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Key Points:

- Upscaling flow resistance with generalized spatial averaging is appropriate for estimating large-scale wetland/floodplain/delta discharge
- Connectivity is an increasingly important driver of flow at low water levels, contributing to large-scale ecogeomorphic feedback
- Flow through well (compared to poorly) connected hydroscapes is more resilient to perturbations in water depth or landscape configuration

Supporting Information:

- Supporting Information S1

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How Important is Connectivity for Surface Water Fluxes? A Generalized Expression for Flow Through Heterogeneous Landscapes

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Abstract How important is hydrologic connectivity for surface water fluxes through heterogeneous floodplains, deltas, and wetlands? While significant for management, this question remains poorly addressed. Here we adopt spatial resistance averaging, based on channel and patch configuration metrics quantifiable from aerial imagery, to produce an upscaled rate law for discharge. Our model suggests that patch coverage largely controls discharge sensitivity, with smaller effects from channel connectivity and vegetation patch fractal dimension. However, connectivity and patch configuration become increasingly important near the percolation threshold and at low water levels. These effects can establish positive feedbacks responsible for substantial flow change in evolving landscapes (14–36%, in our Everglades case study). Connectivity also interacts with other drivers; flow through poorly connected hydroscapes is less resilient to perturbations in other drivers. Finally, we found that flow through heterogeneous patches is alone sufficient to produce non-Manning flow–depth relationships commonly observed in wetlands but previously attributed to depth-varying roughness.

Plain Language Summary Hydrologists can readily predict the flow of water in uniform channels or over fields of vegetation, but when both vegetated patches and flowing channels are present (as in a wetland, river delta, or floodplain), it can be difficult to estimate the volume of flow attainable without resorting to complicated two-dimensional models. This makes it difficult to achieve a general understanding of the aspects of landscape structure that really matter for conveyance of flow. Such an understanding would benefit a variety of engineering practices and restoration design, enabling us to address questions such as, "Does the connectivity of flowing channels for water really matter to restoration of the Everglades landscape?" or "How should vegetation be planted in a wetland designed for wastewater treatment to optimize treatment efficiency?" Here, the authors developed a simple expression for estimating flows through a vegetated landscape as a function of metrics of the landscape's configuration. Their results come from analysis of over 11,000 numerical models that simulate flow through landscapes with different structures. They found that flows are very sensitive to channel connectivity when water levels are low but much more sensitive to the sheer area of vegetation patches when water levels are high.

1. Introduction

Feedbacks between biotic and abiotic components of environmental systems can produce emergent behavior, such as threshold-type transitions or the tendency to remain in a particular state despite perturbation. These behaviors can stymie efforts to maintain or restore ecosystem function (Larsen & Harvey, 2010; Suding et al., 2004). In aquatic landscapes, feedbacks between flow and vegetation can structure the development of ecosystems and their physical templates through fluvial biogeomorphic succession (Corenblit et al., 2007, 2015), in which hydrologic connectivity to river channels controls the balance between abiotic and biotic interactions engaged in ecogeomorphic feedback. The fluvial biogeomorphic succession theory augments a growing focus on large-scale feedbacks in ecology and geosciences (De Lima et al., 2015; Meire et al., 2014; van de Koppel et al., 2015). In particular, there has been a call to better understand how connectivity (used here in the sense of structural connectivity, which describes the physical contiguity of landscape elements such as flow channels) impacts delivery of sediment and nutrients and associated feedbacks in low-gradient landscapes such as floodplains and deltas (Paola et al., 2011; Passalacqua, 2017; Sendrowski & Passalacqua, 2017) and in wastewater treatment wetlands (Sabokrouhiyeh et al., 2016). Here we quantify the sensitivity of large-scale flow to landscape spatial configuration and develop a relationship that predicts landscape-scale discharge from spatial configuration metrics, flow resistance properties, and water levels.

To develop a relationship that predicts free-surface discharge at large scales, we invoke the ergodic hypothesis, whereby properties influencing flow at large scales can be represented as spatial averages of these properties at smaller scales (Lumley & Panofsky, 1964). Here, we adopt the Manning equation (1) (but see Text S1 in the supporting information for additional generalizations) to predict discharge per unit width, q [$L^2\ T^{-1}$], using an upscaled resistance term, H_{eff} [L], computed as a generalized spatial average in a binary landscape of roughness patches (subscript p) and channels (subscript c; equation (2)):

$$q = {H_{\mathrm{eff}}}^{5/3} S^{1/2}, \tag{1}$$

where $H_{\mathrm{eff}} \equiv \overline{Kh}$ and $K \equiv n^{-\frac{3}{5}}$, and

$$H_{\mathrm{eff}} = \left[p\left(K_{\mathrm{p}}\left(h - z_{\mathrm{p}}\right)\right)^{\omega} + (1-p)(K_{\mathrm{c}}h)^{\omega}\right]^{1/\omega}. \tag{2}$$

