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The role of reserves and anthropogenic habitats for functional connectivity and resilience of ephemeral wetlands

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Abstract. Ecological reserves provide important wildlife habitat in many landscapes, and the functional connectivity of reserves and other suitable habitat patches is crucial for the persistence and resilience of spatially structured populations. To maintain or increase connectivity at spatial scales larger than individual patches, conservation actions may focus on creating and maintaining reserves and/or influencing management on non-reserves. Using a graph-theoretic approach, we assessed the functional connectivity and spatial distribution of wetlands in the Rainwater Basin of Nebraska, USA, an intensively cultivated agricultural matrix, at four assumed, but ecologically realistic, anuran dispersal distances. We compared connectivity in the current landscape to the historical landscape and putative future landscapes, and evaluated the importance of individual and aggregated reserve and non-reserve wetlands for maintaining connectivity. Connectivity was greatest in the historical landscape, where wetlands were also the most densely distributed. The construction of irrigation reuse pits for water storage has maintained connectivity in the current landscape by replacing destroyed wetlands, but these pits likely provide suboptimal habitat. Also, because there are fewer total wetlands (i.e., wetlands and irrigation reuse pits) in the current landscape than the historical landscape, and because the distribution of current wetlands is less clustered than that of historical wetlands, larger and longer dispersing, sometimes nonnative species may be favored over smaller, shorter dispersing species of conservation concern. Because of their relatively low number, wetland reserves do not affect connectivity as greatly as non-reserve wetlands or irrigation reuse pits; however, they likely provide the highest quality anuran habitat. To improve future levels of resilience in this wetland habitat network, management could focus on continuing to improve the conservation status of non-reserve wetlands, restoring wetlands at spatial scales that promote movements of shorter dispersing species, and further scrutinizing irrigation reuse pit removal by considering effects on functional connectivity for anurans, an emblematic and threatened group of organisms. However, broader conservation plans will need to give consideration to other wetland-dependent species, incorporate invasive species management, and address additional challenges arising from global change in social-ecological systems like the Rainwater Basin.

Key words: *anurans; clustering; functional connectivity; graph theory; irrigation; modularity; Protected Areas as Socioecological Systems; Rainwater Basin, Nebraska, USA; resilience; restoration; wetlands.*

INTRODUCTION

Deterministic changes in local environments that steadily decrease wildlife population sizes and random stochastic events that eliminate large numbers of individuals may each contribute to local extinctions (Atmar and Patterson 1993, Tscharntke et al. 2005, Keith et al. 2008). The regional persistence of species is facilitated by emigration and immigration of individuals among patches of suitable habitat or the presence of patches large enough to support multiple interacting populations (Wahlberg et al. 1996, Gonzalez et al. 1998).

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Ecological reserves, defined here as lands set aside for conservation purposes, provide wildlife with important habitat patches in various landscapes.

Interspecific competition, species- and landscape-specific dispersal components (e.g., dispersal probability, dispersal distance, temporal dispersal patterns, disperser mortality, and search time), and travel costs affect successful colonization of suitable patches (Fahrig and Merriam 1994, D'Eon et al. 2002, Belisle 2005). An extinction threshold is crossed and extinction debt created when the characteristics and/or arrangement of habitat patches in an area no longer satisfy the conditions necessary for the persistence of a population, and without improvements, local extirpation becomes inevitable (Atmar and Patterson 1993, Kareiva and Wennergren 1995, Hanski and Ovaskainen 2002).

Metapopulations are characterized by the occasional migration of individuals between habitat patches, creating a balance between extinction and colonization at larger spatial scales (Pulliam 2000). True metapopulations carry high extinction risks for individual patches and are relatively uncommon in nature; however, the term usefully describes many spatially structured populations (Fronhofer et al. 2012). The consideration of genetically connected populations as metapopulations and the promotion of functional connectivity among habitat patches are important for conserving populations scattered among, or restricted to, isolated habitat patches (Wahlberg et al. 1996, Gibbs 2000, Wiens 2002).

Connectivity within landscapes refers to functional relationships between habitat patches that are derived from their spatial distribution and the movement of organisms among them (Fahrig and Merriam 1994, With et al. 1997, Haig et al. 1998). Certain landscape characteristics may encourage or discourage among patch movements of species that interact with landscapes at different spatial scales (Taylor et al. 1993, Tischendorf and Fahrig 2000, D'Eon et al. 2002). In addition to the spatial aspects of habitat patches, their quality for breeding, foraging, and refuge are important. The availability of suitable habitat patches may be limited in landscapes that have undergone significant change (e.g., agricultural landscapes); therefore, ecological reserves and other publicly or privately owned lands may play important roles in the conservation of unique biodiversity elements (Lindenmayer et al. 2006), and more broadly, the provisioning of ecosystem goods and services in landscapes modified by humans (Fischer et al. 2006). However, conservation efforts can be costly, and the efficiency of protected areas for maintaining imperiled populations may depend on suboptimal habitat patches that are critical for facilitating dispersal among higher quality patches (Urban and Keitt 2001). Thus, explicit spatial modeling is useful for evaluating the role of protected areas and other habitats in providing the functional connectivity required for the conservation of populations of conservation concern in human-modified landscapes.

Connectivity and network analysis have emerged as important tools for the study of complex adaptive systems and their resilience in the face of perturbations. A social-ecological system (SES) is a type of complex, adaptive system that links ecosystems and human societies by considering their interactions and impacts on one another (Cumming 2011). An SES perspective is relevant in agricultural landscapes, where economic interests can conflict with environmental conservation and necessitate complex management trade-offs (Sánchez-Carrillo and Angeler 2010). In addition to asymmetries and information processing, network characteristics are spatially relevant aspects of complexity (Norberg and Cumming 2008). Network theory is useful for illustrating how the position of a system within a network of other systems, interactions among systems, system connectivity, and other network properties affect system function under varying internal and external conditions (Cumming 2011). The spatial arrangement of system components and their connectivity can affect information collection, exchange, and processing within a system, and network resilience has been described as the ability of networks to withstand elimination of components while still maintaining connectivity (Cumming 2011). Intermediate levels of connectivity and modularity (i.e., a network-level metric that measures the separation of networks into smaller, connected clusters [Newman 2006]) are hypothesized to increase the resilience of SESs (Holling 2001, Gunderson and Holling 2002, Walker and Salt 2006, Webb and Bodin 2008, Cumming 2011).

In this study, we assessed the functional connectivity and spatial distribution of wetlands in an intensive agricultural landscape at four assumed, but ecologically realistic, anuran dispersal distances to evaluate anuran community resilience (i.e., the resilience "of what" [Carpenter et al. 2001]) under historic, current, and putatively future conditions (i.e., the resilience "to what"), and evaluate the importance of reserve and non-reserve wetlands and other man-made water bodies for maintaining connectivity. Results may provide insights into how changes in land use, specifically the number and spatial arrangements of remnant, reserve, and anthropogenic wetlands (i.e., irrigation reuse pits), affect the functional connectivity and resilience of these key habitats embedded in an agricultural matrix. This information is relevant for management and conservation of wetlands (Mitsch and Gosselink 2007) and unique semiaquatic biota, including anurans (Baillie et al. 2004, Stuart et al. 2004, Cushman 2006).

Materials and Methods

Study area

The Rainwater Basin is a 15 800-km^2 watershed consisting of all, or portions of, 21 counties of south–central Nebraska, USA (Fig. 1; LaGrange 2005). This intensively farmed landscape is dominated by maize (*Zea mays*) and soybean (*Glycine max*) production, and water is obtained from surface and groundwater sources

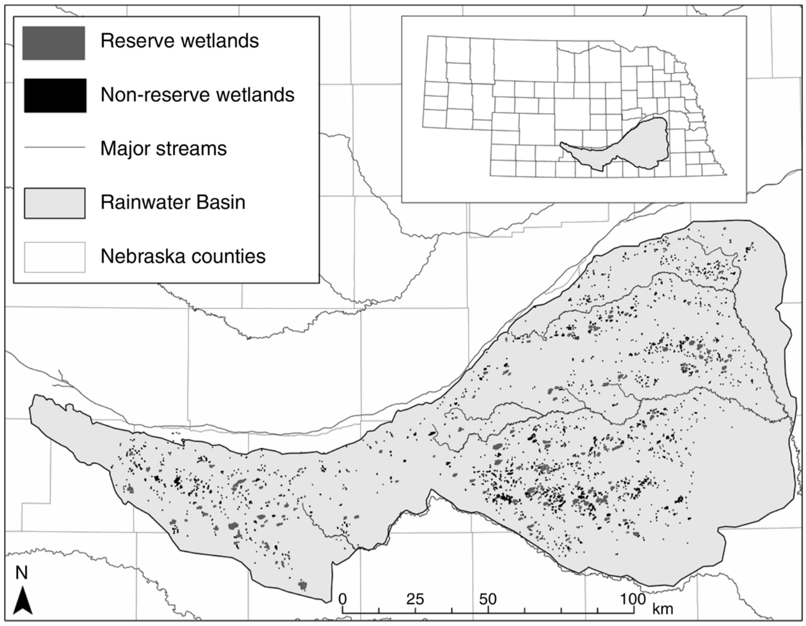

FIG. 1. Location of the Rainwater Basin region in south–central Nebraska, USA, with current reserve and non-reserve wetland locations, major streams, and Nebraska counties displayed.

