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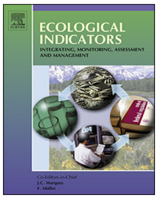

Original Articles

The challenge of assaying landscape connectivity in a changing world: A 27-year case study in the southern Great Plains (USA) playa network

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ABSTRACT

Many habitat resources fluctuate in availability due to natural environmental variability and anthropogenic influences. These fluctuations pose challenges to organisms attempting to move from one habitat patch to another, and also pose challenges to detecting and managing factors impacting landscape connectivity. Our understanding of these relationships is further hampered by lack of precedence on how to quantify dynamic connectivity. The ephemeral freshwater wetlands of the southern Great Plains of the USA (playas) form a dynamic habitat network that serves as a case study of these challenges and allows us to propose a suite of connectivity metrics to monitor changes in network topology and evaluate the management importance of individual wetlands. We used satellite imagery to examine inundation patterns of > 7000 playas in a 29,083 km^2 portion of Texas on 80 dates from 1984 to 2011. Based on historic locations of playa basins, approximately 85% of playas (particularly those $\leq$10 ha) have lost the capacity to hold water even during regionally wet times, resulting in a ~69% reduction of surface water area. These losses were associated with proximity to cropland, with total cropland acreage increasing by 0.07–17.34% of county land area during our focal time span in 10 of the 14 counties in our study area. We examined connectivity at wetland and whole-network scales to determine effects of playa losses on network topology and thus on connectivity. We evaluated 11 metrics for this purpose, which quantified the number of wet playas present on each date, their degree of connectedness, their clustering, path redundancy within the network, overall network topology, the importance of individual playas in various roles, and the size of a single playa that would provide equivalent connectivity (amount of reachable habitat) as in the actual network. Topology has thinned over the past three decades with playa losses, reflected in increasing graph density, average path length, degree of connectivity for highly linked hubs, and average number of cut-points. Similarly, graph diameter is currently less than half of the historic potential maximum, and the equivalent connected area has declined by over 23% since 1984 (and by over 82% relative to historic values). These patterns suggest that path redundancy through the network has declined such that dispersers currently have fewer connectivity options compared to a few decades ago. Relatively high transitivity scores indicate that the playa network is still populated with a large (but diminishing) number of wetlands, and the dwindling surface water present in the remaining playas is not compensating for playa losses over time. Average coalescence distances are currently higher than the dispersal capacity of many organisms, meaning that the playa network is fragmented such that only an extremely vagile disperser (capable of moving at least 18–45 km) would be able to traverse the landscape via the remaining wetlands, even if all were wet simultaneously. These findings illustrate the importance of using multiple indicators in assaying dynamic connectivity and provides a framework of possible metrics to use for monitoring and assessment of any dynamic habitat network.

1. Introduction

Many habitat resources fluctuate in availability due to natural environmental variability but also increasingly as a result of human activities related to large-scale land conversion. Organisms that use these resources must therefore navigate a dynamic habitat network.

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Landscape connectivity, defined as how the spatial arrangement of habitat patches facilitates or impedes the movement of organisms (Taylor et al., 1993), may be enhanced or compromised by such fluctuations. Because compromised habitat connectivity increases extinction risk, quantifying changes in habitat connectivity has become a primary focus in the study of habitat networks (Lookingbill et al., 2010; Estrada, 2012). However, most work has been on static networks or on networks at a single snapshot in time (e.g. Jordan et al., 2003; Baum et al., 2004; Pascual-Hortal and Saura, 2007). It has only been recognized recently that connectivity is dynamic (Matisziw and Murray, 2009; Saura et al., 2011; Ruiz et al., 2014; Tulbure et al., 2014; Zeigler and Fagan, 2014; Bishop-Taylor et al., 2015; Bishop-Taylor et al., 2017; Martensen et al., 2017), with a challenge remaining in assessing changes in connectivity in temporally fluctuating habitat networks. Comparing an ecological network to a null model constructed with a similar number of nodes (habitat patches) and node degree distribution (e.g. by using a power law function to generate a neutral model of a scale-free network, or a random/Poisson model) is relatively well-established (e.g. Watts and Strogatz, 1998; Moore and Newman, 2000; Proulx et al., 2005; Wright, 2010; Estrada, 2012; Lee and Maeng, 2013). However, empirical comparisons across non-theoretical networks are crucial in distinguishing natural intra- and interannual variability in dynamic networks from directional changes resulting from land use changes or climate shifts, and are necessary for natural resource monitoring and management in a changing world.

This challenge is further complicated by the fact that there are numerous indices that quantify various aspects of connectivity at two different scales: that of the entire network, and that of the relative importance of each node within the network (Tischendorf and Fahrig, 2000b; Kindlmann and Burel, 2008; Baranyi et al., 2011; Laita et al., 2011). Common global metrics quantify the structure of ecological networks in terms of the number of nodes, path redundancy within the network, and overall network topology; the role(s) of individual nodes can be quantified in terms of their degree of connectedness. However, there is no consensus on which metrics may be most useful for comparative work (Kupfer, 2012; Ernst, 2014), although Baranyi et al. (2011) had some suggestions on individual-scale metrics useful in ranking nodes, and Estrada (2012) suggested various indices for comprehensively describing network structure with respect to node density and clustering and the importance and roles of individual nodes, as well as some that are more appropriate for a theoretical or social network than for a spatially explicit landscape network. This lack of agreement is particularly problematic when examining dynamic connectivity, which by its very nature requires quantitative comparisons over time. Thus, even though there are numerous metrics that can be used to quantitatively describe structural connectivity, there are few examples of comparing these indices over time. Connectivity in dynamic habitat networks thus represents an important but understudied and growing research need.

Wetlands are a prime example of a dynamic habitat network, fluctuating in availability based on precipitation patterns (droughts, floods) and human activities (drainage, infill, channelization), and thus also impose dynamic connectivity on wetland-associated wildlife. Wetlands are among the most sensitive ecosystems to land conversion and climate change (Brinson and Malverez, 2002). About half of the freshwater wetlands in the U.S. have been lost in the past 200 years due to human activity, mostly in the Great Plains (Dahl, 2011). As part of the United States' breadbasket, corn belt, and cotton belt, the Great Plains have experienced extensive conversion of native grasslands to tillage agriculture, threatening prairie wetlands (Wright and Wimberly, 2013). Examinations of how these activities may have altered connectivity among prairie wetlands have been scarce, however (Ruiz et al., 2014; Uden et al., 2014), so we examined whether temporal trends in the playa network were associated with land use.

