GEOPHYSICAL RESEARCH LETTERS, VOL. 39, L17401, doi:10.1029/2012GL052754, 2012

Orientation matters: Patch anisotropy controls discharge competence and hydroperiod in a patterned peatland

David A. Kaplan,[1,2] Rajendra Paudel,[3] Matthew J. Cohen,[2] and James W. Jawitz[3]

Received 18 June 2012; revised 29 July 2012; accepted 1 August 2012; published 6 September 2012.

[1] Identifying the mechanisms that drive development of self-organized patterned landscapes is essential for guiding ecosystem management and restoration. In this work, we modeled flow through real and geostatistically simulated landscapes to test the hypothesis that feedbacks between patch anisotropy and hydroperiod may be sufficient to explain development of the flow-parallel ridge-slough mosaic of the Everglades (Florida, USA). Results show patch anisotropy to be a strong predictor of hydroperiod, with ecologically significant increases in flooding duration (>40 days/year) in isotropic landscapes compared with areas of the Everglades with the best-conserved anisotropic patterning. Notably, hydroperiod differences among landscapes were largest in dry years, suggesting that low flow periods may be most influential in landscape pattern development, contrary to alternative models of pattern formation. This study demonstrates the potential for coupled feedbacks between landscape geometry and hydrology to drive anisotropic pattern formation via inundation frequency without requiring velocity-driven erosion and redistribution of particulates. **Citation:** Kaplan, D. A., R. Paudel, M. J. Cohen, and J. W. Jawitz (2012), Orientation matters: Patch anisotropy controls discharge competence and hydroperiod in a patterned peatland, *Geophys. Res. Lett.*, *39*, L17401, doi:10.1029/2012GL052754.

1. Introduction

[2] Self-organized patterned landscapes derive from coupled feedbacks between biotic and abiotic systems operating at different spatial scales, with short-range facilitation balanced by the existence of one or more long-range inhibitory mechanisms [*Rietkerk and van de Koppel*, 2008]. Landscape patterning is increasingly recognized as being critical to biological diversity [*Kolasa and Rollo*, 1991], ecological function [*Palmer and Poff*, 1997], and ecosystem resilience [*Scheffer et al.*, 2001] in a number of natural systems. In wetlands, coupled interactions among hydrology, vegetation, and topography have been shown to control landscape patterning in a variety of ecosystems including tidal marshes [*van Hulzen et al.*, 2007], meandering rivers [*Tal and Paola*, 2010], and boreal peatlands [*Glaser et al.*, 2004; *Eppinga et al.*, 2008, 2009]; however the feedback mechanisms that yield landscape pattern vary between systems. Identifying how these feedbacks drive the development and maintenance of landscape pattern is critical to the management and restoration of ecosystems in which they occur.

[3] One such ecosystem is the ridge-slough mosaic of the Everglades (Florida, USA), a patterned peatland which is hypothesized to have developed due to coupled feedbacks between primary production, soil elevation, and landscape hydrology [*Science Coordination Team* (*SCT*), 2003; *Larsen et al.*, 2007; *Cohen et al.*, 2011]. Under historic flow conditions, elongated ridges and connected sloughs were oriented parallel to the flow direction (Figure 1a), with an estimated elevation difference of 60–90 cm between shallow-water ridges and deeper-water sloughs [*McVoy et al.*, 2012] and a distinctly bimodal elevation distribution. Hydrological modifications during the 19th and 20th centuries drastically altered the timing and magnitude of flow [*Davis and Ogden*, 1994], resulting in more topographically uniform [*Watts et al.*, 2010] and isotropic [*Wu et al.*, 2006; *Nungesser*, 2011] landscapes (Figure 1b), with significant implications for the landscape's ability to convey water, as well as a number of detrimental ecological effects [*SCT*, 2003].

