How Vegetation and Sediment Transport Feedbacks Drive Landscape Change in the Everglades and Wetlands Worldwide.
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Source: *The American Naturalist*, Vol. 176, No. 3 (September 2010), pp. E66-E79
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/10.1086/655215
Accessed: 13/01/2011 10:22

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vol. 176, no. 3 the american naturalist september 2010 Ⓔ

E-Article

How Vegetation and Sediment Transport Feedbacks Drive Landscape Change in the Everglades and Wetlands Worldwide

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Submitted June 15, 2009; Accepted March 23, 2010; Electronically published July 16, 2010

Online enhancements: appendixes, video.

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abstract: Mechanisms reported to promote landscape self-organization cannot explain vegetation patterning oriented parallel to flow. Recent catastrophic shifts in Everglades landscape pattern and ecological function highlight the need to understand the feedbacks governing these ecosystems. We modeled feedback between vegetation, hydrology, and sediment transport on the basis of a decade of experimentation. Results from more than 100 simulations showed that flows just sufficient to redistribute sediment from sparsely vegetated sloughs to dense ridges were needed for an equilibrium patterned landscape oriented parallel to flow. Surprisingly, although vegetation heterogeneity typically conveys resilience, in wetlands governed by flow/sediment feedbacks it indicates metastability, whereby the landscape is prone to catastrophic shifts. Substantial increases or decreases in flow relative to the equilibrium condition caused an expansion of emergent vegetation and loss of open-water areas that was unlikely to revert upon restoration of the equilibrium hydrology. Understanding these feedbacks is critical in forecasting wetland responses to changing conditions and designing management strategies that optimize ecosystem services, such as carbon sequestration or habitat provision. Our model and new sensitivity analysis techniques address these issues and make it newly apparent that simply returning flow to predrainage conditions in the Everglades may not be sufficient to restore historic landscape patterns and processes.

Keywords: Everglades, wetlands, alternate stable states, modeling, patterned landscapes, sediment transport.

Introduction

Landscapes with self-organized vegetation patchiness occur worldwide (Swanson and Grigal 1988; Rietkerk et al. 2004*b*; Eppinga et al. 2008) and are important for their heterogeneity, which fosters high biodiversity and an ability to withstand disturbance (Palmer and Poff 1997; Gilad et al. 2004). When the orientation of topographic and vegetation patterning is parallel to surface-water flow (fig. 1), these landscapes are further valued for channel connectivity, which facilitates fish migration and gene flow (National Research Council 2003). Some wetlands with this morphology are Ramsar-listed wetlands of international importance, including large parts of the Florida Everglades, the Brazilian Pantanal, the Cuban Zapata Peninsula, the Yucatán Peninsula, and the Botswanan Okavango Delta (Frazier 1999). Understanding the controls on patterned landscape structure is critical for conservation of their unique and highly valued ecosystem functions.

Most regularly patterned landscapes found throughout the world are governed by some version of scale-dependent feedback, meaning that organisms grouped in patches modify their environment such that environmental factors have a positive effect on their growth at short distances (i.e., local facilitation) but a negative effect on their growth at long distances (i.e., large-scale inhibition; Rietkerk and van de Koppel 2008). In wetlands, scale-dependent feedback often involves the accumulation of nutrients at the scale of the patch, which depletes nutrients at longer spatial scales (Rietkerk et al. 2004*a*). In aggregate, this feedback produces wetlands that are patterned with a mazelike structure or with strings of hummocks and hollows aligned perpendicular to flow, depending on the slope of the landscape (Eppinga et al. 2009). Alternatively, interactions between water levels, plant growth, and peat accretion rate are thought to produce similar forms of landscape self-organization (Belyea and Baird 2006; Eppinga et al. 2008). Flowing water backing up behind low-conductivity strings of hummocks and spreading out along the slope may also produce sharply delineated perpendicular landscape patterns (Swanson and Grigal 1988). On the other hand, irregular patchiness can arise from surface-water flow that scours bare sediment around tidal-marsh tussocks (van Wesenbeeck et al. 2008). However, none of these mech-

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Am. Nat. 2010. Vol. 176, pp. E66–E79.

DOI: 10.1086/655215

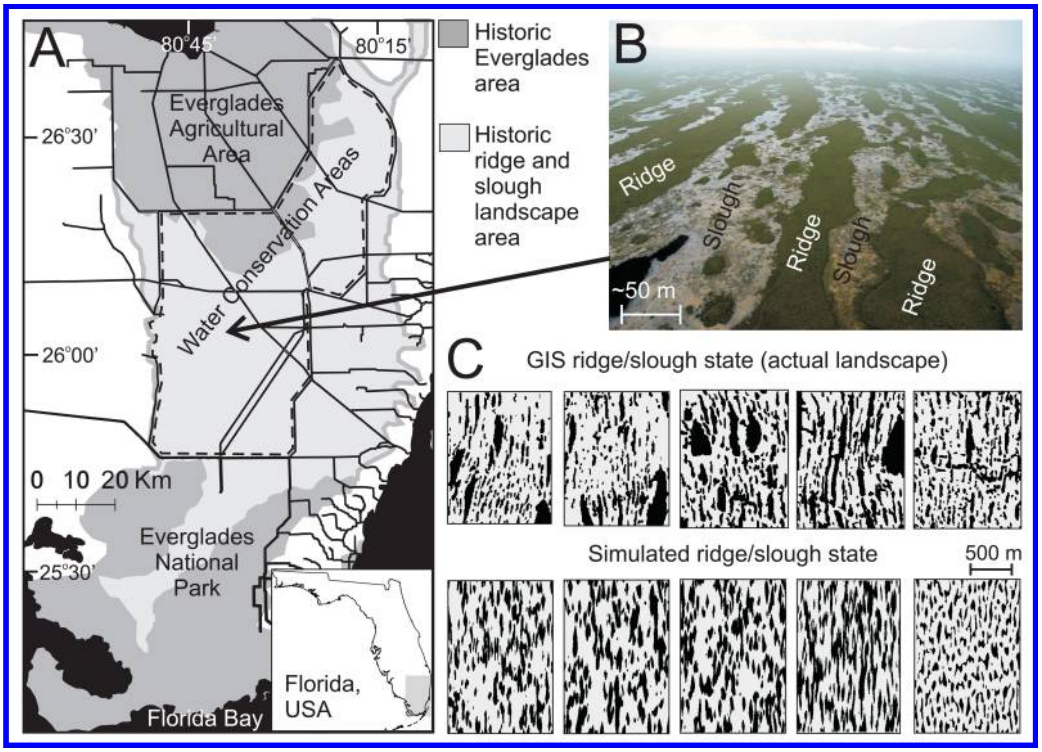

Figure 1: *A*, Historic extent of the parallel-drainage ridge-and-slough landscape within the Everglades; *B*, oblique aerial photograph of well-preserved ridges and sloughs; *C*, actual and simulated geometry of the system. Shallow, nearly uniform flows across this floodplain formerly traveled southward toward the Florida Bay. Now a network of canals and levees (*black lines* in *A*) compartmentalize flows. In *C*, geographical information system (GIS) images of the well-preserved landscape (*black* = ridges and tree islands, *gray* = sloughs; reprinted from Wu et al. 2006, with permission) are compared to several examples of simulated landscapes. Flow is from top to bottom.

anisms have been sufficient to explain the highly regular longitudinal (i.e., parallel-to-flow) vegetation patterning that occurs in the Everglades and elsewhere (Larsen et al. 2007).

