ECOSYSTEMS

Hydrologic Modification and the Loss of Self-organized Patterning in the Ridge–Slough Mosaic of the Everglades

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ABSTRACT

The ridge–slough landscape of the Everglades (Florida, USA), is characterized by elevated ridges dominated by sawgrass (Cladium jamaicense) interspersed among deeper sloughs dominated by floating, submerged and emergent macrophytes and calcareous periphyton. Interactions among hydrologic conditions (water depth, hydroperiod), plant composition and production, and respiration are hypothesized to create alternative peat accretion equilibria at the point scale, while spatial interactions among patches create regular pattern at the landscape scale. Despite significant research on these interactions, few studies have examined the hypothesis that the ridge–slough landscape consists of spatially coupled alternative stable patch states, and none has used diagnostic indicators thereof to assess landscape resilience to hydrologic change. Dense random sampling of water depths (a proxy for soil elevation) along a gradient of hydrologic impairment of drained to relatively natural to impounded conditions was used to evaluate four predictions related to this hypothesis: (1) bimodal soil elevation distributions show strong fidelity to community type; (2) positive autocorrelation at short distances with negative values at longer distances; (3) strong anisotropy (diagnostic of flow orientation), and spatial structure (diagnostic of the strength of landscape self-organization); and (4) loss of these features with hydrologic modification. Our results support the hypothesis that soil elevations are strongly bimodal and anisotropic in areas with minimal hydrologic impact, and spatial autocorrelation patterns indicate the operation of scale-dependent feedbacks. These metrics change markedly with hydrologic modification, although with differences between drainage and impoundment. Moreover, changes in landform precede associated changes in vegetation, suggesting their utility as diagnostic indicators of landscape degradation and recovery.

Key words: biogeomorphology; bi-modality; scale-dependent feedbacks; alternative stable states; peat accretion; patterned landscape.

INTRODUCTION

Self-organized patterned landscapes arise in response to spatial feedbacks, wherein, at a minimum, the presence of one patch type inhibits suitability for that patch type at adjacent sites (Ludwig and others 1999; Rietkerk and others 2004a, b; Rietkerk and van de Koppel 2008). Local positive feedbacks, where biota enhance local site conditions (for example, by altering nutrient content, infiltration rates or soil elevation), can act along with distal negative feedbacks to create diverse landscape pattern geometry (Eppinga and others 2009a). Moreover, coupled local positive and distal negative feedbacks can create conditions of global bi-stability, where both patterned and unpatterned landscapes are stable under the same environmental conditions (van de Koppel and Crain 2006; Rietkerk and van de Koppel 2008). Although several studies have considered feedbacks that control pattern in minimally impacted systems, few have empirically documented changes in patterning that arise from changing environmental drivers (but see Eppinga and others 2009b). This is an important gap because potential hysteresis in shifts between patterned and unpatterned states (Rietkerk and others 2004a) could confound restorative action and prioritizes identifying thresholds beyond which pattern is lost.

Peatlands are formed during persistent periods of net autotrophy (primary production exceeding ecosystem respiration), and maintained under conditions of long-term carbon flux equilibrium; therefore, local feedbacks among hydrology, primary production, and respiration are paramount. By extension, persistent patterning in peatlands suggests that all patch types comprising the mosaic represent alternative ecological configurations to achieve the nominal landscape accretion rate (Belyea and Clymo 2001). Patches whose attributes (hydroperiod, productivity) lead to accretion rates different from the landscape mean are transient. Empirical diagnostic indicators of the existence of alternative stable configurations include multimodal distributions of key ecosystem state variables (for example, peat elevation—Eppinga and others 2008; herbaceous vegetation—Ludwig and others 1999). Moreover, changes in environmental drivers can adjust the prevalence of alternative modes, and may force convergence on one mode. It is conceptually important to distinguish feedbacks that regulate point-scale configurations from landscape scale processes that control the arrangement and size of patches. Describing pattern persistence and loss in peatlands requires attention to both.

The ridge–slough patterned peatland is a dominant feature of the Everglades (Florida, USA) in which isolated elevated ridges, oriented parallel to flow and dominated by sawgrass (*Cladium jamaicense*), are surrounded by deeper sloughs inhabited by floating-leaved, submerged and emergent plant species. These two modes have existed for at least 2,700 years, with patch centers persistent in their present configuration for at least 1,000 years (Bernhardt and Willard 2009). Wu and others (2006) document recent changes in landscape pattern, attributing these to regional water management (that is, compartmentalization and drainage; Light and Dineen 1997) and agricultural nutrient enrichment (Gaiser and others 2005; Hagerthey and others 2008).

In areas where hydrology and water quality are considered least modified (for example, portions of Water Conservation Area (WCA) 3 and Everglades National Park (ENP); SCT 2003), the landscape is characterized by 'corrugation' in the peat surface (Baldwin and Hawker 1915; Loveless 1959; Sklar and others 2004). Elsewhere, hydrologic changes have been linked with changes in patch prevalence and pattern (Wu and others 2006), and topographic flattening (Givnish and others 2007). In particular, contemporary hydrology in WCA 3 (including 3A-N, 3A-S, and 3B) has been modified for water storage (Walters and others 1992) and is affected by the presence of road corridors orthogonal to regional flow in both the north, where conditions are drained relative to historic regimes, and south, where conditions are impounded. Stage and flow control in WCA 3B has dramatically decreased hydrologic variation and longitudinal flux, compounding effects of severe historical drainage. Because the best-conserved landscape falls between the drained northern end and impounded southern end of WCA 3 (SFWMD 1992), our focus is on changes in ridge–slough pattern spanning the existing hydrologic gradient in that unit.

