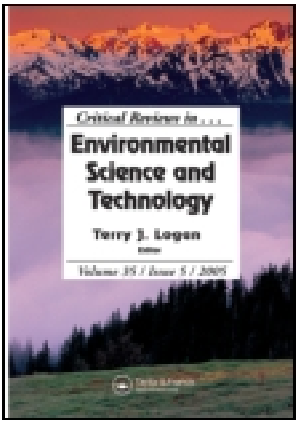

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Recent and Historic Drivers of Landscape Change in the Everglades Ridge, Slough, and Tree Island Mosaic

Laurel Larsen [a], Nicholas Aumen [b], Christopher Bernhardt [a], Vic Engel [c], Thomas Givnish [d], Scot Hagerthey [e], Judson Harvey [a], Lynn Leonard [f], Paul McCormick [e], Christopher Mcvoy [e], Gregory Noe [a], Martha Nungesser [e], Kenneth Rutchey [e], Fred Sklar [e], Tiffany Troxler [g], John Volin [h] & Debra Willard [a]

[a] U.S. Geological Survey, Reston, VA, USA

[b] A.R.M. Loxahatchee National Wildlife Refuge, Boynton Beach, FL, USA

[c] Everglades National Park, Homestead, FL, USA

[d] Dept. of Botany, University of Wisconsin, Madison, WI, USA

[e] Watershed Management Department, South Florida Water Management District, West Palm Beach, FL, USA

[f] Geography and Geology, University of North Carolina Wilmington, Wilmington, NC, USA

[g] Southeast Environmental Research Center, Florida International University, Miami, FL, USA

[h] Natural Resources and the Environment, University of Connecticut, Storrs, CT, USA

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Recent and Historic Drivers of Landscape Change in the Everglades Ridge, Slough, and Tree Island Mosaic

LAUREL LARSEN,[1] NICHOLAS AUMEN,[2]
CHRISTOPHER BERNHARDT,[1] VIC ENGEL,[3] THOMAS GIVNISH,[4]
SCOT HAGERTHEY,[5] JUDSON HARVEY,[1] LYNN LEONARD,[6]
PAUL McCORMICK,[5] CHRISTOPHER McVOY,[5] GREGORY NOE,[1]
MARTHA NUNGESSER,[5] KENNETH RUTCHEY,[5] FRED SKLAR,[5]
TIFFANY TROXLER,[7] JOHN VOLIN,[8] and DEBRA WILLARD[1]
[1]*U.S. Geological Survey, Reston, VA, USA*
[2]*A.R.M. Loxahatchee National Wildlife Refuge, Boynton Beach, FL, USA*
[3]*Everglades National Park, Homestead, FL, USA*
[4]*Dept. of Botany, University of Wisconsin, Madison, WI, USA*
[5]*Watershed Management Department, South Florida Water Management District, West Palm Beach, FL, USA*
[6]*Geography and Geology, University of North Carolina Wilmington, Wilmington, NC, USA*
[7]*Southeast Environmental Research Center, Florida International University, Miami, FL, USA*
[8]*Natural Resources and the Environment, University of Connecticut, Storrs, CT, USA*

More than half of the original Everglades extent formed a patterned peat mosaic of elevated ridges, lower and more open sloughs, and tree islands aligned parallel to the dominant flow direction. This ecologically important landscape structure remained in a dynamic equilibrium for millennia prior to rapid degradation over the past century in response to human manipulation of the hydrologic system. Restoration of the patterned landscape structure is one of the primary objectives of the Everglades restoration effort. Recent research has revealed that three main drivers regulated feedbacks that initiated and maintained landscape structure: the spatial and temporal distribution of surface water depths, surface and subsurface flow, and phosphorus supply. Causes of recent degradation include but are not limited to perturbations to these historically important controls; shifts in mineral and sulfate supply may have

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Address correspondence to Laurel Larsen, U.S. Geological Survey, 430 National Center, Reston, VA 20192, USA. E-mail: lglarsen@usgs.gov

also contributed to degradation. Restoring predrainage hydrologic conditions will likely preserve remaining landscape pattern structure, provided a sufficient supply of surface water with low nutrient and low total dissolved solids content exists to maintain a rainfall-driven water chemistry. However, because of hysteresis in landscape evolution trajectories, restoration of areas with a fully degraded landscape could require additional human intervention.

KEYWORDS: Everglades, ridge and slough, tree islands, hydroecology, feedback, landscape patterning

1. INTRODUCTION

Landscape heterogeneity or patchiness increases environmental complexity and ecosystem resiliency (Gilad et al., 2004; Kolasa and Rollo, 1991; van de Koppel and Rietkerk, 2004). Fluvial dynamics often play a major role in regulating the heterogeneity of lotic ecosystems (Palmer and Poff, 1997), though the mechanisms by which flow promotes environmental heterogeneity vary. Existing physical heterogeneity (e.g., lithology) may create flow patterns that promote biological amplification of existing heterogeneity (e.g., Vallett et al., 1997). Alternatively, self-organization of biological processes occurring in uniform flow may initiate the development of physical and biological heterogeneity (Rietkerk et al., 2004; Rietkerk and van de Koppel, 2008; van de Koppel et al., 2001).

Understanding the processes that maintain environmental heterogeneity and even landscape patterning is a management concern in many aquatic ecosystems. Patchy landscapes are prone to catastrophic shifts between multiple stable states, so that a change in environmental conditions can prompt rapid conversion of a heterogeneous landscape to a homogeneous landscape with comparatively low ecological value (Beisner et al., 2003; Suding et al., 2004). For example, changes in flow management can disrupt the feedbacks that result in heterogeneity, with consequences for species richness (Ward et al., 1999).

The ridge and slough landscape of the Everglades (Figure 1) is a classic example of a patterned landscape that exhibited long-term stability but has undergone rapid conversion to a more homogeneous state under drainage and changes in flow management, with adverse ecological consequences (Science Coordination Team, 2003). This landscape occupied 55% of the historical extent of the Everglades (McVoy et al., 2011) and was characterized by elongated peat ridges that were elevated above (by 30–90 cm; Baldwin and Hawker, 1915; J.O. Wright, 1912) and regularly interspersed among lower, more open peat sloughs. Ridges were dominated by sawgrass (*Cladium jamaicense*), sloughs by open water or water lilies (*Nymphaea odorata*),

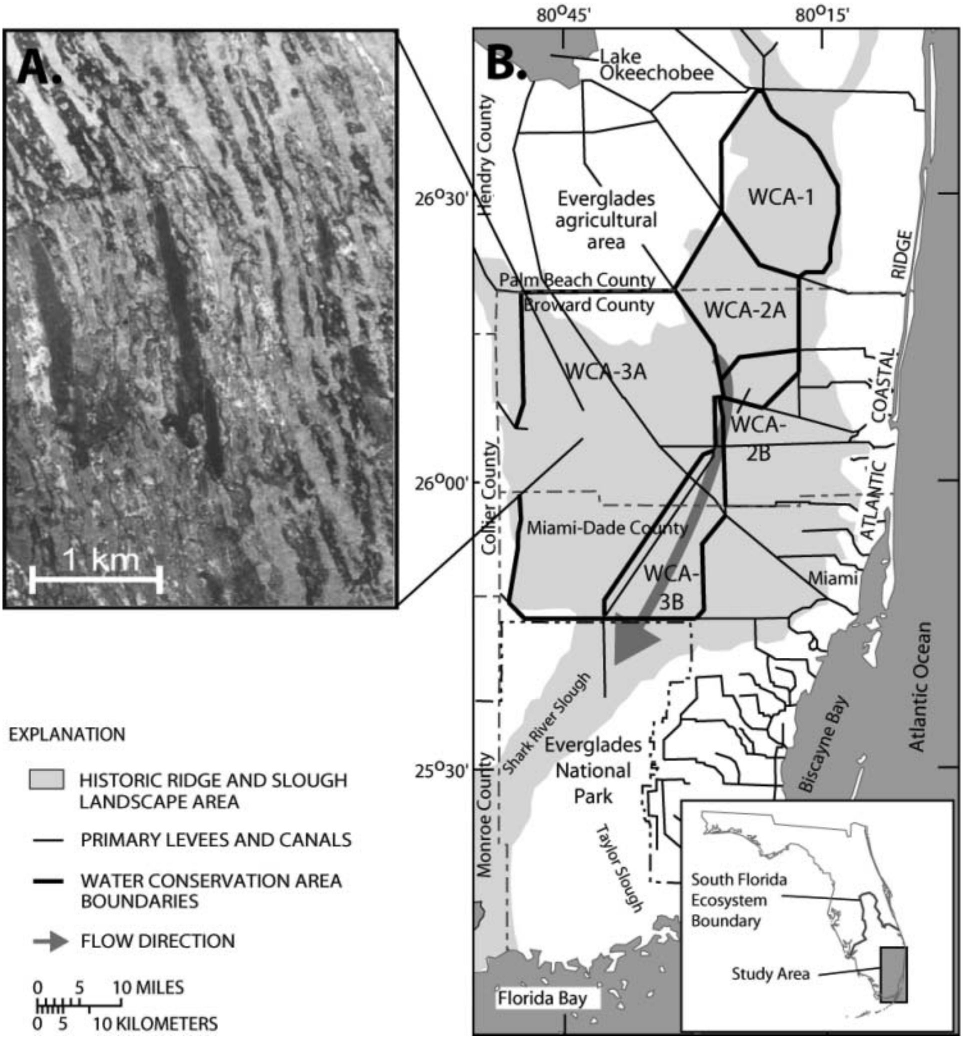

FIGURE 1. Location, extent, and morphology of the Everglades ridge and slough landscape. (A) Satellite image of well-preserved ridge and slough landscape, reprinted from Science Coordination Team (2003). Light features are ridges. Dark features are sloughs, except for the two darkest features, which are recently burned ridges. (B) Historic coverage of the ridge and slough landscape, shown with present-day canals, levees, and WCAs. Ridges and sloughs are aligned parallel to the dominant flow direction, indicated with the gray arrow.

