

ALTERNATIVE STABLE STATES AND SELF-ORGANIZED PATTERNING:
EVERGLADES RIDGE AND SLOUGH MOSAIC

By

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To my friends, my husband, and the Everglades.

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The Everglades in South Florida is a large subtropical peat wetland with important hydrologic, ecologic, and cultural values. The ridge and slough mosaic is a major landscape component of the Everglades, characterized by elevated ridges of sawgrass (*Cladium jamaicense*) interspersed among deeper water sloughs comprised of floating and emergent species as well as calcareous periphyton. Autogenic feedbacks among depth and duration of inundation, plant community composition, and net peat accretion are hypothesized to create and stabilize these multiple ecosystem equilibria. While significant research has focused on processes leading to these potential stable states, few studies have formally examined the hypothesis that ridge and slough represent alternative stable states, and none has examined the resilience of alternative stability domains to hydrologic change. In this study, water depth (a proxy for soil elevation) was measured along a gradient of hydrologic impairment in the ridge-slough region of the central Everglades to evaluate predictions that follow from the multiple stable state hypothesis: 1) soil elevations show strong fidelity to community type with little overlap in elevation distributions in areas with minimum hydrologic impacts; 2) increasing hydrologic modification increases overlap between elevation distributions; 3) hydrologic modification increases the variance of elevations within communities; 4) kurtosis of the joint soil elevation

distribution increases with increasing hydrologic modification; and 5) spatial anisotropy (diagnostic of landscape orientation with flow), and spatial structure (diagnostic of landscape scale self-organization) decline with hydrologic modification. Results accord with predictions; properties of bimodality and spatial structure are strong in sites with minimal hydrologic impact and change significantly with hydrologic modification. These non-linear ecosystem processes and feedbacks need to be incorporated into modeling and restoration planning in the Everglades, as they may act as constraints on restoration goals.

CHAPTER 1 LITERATURE SYNTHESIS

Introduction

Alternative stable states have been described for numerous ecosystems in the recent literature (Scheffer and Carpenter, 2003; Suding et al., 2004; Schröder et al., 2005). These ecosystems exhibit resistance to changes over some range of an ecosystem driver via homeostatic feedbacks; however, thresholds at the edge of that range lead to catastrophic regime shifts to some new self-reinforcing ecosystem state (Scheffer et al., 2001). A key component of these shifts is hysteresis (path dependency) wherein the threshold at which regime shifts occur differ in opposing directions of change. Regime shifts between alternative stable states have been expressed at a population level (e.g., shifts between high biomass and low biomass in the presence of a predator) and at an ecosystem level (e.g., nutrient loading driving a lake system from macrophyte dominance to algal dominance) (see review of concepts in Beisner et al., 2003).

Alternative stable state theory has more recently been extended in landscapes with regular patterning, wherein feedback mechanisms from a plant community engineer ecosystem attributes at the local scale to their favor (e.g., changing nutrient content, infiltration rate, soil elevation) rendering more distal locations unfavorable to them; the result of such scale-dependent autogenic reinforcement is landscape patterning (Ludwig et al., 1999; Rietkerk et al., 2004a; Rietkerk et al., 2004b; Rietkerk and van de Koppel, 2008). Among these feedbacks in patterned landscapes are a redistribution of water in arid systems; competition for limiting resources in savannas; and ponding of water and advective transport of nutrient by differences in transpiration rates in peatlands (Rietkerk et al., 2004a).

The ridge-slough mosaic, the dominant landscape feature of the central peat-dominated Everglades, exhibits corrugated soil elevation patterning suggestive of those landscapes increasingly understood as being structured by alternative stable states. Ridges, which occur at higher soil elevations, are dominated by sawgrass (*Cladium jamaicense*). Interspersed among the ridges are deeper water sloughs, comprised of floating-leaved and emergent species as well as extensive periphyton. This patterning has been in existence for the last 2,700 years, and the centers of the ridges and sloughs have been invariant for the last 1000 years (Bernhardt et al., 2004). However, whether the ridge and slough mosaic represent alternative stable states in the Everglades, with multiple state equilibria, is unknown.

For patterned systems phase shifts can occur at the landscape, from a self-organized patchy state to a homogenous state (Rietkerk et al., 2004a). The model for shifts between homogeneity and self-organized patchiness invokes a ‘region of global bistability’ (Rietkerk et al., 2004a) along a gradient of environmental conditions wherein alternative ecosystem states are stable. Outside of the region, only one state is stable. The implications of this model for the Everglades are outlined by Wu et al. (2006) who described catastrophic shifts from the ridge-slough pattern to a nearly homogenous state driven by landscape hydrologic modifications.

A key line of evidence for assessing whether alternative stable states describe ridges and sloughs is peat elevation differences between the two ecosystems. More specifically, transition zones between the two ecosystems are very distinct and narrow in the least hydrologically-altered parts of the landscape. An analysis of the distributions of elevations should indicate discreteness between the two ecosystems. A histogram of elevations should center around two distinct distributions (ridges and sloughs), suggesting that localized feedbacks maintain discrete ecosystem states. Moreover, soil elevation distributions should allow us to evaluate the effect of

hydrologic modification on the stability of the ridge and slough mosaic. Should ridges and sloughs appear to be alternative stable states, then it is important to incorporate ecosystem thresholds and feedbacks to any model and restoration plan in the Everglades, as these may act as constraints on restoration goals (Suding et al., 2004). Evidence contrary to this model would be in a spatially stochastic structure of peat elevations. That is, if there are not multiple ecosystem equilibria, elevation differences between ridges and sloughs should be random due to non-directional ecosystem development pathways. A lack of bimodal distribution would indicate that the system is in a constant, non-linear transitional state between ridges and sloughs.

In this chapter, I outline what is known about pattern formation and decline in the Everglades ridge-slough landscape, and discuss the relative merits of various proposed mechanism for that phenomenon. In Chapter 2, I evaluate evidence for alternative stable states, and examine the effects of hydrologic modification on alternative state stability. Chapter 3 discusses the implications of this study, and suggests future directions for research on the ridge-slough pattern in the central Everglades, emphasizing inference about alternative hypothetical mechanisms for ridge-slough maintenance.

The Landscape

Much of Florida, south of Lake Okeechobee, is a single large drainage basin that includes the Everglades, the Big Cypress basin, Shark Slough, and the salt marshes and mangrove swamps of the coastal zone. Historically its hydrology was dominated by seasonal rainfall, with great sheets of shallow water moving slowly south over a uniquely flat landscape (vertical gradients of 3 cm per 1 km) and draining into Florida Bay. The Everglades is the largest subtropical wetland complex in the US, and was once comprised of 500,000 ha (5,000km²) of sawgrass marshes, wet prairies, slough aquatic communities, and tree islands (Loveless, 1959). These vegetative communities are associated with specific hydrology and water depths

(Loveless, 1959; Newman et al., 1996; Busch et al., 1998). The central Everglades is a peat-dominated wetland underlain by limestone bedrock which formed wetland environments approximately 5000-4500 YBP (Gleason and Stone, 1997). Gradients in soil depth and plant productivity occur with variations in topography and hydrology (Craft and Richardson, 1993b; Gleason and Stone, 1997). The Everglades has uniquely low topographic relief; increases in soil elevation as little as 10 cm can result in a 45% reduction in mean water depth and a 20% reduction in inundation frequency in some areas (David, 1996).

The central portion of the Everglades is largely a mosaic of ridges and sloughs, where higher elevation peat ridges dominated by sawgrass or tree island vegetation are oriented parallel to water flow (Figure 1-1), interspersed among lower elevation sloughs dominated mainly by either short hydroperiod marsh vegetation or floating aquatic vegetation (Ross et al., 2006). The wet season occurs from May through October with the dry season occurring November through April (Duever et al., 1997). The precipitation in the wet season is primarily from localized thunderstorms and is therefore erratic in distribution both temporally and spatially. The plant communities comprising the historic landscape are adapted to oligotrophic conditions (i.e., surface waters with low concentrations of dissolved minerals and nutrients).

Hydrologic Changes

Since the turn of the 20th century, large sections of the Everglades have been drained via canals (Light and Dineen, 1997), converted to agriculture (Snyder and Davidson, 1997), enriched with phosphorus (Davis and Ogden, 1997), and unnaturally flooded by the construction of impoundments (Kushlan, 1990). Water management projects in the Everglades culminated in the development of 1000 miles of canals, 720 miles of levees, 16 pumping stations, and approximately 200 control structures. The new hydrologic system redirects vast quantities of water to the coasts, resulting in 70% less water reaching Everglades National Park and Florida

Bay (Perry, 2004). The historic Everglades is now partitioned into the Everglades Agricultural Area (EAA), Water Conservation Areas (WCA) 1, 2, and 3, and the Everglades National Park (ENP). While the compartmentalization of the Everglades has helped to preserve the marshes by restricting urban and agriculture development, compartmentalization has also had negative consequences on marsh biota as the water flow and hydroperiod have been altered (Figure 1-1).

Ongoing conflicts over water resources between human users and ecosystem requirements led, in part, to the Central and Southern Florida Project Comprehensive Review Study (C & SF project), authorized by US Congress in 1992 to study the feasibility of modifying water-control structures and operations to restore the south Florida ecosystem and provide for other water-related needs of the region (Perry, 2004). The C & SF project reported a general decline in the health of the Everglades, including a 90-95% loss of wading birds; species loss (there are 68 federally listed species); deteriorated water quality via eutrophication and contaminants; habitat degradation and loss; and a decline in fisheries in estuaries and Florida Bay (Perry, 2004), which led to the creation of the Comprehensive Everglades Restoration Plan (CERP) as a framework for implementing hydrologic restoration. The main goals were improved water quality and restoration of the seasonal water flows to ENP.

Among the restoration goals were distribution of 80% of available water to support ecosystem needs, 20% to urban use, and water delivery with a more natural hydroperiod (Perry, 2004). More than 240 miles of levees and canals are scheduled to be removed, including most of the Miami canal in WCA 3, Tamiami Trail (US-41) will be rebuilt with bridges and culverts, and the levee separating the Big Cypress National Preserve from ENP will be removed (Perry, 2004). Other goals include the removal of contaminants (i.e., pesticides, biological oxygen demand (BOD), bacteria, and suspended solids) and phosphorus.

While anthropogenic nutrient inputs have strong effects on the plant and algal communities in the Everglades in areas adjacent to canal structures, nutrient loads are largely attenuated for ecosystems in the interior of WCA 3A (Childers et al., 2003). As such, this is an ideal area for understanding the role of hydrology in shaping the Everglades, decoupled from nutrient loading effects. WCA 3A is leveed on three sides. Tamiami Trail, constructed between 1915-1928 to connect Miami on the east coast with Naples on the west coast, delineates the southern boundary between WCA 3A and ENP. While the road contains numerous culverts and bridges designed to allow flow from north to south, a levee (Levee 29) still regulates flow, which has increased water depth on the WCA 3A side and, in turn, disrupted the seasonal hydrologic pattern (Childers et al., 2003), reduced vegetative diversity (David, 1996), and increased the proportion of slough area to ridge area (Wu et al., 2006). The northern area of WCA 3A has an inundation period of 32-61% of the year (mean water depth is 10-18cm); in contrast, the impounded southern part of 3A is much wetter, with an inundation period of 96% of the year (mean water depth > 60cm) (David, 1996). Reductions in spatial heterogeneity associated with hydrologic modification (Wu et al. 2006) alter the size and diversity of habitats, with important negative consequences for many wildlife populations (Davis and Ogden, 1997).

Plant Communities

Herbaceous communities in the Everglades are generally grouped according to dominance by one of the following: 1) *Cladium jamaicense* Crantz, either in nearly monospecific stands or sparsely in marl prairies; 2) *Eleocharis cellulosa* in wet prairie habitats usually combined with *Sagittaria* spp and *Rhynchospora* spp; 3) *Panicum* spp and *Paspalidium* spp, also in wet prairies; or 4) *Utricularia* spp and *Bacopa* spp, generally found in sloughs (Busch et al., 1998) (Figure 1-2). Other species, such as *Nymphaea odorata*, are associated with deeper water habitats and frequently are found in sloughs. There is a gradient of increasing water depth and

above water decreasing habitat complexity as one moves from *C. jamaicense* stands toward wet prairies and thence to sloughs (Jordan et al., 1997).

C. jamaicense is a rhizomatous perennial sedge adapted to oligotrophic conditions (Steward and Ornes, 1975; Lorenzen et al., 2001), which may help explain its dominance in the Everglades. It reproduces primarily vegetatively, chiefly through rhizome production, but also through witch's brooms, an unusual vegetative proliferation on the reproductive organs (Miao et al., 1998). Physiological constraints, including low seed germination rates (Lorenzen et al. 2000) and growth responses to oxygen limitation (Lorenzen et al. 2001) restrict the spatial extent of *C. jamaicense* in this landscape.