The most prevalent wetlands of the southern Great Plains are playas (Smith, 2003). Playas are ephemeral freshwater wetlands that are important resources for people and wildlife (Bolen et al., 1989) (Fig. 1). Playas support breeding (e.g. amphibians, invertebrates, waders, waterbirds) and overwintering (e.g. waterfowl, cranes) wildlife, and are continentally important migratory stopover habitats along the Central Migratory Flyway. Playas are filled from precipitation and runoff and as such are influenced by land-use activity in their watersheds as well as by weather variability (Smith et al., 2011). Hydroperiods are highly variable within and between years, ranging from 15 to 185 days depending on rainfall and surrounding land use (Ghioca and Smith, 2008; Collins et al., 2014). Indeed, it is the dynamic drying/inundation patterns of playas that enhance regional biodiversity (Haukos and Smith, 1994). When dry, their clay basins form cracks that, when wetted enough, swell and seal, thereby allowing the playa to hold water. Surrounding land-use can facilitate or impede runoff, thereby affecting playa hydroperiod (Collins et al., 2014), but it is unknown how much precipitation is needed, over what time frame, for a playa within a given land-use type to hold water (Ganesan et al., 2016). During droughts, many playas will be dry for weeks to years, although most are still detectable due to the presence of a depression, hydric soils, and associated vegetation (Smith, 2003). Human activities associated with agriculture, such as drainage and infill, have disrupted the ability of some playas to hold water and have caused some playas to disappear from the landscape altogether (Johnson et al., 2012). Historically, there were an estimated > 30,000 of these ephemeral freshwater wetlands (Smith, 2003), yet it is unknown how many have been lost in terms of their capacity to hold water, in large part because of the inherently dynamic hydrology of playas. Loss estimates range from 17% to over 85%, and even moderate losses may compromise the unique and vital

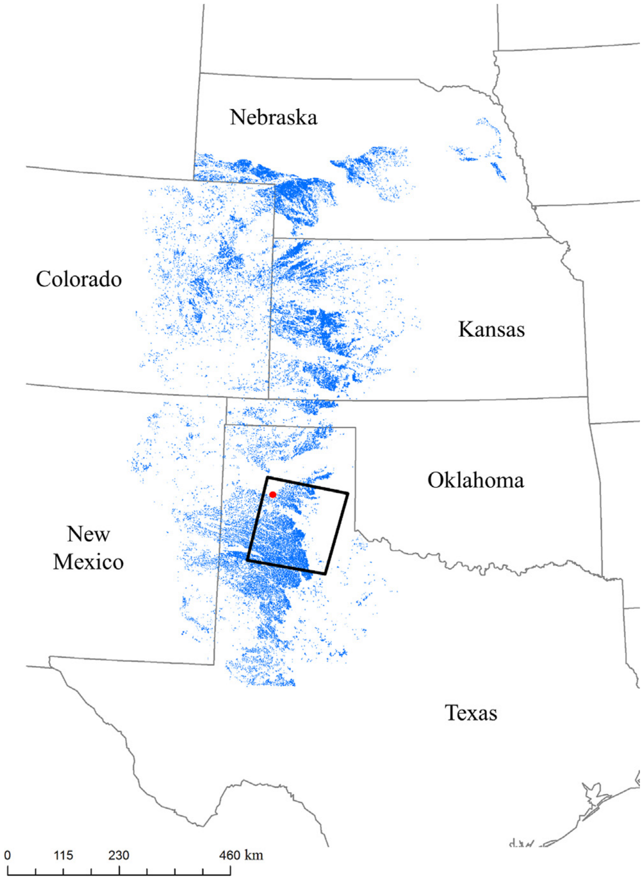

Fig. 1. Playas of the Great Plains (digital data from the Playa Lakes Joint Venture; www.pljv.org/partners/maps-data/playa-maps), showing our focal area (Landsat 5 scene 30/36; parallelogram) and the city of Amarillo, Texas (largest populated place within scene 30/36; red circle). Base map "USA States" from ArcGIS online.

habitat network that is the playa wetland system of the Great Plains (Johnson, 2011; Collins et al., 2014). Patterns of loss with respect to geomorphological patterns, such as playa basin size, are also unknown, but smaller basins should dry out more quickly or be infilled with erosional sediments more readily, meaning that the networks may be altered in predictable ways. Therefore, changes in connectivity of this network from playa losses have far-reaching implications on continental-scale biodiversity. Playas thus represent a model system of dynamic connectivity, but examining long-term patterns in this and other fluctuating systems will depend on using indices that are sensitive enough to capture changes at both the whole-network and individual-node scales.

To complicate matters, there are several dozen indices that measure different structural landscape properties or potential functional outcomes of dispersal at a population or community level (Tischendorf and Fahrig, 2000a, 2000b; Moilanen and Nieminen, 2002; Calabrese and Fagan, 2004; Kindlmann and Burel, 2008; Vogt et al., 2009; Laita et al., 2011). One family of metrics consists of variants of least-cost paths based on landscape resistance or circuit theory (see e.g. Adriaensen et al., 2003; Zeller et al., 2012). These indicators must be parameterized with empirical data (which are lacking for most species) or on expert opinion that may be incomplete, inaccurate, or biased (Spear et al., 2010). In contrast, connectivity metrics from graph theory (a Euclidian distance-based family of metrics; Bunn et al., 2000; Fortuna et al., 2006; Fall et al., 2007) do not need to be parameterized with such data, but also do not incorporate aspects related to the matrix between habitat patches. Although these two approaches are not mutually exclusive (and indeed, resistance-weighted distances derived from least cost or circuit-based modelling can be used as inputs to calculate graph theory-based connectivity metrics), they quantify different aspects of connectivity (structural vs. functional; Calabrese and Fagan, 2004; Kindlmann and Burel, 2008). Since environmental management decisions are typically made based on structural aspects of habitat availability rather than on species-specific functional aspects, it is not surprising that graph theoretical approaches are being increasingly adopted for rapid structural habitat assessment for conservation planning (Minor and Urban, 2007). A graph-theoretical approach is thus ideal for quantitative appraisals of dynamic connectivity because it does not require species-specific demographic data and instead focuses on dispersal distances for a range of organisms (Saura and Rubio, 2010). Even so, there are numerous graph theoretical metrics, and because different indices quantify connectivity at different scales (individual patches vs. the entire network), a suite of metrics that allow for inferences about dynamic connectivity at multiple scales is needed. We therefore undertook a longitudinal analysis of landscape change and dynamic connectivity among playas over the past 30 years. We predicted that we would see fluctuations in the numbers of wet playas (given inherent weather variability) but that there would be an overall loss trend of playas over time (particularly smaller ones) that coincides with conversion of grassland to other forms of land use; we further predicted that this decrease in node density would be reflected in connectivity in terms of limiting the number and distance or efficiency of dispersal options. In testing these predictions, we provide a case study of an approach that examines connectivity within dynamic habitat networks, with suggested metrics to use when assessing changes in connectivity over time.

Table 1
Dates of the Landsat scene 30/36 images that were used in our study. Images were chosen from portions of three decades that included years that were both wetter and drier than the long-term average. During each set of focal years (i.e., decade), all consecutive images that were cloud-free were used.