Recent studies have shown that soil elevation in the ridge–slough landscape (excluding tree islands) is decoupled from the underlying bedrock (Lewis 2005; Givnish and others 2007), indicating that surface morphology results from feedbacks among vegetation production, respiration, and hydrologic conditions. Long-term persistence of elevation differences between ridges and sloughs are hypothesized to reflect equivalence in net peat production (Larsen and others 2007) of approximately 1–6 mm y^{-1} (400–100 years before present; Bernhardt and Willard 2009). Our simplified point-scale conceptual model (Figure 1A) assumes that
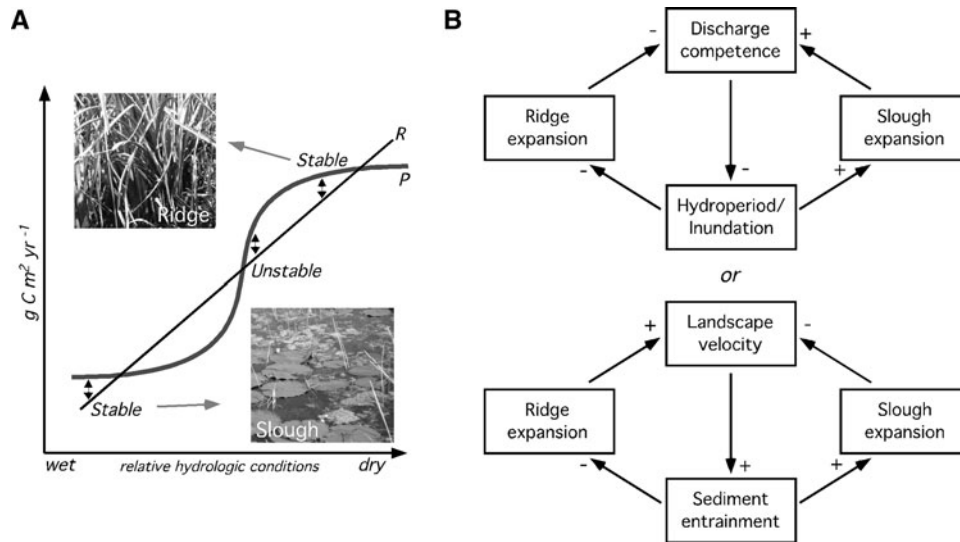
Figure 1. **A** Conceptual model of alternative stable configurations in the carbon budgets of ridges and sloughs, leading to differential peat elevations on the landscape. Under historic hydrological conditions, there are two possible, positive, peat-accreting configurations at the point-scale for the Everglades and one unstable, accreting configuration. Any small perturbation in hydrologic conditions forces the system to push to either a ridge or a slough accreting equilibrium. **B** Although multiple mechanisms for ridge–slough patterning have been suggested in the literature, patterning in the Everglades would arise as a result of scale-dependent feedbacks between local site conditions (ridge or slough) and regional hydrology.

respiration increases monotonically with soil elevation, whereas primary production follows a sigmoid curve, with the inflection due to transition at intermediate water depths from slough vegetation to sawgrass. Two distinct, stable vegetative-elevation configurations yield the same long-term peat accretion rates: ridges at higher elevation with high primary production (Loveless 1959; Craft and Richardson 1993; Childers and others 2003; SCT 2003) balanced by greater respiration due to increased soil exposure. Similarly, sloughs at lower elevations have lower primary production and more labile litter (Vaithiyanathan and Richardson 1998; Lewis 2005; Jorczak 2006), but also lower peat oxidation due to infrequent exposure. This model suggests two landscape modes of peat elevation, but does not address their prevalence and spatial arrangement. It also implies that the effects of extended hydrologic modification would move the entire landscape to the left (wetter) or right (drier), prompting sites in one basin of attraction to converge on the other.

The prevalence and spatial configuration of ridges and sloughs are widely thought to be a response to flow (SCT 2003). Both patch types are oriented parallel to north–south regional flow and the spatial pattern exhibits a characteristic wavelength perpendicular to flow of approximately 100 to 150 m. Despite a general consensus regarding

the importance of flow, contrasting views exist on the precise mechanism via which flow controls pattern formation. The evolution of ridge–slough patterning has most often been attributed to flow velocity; higher flow velocity in sloughs is theorized to entrain organic sediments, which are subsequently deposited in ridges (SCT 2003; Larsen and others 2007; Larsen and others 2010). The implied distal feedback of this mechanism is the effect of lateral ridge expansion on slough velocity; increased prevalence of ridges would concentrate flow in sloughs, increasing velocity and thereby increasing particle entrainment in sloughs (Figure 1B); increased longitudinal expansion of ridges would not create the same effect provided sloughs are hydraulically connected.

In response to several observations about the contemporary and historical Everglades that run counter to the sediment entrainment hypothesis, Cohen and others (2010) posit an alternative mechanism for patch elongation. They note two processes via which ridge or slough expansion could affect regional hydrology in a manner that inhibits further expansion. The first is water displacement, with expanding ridges inducing longer hydroperiods given the same standing water volume (and expanding sloughs similarly shortening hydroperiods); this effect would be spatially isotropic yielding round patch geometry, likely

influencing patch prevalence, and would control patch geometry in the absence of flow. The second is the effect of patch expansion on landscape specific discharge competence, defined as the ability of the landscape to shed water per unit cross-section. Flow through longitudinally connected sloughs dominates landscape discharge (sloughs move ca. 85% of the water; Harvey and others 2009), and reduced slough area principally affects water depth, not velocity (due to high flow friction in both patch types). Cohen and others (2010) suggest that lateral ridge expansion would reduce specific discharge competence, leading to higher water levels for a given discharge, ultimately creating hydroperiod and water depth conditions unfavorable for ridges. The reciprocal process—increased slough area increasing specific discharge competence and shortening hydroperiod, creating conditions unfavorable for sloughs—would also occur. This distal inhibitory effect is anisotropic because longitudinal ridge expansion has minimal effect on specific discharge competence (Figure 1B); given stochastic variation in ridge or slough expansion (for example, mediated by fire, sawgrass senescence, peat pop-ups, alligator holes), a slight selective preference for longitudinal expansion over lateral expansion may be sufficient to yield flow-oriented patches. Although determining the mechanism by which flow controls pattern development is of clear management relevance, it is not essential to describing the loss of pattern with modern hydrologic modification. Specifically, both mechanisms predict anisotropic hydrologic control on pattern geometry, and topographic leveling if water levels are reduced below a threshold that maintains both patches. Our intent here is not to test these two hypotheses but to evaluate changes in spatial patterns of vegetation and topography along the existing hydrologic gradient.

Detecting landscape pattern change requires determining which variables serve as leading or lagging indicators. Responses of the ridge–slough landscape to hydrologic modification have largely been inferred from vegetative patterning (Wu and others 1997; Givnish and others 2007; Zweig and Kitchens 2008), principally because of rapid, remote detection. Efforts to quantify microtopographic changes in response to hydrologic modification are not sufficiently developed to diagnose or predict regime shifts (that is, from ridge–slough mosaic to a homogeneous landscape) in part because quantitative information linking elevation to plant communities is limited (Childers and others 2003; Armentano and others 2006; Zweig and Kitchens 2008, although see Givnish and others 2007).

Importantly, use of plant communities to assess ecosystem change implicitly assumes that vegetation changes first, and that other coupled variables lag in their response. We suggest, however, that the local carbon balance can respond quickly to new hydrologic conditions, specifically via changes in respiration, and that priority effects in community composition might cause lags between hydrologic change and vegetation response. As such, we hypothesize that soil elevation changes (for example, loss of bimodality) will precede changes in vegetation composition, providing an improved diagnostic indicator.

Based on our conceptual models at the point (Figure 1A) and landscape (Figure 1B) scales we sought to test four predictions about the ridge–slough landscape. Two test the hypothesis that point-scale feedbacks between vegetation and soil elevation, mediated by hydrology, produce multiple attractors (ridge and slough) at the local scale; the other two relate to the presence and disruption of spatial patterning feedbacks. First, peat elevation should be bi-modal under the best preserved hydrologic conditions, and vegetative assemblages should show strong fidelity to distinct elevation modes. Second, peat elevation distributions should show marked departure away from bimodality with hydrologic alteration, with corresponding shifts in plant community prevalence and fidelity to elevations. Third, if pattern is maintained due to scale-dependent (that is, local positive and distal negative) feedbacks, auto-correlation plots of soil elevations should indicate strong positive values at short separation distances and then significant negative values at longer separation distances (Rietkerk and van de Koppel 2008; Eppinga and others 2008). Moreover, these feedbacks should be anisotropic due to water flow, with stronger distal negative feedbacks orthogonal to flow. Fourth, metrics of spatial pattern (anisotropy and structure) in topography will decline with increasing hydrologic modification as the distal negative feedbacks presumed to control landscape pattern are altered or removed.

