

# Dynamic connectivity of temporary wetlands in the southern Great Plains

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**Abstract** We quantified fluctuations in the status of individual patches (wetlands) in supporting connectivity within a network of playas, temporary wetlands of the southern Great Plains of North America that are loci for regional biodiversity. We used remote sensing imagery to delineate the location of surface waters in >8,000 playa basins in a ~31,900 km<sup>2</sup> portion of Texas and quantified connectivity in this region from 2007 to 2011. We ranked playas as stepping-stones, cutpoints, and hubs at different levels of environmental conditions (regionally wet, dry, and average periods of precipitation) for dispersal distances ranging from 0.5 to 34 km, representing a range of species' vagilities, to provide baseline dynamics within an area

likely to experience disrupted connectivity due to anthropogenic activities. An individual playa's status as a stepping-stone, cutpoint, or hub was highly variable over time (only a single playa was a top 20 stepping-stone, cutpoint, or hub in >50 % of all of the dates examined). Coalescence of the inundated playa network usually occurred at  $\geq 10$  km dispersal distance and depended on wetland density, indicating that critical thresholds in connectivity arose from synergistic effects of dispersal ability (spatial scale) and wet playa occurrence (a function of precipitation). Organisms with dispersal capabilities limited to <10 km routinely experienced effective isolation during our study. Connectivity is thus a dynamic emergent landscape property, so management to maintain connectivity for wildlife within ephemeral habitats like inundated playas will need to move beyond a patch-based focus to a network focus by including connectivity as a dynamic landscape property.

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## Introduction

Habitat connectivity is a key determinant of extinction risk for many species and, thus, a primary aim of conservation planning (Taylor et al. 1993; Beger et al. 2010). Many conservation activities focus on

identification and management of habitat patches that serve important roles as (1) *stepping-stones*, which facilitate connectivity through a network of patches; (2) *cutpoints*, the loss of which would result in a disproportionately high degree of fragmentation; or (3) *hubs*, which are connected to more patches relative to other patches in the network (Metzger and Décamps 1997; Minor and Urban 2008). However, evaluation of a patch's importance in maintaining functional connectivity (Laita et al. 2011) has typically been done at a single point in time (e.g. Keitt et al. 1997; Jordan et al. 2003; Baum et al. 2004; Pascual-Hortal and Saura 2007), which does not take into account potential temporal variability in a patch's importance. Identification of temporal consistency in a patch's function as a stepping-stone, cutpoint, or hub is critical information for management and conservation in a dynamic habitat network.

Temporary freshwater wetlands are among the more important and vulnerable habitats on Earth (Brinson and Malvarez 2002). The inherent dynamics of these ephemeral wetlands are key for supporting regional biodiversity (Haukos and Smith 1994; Williams 2006). One such group of temporary wetlands is the *playa* wetland network of the southern Great Plains of North America, comprised of >30,000 shallow, closed-basin wetlands that encompass critical habitat for aquatic and amphibious wildlife in the south-central U.S. (Bolen et al. 1989; Smith 2003). Moreover, these wetlands are located within the Central Flyway for migratory birds, linking them to the prairie pothole wetland complex of the northern Great Plains (Ray et al. 2003). Connectivity through the *playa* network is thus crucial for supporting biodiversity at a multiple scales, including the continental scale. *Playas* have been and continue to be degraded and lost due to land-use decisions that lead to *playa* infill and drainage (Johnson et al. 2012). Ecological states of *playas* are predicted to be affected by regional climate change with projections of higher evaporation due to higher temperatures, as well as altered timing and amount of precipitation, which will impact the frequency, timing, and duration of precipitation and, thence, inundation (Smith et al. 2011). A primary conservation focus is thus on identifying *playas* that reliably resist fragmentation and maintain landscape connectivity.

The inundated ecological state of the *playa* wetland network is naturally dynamic in time as a function of rainfall amount and spatial distribution, so the role of a

given *playa* as a stepping-stone, cutpoint, or hub may vary with overall network topology. Moreover, because connectivity is scale-dependent (D'Eon et al. 2002), different patches may serve as stepping-stones, cutpoints, or hubs for organisms that differ in their dispersal capacity (i.e., scale at which they interact with landscape structure). Additionally, the existence of cross-scale pattern-process relationships means that factors that contribute to the importance of a given patch at a given scale could influence the ranking of other patches at other scales (Schooley and Branch 2007). Therefore, if individual *playas* can be identified as serving as key network nodes consistently over time at multiple spatiotemporal scales, that information should prove useful for targeting conservation efforts. We used a graph theory approach (Bunn et al. 2000; Fall et al. 2007) to quantify connectivity among wet *playas* over multiple points in time to (1) compare network configuration during wet and dry periods and at a range of dispersal distances from 0.5 to 34 km, and (2) determine which *playas* (if any) showed consistency in fulfilling a role of stepping-stone, cutpoint, or hub. Graphical approaches to quantifying connectivity within ecological networks have recently become widely used because they do not require species-specific demographic data and as such can be rapidly applied to many species (Minor and Urban 2007; Urban et al. 2009; Dale and Fortin 2010; Rayfield et al. 2011). In a graphical approach, a network is described as a graph of nodes (patches) connected by actual or potential dispersal routes, termed links, which we approximated as Euclidian distances between inundated *playas*. By using this approach, we are focusing on the most direct distance between patches and not on other factors that may influence connectivity such as an organism's dispersive mode (e.g. passive vs. active) or the structure of the landscape between patches, making this approach broadly applicable to a wide range of species, including many invertebrates, vertebrates, and plants with dispersive propagules.

