# Spatiotemporal dynamics of complex ecological networks: Power-law scaling and implications for conservation planning

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**Spatial constraints on the topology of complex networks are just beginning to be appreciated, both theoretically[1-3] and in concrete examples like the Internet[4] and global air transportation network[5]. Ecological networks, composed of habitat patches connected by species dispersal, are intrinsically spatial and show promise as a tool for conservation planning; but while habitat-loss effects on ecological networks have been simulated, such effects have not been directly measured in ecological networks varying over time[6-8]. In this study, I used satellite remote sensing to study ecological networks composed of wetland habitat in the Prairie Pothole Region (PPR) of North America. I find power-law scaling of important topological properties as a function of dispersal ability and as wetland density varies with climate. Prairie wetland networks are 'meso-worlds' with mean topological distance increasing faster with network size than small-world networks[9], but slower than regular lattices[10]. While similar dynamics have been shown in random spatial networks[1,3], these results emphasize the importance of processes determining locations of nodes in a spatial network, with possible implications in other areas like wireless communication networks[11] or disease transmission networks[12]. Wetland networks establish a climate envelope for landscape connectivity in the PPR, and I show that wetland-dependent species face a 'crisis of connectivity' with climate change. The global biodiversity crisis requires that conservation planners act quickly over large areas using limited resources[13,14]; a network-based approach to coarse-filter conservation planning in dynamic landscapes should be broadly applicable to this problem.**

The PPR spans approximately 800,000 km$^2$ of glaciated prairies from Alberta, Canada to northern Iowa in the United States (SI Fig. 1), containing tens of millions of closed-basin, depressional wetlands and encompassing the most productive waterfowl habitat in North

America[15]. In response to a pronounced decadal climate cycle of drought and above-average precipitation, or deluge[16], surface water extent varies widely in the PPR (Fig. 1a).

Wetland networks (Fig. 1b) were extracted from water bodies identified in a time series of Landsat Thematic Mapper (TM) imagery from eastern North Dakota, U.S.A[17]. TM data from 1989 captured the transition from average hydrologic conditions to drought, while a 1991 image was acquired at the height of the 2$^{nd}$ worst drought in the past century; slightly less-severe than the 'dust-bowl' years of the 1930s (Fig. 1a). A 1997 image captured the peak of a wet period unequaled in the past 500 years[16], while subsequent relaxation and drying of the hydrologic landscape was observed in 2003 (image not shown). Euclidean distances between water bodies were calculated on a centroid-to-centroid basis and wetland networks were constructed at three dispersal scales; 500 m, 1000 m, and 1500 m (Fig. 1b). At the 500 m dispersal scale, links were established between all neighboring wetlands separated by no more than 500 m; at the 1000 m scale all wetlands within 1000 m of one another were connected, and so on at the 1500 m scale. These distances are representative of annual dispersal by a number of wetland-dependent bird, amphibian, and plant species resident in the PPR[18-21].

Wetland network topology, and the ensuing potential for species dispersal across the landscape, is determined by wetland density and maximum dispersal distance. Observed variation in wetland density generated an ensemble of wetland networks varying in size by several orders of magnitude (SI Table 1). Despite these differences, I found exponential node degree distributions (SI Fig. 2, SI Table 2) and power-law distributions of cluster size (SI Fig. 3, SI Table 3) across all networks. Comparing distributions across the ensemble, I normalized different-sized networks with respect to their percolation thresholds[10]; thus, distributional parameters were plotted against the proportion of nodes, $G$, belonging to the largest connected

component.  The exponential parameter of node degree distributions, β, and the power-law exponent of cluster size distributions, $\alpha$, both scale as power laws:  $\beta \approx G^{-0.63}$ (Fig. 2a) and $\alpha \approx G^{-0.15}$ (Fig. 2b).  As wetland networks span a greater proportion of the landscape, they disproportionately accumulate nodes linking spatially distinct wetland clusters; subsequently network betweenness centrality, $B$, increases as $B \approx G^{1.98}$ (Fig. 2c).  To the best of my knowledge, these types of power-law regularities are the first to be documented in networks dynamic in both space and time.