[4] Despite significant study, elucidating the processes linking hydrology and landscape patterning in the Everglades remains an unresolved and active area of research that is critical to restoration planning. Three primary hypotheses have been proposed to explain the development and recent degradation of the ridge-slough landscape: 1) phosphorous transport from sloughs to ridges driven by differential evapotranspiration and anisotropic hydraulic conductivity [*Ross et al.*, 2006; *Cheng et al.*, 2011]; 2) sediment entrainment and deposition driven by velocity differences between ridges and sloughs [*Larsen et al.*, 2007; *Larsen and Harvey*, 2010, 2011]; and 3) reciprocal feedbacks among hydroperiod, productivity, peat accretion, and landscape geometry (the "self-organizing canal hypothesis") [*Cohen et al.*, 2011; J. B. Heffernan et al., Discharge competence and pattern formation in peatlands: A meta-ecosystem model of the Everglades ridge-slough landscape, submitted to *Ecosystems*, 2012]. While modeling in support of the nutrient and sediment redistribution hypotheses has shown promise in generating ridge-slough-like patterning, different modeled ecohydrological feedback mechanisms may yield the same spatial structure [*Eppinga et al.*, 2008], making the simulated emergence of pattern insufficient to unequivocally support one hypothesis over another.

[5] Critically, empirical evidence of the hydrologic conditions required to support flow-parallel anisotropic patterning via nutrient accumulation is largely lacking [*Larsen et al.*, 2007]. Similarly, while velocities were likely higher in the historical system [*McVoy et al.*, 2012], it is unclear whether they were sufficient to entrain flocculent sediment,

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[1] Environmental Engineering Sciences Department, University of Florida, Gainesville, Florida, USA.

[2] School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA.

[3] Soil and Water Science Department, University of Florida, Gainesville, Florida, USA.

Corresponding author: D. A. Kaplan, Environmental Engineering Sciences Department, University of Florida, 6 Phelps Lab, P.O. Box 116350, Gainesville, FL 32611, USA. (dkaplan@ufl.edu)

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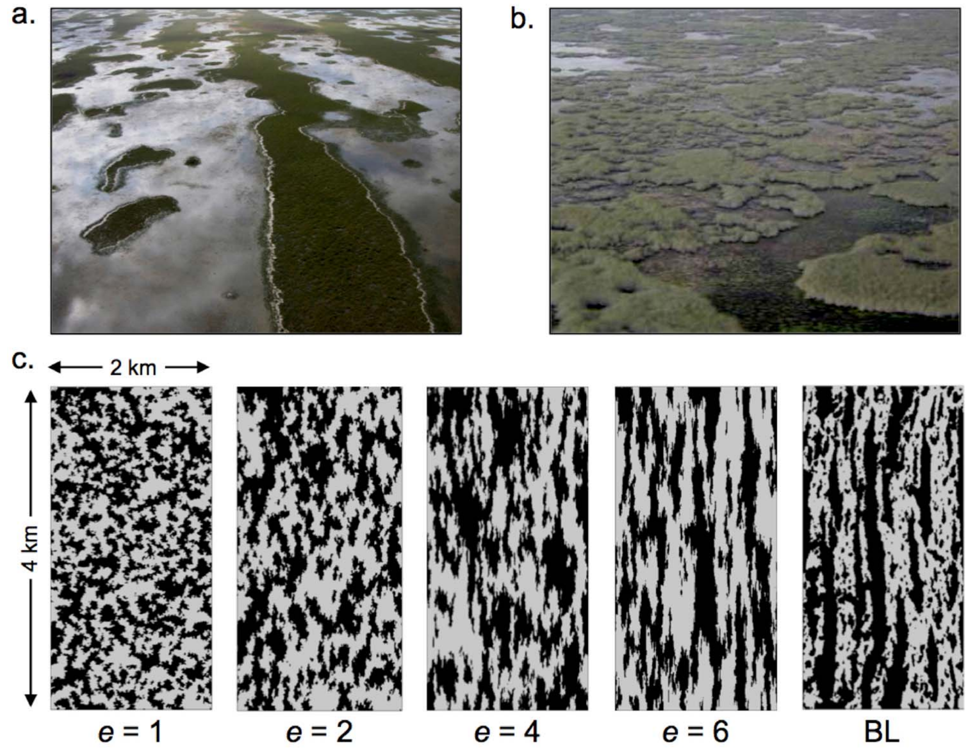