1980’s (1984–1986) 13 dates:	1990’s (1995–1998) 30 dates:	2000’s (2007–2011) 37 dates:
14 April 1984	24 February 1995	8 January 2007
19 July 1984	13 April 1995	19 July 2007
8 November 1984	16 June 1995	31 March 2008
10 December 1984	6 October 1995	16 April 2008
12 February 1985	22 October 1995	2 May 2008
1 April 1985	7 November 1995	18 May 2008
14 January 1986	26 January 1996	3 June 2008
30 January 1986	14 March 1996	21 July 2008
4 April 1986	15 April 1996	6 August 2008
20 April 1986	1 May 1996	22 August 2008
6 May 1986	18 Jun 1996	25 October 2008
11 September 1986	4 July 1996	12 December 2008
13 October 1986	8 October 1996	13 January 2009
	9 November 1996	29 January 2009
	25 November 1996	18 March 2009
	11 December 1996	3 April 2009
	28 January 1997	22 June 2009
	21 June 1997	8 July 2009
	14 August 1997	26 September 2009
	25 September 1997	16 January 2010
	27 October 1997	17 February 2010
	14 December 1997	6 April 2010
	4 March 1998	9 June 2010
	5 April 1998	25 June 2010
	21 April 1998	12 August 2010
	24 June 1998	29 September 2010
	14 October 1998	15 October 2010
	15 November 1998	16 November 2010
	1 December 1998	2 December 2010
	17 December 1998	3 January 2011
		27 May 2011
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		28 June 2011
		14 July 2011
		2 October 2011
		18 October 2011
		3 November 2011

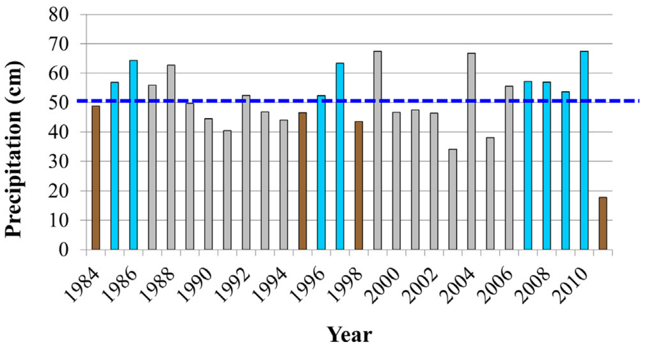

Fig. 2. Annual precipitation data for Amarillo, Texas (largest populated place within scene 30/36). The long-term (1892–2011) average is represented as a dashed blue line (51.38 cm). Our focal years (1984–1986, 1995–1998, 2007–2011) are colored relative to mean annual precipitation (blue = wetter than average, brown = drier than average, gray = years not examined).

2. Materials and methods

Our main objective was to create a framework for assessing changes in connectivity over time. First, we quantified the playa network in terms of numbers of nodes (wet playas) present. We used satellite imagery to enumerate and measure wet playas over three decades (portions of the 1980’s, 1990’s, and 2000’s) within a portion of Texas (Landsat 5 TM scene 30/36; https://glovis.usgs.gov) that contains the highest density of playa basins in the Great Plains (Fish et al., 1998). Eighty images (Table 1) for the years 1984–1986 (13 dates), 1995–1998 (30 dates), and 2007–2011 (37 dates) were processed, spanning dry and wet periods (Fig. 2), following the classification protocol in Ruiz et al. (2014). This dataset encompasses all of the available high-quality, cloud-free images over the focal years. The satellite data (resolution: 30 m × 30 m) were processed in ENVI 4.8 (Exelis Visual Information Solutions, Inc., Boulder, Colorado, USA) to distinguish water from nonwater via a band-math classification method (Collins et al., 2014); detected waters were masked in ArcGIS 10.2.2 (Esri, Redlands, California, USA) against historic locations of playas from a digital map of hydric soils (Fish et al., 1998), following protocols in Collins et al. (2014). The data were clipped to a common extent (29,083 km^2) in UTM Zone 14N.

Our focal period encompassed a range of precipitation levels, including wetter than average and drier than average years during each decade. Annual precipitation data were obtained from the National Weather Service station at the Rick Husband Amarillo International Airport (the most complete long-term weather dataset for the region; http://www.nws.noaa.gov/climate/index.php?wfo = ama).

Coefficients of variation (CV) of precipitation for our focal years and for the span 1892–2011 were calculated to assess norms, variability, and extremes. Due to a paucity of weather stations near playas, we did not attempt to model shorter-term or more localized, accumulated precipitation corresponding to each of the Landsat dates.

We examined playas during wet and dry portions of the three focal decades relative to historic locations of playas based on hydric soil locations from county soil surveys mostly conducted shortly after World War II (Fish et al., 1998). These surveys represent the only comprehensive information available about the locations of playas in this area before the development of satellite technology and likely underestimate the true number of playas originally present in the region. However, because it is unlikely that all basins would have held water simultaneously, these historic numbers should be considered potential maxima.

We plotted the number and basin size distributions of historic locations of playas, playas that held water at least once, and wet surface areas within playas. Kruskal-Wallis χ^2 nonparametric analyses of variance by ranks with Kolmogorov-Smirnov (K-S) pairwise tests of means with Dunn-Ŝidák corrections for multiple comparisons (Cramer and Howitt, 2004) were conducted to compare numbers and sizes of playas over time (means across dates within decades). Coefficients of variation (CV) were calculated to compare variability in playa size distributions over time (see also Van Meter and Basu, 2015). Finally, we used a chi-square test to determine whether losses of playas (in terms of their ability to hold water) in certain size categories (≤ 10 ha in basin area) occurred more frequently than expected. All analyses were performed in SAS 9.3 (SAS Institute, Cary, North Carolina, USA).

To assess whether temporal trends in the playa network were associated with land use, we examined how land use in our focal region changed over our study span. We used the U.S. Department of Agriculture's (USDA) Census of Agriculture (a long-term county-level census performed every 5–10 years since 1840) data from the 1987, 1997, and 2007 censuses for the 14 counties with the majority or entirety of their land area within scene 30/36 (Table 2). These data are relatively coarse in land-use categorization, separating irrigated from total cropland, and cropland from pasture, but finer details are only available for Texas since 2008 from the USDA National Agricultural Statistics Service's CropScape program (https://nassgeodata.gmu.edu/CropScape/). Pasture/grassland included grazed grasslands as well as ungrazed grasslands, including Conservation Reserve Program (CRP) land. The USDA's Conservation Reserve Program was first implemented in 1986 and has effectively reclaimed former cropland to ungrazed and unmowed perennial grasses (Heard et al., 2000), but CRP locations are not publicly available due to landowner privacy regulations. Therefore, we could not distinguish CRP from non-CRP grasslands and therefore consider pasture/grassland as a single category.

