Directional connectivity in hydrology and ecology

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Abstract. Quantifying hydrologic and ecological connectivity has contributed to understanding transport and dispersal processes and assessing ecosystem degradation or restoration potential. However, there has been little synthesis across disciplines. The growing field of ecohydrology and recent recognition that loss of hydrologic connectivity is leading to a global decline in biodiversity underscore the need for a unified connectivity concept. One outstanding need is a way to quantify directional connectivity that is consistent, robust to variations in sampling, and transferable across scales or environmental settings. Understanding connectivity in a particular direction (e.g., streamwise, along or across gradient, between sources and sinks, along cardinal directions) provides critical information for predicting contaminant transport, planning conservation corridor design, and understanding how landscapes or hydroscapes respond to directional forces like wind or water flow. Here we synthesize progress on quantifying connectivity and develop a new strategy for evaluating directional connectivity that benefits from use of graph theory in ecology and percolation theory in hydrology. The directional connectivity index (DCI) is a graph-theory based, multiscale metric that is generalizable to a range of different structural and functional connectivity applications. It exhibits minimal sensitivity to image rotation or resolution within a given range and responds intuitively to progressive, unidirectional change. Further, it is linearly related to the integral connectivity scale length—a metric common in hydrology that correlates well with actual fluxes—but is less computationally challenging and more readily comparable across different landscapes. Connectivity-orientation curves (i.e., directional connectivity computed over a range of headings) provide a quantitative, information-dense representation of environmental structure that can be used for comparison or detection of subtle differences in the physical-biological feedbacks driving pattern formation. Case-study application of the DCI to the Everglades in south Florida revealed that loss of directional hydrologic connectivity occurs more rapidly and is a more sensitive indicator of declining ecosystem function than other metrics (e.g., habitat area) used previously. Here and elsewhere, directional connectivity can provide insight into landscape drivers and processes, act as an early-warning indicator of environmental degradation, and serve as a planning tool or performance measure for conservation and restoration efforts.

Key words: conservation; directional connectivity metrics; Everglades; graph theory; hydroecology; hydrology; landscape ecology; restoration.

INTRODUCTION

Connectivity in hydrology and ecology

Connectivity has received much recent attention in both hydrology and ecology. Ecologists have defined connectivity as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993) or the degree to which it regulates gene flow among populations (Mollanen and Hanski 2001). Hydrologists have defined it as the amount of “water-mediated transfer of matter, energy, and/or organisms within or between elements of the hydrologic cycle” (Pringle 2001). Connectivity may be structural, based on physical adjacency of landscape features such as plant communities, or functional, based on how that adjacency translates to fluxes of water, solutes, or organisms (Fig. 1) (Lexartza-Artza and Wainwright 2009, Wainwright et al. 2011). Process connectivity, the third main type, quantifies not flows of mass but flows of information between physical and biological drivers affecting the evolution of environmental systems (Miller et al. 2012, Wang et al. 2012).

In ecology structural connectivity quantifies connections within or between patches of habitat, whereas functional connectivity often quantifies dispersal rates or gene flow and can be organism-specific (Tischendorf and Fahrig 2000b). For example, ecological connectivity is a fundamental factor in determining species distributions (Fahrig and Merriam 1985) and is often quantified to guide reserve design (Calabrese and Fagan 2004) or prioritize land acquisition for conservation (Crooks and Sanjayan 2006). In hydrology structural connectivity
refers to spatial contact within high-conductivity zones (groundwater) or channels (surface water), whereas functional connectivity refers to the influence of the environment on constituent fluxes and travel times (Knudby and Carrera 2005). Studies often relate hydrological connectivity to processes such as runoff yield and duration (e.g., Bracken and Croke 2007, Moody et al. 2008, Ali and Roy 2010) or contaminant migration (e.g., LaBolle and Fogg 2001). Connectivity is often regarded as critical for hydrologic prediction (Western et al. 2001), and connectivity metrics can better explain hydrologic response than other spatial variables such as vegetation cover, patch density, and patch size (Mayor et al. 2008).

Hydrologists and ecologists use different approaches to characterize connectivity, and even within each discipline, there is little consensus on how to quantify functional connectivity. Tischendorf and Fahrig (2000b) argue that the most relevant indicator of connectivity in ecology is actual immigration or dispersal rates, but it is more common and arguably more practical (Moilanen and Nieminen 2002) to use structural indicators based on spatial analysis or functional indicators developed from both spatial analysis and assumptions about ecological processes. Many of the structural and functional metrics commonly used in ecology are reviewed in Calabrese and Fagan (2004). These raster-based metrics have been subject to much scrutiny (e.g., Schumaker 1996, Tischendorf and Fahrig 2000a, Corry and Nassauer 2005), particularly with regard to their ability to uniquely discriminate between landscapes, reflect qualitative changes in landscapes, and remain relatively insensitive to image resolution or rotation. Furthermore, most ecological connectivity metrics measure only interpatch connectivity, such that connectivity metrics in landscapes with one large contiguous patch are similar to those of highly fragmented systems (Tischendorf and Fahrig 2000a, b). However, measures of intrapatch connectivity are essential for hydrologic systems where transport and dispersion occurs within a large, semi-connected matrix and for ecological systems in which the scale of organism movement is small relative to that of the habitat (Tischendorf and Fahrig 2000b).

Fig. 1. An integrated concept of connectivity across hydrology and ecology. (A) Salient features exhibited by many connectivity metrics in hydrology and ecology, as well as desirable features for connectivity metrics that integrate across disciplines. (B) Different types of connectivity within an integrated scope, which encompass some of the classifications used by previous researchers (BC, Bracken and Croke [2007]; KC, Knudby and Carrera [2005]). This paper focuses primarily on structural and functional connectivity.
As an alternative to raster-based metrics, graph-theory-based metrics are gaining in popularity (Cantwell and Forman 1993, Ricotta et al. 2000, Calabrese and Fagan 2004). In this approach, habitat patches are represented as nodes, with links representing dispersal pathways between patches. Advantages of graph-theory approaches are their ability to identify the importance of individual patches to landscape connectivity, their adaptability to different scales and degrees of detail, and readily available algorithms and analytical tools that make complex computations efficient (Urban and Keitt 2001, Saura 2010). Compared to raster-based metrics of connectivity, graph-theoretic metrics provide a higher ratio of information content to data requirements, making them highly suitable to addressing large-scale conservation problems (Calabrese and Fagan 2004).

