Reciprocal Biotic Control on Hydrology, Nutrient Gradients, and Landform in the Greater Everglades

Matthew J. Cohen [a] , Danielle L. Watts [b] , James B. Heffernan [c] [d] & Todd Z. Osborne [e]

[a] School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA

[b] School of Natural Resources and Environment, University of Florida, Gainesville, FL, USA

[c] Department of Biological Sciences, Florida International University, Miami, FL, USA

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

[e] Soil and Water Science Department, University of Florida, Gainesville, FL, USA

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Reciprocal Biotic Control on Hydrology, Nutrient Gradients, and Landform in the Greater Everglades

MATTHEW J. COHEN,[1] DANIELLE L. WATTS,[2]
JAMES B. HEFFERNAN,[3,4] and TODD Z. OSBORNE[5]

[1]*School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA*
[2]*School of Natural Resources and Environment, University of Florida, Gainesville, FL, USA*
[3]*Department of Biological Sciences, Florida International University, Miami, FL, USA*
[4]*Southeast Environmental Research Center, Florida International University, Miami, FL, USA*
[5]*Soil and Water Science Department, University of Florida, Gainesville, FL, USA*

Restoration can be viewed as the process of reestablishing both exogenous drivers and internal feedbacks that maintain ecosystems in a desirable state. Correcting exogenous and abiotic drivers is clearly necessary, but may be insufficient to achieve desired outcomes in systems with self-organizing biotic feedbacks that substantially influence ecological stability and timing of responses. Evidence from a broad suite of systems demonstrates the prevalence of biotic control over key ecosystem attributes such as hydroperiod, nutrient gradients, and landform that are most commonly conceived of as exogenously controlled. While a general theory to predict conditions under which biotic controls exert such strong feedbacks is still nascent, it appears clear that the Greater Everglades/South Florida landscape has a high density of such effects. The authors focus on three examples of biotic control over abiotic processes: hydroperiod and discharge controls exerted by peat accretion in the ridge-slough landscape; phosphorus (P) gradients that emerge, at least in part, from interactions between accelerated peat accretion rates, vegetation structure and fauna; and reinforcing feedbacks among land elevation, aquatic respiration, and carbonate dissolution that produce local and landscape basin structure. The authors propose that the unifying theme of biogeomorphic landforms in South Florida is low extant topographic variability, which allows reciprocal biotic

Address correspondence to Matthew J. Cohen. E-mail: mjc@ufl.edu

*modification of local site conditions via mechanisms of peat accre-
tion (including via effects of landscape P redistribution on primary
production) or limestone dissolution. Coupling these local positive
feedbacks, which drive patch expansion, with inhibitory or negative
feedbacks on site suitability at distance, which serve to constrain
patch expansion, provide the mechanistic basis for landscape pat-
tern formation. The spatial attributes (range and isotropy) of the
distal negative feedback, in particular, control pattern geometry;
elucidating the mechanisms and properties of these distal feedbacks
is critical to restoration planning.*

KEYWORDS: biogeomorphic, patterned, landscape, self-
organization, conceptual model

INTRODUCTION

A fundamental challenge in ecosystem restoration is the resetting of criti-
cal feedbacks that previously maintained the system in some desired state
(Suding et al., 2004), but frequently these feedbacks are poorly understood.
Thresholds in responses to environmental drivers, past which feedbacks no
longer operate, can induce precipitous declines, long lags in recovery, and
even arrested succession. In many restoration cases the ecological system is
viewed from an engineering perspective, wherein setting the external drivers
(e.g., hydrology) is judged sufficient to create the necessary interactions be-
tween the internal components (Zedler, 2000). This perspective presumes
first that ecological systems change continuously along gradients of exoge-
nous drivers, and second that the arrangement of ecological parts is somehow
manifest in the boundary conditions. An increasingly long list of ecologi-
cal examples, including shallow lakes, coral reefs, patterned peatlands, arid
grasslands, and salt marshes suggests that this perspective is, at best, incom-
plete (Didham et al., 2005; Mayer and Rietkerk, 2004; van Hulzen et al., 2007).
Indeed, an emerging theme in the ecological restoration literature is the need
to reinstate reciprocal controls (sensu Corenblit et al., 2008) between system
elements (Suding and Hobbs, 2009), particularly the action of ecosystem en-
gineers (Byers et al., 2006; Jones et al., 1994; van Hulzen et al., 2007), and
to explicitly monitor those feedbacks to assess restoration performance.

Biotically mediated positive feedbacks play an important role in most, if
not all, multiple-state ecosystems. For example, submerged aquatic vegeta-
tion reduced turbidity and thereby nutrient recycling to the water column in
shallow lakes, creating conditions favorable for their persistence even under
moderately elevated nutrient loading; loss of rooted macrophytes yields a
new set of positive feedbacks that instead favor the dominance and per-
sistence of phytoplankton, even after nutrient loading has been reduced
(Scheffer et al., 2001). Stabilization of sediments by vegetation during severe

floods causes the divergence of desert streams into densely vegetated wet-lands and bare gravelbed channels that constitute alternative biogeomorphic states (Heffernan, 2008).

Similar types of biotic control are likely to be important drivers in self-organizing patterned landscapes (Rietkerk et al., 2004a) wherein multiple, locally stable states exist in a nonrandom spatial mosaic, but the emergence of such patterned landscapes occurs only when such local positive feedbacks are coupled to longer-range negative feedbacks that inhibit patch expansion (Rietkerk and van de Koppel, 2008). Indeed, the directionality, spatial ex-tent, and temporal characteristics (i.e., lags) of these distal negative feed-back mechanisms are crucial to controlling the emergent pattern, which in turn can provide insight into structuring mechanisms (Eppinga et al., 2008; Eppinga et al., 2009). For example, effects of vegetation on the geomor-phic processes of sediment entrainment and deposition create platforms and drainage networks in tidal marshes (Kirwan and Murray, 2007; van Hulzen et al., 2007), and bank stability that constrains braiding and affects fluvial landform in meandering rivers (Corenblit et al., 2009; Smith, 1976). Likewise, vegetation in arid areas can induce pattern formation in response to the local feedbacks between vegetation density and infiltration, and the distal feedbacks between infiltration hotspots and water limitation that generate interpatch impervious areas (HilleRisLambers et al., 2001; Rietkerk et al., 2002). Among the most important attributes of patterned landscapes is the possibility that patterned and unpatterned configurations of the landscape are themselves bistable at some range of environmental condition; that is, both configurations are resilient over some range of global bistability (see Reitkerk et al., 2004a). Catastrophic transitions between a patterned and unpatterned state, and the internal feedbacks that permit the unpatterned state to be stable, are critical to understand since they suggest that restora-tion of environmental drivers alone may be insufficient to restore desired conditions.

Despite the growing list of systems in which reciprocal biological control produces multiple stable states and development of self-organized landscape pattern, a general theory for predicting the circumstances in space and time under which such feedbacks are likely to be dominant, and thus to con-found restoration, is still developing (Suding et al., 2004). One emerging pattern in multiple state ecosystems and self-organized landscapes is the im-portance of strong interactions between biota and processes that structure landform (Francis et al., in press; Heffernan, 2008; Stallins, 2006). Indeed, all of the examples listed involve interactions between the action of vegetation and sediment transport or substrate morphology, though at widely varying temporal scales.

It is not yet known why biotic-geomorphic interactions are so common in patterned and alternative state systems. It may reflect the simplicity of po-tential interactions between biota and geomorphic processes and structures vis-à-vis more complex interactions between species; simpler interactions,

in turn, reduce the potential for short-circuiting of feedback loops that constrain system development. HilleRisLambers et al. (2001) and Didham et al. (2005) posited that alternative stable states are most likely in ecosystems where the biotic community is structured by harsh abiotic conditions rather than competitive interactions (but see Fukami and Lee, 2006). The underlying mechanism is that harsh environments permit competitive dominance of one taxa or functional group (i.e., trait underdispersion), allowing sufficient density thereof to exert action as an ecosystem engineer (Jones et al., 1994) facilitating its own growth via modifications to the microenvironment. Although this hypothesis is consistent with many examples from arid, tidal, dune, and wetland systems, harsh conditions appear neither sufficient nor necessary to effectively predict where biota can act as keystone drivers of hydrologic, edaphic, or geomorphic processes. Numerous adverse environments have not, to date, been described as containing alternative stable states. Moreover, Corenblit et al. (2008) pointed out that biotic feedback can be important even in mildly disturbed, competitively structured ecosystems; examples of self-reinforcing reciprocal actions of biota in such systems include construction of coral reefs, biodissolution in karst landforms, and bioturbation and stabilization of soils.

        If self-organization of ecosystems is facilitated by the unique action of ecosystem engineers present at high density, the converse is that such biotic effects are more likely to structure abiotic environments that exhibit relatively little variation or where processes and forces are small in magnitude (e.g., abiotic erosion resistance on steep hillslopes). As suggested by Heffernan (2008), the ratio of the magnitudes of abiotic and biotic forces (and resulting spatial and temporal variance) may determine the extent to which the density dependence of many biotic processes can exert significant influence on the underlying abiotic template; either large biotic effects or small abiotic variation (or both) may lead to conditions where organisms control landform. Thus, the disturbance-severity hypothesis of HilleRisLambers et al. (2001) and Didham et al. (2005) may describe one important but incomplete subset of the circumstances under which the effects of biota are magnified relative to external abiotic drivers.

        In this study, we address these issues by describing the unique density and variety of landscapes and processes characterized by strong biotic control of landscape patterns in the South Florida/Greater Everglades ecosystem. We hypothesized that reciprocal controls are particularly important in South Florida because biota can engineer meaningful changes in low-variance abiotic processes and characteristics (e.g., in elevation because the landscape is so flat or in nutrient concentration because, in part, phosphorus is so scarce), a contention that may be generalizable to other systems. We focus on three examples of reciprocal biotic control leading to landscape pattern, presented in order of how well understood the underlying processes are: (a) the patterned ridge-slough landscape of the central Everglades (Figure 1a)
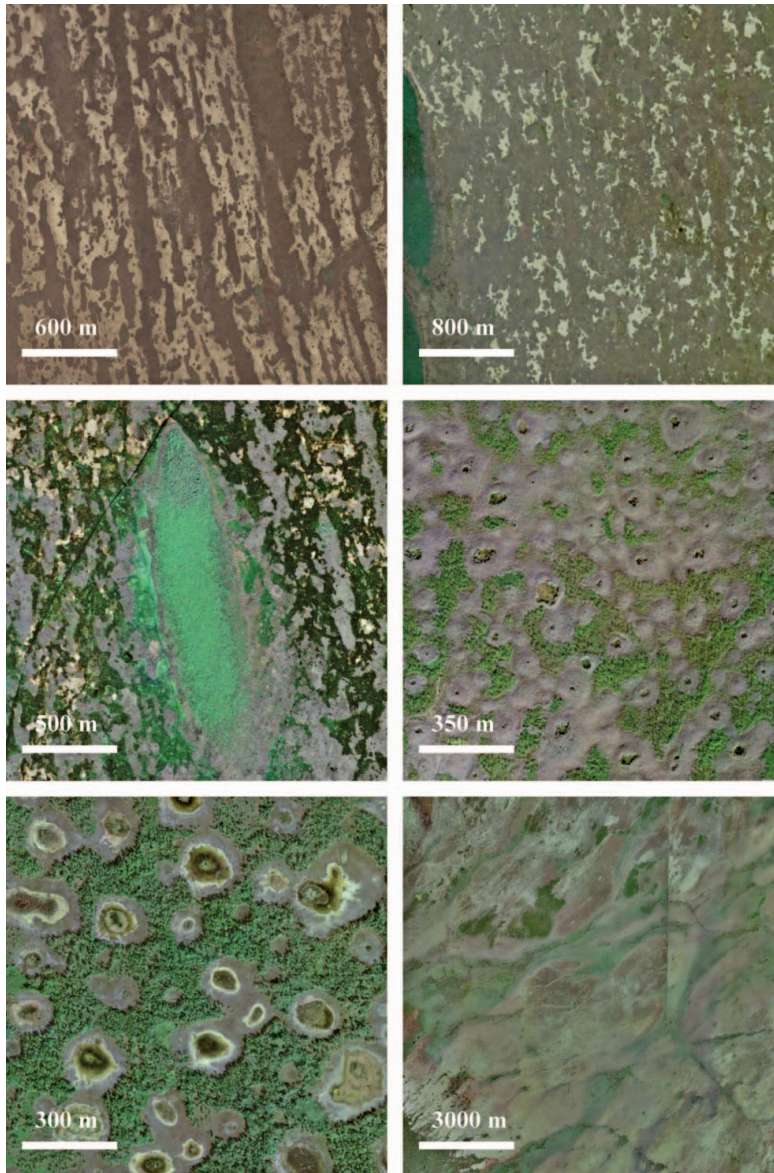
FIGURE 1. Aerial images of patterned landscapes in the Greater Everglades: (a) a relatively well conserved region of the ridge-slough mosaic in northern WCA-3A; (b) a degraded ridge-slough mosaic in WCA-3B, where flow has been dramatically reduced and water level variability virtually eliminated due to water management; (c) typical tree island morphology from southern WCA-3A with dense woody vegetation occupying a teardrop shaped island oriented with flow; (d) isolated cypress domes in central Big Cypress National Preserve (note radial pattern and the absence of trees from the center of most wetlands, possibly indicating excessive water depths); (e) isolated cypress domes in northern Big Cypress National Preserve (note the radial pattern, and the clear boundary zone of apparent marl formation); (f) karst drainage features in southern Big Cypress National Preserve, showing the pronounced biotic effects of hydrologic convergence to self-organizing channels, and the apparent dryness of interchannel areas. (This figure is available in color online).