We used graph theory metrics to quantify structural connectivity within the playa network. In this approach, a network is a graph of nodes (i.e., playas) connected by links (single Euclidian distance between a pair of nodes) (Table 3). Dispersal paths through the network are thus formed from multiple links. We chose a suite of easily interpretable metrics to examine connectivity in terms of the importance of individual playas on connectivity up to overall network topology (Estrada, 2012; Kupfer, 2012); some of these metrics have also been used in other studies on dynamic connectivity (Ruiz et al., 2014; Tulbure et al., 2014; Bishop-Taylor et al., 2015). Using the *igraph* package (Csardi and Nepusz, 2006) in R 3.0.2 (R Core Team, 2014), we first determined the coalescence distance of the network on each date. This distance is the maximum nearest-neighbor distance between nodes; for an organism capable of dispersing at least the coalescence distance, the entire network is potentially traversable (i.e., all playas form a single cluster within the organism's dispersal range). At the coalescence distance, we then calculated the graph density, average path length, graph diameter, and transitivity (Table 3). Graph density is a bidirectional form of linkage density, calculated as the ratio of linkages present to the number of all possible links among nodes; values closer to 1 (maximum possible value) can indicate the presence of more choices of paths through the network (if the numerator increases) or, conversely, a simplified network (if the denominator decreases). Therefore, this metric should be examined with respect to changes in the number of links present to determine which situation is present. Average path length should not be confused with path length in a geographic or physical distance sense: average path length in a graph is the number of connections that a node has with other nodes within the specified (coalescence) distance and as such represents average nodal connectance; as such, lower values indicate more circulation efficiency through the network. Graph diameter is the longest geodesic among the shortest routes through the network, so higher values indicate greater graph complexity. Transitivity is an assay of the degree of clustering in the overall network; this clustering coefficient ranges from 0 (no clusters of at least three nodes are present) to 1 (all nodes are within the coalescence distance of at least two other nodes, forming a perfectly closed graph) and measures the degree to which a graph has groups of nodes with a relatively high density of links among them as opposed to a thinner network. Collectively, these metrics provide assessments of path redundancy, which is associated with network resiliency (Janssen et al., 2006; Rayfield et al., 2011), and network density.

Table 2

Percentages of county area designated as total cropland ("Total") and irrigated ("Irrigated") cropland by the USDA Census of Agriculture for 1987, 1997, and 2007 for the 14 counties with a majority or entirety of their area contained within Landsat scene 30/36. A dash ("–") indicates that data were not reported for that category in the census for that county in that year.

County	County size (km^2)	1987		1997		2007	
		Total	Irrigated	Total	Irrigated	Total	Irrigated
Armstrong	2367	29.03	1.33	–	1.40	27.25	1.02
Briscoe	2336	24.91	4.88	26.71	4.87	28.88	5.48
Carson	2393	48.86	10.76	45.96	12.47	55.97	7.02
Castro	2328	73.82	31.32	71.13	39.42	75.54	37.07
Collingsworth	2380	27.23	1.09	30.05	3.69	32.90	5.05
Donley	2416	13.23	0.66	15.56	2.09	14.02	2.82
Floyd	2572	70.90	22.74	64.31	26.68	66.19	20.42
Hale	2603	78.88	37.46	79.63	48.24	71.88	37.85
Hall	2341	29.84	0.93	29.80	1.54	37.86	4.82
Lamb	2637	61.69	27.36	67.44	33.49	79.03	36.04
Motley	2564	16.55	0.61	–	1.02	16.62	0.52
Potter	2388	9.88	1.29	–	1.37	12.61	1.18
Randall	2388	44.49	5.23	46.88	6.51	45.78	3.35
Swisher	2334	67.37	20.01	61.48	19.89	65.90	14.54
Averages	2431.93	42.62	11.83	48.99	14.48	45.03	12.66

We used the equivalent connected area (ECA) index (Saura et al., 2011) to evaluate changes in habitat connectivity compared to changes in habitat amount, i.e., the number of wet playas as well as the area in hectares of open water (Bishop-Taylor et al., 2017; Martensen et al., 2017). Based on the number and size of nodes at a specified proximity, ECA indicates the size of a single habitat patch (node) that would be needed to provide the same probability of connectivity as the observed fragmented network of nodes currently being evaluated. ECA thus accounts for the habitat available within the individual nodes themselves

Table 3
Glossary of the connectivity metrics that we used.

Metric	Definition
Node	Point of interest (playa centroid)
Link	Euclidian distance between a pair of nodes
Coalescence distance	Distance between the farthest pair of nearest-neighboring nodes
Graph density	Linkage density; ratio of the actual number of links to the number of possible links among all pairs of nodes
Average path length	Mean number of links connecting each node within a specified distance; not used in a geographic or physical distance sense
Graph diameter	Longest shortest path through the network in terms of number of nodes
Transitivity	Global clustering coefficient; ratio of the number of closed clusters of at least three nodes to the number of connected clusters
Kleinberg's hub score	Proportional to the number of links from a node, with a node that is connected to a large number of other nodes (within a specified dispersal distance) receiving a high hub score, meaning that a hub is a node that is connected by a relatively high number of links to other nodes in the network
Cutpoint	Any node whose loss fragments a coalesced (i.e., fully connected) network into pieces isolated by a distance greater than the coalescence distance
Equivalent connectivity area (ECA)	Size of a single node that would provide the same habitat availability as the observed spatially disjunct network of nodes
ECA:Area	Ratio of ECA to total habitat area (wet area within playa basins)

based on their size as well as that which is available to a disperser for a specified distance. Because it takes habitat size into account, this index provides a complementary measure to our other indices in characterizing the dynamic connectivity in our study area. Use of our other connectivity indices not based on habitat area in tandem with ECA thus enriches the characterization of dynamic connectivity in our study area. We used the Conefor tool in ArcMap 10.5.1 (http://www.jennessent.com/arcgis/conefor_inputs.htm) to generate input files of the network of wet playas on each date and then calculated ECA in Conefor 2.6, using the probabilistic PC formulation of ECA with nodes weighted by their size (actual wet area, not basin size) (http://www.conefor.org; Saura and Torné, 2009) for those node pairs located at a distance ≤ the coalescence distance for each date (as recommended in the Conefor manual for large and sparse networks; Saura and Torné, 2012). We also calculated ECA for all historic basins based on their basin size (rather than the number of wet basins and wet area, as was done for each recent date) (Table 3). ECA is well-suited to determine how landscape connectivity is changing relative to the amount of habitat on the landscape. Because network topology and, thus, connectivity through the network are dependent on habitat availability (i.e., number and distribution of nodes within the network), we can use it to tease apart the effects of habitat loss from changes in connectivity. In our study area, a loss in wetlands over time is of course going to constrain connectivity. Therefore, the objective is not only to determine how much connectivity is going to decrease, but also to determine whether this decrease is above or below that which would be expected from habitat loss alone. To do so, we constructed a 1:0.5 line on plots of ECA vs. the number of wet playas, and ECA vs. the wet area. Because the ECA metric is a square root function of the independent variable plotted on the X-axis, a 1:0.5 line would be used rather than a 1:1 line. This line effectively parses the graph space into two section: Values above this line would indicate connectivity higher than expected based on habitat availability, and conversely, values below this line would indicate lower-than-expected connectivity. Because ECA can never assume a value smaller than the size of the largest node in the network, we also calculated the ECA:Area index to provide a scaled assessment of how connectivity may change with habitat area (Bishop-Taylor et al., 2017). A maximally connected network has an index value of 1 (i.e., upper limit is 1); node isolation reduces ECA:Area index values (Bishop-Taylor et al., 2017). ECA:Area thus provides an assay of network fragmentation.

