Implications of discontinuous elevation gradients on fragmentation and restoration in patterned wetlands

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Abstract. Large wetlands around the world face the possibility of degradation, not only from complete conversion, but also from subtle changes in their structure and function. While fragmentation and isolation of wetlands within heterogeneous landscapes has received much attention, the disruption of spatial patterns/processes within large wetland systems and the resulting fragmentation of community components are less well documented. A greater understanding of pattern/process relationships and landscape gradients, and what occurs when they are altered, could help avoid undesirable consequences of restoration actions. The objective of this study is to determine the amount of fragmentation of sawgrass ridges due to artificial impoundment of water and how that may be differentially affected by spatial position relative to north and south levees. We also introduce groundbreaking evidence of landscape-level discontinuous elevation gradients within WCA3AS by comparing generalized linear and generalized additive models. These relatively abrupt breaks in elevation may have non-linear effects on hydrology and vegetation communities and would be crucial in restoration considerations. Modeling suggests there are abrupt breaks in elevation as a function of northing (Y-coordinate). Fragmentation indices indicate that fragmentation is a function of elevation and easting (X-coordinate), and that fragmentation has increased from 1988–2002. When landscapes change and the changes are compounded by non-linear landscape variables that are described herein, the maintenance processes change with them, creating a degraded feedback loop that alters the system’s response to structuring variables and diminishes our ability to predict the effects of restoration projects or climate change. Only when these landscape variables and linkages are clearly defined can we predict the response to potential perturbations and apply the knowledge to other landscape-level wetland systems in need of future restoration.

Key words: elevation; Everglades; fragmentation; FRAGSTATS; LANDSAT, restoration.

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INTRODUCTION

Degraded wetland systems do not always respond to restoration in a linear, predictable manner (Zedler 2000, Suding et al. 2004). A greater understanding of landscape drivers and pattern/process relationships, and what occurs when they are altered, could help avoid undesirable consequences of restoration actions (Briske et al. 2006, Alvarez-Cobelas et al. 2008). Large wetland landscapes often have subtle drivers or gradients that, in concert with fluvial dynamics, create extremely heterogeneous systems with distinct patterning (Ward et al. 1999). Disturbances may have different effects across these landscapes in response to even small
gradient changes, such as discontinuous elevation (e.g., abrupt changes in elevation between relatively flat areas) (Williams et al. 1999). As large wetlands with distinct patterning such as the Pantanal, Okavango Delta, and Everglades are being impacted by human activities on a landscape scale (Ellery et al. 2003, Junk et al. 2006), understanding the spatial dynamics of these systems, particularly when they are non-linear and/or unpredictable, becomes critical when considering restoration.

The Everglades is an example of how human disturbance can alter the patterns and processes within a wetland ecosystem, fundamentally changing landscape drivers within the system. Reduction of spatial extent, and alteration of sheetflow and seasonal hydrology, have created massive changes in the patterns and processes of the Everglades on several scales (DeAngelis 1994). Within a wetland system such as the Everglades, a feedback loop can be created by disturbing either patterns or processes that, in turn, affect system drivers, which may further alter patterns and/or processes of the system, potentially resulting in degradation due to fragmentation of its community components. While still considered ‘functional’ at a larger scale, wetlands in such degrading feedback loops may actually only be functioning superficially or not at all (Sklar et al. 2005). This more pervasive fragmentation can be difficult to detect, and is likely to become important as large wetland systems are increasingly fragmented and further disturbed by anthropogenic activities. We present the Everglades ridge and slough landscape (RSL) as an illustration of how subtle changes in landscape drivers have a profound impact on the spatial ecology of a system.

The historical RSL, a sub-tropical patterned peatland, was a dominant landscape type of the central portion of the Everglades. The RSL consists of long, linear strands of sawgrass (Cladium jamaicense Crantz.), longer hydroperiod sloughs, and occasional tree islands oriented parallel with the slow-moving flow of water from northwest to southeast. This landscape has been fragmented by compartmentalization, impoundment, and reduced flows (Ogden 2005) and is now in a degraded form. Intact portions of the RSL that remain are considered ecologically important, as in its unfragmented form, it was very important to the entire Everglades landscape by providing refugia for aquatic organisms during the dry season, creating a large amount of water storage potential, and was the main site for primary and secondary production (Ogden 2005).