Parallel-drainage topography (intrinsically associated with longitudinal vegetation patterning) is traditionally thought to be unstable on low-to-moderate gradients because of positive feedback between flow velocity, local flow depth, and sediment erosion that causes coalescence into a dominant channel network (Phillips and Schumm 1987). Nonetheless, paleoecological records suggest that longitudinal vegetation patterning was stable in the Everglades for millennia, until recent human manipulation of hydrologic controls (Bernhardt and Willard 2009). Over the past century, this patterning, characterized by ridges of dense emergent sawgrass (*Cladium jamaicense*) interspersed among open, less densely vegetated sloughs, has diminished in extent, with widespread topographic flattening and shifts in vegetation cover to homogeneous sawgrass (National Research Council 2003). The landscape is now a prime focus of the $10.9 billion congressionally funded Everglades restoration effort, which aims to restore near-historic flows. However, similar catastrophic shifts to a homogeneous landscape state in other formerly patterned ecosystems are known to be largely irreversible (Scheffer et al. 2001; Peters et al. 2004; Rietkerk et al. 2004*b*) as a result of positive feedback between vegetation and a limiting resource. The dynamics of landscape evolution trajectories following catastrophic shifts thus play an integral role in determining the potential for restoration of a patterned landscape (Suding et al. 2004).

Through process-based numerical modeling, we aimed to establish whether a sediment transport feedback could interact with a differential peat accretion feedback to explain landscape pattern formation and stability in worldwide parallel-drainage wetlands (see fig. 2). The hypothesis was that at the scale of the vegetation patch, emergent vegetation would promote the accumulation of sediment through differential peat accretion and sedimentation, which would foster the growth of additional emergent vegetation. At the landscape scale, the accumulation of sediment and high-resistance vegetation within ridge patches would divert more flow to open channels or sloughs, which

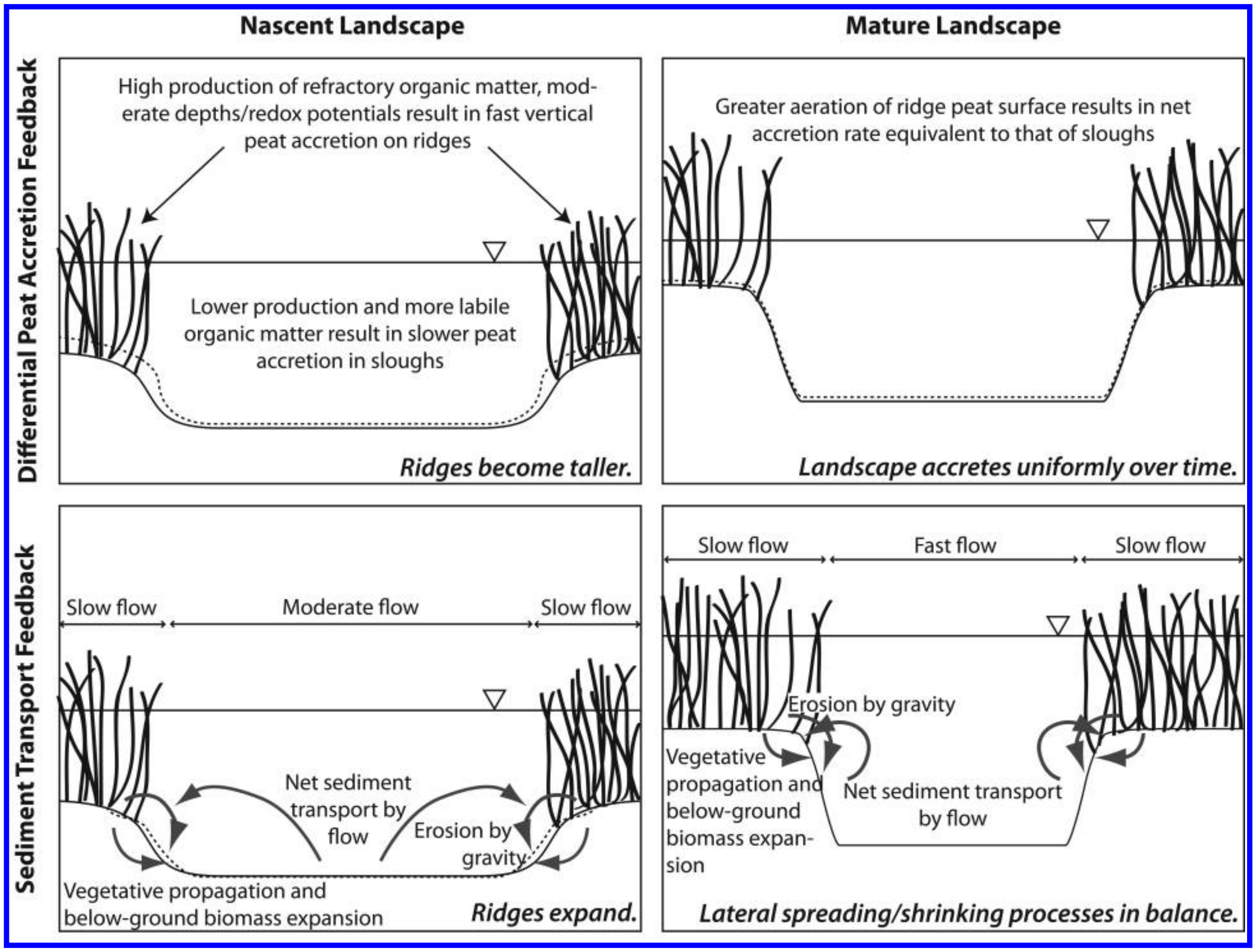

Figure 2: Landscape cross sections (drawn with the dominant flow direction into the page) show the influence of the differential peat accretion feedback and sediment transport feedback at different stages of wetland development. Each row of the diagram shows the influence of a feedback individually; dotted lines show changes in the peat topography that result from that feedback. Arrows indicate sediment transport. Our model tests the hypothesis that, initially, ridges expand because of differential peat accretion, gravity-driven spreading of sediment, lateral biomass expansion, and sediment deposition in transition areas. Eventually, the concentration of flow in sloughs creates velocities sufficient to redistribute enough sediment from transition zones to ridge interiors to counteract spreading processes. Ultimately, we predict that the differential peat accretion feedback controls vertical landscape development, while the sediment transport feedback controls lateral and longitudinal landscape development.

would promote erosion and inhibit the growth of emergent vegetation in those locations.

We developed the model to accept a general range of input parameters that bracketed environmental conditions in the Everglades (chosen as our case study because of the availability of decades of supporting field data), as well as many other low-gradient wetlands. Previous modeling showed that the differential peat accretion feedback alone was not a sufficient cause of longitudinal landscape patterning in the Everglades, suggesting the importance of another mechanism (Larsen et al. 2007). Here we manipulate model input parameters to evaluate the general sensitivity of landscape pattern in low-gradient wetlands to environmental conditions controlling differential peat accretion and sediment transport feedbacks. We also examine the role that twentieth-century human impacts have had on degradation of the ridge-and-slough landscape of the Everglades and its potential for restoration.