To complement these whole-network connectivity metrics, we also calculated two node-level metrics at the coalescence distance (Bodin and Saura, 2010). The Kleinberg hub score calculated for each node on each date reflects the number of links extending from a node; a node connected to a large number of other nodes has a high hub score (Csardi and Nepusz, 2006). Hubs are thus connected to more nodes relative to other nodes within a network (Minor and Urban, 2008). Nodes were also identified as to whether they were cutpoints or not (Csardi and Nepusz, 2006; Galpern et al., 2011). Cutpoints are nodes that, if removed from the network, result in the network becoming fragmented into components that require a greater coalescence distance to link back together (Keitt et al., 1997).

These metrics allowed us to characterize the basic structure of ecological networks in terms of the number of nodes present and at what maximum dispersal distance they are all potentially accessible by a disperser (coalescence distance), their degree of connectedness (number of links, hub score, average path length), path redundancy within the network (graph density, graph diameter, average path length), overall network topology (coalescence distance, graph density, graph diameter), the role(s) of individual nodes (as hubs or cutpoints), and assays of network fragmentation relative to habitat availability (ECA, ECA:Area). Some of these metrics inform multiple facets of network structure, making them especially valuable. All metrics were calculated for each date and then averaged by decade for a more equitable comparison of effects over time.

Because there have been few studies that have examined ecological connectivity at more than one point in time, there was little conceptual guidance from which to try to predict how a change in network topology would be manifested in connectivity metrics. Some studies that have examined connectivity longitudinally plotted trends in mean values over time (e.g. Tulbure et al., 2014) or examined changes in importance rankings over time (e.g. Ruiz et al., 2014), so we also adopted those approaches. We also took the approach used in Saura et al. (2011), Bishop-Taylor et al. (2017), and Martensen et al. (2017), all of which examined changes in ECA over time. We additionally used first principles from the mathematical calculation of the metrics themselves (formulae in Csardi and Nepusz, 2006) to make ecological predictions and determine whether some metrics performed better than others. We predicted *a priori* that the number of wet playas would decrease over time due to playa losses from land-use changes. This was then expected to cause the number of links to decrease because with fewer nodes there would be fewer possible connections. This in turn was predicted to cause a decrease graph density but increases in transitivity and average path length because of the presence of fewer links. We expected coalescence distance to increase because network thinning would mean that it would take a greater distance to move among the remaining nodes. Likewise, graph diameter should decrease as nodes are lost. We expected the average hub score to decrease over time as nodes thinned out and the number of cutpoints to increase as the network was pruned of branches out to nodes. Finally, we expected ECA and ACA:Area to decrease over time as habitat availability declined.

For these metrics to be useful guides in dynamic connectivity, they needed to show significant differences over time. Metrics that are not sensitive to changes in the numbers or placement of nodes in a network would not be well-suited to detect shifts due to natural or

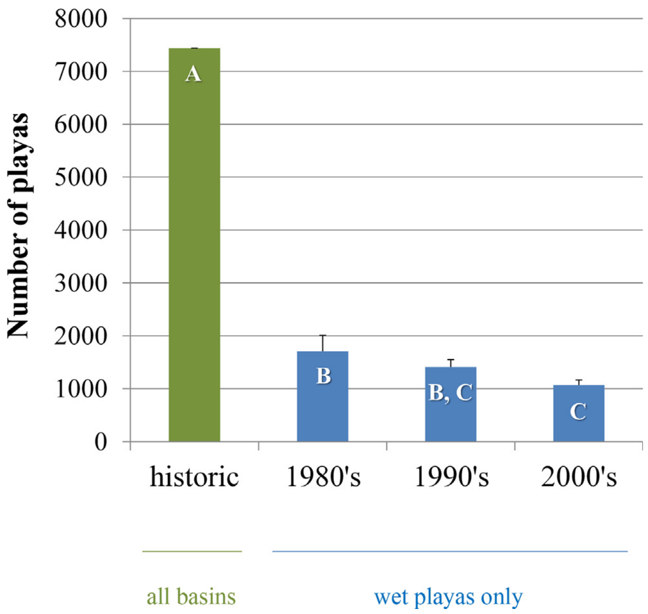

Fig. 3. Numbers of playas across dates. Historic playas included all basins (green column); this was compared to the mean (+standard error) number of playas containing water (blue columns) across dates in the 1980's–2000's. Columns with the same letter are not significantly different (K-S tests). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

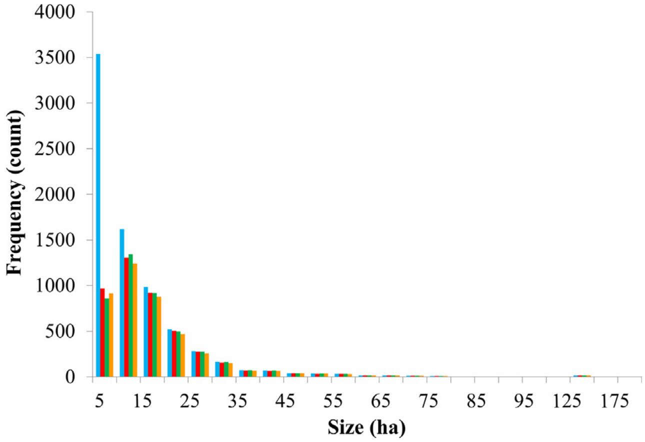

Fig. 4. Histogram of historic playa sizes (in hectares, ha) in our focal area (blue) and those playas that held water at least once during the 1980's (red), 1990's (green), and 2000's (orange). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

anthropogenic fluctuations. But because certain metrics are bounded (ratios must assume values between 0 and 1, for example) whereas others are not, we compared relative changes over time (i.e., percent increases or decreases) rather than absolute metric variations since unbounded metrics would naturally tend to have larger changes stemming from larger values. Metrics with higher ranges would have a disproportionate influence on the analyses, so relative values are necessary to make more valid comparisons among the metrics.