Recently, hydrologists have also begun to use graph theory in connectivity assessments (Phillips et al. 2011), representing stream reaches as links that connect runoff-generating sub-basin nodes. Compared to ecology, though, hydrology exhibits a dearth of connectivity metrics (Ali and Roy 2010), and more critical evaluation of different hydrologic connectivity metrics is needed (Knudby and Carrera 2005, Mayor et al. 2008). Common geostatistical metrics, reviewed in Knudby and Carrera (2005) and Ali and Roy (2009, 2010), include the entropy integral scale and variogram-based metrics. However, two-point correlation techniques like variograms often poorly reflect actual connectivity (i.e., fluxes) because they do not account for non-linear flow paths (Western et al. 2001, Knudby and Carrera 2005). Another class of metrics rooted in percolation theory (Berkowitz and Balberg 1993) overcomes this problem. Based on probability that a connection exists between any two points, the connectivity function (Western et al. 2001) and related integral connectivity scale (Knudby and Carrera 2005) better agree with flux measurements but require complex, unwieldy computations and have large data requirements. Because of the directional nature of water flow, directional versions of hydrologic connectivity metrics (e.g., directional semivariograms or connectivity functions computed along flow paths) generally better capture trends in travel time and fluxes than omnidirectional metrics and are better related to functional connectivity (Knudby and Carrera 2005, Ali and Roy 2010).

The time is ripe for selecting and integrating the most successful and general characterizations of connectivity between the fields of hydrology and ecology (Fig. 1). In doing so, opportunities exist for improving the way connectivity is characterized in both disciplines. For example, ecology would benefit from improved approaches for calculating directional connectivity (Li and Reynolds 1994, Corry and Nassauer 2005), particularly within habitat patches. Many habitats, such as alpine vegetation zones or riparian zones, are linearly or anisotropically distributed (Urban and Keitt 2001). Additionally, dispersal that depends on the directional connectivity of habitat patches can arise from water flow (DiBacco et al. 2006), prevailing wind (Miller et al. 1991), or established migration paths (Gutzwiller and Anderson 1992). Conservation goals would also benefit from quantification of directional connectivity. One example is the Yellowstone to Yukon Conservation Initiative, which aims to establish wildlife corridors along a north-south axis. Another is the US$10.9 billion Comprehensive Everglades Restoration Plan, for which a primary goal is restoration of the ridge and slough landscape, which is characterized by patterned peat ridges and open-water sloughs connected in the direction of flow. In turn, hydrology would benefit from ecology’s use of graph theory to construct normalized connectivity metrics. Common connectivity metrics in hydrology are typically length scales, precluding comparison of connectivity across environments with inherently different spatial scales.

Here we develop the directional connectivity index (DCI), applicable to a general range of problems in hydrology and ecology. The DCI incorporates the best features of connectivity statistics in hydrology and ecology: it is computed using graph theory, normalized, and sensitive to intrapatch as well as interpatch connectivity. Moreover, it employs weighting schemes generalizable to a variety of functional connectivity applications such as dispersal or solute fluxes. Using the Everglades ridge and slough landscape as a case study, we show how the DCI responds to landscape change and compare its response to connectivity metrics prevalent in hydrology and ecology. Additionally, we evaluate tradeoffs between index behavior, computational time, scale, and conventions for defining graph links and nodes. Finally, we show how curves of DCI over a range of angular bearings can be used to identify the dominant orientation of environmental features, leading to deeper understanding of the mechanisms controlling landscape evolution and ecosystem processes. These connectivity-orientation curves summarize an unprecedented amount of topologic information, serving as a tool for comparing actual and model-generated landscapes.

**Methods**

**Definition of graph links and nodes**

Graph theory represents landscapes (loosely defined here as the structural environment, ranging from subsurface aquifers to large-scale ecosystems) as networks of links and nodes (Fig. 2). In ecology, nodes are traditionally individual habitat patches, and links are the dispersal pathways bridging patches (Fig. 2A). Here, because of our interest in quantifying directional connectivity within (e.g., gray patches in Fig. 2A) as well as between habitats (e.g., white patches in Fig. 2A) or flow paths, we test two new approaches for defining nodes within a rasterized landscape. In the first approach, nodes are defined as all pixels comprising a patch type (i.e., the “full” network, Fig. 2B). In the second, nodes are defined as all pixels in a skeleton...
representation of the patch type (Fig. 2C). Patch skeletons are readily computed in most image processing software packages. The algorithm involves progressive “erosion” of patches by repeated removal of edge pixels until a pixel-wide spine remains. Because erosion ceases in areas reduced to spines, the algorithm preserves connectivity of landscape patches while resolving axes of directionality within convoluted patches. Spines represent the most direct routes via which organisms or flow traverse patches.

Landscape graphs are represented by $v \times v$ distance and adjacency matrices, where $v$ is the total number of nodes. Entries of directly connected nodes in the binary adjacency matrix have a value of unity; those in the distance matrix have values equal to $\ell$, the physical or functional distance between connected nodes. Functional distances can be a product of physical distance and a resistance term inversely proportional to hydraulic conductivity or ease of dispersal (Tischendorf and Fahrig 2000a, 2000b), or a hydrologic distance defined along a flow path (Peterson et al. 2006). In undirected graphs, in which transport along links occurs in both directions, the adjacency and distance matrices are symmetric. Undirected graphs are suitable for structural connectivity assessments or functional connectivity assessments in which organisms or material may travel “upstream” along a particular direction to ultimately reach locations further “downstream.” In directed graphs, links connect nodes in one direction only. Directed graphs that connect pixels only along the downslope or zero-slope directions are often most suitable for functional connectivity assessments involving flow of water.

