

ESTIMATING TRANSITION PROBABILITIES AMONG EVERGLADES WETLAND
COMMUNITIES USING MULTISTATE MODELS

By

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To my family

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Abstract of Thesis Presented to the Graduate School
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By

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There has been a drastic loss of wetlands throughout the world with an estimated loss of 53% in the United States since the late 1700s. Half of the Everglades, a south Florida wetland, has been lost to agriculture and urban development in the last hundred years but now efforts are being made to restore it. Managers and decisions makers faced with the task of carrying out Everglades restoration are in dire need of robust statistical estimates that relate changes in water levels to changes in plant communities. To address this need I present a comprehensive framework for investigating multiple competing hypotheses about the factors governing transition probabilities among vegetative community states in the Everglades. The first step in this analysis was to use multivariate analyses to classify vegetation communities into states that are particularly relevant to specified management problems. I then applied likelihood based multistate models in order to evaluate multiple competing hypotheses; and to provide estimates of transition probabilities and associated measures of uncertainty. These estimates can then be incorporated into management models. In addition, to being useful for management of the Everglades I believe that our framework can be used to address adaptive management problems in other ecosystems.

CHAPTER 1 OVERVIEW

Introduction

Wetlands are transition zones between terrestrial and true aquatic ecosystems. By cleansing polluted waters, preventing floods, protecting shorelines and recharging groundwater aquifers, wetlands fill an important ecological role. They function as sources, sinks, and transformers of chemicals, and biological material through their extensive trophic chains and rich biodiversity. Their soils are waterlogged for some portion of the year resulting in anoxic conditions which makes them unlike other ecosystems (Mitsch and Gosselink 1993). The “no net loss” policy, enacted in January of 1989, set a goal for the United States to stop the decrease in wetland area occurring throughout the country (Salzman and Ruhl 2006). “No net loss”, along with increased public knowledge, has led to the undertaking of the Comprehensive Everglades Restoration Plan (CERP), one of the largest wetland restoration efforts ever.

As a part of the restoration effort, certain species have been identified as indicator species of Everglades’s health. The snail kite (*Rostrhamus sociabilis*) is one of these species because it is completely dependent on the South Florida watershed for its entire life cycle (Sykes et al. 1995). The fate of the snail kite is inextricably tied to the health of the Everglades. The attempt to restore the Everglades will be aided by increased knowledge of the habitats necessary for a healthy, proliferating snail kite population. A robust proliferating snail kite population would be a performance measure of restoration success. The snail kite is also an endangered species and as outlined in the Endangered Species Act of 1973, Federal agencies are responsible for protecting and conserving the ecosystems that endangered species depend on. Federal agencies must also cooperate with State and local agencies to resolve water resource issues in concert with conservation of endangered species.

To help meet these aims, this study will track the loss of wet prairie, the preferred foraging habitat of the snail kite (Karunaratne et al. 2006). The proposed reason for this loss of critical habitat is a change in the hydrologic regime due to impoundment. Water Conservation Area 3A (WCA3A) in South Florida was historically very important to the snail kite, so efforts to investigate this link have been focused there (Kitchens et al. 2002). The Water Conservation Areas are also perfect candidates for restoration and critical spatially and functionally to the water management of the Everglades. It is hoped that an improved management strategy for WCA3A and the snail kite will be produced as a result of this study.

Background

Wetlands

It is estimated that there are 7 to 10 million km² of wetlands on Earth which is about 5 to 8 % of the Earth's land surface (Mitsch and Gosselink 2007). About 50% of endangered species, 80% of the U.S. breeding bird population and 50% of protected migratory birds depend on wetlands for their survival. Wetlands also moderate the effects of floods and storms, and improve water quality while recharging the aquifer. Over half the wetlands in the U.S. have been lost and of the total wetlands left 95% are freshwater wetlands (Dahl 2000). The U.S. currently has a no-net loss policy for wetlands, which means that for all wetlands destroyed, new wetlands have to be created or degraded wetlands must be restored. (Dahl 2000) estimated that about 23,675 hectares of wetlands are lost annually. The most important factor in wetland restoration is restoration of the natural hydrologic conditions. Hydrologic conditions affect abiotic factors like soil type and nutrient availability, which in turn determine the flora and fauna that will inhabit a wetland. Hydrology encompasses a variety of parameters, such as hydroperiod, seasonal pulses, flow pattern, and retention times. Hydroperiod is the hydrologic signature of each wetland, which is determined by the seasonal water level pattern of a wetland.

The rise and fall of surface and subsurface water is characteristic for each type of wetland and can be called its hydroperiod (Mitsch and Gosselink 1993). This study will look at the link between hydrology and vegetative communities in the Everglades.

The Everglades

The Everglades formed 5000 years ago in a time of rapid rise in sea level that created the current hydrologic conditions that have been changing ever since (Gunderson and Pritchard 2002). From the regional landscape level the Everglades appear to have a uniform topological gradient and vegetative type. At the local level, however, it is a changing and dynamic mosaic driven by topological features such as water depth, hydroperiod, and geology (rock, peat depth and type, or sand). Since the early 1900's the South Florida freshwater wetlands have been reduced from 3.5 million hectares to about 1.8 million hectares and have been impounded by about 2000 km of dikes and canals (Kitchens et al. 2002). In recent years there has been a massive effort to restore the Everglades and protect the endangered species that are native to it. In order to restore the Everglades, however, a comprehensive monitoring and management plan must be developed and our understanding of the dynamic Everglades system must be improved.

In order to restore what remains of the Everglades, the key ecological driving forces need to be determined (Sklar et al. 2002). As a result of impoundment caused by the building of dams, dikes, and canals, the vegetative communities and subsequently the fauna of the Everglades are being altered. There is a flattening of the topography created by the slow flow, about 2 cm/km, of the watershed before impoundment (Leach et al. 1972). Over time, the Everglades are becoming a monoculture due to lack of flow and lack of variation in hydrology. An ecosystem needs all of the historical natural diversity of abiotic processes to survive disturbance (Gunderson and Holling 2002). The Everglades have lost biotic and process

diversity needed to support the native flora and fauna through disturbances like drought, fire, flood, and hurricanes.

Flora and Fauna of the Everglades

Seven physiographic landscapes comprised the Everglades before drainage. Three of these landscape types have been lost to development and the largest remnant of the wet prairie-slough-tree island-sawgrass mosaic can be found in Water Conservation Area 3A (WCA3A) (Davis et al. 1994). Of these habitats wet prairie has been identified as the type most used for foraging by the endangered snail kite (Karunaratne et al. 2006). Generally wet prairies are found in areas covered by surface water for much of the year and where the water level is not more than 30.48 cm below ground level except in extreme drought. They frequently form transition zones between the sawgrass communities and the slough communities. Some of the indicator species for wet prairies are beak rush (*Rhynchospora spp.*), madiencane (*Panicum spp.*) and spike rush (*Eleocharis spp.*). Sloughs are shallow, from a few centimeters to a meter or two deep, natural channels, which typically have water most of the year. They are characterized by white water-lily (*Nymphaea odorata*) and bladderwort (*Utricularia*). Sawgrass strands are typically drier communities composed primarily of *Cladium jamaicensis* (Loveless 1959).

Changes in hydrology (source, timing, duration, and depth of water) change plant communities (Mitsch and Gosselink 1993). Human induced development and management reduces the natural variation and extremes in hydroperiod. Hydrology and fire are the dominant influences on the current condition of plant communities. Both hydrology and fire have been altered by past human activities and are under management control so they are central parameters in future management schemes. Hydrology influences primary production, decomposition, and export of particulate organic matter. Nutrient cycling and nutrient availability are both significantly influenced by hydrologic conditions.

WCA3A South has a total area of about 62,000 hectares and is bounded by Tamiami Trail (Hwy 41) to the south, Alligator Alley (I-75) to the north, Big Cypress National Preserve to the west, and Water Conservation Area 3B to the east. WCA3A was the main reproductive unit for the snail kite, which is an endangered species whose U.S. population is restricted to the South Florida freshwater wetlands. The snail kite feeds mainly on apple snails (*Pomacea paludosa*) and forages most effectively in a wet prairie habitat where it is easier for them to see the snails when they crawl up the emergent vegetation to breathe (Kitchens et al. 2002). There is a matrix of freshwater habitats in the study area from relatively dry tree islands and sawgrass strands to wet prairies and deep-water sloughs.

It is believed that the foraging and nesting habitat of the snail kite is decreasing in extent and quality, and that this is contributing to a population decline. In recent years wet prairie communities used for foraging by have been transforming to slough communities because of excessive hydriperiods (Kitchens et al. 2002, Zweig and Kitchens 2008a). Before this trend, the water management in the 70's, 80's, and 90's kept WCA3A drier than it historically was. During this time period there was a 25% loss in prairie and slough and a correlated gain in sawgrass (White 1994). Essentially, management has been counter to conditions necessary for wet prairie communities for the past 40 years by moving from one extreme to another. Recognizing the magnitude of this critical habitat lost and understanding the reason it was lost, will lead to better management of the Everglades. A better management plan will lead to a more successful restoration attempt. There have been a number of descriptive studies describing this trend from wet prairie to slough (Wood and Tanner 1990, David 1996) but this study will quantify it for the first time.

CHAPTER 2 METHODS

Study System

Water Conservation Area 3A (WCA3A), the largest intact remnant of ridge and slough landscape left in the Everglades, is located in the South Florida watershed as shown in Figure 2-1. The Everglades formed just 5,000 years ago (Gleason et al. 1984), but have been drastically changed in the last 100 years by impoundment for development. WCA3A South has a total area of about 62,000 hectares and is bounded by Tamiami Trail (Hwy 41) to the south, Alligator alley (I-75) to the north, Big Cypress National Preserve to the west, and Water Conservation Area 3B to the east. There is a matrix of freshwater habitats in WCA3A South ranging from relatively dry tree islands and sawgrass strands to wet prairies and deep-water sloughs. The plots for this study are located in Southern WCA3A. The Study Area does not extend all the way to Alligator Alley but stops in central WCA3A. This central area of 3A is referred to in this thesis as north as it is the location of the northern study plots.

Sampling Design

This is an ongoing study for which biannual sampling has been carried out since November of 2002. The sampling took place in twenty 1 km² plots which were established in a stratified random manner over southern WCA3A (Figure 2-1). Three gradients were considered when deciding plot placement: snail kite nesting density, impoundment effects, and ground elevation. Snail kite nesting activity and density was determined from nesting records for the past six years. The impoundment effect relates to the differing hydrology of central and south WCA3A. Water was not always deeper in southern WCA3A, the deeper water is a result of impoundment, associated with the Tamiami Trail. By placing half of our plots in central 3A in relatively intact ridge and slough habitats with sheet flow and the other half in southern 3A it

was possible to compare vegetation changes in a relatively unimpounded wetland to those in a mostly impounded system. The last gradient considered was peat depth with little to no peat in the west and gradually deeper peat to the east (Powers 2005).

Sampling

In each plot 2 or 3 belt transects were placed perpendicular to the plant community zonation. Transect varied in length because they started in one community and moved into at least one more if not many more. For example a typical transect might have run from a sawgrass strand through a wet prairie to end in a slough. A belt transect consisted of three pairs of sample transects and extended through two or three plant communities. Transects varied in length because they had to start in the middle of a clearly definable reference community and extend until they were in the middle of another clearly definable reference community. There were three 1 meter wide paths/walkways between the sampling transects and the distance between the centers of the walkways/transects was 4 meters. An aerial view of a typical belt transect can be seen in Figure 2-2. Samples, taken every three meters along a single transect, consisted of all the rooted vegetation in a 0.25 m² area. Biannual sampling has taken place since 2002, once at the end of the dry season in April or May and once in October or November at the peak of the standing crop or end of the wet season. The transect within the belt transect to be sampled was selected randomly by choosing a letter C to N excluding any letters that had already been sampled. For example, samples C, D, E, and F were on the same transect but C and D were on one side of the transect and E and F were on the other side. C and E were offset 1.5 meters from D and F and in this way with just 3 transect lines, 12 different sampling events could occur (Powers 2005).