and the dramatic loss of both vertical and horizontal variability with hydro-
logic modification (Figure 1b); (b) the biogeomorphic creation of tree islands
(Figure 1c) based on three-way feedbacks between vertical vegetative struc-
ture, faunal- and dry deposition-induced P enrichment, and elevated primary
productivity; and (c) the carbonate dissolution processes that create surface
water storage features in northern Big Cypress National Preserve (Figures 1d
and 1e) and J.W. Corbett Wildlife Management Area, and Karst drainage fea-
tures in Big Cypress National Preserve on the southwestern coast (Figure 1f).
The evidence suggests that coupled scale-dependent feedbacks emerging
principally from the action of local biotic processes are crucially impor-
tant to the creation and maintenance of patterns in these landscapes, and
that such feedbacks (and scales and thresholds implied therein) should be
more explicitly integrated into ecological conceptual models that guide their
restoration.

BIOTIC CONTROLS ON RELIEF, HYDROPERIOD, AND DISCHARGE IN THE RIDGE-SLOUGH MOSAIC

Background

One of the most characteristic features of the central Everglades is the pat-
terned ridge and slough landscape mosaic. The landscape comprises two
relatively distinct, evenly abundant patch types: sawgrass ridges (dominated
almost completely by *Cladium jamaicense*) and sloughs (ranging from deep-
water habitats dominated by submerged and floating leaved aquatic plants
to prairies with emergent graminoid taxa), with tree islands comprising a
third type or state (discussed in the next section), lower in prevalence but
functionally and biologically important. Ridges and sloughs are distinctly
nonrandom in their arrangement (Figure 1a), exhibiting pronounced elon-
gation in the direction of flow, with patch widths constrained to 50–250 m,
at least where the historical landscape is relatively well-conserved (Science
Coordination Team, 2003), specifically in northern Water Conservation Area
(WCA) 3A-S.

This patterned landscape appears to be structured by processes that
are independent of vertical variability in the underlying limestone. Several
studies have confirmed two key facts: (a) peat surface and limestone eleva-
tions are uncorrelated, except under tree islands where limestone pinnacles
may be important nucleation sites, and (b) the elevations of the underlying
carbonate material have low variability (Givnish et al., 2007; Science Coor-
dination Team, 2003). As such, the differential elevation of the peat surface
between higher ridges and lower sloughs is ascribed to autogenic processes
that regulate the balance of organic matter inputs from primary production
and mineralization due principally to microbial oxidation (Givnish et al.,
2007; Larsen et al., 2007; Science Coordination Team, 2003; Watts et al.,

2010). Contemporary elevation differences in regions of the Everglades with the least impacted hydrologic conditions (specifically, central WCA-3A) are between 25 and 30 cm (Watts et al., 2010). The magnitude of historic elevation differences between ridges and sloughs is speculated to be as large as 60–90 cm (Science Conservation Team, 2003), although a lack of systematic sampling before recent hydrologic modification makes this quantity difficult to ascertain with any certainty.

Local Positive Feedbacks and Peat Elevation Differentiation

It is widely presumed that the two ecosystem states (ridge and slough) are alternative pathways to achieve the same long-term landscape peat accretion rate (approximately 1–6 mm yr^{-1} in unenriched Everglades; Berhardt and Willard, 2009). Regime shifts between patterned and unpatterned states have been described in response to nutrient enrichment (Hagerthey et al., 2008), and in response to hydrologic modification (Watts et al., 2010; Wu et al., 2006). Our conceptual model of the historical system has, at its center, a homeostatic feedback between soil accretion, hydroperiod, and soil redox; increased soil accretion shortens hydroperiod and increases soil redox potential, in turn inhibiting soil accretion via accelerated respiration (Figure 2);

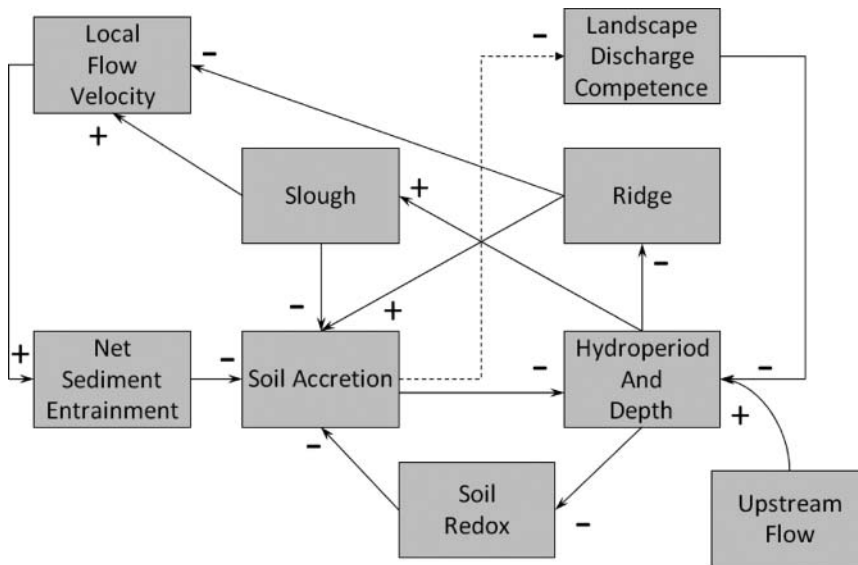**FIGURE 2.** Influence diagram describing the major interactions leading to local positive feedbacks (autocatalysis) and distal negative feedbacks (inhibition) in the ridge-slough mosaic. The dashed line indicates the mode of action in the self-organizing canal hypothesis; note that this mechanism is implicitly anisotropic, with the feedback strength higher when soil accretion occurs orthogonal to flow.

this feedback mechanism is similar to models describing boreal peatland development (Belyea and Clymo, 2001; Clymo, 1984). There are, however, two ecological configurations at which peat accretion rates (production minus respiration) are the same; these alternative equilibria are ridges and sloughs, and they are created by self-reinforcing (i.e., autocatalytic) effects of vegetation on soil accretion and thus elevation (Figure 2). In short, ridges are dominated by sawgrass (*Cladium jamaicense*), which is 2–3 times more productive than vegetation characteristic of adjacent sloughs (Daoust and Childers, 1999; Ewe et al., 2006) and also has higher lignin content, indicating lower mineralization potential (Lewis, 2005). The resulting higher peat accretion potential produces increases in elevation that favors further sawgrass growth (Childers et al., 2006). Conversely, reduced productivity and higher lability of slough vegetation limits soil accretion rates leading to longer hydroperiods and conditions that favor the same deepwater species. The hypothesis that these are distinct stable configurations, and that intermediate peat elevations between the two states are unstable, is strongly supported by histograms of peat elevation in areas considered minimally impacted (northern and central WCA-3A South), which exhibit marked bimodality (Watts et al., 2010).

Positive feedbacks between vegetation and peat production (and therefore elevation) are ultimately inhibited by the homeostatic feedbacks previously described between elevation, hydroperiod, soil redox potential, and peat decomposition (Figure 2). In short, higher peat accretion potential in ridges is ultimately offset by increased peat exposure caused by being situated higher in the water column. As ridge elevation increases, hydroperiod decreases (ca. 310 days in the best conserved areas; see Givnish et al., 2007 for longer estimates), exposing peat in ridges to longer and more frequent periods of aerobic oxidation (i.e., elevated soil redox in Figure 2). Sloughs in contrast are rarely exposed (ca. 350+ day hydroperiod), at least where hydrologic conditions are thought to best approximate pre-drainage conditions (Givnish et al., 2007; Watts et al., 2010). The balance of these positive and negative feedbacks produces two alternative attractors (high productivity–high respiration and low productivity–low respiration; Figure 2) whose similar net peat accretion explains the extended stability (>1000 years; Bernhardt and Willard, 2009) of landscape patch configuration.

Hydrologic modification of the Everglades has resulted in dramatic changes in hydroperiod (Figure 1b; S.M. Davis et al., 1994). In many areas of the historic ridge-slough landscape, the local patterning is exhibiting signs of adjusting to these new conditions (Wu et al., 1997; Wu et al., 2006; Watts et al., 2010). These changes suggest that the key feedbacks (among soil accretion, hydroperiod/water depth, and vegetation) that maintained approximate equivalence of the two states have been overwhelmed by exogenous change, with the associated loss of vertical relief. Importantly, the loss of landscape bimodality occurs in both directions of hydrologic modification; that is, both drier and wetter conditions interrupt the mechanisms

that maintain clustering of peat surface elevations (Watts et al., 2010) and patterning of vegetation communities (Wu et al., 2006). Quantitative prescription of the hydrologic thresholds at which these structuring feedbacks are lost is crucial to successful restoration.

Distal Negative Feedbacks and Landscape Pattern Formation

While there is broad consensus (though still limited confirmatory evidence) about the mechanisms that lead to alternative peat accretion equilibria at a particular location, the mechanisms that produce the patterning of these patches on the landscape are less clear. The two key features to be explained are the linear orientation of ridges and sloughs parallel to prevailing regional flow patterns (generally south in WCA-3A and southwest in Everglades National Park) and the characteristic 50–250 m wavelength of these features orthogonal to flow; additional clear and persistent features of the best-conserved landscape pattern (highly fractal patch geometry, apparent power law distribution of patch sizes) will also ultimately require mechanistic explanations.

Patterns of spatial autocorrelation in soil elevations support the hypothesis that spatial patterning in the Everglades ridge and slough is driven by the spatial coupling of positive local and negative distal feedbacks (Watts et al., 2010). Specifically, statistically significant negative autocorrelations were observed at distances of 50–150 m in comparatively unimpacted regions when evaluated orthogonal to regional flow, and was absent in hydrologically modified sites. This observation is not predicted by simple geostatistical models (Goovaerts, 1997) but is consistent with distal negative feedbacks thought to produce self-organized landscape pattern (Eppinga et al., 2008; Rietkerk and van de Koppel, 2008). However, these patterns do not discriminate among the several candidate mechanisms that might explain how flow (the putative agent of anisotropy) induces patch linearity (Larsen et al., 2007).

The most frequently invoked mechanism of pattern formation in the Everglades ridge and slough is the action of sediment entrainment and deposition and the biotic controls thereon; numerous authors (Larsen et al., 2007; Larsen et al., 2009a, b; Leonard et al., 2006; National Research Council, 2003; Science Coordination Team, 2003) posited that slough water velocities are enhanced due to reduced flow friction to preferentially entrain organic floc particles slowly removing material, while reduced flow velocities and the baffling effect of emergent stems in ridges induce preferential deposition. Analogies to anastomosing rivers (Larsen et al., 2007) wherein episodic sediment redistribution occurs in response to peak flows, have built on and prompted several studies of extant hydraulics (Harvey et al., 2005; Harvey et al., 2009; Ho et al., 2009), sediment properties (critical entrainment velocities, Larsen et al., 2009a; and nutrient content, Noe et al., 2007), and suspended sediment entrainment and transport (Saiers et al., 2003, Huang

et al., 2005, Larsen et al., 2009b). Here we attempt to synthesize the concordance of these findings with the dynamics necessary to produce and maintain ridge-slough patterning via sediment redistribution.