with occasional spatterdock (*Nuphar advena*), and likely widespread bladderwort (*Utricularia* spp.; McVoy et al., 2011). Teardrop-shaped tree islands in the central Everglades and circular or cigar-shaped tree islands in the Loxahatchee National Wildlife Refuge contain a diverse assemblage of trees, shrubs, and ferns (Armentano et al., 2002; Heisler et al., 2002). Unlike the patterned fens common in boreal latitudes, the axis of pattern elongation in the ridge and slough landscape is parallel to the dominant flow direction—a feature shared with several other subtropical wetlands, including parts of the Zapata Peninsula in Cuba, Yucatan Peninsula in northern Belize, morichal wetlands in Colombia and Venezuela (San Jose et al., 2001), and buritizal wetlands in the Brazilian Pantanal (Silva et al., 1999). That these parallel-drainage wetlands are in a quasiequilibrium state is somewhat surprising, given the positive feedback between flow, sediment transport, and channel morphology that often causes channel coalescence and development of a dominant channel network on low gradients (Phillips and Schumm, 1987).

Until recently, the mechanisms responsible for the development and apparent stability of the ridge and slough landscape had remained poorly understood. Interest intensified following congressional authorization of the $10.9 billion Comprehensive Everglades Restoration Plan, which proposed to restore vast portions of the Everglades ridge and slough landscape that had degraded following 20th century drainage and compartmentalization (U.S. Army Corps of Engineers, 1999). These engineering efforts altered hydroperiods, flow depths, and flow directions, diminished flow velocities, and introduced agricultural contaminants into the historically oligotrophic (S.M. Davis, 1994) ecosystem. Concurrently, large portions of the ridge and slough landscape experienced an expansion of sawgrass into sloughs and a loss of slough connectivity and directionality (Figure 2). These changes hindered fish migration and diminished habitat diversity (Science Coordination Team, 2003). Other portions of the landscape upstream of levees experienced longer hydroperiods and a loss of ridges (Science Coordination Team, 2003; Sklar et al., 2004).

Early restoration plans focused on restoring predrainage water levels and hydroperiods, but flow velocities did not become a priority until publication of the Science Coordination Team White Paper (2003). The document proposed several hypotheses, then untested, of the mechanisms by which flow produces and maintains longitudinal landscape patterning. Since then, Everglades researchers have had the opportunity to test many of the original hypotheses and advance others. Aided by increasing communication among researchers, there has been a gradual coalescence of conceptual models toward a unified model describing how feedbacks create and maintain parallel-drainage patterning in low-gradient wetlands and floodplains. Here we synthesize and review that body of work, showing how it provides clear direction for Everglades restoration management.

2 PALEOECOLOGICAL HISTORY OF THE RIDGE-SLOUGH-TREE ISLAND LANDSCAPE

The dynamic equilibrium state of the predrainage ridge and slough landscape has been established by calibrating pollen records of local vegetation

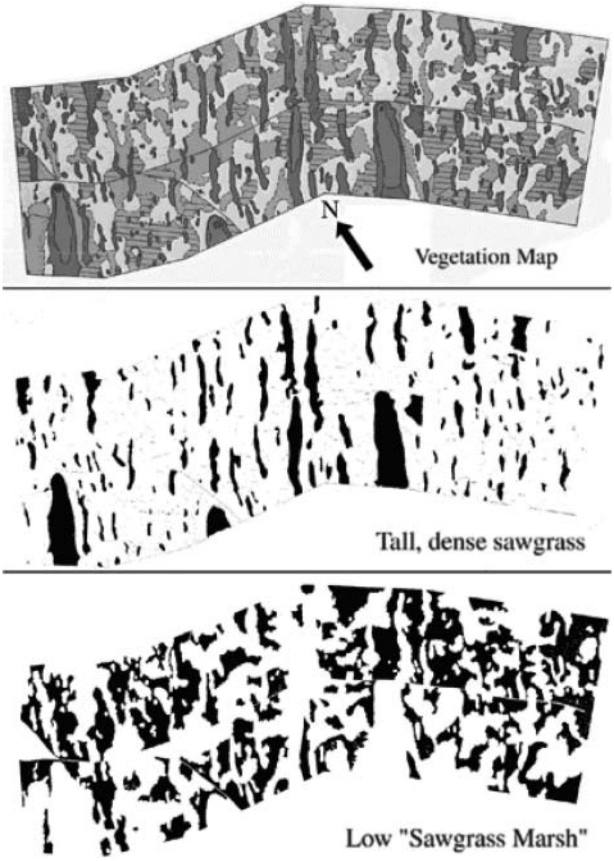

FIGURE 2. Vegetation map from 1980 of area within Shark River Slough, Everglades National Park (top panel; Olmsted and Armentano, 1997), separated into older sawgrass marsh (middle panel) and younger sawgrass marsh (lower panel). The older sawgrass growth, thought to be consistent with the predrainage ridge and slough landscape pattern, is directional, with consistent orientation and well-connected intervening areas. In contrast, the younger sawgrass has randomly invaded sloughs, reducing their connectivity. This expansion of sawgrass into sloughs is a typical form of landscape pattern degradation that has become widespread postdrainage. Figure by Christopher McVoy, reprinted from Science Coordination Team (2003) with permission.

with ^{14}C, ^{210}Pb, and ^{137}Cs dating (Willard et al., 2001). These methods date the earliest tree island deposits to 3500 years before present (YBP; Willard et al., 2006) and suggest that patches of sawgrass marsh and slough vegetation have been distinct since 2700 YBP (Bernhardt et al., 2004). At that time, *Nymphaea* pollen abounded relative to *Cladium* pollen, while pollen from other plants remained nearly absent, indicating wetter, deeper conditions than are present today (Bernhardt et al., 2004). During periods of extended drought likely caused by the southward displacement of the Intertropical Convergence Zone (~1500 YBP, ~1000 YBP, ~400 YBP; Haug et al., 2001), tree islands and ridges expanded across the transects sampled, and emergent taxa indicative of drier conditions became more abundant (Bernhardt and Willard, 2009; Willard et al., 2006). Around 400–300 YBP (the Little Ice Age), the taxa representative of the modern community became dominant on ridges (Bernhardt and Willard, 2009). In sloughs vegetation community compositions have continued to change through the past century in response to anthropogenic influences. Emergent vegetation such as *Eleocharis* spp. has become more abundant relative to predrainage conditions (Bernhardt and Willard, 2009), while historical accounts suggest that floating periphyton mats have also become more widespread (McVoy et al., 2011).

3 CONCEPTUAL MODEL OF THE RIDGE-SLOUGH-TREE ISLAND LANDSCAPE

Consistent with paleoecological history, the conceptual model of landscape processes that we have synthesized in Figure 3 is modified from elements of conceptual models described by previous researchers (Givnish et al., 2008; Larsen et al., 2007; Ross et al., 2006; Wetzel et al., 2005). The model contains interacting feedback cycles that regulate local rates of peat accretion and vegetation colonization and are ultimately governed by surface water stages, flow velocities, and the supply of phosphorus (P), a limiting nutrient (S.M. Davis, 1994; Noe et al., 2001). We propose that feedbacks regulating autochthonous (i.e., in-place) peat accretion provide the dominant control on the vertical aspect of the landscape (i.e., the difference in elevation between ridges, sloughs, and tree islands), whereas feedbacks regulating vegetation colonization through the transport of sediment and nutrients provide the dominant control on the lateral aspect (i.e., the length, width, and planform shape of landscape features). Individually, each of these feedbacks is common in different environments throughout the world (see Larsen et al., 2007). However, it is the combination of these feedback processes, together with the driving variables within certain ranges, that produces the parallel-drainage patterning unique to the Everglades ridge-slough-tree island landscape and other tropical wetlands. In the following sections we describe the studies that detail and support this conceptual model.