Above, K is “conductivity” (i.e., inverse local roughness, which does not account for shear layer formation), h is water depth within channels [L], S is the energy slope (approximated here as the bed slope) [−], n is the metric Manning roughness [$T\,L^{-1/3}$], p is the areal coverage of patches (e.g., of vegetation) [−], z_{p} is the elevation of those patches [L], ω is a fitted averaging exponent [−], and the overbar is the spatial averaging operation.

A primary objective is to develop a quantitative relationship between ω and landscape configuration metrics. To do so, we reanalyze a set of previously published two-dimensional simulations of flow through heterogeneous, binary landscapes with diverse spatial configurations (Kaplan et al., 2012). Based on the discharge solutions (q) from these simulations, we solve for H_{eff} in equation (1) and then for ω in equation (2). Next, we statistically model the fitted ω as a function of landscape configuration metrics and water level. Second, based on the statistical model, we perturb these landscape configuration metrics individually and interactively to evaluate the sensitivity of large-scale discharge to their values.

The sensitivity analysis addresses two questions. First, what is the individual effect of each landscape characteristic in controlling large-scale fluxes? Second, in a landscape evolving through ecogeomorphic feedbacks that alter hydrologic and landscape characteristics simultaneously, what fraction of the change in flux is attributable to each control? The latter question is relevant to understanding mechanisms of landscape pattern development and degradation in the Everglades, which has undergone diminished ridge patch anisotropy and slough (channel) connectedness after extensive hydrologic modifications that reduced water surface slope and depth. Ultimately, pattern degradation has been attributed to lower velocities decreasing or stopping sediment redistribution (Larsen & Harvey, 2010) and/or changing hydroperiods in a way that allows for excess vegetation growth in sloughs (Acharya et al., 2015; Cohen et al., 2011; Heffernan et al., 2013). Here we ask to what extent those diminished flow velocities are due to large-scale landscape configurational feedbacks rather than to the original hydrologic perturbation.

This work builds on a long history of upscaling analyses in groundwater hydrology, as reviewed by Cushman et al. (2002) and Farmer (2002). Groundwater parameters typically upscaled include fracture aperture width, hydraulic conductivity, and dispersivity (Gelhar & Axness, 1983; Tsang & Tsang, 1989). “Equivalent” upscaled values are those representative of an area larger than the small-scale heterogeneity; “effective” values represent the limit of equivalent values as the domain extent increases (Dagan, 2001). While many have approached the challenge of developing upscaled parameters stochastically (Dagan et al., 2013; Rubin, 2003), others have used the generalized average (e.g., equation (2)) to compute effective parameter values heuristically (Desbarats, 1992). It is widely recognized that knowledge of the probability density functions of hydraulic parameters is insufficient to compute effective values; the connectivity of those parameters also matters. Journel et al. (1986) suggested that ω depends on the correlation length, p, and average aspect ratios of porous media features. Ronayne and Gorelick (2006) extended these ideas with formal sensitivity analyses on effective permeability computed from simulated flow through binary, two-dimensional fracture networks and found ω to be positively dependent on fracture-to-matrix permeability ratios and inversely dependent on the network’s fractal dimension and spanning-path tortuosity. Expectedly, orientation of high-permeability regions relative to the head gradient will also influence ω, nudging it toward unity (the arithmetic average) when parallel and -1 (harmonic average) when perpendicular (De Ghislain, 1986).

In contrast, formal upscaling is uncommon in free-surface flow modeling, with the exception of longitudinal dispersion parameters (Li & Zhou, 1997). However, considering that the most general form of a rate law for one-dimensional flow (equation (1)), like Darcy's Law, formulates flux as a product of a gradient and a conductivity term, the generalized average approach to upscaling should apply. Recent studies suggest that surface water hydroperiods are strongly related to vegetation patch anisotropy ratios (Kaplan et al., 2012) and channel connectivity (Yuan et al., 2015), though via unknown functional form. Further, others (Luhar & Nepf, 2013; Nikora et al., 2008) have noted that consistent with Journel et al. (1986), effective Manning roughness n increases nonlinearly with the fraction of stream channels occupied by vegetation, because as this blockage factor increases, flow through vegetation contributes more to the total discharge. In this work, we build on these findings by developing a formal upscaling approach for flow through heterogeneous hydroscapes.

