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ESTIMATING TRANSITION PROBABILITIES AMONG EVERGLADES WETLAND COMMUNITIES USING MULTISTATE MODELS

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Abstract: In this study we were able to provide the first estimates of transition probabilities of wet prairie and slough vegetative communities in Water Conservation Area 3A (WCA3A) of the Florida Everglades and to identify the hydrologic variables that determine these transitions. These estimates can be used in management models aimed at restoring proportions of wet prairie and slough habitats to historical levels in the Everglades. To determine what was driving the transitions between wet prairie and slough communities we evaluated three hypotheses: seasonality, impoundment, and wet and dry year cycles using likelihood-based multistate models to determine the main driver of wet prairie conversion in WCA3A. The most parsimonious model included the effect of wet and dry year cycles on vegetative community conversions. Several ecologists have noted wet prairie conversion in southern WCA3A but these are the first estimates of transition probabilities among these community types. In addition, to being useful for management of the Everglades we believe that our framework can be used to address management questions in other ecosystems.

Key Words: adaptive management, community dynamics, restoration

INTRODUCTION

Over half the wetlands in the U.S. have been lost (Dahl 2000). For example, South Florida freshwater wetlands have been reduced from 3.5 million to 1.8 million ha in extent and have been impounded by 2000 km of dikes and canals as a result of agricultural and urban development in the last 100 years (Mitsch and Gosselink 1993, Kitchens et al. 2002). 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. 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 presents a comprehensive framework for investigating multiple competing hypotheses about the hydrologic factors governing transition probabilities among vegetative community states in the Everglades. This framework allows for the calculation of estimates of transition probabilities and estimates of uncertainty (process and sampling variance associated with these estimates) and is applicable to other wetland communities. The estimation of various types of uncertainty is particularly important for making informed decisions for conservation (Martin et al. 2009b).

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, 2009b). 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, Gunderson 1994). 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, which enables the snail kite to easily see its primary food source, the apple snail, when it emerges to breathe (Kitchens et al. 2002, Karunaratne et al. 2006). Indicator plant species for wet prairies are beak rush (*Rhynchospora*), maidencane (*Panicum*), and spike rush (*Eleocharis*). The other community in the study is slough which is a shallow natural channel that has water most of the year and is characterized by white water-lily (*Nymphaea odorata*) and bladderwort (*Utricularia*) (Loveless 1959). Karunaratne et al (2006) showed that snail densities were lower in sloughs than in wet prairies, and several authors have hypothesized that conversion from wet prairies to slough communities may be detrimental to snails and snail kites (Kitchens et al. 2002, Karunaratne et al. 2006, Martin et al. 2008a).

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. These types of models are now commonly used to estimate movement probabilities of organisms among discrete geographic units or physiologic states (Blums et al. 2003, Martin et al. 2007b). We further use these models 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. Precipita- Precipitation is the main route by which water enters the Everglades ecosystem (Duever et al. 1994) and the dominant source of natural surface freshwater. Rainfall in southern Florida is seasonal with 60% occurring from June to November and only 25% occurring between November and June. The result of this rainfall pattern is a hydroperiod that has strong effects on vegetation composition and structure and which exhibits natural periodicity or

