Spatiotemporal dynamics of prairie wetland networks: power-law scaling and implications for conservation planning

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Abstract. Although habitat networks show promise for conservation planning at regional scales, their spatiotemporal dynamics have not been well studied, especially in climate-sensitive landscapes. Here I use satellite remote sensing to compile wetland habitat networks from the Prairie Pothole Region (PPR) of North America. An ensemble of networks assembled across a hydrologic gradient from deluge to drought and a range of representative dispersal distances exhibits power-law scaling of important topological parameters. Prairie wetland networks are "meso-worlds" with mean topological distance increasing faster with network size than small-world networks, but slower than a regular lattice (or "large world"). This scaling implies rapid dispersal through wetland networks without some of the risks associated with "small worlds" (e.g., extremely rapid propagation of disease or disturbance). Retrospective analysis of wetland networks establishes a climatic envelope for landscape connectivity in the PPR, where I show that a changing climate might severely impact metapopulation viability and restrict long-distance dispersal and range shifts. More generally, this study demonstrates an efficient approach to conservation planning at a level of abstraction addressing key drivers of the global biodiversity crisis: habitat fragmentation and climatic change.

Key words: climate change; complex networks; conservation planning; habitat fragmentation; power-law scaling; Prairie Pothole Region; wetlands.

Introduction

The global biodiversity crisis is driven by habitat loss/fragmentation (Becker et al. 2007) and climatic change (Araújo et al. 2004). In combination, these threats may have particularly serious implications for biodiversity conservation. Existing reserves will likely not meet habitat requirements under future climates (Araújo et al. 2004), while fragmentation limits the ability of species to adjust their ranges as climate shifts (Jetz et al. 2007, Colwell et al. 2008).

Habitat networks are a promising tool for conservation planning in fragmented landscapes. Conceptually, they invoke a metapopulation model (Urban et al. 2009), where the nodes of a habitat network correspond to isolated habitat patches and potential dispersal between nodes is indicated by links (Fig. 1). Habitat networks are attractive as proxies for more complicated spatially explicit population models (Minor and Urban 2007), especially given the time and resource constraints of most conservation planning applications (Wilson et al. 2006). In practice, network models have been used to assess landscape resilience to habitat loss; either by random deletion of nodes (Urban and Keitt 2001) or directed removal consistent with anticipated future

losses of habitat (Fortuna et al. 2006). However, little progress has been made studying *actual* effects of habitat loss as networks vary in space and time.

Here I examine spatiotemporal dynamics of wetland habitat networks from the Prairie Pothole Region (PPR) of North America. The PPR spans a glacial landscape dotted with millions of wetlands from Alberta, Canada to the north-central United States (Appendix A). In response to a decadal climate cycle of drought and above-normal precipitation (or deluge), surface water extent varies dramatically in the PPR (Appendix B). This relatively rapid turnover of discrete wetland patches makes the PPR an ideal setting for exploring the spatiotemporal dynamics of habitat networks.

Methods

Surface water bodies from a 34 000-km^2 area in eastern North Dakota, USA (Appendix A) were identified in Landsat Thematic Mapper imagery (U.S. Geological Survey 2003) using a classification tree methodology (Wright and Gallant 2007). Landsat data from 1997 (Appendix B: Fig. B1A) captured a wet phase unequaled in the past 500 years (Winter and Rosenberry 1998). Subsequent drainage and drying of the wetland landscape was observed in 2003 (image not shown). Satellite imagery from 1989 represents the transition from average hydrologic conditions to drought (Appendix B: Fig. B1B) while a 1991 image was acquired during

the worst drought since the "dust-bowl" era of the 1930s (Appendix B: Fig. B1C).

Distances between water bodies were calculated centroid to centroid. Separate wetland networks were constructed using three different maximum dispersal distances; 500 m, 1000 m, and 1500 m. For each maximum dispersal distance, all wetlands less than the threshold distance apart were connected by undirected links (indicating potential dispersal between wetlands in either direction). These maximum dispersal distances span a range of annual dispersal by a number of wetland-dependent amphibian, plant, and bird species resident in the PPR (Rotella and Ratti 1992, Fairbairn and Dinsmore 2001, Newman and Squire 2001, Galatowitsch 2006), but are not specific to any particular species or groups of species. Instead, my objective was to explore how the connectivity characteristics of a single landscape might vary from the perspective of different species (Bunn et al. 2000), treating variation in dispersal ability in a very general way.