(Dunnigan et al. 2011). Soil surveys from the early 20th century document the existence of as many as 1000 major (i.e., semipermanent) and 10 000 minor (i.e., seasonal or temporary) wetlands in the Rainwater Basin at the time of European settlement, <10% of which remain today (Gersib 1991, Bishop and Vrtiska 2008). Wetlands are classified as semipermanent, seasonal, or temporary, according to hydric soil series, water retention, and plant community composition (Gersib et al. 1989, Gilbert 1989, Rainwater Basin Joint Venture Public Lands Work Group 1994). Semipermanent wetlands are typically the largest and are inundated for the longest durations, whereas the smaller seasonal and temporary wetlands are generally inundated for shorter durations (Gersib et al. 1989, Bishop and Vrtiska 2008). During wetter periods, all three wetland types provide reliable habitat, whereas only semipermanent wetlands provide habitat during drier times (Gersib et al. 1989). Wetland reserves are defined here as publicly and privately owned wetland areas set aside for conservation purposes, while non-reserve wetlands do not have a specific conservation status. More than one-third of existing wetland reserves are classified as semipermanent.

Technological advances and agricultural intensification during the 20th century resulted in wetland destruction and degradation via draining, development, culturally accelerated sediment accumulation, conversion to agriculture, and excavation for the construction of irrigation reuse pits (Gersib 1991, LaGrange et al. 2011). Irrigation reuse pits (hereafter referred to as pits) are typically situated at the lowest elevations on properties and concentrate excess irrigation water runoff for future use, and negatively impact hydroperiods within watersheds by catching precipitation runoff that might otherwise fill wetlands (LaGrange 2005). The characteristics of pits are markedly different from those of natural wetlands, with pits having greater depth, steeper sides, greater and faster water-level fluctuations during the irrigation season, and increased exposure to irrigation runoff, and potentially, agricultural chemicals (Stutheit et al. 2004, Grosse and Bishop 2012). These characteristics may inhibit the growth of aquatic vegetation in pits, which provides important anuran breeding habitat, and likely decrease the value of pits as wildlife habitat in general, despite the fact that pits tend to hold water for longer durations than many wetlands (Haukos and Smith 2003, Smith 2003, Stutheit et al. 2004, LaGrange 2005). All wetland, pit, and reserve geographic information system (GIS) data used in this study were georeferenced and provided by the Rainwater Basin Joint Venture (more information *available online*).[5]

Evaluating functional connectivity

We employed a graph-theoretic approach to assess the functional connectivity of anuran habitats in historic, current, and putative future scenarios of the Rainwater Basin wetlands landscape. The wetlands landscape may be substantially altered in the future through the global change-mediated loss of reserve and non-reserve wetlands and/or the planned removal of pits. Therefore, we considered the following range of landscape scenarios

[5] http://rwbjv.org/

TABLE 1. Nine anuran species occurring in the Rainwater Basin, Nebraska, USA.

Species	SVL (mm)	Nonbreeding habitat
American bullfrog (*Lithobates catesbeiana*)	105–190†	aquatic
Woodhouse's toad (*Anaxyrus woodhousii*)	58–113‡	terrestrial
Northern leopard frog (*Lithobates pipiens*)	55–95‡	semiaquatic
Plains leopard frog (*Lithobates blairi*)	50–95†	semiaquatic
Great Plains toad (*Anaxyrus cognatus*)	52–78‡	terrestrial
Plains spadefoot toad (*Spea bombifrons*)	41–58‡	terrestrial
Grey treefrog (*Hyla chrysoscelis*)	31–50‡	arboreal
Western chorus frog (*Psuedacris triseriata*)	18–34‡	semiterrestrial
Northern cricket frog (*Acris crepitans*)	14–32‡	semiterrestrial

Notes: Dispersal ability is typically contingent on snout–vent length (SVL) and dependence on standing water. All anurans require standing water during the breeding season; therefore, dependence on standing water is best indicated by the nonbreeding habitat of a species.

† Source is Ballinger et al. 2010.

‡ Source is Lynch 1985.

that encompass possible future functional connectivity patterns, based on current wetland distributions: current wetlands excluding reserves, current wetlands excluding pits, current wetlands excluding both reserves and pits, and current wetland reserves excluding pits and nonreserve wetlands. These potential future landscape scenarios were compared with one another, as well as with the historical and current scenarios of the landscape, resulting in six total landscape scenarios. The relative density of wetlands in each landscape scenario was examined with the average nearest neighbor distance tool in ArcGIS, which uses a *z* test to compare the observed mean distance between points with the expected mean distance between the points, assuming a random distribution of the points in the same area (ESRI 2011).

When dispersal distances of target species are unknown or uncertain, comparing the level of connectivity among several nested spatial scales is useful for gaining information about the effects of scale on network-specific connectivity (Calabrese and Fagan 2004). Nine anuran species are known to occur in the Rainwater Basin (Table 1). Because limited information was available concerning the dispersal capabilities of these particular species, we assumed four dispersal distances that represent a range of their dispersal potentials in rowcrop fields: 0.50, 1.00, 1.50, and 2.00 km. The maximum value of this range is nearly identical to the reported mean maximum dispersal distance of anurans (i.e., 2.02 km) in a variety of landscapes (Smith and Green 2005); therefore, the dispersal potentials of Rainwater Basin anurans are likely to lie within it.

In a graph-theoretic approach, individual habitat patches are represented as nodes, and the connections between them (i.e., Euclidian distances) as edges (Bunn et al. 2000, Urban and Keitt 2001, Calabrese and Fagan 2004, Estrada and Bodin 2008). The term network is used to describe the combination of all nodes and edges, including those that are isolated or separated from one another, and the term cluster refers to groups of connected nodes within a specified distance, with ≥ 1 cluster(s) constituting the larger network. Within networks, paths are defined as ≥ 1 edge between any unique set of nodes that does not cross any one node more than once (Bunn et al. 2000, Pascual-Hortal and Saura 2006).

Wetland networks for the six scenarios of the Rainwater Basin wetlands landscape were built and analyzed using ArcGIS and the program R (R Development Core Team 2012), with R functions housed in the rgdal (Bivand et al. 2013), sp (Bivand et al. 2008), SDMTools (VanDerWal et al. 2012), and igraph (Csardi and Nepusz 2006) packages. For each landscape scenario, we converted individual water bodies to point features in ArcGIS, using the geographic coordinates of the location nearest the wetland centroid that was still within the wetland polygon. In R, Euclidian distances between each wetland centroid and every other wetland centroid in the network were calculated, and connections with distances less than or equal to each of the four dispersal distances were retained and used to create lists of edges representing connections between wetland nodes. Wetland nodes and edges were then combined to produce a network for each landscape scenario at each of the four dispersal distances (Fig. 2). Anurans, like many other species, are unlikely to traverse landscapes in straight lines; therefore, true dispersal distances between wetlands may be underrepresented. However, because information related to specific dispersal patterns for many organisms are unavailable (Jacobson and Peres-Neto 2010), including anuran movements in the Rainwater Basin, we used Euclidian distance between sites as a best estimate. Euclidean distance is commonly used in metacommunity studies as a spatial proxy of connectivity and dispersal (Legendre et al. 2005, Baldissera et al. 2012, Angeler et al. 2013). Furthermore, because we lacked information related to the directional movement of anurans in the landscape, we assumed between-node travel to be random (i.e., undirected).

A variety of methods and metrics have been proposed for examining node- and network-level connectivity, and for determining the contributions of individual nodes to network-level connectivity (Calabrese and Fagan 2004, Pascual-Hortal and Saura 2006, Saura and Rubio 2010).