METHODS

Sampling

Eight 2×4 km sampling blocks were located throughout the southern Everglades (WCA 3 and ENP, oriented along historical flow lines; Figure 2). Six blocks were in WCA 3A, which spans hydrologic conditions from drained in the north to impounded in the south; its center is widely viewed as the best-conserved ridge–slough landscape, which we
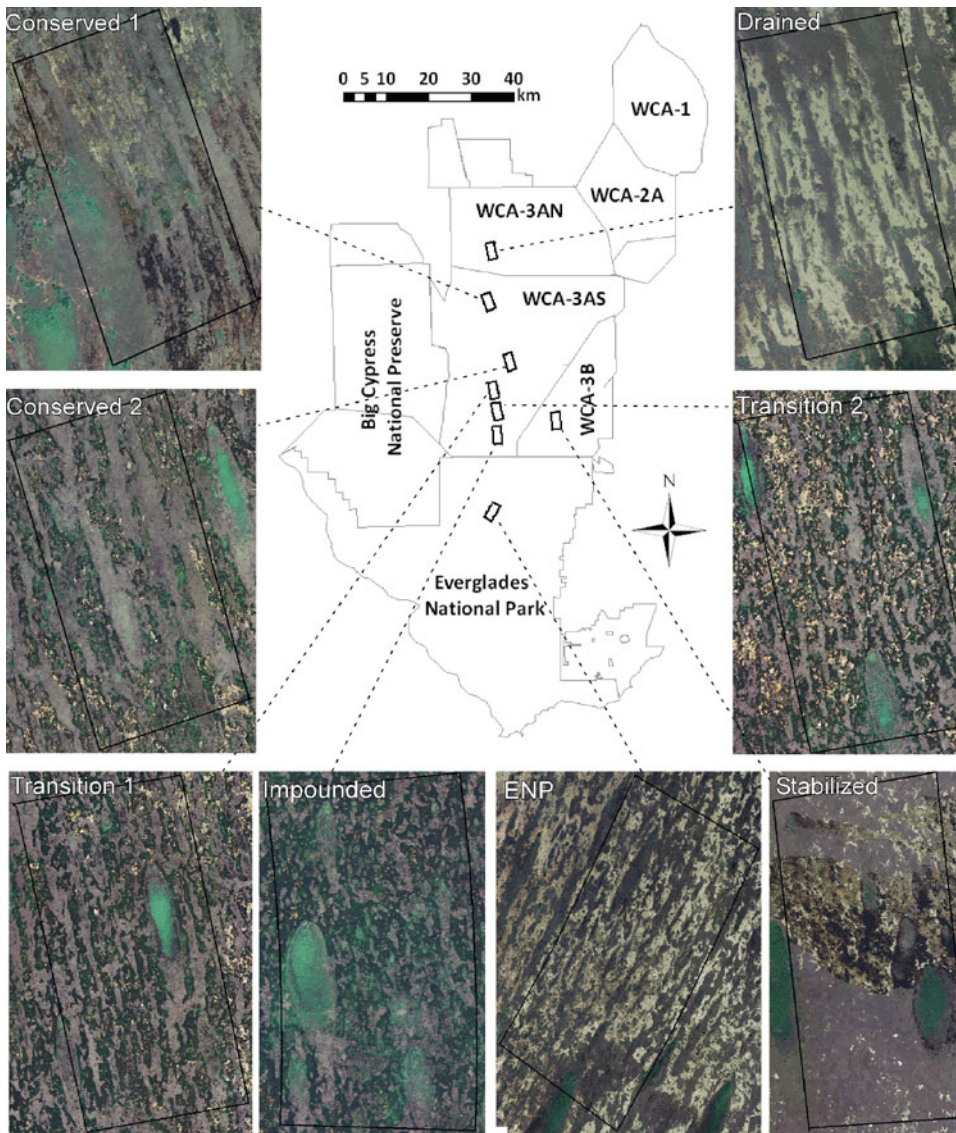
Figure 2. Map of South Florida with aerial photos (ca. 2004) of the eight 4 × 2 km sampling blocks. Ridges are *light*; sloughs are either *dark* (when periphyton is absent) or *very light* (periphyton present). *Dark tear drop shaped areas* are tree islands. The Stabilized block has a clear fire scar.

assume implies hydrologic drivers most similar to historical conditions. One block was located in WCA 3B, which is hydrologically stabilized (that is, low temporal variation) and receives little flow. Finally, one block was placed in northern ENP for which contemporary inundation depths are considered lower than historical conditions, and where many of the sloughs have transitioned to wet prairies.

Each block was sampled on a single day between September and December 2007, except ENP, which was sampled in November 2008. Between 19 and 27 clusters were randomly located in each block; points landing on a tree island (ca. 3% of the landscape) were discarded. At each cluster, nine water depth measurements were made in a fixed frame consisting of a center point and points 5 and 25 m away from center in each cardinal direction

(although flow orientation is not exactly north–south, it is within the 22.5° angular tolerance of all anisotropic spatial analyses). Distances were chosen to ensure sampling of transitions between ridges and sloughs, and to complete sampling in a single day. The water table was above the soil surface at all locations on the day of sampling. Water depths were measured at each point with a precision of 0.5 cm with a meter stick to which a circular foot (10.7 cm dia.) was attached to ensure repeatable detection of the soil–water interface in low bulk density peat. Modest pressure was applied to eliminate litter and floc in the measurement, and repeated local measurements were undertaken to ensure repeatability. At each site, presence of all macrophyte species and calcareous periphyton was noted along with cover (in 10% increments) of dominant taxa.

Historical Water Level Data

Changing water management over time may confound inference of the effects of modern hydrology on pattern. Water elevation data from 1958 to 1993 in WCA 3B (USGS site 254754080344300; http://www.sflorida.er.usgs.gov) suggest severely drained conditions, which were adjusted to permanent moderate inundation by altered water management in the early 1990s (median water levels were 15 cm lower prior to 1994, $P < 0.05$). Long-term hydrologic data are not available in WCA 3A; data available since 1991 show no significant trend. Observations reported by Zafke (1983) indicate varying degrees of change in hydrologic conditions since the 1970s in WCA 3A-N, however. WCA 3A-N has evidently experienced significant hydrologic change, with wetter conditions prior to construction of the C-123 canal in the 1970s (inundation frequency reduced from 0.85 to 0.38 between the late 1960s and late 1970s), and since construction of S-339 control structure (which increased inundation frequency to 0.75).

