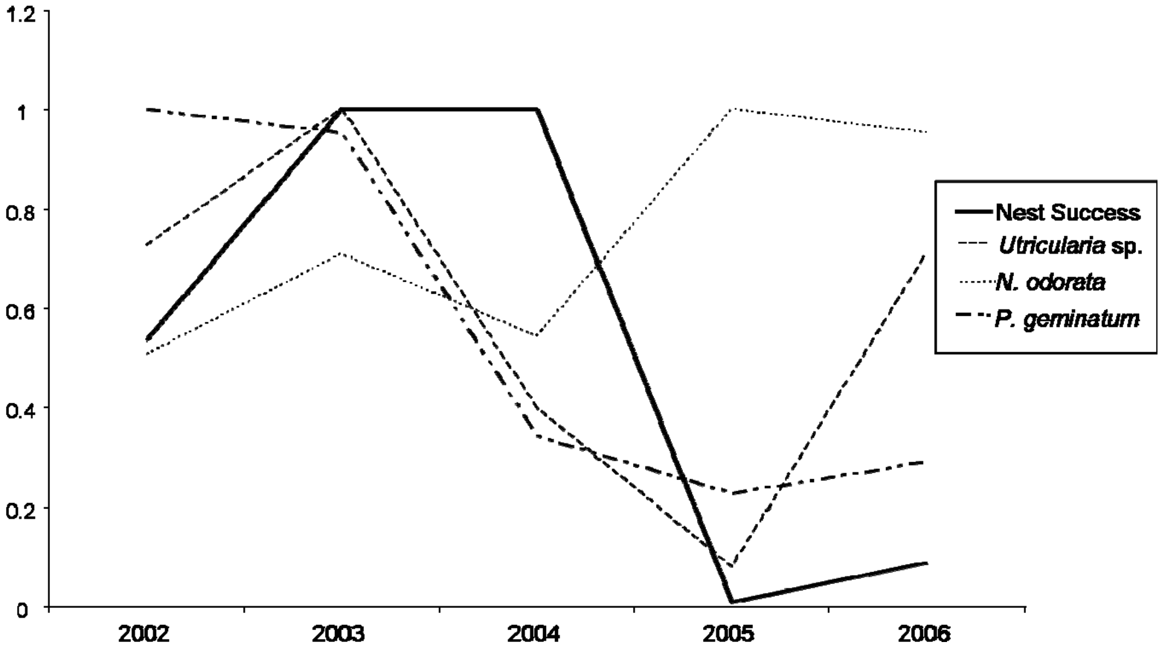


Figure 5-6: Nest success and densities of Snail Kite foraging habitat species in Water Conservation Area 3A. Values have been relativized for display purposes (value/max in group).