In the past decade, much has been made of small-world networks[9].  Like small words, wetland networks exhibit consistently high local clustering (Fig. 3).  However, the average topological distance, $L$, between nodes in a small-world network scales as $L \approx ln(n)$ where $n$ is network size.  In wetland networks inter-node distance increases as $L \approx n^{0.35}$ (Fig. 3); faster than a small world, but slower than a regular 2-dimensional lattice, or 'large-world', where $L$ increases as $n^{0.5}$ (10).  While a lack of long-range connections precludes small-world dynamics in wetland networks, we can think of prairie wetlands as 'meso-world' networks.  Similar intermediate scaling of mean topological distance has been observed in random spatial networks where the probability of connection is a power-law function of Euclidean distance between nodes[3], or where a competition between preferential attachment and distance-selection occurs[1]. However, given that I used fixed dispersal thresholds in assembling wetland networks, observed meso-world properties emerge solely from the spatial configuration of wetlands as they appear and disappear on the prairie landscape.

An exception to approximately cube-root scaling of $L$ was found under very high wetland densities in the 1997 network extracted at the shortest dispersal scale, 500 m.  In Fig. 3, the 500 m network is a clear outlier, with $L$ displaced above the fitted trend.  Paradoxically, we might not expect poorer dispersing species to be disadvantaged in an environment with maximally

available habitat; but in this case better dispersers should be more efficient finding 'shortcuts' in the habitat network they 'see' (relative to the network available to poorer dispersers). Analogous effects are likely important in other spatial networks like wireless communication networks[11] or disease transmission networks[12]. For example, in a wireless network it might be advantageous to increase transmission distance when the density of individual devices exceeds some threshold in order to take advantage of shortcuts arising in the network.

Spatial constraints on network topology have previously been studied by considering nodes fixed in space and treating connection probabilities as a function of inter-node distance[1-4]. Here, I assessed spatial effects arising from changes in node density and location over time. In the PPR, observed power-law regularities emerge from underlying hydrologic processes. Power-law scaling is commonly found in geomorphology and hydrology[22,23], including wetland hydrology where correlations over a range of time scales, or $1/f$ noise have been observed[24]. Complex groundwater flow fields arise in the glacial moraine topography and poorly permeable soils characteristic of the PPR[16]. A potentially powerful future application would be to use power-law scaling of wetland networks to make inferences about landscape hydrologic processes.

**Implications for conservation planning**

Wetland networks were compiled from a remote sensing record spanning a gradient from deluge to severe drought (Fig 1a). This record establishes a climate envelope for landscape connectivity in the PPR. Over the next century, global climate change models (GCMs) predict increasing drought frequency in the PPR with an overall loss of wetland habitat[15]. Given observed power-law scaling of wetland network topology (Fig. 2), such a shift implies nonlinear decreases in wetland connectivity, both locally as expressed in more constricted node degree

distributions (Fig 2a, SI Fig. 2), and across the greater landscape; as larger clusters become more improbable (Fig. 2b, SI Fig. 3) through the disappearance of wetlands with high betweenness centralities (Fig. 2c). Expected negative effects on wetland-dependent species include increased extinction probabilities of local metapopulations[25] and a restricted ability of species to adjust their ranges relative to a shifting climate. For example, consider clusters of 20 wetlands or more, a reasonable lower bound for a viable metapopulation[26]: as the landscape dries, their geographic coverage constricts dramatically (Fig. 4). Clusters first disappear from the study area's central portion; an area with less vertical relief, and subsequently more intensive agricultural cultivation and wetland drainage. This contraction isolates the northern half of the study area from the southern half. At the height of drought, the few remaining clusters are largely confined to a small area in the north (Fig. 4). I conclude that wetland-dependent species in the PPR face a 'crisis-of-connectivity' with climate change.