4 AUTOCHTHONOUS PEAT ACCRETION FEEDBACK

4.1 Theory

In boreal peatlands hummocks maintain a stable equilibrium elevation relative to hollows as a result of an autochthonous peat accretion feedback that

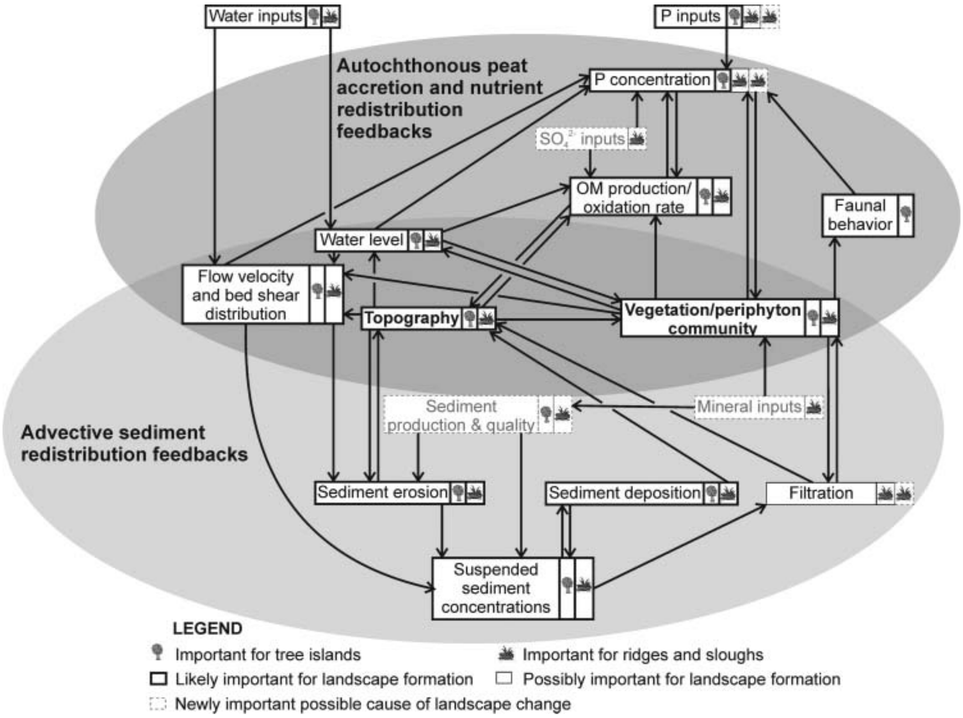

FIGURE 3. Synthesis of historically and newly important drivers in evolution of ridge, slough, and tree island landscape structure. Processes shown are those that are known to or likely have a dominant effect on landscape structure. Interactions are grouped into processes that affect local topography and vegetation community in-place (autochthonous peat accretion feedbacks) and processes involving the transport and redistribution of materials by flow (advective sediment redistribution feedbacks). As noted in the figure, there are uncertainties in the role of some drivers of landscape evolution historically and at present. These uncertainties prioritize future research directions.

governs the local balance between the production and decomposition of organic matter in different vegetation communities (Belyea and Clymo, 2001; Nungesser, 2003). In wetlands dominated by vascular plants, this feedback also applies. Here, water depth is often the dominant driver of differences in net peat accretion rate (Nyman et al., 2006; Redfield and Rubin, 1962; Yu et al., 2001), in part because of its effects on soil redox potential (Koch-Rose et al., 1994) and accumulation of plant toxins (Pezeshki, 2001; Wheeler, 1999). At high water depths, low redox potentials limit plant productivity and decomposition rates. Long stems or flooded leaves that reduce the photosynthetically productive fraction of vegetation tissue also contribute to low plant productivity in deep water (Givnish et al., 2008). While decomposition rates in the Everglades increase monotonically as water depths decrease (DeBusk and Reddy, 1998), the function for plant productivity is concave-up

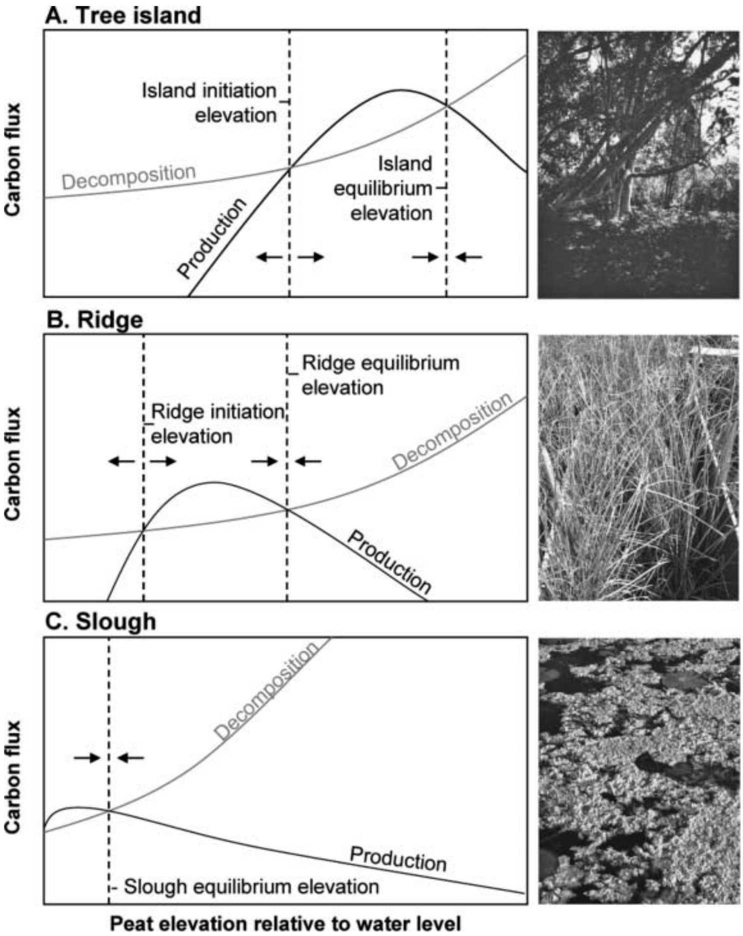

FIGURE 4. Schematic diagram of organic matter production and decomposition as a function of water level in tree island, ridge, and slough vegetation communities (photos at right). Peat accretes when the production of organic matter exceeds organic matter decomposition. These rates depend on the life history strategy of the vegetation community, quality of the organic matter produced, substratum redox potential, soil enzyme activity, and P concentration. Arrows show the direction of peat surface growth or decline over time. Figure modified from Givnish et al. (2008). Photo credits: Top: http://sofia.usgs.gov/sfrsf; Middle: D. Nowacki; Bottom: L. Larsen.

(Figure 4), reflecting the existence of a community specific optimum (Givnish et al., 2008). When primary production exceeds organic matter decomposition, peat accumulates over time, increasing the elevation of the soil surface relative to the water surface. Oxidation of peat occurs when decomposition rates exceed production rates. When rates of organic matter production and decomposition are equal, the topography is in equilibrium with respect to the water surface.

Local equilibrium peat elevations can be stable or unstable. Perturbations of stable equilibria change the rates of organic matter production or decomposition such that, over time, the peat surface again approaches the equilibrium elevation, whereas perturbations to unstable equilibria cause divergent behavior (arrows in Figure 4). In peatlands these unstable equilibria may be regarded as initiation elevations for a vegetation community, above which the community will approach the stable equilibrium through the peat accretion feedback.

Vegetation communities have unique equilibrium peat elevations because of differences in their organic matter production and decomposition curves (Figure 4) that respectively result from context-specific differences in the physiological tolerance and competitive ability of individual species (Givnish et al., 2008) and from detrital organic carbon quality (Busch et al., 2004; DeBusk and Reddy, 1998; Mitsch and Gosselink, 2000) and enzyme activity (Penton and Newman, 2008). Tree species cannot tolerate deeper water but can overtop herbaceous plants on better-drained sites, leading to their dominance on islands; sawgrass outcompetes water lilies and submersed aquatics on inundated ridges but cannot tolerate the deeper water in sloughs (Givnish et al., 2008). Furthermore, detrital material with relatively high lignin content, such as ridge or tree island vegetation, decays less rapidly than the less conjugated organic material with higher C/N ratios found in sloughs (DeBusk and Reddy, 1998; Penton and Newman, 2008). Sloughs also contain greater enzyme activity that contributes to faster decomposition rates relative to ridges (Penton and Newman, 2008). Meanwhile, ridges exhibit primary productivity that is 8 times greater than that of *Eleocharis* communities (Daoust and Childers, 1998). These factors combine to result in sloughs having the lowest equilibrium elevation, followed by ridges and then tree islands (Givnish et al., 2008). Within tree islands, individual plant communities are structured by elevation (Troxler-Gann and Childers, 2006).

Limiting factors such as nutrient concentrations (Amador and Jones, 1993; Koch and Reddy, 1992; Miao and Sklar, 1998) also influence organic matter production and decomposition. The net effect of P enrichment in the Everglades is a monotonic increase in peat accumulation (Craft and Richardson, 1993; Kadlec, 1994; Reddy et al., 1993). Soil elevations on tree islands are likewise positively correlated with P concentration (Wetzel et al., 2009), which influences tree island peat accretion directly, through local effects on organic matter production and decomposition rates, and indirectly, by exerting control over the composition of the vegetation community and its ability to sequester additional P (Figure 3). Givnish et al. (2008) surmised that a nutrient gradient resulting from the leaching of P from tree islands is a secondary driver of vegetation community composition and landscape processes in the surrounding marsh. Directly and indirectly, P availability is thus a third factor that may affect the equilibrium elevations of ridge, slough, and tree island vegetation communities.

4.2 Potential to Promote Long-Term Landscape Heterogeneity

Using a model based on field (Craft and Richardson, 1993; Kadlec, 1994; Reddy et al., 1993) and greenhouse (Kludze and DeLaune, 1996) studies that provided autochthonous peat accretion rates as a function of water level and P concentration, Larsen et al. (2007) showed that differential peat accretion produces a ridge-slough elevation difference consistent with historical records. Still, below-ground biomass growth causing lateral expansion of peat soils and gravitational displacement of unconsolidated organic sediment (i.e., floc) from higher to lower elevations would build the topography of transitional areas between ridges and sloughs or tree islands and sloughs. This topographic growth would incrementally expand the area of soil at elevations above the ridge or tree island initiation elevation, causing expansion of these landscape elements at the expense of sloughs (Larsen et al., 2007). Because indefinite expansion of ridge and tree islands is not consistent with the paleoecological record (Bernhardt et al., 2004), another mechanism must have controlled the stability of ridge and tree island boundaries, ensuring long-term heterogeneity.