One physiological attribute precluding *C. jamaicense* from deeper water habitats may be its root response to reducing conditions. Chabbi et al. (2000) found the root response to plant oxygen demand was limited. A detailed examination of radial oxygen loss to root tips showed a mechanism for developing barriers to leakage along root axes (Chabbi et al. 2000). However, increased alcohol dehydrogenase activity and ethanol concentrations in *C. jamaicense* suggest that this mechanism is not sufficient to prevent oxygen deficiencies under extended inundated conditions. Chabbi et al. (2000) additionally found the development of aerenchyma and subsequent increases in root porosity are also limited in *C. jamaicense*. Further compounding this limitation, oxidation of the rhizosphere after flooding is reduced, which may limit mineralization and availability of nutrients in the root zone. These physiological limitations may be key to understanding the presence of *C. jamaicense* along higher elevation ridges and its absence in deeper water sloughs; moreover, reproductive constraints may be important to understanding the time domain of sawgrass encroachment into sloughs with hydrologic modification.

Sloughs are a few inches to one - two feet below the elevation of adjacent ridges (Loveless, 1959). The dominant vegetation is *Nymphaea odorata* and *Nuphar advena* as well as sparse, stunted *C. jamaicense* and *Utricularia* spp (Loveless, 1959). *Utricularia* is abundant in many slough areas and may play an important role in the formation of organic soils in sloughs (Loveless, 1959). Lewis (2006) found a higher residual fiber content in *Utricularia* than any other slough species, though values were substantially lower than for *C. jamaicense*.

Periphyton is an important component of open water habitats in the Everglades and varies both temporally and spatially in terms of biomass, productivity, and species richness and diversity in relation to macrophyte abundance and nutrients (Gleason and Spackman Jr., 1974; Wood and Maynard, 1974; McCormick et al., 1998; McCormick and Stevenson, 1998). Periphyton plays an important role in soil formation, as calcium carbonate (CaCO_3) can represent more than 90% of the weight of periphyton in some Everglades communities (Browder et al., 1982). High pH conditions cause CaCO_3 to precipitate, which can yield material for sediment building. Where *C. jamaicense* is abundant, periphyton is sparse ($7\text{-}52\text{g AFDM m}^{-2}$) and less productive ($0.25\text{-}0.70\text{ g C m}^{-2}\text{ d}^{-1}$) than in sloughs ($100\text{-}1600\text{g AFDM m}^{-2}$; $1.75\text{-}11.49\text{g C m}^{-2}\text{ d}^{-1}$) (McCormick et al., 1998). Interestingly, unlike with macrophytes, water depth does not appear to be a factor influencing biomass and species composition of periphyton (Wood and Maynard, 1974; Browder et al., 1982; McCormick et al., 1998). However, phosphorus loads do regulate periphyton production and respiration rates (Iwaniec et al., 2006). Even small changes in phosphorus, from less than 7 to $10\text{-}20\ \mu\text{g L}^{-1}$ can change the periphyton community to one dominated by filamentous green algae (McCormick et al., 1998). Periphyton acts as a phosphorus sink, and therefore has a role in preserving the oligotrophic nature of the Everglades (McCormick et al., 1998; Vaithyanathan and Richardson, 1998). Clear differences in the

characteristics and life history of the vegetation between ridges, sloughs and wet prairies sets the stage for associated and critically important differences in ecological processes.

The Processes

Proposed explanations for the development of ridges and sloughs have included the dislodging of patches of water lily marsh peat under deep water conditions (Gleason and Stone, 1997); flocculent transport and sediment deposition resulting in the creation of ridges (Jorczak, 2006); high-energy events depositing floc and organic matter on the interior of ridges, thus depositing greater amounts of nutrients on ridges (Leonard et al., 2006); or high flow volumes with a scouring action on sloughs, maintaining a distinct elevation difference between ridges and sloughs (Ogden, 2005).

The velocity of water and its action on elevation does not appear to be an important factor, as it does not vary among ridges and sloughs (Leonard et al., 2006); however, there is seasonal variation of the velocity of water between adjacent ridges and sloughs, an observation that Jorczak (2006) links to water levels. The same study showed an increase in total suspended solids in the water column moving from north to south from northern WCA3A to Everglades National Park, and slightly higher suspended solids in sloughs compared to ridges. Another study similarly found accumulation rates of particulates to be lower on ridges than in sloughs (Leonard et al., 2006). Accumulation rates are generally low in Shark River Slough (mean rate of particulate accumulation in Oct. 2003 of $44.8 \text{ gdw d}^{-1} \text{ m}^{-2}$ and $122.4 \text{ gdw d}^{-1} \text{ m}^{-2}$ for ridges and sloughs, respectively). As such, sediment deposition from the water column as the mechanism of ridge formation and maintenance is unlikely. It is possible that physical structure of sawgrass on a ridge may act as a baffle, allowing fine organic matter and nutrients to settle out of the water column, and thereby increase the nutrient status of the ridge. If so, this could help explain higher

productivity on ridges. Unfortunately, an analysis of the mass and characteristics of particulates deposited on ridges has not yet been done.

Another mechanism proposed for maintaining multiple stable equilibria focuses on autogenic feedbacks between soil elevation, plant productivity and peat oxidation (Givnish et al., 2007; Larsen et al., 2007). As Odum (1971) elegantly stated “Ecosystems are capable of self-maintenance and self-regulation as are their component populations and organisms.” The processes of maintenance and self-regulation of the Everglades center around hydrological effects on community composition, decomposition and productivity. As discussed above, water depth has an influence on the species present at any particular location, and is an important control on ecosystem productivity via both changes in composition and inundation stress. Decomposition of plant matter is also influenced by soil elevation by affecting both the diffusion of oxygen through the water column to the sediment and the probability that a particular location will be exposed to the air with natural variation in water depth. The combined processes of plant (and litter) production and subsequent mineralization control peat accretion; changes in water depth that occur in response to changes in peat accretion act as a feedback mechanism controlling plant community composition (Figure 1-3).

Despite strongly differential rates of primary productivity, ridges and sloughs must accrete peat at roughly the same rate in order for the landscape pattern to be persistent. To compensate for large differences in productivity, carbon mineralization from the soil and water column (as CO_2 and CH_4), must be higher in ridges. Oxidation differences are likely to be most pronounced during seasonal low water, when ridge sites have a higher probability of exposure and therefore aerobic oxidation. This mechanism is supported by other studies showing that water depth has a strong influence on CO_2 evolution in the Everglades (Debusk and Reddy, 2003; Jorczak, 2006).

Time integrated ecosystem carbon accretion rates at equilibrium must be equal between ridges and sloughs (Fig 1-4a); were this not true, elevation differences between ridge and slough would continue to grow unchecked by feedbacks such as accelerated respiration. Moreover, if ridges and sloughs represent alternative stable states, any location that is accreting peat at rates different from the equilibrium state would be unstable; that is, ecosystem feedbacks in the form of changes in production and/or respiration would force the carbon balance back to the equilibrium state. For example, a particularly shallow location would experience accelerated soil respiration such that soil elevations would decline and the system would move back to equilibrium. Similarly, oxidation rates at deep water sites would force the system to accrete soil, moving that location towards the slough equilibrium. What happens in the systems falling between equilibrium states may be more varied, where the elevation may be either rising, moving towards ridge systems, or lowering, moving towards the slough system; moreover, community composition shifts may lead to catastrophic transitions between states. The keystone driver for these feedback controls on the carbon balance is hydrology (water depth); as such, when hydrology is altered, shifts between ridges and sloughs are expected to ensue.

The transition from ridge to slough is expected to be strongly influenced by competition between sawgrass and slough species (Fig 1-4b). The directionality of change should be indicated by the carbon balance: If the net carbon accretion is higher than the landscape equilibrium rate, then the system is moving towards a ridge. Alternatively, if the net carbon accretion is less than equilibrium, then the system is moving towards a slough. Understanding peat formation, then, is necessary to understand the variations in the topography found in the ridge and slough mosaic.

The characteristics of peat formed in ridges and sloughs differ in many ways. Vegetation on ridges has greater residual fiber content and a higher C:N ratio (Lewis, 2005). Many slough species require buoyancy in leaf structures and therefore lack the carbon structures necessary in emergent plants such as *C. jamaicense* (Lewis, 2005). While hydroperiod has an effect on litter decomposition (Lewis, 2005), it may be the recalcitrant nature of *C. jamaicense* dictating the litter decomposition rate on ridges. However, when peat is exposed to oxygen, it decomposes at a much higher rate. Peat has been estimated to accrete at rates of 2.8-3.2 mm yr⁻¹ at reduced hydroperiod areas, 1.6-2.0 mm yr⁻¹ at higher hydroperiod areas, and as fast as 4.0-5.67 mm yr⁻¹ in phosphorus enriched areas (Craft and Richardson, 1993a, b).

Another factor essential to understanding peat formation is in the recalcitrance of the peat. Jorczak (2006) found no difference in carbon dioxide (CO₂) emission from ridge soils versus slough soils. This finding suggests that although vegetative matter decomposes more readily in sloughs, the recalcitrance of the soils is similar once the litter becomes soil. Jorczak (2006) also reported a threefold increase in soil respiration when the water table fell below the soil surface. Other studies have shown a similar increase in CO₂ flux when water tables are decreased. Debusk and Reddy (2003) reported an increasing flux of CO₂ in Everglades peat profiles as water levels were decreased incrementally between 0 and -15 cm. However, while studies have correlated methane (CH₄) production to water table depth, temperature, and pH fluctuations, a thorough understanding of methane production has thus far proven elusive (Bachoon and Jones, 1992; Drake et al., 1996; Debusk and Reddy, 2003; Chauhan et al., 2004; Jorczak, 2006): CH₄ may be oxidized through the rhizosphere, lost to methanogenesis, or fluxed through vegetative matter. The flux through vegetative matter is a particularly important factor,

as increases in *C. jamaicense* biomass in a marl prairie were closely correlated with rates of methane emission for the ecosystem (Whiting et al., 1991).

Sawgrass communities are highly productive, with net aboveground primary productivity (NAPP) values ranging from 300 to 5656 gdw m⁻² yr⁻¹ (Table 1-1), and are consistently higher than either slough or wet prairie communities. Increasing annual water depths and hydroperiod reduce the productivity of sawgrass-dominated communities (Childers et al., 2006), which may help explain the transition of ridges to sloughs in areas affected by impounded water.

Productivity of *C. jamaicense* also varies concurrently with phosphorus (Daoust and Childers, 1999). While ridges are dominated by *C. jamaicense*, slough vegetation is much more variable, and therefore the productivity of the ecosystem is expected to be much more variable (Table 1-1). This is particularly true as sloughs may be dominated by sedges, *N. odorata*, *Eleocharis* spp, periphyton, or change over the course of a year in plant dominance (Daoust and Childers, 1999), with reciprocal changes in ecosystem productivity.

This study has two objectives: First, test hypotheses drawn from alternative stable state theory in the Everglades ridge-slough region. Second, quantify the effects of altered hydrologic regimes on the properties of the bi-stable ridge-slough landscape. To accomplish these tasks, I examined the distribution of soil elevations across large landscape blocks (2x4 km) spanning a gradient of hydrologic impairment in the central Everglades. The hypothesis that ridges and sloughs represent alternative stable states leads to the predictions that: 1) soil elevations show strong fidelity to community type with little overlap in probability density functions (pdf) of elevation in minimally hydrologically impacted areas; 2) increasing hydrologic modification decreases pdf separability; 3) hydrologic modification increases the variance of elevations within communities; 4) kurtosis of the joint soil elevation distribution decreases with increasing

hydrologic modification; and 5) spatial anisotropy declines with hydrologic modification. The results born out of this project, presented in Chapter 2, have a third intention- to develop simple, diagnostic measures of ecosystem health in the Everglades.

Research Objectives

Objective 1

Determine the extent to which ridges and sloughs are discrete ecosystems via an analysis of the distributions of elevations.

Hypothesis 1: The ridge-slough landscape is an expression of alternative stable states.

Prediction 1-1: There is a bimodal distribution of elevation heights.

Rationale: If the system is comprised of a series of gradients leading from ridges to sloughs, then water depths are clustered around a mean, which is the intermediary between ridges and sloughs. Thus, bimodality should indicate the discreteness of the boundary between ridges and sloughs.

Prediction 1-2: Vegetative communities exhibit a fidelity to discrete soil elevations.

Prediction 1-3: Autocorrelation is high in near-point neighbors, decreasing with distances.