## Methods

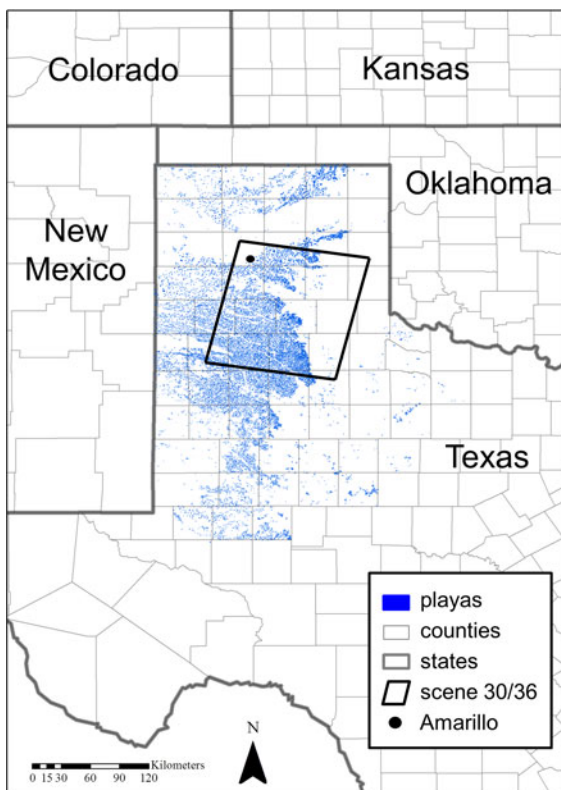
We analyzed a Landsat 5 Thematic Mapper scene that covered a portion of the Texas panhandle (WRS-2 Path 30/Row 36, hereafter, scene 30/36). The extent of scene 30/36 was  $185 \times 185$  km ( $34,225$  km<sup>2</sup>) and

contained the region with the highest density of playas in North America (Fish et al. 1998; Johnson et al. 2012) (Fig. 1). GeoTIFF files from dates with cloud cover flagged at <10 % were downloaded from the USGS Earth Resources Observation and Science Center (<http://glovis.usgs.gov>). Images nominally at <10 % cloud cover but with extensive coverage of small “popcorn” clouds and their shadows were excluded. Optical band data were calibrated to top-of-atmosphere reflectance in ENVI 4.8 (Exelis Visual Information Solutions, Boulder, Colorado). Similar to Cariveau et al. (2011), we used a rule-based classification of TM band 5 < TM 3 band = open water (formulated in ENVI 4.8) to map inundated playas. TM band 5 (1.55–1.75  $\mu\text{m}$ ) is often used to identify wetlands (Ozesmi and Bauer 2002). Rule-based wetland classification has been shown to be more accurate and rapid than unsupervised and supervised classification protocols (Sader et al. 1995). This type of

classification is able to distinguish open water from dark soils because infrared light does not penetrate into water to the same extent that visible light does, but would not include wet playas where the open water was obscured by a closed canopy of emergent vegetation; thus, our technique is a conservative estimate of the number of wet playas. While open water extent is not always synonymous with wetland extent, this approximation was appropriate in this region at the spatial resolution of the data (30 m).

Open water was classified for each date from 2007 to 2011 meeting the cloud-free quality criteria ( $N = 37$  dates total: 2 from 2007, 10 from 2008, 7 from 2009, 10 from 2010, and 8 from 2011 until failure of Landsat 5 in mid-November 2011) (Table 1). This time span included one relatively average year in terms of annual precipitation (2009), 3 years with above-average precipitation (2007, 2008, 2010), and one with a record-low amount (2011) (average annual precipitation  $\pm 95\%$  confidence interval (CI), 1892–2006: 51.41  $\pm$  2.44 cm). These precipitation data are from the National Weather Service’s first-order station in Amarillo, Texas, the largest metropolitan area in scene 30/36, and are reported here for descriptive purposes ([http://www.srh.noaa.gov/ama/?n=yearly\\_precip](http://www.srh.noaa.gov/ama/?n=yearly_precip).) Precipitation in 2009 (53.67 cm) fell within the 95 % CI of the long-term average. The wet years exceeded the upper CI (2007: 57.15 cm; 2008: 56.99 cm; 2010: 67.41 cm), and the dry year exceeded the lower 95 % CI (2011: 17.78 cm, 34.55 % of average, the driest year on record for the southwestern U.S.).