Figure 1. (a) Under historic flow conditions, elongated ridges and connected sloughs were oriented parallel to the flow direction. This patterning remains only in the best-conserved areas of the Everglades. (b) Elsewhere, compartmentalization and water management activities have led to the loss of linear patterning. (c) Example ridge (black) and slough (gray) simulated landscapes with varying degrees of anisotropy (*e*). 120 landscapes were simulated (n = 30 for each value of *e*) and compared to a reference benchmark landscape (BL). Each domain contained 181,804 square cells that were 6.67 m on each side. Photos courtesy of Scot Hagerthy and Christopher McVoy.

and if so, whether velocity differences between ridges and sloughs supported sediment distribution from sloughs to ridges [*Cohen et al.*, 2011]. Ongoing field-based research is focused on further elucidating the plausibility of velocity-driven pattern formation; however, given the persistence of ridge-slough patterning in areas with contemporary flow velocities too low to support sediment redistribution, alternative hypotheses of pattern formation and maintenance merit investigation.

[6] The self-organizing canal (SOC) hypothesis suggests that landscape patterning in the Everglades may arise without sediment or nutrient redistribution [*Cohen et al.*, 2011]. Briefly, the SOC hypothesis proposes that anisotropic landscape patterning in the ridge-slough mosaic can arise from local positive feedbacks among hydroperiod, productivity, and carbon accretion that create two stable carbon equilibria (i.e., two elevations: shallow-water ridges and deeper-water sloughs) coupled with a distal negative feedback between ridge expansion and the ability of the landscape to convey water (i.e., landscape-scale specific discharge competence, q [$L^2\ T^{-1}$], defined as discharge per unit width). Crucially, the SOC hypothesis posits that this negative feedback is anisotropic, with *lateral* expansion of ridges into sloughs substantially reducing q, requiring deeper overall flooding to convey the same flow, which in turn inhibits expansion of shallow-water ridges. In contrast, *longitudinal* ridge expansion has a minimal effect on q. In other words, ridge prevalence and orientation have a direct (and directional) effect on landscape flooding dynamics, which in turn affect the prevalence and orientation of ridges. The anisotropic patterned landscape evolves via the recursive growth and decline of ridges as sloughs become longitudinally connected to provide the requisite landscape drainage capacity.

[7] In this work we quantify the magnitude of the anisotropic negative feedback proposed in the SOC hypothesis by modeling the relationship between flow and depth in a series of geo-statistically simulated landscapes and enumerating the effect of patch anisotropy on q and hydroperiod. Specifically, we hypothesize that patch anisotropy impacts flooding dynamics in a flowing, patterned peatland such as the Everglades and propose that this directional hydrological phenomenon may be sufficient to exert the distal negative feedback mechanism that drives development of the flow-parallel ridge-slough mosaic.

2. Methods

[8] For a given set of boundary conditions, flooding dynamics in a lotic wetland are determined by topography, flow-path connectivity, and bed and vegetative friction, which together describe “landscape hydraulic geometry.” Metrics of hydraulic geometry driven by landscape pattern include patch prevalence (i.e., the proportion of the landscape inhabited by each patch type), patch elevation differences, and patch geometry (i.e., parallel vs. orthogonal to flow, isotropic vs. anisotropic). To test the effects of varying patch anisotropy on landscape-scale flooding dynamics, we created 120 2 × 4-km ridge-slough synthetic landscapes (SLs) with anisotropy (*e*, defined as the ratio of the major and minor