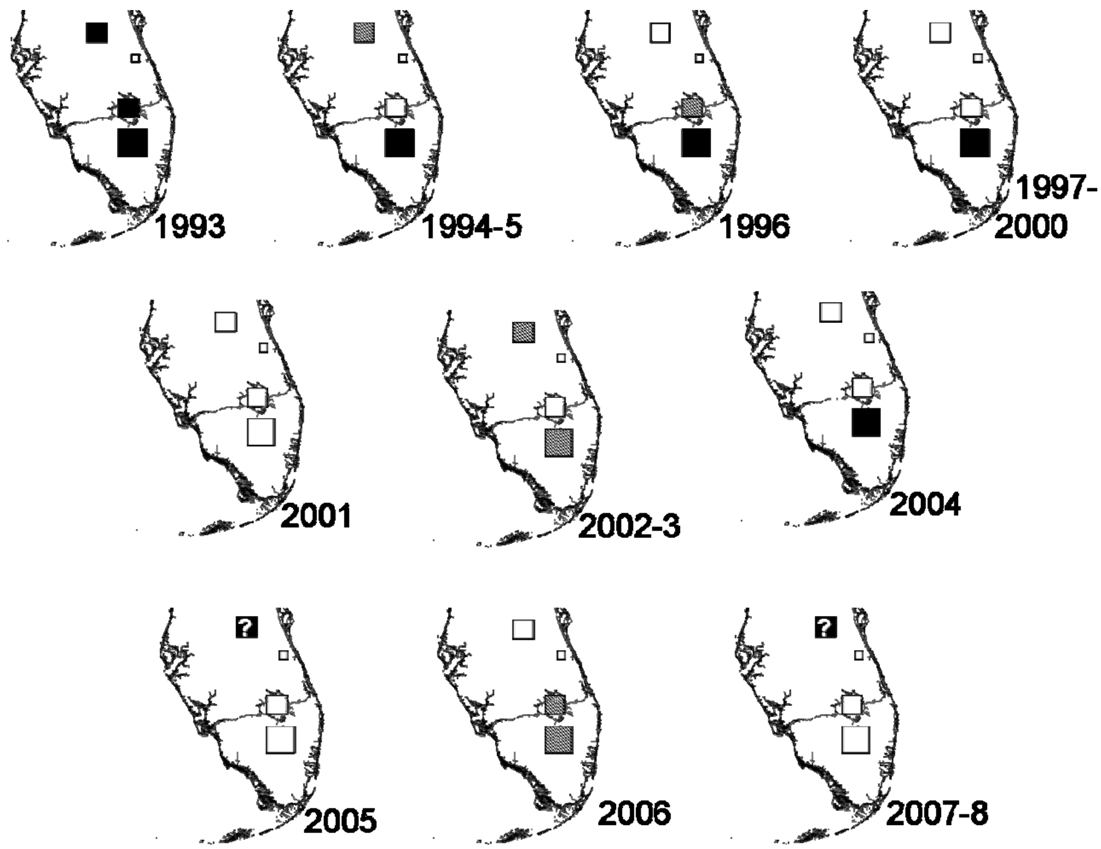


Figure 5-7: Snail kite habitat network in FL, USA. Black squares = region is online for reproduction, diagonal lines = area is questionable, and white squares = offline. "?" for a region indicates that I am unsure if it is a source or a sink due to widespread presence of an exotic apple snail. Offline = production index <= 5%. Questionable = production index <=15%. Production index = # young produced in area in year/ Total # young produced in year * production potential. Production potential = Total # young produced in year/ maximum total of young produced per year.

CHAPTER 6
DISCUSSION

An essential function of science within restoration is to provide the knowledge to predict outcomes of management actions (Zedler 2000). Lockwood et al (2000) identified a lack of knowledge concerning Everglades processes that are needed to complete, or even begin, restoration. This dissertation explores the complex interactions between wildlife, hydrology, and vegetation ecology in the Everglades, and provides links between conceptual and applied information and baseline data for its restoration.

Wetland Restoration

Zedler (2000) provided 10 ecological principles that are often neglected in many wetland restoration efforts:

1. Landscape context and position are crucial to wetland restoration
2. Natural habitat types are the appropriate reference system
3. The specific hydrological regime is crucial to restoring biodiversity and function
4. Ecosystem attributes develop at different paces
5. Nutrient supply rates affect biodiversity recovery
6. Specific disturbance regimes can increase species richness
7. Seed banks and dispersal can limit recovery of plant species richness
8. Environmental conditions and life history traits must be considered when restoring biodiversity
9. Predicting wetland restoration begins with succession theory
10. Genotypes influence ecosystem structure and function

This dissertation addresses 5 of 10 of these principles in reference to Everglades restoration: numbers 2, 3, 4, 8, and 9.

Point 2 and 3: Choosing reference habitat types is difficult in Everglades restoration, because there are only general descriptions of the plant communities and their arrangement at the multiple scales required. Drainage began in the 1880's (Sklar et al 2005), so most accounts describe an altered system. While the communities described in Chapter 2 would not be reference communities, they are the most detailed descriptions available of vegetation in Water Conservation Area 3A South and should be references for water management decisions, particularly considering the hydrologic correlates I provide for community composition. These correlates in both Chapters 2 and 3 relate specific hydrologic characteristics to vegetation communities, which provide initial data for restoration water regime alternatives, especially when restoring a specific sub-community type.

Point 4: Ecosystem attributes of the Everglades develop at three different temporal scales: long-term, periodic, and discrete (DeAngleis and White 1994). Chapter 4 explores the complex pattern/process relationships of two scales (periodic and discrete) in the Everglades and how degraded feedback loops are created and maintained. I also quantify the degradation of the characteristic ridge and slough landscape from the disturbance of the pattern and process on both periodic and discrete levels.