Each classified binary image (open water or not open water) was then converted into a shapefile in ArcGIS 10 (Esri, Redlands, California). An image acquired on a given date does not align perfectly with the spatial extent covered by the previous date’s image because of planetary and satellite movement that results in scenes not aligning perfectly in space across dates. Therefore, we layered all of the images and then defined a polygon to bound the maximal common area to all of the images. This polygon was 31,935.10  $\text{km}^2$  in size and used to clip each classified image to the common extent. Playas that fell on the scene edge ( $N = 34$ ) were included in their entirety. We then converted each date’s clipped shapefile to a raster file (30  $\times$  30 m cells) and overlaid it onto a rasterized mask of playa basin locations  $\geq 0.11$  ha that had been defined by the presence of playa-specific hydric soils



**Fig. 1** Map of playa basins within Texas (based on hydric soils; Fish et al. 1998), showing the location of our focal area, Landsat scene 30/36, and the approximate location of the city of Amarillo

**Table 1** List of cloud-free dates by year of Landsat images for scene 30/36 that we used to examine changes in inundated playa occurrence over time

| 2007      | 2008        | 2009         | 2010         | 2011       |
|-----------|-------------|--------------|--------------|------------|
| 8 January | 31 March    | 13 January   | 16 January   | 3 January  |
| 19 July   | 16 April    | 29 January   | 17 February  | 27 May     |
|           | 2 May       | 18 March     | 6 April      | 12 June    |
|           | 18 May      | 3 April      | 9 June       | 28 June    |
|           | 3 June      | 22 June      | 25 June      | 14 July    |
|           | 21 July     | 8 July       | 12 August    | 2 October  |
|           | 6 August    | 26 September | 29 September | 28 October |
|           | 22 August   |              | 15 October   | 3 November |
|           | 25 October  |              | 16 November  |            |
|           | 12 December |              | 2 December   |            |

(the resolution of 0.11 ha was the resolution of the digital data from Fish et al. 1998). This masking simultaneously removed non-playa open water features (e.g. rivers, reservoirs) and only accounted for actual surface water on any given date within a playa basin. The result was a binary output raster with “1” in wet playa cells and “no data” elsewhere; cells were denoted based on a “majority rule” (Turner et al. 2001). Each of those files was then converted back to a shapefile. We used a 4-neighbor (rook’s case) rule in forming polygons from raster cells (Turner et al. 2001) to include surface waters as small as a single pixel (0.09 ha). The UTM coordinates of the centroid of each confirmed wet basin were then calculated and used in subsequent connectivity analyses.

Inundated playa networks were analyzed with the *igraph* package (Csardi and Nepusz 2006) in R 2.15.2 (R Core Team 2012). We quantified connectivity between centroids of inundated playas over a range of dispersal distances (0.5–34 km) to represent a spectrum of organisms within the playa system that differ in relative vagility (i.e., dispersal capacity, or distance that an organism can travel in a single bout to obtain resources), such as amphibians and birds. For those organisms that may not have straight-line dispersal routes (e.g. overland dispersers in a heterogeneous matrix, such as amphibians), a graphical approach using Euclidian distances may overestimate connectivity among patches. More vagile organisms such as birds may engage in more direct dispersal, making our approach more directly applicable to them. The dispersal distance was increased by 1 km increments until network coalescence was observed (a critical threshold where the network goes from being

fragmented to completely traversable). In other words, playa centroids that were located within a given distance were considered functionally connected to each other and as such were part of the same cluster; this distance was increased until there was a single cluster that spanned the entire network (a “distance to neighbors” form of network construction; Fortin and Dale 2005). Thus, each date’s image had a single coalescence distance at which connectivity was achieved.

We examined the effect of precipitation on connectivity among wet playas. Precipitation data were obtained from the National Weather Service’s Amarillo station and 12 West Texas Mesonet stations (<http://www.mesonet.ttu.edu>) located within scene 30/36 that had data with no gaps over our 5-year focal period (Abernathy, Amherst, Clarendon, Dimmitt, Floydada, Hart, McLean, Memphis, Olton, Plainview, Roaring Springs, Silverton). The precipitation data for all 13 stations were averaged for each day and used in our analyses to determine the relationship between coalescence distance and cumulative precipitation. To determine how far back in time we needed to go over which to calculate cumulative precipitation to explain the highest proportion of variance ( $R^2$ ) in coalescence distance for our 37 focal dates, we ran a regression of cumulative precipitation from 1 day to 400 days. There was an increasing trend of  $R^2$  values with number of days that plateaued around 6 months and decreased after that, indicating that connectivity among wet playas was a function of rainfall over the previous 6 months. We then chose the dates from our 37 focal dates that were spaced at ~6-month intervals ( $N = 8$  dates) for statistical independence and

performed a nonlinear (negative exponential) regression of coalescence distance against precipitation accumulated over the previous 6 months.