Cross-scale feedback within the autochthonous peat accretion mechanism provides one possible explanation for historical landscape stability under constant climatic forcing. As the volume of submerged peat expands throughout the landscape, water levels increase. At some point, the rate of soil addition to the portion of the topography just below the ridge or tree island initiation elevation could equal the rate at which water surface rises, causing the distribution of surface water depths to remain unchanged and stabilizing the boundary (Givnish et al., 2008; Larsen et al., 2007). Increased resistance to flow by expanding ridges (Section 5.1) could further contribute to rising water levels. However, recent simulations (Larsen, 2008) of hydrologic and autochthonous peat accretion feedbacks suggest that rising water levels stabilize ridge edges only after ridge vegetation coverage exceeds that of the predrainage system (55%; McVoy et al., 2011).

Another possible explanation for historic ridge stability could be that low P concentrations limit sawgrass colonization. Total dissolved P concentrations in ridge surface water and soil are slightly elevated (8% greater in surface water; Noe et al., 2010; 13% greater in pore water; Ross et al., 2006) above those of the slough. Relatively high leaching rates of sawgrass detritus (S.E. Davis et al., 2006) and evaporative concentration of P during the dry season (Larsen et al., 2007) contribute to higher P concentrations on the ridge. Though it is known that sawgrass responds to low-level P enrichment with higher productivity and density over two to three years (S.M. Davis, 1989, 1991; Miao and Sklar, 1998; Smith et al., 2009) and exhibits sustained growth at 10 μg P L^{-1} (Kuhn et al., 2002; Lissner et al., 2003), less is known about whether highly oligotrophic conditions (6–8 μg L^{-1}) characteristic of sloughs (S.M. Davis, 1994; Miao et al., 1998; Newman et al., 2001) restrict its colonization. Physiological studies suggest that sawgrass is well equipped for extremely oligotrophic conditions through its high P use efficiency at low P levels (Chen et al., 2005; Lorenzen et al., 2001), though P uptake rates diminish when soil redox potentials are low ($\leq$150 mV; Lissner et al., 2003), as is common in sloughs (Koch-Rose et al., 1994). Sawgrass also exhibits high root phosphatase activity (Kuhn et al., 2002; Rejmankova and Macek, 2008) and high tissue N:P ratios (Daoust and Childers, 1999; Newman et al., 1996). However, knowing the controls on the vegetative propagation of rhizomes from sawgrass may be more important for understanding limits on ridge expansion (Goslee and Richardson, 2008; Miao et al., 1997). Preliminary work by P. McCormick (personal communication, 2009) showed that rhizome production from sawgrass seedlings is maximal at low levels of P enrichment, but additional research on rhizome production from mature sawgrass stands is needed.

Even if P concentrations restricted sawgrass colonization historically, the autochthonous peat accretion mechanism alone may still be unable to restrict the width of ridges. Hydrologic models that use Priestley-Taylor evapotranspiration routines calibrated to ridge and slough vegetation communities (German, 2000) predict a slight water-table mound under ridges during the dry season, which causes an advective flux of water from ridges to sloughs (Larsen et al., 2007). This advective flux would add to a diffusive transfer of dissolved P from ridges to sloughs, permitting gradual ridge expansion.

In contrast to ridges, tree island evapotranspiration draws down the water table relative to the surrounding marsh (Ross et al., 2006; Wetzel et al., 2011), creating an advective flux of water toward tree islands. Whether this flux is a primary contributor to elevated P concentrations on tree islands or whether deposition of P in guano from wading bird roosts is a more significant cause is debatable (e.g., Givnish et al., 2008; Wetzel et al., 2005; Wetzel et al., 2009), but it is known that tree islands concentrate P to a much greater extent than ridges (Ross et al., 2006; Troxler-Gann et al., 2005). It has been estimated that tree islands historically stored more than half of the total P in the central Everglades (Wetzel et al., 2009). Recent studies of tissue nutrient composition and turnover rates have suggested that the P demand of vegetation communities on the relatively dry and nutrient-rich tree island heads is 4 times greater than that of communities on the relatively wet and nutrient-poor tails. These relatively high nutrient demands suggest that the indefinite expansion of tree islands may be restricted by P availability in the surrounding marsh (C. Coronado, personal communication, 2009; T.G. Troxler, personal communication, 2009), while downstream advection of subsurface plumes of elevated P concentrations may support tree island elongation (Givnish et al., 2008; Ross et al., 2006; Wetzel et al., 2011).

5 ADVECTIVE SEDIMENT REDISTRIBUTION FEEDBACK

Alone, autochthonous peat accretion is insufficient to explain the planform shape of ridges and some tree islands, indicating that a directional feedback process must also exert control over the landscape. Our conceptual model proposes that in a stable system, processes that build topography in transition zones between landscape elements may be balanced by flow that removes material from this zone, displacing it downstream and to regions just inside the sawgrass boundary (Larsen et al., 2007). According to this conceptual model, landscape stability would require flow velocities that are sufficiently high for entrainment of floc in sloughs and transition zones. In an evolving landscape, as peat accretion on ridges displaced more water into sloughs, velocities and water depths within sloughs would increase, bolstering floc entrainment. Similarly, declining water inputs to the system would cause ridge expansion until the volume of ridges across the landscape displaced enough water into sloughs that velocities became sufficient to again promote landscape equilibration (Givnish et al., 2008; Larsen et al., 2007). This hypothesis is consistent with the limited ridge expansion that occurred during the relatively dry Medieval Warm Period and Little Ice Age (Bernhardt et al., 2004). Additional support lies in recent work performed within the ridge and slough landscape to understand controls on surface water flow velocities and relationships between velocities, bed shear stresses, and sediment transport.

5.1 Controls on Surface Water Flow Velocities

Wetland flow velocities vary with water depth, water-surface slope, and vegetation community (Nepf, 2004). The influence of wind, which can drive flow in unvegetated basins, diminishes in wetlands within a few centimeters of the water surface (Bazante et al., 2006; Harvey et al., 2009). Long-term mean velocities throughout the Everglades have a range of 0.3–1.4 cm s^{-1} (Bazante et al., 2006; Harvey et al., 2009; Leonard et al., 2006; Riscassi and Schaffranek, 2002, 2003, 2004). At present mean slough velocities are greater than ridge velocities by 29–55% (Table 1). At a tree island head in upper Shark River Slough, Everglades National Park, velocities were even higher, averaging 0.9–1.4 cm s^{-1} for the 2003–2004 wet season (Bazante et al., 2006).

TABLE 1. Reported long-term mean flow velocities in adjacent ridges and sloughs

Location	Upper Shark River Slough, Everglades National Park	WCA-3A-5 (26° 03′ 23.7″ N, 80° 42′ 19.2″ W)
Years of record	2002–2007	8/2005–2/2008
Mean ridge velocity, cm s^{-1}	0.2	0.3
Mean slough velocity, cm s^{-1}	0.3	0.4
Source	Leonard et al., 2006	Harvey et al., 2009

The relatively high velocities of sloughs are primarily attributable to their lower vegetative drag (Harvey et al., 2009). Drag forces are proportional to vegetation frontal area, flow velocity squared, and a dimensionless drag coefficient related to hydromechanical properties of the vegetation stems and leaves (Nepf, 2004). Vegetation biovolumes are an order of magnitude greater in ridges than in sloughs, and frontal areas are likewise higher (Harvey et al., 2009). At Everglades field sites in Chekika (25.7463° N, 80.6537° W) and Frog City (25.7518° N, 80.5905° W), flow velocity was negatively correlated with biovolume (r^2 of linear regression = .54, p = .004, and $r^2 = .52$, $p = .04$, respectively; L. Leonard, personal communication). Substantial reductions in velocities occurred in the vicinity of dense submersed litter or floating mats containing periphyton and *Utricularia* (Harvey et al., 2005; Leonard et al., 2006). Tracer gas (SF_6) showed preferential movement of water in areas unobstructed by sawgrass patches (Ho et al., 2009). Likewise, the high velocities observed around tree island heads have been attributed to the sparse understory vegetation beneath the shaded forest canopy (Bazante et al., 2006). Hydromechanical differences between ridge and slough vegetation stems and leaves further contribute to the relatively high velocities of sloughs: drag coefficients of ridge vegetation, calibrated from hydrologic monitoring records, are substantially higher than those of slough vegetation (Harvey et al., 2009).

A scaling assessment based on dimensional analysis and the physics of flow through vegetation revealed that temporal variation in flow velocity is dominantly caused by changes in the water-surface slope rather than changes in flow depth (Harvey et al., 2009). Because emergent vegetation protrudes through the water column, vegetative resistance increases as water depths increase, and flow depth cancels out of the force balance equation. Instead, velocity depends on vegetation frontal areas, stem diameters, and water-surface slope, with temporal changes in the latter driving most of the variability in velocity. Continuous records of velocity, water level, and water-surface slope acquired over three wet seasons in central Water Conservation Area (WCA) 3A supported these predicted relationships (Harvey et al., 2009).

The dominant role of water-surface slope in governing flow velocity also explains regional differences in surface water flow. Mean flow velocities measured at five sites in Shark River Slough are approximately double those measured in central WCA-3A, despite shallower water depths and generally similar vegetation. The difference in flow velocities is attributed to a difference in water-surface slope, which is approximately twice as great in Everglades National Park than in WCA-3A (Harvey et al., 2009). Shallower water-surface slopes in WCA-3A result both from a shallower bed slope and backwater effects due to the impoundment of water by levees (Harvey et al., 2009; C. McVoy, personal communication, 2009). Operation of water-management structures likewise affects water-surface slopes and flow direction. Variano et al. (2009) reported large-scale movement of water in a direction that contrasted with bed slope and remnant directionality of the vegetation patterning, which they attributed to water-management operations.