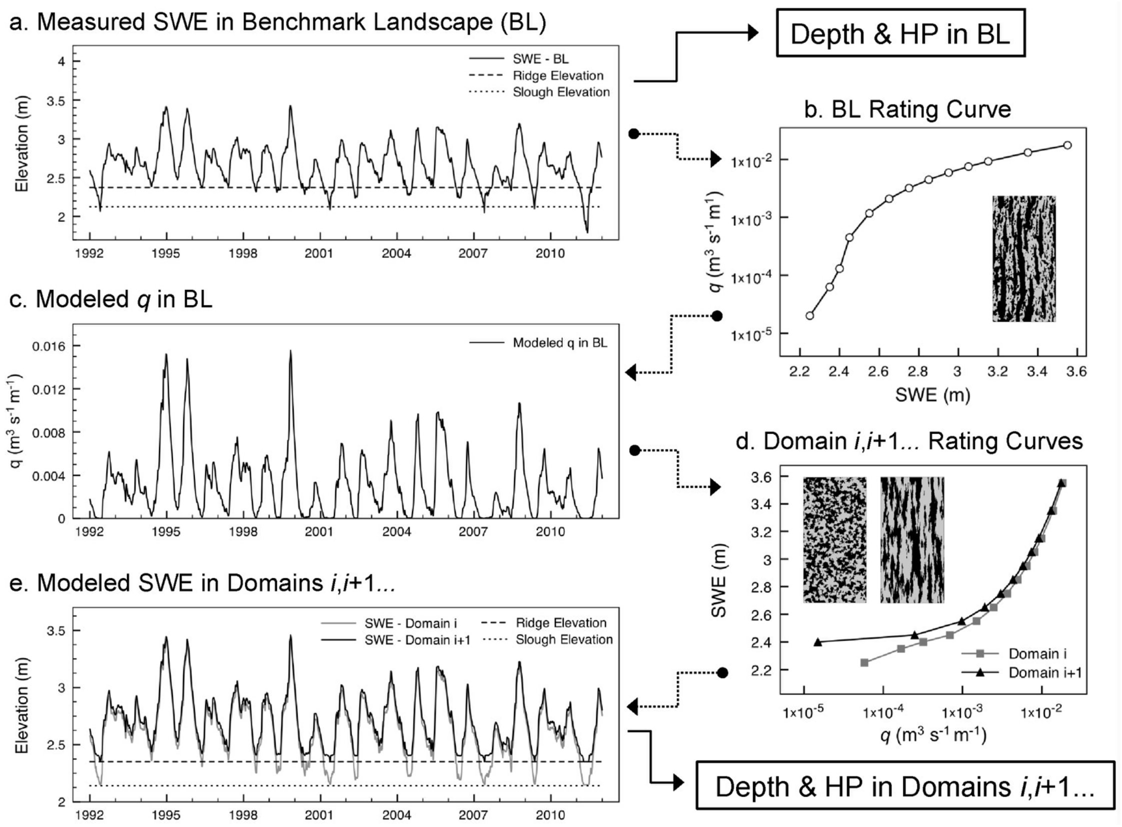

Figure 2. Method for evaluating hydrologic effect of patch anisotropy. (a) First, surface water elevation (SWE) data were used to calculate depth and hydroperiod (HP) in a benchmark landscape (BL) in the Florida Everglades. Next, (b) a rating curve relating SWE to discharge competence (q) in the BL was used to estimate (c) q in the BL. (d) Rating curves for all other domains were then used to predict (e) SWE time series, flooding depths, and hydroperiod in all domains.

ranges) ranging from e = 1 (perfectly isotropic) to e = 6 (highly elongated in the direction of flow) using sequential indicator simulation in GSLib [*Deutsch and Journel*, 1998] (Figure 1c). To isolate the effects of anisotropy, ridge prevalence (%R) was fixed at 50% [*Wu et al.*, 2006], the ridge-slough elevation difference (Δz) at any domain cross-section was fixed at 0.25 m [*Watts et al.*, 2010], the overall landscape slope (s) was 3×10^{-5} m/m [*Egler*, 1952], and the scale of pattern geometry was constrained using a minor range of 100 m [*Watts et al.*, 2010] in all SLs.