Climate envelope models based on GCM forecasts have been used to identify regions at risk of losing species through climate change[27,28] and to target reserves accessible by dispersal as existing habitats become unsuitable[29]. However, the precision of such models has recently come into serious question[30]. Here, I establish a climate envelope for landscape connectivity by direct observation; identifying where better-connected wetland networks are likely to persist in drier landscapes. These sites are obvious candidates for protection. Observations under improved conditions indicate pathways for dispersal from drought refugia to newly available habitat. A more subtle conservation strategy would be to protect important 'stepping stones' for recolonization; these wetlands are identified by high betweenness centralities (Fig 1b), analogous to airports (e.g. Melbourne, Australia) connecting different communities or modules in the global air transportation network[5]. Adding long-range links to wetland networks through directed

dispersal by conservation planners might shift meso-world networks into a small world regime, accelerating recolonization.

Obviously, I've made a number of simplifying assumptions in this study; the intervening landscape between wetlands may not be traversable, all wetlands are not similarly suitable habitat for all species, etc. More sophisticated, spatially-explicit metapopulation models exist to assess population viability[25]. However, the current global biodiversity crisis requires that conservation planners act quickly over large areas using limited funding[13,14]. As a coarse filter planning tool, a network approach is relatively easy to implement and could be extended to the entire PPR, or other climate-driven, temporally variable aquatic systems. Terrestrial habitats expected to be altered by climate change do not appear and disappear on short enough timescales to make similar retrospective studies feasible in other landscapes. However, as climate and land-cover projections become more fine-grained and accurate, a similar, but prospective network approach to conservation planning should be broadly applicable.

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**Fig. 1.  Determinants of wetland network topology – wetland density and dispersal distance.  a**, Three Landsat Thematic Mapper images from a subset of the study area illustrating surface water variability as a function of climate.  1991 was the height of drought, 1997 was the height of deluge, and 1989 was an average-to-dry year.  Images are false color composites of mid-infrared (red), near-infrared (green), and visible blue (blue) spectral bands.  Surface water appears blue. **b**, Three sub-networks given maximum dispersal distances of 500 m, 1000 m, and 1500 m extracted from the 1997 wetland landscape, at the height of deluge.  Node sizes are scaled by their betweenness centrality, a measure of node importance in connecting pairs of wetlands by a shortest path, i.e., betweenness centrality increases as the number of shortest paths transiting through a node increases[5].

**Fig. 2.  Power-law scaling of wetland network topology.  a**, Exponential parameters of node degree distributions. **b**, Power-law exponents of cluster size distributions.  **c**, Network betweenness centrality.  Maximum dispersal distance: 500 m (squares), 1000 m (triangles), 1500 m (circles).  Year: 1989 (green), 1991 (red), 1997 (blue), 2003 (violet).