Hydrology

To quantify the independent variables associated with hydroperiod, water levels have been monitored since 2002. There is spatial variability in rainfall so data from 17 wells spread throughout south WCA3A at our sampling plots was used. Water depths at our sampling sites can be hindcast back using wells in place before 2002 to look at the historical hydrology of the site (Conrads et al. 2006). The hydrologic variables thought to be of the most importance in determining which seasons are wet and which are dry are minimum, maximum, and mean seasonal water depths as well as the duration of the wet or dry event (calculated by taking the percent of time water levels fell in the lower quartile of water levels for that season and the percent of time water levels fell in the upper quartile of water levels for that season). Lower and upper quartiles for wet and dry seasons were determined by combining all depths for a season from 1992 to 2007 and dividing them into quartiles. Using quartiles made it possible to obtain an idea of inundation and exposure time, which could not be obtained from a minimum or a maximum, and has a significant effect on vegetative communities. The dry season was defined as occurring from November to June and the wet season was from June to November.

Water levels back to 1992 were used because it was the beginning of the newest hydrological era in WCA3A (Figure 2-3). Hydrologic alterations of the natural system began in South Florida around the turn of the century. A consequence of these alterations is the management or regulation of the natural system for a variety of uses. Water levels in WCA3A were not recorded until 1953 but from that time on changes can be seen in regulation schedules starting with a relatively dry era in the 1950's and getting progressively wetter as the needs of wildlife began to be considered. The hydrological eras in WCA3A do not correspond to natural droughts or floods lasting 15 to 20 years but to changes in management priorities and consequent changes in regulation schedules.

Data Analysis

There were several steps in the analysis to look at the transition probabilities of various Everglades vegetative communities and the factors driving the transitions. The first step was to use a multivariate community classifying technique in program PC-ord to classify the communities in WCA3A at each sampling occasion. Hydrological variables were used to cluster water levels for each season into categories of dry, normal, and wet time periods. This data was then put into a matrix for use in program MARK which estimates the transition probabilities for the vegetative communities in WCA3A.

Multivariate Community Classifying Analysis

The vegetation sampled for this study had a wide variety of growth forms from *Cladium Jamaicense* with a few blades per sample, but considerable biomass per blade, to *Eleocharis elongata* with many stems per sample, but low biomass per stem. To deal with this problem a relativizing index termed importance values (IV) from McCune and Grace (2002) was used. Calculating IV helps when high density and low biomass species need to be compared to low density high biomass species. It was important to know the relative importance of each species in each *a priori* community so that each community with its specific ratio of importance values could be clustered to find which communities were similar to each other.

To calculate IV the first step is to determine the relative density and biomass for each species present in a community group. Relative density is calculated by taking the density of a species in a particular 0.25 meter sample and dividing it by the sum of the density of all the species in the plot. Relative biomass is calculated in the same way using the biomass of an individual species in an individual sample and dividing it by the sum of the biomass of all the species in the plot. IV is simply relative density plus relative biomass divided by 2 and then

multiplied by 100 (McCune and Grace 2002). Each species in each sample has an IV which can be grouped with the IVs of the same species in each *a priori* designated community.

Using the multivariate statistics program, PC-ORD (McCune and Grace 2002), a hierarchical, agglomerative cluster analysis was done using the IV for each species from each of these communities for each sampling occasion to determine if the communities remained in the same cluster or moved to a different one at each sampling occasion. Sixty six *a priori* community groups were used in the cluster analysis with about 9 sampling occasions in each *a priori* community group for a total of 477 communities for PC-ord to cluster. The distance measure used to cluster was Sorensen or Bray-Curtis which is shared abundance divided by total abundance. This is a good distance measure for non-negative proportion (IV) data (McCune and Grace 2002). The group linkage method was flexible beta which is combinatorial and flexible with respect to space.

The optimal number of clusters was chosen using an indicator species analysis which also allowed us to identify the most important species in each cluster. A species which has an indicator value of 100 is a perfect indicator of that group or occurs exclusively and always in that group. Indicator values of 0 mean no indication. Indicator values were also tested for statistical significance using 1000 Monte Carlo runs. If groups are too finely divided, their indicator values will be low and if groups are too large, their internal heterogeneity will reduce indicator values. Indicator values were calculated for each species at 20 clustering levels (from 1 to 20 clusters) and the p-values for all species at each clustering level were averaged. The cluster level with the smallest average p-value is the most informative and best fitting (McCune and Grace 2002). The clusters were then designated as wet prairie, slough, sawgrass, or tree island using our knowledge of the species compositions of each of these community types.

Hierarchical Clustering Analysis to Categorize Wet and Dry years

Water levels from the 17 wells placed in WCA3A near the sampling sites were hindcast to 1992 using artificial neural networks (Conrads et al. 2006). Figure 2-3 explains why water levels from 1992 to present are considered to be in the same era. The hydrologic variables from the hindcast water levels that were thought to be of the most importance in determining which years were wet or dry were; minimum, maximum, and mean seasonal water depths as well as a duration of high and low water proxy which was the percent of time water levels fell in the lower quartile of water levels for that season and the percent of time water levels fell in the upper quartile of water levels for that season. These values were calculated for each wet and dry season and run through separate hierarchical cluster analyses; one for wet seasons and one for dry seasons.

The hierarchical cluster analysis was run in program R using a set of dissimilarities for the objects being clustered. When R clustered, it initially assigned each object to its own cluster and then used an algorithm to proceed iteratively, at each stage joining the two most similar clusters, continuing until there was just a single cluster. At each stage distances between clusters were recomputed by the Lance–Williams dissimilarity update formula according to the complete clustering method. The complete clustering method finds similar clusters. The algorithm used in `hclust` command in R orders the subtrees so that the tighter cluster is on the left (the last, i.e., most recent, merge of the left subtree is at a lower value than the last merge of the right subtree). The results from these cluster analyses allowed us to classify each wet season as either wet or normal and each dry season as either dry or normal.

Multistate Modeling

Only wet prairie and slough community states from the multivariate community classifying analysis were used in the input matrix for program MARK. For each sampling occasion each a

priori community was labeled either P for wet prairie or S for slough based on the results of the community cluster. Each *a priori* community was also grouped as either N or S depending on whether it was located in the north or south of our sampling area. This input matrix was put in MARK where it was possible to classify each sampling occasion as either wet, normal, or dry by assigning it a parameter. Models were run to test for a north/south effect, a seasonal effect, and a wet/dry time period effect.

Likelihood based multistate models were used to estimate transition probabilities among vegetative community states. I defined ψ^{AB} as the probability that a community in state *A* at time *t* is in state *B* at time *t*+1. In our application, there were two states; slough communities denoted *S* and wet prairies communities denoted *P*. Communities had two options from one sampling occasion to the next, they could start as wet prairie (*P*) and persist as wet prairie (*P*) or transition to slough (*S*). Accordingly if they started as sloughs (*S*) they could persist as sloughs (*S*) or transition to wet prairies (*P*). I wanted to know what the probabilities of these transitions were for each sampling occasion and what environmental drivers could be linked to these transitions.

Four environmental factors that could influence transition probabilities were considered. The effect of wet and dry season on ψ was denoted SEAS, and, by extension, the model that included a seasonal effect on ψ was denoted ψ (SEAS). We also included wet and dry years as a factor (denoted WDyr). Models that had three groups of years (WDyr3cat), wet, dry, and normal were used, as were models with just two groups (WDyr2cat), wet or dry, to determine the effect of wet and dry years. A covariate (covar) of percent of time water levels were in the lower quartile of all water levels for that season was also used to test for the effect of wet and dry years. The effect of the spatial location of the study site, north versus south, was denoted (NS) and can be considered an indicator of impoundment effects. In addition, we considered two

temporal structures: time variation denoted (t , which assumed that ψ vary over time), and no time variation denoted (“.”, which assumed that ψ remain constant over time). Finally we allowed some of the factors to interact (the interaction between two factors was denoted “*”, for instance model ψ (WDyr*NS)).

In general when running models in MARK the sin link function was used because provides constraints that keep the real parameters in the $[0,1]$ interval, yet allows the number of parameters to be correctly estimated. The identity matrix was used for all the models except the models containing real covariates (covar) when the design matrix had to be used. When models with covariates were run the logit link function was used. The logit link function is used with design matrices and real covariates because the logit link function is monotonic and the sin link function is not. This means that multiple values of the sin function will produce exactly the same transformation ($\sin(x)$, $\sin(x+2\pi)$, and $\sin(x+4\pi)$ all produce the same transformation) which is not true for the logit function (Cooch and White 2008).

All link functions are transformations of probability such that the transformed probability changes from being either 0 or 1 (P or S) to $-\infty, \infty$. They make it so that the probability of an event (transition) is a linear function of a vector of explanatory variables. Link functions are essentially performing a regression (in the case of the logit link function a logistic regression) and the resulting parameters are the estimates of the slope in the linear model. Logit link functions have problems estimating parameters that are close to 0 or 1. For this reason the sin link function should be used when possible but when the design matrix and therefore the logit link function must be used and there are problems with the transitions from a stratum not summing to one, mlogit should be used to constrain the parameters to sum to 1. It was not

necessary in my analysis to use mlogit as the transitions from a stratum summed to one because there were only 2 transitions (Cooch and White 2008).

The parameters for survival (S) and detection (p) were both fixed to 1 as we were not trying to estimate those quantities. In our application survival and detection of plant communities were set to 1 because communities were always detected and transitioned to one of the two states but never “died”. The alternate optimization method used for these models was simulated annealing which made sure that the global maximum and minimum and not the local maximum and minimum were found (Cooch and White 2008).

Model selection

We developed a set of candidate models in order to evaluate our *a priori* hypotheses. Each model corresponded to a mathematical formulation of our hypotheses. For example $\Psi^{[ps \neq sp]}(WDyr3cat)$ means that the probability of transitioning from wet prairie to slough is not equal to the probability of transitioning from slough to wet prairie and that this shift is a function of wet, normal, and dry time period classifications. We used Akaike Information Criterion (AIC) to select the models that provided the most parsimonious description of the variation in the data (i.e., model with the lowest AIC) (Burnham and Anderson 2002). Adding parameters to a model increases the fit of the model but reduces the precision of parameter estimates. AIC values account for this by penalizing the better fit or lower deviance of more parameterized models for the reduced precision of the estimates themselves.

$$AIC = -2\ln(L) + 2K,$$

L is the model likelihood which goes up as fit gets better and makes the AIC go down. K is the number of parameters which causes the AIC to increase or get worse.

We used AICc weight (w) as a measure of relative support for each model. Values of w range from 0 to 1 with 0 indicating no support from the data, and 1 indicating maximum support

(Burnham and Anderson 2002). We also presented $\Delta AICc$ ($\Delta AICc$ for the i th model was computed as $AICc_i - \min(AICc)$, see Burnham and Anderson 2002).

Effect size

Effect size is used to determine whether the size of the difference between two estimates is significant. The difference between two estimates of transition probabilities were computed by calculating the arithmetic difference between these estimates to get an effect size (ES). The difference between the two estimates of transition probabilities were considered to be statistically significant when the 95% CI of the ES did not overlap 0 (Cooch and White 2008).

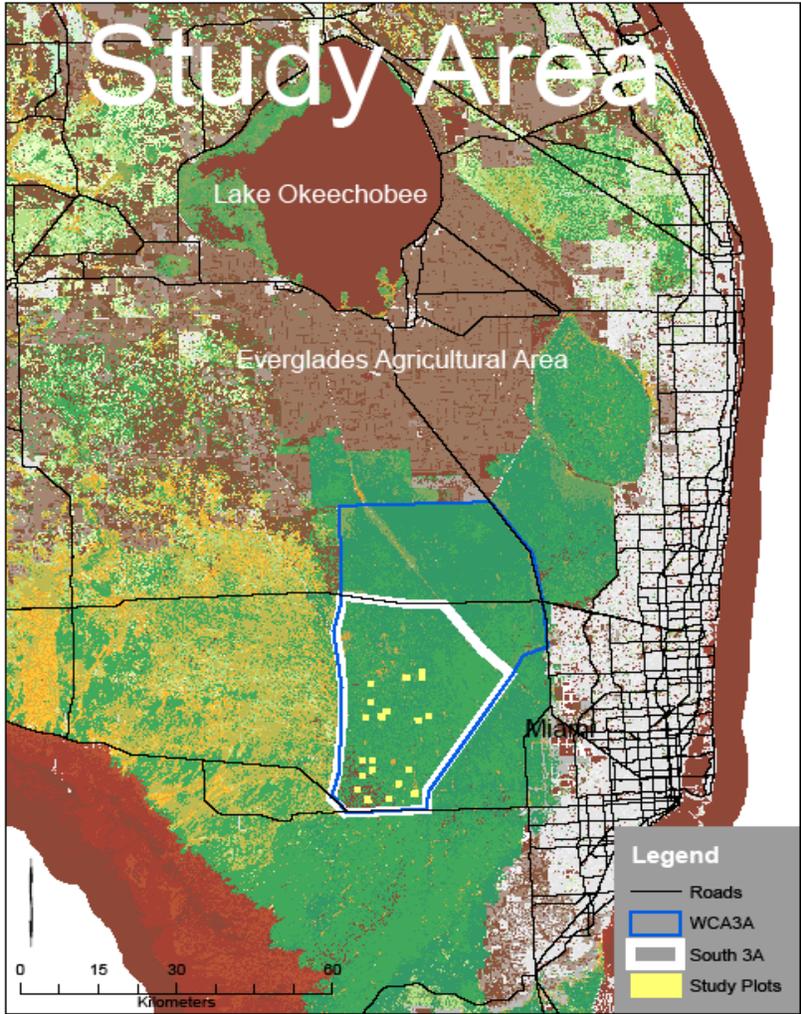


Figure 2-1. Location of WCA3A and the study plots.