Methods

The Model

In appendix A, we present a detailed description of the model, using the standard ODD (overview, design concepts, details) protocol (Grimm et al. 2006) for model description. Below is an abridged version; many of the assumptions, the design concept and algorithm details, and descriptions of coefficients can be found in appendix A.

Entities, State Variables, and Scales. The model environment represents a landscape 1.27 km wide × 1.86 km long. The domain is divided into two-dimensional grid cells with a length of 10 m in the direction parallel to flow and a width of 5 m. Grid cells are distinguished by four state variables: (1) vegetation state (either ridge or slough vegetation) and the associated rates of organic-matter production and decomposition and degree of flow resistance, (2) the elevation of the peat surface, (3) local flow velocity and associated bed shear stress, and (4) suspended-sediment concentration. Global environmental variables are the annual duration and discharge of high-flow pulses, the water-surface slope during high-flow periods, water level, and the depth of potentially erodible bed sediment (loosely consolidated, compound organic aggregates, or "floc") before the high-flow period. The water surface is assumed to be planar, with a constant elevation relative to the mean bed plane.

Process Overview and Scheduling. Vegetation state and topography are updated on 1-year time steps, beginning with the assignment of vegetation state based on local topography relative to water level (fig. A1). Vegetation state influences local flow velocity, for which a steady state solution is obtained. Although flow velocities vary throughout the year, velocities are assumed to be important only for the evolution of topography and vegetation state during the high-flow pulses, when flows are high enough to entrain sediment. The steady state solution of flow velocity obtained within each time step of the model is representative of flows during these pulsed events.

Next, the velocity and the associated bed shear stress solution are used to compute the distribution, entrainment, and deposition of suspended sediment. Finally, the topography is updated on the basis of the total erosion and deposition of sediment during the high-flow pulses and the other physical and biological processes that affect topography throughout the year: the gravity-driven erosion of topographic gradients, the lateral spreading of soil that results from vegetative propagation and belowground biomass production, and the accumulation of peat that results from an imbalance between the production and the decomposition of organic matter.

Initialization. Cell elevations were initialized with a Gaussian random number distribution in which the standard deviation was varied as an input parameter to yield different values of the initial ridge coverage. The specified water-surface slope and input initial maximum slough depth for the high-flow periods determined the high-flow discharge. Subsequent time steps retained the input water-surface slope but adjusted water level to maintain a constant high-flow-pulse discharge. In some simulations, the effects of altered environmental parameters on mature landscape structure were examined. These runs were initialized with the topography and hydrology generated at an advanced stage of a previous simulation.

Input Data. Field data and results from more detailed but less spatially extensive numerical modeling were used in the formulation of key processes. Lookup tables that provided flow-parallel and flow-perpendicular dispersion coefficients (D_x and D_y, respectively), drag coefficients (C_D), and bed shear stress (τ_0) as functions of the water-surface slope (S) and depth-averaged velocity ($\bar{u}$) were obtained from one-dimensional simulations of vertical velocity profiles in vegetation canopies (see Larsen et al. 2009*b* and fig. A2). Different lookup tables were available for each vegetation community. Community frontal areas per unit volume (a) and stem diameters (d) as a function of water depth (H) were obtained from field measurements, and the expressions for ridge and slough drag coefficients were derived from dimensional analysis, fitted empirically to a record of flow velocity and water depth data (Harvey et al. 2009).

Submodels. Assignment of vegetation state. Slough communities were assigned to cells with high (≥61.2 cm) water depth and ridges to cells with low (≤50.4 cm) water depth on the basis of the Givnish et al. (2008) data. Between these thresholds, ridge and slough vegetation occurred stochastically, according to an error-function-shaped probability distribution. The probability distribution function was multiplied by a coefficient that favored ridge vegetation colonization when the surrounding cells were ridge cells or when the cell had been occupied by ridge vegetation in the previous time step (Larsen 2008).

Hydraulics: two-dimensional flow velocities, water level, and bed shear stress. The governing equations for flow velocity and water level were an approximation of the steady state momentum (eqq. [1], [2]) and the continuity (eq. [3]) equations:

$$\underbrace{\overline{(1-ad)u_x}\frac{\partial\bar{u}_x}{\partial x}+\overline{(1-ad)u_y}\frac{\partial\bar{u}_x}{\partial y}}_{\text{advection}}+\frac{1}{2}\underbrace{\overline{C_{\mathrm{D}}au_x^2}}_{\text{vegetative drag}}=\underbrace{\overline{g\left(1-\frac{\pi}{4}ad\right)S}}_{\text{gravitational forcing}}$$

$$+\underbrace{\overline{\left(1-\frac{\pi}{4}ad\right)}\frac{\partial}{\partial x}\left(D_x\frac{\partial\bar{u}_x}{\partial x}\right)+\overline{\left(1-\frac{\pi}{4}ad\right)}\frac{\partial}{\partial y}\left(D_y\frac{\partial\bar{u}_x}{\partial y}\right)}_{\text{dispersion}},\tag{1}$$

$$\underbrace{\overline{(1-ad)u_y}\frac{\partial\bar{u}_y}{\partial y}+\overline{(1-ad)u_x}\frac{\partial\bar{u}_y}{\partial x}}_{\text{advection}}+\frac{1}{2}\underbrace{\overline{C_{\mathrm{D}}au_y^2}}_{\text{vegetative drag}}=$$

$$\underbrace{\overline{\left(1-\frac{\pi}{4}ad\right)}\frac{\partial}{\partial x}\left(D_x\frac{\partial\bar{u}_y}{\partial x}\right)+\overline{\left(1-\frac{\pi}{4}ad\right)}\frac{\partial}{\partial y}\left(D_y\frac{\partial\bar{u}_y}{\partial y}\right)}_{\text{dispersion}},\tag{2}$$

$$\frac{\partial(\bar{u}_xH)}{\partial x}+\frac{\partial(\bar{u}_yH)}{\partial y}=0.\tag{3}$$

In equations (1)–(3), the x-direction is parallel to the water-surface slope, the y-direction is perpendicular to the water-surface slope, and g is the acceleration due to gravity. Overbars denote depth-averaged quantities. Periodic boundary conditions were imposed, with the solution constrained by the imposed high-flow discharge, $Q=\int\bar{u}_xHdy$.

The cellular-automata approximation of equations (1)–(3) assumes that the water surface is a plane with slope S. Local values of H were thus determined from topography alone, and equations (1)–(3) were solved for $\bar{u}_x$ and $\bar{u}_y$ (e.g., Parsons and Fonstad 2007). Next, local water depth and local velocity magnitude were input into the vegetation community–specific lookup tables to obtain bed shear stress (Larsen et al. 2009*b*; fig. A2).