For each date at its threshold (coalescence) distance, we ranked individual inundated playas according to their importance in supporting connectivity. Ranking patches according to their importance in supporting connectivity through a network is common practice (Bodin and Saura 2010), although the rankings can be influenced by the connectivity metric used (Laita et al. 2011). Therefore, we used three conceptually and computationally different measures of connectivity, identifying patches as stepping-stones, cutpoints, or hubs (see Csardi and Nepusz 2006 for the mathematical formulations of each). Identifying patches as stepping-stones is perhaps the most common approach in examining connectivity, particularly when using graph theory (Tischendorf and Fahrig 2000; Baum et al. 2004; Minor and Urban 2007). Stepping-stones were determined using betweenness centrality, a standard network metric (Girvan and Newman 2002; Bodin and Saura 2010) that identifies the number of shortest paths through each node within the network, with a stepping-stone being a node through which most of the shortest paths pass (Newman and Girvan 2004). However, there are also roles other than as a stepping-stone that a patch may play in an ecological network. For example, a cutpoint (also called a cut-node or articulation point; Csardi and Nepusz 2006; Galpern et al. 2011) is a node that, if removed, causes the network to become fragmented (i.e., increases the number of components or clusters of inundated playas linked within a specified distance) (Keitt et al. 1997; Csardi and Nepusz 2006). Kleinberg's hub scores are proportional to the number of links from a node; a node that connects to a large number of other nodes receives a high hub score (Csardi and Nepusz 2006). There are many other ways to quantify landscape connectivity (see Tischendorf and Fahrig 2000 for a review); our focus was on individual habitat patches and the change in the importance of those patches in network coalescence over time.

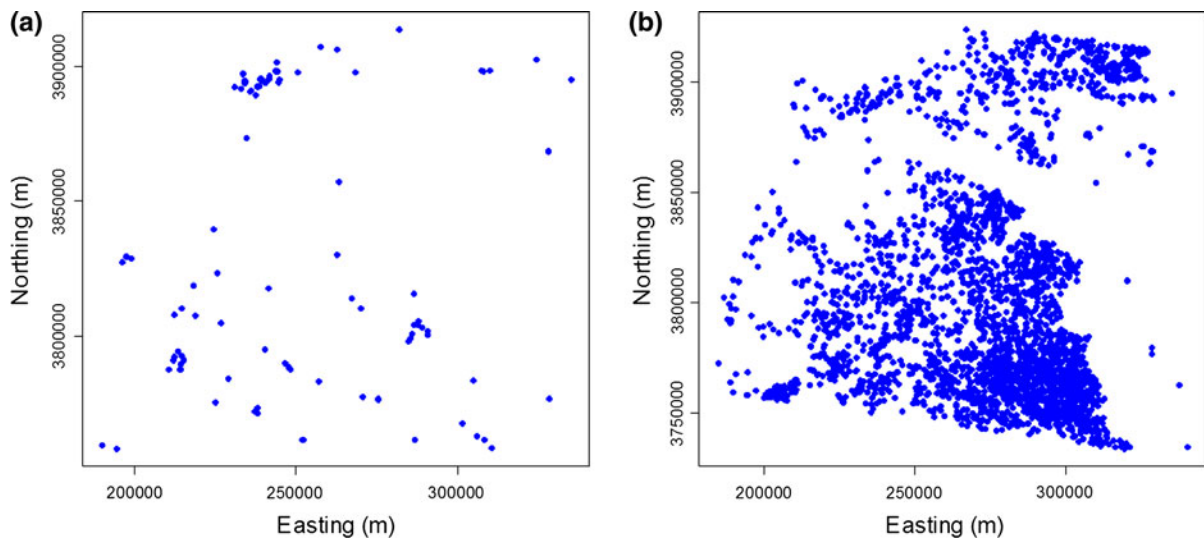
We ranked playas according to their betweenness centrality score and their hub score, for each date at each of the focal dispersal distances. Designation as a cutpoint is Boolean and so could not be ranked. We assumed the playa network to be an undirected graph (that is, movements between playas could occur in

either direction). Playas on or near the scene edge could have been linked to playas that fell outside the scene, meaning that it is possible that the importance of playas on the edge of the scene in maintaining connectivity may have been underestimated. We used the *plyr* package (Wickham 2011) in R to quantify how frequently a playa basin appeared as a top 20 stepping-stone, top 20 hub, or as a cutpoint for the 37 dates at the critical distance at which network coalescence was achieved for each date.

## Results

There were 8,404 hydric soil-defined playa basins within the clipped portion of scene 30/36. However, the number of basins that contained water at any time during our time series was 4,678 and ranged by date from 127 (2 October 2011, driest year) to 2,955 (9 June 2010, wettest year), indicating a highly dynamic and fragmented network dependent on the amount and spatial distribution of rainfall (Fig. 2). Topology of important nodes within the inundated playa network varied over time: only a single playa basin consistently served as a top 20 stepping-stone over a majority of the dates examined (18 out of 37 dates) as well as a cutpoint (9 out of 37 dates), and no playas served as a top 20 hub more than 24 % of the time (9 out of 37 dates) (Table 2). In addition, there was no consistency in regions of the network where stepping-stones or cutpoints tended to occur, although ~5 clusters of hubs (or “communities” of highly connected patches; Girvan and Newman 2002; Newman and Girvan 2004) were detected (Fig. 3).