Freely available network analysis software, Pajek (de Nooy et al. 2005), was used to calculate a number of network metrics including node degree, sizes of connected components, mean topological distance, clustering coefficients, and betweenness centrality. Parameters of node degree distributions and connected component size distributions were estimated by linear regression analysis of inverse cumulative distributions (Newman 2003, White et al. 2008). Definitions of network terms/metrics are summarized in Table 1 and readers are referred to reviews by Urban and Keitt (2001) and Urban et al. (2009) for more detailed discussion of graph theoretic methods in ecology.

RESULTS AND DISCUSSION

Climate-driven wetland variability in the PPR, in combination with different maximum dispersal distances, generated an ensemble of wetland networks varying in size by several orders of magnitude (Table 2). Despite these differences, exponential distributions of node degree (the number of neighbors connected to a node) were found across all networks (Appendix C, Appendix E), indicating that prairie wetland networks are not scale-free networks. This appears to be a general feature of spatially constrained networks (Barthélémy 2003) and, here, likely reflects finite limits on local wetland density, or how tightly wetland basins can be packed into the landscape. By contrast, the size of connected components (nodes connected to each other but isolated from other connected components) exhibited power-law scaling across the ensemble of wetland networks (Appendix D, Appendix F).

As the wetland landscape dries, or maximum dispersal distance is reduced, exponential tails of node degree distributions shift inward (Appendix C), accompanied by a decline in average node degree (Table 2). This drop in node degree, a measure of local habitat connectivity, implies a reduced capacity of wetland patches to
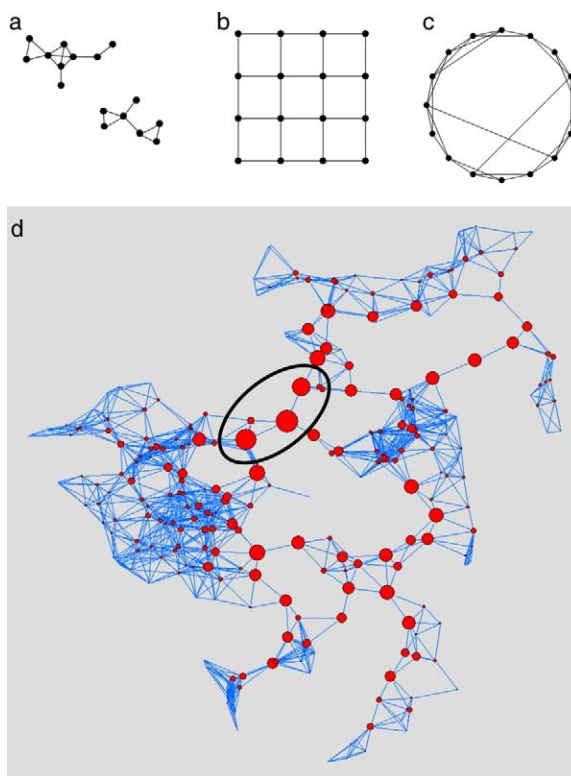

FIG. 1. Examples of networks. Circles represent nodes; lines represent undirected links between nodes indicating potential movement between nodes in either direction. (a) A network where nodes are linked if they are less than a threshold distance apart; in this example the network is not fully connected, i.e., there are two separate components; (b) a regular two-dimensional lattice where nodes are connected only to their nearest neighbors; (c) a small-world network plotted on a circle (for ease of representation) in which most nodes are connected only to their immediate neighbors or second-closest neighbors, but a few long-range links enable relatively rapid movement through the network (in terms of the number of links which must be transited in order to move between any given pair of nodes); and (d) an example of a single connected component from the 1997 wetland network constructed using a maximum dispersal distance of 1000 m; node sizes are scaled by their betweenness centralities; the three large nodes enclosed by the black oval are critical in connecting wetlands in the left half of the component with wetlands on the right.

contribute emigrants to neighboring patches. With respect to conservation planning, this type of retrospective network analysis could be used to identify potential source patches across a range of hydrologic conditions and dispersal abilities (i.e., for multiple species).

Under wetter conditions, the proportion of nodes belonging to the largest connected component increases (Table 2) as previously separate network components are linked. During a deluge phase, such elevated habitat connectivity likely contributes positively to long-distance dispersal, with corresponding influences on gene flow, rescue effects (Brown and Kodric-Brown 1977), and potential range shifts in response to climatic extremes, variation, and change.