Best estimates of the entrainment velocity of slough material (principally flocculent detritus) range from 4 cm s^{-1} (Larsen et al., 2009a) to 7 cm s^{-1} (Bazante et al., 2006). These are generally higher than observed velocities even in areas where the ridge-slough mosaic is best conserved, though passage of Hurricane Wilma induced higher velocities (max. = 5 cm s^{-1}) orthogonal to north-south orientation for a short period of time (Harvey et al., 2009). Typical velocities in the best conserved ridge-slough landscape in central WCA-3A range from 0.3 to 0.8 cm s^{-1} (Harvey et al., 2009); values elsewhere vary widely, in the range of 0.5–1.5 cm s^{-1} in southern Everglades National Park (Riscassi and Schaffranek, 2004) and 0.2–0.8 cm s^{-1} in northern ENP (Leonard et al., 2006). Values at the heads of tree islands, where water is routed around an emergent peat formation, have been measured between 0.9 and 1.4 cm s^{-1} (Bazante et al., 2006). In short, the contemporary Everglades hydrology does not support the redistribution of floc material via entrainment to any appreciable extent. Proposals to create episodic pulses of water through upstream flow control structures to achieve desired velocities (Harvey et al., 2009; Larsen et al., 2009b) may provide additional insight into the plausibility of this mechanism for reversing slough infilling, but run the risk of reducing landscape inundation depths at other times of the year (and thereby hydroperiod) if more water at the upstream boundary is not also made available. Moreover, contemporary patterns of velocity (highest in ENP and lowest in northern WCA-3A) are not consistent with where the best preserved ridge-slough mosaic is observed (in northern WCA-3A-S).

Equally vexing to the sediment redistribution hypothesis is the observation of relatively subtle differences in velocities between ridges and sloughs (e.g., 0.51 in ridges vs. 0.74 cm s^{-1} in sloughs; Leonard et al., 2006). Harvey et al. (2009) refined this by demonstrating that differences in velocity are negligible at shallow depths (ca. 30 cm in sloughs) and peak at 0.3 cm s^{-1} when slough water depths are over 70 cm. Modest differences in velocity may reflect similar frictional effects of dense emergent stems in ridges and appreciable biovolume of submerged aquatic vegetation in sloughs. Whether observed velocity differences are sufficient to permit preferential entrainment in sloughs while simultaneously allowing preferential deposition in ridges remains unclear, but observed noise in the observations of critical entrainment velocities would generally suggest that these differences are far too small to induce such clear landscape differentiation. Moreover, Larsen et al. (2009) reported an impact of simulated stems on organic floc entrainment that is counter to the general expectations of the conceptual model, with higher concentrations of floc entrained at typical Everglades velocities when stems are present. Huang et al. (2005) examined transport, dispersion, and capture of small (1 μm) synthetic particles and report both markedly increased

particle capture efficiencies and markedly lower dispersion in a site dominated by wet prairie species (*Eleocharis* spp.) than in a site dominated by *C. jamaicense*. In short, the distal negative feedbacks induced by differential entrainment and deposition in ridges vis-à-vis sloughs appear to be comparatively weak, at least under contemporary hydrologic conditions.

One way to assess the plausibility of this sediment redistribution mechanism for landscape pattern formation is to back-cast estimates of specific discharge (i.e., m^3 of flow per m of cross-sectional width per second) prior to contemporary modification using the two most important assumptions about the historical Everglades landscape (elevation differences of 60–90 cm; Science Coordination Team, 2003; and flow velocities markedly higher than today, Harvey et al., 2009). That is, are the estimated historical water inputs at the upstream boundary of the Everglades sufficient to maintain specific discharge values that are implied by these two attributes of the landscape? To bound the range of plausible upstream boundary conditions, we note that Sklar et al. (2005) reported a 55% decline in discharge to the Gulf of Mexico via Shark Slough between model-predicted contemporary (871×10^6 m^3 yr^{-1}) and historical (1932×10^6 m^3 yr^{-1}) conditions.

Contemporary discharge velocities (0.3 and 0.5 cm s^{-1} in ridges and sloughs, respectively) and landscape elevation differences in northern WCA-3A (ca. 30 cm) yield a modern specific discharge of 0.0015 m^3 m^{-1} s^{-1} (133 m^3 m^{-1} d^{-1}, roughly concordant with the estimate of 115 m^3 m^{-1} d^{-1} mean discharge for ridge and slough in Harvey et al., 2009). Assuming no increase in median ridge water depth (necessary to maintain peat accretion processes), and using historical average velocities of 1.5 and 3.0 cm s^{-1} in ridges and sloughs, respectively, and an elevation difference of 60 cm, the specific discharge increases 0.0144 m^3/m/s (1246 m^3 m^{-1} s^{-1}), an increase in total water flux of 930%. Assuming that rainfall represents over 80% of the historical water inputs to the Everglades (Davis et al., 1994) and can, along with ET, reasonably be presumed to have remained largely unchanged, specific discharge due to upstream boundary inputs of water (presently ca. 0.0003 m^3 m^{-1} s^{-1}) would have to increase 42-fold (to 0.0132 m^3 m^{-1} s^{-1}) to achieve the predicted flux rate. Such a large difference between present and historical inputs seems implausible, though we reiterate that this analysis considers sustained higher velocity, and does not therefore evaluate the plausibility of pulsed water release. We note that to achieve short-term velocity conditions that achieve any sediment redistribution appears to require water slopes approximately double bed slopes (Larsen et al., 2009b), a condition that would only historically occur under very specific weather events that deliver rainfall only to the upper part of the catchment.

Notably, relaxing only the assumption regarding historical flow velocities (i.e., assuming that present conditions in the best conserved part of the ridge-slough landscape are sufficient) yields a specific discharge of 0.0024 m^3 m^{-1} s^{-1}, which would still require boundary inputs to increase 25-fold.

Given the finite quantity of water available, we propose that both assumptions (about historic differences in velocity and elevation between ridges and sloughs) require considerable additional scrutiny given their central importance in restoration planning.

The capacity of floc entrainment and redistribution to maintain vertical differentiation and therefore patterning is further challenged by the characteristics of the material being entrained. Floc is generally highly labile, with the finer particles (0.45–2.7 μm) that are most easily entrained (Larsen et al., 2009) also being most bioavailable, typically consisting of microbes and little refractory material (Noe et al., 2007). Cohen et al. (2010) observed microbial mineralization rates of floc material under controlled conditions that were nearly 2 orders of magnitude more rapid than the underlying peat, severely challenging the plausibility that floc material can meaningfully contribute refractory mass to accelerate accretion, even with dramatically elevated rates of deposition on ridges vis-à-vis contemporary observations. A more plausible mechanism for the action of entrainment and deposition on peat accretion is via the stimulatory action of P transport in a severely P limited ecosystem (Noe et al., 2001); Noe et al. (2007) noted that a large fraction (ca. 43%) of the total water column P transport is as particulates. Moreover, Cohen et al. (2009) observed strongly significant negative associations between soil elevation and surface peat total P concentrations in areas where peat bimodality has been maintained. That is, patterns of soil P concentrations appears to be spatially structured (ca. 100–150 mg/kg higher in ridges than sloughs) in areas where the maintenance processes are best conserved, whereas the mechanisms that create and maintain this spatial pattern are substantially interrupted elsewhere. While the mechanism for this differential P enrichment is unknown, preferential deposition of P-rich labile floc is one plausible hypothesis. The effect of this enrichment on productivity is unknown, but could enhance the peat production feedbacks that maintain ridge elevations.

Whether flow-driven nutrient redistribution could account for observed ridge-slough patterning remains less clear. In the absence of landscape relief, a nutrient redistribution mechanism based on evaporative concentration creates radial patterning in northern peatlands; the addition of landscape gradients (i.e., anisotropy in the distal negative feedbacks) creates linear hummocks and hollows, but oriented perpendicular, not parallel, to flow (Eppinga et al., 2008; Rietkerk et al., 2004b). The distal feedback mechanism to create nutrient redistribution is different in the Everglades, where extended inundation limits the potential for evapoconcentration processes, at least in the long hydroperiod marshes. In arid landscapes, nutrient redistribution via overland flow produces banded vegetation patterns oriented parallel to topographic contours and perpendicular to overland flow patterns (Ludwig et al., 1999); redistribution of limiting materials (nutrients in peatlands, water in arid landscapes) requires an upstream source area and downstream sink area, which explains why patterns run perpendicular to the direction

of advection. Thus, evidence from several systems suggests that nutrient redistribution produces patterning that is orthogonal to that observed in the Everglades ridge and slough; further explication is needed to determine if longitudinal patch expansion in response to nutrient redistribution emerges from the special case in the Everglades where P transport is principally as particles rather than solutes (Noe et al., 2007).

The persistence of ridge-slough pattern in areas with contemporary flow velocities too low to support sediment redistribution, and the implausibility of peat accretion due to floc deposition, suggest the need for alternative hypothesis describing anisotropic distal negative feedback, but such mechanisms have not been well developed. In the Everglades, the feedback mechanism must act to preferentially constrain lateral ridge expansion, and permit longitudinal expansion; that is, the magnitude of the negative feedback is stronger orthogonal to flow that parallel to flow, as shown by the red arrow in Figure 4 (process D). Here we consider an alternative, which we term the *self-organizing canal hypothesis*, based on the action of lateral patch expansion on landscape discharge competence (Figure 3).

To start, we consider a landscape without flow and with a fixed quantity of surface water. We note that in such a landscape the autocatalytic growth of ridges (process A in Figure 4) implies hydraulic displacement wherein lateral or vertical expansion deepens water elsewhere (process B in Figure 4), making distal sites increasingly unsuitable for ridges (process C in Figure 4) and thereby more favorable for sloughs. This process would be slow because it is based on peat accretion, but would ultimately result in a prevalence of the two stable state patch types governed by the nominal amount of water present on the landscape (more water, more sloughs). In a landscape without a natural hydrologic gradient (and therefore a prevailing orientation to flow), this distal negative feedback on ridge expansion would produce an isotropic (i.e., round or at least nondirectional) landscape pattern; in the Everglades, where there is a strong north-south geologically imposed flow gradient, ridge expansion perpendicular to flow creates stronger hydrologic impacts (via effects on landscape specific discharge competence, described subsequently) than ridge expansion parallel to flow. This anisotropy in the distal negative feedback mechanism may be sufficient to explain the pronounced flow orientation of the patches.