Sediment transport. An advection-dispersion equation controlled sediment transport:

$$\frac{\partial\overline{C}H}{\partial t}=-\underbrace{w_{\mathrm{s}}\overline{C}H}_{\text{settling}}-\underbrace{\overline{u_x(1-ad)}H\frac{\partial\overline{C}}{\partial x}-\overline{u_y(1-ad)}H\frac{\partial\overline{C}}{\partial y}}_{\text{advection}}$$

$$+\underbrace{\left(1-\frac{\pi}{4}ad\right)M\max\left(\left(\frac{\tau_0-\tau_{\mathrm{e}}}{\tau_{\mathrm{e}}}\right)^n,0\right)}_{\text{entrainment}}$$

$$+\underbrace{\overline{\left(1-\frac{\pi}{4}ad\right)}\frac{\partial}{\partial x}\left(D_x\frac{\partial\overline{C}H}{\partial x}\right)+\overline{\left(1-\frac{\pi}{4}ad\right)}\frac{\partial}{\partial y}\left(D_y\frac{\partial\overline{C}H}{\partial y}\right)}_{\text{dispersion}},\tag{4}$$

where C is the suspended-sediment concentration, τ_{e} is the threshold shear stress of sediment entrainment (an input parameter), w_{s} is the settling velocity (0.11 cm s^{-1}; see Larsen et al. 2009*c*), and M and n are constants (see table A1).

Changes in bed elevation. The governing equation for changes in bed elevation (η) was

$$\frac{\partial\eta}{\partial t}=\underbrace{\frac{w_{\mathrm{s}}\overline{C}}{\rho_{\mathrm{b}}}\overline{\left(1-\frac{\pi}{4}ad\right)^{-1}}}_{\text{deposition}}-\underbrace{\min\left(\frac{M}{\rho_{\mathrm{b}}}\max\left(\left(\frac{\tau_0-\tau_e}{\tau_e}\right)^n,0\right),r\right)}_{\text{erosion by flow}}$$

$$+\underbrace{D_{\mathrm{sed}}\left(\frac{\partial^2\eta}{\partial x^2}+\frac{\partial^2\eta}{\partial y^2}\right)}_{\text{gravity-driven erosion}}+\mathrm{DPA}+f\cdot\mathrm{DPA}_{\mathrm{edge}},\tag{5}$$

where ρ_{b} is bulk density of the peat soil (0.06 g cm^{-3}; Harvey et al. 2004), r is the rate of production of new floc (i.e., the erodible bed sediment layer), D_{sed} is the input diffusivity of the bed sediment, DPA is differential peat accretion, and f is an input scaling coefficient that governs vegetative propagation and belowground biomass expansion in slough cells adjacent to ridge edge cells. DPA represents the additional vertical accretion of ridges relative to sloughs resulting from the higher rates of primary production and more refractory biomass of ridge vegetation (Saunders et al. 2006). Summarizing the field-based numerical modeling of autogenic accretion processes described by Larsen et al. (2007), DPA is formulated as

$$\mathrm{DPA}=S_1\left[c_1\left(\frac{\eta^*}{S_2}\right)^3+c_2\left(\frac{\eta^*}{S_2}\right)^2+c_3\left(\frac{\eta^*}{S_2}\right)+c_4\right],\tag{6}$$

where c_1–c_4 are empirical coefficients (table A2) that result in a concave-up, single-hump DPA curve over the ridge elevations of interest. Input parameters S_1 and S_2 govern the maximum differential rate of peat accretion on ridges and the maximum ridge elevation relative to sloughs, respectively. Parameter η^* is the bed elevation adjusted for changes in water level (Z_{s}) relative to the mean water level at which the simulations of Larsen et al. (2007) were run (Z_{L}), so that $\eta^*=\eta-Z_{\mathrm{s}}+Z_{\mathrm{L}}$.

Because high-flow events occurred during just a fraction of each 1-year time step, the finite-difference algorithm for solving equation (5) multiplied the flow-driven erosion and deposition terms by that fraction. The remaining three terms represented average rates over the duration of the time step. All floc mass remaining at the end of the time step was assumed to be converted conservatively into peat.

Simulation Experiments

We executed the model in 137 Monte Carlo runs, in which 10 input parameters were varied within their plausible ranges (table A3) in a space-filling Latin hypercube design. For each combination of input parameters, the model was run for 2,700+ years, until stability in topography and vegetation state was reached. Model outcomes were classified according to whether they exhibited one, both, or neither of the behaviors associated with critical ecosystem functions in the Everglades: development of distinct longitudinal vegetation patterning with well-connected sloughs (e.g., fig. 1*B*) and equilibration of the landscape at high vegetation heterogeneity (28%–55% ridge). Quantitative criteria for these behaviors (table A4) were assigned on the basis of Everglades spatial analysis (Wu et al. 2006).

We identified threshold values of input parameters that cleanly divided model outcome behaviors through a cross-validated recursive-partitioning analysis (see app. B). We also assessed parameter sensitivity through stepwise multiple logistic regression using the main effects of the standardized, centered input parameters, quadratic terms, and two-way interaction terms. Sensitive input parameters that best predicted emergence of the two landscape behaviors were identified as the variables with the largest effect sizes in the most parsimonious regression model.

To evaluate the hypothesis of multiple stable states, we performed a one-dimensional numerical bifurcation analysis to identify stable and unstable equilibrium ridge coverages over a range of flow velocities (see app. B for details). Except for water-surface slope (a control on flow velocity) and initial ridge coverage, all input parameters were set equal to values that produced a landscape with both ecologically important behaviors of interest.

Finally, we performed perturbation experiments on a landscape that exhibited the behaviors of interest. In one experiment, the equilibrium landscape was subject to a decrease in water-surface slope, and in the other, it was subject to a combined decrease in water-surface slope and water level. Resulting changes in sediment fluxes affecting topography and vegetation distribution were monitored across the model domain to achieve a better mechanistic understanding of how patterned landscapes respond when subject to disturbance.

Results

General Dynamics of Evolution of Longitudinal Vegetation Patterning

Simulated flows exhibited quantitative and qualitative agreement with measured flow patterns in the field. Flows were highly heterogeneous, with slower flow over ridges, faster flow in sloughs, and divergence and convergence around the heads and tails of ridges, respectively (fig. C1; app. C). Velocities simulated over a daily time series of measured Everglades surface-water slopes and depths were found to be consistent with field measurements in ridges and sloughs (Harvey et al. 2009) to within 0.1 cm s^{-1} (root mean square error; $N = 149$). For simulated flow conditions representing a field tracer test, the computed slough dispersion coefficient matched the experimental value (0.01 m^2 s^{-1}; Variano et al. 2009).

When flows were sufficient to entrain bed sediment, emerging ridges first elongated because of sediment deposition in low-velocity regions upstream and downstream of ridges (video; app. C). As expanding ridges across the landscape displaced more flow toward sloughs, water levels, flow velocities, and bed shear stresses increased in sloughs, ridge elongation slowed, and net erosion occurred in sloughs just outside the ridge vegetation boundary, with net deposition occurring just inside the boundary (fig. C1).

Feedback processes governing sediment fluxes at ridge edges were essential in determining whether emerging landscapes attained planform stability at later stages of evolution. Ridges expanded radially through vegetative propagation, belowground biomass production, and gravitational erosion of sediment on topographic gradients (fig. 3*A*) until one of two negative feedbacks maintained stability. Under a "flow-induced" negative feedback, net elevation change of areas just outside the ridge boundary became 0, reflecting a balance between sediment erosion by flow and sediment additions from ridge expansion (fig. 3*B*). Alternatively, under a "water level–induced" negative feedback, the overall rate of increase in water surface elevation (due to displacement by accreting peat) equaled the rate of sediment accretion in regions just outside the ridge boundary, preventing emergent ridge vegetation from spreading. The relative dominance of these feedbacks at each time step was assessed by quantification of gross contributions of different peat aggradation and degradation processes (fig. 3) to changes in ridge edge elevation and comparison to changes in water-surface elevation.