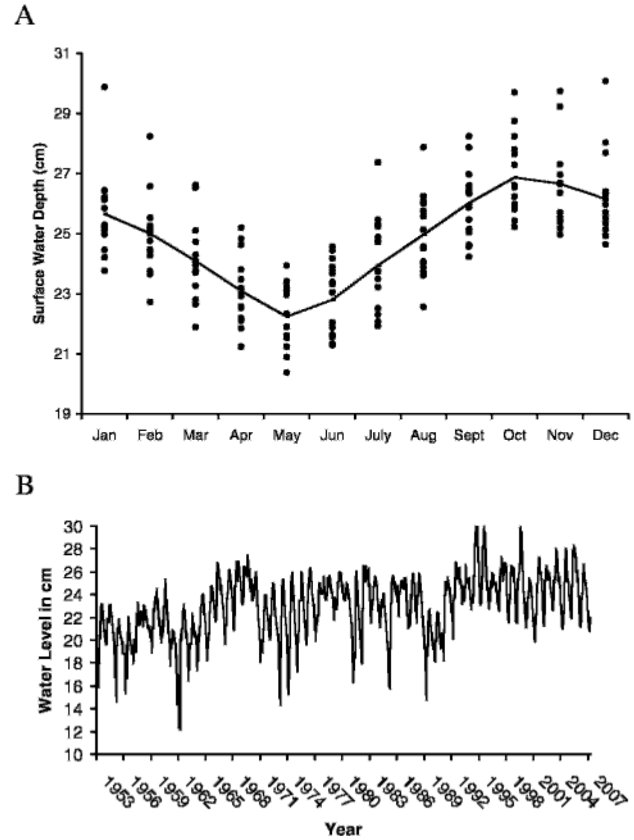

Figure 1. A) Hydrograph of water levels in Water Conservation Area 3A from 1992 to 2006, which demonstrates the seasonal pattern in water levels and annual variation. B) Stage water levels in WCA3A since 1953 to 2006, where different water regulation schedules can be seen with the driest schedule in the 1950's and 1960's. The dashed box indicates the newest era in water regulation schedule that started in 1992. Stage water levels for both graphs are from USGS gauge station 3–65, which is also known as 3A-28.

substantial and predictable within year seasonal variation (White 1994) (Figure 1A). The vegetation of the Everglades is adapted to this seasonal environment in its rhythms of production, decomposition, mortality, and reproduction. Therefore, we predict the transition probabilities from wet prairie communities to sloughs to be greater during wet seasons that occur in the interval from June to November. In contrast, we predict the transition probabilities from slough communities to wet prairie communities to be greater during dry seasons that occur in the interval from November to June. Most of these species are perennials so they do not appear or disappear from a community during a season but the dominant species (as seen in their biomass and density) in the community can shift over short time scales.

Hypothesis 2: Wet and Dry Years Substantially Influence the Process of Conversion of Sloughs and Wet Prairies. In South Florida wetlands precipitation, which has a significant impact on hydroperiod, has high interannual variability ranging 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 (Figure 1A,B) 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 (Duever et al. 1994). With this in mind, we predict the transition probabilities from slough communities to wet prairies to be greatest during dry intervals. In contrast, we predict the transition probabilities from wet prairie to slough communities to be greater during wetter intervals.

Hypothesis 3: Probabilities of Transition Between Sloughs and 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 that 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, we predict there will be more conversion from wet prairies to sloughs and less conversion from sloughs to wet prairies. In the northern sites, we predict less conversion from wet prairies to sloughs and more conversion from sloughs to wet prairies.

METHODS

Study Area and Sampling Methods

This study was located in the southern portion of Water Conservation Area 3A (WCA3A) in the Everglades of South Florida, USA (Figure 2). In the fall of 2002, 20 1-km^2 plots were placed across three landscape strata: an east-west peat depth gradient, and artificial north-south water depth gradient, and a Florida snail kite nesting activity gradient in a random stratified manner. Two or three 10-m wide belt transects, which varied in length depending on the dimensions of the communities and contained 12