[9] Since local flows at specific locations in the Everglades are not known, but local stages are, we created a 2 × 4-km benchmark landscape (BL; Figure 1c) to estimate flow based on measured surface water elevation data (see below), enabling us to compare flooding dynamics between the BL and SLs across a benchmark flow time series. The BL was selected from the portion of the Everglades with the most well-conserved remnant landscape patterning (central Water Conservation Area 3A) [*Nungesser*, 2011] and was generated using remotely-sensed vegetation data [*Rutchey et al.*, 2006] and the values of Δz and s above. Major and minor ranges in the BL were estimated by fitting an exponential semivariogram model in GS+ (Gamma Design Software, Plainwell, MI), yielding e = 4.5. Finally, domains with uniformly distributed, 100-m wide, rectangular ridges oriented parallel and orthogonal to flow (not shown) were created using the values of %R, Δz and s above to serve as landscape orientation end-members.

[10] Domain-specific relationships between surface water elevation (SWE) and steady state q (i.e., landscape "rating curves") were developed for each of the SLs and the BL using a spatially distributed numerical flow model (SWIFT2D) that solves the vertically integrated mass and momentum equations [*Schaffranek*, 2004]. Rating curves were created by applying a series of constant head boundary conditions (BCs) at the up- and downstream model domain boundaries assuming uniform flow (i.e., parallel bed and surface water slopes), with no-flow BCs at the domain lateral boundaries. While *Harvey et al.* [2009] observed temporally variable water surface slopes that were most often less than the bed slope in the present-day, compartmentalized system, deviations from uniform flow conditions are thought to have been rare under historic conditions [*McVoy et al.*, 2012]. Rating curves were developed over a range of SWE equivalent to slough depths of 0–1.4 m based on observed stage data, allowing us to compare flooding depths across domains at any value of q. While several studies have found Manning's roughness (n_m) to vary spatially and temporally in ridges and sloughs [e.g., *He et al.*, 2010; *Min et al.*, 2010], we applied a homogenous, depth-independent *nm* value of 0.45 in both ridges and sloughs to further isolate the specific effects of patch anisotropy. This simplification yields conservative