**Directional connectivity index (DCI)**

The DCI is essentially a measure of the linearity of patches along a particular direction and over multiple scales, formulated so that it is maximized when transport or dispersal takes the shortest path along that direction. It is constructed as a weighted or unweighted sum of the ratio of a projected distance between nodes along an axis (i.e., the distance between rows of pixels) to the shortest path distance between nodes at that projected distance, summed over all nodes and all projected distances (Fig. 3A). Scaled between 0 and 1, it has a value of 0 when patches have no connectivity along the direction of interest (Fig. 3B) and 1 when patches have complete linear connectivity (Fig. 3C). The DCI is formulated as follows:

$$
DCI = \frac{\sum_{i=1}^{v} \sum_{j=r+1}^{R} w_{ij} \frac{dx(j-r)}{d_{ij}}}{\sum_{i=1}^{v} \sum_{j=r+1}^{R} w_{ij}}
$$

where $i$ is a node index, $j$ is a row index, $r$ is the row containing node $i$, $R$ is the total number of rows in the direction of interest, and $dx$ is the relative pixel length along that direction; $d_{ij}$ is the shortest connected structural or functional distance between node $i$ and any node in row $j$, computed from the distance matrix using Johnson’s shortest path algorithm (Johnson 1977). Though the computation integrates across all length scales, a DCI that emphasizes a particular length scale can be selected by tuning the weighting function $w_{ij}$. In our application, we use $w_{ij} = dx(j-r)$ to emphasize large-scale directional connectivity. To illustrate the effects of $w_{ij}$, isolated but linear habitat patches (e.g., Fig. 3D) have moderate DCI when $w_{ij} = 1$ but low DCI when $w_{ij} = dx(j-r)$, reflecting substantial directional connectivity at the small scale but no connectivity at the large scale.

**Comparison to common connectivity metrics in hydrology and ecology**

We compared the DCI to connectivity metrics commonly used in hydrology and ecology. Freely available spatial analysis software packages such as FRAGSTATS (McGarigal et al. 2002) have popularized...
use of several isotropic connectivity metrics in ecology: cohesion, aggregation index (AI), and contagion. Cohesion measures the physical connectedness of a patch type, increasing as patches become more aggregated. It is computed based on the perimeter \( P_i \) and area \( a_i \) of each patch \( i \) and the total area \( A \) and number of patches \( n \) in the landscape (Schumaker 1996):

\[
\text{cohesion} = 100 \left( 1 - \frac{\sum_{i=1}^{n} P_i}{n \sqrt{a_i}} \right) \left( 1 - \frac{1}{\sqrt{A}} \right)^{-1}.
\]

Similarly, AI is maximal when the cells of a patch type are configured as a single, compact mass. It is constructed from the ratio of the number of shared edges (adjacencies) between pixels of a patch type \( g_{ij} \) to the maximum possible number of adjacencies between pixels of that patch type (He et al. 2000):

\[
\text{AI} = 100 \frac{g_{ij}}{g_{ij,\text{max}}}. \tag{3}
\]

In contrast to AI and cohesion, contagion is a measure of overall landscape clumpiness computed across all patch types \( (j \text{ and } k) \). Inversely related to edge density, it is highest when patch dispersion and interspersion are both low, resulting in a high proportion of like adjacencies and an inequitable distribution of unlike adjacencies, respectively (Li and Reynolds 1993):

\[
\text{contagion} = 100 \left[ 1 + \left( \sum_{j=1}^{n} \sum_{k=1}^{n} \frac{a_j g_{jk}}{A \sum_{k=1}^{n} g_{jk}} \right) \ln \left( \frac{a_j g_{jk}}{A \sum_{k=1}^{n} g_{jk}} \right) \right] \frac{\ln(n)}{2 \ln(n)}. \tag{4}
\]

The directional semivariogram range used in hydrology gives a length scale over which patches are contiguous in a particular direction, typically a linear direction. The experimental semivariogram for a binary image is as follows (Western et al. 1998):

\[
\Gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left[ I(x_i + h) - I(x_i) \right]^2 \tag{5}
\]

where \( I(x_i) \) is the value of “on” pixel \( x_i \), \( h \) is a lag distance along a particular direction, and \( N(h) \) is the number of pixel pairs separated by \( h \). The experimental semivariogram is then fit with an exponential model using a least-squares procedure:

\[
\Gamma(h) = c_0 + C(1 - e^{h/s_i}) \tag{6}
\]

where \( c_0 \) is the nugget variance, \( C \) is the amplitude, and \( s_i \) is the semivariogram range.

Unlike the semivariogram range, the topographic integral connectivity scale (ICS) is quantified based on the probability \( \tau(h) \) that two pixels \( x \) and \( x + h \), separated by a lag distance \( h \) along a particular direction within the image domain \( G \), are connected along a flow path (i.e., a contiguous patch of pixels in \( A \), the set of “wet” or “on” pixels, along which elevation is monotonically decreasing) (Ali and Roy 2010). In our computation of the topographic ICS, we denote this connection as \( x \to x + h \), computed based on whether \( x \) flows into \( x + h \) in a “full” directed network. That is,

\[
\tau(h) = P(x \to x + h | x \in A, x + h \in G). \tag{7}
\]

The topographic ICS is then defined as

\[
\text{ICS} = \int_0^\infty \tau(h) dh. \tag{8}
\]

Last, the gamma index (Ricotta et al. 2000) is one of the most common graph-theoretic, isotropic connectivity metrics employed in many fields. It is a ratio of the
actual number of linkages \((e)\) within a network to the maximum possible number of linkages:

\[
\gamma = \frac{e}{0.5(v^2 - u)}.
\]

\[(9)\]

Study site description

We computed the above suite of connectivity metrics from GIS images and simulation outcomes of one of the best studied directionally patterned landscapes in the world. The Everglades ridge and slough landscape is characterized by kilometer-scale elongated peat ridges colonized by sawgrass \((Cladium jamaicense)\) and interspersed among sloughs. The more open sloughs are highly connected along the direction of flow and convey 86\% of the total discharge through the marsh (Harvey et al. 2009). Degradation of the ridge and slough landscape, which has occurred at an accelerated rate over the past century, typically refers to rapid expansion of sawgrass in hydrologically impacted areas or cattail \((Typha domingensis)\) in nutrient-impacted areas at the expense of open sloughs. The resulting homogenization inhibits fish dispersal through sloughs and decreases fish and wading bird diversity (Ogden 2005). Degradation can be induced by perturbations involving some combination of a reduction in water depth, decrease in water-surface slope, nutrient enrichment, or choking of sloughs with emergent spikerush \((Eleocharis spp.)\) (Larsen and Harvey 2011).