The designation of playas as stepping-stones, cutpoints, or hubs (and thus also the occurrence of multi-node communities), however, differed if one examined connectivity through the network for a relatively vagile species compared to one with limited dispersal capability. Network topology was compared between those dates when coalescence was achieved at <15 km versus those that became traversable at ≥15 km to represent groups of species with more limited dispersal abilities (e.g. overland dispersers) versus more vagile (e.g. aerial) species; a cutoff of 15 km was chosen because it represented a natural break of the coalescence distance of a nearly equal number of dates (18 vs. 19, respectively). Differences in the distribution of stepping-stones, cutpoints, and



**Fig. 2** Map of centroids (*blue dots*) of wet playas in scene 30/36 on **a** the single date with the lowest number of wet basins detected (127, 2 October 2011) and **b** the single date with the highest number of wet basins detected (2,955, 9 June 2010) during our 2007–2011 focal period. Axes are UTMs (zone

14 N). Wet playa centroids (this figure, Figs. 3, 4) are not drawn to scale, for playas occupy only  $\sim 2\%$  of the land surface in the southern Great Plains (Haukos and Smith 1994). See Fig. 1 for geographic context. (Color figure online)

**Table 2** List of all of the wet playas (in UTM coordinates) from scene 30/36 that were ranked as top 20 stepping-stones, top 20 hubs, or cutpoints for at least 9 out of the 37 cloud-free dates we examined from 2007 to 2011 (i.e., upper quartile of

occurrences), as calculated for the single critical distance (distance at which network coalescence was achieved) for each date

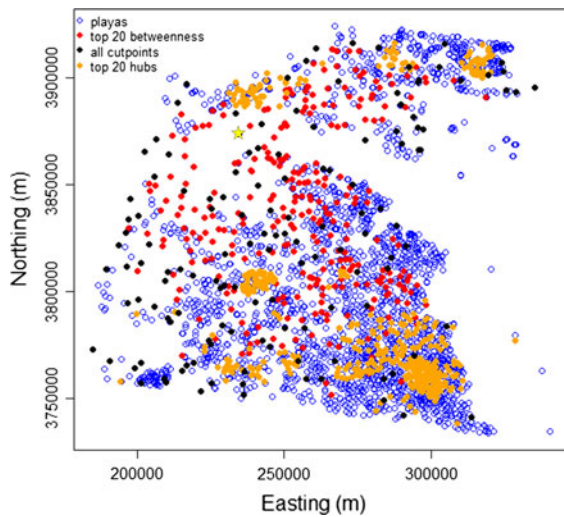
| Eastings (m) | Northing (m) | Connectivity metric | Total number of occurrences | Range of critical distances (km) |
|--------------|--------------|---------------------|-----------------------------|----------------------------------|
| 234510       | 3873720      | Stepping-stone      | 18                          | 10–33                            |
| 256975       | 3783090      | Stepping-stone      | 11                          | 10–33                            |
| 268410       | 3898250      | Stepping-stone      | 11                          | 9–34                             |
| 246480       | 3790100      | Stepping-stone      | 9                           | 10–33                            |
| 255810       | 3813480      | Stepping-stone      | 9                           | 14–33                            |
| 299629       | 3759650      | Hub                 | 9                           | 10–18                            |
| 298559       | 3757410      | Hub                 | 9                           | 10–18                            |
| 234510       | 3873720      | Cutpoint            | 9                           | 10–33                            |

The range of critical distances (min–max) for those occurrences is provided

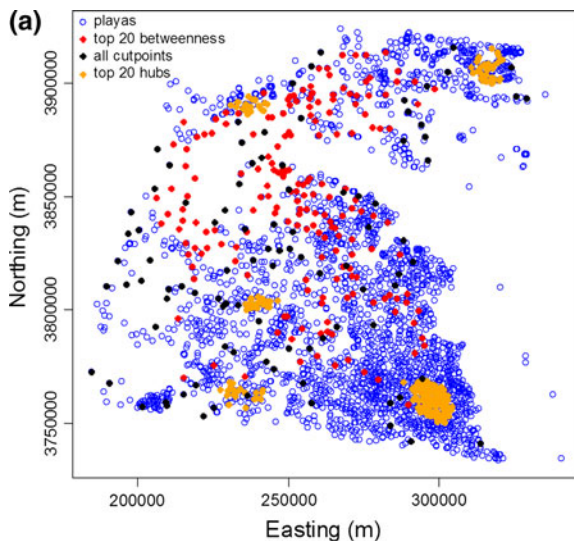
especially hubs were seen, with more playas playing important roles for less-vagile species (those with a dispersal capability  $<15$  km) in the sparser regions of the network (the north-central and western portions, where playa density is lower; Fig. 4) and hubs occurring in clusters, whereas for more vagile species ( $\geq 15$  km) the important playas were typically found in denser regions of the network and the hubs were more dispersed (Fig. 4).