Rationale: It has been suggested that scale-dependent feedbacks (locally positive, distally neutral or negative) lead to landscape patterning (Rietkerk and van de Koppel, 2008). These feedbacks would be evidenced by initially high autocorrelation followed by decreasing correlation at each site.

Objective 2

Determine the extent to which hydrologic modification has altered the underlying characteristics of ridge-slough patterning.

Hypothesis 2: Recent hydrologic modifications have led to a loss of the characteristics of the patterning of the ridge-slough landscape.

Prediction 2-1: Probability density function separability decreases at sites with hydrologic modification.

Prediction 2-2: The occurrences of vegetative communities shifts under hydrologic modification.

Prediction 2-3: The variance of elevations within each community increases in areas with hydrologic modification.

Rationale: As each community nears its water depth threshold, increases in transitional areas are observed.

Prediction 2-4: Spatial anisotropy is lost under hydrological modification.

Rationale: Given that the conserved portions of the ridge-slough mosaic are anisotropic, and have long been long thought to be related to water flow, then hydrologic alteration (drainage and thus reduced flow rates; impoundment) should reduce anisotropy.

Prediction 2-5: Spatial structure is lost under hydrologic modification.

Rationale: While there is a certain amount of stochasticity to soil characteristics, if predictions 1-1 and 1-2 are correct, that is, vegetative communities have a strong fidelity to non-overlapping peat elevations, then we can assume there is a high amount of non-stochastic spatial structure. The processes leading to this spatial structure (community dynamics, respiration, etc), however, can be assumed to be functioning differently under hydrologic modification, increasing the stochastic nature of any patterning present.

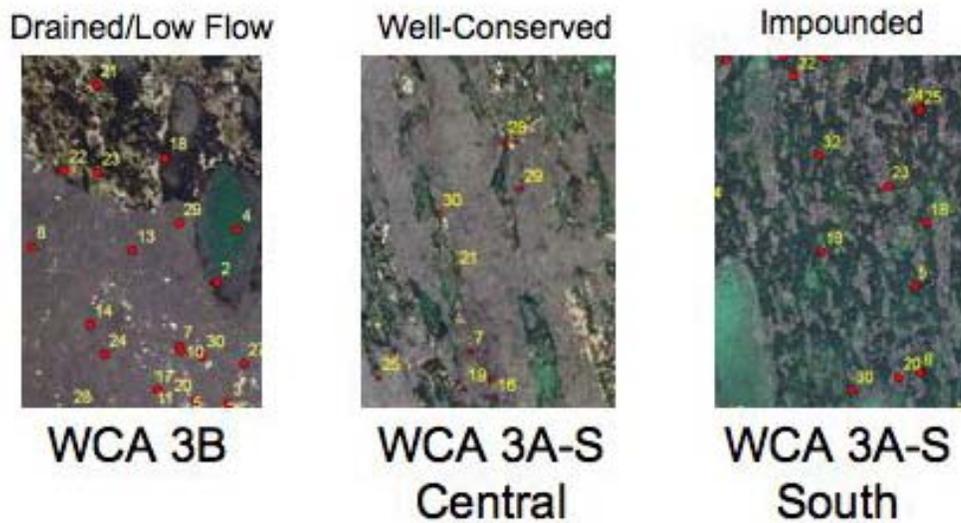


Figure 1-1. Aerial views of the ridge-slough mosaic. Recent (last 100 year) hydrologic modifications have resulted in a general loss of the historic patterning of the landscape. WCA 3B has significantly reduced flow volumes and rates, whereas the southern portion of WCA 3A-S has impoundment of water. The central portion of WCA 3A-S is considered to have the most well conserved hydrologic conditions, and thus the most well conserved ridge-slough patterning. The areas shown are sections of the landscape blocks sampled, as described in Chapter 2.

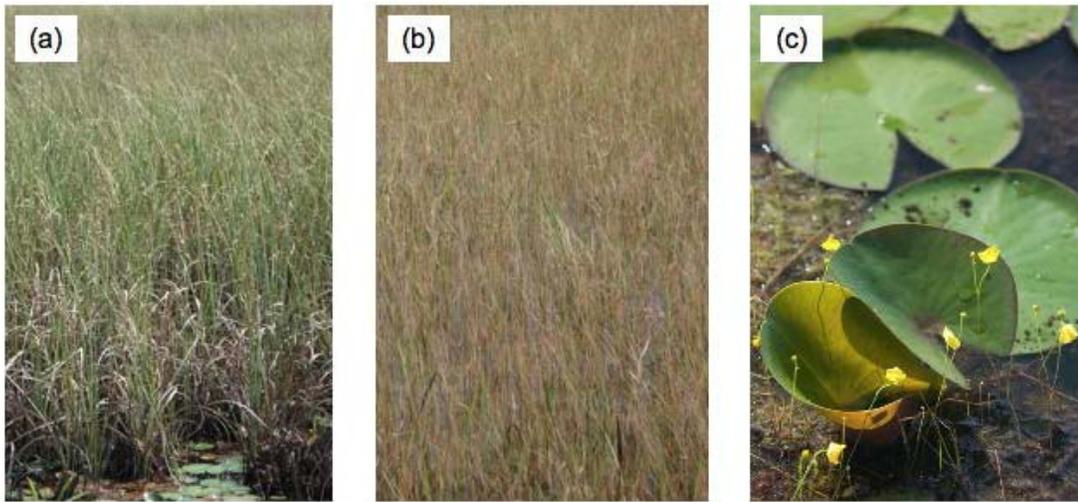


Figure 1-2. Vegetative communities of the ridge-slough portion of the Everglades (excluding tree islands): (a) sawgrass ridge; (b) wet prairie, generally dominated by either *Panicum* spp or *Eleocharis* spp; and (c) sloughs, generally dominated by *Utricularia* spp and *N. odorata* (picture (c) courtesy of Tyler Jones).

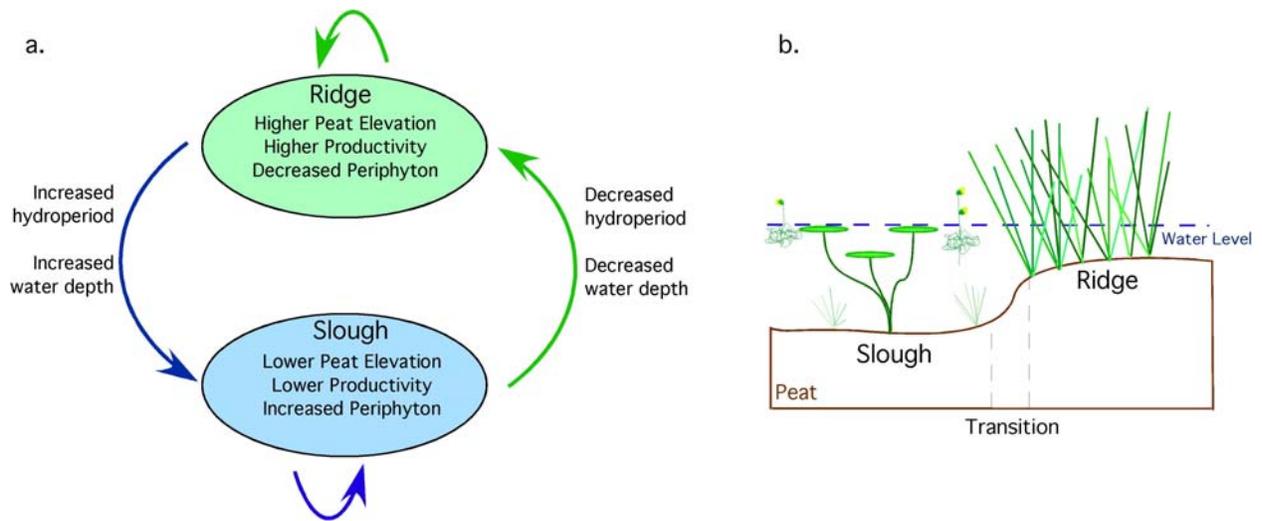


Figure 1-3. Feedbacks to the multiple steady states of the ridge and slough portion of the Everglades. Interactions between hydrologic conditions and productivity/respiration (a) lead to the maintenance of either a ridge or a slough (b), with differing communities and peat elevations. Large changes to the hydrologic conditions could, however, cause a shift from one ecosystem type to another.

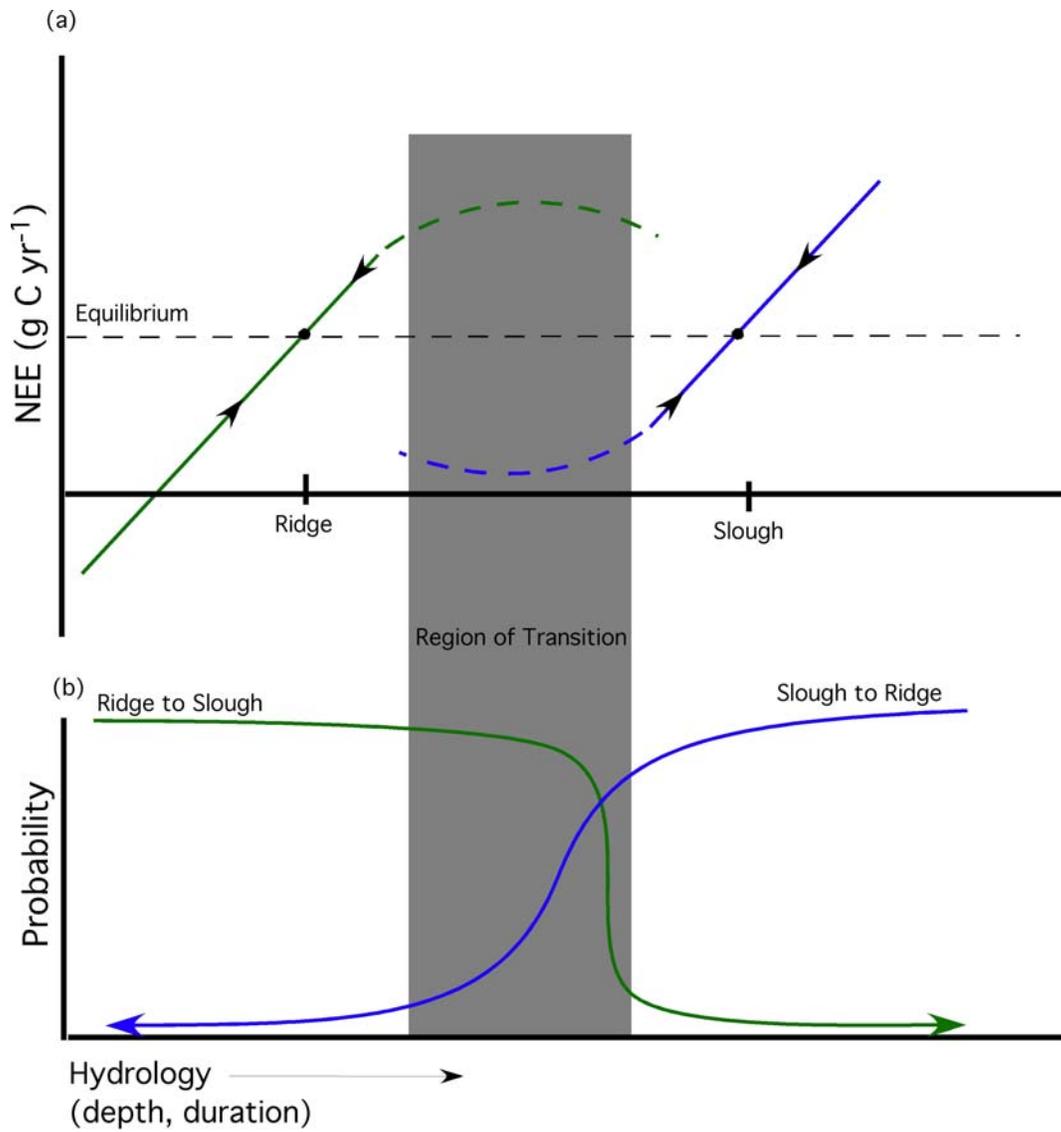


Figure 1-4. Point model for theoretical relationship of the carbon balance in ridges and sloughs. There is a range of water depths ideal for ridges and sloughs, where the ecosystem carbon balance at any point will move towards the equilibrium state over any time period (a). When the water depth is at some intermediate level for an extended period of time, the effect of competition between the ridge and slough communities is seen (b), where sawgrass reaches a threshold level whereby it can no longer compete with the more opportunistic species found in sloughs, causing a community and thereby ecosystem shift.

Table 1-1. Net aboveground primary productivity estimates in the Everglades.