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TABLE 1.   Definitions of network metrics and terms.

Metric/term	Definition
Node degree	The number of neighbors attached to a node
Connected component	A set of nodes connected to each other but isolated from other connected components; the size of a connected component is in number of nodes
Topological distance	The minimum number of links that must be transited to travel from one node to another node; typically averaged over all connected pairs of nodes in a network
Clustering coefficient	The fraction of a node's neighbors that are neighbors of each other, averaged over all nodes in a network
Shortest path	The minimal set of links which must be transited to travel from one node to another node; the length of a shortest path is equivalent to the topological distance between two nodes
Betweenness centrality	For a given node, the number of shortest paths transiting through that node; also can be averaged over all nodes in a network as network betweenness centrality

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Connected component size might be useful for conservation planning as a coarse-level indicator of metapopulation viability. For example, consider connected components of 20 or more wetlands, a reasonable lower bound for a viable metapopulation in the most general terms (Vuilleumier and Possingham 2006). Along a hydrologic gradient from deluge to drought, the number of wetlands belonging to connected components meeting this lower bound declines substantially as the wetland landscape fragments (Fig. 2). Also note that while drought substantially reduces the total amount of available habitat (Table 2), wetlands persisting under drier conditions were still relatively well-distributed across the study area in 1989 and 1991 (Fig. 2c, d). Network analysis shows that most of these wetlands may be isolated within connected components too small to support viable metapopulations.

Power-law tails of component size distributions (Appendix D) may confer a degree of drought resilience to prairie wetland networks. Even under drought, there is a subset of connected components much larger than the mean component size (Table 2). With respect to conservation planning, these larger components persisting in the face of drought, e.g., wetlands in the northern portion of the study area (Fig. 2d), are obvious candidates for protection as drought refugia.

Over the next century, global climate models predict more frequent drought in the PPR (Johnson et al. 2005). Thus, we might expect future wetland landscapes to more frequently resemble configurations like those found in 1989 (Fig. 2c) and 1991 (Fig. 2d), with both less wetland habitat and reduced connectivity. In turn, a reduced frequency of hydrologic landscapes resembling the 1997 and 2003 deluge years (Fig. 2a, b) would have a negative impact on long-distance dispersal and potential range shifts.

In order to look for general relationships across the ensemble of wetland networks, I normalized different-sized networks with respect to the proportion of nodes, G, belonging to the largest connected component in each network. This is equivalent to normalizing networks with respect to their percolation threshold, or the point at which the wetland landscape becomes fully connected (Dall and Christensen 2002). Here, a number of power-law relationships emerged. The exponential parameter of node degree distributions, β, decreases as $\beta \approx G^{-0.63}$ (Appendix G: Fig. G1A). The power-law exponent of connected component size distributions, γ, scales as $\gamma \approx$

TABLE 2.   Network summary statistics along a hydrologic gradient from deluge (1997) to drought (1991) for wetland networks constructed at three maximum dispersal distances (500, 1000, and 1500 m).