2. Methods

The set of previously published simulations that supplied q in equation (1) employed the USGS SWIFT2D model (Schaffranek, 2004) to solve the vertically averaged equations for mass and momentum conservation under constant-head boundary conditions, local Manning roughness values, and steady flow. As described in Kaplan et al. (2012), domains comprised 840 2 × 4 km synthetic landscapes with n (0.45 s m$^{-1/3}$) and z_{p} (0.25 m) representative of the Everglades ridge-slough landscape (Florida, USA) and simulated using sequential indicator simulation (Deutsch & Journel, 1998): 30 realizations each of four anisotropy and seven coverage classes. Anisotropy values ranged from 1 to 6, representing landscapes for which surface water flow and sediment transport play some role in geomorphic development (Larsen & Harvey, 2011). To develop landscape-scale stage–discharge relationships, 14 simulations with h ranging from 10 to 150 cm were run for each landscape, yielding 11,760 total simulations. Additional solutions for q were generated analytically, from a force balance, for limiting-case landscapes with infinite patches aligned in parallel and in series with respect to the flow direction (Text S2).

Next, statistical models were developed to formulate the fitted ω values as a function of landscape configuration and h. Landscape configuration metrics consisted of the coverage (p), anisotropy (e), and box-counting fractal dimension of patches (f_{d}), mean spanning-path tortuosity (Ronayne & Gorelick, 2006), and large-scale and multiscale directional connectivity index (DCI; Larsen et al., 2012; Text S3) for islands and channels. The latter is a composite measure of the linearity and contiguity of channels along a primary direction (e.g., valley slope) and varies between 0 and 1. Appropriate models were determined by isolating variables hierarchically and performing least-squares linear or nonlinear regression. When the appropriate functional form was unclear, stepwise multiple linear regression was used to identify the critical terms. Once the appropriate functional form for independent components of each model was identified, the model was optimized as a whole through nonlinear least squares regression (see Text S4–S6).

In the first part of the sensitivity analysis, each control on large-scale fluxes in equation (1) and the statistical model for ω was perturbed independently, within one standard deviation of its mean (Table S4), to calculate $\Delta;u'$, the average change in large-scale velocity over positive and negative parameter perturbations, normalized by the base-case velocity. The base-case velocity was computed separately for two representative landscapes: highly connected (DCI = 0.75, e = 4.5; Figure 2d) and poorly connected (DCI = 0.4, isotropic, e = 1; Figure 2e). Next, we used our statistical model to calculate large-scale fluxes through the simulated landscapes produced by the ecogeomorphic model RASCAL along a degradation trajectory (Larsen et al., 2012). Degradation ensued over 60 years following a 20 cm step decrease in water level and 10^{-5} decrease in water surface slope. We perturbed the landscape configuration metrics in the fitted model for ω, individually and in tandem, in accordance with the observed changes (Table S5) to determine their relative influence on landscape-scale fluxes (Text S7).

As a measure of validation of our overall approach, we developed an upscaled Manning model to replicate velocities modeled by Choi and Harvey (2014; hereafter CH) for a portion of the Everglades landscape. CH's model (Text S9) was calibrated to long-term field observations and employs the Kadlec (1990) equation for modeling flow through wetlands, which assumes depth-variable drag and an energy slope exponent equal, here, to 1. Using values of z_p given by CH and DCI, *e*, and *p* values quantified from a 2 × 2 km vegetation map (Table S7) in our model of ω (i.e., Tables S1 and S2), we generated estimates of velocity that we compared to CH's model velocities over a range of water depths greater than z_p. Roughness values n_p and n_c were calibrated by minimizing error to CH's model velocities. As a further comparison of alternative large-scale flow modeling strategies, we also developed a standard Manning flow model for that system, assuming flow through a homogeneous landscape, in which *n* was obtained through calibration.

3. Results and Discussion

3.1. Physical Behavior of ω

The resistance averaging exponent, ω, is an indicator of the relative influence of high-resistance patches on flow. High values of ω indicate that the mean discharge is more influenced by flow through the preferential channels, whereas low values indicate that flow over patches has the greater influence. Because of the power law relationship between water depth and discharge in the Manning equation, for the limiting case of a landscape with infinitely long patches oriented in parallel, ω will asymptotically approach 5/3 as water level approaches the patch surfaces (Figure 1a). For the opposite limiting case, with infinitely wide patches in series, ω will approach negative values, near -1 but dependent on the patches' length and areal coverage (Figure 1b). The analytical analysis (Text S2) indicates that as water levels increase, ω changes approximately—but not exactly—linearly for either limiting case, with a slope that varies as a function of patch coverage, dimensions, and roughness. Slopes are steeper for narrower channels, reflecting greater frictional influence within those landscapes (Figure 1a). Slopes can be positive for landscapes with few wide channels and relatively low bed drag, because of the diminished relative influence of friction from the patch edges (see Luhar & Nepf, 2013).