Community	Location	g DW m ⁻² yr ⁻¹	Citation
Sawgrass		2991±891	(Daoust and Childers, 1998)
Sawgrass		802-3035	(Davis, 1989)
Sawgrass	Northern ENP	300-850	(Daoust and Childers, 1999)
Wet Prairie	Northern ENP	30-135	(Daoust and Childers, 1999)
Wet Prairie		409±160	(Daoust and Childers, 1998)
Wet Prairie	Eastern Big Cypress	43.8-317.55	(Porter Jr., 1967)
R/S Sawgrass	Shark River Slough	166-800*	(Ewe et al., 2006)
Tall Ridge Sawgrass	North 3A	4295.2±19	(Lewis, 2005)
	Central 3A	3667.7±225	
	North ENP	5656.2±100.8	
	Central ENP	3765.6±420.2	
Short Ridge Sawgrass	North 3A	2486.7±160.9	(Lewis, 2005)
	North ENP	1094.6 ± 13.4	
	Central ENP	3487.4±280.6	
Slough	North 3A	1683.5 ±266.1	(Lewis, 2005)
	Central 3A	844.9 ± 406.6	
	North ENP	663.8 ± 213.7	
	Central ENP	1515.7 ±158.7	

* Converted from g C m⁻² yr⁻¹ assuming 48% C content in sawgrass vegetation.

CHAPTER 2
EVIDENCE FOR PERSISTANCE AND LOSS OF ALTERNATIVE STABLE STATES IN
THE RIDGE SLOUGH MOSAIC OF THE EVERGLADES

Introduction

Alternative stable state theory suggests that within ecosystems with the same exogenous drivers, two or more distinct stable states can exist. Generally, these stable states exhibit shifts between alternative “basins of attraction” in community composition (Holling, 1973) that are internally maintained via positive feedbacks between communities and ecosystem variables. These systems undergo catastrophic shifts between system states as ecosystem driver variables change (Scheffer and Carpenter, 2003; Suding et al., 2004; Schröder et al., 2005), and are characterized by path-dependent hysteretic behavior. That is, changes in ecosystem state lag changes in an ecosystem driver because of positive feedbacks that resist change; resistance in both directions results in transition thresholds that differ with the direction of the shift (Scheffer et al., 2001).

A number of ecosystems exhibit regime shifts characteristic of alternative stable states (reviewed in Didham et al., 2005; Schröder et al., 2005). Systems that manifest multiple stable states in space rather than time (i.e., patterned landscapes) have been the subject of recent interest (reviewed in Rietkerk et al., 2004a). These systems form landscape pattern from local and regional feedback mechanisms wherein organisms (principally plants) change the nutrient content, water status, and/or soil elevation with reciprocal implications in ecosystem structure, composition and function (Ludwig et al., 1999; Rietkerk et al., 2004a; Rietkerk et al., 2004b). These scale dependent feedbacks (positive feedbacks locally, negative feedbacks at distance) lead to patterned structure in the landscape (Rietkerk and van de Koppel, 2008). Among the feedbacks that create these patterns are a redistribution of water in arid systems; competition for limiting resources in savannas; and ponding of water and convective transport of nutrient by

differences in transpiration rates in peatlands (Rietkerk et al., 2004a). Regime shifts in these systems occur not only as local shifts between alternative ecosystem states, but also landscape-level shifts from self-organized patchy states to homogenous states as conditions change (Rietkerk et al., 2004a); that is, under some environmental conditions, only one state is stable, and landscape patterning is lost. The Florida Everglades provides an excellent model system for testing predictions of alternative stable state theory, as well as increasing our understanding of the mechanisms underlying ecosystem patterning.

The central portion of the Everglades is comprised of the patterned ridge-slough mosaic. The system was historically a flow-through, oligotrophic system which has since been compartmentalized into water conservation areas (WCA) with distinct hydrologic regimes (SCT, 2003) and, in areas, enriched with phosphorus. Ridges are dominated by sawgrass (*Cladium jamaicense*), and are more productive systems with high peat accretion potential (Loveless, 1959; Craft and Richardson, 1993a; Childers et al., 2003; SCT, 2003). Sloughs are commonly dominated by *Nymphaea odorata*, *Nymphoides aquatica*, and *Utricularia* species, although they may be dominated by various graminoid and rush species in an assemblage frequently referred to as wet prairies (Loveless, 1959; Jordan et al., 1997; Childers et al., 2003). Sloughs are generally lower in elevation than ridges, with characteristic vegetation that produces more labile litter leading to lower peat accretion potential (Vaithiyathan and Richardson, 1998; Lewis, 2005; Jorczak, 2006). In areas where historic conditions persist, vegetation patterning is highly regular, and oriented with landscape water flow; the soil elevation differences between communities have led to the landscape being referred to as ‘corrugated’ (Baldwin and Hawker, 1915; Loveless, 1959; Sklar et al., 2004). Recent loss of this spatial vegetative patterning in some areas has been identified as a major concern for restoration activities (SCT, 2003; Ogden, 2005). Wu et al.

(2006) have suggested that loss of spatial pattern towards a homogenous landscape represents a catastrophic shift *sensu* Rietkerk (2004a), and have developed spatial indices for pattern degradation. This vegetative pattern loss has not been correlated to soil elevation changes; elevation is inferred from vegetative cover. Recent studies have established that soil elevation in this region (excluding tree islands) is decoupled from the underlying bedrock (SCT, 2003; Givnish et al., 2007), suggesting that some other process, presumably autogenic feedback from the vegetative communities, has led to spatial patterns of peat elevations across the landscape. Further, this implies that the loss of spatial patterning is driven by alterations in these autogenic feedbacks.

Our conceptual model for patterning in the Everglades ridge-slough proposes autogenic feedback mechanisms in carbon budgets maintain stable landscape patterning. Feedbacks among depth and duration of inundation, plant community composition, net primary production, and peat accretion and decomposition are hypothesized to create and maintain multiple peat accretion equilibria (high production, high respiration ridges; low production, low respiration sloughs). To maintain landscape patterning, long-term accretion rates in ridges and sloughs must be similar, despite strongly differential primary productivity, presumably because of a dynamic balance between production and respiration rates (Figure 2-1). Alterations in hydrologic conditions, which are emblematic of human management of the Everglades, are expected lead to changes in the carbon budget and disequilibrium in peat accretion and ultimately to shifts between ecosystem states. Recent literature describes elevation differences between intact ridges and sloughs and the loss of these differences with hydrologic alteration (Givnish et al., 2007). However, efforts to quantify elevation differences in response to known hydrologic changes are not sufficiently developed to be diagnostic of regime shifts (from ridge-slough to a flattened

landscape), nor can we predict the hydrologic conditions under which transitions between ridge and slough states will occur. Finally, quantitative information linking elevation differences to changes in the plant communities is limited, which represents a critical knowledge gap since this relationship is hypothesized to be the foundation of bi-modality maintenance in the ridge-slough mosaic.

Here we consider the use of peat elevation distributions to indicate autogenic state stability and examine how elevation distribution properties change along a gradient of hydrologic impairment. Using a bifurcation point model for alternative stable states (adapted from Sheffer et al., 2001, Figure 2-2), we developed a series of predictions emerging from the hypothesis that the ridge-slough landscape represents alternative stable states. First, distinct bimodality in peat elevations should be evident in what is considered the most well conserved hydrologic conditions in the ridge-slough mosaic. Second, these peat elevation distributions should show significant shifts away from bimodality with hydrologic alteration, with corresponding shifts in plant community prevalence and fidelity to soil elevations. Consequently, self-organizing spatial macro-structure in the landscape is lost with hydrologic alteration. If true, we predict that statistical metrics of pattern (spatial anisotropy and relative spatial structure) in the peat topography evident in conserved areas will be lost with hydrologic modification. While the metric of interest is peat elevation, we use water depth as a local elevation proxy throughout.

Methods

Study Area

For at least the last 2,700 years, most of the central Everglades has consisted of the ridge-slough mosaic, with the centers of ridges and sloughs persistent in their present configuration for at least 1,000 years (Bernhardt et al., 2004). Presently, the ridge-slough region is restricted to Water Conservation Area (WCA) 3 and ENP (SCT, 2003), with the largest area of peat-based

ridge-slough mosaic located in WCA 3. This change is attributed, at least in part, to hydrologic changes in the 20th century (Light and Dineen, 1997) associated with the compartmentalization of the Everglades. Recent (100 years) hydrologic changes has been linked with sawgrass expansion, producing or exploiting topographic flattening (Bernhardt et al., 2004). The modern hydroperiod of WCA 3 has been modified for use as a shallow storage reservoir (Walters et al., 1992), and the presence of road corridors orthogonal to flow has led to hydroperiod shortening in the north, and impoundment in the south. These landscape modifications to regional hydrology in WCA3A comprise a hydrologic gradient, with the central area considered well conserved, and dry and impounded end-members in the north and south (District, 1992).

Seven 2x4 km landscape-sampling blocks were located throughout WCA 3, oriented along flow lines (Figure 2-3). Six of these landscape blocks were located in hydrologic partitions that represent the modern hydrologic conditions in WCA3A (drained, conserved, and impounded conditions), as well as a dry, low-flow end member located in WCA 3B.

Sampling

Sampling in each unit was done over a single day between September and December 2007. Since our metric of interest was relative elevation differences between ridges and sloughs, benchmarked water depths are not essential to the analysis. As such, water depths are not comparable among sampling units due to changes in hydrologic conditions over the sampling period; all analyses were performed within sampling units. Up to 30 randomly located clusters were placed in each sampling unit. Clusters consisted of measurements of water depth at the center point and points at 5 m and 25 m away from center in the ordinal directions (north, south, east and west). Water depth data act as surrogates for peat elevation, and are analyzed with respect to distributions of depths. All plant species were recorded at each location, and the cover of the dominant species noted.

Data Analysis

To avoid pseudoreplication resulting from 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.

To test for bimodal distribution of water depth, the Bayes' information criterion (BIC), a model comparer, was used to determine whether a single normal or a bimodal (two normal) distribution better fits the joint probability density function. The BIC penalizes additional parameters more strongly than does the Akaike information criterion (AIC), and thus at large sample sizes is a more conservative comparison of models (Burnham and Anderson, 2004). Water depth frequency in each sampling unit was fit to single normal (1) and mixed normal (2) distributions:

$$P_s = N(\mu_i, \sigma_i) \quad (1)$$

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

where q is a variable representing the probability of falling within the first of the two normal distributions, and N is a normal distribution with mean μ_i and standard deviation σ_i . To understand the separation of the joint probability function across the hydrologic gradient, a measurement of the joint probability function kurtosis (increasing density of points in the shoulders of the probability density function), the fourth moment of the pdf, was modeled as:

$$N^{(-1)} \sigma^{-4} \sum_i (x_i - \mu)^4 - 3 \quad (3)$$

where N is the length of (x) . Negative kurtosis indicates a higher density of observations in the shoulder of the distribution than expected with a standard normal; extreme kurtosis indicates a bi-modal density function, and as such serves as a simple diagnostic of joint probability function separation.

A priori vegetative classifications were used to separate water depth data into separate distributions to test for significant differences in water depths between communities. *C. jamaicense* dominance led to a label of ‘ridge’, *N. odorata* or *Utricularia spp.* dominance was labeled ‘slough’, and areas dominated by graminoids or sedges other than *C. jamaicense* were labeled ‘wet prairie’. All data points not falling into one of these classifications were not used for vegetative analyses. The resulting community-specific mean water depth values were compared within each sampling unit using a Student’s t-test. Linear regression between latitude and water depth within each landscape block was used to determine if the assumption of within-unit hydrologic uniformity is valid. Because ridges and sloughs each exhibit separate normal distributions, we regressed only the slough water depths (Table 2-1). The assumption of uniform hydrologic conditions within each landscape block was validated in most units, which exhibit non-significant slopes of slough water depth with latitude. However, the Drained and Conserved 1 landscape blocks both have significant negative slopes, suggesting hydrologic conditions are not uniform across their 4-km length and, specifically, that water gets deeper at the southern end of the unit. Ridge water depths also exhibit a significant negative slope for the Drained landscape block (Table 2-2), but exhibited a significant positive slope in the Conserved 1 landscape block, suggesting that the ridge-slough elevation difference in that sampling unit increases dramatically with distance south.

To test our conceptual model for scale-dependent feedbacks, patterns of spatial autocorrelation were determined within each landscape block (Rietkerk and van de Koppel, 2008) using GS⁺ software (Gamma Design Software, Plainwell, MI USA). As the landscape is expected to show declining correlation as distances increase, a measure of autocorrelation was done first in the near-neighbors, using 5m lag classes, and then at larger distances, using 20m lag

classes. Autocorrelation was used to find repeating patterns over space. A covariance matrix was created, where the covariance for an interval distance (class h) is

$$\text{cov}(h) = \frac{\sum x_i x_{i+h} - \overline{x_i} \overline{x_{i+h}}}{N_h} \quad (4)$$

where N_h is the total number of paired samples for the lag class h , x_i is the measured value of point i , x_{i+h} is the measured value of point $i+h$, $\overline{x_i}$ is the mean of all x_i for lag class h , and $\overline{x_{i+h}}$ is the mean of all x_{i+h} .