The landscape-scale flow-induced and water level–induced feedbacks, which result from local-scale differential peat accretion and sediment transport feedbacks, governed the landscape's equilibrium morphology. When the flow-induced feedback was dominant, two outcomes were possible. Under moderate water-surface slopes (i.e., moderate flow velocities), the landscape typically achieved equilibrium at <55% ridge coverage (fig. 4), which is considered to be the threshold ridge coverage that distinguishes between well-preserved and deteriorating ridge-and-slough landscapes (Wu et al. 2006). At higher water-surface slopes, ridge growth would initially slow, but then emerging preferential channels (see app. C) would destabilize the landscape, causing ridge expansion to a much higher equilibrium coverage. Although the water level–induced negative feedback was present to some degree in all simulations, it was the dominant cause of landscape stability only at high ridge coverage (>80%), when sloughs had lost connectivity. Simulations without flow maintained minimal heterogeneity. Flow that redistributed sediment from sloughs to ridges was necessary for permanent or long-term persistence of well-connected sloughs (fig. C2).

Over a range in water-surface slope (which drives a range in flow velocities), simulated landscapes had multiple stable equilibria: one at zero ridge coverage and a family of equilibria at moderate to high coverage (fig. 4). Starting from low vegetation coverage, landscapes approached the lowest stable equilibrium (arrow *0* in fig. 4). Subsequently, a heterogeneous ridge-and-slough landscape could be destabilized through perturbations that decreased flow velocities and/or water levels (fig. 3*C*, 3*D* and arrow *1* in fig. 4). Both of these situations caused a shift in the balance of sediment redistribution and autogenic peat accretion processes at ridge edges that led to ridge encroachment into sloughs (arrow *2* in fig. 4) and ridge edges more rounded than those of a stable landscape (fig. 3). Changes in ridge coverage resulting from perturbations to flow velocity were unlikely to be reversed by removing the perturbation (arrow *3* in fig. 4), as indicated by the landscape's position within the family of stable equilibria. Multiple equilibria within this region exist because of the high resistance of vegetated ridge patches to erosion under the flows examined, which prevents the loss of preestablished ridges.

Sensitivity of Landscape Pattern to Environmental Conditions

Simulated landscapes that exhibited the behaviors of interest occupied a small portion of the parameter space (fig. 5). Recursive partitioning ($R^2 = 0.44$) and multiple logistic regression ($R^2 = 0.55$ and 0.48 for the top and bottom sections of table 1, respectively) indicated that landscape behaviors were sensitive to a consistent set of hydrologic, sediment, and vegetation properties. The initial water depth in sloughs was greater than 63 cm in all simulations that developed longitudinal vegetation patterning with well-connected sloughs and in 86% of all simulations that stabilized at high vegetation heterogeneity. Relatively high values of the water-surface slope, which is

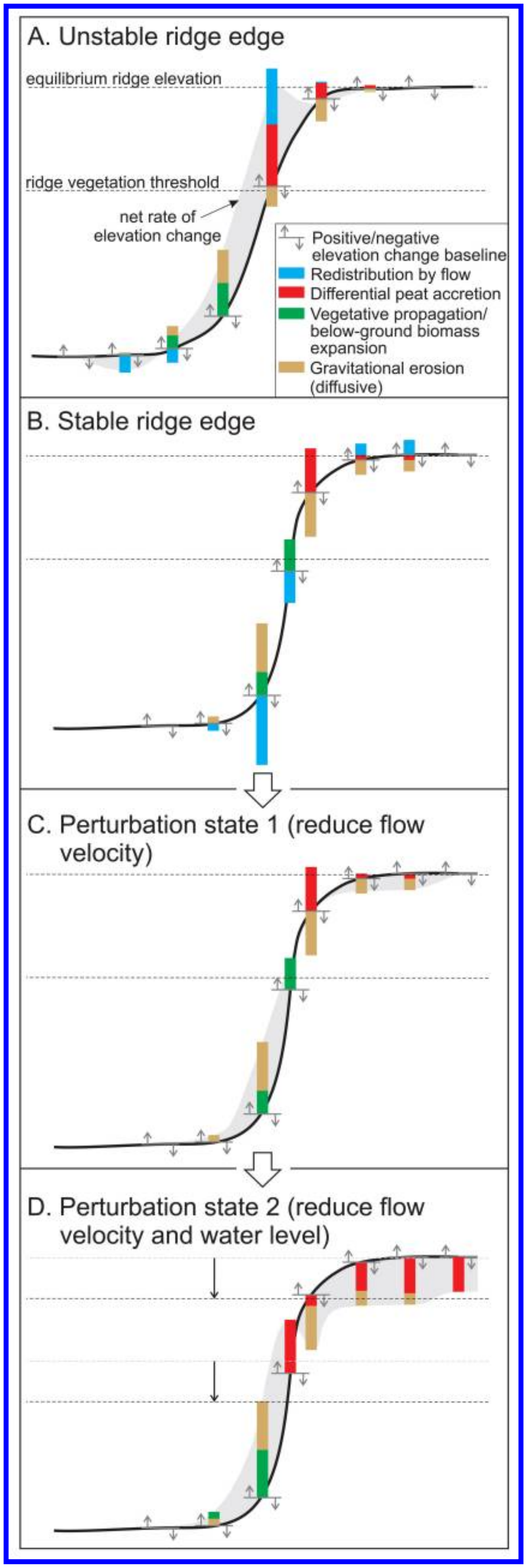

Figure 3: Cross sections show the magnitude of topographic rates of change at unstable ridge edges (*A*), stable ridge edges (*B*), and formerly stable ridge edges that become destabilized through perturbation (*C*, *D*). Lateral stability occurs when local rates of elevation change (relative to a constant baseline rate of peat accumulation) due to different processes (*stacked bars*) are in balance. Depicted topographies and rates of elevation change were acquired from unique simulation results chosen to illustrate likely outcomes of water management actions in the Everglades during the past century; other combinations of rates of elevation change that produce ridge stability or instability are also possible.