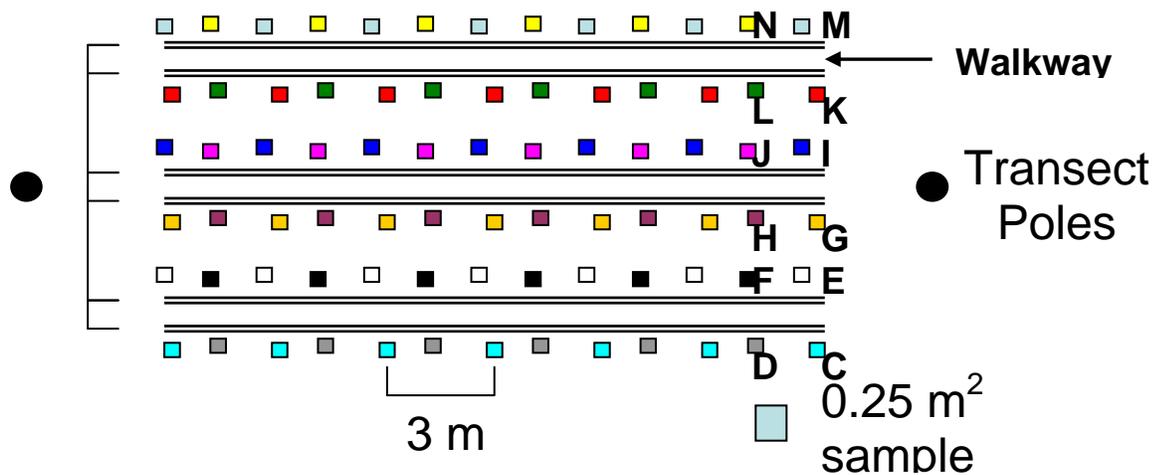


Figure 2-2. Aerial schematic of belt transect sample collection. A belt transect consists of 3 sets of four sample transects, labeled C through N. A 1 m wide walkway is exists between each pair of sample transects. The distance between the center of a walkway and the center of the next walkway is 4 m. The transect to be sampled on a particular date is randomly selected (see Belt Transect field book). All the vegetation rooted in 0.25 m² plots will be collected every 3 m along the transect that is sampled on that date. The second time that transect is sampled the plots are offset 1.5 m from the previous starting point. Poles have been placed in the field at the beginning and end of transect G/H/I/J to guide future placement of the other transects. Transect E is always to be positioned to the left of the G/H/I/J transect poles from the slough end (start) of the transect.

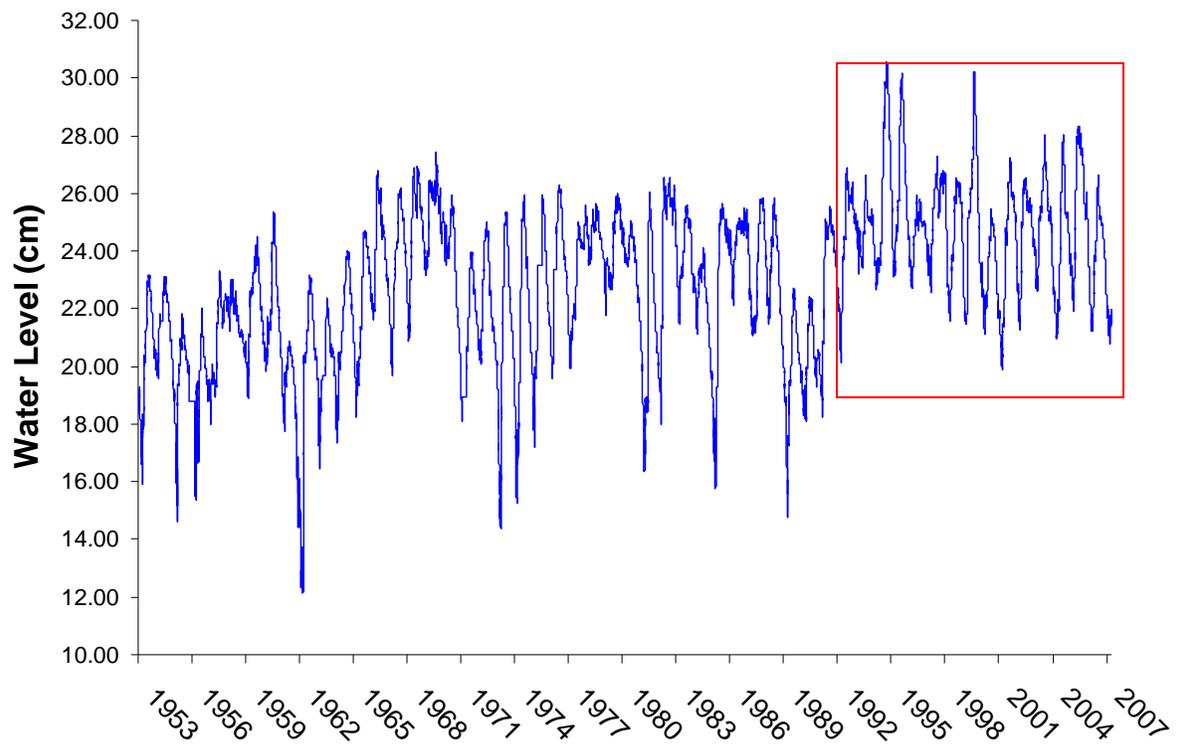


Figure 2-3. Water levels at S65 and S64: a new hydrological era began in 1992.

CHAPTER 3
ESTIMATING TRANSITION PROBABILITIES AMONG EVERGLADES WETLAND
COMMUNITIES USING MULTISTATE MODELS

Introduction

South Florida freshwater wetlands have been reduced from 3.5 million hectares to 1.8 million hectares in extent and have been impounded by 2000 km of dikes and canals as a result of agricultural and urban development in the last hundred years (Mitsch and Gosselink 1993, Kitchens et al. 2002). In order to reverse some of the adverse impacts of impoundment one of the most ambitious ecosystem restoration projects ever, the Comprehensive Everglades Restoration Project (CERP) has been undertaken (RECOVER 2005). One of the stated goals of this project is to promote conditions that will increase the abundance and diversity of native species by regulating water in the system (RECOVER 2005). In order to accomplish this goal, it is critical to develop reliable models of how hydrology affects the dynamics of plant communities in the Everglades. Unfortunately, there is very little information in this critical area. To address this issue, our study will present a comprehensive framework for investigating multiple competing hypotheses about the factors governing transition probabilities among vegetative community states in the Everglades. This framework allows for the calculation of robust estimates of transition probabilities and estimates of uncertainty (process and sampling variance associated with these estimates). The estimation of various types of uncertainty is particularly important for making informed decisions for conservation (Martin et al. 2008c).

Our study focused on the transition probabilities between wet prairie and slough community states because of their importance to the endangered snail kite (*Rostrhamus sociabilis*) population, which has been selected as one of the key performance measures of the ongoing restoration activities associated with CERP (RECOVER 2005, Martin et al. 2007a, Martin et al. 2008c). Wet prairies are defined as areas that are covered in surface water for much

of the year and where the water level does not drop more than a foot below ground level except in extreme drought (Loveless 1959). They frequently form transition zones between drier sawgrass communities and wetter slough communities. Wet prairie habitat is ideal for snail kite foraging because of its sparse emergent vegetation. Sparse emergent vegetation enables the snail kite to easily see its primary food source, the apple snail, when it emerges to breathe, making wet prairie the habitat in which they forage most effectively (Kitchens et al. 2002, Karunaratne et al. 2006). Some of the indicator species for wet prairies are beak rush (*Rhynchospora spp.*), maidencane (*Panicum spp.*), and spike rush (*Eleocharis spp.*). Sloughs are shallow, a few inches or feet deep, natural channels, that have water most of the year. They are characterized by white water-lily (*Nymphaea odorata*) and bladderwort *Utricularia* (Loveless 1959).

The primary objective of our study was to provide the first estimates of transition probabilities between wet prairie and slough communities using multistate models. Although a number of authors (Kolipinski and Higer 1969, McPherson 1973, Dineen 1974, Alexander and Crook 1975, Zaffke 1983, Wood and Tanner 1990, Davis et al. 1994, David 1996) have proposed verbal or conceptual models of how these transitions may proceed, there are few mechanistic mathematical models that can translate consequences of environmental variation or management actions on community dynamics in the Everglades. Here we use likelihood-based multistate models to estimate transition probabilities among wet prairie and slough communities. This type of model is now commonly used to estimate movement probabilities of organisms among discrete geographic units or physiologic states (Blums et al. 2003, Martin et al. 2007b). However, these models have rarely been used to evaluate multiple competing hypotheses about factors governing the dynamics of plant communities.

Hypotheses and Predictions

Hypothesis 1: Wet and Dry Seasons Influence the Conversion of Sloughs and Wet Prairies

Precipitation is the main route by which water enters the Everglades ecosystem (Duever et al. 1994) and the dominant source of natural surface freshwater in this part of the Everglades. Rainfall in southern Florida is highly seasonal with 60% occurring from June to September and only 25% occurring between November and April. The result of this rainfall pattern is a hydroperiod that has strong effects on vegetation composition and structure and which exhibits natural periodicity or substantial and predictable within year seasonal variation (White 1994) (Figure 3-1). The vegetation of the Everglades is adapted to this seasonal environment in its rhythms of production, decomposition, mortality, and reproduction. Therefore, I predict the transition probabilities from wet prairie communities to sloughs to be greater during wet seasons which occur in the interval from June to November. In contrast, I predict the transition probabilities from slough communities to wet prairie communities to be greater during dry seasons which occur in the interval from November to June.

Hypothesis 2: Wet and Dry Years Substantially Influence the Process of Conversion of Sloughs and Wet Prairies

The hydroperiods of most wetlands vary significantly from year to year with 10 to 20 year cycles (Mitsch and Gosselink 2007) (Figure 3-1). In South Florida wetlands, precipitation which has a significant impact on hydroperiod has high interannual variability with documented extremes from 86 cm to 224 cm for the period from 1951 to 1980 (NOAA 1985, Obeysekera et al. 1999). The El Nino Southern Oscillation is responsible for much of the variability in rainfall (Puckridge et al. 2000), but it is difficult to detect a clear interannual wet dry cycle in South Florida as hurricanes are frequently the cause of wet years. Extreme values of precipitation are encountered in the Everglades on a time period of 3 to 10 years. With this in mind, I predict the

transition probabilities from slough communities to wet prairies to be greatest during dry intervals. In contrast, I predict the transition probabilities from wet prairie to slough communities to be greater during wetter intervals.

Hypothesis 3: Probabilities of Transition between Sloughs and Wet Prairies are Substantially Influenced by Impoundment

Impoundment has eliminated sheet flow from the Everglades and caused excessive ponding in the southern ends of the Water Conservation Areas (WCAs) while over-draining the northern ends (Dineen 1972, Light and Dineen 1994). Impounded wetlands have vertical rather than lateral expansions/retractions which cause a loss in intra and inter wetland heterogeneity (Kitchens et al. 2002). This is causing conversion from wet prairie and sawgrass communities to deeper, more aquatic slough habitats in the southern area of the WCAs due to prolonged hydroperiods (Kitchens et al. 2002). In southern sites, I predict there will be more conversion from wet prairies to sloughs and less conversion from sloughs to wet prairies. In the northern sites, I predict less conversion from wet prairies to sloughs and more conversion from sloughs to wet prairies.