Autocorrelation is then defined as

$$C(h) = \frac{\text{cov}(h)}{\sigma_i \sigma_{i+h}} \quad (5)$$

where σ_i is the standard deviation of the measured values. The function $C(h)$ gives a value in the range $[-1,1]$, where 1 indicates perfect correlation and -1 indicates perfect anti-correlation.

Spatial analyses were performed using ArcGIS v. 9.2 (ESRI, Redlands, CA USA).

Spatial characteristics of variables are modeled by the semi-variogram function $\Upsilon(h)$. A semi-variogram describes the degree of spatial dependence between observations as a function of distance (lag). The semi-variogram then has properties of a sill, which is a measure of the lag variance; a range, which is the distance at which the semi-variogram reaches the sill; and a nugget effect, which is the sum of microstructure and measurement error. A ratio of the nugget to sill gives a value of Q which is a measure of the spatial dependence of soil properties (Cambardella et al., 1994). Strong spatial structure is represented by values greater than 75%. Values 25- 75% suggest moderate spatial structures, and values less than 25% indicate low spatial structures.

Spatial anisotropy was determined by examining the range of autocorrelation in orthogonal directions. Anisotropy factor is calculated as the ratio of the major range (direction of

maximum autocorrelation) to the minor range (autocorrelation range orthogonal to the major axis). Values of 1 indicate isotropic semivariance; the expected condition for a conserved ridge slough landscape is strong anisotropy. As our main interest was evidence for highly localized anisotropy, we restrained the analysis to 100m.

Results

In conserved sites, the water depth density function exhibited distinct bimodality (Figure 2-4). This bimodal signature is lost with both increasing drainage and increasing impoundment. Kurtosis follows a similar trend (Table 2-3), in which drained conditions have positive values, conserved conditions have negative values (i.e., density functions in these areas are highly kurtotic) and impounded conditions exhibit a shift back towards positive values.

When probability density functions are evaluated on a community basis, significant differences are observed between mean water depths in ridge and slough communities (Figure 2-5). However, the separation of the means, inferred from the *t*-value, decreases in both directions of hydrologic impairment compared with conserved conditions, indicating greater overlap in water depths between communities (Table 2-4). Moreover, the variance in water depths in both vegetative communities clearly increases with impoundment, and may decrease under drained conditions.

The distribution of vegetative community types varied with position within the hydrologic gradient. A substantially large fraction of sites were ridges in the drained/low flow site (WCA 3B) than at other sites (Figure 2-6). Ridge incidence decreases systematically with impoundment, while sloughs increase in incidence. When slough sites are partitioned into wet prairies (dominated by emergent vegetation) and deep sloughs (submerged and floating-leaved aquatics), a clear decline in the incidence of wet prairies is observed from conserved through impounded conditions (Fig. 2-6).

Near-distance autocorrelation for the well-conserved sites and the first transition site was highest among all the sites (between 0.85 and 1), with autocorrelation the lowest among the drained sites (between 0.5 and 0.6) (Figure 2-7). With larger ranges and lag distance, a periodicity is observable at all sites, with autocorrelation varying between strongly positive and negative correlation (Figure 2-7). In all cases, positive and negative correlation reduces with increased distance, however, so the autocorrelation becomes increasingly weak.

Relative spatial structure (Q) was high ($Q > 75$) for conserved and impounded sites, but low (< 40) for both of the drained sites (Figure 2-8). Anisotropy, however, was much lower for both the impounded sites (Transition 1, 2, and Impounded), and high (> 1.5) for both conserved and drained sites. Values for the anisotropy factor ranged from 1.1 in the Impounded block (effectively isotropic) to 2.2 (strongly anisotropic) in the Conserved 2 block.

Discussion

The evolution of patterning in the Everglades has been variously attributed to sediment transport (Leonard et al., 2006), differential flow volumes (Sklar 2005), and the redistribution of limiting nutrients, particularly phosphorus (Ross et al., 2006; Givnish et al., 2007; Rietkerk and van de Koppel, 2008). We propose a different model, in which peat accretion processes, and autogenic feedbacks therein, coupled with hydrology regulate landscape patterning. While there have been a number of studies concluding that anthropogenic hydrologic modification has resulted in community shifts in composition and extent (reviewed in Ogden, 2005), there have been few comprehensive studies on corresponding changes in the topography in the ridge-slough landscape (although see Givnish et al., 2007). As our results are highly suggestive that ridges and sloughs are a synthesis not only of vegetative community, but also of autogenic processes leading to peat elevation differences, from here on ‘ridge’ and ‘slough’ will represent these combined ecosystem variables.

Alternative stable states in patterned landscapes are predicted to exist within a discrete range of ecosystem drivers (Rietkerk et al., 2004a). Outside of that region of bistability, environmental conditions are such that feedbacks cannot maintain one or the other of the ecosystem types, and the system trends towards spatial homogeneity. Alternative stable states, then, exist not only as phase shifts from one ecosystem to another, but also as the landscape possibility of self organized patchy vs homogenous states. Our data support the hypothesis that changes in environmental drivers (i.e., hydrologic modification) lead to conditions where landscape bimodality is removed. These results are strongly consistent with predictions that emerge from the alternative stable state theory.

That the system is made of two phases (ridge and slough) with sharp boundaries is evidenced by the bimodality in conserved and transitional landscape blocks. Patterning comprised of gradual transitions would exhibit unimodal distributions in water depths. The loss of bimodality with hydrologic modification suggests that vegetative patterning in the drained and impounded sites is a residual signature; the sharp boundaries between ridges and sloughs have disappeared altogether, and it can be surmised that vegetative differences will ultimately disappear as well. Soil elevation, then, is the keystone variable in this system. Studies of vegetation change are forced to infer soil elevation changes from vegetation, but with key model failures. For example, Wu et al. (2006) infer from aerial photography that northern 3A (near our 'Drained' block) and southern 3A (near our 'Impounded' block) exhibits intact (or nearly so) ridge-slough patterning. Our data, however, show that vegetative changes lag behind soil elevation parameters.

Increased water depth variance within each vegetative community was expected to occur with hydrologic modification in both directions. Evidence supports this prediction with

impoundment but not with drainage, which was at first contrary to our expectations. The rationale for the original expectation was that vegetative communities would exhibit hysteretic behavior in response to hydrologic change. Thus we would expect to see species diagnostic of a community (e.g., *C. jamaicense*) over a wider range of soil elevation conditions when the landscape is in transition. We attribute the observation of increased variance behavior with impoundment, but not with drainage, to ecophysiological attributes of sawgrass. Despite sawgrass physiological stress and decreased growth with increasing inundation (Newman et al., 1996), which limits its spatial expansion except during periods of drought (Brewer, 1996; Pezeshki et al., 1996; Weisner and Miao, 2004), sawgrass appears to persist in deep water via rhizome extension upwards in the water column (presumably overcoming redox induced stress). Slough vegetation, in contrast, is easily out competed, and responds rapidly to both interannual variation, as well as long-term hydrologic change associated with both drainage and impoundment (David, 1996; Busch et al., 1998). The differences in vegetative response dynamics to hydrologic change (slow loss of sawgrass with impoundment, rapid loss of slough vegetation with drainage) results in increasing presence of emergent vegetation under drained conditions, but asymmetrical rates of change with impoundment.

Strong positive autocorrelation was observed at short-range in all landscape blocks, with clear declines with distance. More importantly for understanding landscape patterning, negative autocorrelations are observed at moderate distance and periodicity is evident at the block scale for sites with conserved pattern (Figure 2-7). This is consistent with expectations from self-organizing patterned landscapes. As communities exhibit fidelity to restricted ranges for water depths, autocorrelation would be expected to be high over distances coinciding with the spatial wavelength of ridge and slough patterning.

Rietkerk and van de Koppel (2008) postulate that short-scale positive feedbacks explain the sharpness of ecosystem boundaries, while large-scale negative feedbacks determine the pattern of self-organized, patchy systems. They further propose that the density of the organism engineer (in this case sawgrass) in a landscape determines the strength of scale-dependent feedbacks. This scale-dependency is exhibited by the periodicity and reduction in autocorrelation of water depths in our study. Further, the catastrophic shift from patterned to homogenous states is evidenced by the concurrent loss of peat bimodality, spatial structure, and the loss of anisotropy at the hydrologically modified sites.

Hydrologic changes over the last 50 years in WCA 3, considered widely to be the most well conserved ridge-slough mosaic, are driving the system away from the conditions that maintain patterned ridge-slough landscapes. Drained sites exhibited dramatic leveling of the landscape, decreased incidence of slough ecosystems (replaced by wet prairies), and decreasing spatial structure, suggesting that the ridge-slough mosaic is changing towards a sawgrass prairie. The residual signature of bi-modal vegetative communities under drained conditions is likely an artifact of sawgrass autecology; sawgrass expands primarily via vegetative growth (Brewer, 1996; Daoust and Childers, 1999; Lorenzen et al., 2000; Lorenzen et al., 2001) and thus is not an effective colonizer of disturbed areas. With increasing drainage leading to the succession of slough to wet prairie, and a complete loss of peat height bimodality (observed at the drained end-member block), it seems likely that the wet prairie state is transitional, and will succeed to sawgrass given time required for vegetative propagation. That is, transition from slough to emergent vegetation suggests that these locations are out of equilibrium; loss of soil elevation differences suggests that future plant community composition will be determined by competitive interactions, with the expectation that sawgrass will eventually dominate. Further, it appears that

the responses of landscape structuring to drainage and impoundment differ. Spatial structure (diagnostic of landscape self-organization) is lost in the drained areas, suggesting that sawgrass expansion and slough conversion to wet-prairie have flattened the landscape. In contrast, impoundment does not lead to a loss of spatial structure (that is, autocorrelation remains strong), but does appear to lose anisotropy, or directionality. The mechanism maintaining anisotropy under drained conditions is unknown, though maintenance of flow velocities despite changes in hydroperiod are likely to be a factor.

Among the long-term goals of the Comprehensive Everglades Restoration Plan (CERP) is the restoration of the depth, duration, timing and velocity of water across the landscape (SCT, 2003; Perry, 2004). Since much of the fish, insect, and plant diversity occurs in sloughs, there is a clear biological imperative to understand how to maintain the ridge-slough pattern (Davis and Ogden, 1997). Our results show that simple statistical descriptions of water depth distributions, including anisotropy, spatial structure, and bimodality, can act as diagnostic measures of ridge-slough health. Further, these measures are sensitive and specific to the magnitude and direction of hydrologic modification and may therefore be useful for effective ecosystem monitoring. We can also infer from our data that restoring historic water flows to WCA 3 will not necessarily quickly restore the original ridge-slough conditions. There appear to be lags in the shifts from intact ridge-slough to a degraded pattern; if these lags exist in reverse then we can expect a long ecosystem recovery. Where the landscape has lost patterning altogether, recovery can be expected to take even longer, constraining restoration goals (Zedler, 2000; Suding et al., 2004).