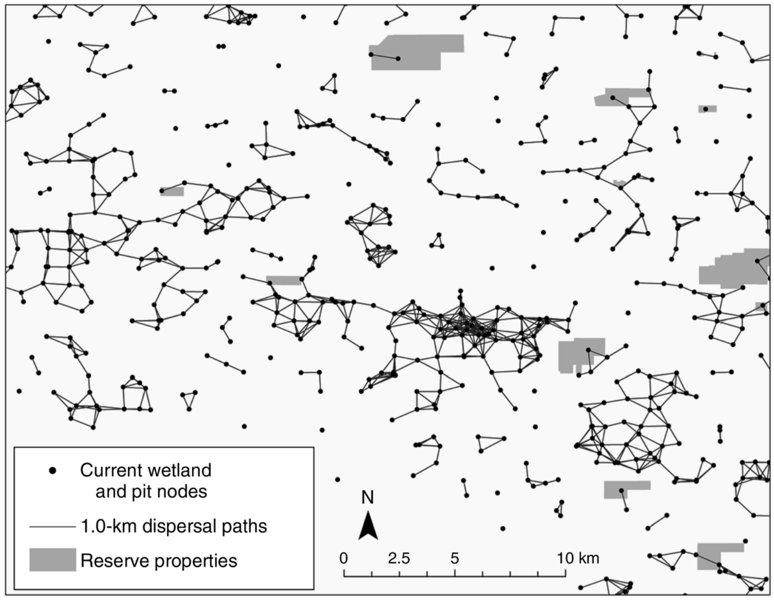

FIG. 2. A graph-theoretic representation of functional connectivity for anurans in a portion of the current wetlands landscape scenario, assuming a 1.00-km dispersal distance. Wetland habitats (i.e., nodes) are represented by points, and the dispersal paths (i.e., edges) between them as straight lines.

We assessed node-level connectivity with degree centrality, which is simply the number of direct connections a node maintains with adjacent nodes (Estrada 2007, Estrada and Bodin 2008). The importance of individual nodes for overall network connectivity was also determined by sequentially removing each node from the network, calculating the mean degree centrality among the remaining nodes, and then replacing it before repeating the process. To visually represent the spatial distribution of node-level connectivity, we produced continuous inverse distance weighted (IDW) raster surfaces for interpolating degree centrality values among nodes. Species occupying a habitat patch (i.e., node) with a high degree centrality may emigrate to various neighboring patches in the event that the patch they are occupying becomes unsuitable as habitat. Similarly, if a local extinction occurs in a patch with a high degree centrality, species from neighboring patches may immigrate to recolonize it.

Network-level connectivity, which has been identified as a determinant of system resilience (Holling 2001, Gunderson and Holling 2002, Walker and Salt 2006, Cumming 2011), was evaluated according to mean degree centrality, the total number of clusters in the network, the mean number of nodes composing clusters, the percentage of total nodes contained in the largest cluster, and a network modularity score. The more distinct clusters of connected habitat patches that exist in a network, the more disconnected the patches and the species inhabiting them become, with the maximum possible number of clusters being equal to the total number of patches. Alternatively, the greater the percentage of total patches that are contained in the single largest cluster, the more patches in the network a species can reach from any given patch within that cluster, until connectivity increases to the point that the entire network consists of a single cluster and any given patch can be directly or indirectly reached from any other patch. Therefore, habitat networks with fewer, but larger and more encompassing, clusters provide species with the greatest opportunities for movement throughout the network. Although high levels of connectivity maximize the potential for among-patch movement and the resulting exchange of genetic information within metapopulations, it may also facilitate biological invasions and the spread of disease and other detrimental elements through habitat networks and spatially structured populations. Modularity is a network-level metric that measures the separation of networks into smaller connected clusters and is greatest in networks where connections are dense within clusters and sparse between them (Newman 2006). Habitat networks with intermediate levels of connectivity and modularity are hypothesized to permit the movement of species among patches and clusters, while still restricting detrimental events to individual clusters, thereby minimizing the potential for their spread through, and negative effect on, the larger network (Ash and Newth 2007, Webb and Bodin 2008).

RESULTS

Landscape scenario comparisons

Functional connectivity.—Of the six compared scenarios of the Rainwater Basin landscape, the historical wetlands landscape had the most wetlands, the densest distribution of wetlands (Table 2), the greatest mean

TABLE 2. Spatial clustering of wetlands in the six wetland landscape scenarios.

Landscape scenario	No. wets	ExpDist	ObsDist	DistDiff	z	P
Historical	11 711	808.90	482.07	326.83	−83.65	<0.01
Current	10 161	872.53	590.52	282.00	−62.33	<0.01
Current without reserves	9910	883.51	591.55	291.95	−62.93	<0.01
Current without pits	1856	1800.62	1093.92	706.70	−32.35	<0.01
Current without pits or reserves	1615	1912.91	1133.76	779.16	−31.31	<0.01
Reserves without pits or non-reserves	241†	4658.91	2294.31	2364.60	−15.07	<0.01

Notes: For each scenario, a z score was calculated for comparing the observed mean distance between wetlands to the expected mean distance between them, if their distribution is assumed to be random and in the same area. The P value represents the probability that the null hypothesis (i.e., wetlands are randomly distributed) is true. Wetlands in all six scenarios were significantly clustered, with lower z scores indicating more clustering. Analysis was conducted with the average nearest neighbor tool in ArcGIS (ESRI 2011). No. wets is the total number of wetlands in the landscape scenario; ExpDist is the expected mean distance between wetland centroids, in meters, assuming a random distribution of points; ObsDist is the observed mean distance between wetland centroids, in meters; and DistDiff is the difference in expected and observed mean distances between wetland centroids, in meters.

† A mismatch exists between the total number of current wetlands, the number of current wetlands without reserves, and the number of reserves without irrigation reuse pits or non-reserve wetlands, because of the fact that 10 pits are located on reserve properties.