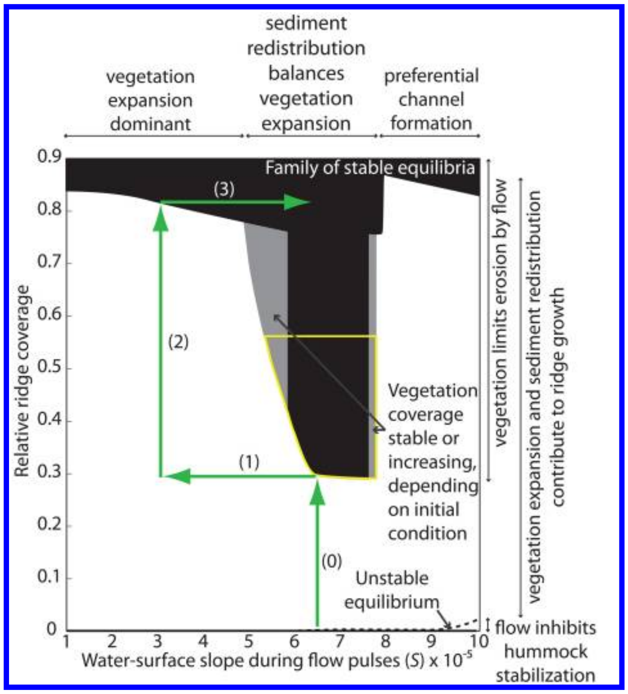

Figure 4: Landscape-scale bifurcation diagram, showing landscape evolution toward an equilibrium ridge coverage over a range of water-surface slopes. All other parameters were held constant, set equal to values that produce a parallel-drainage-patterned landscape at an S of 6.5×10^{-5}. The dashed line represents an unstable equilibrium, while the X-axis represents a stable equilibrium and the black portion of the plot represents a family of stable equilibria. The gray regions represent areas where vegetation is either stable or expanding, depending on the preexisting configuration of vegetation patches (i.e., depending on the trajectory by which the region was approached; see app. B). Areas in white represent regions of evolving landscapes. Parallel-drainage-patterned landscapes occupy a subset of the space that contains stable, highly heterogeneous landscapes (*yellow outline*) and are further distinguished by elongated ridges and well-connected sloughs. Arrows show a sample trajectory of evolution of a parallel-drainage landscape that evolved naturally (*0*), was subject to a step perturbation (*1*), evolved in response to that perturbation (*2*), and then experienced removal of the perturbation (*3*). Arrows *0–2* characterize the long-term and recent history of the Everglades ridge-and-slough landscape. For further description of the bifurcation analysis, see appendix B.

the dominant control on velocity and bed shear stress in emergent wetlands (Harvey et al. 2009), improved the probability of development of these landscape behaviors (fig. 5; table 1). However, the negative effect size for the square of water-surface slope (table 1) implied that the highest slough velocities impeded the development of longitudinal vegetation patterning with well-connected sloughs. Further, the positive effect of the interaction term between water-surface slope and the critical bed shear stress for sediment entrainment suggested that water-surface slopes only slightly above the entrainment threshold contributed to development of these valued behaviors. Relatively long annual high-flow durations generally improved the probability of longitudinal vegetation pattern development but also had a long-term destabilizing influence (table 1).

The equilibrium elevation of ridges, the spreading rate of ridges due to vegetative propagation and belowground biomass expansion, and the differential rates of vertical peat accretion on ridges relative to sloughs are properties controlled by the ridge vegetation community that were influential in determining landscape behaviors. To improve the probability of developing stable, heterogeneous landscapes, ridges had to be low and submerged (low ridge elevation scaling factor) to serve as sinks for sediment from sloughs during high flows (fig. 5). In systems like the Everglades, with relatively low rates of sediment mass transfer, preferential expansion of ridges parallel to flow at the initial stages of landscape development was essential for maintaining well-connected sloughs at later stages of landscape evolution. Thus, moderately high rates of vegetative propagation and belowground biomass production facilitated development of longitudinal vegetation patterning (table 1). In contrast, high vertical accretion rates (i.e., high differential peat accretion scaling factors) inhibited emergence of the longitudinal pattern structure. However, extremely low differential peat accretion rates were associated with landscapes that remained mostly (>90%) slough and never entered the positive-feedback cycle that promoted initial ridge growth. Other factors that contributed to the evolution of mostly-slough landscapes were low initial ridge coverage and sediment that required high bed shear stresses to entrain (fig. 5).

Landscape patterning was also sensitive to the ridge and slough sediment diffusion coefficients. Whereas high slough sediment diffusion coefficients had a strong negative effect on the probability of emergence of both behaviors, high ridge sediment diffusion coefficients had a positive effect, although extreme high values inhibited development of longitudinal vegetation patterning with well-connected sloughs (table 1).

Discussion

The model we present is the first coupled morphological, hydrological, and biological model of wetland landscape evolution that is complex enough to simulate detailed distributions of bed shear stress and sediment fluxes yet simple enough to enable Monte Carlo tests of sensitivity. It provides the first demonstration of how highly regular vegetation patterning parallel to flow can arise from scale-dependent feedbacks involving vegetation, flow hydraulics (i.e., patterns in bed shear stress), and hydrology (water levels) over certain bounds in environmental parameters.

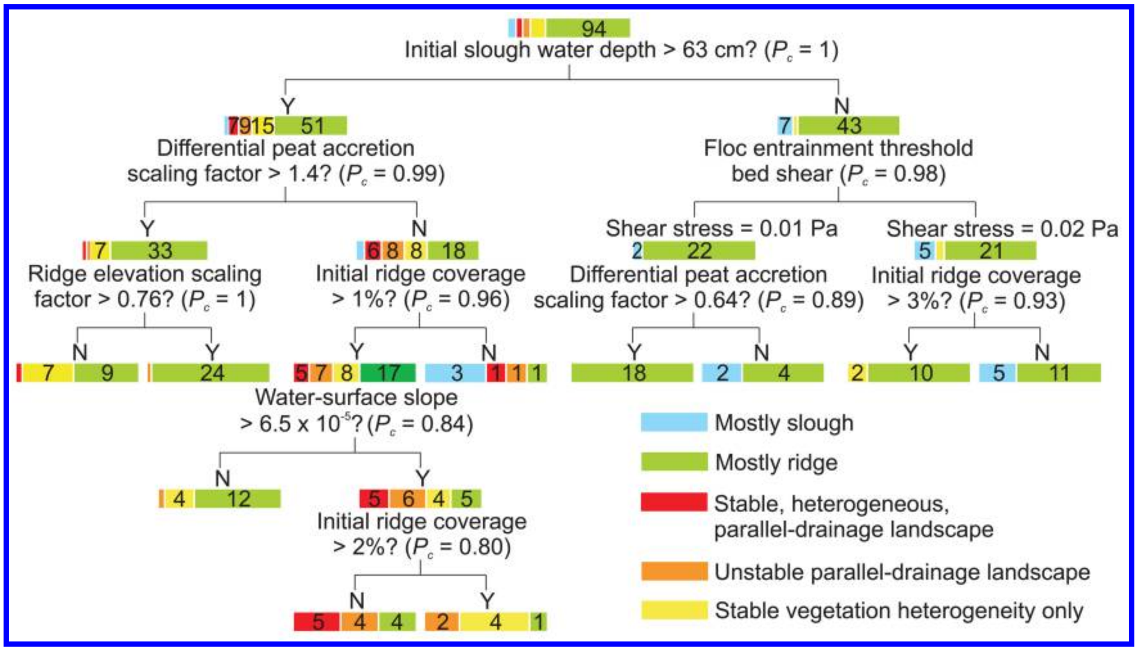

Figure 5: Recursive-partitioning tree of simulation outcomes. Simulations shown in red (e.g., fig. C2*B*) exhibit the behaviors with highest ecological value, meeting the criteria for heterogeneity, stability, elongation, and connectivity (table A4). Orange and yellow simulations exhibit some of these behaviors, with orange simulations meeting the criteria for elongation and connectivity (e.g., fig. C2*C*) and yellow simulations exhibiting stable heterogeneity. Blue and green simulations never exhibit these behaviors; blue simulations (>90% slough) never experience the positive feedback that promotes ridge growth. Depicted numbers are counts of the simulations falling into each category, and P_c values provide the percent confidence in each branch of the tree, based on a jackknife analysis (see app. B).