The sediment redistribution hypothesis, discussed previously, posits implicitly that the anisotropic distal negative feedback occurs as sloughs contract, increasing local velocities to compensate for reduced landscape cross-sectional area, and leading to increased sediment entrainment and ultimately wider channels. We invoke a similar argument for the action of patch expansion of regional hydrology. Specifically, our proposed alternative mechanism follows from biotic control over landscape discharge competence (Figure 3), measured as specific discharge, or discharge per unit width of cross-section. Harvey et al. (2009) reported that, despite occupying roughly half the
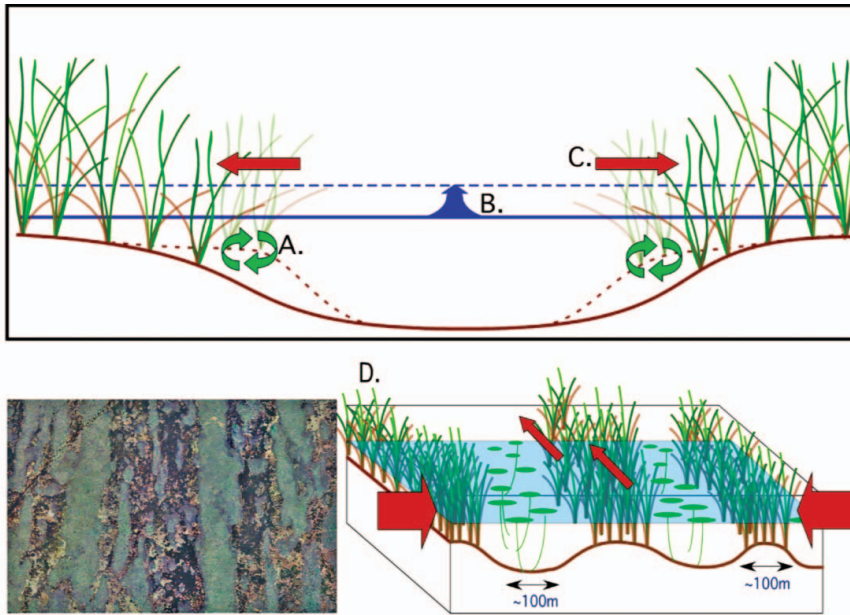
FIGURE 3. Conceptual diagram of feedbacks to the self organizing canal hypothesis for flow orientation of the ridge-slough landscape. (a) Local scale positive feedbacks: Sawgrass expansion into sloughs is catalyzed by internal feedbacks between peat accretion, hydroperiod and productivity; the reverse process can also occur, with sloughs representing an alternative stable state. (b) Distal negative feedbacks (without regional flow) are the prevalance of ridges and sloughs is controlled at the landscape level by the action water displacement, leading to changes in water depth and hydroperiod. (c) The altered hydrologic regime due to ridge expansion lowers habitat suitability for sawgrass in marginal areas (i.e., ridge edges), causing ridge contraction. For a fixed water volume across the landscape, an equilibrium prevalence of ridges and sloughs arises from interactions between the differential storage of water in ridges and sloughs and their particular hydrologic optima. (d) Landscape self-organization with regional flow: The requirements that landscape have competence to allow passage of water from north to south induces anisotropic distal feedbacks (indicated by the size of red arrows), where the negative feedback to the lateral expansion of ridges is large (because lateral expansion alters discharge competence), and the negative feedback on longitudinal expansion of ridges (i.e., parallel to water flow) is low. This anisotropic distal negative feedback is potentially sufficient to explain the linear pattern without sediment redistribution. (This figure is available in color online).

landscape area, the vast majority (86%) of water flux occurs through sloughs due to their greater depth (ca. 30 cm deeper), and modestly higher flow velocity vis-à-vis ridges. Higher discharge competence in sloughs suggests that even a modest lateral expansion of ridges would reduce the landscape discharge competence dramatically because of large differences between ridges and sloughs in specific discharge.

In order for the landscape to compensate for reduced discharge competence associated with ridge expansion given a fixed upstream volumetric
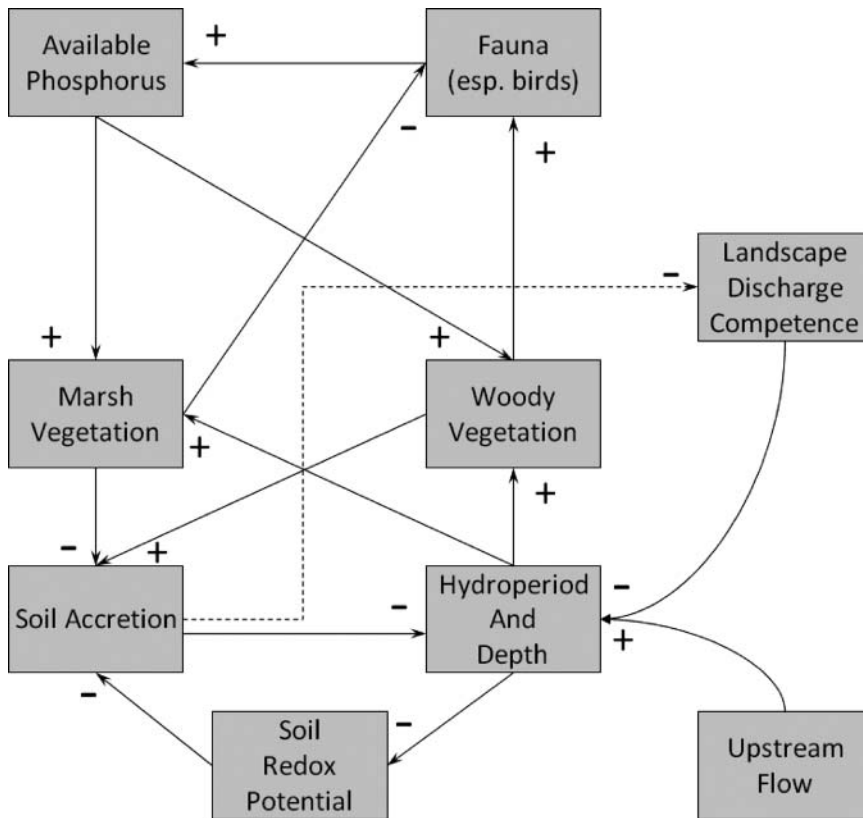
FIGURE 4. Influence diagram depicting the major interactions that lead to the self-organized tree island pattern. Notably, the core negative feedbacks are the same as for the ridge-slough, but the addition of faunal P enrichment creates a third alternative stable state in the ridge-slough scheme (i.e., ridges and sloughs and embedded in marsh vegetation). Two distal negative feedbacks constrain tree island expansion; the first is due to the water impoundment effects associated with tree island morphology, and the second is due to the hyperconcentration of phosphorus to tree islands from surrounding marshes, starving the source landscape of P that maintains the secondary productivity (e.g., fish, amphibians) that draw the avifauna to them.

input, water depths and flow velocities would have to increase. Steady-state solutions for water depth and velocity based on Manning's equation reveal more biologically relevant changes in depth than in velocity with increasing specific discharge. As water depths increase, deeper sites become increasingly unfavorable to sawgrass, producing a distal negative feedback loop that would inhibit expansion of sawgrass at the landscape scale by forcing the deepest ridge sites out of the range of sawgrass persistence. Conversely, the lateral expansion of sloughs (and contraction of ridges) dramatically increases discharge competence, permitting hydrologic conveyance through the landscape at lower nominal water depths, thereby reducing site suitability for sloughs. It is relevant to reiterate that the effect of ridge expansion on

water levels would be anisotropic: ridge expansion parallel to flow would have a minimal impounding effect (i.e., mostly due to the action of displacing water) whereas lateral expansion would constrain the passage of water much more directly, creating incremental impoundment that is disfavorable for ridge persistence at lower elevation sites. This self-organizing canal mechanism would, over long periods, calibrate landscape patch prevalence, linearity, and connectivity for particular climatic conditions, and could produce the observed landscape pattern even in the absence of sediment- or nutrient-redistribution mechanisms. In short, sloughs self-organize to behave in much the same way that manmade canals do, with biota constantly exerting reciprocal adjustments to their area that maintain a long-term equilibrium water level at landscape scale. Van Hulzen et al. (2007) reported a similar phenomenon in coastal marsh self-organization, wherein drainage competence from a tidal platform is inhibited by the presence of *Spartina anglica*, and enhanced in locations where that vegetation has been removed. We also note that this is a weak distal feedback—it operates at the landscape scale, not on each patch individually; this could explain the persistence of highly fractal patch edges, evident even in 1941 aerial imagery.

The long time scales of landscape evolution in the ridge and slough peatland complicate evaluation of alternative mechanisms for their maintenance; moreover, the mechanisms underlying the two hypotheses are sufficiently similar (both having to do with flow) that predictions that reliably distinguish between them are challenging. Support for the self-organizing canal hypothesis could come from three lines of evidence. The first is inference by elimination; that is, available evidence acting counterfactual to other hypotheses. For example, we assert that the finite quantity of water delivery from rainfall and upstream sources constrains landscape specific discharge to values within a factor of 2–3 of contemporary values. That these discharge quantities are insufficient to maintain either 60–90 cm ridge-slough elevation differences or greatly elevated water velocities suggests that some other assemblage of feedbacks is worth exploring. Similarly, in the region of the central Everglades (northern and central WCA-3A) that represents the best conserved ridge-slough mosaic, strong bimodality has persisted through 60 years of regional water flow modification (Watts et al., 2010) that have clearly would have interrupted sediment entrainment and deposition processes. Future inverse inference will be made possible by evaluating landscape responses to hydrologic changes associated with restoration activities. Activities that increase discharge but not velocity, or conversely that increase velocity in pulses but leave annual specific discharge unchanged, and fail to engender early signs of patterned landscape response (e.g., bimodality and spatial structure, Watts et al., 2010) would provide evidence for the dominant mechanisms underlying pattern. We note in particular that the raising of Tamiami Trail, which would alter hydroperiods in both southern WCA-3A and northern ENP, would be restorative if the landscape

discharge hypothesis operates, and not if patterning requires sediment redistribution.

A second, more direct set of predictions that emerge from the self-organizing canal hypothesis have to do with landscape patch shapes and longitudinal connectivity. First, longitudinal connectivity of sloughs should be continuous; the longitudinal connectivity of ridges is largely irrelevant, but if water cannot easily percolate from upstream to downstream though a relatively constant cross-section of sloughs, impoundment would result. As such, longitudinal connectivity should be strong, and cross-sectional area (i.e., orthogonal to flow) constant, in the best conserved regions of the Everglades. Further, landscape connectivity of sloughs should respond predictably to both natural and anthropogenic hydrologic gradients (i.e., by increasing in response to extended inundation and decreasing in response to flow reductions). Second, sediment redistribution that accelerates peat accretion at ridge edges due to a subsidy of material entrained in sloughs should leave a clear chemical signal. For example, calcite present in abundance in slough floc would be higher in ridge edges than ridge centers, as would total P. Preliminary evidence (D. Watts, unpublished data) found no evidence to support this prediction, but further examination is warranted. Finally, where velocities are consistently below the critical floc entrainment threshold, patches should rapidly lose their anisotropy if sediment redistribution dominates. The remarkable persistence of linearity in WCA-3A-N (Wu et al., 2006) despite the near total loss of landscape bi-modality (Watts et al., 2010) offer some tentative evidence to the contrary.

A third line of evidence that may eventually be testable has to do with differences between the two hypotheses in how patches form, and regarding the carbon balance that ought to be observed for each. During incipient landscape formation, the self-organizing canal hypothesis would predict first radial expansion of ridges, and only when the cross-sectional area of the landscape begins to impound water would linearity ensue. Detailed palynological or soil chemical analyses would be necessary to distinguish ridge and slough peat layers, but the specific discharge competence hypothesis would predict that lateral expansion of ridges would predate longitudinal expansion. Larsen et al. (2008) used a cellular automata model of the sediment redistribution hypothesis in which longitudinal expansion predates lateral expansion. Since both ridge and sloughs are thought to be stable components within a peat-accreting landscape, both must achieve the same nominal rates of landscape accretion. That is, the net production (production minus respiration) must be equal for both to ensure their stability. The sediment transport hypothesis predicts that, at least under historical hydrologic conditions, elevated respiration in ridges is compensated for by the deposition of material entrained in sloughs. As such, it makes the implicit prediction that, where sediment redistributive processes have been interrupted, ridges should exhibit markedly lower net ecosystem production than sloughs.

Ongoing measurements of net carbon fluxes in ridge and slough sites spanning a hydrologic gradient from drained to impounded, and including the regions of the Everglades where the ridge-slough mosaic is best conserved, will provide a test of this prediction (D. Watts, unpublished data).

Discriminating between these two hypotheses for explaining ridge-slough linearity is important because water management actions to reinforce each would be substantially different. For example, discharge management based on sediment redistribution might focus on creating episodic pulses that allows temporary high flow velocities, but at the possible expense of landscape median depths and thus hydroperiods, affecting the local conditions that permit bistability in peat accretion rates. Similarly, water management based on ensuring water fluxes that are twofold larger than contemporary conditions and that are constant between seasons (as reported for the historical system by Sklar et al., 2005) may be at odds with creating high velocity excursions. Regardless of which hypotheses holds true, and considering the possibility that both act simultaneously, the most important implication of thresholds in self-organized feedbacks are potential time lags and unexpected trajectories in restoration efforts, and thus the urgent need for large scale experiments.