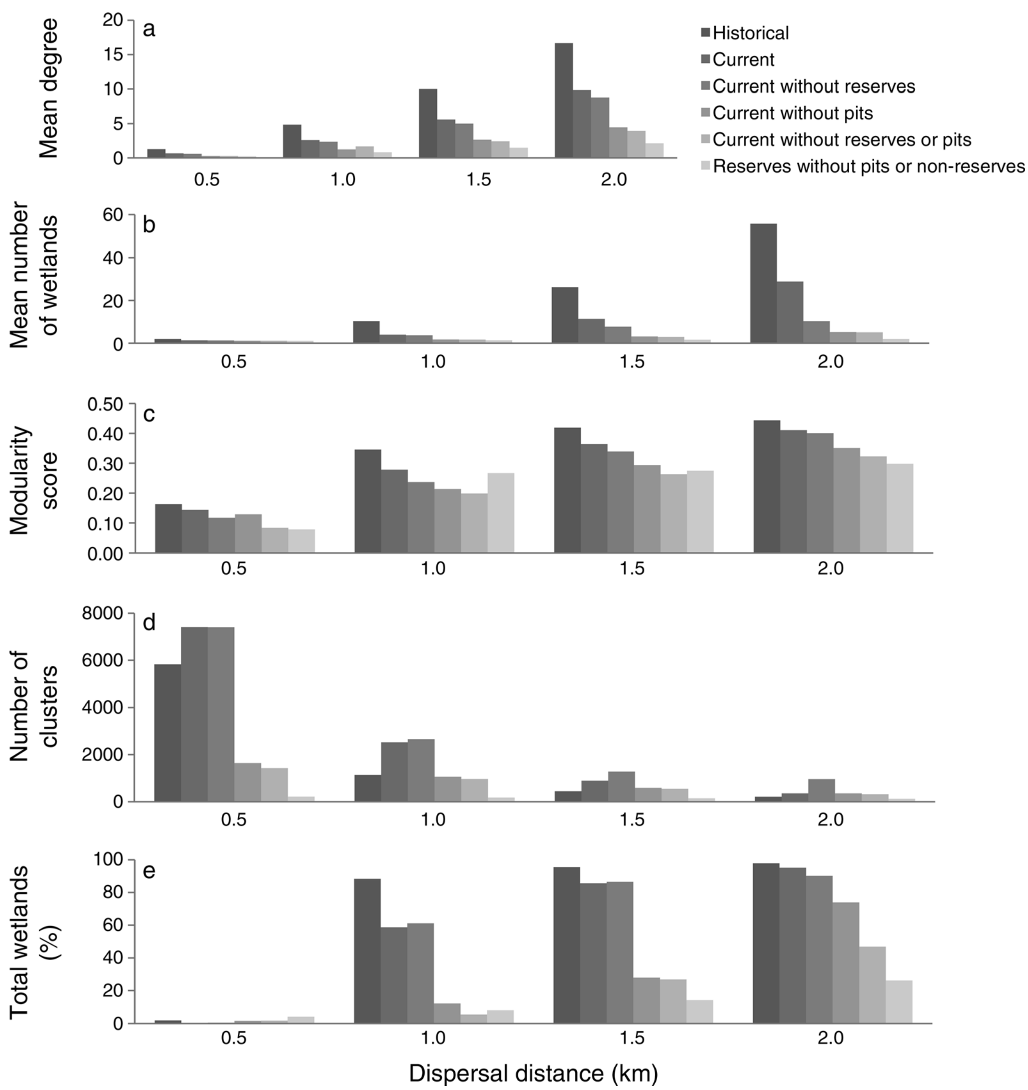

FIG. 3. Connectivity metrics among the six landscape scenarios at four assumed anuran dispersal distances. (a) Wetland degree (i.e., the number of direct connections a wetland has with other wetlands); (b) the mean number of wetlands per cluster; (c) modularity scores (i.e., the level of within- and between-cluster connectivity); (d) the number of wetland clusters in the entire network; and (e) the percentage of wetlands in the largest cluster.

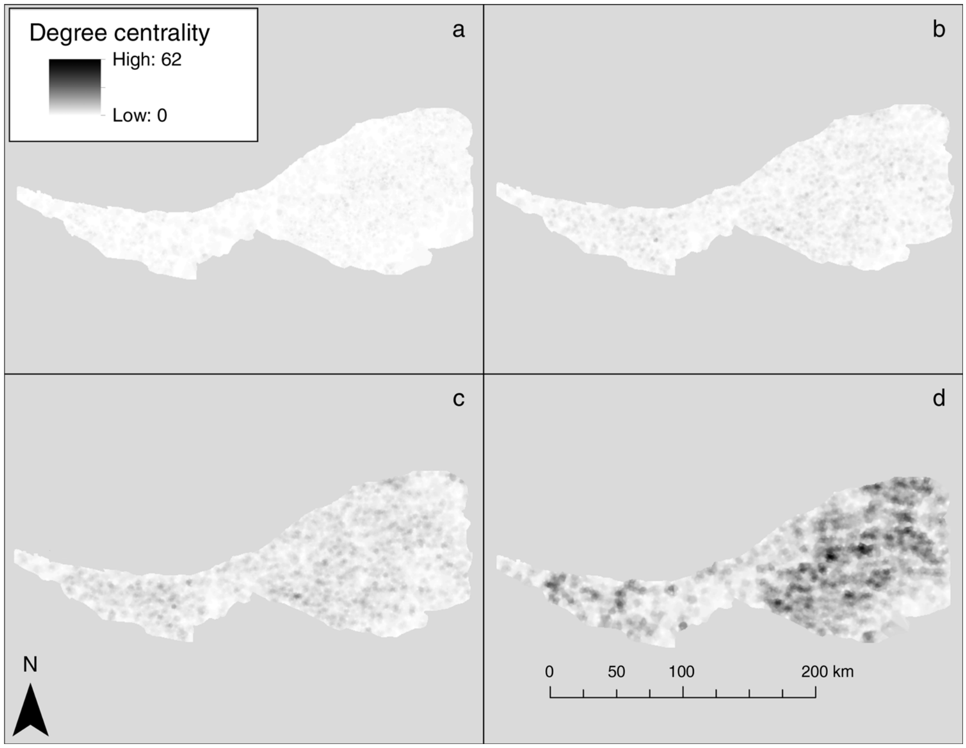

FIG. 4. Inverse distance weighted continuous raster surface of wetland degree centrality in the historical wetlands landscape scenario at the (a) 0.50-km, (b) 1.00-km, (c) 1.50-km, and (d) 2.00-km dispersal distances. Wetland degree centrality refers to the number of direct connections between a wetland and other wetlands, and wetlands in darker shaded areas tend to be more connected.

degree centrality, and the greatest mean number of wetlands per cluster at each of the four dispersal distances (Fig. 3a, b), indicating the greatest level of overall connectivity. The historical landscape scenario also had the highest modularity score at all four dispersal distances (Fig. 3c). Following the historical landscape scenario, connectivity for the current landscape scenario was > the current landscape excluding reserves scenario, which was > the current landscape excluding pits scenario, which was > the current landscape excluding pits and reserves scenario, which was > reserves excluding pits and non-reserve wetlands scenario. Although exceptions to this ranking occurred at several connectivity metric–landscape scenario–dispersal distance combinations, the ranking describes the general pattern in connectivity among landscape scenarios and dispersal distances, and highlights the contributions of reserve wetlands, non-reserve wetlands, and pits to functional connectivity for anurans in the current, and potentially future, wetlands landscapes.

Wetland spatial distributions.—The spatial distributions of wetlands in the historical, current, and future landscape scenarios were all significantly clustered (i.e., the observed mean distance between wetlands was significantly greater than the expected mean distance between them, assuming their random distribution in the same area); however, the distribution of wetlands was most dense in the historical landscape scenario and least dense in the reserves without pits and non-reserve wetlands landscape scenario (Table 2). Although there was a similar, but greater, number of wetlands in the historical landscape scenario than the current landscape scenario (Table 2), there were fewer wetland clusters in the historical landscape scenario at each dispersal distance (Fig. 3d), and accordingly, the mean number of wetlands per cluster was greater in the historical landscape scenario at each dispersal distance (Fig. 3b). The exclusion of pits from the current landscape scenario resulted in a noticeable decrease in wetland density (Table 2).

Differences in wetland distributions and densities among landscape scenarios and dispersal distances were also evident from comparisons of wetland degree centrality hotspot maps (Figs. 4–6). As expected, among-wetland connectivity tended to be greater in landscape scenarios with more wetlands and at greater dispersal distances. More localized areas of relatively high among-wetland connectivity were present in the historical wetlands landscape scenario than in the current wetlands landscape scenario or the current wetlands excluding pits landscape scenario. Furthermore, the current wetlands landscape scenario tended to contain more, and more uniformly-distributed, areas with moderate levels of among-wetland connectivity

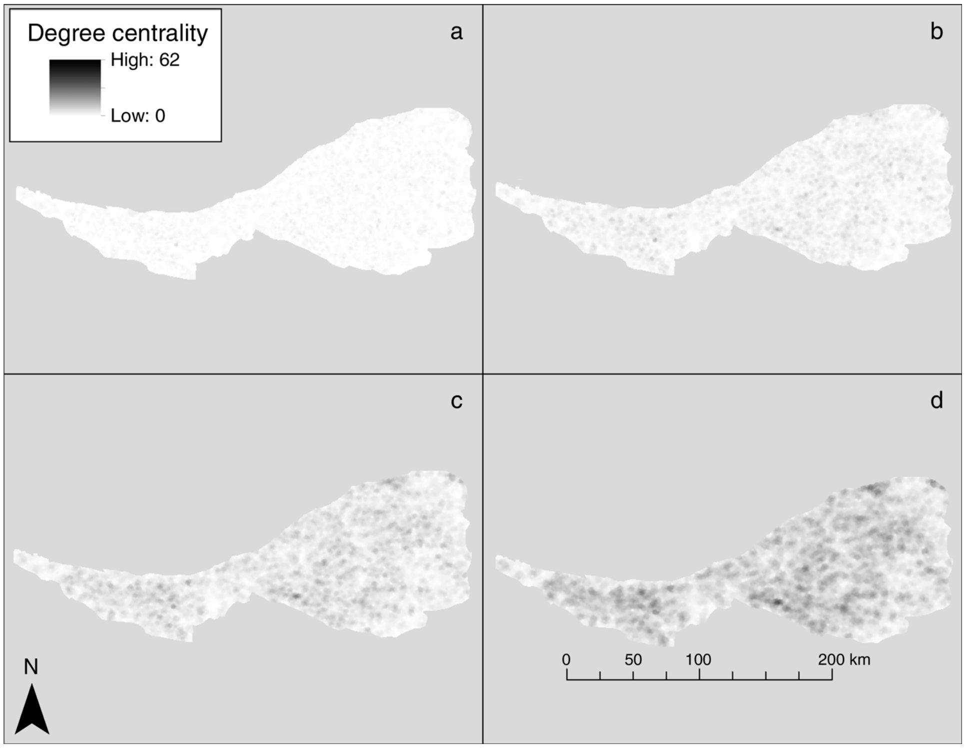

FIG. 5. Inverse distance weighted continuous raster surface of wetland degree centrality in the current wetlands landscape scenario at the (a) 0.50-km, (b) 1.00-km, (c) 1.50-km, and (d) 2.00-km dispersal distances. Wetland degree centrality refers to the number of direct connections between a wetland and other wetlands, and wetlands in darker-shaded areas tend to be more connected.

than the historical landscape scenario. Although the current wetlands excluding pits landscape scenario displayed lower overall levels of connectivity than the historical or current landscape scenarios, hotspots of connectivity within it still appeared to be more localized than in the current wetlands landscape scenario.