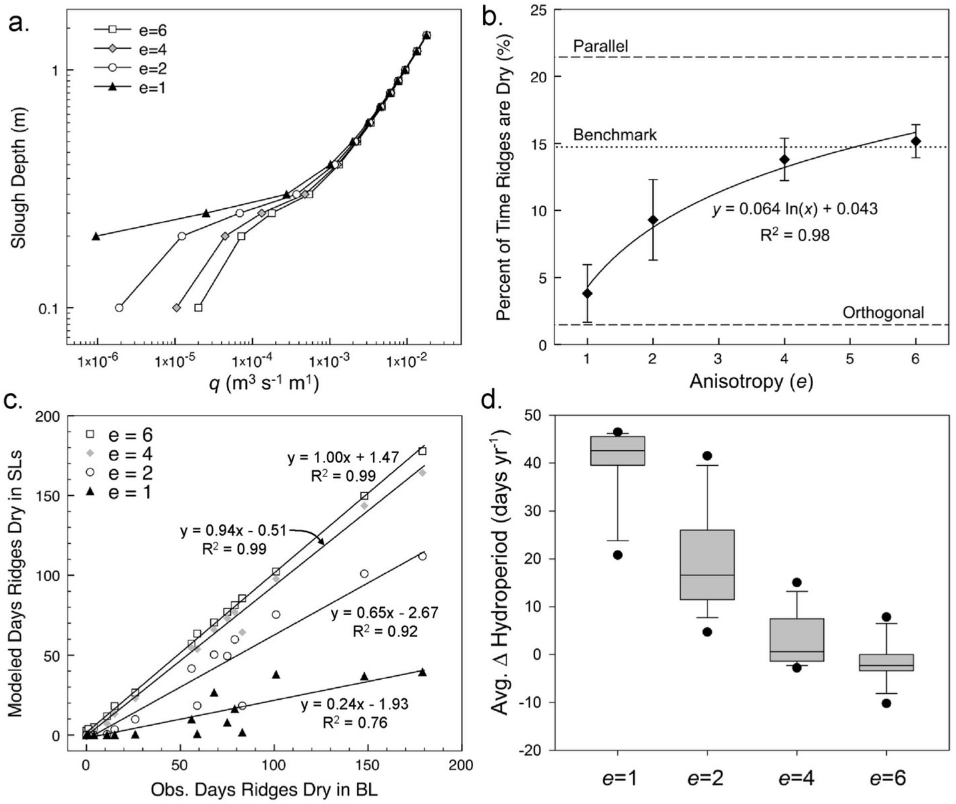

Figure 3. (a) Landscape rating curves illustrating average discharge competence (q) in domains with different anisotropy (e) values at depths of 0.1–1.4 m. (b) The proportion of time ridges were exposed as a function of e. Error bars denote standard deviation. (c) The yearly number of days ridges were exposed in the benchmark landscape (BL) vs. the average number of days ridges were exposed in simulated landscapes (SL) with different e-values. (d) Box plots showing average yearly changes in hydroperiod relative to the BL (Δ hydroperiod) as a function of e. Symbols denote 95% CI.

estimates of differences in flooding dynamics between landscapes, which would be magnified by applying higher n_m values in ridges (vis-à-vis sloughs) and at low flows. SWIFT2D results were validated by comparing modeled flows in the domain with ridges oriented parallel to flow (for which analytical solutions exist) to Manning's-calculated flows over the range of BC heads with excellent results (Nash-Sutcliffe coefficient of efficiency = 0.99).

[11] Differences in flooding dynamics across domains were assessed based on two ecologically significant hydrologic metrics: inundation depth and hydroperiod. Hydroperiods were calculated following the algorithm in Figure 2 using a 20-yr record of daily SWE data from the Everglades Depth Estimation Network – Site 64, located ca. 7.5 km south of the BL (http://sofia.usgs.gov/eden/). First, depth and hydroperiod in the BL were calculated using the observed SWE time series (Figure 2a), based on ridge and slough elevations at Site 64. Next, SWE in the BL was used with the BL rating curve developed from the hydrologic model (Figure 2b) to calculate a daily q time series in the BL (Figure 2c). This discharge was then routed through all domains using domain-specific rating curves (Figure 2d) to predict daily SWE (Figure 2e), flooding depths, and hydroperiods in all domains. The use of steady state landscape rating curves to compare time series of flooding depths and hydroperiods assumes that non-uniform flow behavior was rare in the historic system [*McVoy et al.*, 2012] and that its effects on overall flooding dynamics are small, particularly given the strong autocorrelation of flow and depth time series.

3. Results

[12] Differences in flooding depths (Δd) between landscapes with different e-values were largest at low q and decreased with increasing flow (Figure 3a). At extremely low flows, average Δd between landscapes with $e = 1$ and $e = 6$ approached 20 cm, but decreased to ca. 1 cm at the highest values of q. Notably, mean Δd between these landscapes was only 3.2 cm at the median contemporary value of q in WCA-3A (ca. 1.33×10^{-3} m^3 s^{-1} m^{-1} [*Harvey et al.*, 2009]), suggesting that patch anisotropy may only weakly affect long-term average flooding depths. However, given the seasonal flood pulse that characterizes the hydrology of the Everglades (e.g., Figure 2a), a more integrated measure of flooding dynamics (e.g., hydroperiod) is likely required to characterize the ecologically relevant effect of anisotropy on dynamic landscape hydrology.

[13] Since dry periods exert critical control on carbon oxidation and accretion [e.g., *Sulman et al.*, 2012]), the effect of e on ridge hydroperiod is presented as the proportion of time that ridges were *not* inundated over the 20-yr period of record (Figure 3b). Patch anisotropy dramatically influenced ridge hydroperiod, with ridges in the most

anisotropic landscapes ($e = 6$) exposed approximately 300% longer than those in the most isotropic landscapes ($e = 1$). Measured ridge hydroperiod in the BL ($e = 4.5$) fell between those in the $e = 4$ and $e = 6$ landscapes, demonstrating that patch anisotropy is predictive of hydroperiod in real, as well as simulated landscapes. As expected, ridge hydroperiods in the BL and SLs were bounded by those in end-member parallel and perpendicular domains (Figure 3b).