3. Results

There were 7437 hydric soil-defined playa basins in our study area; only 144 of these basins held water on the driest date (24 February 1995), and only 4950 held water on the wettest date (13 October 1986). There was a significant decrease in the number of playas in our focal area that held water through the 1980's, 1990's, and 2000's, relative to historic basin numbers ($\chi^2 = 9.60$, $P = 0.0223$; Fig. 3). Most of those playas that were lost were small in size (basins ≤ 10 ha), with proportionally greater losses in this size category than expected from their frequency ($\chi^2 = 4825.25$, $P < 0.0001$; Fig. 4). There also were differences in the surface areas of water within playas in recent decades compared to historic basin sizes, driven by losses of small playas rather than by any increase in the size of wet area (Table 4). This was expected since historic data were based on the sizes of hydric soil basins, which are static, whereas data from the 1980's to 2000's were based on the actual presence of water within the basins, which fluctuates with precipitation as well as surrounding land use that influences runoff. The drop in surface water availability was not due to marked differences in annual rainfall among decades, although there was greater variability in precipitation from 2007 to 2011 compared to our other two focal decades as well as to the overall long-term pattern, due to a record drought in 2011 (Table 4). The decrease in CV values from historic to more recent decades indicates there is now a narrower range of sizes of functional playas than historically (Table 4). There was no statistically significant difference in the average sizes of surface water areas within playa basins in the 1980's–2000's ($\chi^2 = 0.90$, $P = 0.6379$; blue columns in Fig. 5); however, those playa basins that held water at least once during the 1980's–2000's were larger on average than historic basins overall ($\chi^2 = 1486.91$, $P < 0.0001$; green columns in Fig. 5), consistent with losses of smaller playas. By the 1980's, there was a loss of 61.9% in surface water since historic times, comparing maximum numbers of wet playas present (Table 5). From the 1980's to the 2000's, there was a further loss of 36.4% of wet playas and 18.3% in surface water. The fewest wet playas were encountered in the 2000's. By the 2000's, 85.1% of playas were lost (that is, from historic to the 2000's, 85.1% of the playa basins examined never held water on any of the 80 dates). These trends indicate that playa dynamics are driven by more than simply precipitation patterns, including drought/deluge periods; land conversion is also a contributing factor. Most of our focal area was converted to agriculture during the early 20th century, with an expansion of irrigation after World War II. Currently, some counties have relatively more cropland than others for a variety of reasons, including geographical differences in soil types, precipitation amounts, and accessibility to the aquifer, the primary source for irrigation in this region; Donley, Motley, and Potter counties consistently have the least cropland, both total and irrigated, and Castro, Floyd, and Hale counties consistently have the most (Table 2).

As predicted, the numbers of wet playas fluctuated by date, but there was an overall decrease in the numbers of playas that held water over time, particularly smaller ones, and these loss trends coincide with an increase in cropland acreage from 1987 to 2007 in 10 out of 14 counties (by an average of 4.8%), and in irrigated cropland (by an average of 3.6%) for 7 out of 14 counties (Table 2). These landscape changes were reflected in changes in playa network connectivity: Coalescence distances ranged from 18 to 45 km by date, meaning that an overland disperser traveling from wet playa to wet playa would need to be able to travel at least 18 km in the best-case scenario and 45 km in the worst-case scenario, ignoring intervening landscape structure. Coalescence typically occurred at ≥20 km (79 out of 80 dates). On 14 dates, coalescence occurred at even greater distances (≥30 km). Mean coalescence varied by year, being nearly 1.5 times as long in the drought-stricken year of 2011 (31.8 km) compared to the relatively wet year of 2010 (23.6 km). These distances are much longer than the daily or even lifetime dispersal distances of many organisms (e.g. amphibians; Smith and Green, 2005) and twice as high compared to the historic value of a fully intact network (12.7 km; Table 5).

As the numbers of nodes decreased through time, the number of linkages likewise decreased (Table 5). As a consequence, the playa network has become less connected overall, manifested in our focal metrics (Table 5). For example, graph density has increased over time;

Table 4
Sizes of wet area within playa basins for each time period, relative to historic basins, annual precipitation totals, and coefficients of variation (CV) for the size distributions of playas in Fig. 4.

Within clipped scene 30/36	Historic (hydric soils)	1980’s (1984–1986)	1990’s (1995–1998)	2000’s (2007–2011)
Mean (and range) size, ha	9.27 (0.12–163.38)	4.56 (0.09–116.46)	4.82 (0.18–117.81)	4.66 (0.18–125.10)
Median size, ha	5.41	1.62	1.62	1.53
CV playa sizes, ha	1.27	0.23	0.29	0.32
Mean (range) yearly precipitation, cm	51.38 (17.80–100.96)	56.69 (48.84–64.34)	51.46 (43.56–63.37)	50.61 (17.80–67.41)
CV precipitation, cm	–	13.67	16.96	37.64

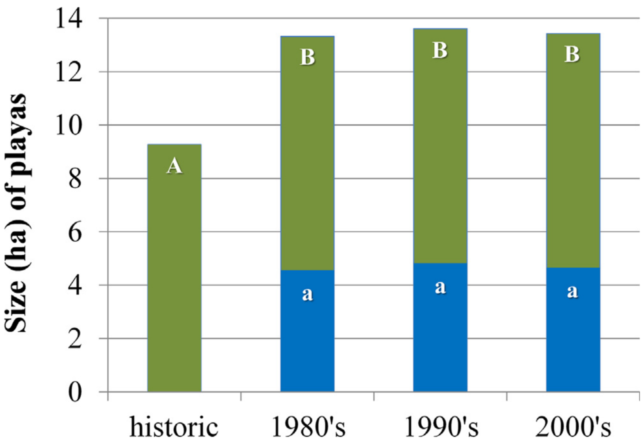

Fig. 5. Mean sizes in hectares (ha) of playas over time. Green columns indicate playa basins whereas blue columns indicate wet area within basins detectable via satellite imagery in the 1980’s–2000’s. Green basins in the 1980’s–2000’s were only those that held water at least once; these were larger basins on average than the historic distribution, indicating loss of small playas. Green columns with the same capital letter and blue columns with the same lowercase letter are not significantly different (K-S tests). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

because this metric is the ratio of the number of links present to all possible pairwise links, an increase in this value that occurs with a simultaneous decrease in the number of links present indicates that the network is thinning (i.e., denominator is decreasing). Average path length at coalescence for the recent networks were lower than the historic value, suggesting that there are fewer connections among nodes now than previously; however, this metric has been increasing in recent decades, suggesting a channelization of pathways. Graph diameter is also currently lower than historically, likewise indicating fewer direct path options through the network. Transitivity has increased, indicative of thinning of paths through the network and loss of path redundancy. Additionally, hub scores surprisingly have increased over time, suggesting that the playa network is becoming fragmented into clusters, which have a high number of connections among the nodes within a cluster, but few connections among clusters; this suggestion is supported by relatively high and increasing transitivity scores. The number of cutpoints is lower now than historically, but with an upward recent trend, signaling greater risk of network fragmentation. Finally, the status of any given playa as a cutpoint or hub for maintaining connectivity was not constant through time.

The equivalent connected area (ECA) index was positively related to the number of wet playas present and on the availability of water on the landscape (Fig. 6), which is to be expected given that ECA is calculated based on the number and sizes of nodes. Similarly, ECA values decreased over time, as would be expected as playas were lost (Table 5). Most ECA values were at or above a 1:0.5 line with respect to the numbers of wet playas present, indicating that connectivity among the remaining playas was higher than expected, but was below the 1:0.5 line with respect to the size of wet playas present (surface water area), suggesting that the amount of habitat area is of less importance than habitat placement (Fig. 6). Likewise, the ECA:Area index decreased as habitat availability increased on the landscape, with a curvilinear relationship between ECA:Area and the number and size of wet playas present (Table 5, Fig. 7). This decrease was expected because this metric indicates network fragmentation, which logically should decrease with increasing habitat availability. Low ECA:Area values indicate network fragmentation. Furthermore, an examination of Fig. 7 shows that the lowest values (and declines) are from the 1990’s and less so in

Table 5
Connectivity metrics values at coalescence, averaged over all dates examined within each decade.