Dispersal distance connectivity thresholds.—Functional connectivity was affected by dispersal distance, and dramatic shifts in network-wide connectivity in different landscape scenarios were detected between certain dispersal distances. For example, in the historical landscape scenario, the percentage of total wetlands in the largest cluster increased from 1.8% to 88.4% between the 0.50- and 1.00-km dispersal distances, and then more gradually increased to 97.9% total inclusion at the 2.00-km dispersal distance (Fig. 3e), indicating a dispersal threshold between 0.50 and 1.00 km, where the majority of wetlands were all directly or indirectly connected with one another. A more gradual increase in connectivity was evident in the current landscape scenario, where the percentage of wetlands in the largest cluster increased from <0.1% to 58.7% between the 0.50- and 1.00-km dispersal distances, and then to 85.7% and 95.2% at 1.50- and 2.00-km dispersal distances, respectively (Fig. 3e), making any connectivity thresholds less apparent. In the current landscape scenario without pits, the greatest increase in the percentage of wetlands in the largest cluster occurred between the 1.50- and 2.00-km dispersal distances, with 73.9% of all wetlands being in the largest cluster; however, only 26.1% of wetlands were in the largest cluster in the reserves without pits and non-reserves landscape scenario at the 2.00-km dispersal distance (Fig. 3e).

Node contributions to connectivity

Specific wetland nodes that contributed most to connectivity varied with the landscape scenario and dispersal distance considered; however, some general trends in their spatial distributions and statuses as natural wetlands, pits, and reserves were evident. In the historical landscape scenario, at dispersal distances $\geq$1.00 km, all but one of the top 10 wetland contributors to mean degree centrality were located within ~20 km of one another in two portions of the same wetland cluster (Fig. 7). In the current landscape scenario, wetlands in this area are less dense, more uniformly distributed, and consist primarily of pits. In fact, at each of the four dispersal distances, the number of the top 10 historical landscape scenario contributors to mean degree centrality that are still in existence today is 1, 2, 0, and 0, respectively; and none of these are presently reserves.

In the current landscape scenario, at dispersal distances $\geq$1.00 km, the majority of the top 10 contributors to mean degree centrality were located

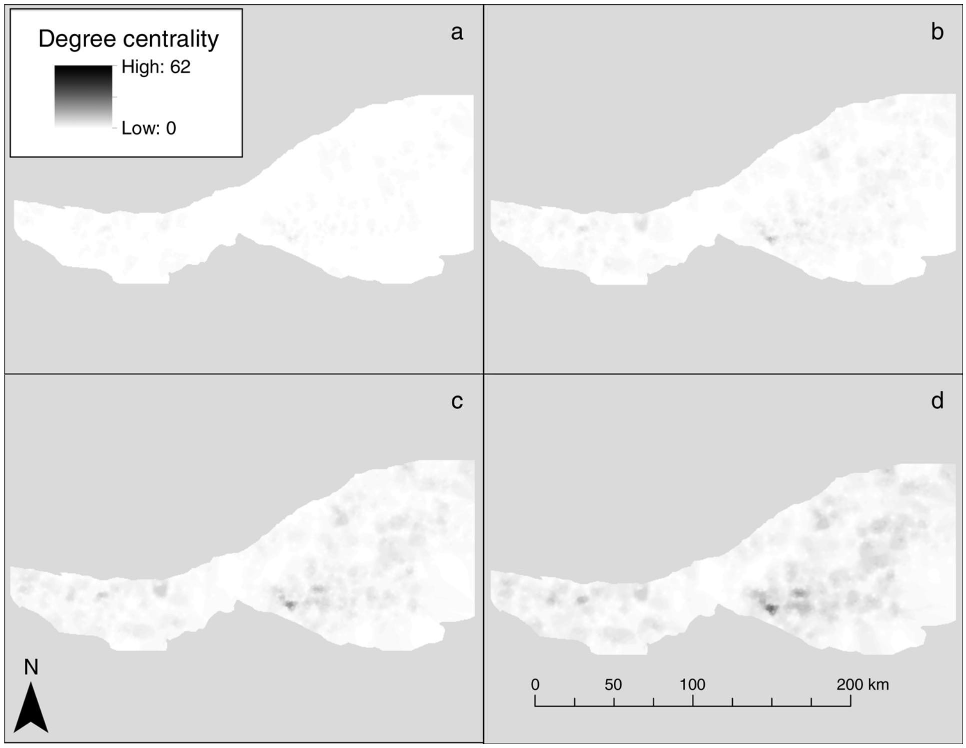

FIG. 6. Inverse distance weighted continuous raster surface of wetland degree centrality in the current wetlands without irrigation pits landscape scenario at the (a) 0.50-km, (b) 1.00-km, (c) 1.50-km, and (d) 2.00-km dispersal distances. Wetland degree centrality refers to the number of direct connections between a wetland and other wetlands, and wetlands in darker shaded areas tend to be more connected.

>40 km to the southwest of the top contributors in the historical landscape scenario (Fig. 8). Furthermore, the number of these 10 in the current landscape that are natural wetlands (i.e., not pits) at the four dispersal distances is 0, 6, 10, and 10, respectively; and none are presently reserves. In the current landscape without pits scenario, at all four dispersal distances, all but one of the top 10 contributors to mean degree centrality are situated in the same wetland cluster as the top contributors in the current landscape scenario (Fig. 9), with the single isolated contributor at the 0.50-km dispersal distance being a reserve.

DISCUSSION

The current wetlands landscape scenario of the Rainwater Basin, in addition to four putative future scenarios of it, all exhibited lower levels of functional connectivity, modularity, and spatial wetland clustering for anurans than the historical wetlands landscape scenario. Thus, management action is required to enhance the future sustainability of wetland networks in the Rainwater Basin and similar agricultural landscapes. Important information for increasing the functional connectivity of wetland landscapes in these areas, and maintaining resilient anuran communities within them, can be derived from our results. Because this study evaluated functional connectivity of wetlands in historic, current, and future scenarios of the wetland landscape, it provides insights not only into how the spatial arrangement and connectivity of habitat patches may be influencing anuran species with different dispersal abilities presently, but also as to how those influences may have changed over the past century, and may again in the future.

Relative hotspots of connectivity are apparent in the different landscape scenario–dispersal distance combinations (Figs. 4–6). Areas that had the highest levels of connectivity historically are not only less connected today, but are also less connected than other areas of the current landscape, especially when pits are excluded. The overall distribution of wetlands in the current landscape is less dense than it was historically, even though the number of wetland nodes in the historical and current landscape scenarios is similar (Table 2). The fact that pits are situated in agricultural fields that are typically divided into square ~64-ha properties (Mitchell et al. 2012) could contribute to this more uniform distribution.