As we describe below, the results provide new recognition of autogenic peat accretion and sediment transport feedbacks as primary drivers of catastrophic shifts and multiple stable states in some ecosystems. These findings add to a growing awareness of the importance of sediment erosion and deposition feedbacks in structuring marsh ecosystems (Fagherazzi and Furbish 2001; D'Alpaos et al. 2007; Kirwan and Murray 2007), riparian wetlands (Heffernan 2008), and tidal flats (van de Koppel et al. 2001; Temmerman et al. 2007; van Wesenbeeck et al. 2008).

Over certain sets of environmental conditions, our model predicted emergence of well-connected parallel-drainage landscapes that exhibited good qualitative agreement with the Everglades ridge-and-slough landscape (fig. 1*C*). Small discrepancies between the morphologies of actual and simulated vegetation patches could be accounted for by field complexities not simulated in the model. For instance, the more linear nature of simulated ridges resulted from strict alignment of the hydraulic gradient with the long axis of the model domain, whereas in the field the underlying bedrock topography has a legacy effect of inducing flow that is not strictly unidirectional (Gleason and Stone 1994). Second, our model does not simulate tree islands, the largest but rarest vegetation patches observed in the field. The distribution of vegetation patch size in the field is also known to be sensitive to fire frequency and intensity (Brandt et al. 2002). Future refinements of the model to simulate flow resistance and peat accretion in tree islands and stochastic fire occurrence could improve the agreement between simulated and actual vegetation patch size distribution.

For longitudinal vegetation patterning to develop in our simulations, flow-induced redistribution of sediment from sloughs to ridges was needed (fig. 3). Beyond this basic hydraulic requirement, factors that restricted the formation of preferential flow channels were important in determining whether a highly heterogeneous ridge-and-slough-type landscape would be an equilibrium configuration. Preferential flow channels were the typical cause of loss of initially well-connected sloughs in the simulations because they captured surface-water discharge as they deepened, decreasing flow depths across the rest of the landscape and permitting ridge vegetation to expand rapidly (app. C). The end result was relatively deep parallel-flow channels with low coverage, similar to those that develop on tidal flats during marsh formation (Temmerman et al. 2007). The highest water-surface slopes, particularly when paired with a low critical shear stress for

Table 1: Sensitive simulation parameters that produce landscape behaviors linked to desirable ecosystem functions, assessed by stepwise multiple logistic regression

Behavior, parameter	Effect size β_i[a]	Likelihood ratio χ^2	P
Landscape develops a well-connected parallel-drainage morphology:			
Slough sediment diffusion coefficient	−16.4	18.8	<.0001*
Scaling factor for differential rate of peat accretion between ridge and slough	−6.3	6.4	.01*
Ridge sediment diffusion coefficient	5.8	4.0	.05*
Slough sediment diffusion coefficient × annual duration of high-flow events	5.1	15.0	.0001*
Annual duration of high-flow events	3.8	8.2	.004*
Scaling factor for ridge expansion by vegetation processes	3.1	12.1	.0005*
(Water-surface slope)^2	−2.8	11.0	.0009*
Water-surface slope	2.4	8.7	.003*
Initial water depth in deepest slough	2.0	8.3	.004*
Water-surface slope × critical bed shear stress for sediment entrainment	1.9	4.7	.03*
(Ridge sediment diffusion coefficient)^2	−1.7	7.9	.005*
Critical bed shear stress for sediment entrainment	.9	3.3	.07
Landscape stabilizes at high vegetation heterogeneity:			
Slough sediment diffusion coefficient	−20.4	28.7	<.0001*
Ridge sediment diffusion coefficient	16.5	28.2	<.0001*
Annual duration of high-flow events	−3.6	9.3	.002*
Initial water depth in deepest slough	3.4	27.8	<.0001*
Scaling factor for maximum ridge elevation	−2.9	20.1	<.0001*
(Scaling factor for maximum ridge elevation)^2	1.4	5.4	.02*
Water-surface slope	.8	5.1	.02*

[a] Positive values indicate a positive relationship between the parameter and the probability of occurrence (P) of the behavior, according to the multiple–logistic regression equation $P = \left(1 + e^{-\Sigma X_i \beta_i + \gamma}\right)^{-1}$, where X_i is the standardized, centered value of parameter i and γ is an intercept.

* Significant parameter at the $\alpha = 0.05$ level.

sediment erosion, resulted in a large variance in sediment erosion rates in sloughs, which facilitated preferential channel development (fig. 4) and decreased the probability of emergence of well-connected sloughs. Likewise, the combination of long flow durations and low slough sediment diffusivity favored preferential channel development (table 1).

Dynamics governing the topography of patch edges were also critical regulators of landscape morphology and stability. Edge topography affected the spreading rate of ridge vegetation, which could move only sloughward when the elevation of the peat just outside the ridge vegetation boundary was sufficiently high. The shape of the edge gradient also influenced rates of sediment entrainment outside the ridge boundary, with lower locations experiencing relatively high net entrainment and higher locations sometimes experiencing net deposition by settling, depending on global hydrologic variables. By reducing the topographic gradient on the slough side of ridge edges (e.g., fig. 3*A*), high slough sediment diffusion coefficients assisted radial expansion of ridges and inhibited development of the landscape behaviors of interest. In contrast, moderately high ridge sediment diffusion coefficients promoted development of these behaviors (table 1) by competing with differential peat accretion to limit the net accumulation of peat at the sawgrass boundary.

Catastrophic Shifts and Alternate Stable States

Our modeling supports the hypothesis that, because of cross-scale flow-vegetation feedbacks, longitudinally patterned wetlands are subject to catastrophic shifts to an alternately stable, more homogeneous state. After perturbations that cause preferential channel incision, decrease water levels, or reduce flow velocities and sediment redistribution (or, equivalently, increase plant production and peat accretion rates relative to flow), emergent ridge vegetation expands rapidly (figs. 3, 4), which dissects sloughs nondirectionally. Higher peat accretion rates and growth of the peat topography follow the emergent vegetation (Larsen et al. 2007), increasing its long-term stability. To reverse that expansion, the relative elevation of the soil colonized by emergent vegetation would have to decline to prevent ridge vegetation survival. However, flow velocities and bed shear stresses are greatly reduced in ridge vegetation patches, suppressing erosion (Larsen et al. 2009*b*). As a result, when high discharges are restored to an ecosystem subject to a period of lower flows (see arrows

1, *2* in fig. 4), ridges will remain wide (see arrow *3* in fig. 4) but water levels will be higher and flow velocities lower than in the original system. Consequently, longitudinally patterned wetlands with wide, connected sloughs are an indicator of a metastable ecosystem that is particularly sensitive to change.

Many of the factors to which longitudinally patterned landscapes are most sensitive are prone to alteration by human activity and climate change. For instance, because of compartmentalization of the Everglades, water depths, water-surface slopes, and the duration of high-flow events have decreased relative to predrainage conditions (National Research Council 2003). Furthermore, the ridge elevation scaling factor in peat systems is a function of redox potential and temperature (Larsen et al. 2007), and the slough sediment diffusion coefficient and entrainment threshold shear stress, both related to the cohesion of the flocculent bed sediment layer, can be altered by water quality conditions that change the abundance of periphyton (McConnachie and Petticrew 2006). Although changing environmental conditions make these diverse and ecologically valued landscapes vulnerable, the corollary is that these landscapes are particularly conducive to conservation and restoration management.