Point 8: The range of possible environmental conditions should be taken into account when considering targets for Everglades restoration. A complete restoration is not possible as the human population of south Florida still requires water storage and flood control from the remnants of the Everglades (Sklar et al 2005). I need to be conscious of the feasible environmental conditions and the vegetation communities that are suited to those conditions, and analyses within this dissertation contribute to the required knowledge base of vegetative/hydrologic interactions. I also suggest species that are possible indicators of restoration based on life-history traits and how they interact with the environmental conditions.

Point 9: Chapter 3 provides a general wetland and applied succession model in the form of state and transition models. I explore the non-linearity of wetland succession (Zedler 2000), potential hysteresis, and transitory communities that are possible within restoration. Awareness of these possibilities allows managers to avoid unwanted states that could occur from uninformed water management decisions.

Habitat Restoration

I provide evidence for the alteration and possible degradation of an endangered species' habitat within the Everglades, and how nest success of the Snail Kite is linked to community composition and hydrologic factors. By identifying the hydrology correlated to vegetation community composition, I also provide possible pathways for habitat restoration. Foraging habitats respond relatively quickly to altered hydrology, especially maximum and minimum water depths in the dry seasons, which encompass a large part of the Snail Kite's breeding season. Restoring and maintaining quality foraging habitat for reproduction of Snail Kites in WCA3A, using the provided hydrologic variables as input, might be completed quickly and should be a primary consideration in water management decisions for the future.

Information for Large-Scale Restoration

I provide a detailed look at the vegetation ecology of an Everglades remnant and explore how vegetation communities interact with environmental characteristics. The most important use of this information is to information for the restoration of the Everglades. The political and scientific process of Everglades restoration will serve as a model (either positive or negative) for future large-scale restoration efforts (Sklar et al 2005), and I attempt to provide current vegetation information and contribute as scientists to the process.

APPENDIX
DETAILED VEGETATION SAMPLING PROTOCOL AND SITE INFORMATION

Sampling began in November 2002 and concluded in July 2005. We selected 20 1-km^2 plots by randomly choosing 20 points on an 1 km x 1 km grid over the study area to represent the northwest corner of each plot (Table A-1). Two or three belt transects were located in each plot (Table A-2) by dividing each plot into a 100 m x 100 m grid. Two random numbers were generated between 1 and 10 (a and b). Using an airboat and starting in the northwest corner of a plot, we drove 100*a meters due east and 100*b meters due south. At that point, a transect was placed perpendicular to an ecotone between two representative *a priori* communities (ex: slough to sawgrass). PVC poles were placed at the start and end of a transect, and at the transition(s) between *a priori* communities. The length, orientation, and number of samples on the transect were recorded (Table A-3).

Belt transects were used to allow the removal of biomass at every sample site for multiple sample events. Each belt transect (Figure A-1) consists of three pairs of lettered transects spaced 4 m apart. Each lettered transect has a 1 m walkway to keep trampling of the sample area to a minimum, and two alternating sample events on each side of the walkway. For example, sample event B would start at the bottom lettered transect and a 0.25m^2 sample would be taken at the transect pole and every 3 m after that. The first 0.25m^2 sample of C would start 1.5m from the bottom transect pole and continue every 3 m from that point. Quarter-meter squared vegetation samples were taken every 3 meters at an arm's length away from the walkway. A wooden dowel was placed at the sample point as a reference for the sampling hoop, and we collected any floating vegetation and clipped other vegetation at substrate level. Approximately 1200 samples per sample event were cut. Plants were sorted by species, dried to a constant weight, and weighed to the nearest 0.01 g.

We scheduled two sample events each year—one in the wet and one in the dry season. The dry season sample event typically occurred in June or early July. Criterion for the start date of the dry season sample event was accessibility of the area by airboat after the lowest water depths of the season had occurred. The wet season sample event occurred in November or early December. Criterion for the start of the wet season sample was to sample as near peak water depths as possible without sacrificing accurate sampling protocols due to deep water depths and poor water visibility.

Table A-1: GPS coordinates for study plot corners in Water Conservation Area 3AS. Coordinates are UTM, NAD83. N = north, S = south, E = east, W = west.