Fitted values of ω for the synthetic landscapes (Figure 1c) varied with water level in a manner similar to the analytical solutions for the limiting cases, with higher values characterizing the more anisotropic cases and lower values characterizing the isotropic cases, particularly as water levels approached patch surfaces. As patch orientation for all anisotropic landscapes is parallel to flow, the behavior of ω was most similar to the patches-in-parallel limiting case, although a shift toward the patches-in-series limiting case was apparent as anisotropy decreased toward 1. Among replicate simulated landscapes, the greatest variability in the slope of the linear portion of the curve occurred for landscapes with high anisotropy and patch coverages of 0.1, 0.5, and 0.9. Based on the analytical analysis of patches in parallel (Figure 1a), this high variability is expected for $p = 0.1$, for which ω is particularly sensitive to variability in patch geometry. However, for the $p = 0.5$ and 0.9 cases, the high variability in slope must be due to factors not considered in the simple force balance, such as lateral interactions (e.g., large-scale flow separation effects). Notably, for the simulated landscapes, the percolation threshold occurs near $p = 0.5$. Landscapes near the percolation threshold that have contiguous channels experience topographic steering into those channels, resulting in ω values that are higher than expected for the limiting case of patches in parallel, whereas those without contiguous channels experience lower-than-expected values. At $p = 0.9$, the slopes of ω as a function of water level vary the most between the patches-in-parallel and patches-in-series limiting cases (Figures 1a and 1b). While the patches-in-series case may be more physically representative of the synthetic landscapes below the percolation threshold, there is a larger chance that remnant channels will align for the high-anisotropy case than the low-anisotropy case, resulting in a large divergence in slope for the $p = 0.9$, high-anisotropy replicates.

Variability in ω when water levels were beneath patch surfaces (Figure 1c) was likewise solely attributable to landscape spatial configuration as, for a landscape with patches in parallel, ω is exactly equal to 5/3 for flow in channels only. For a landscape with patches in series, complete blockage would result in no flow and ω of $-\infty$, depicted as missing in the figure. A large number of simulations experience no flow for high values of *p*, particularly when patches are isotropic. For landscapes that do flow at low water levels, variability in ω is highest for anisotropic patches, attributable to a lower portion of patch edges potentially in the lee orientation (and hence a higher portion of patch edges exerting a substantial frictional influence on flows, which would vary with edge configuration) than for isotropic, low *p* cases.