Managers are interested in understanding the negative impacts that altered hydrology has had on the remaining RSL and how to alleviate further fragmentation through restoration (Science Coordination Team 2003). The majority of the remaining RSL in the Everglades is within Water Conservation Area 3A South (WCA3AS; Fig. 1), the focus of the Decompartmentalization and Sheetflow Enhancement Project (DECOMP), a main project in the Comprehensive Everglades Restoration Plan (http://www.evergladesplan.org/). DECOMP aims to restore WCA3AS by removing levees and canals that restrict sheetflow across the system. Updated knowledge of the system and very careful consideration of landscape gradients are vital for a successful project. Most literature concerned with fragmentation of the RSL describes Typha sp. invasion (Childers et al. 2003, McCormick et al. 2009), loss of sloughs to sawgrass (Larsen et al. 2007) or tree island disappearance (Willard et al. 2006), but do not address the loss of RSL to the effects of pooled, deep water, which is a common problem in the downstream end of impounded wetlands.

The objective of this study is to estimate the amount of fragmentation (fragmenting of linear sawgrass ridges into non-linear patches) due to artificial impoundment of water and to determine whether fragmentation may be differentially affected by spatial position relative to north and south levees. We test the hypothesis that discontinuous elevation gradients on the landscape-level exist within WCA3AS, as relatively abrupt breaks in elevation may have non-linear effects on hydrology and vegetation communities and would be crucial in restoration considerations.

**METHODS**

**Study area**

WCA3AS (Fig. 1) was established in the 1960s to provide water storage and flood control for the south Florida population (Light and Dineen 1994). The surrounding levees and water control
structures altered the seasonal flooding and sheetflow that were defining characteristics of historical Everglades hydrology and shaped the landscape over the past 5000 years (Kitchens et al. 2002). The northern section of WCA3AS has been chronically over-drained and disconnected from the characteristic sheetflow of the Everglades by Alligator Alley (Interstate 75)—the north boundary of WCA3AS, causing sawgrass (shorter hydroperiod vegetation community) to encroach into the sloughs. Culverts were installed under Alligator Alley to create wildlife crossings in 1992, which improved flow for the northern section of WCA3AS (Gunderson et al. 1995). An era of increased water depths (higher maximum water depths; Fig. 2) and longer hydroperiods also began circa 1991 (Zweig and Kitchens 2008), possibly affecting conditions within WCA3AS. WCA3AS was already managed as the wettest compartment within the water conservation areas of the Everglades (Childers et al. 2003) and higher water levels could be expected to exacerbate the disappearance of ridges within the system.

Elevation data and elevation breaks

When examining the hydrology of WCA3AS in a previous study (Zweig and Kitchens 2008), we observed possible evidence of an elevation break—a relatively abrupt change in topography on an otherwise continuous surface. To further investigate the possibility of discontinuous elevation gradients, we used the most comprehensive elevation data for the Everglades: the High Accuracy Elevation Database (HAED) from the U.S. Geological Survey ([http://sofia.usgs.gov/exchange/desmond/desmondelev.html](http://sofia.usgs.gov/exchange/desmond/desmondelev.html)). HAED data (±15 cm) was recorded at the peat surface at 400 m increments across the entire Everglades.

It is difficult to visualize landscape elevation changes within the RSL when local elevation changes (e.g., between adjacent slough, saw-
grass, and tree island communities) can be greater than landscape changes in elevation (e.g., between points separated by many kilometers along the direction of flow) (Gunderson 1994). Such subtle landscape-level elevation gradients in WCA3AS (<2 m over ~44 km) can be dominated by local community elevation changes (~1 m difference in elevation from slough floor to tree island surface over a distance of ~3 m). We chose to focus on a single community type (sloughs) to reduce this issue and created an elevation surface of only sloughs for our study area to aid in visualization of the elevation breaks. Only one third of the HAED points had vegetation data associated with them, so to isolate HAED points within sloughs, we overlaid the point elevation data on the slough/sawgrass/tree island classification described below and only the HAED points within sloughs were included in the analysis.

To aid in visualization of the elevation breaks, we kriged a slough elevation surface in Spatial Analyst in ArcGIS 9.3 (ESRI 2008) and displayed it in ArcGIS using the natural breaks (Jenks) classification (Fig. 1). This classification is user-defined and based on natural groupings and divides the surface where there are distinct differences in data values (Jenks 1967). Varying the number of breaks from two to six yielded slightly different groupings; however, the break

Fig. 2. Daily maximum water levels from 1978–2002 in Water Conservation Area 3A South, Florida, USA. This demonstrates the change in water levels circa 1992, highlighting the current, wetter hydrologic era that is affecting sawgrass ridge communities.
point along the 2.0 m contour remained constant in all trials. To provide a visual representation of potential discontinuous elevation gradients in WCA3AS we used five classes or four breaks (Fig. 1). For our analysis of differential fragmentation between northern and southern analysis, we used the 2.0 m contour.