Most of the top 10 wetlands contributing to mean degree centrality in the historical wetlands landscape scenario at each dispersal distance have been lost, and as the distribution of wetlands in the landscape changed, the relative importance of specific wetlands for maintaining mean degree centrality shifted. Following Euro-

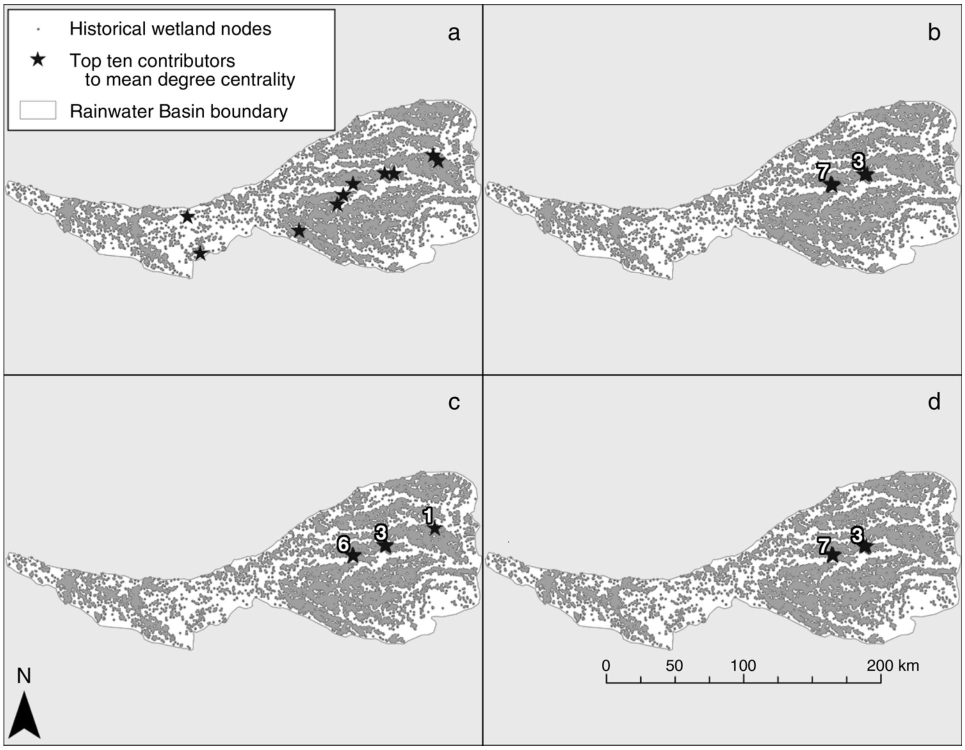

FIG. 7. Historical wetland nodes, together with the top 10 wetland contributors to mean network degree centrality at four anuran dispersal distances (stars). (a) At the 0.50-km dispersal distance, the top contributors to degree centrality are more evenly distributed throughout the region than at the (b) 1.00-km, (c) 1.50-km, and (d) 2.00-km dispersal distances, where all but one of the contributors are located near one another in two portions of the same wetlands cluster. The numbers in panels (b), (c), and (d) correspond to the number of the top 10 contributors in specific vicinities.

pean settlement, connectivity in the Rainwater Basin decreased via agricultural land use change, a stressor that threatens the ecological integrity of wetlands worldwide (Mitsch and Gosselink 2007). More than 9000 artificial water bodies (i.e., pits) have been constructed with the main purpose of agricultural irrigation, rather than environmental conservation, and because of differences between them and natural wetlands (e.g., greater depth, steeper sides, greater water-level fluctuations associated with irrigation practices rather than natural meteorological phenomena, more agricultural chemicals, and less aquatic vegetation), these may provide suboptimal anuran habitat. Indeed, previous research has shown that the presence of pits does not improve the regional occurrence of anurans in a boreal landscape (Anderson et al. 1999). Also, irrigation pits may alter hydrological disturbance regimes, negatively affecting natural wetlands. Our results show that the construction of pits did not compensate for the loss of natural wetlands in the area, as connectivity was not restored to its former level.

Although our results suggest that the use of pits as stepping stones for anuran dispersal may be limited, the analysis of four dispersal distances, in combination with the spatial distribution of pits, allows us to make broader inferences about the importance of artificial vs. natural water bodies for anurans. Although a large proportion of wetlands in the historical wetlands landscape scenario were connected as a single cluster at a 1.00-km dispersal distance, the current wetlands landscape scenario only obtains the same percentage of single-cluster connectivity at dispersal distances >1.50 km (Fig. 3e). Furthermore, many of the most critical wetland nodes for maintaining mean degree centrality in the current landscape scenario at dispersal distances <1.00 km are pits, whereas natural wetlands become more important at dispersal distances ≥1.00 km. Therefore, post-European settlement changes in network-level connectivity may be favoring larger, longer distance dispersers (e.g., American bullfrog and plains leopard frog) over smaller, shorter distance dispersers (e.g., northern cricket frog). The cricket frog, small bodied and short lived, is in decline in much of its range and is listed as endangered in the States of Minnesota, Wisconsin, and New York, and as a species of concern in Indiana, Michigan, and West Virginia (Lanoo 2005). Cricket frogs are reported to live an average of four months, and may experience population turnover in as few as 18 months (Burkett 1984). A well-connected landscape that allows for dispersal to suitable wetlands under a variety of climatic conditions is important for the local persistence of cricket frogs and other short-

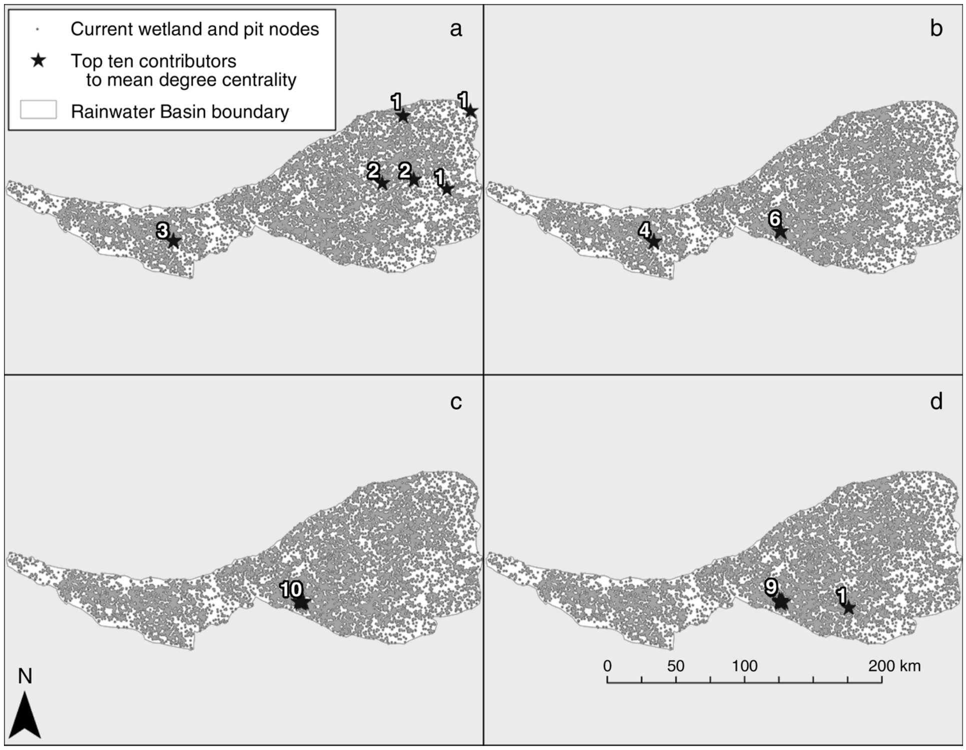

FIG. 8. Current wetland and pit nodes, together with the top 10 contributors to mean network degree centrality at four anuran dispersal distances (stars). (a) At the 0.50-km dispersal distance, the top contributors are spread fairly evenly throughout the region. (b) At the 1.00-km dispersal distance, the top contributors are split between two clusters in the western and eastern portions of the region, and at the (c) 1.50-km and (d) 2.00-km dispersal distances, all but one of the top contributors are in the eastern cluster. The numbers in each panel correspond to the number of the top 10 contributors in specific vicinities.

distance dispersers, which may have been able to move freely throughout the historical wetlands landscape, but now are more restricted to intact clusters, with inter-cluster movements limited. In addition to species-specific dispersal abilities, it is important to consider the invasive status of anurans. For example, the bullfrog is a nonindigenous species that may prey upon, or out-compete, other frog species (Werner et al. 1995, Adams 1999). Thus, a landscape that facilitates bullfrog dispersal while impeding short-distance dispersal could further threaten persistence of smaller species that are already in peril.

Reserves play an important role in biodiversity conservation (Lindenmayer et al. 2006). Many wetland reserves in the Rainwater Basin that have best retained natural hydroperiods and flood frequency regimes, and thus ecological integrity, are large, semipermanent wetlands. These reserves may be the most suitable sources of anuran habitat; however, when considered in isolation, they contribute less to network-level connectivity than non-reserve wetlands or pits. This lower level of connectivity among reserves is likely a result of only ~2.4% of water bodies in the current wetlands landscape being reserves. Thus, the spatial isolation and low number of wetland reserves may currently represent two impediments toward an efficient use of wetland reserves for conserving important biodiversity elements like anurans. Non-reserve wetlands and other unmapped temporary water bodies (e.g., temporarily flooded road ditches, pools of irrigation runoff, and so on) may also be important for maintaining connectivity, and could serve as important stepping stones between more permanent water bodies.