Within clipped scene 30/36	Historic[1]	1984–1986	1995–1998	2007–2011	Relative change, historic to most recent[2]	Relative change, 1980’s to most recent[3]
Number of nodes (wet playas)	7176[4]	1677[5]	1409.23[5]	1065.59[5]	−85.1	−36.4
Average wet area, hectares	9.61	3.66	3.71	2.99	−68.9	−18.3
Number of links	875,603	258,409.20	156,816.00	120,975.80	−86.2	−53.2
Coalescence distance, km	12.65	25.85	25.80	26.35	108.3	1.9
Graph density	0.03	0.13	0.14	0.18	500	38.5
Average path length	6.90	3.59	3.61	4.14	−40	15.3
Graph diameter	30.00	12.38	11.90	14.59	−51.4	17.8
Transitivity	0.66	0.70	0.72	0.77	16.7	10
Hub score	0.10	0.28	0.27	0.31	210	10.7
Number of cutpoints	4.00	0.85	1.83	2.00	−50	135.3
ECA, hectares	3932.64	904.12	792.62	694.54	−82.3	−23.2
ECA:Area	0.05	0.18	0.18	0.30	500	66.7

[1] Connectivity metric values for historic playas are not averages because they are from a single point in time; values for the 1980’s, 1990’s, and 2000’s represent means across dates (each date represents a network).

[2] Difference between historic and values from the 2000’s, divided by historic values and multiplied by 100 to yield a% change.

[3] Difference between values from the 1980’s and the 2000’s, divided by earlier values and multiplied by 100 to yield a% change.

[4] Number of hydric soil basins, assuming all playa basins were wet simultaneously.

[5] Mean number of wet playas across dates.

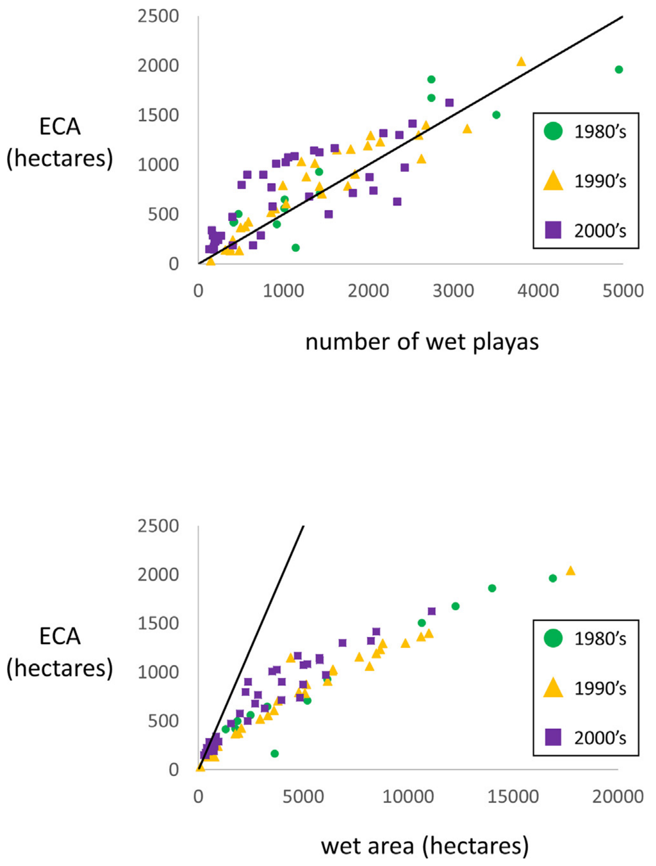

Fig. 6. Plots of ECA in hectares vs. the number of wet playas (nodes) (top) and wet area in hectares (bottom) for each of our 80 dates, with each of the three decades denoted by different symbols (1980's: green circles; 1990's: orange triangles; 2000's: purple squares). The line is a 1:0.5 line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the 2000's, which would seem counterintuitive, given the other metrics. However, coalescence distances were highest in the 2000's (Table 5), and since we used the unique coalescence distance on each date to calculate ECA, the networks from this decade may appear less fragmented than if a lower coalescence distance had been used.

Although all of the metrics displayed variation over time, particularly relative to the historic number of playa basins (which is necessary to document changes in network structure), some showed much less change on an absolute basis than did others (Table 5), which was influenced by the possible range of values each metric could be. This was particularly true for those indices that had a range from 0 to 1 (graph density, transitivity, hub score, and ECA:Area). The other metrics did not have such mathematical bounds on what value they could take (could be any value ≥ 0) and so displayed relatively greater variability. Even with these differences, however, there was agreement in the trends that the metrics indicated, and when the relative values were examined, the patterns of compromised connectivity were more evident (Table 5). For example, the increase in graph density seen from 1984–1986 to 2007–2011 (0.13 to 0.18, respectively) was 38.5%; this change, combined with a 53.2% decrease in the number of links over that same span, indicates a loss in path redundancy in the playa network over time. Relative changes in other metrics likewise reveal similarly steep losses in habitat availability (ECA), and increases in network fragmentation (number of cutpoints and ECA:Area), and these changes are even larger when comparing the most recent values to historic ones (Table 5).