Plot corner	UTM X	UTM Y
0NE	525847	2852281
0NW	524847	2852281
0SE	525847	2851281
0SW	524847	2851281
1NE	520847	2857281
1NW	519847	2857281
1SE	520847	2856281
1SW	519847	2856281
2NE	519847	2854281
2NW	518847	2854281
2SE	519847	2853281
2SW	518847	2853281
3NE	521847	2852281
3NW	520847	2852281
3SE	521847	2851281
3SW	520847	2851281
4NE	527847	2855281
4NW	526847	2855281
4SE	527847	2854281
4SW	526847	2854281
5NE	530847	2853281
5NW	529847	2853281
5SE	530847	2852281
5SW	529847	2852281
6NE	529847	2858281
6NW	528847	2858281
6SE	529847	2857281
6SW	528847	2857281
7NE	522847	2860281
7NW	521847	2860281
7SE	522847	2859281
7SW	521847	2859281
8NE	522847	2858281
8NW	521847	2858281
8SE	522847	2857281
8SW	521847	2857281
9NE	520847	2860281
9NW	519847	2860281
9SE	520847	2859281
9SW	519847	2859281
10NE	524847	2869281
10NW	523847	2869281

Table A-1. Continued

Plot corner	UTM X	UTM Y
10SW	523847	2868281
11NE	525847	2870281
11NW	524847	2870281
11SE	525847	2869281
11SW	524847	2869281
12NE	531847	2868281
12NW	530847	2868281
12SE	531847	2867281
12SW	530847	2867281
13NE	532847	2877281
13NW	531847	2877281
13SE	532847	2876281
13SW	531847	2876281
14NE	533847	2869281
14NW	532847	2869281
14SE	533847	2868281
14SW	532847	2868281
15NE	532847	2878281
15NW	531847	2878281
15SE	532847	2877281
15SW	531847	2877281
16NE	529847	2877281
16NW	528847	2877281
16SE	529847	2876281
16SW	528847	2876281
17NE	521847	2869281
17NW	520847	2869281
17SE	521847	2868281
17SW	520847	2868281
18NE	522847	2876281
18NW	521847	2876281
18SE	522847	2875281
18SW	521847	2875281
19NE	522847	2872281
19NW	521847	2872281
19SE	522847	2871281
19SW	521847	2871281

Table A-2: Characteristics of transects and GPS coordinates of transect start (STA), ecotone (BND), and end poles (END) in Water Conservation Area 3AS. Coordinates are UTM, NAD83.

Plot-Transect	Community types	Orientation (degrees)	Length (m)	# of samples	Point Type	UTM X	UTM Y
0-1	slough/sawgrass	262	57.8	21	BND	525655	2852133
0-1					BND2	525614	2851796
0-1					END	525628	2852121
0-1					STA	525683	2852142
0-2	prairie/sawgrass/slough/ghost island	91	98.4	33	BND2	525588	2851797
0-2					BND3	525643	2851803
0-2					END	525662	2851801
0-2					STA	525566	2851796
0-3	slough/sawgrass	91	45.6	16	BND	525161	2851697
0-3					END	525186	2851703
0-3					STA	525130	2851694
1-1	prairie/sawgrass	100	75	26	BND	519939	2856715
1-1					END	519966	2856715
1-1					STA	519888	2856720
1-2	slough/sawgrass	120	36	13	BND	520781	2856743
1-2					END	520789	2856741
1-2					STA	520751	2856742
1-3	prairie/sawgrass	120	28.8	10	BND1	520817	2857044
1-3					BND2	520830	2857036
1-3					END	520852	2857026
1-3					STA	520814	2857051
2-1	prairie/typha	270	60	21	BND	519013	2853940
2-1					END	518979	2853938
2-1					STA	519064	2853944
2-2	prairie/typha	279	63	22	BND	519234	2854116
2-2					END	519204	2854118
2-2					STA	519267	2854115
2-3	sawgrass/prairie/sawgrass	110	66	23	BND1	519343	2853608
2-3					BND2	519371	2853593