Coalescence of the inundated playa network was usually (36 out of 37 instances) at  $\geq 10$  km dispersal

distance and depended on wet playa density (number of playas with open water within scene 30/36). During five dates (all during the extreme drought of 2011), the networks only coalesced at dispersal distances  $\geq 30$  km, with the largest distance being 34 km (Table 2). Not surprisingly, the only coalescence seen at  $<10$  km was in the wet year of 2010 (9 km). The distance at which coalescence was achieved reflected accumulated precipitation over the previous 6 months ( $F_{1,6} = 31.1$ ,  $R^2 = 0.81$ ,  $P = 0.001$ ), with the smallest coalescence distances (i.e., greatest network connectivity) occurring



**Fig. 3** Map of centroids (*blue circles*) of wet playas in scene 30/36 on the single date with the highest number of wet basins detected (9 June 2010), superimposed with the top 20 betweenness centrality stepping-stones (*red dots*), top 20 hubs (*orange dots*), and all cutpoints (*black dots*) for all dates as calculated for the coalescence distance at each date during our 2007–2011 focal period. The *gold star* indicates the single playa in scene 30/36 that was a top 20 stepping-stone for a majority of dates and a top 20 hub for the top quartile of dates. Axes are UTM's (zone 14 N). See Fig. 1 for geographic context. (Color figure online)

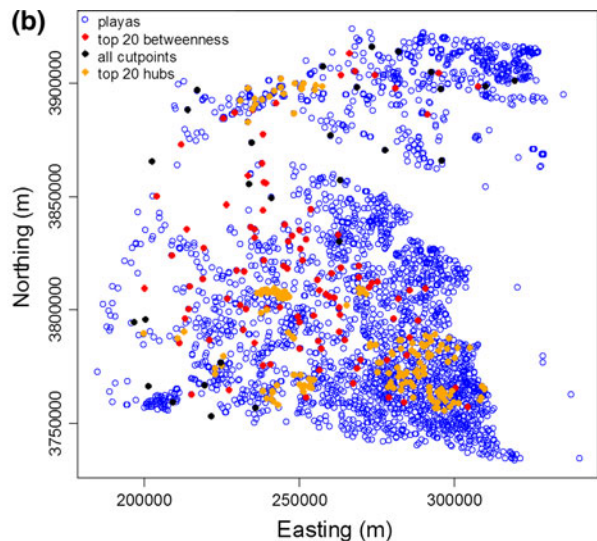


**Fig. 4** Map of centroids (*blue circles*) of wet playas in scene 30/36 on the single date during our 2007–2011 focal period with the highest number of wet basins detected (9 June 2010), superimposed with the top 20 betweenness centrality stepping-stones (*red dots*), top 20 hubs (*orange dots*), and all cutpoints (*black dots*) for **a** those dates where coalescence occurred

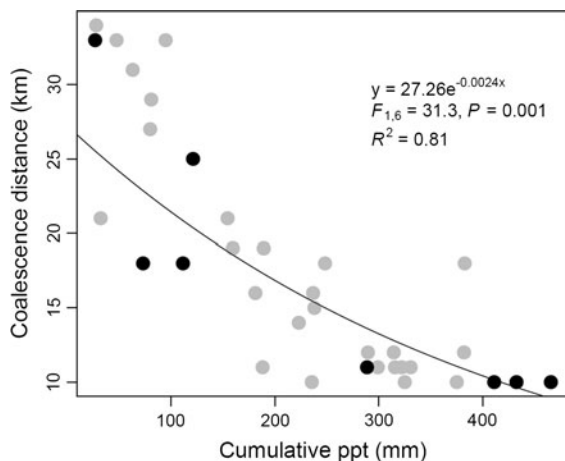
when precipitation over the previous 6 months had been high (Fig. 5). This pattern reflects the synergistic influence of ecological state of playas (inundation extent as driven by wet/dry conditions) and dispersal capability on landscape connectivity.

## Discussion

Greater than 44 % of the playa basins in scene 30/36 never contained any open water as detectable via our satellite classification on the dates we examined (possibly due to anthropogenic land conversion; Collins et al. in review), suggesting that the inundated playa network was highly fragmented during our study period. Indeed, Johnson et al. (2012) have estimated losses of 17 % (hydic soil basin no longer apparent) to 60 % (water entirely displaced by sediment) of playas in the southern Great Plains. For playa-associated species incapable of dispersing  $\geq 10$  km, the inundated playa wetland network was typically not contiguous (i.e., was fragmented into isolated components) during our study period, even during times of relatively high open-water availability (wet periods).



<15 km (18 dates) to represent species with more limited dispersal abilities and **b** for those dates where coalescence occurred  $\geq 15$  km (19 dates) to represent relatively more vagile species. Axes are UTM's (zone 14 N). See Fig. 1 for geographic context. (Color figure online)



**Fig. 5** Plot of coalescence distance in kilometers for wet playas in scene 30/36 for each of our 37 focal dates (*dots*) during our 2007–2011 study period as a function of precipitation accumulated over the previous 6 months (“Cumulative ppt”) in millimeters. Our 37 focal dates are shown as *gray dots*; the *black dots* show the eight statistically independent dates at 6-month intervals (based on examination of residuals; see text). Trend line is a negative exponential function of the eight dates (with equation,  $F$  statistic,  $P$  value, and coefficient of determination). (Color figure online)

Moreover, there were differences in which playas supported connectivity as stepping-stones, cutpoints, or hubs depending on species vagility, which indicates the challenges of multi-species conservation of the same network for the same property (connectivity at network coalescence). Although anurans and salamanders may be capable of dispersing 8–13 km, most move  $\leq 2$  km (Smith and Green 2005). Likewise, although many birds that use playas are migratory and thus capable of flying thousands of kilometers, most waterfowl and shorebirds move among wetlands within 10 km for daily activities (Farmer and Parent 1997; Webb et al. 2010). Even some amphibious insects like odonates (dragonflies) are capable of flying  $>400$  km, although most remain within 3 km of their natal wetland (Corbet 1999). Thus, although many species have a great potential capacity to disperse among habitat patches, most individuals do not move more than a few kilometers, far less than the critical thresholds of connectivity we saw (9–34 km) in the inundated playa network during our 5-year study period. Fluctuations in those critical thresholds were functions of the occurrence and spatial distribution of wet playas and spatial scale (dispersal distance), and

likely have important implications for the metapopulation dynamics of playa-dependent organisms. Specifically, reductions in dispersal among patches can delay a rescue effect and lead to increased demographic or genetic isolation of subpopulations (Hanski 1999; Johst et al. 2002).