Daily water levels for 8 years prior to sampling (30 June 2000 to 29 June 2008) were obtained at the center point of each landscape block from the Everglades Depth Estimation Network (EDEN; http://sofia.usgs.gov/eden/); we used both actual observations and model-hindcasted predictions (Conrads and Roehl Jr. 2007). Using EDEN estimates of water elevation on the day of sampling, we estimated peat surface elevation as the difference between water elevation and measured water depth at each sampling location; all subsequent analyses use this peat elevation. We implicitly assume that the water and land slopes are equal, and intentionally ignore nominal longitudinal changes in peat surface elevation (ca. 1.5 cm per 1000 m) to allow peat elevations within blocks to be analyzed together. Historical daily water elevation data were used to compute a cumulative elevation exceedance probability curve, which, when compared to measured peat elevations, yield an inundation probability (that is, long-term average hydroperiod) for each site. Median landscape water depth, defined as the difference between the median water elevation (over time) and the median peat elevation (over space), and water elevation variance (over time) were used to verify our a priori hydrologic categorization of the landscape blocks.

Linear regression between latitude and water depth within each landscape block was performed to test the assumption that land and water slopes are uniform within a sampling block. Because ridges and sloughs were expected to have different peat elevations, and because these distinct ecosystem types appear to respond differentially to exogenous shifts in other stressors (Hagerthey and others 2008), they were regressed separately. The assumption of longitudinal homogeneity was validated in most blocks, which exhibited no association between slough water depth and latitude (that is, land and water changes in elevation are occurring at the same rate). However, both Drained and Conserved 1 landscape blocks had significant negative trends in slough water depth with latitude (slope = -2 cm km^{-1} and -1.4 cm km^{-1} with an $R^2 = 0.16$ and 0.17, respectively, $P < 0.01$), suggesting an increase in slough water depth towards the southern end of each unit. Ridge water depths in the Drained block exhibited an identical trend with latitude (slope = -2.1 cm km^{-1}, $R^2 = 0.17$), suggesting that the water slope diverges slightly from the land slope, possibly due to impoundment resulting from proximity to a major road (Alligator Alley) orthogonal to flow at the southern boundary between WCA 3AN and WCA 3AS (Figure 2). In contrast, a significant positive trend in water depths was observed with latitude for ridges in the Conserved 1 landscape block (slope = 2.6 cm km^{-1} and $R^2 = 0.12$). This increasing bed slope for ridges, simultaneous with a decreasing bed slope for sloughs suggests that ridge–slough elevation difference in that block increases markedly with distance south from the boundary between WCA 3AN and WCA 3AS (Figure 2). This suggests a spatially compact hydrologic transition, with shallower waters in upper portions of the block in relation to lower portions; whether this represents a stable configuration or a slow-moving transient response is unknown.

Data Analysis: Bimodality

To test for bimodality in peat elevation distributions, we compared goodness-of-fit between the observed peat elevations and (1) a single normal and (2) mixed double normal model:

$$P_s = N(\mu_i, \sigma_i) \tag{1}$$

$$P_m = q \cdot N(\mu_1, \sigma_1) + (1 - q) \cdot N(\mu_2, \sigma_2) \tag{2}$$

where q represents the probability of falling within mode 1, and N is a normal distribution with mean μ_i and standard deviation σ_i. Model fit was compared using Bayes' information criterion (BIC). To avoid pseudo-replication resulting from strong short-range spatial autocorrelation (Legendre 1993), the 5-m data points within each cluster

were removed from distribution and vegetation analyses. The full data set was included for all spatial analyses.

Data Analysis: Community Fidelity

A priori vegetation community classifications were used to test whether communities occurred on different peat elevations. Sites dominated by *C. jamaicense* were classified as 'ridges', sites dominated by *Nymphaea odorata* or *Utricularia* spp. were 'sloughs', and sites dominated by emergent species (such as graminoids or sedges other than *C. jamaicense*) were 'wet prairies'. In our conceptual model of a bimodal landscape, wet prairie systems are hypothesized to be transitional states through which a site passes as it changes from a slough to a ridge; notably, we assume significant asymmetry in vegetation change such that the successional trajectory from ridge to slough does not necessarily include wet prairies. This hypothesis arises because (1) ridges have substantial staying power (for example, via adjusted growth patterns), and (2) if the land never dries out enough to permit the seed bank of wet prairie species to be expressed (that is, permanently inundated), wet prairie communities are very rare (Loveless 1959; Zafke 1983; Zweig and Kitchens 2008; among others). In contrast, drying permits the establishment of wet prairie species quickly because of the seed bank, whereas sawgrass encroachment is a much slower process (Loveless 1959; Zafke 1983; Smith and others 2002; among others). Wet prairies, therefore, are grouped with sloughs for this analysis. All data points ($n = 45$ across all blocks) falling outside one of these classifications (for example, edges of tree islands and alligator holes) were discarded from the analysis. Community-specific mean elevation values were compared within each sampling unit using a Student's *t*-test.

Data Analysis: Spatial Autocorrelation

We used spatial autocorrelation within each block to test for scale-dependent feedbacks (Rietkerk and van de Koppel 2008; Eppinga and others 2008). We extracted autocorrelation values at zero-separation distance and enumerated declines with increasing distance in directions both orthogonal and parallel to flow using an angular tolerance of 22.5°, a lag spacing of 30 m, and a range of 500 m; lag classes were combined if there were fewer than 20 data pairs. Due to low numbers of sample pairs in mid-range lag classes, additional data (Cohen and others 2009a), collected in an identical manner for an unrelated study, were included where available;

transitional sites (Transition 1, 2—Figure 2) lacked these additional data and thus had insufficient power at some separation distances. These additional data were not included in analyses that explicitly consider vegetation due to differences in plant cover assessment methods.

Spatial structure was explored using semi-variograms, which describe spatial dependence between paired observations as a function of distance between them (lag) (Goovaerts 1997). We estimated semi-variances with lag spacing of 15 m, and fit a spherical model to those observations from which we extracted the sill (semi-variance outside the range of autocorrelation, or between spatially independent observations), the range (the distance at which semi-variance reaches the sill) and the nugget (semi-variance at zero-separation, indicative of microstructure and measurement error). The ratio of the partial sill (sill minus nugget) to sill provides a measure, Q, of the degree of spatial structuring of the peat surface.

Anisotropy was determined by comparing the semi-variance range in orthogonal directions (parallel and perpendicular to flow); anisotropy is defined as the ratio of the major range (determined in the direction of maximum autocorrelation) to the minor range (orthogonal to the major axis), with values of 1 indicating isotropic semi-variance. As with the autocorrelation analysis, the anisotropic semi-variance analysis used an angular search tolerance of 22.5° to identify sample pairs in the major and minor directions.

RESULTS

Our site designations (that is, Drained, Stabilized, Impounded) were confirmed by evaluating hydrologic conditions in each landscape block (for example, landscape median water depth and temporal water depth variance, Figure 3). The lowest median water depth was observed in the Drained site; median depth increases nearly monotonically through the ENP/Conserved and Transition sites to the Impounded site in southern WCA 3A-S. The Stabilized block (median water depth = 33 cm) and Conserved 1 (median water depth = 19 cm) were exceptions. Temporal variance in water depth is relatively uniform across sites (SD $\sim$ 22 cm) except at the Stabilized site where water levels were approximately half as variable.