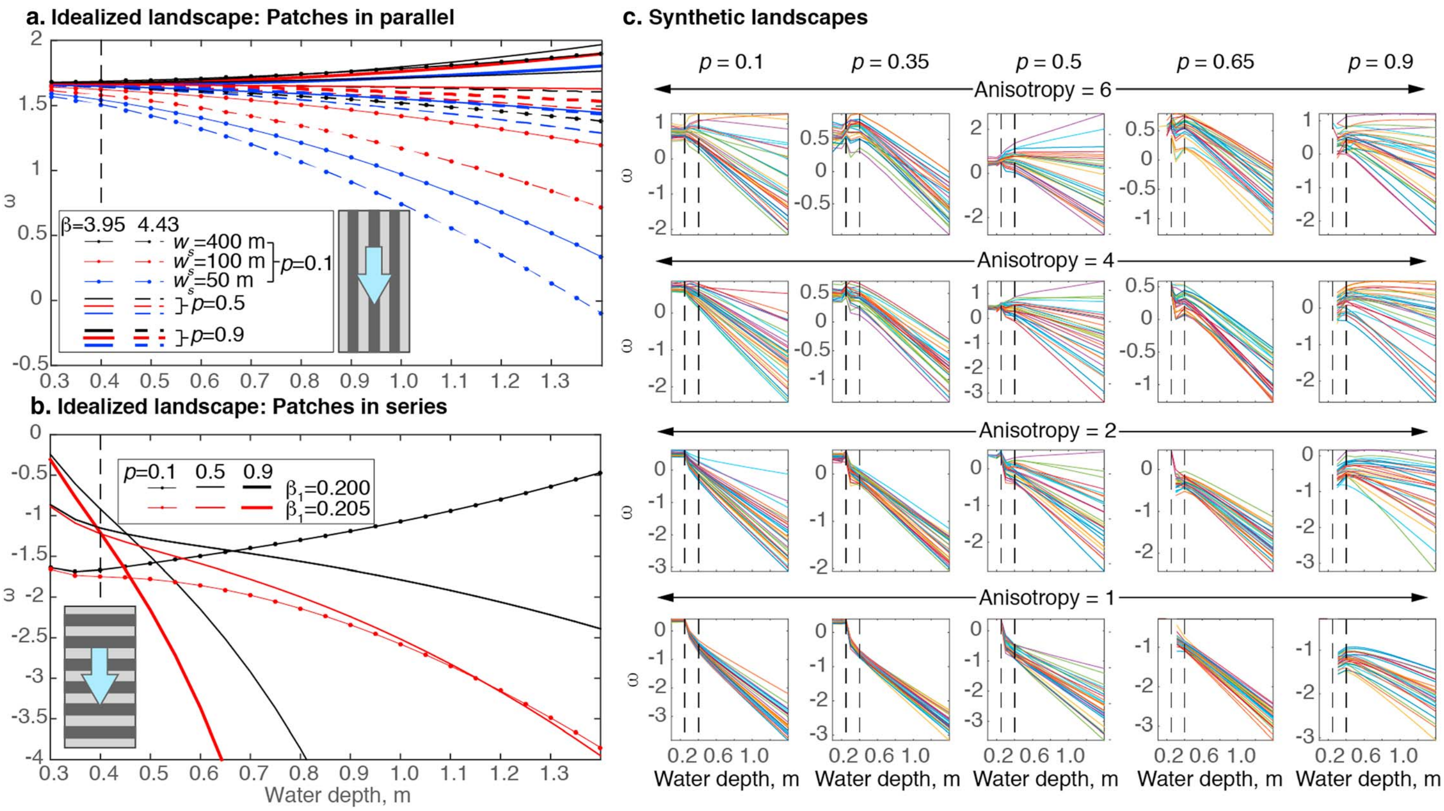

Figure 1. Fitted values of ω, the generalized averaging exponent, to (a, b) analytical and (c) simulated flow through binary, heterogeneous landscapes over a range of water depths. In Figures 1a and 1b, solutions are provided for different channel widths w_s, patch coverage p, and lumped roughness factors β and β_1, both of which are proportional to the bed drag coefficient (see Text S2). In Figure 1b, the lumped form drag coefficient (β_2 in equation S12 of the supporting information) is assumed to be an order of magnitude higher and is set equal to $10\beta_1$. In Figure 1c, the 30 lines in each subplot represent solutions for synthetic landscape replicates, which differ randomly in their connectivity, fractal dimension, and channel/island dimensions. Vertical dashed lines distinguish $h = z_p$ (25 cm) and $h = z_p + 15$ cm, where ω curves begin to become approximately linear. See Figure S1 for the full version of Figure 1c, including all p values analyzed.

3.2. Sensitivity of Flow to Landscape Configuration

The physical interpretation of ω above suggests that landscape-scale patch configuration is particularly important at very low and very high patch coverage, low water levels, and near the percolation threshold. To quantify these effects, we statistically modeled the approximately linear relation ($R^2 = 0.97$) between ω and water depth at $h - z_p \geq 15$ cm (a threshold that would vary for landscapes with different z_p and n) and the approximately constant values of ω at $h = z_p$ ($R^2 = 0.75$) and $h < z_p$ ($R^2 = 0.78$; Text S5 and S6) as a function of the candidate landscape spatial configuration metrics. We then performed the perturbation analysis on each of these three models. Unsurprisingly, water depth emerged as the dominant driver of velocity for "high" water levels ($h - z_p \geq 15$ cm; Figure 2a). Patch coverage had a secondary effect, although of the same order of magnitude as water level (inducing changes in velocity of O(10%)). In the well-connected landscape, anisotropy had a tertiary effect (O(0.1–1%)), followed by fractal dimension (O(0.1%)) and finally DCI (0.01%). Comparatively, in the poorly connected landscape, both DCI and anisotropy had an order-of-magnitude greater effect, while perturbations in other parameters also had the same or greater effect, although of the same order of magnitude.