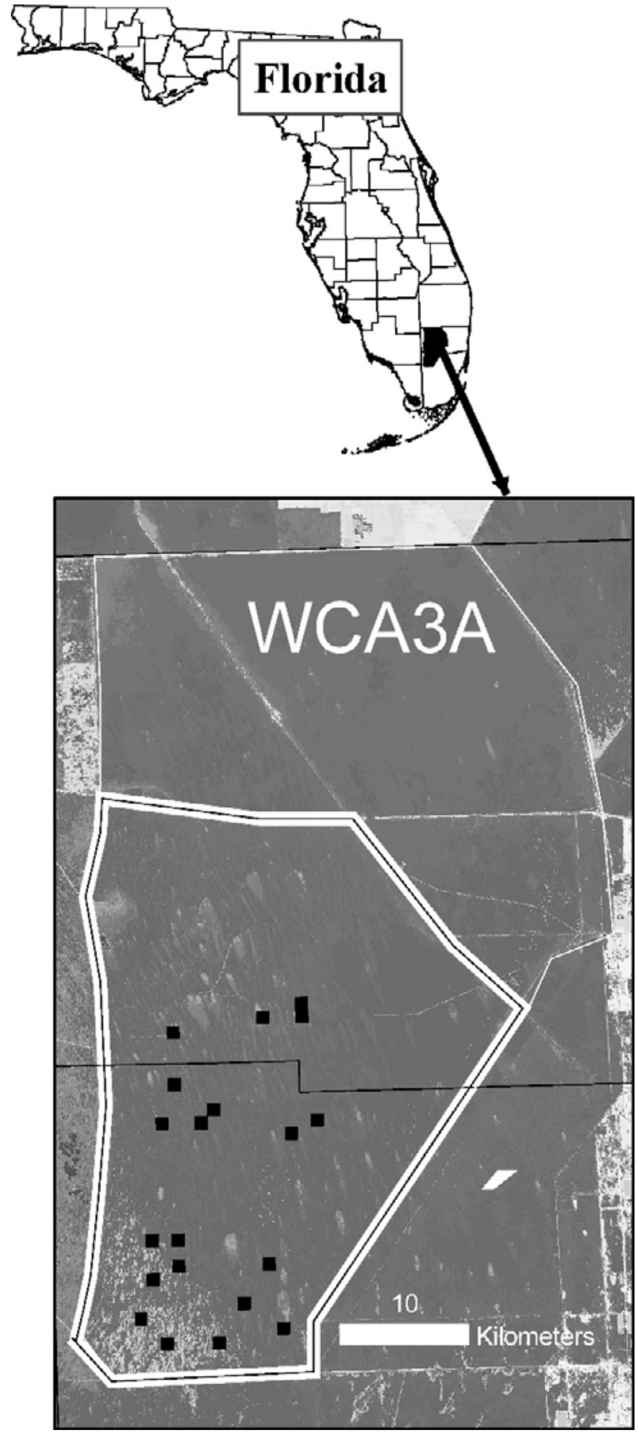

Figure 2. The southern WCA3A study area with the 20 study plots in black. Plots were placed in a stratified random manner across landscape level gradients of peat depth, water level, and snail kite nesting concentration. All data used in this analysis came from transects placed in these plots.

Table 1. Importance Values (%) of seven main species for the 11 communities found in the hierarchical, agglomerative cluster analysis. The importance value of each species to each cluster allowed us to determine what type of community the cluster represented. For example all communities that were labeled Wet Prairie had high importance values for either *Eleocharis elongata* or *Eleocharis cellulosa*.

Community	*Cephalanthus occidentalis*	*Cladium jamaicense*	*Eleocharis elongata*	*Eleocharis cellulosa*	*Nymphaea odorata*	*Pontederia cordata*	*Utricularia spp.*
Tree Island	14.4	13.6	5.2	0.5	2.8	41.9	1.5
Tree Island	9.2	46.1	1.8	0.8	1.1	13.4	1.2
Sawgrass	2.5	63.6	7.5	1.6	2.0	5.0	1.4
Sawgrass	0.7	48.0	0.6	22.3	1.8	3.5	1.3
Sawgrass	5.3	41.1	8.4	3.0	2.4	2.8	3.3
Sawgrass	2.8	43.6	36.6	2.1	1.3	2.4	1.0
Wet Prairie	0.0	17.5	2.3	64.3	1.7	0.0	2.7
Wet Prairie	0.8	4.1	53.1	12.6	4.6	2.1	7.9
Wet Prairie	0.0	2.9	5.9	35.7	10.5	0.1	18.9
Slough	0.0	2.9	46.3	2.8	13.8	0.4	23.6
Slough	0.7	3.0	24.3	4.9	33.6	0.7	22.3

sampling transects, were placed in each plot moving from one *a priori* community type (slough, sawgrass, tree/shrub island, *Typha*, and wet prairie) into another. Enough transects were placed in each plot to have several community replicates in each identified strata. Samples were collected every 3 m along belt transects twice a year at the end of the dry (May/June) and wet (November/December) seasons. A sample was a 0.25 m^2 area from which all standing biomass was clipped at peat level, including any submerged aquatic plants. Each sampling event occurred at a specific location on the belt transect, on the right or left side of the transect and staggered ever 1.5 m, which allowed us to sample the same communities but not the exact same location on the transect. Samples were sorted by species, counted (stems or blades), dried, and weighed. There were eight sampling events from November 2002 to June 2006. In addition, 17 water level monitoring wells were placed in the plots to take twice daily water level readings. Plots that were very close to each other or had adjacent corners shared wells. Sampling methods were the same as those used in Zweig and Kitchens (2008).