The landscape prevalence of vegetative community types also varied along the hydrologic gradient (Figure 3). Ridge prevalence was highest in the Stabilized site (WCA 3B), and responded only modestly to the gradient in impoundment. Ridge
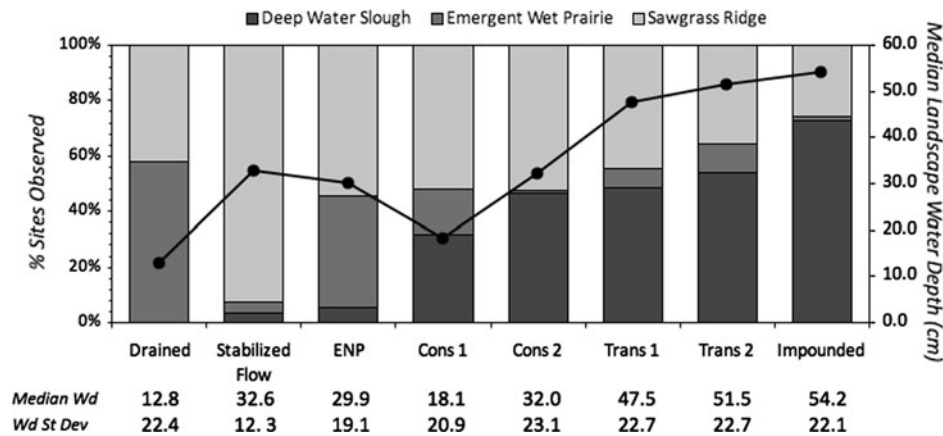
Figure 3. Relative incidence of plant communities by block. A priori classifications were based on dominance by *C. jamaicense* (ridges), *N. odorata* or *Utricularia* spp. (sloughs), or wet graminoids or sedges, excluding *C. jamaicense* (wet prairies). Median landscape water depth (that is, the difference between median water elevation (from 2000 to 2008) and median peat elevation (over space) in each landscape block) is indicated by the *solid black line*. Median landscape water depth and standard deviation are reported beneath.

prevalence was best correlated, albeit weakly, to median water depth ($R = +0.56$, $P = 0.12$; we removed the Stabilized due to possibly confounding dry conditions prior to 1993). Slough prevalence also varied with hydrologic conditions: a dramatic increase in deep water slough prevalence is evident in both Drained and Stabilized sites, where they are almost entirely absent, to the Impounded site where deep water sloughs were found at over 70% of the sites. Moreover, a clear decline in the prevalence of wet prairies is observed from conserved through impounded conditions (Figure 3). The effects of median water depth were significantly correlated with deep water slough prevalence ($R = +0.79$, $P < 0.05$). Wet prairie prevalence was less well correlated with hydrologic variables, though the effect of the interaction between temporal water elevation variance and landscape median water depth was weakly significant ($R = +0.68$, $P = 0.055$).

More detailed insight into extant hydrologic conditions in each block emerges from comparing the distribution of peat elevations and exposure probability derived from water level time series (Figure 4). In the Conserved 2, Transition 1, and Transition 2, and Impounded blocks the inundation probability for sites classified a priori as sloughs was 100%. Similarly, water levels exceeded the peat elevation in sites classified a priori as ridges 86, 95, and 91% of the time for Conserved 2, Transition 1, and Transition 2, respectively. The same comparison at the Drained site suggests that nearly the entire landscape is exposed at some point, despite the fact that the inundation probability at the

landscape median elevation still exceeds 80%. In contrast, peat exposure is almost never observed in the Stabilized block. Conversion to an increasingly slough-dominated landscape in the Transition 2 and Impounded sites appears to be strongly linked to inundation probability: nearly all peat elevations within those blocks are permanently inundated with median inundation depths approximately 20 cm higher than the Conserved sites.

In both Conserved and both Transitional blocks, peat elevations exhibited distinct bimodality (Figure 4; Table 1). Bimodality was lost in both directions of hydrologic modification, with no residual evidence of bimodality in the Drained, Stabilized or Impounded blocks. Model selection for the ENP site was less clear; BIC values for the single normal model was only slightly higher than for the mixed normal model, suggesting nearly equivalent goodness-of-fit.

Significant differences in mean peat elevation were observed between a piori defined ridge and slough communities (where wet prairies are a part of the slough community) across all sampling blocks ($P < 0.05$), with differences between community types ranging from 6 to 25 cm (Figure 5B). Comparisons of the peat elevations for the a priori community designations with the peat elevation distributions (Figure 4), however, show considerable overlap between ridge and slough communities for all but the two Conserved and Transition 1 landscape blocks.

Relative spatial structure (Q) was high ($>75\%$) for ENP, Conserved and Transitional blocks, and markedly lower for the Drained, Stabilized and
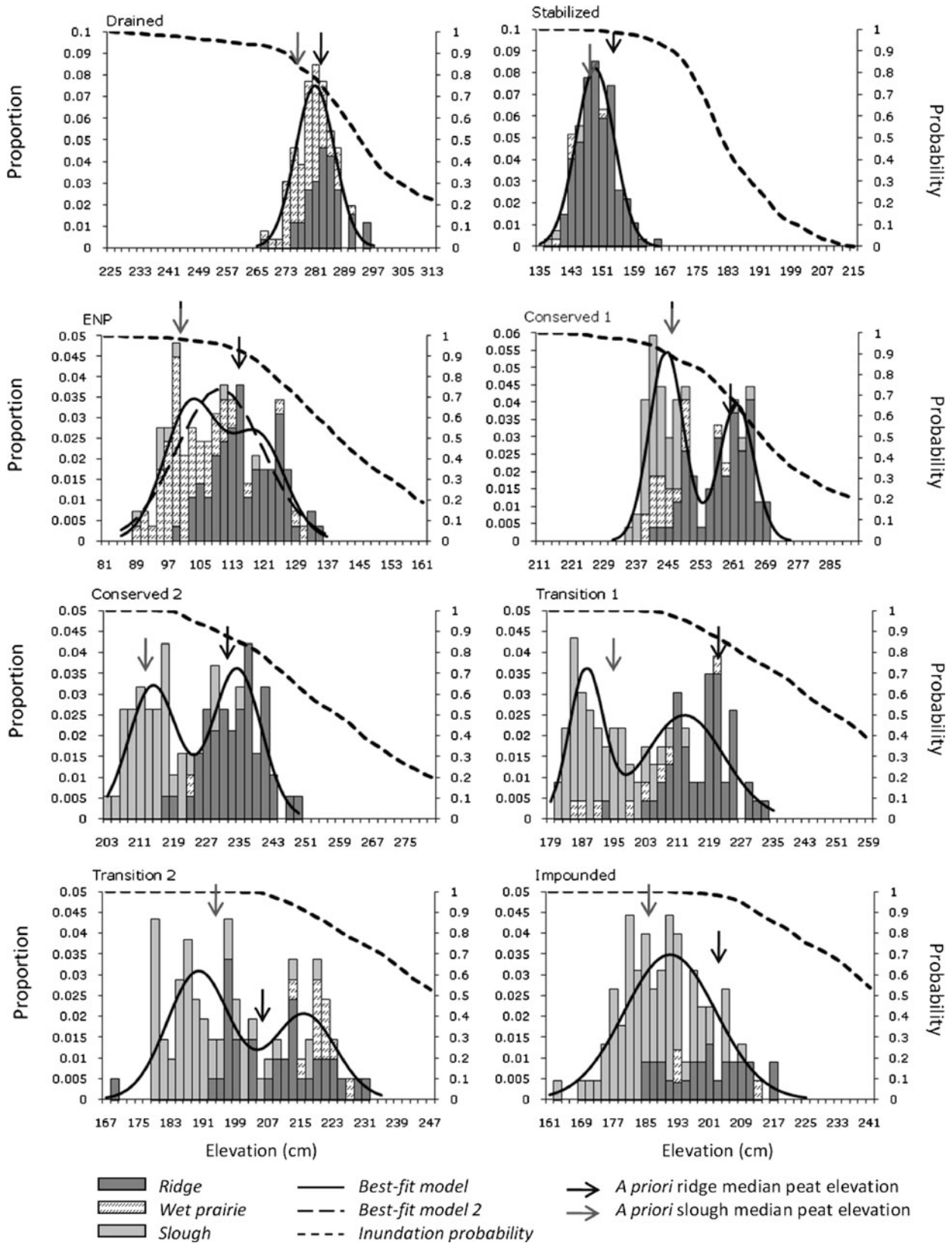
Figure 4. Peat elevation histograms within each block. *Solid lines* indicate the best-fit probability density function; unimodal and bimodal models are shown for ENP. *Thick dashed lines* indicate the water elevation exceedance probability (for values less than 1.0). *Arrows* (*black* for ridge, *dark gray* for slough) indicate median elevations of a priori defined communities.