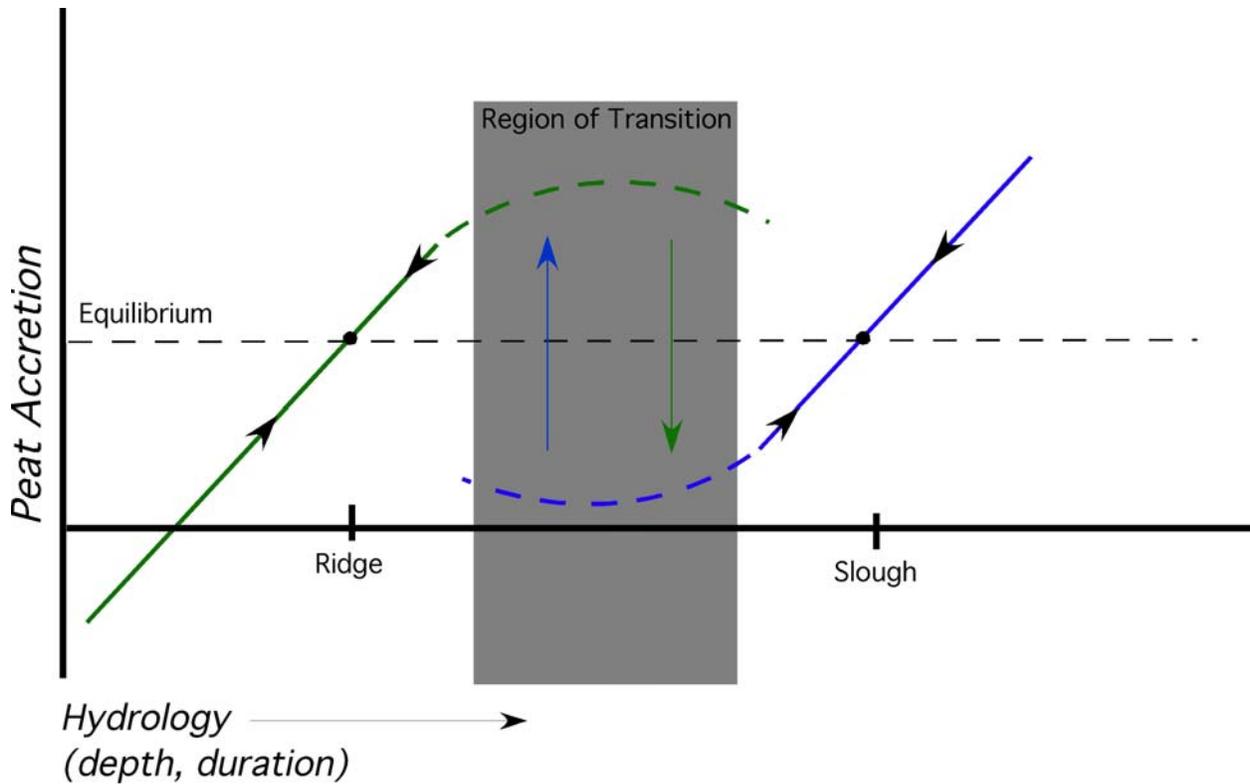


Figure 2-1. Conceptual model for autogenic feedbacks maintaining stable alternative ecosystems. Peat accretion is a net ecosystem variable, synthesizing the ecosystem processes of productivity and respiration. At the localized level, both ridges and sloughs have a hydrologic condition (water depth, inundation duration, velocity, etc) at which either a ridge or a slough is the likely community to be found. Changes in the hydrologic condition may alter the peat accretion rates, but the autogenic feedbacks within the communities will drive the system back to an equilibrium point. However, the system can be driven to whole-scale shifts if hydrologic alterations are of a large enough magnitude within a parameter space that would be the region of transition.

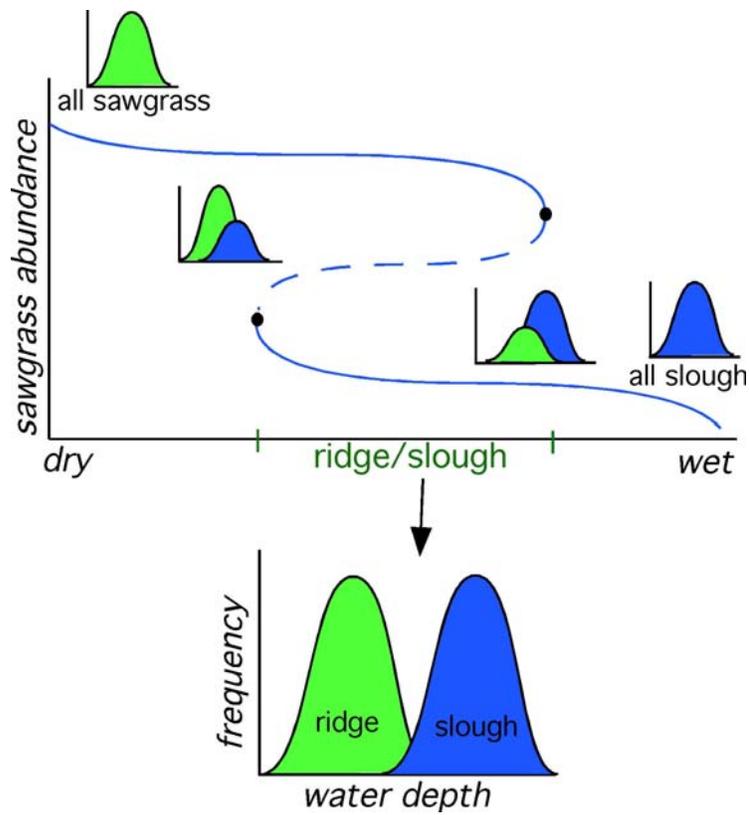


Figure 2-2. Bifurcation model for alternative stable states with hypothetical water depth distributions super-imposed. Under natural hydrologic conditions, the ridge-slough pattern is the most stable state. However, a movement away from those hydrologic conditions leads to a uniform, unimodal state of either all ridge (sawgrass prairie) or all slough.

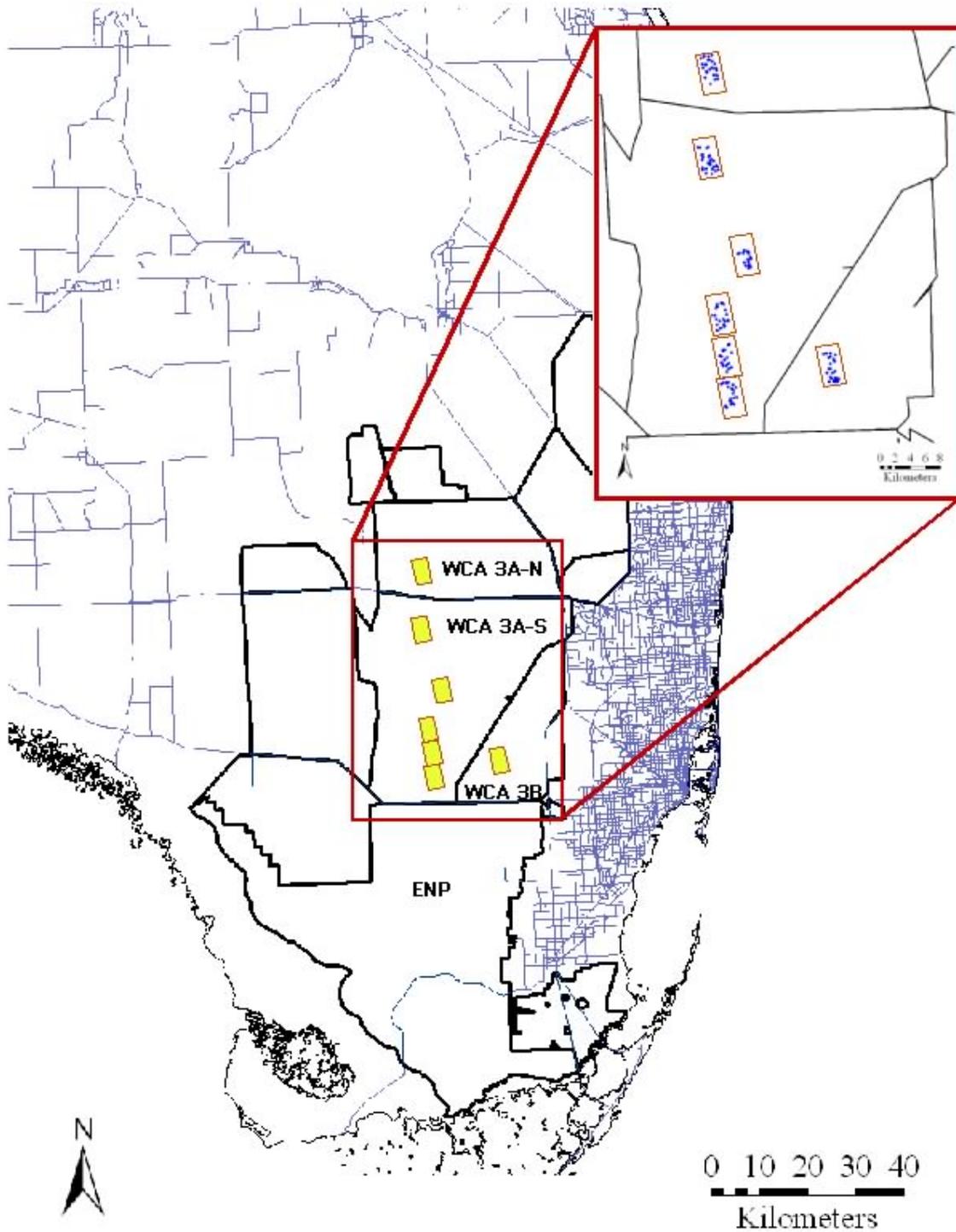


Figure 2-3. Map of South Florida with landscape sampling blocks. Insert: Locations of nested, randomly-located sites within the sampling blocks.

Table 2-1. Summary of regressions for slough water depths as a function of latitude.

Site designation	Intercept	Slope	R ²
Drained/Low flow	5.4e+02	-1.2e-03	0.06
Drained	5.3e+02	-2.0e-03 ***	0.16
Conserved 1	3.6e+02	-1.4-03 ***	0.17
Conserved 2	-7.6e+01	5.6e-04	-0.02
Transition 1	1.7e+02	-5.2e-04	-0.01
Transition 2	-2.6e+02	1.5e-03	0.02
Impounded	-4.4e+01	3.9e-04	-0.01

Regression summary for Slough water depth where water depth = a + b (latitude)

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

Table 2-2. Summary of regressions for selected areas for ridge water depths.

Site designation	Intercept	Slope	R ²
Drained/Low flow	1.9e+02	-7.6e-04*	0.01
Drained	5.5e+02	-2.1e-03 ***	0.17
Conserved 1	-5.9e+02	2.6e-03 **	0.12
Conserved 2	545.7	0.0	0.08
Transition 1	-3e+02	1.2e-03	0.17
Transition 2	797.5	0.0*	0.08
Impounded	-2.1e+02	1.1e-03	0.52

Regression summary for Ridge water depths where water depth = a + b (latitude).

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

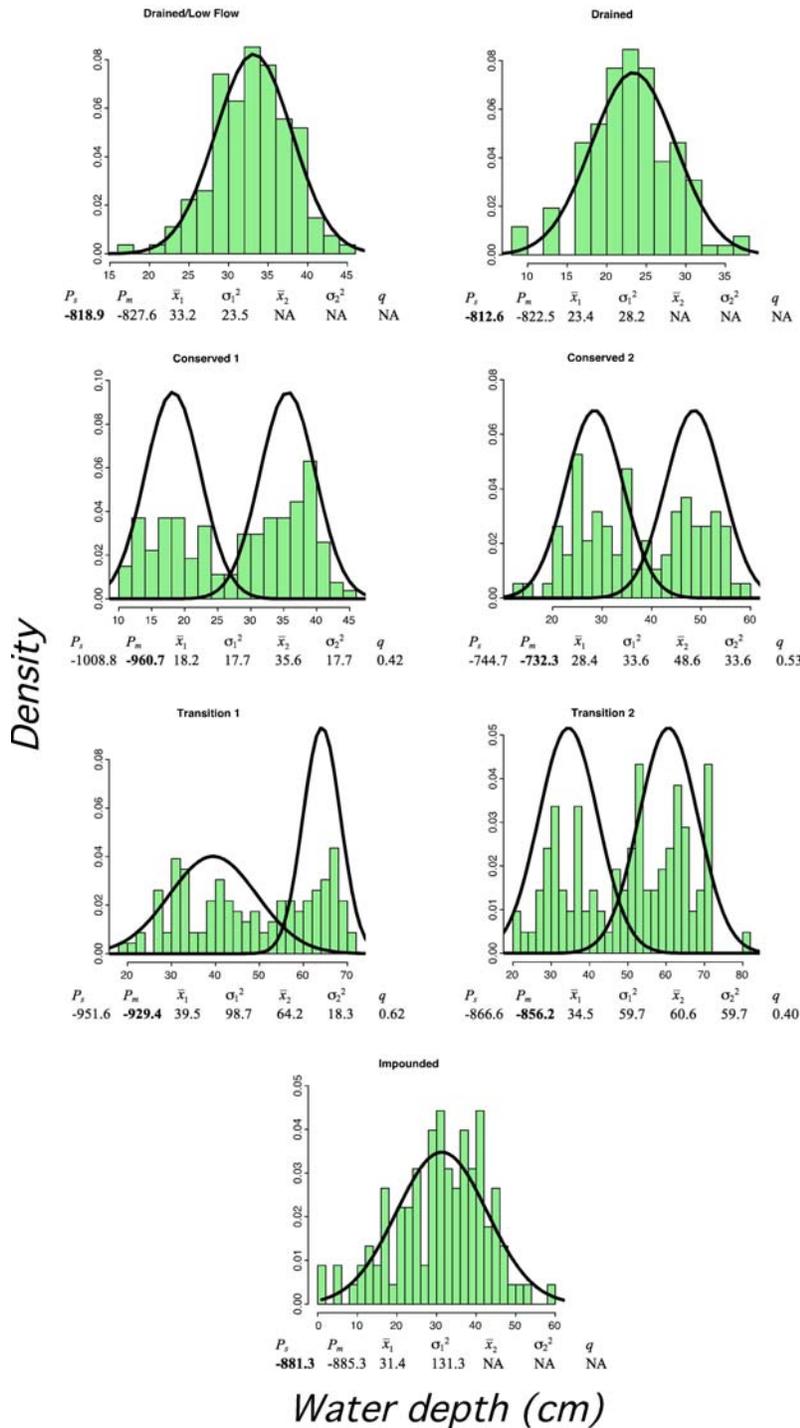


Figure 2-4. Water depths (local proxy for peat elevation) within each landscape block are shown as histograms. The lines indicate the probability density function of the best model indicated by the BIC score. The greater BIC fit (indicated in bold) indicates whether a single normal distribution (P_s) or a mixture of two normal distributions (P_m) 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. Note: NA=not applicable.