Data acquisition and pre-processing

Conserved1 and Conserved2 are GIS images representing well-preserved portions of the ridge and slough landscape (Fig. 4). Conserved1 was digitized from 30-m resolution Landsat satellite imagery at approximately 1:10 000 (Wu et al. 2006, Watts et al. 2010); Conserved2 (Nungesser 2011) was digitized from 1–2 m resolution aerial photographs at approximately 1:5000. The images were digitized manually; visual differences between colors and textures were used to discriminate between water and emergent vegetation. Metrics computed for these landscapes were also compared to those of Sim1, a synthetic ridge and slough landscape generated from the RASCAL simulation model (Larsen and Harvey 2010, 2011), and Degraded1, a GIS image of a portion of the landscape that exhibits aggregated ridges and a few fragmented sloughs, digitized in the same manner as Conserved2 (Nungesser 2011).

Connectivity metrics are computed on a binary, rectangular base image. If the direction of interest for the DCI computation (e.g., a streamwise direction) is not linear, a coordinate transformation of the image is necessary to project that direction of interest parallel to image columns (e.g., Legleiter and Kyriakidis 2006). For the connectivity computations here, base images with numeric pixel values (e.g., hydraulic conductivity, vegetation density or composition, flow roughness) must be binarized, typically done through thresholding (Western et al. 2001, Knudby and Carrera 2005). Adjacency and distance matrices are then created from the thresholded image, and DCI is computed using Matlab’s image processing toolbox (MathWorks, Natick, Massachusetts, USA), the open-source MatlabBGL library \(available online\), \(^4\) and code provided in the Supplement.

Connectivity-orientation curves are computed by rotating the image with respect to the computational grid. Rotated images are resampled to the computational grid using bilinear interpolation and cropped to a square with length \(2^{4.5}\) times that of the shortest dimension of the original image, ensuring that even at a 45\(^\circ\) rotation angle, computations are performed only on cells containing image pixels and that, at all bearings, image extent is equivalent. Because of cropping, users must select images extending beyond the immediate area of interest.

Connectivity metrics computations

Because historical aerial imagery of the ridge and slough landscape is available for only a few years (Nungesser 2011), we used simulation outcomes from the RASCAL (Ridge and Slough Cellular Automata Landscape) model (Larsen and Harvey 2011) to examine how DCI reflects landscape degradation processes. We

\[^4\] \url{https://github.com/dgleich/matlab-bgl}
computed the suite of connectivity metrics at multiple points along simulated degradation trajectories. Degradation was induced in the model by decreasing mean annual water level (from 65 cm to 45 cm), decreasing mean water-surface slope during the high-flow pulses (from $6.5 \times 10^{-5}$ to $2.5 \times 10^{-5}$), and/or increasing abundance of emergent spikerush (*Eleocharis* spp.) choking sloughs.

Many common connectivity metrics exhibit high sensitivity to image resolution and/or rotation (Wickham and Riitters 1995, Frohn 1998, Wu 2004). We tested sensitivity of the DCI to resolution by repeating computations at full, one-half, and one-quarter the original resolution using bilinear downsampling. In addition, we tested for rotational sensitivity by comparing the DCI of Sim1 to that of Rotated1 (Fig. 4), a landscape identical to Sim1 but at a 40° offset.

**RESULTS**

**Comparison of alternate constructions of the DCI**

Key decisions in formulating the DCI include whether to use (1) the full network or skeleton network representation of landscapes, (2) weighting to favor certain scales, and (3) directed or undirected landscape graphs. Although the full network representation simplifies landscape structure the least, there is a large tradeoff in computational time, which grows with number of nodes according to a power law (Fig. 5A). For landscapes based on skeleton networks, DCI is generally computed in less than one minute on a 2.13-GHz processor with 4 Gb memory. Fortunately, DCI values calculated based on skeleton networks correlate strongly with ($R^2 = 0.98$, $P < 0.0001$) but are generally lower than those based on the full networks (Fig. 5B). The relationship between both versions of DCI is equivalent for weighted or unweighted formulations. Because there are fewer paths between sets of points in directed networks relative to undirected networks, DCI values tend to be lower for computations based on directed networks (Fig. 6). The difference between the two computations is dependent on the specific landscape and, to some extent, on image resolution. Generally, relative comparisons between landscapes using metrics consistently computed with full or skeleton network representations, weighted or unweighted formulations, and directed or undirected graphs should be robust.

The extent to which changes in image resolution affect the DCI depends on the nature of the landscape and the magnitude of change in resolution. Coarse raster grid resolutions simplify landscape features, which tends to produce higher DCI values than fine grid resolutions (Fig. 6). Features with relatively simple structures (e.g., Conserved1 sloughs) tend to have DCI values insensitive to resolution because their skeletons do not change substantially with pixel size. These types of landscapes exhibit changes in DCI on the order of 0.01 with twofold or fourfold coarsening of grid resolution. More complex landscape elements (e.g., Conserved2 sloughs) exhibit changes in DCI an order of magnitude higher for each twofold coarsening of grid resolution. Even relatively simple features that are initially insensitive to resolution coarsening eventually become sensitive to resolution. For example, although DCI changes little as Sim1 is coarsened twofold or Conserved1 is coarsened fourfold, they increase substantially with further coarsening (Fig. 7). At the finest and coarsest grid resolution extremes (7.6-m and 61-m pixels), connectivity-orientation curves are noisy (Fig. 7A), indicating rotational sensitivity. The $5^\circ$ rotational precision (i.e., 95% confidence interval...
around a 5° moving average) in DCI for the finest and coarsest resolution versions of Conserved1 is 0.04 and 0.06, respectively. For intermediate grid resolutions (15.2–30.5 m), DCI is more robust to image rotation (5° rotational precision of 0.03 for Conserved1). Across the full eightfold coarsening in resolution, the 95% confidence interval in DCI for the Conserved1 connectivity-orientation curves is 0.16, but across a fourfold coarsening it is only 0.07. Rotation and resampling during image processing have little effect on DCI computations; when shifted by 40°, the connectivity-orientation curves for Rotated1 and Sim1 (Fig. 7B) are statistically equivalent, with a Tucker’s congruence coefficient of 1.00 (Lorenzo-Seva and ten Berge 2006) and 95% confidence interval in DCI of 0.02.

