

Graph theory as an invasive species management tool: case study in the Sonoran Desert

Joseph C. Drake · Kerry L. Griffis-Kyle · Nancy E. McIntyre

Received: 29 April 2016 / Accepted: 1 June 2017 / Published online: 28 June 2017
© Springer Science+Business Media B.V. 2017

Abstract

Context Biodiversity in arid regions is usually concentrated around limited water resources, so natural resource managers have constructed artificial water catchments in many areas to supplement natural waters. Because invasive species may also use these waters, dispersing into previously inaccessible areas, the costs and benefits of artificial waters must be gauged and potential invasion- and climate change-management strategies assayed.

Objectives We present a network analysis framework to identify waters that likely contribute to the spread of invasive species.

Methods Using the Sonoran Desert waters network and the American bullfrog (*Lithobates catesbeianus*)—a known predator, competitor, and carrier of pathogens deadly to other amphibians—as an example, we quantified the structural connectivity of the network to predict regional invasion potential under current and two future scenarios (climate change and management reduction) to identify waters to manage and monitor for invasive species.

Results We identified important and vulnerable waters based on connectivity metrics under scenarios representing current conditions, projected climate-limited conditions, and conditions based on removal of artificial waters. We identified 122,607 km² of land that could be used as a buffer against invasion and 67,745 km² of land that could be augmented by artificial water placement without facilitating invasive species spread.

Conclusions Structural connectivity metrics can be used to evaluate alternative management strategies for invasive species and climate mitigation.

Electronic supplementary material The online version of this article (doi:[10.1007/s10980-017-0539-2](https://doi.org/10.1007/s10980-017-0539-2)) contains supplementary material, which is available to authorized users.

Present Address:

J. C. Drake (✉)
Department of Environmental Conservation, University of Massachusetts, 160 Holdsworth Way, Amherst, MA 01003-9285, USA
e-mail: jdrake@umass.edu

K. L. Griffis-Kyle
Department of Natural Resources Management, Texas Tech University, Lubbock, TX 79409-2125, USA

N. E. McIntyre
Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409-3131, USA

Keywords Network analysis · Fragmentation · Dispersal · Invasion · Spatial ecology · Catchments

Introduction

Invasive species impact native species and economies at a cost that exceeds \$120 billion annually (Pimentel

et al. 2005). Furthermore, approximately 42% of listed endangered and threatened species in the United States are primarily threatened by invasive species (Pimentel et al. 2005). As such, invasive species, considered in tandem with climate change, are leading contributors to biodiversity declines. Habitats that are sensitive to climate change, such as wetlands, are subject to climate change-mitigation strategies that can inadvertently increase their chance of invasion by non-native species (Letnic et al. 2014; Román 2014).

For example, biodiversity in arid regions is concentrated around mostly small and isolated water sources (Souza et al. 2006; Stevens and Meretsky 2008) and are home to rare and endemic species (Hendrickson and Minckley 1985). In the Sonoran Desert of North America, these waters include intermittent streams, seeps, springs, and rock pools called tinajas. These aquatic resources are home to several rare and endemic species, so managers have constructed >6000 artificial catchments to increase water availability for them and for economically important game species (e.g., Gambel's Quail and mule deer) throughout the western U.S. since the 1940's (Wright 1959; Rosenstock et al. 1999). Because the Sonoran Desert is projected to experience reduced water availability from climatic shifts in the coming decades (Seager et al. 2007; Karl et al. 2009; IPCC 2014), these water-augmentation measures are now being seen as climate change-mitigation strategies to prepare for more pronounced water limitations in the future (Longshore et al. 2009). This potential utility must be weighed against the non-trivial costs to build and maintain these catchments under dwindling natural resource management budgets. For example, hauling water to catchments cost an average of \$144,000 per year between 1996 and 2001 in Arizona (Bloom 2003), and construction of a single artificial catchment may exceed \$70,000 (AZGFD 2015).

In addition, there is increasing evidence of negative biotic effects of catchments (Griffis-Kyle et al. 2014). These artificial catchments have much longer hydroperiods than do natural waters because they have water storage tanks and may be refilled by managers during droughts. These characteristics provide suitable conditions for invasive species to spread and outcompete native species. One such invasive species, the American bullfrog (*Lithobates catesbeianus*), has been linked to the decline of native species like the threatened Chiricahua leopard frog