Table A-3. continued

Plot-Transect	Community types	Orientation (degrees)	Length (m)	# of samples	Point Type	UTM X	UTM Y
2-3					END	519385	2853587
2-3					STA	519325	2853615
3-1	slough/wet prairie	122	76	26	BND1	521502	2851785
3-1					BND2	521539	2851770
3-1					END	521555	2851762
3-1					STA	521488	2851794
3-2	slough/ sawgrass	180	51.5	17	BND	521088	2851700
3-2					END	521055	2851701
3-2					STA	521102	2851697
4-1	slough/sawgrass/slough	74	76.3	27	BND1	527351	2854845
4-1					BND2	527367	2854850
4-1					END	527383	2854859
4-1					STA	527285	2854830
4-2	slough/shrub island	108	37.6	12	BND	527272	2854538
4-2					END	527310	2854533
4-2					STA	527236	2854545
4-3	slough/sawgrass	81	48	16	BND	527791	2855072
4-3					END	527820	2855068
4-3					STA	527773	2855061
5-1	slough/sawgrass	283	60	21	BND	530083	2852784
5-1					END	530043	2852793
5-1					STA	530101	2852782
5-2	slough/sawgrass	210	50.4	18	BND	530594	2852337
5-2					END	530582	2852306
5-2					STA	530598	2852352
5-3	slough/sawgrass	58	27	10	BND	530556	2852717
5-3					END	530570	2852728
5-3					STA	530547	2852711
6-1	slough/sawgrass/slough	63	66	24	BND1	529102	2858010
6-1					BND2	529116	2858021

Table A-3. continued

Plot-Transect	Community types	Orientation (degrees)	Length (m)	# of samples	Point Type	UTM X	UTM Y
6-1					END	529141	2858035
6-1					STA	529086	2858003
6-2	slough/sawgrass	78	40.8	14	BND	529262	2857430
6-2					END	529290	2857434
6-2					STA	529248	2857426
6-3	slough/sawgrass	270	39.3	14	BND	529485	2857747
6-3					END	529470	2857739
6-3					STA	529507	2857743
7-1	slough/sawgrass	60	42	15	BND	522569	2859938
7-1					END	522586	2859947
7-1					STA	522550	2859923
7-2	prairie/sawgrass/shrub island	290	41.3	14	BND	521914	2859473
7-2					END	521905	2859473
7-2					STA	521943	2859475
7-3	slough/light sawgrass/slough	124	83	29	BND1	522317	2859722
7-3					BND2	522306	2859728
7-3					END	522350	2859704
7-3					STA	522277	2859742
8-1	slough/sawgrass	105	45	16	BND	522533	2858025
8-1					END	522559	2858030
8-1					STA	522515	2858034
8-2	slough/sawgrass	213	30	11	BND	522644	2857588
8-2					END	522633	2857576
8-2					STA	522663	2857594
8-3	slough/sawgrass	270	30	11	BND	522585	2857319
8-3					END	522576	2857318
8-3					STA	522605	2857319
9-1	slough/sawgrass	282	39	14	BND	520170	2860114
9-1					END	520155	2860118
9-1					STA	520189	2860113

Table A-3. continued

Plot-Transect	Community types	Orientation (degrees)	Length (m)	# of samples	Point Type	UTM X	UTM Y
9-2	slough/sawgrass/shrub island/sawgrass/slough	92	94.3	32	BND1	520686	2859967
9-2					BND2	520731	2859969
9-2					END	520762	2859971
9-2					STA	520669	2859963
10-1	slough/sawgrass/slough	114	87	30	BND2	524325	2868818
10-1					BND1	524473	2869064
10-1					END	524379	2868801
10-1					STA	524298	2868829
10-2	slough/sawgrass/slough/sawgrass	88	99	34	BND2	524493	2869070
10-2					END	524549	2869075
10-2					STA	524450	2869062
10-3	slough/sawgrass	240	45	16	BND	524614	2868518
10-3					BND1	524624	2868520
10-3					END	524603	2868511
10-3					STA	524643	2868530
11-1	slough/sawgrass/slough	76	82	28	BND	525528	2870138
11-1					END	525578	2870158
11-1					STA	525501	2870129
11-2	prairie/sawgrass	58	72	25	BND	525520	2869521
11-2					END	525542	2869535
11-2					STA	525485	2869492
11-3	slough/sawgrass	43	29	10	BND	525704	2869725
11-3					END	525718	2869735
11-3					STA	525681	2869716
12-1	slough/light sawgrass/slough	80	51.2	18	BND	531164	2868038
12-1					END	531195	2868044
12-1					STA	531122	2868014
12-2	slough/sawgrass	80	66.2	23	BND	531740	2867605
12-2					END	531762	2867603