**Case study: Comparison of DCI values between Everglades landscapes**

Changes in DCI agree qualitatively with apparent changes in the connectivity of landscape elements and orientation. In a strongly linear landscape (e.g., Conserved1), DCI varies sinusoidally with orientation, obtaining maximum values at bearings of approximately 0° and 180° (parallel to the axis of elongation of landscape elements) and a minimum value perpendicular to that axis (Fig. 7A). The maximum value of DCI is higher for landscapes with distinct linear features (e.g., Conserved1 sloughs) than for those with obviously disconnected features (e.g., Degraded1 sloughs) (Fig. 6). Sim1 and Conserved2 sloughs have intermediate DCI, with Sim1 falling between Conserved1 and Conserved2. When slough DCI is high (e.g., 0.72 for Conserved1), ridge DCI tends to be low (0.29). Conversely, when slough DCI is low (e.g., 0.02 for Degraded1), ridge DCI tends to be high (0.64). Conserved2 exhibits intermediate DCI values for ridges and sloughs (0.35 sloughs; 0.31 ridges), reflecting the qualitatively lesser connectivity of sloughs compared to Conserved1 (Fig. 4).

Sim1 experienced expansion of sawgrass patches and loss of slough connectivity in all landscape degradation scenarios examined with the RASCAL model (Fig. 8). Loss of slough coverage and connectivity was fastest in response to perturbations involving decreased water depth (Fig. 8A and B), but DCI declined more rapidly than coverage, with most connectivity lost over hundreds of simulated years as opposed to millennia. The threshold for connectivity loss was around 50–60% aerial coverage of sawgrass (Fig. 9A), which corresponds to the percolation threshold (Fig. 9B), the point at which the landscape loses all spanning paths along the direction of interest (i.e., sloughs that are connected from one end of the model domain to the other). Based on changes in the number of spanning paths, trajectories of landscape change can be divided into three phases: phase I, an early phase, where, as increasing numbers of ridges are stabilized by vegetation and made permanent, subdivision of the surrounding slough matrix results in a larger number of spanning paths; phase II, approach of the percolation threshold, where further ridge growth cuts off formerly connected sloughs and the number of spanning paths declines; and phase III, post-percolation threshold, where no spanning paths exist, yet directional connectivity continues to decline through a decrease in the size and linearity of remnant sloughs. Most DCI loss occurs during the approach of the percolation threshold, with only slight losses during the early and post-percolation threshold phases (Fig. 9A).

**Comparison between the DCI and other connectivity metrics**

Common isotropic connectivity metrics poorly reflect apparent differences in ridge or slough directional...
Fig. 7. Connectivity-orientation curves for the Everglades ridge and slough landscape at different resolutions: (A) Conserved1; (B) Sim1 and Rotated1. The grid resolution for Rotated1 is 7.6 m, and computations were performed on landscape graphs configured as undirected networks.
connectivity and changes in that connectivity with landscape degradation. The graph-theory-based metric, $\gamma$, remains low (0.0002–0.0007) in all computations and does not vary in the expected manner; for instance, disparate ridges in Conserved1 have a higher $\gamma$ (0.0006) than well-connected sloughs (0.0005). In contrast, AI and cohesion for sloughs remain near the top of their range for all landscapes examined, even the most degraded (Table 1). These metrics also do not reflect the relative differences in connectivity across landscapes apparent in the DCI. For instance, ridge AI does not reflect the high DCI of Conserved2 ridges relative to that of Conserved1 and Sim1. Also, cohesion does not reflect differences in slough connectivity between Conserved1 and Sim1.

Common directional connectivity metrics differ in their agreement with the DCI and in their reflection of qualitative differences between the test landscapes. Like DCI, the ICS reflects relative differences in connectivity between the four test landscapes (Table 1). However, the semivariogram range is not consistent with the DCI. For example, ridge AI does not reflect the high DCI of Conserved2 ridges relative to that of Conserved1 and Sim1. Also, cohesion does not reflect differences in slough connectivity between Conserved1 and Sim1.

Differences between the DCI and other common connectivity metrics are more apparent in the trajectories of landscape change simulated with the RASCAL model (Fig. 9). Like the DCI, slough cohesion, AI, and ICS decline with increasing sawgrass coverage. In fact, the DCI and ICS are linearly related, with an $R^2$ of 0.98 (Fig. 9C). However, unlike the DCI, cohesion is only sensitive to landscape change at and beyond the percolation threshold (phase III, Fig. 9E). AI is sensitive during phase I of landscape development (subdivision) and again during phase III (post-percolation threshold), but only for some of the perturbation scenarios (Fig. 9F). For the perturbation scenario involving decreased water surface slope, AI is flat at and beyond the percolation threshold and does not reflect the real losses in slough connectivity and area apparent in Fig. 8C.

In contrast to the other connectivity metrics, contagion and the directional semivariogram range do not change monotonically with increasing sawgrass coverage. Contagion, which depends on the distribution of both ridge and slough landscape elements, declines with increasing maturity of a stabilizing ridge and slough landscape but ultimately increases with perturbations that cause sloughs to become more fragmented (Fig. 9G). The minimum value of contagion occurs just before the percolation threshold. Changes in the semivariogram range with sawgrass coverage are less smooth and more erratic, with many perturbation scenarios exhibiting a shallow local maximum near the percolation threshold. However, the location of the local maximum is not consistent across perturbation scenarios (Fig. 9D).
Fig. 9. Changes in new and established connectivity metrics with landscape evolution over the trajectories shown in Fig. 8. Changes are divided into three phases: I, an early phase, where subdivision of the slough patch results in a larger number of spanning paths; II, approach of the percolation threshold, where further ridge growth cuts off formerly connected sloughs, and the number of spanning paths declines; and III, post-percolation threshold, where no spanning paths exist, yet connectivity can continue to decline through a decrease in the size of remnant sloughs. Abbreviations are: AI, aggregation index; and ICS, integral connectivity scale.
Cohesion exhibits a nominal precision of 2 (i.e., 2 with small differences in connectivity. For example, create problems in discriminating between landscapes full time series of landscape degradation, which may characterized some of the landscape degradation trajectories, which were noisy and/or exhibited a lack of abundance and connectivity (Fig. 9G), reflecting its variation here) and resolution precision (for fourfold changes in resolution) of 0.07.