As a formal test for non-linear change in elevation, we compared generalized linear models (GLM) with generalized additive models (GAM) with the same set of explanatory variables and gamma error distributions. GLM and GAM are regression methods used for predictive modeling (Guisan and Zimmerman 2000, Guisan et al. 2002). GLM assumes a linear relationship between the dependant and predictor variables, while GAM relaxes this assumption by using smoothing functions (Davidson and Knapp 2007) and allows for non-linear solutions (e.g., discontinuous elevation gradients). Significant GAMs with approximate estimated degrees of freedom larger than one were considered non-linear (Zuur et al. 2009). We used an analysis of variance (F-test) comparing model deviance of the models (Andersen 2009) to determine which better fit the data—a linear (GLM) or non-linear (GAM) solution.

We established nine transects along the historical flow pattern (Fig. 1) and extracted HAED for all points in sloughs that fell within one km to the left and right of each transect. We modeled change in elevation along each transect as a function of spatial location by northing (Y) and easting (X) to determine approximately where on the landscape non-linear elevation changes may occur. We conducted the current models using the statistical software R (version 2.12.2, CRAN 2011, packages “mgcv” and “stats”, procedures “gam” and “glm”) as:

Model 1 (GLM): elevation = Y + X,

Model 2 (GAM): elevation = s(Y) + s(X),

where X = X-coordinate in UTM(WGS84), Y = Y-coordinate in UTM(WGS84), and ‘s’ is a smoothing function (i.e., thin plate regression spline) applied to predictor variables in generalized additive models (Wood 2006). The statistical significance of X and Y were assessed at the 5% level.

Landscape analysis

Two cloud-free satellite images (Fig. 3) were obtained of the study area from approximately the same season (dry season) and water depth. Water depth between the images varied less than four inches and while it may affect finer-scale classifications (e.g., emergent communities vs. floating leaf aquatic communities) it would not have a considerable effect on this classification of dense sawgrass and open-water slough habitats in the same pixel. The images obtained were from 1988 and 2002–2002 approximating present conditions and 1988 representing the drier hydrologic era. The images—March 5, 1988 (Landsat TM) and February 5, 2002 (Landsat ETM+)—were radiometrically corrected and geometrically corrected to UTM WGS84, Zone 17, using DOQQ aerial imagery until the root mean square errors were less than 0.5 pixel. Both images were classified with a minimum of 30 training points per class (90+ points), and non-parametric, paralleleipped supervised classification in ERDAS Imagine, with three vegetation classes: slough, sawgrass, and tree island (Fig. 3b). Thirty randomly chosen GPS points of each vegetation class (90 total) were obtained from the field in 2007 as references for classification accuracy testing.

To assess landscape response to the potential effect of discontinuous elevation, we randomly chose 1-km² plots from the 2002 classified image (n = 107) and calculated an average elevation, slope, and aspect for each pixel. Elevation was used to link fragmentation response to the discontinuous elevation analysis. Slope and aspect were used as secondary terrain attributes that describe the geomorphology and flow of water on the landscape (Franklin 2009). The plots were analyzed separately using FRAGSTATS (McGarigal et al. 2002), a public domain software that computes landscape metrics on spatial categorical data. We chose four class metrics (Table 1) for sawgrass—the focal class of interest—to represent fragmentation of ridges in the RSL. The calculated metrics for the 107 1-km² plots were modeled independently using GLM and GAM methods as:

Model 3 (GLM): metric = elevation + X + slope + aspect

Model 4 (GAM): metric = s(elevation) + s(X) + s(slope) + s(aspect)
where elevation = height above sea level (m), X = X-coordinate in UTM(WGS84), slope = steepest change in altitude within the pixel of interest and its eight neighboring pixels, and aspect = direction of slope (°). Elevation and Y-coordinates (the horizontal position in the landscape) were highly correlated ($r^2 = 0.8$), so Y was excluded from the analysis. Models were optimized by...
testing the significance of each of the explanatory variables at the 5% level. As a formal test for non-linearity, we compared the deviance of model 3 to model 4 (ANOVA, F-test) (Andersen 2009). Significant smoothing functions with approximate estimated degrees of freedom larger than one were considered non-linear (Zuur et al. 2009). Statistical modeling was conducted using the statistical program R (version 2.12.2, CRAN 2011, packages “mgcv” and “stats”, procedures “gam” and “glm”).