**Fig. 3.  Meso-world scaling of wetland networks.**  Mean topological distance and local clustering coefficients as a function of the size of a network's largest cluster.  Plots of $L = n^{0.5}$ (scaling of a regular 2-D lattice, short dashes) and $L = \log n$ (small-world scaling, long dashes) included as a guide to the eye.  Maximum dispersal distance: 500 m (squares), 1000 m (triangles), 1500 m (circles).  Year: 1989 (green), 1991 (red), 1997 (blue), 2003 (violet).  Open symbols represent local clustering coefficients.
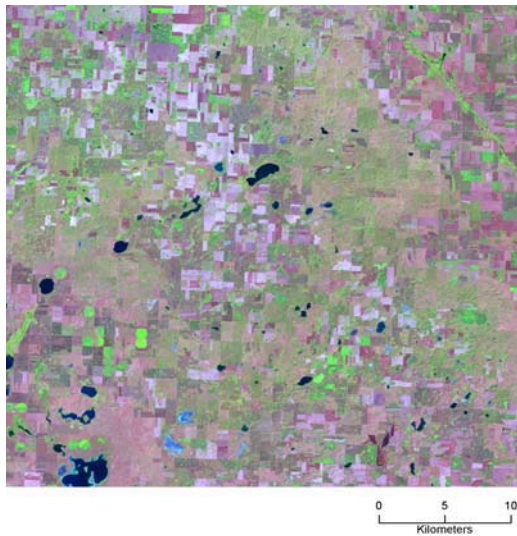
**Fig. 4. Fragmentation of the wetland landscape.** Wetlands belonging to clusters composed of 20 wetlands or more in networks constructed using a maximum dispersal distance of 1000 m over a gradient from deluge to drought. Wetland locations are plotted on top of a digital elevation model (elevations above sea level) where lighter values correspond to higher elevations (maximum = 598 m) and darker values represent lower elevations (minimum = 492 m).
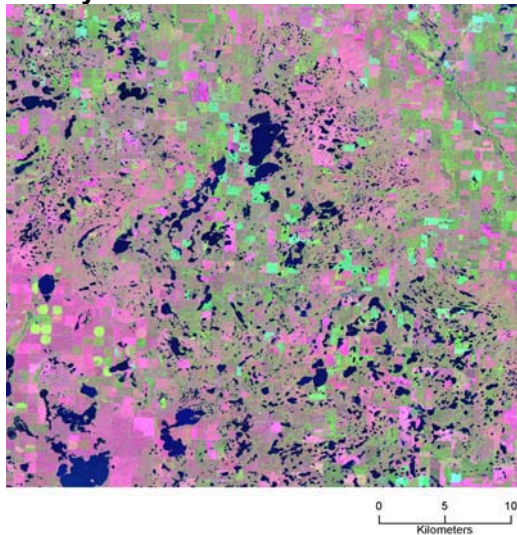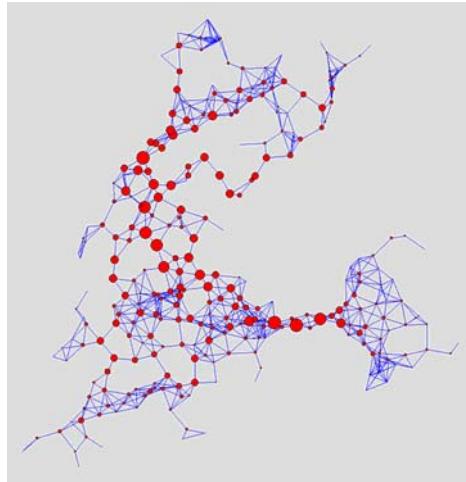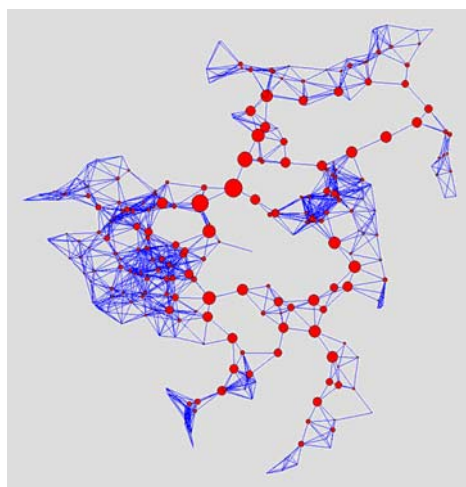
**a**

**b**

**12 May 1989**

**500 m**



**12 June 1991**

**1000 m**



**14 July 1997**

**1500 m**

**a**

$\alpha = -0.63$
$r^2 = 0.82$

Degree dist. decay parameter

Proportion of nodes in largest cluster

**b**

$\alpha = -0.15$
$r^2 = 0.87$

Cluster size dist. exponent

Proportion of nodes in largest cluster

**c**

$\alpha = 1.98$
$r^2 = 0.95$

Network betweenness

Proportion of nodes in largest cluster

**1997**



**2003**



**1989**



**1991**