Table A-3. continued

Plot-Transect	Community types	Orientation (degrees)	Length (m)	# of samples	Point Type	UTM X	UTM Y
12-2					STA	531702	2867596
13-1	prairie/sawgrass	60	69.2	24	BND	532651	2876890
13-1					END	532667	2876889
13-1					STA	532619	2876868
13-2	slough/sawgrass,typha	259	60.2	21	BND	532544	2876668
13-2					BND2	532486	2876668
13-2					END	532478	2876669
13-2					STA	532601	2876666
13-3	slough/prairie/sawgrass	244	97	33	BND1	532319	2876426
13-3					BND2	532301	2876434
13-3					END	532264	2876411
13-3					STA	532344	2876455
14-1	slough/sawgrass	80	58	20	BND	533148	2869079
14-1					END	533171	2869085
14-1					STA	533116	2869067
14-2	slough/light sawgrass/slough	80	63	22	BND	533853	2868895
14-2					END	533890	2868896
14-2					STA	533833	2868890
14-3	slough/sawgrass	100	42	15	BND1	533214	2868748
14-3					BND2	533231	2868752
14-3					END	533236	2868744
14-3					STA	533193	2868752
15-1	slough/sawgrass	310	92	31	BND	532503	2877856
15-1					END	532429	2877888
15-1					STA	532511	2877855
15-2	slough/ghost island	235	78	27	BND1	532529	2877522
15-2					END	532466	2877490
15-2					STA	532606	2877572
16-1	sawgrass/prairie/sawgrass	105	99.2	34	BND1	529598	2877096
16-1					BND2	529638	2877092

Table A-3. continued

Plot-Transect	Community types	Orientation (degrees)	Length (m)	# of samples	Point Type	UTM X	UTM Y
16-1					END	529681	2877084
16-1					STA	529584	2877100
16-2	prairie/sawgrass	240	44.2	16	BND	529576	2876445
16-2					END	529555	2876431
16-2					STA	529595	2876453
16-3	ghost island/sawgrass, shrub	95	93.4	32	BND	528904	2876819
16-3					END	528951	2876816
16-3					STA	528859	2876805
17-1	prairie/sawgrass/shrub island	94	17.8	25	BND1	521188	2868735
17-1					BND2	521213	2868756
17-1					END	521228	2868738
17-1					STA	521162	2868734
17-2	slough/sawgrass/slough	90	87.3	30	BND1	521851	2868722
17-2					BND2	521887	2868724
17-2					END	521896	2868722
17-2					STA	521822	2868722
17-3	prairie/sawgrass/prairie	100	67.3	23	BND	521573	2868907
17-3					BND2	521591	2868903
17-3					END	521621	2868895
17-3					STA	521553	2868909
18-1	sawgrass/prairie/sawgrass,shrub	110	58.7	21	BND1	522207	2876156
18-1					BND2	522171	2876167
18-1					END	522161	2876168
18-1					STA	522219	2876153
18-2	sawgrass/prairie/slough/sawgrass	105	70.3	24	BND1	522165	2875526
18-2					BND2	522178	2875524
18-2					BND3	522211	2875522
18-2					END	522223	2875523
18-2					STA	522151	2875528
18-3	slough/sawgrass/slough	270	73	25	BND1	522607	2875941

Table A-3. continued

Plot-Transect	Community types	Orientation (degrees)	Length (m)	# of samples	Point Type	UTM X	UTM Y
18-3					BND2	522563	2875939
18-3					END	522553	2875941
18-3					STA	522623	2875938
19-1	slough/prairie/sawgrass	261	48	17	BND	522135	2871678
19-1					END	522155	2871684
19-1					STA	522108	2871673
19-2	prairie/light sawgrass/prairie	274	72	25	BND1	522566	2871978
19-2					BND2	522547	2871979
19-2					END	522521	2871979
19-2					STA	522593	2871978
19-3	slough/sawgrass	90	42.2	15	BND	522530	2871411
19-3					END	522552	2871413
19-3					STA	522512	2871411