To account for the effects that an elevation break might have on hydrology in an impounded system (such as pooling), and the differential effects of hydrology previously described in WCA3AS, the 1988 and 2002 classifications were split into northern and southern sections along the 2.0 m contour derived from the kriged surface. This split is supported by the modeled elevation breaks (Fig. 1), the Jenks natural breaks method, and visual differences from the satellite imagery. It is a general contour to facilitate comparisons between the northern and southern sections of WCA3AS which have been subject to different hydrologies since impoundment. The entire northern and southern sections were analyzed in FRAGSTATS using the same four metrics (Table 1) for slough and sawgrass to quantify the degree of fragmentation over time (McGarigal and Marks 1995).

**RESULTS**

**Elevation breaks**

The X-coordinate variables were dropped from models 1 and 2 as they were not significant at the 5% level. The resulting models included effects of Y-coordinates on changes in elevation. Changes in elevation were best modeled using a GAM over a GLM approach along seven out of nine transects in WCA3AS (Table 2). In addition, the relatively high number of estimated degrees of freedom (> 1 df indicates non-linearity) associated with each of the smoothing functions

| Transect | Estimated df | r² | Deviance explained (%) | GLM or GAM | n | F-stat | p-value |
|----------|--------------|----|------------------------|------------|---|--------|---------|
| 1        | 6.9          | 0.961 | 96.5                | GAM        | 79 | 235.2  | <0.001  |
| 2        | 3.093        | 0.896 | 88.6                | GAM        | 77 | 139.3  | <0.001  |
| 3        | 6.695        | 0.927 | 93.8                | GAM        | 91 | 145.2  | <0.001  |
| 4        | 8.501        | 0.854 | 86.5                | GAM        | 105 | 66.07  | <0.001  |
| 5        | 7.692        | 0.824 | 83.2                | GAM        | 109 | 57.82  | <0.001  |
| 6        | 3.628        | 0.664 | 67.6                | GAM        | 80 | 34.28  | <0.001  |
| 7        | 4.93         | 0.548 | 58.1                | GAM        | 67 | 13.53  | <0.001  |
| 8        | 1            | 0.155 | 0.2                 | neither    | 67 | 12.99  | <0.001  |
| 9        | 1            | 0.0271 | 4.8              | neither    | 48 | 2.296  | 0.137   |

Notes: Estimated degrees of freedom (1 df = linear predictor), r², and deviance explained are from the GAM analysis. Greater than 1 df is indicative of non-linearity, but is not directly equivalent to the number of significant changes in elevation. The F-statistics and p-values represent results from ANOVAs comparing the model deviance of the GAM to the GLM.
provide further indication of non-linear or discontinuous changes in elevation along the historical flow gradient (Table 2).

Our results suggest that there are multiple elevation breaks and that the number and position differ by where they occur on the landscape (Fig. 1). The elevation gradient is steepest in the northeast (upstream) and flattens out considerably in the southwest (downstream) (Fig. 4). The more southern, flatter transects were not well represented with either modeling procedure, indicating no statistically distinct spatial pattern in elevation. These elevation breaks along the modeled transects support the five elevation classes in the Jenks natural method chosen a priori to visually represent the discontinuous elevation within WCA3AS, and suggest that there are more breaks than we previously suspected.

**Landscape analysis**

The 1988 and 2002 images were classified with an overall accuracy of 88.76% and 95.51% respectively. The difference in accuracy could be explained by the time lag between the image and field data and the obvious vegetation community changes that have occurred. Visually, WCA3AS still has remnants of the characteristic linear landscape pattern that was formed by historic sheetflow. Much of the sawgrass loss occurs along the south and east levees, and the southern section of WCA3AS has a particular pattern of sawgrass disappearing from the fringes of tree islands.

Fig. 4. Average elevations along transects following the historical flow pattern of Conservation Area 3A South, Florida, USA. 1 is the northeastern most transect and 9 is in the extreme southeast of the study area.
The landscape metrics calculated in FRAGSTATS are reported only for sawgrass and slough, as tree islands and cattail were combined in the classification, and we were not interested in changes in tree islands. The metrics illustrate a decline in the area and an increase in the fragmentation of sawgrass (Table 3) in both the north and south sections of WCA3AS. In 1988, there was approximately 200% more sawgrass in the north than in the south, and 260% more sloughs in the south. The area (area-weighted mean) decreased for sawgrass in both the north and south between 1988 and 2002, and slough area increased for both (Table 3). The cohesion and division metrics indicate sawgrass became less cohesive and more divided over time, while the converse was true for slough. There was a greater loss of sawgrass in the northern section, but the density of sawgrass patches increased by almost two times more in the southern end than in the north, indicating greater fragmentation of the south’s RSL.