Biotic Controls on Patch Size

Another area that requires some investigation is why the ridge and slough patches are the characteristic size that they are. There are few explicit hypotheses that we are aware of. Neither distal negative feedback to constrain patch expansion (i.e., sediment redistribution or self-organized canals) explicitly evokes a characteristic geometric scale, focusing more on the linearity emerging as a consequence of anisotropic feedback action. We note that the sediment redistribution hypothesis may imply a certain patch size based on the transport distances associated with predominant floc particles, but the specifics of this have yet to be explored.

Patch sizes in other self-organizing landscapes vary dramatically (Rietkerk and van de Koppel, 2008), though there appears to be some concordance between the size of the ecosystem engineer (ranging from mussels to trees) and the size of the patches. We infer that another plausible mechanism that controls the area of ridge patches is due to the size of a single *C. jamaicense* individual, which may span 10 m or more. Sawgrass disperses almost exclusively via vegetative propagation, which further constrains the size of patches because the likelihood of a new patch arising via seed dispersal is low. Moreover, if ridge patch sizes are controlled by physiological attributes of sawgrass, no additional mechanism would be necessary to control the patch size of sloughs because of complementarity between the two patch types. We note that ridges occur as islands within a matrix of sloughs in the most well conserved areas of the Everglades (Figure 1a), suggesting that the

mechanisms controlling characteristic ridge patch size and geometry create approximately equal patch size and geometry in sloughs.

BIOTIC CONTROLS OF NUTRIENT GRADIENTS, RELIEF, AND DISCHARGE ON TREE ISLANDS

Background

The Everglades is a severely P-limited system (Noe et al., 2001), due to the convergence of three primary factors: high geochemical affinity for P, high microbial and primary productivity, and low historical levels of exogenous inputs (Noe et al., 2001). Several important aspects of the Everglades ecology is driven by these exogenous controls on nutrient availability, and set the stage for dramatic effects of processes that concentrate P, whether they be exogenous (due to contamination from fertilizers used in agricultural production) or endogenous (controlled by local biotic concentration mechanisms).

The effects of P enrichment due to exogenous anthropogenic loading are exceedingly well documented in the Everglades (Craft and Richardson, 1993; Dong et al., 2002; Hagerthey et al., 2008; McCormick et al., 2009; McCormick et al., 1996; White and Reddy, 2003). Those affects include the interruption of ecological feedbacks that previously maintained areas such as northern WCA-2A and the perimeter of WCA-1 as ridge-slough mosaics (Childers et al., 2003). The most dramatic change is the expansion of monotypic stands of cattails (*Typha domingensis*), through a suite of changes along the gradient of enrichment (Hagerthey et al., 2008). For a frame of reference, it is worth noting that historical P concentrations in the peat soils of the Greater Everglades generally were between 200 and 500 mg/kg (McCormick et al., 2009); indeed, a P concentration of 500 mg/kg is frequently asserted as a useful diagnostic indicator of unnatural enrichment (Sklar et al., 2005). P concentrations along the nutrient enrichment gradient in northern WCA-2A, in contrast, can be as high as 1,500 mg/kg. As such, the evidence of artificial enrichment is clear, making the expansion of the P-enriched zone in that region a subject of considerable management interest.

Massive P enrichment gradients P have also been observed at a smaller scale in the interior and periphery of tree islands. Wetzel et al. (2009) demonstrated conclusively that (a) P enrichment is strongly a function of island height, suggestive of a biotic feedback mechanism; and (b) the magnitude of enrichment, though highly localized, is the same as what is observed in WCA-2A, with P concentrations as high as 1,600 (±350) mg/kg in some islands. Moreover, there is evidence to suggest that the highly elevated levels of P in tree island peat soils radiates outwards from the tree island into the adjacent ridges, supporting a flora that is typical of nutrient rich conditions (*Typha* spp., *Pontedaria cordata*; Givnish et al., 2007).

Mechanisms of P Enrichment

The magnitude and extent of elevated P concentrations indicates a local enrichment mechanism, possibly induced by the action of biota (Figure 5), and several have been proposed; Wetzel et al. (2005) offered the most compelling synthesis of the four main mechanisms proposed. The first is that P-rich groundwater inputs emanate to the surface via limestone pinnacles (Bevier and Krupa, 2001; Wetzel et al., 2005); this strictly endogenous mechanism is plausible, though the hydraulics would presumably be confounded by low permeability subsurface layers (Harvey et al., 2000). Moreover, tree islands appear to be distributed across the landscape in a distinctly nonrandom way (i.e., they appear more evenly dispersed than would be expected by chance or by the arrangement of groundwater conduits) suggesting at least some biotic control over whether a tree island develops around a particular groundwater discharge site. Moreover, tree islands coalesce around nucleation sites (e.g., peat popups, or even some ridges; Givnish et al., 2007)
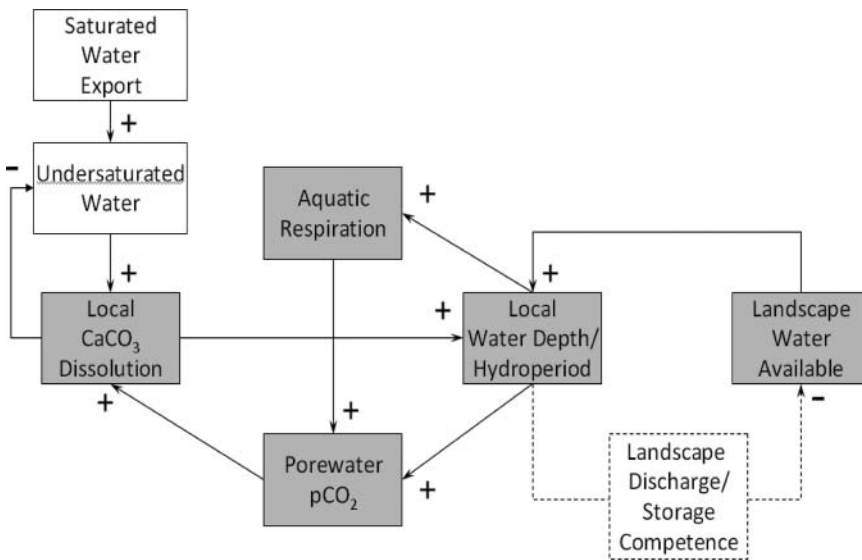
FIGURE 5. Influence diagram depicting the major interactions driving the dissolution of cypress dome basin forms in Big Cypress National Preserve. The core positive feedback is between water depth and the partial pressure of CO_2 (enhanced by aquatic respiration) driving the dissolution of $CaCO_3$. The continual export of saturated water and replacement by undersaturated water (white boxes) is necessary to permit basin formation. The distal negative feedback that constrains expansion is due to the preferential allocation of finite water available across the landscape to dissolution basins. The action of this distal feedback is isotropic in some areas of the Preserve (where round landscape features emerge; Figure 1d and 1e) and anisotropic in others (where flow induces directionality and the emergence of a karst drainage network; Figure 1f).

that would not be subject to elevated groundwater interaction (Wetzel et al., 2005).

A second proposed mechanism follows from predicted differences in productivity between tree islands and adjacent ridges; the associated differences in transpiration, amplified by the effects of tree-island soil specific yield, would drive subsurface hydraulic gradients toward tree islands, focusing P there via evapoconcentration (Ross et al., 2006; Wetzel et al., 2005). This mechanism, which has been demonstrated in the islands of the Okavango Delta for the translocation of salts (Ramberg and Wolski, 2008), is plausible if hydraulic conductivities are comparatively high (as they are in the mineral sediments of Okavango), and if islands are exposed for a significant fraction of the year, forcing water to be routed via subsurface flowpaths. Givnish et al. (2007) pointed out that while this mechanism is conceptually plausible, it is not supported by local measures of peat hydraulic conductivity (0.01–10 m day^{-1}; Harvey et al., 2000), where models require conductivities of 1000 m day^{-1} (Ross et al., 2006). Given that peat accretion occurs due to prolonged seasonal saturation, and the comparatively low observed hydraulic conductivity values, demonstration of the primacy of this mechanism requires additional measurements of pore water concentrations of conservative tracers (e.g., chloride) that would presumably be similarly enriched via evapoconcentration.

The third possible mechanism explaining the dramatic local P gradients derives from the interaction between the vertical structure that exists on tree islands (and nowhere else in the landscape), and fauna, principally birds. A fourth mechanism also derives from the action of vertical structure, but on atmospheric dryfall deposition rates, a hypothesis that we do not expound on here, and for which limited empirical data exist. Several authors (e.g., Frederick and Powell, 1994) have proposed this avifauna mechanism, arguing that biotic concentration of P from the surrounding landscape occurs because alternative roosting habitat is absent; a similar argument can be made for a variety of other fauna, including the compounding effect of birds attracting both bird predators and scavengers (Frederick and Powell, 1994). While there remains some uncertainty about the relative importance of these multiple mechanisms, enrichment of ^{15}N on tree islands (ca. 1–2‰ heavier on tree islands than in the surrounding sloughs; Diamond, 2008 unpublished data), and strong covariance between TP and δ^{15}N on tree island heads ($r = .87$; J. Diamond unpublished data) suggest that animal waste is a substantial component of tree island nutrient budgets.

The systematic loss of tree island area and head elevation across the Everglades over the last 50 years (Wetzel et al., 2009) would likely interrupt any self-organized mechanisms (i.e., not including groundwater inputs) that entrained such large quantities of P on islands. As tree islands lose their influence over landscape P dynamics, P concentrations on the remaining landscape would be expected to rise, leading to a potential nutrient effect

due to hydrological change alone. The magnitude of this effect is unknown, but the presence of ghost islands in southern WCA-2A (i.e., islands that are no longer capable of supporting woody vegetation and are inexorably subsiding to elevations where ridge feedbacks can stabilize peat) offer a useful test of this possible mechanism. Similarly, changes in the abundance of avifauna (Davis and Ogden, 1994) could have dramatic consequences for P redistribution over the long term, leading to reduced P gradients on tree islands, and, by association, increased P concentrations in the surrounding marshes. This potential biotic control over creation and maintenance of landscape patches is of considerable restoration importance, and, crucially, demonstrates the interconnection of landscape and fauna restoration goals. In a broader sense, if tree islands represent a biotically reinforced stable state in the Everglades (Givnish et al., 2007; Wetzel et al., 2009), they support the hypothesis of Didham et al. (2005) where, despite high biodiversity characteristic of tree islands, abiotic conditions, not principally competitive interactions, preclude dispersion of woody species to other parts of the landscape.

Local Positive Feedbacks on Peat Elevation

Self-organized nutrient gradients are thought to be autocatalytic in the process of tree island formation (Givnish et al., 2007); as vertical structure is established and avifauna use increases, nutrients are locally concentrated from some larger source area, which in turn increases primary productivity, which is relatively high on tree islands (Troxler-Gann et al., 2005). The feedback loop is closed by observing that high primary production is crucial to maintain high peat elevations (Figure 5) because comparatively short hydroperiods lead to high oxidation rates as a result of regular exposure; this in turn permits the persistence of woody vegetation that cannot persist in the longer hydroperiod marshes (ridges and sloughs). That tree islands accrete organic matter at a rate equal to the remaining landscape is an extension of the processes thought to create two alternative stable states in the ridge-slough mosaic. Thus, tree islands may constitute a third stable configuration (extremely high productivity and respiration) of vegetation-elevation-hydrology interactions, for which two states are shown in Figure 2.

Distal Negative Feedbacks and Pattern Formation

P enrichment at tree island nucleation sites (i.e., limestone pinnacles or large peat popups) inexorably releases P into the surrounding marshes due to diffusion gradients established by enormous (ca. 1 order of magnitude) concentration differences. Monotonic declines from tree island head to tail in pore water P concentrations (Wetzel et al., 2005), soil TP (Wetzel et al., 2009), and $\delta^{15}N$ (J. Diamond, unpublished data) suggest a point source for P at the tree island head and a decline in concentrations with distance. While

it seems reasonable to assume that tree islands expand from nucleation sites via the transport of phosphorus from nucleation sites at the head of each island, several key questions remain: (a) what constrains the tree island stable state to a minor prevalence in the landscape, (b) why do the feedbacks that constrain landscape prevalence not appear to constrain the size of any individual patch, and (c) what constrains expansion principally orthogonal to flow (i.e., why are tree islands 4–5 times longer than they are wide).