Effects of perturbations in landscape configuration factors on flow varied as a function of water depth and patch coverage. All factors became more important at low water depth, a trend most pronounced for DCI and anisotropy (Figure 2a). Perturbations to these "connectivity factors" had the most substantial effect at intermediate values of patch coverage, just below the percolation threshold (50–60% coverage in anisotropic landscapes, 30–40% coverage in isotropic landscapes; Stauffer & Aharony, 1994). In contrast, landscapes with low patch coverage were more sensitive than those with high coverage to perturbations in fractal dimension. In other words, flow through landscapes with few patches is likely to change

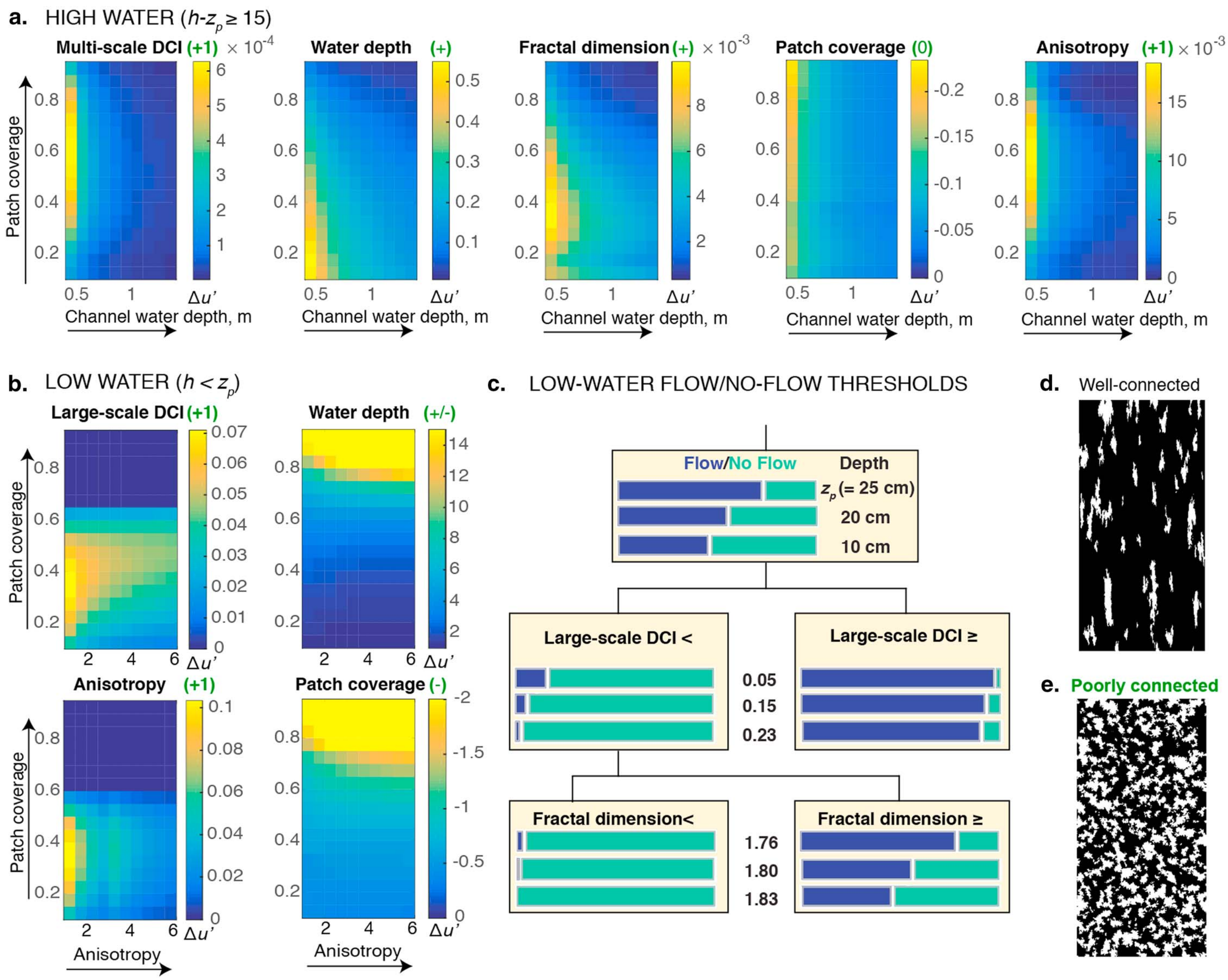

Figure 2. Sensitivity of large-scale flows to configurational and hydrological factors. (a) and (b) depict $\Delta u'$ computed for a well-connected landscape (for example, (d); white = ridges, black = channels). Positive values indicate an increase in velocity with an increase in parameter value. Green parentheses indicate whether sensitivities are higher (+), lower (−), or equivalent (0) for a poorly connected landscape (e.g., (e)) and whether the change is over an order of magnitude (1) or not (no number). (c) Threshold values of the large-scale DCI and patch fractal dimension that best distinguish between flowing and nonflowing landscapes at three water levels, based on a recursive partitioning analysis. Full statistical details for the recursive partitioning analysis and complete results of the sensitivity analyses are provided in Text S7 and S8.

substantially with changes to the patch perimeter or area, whereas landscapes with more patches are more sensitive to the linearity and connectivity of the remaining through-flow channels. At levels equal to z_p and below, sensitivity to anisotropy and DCI (Figures 2b; Text S18 and S19) continued to increase, with small perturbations resulting in up to 100% (but mostly <10%) changes in velocity. In general, sensitivity of flows to perturbations in DCI and anisotropy was greatest for poorly connected, isotropic landscapes with patch coverage at or near the percolation threshold. At higher patch coverage (>0.60), only changes in coverage or water depth could measurably change flow velocities, by O(100%) and O(1,000%), respectively.