Table 1. Sampling Site Means and Variances for Peat Elevations Based on BIC Model Fitting

Site designation	Best fit parameters from BIC model selection[a]				
	$\bar{x}_1$	$\bar{x}_2$	σ_1^2	σ_2^2	q
Drained	280.9	NA	28.2	NA	NA
Stabilized	149.0	NA	23.5	NA	NA
ENP[b]	102.7	119.6	46.1	46.1	0.57
	109.9	NA	116.5	NA	NA
Conserved 1	244.3	261.7	17.7	17.7	0.58
Conserved 2	214.0	234.2	33.6	33.6	0.47
Transition 1	187.9	212.6	18.3	98.4	0.38
Transition 2	189.8	215.9	59.7	59.7	0.60
Impounded	191.0	NA	131.3	NA	NA

NA not applicable.
[a]The greater maximum BIC fit indicates whether a single normal distribution or a mixture of two normal distributions best describes the data. Best-fit parameters are shown, where q is the weight of the first distribution when a mixed distribution has the better fit.
[b]For ENP model selection, the BIC test statistic was nearly indistinguishable between uni- and bi-modal models and thus both are considered equally viable, and both model parameters are shown.

Impounded blocks (Figure 5C). Higher anisotropy was observed for Conserved and Drained blocks, with a maximum of 2.8 in Conserved 1 (Figure 5D). In contrast, substantially lower anisotropy was observed in the Impounded and Stabilized blocks. We also observed that the spatial range was short (<100 m) in the Impounded block, moderate (100–200 m) in the Stabilized and Drained blocks, and longest (>220 m) in the other blocks where bimodality is relatively well conserved (Figure 5D).

Short-range autocorrelation using 30-m lags was high at the two Conserved and the Transition 1 blocks (short-range autocorrelation between 0.83 and 1), but weaker for the Drained and Impounded blocks (short-range autocorrelation between 0.5

and 0.75) (Figure 6). To test the assumption that led to our omission of the 5 m samples for analysis of bimodality, we examined short-range autocorrelation at both 5 m and 25 m lag distances; values at 5-m ranged from 0.43 (Drained) to 0.95 (ENP), and at 25 m from 0.35 (Stabilized) to 0.71 (Conserved 2). Autocorrelation pattern differed markedly between parallel and orthogonal to flow, particularly for the Conserved, ENP and Transition 1 blocks, which exhibited significant ($P < 0.05$) negative autocorrelation with a range between 100 and 200 m in all cases. We note that the analysis has low power at this distance in the Transitional blocks.

DISCUSSION

Our field measurements strongly support predictions derived from our point-scale conceptual model (Figure 1a). Peat elevations were significantly bimodal in the 4 conserved and transitional blocks, and vegetation community displayed strong fidelity to site elevation (Figure 4). These observations suggest that, under the best-conserved hydrologic conditions, ridge and slough landscape elements reflect multiple elevation equilibria generated by feedback among site vegetation (which affects primary production), soil elevation (which affects respiration), and local hydrology. Because soil elevation is independent of underlying geology, ridges and sloughs should be viewed as discrete self-organized ecosystem states that control local elevation (and thus hydrology), not simply as vegetation assemblages.