(*Lithobates chiricahuensis*) through competition and predation (Schwalbe and Rosen 1988), and bullfrogs are also known carriers of the fungal pathogen *Batrachochytrium dendrobatidis* (Bd), which has been implicated in the decline and extinction of amphibians worldwide (Garner et al. 2006; Schlaepfer et al. 2007). Although native to the U.S., bullfrogs were absent from the Sonoran Desert until they were introduced for sport hunting (Tellman 2002). Unlike many native Sonoran Desert amphibians that are adapted to take advantage of ephemeral water sources through explosive breeding and rapid development (Newman 1988; Sullivan 2005), the American bullfrog needs at least nine months to complete metamorphosis, resulting in a need for more permanent water sources. Constructed water sources, including artificial catchments, thus provide a resource the American bullfrog can use for breeding and dispersal to new areas (Rosen and Schwalbe 1994). This is evident from bullfrog presence in now-permanent waters in areas that originally had been seasonally dry (and bullfrog-free) in southern Arizona (Maret et al. 2006).

Calculating invasion risk in this system and elsewhere hinges upon understanding landscape connectivity (With 2002). Percolation modeling through neutral landscapes has been used to explore how landscape structure theoretically affects the spread of invasive species and has shown that quantifying connectivity is necessary to accurately determine risk (With 2004). Graph theory has been developed as a way of quantifying connectivity among discrete habitat patches (Minor and Urban 2008) but has been underutilized to map or predict invasive species spread (Perry et al. 2016). Moreover, a graph theory approach has been shown to be useful in evaluating different scales of connectivity (Calabrese and Fagan 2004). Dispersal and other ecological and evolutionary processes, particularly those influenced by connectivity, can be influenced at separate spatial scales (Benard and McCauley 2008). Because invasive species removal or mitigation is typically done at the local scale by managers or private landowners at specific localities (Giovanelli et al. 2008), a method that can address local vulnerability within the context of regional connectivity is clearly needed. A graphical approach to quantifying connectivity should therefore be particularly relevant in examining invasion risk.

We took a graph-theoretic approach to quantify the current structural landscape of invasion risk by

American bullfrogs in the natural and anthropogenic waters of the Sonoran Desert. We then compared the current invasion-risk landscapes to that projected under climate change (losses of natural waters) and to a landscape in which management decisions are made to halt water supplementation (loss of artificial catchments). We predict both of these alternative scenarios will compromise connectivity for native species, but perhaps not for invasives with greater dispersal capabilities. In addition, such changes are likely to alter which waters are deemed high priorities for management, based on a determination of how these ultimately contribute to the local versus regional connectivity of the desert waters network. Furthermore, we explored how connectivity varied with dispersal distance for each of the scenarios to determine whether connectivity was compromised more by climate change or by management, relative to current conditions. Our objective was to illustrate how graph theory can be used to target monitoring and mitigation efforts from large regions down to specific waters, based on connectivity metrics, so that early detection of and rapid response to invasive species could be possible through identification of specific at-risk areas. Such an approach can also help guide the creation of quarantine zones against the spread of invasive species similar to those suggested for the prevention of spreading localized zoonotic diseases (Cromie et al. 2012). This framework is designed to help guide management decisions (e.g., catchment placement or removal; Drake et al. 2017) and invasive species mitigation, as an easily replicated, stand-alone method applicable to a variety of habitat networks that may be susceptible to invasion.

Methods

Study area

We focused on the waters found in the United States portion of the Sonoran Desert, an $\sim 140,000$ km² ecoregion (Strittholt et al. 2012). To minimize boundary effects (Koen et al. 2010) within our spatial calculations, we added a 32.2-km buffer around this area in ArcGIS 10.2 (ESRI, Redlands, CA). This buffer size was chosen because it is more than twice the largest dispersal distance we examined, which was

15 km (representing 1.5 times the known maximum American bullfrog dispersal distance; Kahrs 2006).

Data

We compiled locations of waters from the Spring Stewardship Institute (Flagstaff, AZ), Sky Island Alliance (Tucson, AZ), Arizona Game and Fish Department (AZGFD), BLM (Strittholt et al. 2012), 56th Range Office (Luke Air Force Base, AZ), and scientists familiar with the area (Online Appendix S1). Duplicated waters were found using one of two methods. The first was a 2-m proximity selection between spatial databases; the second was performed by sorting attributes such as locations and names to identify redundant entries. These were resolved using visual confirmation with Google Earth imagery, and the water body with the larger spatial error was removed.

Connectivity was assessed as Euclidian distances between the centroids of the waters. Using straight-line distances is often done in ecological applications of graph theory (e.g., Urban and Keitt 2001; Ruiz et al. 2014; Bishop-Taylor et al. 2015; McIntyre et al. 2016), although it does not take into account the cost of movement between habitat patches in the network which typically results in actual animal movements being more tortuous than straight. Graph theory is a superb tool for a quick yet accurate assessment of resource connectivity for a variety of species (Urban and Keitt 2001; Lookingbill et al. 2010), although it likely overestimates the ability of non-volant species to disperse through a network that is tacitly assumed to be homogeneous (Fletcher et al. 2011). The Sonoran Desert's "sky island" mountains and desert lowlands present formidable challenges to overland dispersers, but conducting more detailed or realistic movement assessments (e.g., via least-cost paths or landscape resistance routes) requires data that do not exist for most species in this area (Drake et al. 2017).