Coalescence of the playa wetland network was dependent on a synergistic effect of dispersal ability (spatial scale) and inundated playa availability (wet vs. dry periods), with network topology differing across spatial scales on the same date, as well as during different dates at the same spatial scale. Connectivity is thus an emergent landscape property in a region that is likely to be impacted by a changing climate and future land-use decisions (e.g. conversion of grassland to agriculture, restoration of cropland to grassland, changes in crop types grown, irrigation practices, etc.). Playas are naturally highly ephemeral; the concern is whether climate change will alter the network—in term of changes in the timing, locations, and amounts of precipitation—to such an extent that playa-associated wildlife will not be able to adapt to these altered inundation dynamics in tandem with landscape fragmentation resulting in further losses of wet playas due to drainage or sedimentation (Smith et al. 2011).

The same playas typically did not serve as stepping-stones, cutpoints, or hubs year after year. The single playa most often associated with maintaining network connectivity was a basin in the city of Canyon, Texas, now maintained as an urban recreation area (Southeast Park). Playas in urban settings in Texas are often used for recreation and stormwater impoundment and have artificially prolonged hydroperiods relative to playas in non-urbanized settings (Collins et al. in review), meaning that they may play outsized roles in supporting connectivity during regionally drier times, with their urban context potentially isolating these topologically important playas for many native species that are intolerant of urbanization. These roles must also be weighed against the fact that urban playas are also subject to contaminants in urban runoff and are often highly modified: for example, the Southeast Park playa has two fountains, is partially surrounded by mowed lawn, and is stocked with fish (playas are naturally fishless; Smith 2003). Such urban playas may thus function quite differently from non-urban playas.

Individual habitat patches are typically identified as irreplaceable connecting elements only under



narrowly defined conditions (e.g. low habitat availability, high degree of fragmentation, and moderate [5–35 km] dispersal abilities) (Rubio and Saura 2012). Playa conservation will be challenging because of a lack of consistency in which wet playas were most important in maintaining landscape connectivity. Moreover, most assessments of landscape connectivity (and the roles of individual patches in supporting connectivity) have been done on static networks. But intermittent habitats such as playas (i.e., inherently dynamic wetlands) illustrate the necessity of moving beyond a static patch-based focus to one of connectivity as a dynamic landscape property. The conservation task thus becomes one of maintaining connections both within and between multi-patch units over time.