Methods

Study Area and Sampling Methods

Our study was located in the southern portion of Water Conservation Area 3A (WCA3A) in the Everglades of South Florida, USA (Figure 3-2). In the fall of 2002, twenty 1 km² plots were placed across three landscape gradients: an east-west peat depth gradient, an artificial north-south water depth gradient, and a Florida snail kite nesting activity gradient in a random stratified manner. Two or three belt transects were placed in each plot perpendicular to ecotones or moving from one *a priori* community type (slough, sawgrass, tree/shrub island, *Typha*, and wet prairie) into another. Samples were collected every 3 meters along belt transects twice a year

at the end of the dry (May/June) and wet (November/December) seasons. A sample is a 0.25 m² area from which all standing biomass has been clipped at peat level including any submerged aquatic plants. The 0.25 m² samples represent pseudorepeated measures, as destructive samples were taken and I could not resample the exact location. There were eight sampling events from November 2002 to June 2006 during which 33,501 samples were taken. The samples were sorted by species, counted, dried, and weighed. In addition, 17 water level monitoring wells were placed in the plots to take twice daily water level readings.

Data Analysis

Multivariate analysis to classify communities

The relative density and biomass for each species present in a plot were calculated to determine an importance value (IV) for each species in each *a priori* community in the plot. Relative density or biomass is calculated by taking the sum of the density or biomass for each species and dividing it by the sum of the density or biomass of all species in the plot. IV is simply relative density plus relative biomass divided by 2 and then multiplied by 100. IV is a relativizing index that helps to account for high density and low biomass species and high biomass low density species (McCune and Grace 2002).

A priori community designations were used to group each 0.25 m² sample into communities for each plot. Using the multivariate statistics program, PC-ORD (McCune and Grace 2002), a hierarchical, agglomerative cluster analysis was done using IV from each of these communities for each sampling occasion to determine if the communities remained in the same cluster or moved to a different one. The optimal number of clusters was chosen using an indicator species analysis which also allowed us to identify the most important species in each cluster. The clusters were then designated as wet prairie, slough, sawgrass, or tree island using our knowledge of the species compositions of each of these community types.

Hierarchical clustering analysis to categorize wet and dry years

Water levels at our sampling sites were hindcast using artificial neural networks to look at the historical hydrology of the site (Conrads et al. 2006). As the newest hydrological era in WCA3A began in 1992, water levels from the past 16 years have been featured in Figure 3-3 and used in the cluster analysis. The hydrologic variables that were thought to be of the most importance in determining which years were wet or dry were; percent of time water levels fell in the lower quartile of water levels for that season, minimum seasonal water level, percent of time water levels fell in the upper quartile of water levels for that season, maximum seasonal water level, and mean seasonal water depth. These values were calculated for each wet and dry season since 1992 and run through separate agglomerative cluster analyses; one for wet seasons and one for dry seasons. This allowed us to classify each wet season as either wet or normal and each dry season as either dry or normal.

Multistate modeling

Likelihood based multistate models were used to estimate transition probabilities among plant community states. I defined ψ^{AB} as the probability that a community in state A at time t is in state B at time $t+1$. In our application, there were two states; slough communities denoted (s) and wet prairies communities denoted (p) (Figure 3-4). I considered four factors that could influence transition probabilities. The effect of wet and dry season on ψ was denoted $SEAS$, and, by extension, the model that included a seasonal effect on ψ was denoted $\psi(SEAS)$. I also included wet (W) and dry (D) years (yr) as a factor (denoted $\psi(WDryr)$). Models that had three categories ($\psi^{[ps \neq sp]}(WDYr3cat)$) for years, wet, dry, and normal were used, as were models with just two categories ($\psi^{[ps \neq sp]}(WDYr2cat)$), wet or dry, to determine the effect of wet and dry years. A covariate ($cov\ ar$) of percent of time water levels were in the lower quartile of all water

levels for that season was also used to test for the effect of wet and dry years. The effect of the spatial location of the study site, north versus south, was denoted ($\psi(NS)$) and can be considered an indicator of impoundment effects. In addition, I considered two temporal structures: time variation denoted (t , which assumed that ψ vary over time), and no time variation denoted (“.”, which assumed that ψ remain constant over time). I allowed some of the factors to interact (the interaction between two factors was denoted “*”, for instance model $\psi(WDryr * NS)$). Finally, for all models I assumed that transition probabilities ψ^{ps} and ψ^{sp} were either identical (denoted $\psi^{[ps=sp]}$); or were different (denoted $\psi^{[ps\neq sp]}$).

I used program MARK to develop and analyze multistate models (White and Burnham 1999).

Model selection

I developed a set of candidate models in order to evaluate our *a priori* hypotheses. Each model corresponded to a mathematical formulation of our hypotheses. I used Akaike Information Criterion (AIC) to select the models that provided the most parsimonious description of the variation in the data (i.e., model with the lowest AIC) (Burnham and Anderson 2002).

I used AICc weight (w) as a measure of relative support for each model. Values of w range from 0 to 1 with 0 indicating no support from the data, and 1 indicating maximum support (Burnham and Anderson 2002). I also presented $\Delta AICc$ ($\Delta AICc$ for the i th model was computed as $AICc_i - \min(AICc)$, see Burnham and Anderson 2002).

Effect size

Effect size (ES) was calculated by taking the arithmetic difference between the two estimates of transition probabilities from the same model that were being compared. The

difference between the two estimates of transition probabilities was considered to be statistically significant when the 95% CI of the ES did not overlap 0 (Cooch and White 2008).

Results

Multivariate Analysis to Classify Communities

The indicator species analysis, based on hierarchical, agglomerative cluster analysis of the Everglades WCA3A vegetation monitoring data, indicated that there were eleven communities/clusters (Figure 3-5). Using our knowledge of the system, I determined that there were 2 slough, 3 wet prairie, 4 sawgrass strand, and 2 tree island communities. Communities that were not initially classified as slough or wet prairie were removed from the data set used in the multistate analysis. There are several reasons why I removed the other communities from the data set. Most importantly, the data available would not have supported models with more than two vegetation states. Secondly, slough and wet prairie are the community types that are most relevant to management of snail kite habitat. Finally, one motivation of our study is to provide models of system behavior for the adaptive management of Everglades and WCA3A and most decision making tools require simple system models (e.g., Stochastic Dynamic Programming, (Martin et al. 2008c). Indeed, using more parameterized models (models with more states) would substantially increase the state space and, therefore, would increase the difficulty of solving the decision problem.

Hierarchical Clustering Analysis to Categorize Wet and Dry Years

The agglomerative hierarchical cluster analysis of all dry seasons since 1992 found that the dry seasons of water years 1992, 2000, 2001, 2004, and 2006 clustered together and were dry. The dry seasons of water years 1993, 1994, 1995, 1996, 1997, 1998, 1999, 2002, 2003, and 2005 clustered together and could be considered wet or normal (Figure 3-6). The wet seasons of water years 1995, 1996, 1998, 2000, 2004, and 2006 clustered together and were wet. The wet seasons

of water years 1993, 1994, 1997, 1999, 2001, 2002, 2003, 2005, and 2007 clustered together and were normal to dry (Figure 3-7). This led to the designation of two dry time periods November 2003 to June 2004 and November 2005 to June 2006 and two wet to normal time periods November 2002 to November 2003 and November 2004 to November 2005. This designation could be further broken down to include two wet time periods June 2003 to November 2003 and June 2005 and November 2005 and two normal time periods November 2002 to June 2003 and November 2004 to June 2005 for a total of three water categories: wet, dry, and normal.

Multistate Modeling

The most parsimonious model based on AIC weight was model $\psi^{[ps \neq sp]}(WDyr3cat)$ (AIC (w)=0.685) (Table 1). This model is a mathematical formulation of the hypothesis that wet and dry years influence transition probabilities between slough and wet prairie communities. Based on this model, I found that estimates of ψ^{ps} were greater during normal years ($\psi^{ps}=0.119$ (SE=0.050)) than during dry years ($\psi^{ps}=0$ (SE=0)) and wet years ($\psi^{ps}=0.042$ (SE=0.041)). The difference in ψ^{ps} between normal and dry years was statistically significant (ES=0.119 (95%CI= 0.019 to 0.219)), but it was not statistically significant between normal and wet years (ES=0.077 (95%CI= -0.052 to 0.206)), nor between wet and dry years (ES=0.042 (95%CI= -0.039 to 0.123)). Also, based on model $\psi^{[ps \neq sp]}(WDyr3cat)$, I found that that estimates of ψ^{sp} were greater during dry years ($\psi^{sp}=0.181$ (SE=0.067)) than during wet years ($\psi^{sp}=0.111$ (SE=0.052)) and that there were no transitions from sloughs to wet prairies during normal years ($\psi^{sp}=0$ (SE=0)). The difference in ψ^{sp} between normal and dry years was statistically significant (ES=0.181 (95%CI=0.047 to 0.316)), as was the difference between normal and wet years (ES= 0.111 (95%CI=0.006 to 0.216)). However, the difference in ψ^{sp} from wet to dry

years was not statistically significant (ES=0.071 (95%CI= -0.099 to 0.241)) (Figure 3-8). Based on AIC weight, all the other models received less support from the data. However, it is interesting to note that based on our second most parsimonious model $\psi^{[ps \neq sp]}(WDyr 2cat)$ (AIC (w)=0.089), which used only wet and dry to categorize years, estimates of ψ^{ps} were greater during wet years ($\psi^{ps} = 0.091$ (SE=0.035)) than during dry years ($\psi^{ps} = 0$ (SE=0)), and this difference was statistically significant (ES=0.091 (95%CI=0.020 to 0.162)). Similarly, based on model $\psi^{[ps \neq sp]}(WDyr 2cat)$, estimates of ψ^{sp} were greater during dry years ($\psi^{sp} = 0.182$ (SE=0.067)) than during wet years ($\psi^{sp} = 0.048$ (SE=0.023)), but this difference was not statistically significant (ES=0.134 (95%CI= -0.008 to 0.276)) (Figure 3-9).

Discussion

This study provides the first estimates of transition probabilities between slough and wet prairie communities in the Everglades ecosystems from likelihood based multistate models. This approach allowed us to evaluate hypotheses about the factors governing the shifts from one community type to another and to relate such shifts to water conditions. Our results provided support for our 2nd hypothesis, that the probability of conversion from wet prairie to slough is greater during normal and wet years than during dry years, whereas the probability of transition from slough to wet prairie is greater during dry years than normal and wet years. In determining which years were wet, normal, and dry I used mean, minimum, maximum water depths, as well as a duration proxy which was the percent of time water levels were in the upper or lower quartile of all water levels for that season. In essence I combined many of the factors found in other studies (Kolipinski and Higer 1969, Dineen 1974, Zaffke 1983) to be correlated with plant community conversion to categorize each year for which I had plant community data. It is not therefore, surprising that the model $\psi^{[ps \neq sp]}(WDyr 3cat)$ was the most parsimonious in the model

set. The estimates found here support the conceptual models posed by (Kolipinski and Higer 1969, Dineen 1974, Zaffke 1983, Zweig and Kitchens 2008b) but are based on empirical data and on statistically robust estimators.

In the most parsimonious model $\psi^{[ps\neq sp]}(WDyr3cat)$ there were a few anomalous transitions from slough to wet prairie, during wet years, for which there is a logical explanation. Almost all the anomalous transitions occurred in northern WCA3A in 2005. Hurricane Wilma passed over the Everglades in October 2005. There was not a lot rainfall in the Everglades from this hurricane but there were wind speeds up to 195 km/h. The hurricane force winds caused an interesting phenomenon, which has been noted in other studies as well, to occur (ScienceCoordinationTeam 2003, Larsen et al. 2007). The wind blew the submerged aquatic vegetation, a main indicator of sloughs, out of the sloughs making samples taken in November appear like wet prairie samples in the cluster analysis because they had lost their main slough indicator species.