Modeling of class-level (sawgrass) FRAGSTATS metrics by elevation, aspect, slope, and spatial positioning (northing and easting) demonstrate a consistent relationship between elevation and fragmentation (Table 4). Elevation was a significant predictor for all metrics and easting (X) was a significant predictor of two of four metrics (i.e., cohesion and division) (Table 4).

**DISCUSSION**

We present elevation as an example of a subtle measure that is a profound landscape driver. Our analysis emphasizes the need to look beyond general assumptions (the Everglades as a ‘flat’ system), particularly in a restoration setting. Our results have clear management implications for large-scale systems similar to the Everglades, especially where changes in elevation have been identified as an important ecological component (Ellery et al. 1993, Gumbricht et al. 2005, Hamilton 2002, Heckman 1998). Accounting for subtle changes in landscape patterns that drive ecological processes is important for understanding the complete spatial dynamics of the system, including changes to habitat and wildlife populations, and reduces uncertainty for future conservation.

**Elevation break**

Literature research of site geology reveals that the contour used to separate the north and south study areas (Fig. 5) follows the general boundary between the underlying Miami and Fort Thompson geological formations (Gleason and Stone 1994). The relatively steep slope in the northeast

Table 3. FRAGSTATS metrics calculated for slough and sawgrass communities in the northern and southern sections of Water Conservation Area 3A South, Florida, USA.

| Section/community | Patch area (ha) | Patch density | Cohesion | Division |
|-------------------|----------------|--------------|----------|----------|
| North             |                |              |          |          |
| Slough 1988       | 1151.42        | 6.54         | 98.77    | 0.99     |
| Slough 2002       | 2633.84        | 6.24         | 99.29    | 0.98     |
| Difference        | 1482.42        | 0.30         | 0.51     | 0.01     |
| Sawgrass 1988     | 23928.43       | 4.69         | 99.90    | 0.66     |
| Sawgrass 2002     | 17382.97       | 7.19         | 99.86    | 0.79     |
| Difference        | -6545.46       | -2.50        | -0.04    | 0.13     |
| South             |                |              |          |          |
| Slough 1988       | 36908.07       | 2.26         | 99.95    | 0.53     |
| Slough 2002       | 40940.99       | 2.01         | 99.97    | 0.45     |
| Difference        | 4032.92        | 0.24         | 0.02     | -0.08    |
| Sawgrass 1988     | 1265.36        | 13.19        | 97.90    | 0.99     |
| Sawgrass 2002     | 75.00          | 17.14        | 92.74    | 1.00     |
| Difference        | -1190.36       | 3.95         | -5.15    | 0.01     |

*Note: Data is from classified LANDSAT TM and ETM+ satellite images from 1988 and 2002.*

The landscape metrics calculated in FRAGSTATS are reported only for sawgrass and slough, as tree islands and cattail were combined in the classification, and we were not interested in changes in tree islands. The metrics illustrate a decline in the area and an increase in the fragmentation of sawgrass (Table 3) in both the north and south sections of WCA3AS. In 1988, there was approximately 200% more sawgrass in the north than in the south, and 260% more sloughs in the south. The area (area-weighted mean) decreased for sawgrass in both the north and south between 1988 and 2002, and slough area increased for both (Table 3). The cohesion and division metrics indicate sawgrass became less cohesive and more divided over time, while the converse was true for slough. There was a greater loss of sawgrass in the northern section, but the density of sawgrass patches increased by almost two times more in the southern end than in the north, indicating greater fragmentation of the south’s RSL.

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**Elevation break**

Literature research of site geology reveals that the contour used to separate the north and south study areas (Fig. 5) follows the general boundary between the underlying Miami and Fort Thompson geological formations (Gleason and Stone 1994). The relatively steep slope in the northeast
of WCA3AS, visible in our analysis, possibly reflects this underlying geology as the landscape grades into Tamiami Basin and the Shark River Bedrock Slough (Gleason and Stone 1994) on the east side of the study area (lightest green area in Fig. 1). Slope flattens out considerably in the southwest and is likely due to autogenic processes instead of underlying geology. Peat has accumulated in this area from increased inundation caused by downstream impoundment (Craft