Data Analyses

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 was 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. Relative density plus relative biomass divided by 2 and then multiplied by 100 is IV. Importance values are 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 m^2 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 IVs 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 that 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. Further clarification of this methodology can be found in Zweig and Kitchens (2008) who preformed a similar analysis with different objectives in mind on a subset of the data set used here that included only wet seasons and samples through 2005.

The indicator species analysis, based on hierarchical, agglomerative cluster analysis of the Everglades WCA3A vegetation monitoring data, indicated that there were 11 communities/clusters (Table 1). Using our knowledge of the system, we determined that there were 2 slough, 3 wet prairie, 4 sawgrass ridge, 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 we 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. 2009b). 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 Seasons. Water levels at our plots were hindcast using artificial neural networks to look at the historical hydrology of the plot (Conrads et al. 2006). Artificial neural network models were used in this instance to perform multivariate, non-linear interpolation between gauging stations that had historical data and stations placed in WCA3A for this project. As the newest hydrological era or water management regime began in WCA3A in 1992, water levels from the past 16 years have been featured in Figure 1B 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 included: 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. We 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 prairie communities denoted (p) (Figure 3). We 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 $\psi(SEAS)$. We also included wet (W) and dry (D) years (yr) as a factor (denoted $\psi(WDyr)$). Models that had three categories ($\psi^{[ps \neq sp]}(WDyr3cat)$) for

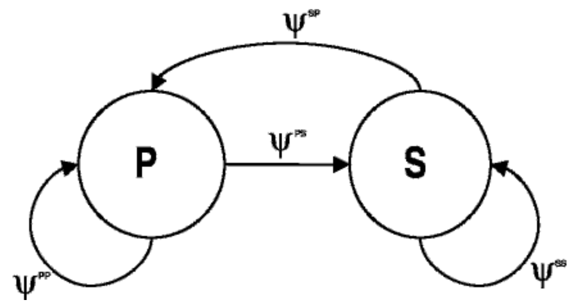

Figure 3. This diagram of transition probabilities shows that sloughs will transition to wet prairies with a certain probability or remain as sloughs. Wet prairies behave in the same manner, either transitioning to sloughs with a certain probability or continuing on as wet prairies.

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. Models in which the northern communities were grouped together and allowed to have different transition probabilities from the group of southern communities were used as well as models in which the transition probability of northern communities were set equal to southern communities. In addition, we considered two temporal structures: time variation denoted (t, which assumed that Ψ varies over time), and no time variation denoted (".", which assumed that Ψ remains constant over time). We allowed some of the factors to interact (the interaction between two factors was denoted "$*$", e.g. model $\psi(WDyr * NS)$). Two models that tested for the lag effects of hydrology, specifically hydrology from the season previous to sampling $\psi^{[ps \neq sp]}(WDyr_{prevSEAS})$ and the year previous to sampling $\psi^{[ps \neq sp]}(WDyr_{prevYEAR})$, were also included. Finally, for all models we assumed that transition probabilities ψ^{ps} and ψ^{ps} were either identical (denoted $\psi^{[ps = sp]}$) or were different (denoted $\psi^{[ps \neq sp]}$). We used program MARK to develop and analyze multistate models (White and Burnham 1999). We computed confidence intervals based on the profile likelihood method available in program MARK.

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. We used Akaike Information Criterion (AIC) to select the models that provided the most parsimonious description of