When floating vegetation such as mats of periphyton and *Utricularia* are present, water depth remains a significant term in the force balance (Larsen et al., 2009b) and exerts a direct control over flow velocity. In all vegetation communities, water depth also exerts an indirect control on velocity, through its exposure of different portions of the vegetation canopy to flow. According to a scaling analysis, flow velocities are strongly and positively related to stem diameters and inversely related to frontal areas, which are roughly proportional to biomass (Harvey et al., 2009). As flow depths increase, the depth-averaged frontal areas of slough vegetation generally decrease, because stem count decreases and vegetation stems taper away from the bed. High flow depths also displace floating mats of periphyton and *Utricularia* away from the bed, diminishing their contribution to the depth-averaged frontal area (Larsen et al., 2009b). In addition, many wetland emergent species, including *Eleocharis* spp., respond to high water levels by increasing their stem diameter (Baksh and Richards, 2006; Edwards et al., 2003) while decreasing overall biomass and number of shoots (Edwards et al., 2003). For these reasons, researchers have observed a positive relationship between flow velocity and flow depth in Shark River Slough (He et al., 2010; Lee et al., 2004; Leonard et al., 2006), Taylor Slough (Lee et al., 2004), and WCA-2A (Lee et al., 2004).

Overall, data and theory indicate that flow velocities in the ridge and slough landscape are highly sensitive to water-surface slope and vegetation coverage, with water-surface slope the dominant control over regional flow direction. In thickly vegetated areas and particularly when floating periphyton mats abound (both conditions associated with altered, postdrainage water management), water depth is also an important control, mainly through indirect interactions with the vegetation canopy.

5.2 Relationship Between Velocity and Bed Shear Stress

Though flow velocities are more readily measurable, bed shear stress is most relevant to bed sediment entrainment. The depth-averaged velocity associated with the critical bed shear stress for sediment entrainment may vary with water depth, water-surface slope, and vegetation community. These factors affect the shape of velocity profiles, determining the distribution of velocities close to the bed, which are most directly related to bed shear stress. Vegetation communities with near-surface frontal areas that are relatively high compared to near-bed frontal areas (e.g., sloughs with thick floating mats of periphyton and *Utricularia*) have velocities that are faster close to the bed than higher in the water column (Leonard et al., 2006) and attain the critical bed shear stress for sediment entrainment at a low depth-averaged velocity relative to vegetation communities with frontal areas that decrease monotonically away from the bed (Larsen et al., 2009b).

Using field-calibrated drag coefficients unique to ridge and slough vegetation communities (Lee et al., 2004; Harvey et al., 2009), theory relating drag coefficients to vertical eddy diffusivities (Nepf et al., 1997), and representative vegetation architectures based on clip plots harvested throughout the ridge and slough landscape (Carter et al., 1999a, 1999b; Harvey et al., 2009; Rybicki et al., 2001), Larsen et al. (2009b) solved for velocity profiles over a range of water-surface slopes and surface water depths. They then used a force balance to solve for bed shear stress from the velocity profiles. Bed shear stress contours constructed from the solution revealed that bed shear stress is lower in ridges than in sloughs for a given set of hydraulic forcing conditions (Figure 5). Similar to flow velocity, bed shear stress is more sensitive to water-surface slope than to water depth, though depth becomes a more important control when floating mats of periphyton and *Utricularia* are present. Additionally, bed shear stress is highly sensitive to emergent vegetation in sloughs and is lowest in communities with abundant spikerush.

5.3 Entrainment of Sediment by Flowing Water

At present, Everglades surface water contains low concentrations (0.5–1.5 mg L^{-1}) of fine suspended sediment, with mean diameters of 3–11 μm (Bazante

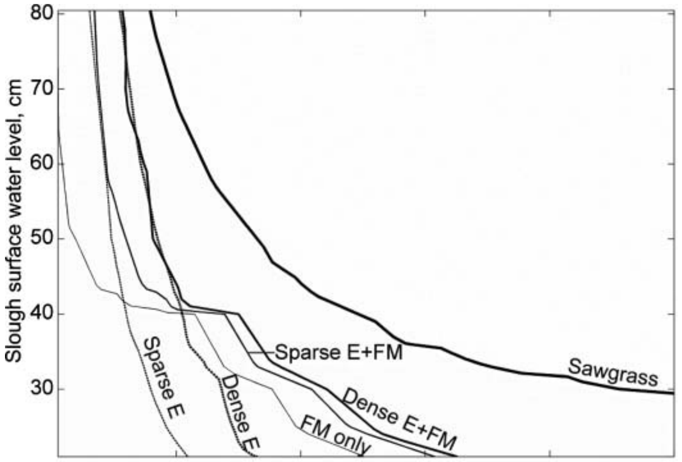

FIGURE 5. Combinations of slough surface water level (assumed to be 20 cm higher than ridge water level) and water-surface slopes that produce bed floc entrainment in different vegetation communities (E = *Eleocharis* spp., FM = floating mats, consisting of *Utricularia* spp. and periphyton). Lines represent contours of constant bed shear stress, equal to the value (1 × 10^{-2} Pa) that entrained bed floc in laboratory flume studies (Larsen et al., 2009a). Figure modified from Larsen et al. (2009b).

et al., 2006; Noe et al., 2007). Concentrations of larger detrital floc in suspension, measured with a digital floc camera over one day at a single site in central WCA-3A, were even lower (0.001–0.3 mg L^{-1}; Larsen et al., 2009c). Concentrations of suspended sediment are generally unrelated to flow velocities (Larsen et al., 2009c; Noe et al., 2010), suggesting that ambient flow velocities are below the sediment entrainment threshold. The dominant size class of fine sediment (0.45–2.7 μm) and dominance of particulate P by the microbial, acid-hydrolyzable fraction suggest a bacterial origin within the water column (Noe et al., 2007), whereas entrainment of larger aggregates in ambient conditions is likely associated with bioturbation (see subsequent paragraphs). Suspended sediment biogeochemical characteristics, size distributions, and concentrations do not significantly differ between ridge and slough, though the greater discharge through sloughs results in greater unit-width loading of suspended material compared to ridges (Noe et al., 2010).

Episodic events elevate suspended sediment concentrations above ambient levels. Pulses (lasting less than a half-hour) of suspended sediment observed during a diel time series were not correlated with hydrologic and meteorological parameters and were likely caused by bioturbation by grass shrimp (*Palaemonetes paludosus*) and crayfish (*Procambarus* spp.; Larsen et al., 2009c; Noe et al., 2010). Hurricane effects, while infrequent, are more widespread and long-lasting. Fifteen days after the eye of Hurricane Wilma passed over a measurement station in central WCA-3A, suspended sediment concentrations were three to 4 times higher than measurements taken prior to the storm (Noe et al., 2010). The hurricane caused velocities as high as 4.9 cm s^{-1} at this research site, gusts of wind as high as 14.2 m s^{-2}, and water levels that increased by 20 cm over several hours (Harvey et al., 2009). These conditions eliminated surface mats of periphyton and *Utricularia* from sloughs and redistributed macrodetritus into lines of wrack that surrounded the edges of ridges and tree islands (Zweig and Kitchens, 2008).

Recent experiments to obtain the entrainment threshold for Everglades bed floc involved simultaneous measurement of suspended sediment concentrations and flow velocities over a range of induced flows in a laboratory racetrack flume (Larsen et al., 2009a), a portable benthic annular flume deployed in unvegetated field locations (S. Hagerthey, personal communication, 2008), and a field flume located in an Everglades slough (J. Harvey, personal communication, 2010). Despite different methodologies, results were broadly consistent. Bed shear stress measured at the point of bed floc entrainment in the racetrack flume was 0.01 Pa (Larsen et al., 2009a). In all experiments corresponding velocities 5 cm above the bed at the bed floc entrainment threshold were 1.6–2.8 cm s^{-1} (S. Hagerthey, personal communication, 2008; J. Harvey, personal communication, 2010; Larsen et al., 2009a). For sustained entrainment, velocities of 3–5 cm s^{-1} at 5 cm above the bed were required (S. Hagerthey, personal communication, 2008; Larsen et al., 2009a). Because velocities in these experiments tended to increase with distance from the bed, depth-averaged velocities at the bed floc entrainment threshold were slightly higher: between 3.2 and 5.3 cm s^{-1} in the field flume entrainment experiment (Harvey et al., 2011). This range was consistent with the predicted depth-averaged velocity (3.7 cm s^{-1}) in the field flume at the entrainment threshold using the velocity profile model of Larsen et al. (2009b).

5.4 Potential for Sediment Redistribution Within the Ridge and Slough Landscape

Though present-day differentiation in suspended sediment concentrations between ridges and sloughs is negligible (Noe et al., 2010), sediment redistribution from sloughs to ridges will occur when flows are above the floc entrainment threshold in sloughs. Over a range of water-surface slopes and surface water depths, bed shear stresses are sufficient for bed floc entrainment from sloughs but not ridges (Figure 5), though this range becomes narrower with increasing abundance of spikerush in sloughs. Because of advective flow paths and large lateral dispersion coefficients (0.003–0.01 m^2 s^{-1}; Variano et al., 2009), some of the flow carrying floc entrained from sloughs will intercept the ridge. Floc has a mean settling velocity of 0.11 cm s^{-1} (S. Hagerthey, personal communication, 2008; Larsen et al., 2009a), ensuring that much of the floc transported to the ridge will settle just inside the ridge boundary. Data collected from sediment traps deployed at the end of dead-end sloughs in Everglades National Park support this hypothesis (Leonard et al., 2006).