Fig. 5. Non-parametric, supervised classification of 1988 and 2002 images of Water Conservation Area 3A South, Florida, USA from the north and south split from elevation analysis.
and Richardson 2008). The heterogeneous, distinct changes in elevation over the landscape, both northing and easting, are very different from descriptions of the Everglades that indicate a wide expanse of marsh with flat relief (e.g., Loveless 1959, Kerry and Ornes 1975). What literature there is on elevation differences in the Everglades is concerned with microtopography between vegetation classes, which does not necessarily reflect the underlying bedrock (Loveless 1959, Sklar and van der Valk 2002). This spatial variability of elevation may not be a novel concept to scientists involved in research in the Everglades (DeAngelis 1994), but this is the first description of such heterogeneous elevation on a landscape scale. The importance of local microtopography cannot be denied, but it occurs on top of the landscape-level heterogeneity that we describe in WCA3AS, creating a compound effect of elevation on landscape processes and patterns.

Describing the topography of the landscape is important, as water depths in WCA3AS are monitored using a 3-gauge average. According to our data, this average would not adequately represent the way water will move across the landscape. A stage of 2.0 m at the average gage will translate into different water depths for the northeast as opposed to the southwest. A better understanding of how water will flow and pool due to the discontinuous elevation on the landscape would be key for hydrologic restoration and management decisions, as the depth of water affects the vegetation communities that will be present or are desired (Zweig and Kitchens 2008).

Discontinuous elevation is also an important consideration, as it will increase the area that is affected by small hydrologic changes, controlling how water progresses up the gradient, and causing non-continuous change in vegetation communities (Williams et al. 1999) and habitat for critically endangered fauna (Kitchens et al. 2002). For example, the emergent communities which serve as foraging habitat for the endangered Florida snail kite are being drowned out in the southern end of WCA3AS by extended hydroperiods from impounded water (Kitchens et al. 2002). On a continuous elevation gradient, these emergent communities could simply displace upslope, keeping pace with higher water levels. However, the stepped nature of WCA3AS impedes that process, drowning out large portions of foraging habitat as water pools below elevation breaks. Knowledge of discontinuous elevation gradients, and perched and depressed areas within WCA3AS and considering them for restoration decisions reduces uncertainty of restoration actions; particularly when hydrology is such an important factor (Fuller et al. 2008) and small changes in elevation lead to large differences in water depths and nutrient cycles (Saha et al. 2010).

**Landscape analysis**

Restoring the RSL pattern in WCA3AS is of particular interest for the Everglades ecosystem restoration (Science Coordination Team 2003). Here we provide information for restoration by demonstrating the relationship between elevation/spatial position and fragmentation, and by quantifying the amount of fragmentation and loss of sawgrass ridges from altered hydrology. According to recent models (Larsen et al. 2007), water depths within the RSL are important to vertical peat accretion, and our data support this by demonstrating the general replacement of sawgrass ridges by more aquatic sloughs, presumably due to pooling and higher water depths in the wet era beginning circa 1991 (Fig. 2) or improvements to Alligator Alley around the same time period.

An important distinction to note is the differential effect altered hydrology has on WCA3AS, particularly between the northern and southern sections separated by the 2.0 m contour (Fig. 5). We can state that our study area, as a whole, is losing sawgrass ridges, but the manner in which they are lost and fragmented is important to our understanding of how the area will respond to restoration. The northern section of our study site was historically over-drained and dry, allowing sawgrass to encroach into the sloughs. The 1988 image shows cohesive patches of sparse sawgrass (i.e., sawgrass that had encroached in to sloughs) that are fragmented in the 2002 image. This fragmentation appears to be a restoration, not degradation, of the RSL pattern and is supported by the increase of linearity of both slough and sawgrass in 2002. The southern section, however, has lost a considerable amount of sawgrass to slough, but the fragmentation appears to be degradation of the RSL pattern and
drowning of the sawgrass ridges from high water and levee effects. Our analysis for the southern section suggests fragmentation via a loss of cohesion of sawgrass ridges and consolidation of sloughs, but not a total disappearance of sawgrass. The sympodial growth form of sawgrass allows it to persist in less than ideal conditions for an extended period (Snyder and Richards 2005) by growing up, forming tussocks—or fragmenting at a local scale—instead of growing in continuous strands. This appears to be the pattern reflected in the southern portion of WCA3AS. Reduced ponding of the southern section of WCA3AS could initiate restoration of the RSL where the pattern is still somewhat intact. However, drying out the southern section without increasing water delivery to the north could create conditions conducive to destructive fires.