The 3rd most parsimonious model in the model set supported to some extent the 1st hypothesis and included the interacting affects of wet/dry years and seasons while the 4th most parsimonious model showed some support for the 3rd hypothesis and included the interacting effects between wet/dry years and the north/south impoundment affect. The vegetation of the Everglades is adapted to cyclical seasonal changes in water levels and has shown a high resilience to seasonal change as explained in our 1st hypothesis (White 1994). Species of *Eleocharis* have been shown to recover from complete die off due to drought in just 9 weeks when the water returns (Edwards et al. 2003). It is not, therefore surprising that although seasonality is important in community transitions it is not the main driver and that longer time scale cycles of wet and dry years are. It was surprising to learn that impoundment as outlined in

our 3rd hypothesis did not have more of an effect on community transitions showing up first as an interacting factor in our 4th model but this may be a question of time scale. The impoundment effect in WCA3A started when levee 29 was constructed in 1962, which means that all of the plots in the southern area of WCA3A had been subjected to the effects of inundation for 40 years before the first samples were taken. Much of the plant community conversion due to deep water in southern WCA3A had probably already occurred by 2002 as it was noted in a number of past studies (Alexander and Crook 1975, Zaffke 1983, Wood and Tanner 1990, David 1996). Our results show that the over riding driver of plant community conversion in WCA3A at the 4 year time scale are cycles of wet and dry years.

The estimates provided in this study from our most parsimonious models are very valuable for Everglades restoration and management. Indeed, our estimates can be incorporated into management models (e.g., Markov chain models) to predict how management actions, like water level regulations, will affect the proportion of habitat occupied by wet prairie or slough communities (Martin et al. 2008c). These models can also be used to predict the effect of global changes on the dynamics of vegetative communities in the Everglades.

Dynamics of wet prairie and slough communities can be described by the expression below

$$\Pi_{t+1} = \Phi \Pi_t$$

Where $\Phi = \begin{bmatrix} \psi^{pp} & \psi^{sp} \\ \psi^{ps} & \psi^{ss} \end{bmatrix}$ is a projection matrix, $\Pi_t = \begin{bmatrix} \varphi^p \\ \varphi^s \end{bmatrix}$ is a vector with φ^p representing the

occupancy of wet prairies (i.e., proportion of habitat occupied by wet prairies) and

φ^s representing the occupancy of slough communities. If the probability of transition among the community states can be assumed to be constant over time then a system governed by the above expressions will attain dynamic equilibrium (Caswell 2001, MacKenzie et al. 2006, Martin et al.

2008b). The equilibrium occupancy for each community state, or the proportion of habitat occupied by each community type, can be computed by calculating the first element of the right eigenvector associated with the dominant eigenvalue of the transition matrix Φ . For instance, let's assume a 10 year scenario in which there are 4 wet years, 3 normal years, and 3 dry years. One can compute the average probabilities for each transition

(e.g. $\psi^{sp} = \frac{(\psi_{Wet}^{sp} \times 4 + \psi_{Normal}^{sp} \times 3 + \psi_{Dry}^{sp} \times 3)}{10}$), which if I used estimates from model

$\psi^{[ps \neq sp]}(WDyr3cat)$ would lead to an average probability of 0.099 for ψ^{sp} and an equilibrium occupancy by wet prairies of 0.65 (i.e., at equilibrium occupancy for this scenario, 65% of the habitat would be occupied by wet prairies and the remaining 35% by sloughs). This is just one example among many of how our estimates can be used to investigate the dynamics of vegetation communities.

Our estimates can also be incorporated into more complex and realistic analyses (e.g., explicit incorporation of environmental stochasticity) (Caswell 2001). For instance several scenarios of how alterations associated with global change would affect the dynamic of vegetative communities in the Everglades could be examined by varying the frequency of dry and wet years, see (IPCC 2007). Perhaps, of even greater relevance to management of the Everglades, one could use our approach to parameterize management models as part of a process of structured decision making and adaptive management (Martin et al. 2008c). The goal of such structured decision process is to determine decisions that are optimal with respect to management objectives (Williams et al. 2002, Martin et al. 2008c). For instance, managers may be interested in attaining historical proportions of wet prairie in the Everglades without compromising the socioeconomic status of South Florida. This goal would be important to many

native species that use wet prairies but especially for the snail kite whose population is at great risk of extinction (Martin et al. 2007a, Martin et al. 2008a).

Advocates of structured decision making and adaptive management emphasize the importance of considering several important sources of uncertainty: model uncertainty, sampling uncertainty and environmental uncertainty. The approach that I have developed to model the dynamics of vegetative communities in the Everglades, explicitly measures all of these sources of uncertainty. Model uncertainty can be measured by AICc weight, at least as an initial step, but a Bayesian approach is necessary for further updating of the model weights at each implementation of management actions (Williams et al. 2002). Environmental uncertainty can be incorporated into the models by providing estimates for contrasted environmental conditions like wet and dry years. Environmental stochasticity can also be measured by computing the process variance associated with each transition probability. Unfortunately, our monitoring data did not include enough years of record to measure process variance, but I believe that it will be possible to estimate this quantity as more monitoring data is collected. Finally, the sampling variance associated with each estimate of transition probabilities can be incorporated into the management models to account for the uncertainty associated with sampling methods.

In conclusion, our approach involved three steps. First, vegetation communities in areas that have been deemed key to Everglades restoration projects were monitored. Second, multivariate analyses were applied to classify vegetative communities into states that are particularly relevant to management problems (e.g., management of vegetative communities that can affect performance measures such as Snail kites). Third, I applied likelihood based multistate models in order to evaluate multiple competing hypotheses about factors governing the dynamics of vegetative communities and to provide estimates of transition probabilities and associated

measures of uncertainty which can then be incorporated into management models. Although, the models I developed for this study were fairly simple, they provide a starting point from which additional levels of complexity can be added (as more data becomes available). It is also worth noting that most methods to determine optimal decisions require relatively simple models (Williams et al. 2002, Fonnesebeck 2005). I hope that ecologists and managers will find our framework useful for investigating the dynamics of other vegetation communities and for implementing this new knowledge into the adaptive management of other parts of the Everglades and possibly other ecosystems.

Table 3-1. Multistate models of transition probabilities (ψ) for wet prairie to slough conversions (ps) and slough to wet prairie conversions (sp).

Model	AICc	Δ AICc	w	K	DEV
$\psi^{[ps \neq sp]}(WDyr3cat)$	107.798	0	0.685	6	52.724
$\psi^{[ps \neq sp]}(WDyr2cat)$	111.863	4.064	0.090	4	61.006
$\psi^{[ps \neq sp]}(WDyr * SEAS)$	112.056	4.258	0.081	8	52.679
$\psi^{[ps \neq sp]}(WDyr * NS)$	112.916	5.117	0.053	12	44.671
$\psi^{[ps \neq sp]}(cov ar * NS)$	115.153	7.355	0.017	4	64.297
$\psi^{[ps=sp]}(NS)$	116.098	8.299	0.011	2	69.379
$\psi^{[ps=sp]}(WDyr * NS)$	116.111	8.313	0.011	6	61.036
$\psi^{[ps=sp]}(WDyr2cat)$	116.547	8.748	0.009	2	69.828
$\psi^{[ps=sp]}(SEAS * NS)$	116.939	9.14	0.007	4	66.082
$\psi^{[ps=sp]}(cov ar)$	116.947	9.149	0.007	2	70.228
$\psi^{[ps=sp]}(SEAS)$	117.186	9.387	0.006	2	70.466
$\psi^{[ps \neq sp]}(cov ar)$	117.537	9.738	0.005	4	66.680
$\psi^{[ps \neq sp]}(cov ar * NS)$	118.068	10.269	0.004	8	58.690
$\psi^{[ps=sp]}(WDyr3cat)$	118.167	10.369	0.004	3	69.390

The effect of wet and dry years were tested (WDyr), as was the effect of seasons (SEAS) and the north south water impoundment effect (NS). AICc is the Akaike Information Criterion, Δ AIC is adjusted for sample size, w is AICc weight, K is the number of parameters, DEV is the deviance given by program MARK.

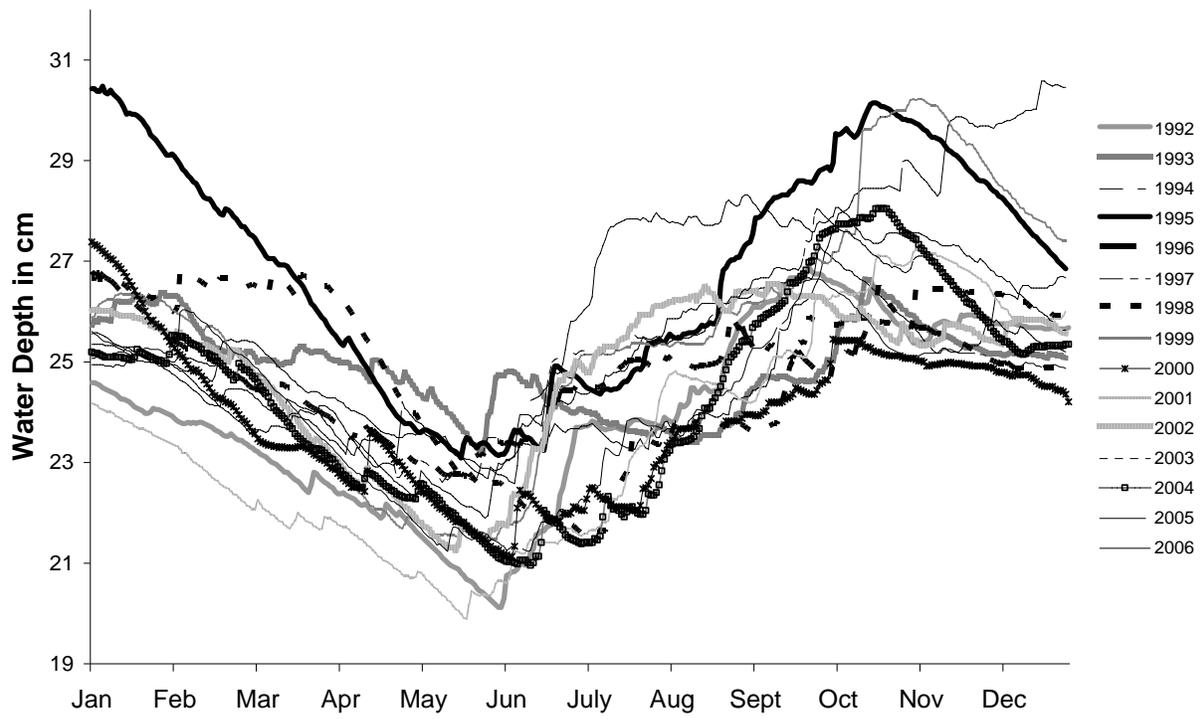


Figure 3-1. Hydrograph of water levels in Water Conservation Area 3A from 1992 to 2006. The graph demonstrates the defined seasonal pattern in water levels as well the clear variation from year to year.

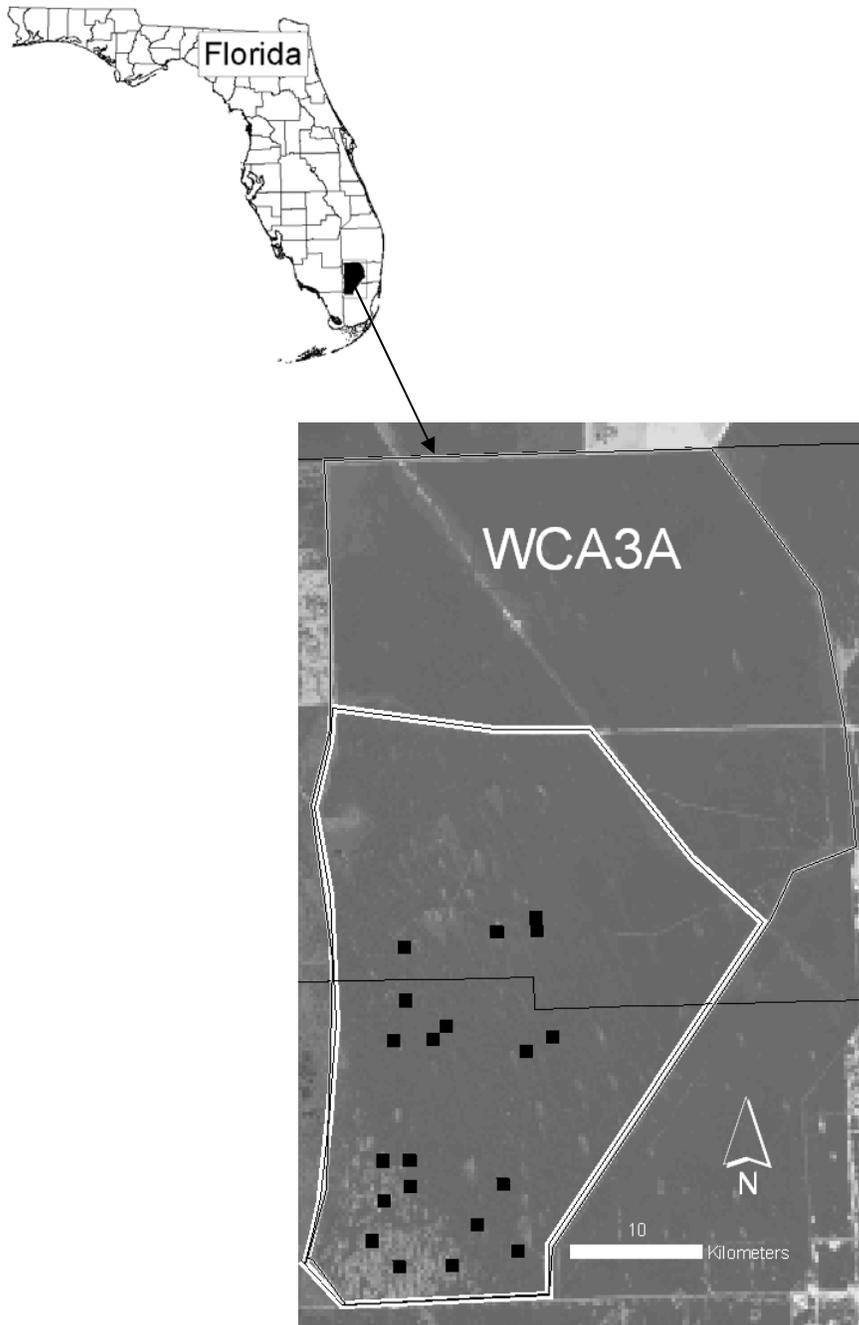


Figure 3-2. Our study area, southern WCA3A, is shown here with the twenty study plots in black. The plots were placed in a stratified random manner across landscape level gradients like peat depth, water level, and snail kite nesting concentration. All data used in this analysis came from transects placed in these plots.