Unstable thresholds between ridge and slough attractors occur at intermediate elevations where respiration and primary production are moderately high and carbon balance is highly sensitive to variation in vegetation production (Larsen and
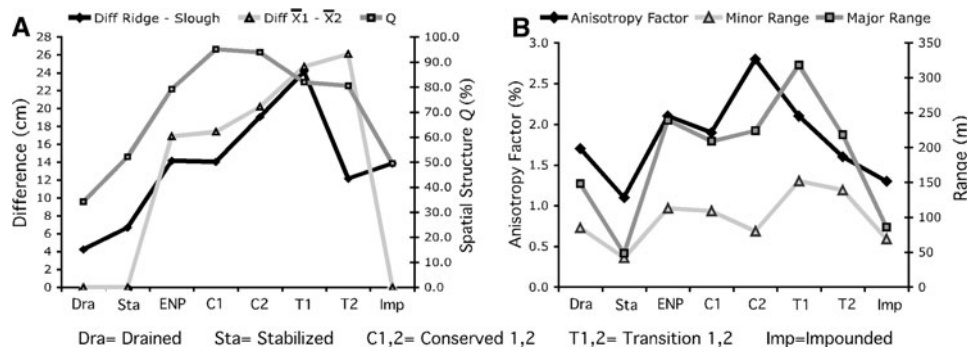
Figure 5. Relationship of select parameters (spatial and hydrologic) ordered along a hydrologic gradient incorporating both median water depths and water depth variance. Diff $x_2 - x_1$ is the mode peat elevation differences of the BIC-selected models; Diff ridge–slough indicated the mean peat elevation differences of a priori defined ridges and sloughs.
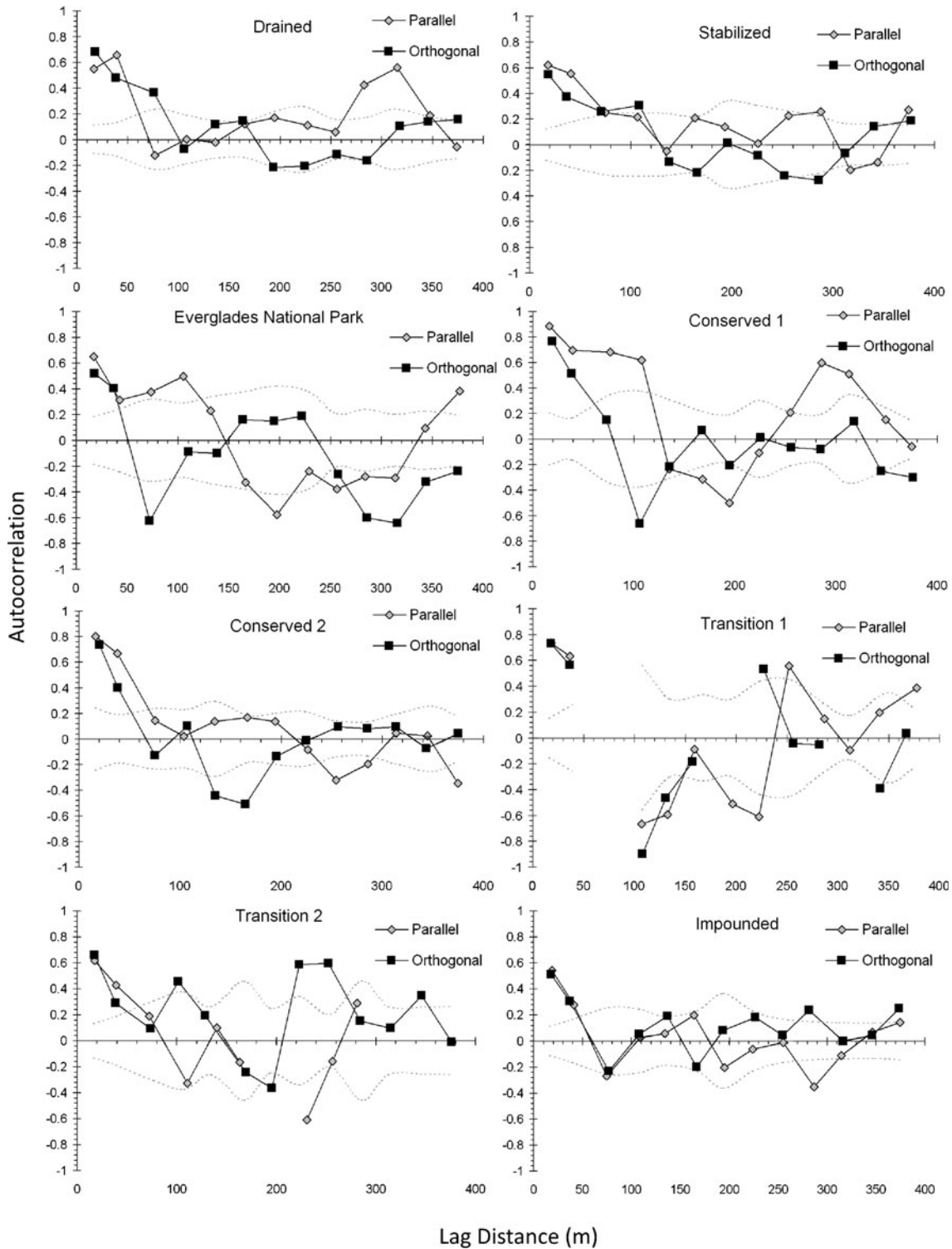
Figure 6. Correlograms of water depths with lag distances (*h*) of 30 m. The 95% confidence limits of the cross correlation values are based on the number of pairs within each lag class *h*. The distances along the *x*-axis are the average distances among all pairs within each lag class.

others 2007); these water levels are located at the saddles in the bimodal distributions. Under the best-conserved, modern hydrologic conditions, this

threshold occurs near the point of non-zero exposure probability (Figure 4). In Conserved 1 and ENP blocks, where wet prairie vegetation is

common, the slough elevation mode occurred at regularly exposed depths and raises the question of whether vegetation and peat patterning there will persist or degrade if present conditions continue. The Conserved 1 block, where sloughs have experienced exposure roughly 10% of the time over the last decade, may be in transition to a unimodal landscape; evidence of a spatially compact hydrologic gradient within this block (the ridge–slough elevation difference increases markedly with distance south) underscores the utility of future monitoring of this location.

Our data provide preliminary guidance regarding hydroperiod requirements for the two landscape modes. Median ridge elevations in conserved blocks occurred at exposure probabilities of 10–30% (Figure 4), suggesting that 1–3 months of accelerated respiration approximately balances the marginal productivity of ridges compared to sloughs. Sloughs appear to be permanently inundated in the Conserved 2 and two Transitional blocks, suggesting that any peat exposure causes excess respiration and allows wet prairie species recruitment and increased productivity. These hydroperiods for ridges and sloughs are strikingly similar to pre-drainage hydroperiods reported by McVoy and others (2010).

Historical accounts suggest differences between ridge and slough elevations (60–90 cm; SCT 2003, McVoy and others 2010) larger than any we observed in this study. However, the lack of systematic sampling prior to hydrologic modification in the Everglades makes direct comparisons with modern peat elevations impossible. Further, no records exist for central WCA 3A that would allow comparisons of modern and historic hydrology (although see McVoy and others 2010). At best, the data indicate that the central WCA 3A landscape has maintained significant bimodality (that is, distinct patch edges) and a 25 cm elevation difference between ridges and sloughs despite 50+ years of hydrologic modification, which suggests surprising landform stability given rates of landscape degradation observed over the same period in other parts of the Everglades system. Further monitoring of soil elevation distributions as part of the Comprehensive Everglades Restoration Plan (CERP) will allow the persistence or amplification of elevation differences in well-conserved sites to be evaluated.

Less severe hydrologic modification appears to be associated with smaller changes in elevation distributions and vegetation. For example, ENP appears transitional between Drained and Conserved areas, with increased abundance of ridges and wet prairie, and reduced elevation differences between ridges and sloughs as compared to conserved blocks. The Transition blocks had slightly higher deep slough vegetation abundance than Conserved blocks, and also higher elevation variance. Differences between ridge and slough elevations were similar, however, suggesting that landform changes in response to longer hydroperiod may be lagged (hydrologic conditions in southern WCA-3AS have changed little over the last 40 years; Zafke 1983). This delayed response may be due to the ability of sawgrass to resist deep and extended inundation.

Although loss of peat elevation bimodality appears to be a general response to hydrologic modification, trajectories of transition from a bimodal to unimodal peat surface appear to differ based on the direction, magnitude, and character of hydrologic modification. Acknowledging that our findings are based on a limited number of observations, and confounded by uncertainty of past hydrologic management, we suggest that further attention to three pathways of pattern loss may provide insight into potential responses to future hydrologic alteration and restoration.