Compared to bed floc, fine particles and aggregates have a much slower settling velocity, with a mean of 0.03 cm day^{-1} for small particles (2.9–3.6 μm in diameter) suspended in ambient flow in Everglades National Park (Bazante et al., 2006) upwards to a maximum of 1 mm s^{-1} for aggregates of 100 μm in diameter (Larsen et al., 2009a). This fine sediment is less likely to undergo substantial redistribution from slough to ridge through single-particle settling. However, fine sediment may be intercepted by larger settling flocs (Larsen et al., 2009c) or undergo filtration (interception) on vegetation stems (see Stumpf, 1983). Tracer tests using 1 μm TiO_2 particles in an *Eleocharis* slough in Everglades National Park (Saiers et al., 2003) and 0.2 μm particles in a ridge in central WCA-3A (Huang et al., 2008) suggested that the emergent vegetation now common in postdrainage sloughs is two orders of magnitude more efficient in the capture of fine sediment than ridge vegetation. In these experiments filtration reduced the tracer concentration by one half over a transport distance of 128 m in the ridge versus 1 m in the slough. Huang et al. (2008) attributed the difference in capture efficiency to sticky epiphyton coatings on spikerush stems in sloughs and to the smaller diameter of spikerush stems compared to sawgrass stems (see Palmer et al., 2004). Whether the higher capture of fine sediment on slough vegetation stems is balanced by a larger net settling flux of fine sediment on ridges (through both single-particle settling and interception of fine sediment by settling floc) remains uncertain and constitutes a future research priority.

Preliminary flume studies suggest that fine sediment (e.g., aggregates $<100\ \mu$m of epiphyton and the associated extracellular matrix) from vegetation stems is entrained at lower velocities than bed floc (Harvey et al., 2011). Thus, any landscape-forming processes that involve fine sediment from stems may occur over a wider range of flow velocities than those that entrain bed floc. Understanding the differential transport of fine and coarse sediment and the relative importance of each to landscape evolution is a critical need, well-suited to flume, mesocosm, or landscape-scale experiments that are coupled to modeling efforts.

6 LANDSCAPE EVOLUTION THROUGH AUTOCHTHONOUS PEAT ACCRETION, FLOW, AND SEDIMENT REDISTRIBUTION

6.1 Simulation Studies

Fieldwork in the ridge and slough landscape has made possible the construction of spatially explicit models of flow, sediment transport, and vegetation and peat dynamics. Larsen and Harvey (2010, 2011) used cellular automata modeling techniques to show that the combination of an autochthonous peat accretion feedback and advective sediment redistribution feedback were sufficient to produce the geometry characteristic of the ridge and slough

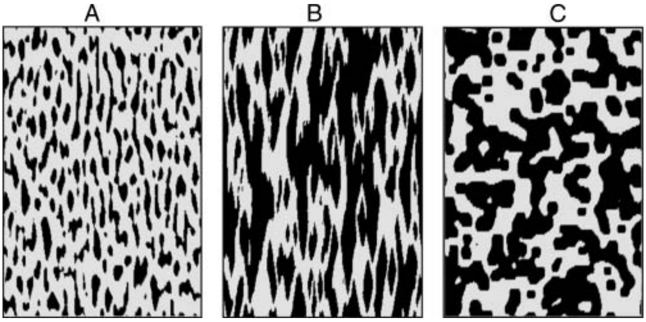

FIGURE 6. Ridge and slough landscape simulation results from Larsen and Harvey (2010, 2011), with ridges in black and sloughs in gray. Landscapes in A–C evolved from an initially rough topography through the autochthonous peat accretion and advective sediment redistribution feedbacks, using different combinations of input parameters. (A) An equilibrium ridge and slough landscape with flow, with elongated ridges and well-connected sloughs. (B) A disequilibrium landscape with flow. Ridge coverage is 55%, but sloughs remain interconnected. (C) A disequilibrium landscape without flow. Ridge coverage is 55%, and sloughs are disconnected. The domain size is 1.27 × 1.86 km.

landscape from an initially rough topography (Figure 6). Consistent with paleoecological studies (Bernhardt and Willard, 2009; Willard et al., 2006), the simulated landscapes evolved from wetter-than-present conditions. Simulations assumed modern ridge vegetation, deepwater sloughs with periphyton, *Utricularia*, and sparse *Eleocharis*, and bed floc redistribution by entrainment and settling only. Entrainment of fine material from vegetation stems and filtration by stems were not simulated. Although even simulations without flow sufficient to entrain bed floc maintained long-term heterogeneity through water-level limitation of sawgrass colonization, flow that entrained floc was required for long-term slough connectivity (Figure 6).

6.2 Uncertainty About the Fate and Role of Particulate Organic Material

The simulation model of Larsen and Harvey (2010, 2011) assumed oligotrophic conditions and did not explicitly incorporate P transport. It also assumed that all floc was converted to peat conservatively. However, floc is more enriched in P than peat (Noe and Childers, 2007; Troxler and Richards, 2009) and therefore more biogeochemically reactive (Amador and Jones, 1993; Noe et al., 2010). Though organic biomarker data suggest partial incorporation of floc organic matter into the peat (Neto et al., 2006), it is apparent that some decomposition of floc occurs, which decreases the carbon input to peat and releases bound P. Decomposition of floc and the redistribution of P bound to sediment may play important roles in evolution of the ridge and slough landscape.

Long-term studies of floc decomposition are not yet available, but 10-day laboratory incubations of floc at 30°C resulted in aerobic carbon losses of 0.3–1.2% ($N = 4$) of the initial mass of floc and anaerobic carbon losses of 0.8–4% ($N = 4$; A.L. Wright et al., 2009). Although decomposition rates are expected to decrease nonlinearly over time as the labile fraction of the floc organic matter pool is preferentially removed (Dai et al., 2005; Wickland et al., 2007), metabolism of a significant fraction of the floc prior to its conversion to peat is likely. Using a mixing model based on $\delta^{13}C$ signatures, Troxler and Richards (2009) estimated that in sloughs with low periphyton coverage, floc organic matter is 100% *Utricularia* spp. detritus, which comprises 59%, 47%, and 43% of the carbon in peat at depths of 0–2.5, 2.5–5.0, and 5.0–10.0 cm, respectively, with the remainder derived from below-ground biomass. Models that assume conservative conversion of floc to peat thus underestimate the timescales over which floc transport by flow can impact landscape formation. Due to the low number of replicates in the A.L. Wright et al. (2009) floc decomposition study and the apparent similarity between rates of aerobic and anaerobic decomposition, it remains unclear whether oxidation of transported floc on the ridge would be different from that of native floc in the slough.

When decomposing floc releases bound P, it first enters microbial food webs but can eventually stimulate macrophyte primary production and peat accretion (Noe et al., 2003). In this way, floc entrainment and transport may have an indirect effect on peat topography, by restricting some of the organic matter production that would otherwise build topography in ridge-slough transition zones, and by augmenting organic matter production within the ridge. Though not yet quantified, fine aggregates from the vegetation stems and coarse bed floc may have different significance in particulate P redistribution. To first order, the differential entrainment and settling of fine and coarse sediment (see Section 5.4) would result in different mass transport fluxes from sloughs to ridges. Second, P concentration on sediment varies as a function of its size (Noe et al., 2007), with bed floc often containing higher mass concentrations of P than finer periphyton aggregates but lower P turnover rates (Noe and Childers, 2007). In summary, whether fine aggregates from stems or coarse bed floc contribute more to particulate P redistribution in a well-functioning ridge and slough landscape is unclear. Attaining a better understanding of the differential contributions of these sediment sources to carbon and P budgets is important in determining target flow velocities, durations, and P concentrations, as well as estimating timescales of landscape response to altered flows.

6.3 Dominant Processes on Tree Islands Versus Ridges

Differences in the relative importance of autochthonous peat accretion versus advective sediment redistribution feedbacks can explain many of the morphological differences between tree islands and ridges. Through autochthonous peat accretion, ridges may become sufficiently aerated for ferns and woody species, which then promote further peat accretion to a new, higher equilibrium elevation (Givnish et al., 2008; Stone et al., 2002). This transition can occur during extended periods of drought, as observed in the paleoecological record (Willard et al., 2006), or when masses of peat become buoyant and float on the water surface (Wetzel, 2002). The former is thought to be the origin of many cigar-shaped tree islands, whereas the latter is thought to be the origin of round, pop-up tree islands (Stone et al., 2002; Willard et al., 2002). Tear-shaped tree islands are commonly tied to high points in the limestone bedrock, though this may not always be the case (Mason and van der Valk, 2002; Willard et al., 2002; see also Givnish et al., 2008).

Our conceptual model predicts that ridge elongation occurs in upstream and downstream directions predominantly through vegetative propagation and sediment deposition. In contrast, tear-shaped tree island elongation may occur predominantly in the downstream direction, limited by the surface and subsurface advection of high-concentration P plumes from the tree island head (Givnish et al., 2008; Ross et al., 2006; van der Valk and Sklar, 2002). It is also plausible that the advective sediment redistribution feedback contributes to the teardrop shape. In alluvial environments without biological processes, the teardrop shape, or lemniscate, is the minimum-drag configuration for depositional features (Komar, 1983, 1984). The heads of fixed tree islands in the Everglades are generally larger and higher than those of ridges, which would induce more flow separation and faster flow around the edges. As a result, erosional processes that historically restricted island expansion would become larger relative to the biological processes that promoted island expansion, causing the island's equilibrium configuration to be more similar to the fully abiotic (lemniscate) end member than the equilibrium configuration of ridges. However, while it is known that tree island morphology is highly sensitive to flow magnitude, direction, and hydroperiod (Brandt et al., 2000; Wetzel, 2002; Wu et al., 2002), not enough is known about mechanisms and rates of sediment accumulation and loss on tree islands to determine the optimal combination of hydrologic and hydrodynamic conditions for their persistence.