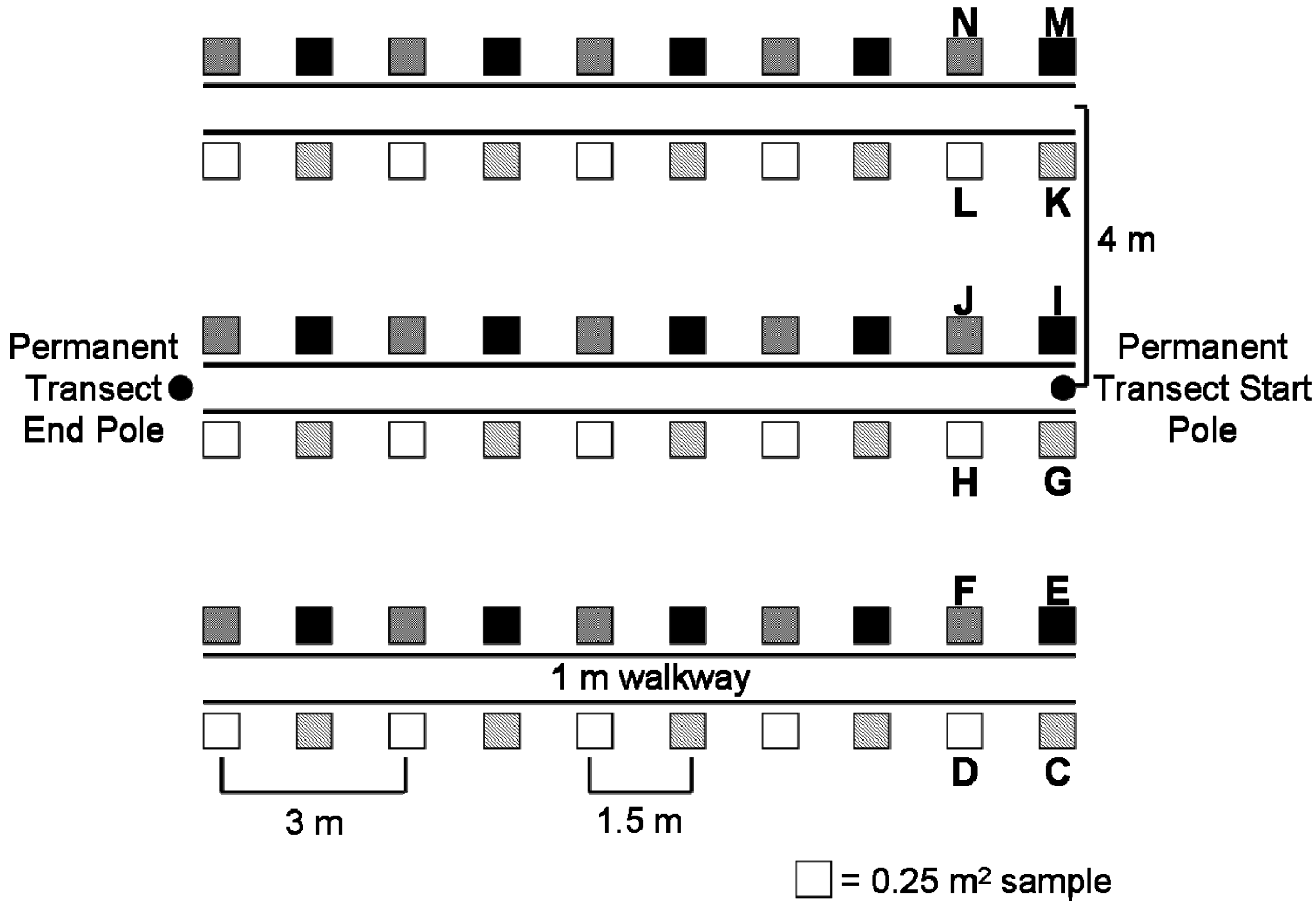


Figure A-1: Belt transect diagram for vegetation sampling in Water Conservation Area 3AS

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BIOGRAPHICAL SKETCH

Christa Zweig grew up in Springfield, MO and spent a significant portion of her summer breaks on the beach in coastal GA. She earned her B.S. in Biology at the University of Richmond, VA, and tried out life as a biologist at her first field technician job in the Great Smoky Mountains during her summers in Richmond. This led to technician jobs across the country, from Florida to Texas and California. She found herself back in Florida in 1999 starting a M.S. degree at the University of Florida. She studied the body condition of alligators as an indicator of restoration success and transitioned into her PhD at the University of Florida, still working in the Everglades.