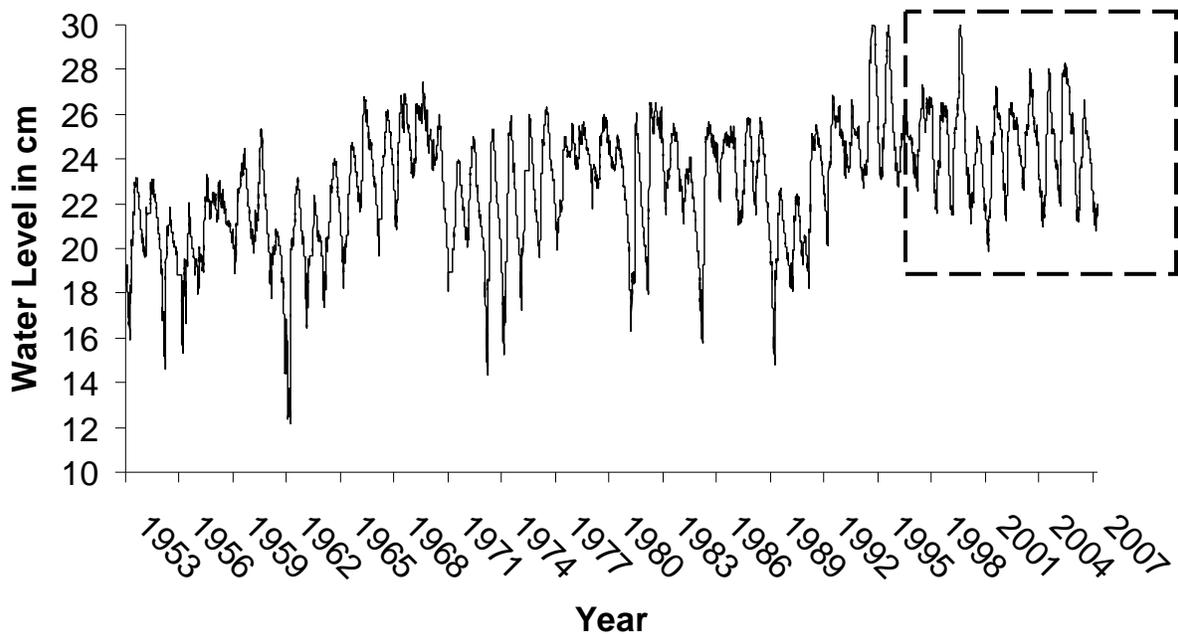


Figure 3-3. Stage water levels in WCA3A since 1953 from gauge station 3-65, site 3A-28. Several different water regulation schedules can be seen in the graph with the driest schedule in the 50's and 60's. Dashed box indicates newest era in water regulation schedule which started in 1992.

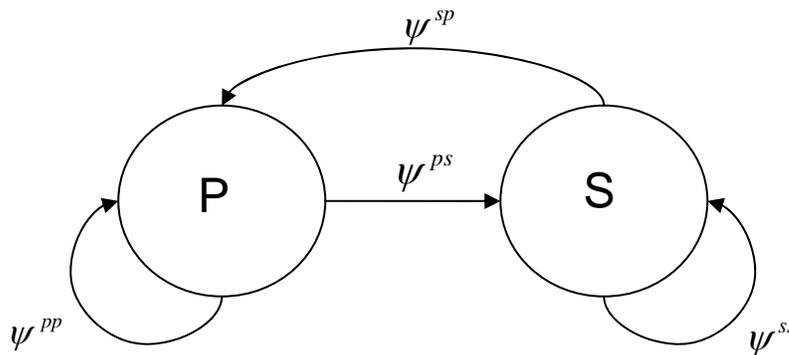


Figure 3-4. Transition probabilities shows that sloughs will transition to wet prairies with a certain probability or remain as sloughs. Wet prairies behave in the same manner, either transitioning to sloughs with a certain probability or continuing on as wet prairies.

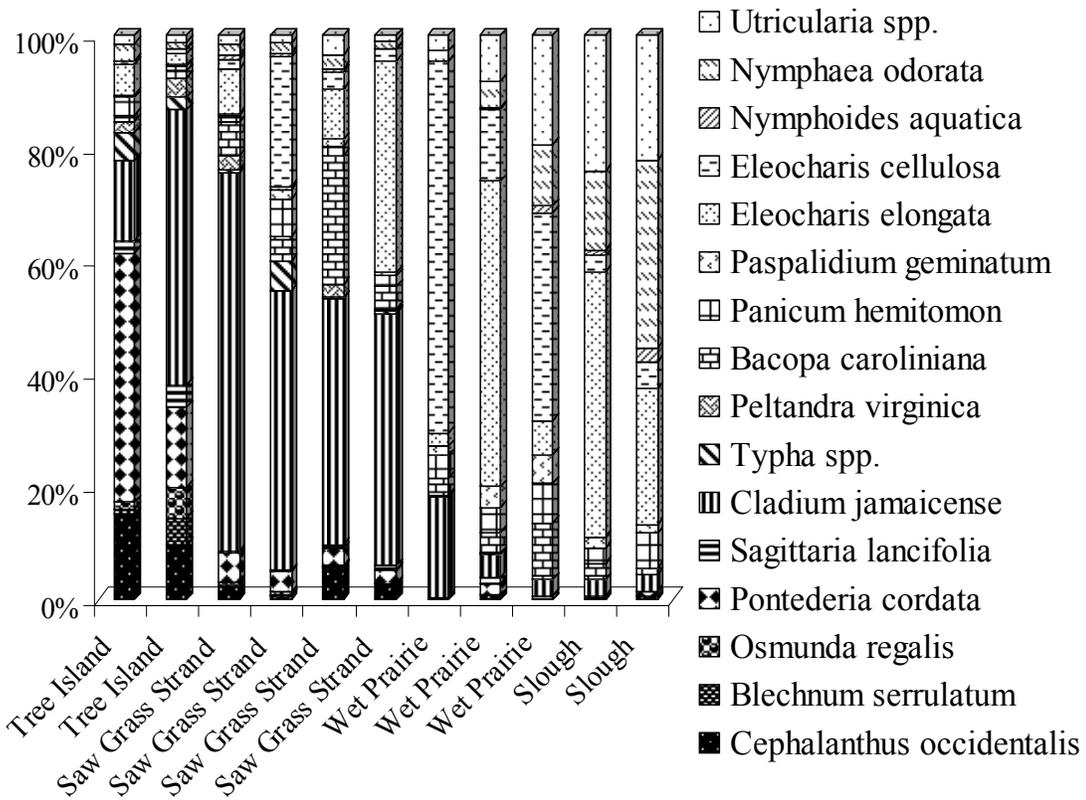


Figure 3-5. Results from the Agglomerative Cluster analysis used to determine the vegetation communities in WCA3A at each sampling event. An indicator species analysis was also done and used in combination with our knowledge of the system to label the communities.

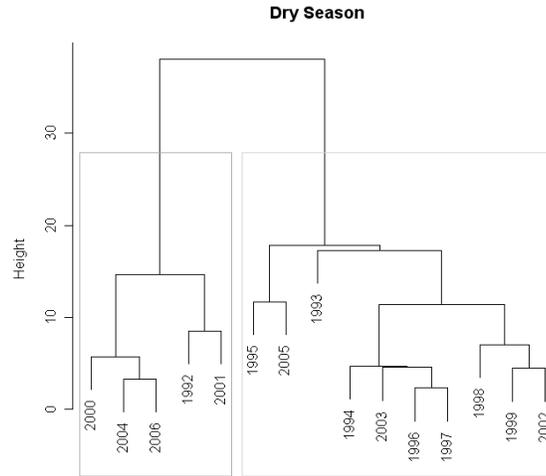


Figure 3-6. Cluster analysis used for all dry seasons since water year 1992 to determine which dry seasons were dry (dark grey) and which were normal/wet (light grey).

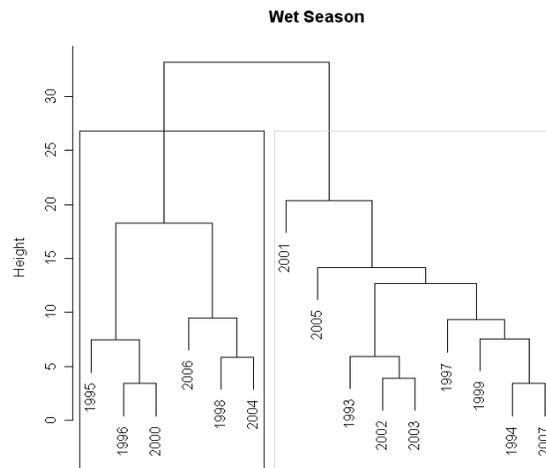


Figure 3-7. Cluster analysis used for all wet seasons since water year 1992 to determine which wet seasons were wet (black) and which were normal/dry (light grey).

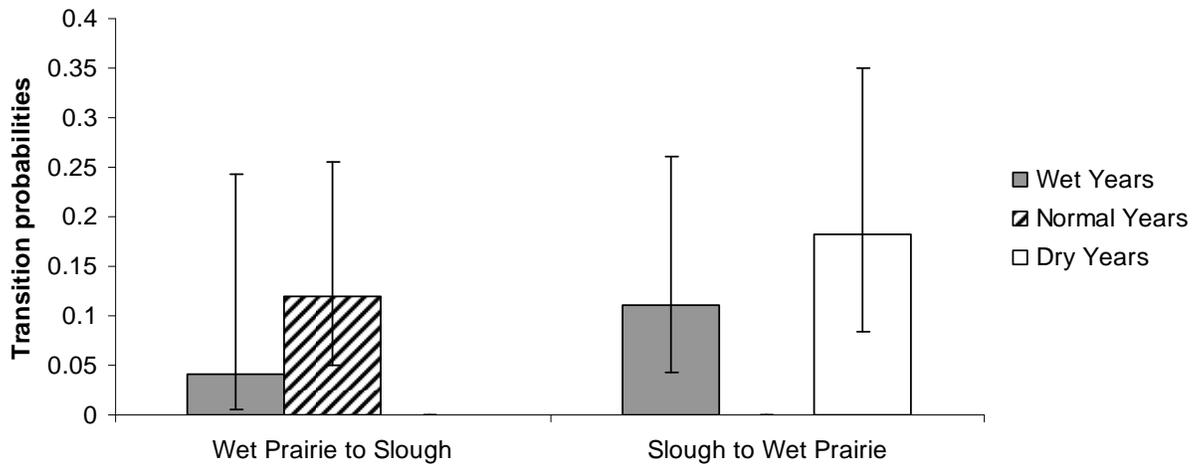


Figure 3-8. Transition estimates from our most parsimonious model $\psi(WDyr3cat)$ ($AIC(w) = 0.685$) for wet prairie and slough communities using wet, normal and dry year classifications. For transition estimates from wet prairie to slough the difference between normal and dry years was statistically significant (ES=0.119, 95%CI= 0.019 to 0.219), but the difference in ψ^{ps} between normal and wet years as well as the difference in ψ^{ps} between dry and wet years was not significant. For slough to wet prairie conversions, the difference between normal and dry years was significant (ES=0.181; 95%CI=0.047 to 0.316) as was the difference between normal and wet years (ES= 0.111; 95%CI=0.006 to 0.216). However, the difference in ψ^{sp} between dry and wet years was not significant.