[14] Interannual hydrologic variability markedly affected the relationship between e and hydroperiod. A linear relationship was observed between the modeled number of days ridges were exposed (per year) in SLs vs. the observed number of days ridges were exposed in the BL (Figure 3c). Differences in ridge hydroperiod ($\Delta HP_{\mathrm{i,j}} = HP_{\mathrm{i,j}} - HP_{\mathrm{BL,j}}$ for domain i and year j) were minimal in wet years (i.e., the cluster of points near the origin in Figure 3c), but diverged greatly as a function of e in dry years. For example, ridges in landscapes with $e = 1$ were flooded an average of 140 days longer than the BL in 2007, the driest year in the period of record. Slopes of the linear regressions in Figure 3c indicate the overall effect of e on ridge hydroperiod relative to the BL (i.e., 76 and 35% reduction in the number of dry ridge days in landscapes with $e = 1$ and 2, respectively; little change in landscapes with $e = 4$ or 6). Values of ΔHP averaged over the 20-yr period of record were largest in the most isotropic landscapes (avg. $\Delta HP = 40$ days) and decreased with increasing anisotropy (Figure 3d), highlighting the potential for patch anisotropy to exert ecologically meaningful control on hydroperiod on longer-term time scales.

4. Discussion

[15] Correctly identifying the feedback mechanisms responsible for landscape pattern formation (and degradation) is critical to planning ecosystem restoration and management. While Everglades restoration efforts have appropriately focused on “getting the water right” [e.g., *Sklar et al.*, 2005], presuming that the desired ecological recovery will follow, a lack of historical data makes setting specific hydrological restoration goals a challenge. In particular, determining the primacy of hydroperiod vis-à-vis velocity as the principal hydrologic driver organizing landscape patterning is fundamental to developing the appropriate restoration approach; achieving the velocities required to entrain and transport sediment [*Larsen et al.*, 2009] would likely require upstream storage and episodic release of water, which may be antagonistic to maintaining appropriate hydroperiods across the landscape. While it is possible, even likely, that both hydroperiod and velocity-driven sediment redistribution are important to landscape pattern development [*Cohen et al.*, 2011], this study demonstrates the sufficiency of landscape hydraulic geometry to create ecologically significant effects on flooding dynamics (i.e., hydroperiod) as a function of patch anisotropy, which supports the self-organizing canal hypothesis.

[16] The effects of e on flooding depths across a range of flows highlighted the particular importance of low flows in driving hydroperiod differences among landscapes. Fundamentally, these differences are driven by the ability of a landscape to route water at different depths. When depths are high, ridges and sloughs in all domains are inundated, and flow is driven primarily by s and n_m, yielding minor differences in q across domains (i.e., top-right portion of Figure 3a). As depths decrease, landscape hydraulic geometry has an increasingly strong effect on q, with the greatest divergence between landscapes at the lowest depths (i.e., bottom left portion of Figure 3a). At depths $< \Delta z$, differences in q are increasingly driven by the presence of connected slough flow paths. In our SLs, slough connectivity (defined as the presence of at least one cell-width of continuous slough connection between upper and lower domain boundaries) was strongly dictated by e: 97% of landscapes with $e = 6$ had slough flow connectivity compared to only 3% of landscapes with $e = 1$ (37 and 67% of landscapes were connected for $e = 2$ and $e = 4$, respectively). While low flows are routed through sloughs at low depths in well-connected landscapes, water must overtop ridges to move the same flow downstream in disconnected landscapes. For landscapes with the same e-values, variance in hydroperiod (i.e., error bars in Figure 3b) is likely driven by the “quality” of connectivity, a property describing the location and geometry (width, tortuosity) of slough connectivity that is likely to be more precisely enumerated by new percolation metrics [*Larsen et al.*, 2012].