Loss of topography is extremely important, as ridges are thought to be formed and maintained from already existing ‘bumps’ or proto-ridges (Larsen et al. 2007, Givnish et al. 2008). Disturbance and removal of a ridge by fire or drowning can completely arrest the pattern and process that create ridges. The altered system reinforces the trend of ridge fragmentation and slough proliferation with reduced chances of reversing the direction of change. Our data support the hypothesis that the mechanisms of current fragmentation are prolonged ponding and reduction of flow by compartmentalization and deeper water, exacerbated by discontinuous elevation within WCA3AS.

**Conclusion**

There is an attempt to restore flow and natural hydrologic regimes to WCA3AS within Everglades restoration, but more direct evidence of the pattern/process linkages, consideration of the stepped nature and altered elevation patterns of WCA3AS, and monitoring of the RSL pattern are critical to the success of the complete Everglades ecosystem. Only when these landscape variables and linkages are clearly defined can we predict the response to potential perturbations and apply the knowledge to other large wetland systems in need of conservation or restoration.

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**Literature Cited**

Alvarez-Cobelas, S., S. Sánchez-Carrillo, S. Cirujoano, and D. G. Angeler. 2008. Long-term changes in spatial patterns of emergent vegetation in a Mediterranean floodplain: Natural versus anthropogenic constraints. Plant Ecology 194:257–271.

Andersen, R. 2009. Nonparametric methods for modeling nonlinearity in regression analysis. Annual Review of Sociology 35:67–85.

Briske, D. D., S. D. Fuhlen-dorf, and F. E. Smeins. 2006. A unified framework for assessment and application of ecological thresholds. Rangeland Ecology and Management 59:225–236.

Childers, D. L., R. F. Doren, R. Jones, G. B. Noe, M. Rugge, and L. J. Scinto. 2003. Decadal change in vegetation and soil phosphorous pattern across the Everglades landscape. Journal of Environmental Quality 32:344–362.

Craft, C. B. and C. J. Richardson. 2008. Soil characteristics of the Everglades Peatland. Pages 59–72 in C. J. Richardson, editor. The Everglades experiments: lessons for ecosystem restoration. Springer Science, New York, New York, USA.

CRAN. 2011. Comprehensive R Archive Network. (http://cran.r-project.org/)

Davidson, C. and R. A. Knapp. 2007. Multiple stressors and amphibian declines: dual impact pesticides and fish on yellow-legged frogs. Ecological Applications 17:587–597.

DeAngelis, D. L. 1994. Synthesis: spatial and temporal characteristics of the environment. Pages 307–320 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. CRC Press, Boca Raton, Florida, USA.

Ellery, W. N., T. S. McCarthy, and N. D. Smith. 2003. Vegetation, hydrology, and sedimentation patterns on the major distributary system of the Okavango fan, Botswana. Wetlands 23:357–375.

Ellery, W. N., K. Ellery, and T. S. McCarthy. 1993. Plant distribution in islands on the Okavango Delta, Botswana: determinants and feedback interactions. African Journal of Ecology 31:118–134.