The low prevalence of tree islands (ca. 4% in the 1940s; Wetzel et al., 2009) may be due to several distal feedbacks operating principally at the landscape scale (i.e., not necessarily on individual patches). The first distal negative feedback has to do with the finite mass flux of P entering the system (principally from both dry and wet atmospheric deposition, S.M. Davis 1994; though this may discount root mobilization and groundwater P advection, Wetzel et al., 2005). In effect, any mechanism that hyperconcentrates P on tree islands is mining that P out of other areas of the Everglades, notably sloughs. Wetzel et al. (2009), the source of this assertion, estimated that nearly 70% of the P flux into the central Everglades was historically sequestered in tree islands. If large P translocation is necessary for tree island maintenance, and the ca. 4% of the landscape that was historically tree islands sequesters most of the P, it follows that any increase in the prevalence of tree islands would produce density dependent negative feedbacks wherein insufficient P is available to stimulate enhanced productivity on all islands. In short, landscape-scale P mass balance may limit the abundance of tree islands.

Another negative feedback at distance is exerted as a result of tree island morphology, and has as its basis the same hydrologic constraints that we posit above to produce ridge-slough patterning. The relevance of hydrology to tree island ecosystem processes, and thereby the potential for strong selection pressure for ecosystem engineers that exert reciprocal control is clear in Troxler-Gann et al. (2005). Tree island heads typically extend substantially above the median water elevation (Ross et al., 2006; Wetzel et al., 2009), meaning that they impede surface flow entirely, with consequences for landscape discharge competence and therefore on local hydroperiod (Figure 4). This distal feedback has three attributes that make it of interest for further consideration. First, it would constrain tree island landscape prevalence by linking tree island expansion to changes in hydrology that are ultimately disfavorable for tree islands (i.e., increase hydroperiod and inundation). Second, this feedback is anisotropic because expansion of tree islands longitudinally exerts no additional impoundment effect, but lateral expansion lowers the landscape cross-section through which flow passes, leading to incremental impoundment. This mechanism could serve to limit the cross-sectional area of tree islands at the landscape scale. Thirdly, however, it would not necessarily influence the width of any given tree island. Where the characteristic wavelength of the ridge-slough pattern may be due to the physiological particulars of the dominant species (sawgrass); no such

intrinsic biotic geometry constrains the expansion of tree islands. Indeed, since tree islands are relatively evenly distributed in space but vary tremendously in size (0.01–70 ha; Wetzel et al., 2009), whatever distal negative feedbacks constrain patch expansion do so principally via effects on landscape prevalence, not patch size. We note that the P mining process outlined in Wetzel et al. (2009) actually acts to reinforce not inhibit individual large tree islands, suggesting that it satisfies this criterion. Notably, sediment redistribution due to elevated velocities around tree island heads does not because the magnitude of that negative feedback on expansion acts on individual patches, a point to which we return subsequently.

One explanation for the observed shape orthogonal to flow follows from the advection of P by water flows (in both surface and groundwater), which is thought (Givnish et al., 2007) to create regions of enrichment downstream of the tree island heads, in turn stimulating higher productivity, higher peat elevations, and woody plant recruitment. The preferential advection in the direction of regional flow is thought to create anisotropy in the local positive feedback leading to the characteristic tear-drop tree island shape (Figure 1c).

While this explanation is highly intuitive, low flow velocities in the Everglades (0.9–1.4 cm s^{-1} around tree islands; Bazante et al., 2006) result in rates of solute dispersion, which acts isotropically, that are far larger relative to advection rates than in other lotic systems where elongated patches are typical. While hydrologic fluxes tend to transport P preferentially in the direction of flow, high lateral dispersion should create fan shaped enrichment patterns, leading to a morphology of tree islands quite different from that observed. Erosive forces (i.e., particle entrainment) are one plausible explanation for a process that constrains tree island lateral expansion. However, as with sloughs in the previous example, the extant velocities are too low for substantial entrainment, at least under present hydrologic conditions, even proximate to large tree islands that force water around their emergent heads. Further, the edges of tree islands are extremely densely vegetated, a condition that would presumably lead to reduced velocities, and therefore reduced entrainment. Given that the distal feedbacks that operated on tree islands appear to constrain the prevalence of tree islands but not the size of individual patches, further attention to the role of landscape level feedbacks appears worth considering.

While the mechanisms for the maintenance of tree island area and shape (both vertically and horizontally) remain foci of active research, it is clear that biota exert substantial control over the process. Indeed, our conceptual model (Figure 4) suggests that the vertical structure offered by trees provides habitat for avifauna phosphorus miners, which in turn creates conditions favorable for the persistence of trees. This biotic control over the persistence of an important component of the landscape is also fragile. The loss of avifauna to early hunting, mercury toxicity, and habitat loss, plus exogenous changes in hydrology that alter the frequency and duration of tree island exposure,

have already changed the underlying processes that maintained the land-scape. Where hydroperiods are markedly longer than they were historically (e.g. WCA-2A) ghost tree islands have become widespread, presumably be-cause conditions there no longer favor the woody vegetation necessary to close the biotic feedback loop. Similarly, in areas where hydroperiod has been reduced (e.g., WCA-3A-N and Everglades National Park) peat oxidation threatens the topographic separation (between tree islands and surrounding marshes) that permits the localized persistence of woody patches, and thus P enrichment gradients. The potential for positive feedbacks between bird populations and the maintenance of their habitat (including the hydrologic exclusion of nest predators, Frederick and Powell, 1994) has the potential to confound tree island restoration executed strictly on the basis of hydrologic drivers, and inextricably links landscape and faunal restoration objectives.

BIOTIC CONTROLS ON KARST STORAGE AND DRAINAGE IN BIG CYPRESS NATIONAL PRESERVE

Karst landforms are created by the interactions between a soluble mineral matrix and water undersaturated in that mineral (i.e., capable of dissolu-tion; Ford and Williams, 2007). Typically, *karst* refers to carbonate systems, though any soluble mineral (including ice; Gulley and Benn, 2007) self-organizes in analogous ways, wherein sites of hydrologic convergence (e.g., bedding planes, water tables, fractures) dissolve the matrix preferentially and thereby accelerate further hydrologic convergence. This process can be accentuated dramatically by the actions of biota (Viles, 1984). The obvious relevance of karst landforms in South Florida makes it uniquely well suited to analyses of emergent patterns from geochemical-biotic interactions, which have received relatively little attention and are an area in much need of further research (Bonacci et al., 2009). What follows is a primarily specula-tive description of the scale-dependent feedbacks that may generate what are clearly nonrandom patterns in the landscape observed most dramat-ically in Big Cypress National Preserve (dissolution storage in the north, Figure 1d; dissolution drainage in the south, Figure 1f), but also evident in both J.W. Corbett Wildlife Management Area (Figure 1e) on the other side of the peninsula and the tranverse channels that connected the Everglades to the Atlantic and Biscayne Bay (now the paths of major canals). The shape, spatial dispersion, density, and geologic history of these landforms strongly suggest self-organized biotic structuring, presumably via dissolution. How-ever, similar patchy landscapes exist in the Midwestern United States (prairie potholes) due to the abiotic effects of glacial erosion; while that mechanism is not relevant in South Florida, the existing literature on Big Cypress bio-geomorphology does not allow us to rule out other abiotic sources of the pattern.

The Big Cypress National Preserve basin lies in southwest Florida, immediately adjacent to the historic Everglades and a part of the historic regional hydrologic system (Science Coordination Team, 2003). The landscape is a mosaic of upland pine systems, cypress domes (circular, isolated wetlands where the cypress canopy is clearly dome shaped with the shortest trees at the edges) and strands (flow-oriented cypress dominated wetlands without a clear channel), and various marsh communities, spanning a hydrologic gradient from short (pinelands and shallow marshes) to long hydroperiod (cypress forests; Drew and Schomer, 1984). The principal controls on vegetation communities are hydrology and fire regimes (J.H. Davis, 1943), which in turn respond to small-scale heterogeneity in surface elevations. The ecosystems that occupy the lowest elevation locations are cypress domes, flag marshes, and willow heads, where hydrologic conditions support the accumulation of organic matter (Drew and Schomer, 1984); the implied local-scale vertical variation in the top of the mineral surface is large compared with the extremely low relief of the broader landscape. A clear distinction in surface landform exists between the north (Figure 1d), where isolated round cypress domes are interspersed in a matrix of upland and shallow wetland communities, and the south (Figure 1f) where flow orientation in the mosaic is clear. Possible reasons for this distinction are considered subsequently.

Local variation in microtopography is plausibly attributed to dissolution of limestone, which occurs in response to any water undersaturated in calcium (e.g., rainfall in equilibrium with atmospheric CO_2). However, abiotic dissolution processes due to the action of rainfall alone cannot explain the pronounced nonuniformity and overdispersion expressed in the regular radial patterning in some areas (Figures 1d, 1e) and strand formation in others (Figure 1f). The dissolution process can be amplified where the partial pressure of CO_2 (PCO_2) can be increased (Figure 5); for example, CO_2 production due to high rates of aquatic respiration and slow diffusion rates out of wetland sediment pore water can substantially increase the dissolution rate by lowering pH. Moreover, the pH of water incubated with plant material typical of the region is low (Osborne et al., 2007), as presumably are the organic compounds associated with root exudates. Both mechanisms create a positive feedback between increased hydroperiod and water depth and calcite dissolution (Figure 5). Moreover, in Big Cypress, where shallow carbonate soils represent a significant P sink, extended hydroperiods and the associated accumulation of organic matter can dramatically enhance primary productivity, both via the storage of water and the pH induced release of P associated with the mineral substrate. In short, small initial variation in topography is induced by accelerated dissolution at low spots due higher productivity and lower gas diffusion. While this positive feedback is necessary, two additional elements of the process are also required for the observed pattern to emerge. The first is a mechanism to ensure continual contact between undersaturated water and the limestone rock substrate,

which in turn requires that the dissolved material be advected out of the system either vertically or laterally (Figure 5; white boxes). The second is a distal negative feedback that constrains the expansion of the deep water patches (Figure 5; dashed lines).

To facilitate an ongoing local positive feedback, the mineral interface needs to be consistently supplied with under saturated water. This requires some vertical or horizontal flow path via which the dissolved calcium can be transported out of the system (Figure 5); without this advection, the pore water will reach equilibrium, and no additional dissolution will occur. Two plausible export pathways exists, and visual evidence supports the action of both in different areas of Big Cypress (Figures 1d, 1e): vertical export to groundwater and lateral export via shallow water table flowpaths.

Exporting the dissolved calcium vertically to groundwater would lead to preferential dissolution along primary flowpaths, and likely to areas of the cypress dome basin where the rate of peat accretion cannot keep pace with the dissolution-induced deflation of the surface. Rates of groundwater exchange in this landscape are unknown. If this mechanism operates, one effect would be a central zone of particularly rapid dissolution that might be hydrologically unsuitable for cypress trees. The hole-in-the-donut effect observed in the cypress domes in central Big Cypress National Preserve may indicate that this vertical export process is occurring (Figure 1d), a prediction that could readily be tested with measurements of peat and rock elevations, as well as wetland water budgets. The process of vertical groundwater export is observed in North Florida, where cypress domes apparently form via the same general process of hydrologic convergence leading to dissolution of the soluble geologic substrate below the surface (Odum, 1984). Based on vertical water flux rates, Odum (1974) estimated that to create 1 m of basin form via biotically enhanced dissolution requires ca. 3000 years. Because advection of dissolved calcium is via groundwater flowpaths, the pCO_2 can remain high because water is effectively disconnected from atmospheric interactions. The ultimate fate of this dissolved calcium delivered to deep groundwater is unknown, but submarine groundwater discharge to Florida Bay (Corbett et al., 1999) is one possible sink.