Effective permeability (cm\(^{-1}\))

<table>
<thead>
<tr>
<th>Metric</th>
<th>Conserved1</th>
<th>Conserved2</th>
<th>Sim1</th>
<th>Degraded1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent ridge area</td>
<td>38</td>
<td>55</td>
<td>41</td>
<td>86</td>
</tr>
<tr>
<td>Ridge DCI</td>
<td>0.29</td>
<td>0.31</td>
<td>0.08</td>
<td>0.64</td>
</tr>
<tr>
<td>Ridge cohesion</td>
<td>98.4</td>
<td>99.2</td>
<td>98.0</td>
<td>99.9</td>
</tr>
<tr>
<td>Ridge AI</td>
<td>94.5</td>
<td>93.0</td>
<td>93.3</td>
<td>96.2</td>
</tr>
<tr>
<td>Ridge γ index</td>
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<td>0.0003</td>
<td>0.0007</td>
<td>0.0002</td>
</tr>
<tr>
<td>Ridge ICS (m)</td>
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<td>862</td>
<td>251</td>
<td>1348</td>
</tr>
<tr>
<td>Ridge semivariogram range (m)</td>
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<td>106</td>
<td>79</td>
<td>475</td>
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<tr>
<td>Slough DCI</td>
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<td>0.57</td>
<td>0.02</td>
</tr>
<tr>
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<td>99.4</td>
<td>99.9</td>
<td>96.3</td>
</tr>
<tr>
<td>Slough AI</td>
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<td>95.4</td>
<td>77.0</td>
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<tr>
<td>Slough γ index</td>
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<td>0.0003</td>
<td>0.0006</td>
<td>0.0005</td>
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<tr>
<td>Slough ICS (m)</td>
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<tr>
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<tr>
<td>Contagion</td>
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<td>35.8</td>
<td>55.5</td>
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<tr>
<td>Effective permeability (cm(^{-1}))</td>
<td>0.32</td>
<td>0.26</td>
<td>0.31</td>
<td>0.19</td>
</tr>
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</table>

Notes: Abbreviations are: DCI, directional connectivity index; AI, aggregation index; ICS, integral connectivity scale. The γ index is defined in Eq. 9.

### Discussion

Quantifying connectivity in hydrology and ecology

The DCI meets the criteria outlined in Fig. 1 and improves upon some of the other structural connectivity metrics common in hydrology and ecology. Within an intermediate range of grid resolutions, the DCI is robust to twofold resolution changes and is insensitive to image rotation during pre-processing (Fig. 7). Unlike the semivariogram range and ICS, the DCI is bounded between 0 and 1, providing an intuitive measure of connectivity that is transferable across landscapes with inherently different scales. Although cohesion and AI are also bounded, they vary over a much smaller portion of their range (3% and 8% for cohesion and AI, respectively, compared to >80% for the DCI) across a full time series of landscape degradation, which may create problems in discriminating between landscapes with small differences in connectivity. For example, cohesion exhibits a nominal precision of 2 (i.e., 2% of its total range but 67% of its variation here) (Schumaker 1996), while DCI for Conserved1 had a rotational precision of 0.03 (3% of its total range, but 4% of its variation here) and resolution precision (for fourfold changes in resolution) of 0.07.

Nonuniqueness is another shortcoming associated with many connectivity metrics but not with the DCI. Over the course of progressive slough loss, slough DCI changed monotonically. In contrast, contagion was high in landscapes with both very high and very low slough abundance and connectivity (Fig. 9G), reflecting its construction from multiple patch types, which has been recognized for leading to ambiguity (Frohn 1998, He et al. 2000, Corry and Nassauer 2005). To a lesser extent, nonuniqueness in semivariogram range and AI also characterized some of the landscape degradation trajectories, which were noisy and/or exhibited a lack of sensitivity to changes in landscape configuration near the percolation threshold (Fig. 9D). The index γ also exhibited nonuniqueness in that its value was invariant between Conserved1 and Degraded1 sloughs (Table 1). That index compares the number of direct connections between nodes to the total number of possible connections between nodes but does not recognize higher-degree connectivity between distant nodes connected via other nodes. As a result, when coverage of a patch type is high (and hence, the number of nodes is high) γ can be very low, even in a highly connected system, simply because of the large number of possible connections between nodes.

The primary reason for quantifying structural connectivity is to gain insight about functional connectivity, such as fluxes of water, solutes, and/or organisms. Here we examined the behavior and characteristics of the DCI in a purely structural way, although, as will be discussed in section 4.2, it is possible to formulate more inherently functional versions of the DCI. Nevertheless, our analyses suggest that the DCI shows promise for functional connectivity assessments in a way that is complementary or preferable to other connectivity metrics. For instance, DCI is linearly related to the ICS, which correlates with peak and total discharge (Western et al. 2001). Only the DCI and ICS trajectories had an inflection point at the percolation threshold (Fig. 9A), where landscapes lose a spanning path for flow or a contiguous corridor for wildlife migration, which has significant ramifications for fluxes. Management problems in hydrology and ecology often involve quantifying fluxes between defined locations, such as contributions of an agricultural field to nutrient loading within a stream, or dispersal of organisms between distinct subpopulations or habitats. For these problems, connectivity will impact fluxes primarily before the percolation threshold; after the percolation threshold, exchange will be minimal.

We also observed a distinct increase in the slope of DCI trajectories at the point at which subdivision of the slough matrix ceased and the number of spanning paths...
was at a maximum (i.e., the transition between phase I and phase II in Fig. 9). Beyond this point, true decreases in slough connectivity were initiated as further ridge expansion cut off formerly contiguous sloughs. None of the other metrics examined exhibited a distinct change at this point; cohesion was not at all sensitive within this region, whereas the slough AI, semivariogram range, and contagion changed roughly linearly. These differences suggest that changes in metrics such as AI and semivariogram range are dominated by changes in patch area, while DCI, though somewhat sensitive to patch area, better reflects actual connectivity differences.

Ecologists commonly advocate using a suite of connectivity metrics, each of which is sensitive to different environmental attributes and may relate to different aspects of ecosystem function (Li and Reynolds 1994). Indeed, we find that when management problems require evaluation of connectivity over a wide range, it may be most advantageous to use complementary metrics, such as the DCI above the percolation threshold and cohesion below the percolation threshold. Although the ICS has essentially equivalent behavior to the DCI ($R^2 = 0.98$, Fig. 9C), it is substantially less computationally efficient and, as an unbounded metric, is scale-dependent and less intuitive.