Additionally, fire may exert more control over tree island pattern dynamics than over ridge and slough pattern dynamics. In both landscape elements, severe fires that burn the peat can convert large patches of landscape or the transitional areas around high patches to slough (S.M. Davis et al., 1994; Gunderson, 1994). Less severe fires are more frequent (Gunderson and Snyder, 1994), and these fires have a disproportionate effect on tree islands. While sawgrass is known to be highly adapted to fire (Craighead, 1971; Gunderson and Snyder, 1994) and resprouts within weeks following a burn (Forthman, 1973), woody species can be lost from smaller tree islands post-burn (Silveira, 1996). Intermediate-severity fires may oxidize some of the higher, drier peat on tree islands while leaving the peat topography of wetter ridges intact, converting some of the smaller tree islands to ridge habitat. Regardless of the mechanism, fire alters the distribution of tree island sizes, with more frequent fires preferentially eliminating smaller tree islands while leaving larger ones, which because of their size contain cores that are resistant to fire, intact (Brandt et al., 2002; Silveira, 1996). Locally, tree island fires reset successional trajectories (Wetzel, 2002; Wu et al., 2002), which impacts the autochthonous peat accretion feedback process.

7 DEGRADATION OF THE RIDGE AND SLOUGH LANDSCAPE

Key features required for the autochthonous peat accretion and advective sediment redistribution feedbacks to produce stable, elongated ridges and sloughs are periods of flow sufficient to entrain floc from sloughs and transition zones and water levels sufficient to inhibit the lateral expansion of sawgrass into sloughs (Figure 3). Perturbation to either of these driving variables could have contributed to widespread degradation of the ridge and slough landscape. In a three-year field study, Zweig and Kitchens (2009) found that slough communities became invaded by sawgrass when sloughs experienced a minimum water level of 2 cm beneath the peat surface for three consecutive dry seasons and relatively dry conditions for intervening wet seasons. Conversely, sawgrass fragmented after more than two years of sustained wet season depths greater than 61 cm above the ridge surface. Similarly, Armentano et al. (2006) observed replacement of sawgrass with slough species following a 30–40 cm increase in mean water level in Taylor Slough between 1980 and 1990, with a subsequent increase in sawgrass coverage once water levels subsided. Ponding of water at the downstream portions of the WCAs and lower mean water levels at the upstream portions may thus explain the respective fragmentation of ridges and loss of sloughs in these areas. Diminished flow, combined with a lack of clear elevation differences between sawgrass and slough habitats, may be responsible for sawgrass expansion into sloughs (e.g., Figure 2) at rates of up to 30 cm yr^{-1} in portions of Loxahatchee National Wildlife Refuge (P. McCormick, personal communication, 2009).

Even if changes in water level are not sufficient to cause invasion of sloughs by sawgrass, they can instigate the spread of other emergent species that accelerate slough degradation through positive feedback. Because decreases in wet season water depths can cause a shift from *Nymphaea*-dominated sloughs to sloughs with more abundant emergent species (Busch et al., 1998; Zweig and Kitchens, 2008), widespread drainage of the Everglades might have been partially responsible for the abundance of emergent species in the landscape today relative to historic conditions (Bernhardt and Willard, 2009; McVoy et al., 2011). An increase in slough emergent species abundance could accelerate slough infilling through both autochthonous peat accretion (Larsen et al., 2007) and the advective sediment redistribution feedback. Relative to more open sloughs, postdrainage *Eleocharis* sloughs require substantially higher surface water slopes for floc entrainment to occur (Figure 5) and tend to acquire dense epiphytic periphyton (Gaiser et al., 2006), which contributes to high filtration efficiencies (Huang et al., 2008; Saiers et al., 2003).

Possible causes of landscape degradation are not limited to changes in the dominant drivers of its formation (Figure 3). For example, though it seems unlikely that historic spatial differences in P concentration caused ridge edges to stabilize, additions of P above historic oligotrophic levels may promote destabilization of ridges and reduce landscape heterogeneity in several ways. First, sawgrass is stimulated by low-level P enrichment (Smith et al., 2009), and under enriched conditions, sawgrass germinates (Goslee and Richardson, 2008) and is optimally productive at deeper water levels than under unenriched conditions (Lissner et al., 2003). P enrichment may thus shift the threshold elevation for sawgrass growth downward and further into the slough (Newman et al., 1996). Second, enrichment increases the abundance and productivity of emergent slough vegetation (Busch et al., 2004; Daoust and Childers, 2004; Rejmankova et al., 2008) and can convert sparsely vegetated sloughs to dense stands of *Nymphaea* and *Typha* (Hagerthey et al., 2008; McCormick et al., 2009). Ridges likewise experience regime shifts from *Cladium* to *Typha* when subject to moderate (11 mg L^{-1}) P enrichment (Hagerthey et al., 2008). Under enriched conditions, both ridges and sloughs are more susceptible to invasion by exotic macrophytes (Childers et al., 2003).

In interior portions of the Everglades that receive minimal canal water, P enrichment may result from degradation of tree islands (Wetzel et al., 2009), which accumulate P in soil and litter (Orem et al., 2002; Troxler and Childers, 2009). Significant gradients in vegetation community composition occur with proximity to tree islands, which Givnish et al. (2008) attributed to a subtle P gradient. Evidence for low-level P enrichment beyond background oligotrophic levels, apparent in the composition of periphyton communities, is widespread through WCA-3A, WCA-2, and parts of Everglades National Park (Figure 7).

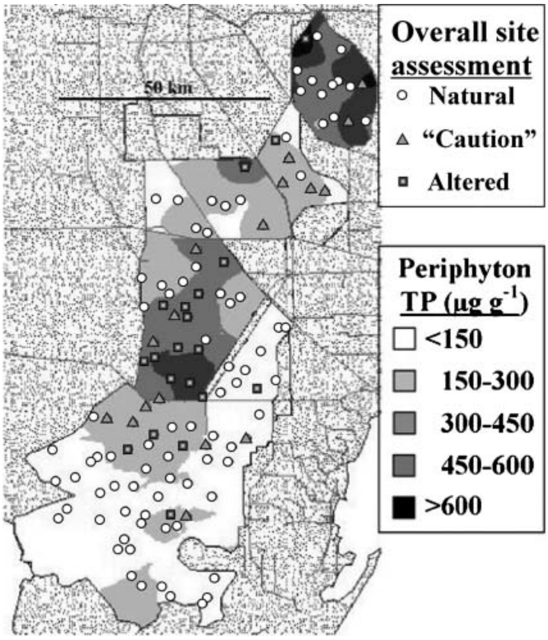

FIGURE 7. Impact of low-level P enrichment on indicator periphyton communities in the greater Everglades. Overall assessments are determined by comparing sampled periphyton biomass, quality, and community composition to unimpacted reference values. Natural sites have values within one standard error of the mean, caution sites within two standard errors, and altered sites within three standard errors. Figure modified and reprinted with permission from Gaiser (2009).

Factors other than P enrichment may have contributed to an increase in slough emergent species and accelerated slough degradation. The ridge and slough landscape was historically a relatively mineral-poor, low-conductivity system, as reflected in the siliceous microfossil record (Slate and Stevenson, 2000) and extensive coverage of highly organic peat (McCormick and Harvey, 2011). However, mineral inputs have increased over the past century (Harvey and McCormick, 2009) via canals and increased groundwater discharge resulting from peat subsidence and altered hydrologic gradients near water control structures (Harvey et al., 2006). Sawgrass seedling growth and rhizome production are stimulated by a combination of low-level P enrichment and mineral enrichment, conditions which would be expected downstream of canal discharges. The intrusion of canal water into remnant soft-water areas such as the Loxahatchee National Wildlife Refuge is associated with an increase in the cover of sawgrass relative to slough habitat, although cause-effect relationships for this pattern have not been clearly established (McCormick and Harvey, 2011).

Changes in slough periphyton composition and abundance as a result of mineral enrichment, low-level P enrichment, or hydrologic changes (Busch et al., 1998; Gaiser, 2009) may have also contributed to degradation of sloughs. Lower water depths and shorter hydroperiods are associated with higher periphyton biomass (Gottlieb et al., 2006; Iwaniec et al., 2006), with possible implications for floc production rates, transport characteristics (Larsen et al., 2009a), and degree of consolidation (C. McVoy, personal communication, 2009). Also, floc with a low organic content tends to have a higher threshold shear stress for erosion and a higher settling velocity than more organic floc (Larsen et al., 2009a). Therefore, an increase in the degree of periphyton $CaCO_3$ encrustation resulting from increased surface water Ca^{2+} concentrations (McCormick et al., 2000) could contribute to slough infilling by reducing floc entrainment and increasing deposition. In addition, Ca^{2+} enrichment favors the development of benthic periphyton mats (S.M. Davis et al., 2005), which, as in situ erosion studies have demonstrated, inhibit floc entrainment (S. Hagerthey, personal communication, 2009).