ESRI. 2008. ArcGIS—a complete and integrated system. Environmental Systems Research Institute,
Redlands, California, USA.
Franklin, J. 2009. Mapping species distributions: spatial inference and prediction. Cambridge University Press, New York, New York, USA.
Fuller, M. M., L. J. Gross, S. M. Duke-Sylvester, and M. Palmer. 2008. Testing the robustness of management decisions to uncertainty: Everglades restoration scenarios. Ecological Applications 18:711–723.
Givnish, T. J., J. C. Volin, V. D. Owen, V. C. Volin, J. D. Muss, and P. H. Glaser. 2008. Vegetation differentiation in the patterned landscape of the central Everglades: importance of local and landscape drivers. Global Ecology and Biogeography 17:384–402.
Gleason, P. J. and P. Stone. 1994. Age, origin, and landscape evolution of the Everglades peatland. Pages 149–198 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. CRC Press, Boca Raton, Florida, USA.
Gumbricht, T., T. S. McCarthy, and P. Bauer. 2005. The micro-topography of the wetlands of the Okavango Delta, Botswana. Earth Surface Processes and Landforms 30:27–39.
Gunderson, L. H., S. S. Light, and C. S. Holling. 1994. Lessons from the Everglades. BioScience 45:566–573.
Gunderson, L. H. 1994. Vegetation of the Everglades: determinants of community composition. Pages 323–340 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. CRC Press, Boca Raton, Florida, USA.
Guisan, A. and N. E. Zimmerman. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.
Guisan, A., T. C. Edwards, Jr., and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157:89–100.
Hamilton, S. K. 2002. Hydrological controls of ecological structure and function of the Pantanal wetland (Brazil). Pages 133–158 in M. E. McClain, editor. The ecohdrology of South American rivers and wetlands. International Association of Hydrological Sciences Press, Wallingford, Oxforshire, UK.
Heckman, C. W. 1998. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dry climatic zone: V. Aquatic invertebrate communities in the Pantanal of Mato Grosso, Brazil. International Review of Hydrobiology 83:31–63.
Jenks, G. F. 1967. The data model concept in statistical mapping. International Yearbook of Cartography 7:186–190.
Junk, W. J., C. N. da Cunha, K. M. Wantzen, P. Petermann, C. Strüssmann, M. I. Marques, and J. Aidis. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. Aquatic Science 68:278–309.
Kerry, K. K. and W. H. Ornes. 1975. The autecology of sawgrass in the Florida Everglades. Ecology 56:162–171.
Kitchens, W. M., R. E. Bennett, and D. L. DeAngelis. 2002. Linkages between the snail kite population and wetland dynamics in a highly fragmented south Florida hydroscape. Pages 183–204 in J. W. Porter and K. G. Porter, editors. The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: an ecosystem sourcebook. CRC Press, Boca Raton, Florida, USA.
Larsen, L. G., J. W. Harvey, and J. P. Crimoldi. 2007. A delicate balance: ecohydrological feedbacks governing landscape morphology in a lotic peatland. Ecological Monographs 77:591–614.
Light, S. S., and J. W. Dineen. 1994. Water control in the Everglades: a historical perspective. Pages 47–84 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. CRC Press, Boca Raton, Florida, USA.
Loveless, C. M. 1959. A study of the vegetation in the Florida Everglades. Ecology 40:1–9.
McCormick, P. V., S. Newman, and L. W. Vilchek. 2009. Landscape responses to eutrophication: loss of slough habitat in the Florida Everglades. Hydrobiologia 621:105–114.
McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. (http://www.umass.edu/landeco/research/fragstats/fragstats.html)
McGarigal, K. and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA Forest Service General Technical Report PNW–351.
Ogden, J. C. 2005. Everglades ridge and slough conceptual ecological model. Wetlands 25:810–820.
Saha, A. K., L. D. O. Sternberg, M. S. Ross, and F. Miralles-Wilhelm. 2010. Water source utilization and foliar nutrient status differs between upland and flooded plant communities in tree islands. Wetland Ecology and Management 18:343–355.
Science Coordination Team. 2003. The role of flow in the Everglades ridge and slough landscape. South Florida Ecosystem Restoration Working Group, U.S. Geological Survey, Washington, D.C., USA.
Sklar, F. H., M. J. Chimney, S. Newman, P. McCormick, D. Gawlik, S. Miao, C. McCoy, W. Said, J. Newman, C. Coronado, G. Crozier, M. Korvela, and K. Rutcheon. 2005. The ecological-societal underpinnings of Everglades restoration. Frontiers in Ecology and the Environment 3:161–169.
Sklar, F. H. and A. van der Valk. 2002. Tree islands of the Everglades: an overview. Pages 1–18 in F. H. Sklar and A. van der Valk, editors. Tree islands of the Everglades. Kluwer Academic, Norwell, Massachusetts, USA.
Snyder, J. M. and J. H. Richards. 2005. Floral
phenology and compatibility of sawgrass, Cladium jamaicense Cyperaceae. American Journal of Botany 92:736–743.
Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology and Evolution 19:46–53.
Ward, J. V., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers 15:125–139.
Willard, D. A., C. E. Bernhardt, C. W. Holmes, B. Landacre, and M. Marot. 2006. Response of Everglades tree islands to environmental change. Ecological Monographs 76:565–583.
Williams, K., K. C. Ewel, R. P. Stumpf, F. E. Putz, and T. W. Workman. 1999. Sea-level rise and coastal forest retreat on the west coast of Florida, USA. Ecology 80:2045–2063.
Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall, CRC Press, Boca Raton, Florida, USA.
Zedler, J. B. 2000. Progress in wetland restoration ecology. Trends in Ecology and Evolution 15:402–407.
Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Science, New York, New York, USA.
Zweig, C. L. and W. M. Kitchens. 2008. Effects of landscape gradients on wetland vegetation communities: information for large-scale restoration. Wetlands 28:1086–1096.