**Adaptability of DCI for structural and functional applications in hydrology and ecology**

The DCI is generalizable to a variety of applications in hydrology and ecology, but that adaptability requires informed decisions about its construction. Users of the DCI have choices about image resolution and extent, the construction of the landscape graph (full or skeleton, directed or undirected) and distance matrix ($\ell =$ physical or functional distance), preferential weighting of large or small scales ($w_{ij}$), and the direction(s) along which to quantify connectivity (e.g., linear or streamwise). The optimal image resolution and extent depend on the scale of the phenomenon of interest (Wiens 1997, Calabrese and Fagan 2004). For example, if a fish species uses only large-scale flow-ways and is not found in small, isolated sloughs surrounded by sawgrass, a coarser image resolution may produce DCI values more relevant for conservation. Image extent should be large enough to encompass a representative distribution of link lengths. In general, we recommend using the maximum extent practical and the minimum resolution that resolves all relevant connections and produces an index that varies smoothly with the angle of rotation (and is therefore minimally sensitive to small changes in image alignment). The precedent for defining minimum relevant resolution is that which is 2–5 times smaller than the ecological phenomenon of interest (O’Neill et al. 1996) or 10–20 times smaller than the area of the hydrologic unit of interest (Shrestha et al. 2006). Images acquired at different resolutions should be resampled to a consistent resolution to ensure comparability.

The preferred convention for defining landscape graphs will depend on the application. In all cases, we recommend using the skeleton network convention for landscape graphs. Although resulting DCI values are generally 10% lower than those generated from full networks, the two sets of values are tightly correlated, and computational time is an order of magnitude lower with the skeleton network. Generally, we recommend using directed networks for applications involving flow or when transport in a particular direction (e.g., up slope, upwind) is hindered and undirected networks when the physical adjacency of landscape elements is the primary factor influencing transport. Preferential weighting of certain scales with the $w_{ij}$ weighting scheme provides additional flexibility for formulating directional connectivity metrics that are most relevant to the scale of the phenomenon of interest. In the Everglades case study, kilometer-scale slough directional connectivity is more relevant to conservation objectives than small-scale connectivity, so our choice of $w_{ij}$ gave more emphasis to directional connectivity over long distances. Other phenomena (e.g., gene flow in populations with limited mobility) may merit preferential weighting of small-scale connectivity by, for example, setting $w_{ij}$ to $dx^{-1}((j - r)^{-1}$. On the other hand, hierarchy theory (in which small-scale systems are nested within graph nodes) may provide the best approach for problems in which the phenomena of interest span multiple scales (Cantwell and Forman 1993, Kunin 1998).

**Information content of connectivity-orientation curves**

One advantage of performing DCI computations over a range of linear directions is that connectivity-orientation curves provide information about a variety of hydrological, geomorphological, and ecological processes. Secondary peaks within a 180° span suggest that multiple directional processes influence landscape development. Broad peaks may reflect temporal variability in the direction of the process (e.g., wind or water flow) driving landscape development and/or limited sensitivity of landscape structure to slight variations in the direction of the sculpting force. Anisotropic landscapes have peaks at 0° and 180° if the image is aligned with landscape features. Any difference in the magnitude of those peaks conveys additional information about landscape structure relevant for transport and dispersal. Because DCI is computed based on the shortest connection between a node and any node at a particular projected distance along the direction of interest, landscapes with patches that diverge along that direction will have a higher DCI than those that converge (i.e., those with divergence contain more options for reaching distant nodes.) When the two DCI peaks differ, processes like dispersal may be favored along the direction with the highest peak, whereas the probability of encountering a mate may be favored along the opposite direction. In hydrology mechanical dispersion
(i.e., of solutes) would be highest when flow is in the direction of the highest peak in DCI.

Because of their high information content, connectivity-orientation curves can be powerful tools for quantitatively comparing landscapes. Quantitative comparisons are important for determining whether processes controlling landscape formation are universal, whether the same processes control landscape evolution at multiple scales, and whether models accurately recreate landscape structure. As reviewed in Murray and Paola (1996), methods for quantitatively comparing landscapes include basic statistics (e.g., mean width of patches), spectral routines for computing the periodicity of landscape features (e.g., bedforms in a river), fractal methods for computing the self-similarity of features under changes in scale, and dynamical systems methods that treat a sequence of measurements in space as a series of measurements in time. Many of these methods distill landscape pattern to a small set of summary numbers, which are then compared across landscapes. However, information is lost in this approach compared to one that compares whole patterns and then reduces the result of that comparison to a set of summary numbers.

There are a few examples of the latter approach for comparing landscape patterns in an information-preserving way (Sapozhnikov and Foufoula-Georgiou 1995, Murray and Paola 1996), but they are not widespread. Statistical differences in connectivity-orientation curves across landscapes, summarized using a Tucker’s congruence coefficient (see Results: Comparison of alternate constructions of the DCI and Lorenzo-Seva and ten Berge [2006]) or Kolmogorov-Smirnov statistic, would be a complementary approach. One advantage of the connectivity-orientation method of comparison over other published approaches is that the information about landscape pattern is captured in a relatively simple, intuitive plot, and for many applications a summary statistic may not even be necessary to assess landscape similarity or simulation model performance. For example, although Sim1 was previously considered an excellent reproduction of an actual Everglades ridge and slough landscape based on standard summary statistics (Larsen and Harvey 2011), clear differences between its morphology and that of Conserved1 emerge from the connectivity-orientation curves (Fig. 7). Hence, connectivity-orientation curves can guide improvement of simulation models to an extent that many summary statistics cannot.