First, under dry conditions (Drained and to a lesser extent in ENP and Conserved 1) landscape leveling probably occurs as a result of both slough infilling (via increased production) and ridge deflation (due to excess peat exposure and accelerated oxidation). Peat exposure in sloughs permits recruitment of wet prairie species (notably not sawgrass, which propagates principally vegetatively) from the prolific Everglades seedbank (Leeds and others 2002). Competitive interactions between sawgrass and periphyton and/or emergent wet prairie species may retard vegetative colonization of sloughs by sawgrass, but ultimately, ongoing landscape flattening is likely to yield monotypic sawgrass marshes. Some 30% of wet prairie sites contained sawgrass, indicating the process may already be occurring; it remains unknown why sawgrass has not expanded more rapidly given favorable hydrologic conditions in the Drained block. Notably, this pathway temporarily preserves the visual character of an intact ridge–slough landscape, retaining modest anisotropy in elevations, but exhibiting markedly reduced bimodality and spatial structure. These observations together indicate substantial weakening of local positive feedbacks that maintain patches; ultimately distal feedbacks that maintain patterning will likely also be lost as vertical differences between patch types disappear.

A second pathway to a flattened landscape may occur with reduced water variance and flow, as in the Stabilized block. Permanent, moderate

inundation precludes seed bank recruitment, and absence of competition could expedite sawgrass expansion to favorable sites. Reduced flow interrupts distal feedbacks that generate landform (for example, sediment redistribution—Larsen and others 2007). Sawgrass-colonized sloughs then rapidly fill due to high peat production by sawgrass and low respiration of inundated peat. Despite the possible role of reduced hydrologic variance on vegetation and peat dynamics, it is important to consider historical contingency in this landscape block. After the 1960s construction of a major canal (L-67) along northern WCA 3B segmented this area from adjoining WCA 3AS, this severely drained area experienced extended periods of winter drying. Only in the 1990s was a revised water management strategy adopted for WCA 3B that stabilized water levels at permanent moderate inundation. Although we could not evaluate the influence of extreme historical drying versus recently stabilized water levels on topographic flattening, simply reversing drained hydrologic conditions does not lead to re-establishment of sloughs or landscape pattern, at least over the last 20 years. Restoration of flow as well as hydroperiod is likely to be required.

A third pathway for bimodality loss, based on observations in our Impounded block, occurs from deep and prolonged inundation that induces sawgrass physiological stress (Brewer 1996; Pezeshki and others 1996; Weisner and Miao 2004). Despite reduced productivity and vegetative propagation (David 1996; Busch and others 1998), sawgrass persists at the highest elevations at relatively low density via upward rhizome growth. Bimodality loss suggests sawgrass productivity at these microsites is insufficient to maintain a distinct ridge elevation mode. Loss of spatial structure with impoundment suggests that new organizing feedbacks occur at a fine spatial scale (that is, sawgrass individual death). The dramatic loss of anisotropy may arise from interruption of landscape distal feedbacks or from the random spatial distribution of sawgrass death; field observations of highly localized sawgrass patches on what was historically a continuous ridge suggests the latter may be dominant. Flow restoration from elevating Tamiami Trail (which creates impounded conditions) may reinstate the coherence and orientation of ridges, and constitutes an effective test of underlying mechanisms.

Hydrologic modification appears to have disrupted both local positive and distal negative feedback mechanisms; local autocorrelation was weaker in Drained and Impounded blocks, and

evidence of distal negative feedbacks was absent. Autocorrelation has been used to understand processes underlying pattern development; but to our knowledge, this study is the first to compare field measurements within patterns along an environment gradient. We propose that patterns of autocorrelation are diagnostic of the persistent action of a distal feedback in the conserved areas, and of loss of that feedback in other areas. Given that observed flow velocities in the best-conserved areas are uniformly too low for regular floc entrainment (Bazante and others 2006; Harvey and others 2009; Larsen and others 2009), this observation suggests either that some other distal feedback mechanism is required, or that pattern loss processes are surprisingly slow. Although our data cannot be used to discriminate between plausible mechanisms that create a distal negative feedback, they do show that the effects of one or more distal feedbacks persist in areas of the Everglades, and decline with hydrologic modification.

Consistent with expectations of coupled feedbacks in patterned landscapes, (Rietkerk and van de Koppel 2008), declines in autocorrelation of peat elevation with distance were more rapid and greater in magnitude, becoming significantly negative, in landscape blocks where bimodality and vegetation fidelity to one mode was conserved (Figure 6). Further, the peat surface was highly structured in space (Figure 5B) and was strongly anisotropic, with elongation occurring along the historic direction of prevailing flow (Figure 5C) in those same landscape blocks.

Change Detection in Patterned Landscapes and Implications for Monitoring and Assessment

Our results illustrate that simple statistical descriptions of peat elevation distributions—measures of bimodality, anisotropy, spatial structure, and autocorrelation—provide diagnostic condition measures for the ridge–slough landscape. These measures are both sensitive and specific to magnitude and direction of hydrologic modification; therefore, they may be useful for restoration monitoring. Importantly, and perhaps surprisingly, changes in distribution and spatial pattern of the peat surface appear to precede responses in community composition. For example, Wu and others (2006) conclude from aerial vegetation mapping that northern 3A (near our 'Drained' block) and southern 3A (near our 'Impounded' block) retain healthy (or nearly so) ridge–slough patterning. Despite the apparent discreteness and elongation of

vegetation patches (Figure 2), we observed advanced loss of topographic patterning (that is, loss of bimodality, changes in anisotropy and spatial structure) in these landscape blocks.

We conclude that vegetative patterning at these drained and impounded sites is a vestigial signature. Landscape soil elevation differences between patch types there have been almost entirely lost, and it can be surmised that as the soil surface continues to converge on a single peat elevation equilibrium, vegetative differences will eventually disappear as well. That patterns in peat elevation actually appear to be leading indicators of landscape change underscores the need to view the restoration of the ridge–slough landscape in terms of the re-initiation of reciprocal interactions among vegetation, soil elevation, and hydrology, rather than as a response of vegetation communities to externally imposed hydrologic conditions (Cohen and others 2010).

A central goal of Everglades management and restoration is the maintenance and re-establishment of landscape patterning, which will require resolution of several uncertainties regarding mechanisms controlling landscape pattern. One outstanding question is the relative importance of material redistribution (Larsen and others 2007) and maintenance of hydrologic competence (Cohen and others 2010) as mechanisms of distal feedback that organize landscape pattern and patch prevalence. In addition, transitions between homogenous landscapes and those with self-organized patterning often exhibit hysteretic behavior (Rietkirk and van de Koppel 2004). Determining whether the ridge–slough mosaic exhibits such behavior has important implications for responses to hydrologic restoration, because directionally dependent thresholds may dramatically delay restoration goals (Suding and others 2004). Leading indicators of pattern loss, which our data suggest should focus on measures of the peat surface, could allow focused efforts to conserve the most vulnerable portions of the landscape.

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