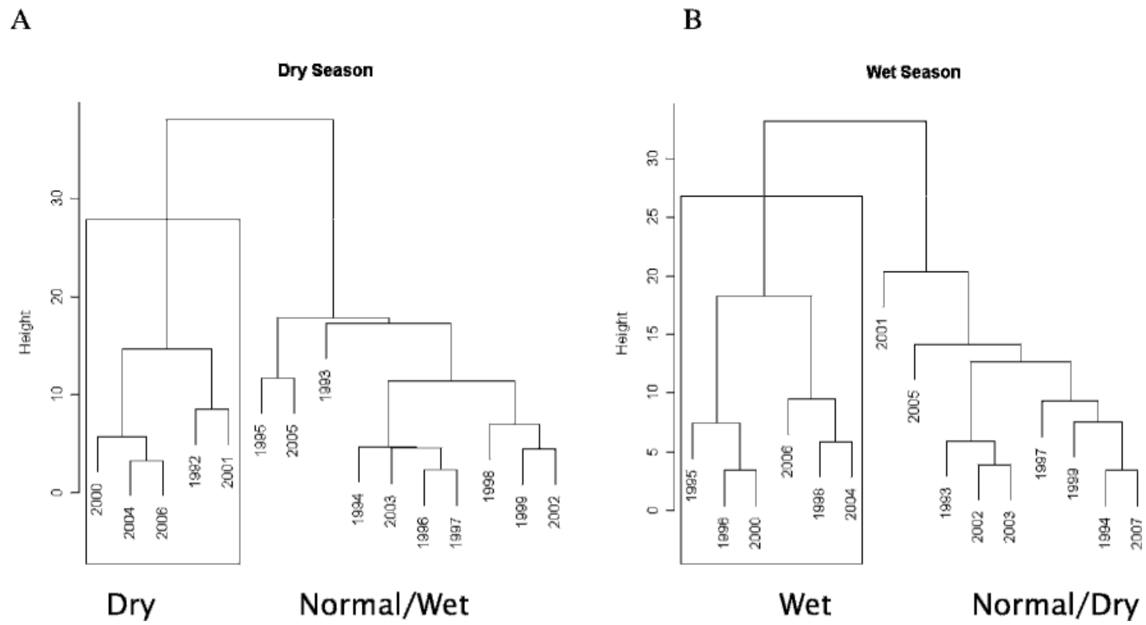

Figure 4. Cluster analyses used for A) dry and B) wet seasons since water year 1992 to determine which dry seasons were dry and which wet seasons were wet (boxes). Seasons not within boxes can be considered normal to wet for the dry seasons and normal to dry for the wet seasons.

the variation in the data (i.e., model with the lowest AIC) (Burnham and Anderson 2002). 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. We also presented ΔAICc (ΔAICc for the ith model was computed as $AICc_i$ - min (AICc), see Burnham and Anderson 2002). Models with a ΔAICc $<$ 2 were considered to receive good support from the data.

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

Hierarchical Clustering Analysis to Categorize Wet and Dry Seasons

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 4A). 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 4B). This lead to the designation of two dry time periods for which there was plant community data, November 2003 to June 2004 and November 2005 to June 2006, and four wet to normal time periods, November 2002 to June 2003, June 2003 to November 2003, November 2004 to June 2005, and June 2005 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) = 0.651) (Table 2). The second most parsimonious model, $\psi^{[ps \neq sp]}(WDyr2cat)$, had a AIC weight of on only 0.085. Model $\psi^{[ps \neq sp]}(WDyr3cat)$ 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, we 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

Table 2. Multistate models of transition probabilities (Ψ) for wet prairie to slough conversions (*ps*) and slough to wet prairie conversions (*sp*). The effect of wet and dry years were tested (*WDyr*), as was the effect of seasons (*SEAS*) and north-south water impoundment (*NS*). AIC_C is the Akaike Information Criterion, Δ AIC is adjusted for sample size, *w* is AIC_C weight, *K* is the number of parameters, and *DEV* is the deviance given by program MARK. Models with lower AIC_C and higher *w* are more parsimonious. Models that are within 2 AIC units of each other can be seen as equally parsimonious. The top model in this model set is 4 AIC units better than the second best model and has a weight of 0.651 making it a fairly good fit for our data. Models that received < 1% support from the data are not shown.

Model	AICc	Δ AIC_C	*w*	K	*DEV*
$\psi^{[ps \neq sp]}(WDyr3cat)$	107.798	0	0.651	6	52.724
$\psi^{[ps \neq sp]}(WDyr2cat)$	111.863	4.064	0.085	4	61.006
$\psi^{[ps \neq sp]}(WDyr * SEAS)$	112.056	4.258	0.077	8	52.679
$\psi^{[ps \neq sp]}(WDyr * NS)$	112.916	5.117	0.050	12	44.671
$\psi^{[ps \neq sp]}(WDyr_{prevSEAS})$	114.075	6.277	0.028	6	59.000
$\psi^{[ps \neq sp]}(WDyr_{prevYEAR})$	114.795	6.996	0.020	6	59.720
$\psi^{[ps \neq sp]}(\mathrm{cov}\,ar * NS)$	115.153	7.355	0.016	4	64.297
$\psi^{[ps = sp]}(NS)$	116.098	8.299	0.010	2	69.379
$\psi^{[ps = sp]}(WDyr * NS)$	116.111	8.313	0.010	6	61.036