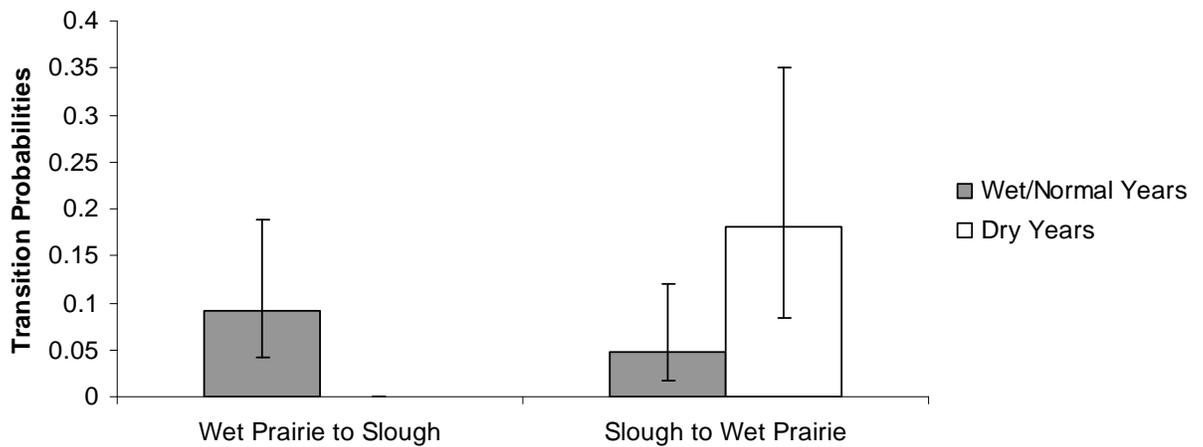


Figure 3-9. The transition estimates for wet prairie and slough communities from our second most parsimonious model $\psi(WDyr2cat)$ ($AIC(w)=0.089$) which used wet and dry year classifications instead of wet, dry, and normal year classifications. The difference in ψ between wet and dry years is significant for wet prairie to slough estimates ($ES=0.091$, $95\%CI=0.020$ to 0.162) but not for slough to wet prairie estimates.

CHAPTER 4 CONCLUSIONS AND NEXT STEPS

It was determined in the last Chapter that multistate models could be used to obtain transition probability estimates for vegetative communities. The next step is to increase sample size by dividing up the *a priori* community groups. With more samples it will be possible to evaluate a number of hypotheses about the vegetative community dynamics of WCA3A. It will also be possible, with a larger sample size, to obtain annual transition estimates by using data from just the wet season. The selection of a single season to define transitions was prompted by the confusion of within year transitions complicating the year to year transitions across the landscape. The last set of analyses pointed to hydrology as the main driver of community transitions. In this step the five different aspects of hydrology (mean, minimum, maximum, % time in upper quartile, and % time in lower quartile) that were combined before, will be separated to determine which aspect of hydrology is most correlated with community transition.

Hypotheses and Predictions

Hypothesis 1: Transition Probabilities Will Be Higher in the North Than in the South

The northern study area is more hydrologically dynamic, reflecting sheet flow rather than impoundment influences. In theory natural wetland hydrology is associated with high transition probabilities, meaning that community transitions are occurring at a high rate, and communities are not stagnant, or tending toward monoculture (Kitchens et al. 2002). In effect wetland vegetative communities should change in concert naturally with changing water conditions (Mitsch and Gosselink 1993). It is expected that transition probability estimates will be higher for the northern plots than for the southern plots at all times.

Hypothesis 2: The Hydrological Variables That Drive Transitions in the North Will Be Different from the Hydrological Variables That Drive Transitions in the South

The northern study area is more hydrologically dynamic and drier than the southern study area. This leads to the hypothesis that the hydrological variables of maximum and % of time in the upper quartile will be most correlated with community transitions in the north. In other words the north has been kept fairly dry so it is expected that most transitions will occur during periods of high water. The opposite is true in the south which has been kept very wet. This leads to the hypothesis that the hydrologic variables of minimum and % of time in the lower quartile will be most correlated with community transitions in the south. Only during extreme dry down will the southern communities begin transitioning.

Hypothesis 3: Transition Probabilities Will Have a Directionality That is Related to Water Levels

The wetland communities in the slough/wet prairie/sawgrass strand/tree island landscape type occur on a hydrologic gradient. Sloughs are typically the wettest communities followed by wet prairies and then sawgrass strands with tree islands as the driest communities in this landscape. As conditions dry down, communities should begin transitioning up the hydrological gradient to drier physiognomic types. As the system rewets, the communities should begin transitioning back down the hydrological gradient to wetter physiognomic types. It is predicted that the transition probabilities from slough to wet prairie communities will be higher in dry time periods. Conversely, the transition probabilities from wet prairie to slough communities will be higher in wet time periods. This trend was seen in the last analyses and is expected to be seen again when the larger data set is used.

Preliminary Results

All of the preliminary analyses presented below will be rerun using the new larger data set but some very ecologically significant trends were found even with a small data set.

Annual Transition Probability Estimates

Obtaining annual transition estimates from this data set was difficult as using data from only wet seasons left just 4 occasions from which transition probabilities could be estimated. This decreased sample size caused an increase in standard errors and confidence intervals from those found when all 8 occasions were used. The candidate model set, including a north-south interaction and different hydrologic variables, was essentially the same as the model set in the last chapter although the effect of seasonality could no longer be tested. The results can be seen in table 4-2.

The most parsimonious model in this model set suggested that there were more transitions in the north than in the south but did not include the effect of time or hydrology $\Psi(ps \diamond sp *NS)$ ($AIC(w)=0.43350$) (Figure 4-1). In the north there were significantly more transitions from slough to wet prairie than from wet prairie to slough ($ES= 0.434$ ($95\%CI=0.084$ to 0.785)). There was also significantly more transition in the north than in the south from slough to wet prairie ($ES=0.402$ ($95\%CI=0.015$ to 0.789)). These findings provided support for hypothesis one which was that transition probabilities would be higher in the north than in the south. Communities in the north also transitioned more to drier states than wetter states which was predicted in hypothesis three although the effect of time was not included in this model.

The model-averaged results are also presented here as model averaging was used because there was some model selection uncertainty (Figure 4-2). Confidence intervals on the estimates are very large and there were no statistically significant effect sizes. Still the model averaged results indicate that transition probabilities were higher in the north than in the south. This is more support for hypothesis one which was related to the fact that the south is severely impounded and stagnant while the north is more hydrologically dynamic, reflecting sheet flow rather than impoundment influences.

Separate Estimates for the North and South

Two-community states: wet prairie and slough

Two separate analyses were performed with two smaller sets of data created from the initial larger data set. Essentially the same candidate model set was used, with the readdition of seasonality this time. Results from model averaging are presented in Figure 4-3. These results showed that in the south wet prairies were transitioning to sloughs with more frequency than sloughs were transitioning to wet prairies in all time periods except the dry seasons of 2004 and 2006. On these occasions sloughs were more likely to transition to wet prairies than wet prairies were to transition to sloughs. This supports hypothesis three as the dry seasons of 2004 and 2006 had long duration dry- downs that should have moved communities toward the drier wet prairie state. These trends are ecologically interesting although the effect sizes on them were not statistically significant. In the north sloughs were more likely to transition to wet prairies than wet prairies were to transition to sloughs on all occasions except the wet season of 2004 and the dry season of 2005. During these relatively wet time periods, wet prairies were more likely to transition to slough than sloughs were to transition to wet prairies so during wet time periods most movement in the north was toward a wetter community state. Although all these findings are ecologically significant and support hypothesis three, the confidence intervals of the effect sizes overlapped 0 and are therefore not statistically significant.

Three-community states: wet prairie, transition, and slough

Wet prairie and slough represent two physiognomic types within which there are multiple community states. Two community states from the vegetative community cluster analysis that had been classified as physiognomic types slough and wet prairie were reclassified as transition states between slough and wet prairie. The same candidate model set as in the previous analysis was used.

As in the previous analysis, transition probabilities were generally higher in the north than in the south, with the exception of the dry seasons of 2004 and 2006. The hydrological variables that were driving community transitions were easier to identify in this set of analysis. In the north the third most parsimonious model included the effect of the percent of time spent in the upper quartile of water levels for that season. Models that included this interaction had a combined AIC weight of 0.16061. This appeared to be the hydrologic variable that best explained community transition in the northern part of the study site. In the south the most parsimonious model included the effect of the percent of time spent in the lower quartile of water levels for that season. Models that included the effect of percent of time spent in the lower quartile of water levels for the season had a combined AIC weight of 0.33407. These results showed the first support for hypothesis two which predicted maximum and % of time in the upper quartile would relate best to community transition in the north and that minimum and % of time in the lower quartile would relate best to community transition in the south.

Discussion

These analyses can be seen as the comparison of an intact wetland to a degraded and impounded wetland. The preliminary results presented here are the first step to further untangling the vegetative community dynamics of WCA3A. Similar analysis will now be run on a larger data set to determine if the findings are correct and statistically significant. With annual transition probabilities and the hydrologic drivers of transitions in hand, planning appropriate hydrologic regimes to maintain desired vegetative communities in WCA3A, and predicting vegetative community shifts under certain management schedules becomes possible. In an era of restoration, particularly Everglades restoration the goal of management schedules is a return to natural community transition probabilities. This analysis will provide a path toward

that goal by identifying the aspects of hydrology that are the main drivers of vegetative community transition.

Table 4-1. Results when the cluster including both wet and dry season data was used to make the input file for annual transition estimates.

Model	AICc	Delta AICc	AICc weights	Model likelihood	Num. par	Deviance
{sp=ps}	42.759	0	0.269	1	2	15.367
{sp=ps*NS}	42.866	0.108	0.254	0.948	3	13.334
{sp=ps*WDyr}	44.439	1.681	0.116	0.432	3	14.907
{sp<>ps}	44.456	1.697	0.115	0.428	3	14.923
{sp<>ps*NS}	45.544	2.785	0.067	0.248	5	11.576
{sp=ps*NS*WDyr}	46.336	3.577	0.045	0.167	5	12.368
{sp=ps*t}	46.631	3.872	0.039	0.144	4	14.907
{sp=ps*WDyr3states}	46.631	3.872	0.039	0.144	4	14.907
{sp<>ps*WDyr}	47.268	4.509	0.028	0.105	5	13.300
{sp=ps*t*NS}	49.190	6.431	0.011	0.040	7	10.571
{sp=ps*NS*WDyr3states}	49.190	6.431	0.011	0.040	7	10.571
{sp<>ps*t}	51.914	9.156	0.003	0.010	7	13.295
{sp<>ps*WDyr3states}	51.914	9.156	0.003	0.010	7	13.295
{sp<>ps*NS*WDyr}	52.591	9.832	0.002	0.007	9	9.088
{sp<>ps*t*NS}	60.358	17.599	0.000	0.000	13	6.315

The estimate of the probability of wet prairie transitioning to slough was equal to the probability of slough transitioning to wet prairie in the most parsimonious model and received a combined AIC (w) of 0.783.

Table 4-2. When the communities were reclustered using only wet season sampling data, the results, as seen here, were quite different and more ecologically reasonable.