Table 2-3. Kurtosis of the water depth distributions for each sampling unit.

Site designation	Kurtosis
Drained/Low flow	0.24
Drained	0.32
Conserved 1	-1.37
Conserved 2	-1.23
Transition 1	-1.34
Transition 2	-1.17
Impounded	0.10

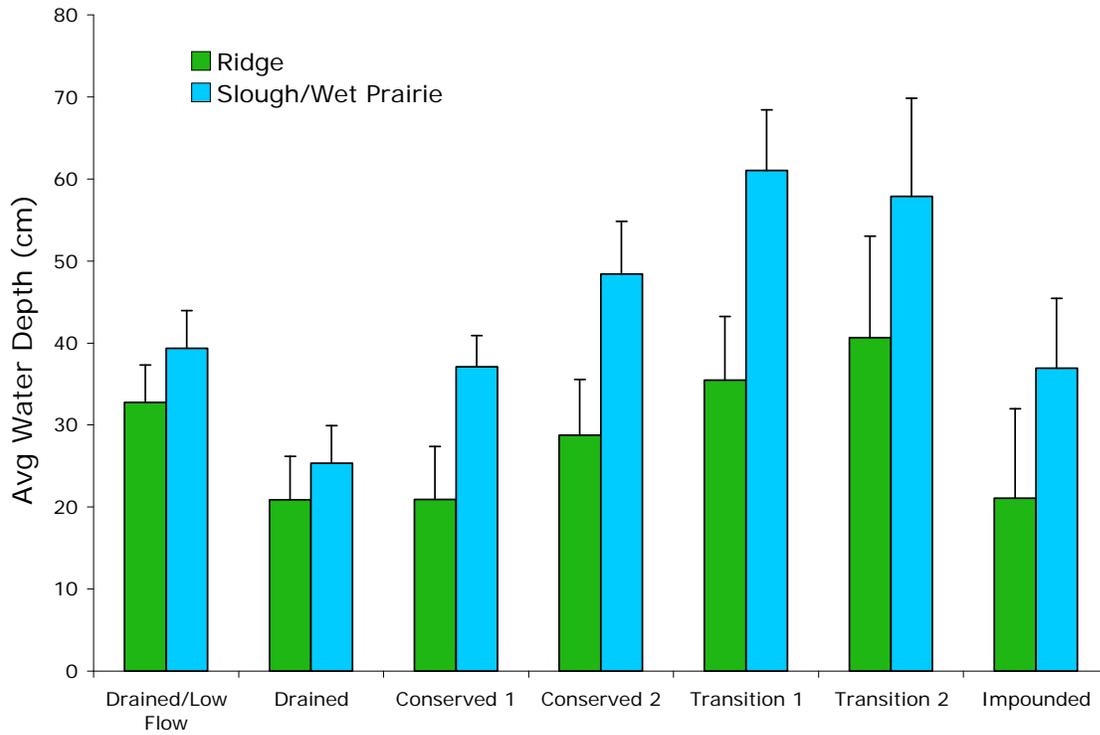


Figure 2-5. Average water depths of each community of the landscape sampling units. Error bars indicate standard deviation (summary of results are found in Table 2-3).

Table 2-4. Results of a-priori defined community water depth analysis

Site designation	Community	t-value	p-value	mean (cm)	var (cm ²)
Drained/Low flow		-3.98	0.004		
	Ridge			32.73	21.20
	Slough/Wet Prairie			39.38	20.98
Drained		-4.92	3.03E-06		
	Ridge			20.88	28.02
	Wet Prairie			25.32	21.34
Conserved 1		-17.33	< 2.2E-16		
	Ridge			20.94	41.62
	Slough			37.09	14.71
Conserved 2		-14.21	< 2.2E-16		
	Ridge			28.73	46.51
	Slough			48.43	41.00
Transition 1		-17.52	< 2.2E-16		
	Ridge			35.47	60.55
	Slough			61.03	54.89
Transition 2		-6.82	1.41E-09		
	Ridge			40.65	153.13
	Slough			57.88	143.25
Impounded		-7.01	1.26E-08		
	Ridge			21.07	118.51
	Slough			36.94	72.43

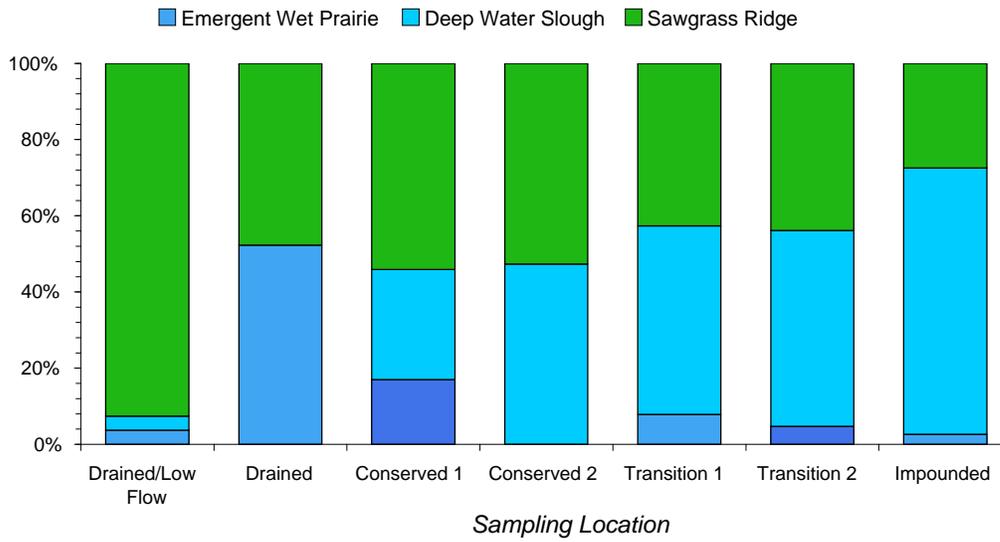


Figure 2-6. Relative incidence of vegetation communities by sampling unit. A priori classifications were designated by community dominance, i.e., sawgrass ridges are dominated by *C. jamaicense*, sloughs are dominated by either *N. odorata* or *Utricularia spp*, and wet prairies are dominated by graminoids or sedges, excluding *C. jamaicense*.

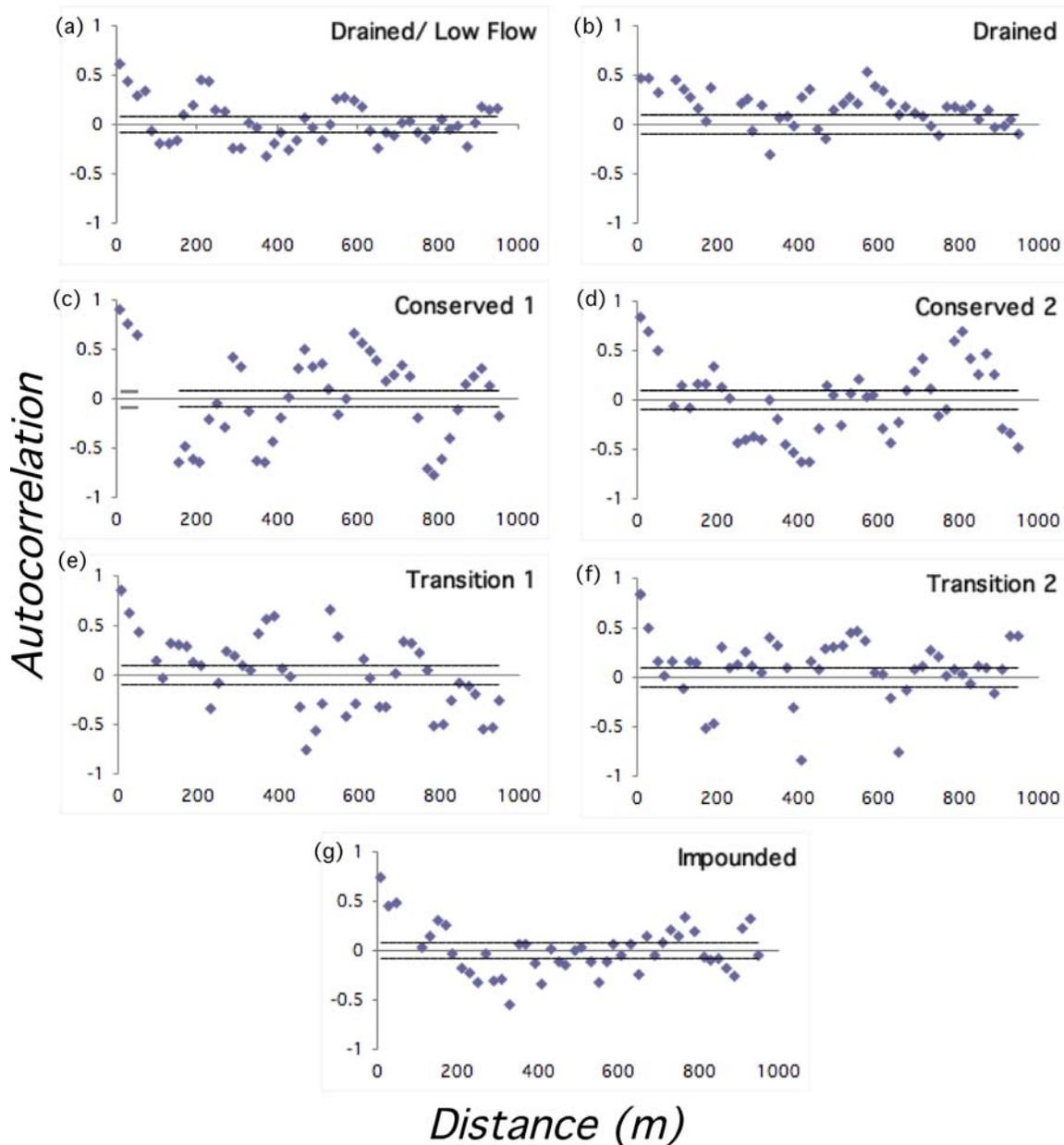


Figure 2-7. Correlograms of water depths with lag distances of $h=20\text{m}$, demonstrating that water depths (cm) are significantly positively correlated at short distances (0-50m), but either uncorrelated or negatively correlated at larger distances (around 100m for all sites). Autocorrelation periodicity, most evident in the conserved and transitional sites is suggestive of the wavelength of landscape pattern. Black lines indicate 95% confidence limits of the cross correlation values based on the number of pairs within the initial lag class h . The distances along the x-axis are the average distances among all pairs within each lag class.

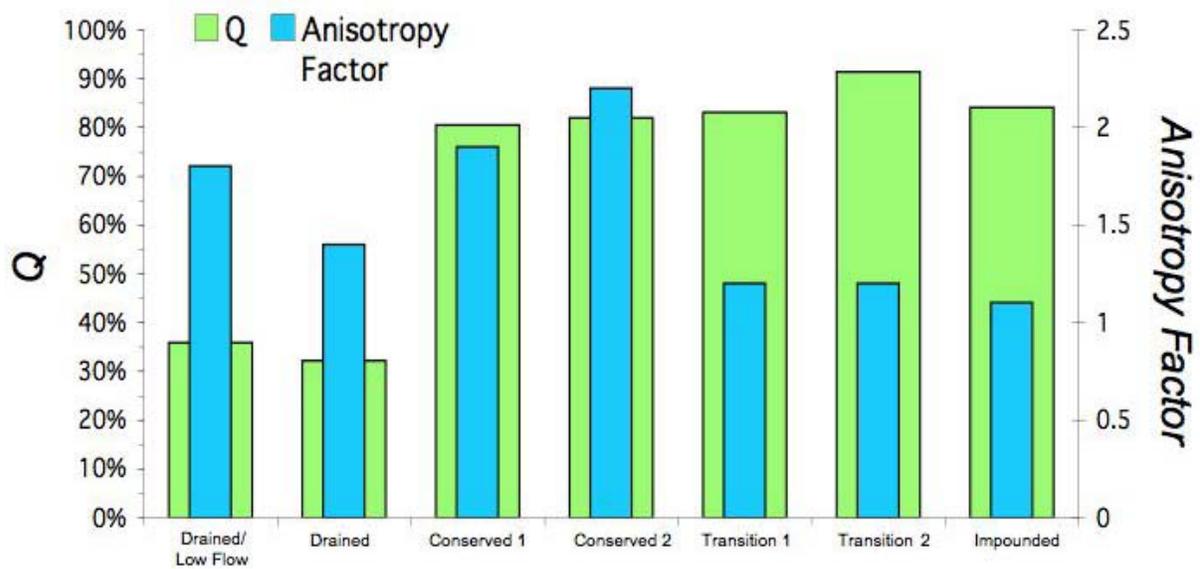


Figure 2-8. Metrics of spatial pattern for sampling units. Relative structure (Q) indicates the percentage of spatial semi-variance explained by the model (i.e., non-random spatial variability) while the anisotropy factor is the ratio of the ranges in the major and minor directions (1.0 where spatial pattern is isotropic). Summary of analyses is found in Table 2-5.