Last, increases in SO_4^{2-} concentrations may contribute to slough degradation. Increased inputs of SO_4^{2-} originate from oxidizing peat in the Everglades Agricultural Area, fertilizer additives, and increased groundwater–surface water exchange (see Harvey and McCormick, 2009). In the central Everglades, higher SO_4^{2-} concentrations have contributed to lower redox potentials (Orem, 2007), which could increase slough peat accretion rates (Larsen et al., 2007). Higher SO_4^{2-} concentrations also raise concentrations of bioavailable P because of competitive binding of S with Fe and the release of Fe-bound P (Orem, 2007).

To summarize, flow was the critical driver that produced the longitudinal pattern structure of the ridge and slough landscape during its formation, though water level and water quality needed to be within an appropriate range to maintain distinct vegetation communities. However, pattern degradation is sensitive to other drivers. Based on response time scales for different ecosystem components, it is possible to rank the potential importance of these drivers of landscape degradation. In relatively oligotrophic areas, vegetation communities respond rapidly (within < 4 years) to water level (Armentano et al., 2006; Childers et al., 2006; Zweig and Kitchens, 2008). Vegetation responds over similar timescales to P enrichment (S.M. Davis, 1994), though P is preferentially taken up by and cycled within microbial communities before uptake by plants (Noe et al., 2003). Changes in primary production rates that cause changes in the equilibrium elevation of the peat surface ensue. Thus, changes in water level, followed by changes in water quality, are likely the factors that can most rapidly cause broad vegetation community shifts and landscape pattern degradation. Over longer (though more uncertain) timescales, decreases in flow velocity cause ridges to gradually encroach on sloughs.

8 RESTORATION RECOMMENDATIONS

In the Everglades, the patterned ridge and slough landscape structure is inseparable from its highly valued ecosystem services, including flood control and groundwater recharge. Two aspects of the landscape structure particularly impact overall ecosystem functioning: (a) Persistent topographic heterogeneity that permits the coexistence of multiple vegetation communities and habitat types (Ogden, 2005) and (b) slough connectedness, required for fish migration (Trexler et al., 2002). In areas with remnant topographic variability, heterogeneity of vegetation communities and maintenance of their distinct equilibrium elevations can best be sustained through appropriate management of water level. Water levels should be such that the possibility of sloughs drying completely in consecutive years is minimal, that ridges do not experience sustained wet season depths greater than about 60 cm (Zweig and Kitchens, 2009), and that tree islands are not exposed to excessive inundation or intense muck fires (Sklar and van der Valk, 2002). However, without flows that entrain floc from sloughs and transition zones, ridges gradually expand into sloughs, and the system loses long-term heterogeneity and slough connectivity. The needed flow velocities (Section 5.3) could be achieved through pulsed releases of water from impounded areas that increase water-surface slope and flow velocity. Flows would need to be aligned parallel to the remnant pattern axis of the landscape to ensure that sediment redistribution maintains slough connectivity (Variano et al., 2009). Still, in regions with dense emergent vegetation in sloughs or with sloughs that have been invaded by sawgrass, it may not be feasible to increase water-surface slopes to the degree required for bed floc entrainment (Figure 5). In these cases, vegetation management may be needed to reinitiate deepwater sloughs.

Several studies suggest strategies for reducing emergent vegetation in sloughs and increasing opportunities for floc entrainment. Prolonged flooding in southern WCA-3A (Zweig and Kitchens, 2008) and in Taylor Slough (Childers et al., 2006) has greatly reduced the annual net productivity of sawgrass and converted areas of sawgrass or wet prairie to sloughs. Fires that burn ridge peat, followed by two years of relatively deep conditions, have also transformed sawgrass communities to slough (Zweig and Kitchens, 2009).

Although reversing landscape degradation associated with abundant emergent vegetation in sloughs requires measures that go beyond restoration of predrainage flows and water levels (because of feedback between flow and vegetation architecture), landscape degradation associated with loss of ridges can likely be more readily reversed. If near predrainage hydrology is restored to these areas, the combination of the autochthonous peat accretion and advective sediment redistribution feedback should be sufficient to cause ridge growth and elongation from initial high portions of the peat surface, as occurred during the original evolution of the landscape (Larsen, 2008).

All of these recommendations for preservation and restoration of the ridge and slough landscape presume that highly oligotrophic, mineral-poor water chemistry is maintained. Nonetheless, flows originating from canals will likely be enriched in P, SO_4^{2-}, and total dissolved solids. Even without canal inputs, legacy effects of P accumulated in the peat soils of WCA-2 (Harvey et al., 2006; Noe and Childers, 2007), combined with possible loss of tree islands (Wetzel et al., 2009), will likely contribute to low-level P enrichment of surface water for decades to come. It is known that any P enrichment causes an increase in slough productivity, sawgrass productivity and spreading rate, and the abundance of emergent vegetation in sloughs (Section 7), but the extent to which these conditions destabilize ridge edges and diminish slough connectivity and the time scales over which they act remain to be quantified. Likewise, levels of surface water SO_4^{2-} and total dissolved solids suitable for maintaining the valued ecological functions of the ridge and slough landscape are uncertain. Appropriate synoptic water quality standards for sustaining the ridge and slough landscape need to be defined and adhered to for restoration to be successful.

Without flow, well-connected sloughs and the ecosystem attributes that they sustain would likely not persist. However, if flows could not meet the needed water quality criteria, restoration planners would be faced with the option to maintain partial ecosystem function by managing the Everglades for topographic heterogeneity only, through adjustment of water levels. Gradual ridge expansion in a topographically heterogeneous system could be inhibited or reset by natural episodic events or managed events such as controlled burns and periodic flooding, but these options require further study.

TABLE 2. Key remaining uncertainties for predicting ridge-slough-tree island landscape dynamics

Role of redistributed sediment in landscape evolution

(1) To what extent does particulate organic matter (bed floc and fine aggregates from vegetation stems) become incorporated into peat over a wide range of flow and biogeochemical conditions?
(2) To what extent does sediment redistribution by flow impact tree island growth and expansion relative to downstream P advection?
(3) What is the fate of P associated with bed floc and fine aggregates from vegetation stems that are redistributed by flow? Does it become available to support macrophyte growth, germination, and ultimately peat accretion?

Mechanisms of landscape degradation

(4) How does the lateral spreading ability of sawgrass change with P enrichment and/or mineral enrichment over a range of water depths?
(5) How do changes in periphyton community composition affect the rates of floc production and floc transport properties?
(6) How efficiently do sawgrass and slough vegetation stems and associated periphyton capture and immobilize natural sediment? Do filtration and settling of floc result in different ecosystem responses?
(7) To what extent do P, SO_4^{2-}, and total dissolved solids enrichment alter the abundance of slough emergent vegetation and autochthonous peat accretion rates in sloughs relative to ridges?

Restoration strategies

(8) What flow durations are needed to ensure sufficient redistribution of sediment to maintain laterally stable ridges?
(9) What are the maximum allowable concentrations of P, SO_4^{2-}, and total dissolved solids needed to maintain long-term topographic heterogeneity and slough connectivity?
(10) Are model predictions of flow velocity and sediment redistribution consistent with field observations over a range of hydrologic forcing scenarios?
(11) What are the most effective means of regenerating sloughs with low resistance to flow where sloughs are invaded by sawgrass or thick emergent vegetation?
(12) What was the historic role of episodic events in inhibiting ridge expansion? Can controlled fire and flood likewise be used today as a resetting mechanism to maintain open sloughs?
(13) Over what timescales does the landscape respond to changes in flow and water quality? How do degradation timescales differ from restoration timescales?

9 REMAINING UNCERTAINTIES AND RECOMMENDATIONS

Much progress has been made on testing the hypotheses of the Science Coordination Team (2003), particularly with regard to establishing and validating the conceptual model of formation of the ridge and slough landscape. However, several key uncertainties about mechanisms of landscape degradation, restoration strategies, and the biogeochemical role of redistributed sediment in landscape evolution remain (Table 2). Though some of these uncertainties can be readily addressed by simple field or laboratory experiments, others that require understanding the effects of interactions among multiple potential drivers necessitate complex experimental designs.

Rather than attempting to fully address these questions, it may be more prudent to ask whether certain combinations of driving variables cause the system to evolve in an acceptable direction, which can be addressed through an adaptive management scheme that tests restoration strategies on a pilot scale before large-scale implementation. Landscape-scale experiments that occur through this management scheme could expose different parts of the landscape to gradients in flow velocities and solute concentrations. Monitoring physical and biological responses over these gradients would yield insight about the combinations of parameters that induce landscape evolution in an acceptable direction. Measured responses could be used in combination with predictive models to refine a final design for larger-scale restoration.

There are many advantages to addressing remaining uncertainties using an adaptive management approach with landscape-scale experiments, but restoration planners should also be cautioned that surprising outcomes could be costly. Feedback processes in this ecosystem can cause hysteresis in landscape evolution trajectories, such that while actions that cause a loss of ridges may be readily reversible through hydrologic manipulation, actions that cause a loss of sloughs together with a loss of topographic heterogeneity are not, requiring more complex and expensive strategies for reducing the abundance of emergent vegetation. Nevertheless, it is clear that the most costly alternative will be to do nothing. Moderately elevated slough P and SO_4^{2-} concentrations, the loss of tree islands, flow velocities below the threshold for sediment entrainment, and changes in water levels all suggest that the best-preserved portion of the ridge and slough landscape may be in danger of rapid degradation. Because preservation and enhancement of extant patterning is cheaper and more feasible than restoration of a fully degraded landscape, time is of essence in addressing uncertainties and implementing solutions.

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