| Network	Number of nodes	Number of links	Mean node degree	Largest connected component (nodes)	Mean connected component size
500 m					
1997	110 621	406 951	7.4	24 926	17.6
2003	55 508	127 038	4.6	4478	8.9
1989	28 608	52 972	3.7	1016	5.4
1991	4728	7452	3.2	177	3.9
1000 m					
1997	115 120	1 364 352	23.7	50 462	148.4
2003	60 615	423 352	14.0	17 143	44.7
1989	33 789	163 402	9.7	11 603	19.3
1991	5970	18 133	6.1	984	6.4
1500 m					
1997	115 540	2 824 713	48.9	113 714	917.0
2003	61 296	874 082	28.5	49 307	175.6
1989	34 729	326 667	18.8	15 341	63.5
1991	6424	31 970	10.0	1711	9.8
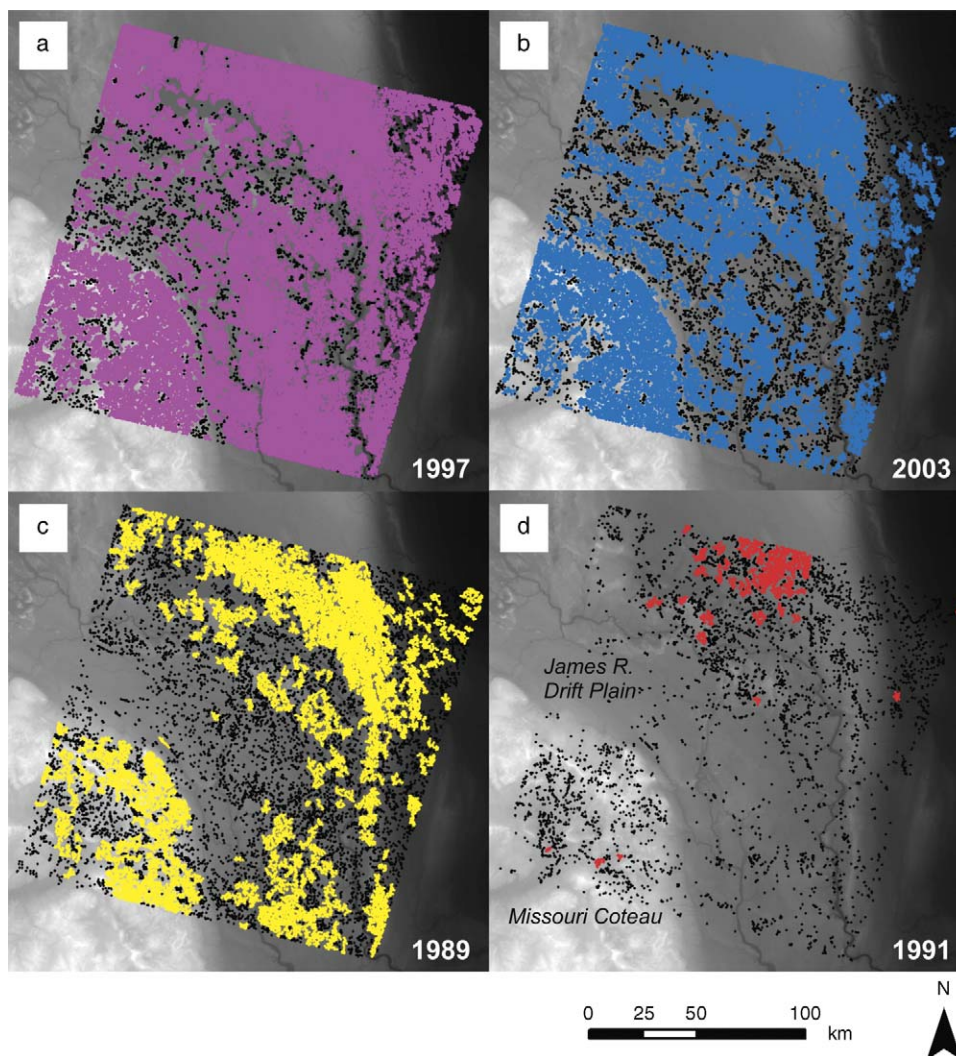
FIG. 2. Fragmentation of the wetland landscape along a hydrologic gradient from deluge to severe drought. Networks were assembled using a maximum dispersal distance of 1000 m. Colored points represent wetlands belonging to connected components containing 20 or more nodes. Black points represent wetlands belonging to connected components containing fewer than 20 nodes. Wetland locations are plotted over a digital elevation model (height above sea level) where lighter values correspond to higher elevations (maximum = 598 m) and darker values represent lower elevations (minimum = 492 m). Connected components containing 20 or more nodes persisting at the height of drought in the north of the study area are located in the vicinity of Devil's Lake, a regional groundwater discharge site (Winter and Rosenberry 1998).

$G^{-0.15}$ (Appendix G: Fig. G1B). Last, network betweenness centrality (see Table 1 for definition), B, increases as $B \approx G^{1.98}$ (Appendix G: Fig. G1C).

The strength of power-law scaling observed across a wide range of hydrologic conditions suggests that future wetland networks will be similarly constrained. Thus, the retrospective analysis described here may sufficiently define a climatic envelope for habitat connectivity in the PPR. Under projected climatic change, wetland networks will likely be biased toward the drier portion of this envelope. Additionally, the dependence of topological parameters on landscape wetness suggests a strong link with conservation planning. At any level of landscape wetness, there will be some subset of wetlands

systematically critical to maintaining habitat connectivity that can be identified by network analysis.