Many landscapes, particularly those with high patch coverage, exhibited no flow at low water levels. A recursive partitioning analysis (Figure 2c) suggested that DCI was the primary factor distinguishing between landscapes that did and did not flow. The threshold value of DCI for flowing landscapes increased as water levels

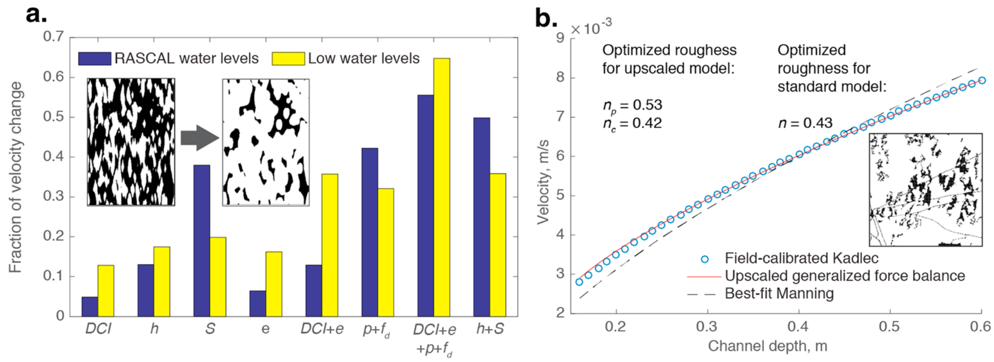

Figure 3. Case study application of spatial resistance upscaling to the Everglades landscape. In (a), the model is applied to assess sensitivity of large-scale velocity to changes in hydrologic and landscape configurational factors as a simulated landscape undergoes change due to ecogeomorphic feedback. Blue bars represent the fraction of the change in velocity attributable to changes in each listed parameter singly and in combination under the actual water levels in the simulation. Yellow bars present this fraction of change had water levels been lower by 20 cm. White and black features in the insets are ridges and channels, respectively. In (b), the performance of the upscaled Manning model is compared to that of Choi and Harvey's (2014) field-calibrated model, with roughness parameter values selected through optimization (see text). A non-upscaled Manning model is also included for comparison. The 2 × 2 km area from which landscape parameters were extracted is depicted in the inset, with flow from top (north) to bottom (south).

declined. Patch fractal dimension played a secondary role in determining whether a landscape flowed, with higher fractal dimensions (i.e., more Euclidean patch shapes) required for flow at lower water levels.

That landscape-scale fluxes become most sensitive to patch configuration when water levels approach patch surfaces is consistent with other studies (Acharya et al., 2015, 2017; Choi & Harvey, 2014; Kaplan et al., 2012). Choi and Harvey (2014) identified how water level divides controls on large-scale fluxes into two regimes, separated by a threshold coincident with patch surfaces: a high-water regime, in which vegetative drag governs fluxes, and a low-water regime, in which microtopography governs fluxes. Like these authors, we found that in low-water conditions, microtopography can effectively block flow; Choi and Harvey (2014) found a threshold patch coverage (0.85) at which blockage occurs, while Kaplan et al. (2012) found anisotropy to be a dominant flow-blocking control (given fixed patch density of 0.5). In the more robust test of structural connectivity metrics presented here, we found a threshold DCI that varies with water level to be most relevant (Figure 2c).

3.3. Case Study Application: Everglades

A general (i.e., one-at-a-time) perturbation analysis does not necessarily reflect the effects of different aspects of hydrology and landscape configuration on flow as a landscape actively undergoes ecogeomorphic change. In the ecogeomorphic simulation model of a degrading Everglades landscape, just under half of the change in velocity along a trajectory of landscape degradation was attributable to hydrologic perturbation ($h + S$), whereas slightly more than half was due to changes in patch configuration ($DCI + e + p + f_d$; blue bars in Figure 3a). Of this change in velocity due to configurational changes, approximately 75% was due to the combined effect of patch coverage and fractal dimension; the other 25% was due to anisotropy and DCI, which had comparable importance. To stress the importance of water level interactions with the elements of landscape configuration that most affect flow velocity, we repeated the analysis assuming these landscapes evolved under water levels 20 cm lower (yellow bars in Figure 3a). In that case, the importance of landscape configuration was even more pronounced, explaining over 60% of the modeled reduction in velocity. Of that 60%, DCI and anisotropy were responsible for more than half of the velocity reduction (approximately 36% of the total and equivalent to the combined effects of water depth and slope).