A second possible export pathway for the dissolved calcium is lateral export via shallow subsurface pathways, either due to regional groundwater flow or due to the radial outflow of accumulated water from centers of hydrologic convergence. This would occur where vertical water export is inhibited, either due to low permeability layers or higher potentiometric elevations. One effect of this process dominating export would be a region of accelerated marl accumulation at the surface some distance from each wetland, arising both from the re-equilibration of enriched CO_2 in lateral groundwater flows with the atmosphere, and algal photosynthesis (CO_2 uptake and consequent pH increases). Strong visual evidence of this (white margins around depressions in Figure 1e) suggests that this export pathway may be important,

at least in more northern locations in Big Cypress National Preserve. The action of periphyton and other submerged aquatic primary producers in short hydroperiod marshes accelerates this marl production process due to CO_2 and bicarbonate consumption. Over time, this preferential marl deposition would lead to distal accretion, which represents a second-order positive feedback that would further reinforce landscape vertical differentiation.

A second necessary process is a distal negative feedback that constrains the prevalence, size and shape of the landscape patches (Rietkerk and van de Koppel, 2008). The most plausible negative feedback arises from the finite volume of water available across the landscape to fill the created storage volume; we refer to the self-organized storage volume as landscape storage competence (Figure 5). Increasing landscape storage competence increases the proportion of available water stored, in turn limiting water availability to engender the same feedbacks in other areas. Stated another way, increases in landscape storage via wetland basin dissolution reduce the availability of water to fuel dissolution elsewhere. As such, the lateral expansion of cypress domes is ultimately inhibited by the local positive feedback that created the storage; this mechanism remains untested, but could be demonstrated by examining the spatial autocorrelation of surface elevations and testing for significant negative correlation at some characteristic distance defined by the size of patches. We note that the water budgets of cypress domes in North Florida indicate a highly local catchment area (i.e., domes are the centers of generally closed basins; Odum 1974); if this holds true for the domes in Big Cypress, it could explain the characteristic geometry of the observed pattern, with the wetland expanding to fill as much of the local catchment as can be supported by the water available therein. The characteristic round shape of the cypress wetlands likely emerges from the fact that the local hydrologic convergence process is spatially isotropic.

The premise that the distal negative feedback acting in the landscapes in Figures 1d and 1e are isotropic leads to the inference that the distal feedback happening in Figure 1f is not. Strong flow orientation to the dissolution features initiates spontaneously 10–12 km north of Alligator Alley, possibly suggesting a geomorphic threshold in slope that permits hydrologic export. We note that this is the approximate location or the contact between the Tamiami Formation and Miami Limestone, which may indicate geomorphic controls on the expression of biotic feedbacks. Alternatively, accrual of groundwater or surface water inflows along shallow topographic gradients may at some point in the catena produce surface water in excess of what can exported vertically, necessitating surface drainage. We presume that the strand features (including Turner River) represent the same local positive feedback (longer hydroperiod leading to accelerated dissolution; Figure 5), but that the density and cross-sectional area of the dissolution channels are maintained by landscape discharge competence. As channels expand laterally and vertically, they move more water, inhibiting channel dissolution elsewhere by limiting

water availability at distal locations. This argument parallels the one made for the ridge-slough landscape, where self-organizing landscape discharge competence controls the linearity and relative abundance of patches.

Although the mechanisms for the origin and maintenance of cypress domes and strands in the Big Cypress basin represent an area for substantial additional research, it appears plausible that interactions between vegetation and hydrology play an important role. While the consequences of interrupting these feedbacks via changes in regional hydrologic regimes may not be immediately felt due to the characteristic time scales of the process, the presence of such dramatic consequences of local biotic processes underscore their importance and relevance to restoration planning.

SYNTHESIS AND CONCLUSIONS

The presence of reciprocal biotic controls on system attributes (e.g., hydroperiod, discharge, nutrient gradients, landform) are not unique to the Everglades. Indeed, the number of systems in which the effects of biota are recognized as critical for engendering familiar geomorphic, biogeochemical and hydrologic patterns has been growing. What is not clear is where these reciprocal controls are large enough to substantially affect the restoration of desired ecological conditions, nor indeed how to proceed with restoration in those areas where feedbacks limit the ecosystem response of returning exogenous drivers to their previous settings. While it may be intuitive at the outset to assert that biota exert reciprocal control on the abiotic template in all systems, and conclude therefore that all systems demand deep knowledge of internal interactions to achieve restoration, it is also likely that the time domains and magnitude of those biotic effects vary sufficiently widely to limit the value of such a perspective. A conceptual model that can predict the circumstances in which reciprocal biotic feedbacks may confound restoration is of significant potential utility to the restoration of such systems, but would also identify the converse set of conditions in which resetting of abiotic drivers would suffice to achieve system recovery.

Multiple settings in the Everglades exhibit the emergence of landscape pattern from the interactions of feedbacks; positive feedbacks that maintain patch homogeneity over some local extent, and a distal negative feedback that inhibit patch expansion. We raise several areas of important uncertainty about the prevailing conceptual models of distal feedbacks that create pattern in South Florida ecosystems, particularly in the ridge-slough landscape and, by extension, for tree islands. Of particular importance is that the patterns resulting from such interactions are often subject to catastrophic loss when system drivers move outside some bi-stable region (Rietkerk et al., 2004a). Present uncertainty about such thresholds in the South Florida landscape is among the most important constraint on landscape restoration. Moreover,

the examples discussed here are not the only examples of possible self-organized behavior in the South Florida/Everglades landscape (Dong et al., 2002; Gunderson, 2001). Effective protection and restoration of these systems will require further research that identifies and enumerates the mechanisms of spatial- and temporal-dependent feedbacks, as well as a concerted effort to incorporate these complex interactions into conceptual models that guide their management.

The abundance and importance of self-organized patterning in the South Florida landscape has important implications for both efforts to conserve and restore its ecosystems. It also suggests a more general pattern about the factors precluding and facilitating biotic control of landscape pattern. Specifically, in all three examples, low variation in relief permits conditions where even modest biotic effects on elevation can be hydrologically significant; those include the action of peat accretion (in the case of the ridge-slough mosaic), focused P enrichment (in tree islands) or dissolution (in the case of cypress domes and strands in Big Cypress National Preserve). Further, changes in hydrology influence species assembly and ecosystem processes (e.g., primary production, avifauna roosting, elevated partial pressure of CO_2), which in turn amplify elevation differences. Such local self-reinforcing feedbacks are ultimately self-limiting: increasing landscape water storage due to wetland basin dissolution limits the extent of sites that can support wetland conditions, focusing phosphorus toward tree islands limits P availability elsewhere, and landscape scale displacement and discharge effects from the expansion of ridges raises water levels and extends hydroperiods, creating conditions unfavorable for ridges. The character of these negative feedbacks, specifically their strength, spatial range, and directionality, specify the characteristic geometry of the landscape pattern. Whether the magnitude of variation in the abiotic template, low levels of which permits increased biotic control, helps predict the presence of multiple-state ecosystems and self-organized patterned landscapes is a question worthy of further investigation.

REFERENCES

Bazante, J., Jacobi, G., Solo-Gabriele, H. M., Reed, D., Mitchell-Bruker, S., Childers, D. L., Leonard, L., and Ross, M. (2006). Hydrologic measurements and implications for tree island formation within Everglades National Park. *Journal of Hydrology* 329, 606–619.

Belyea, L. R., and Clymo, R. S. (2001). Feedback control on the rate of peat formation. *Proc. R. Soc. Lond. B*, 268, 1315–1321.

Bernhardt, C. E., and Willard, D. A. (2009). Response of the Everglades ridge and slough landscape to climate variability and 20th century water management. *Ecological Applications*, 19, 1723–1738.

Bevier C., and Krupa, S. (2001). *Groundwater–surface water interaction in tree islands: Water Conservation Area 3. Part 1: Phase 1 well installation.* Technical

Publication WS-4. West Palm Beach, FL: South Florida Water Management District.

Bonacci, O., Pipan, T., and Culver, D. C. (2009). A framework for karst ecohydrology. *Environmental Geology*, 56, 891–900.

Byers, J. E., Cuddington, K., Jones, C. G., Talley, T. S., Hastings, A., Lambrinos, J. G., Crooks, J. A., and Wilson, W. G. (2006). Using ecosystem engineers to restore ecological systems. *Trends in Ecology and Evolution*, 21, 493–500.

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

Childers, D. L., Iwaniec, D., Rondeau, D., Rubio, G., Verdon, E., and Madden, C. J. (2006). Responses of sawgrass and spikerush to variation in hydrologic drivers and salinity in Southern Everglades marshes. *Hydrobiologia*, 569, 273–292.

Clark, M. W., Cohen, M. J., Osborne, T. Z., Watts, D. L., and Oh, T. (2010). Evaluating Decomposition Dynamics, Community Composition and Ridge-Top Senescence in the Ridge-Slough Mosaic in Response to Climate Change and Water Management.˜ Final Report to the US Army Corps of Engineers and MAP/Recover. Research Work Order # 241.

Clymo, R. S. (1984). The limits to peat bog growth. *Phil. Trans. R. Soc. Lond. B.*, 303, 605–654.

Cohen, M. J., Lamsal, S., Osborne, T. Z., Reddy, K. R., and Newman, S. (2010). *Soil organic matter quality across the Greater Everglades*. Manuscript in review.

Cohen, M. J., Osborne, T. Z., Lamsal, S., and Clark, M. W. (2009). *Regional distribution of soil nutrients: Hierarchical soil nutrient mapping for improved ecosystem change detection*. SFWMD Final Report, West Palm Beach, FL, USA.

Corenblit, D., Gurnell, A. M., Steiger, J., and Tabacchi, E. (2008). Reciprocal adjustments between landforms and living organisms: extended geomorphic evolutionary insights. *Catena*, 73, 261–273.

Corenblit, D., Steiger, J., Gurnell, A. M., and Naiman, R. J. (2009). Plants intertwine fluvial landform dynamics with ecological succession and natural selection: A niche construction perspective for riparian systems. *Global Ecology and Biogeography*, 18, 507–520.

Craft, C. B., and Richardson, C. J. (1993). Peat accretion and N, P, and organic C accumulation in nutrient-enriched and unenriched Everglades peatlands. *Ecological Applications*, 3, 446–458.

Daoust, R. J., and Childers, D. L. (1999). Controls on emergent macrophyte composition, abundance, and productivity in freshwater Everglades wetland communities. *Wetlands*, 19, 262–275.

Davis, S. M. and Ogden, J. C. (1994). Everglades: The Ecosystem and its Restoration. St. Lucie Press, Delray Beach FL, p. 837.

Davis, J. H. Jr. (1943). *The natural features of southern Florida*. Tallahassee, FL: Florida Geological Survey Bulletin.

Davis, S. M., Gunderson, L. H., Park, W. A., Richardson, J. R., and Mattson, J. E. (1994). Landscape dimension, composition, and function in a changing Everglades ecosystem. In S. M. Davis and J. C. Ogden (Eds.), *Everglades: The ecosystem and its restoration* (pp. 419–444). Delray Beach, FL: St Lucie Press.

Diamond, J. 2008. Isotopic Evidence for Faunal Deposition of Nutrients in Tree Islands of the Everglades. Independent Study Final Report, University of Florida, Gainesville, FL, USA.

Didham, R. K., Watts, C. H., and Norton, D. A. (2005). Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? *Oikos*, 110, 409–416.

Dong, Q., McCormick, P. V., Sklar, F. H., and DeAngelis, D. L. (2002). Structural instability, multiple stable states, and hysteresis in periphyton driven by phosphorus enrichment in the Everglades. *Theoretical Population Biology*, 61, 1–13.

Drew, R. D., and Schomer, N. S. (1984). *An ecological characterization of the Caloosahatchee River/Big Cypress watershed*. FWS/OBS-82/58. Washington, DC: Minerals Management Service and Fish and Wildlife Service, U.S. Department of the Interior.

Eppinga, M., Rietkerk, M., Borren, W., Lapshina, E., Bleuten, W., and Wassen, M. (2008). Regular surface patterning of peatlands: Confronting theory with field data. *Ecosystems*, 11, 520–536.

Eppinga, M. B., Rietkerk, M., Wassen, M. J., and De Reuiter, P. C. (2009). Linking habitat modification to catastrophic shifts and vegetation patterns in bogs. *Plant Ecology*, 200, 53–68.

Ewe, S. M. L., Gaiser, E. E., Childers, D. L., Iwaniec, D., Rivera-Monroy, V. H., and Twilley, R. R. (2006). Spatial and temporal patterns of aboveground net primary productivity (ANPP) along two freshwater-estuarine transects in the Florida Coastal Everglades. *Hydrobiologia*, 569, 459–474.