In the past decade, much has been made of "small-world" networks (Watts and Strogatz 1998, Moore and Newman 2000, Guimerà et al. 2005). By definition, the average topological distance between nodes (see Table 1 for definition), L, in a small-world network increases logarithmically with network size as $L \approx \ln(n)$, where n is the number of nodes. In wetland networks, mean topological distance increases as $L \approx n^{0.35}$ (Fig. 3), faster than a small world, but slower than a regular two-dimensional lattice (Fig. 1b), or "large world," where L scales as $n^{0.5}$ (Kosmidis et al. 2008). Like small worlds, wetland networks also exhibit consistently high cluster-
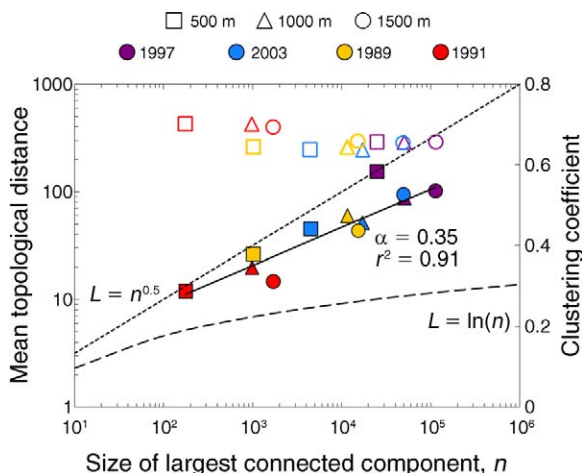
Fig. 3. Meso-world scaling of wetland networks. Mean topological distance L (solid symbols) and local clustering coefficients (open symbols) are plotted as a function of the size of a network's largest connected component. Regression analysis conducted only on the mean topological distance data (not including the 1997 network constructed using a 500-m maximum dispersal distance). Symbol shapes represent maximum dispersal distance. Symbol color indicates network year. Plots of $L = n^{0.5}$ (scaling of a regular two-dimensional lattice, short dashes) and $L = \log n$ (small-world scaling, long dashes) are included as a guide to the eye. Regression slope = α.

ing coefficients (Fig. 3; see Table 1 for definition). Thus, we can think of wetland networks as "meso-worlds."

Such meso-world scaling likely implies a balance between relatively rapid dispersal through wetland networks without some of the risks associated with small-world networks, namely extremely rapid spread of disturbances like disease (Moore and Newman 2000) and invasive species (Minor and Urban 2008). In the networks studied here, note that linking nodes only if they are less than some threshold distance apart precludes small-world behavior, as the requisite long-distance links necessary for small-world scaling are not present (Fig. 1c). In some instances, it could be advantageous for conservation planners to deliberately introduce long-distance dispersal events to shift, albeit temporarily, wetland networks toward a small-world configuration to promote, say, the rapid occupation of newly available habitat during deluge, or to facilitate range shifts.

One exception to meso-world scaling was found under very high wetland densities in 1997 given a maximum dispersal distance of 500 m. In Fig. 3, this network is a clear outlier with a value of L more characteristic of a regular lattice. Paradoxically, one might not expect poorer-dispersing species to be disadvantaged in an environment with maximally available habitat. But, in this case, poorer dispersers may be less efficient at utilizing "shortcuts" in the habitat network that they encounter, as opposed to networks available to species with longer maximum dispersal distances.

Nodes that play a critical role within such shortcuts are identified by high betweenness centralities (Guimerà et al.

2005). In an example from the 1997 1000-m network (Fig. 1d), three nodes with high betweenness centralities (circled in black) are important in connecting wetlands by a relatively direct path rather than a longer, more circuitous route. Similar analyses, repeated for drier years and/or different dispersal thresholds, would identify different critical nodes; again allowing conservation planners to identify potential sites for protection across a range of future environments and for multiple species.

Meso-world wetland networks should also be robust to random habitat loss given the prevalence of redundant links indicated by high clustering coefficients (Watts and Strogatz 1998). This resilience to random node loss typically implies a tradeoff with respect to the vulnerability of networks to targeted disturbance of high degree nodes (Albert et al. 2000). However, in these wetland networks, plots of node betweenness centrality against node degree show that the most connected wetlands are not the most central (Appendix H). This "anomalous centrality" is symptomatic of networks composed of distinct spatial modules (Guimerà et al. 2005), reinforcing the importance of protecting wetlands with high betweenness centralities connecting those modules. Although high degree wetlands may be locally important as source patches, they do not appear to pose a systemic risk to the connectivity of wetland networks.

