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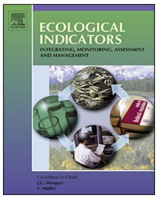

Original Articles

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

Nancy E. McIntyre[a,*], Steven D. Collins[b,1], Lucas J. Heintzman[a,1], Scott M. Starr[a,1], Natasja van Gestel[c,1]

[a] Department of Biological Sciences, Mailstop 3131, Texas Tech University, Lubbock, TX 79409, USA
[b] Johnson, Mirmiran & Thompson, 615 Crescent Executive Court, Suite 106, Lake Mary, FL 32746, USA
[c] Texas Tech Climate Science Center, Texas Tech University, 2500 Broadway, Lubbock, TX 79409, USA

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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 ≤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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[*] Corresponding author.
E-mail address: nancy.mcintyre@ttu.edu (N.E. McIntyre).
[1] Authors after the first are listed alphabetically.

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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

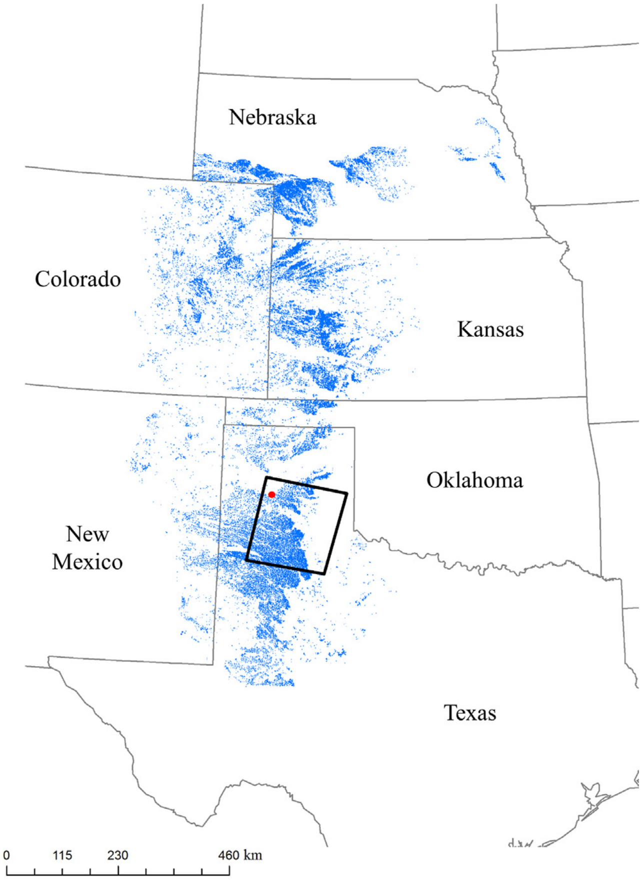

Fig. 1. Playas of the Great Plains (digital data from the Playa Lakes Joint Venture; www.pljv.org/partners/maps-data/playa-maps), showing our focal area (Landsat 5 scene 30/36; parallelogram) and the city of Amarillo, Texas (largest populated place within scene 30/36; red circle). Base map "USA States"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