Structural connectivity—global metrics

Using the package *igraph* (Csardi and Nepusz 2006) in R v3.1.3 (R Core Team 2015), we built a script to calculate structural connectivity metrics (Online Appendix S2) similar to those used for networks of ephemeral wetlands in the Texas panhandle (Ruiz et al. 2014) and the waters on the Barry M. Goldwater

Air Force Range, AZ (McIntyre et al. 2016). As in those studies, we used two scales of common connectivity metrics to bridge the gap between structural and functional landscape connectivity (Tischendorf and Fahrig 2000a; Drake et al. 2017). The first category consisted of global metrics, i.e., those measuring properties of a wholly connected system. System coalescence occurs when the network is no longer fragmented and exists (figuratively) as a single cluster of spatially separate patches (in our case, waters) that function as a single unit in terms of habitat accessibility because they are within range of a disperser. The *coalescence distance* is effectively the farthest distance between nearest neighbors. At this distance, we calculated the *average number of links* per water present and graph density, which is the ratio of waters linked within that distance to all possible waters within the network (Csardi and Nepusz 2006). We also ranked the waters according to importance to connectivity using different measures of graph connectivity, each with its own biological significance. Specifically, we measured global connectivity by identifying and ranking waters as *stepping stones* (Tischendorf and Fahrig 2000b; Minor and Urban 2007), *hubs* (Csardi and Nepusz 2006), and *cutpoints* (Galpern 2012). Stepping stones were identified by calculating the betweenness centrality (i.e., the measure of nodes lying in a path between other nodes, where a node is an individual water within the network) for each water, with high values indicating waters located along the most shortest paths passing through the network (Newman and Girvan 2004). Hubs, which are waters connected to many other waters, were ranked according to Kleinberg's hub score (Csardi and Nepusz 2006), which is proportional to the number of links from a water connecting it to other, nearby waters: more links equals a higher score and indicates potential to provide access easily to more resources and habitat. Cutpoints represent waters that if removed increase the coalescence distance of the system (Keitt et al. 1997); these can represent bottleneck sites whose loss can cause reduced connectivity in the system. With respect to bullfrogs (and other invasive species), identifying stepping stones is important for predicting spread. Identifying hubs is important because the presence of bullfrogs in a water associated with a hub has higher spread risk. Finally, waters identified as cutpoints can be used as a tool to quarantine "infected" waters (Adams 2000; Maret et al. 2006).

Structural connectivity—node-level metrics

The second set of metrics consisted of node-level metrics calculated at distances smaller than the coalescence distance. Because many organisms have relatively limited dispersal capabilities, they experience more localized (rather than entire network scale) connectivity. Therefore, we quantified network connectivity at a range of distances representing dispersal capabilities for a range of organisms: 0.5, 1.0, 2.0, 5.0, 10, and 15 km. The first four distances are relevant to native amphibians in our focal region (Table 1). The 10-km distance represents potential long-distance dispersal by American bullfrogs, which are known to travel upwards of 10 km (Kahrs 2006). Quantifying network structure at distances smaller than 10 km allowed us to determine whether waters identified as important for maintaining connectivity at a "bullfrog-centric" scale were likewise important at finer scales more relevant to native species. Finally, to be prudent in accounting of the uncertainty in maximum movement distances, we also included a 15-km distance as a 150% of maximum known distance moved by bullfrogs.

For each of these six distances below the global coalescence distance, we counted the *number of clusters* of waters present (i.e., waters within each smaller distance of each other) and calculated *mean cluster size* (MCS; i.e., mean number of waters per cluster) and *maximum cluster size* to calculate *percent system fragmentation*. The number of clusters decreases with dispersal distance, being equal to 1 at the coalescence distance (the network is a single cluster). MCS increases with dispersal distance, reaching a maximum at the coalescence distance; it indicates habitat density and, thus, potential risk for bullfrog invasion. To understand potential path redundancy of the Sonoran Desert waters system, we calculated the *network modularity* at each dispersal distance. Network modularity shows how dense the connections are between waters within a graph: a low modularity score would suggest a system of diffuse connections with many alternative routes for bullfrog spread across the landscape (Newman and Girvan 2004; Csardi and Nepusz 2006). Finally, *average diameter* (the longest path between the farthest two connected points within a cluster; Csardi and Nepusz 2006) can give a sense of the travel distance between the most separated wetlands.