**Advancing the functional connectivity concept in hydrology**

Rivers and watersheds are inherently heterogeneous systems, consisting of mosaics of patches that are connected by boundary flows (Ward et al. 2002). In surface-water environments, there is growing interest about how the structural connectivity of landscape elements affects fluxes and exchange of constituents between different parts of the watershed. For instance, Chesapeake Bay restoration scientists seek to understand how the spatial arrangement of riparian buffers impacts the delivery of nutrients from agricultural fields to streams (Baker et al. 2006). Spatiotemporal patterns in floodplain–lake–river connectivity in large river systems have additionally been recognized as a significant and complex driver of fish productivity (van de Wolfshaar et al. 2011). However, little consensus about how to quantify functional connectivity for surface-water applications has emerged. On the other hand, hydrogeology has a rich history of predicting spatially averaged fluxes from patch area and connectivity using an upscaled, effective permeability, \( k_{\text{eff}} \) (Gelhar 1986, de Dreuzy et al. 2010) that is constructed as a power-law area-weighted average of the permeability \( k_i \) of the different patch types (Ronayne and Gorelick 2006):

\[
k_{\text{eff}} = \left( \sum_i f_i^{k_{ik}} \right)^{1/a}
\]  

where \( f_i \) is the volume fraction occupied by patch \( i \), and the averaging exponent \( a \) depends empirically on the connectivity of preferential flow channels, quantified in the hydrogeology literature using a mean spanning path tortuosity (Ronayne 2008). Mean spanning path tortuosity is similar to the inverse of the DCI, though unlike the DCI it does not integrate over multiple scales and is sensitive only to the scale of the image.

Presently, theory for scaling up permeability terms in surface-water hydrology does not exist. However, there are analogies to effective permeability terms in rate laws for surface-water flow. To illustrate, in groundwater hydrology the product of a potential gradient (\( \nabla P \)) and \( k_{\text{eff}} \) is linearly related to discharge, \( Q \) (and therefore, mean flow velocity, \( U \)) through Darcy’s Law:

\[
\nabla P k_{\text{eff}} = -\mu \frac{Q}{L_z} \Rightarrow \frac{\partial H}{\partial x} k_{\text{eff}} = -\frac{v}{g} U
\]

where \( \mu \) is dynamic viscosity, \( v \) is kinematic viscosity, \( \partial H/\partial x \) is the hydraulic head gradient, \( g \) is the gravitational constant, and \( L_z \) and \( L_x \) are the width and thickness of the aquifer. Analogously, in fully turbulent open-water environments, the Manning equation relates the product of a potential gradient (the slope of the water surface, \( S \)) and a “permeability” term to the square of velocity:

\[
S \frac{\alpha R^{4/3}}{n^2} = -\frac{v}{g} U^2
\]

where \( \alpha \) is the product of \( v/g \) and a constant, \( R \) is hydraulic radius, and \( n \) is the Manning roughness. In emergent wetland environments, the product of the potential gradient and a “permeability” term (\( \beta \)) scales with \( U^\alpha \) (Harvey et al. 2009):

\[
S K_0^{-1} a^{2.5-\alpha} v^{-1} U^\alpha = S \beta = \frac{v}{g} U^\alpha
\]
where \( \alpha \) is vegetation frontal area per unit volume, \( d \) is vegetation stem diameter, and \( K_0 \) and \( \varphi \) are empirical constants depending on vegetation biomechanical properties, with \( 0 < \varphi < 1.2 \) (Wu et al. 1999).

As a start, we examined the possibility of upscaling \( \beta \) using the power-law averaging scheme of Ronayne and Gorelick (2006). Rather than using mean spanning path tortuosity in the model for \( \alpha \), we developed an empirical relationship between mean spanning path tortuosity and the DCI (Fig. 10A) and used the DCI, which is bounded and not scale dependent and varies more smoothly with changing landscape condition. Values of \( \beta \) for individual ridge and slough landscape patches were solved by power-law regression on point-scale modeling outputs that predicted \( U \) as a function of \( S \) for a constant value of \( H \) (Larsen et al. 2009). We then used RASCAL to solve for mean flow velocity through each test landscape, subject to a specified \( H \) and \( S \), and compared the outcome to the predicted \( \beta \) (Fig. 10B).

Promisingly, all trajectories plotted onto a single, smooth curve, suggesting that with further advances in theory, surface-water velocities may be predicted by an effective permeability term that depends on the DCI. However, the line was not well fit with a power-law regression, underscoring the need for further advances in theory. One need is for reevaluation of the form of the spatial averaging scheme for \( \beta \) as well as the model used to solve for \( \alpha \). Because aquifers have relatively high mean spanning path tortuosity (e.g., low DCI), our construction of Fig. 10B requires extrapolation into a region where \( \beta \) is minimally sensitive to changes in connectivity (Fig. 10C). In particular, use of the DCI instead of tortuosity in the solution for \( \alpha \) will make the concept of permeability upscaling more relevant to surface-water systems and can improve permeability upscaling in any system that lacks a spanning path.

**Addressing conservation and restoration needs with the DCI**

Case-study application of the DCI to the Everglades illustrates its utility for addressing conservation and restoration problems worldwide. In the simulated Everglades landscapes, slough directional connectivity was lost more rapidly than slough coverage (Fig. 8), highlighting the advantages of regularly quantifying DCI to detect areas of the landscape that may be susceptible to imminent degradation. The precipitous decline in slough connectivity prior to the main decline in slough area suggests feedback between connectivity and area; rapid loss of slough area may result from loss of slough connectivity that changes the large-scale flow field in a way that facilitates slough invasion by sawgrass (Larsen and Harvey 2011). Interestingly, large-scale slough directional connectivity was lost most abruptly near the percolation threshold, at 50–60% sawgrass coverage, regardless of type of hydrologic perturbation (Fig. 9A). Previously, 55% sawgrass coverage had been recognized through qualitative analysis as the threshold for slough invasion by sawgrass.
that distinguishes intact from degraded ridge and slough landscape (Wu et al. 2006). Emergence of this threshold from both image analysis and directional connectivity analysis of the simulated landscapes provides confidence in the validity of the processes simulated by RASCAL, even as configurational differences exist between actual and simulated landscapes.

Applications of these new directional connectivity computations could lead to a better understanding of connectivity not just as a dependent variable, which remains largely uncharted territory in hydrology and ecology (Goodwin 2003). Quantification of directional connectivity in the Everglades has led to novel demonstration that decreases in slough directional connectivity are rapid once initiated and may precede losses in slough aerial coverage (Fig. 8). Efforts to restore historical flow patterns are now underway, and it will become increasingly important to quantify the effects of those actions not just on patch coverage but also the directional connectivity of sloughs. This example highlights use of the DCI as both an early-warning indicator of environmental degradation and a performance indicator of the success of restoration efforts here and around the globe.

Acknowledgments

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Literature Cited


**Supplemental Material**

**Supplement**

MATLAB script files used to perform directional connectivity analyses (Ecological Archives A022-119-S1).