Ford, D., and Williams, P. (2007). *Karst hydrogeology and geomorphology*. Chichester, England: Wiley.

Francis, R. A., Corenblit, D., and Edwards, P. J. (in press). Perspectives on biogeomorphology, ecosystem engineering and self-organisation in island-braided fluvial ecosystems. *Aquatic Sciences*. doi:10.1007/s00027-009-9182-6

Frederick P. C., and Powell, G. V. N. (1994). Nutrient transport by wading birds in the Everglades. In S. M. Davis and J. C. Ogden (Eds.), *Everglades: The ecosystem and its restoration*, Delray Beach, FL: St. Lucie Press, 571–584.

Fukami, T., and Lee, W. G. (2006). Alternative stable states, trait dispersion, and ecological restoration. *Oikos*, 113, 353–356.

Givnish, T. J., Volin, J. C., Owen, D., Volin, V. C., Muss, J. D., and Glaser, P. H. (2007). Vegetation differentiation in the patterned landscape of the central Everglades: importance of local and landscape drivers. *Global Ecology and Biogeography*, 1–19.

Goovaerts, P. (1997). *Geostatistics for natural resources evaluation*. New York: Oxford University Press.

Gulley, J., and Benn, D. I. (2007). Structural control of englacial drainage systems in Himalayan debris-covered glaciers. *Journal of Glaciology*, 53, 399–412.

Gunderson, L. H. (2001). Managing surprising ecosystems in southern Florida. *Ecological Economics*, 37, 371–378.

Hagerthey, S. E., Newman, S., Rutchey, K., Smith, E. P., and Godin, J. (2008). Multiple regime shifts in a subtropical peatland: Community-specific thresholds to eutrophication. *Ecological Monographs*, 78, 547–565.

Harvey, J. W., Krupa, S., Gefvert, C. J., Choi, J., Mooney, R. H., and Giddings, J. B. (2000). *Interaction between ground water and surface water in the Northern*

Everglades and relation to water budgets and mercury cycling: study methods and appendices. Open-File Report 00–168. U.S. Geological Survey, Reston, VA.

Harvey, J. W., Saiers, J. E., and Newlin, J. T. (2005). Solute transport and storage mechanisms in wetlands of the Everglades, south Florida. *Water Resources Research*, 41. doi:10.1029/2004WR003507.

Harvey, J. W., Schaffranek, R. W., Noe, G. B., Larsen, L. G., Nowacki, D. J., and O'Connor, B. L. (2009). Hydrecological factors governing surface water flow on a low gradient floodplain. *Water Resources Research*, 45, W–3421, doi:10.1029/2008WR007129.

Heffernan, J. B. (2008). Wetlands as an alternative stable state in desert streams. *Ecology*, 89, 1261–1271.

HilleRisLambers, R., Rietkerk, M., Van Den Bosch, F., Prins, H. H. T., and de Kroon, H. (2001). Vegetation pattern formation in semi-arid grazing systems. *Ecology*, 82, 50–61.

Ho, D. T., Engel, V. C., Variano, E. A., Schneider, P. J., and Condon, M. E. (2009). Tracer studies of sheet flow in the Florida Everglades. *Geophysical Research Letters*, 36, L09401. doi:10.1029/2009GL037355.

Huang, Y. H., Saiers, J. E., Harvey, J. W., Noe, G. B., and Mylon, S. (2005). Advection, dispersion and filtration of fine particles within emergent vegetation of the Florida Everglades. *Water Resources Research*, 44, W04408. doi:10.1029/2007WR006290.

Jones, C. G., Lawton, J. H., and Schachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373–386.

Kirwan, M. L., and Murray, A. B. (2007). A coupled geomorphic and ecological model of tidal marsh evolution. *Proceedings of the National Academy of Sciences*, 104, 6118–6122.

Larsen, L. G., Aumen, N., Bernhardt, C., Engel, V., Givnish, T., Hagerthey, S., Harvey, J., Leonard, L., McVoy, C., Noe, G., Nungesser, M., Rutchey, K., Sklar, F., Troxler, T., Volin, J., and Willard, D. (in press). The role of flow and transport processes in ridge/slough/tree island pattern dynamics. *Critical Reviews in Environmental Science and Technology*.

Larsen, L. G., Harvey, J. W., and Crimaldi, J. P. (2007). A delicate balance: Eco-hydrological feedbacks governing landscape morphology in a lotic peatland. *Ecological Monographs*, 77, 591–614.

Larsen, L. G., Harvey, J. W., and Crimaldi, J. P. (2009a). Morphologic and transport properties of natural organic floc. *Water Resources Research*, 45, W01410. doi:10.1029/2008WR006990.

Larsen, L. G., Harvey, J. W., and Crimaldi, J. P. (2009b). Predicting bed shear stress and its role in sediment dynamics and restoration potential of the Everglades and other vegetated flow systems. *Ecological Engineering*, 35, 1773–1785.

Leonard, L., Croft, A., Childers, D. L., Mitchell-Bruker, S., Solo-Gabriele, H., and Ross, M. S. (2006). Characteristics of surface-water flows in the ridge and slough landscape of Everglades national Park: Implications for particulate transport. *Hydrobiologia*, 569, 5–22.

Lewis, C. G. (2005). *Linkages among vegetative substrate quality, biomass production, and decomposition in maintaining Everglades ridge and slough vegetative communities.* Gainesville, FL: Soil and Water Science.

Ludwig, J. A., Tongway, D. J., and Marsden, S. G. (1999). Stripes, stands, or stipples: Modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia. *Catena*, 37, 257–273.

Mayer, A. L., and Rietkerk, M. (2004). The dynamic regime concept for ecosystem management and restoration. *Bioscience*, 54, 1013–1020.

McCormick, P. V., Newman, S., and Vilchek, L. W. (2009). Landscape responses to wetland eutrophication: loss of slough habitat in the Florida Everglades, USA. *Hydrobiologia*, 621, 105–114.

McCormick, P. V., Rawlik, P. S., Lurding, K., Smith, E. P., and Sklar, F. H. (1996). Periphyton-water quality relationships along a nutrient gradient in the northern Florida Everglades. *Journal of the North American Benthological Society*, 15, 433–449.

National Research Council. (2003). *Does water flow influence Everglades landscape patterns?* Washington, DC: National Academies Press.

Noe, G. B., Childers, D. L., and Jones, R. (2001). Phosphorus biogeochemistry and the impact of phosphorus enrichment: Why is the Everglades so unique? *Ecosystems*, 4, 603–624.

Noe, G. B., Harvey, J. W., and Saiers, J. E. (2007). Characterization of suspended particles in Everglades wetlands. *Limnology and Oceanography*, 52, 1166–1178.

Odum, H. T. (1984). Summary: Cypress swamps and their regional role. In K. C. Ewel and H. T. Odum (Eds.), *Cypress swamps* (pp. 416–443). Gainesville, FL: University of Florida Press.

Osborne, T. Z., Inglett, P. W., and Reddy, K. R. (2007). The use of senescent plant biomass to investigate relationships between potential particulate and dissolved organic matter in a wetland ecosystem. *Aquatic Botany*, 86, 53–61.

Ramberg, L., and Wolski, P. (2008). Growing islands and sinking solutes: processes maintaining the endorheic Okavango Delta as a freshwater system. *Plant Ecology*, 196, 215–231.

Riscassi, A. L., and Schaffranek, R. W. (2003). *Flow velocity, water temperature, and conductivity in Shark River Slough, Everglades National Park, Florida: August 2001–June 2002*. Geol, U.S. Survey Open File Report 03-348.

Rietkerk, M., Boerlijst, M. C., and van Landevelde, F. (2002). Self-organization of vegetation in arid ecosystems. *American Naturalist*, 160, 524–530

Rietkerk, M., Dekker, S. C., de Ruiter, P. C., and van de Koppel, J. (2004a). Self-organized patchiness and catastrophic shifts in ecosystems. *Science*, 305, 1926–1929.

Rietkerk, M., Dekker, S. C., Wasse, M. J., Verkroost, A. W. M., and Bierkens, M. F. P. (2004b). A putative mechanism for bog patterning. *American Naturalist*, 163, 699–708.

Rietkerk, M., and van de Koppel, J. (2008). Regular pattern formation in real ecosystems. *Trends in Ecology and Evolution*, 23, 169–175.

Ross, M. S., Mitchell-Bruker, S., Sah, J. P., Stothoff, S., Ruiz, P. L., Reed, D. L., Jayachandran, K., and Coultas, C. L. (2006). Interaction of hydrology and nutrient limitation in the ridge and slough landscape of the southern Everglades. *Hydrobiologia*, 569, 23.

Saiers, J. E., Harvey, J. W., and Mylon, S. E. (2003). Surface water transport of suspended matter through wetland vegetation of the Florida Everglades. *Geophysical Research Letters*, 30. doi:10.1029/2003GL018132.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.

Science Coordination Team. (2003). *The role of flow in the Everglades ridge and slough landscape*. Miami, FL: South Florida Ecosystem Restoration Working Group.

Sklar, F. H., Chimney, M. J., Newman, S., McCormick, P., Gawlik, D., Miao, S., McVoy, C., Said, W., Newman, J., Coronado, C., Crozier, G., Korvela, M., and Rutchey, K. (2005). The ecological–societal underpinnings of Everglades restoration. *Frontiers of Ecology and Environment*, 3, 161–169.

Smith, D. G. (1976). Effect of vegetation on lateral migration of anastamosed channel of a glacier meltwater river. *Bulletin of Geological Society of America*, 87, 857–860.

Stallins, J. A. (2006). Geomorphology and ecology: Unifying themes for complex systems in biogeomorphology. *Geomorphology*, 77, 207–216.

Suding, K. N., Gross, K. L., and Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, 19, 46–53.

Suding, K. A., and Hobbs, R. J. (2009). Threshold models in restoration and conservation: A developing framework. *Trends in Ecology and Evolution*, 24, 271–279. doi:10.1016/j.tree.2008.11.012

Troxler-Gann, T. G., Childers, D. L., and Rondeau, D. N. (2005). Ecosystem structure, nutrient dynamics and hydrologic relationships in tree islands of the southern Everglades, Florida, USA. *Forest Ecology and Management*, 214, 11–27.

Van Hulzen, J. B., van Soelen, J., and Bouma, T. J. (2007). Morphological variation and habitat modification are strongly correlated for the autogenic ecosystem engineer *Spartina anglica* (common cordgrass). *Estuaries and Coasts*, 30, 3–11.

Viles, H. A. (1984). Biokarst: Review and prospect. *Progress in Physical Geography*, 5, 523–548

Watts, D. L., Cohen, M. J., Heffernan, J. B., Osborne, T. Z., and Clark, M. W. (2010). *Hydrologic modification and the loss of self-organized patterning in the ridge slough mosaic of the Everglades*. Manuscript in review.

Wetzel, P. R., Van Der Valk, A. G., Newman, S., Coronado, C. A., Troxler-Gann, T. G., Childers, D. L., Orem, W. H., and Sklar, F. H. (2009). Heterogeneity of phosphorus distribution in a patterned landscape, the Florida Everglades. *Plant Ecology*, 200, 83–90.

Wetzel, P. R., Van Der Valk, A. G., Newman, S., Gawlik, D. E., Gann, T. G. T., Coronado-Molina, C. A., Childers, D. L., and Sklar, F. H. (2005). Maintaining tree islands in the Florida Everglades: Nutrient redistribution is the key. *Frontiers in Ecology and the Environment*, 3, 370–376.

White, J. R., and Reddy, K. R. (2003). Nitrification and denitrification rates of Everglades wetland soils along a phosphorus-impacted gradient. *Journal of Environmental Quality*, 32, 2436–2443.

Wu, Y., Sklar, F. H., and Rutchey, K. (1997). Analysis and simulations of fragmentation patterns in the Everglades. *Ecological Applications*, 7, 268–276.

Wu, Y., Wang, N., and Rutchey, K. (2006). An analysis of spatial complexity of ridge and slough patterns in the Everglades ecosystem. *Ecological Complexity*, 3, 183–192.

Zedler, J. (2000). Progress in wetland restoration ecology. *Trends in Ecology and Evolution*, 15, 402–407.