Implications for Restoration

Our results suggest that in the Everglades, remnant patterned portions of the ridge-and-slough landscape can likely be preserved through hydrologic management. Maintaining relatively high water depths (>63 cm in sloughs) is sufficient to preserve some topographic and vegetation heterogeneity (table 1). However, longitudinally patterned wetlands with well-connected sloughs require flows that redistribute sediment in order to promote initial ridge lengthening and restrict ridge widening caused by gravitational erosion and other processes at ridge edges (fig. 3). Flows that redistribute sediment generally require water-surface slopes near 6.5×10^{-5} (figs. 4, 5), two times the bed slope of the central Everglades but only slightly greater than that of Shark River Slough in the southern Everglades, which has a bed slope of 5.6×10^{-5}. The southern Everglades regularly experiences water-surface slopes of 6×10^{-5} (Harvey et al. 2009), but elsewhere, transient events, including pulsed releases of water from impoundments, are required to produce these water-surface slopes. Small-scale but intense precipitation cells and present-day water management may sometimes induce hydraulic gradients aligned transverse to the bed slope (e.g., Variano et al. 2009), but these events are not expected to contribute to parallel-drainage patterning. In contrast, a hydrological connection between Lake Okeechobee and the Everglades that was likely present during most years historically may have had substantial contributions to landscape formation and maintenance (McVoy et al., forthcoming). Recent simulations of lake overflow using the large-scale Everglades Natural Systems Model (Fennema et al. 1994), which predicts flow over 2 × 2-mile grid cells, suggest that these events may have produced sustained water-surface slopes of up to 1×10^{-4} (SFWMD 2007) that doubled surface-water discharge through the central Everglades in a direction parallel to the axis of ridge and slough elongation (Fennema 2008).

In our simulations, annual high-flow durations required to produce well-connected parallel-drainage landscapes are characteristic of a pulsing flow regime, averaging 3.6 days, although some successful simulations had annual high-flow durations as low as 1–2 days. However, since the assumption that floc was conservatively converted to peat is an oversimplification (Neto et al. 2006; Noe and Childers 2007; Wright et al. 2009), actual durations required for flow to sculpt a parallel-drainage landscape may be longer. Stable-isotope studies suggest that Everglades floc comprises 59%, 47%, and 43% of the carbon in peat at depths of 0–2.5, 2.5–5.0, and 5.0–10.0 cm, respectively (Troxler and Richards 2009). Future model refinements will be necessary to improve predictions of high-flow durations needed to sustain a well-connected parallel-drainage landscape.

Many portions of the Everglades have lost remnant heterogeneity after prolonged reductions in flow and water levels. Our results show how ridges would have expanded slowly into sloughs in areas where flow had been curtailed (fig. 3*C*), regulated by vegetative propagation, gravitational erosion of topographic gradients, and water level (the sensitive driver of differential peat accretion). Where water levels also dropped (fig. 3*D*), ridge vegetation, responding to a concurrent drop in the threshold elevation for colonization, would have rapidly encroached on sloughs. Because the presence of emergent vegetation suppresses local sediment erosion over the full range of realistic wetland flows (Larsen et al. 2009*b*), expansion of ridge vegetation into sloughs may not be easily reversed by restoring the original discharge, unless an external resetting mechanism is involved. This behavior suggests that although biological functions of remaining parallel-drainage areas of the Everglades can be preserved by managing water levels and flows under a pulsing regime that periodically increases water-surface slopes and bed shear stresses, restoration of degraded areas may require initial removal of emergent vegetation from historic sloughs.

General Influence of Vegetation and Particle Transport Feedbacks on Worldwide Wetland Evolution

The range of parameter values (table A1) that we examined encompasses many low-gradient ($S < 10^{-4}$) wetlands worldwide. The hydrology is broadly representative, and varying the equilibrium elevation of ridges and maximum differential peat accretion rate has the effect of varying the vegetation community type. Although we do not consider wetlands that lack autogenic sediment production, we do consider ecosystems with vast differences in allogenic sediment delivery, from those in which no sediment is transported to those in which channels completely erode their beds.

Our model assumes that conservative transport of carbon in suspended particles regulates the peat dynamic at ridge edges that restricts edge expansion. However, this mechanism is but one example in a range of global phenomena that would produce similar landscape behavior. For example, flow removing particles from just outside of ridge boundaries could transport limiting nutrients away from this zone, restricting the outward expansion of plants. In the Everglades, suspended particles are enriched in phosphorus (Noe et al. 2007), a limiting nutrient that could further contribute to landscape dynamics. Conversely, deposition of particles enriched in constituents that inhibit plant growth just inside ridge vegetation boundaries could also restrict boundary expansion. While these processes would produce landscapes with morphologies slightly different from those of our simulated systems, the direction of landscape change in response to perturbations would be the same (Othmer and Pate 1980). Mechanistically, our model encapsulates landscape response to redistribution of any particulate material that influences vegetation growth and/or bed elevation and is ubiquitously available throughout sloughs/channels.

Other factors not simulated in our model could also influence evolution trajectories of vegetated aquatic landscapes. In particular, episodic events such as fire (Givnish et al. 2008) or storms that scour ridge edges and deposit detritus on the ridge side of the emergent vegetation boundary (Zweig and Kitchens 2008) can act as resetting mechanisms that prevent the simulations classified as orange in figure 5 from diverging to a more homogeneous condition. In peat-based systems, fire would both reduce ridge spreading rates (by decreasing the height of the peat in the vicinity of the ridge/slough transition) and hinder the development of preferential flow channels (by equalizing slough peat elevations during drydowns, when water ponds in emerging preferential channels but not on higher elevations within the sloughs). Consideration of these resetting mechanisms effectively expands the region of the parameter space within which longitudinal vegetation patterning is a long-term configuration.

Overall, the greater mechanistic understanding of the similarities and differences between the dynamics of water-controlled ecosystems that we achieve will improve classification of these systems and aid in identifying interactions among key controlling factors and their relative importance. The Everglades example illustrates how new understanding about feedbacks between flow, vegetation, and sediment dynamics can help identify key variables, such as water depth and water-surface slope, that can be manipulated by water managers to restore beneficial ecosystem functions. Our modeling and sensitivity analysis approaches are general enough to be widely applicable to predicting how changing environmental conditions and water management strategies will affect ecosystem services in wetlands throughout the world.

Acknowledgments

This work was funded by National Science Foundation award EAR-0636079, the U.S. Geological Survey (USGS) Priority Ecosystems Studies Program, the USGS National Research Program, and the National Park Service, through interagency agreement F5284-08-0024. Reviews by L. Blum, G. Hornberger, C. Hupp, M. Voytek, and three anonymous reviewers improved the article.

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Associate Editor: Egbert H. van Nes
Editor: Donald L. DeAngelis

Setting sun casts its light on an Everglades slough (*foreground*) before sinking behind a ridge (*background*). Photograph by L. G. Larsen.