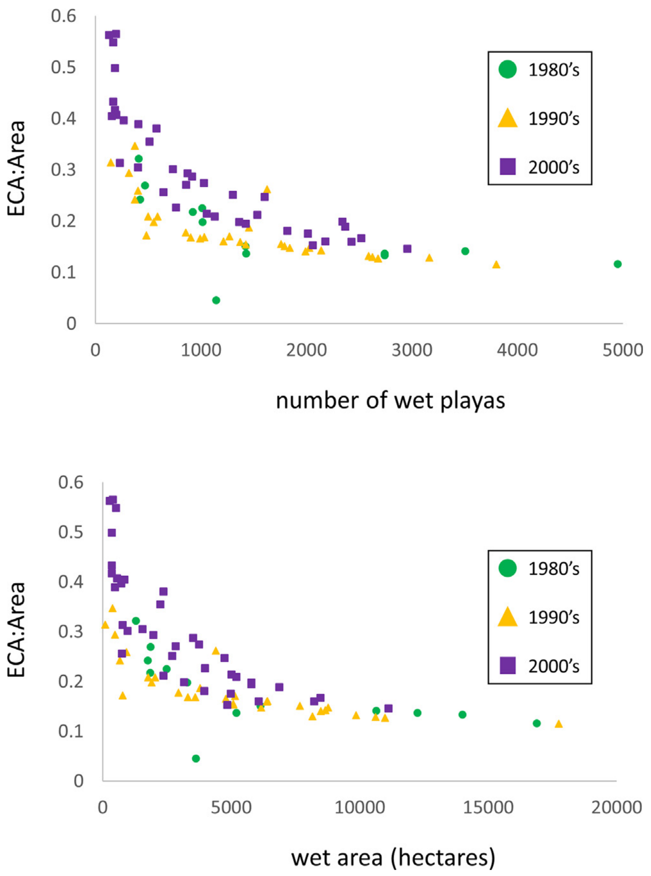

Fig. 7. Plot of ECA:Area index vs. the number of wet playas (nodes) (top) and wet area in hectares (bottom) for each of our 80 dates, with each of the three decades denoted by different symbols (1980's: green circles; 1990's: orange triangles; 2000's: purple squares). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Playa loss estimates in the southern Great Plains range from 17 to 60% (Johnson et al., 2012). Our estimates (44–70%) are comparable even though we used a different technique (remote sensing rather than their low-altitude aerial imagery) and examined many more basins over a longer span. Most of the playa basins that no longer hold water, even during rainy periods, have cropland in their watersheds, which promotes erosion and infill with sediments (Collins et al., 2014; Starr et al., 2016). Playa availability is thus a function of precipitation and nearby land use (Ghioca and Smith, 2008; Collins et al., 2014); this has implications on whether playas within different landscape contexts can support the development of aquatic wildlife that require certain hydroperiods (which range from as little as 21 days for some anurans but as long as 70 days for others; Venne et al., 2012). Moreover, the smallest playas in our focal area have been disproportionately lost. Johnson et al. (2012) similarly found that smaller basins no longer functioned as wetlands in terms of holding water. Small wetlands can play important roles despite their size (Marton et al., 2015), so losing small wetlands can compromise biogeochemical functions, including groundwater recharge, carbon sequestration, and denitrification (Van Meter and Basu, 2015).

Although relatively high transitivity scores indicate that the playa network is populated with a large (but diminishing) number of wetlands, we saw some greater constraints in connectivity than would be expected from habitat loss alone (Figs. 6 and 7). Indeed, changes in the other metrics indicate a loss of path redundancy through the network, meaning that dispersers have fewer connectivity options now than just a few decades ago. These findings indicate that the playa network is highly fragmented, such that only an extremely vagile disperser would be able to traverse the landscape via the remaining wetlands. Percolation models have suggested that a loss of 60–80% of basins could represent a tipping point of connectivity in the playa network (Albanese and Haukos, 2017), with our results indicating that the playas in our focal area already intermittently experience such losses in terms of water availability. This finding is ominous given that our focal area (Landsat scene 30/36) was selected because it had the highest playa density in the Great Plains; the playa network in other portions of the Great Plains is less dense, meaning that if the changes in connectivity we documented in scene 30/36 are likewise represented where the network is already stretched thin, those areas have likely experienced an even greater diminution in connectivity.

The metrics that we used were able to reveal that “small-world” properties were evident for the playa network and increasing over time (Table 5). Small-world networks have properties between completely random and completely regular networks (Watts and Strogatz, 1998), being characterized by containing clusters of nodes with high average path length, high transitivity, and many hubs (Estrada, 2012). Their few but dense connections makes small-world networks vulnerable to overall network failure from losses of highly connected nodes, such as hubs (Dunne et al., 2002). The apparent ubiquity of playas on the landscape may belie the impact of their losses, but this collective is now sparser than it was historically. Beyond reduction in habitat area and resource availability, these losses have also compromised connectivity in several ways, and one of the major challenges of connectivity conservation is that efforts cannot focus on a single site because the importance of a given site changes over time (Ruiz et al., 2014).

Using the ECA metric, Bishop-Taylor et al. (2017) found that for an intermittently flooded river system in Australia, connectivity was higher than expected given decreases in surface water during periods of drought, suggesting that the structure of this riverine network provided a degree of resistance to dry conditions. Something similar appears to be the case in our study area: Results from the ECA index analyses suggest that connectivity within the playa network is higher than would have been expected from habitat loss alone, at least most of the time. The amount of water present in the remaining habitat is not compensating for large-scale habitat loss in the playa network (Fig. 6), but key placement of nodes as stepping-stones can cause connectivity to be higher than expected, given habitat availability (Bishop-Taylor et al., 2017; Martensen et al., 2017). These factors suggests that even when the nodes present are small, their configuration can, at least on some dates, provide a degree of resistance to dry conditions (see also Bishop-Taylor et al., 2017).

Our approach could potentially be scaled up to the global level, owing to the recent availability of high spatial- and temporal-resolution products characterizing the dynamics of surface water (Pekel et al., 2016). Such products are freely available online with the Global Surface Water Explorer for the period 1984–2015 at a 30 m spatial resolution and a monthly temporal resolution (https://global-surface-water.appspot.com/). This dataset uses monthly water recurrence as a measurement of interannual changes but acknowledges that finer-scaled dynamics are not well-captured, noting that “short-duration seasonal water…is likely to be underestimated” (Pekel et al., 2016). Thus, wetlands with short and highly variable hydroperiods, such as playas, may not be well-represented, and so this dataset may need to be supplemented with additional satellite images (which are available at 16-day intervals) to examine dynamic connectivity in ephemeral, seasonal, or temporary waters. Other limitations are discussed in Pekel et al. (2016).

Previous studies that have used the ECA metric (and, by extension, ECA:Area) used a constant threshold distance between node pairs across dates, and picked an arbitrary distance to represent some biologically relevant dispersal distance (e.g. 5000 m). In our case, we used the coalescence distance found for each date, meaning that each date’s ECA value was calculated for a unique distance rather than a common distance, in order to evaluate each network independently based on maximal connectivity rather than a fixed distance. Similarly, our approach calculated the other network metrics for each date independently from the others, as has been done in other assessments of dynamic connectivity (e.g. Ruiz et al., 2014; Tulbure et al., 2014; Bishop-Taylor et al., 2015). A different spatio-temporal approach has been used by Martensen et al. (2017), who proposed a way to deal jointly with connections through space and time, rather than just comparing connectivity values as obtained from each date independently. Indeed, Martensen et al. (2017) have suggested that connectivity as assessed by 'standard' metrics may significantly underestimate actual connectivity, with a more comprehensive picture provided by a fully spatiotemporal network analysis. There are many ecological indicators of landscape connectivity, but relatively few have been evaluated as to whether they can track temporal dynamics (Saura et al., 2011). Our ability to understand the drivers behind network dynamics is compromised by a lack of understanding of how much change in connectivity metrics is needed to signal environmental trends and not merely natural variation. For naturally dynamic systems that are also experiencing trends in occurrence, this ability is crucial. Not all metrics were equally sensitive for monitoring purposes, however. Using relative rather than absolute differences can reveal more striking patterns, given that comparing metrics that have finite distributions (such as proportions bounded between 0 and 1) to unbounded metrics is, by its very nature, an unfair comparison. Having multiple and comparable evaluations can thus determine whether there is consensus in a trend.

5. Conclusions

Our case study illustrates the importance of using multiple metrics in assaying dynamic landscape connectivity and provides a framework of 11 metrics from different network scales for longitudinal comparisons. Because many other ecological networks are experiencing natural and/or anthropogenic alterations that may be inducing downstream effects on connectivity, an approach and suite of metrics that can provide quantitative documentation of topological changes over time, such as provided here, will be necessary for adaptive natural resource management.

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