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## References

- Baum KA, Haynes KJ, Dilleuth FP, Cronin JT (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology* 85:2671–2676
- Beger M, Grantham HS, Pressey RL, Wilson KA, Peterson EL, Dorfman D, Mumby PJ, Lourival R, Brumbaugh DR, Possingham HP (2010) Conservation planning for connectivity across marine, freshwater, and terrestrial realms. *Biol Conserv* 143:565–575
- Bodin Ö, Saura S (2010) Ranking individual habitat patches as connectivity providers: integrating network analysis and patch removal experiments. *Ecol Model* 221:2393–2405
- Bolen EG, Smith LM, Schramm HL (1989) Playa lakes: prairie wetlands of the Southern High Plains. *Bioscience* 39:615–623
- Brinson MM, Malvarez AI (2002) Temperate freshwater wetlands: types, status, and threats. *Environ Conserv* 29: 115–133
- Bunn A, Urban D, Keitt T (2000) Landscape connectivity: a conservation application of graph theory. *J Environ Manag* 59:265–278
- Cariveau AB, Pavlacky DC Jr, Bishop AA, LaGrange TG (2011) Effects of surrounding land use on playa inundation following intense rainfall. *Wetlands* 31:65–73
- Corbet PS (1999) Dragonflies: behaviour and ecology of Odonata. Comstock, Ithaca
- Collins SD, Heintzman LJ, Starr SM, Wright CK, Henebry GM, McIntyre NE (in review) Hydrological dynamics of temporary wetlands in the southern Great Plains as a function of surrounding land use. *J Arid Environ*
- Csardi G, Nepusz T (2006) The igraph software package for complex network research. *InterJournal, Complex Systems* 1695. <http://igraph.sourceforge.net>. Accessed 4 Jun 2013
- D’Eon RG, Glenn SM, Parfitt I, Fortin M-J (2002) Landscape connectivity as a function of scale and organism vagility in a real forested landscape. *Conserv Ecol* 6(2):10. <http://www.consecol.org/vol6/iss2/art10/>. Accessed 10 Jun 2013
- Dale MRT, Fortin M-J (2010) From graphs to spatial graphs. *Annu Rev Ecol Evol Syst* 41:21–38
- Fall A, Fortin M-J, Manseau M, O’Brien D (2007) Spatial graphs: principles and applications for habitat connectivity. *Ecosystems* 10:448–461
- Farmer AH, Parent AH (1997) Effects of the landscape on shorebird movements at spring migration stopovers. *Condor* 99:698–707
- Fish EB, Atkinson EL, Mollhagen TR, Shanks CH, Brenton CM (1998). Playa lakes digital database for the Texas portion of the Playa Lakes Joint Venture region. Technical Publication #T-9-813, Department of Natural Resources Management, Texas Tech University, Lubbock, TX
- Fortin M-J, Dale M (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, New York
- Galpern P, Manseau M, Fall A (2011) Patch-based graphs of landscape connectivity: a guide to construction, analysis and application for conservation. *Biol Conserv* 144:44–55
- Girvan M, Newman MEJ (2002) Community structure in social and biological networks. *PNAS* 99:7821–7826
- Hanski I (1999) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* 87:209–219
- Haukos DA, Smith LM (1994) The importance of playa wetlands to biodiversity of the Southern High Plains. *Landsc Urban Plan* 28:83–98
- Johnson LA, Haukos DA, Smith LM, McMurry ST (2012) Physical loss and modification of Southern Great Plains playas. *J Environ Manag* 112:275–283
- Johst K, Brandl R, Eber S (2002) Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos* 98:263–270
- Jordan F, Baldi A, Orci K-M, Racz I, Varga Z (2003) Characterizing the importance of habitat patches and corridors in maintaining the landscape connectivity of a *Pholidoptera transsylvanica* (Orthoptera) metapopulation. *Landscape Ecol* 18:83–92
- Keitt TH, Urban DL, Milne BT (1997) Detecting critical scales in fragmented landscapes. *Conserv Ecol* 1:4. <http://www.consecol.org/vol1/iss1/art4/>. Accessed 24 July 2013
- Laita A, Kotiaho JS, Mönkkönen M (2011) Graph-theoretic connectivity measures: what do they tell us about connectivity? *Landscape Ecol* 26:951–967
- Metzger J-P, Décamps H (1997) The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. *Acta Oecol* 18:1–12

- Minor ES, Urban DL (2007) Graph theory as a proxy for spatially explicit population models in conservation planning. *Ecol Appl* 17:1771–1782
- Minor ES, Urban DL (2008) A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conserv Biol* 22:297–307
- Newman MEJ, Girvan M (2004) Finding and evaluating community structure in networks. *Phys Rev E* 69:026113
- Ozesmi SL, Bauer ME (2002) Satellite remote sensing of wetlands. *Wetl Ecol Manag* 10:381–402
- Pascual-Hortal L, Saura S (2007) Impact of spatial scale on the identification of critical habitat patches for the maintenance of landscape connectivity. *Landsc Urban Plan* 83:176–186
- R Core Team (2012) R: a language and environment for statistical computing. R Foundation, Vienna
- Ray JD, Sullivan BD, Miller HW (2003) Breeding ducks and their habitats in the High Plains of Texas. *Southwest Nat* 48:241–248
- Rayfield B, Fortin M-J, Fall A (2011) Connectivity for conservation: a framework to classify network measures. *Ecology* 92:847–858
- Rubio L, Saura S (2012) Assessing the importance of individual habitat patches as irreplaceable connecting elements: an analysis of simulated and real landscape data. *Ecol Complex* 11:28–37
- Sader SA, Ahl D, Wen-Shu L (1995) Accuracy of Landsat-TM and GIS rule-based methods for forest wetland classification in Maine. *Remote Sens Environ* 53:133–144
- Schooley RL, Branch LC (2007) Spatial heterogeneity in habitat quality and cross-scale interactions in metapopulations. *Ecosystems* 10:846–853
- Smith LM (2003) *Playas of the Great Plains*. University of Texas Press, Austin
- Smith MA, Green DM (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* 28:110–128
- Smith LM, Haukos DA, McMurry ST, LaGrange T, Willis D (2011) Ecosystem services provided by playas in the High Plains: potential influences of USDA conservation programs. *Ecol Appl* 21(Suppl):S82–S92
- Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. *Oikos* 68:571–573
- Tischendorf L, Fahrig L (2000) On the usage and measurement of landscape connectivity. *Oikos* 90:7–19
- Turner MG, Gardner RH, O'Neill RV (2001) *Landscape ecology in theory and practice*. Springer-Verlag, New York
- Urban DL, Minor ES, Treml EA, Schick RS (2009) Graph models of habitat mosaics. *Ecol Lett* 12:260–273
- Webb EB, Smith LM, Vrtiska MP, LaGrange TG (2010) Effects of local and landscape variables on wetland bird habitat use during migration through the Rainwater Basin. *J Wildl Manag* 74:109–119
- Wickham H (2011) The split-apply-combine strategy for data analysis. *J Stat Softw* 40: 1–29. <http://www.jstatsoft.org/v40/i01/>. Accessed 3 Jun 2013
- Williams DD (2006) *The biology of temporary waters*. Oxford University Press, New York