Fortuna et al. (2006) analyzed a similar system of wetland networks in Spain. Assuming that pond persistence was a function of pond size, they simulated habitat loss by deleting ponds from habitat networks sequentially, starting from the smallest ponds. This approach allowed them to build habitat networks with a combination of directed and undirected links, where directed links indicated dispersal of amphibians from dry ponds to persistent ponds (Fortuna et al. 2006). By contrast, I analyze the static structure of wetland networks at four temporal snapshots, ignoring the past state of those networks. In the PPR, surface water persistence is a complicated function of climatic forcing and groundwater discharge (Winter and Rosenberry 1998), making simulation of wetland presence/absence difficult (Johnson et al. 2005). One area for future research would be to compile remote sensing time series of wetland locations on a seasonal basis across many years. As wetlands appear and disappear from year to year, directed links could be used to represent potential dispersal from drying wetlands to persistent wetlands, or from persistent wetlands to newly available habitat. With respect to conservation planning, such an analysis might identify wetlands critical for facilitating dispersal to drought refugia, or rapid recolonization when landscape wetness increases. This technique is analogous to identifying nodes with high betweenness centralities in both space and time.

The methodology developed in the PPR could be used to assess habitat connectivity in other globally important wetland landscapes (Keddy et al. 2009), specifically boreal peatlands which appear to be acutely sensitive to

climatic change (Camill 2005). Tidal wetlands—where patch dynamics occur on multiple timescales, driven by tidal inundation, episodic sedimentation, and sea-level rise (Ward et al. 2003)—might be particularly interesting from a network perspective. More widely, the types of network analyses demonstrated in wetland landscapes should be generalizable to other patchy landscapes that exhibit significant spatiotemporal dynamics in response to climatic forcing, e.g., tree–grass savannas (Meyer et al. 2007). However, most terrestrial habitats do not respond to climatic forcing on short enough timescales to make similar retrospective studies feasible. But as climate and land-cover projections become more fine-grained and accurate (e.g., Soares-Filho et al. 2006, Jetz et al. 2007), a similar, but prospective network approach should be applicable to conservation planning in terrestrial landscapes.

Conclusions

In the wake of the global biodiversity crisis, conservation planners must make both tactical and strategic decisions: tactical decisions in order to maintain viable metapopulations given near-term impacts of habitat fragmentation, and strategic decisions to identify critical habitat under future climates and facilitate potential range adjustments over longer time spans. The network methodology described here accommodates both of these planning horizons within the same analytical framework. Obviously, network models require a number of simplifying assumptions violated to varying degrees in reality. In the PPR, least-cost paths for dispersal are a more complicated function of intervening land cover and species physiology than straight-line distances; and all wetlands are not similarly suitable habitat for all species. But in the context of the global biodiversity crisis, there simply may not be sufficient time or capability to estimate parameters of more sophisticated, spatially explicit population models in many planning applications. It remains to be seen whether emergent properties of complex habitat networks, e.g., nonlinear fragmentation (Fig. 2) or meso-world scaling (Fig. 3), are more (or less) significant determinants of long-term species persistence than processes operating at finer scales, say, patch-specific demographic rates (North and Ovaskainen 2007). This paper is intended to stimulate that debate.

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APPENDIX A

The Prairie Pothole Region and study area in eastern North Dakota: Landsat Path 31 Row 27 (*Ecological Archives* E091-131-A1).

APPENDIX B

Landsat imagery illustrating surface water variability across a hydrologic gradient from deluge to drought (*Ecological Archives* E091-131-A2).

APPENDIX C

Inverse cumulative distributions of node degree from deluge (1997) to drought (1991) at three maximum dispersal distances (*Ecological Archives* E091-131-A3).

APPENDIX D

Inverse cumulative distributions of connected component size from deluge (1997) to drought (1991) at three maximum dispersal distances (*Ecological Archives* E091-131-A4).

APPENDIX E

Estimated exponential parameters of node degree distributions from deluge (1997) to drought (1991) at three maximum dispersal distances (*Ecological Archives* E091-131-A5).

APPENDIX F

Estimated power-law exponents of connected component size distributions from deluge (1997) to drought (1991) at three maximum dispersal distances (*Ecological Archives* E091-131-A6).

APPENDIX G

Power-law scaling of network topological parameters (*Ecological Archives* E091-131-A7).

APPENDIX H

Node betweenness centrality plotted against node degree for networks constructed using a maximum dispersal distance of 1500 m in 1997 and 1991 (*Ecological Archives* E091-131-A8).