($\psi^{ps} = 0.042$, SE = 0.041). The difference in ψ^{ps} between normal and dry years was statistically significant (ES = 0.119, 95% CI = 0.019–0.219), but it was not statistically significant between normal and wet years (ES = 0.077, 95% CI = −0.052–0.206), nor between wet and dry years (ES = 0.042, 95% CI = −0.039–0.123). Also, based on model $\psi^{[ps \neq sp]}(WDyr3cat)$, we 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 significant (ES = 0.181, 95% CI = 0.047–0.316), as was the difference between normal and wet years (ES = 0.111, 95% CI = 0.006–0.216). However, the difference in ψ^{sp} from wet to dry years was not (ES = 0.071, 95% CI = −0.099–0.241) (Figure 5). Based on AIC weight, all the other models received minimal support from the data.

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 we used mean, minimum, and maximum water depths, as well as a duration proxy that was the percent of time water levels were in the upper or lower quartile of all water levels for that season. In essence we combined many of the factors found in other studies (Kolipinski and

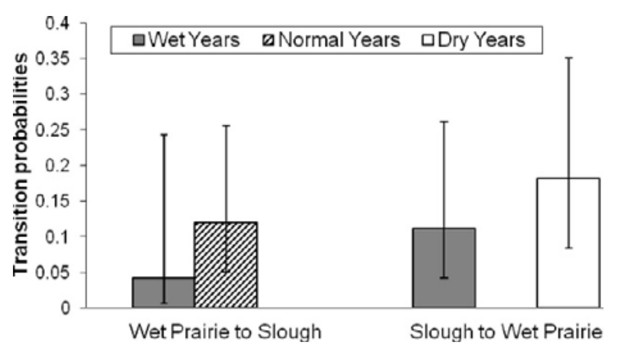

Figure 5. Transition estimates from the most parsimonious model $\psi^{[ps \neq sp]}(WDyr3cat)$ (see Table 2) for wet prairie and slough communities using wet, normal, and dry year classifications. Error bars correspond to 95% confidence intervals.

Higer 1969, Dineen 1974, Zaffke 1983) to be correlated with plant community conversion to categorize each year for which we had plant community data. It is not therefore, surprising that the model $\psi^{[ps \neq sp]}(WDyr3cat)$ was the most parsimonious in the model set. Our estimates support the conceptual models posed by Kolipinski and Higer (1969), Dineen (1974), Zaffke (1983), Zweig and Kitchens (2008), but are based on empirical data and statistically robust estimators.

Zweig and Kitchens (2008) preformed a different set of analysis on a subset of data from this study. They were interested in determining which aspects of previous hydrology (hydrology 6 months to 5 years prior to sampling) were most correlated to current community composition. The two models included in our model set that considered such lag effects had AIC weights of only 2% and 3%, whereas the top model that used hydrology at the time the sample was taken received 65% weight.

In the most parsimonious model $\psi^{[ps \neq sp]}(WDyr3cat)$ there were some anomalous transitions from slough to wet prairie, during wet years, for which there is a logical explanation. Most of the anomalous transitions occurred in northern WCA3A in 2005 when Hurricane Wilma passed over the Everglades in October. Although this hurricane did not produce copious rainfall in the Everglades, wind speeds up to 195 km/h occurred. 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 (Science Coordination Team 2003, Larsen et al. 2007).

It is worth noting that the 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. 2009). 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., $\psi^{sp} = \frac{[(\Psi]^{sp}_{Wet} \times 4 + \Psi^{sp}_{Normal} \times 3 + \Psi^{sp}_{Dry} \times 3)}{10}$), which if we 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. 2009b). 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. 2009b). For instance, managers may be interested in attaining target 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, 2008)

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 we 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 we believe that it will be possible to estimate this quantity as more data are 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.

The estimates provided in this study from our most parsimonious models are 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, and although the models we developed for this study were fairly simple, they provide a starting point from which additional levels of complexity can be added (as more data become available) (Martin et al. 2009b). In fact most methods to determine optimal decisions require relatively simple models (Williams et al. 2002). We 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.

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