[17] The ecological significance of changes in hydroperiod due to varying landscape geometry derives from impacts on vegetation zonation [e.g., *Zweig and Kitchens*, 2008] and the point-scale carbon balance [*Watts et al.*, 2010], both of which have the potential to feed back to the landscape by altering hydraulic geometry. The results of this study demonstrate that decreasing e increases ridge hydroperiod (i.e., decreases the proportion of time that ridges are dry). Ridges in SLs with $e = 1$ were exposed to an average of 40 fewer days of aerobic oxidation per year than the BL ($e = 4.5$), a decrease of 74%. Applying patch-specific, depth-dependent n_m values would amplify these differences, with particularly strong effects during low flows, when depth-dependent n_m formulations drive the largest divergence in roughness between ridge and slough patches [*Min et al.*, 2010]; quantifying the magnitude of these effects is the focus of ongoing work. Given contemporary estimates of mean annual ridge exposure in central WCA-3A ranging from ∼10 days [*Givnish et al.*, 2008] to ∼55 days (this study and *Cohen et al.* [2011]), a 40-day increase in ridge hydroperiod appears to be profoundly ecologically significant. While previous studies have shown the importance of water level to soil respiration rates [*DeBusk and Reddy*, 2003] and the overall carbon balance [*Sulman et al.*, 2012], further work is needed to explicitly tie respiration rates to functional hydrologic metrics such as hydroperiod.

[18] The conceptual model of ridge-slough formation based on velocity-driven entrainment and deposition of sediment [*Larsen et al.*, 2007; *Larsen and Harvey*, 2010, 2011] focuses on the influence of large, episodic flow pulses (i.e., high flows and wet years) to achieve entrainment velocities to transport and deposit flocculent sediment. That contemporary velocities are too low to support this process [*Harvey et al.*, 2009] may suggest that large pulses need to be engineered. This study, in contrast, indicates that differences in hydrology among landscapes are most profound during low flows and dry years (Figure 3c), suggesting that dry years are likely to be more influential in modifying landscape patterning than wet years. This outcome may be in better concordance with a palynological study [*Bernhardt and Willard*, 2009] that suggests ridge formation was initiated by short term regional drying (i.e., during the Medieval

warm Period and the Little Ice Age), after which ridges persisted in roughly their current configuration until the initiation of water management in the 20th century.

[19] The complexities of coupled feedbacks among hydroperiod, productivity, peat accretion, and landscape geometry make modeling a vital tool in the exploration of hypotheses about ridge-slough landscape pattern development and maintenance. In this study, hydrologic modeling yielded critical insights about the hydrologic effects of patch anisotropy in a flowing wetland, providing support for the assertion that patch anisotropy controls discharge competence and thus landscape flooding duration. These results complement recent analytical model support for the sufficiency of the SOC hypothesis to explain development of a bimodal, anisotropic landscape (Heffernan et al., submitted manuscript, 2012), however further field-based research is required to unequivocally discriminate between different hypotheses of pattern formation [*Eppinga et al.*, 2008].

[20] The SOC hypothesis has two components: 1) the effects of pattern on hydrology and 2) the effects of hydrology on changing pattern. This study provides support for the former, but the latter requires a spatially distributed model in which hydrologic outputs are used to drive spatial variation in organic matter accumulation and vegetation transitions based on relationships developed at the point scale. Coupling this model with topography and vegetation monitoring efforts will further elucidate the mechanisms that control landscape development and degradation in the Everglades and help to guide future restoration and management efforts.

[21] **Acknowledgments.** Support for this work was provided by the Army Corps of Engineers through the Restoration, Coordination, and Verification program of the Comprehensive Everglades Restoration Plan. R.P. and J.W.J. were supported by the Florida Agricultural Experiment Station. The authors thank Stuart Muller, Zuzanna Zajac, and Eric Swain for their invaluable insight and assistance. The authors thank Laurel Larsen and an anonymous reviewer for their assistance in reviewing and improving this paper.

[22] The Editor thanks Laurel Larsen and an anonymous reviewer for their assistance in evaluating this paper.

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