Model	AICc	Delta AICc	AICc weights	Model likelihood	Num. par	Deviance
{PS<SP*NS}	72.029	0	0.434	1	4	28.118
{PS<SP}	72.784	0.755	0.297	0.686	2	33.194
{PS=SP*NS}	75.82	3.791	0.065	0.150	2	36.230
{PS<SP*wetdry223}	76.095	4.066	0.057	0.131	4	32.184
{PS=SP}	77.295	5.266	0.031	0.072	1	39.794
{PS<SP*NS*%25}	78.233	6.205	0.019	0.045	8	25.063
{PS<SP*NS*min}	78.538	6.509	0.017	0.039	8	25.367
{PS<SP*NS*dist}	78.786	6.757	0.015	0.034	8	25.615
{PS<SP*NS*avg}	79.111	7.083	0.013	0.029	8	25.941
{PS<SP*NS*wetdry223}	79.291	7.262	0.011	0.027	8	26.120
{PS<SP*%25}	79.407	7.378	0.011	0.025	4	35.496
{PS<SP*NS*%75}	79.411	7.382	0.011	0.025	8	26.240
{PS<SP*t}	80.302	8.273	0.007	0.016	6	31.869
{PS=SP*t}	80.765	8.737	0.005	0.013	3	39.039
{PS<SP*NS*max}	80.945	8.916	0.005	0.012	8	27.774
{PS=SP*t*NS}	83.288	11.259	0.002	0.004	6	34.855
{PS<SP*t*NS}	86.412	14.383	0.000	0.001	12	23.055
{PS<SP*NS*min*dist}	86.868	14.839	0.000	0.001	12	23.512

The most parsimonious model in this model set showed that there were more transitions in the north than in the south but did not include the effect of time or hydrology $\Psi(\text{ps} < \text{sp} * \text{NS})$ (AIC(w)=0.43350). In the north there were significantly more transitions from slough to wet prairie than from wet prairie to slough (ES= 0.434 (95%CI=0.084 to 0.785)). There was also significantly more movement in the north than in the south from slough to wet prairie (ES=0.402 (95%CI=0.015 to 0.789)).

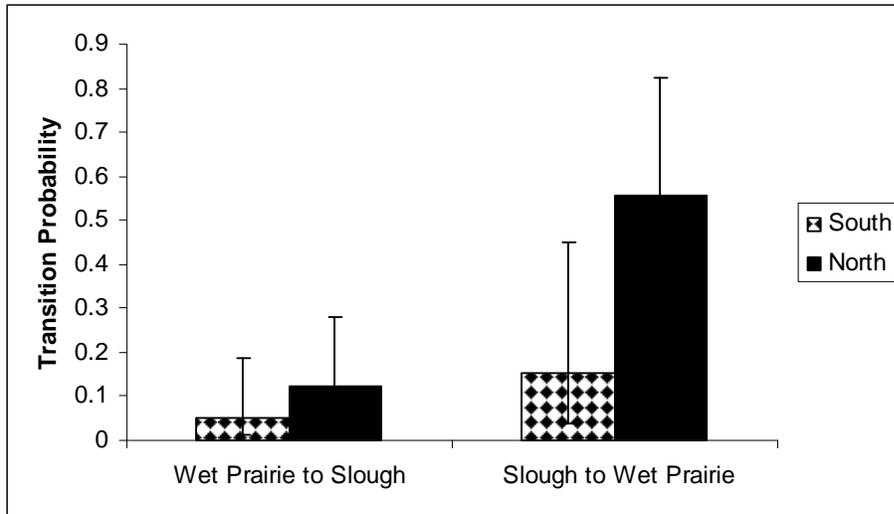


Figure 4-1. Most parsimonious model in model set that attempted to get annual transition probability estimates. It showed that there were more transitions in the north than in the south but did not include the effect of time or hydrology $\Psi(ps \diamond sp *NS)$ ($AIC(w)=0.43350$). In the north there were significantly more transitions from slough to wet prairie than from wet prairie to slough ($ES= 0.434$ ($95\%CI=0.084$ to 0.785)). There was also significantly more movement in the north than in the south from slough to wet prairie ($ES=0.402$ ($95\%CI=0.015$ to 0.789)).

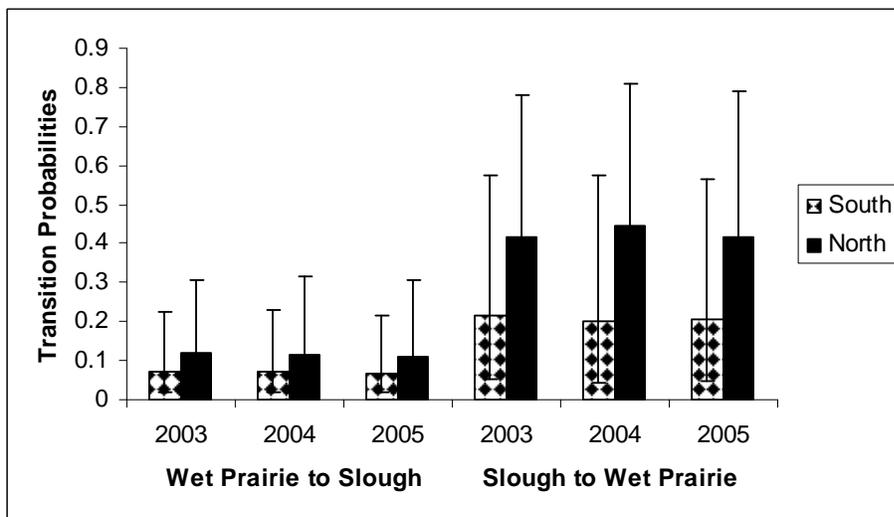


Figure 4-2. Model averaged results from the model set used to get annual transition probability estimates. Confidence intervals on the estimates are very large and there were no statistically significant effect sizes. The results show that the transition probabilities were higher from sloughs to wet prairies than from wet prairies to sloughs at all times. Transition probabilities were also higher in the north than in the south although the effect sizes for these comparisons were not significant.

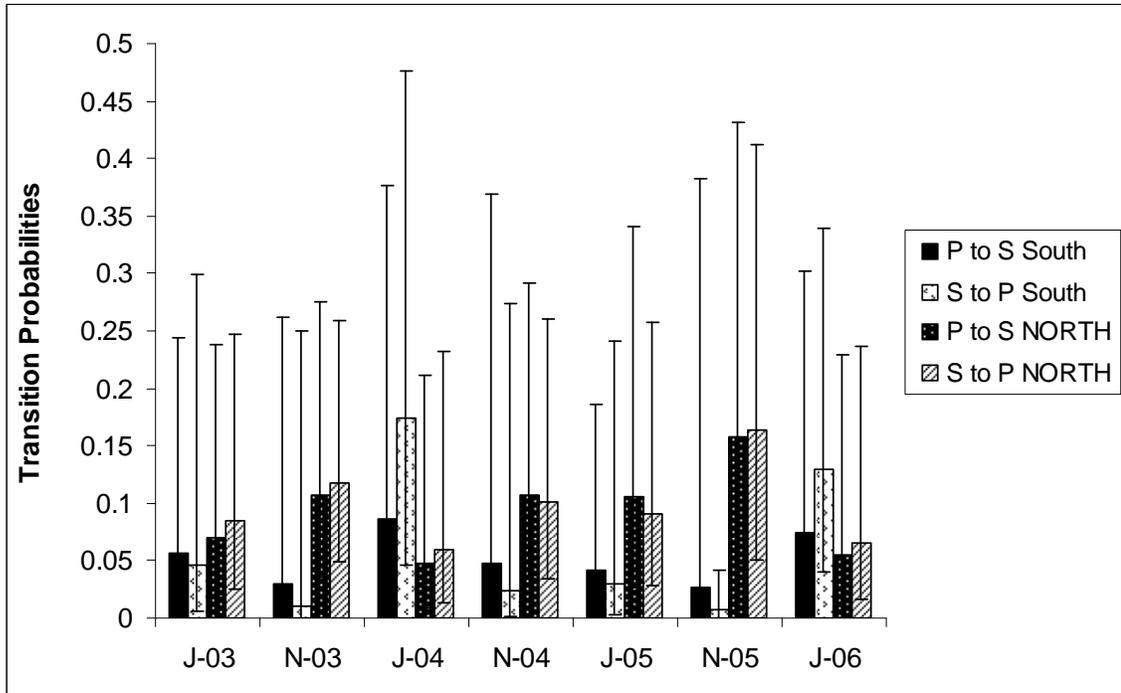


Figure 4-3. Results from 2 model sets, one for the north and one for the south, with 2 community states, slough and wet prairie that were used to determine what the hydrologic drivers are for each area. These results show that in the south wet prairies were transitioning to sloughs with more frequency than sloughs were transitioning to wet prairies in all time periods except the dry seasons of 2004 and 2006. On these occasions sloughs were more likely to transition to wet prairies than wet prairies were to transition to sloughs. In the north sloughs were more likely to transition to wet prairies than wet prairies were to transition to sloughs on all occasions except the wet season of 2004 and the dry season of 2005. During these relatively wet time periods, wet prairies were more likely to transition to slough than sloughs were to transition to wet prairies so during wet time periods most movement in the north was toward a wetter community state. Although all these findings are ecologically significant, the confidence intervals of the effect sizes overlapped 0 and are therefore not statistically significant.

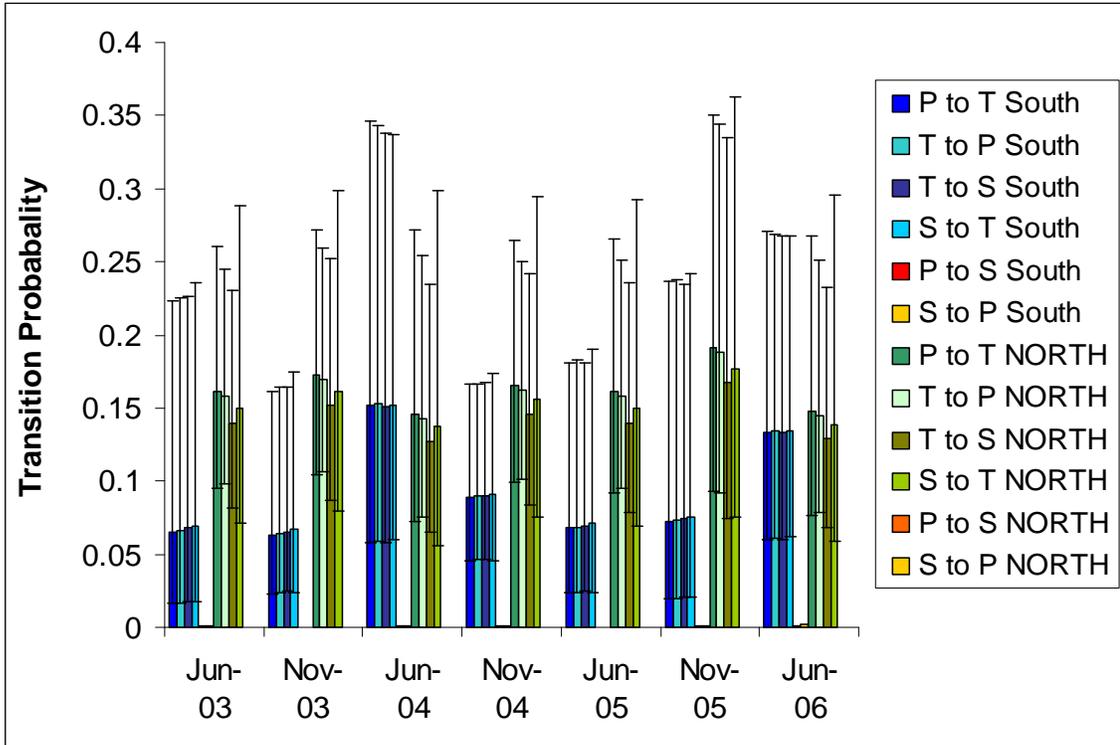


Figure 4-4. Results from two model sets (north and south) with 3 community states: slough, transition, and wet prairie used to determine hydrologic drivers for each area. There was no movement from wet prairies directly to sloughs; all movement occurred through the transition state. As in the previous analysis, transition probabilities were generally higher in the north than in the south, with the exception of the dry seasons of 2004 and 2006. There was still no clear directionality of movement.

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BIOGRAPHICAL SKETCH

Althea Hotaling was born in Athens, Georgia in 1982. She grew up in the countryside around Athens until her family moved to Central Florida. Her love for nature and being outside developed early in these woods and has not waned. She obtained a BS in marine biology from the University of West Florida in 2003. As an undergraduate she worked on a variety of research projects and decided she would like to focus on applied research that really made a difference. Immediately after graduation she married Donald Hagan and joined the Peace Corps, where she served for over 2 years in Bahia de Caraquez, Ecuador, as a natural resources volunteer. During her Peace Corps service, she grew to understand that conservation and restoration of natural ecosystems must be something everyone in the community is invested in or it will surely fail and that it is a delicate balance of needs. She entered the graduate program at the School for Natural Resources and the Environment in 2006.