Resilience has been defined as the ability of a system to absorb disturbances without fundamentally altering its structures and functions (Holling 1973). However, when disturbance thresholds are exceeded, a system tips into an alternative state and rearranges around a new set of processes, structures, and feedbacks. The historical wetlands landscape of the Rainwater Basin had the highest levels of connectivity and modularity, and likely allowed anurans to spread across it, using suboptimal habitats as stepping stones for accessing higher quality sites. These spatial processes may have played a major role in maintaining structural and functional attributes of anuran communities, and likely conferred them high resilience. It is unclear if changes to the historical wetlands landscape have already initiated a state shift, or if the sustained, slow erosion of historical resilience will tip the system into a new state in the future. Notwithstanding, our results suggest that a potential future regime shift might be avoided, or if a shift has

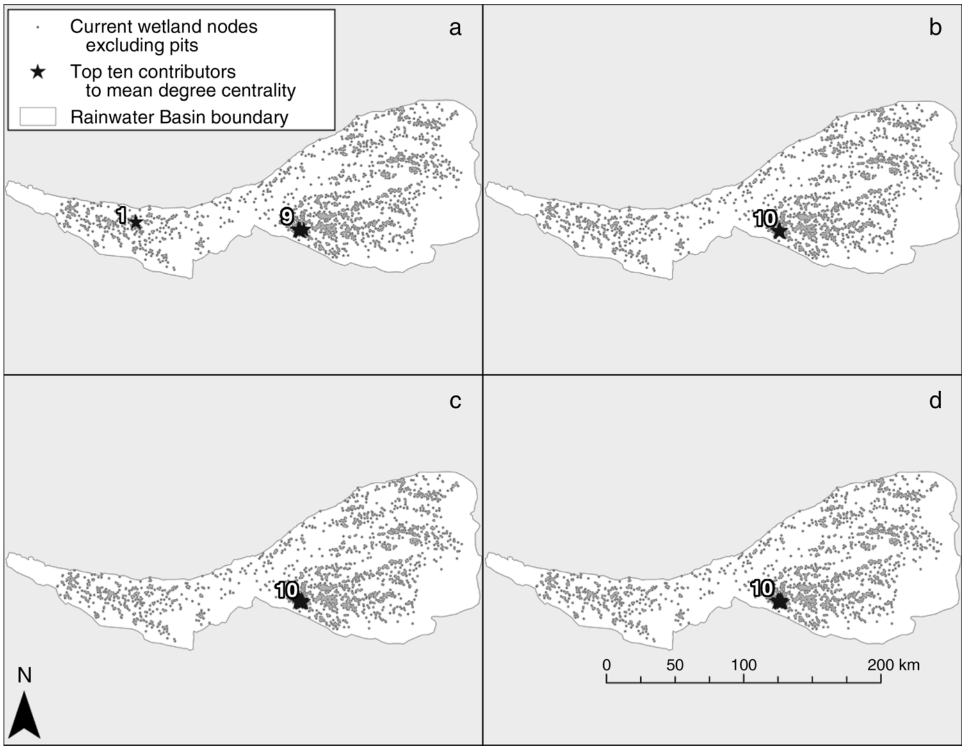

FIG. 9. Current natural wetland nodes (i.e., excluding pits), together with the top 10 wetland contributors to mean network degree centrality at four anuran dispersal distances (stars). At the (a) 0.50-km, (b) 1.00-km, (c) 1.50-km, and (d) 2.00-km anuran dispersal distances, all but one of the top contributors is located in a single wetland cluster. The single outlier in panel (a) is the only node among the top contributors to mean degree centrality in the historical wetlands, current wetlands, or current wetlands excluding pits landscape scenarios, at any of the four dispersal distances, that is presently a reserve. The numbers in each panel correspond to the number of the top 10 contributors in specific vicinities.

already occurred, the resilience of the presently degraded wetlands landscape state could be weakened, through management. This is important for maintaining biodiversity, in addition to the broader provisioning of ecosystem goods and services in agricultural landscapes where production services are otherwise prioritized (MEA 2005, Bennett et al. 2009).

Current wetland management efforts in the Rainwater Basin do not focus on the purchase of all remnant wetlands as new reserves, although conservation easements are still actively sought and were classified as reserves in this analysis. One active area of management is pit removal. Pits in the current landscape enhance connectivity, but may bias it toward the largest species. Therefore, substantially reducing the number of pits could negatively affect overall functional connectivity. To increase resilience of the wetland network and anuran communities inhabiting it, the following actions could be taken: (1) continuing to improve the conservation status of remnant natural wetlands from non-reserves to reserves; (2) restoring historical wetlands that have been converted to pits at spatial scales that facilitate dispersal of native taxa with limited migration capacities; and (3) further scrutinizing pit removals by considering potential effects on the functional connectivity of habitats for wetland-dependent species. These actions are initial steps toward the maintenance of habitat network structures that are important for anurans. However, broader management plans will also need to incorporate waterfowl and invasive species management, and address other challenges arising from global change that will influence the broader social-ecological systems of the Rainwater Basin and other landscapes.

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Literature Cited

Adams, M. J. 1999. Correlated factors in amphibian decline: Exotic species and habitat change in western Washington. Journal of Wildlife Management 63:1162–1171.

Anderson, A. M., D. A. Haukos, and J. T. Anderson. 1999. Habitat use by anurans emerging and breeding in playa wetlands. Wildlife Society Bulletin 27:759–769.

Angeler, D. G., E. Göthe, and R. K. Johnson. 2013. Hierarchical dynamics of ecological communities: Do scales of space and time match? PLoS ONE 8:e69174.

Ash, J., and D. Newth. 2007. Organizing complex networks for resilience against cascading failure. Physica A 380:673–683.

Atmar, W., and B. D. Patterson. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96:373–382.

Baillie, J. E. M., C. Hilton-Taylor, and S. N. Stuart. 2004. IUCN Red List of threatened species. A global species assessment. IUCN, Gland, Switzerland.

Baldissera, R., E. N. L. Rodrigues, and S. M. Hartz. 2012. Metacommunity composition of web-spiders in a fragmented Neotropical forest: Relative importance of environmental and spatial effects. PLoS ONE 7:e48099.

Ballinger, R. E., J. D. Lynch, and G. R. Smith. 2010. Amphibians and reptiles of Nebraska. Rusty Lizard Press, Oro Valley, Arizona, USA.

Belisle, M. 2005. Measuring landscape connectivity: the challenge of behavioral landscape ecology. Ecology 86:1988–1995.

Bennett, E. M., G. D. Peterson, and L. J. Gordon. 2009. Understanding relationships among multiple ecosystem services. Ecology Letters 12:1394–1404.

Bishop, A. A., and M. P. Vrtiska. 2008. Effects of the Wetland Reserve Program on waterfowl carrying capacity in the Rainwater Basin region of south-central Nebraska. USDA NRCS, Lincoln, Nebraska, USA.

Bivand, R., T. Keitt, and B. Rowlingson. 2013. rgdal: bindings for the Geospatial Data Extraction Library. R package version 0.8-5. R Foundation for Statistical Computing, Vienna, Austria. http://CRAN.R-project.org/package=rgdal

Bivand, R., E. J. Pebesma, and V. Gomez-Rubio. 2008. Applied spatial data analysis with R. Springer, New York, New York, USA. http://www.asdar-book.org/

Bunn, A. G., D. L. Urban, and T. H. Keitt. 2000. Landscape connectivity: A conservation application of graph theory. Journal of Environmental Management 59:265–278.

Burkett, R. D. 1984. An ecological study of the cricket frog *Acris crepitans*. Pages 89–103 *in* R. A. Siegel, L. E. Hunt, J. L. Knight, L. Malaret, and N. L. Zuschlag, editors. Vertebrate ecology and systematics: a tribute to Henry S. Fitch. Museum of Natural History, University of Kansas, Lawrence, Kansas, USA.

Calabrese, J. M., and W. F. Fagan. 2004. A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment 2:529–536.

Carpenter, S. R., M. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems 4:765–781.

Csardi, G., and T. Nepusz. 2006. The igraph software package for complex network research. InterJournal, Complex Systems 1695. R Foundation for Statistical Computing, Vienna, Austria. http://igraph.sf.net

Cumming, G. S. 2011. Spatial resilience in social-ecological systems. Springer, London, UK.

Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation 128:321–240.

D'Eon, R. G., S. M. Glenn, I. Parfitt, and M.-J. Fortin. 2002. Landscape connectivity as a function of scale and organism vagility in a real forested landscape. Conservation Ecology 6:1–14.

Dunnigan, B., et al. 2011. Annual evaluation of availability of hydrologically connected water supplies. Nebraska Department of Natural Resources, Lincoln, Nebraska, USA.

ESRI [Environmental Systems Research Institute]. 2011. ArcGIS desktop: release 10. ESRI, Redlands, California, USA.

Estrada, E. 2007. Characterization of topological keystone species: Local, global and "meso-scale" centralities in food webs. Ecological Complexity 4:48–57.

Estrada, E., and O. Bodin. 2008. Using network centrality measures to manage landscape connectivity. Ecological Applications 18:1810–1825.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8:50–59.

Fischer, J., D. B. Lindenmayer, and A. D. Manning. 2006. Biodiversity, ecosystem function, and resilience: Ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment 4:80–86.

Fronhofer, E. A., A. Kubisch, F. M. Hilker, T. Hovestadt, and H. J. Poethke. 2012. Why are metapopulations so rare? Ecology 93:1967–1978.

Gersib, R. A. 1991. Nebraska wetlands priority plan. Nebraska Game and Parks Commission and U.S. Fish and Wildlife Service, Lincoln, Nebraska, USA.

Gersib, R. A., B. Elder, K. F. Dinan, and T. H. Hupf. 1989. Waterfowl values by wetland type within Rainwater Basin wetlands with special emphasis on activity time budget and census data. Nebraska Game and Parks Commission and U.S. Fish and Wildlife Service, Lincoln, Nebraska, USA.

Gibbs, J. P. 2000. Wetland loss and biodiversity conservation. Conservation Biology 14:314–317.

Gilbert, M. C. 1989. Ordination and mapping of wetland communities in Nebraska's Rainwater Basin Region. CEMRO Environmental Report 89-1. Omaha District, U.S. Army Corps of Engineers, Omaha, Nebraska, USA.

Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281:2045–2047.

Grosse, R., and A. Bishop. 2012. Scoring criteria and ranking for Wildlife Habitat Incentive Program Rainwater Basin Public Wetland Watershed Special Initiative. Rainwater Basin Joint Venture, Grand Island, Nebraska, USA. http://rwbjv.org/rainwater2012/wp-content/uploads/2013/04/Summary-of-WHIP-SI-Pit-Fill-model-2012.pdf

Gunderson, L. H., and C. S. Holling. 2002. Panarchy: Understanding transformations in human and natural systems. Island Press, Washington, D.C., USA.

Haig, S. M., D. W. Mehlman, and L. W. Oring. 1998. Avian movements and wetland connectivity in landscape conservation. Conservation Biology 12:749–758.

Hanski, I., and O. Ovaskainen. 2002. Extinction debt at extinction threshold. Conservation Biology 16:666–673.

Haukos, D. A., and L. M. Smith. 2003. Past and future impacts of wetland regulations on playa ecology in the Southern Great Plains. Wetlands 23:577–589.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Holling, C. S. 2001. Understanding the complexity of economic, ecological, and social systems. Ecosystems 4:390–405.

Jacobson, B., and P. R. Peres-Neto. 2010. Quantifying and disentangling dispersal in metacommunities: How close have we come? How far is there to go? Landscape Ecology 25:495–507.

Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299–302.

Keith, D. A., H. R. Akcakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araujo, and T. G. Rebelo. 2008. Predicting extinction risks under climate change: Coupling stochastic population models with

dynamic bioclimatic habitat models. Biology Letters 4:560–563.

LaGrange, T. 2005. Guide to Nebraska's wetlands and their conservation needs. Nebraska Game and Parks Commission, Lincoln, Nebraska, USA.

LaGrange, T. G., R. G. Stutheit, M. Gilbert, D. Shurtliff, and P. M. Whited. 2011. Sedimentation of Nebraska's playa wetlands: A review of current knowledge and issues. Nebraska Game and Parks Commission, Lincoln, Nebraska, USA.

Lanoo, M. J., editor. 2005. Amphibian declines: The conservation status of U.S. amphibians. University of California Press, Berkeley, California, USA.

Legendre, P., D. Borcard, and P. R. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75:435–450.

Lindenmayer, D. B., J. F. Franklin, and J. Fischer. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131:433–445.

Lynch, J. D. 1985. Annotated checklist of the amphibians and reptiles of Nebraska. Transactions of the Nebraska Academy of Sciences 13:33–57.

MEA [Millennium Ecosystem Assessment]. 2005. Ecosystems and human well-being: Biodiversity synthesis. World Resources Institute, Washington, D.C., USA.

Mitchell, R. B., K. P. Vogel, and D. R. Uden. 2012. The feasibility of switchgrass for biofuel production. Biofuels 3:47–59.

Mitsch, W. J., and J. G. Gosselink. 2007. Wetlands. Fourth edition. John Wiley and Sons, Hoboken, New Jersey, USA.

Newman, M. E. J. 2006. Modularity and community structure in networks. Proceedings of the National Academy of Sciences USA 103:8577–8582.

Norberg, J., and G. S. Cumming, editors. 2008. Complexity theory for a sustainable future. Columbia University Press, New York, New York, USA.

Pascual-Hortal, L., and S. Saura. 2006. Comparison and development of new graph-based landscape connectivity indices: Towards the prioritization of habitat patches and corridors for conservation. Landscape Ecology 21:959–967.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

Rainwater Basin Joint Venture Public Lands Work Group. 1994. Best management practices for Rainwater Basin wetlands. North American Waterfowl Management Plan. Central Nebraska Public Power and Irrigation District, Holdrege, Nebraska, USA.

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sánchez-Carrillo, S., and D. G. Angeler, editors. 2010. Ecology of threatened semiarid wetlands: long-term research in Las Tablas de Daimiel. Springer, Dordrecht, The Netherlands.

Saura, S., and L. Rubio. 2010. A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography 33:523–537.

Smith, L. M. 2003. Playas of the Great Plains. University of Texas Press, Austin, Texas, USA.

Smith, M. A., and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110–128.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

Stutheit, R. G., M. C. Gilbert, P. M. Whited, and K. L. Lawrence, editors. 2004. A regional guidebook for applying the hydrogeomorphic approach to assessing wetland functions of Rainwater Basin depressional wetlands in Nebraska. ERDC/EL TR-04-4. U.S. Army Engineer Research and Development Center, Vicksburg, Mississippi, USA.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Tischendorf, L., and L. Fahrig. 2000. On the usage and measurement of landscape connectivity. Oikos 90:7–19.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity: ecosystem service management. Ecology Letters 8:857–874.

Urban, D., and T. Keitt. 2001. Landscape connectivity: a graph–theory perspective. Ecology 82:1205–1218.

VanDerWal, J., L. Falconi, S. Januchowski, L. Shoo, and C. Storlie. 2012. SDM Tools: Species distribution modelling tools: Tools for processing data associated with species distribution modelling exercises. R package version 1.1-13. R Foundation for Statistical Computing, Vienna, Austria. http://CRAN.R-project.org/package=SDMTools

Wahlberg, N., A. Moilanen, and I. Hanski. 1996. Predicting the occurrence of endangered species in fragmented landscapes. Science 273:1536–1538.

Walker, B., and D. Salt. 2006. Resilience thinking: Sustaining ecosystems and people in a changing world. Island Press, Washington, D.C., USA.

Webb, C., and O. Bodin. 2008. A network perspective on modularity and control of flow in robust systems. Pages 85–111 *in* J. Norberg and G. S. Cumming, editors. Complexity theory for a sustainable future. Columbia University Press, New York, New York, USA.

Werner, E. E., G. A. Wellborn, and M. A. McPeek. 1995. Diet composition of postmetamorphic bullfrogs and green frogs: Implications for interspecific predation and competition. The Journal of Herpetology 29:600–607.

Wiens, J. A. 2002. Riverine landscapes: Taking landscape ecology into the water. Freshwater Biology 47:501–515.

With, K. A., R. H. Gardner, and M. G. Tuner. 1997. Landscape connectivity and population distributions in heterogeneous landscapes. Oikos 78:151–169.

Supplemental Material

Supplement

Ten R scripts demonstrating construction and analysis of wetland landscape scenario habitat networks (*Ecological Archives* A024-192-S1).