Table 2-5. Results of spatial analyses.

	Major range	Minor range	Anisotropy factor	Direction	Nugget	Sill	Q
Drained/Low flow	49.6	28.1	1.8	350	9.7	15.1	35.8
Drained	53.0	37.0	1.4	356	11.0	16.2	32.1
Conserved 1	52.6	28.1	1.9	360	4.8	24.5	80.4
Conserved 2	125.0	58.0	2.2	315	12.3	67.9	81.9
Transition 1	52.5	42.9	1.2	33	16.5	97.0	83.0
Transition 2	89.3	72.4	1.2	295	16.2	189.2	91.4
Impounded	51.6	44.9	1.1	46	14.2	89.1	84.1

The major and minor range, nugget, and sill are values interpreted from the semivariogram generated for each landscape block. All analyses were done within 100m. The anisotropy factor is ratio of the major range to the minor range. Values of 1 indicate isotropic semivariance; the expected condition for a conserved ridge slough landscape is strong anisotropy. Q is then calculated as the partial sill/(partial sill + nugget) * 100, which is a measure of the spatial variation not explained by error. Values greater than 75 indicated a strong spatial structure to the variable; values less than 75 indicate weak to moderate spatial structure

CHAPTER 3 SUMMARY AND CONCLUSIONS

The descriptive information in Chapters 1 and 2 provide evidence of alternative stable states, but lead to the key question of the mechanisms that maintain the sharp boundaries between ridges and sloughs. The use of alternative stable state and ecosystem pattern theories incorporates community dynamics and ecosystem and landscape level processes together to help explain patterns observed in the ridge-slough mosaic of the central Everglades. Chapter 2 examined evidence for bimodality in peat elevations and clearly demonstrated two distinct ecological states, with tightly bounded transitional zones. These states, ridge and slough, are defined based on two linked factors: water depths and vegetative communities. Moreover, the patterning of this landscape is highly structured and anisotropic under historic hydrologic regimes. All of these variables are altered with hydrologic modification, although not always in the same direction (i.e., loss of anisotropy with impoundment but apparently not with drainage). The loss of peat elevation bimodality occurs with both drainage and impoundment, however, suggesting that bimodality is a key indicator of landscape stability.

Bimodality in keystone ecosystem variables (e.g., phytoplankton abundance in shallow lakes, soil elevation in patterned peatlands, tree density in semi-arid grasslands, macrophyte density in desert streams) has been used as evidence of alternative stable states. The presence of bimodality suggests regime shifts between alternative states; intermediate states are unstable, transitory by definition, and therefore not widely observed. Examples of variables exhibiting bimodality are chlorophyll *a* concentrations in lakes (Bayley and Prather, 2003); mating systems in plants (Vogler and Kalisz, 2001); vegetative features of hydrologically influenced calcareous dunes in the Netherlands (Adema et al., 2002); and a number of variables in marine systems (reviewed in Petraitis and Dudgeon, 2004). While bimodality is in concordance with predictions

emerging from alternative stable state theory, other explanations supporting predictions of bimodality are still possible and further evidence, preferably experimental, is necessary (Schröder et al., 2005). That is, despite strong evidence of bimodality in the ridge-slough mosaic, we still lack mechanistic understanding of scale-dependent feedbacks that lead to alternative stable states, which constrains our ability to restore and maintain the landscape.

A number of hypothesized mechanisms have been suggested for ridge-slough maintenance (Table 3-1). These alternative hypotheses for ridge-slough creation and maintenance lead to predictions which future work will empirically evaluate. It is plausible that two or more of these processes are occurring simultaneously. Future work should involve not only evaluating these mechanisms, but also attempting to determine their relative importance.

The first hypothesis and prediction outlines peat accretion equilibrium. The conceptual model as presented (Fig. 1-4) posits that the carbon budget, and the autogenic feedbacks therein, are the key unknowns in this system. Specifically, a theoretical point model for peat accretion suggests that there is a landscape-scale equilibrium accretion state. This mean accretion rate across the landscape can arise along two separate, self-organizing pathways: one high production and high respiration (ridge), and the other low production and low respiration (slough). These two pathways, then, are the multiple state equilibria of interest. Under historic hydrologic conditions, locations with elevations different from an equilibrium level are driven towards one of those equilibria by changes in peat accretion rates. For example, shallow water conditions will generally increase productivity on ridges in response to increased oxygen availability. However, oxygen availability also increases respiration rates, canceling out or surpassing the incremental increases in productivity, leading to peat oxidation until the soil elevation is at the equilibrium. Similarly, sloughs at lower elevation than the equilibrium slough elevation will tend to

accumulate peat more rapidly due to reduced exposure probability. Peat accretion will raise the local elevation until it is again at the equilibrium level.

The second hypothesis, related to peat accretion equilibrium, invokes a scale-dependent negative feedback. To regulate the point-based equilibria at a landscape level, the hydraulic requirements of moving necessary flow volumes off the landscape will act as the negative feedback. Specifically, as peat elevation rises locally, water depths in the surrounding landscape increase to accommodate a fixed flow. The simplicity of this process is attractive as the mechanism is sufficient to explain the orientation and prevalence of ridge and slough system, and requires no invocation of sediment transport in the face of low velocities.

Since peat accretion rates are an emergent property of the local scale carbon budget, hypotheses about the mechanisms that create and maintain alternative stable states involve interactions of productivity, respiration (decomposition), community composition shifts (and associated changes in carbon inputs) and hydrology. Demonstrating peat accretion equilibria would provide mechanistic evidence for the existence of alternative stable states in the ridge-slough region, and aid in understanding the hydrologic requirements for landscape maintenance. The hydrologic gradient present in WCA 3A allows for an excellent natural experiment for these hypotheses. That is, directionality at the landscape-scale can be inferred from carbon budgets spanning the drained areas to the impounded areas. Further, modeling the negative feedback would give us the hydrologic regime within which patterning is stable. This information would be vital to management and restoration schemes, where the goal is to maintain the historic ridge-slough patterning.

Other mechanisms that have been postulated to lead to the maintenance of ridges and sloughs revolve primarily on water flow and the movement of particles. The literature primarily

focuses on erosive and depositional mechanisms (see review of hypotheses in Larsen et al., 2007). While a great deal of work has been done on modeling potential contributions of either scour or depositional processes (Leonard et al., 2006; Ross et al., 2006; Larsen et al., 2007), field observations of both processes are lacking. The plausibility of movement of any material other than that which is neutrally buoyant is very low; observed flow rates are generally less than 2 cm s⁻¹ (Leonard et al., 2006), far below entrainment velocities for even soil floc particles. This makes the third hypothesis (Table 3-1) difficult to find credible. However, legacy signatures of processes that accelerate or reduce accretion rates (i.e., via deposition of exogenous material or nutrient subsidies, the final two hypotheses) should be observed in the soils. Sediment deposition of calcitic material derived from sloughs and deposited at ridge edges would result in higher concentrations of Ca in ridge soils. Similarly, deposition of nutrient-rich organic particles on ridge edges would lead to localized enrichment, allowing increased sawgrass production despite anoxic stress at ridge edges. Nutrient stoichiometry in peat soils at the edges and centers of ridge and slough ecosystems will be indicative of this mechanism.

It is evident that our understanding of the processes that creates and maintains patterning in the central Everglades is incomplete. Regardless of the mechanisms that develop and maintain this region, consideration of the scale of their action and interaction is an important unknown. As Rietkerk and van de Koppel (2008) propose--and this study demonstrates--there are multiple scales at which processes act, and their relative importance differs accordingly. Failure to incorporate scale into studies of patterned landscapes could lead to misinterpretation of results, and ultimately to poor management or restoration plans (Zedler, 2000).

The variables measured in this study respond to hydrologic modification, and are sensitive to the direction and magnitude of that modification. Simple statistical descriptions of the

distributions of elevation, particularly anisotropy and bimodality, therefore provide diagnostic measures of ridge-slough health. Effective (i.e., sensitive and specific) diagnosis of ecosystem change is increasingly important, as managers of CERP have focused on the “Field of Dreams” method of restoration (Hilderbrand et al., 2005). That is, there is a tacit expectation that restoring historic water regimes will restore the ridge-slough mosaic (SCT, 2003; Perry, 2004). Given evidence for alternative stable states and the time domain of the keystone variable that responds to bi-modal ecological conditions (i.e., peat accretion), there is a high likelihood that ecological restoration will lag hydrologic restoration by a long time, particularly where landscape flattening has occurred. Providing realistic expectations for the restoration timeline will require a well-developed understanding of the processes that create and maintain the desired ecological condition.

Table 3-1. Hypotheses of mechanisms governing ridge-slough maintenance.

Hypothesis	Source	Predictions
Feedbacks of community carbon budgets lead to multiple system equilibria.	This study	Peat accretion rates are, on average, the same between ridges and sloughs. For areas not falling within the peat accretion equilibrium, there is directionality to the carbon budget, forcing the system back to the equilibrium.
Locally positive feedbacks (productivity and respiration) and landscape negative feedbacks (hydrology) leads to regular pattern formation	(This study, Rietkerk and van de Koppel, 2008)	Associated with autogenic hypothesis; a parameter space exists in hydrology (water depth, duration, pattern) wherein a patterned landscape is more stable than a homogenous landscape.
Sloughs are formed via erosive processes (scour).	(SCT, 2003)	Flow velocities in sloughs are lower than ridges, which lead to erosion and lowered peat elevation.
Sediment transport in the form of neutrally buoyant, inorganic material preferentially settles on ridges.	(Leonard et al., 2006; Larsen et al., 2007)	Soil calcium concentrations are higher at ridge edges than either ridge or slough centers.
Sediment transport in the form of neutrally buoyant, nutrient-rich material enriches ridge edges preferentially to ridge centers, leading to increased sawgrass productivity.	(Larsen et al., 2007)	Nutrient stoichiometry at ridge edges is an intermediate between ridges and sloughs (e.g., lower C:N on ridges, higher C:N in sloughs).

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BIOGRAPHICAL SKETCH

Danielle Watts was born in 1979, in Oklahoma City, Oklahoma, the only child of an only child. Danielle was raised in the Florida Keys by her mother and grandmother, and in this environment lay the genesis of her later interests.

After graduating from Key West High School in 1997, Danielle continued her education, graduating with an Associates in Arts from the Florida Keys Community College in 1999. After effectively throwing a dart at a map of Florida, Danielle moved on to gaining a degree in Wildlife Ecology and Conservation at the University of Florida in Gainesville, FL. It was during this time that she realized that her real interests lay in ecosystem development, and performed an independent study for Dr. Tim Martin on the ecophysiology of two pineland species, *Ilex glabra* and *Serenoa repens*. A year's experience working for Drs. Ted Schuur and Michelle Mack after her graduation helped further refine her interests in plant-soil interactions.

It was at this time, however, that Danielle chose to realize a life-long dream of living in Africa. Early in 2003, Danielle fell in love and married Adam Watts. Together, the two joined Peace Corps, and spent 2004-2006 working as Agroforestry Extension Agents in the Fouta Djallon of the Republic of Guinea. It was at the top of a plateau, during a particularly brutal sub-Saharan day that Danielle realized that her true environmental passion laid in low-lying, tropical wetlands.

Danielle was then accepted into the Interdisciplinary Ecology program, returning to the University of Florida. Chasing after opportunities to work in the Florida Everglades has culminated Danielle's ecological, intellectual, and emotional passions. She continues to explore her interests concerning processes influencing ecosystem development, expanding on her master's research and continuing on for her PhD.