The case study provides insight into why landscape configurational changes may be rapid and difficult to reverse once set into motion. Here a step decrease in water level and water surface slope triggered patch expansion, eventually to the percolation threshold (Larsen et al., 2012), which further decreased the landscape's capacity to convey water. This landscape-scale feedback was responsible for about half of the change in flow velocity over the examined trajectory of degradation (Figure 3). Halting this degradation process in the Everglades requires restoration of higher flows (Choi & Harvey, 2016; Heffernan et al., 2013; Larsen & Harvey, 2011), which will be more difficult to achieve in a landscape that has already lost anisotropy, connectivity, and slough coverage (Figure 3a), a condition that characterizes much of the Everglades

(Casey et al., 2016). This sensitivity analysis suggests that efforts to increase water level or reduce ridge coverage—irrespective of its configuration—would go the furthest toward restoring the flow velocities needed to reinstate sediment transport at high water levels. However, when water levels are close to the surface of the patches (within about 20 cm), resource managers seeking to increase fluxes and interrupt positive feedbacks leading to further channel loss would be well served in efforts to reestablish channel connectivity.

Finally, in the validation exercise, the optimized, upscaled Manning model of velocity produced a near-perfect fit to the field-calibrated CH model velocity (R^2 = 1.00; Figure 3b). The poorest part of this fit, while still strong, was in the transitional water depths ($z_p < h < z_p + 15$ cm), where ω values were linearly interpolated between that of the $h = z_p$ model and that of the h – 15 cm ≥ zp model. Optimized roughness parameters were within the range of values typically used to model the Everglades ridge and slough landscape (South Florida Water Management District (SFWMD), 2005). Meanwhile, the standard Manning model produced a poorer (R^2 = 0.97), biased fit. These findings suggest that the large-scale flow dynamics through heterogeneous patches (i.e., as modeled by the upscaled Manning model) provide an alternative to the depth-variable drag explanation for why flow through floodplains and wetlands does not often conform to a standard Manning equation.

4. Conclusions

It is broadly recognized that connectivity critically impacts fluxes and biogeochemical transformations (Covino, 2017; Gooseff et al., 2017), yet quantifying it appropriately remains a challenge (Bracken et al., 2013). This analysis suggests that multiple components of structural connectivity independently influence functional connectivity—a landscape's ability to transmit surface water flows. The anisotropy of patches (oriented parallel to flow) is the most important aspect of connectivity at high water levels, while the DCI, considered independently, plays little role. However, the relative importance of connectivity metrics varies with the landscape's configuration, indicating a potential for hysteresis. Near the percolation threshold and at low water levels, the DCI's relative importance increases; at low water levels, it becomes the factor most strongly associated with complete flow blockage. Higher relative importance near the percolation threshold, combined with a tendency to change rapidly, gives it about equal importance as anisotropy for changes in flow over a trajectory of landscape change (Figure 3a). Further, interactions among DCI and other controls on large-scale flow are important, with flow through poorly connected landscapes exhibiting less resilience to perturbations in the other controls than flow through well-connected landscapes.

Although our model for ω (Tables S1–S3) is a useful starting point for understanding the sensitivity of large-scale fluxes to changes in landscape configuration, it is based on a simplified representation of flow through vegetated landscapes. Modification of the statistical fits would be necessary for environments with different roughness ratios (Ronayne & Gorelick, 2006) or anisotropy values less than 1. Based on results of detailed hydrodynamic modeling of flow through deltaic marsh/channel mosaics that indicate strong topographic steering by vegetation patches (Nardin & Edmonds, 2014), we expect the sensitivity of flow to all configurational factors in our final model to increase with higher roughness ratios between channels and patches. Further, for emergent marshes where roughness elements extend through the water column, variation in sensitivity with depth would be damped relative to Figure 1 (see Text S1), and the relative importance of DCI and anisotropy over a range of flow depths would increase. Hence, this analysis likely provides a conservative assessment of the role of landscape configuration on large-scale flow. Our model provides insight into the form of the expression appropriate for upscaling resistance in surface water flows and serves as a foundation for investigation of the higher-complexity relationships between large-scale fluxes and landscape configuration over a range of patch roughnesses and vertical morphologies.

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