Table 1 Dispersal data from various Sonoran Desert amphibians used to justify our distances for node-level metrics

Modeled distance (km)	Representative species	Description; distance
0.5	Tiger salamander species (<i>Ambystoma mavortium</i> spp.)	Average dispersal; 0.5 km ^a
1	Red spotted toad (<i>Anaxyrus punctatus</i>)	Observed dispersal; 0.9 km ^b
	Plains spadefoot (<i>Spea bombifrons</i>)	Observed dispersal; 1.0 km ^c
	Great Plains toad (<i>Anaxyrus cognatus</i>)	Observed dispersal; 1.3 km ^d
2	Anuran species	Average dispersal distance; 2.02 km ^a
5	Chiricahua leopard frogs (<i>Lithobates chiricahuensis</i>)	Known recorded movement; 3.5 km ^e
10	American bullfrog (<i>Lithobates catesbeianus</i>)	Movement over arid grassland; 10 km ^f
	Eastern United States leopard frog species	Yearly dispersal; 12 km ^g

^a Smith and Green (2005)

^b Weintraub (1974)

^c Landreth and Christensen (1971)

^d Ewert (1969)

^e Sredl and Jennings (2005)

^f Kahrs (2006)

^g Rosen and Schwalbe (1994)

Current and future scenarios

We calculated these metrics for each of three management/climate scenarios to determine whether network structure is likely to be relatively stable or to vary with climate change and management decisions. We first examined all waters currently present, referred to hereafter as the *current landscape* scenario; this scenario represents current conditions on the landscape. The next scenario explored the possibility of reduced water availability due to climate change in the American southwest—the *climate-limited waters* scenario. To build this scenario, we excluded all waters not managed by a resource agency or identified as a spring to represent the loss of the most ephemeral natural waters in a drier and hotter projected future. If climate change proceeds as predicted and human population growth continues to place unsustainable demands on groundwater and surface water, then this scenario is almost certainly overly optimistic. Finally, the third scenario (*management reduction*) excluded any artificial catchments and thus can be thought of as either one of two perspectives: (1) the “historical” representation of the system before managers placed artificial waters on the landscape or (2) the future outcome of a landscape where management ceases to supplement natural waters. All of these scenarios

assume that all of the waters present are accessible and flowing, which may only occur intermittently (e.g., after extensive regional rain events); all of our scenarios thus represent potential connectivity maxima. Water locality data for each scenario were exported as *.csv files for structural connectivity calculations in R (sample data input file in Online Appendix S3).

We calculated global and node-level connectivity metrics for each of our three scenarios. We compared ranks of hub scores and stepping stones to determine which waters occurred within the top ten percent in each scenario, and which were most likely to contribute highly to system connectivity (McIntyre et al. 2016). In this way, we could identify waters that are important across a wide variety of scenarios for various metrics. As an alternative approach to identifying waters that play multiple connectivity roles, we also analyzed the ranked waters in the *current landscape* scenario with a Spearman rank correlation test in R (Online Appendix S4) to determine whether there was a relationship between being a hub and an important stepping stone. Because a water’s status as a cutpoint is binary (is/is not a cutpoint), we could not conduct similar analyses with them. We only conducted this analysis on the current waters and not for either of the future scenarios because we wanted to be

able to provide managers with information on which waters currently merit special consideration because they play multiple connectivity roles. The uncertainty inherent in both of the future scenarios would limit the utility of such information. Finally, for the finer node-level scales, we divided the number of clusters by the total number of waters in a scenario to compare fragmentation across scenarios; lower percentages equate to less-fragmented systems. This measurement provides a single number that can be used to compare fragmentation regardless of the number of waters present in any given scenario.

Invasive species buffering

One of our objectives was to identify waters that were isolated to a degree that made them relatively unlikely to be colonized by bullfrogs, as well as those waters that were susceptible to invasion risk because they were within the bullfrog's dispersal range from other waters. One way to prevent the further spread of invasive species is to deny them new avenues of dispersal. In the Sonoran Desert, this means the prevention of new artificial catchments being constructed in areas that could join fragmented clusters at an invasive species' dispersal range. Using ArcMap 10.2.2, we created two different sets of subsets for the *current landscape* dataset based on the clusters found in the 10- and 15-km dispersal scenarios. Waters within clusters identified within 10 km were designated as potentially at-risk for bullfrog invasion, and those farther than 15 km were considered to be sufficiently isolated as to be at low risk. We therefore created 10- and 15-km buffers around the clusters of waters to identify portions of the landscape where new catchments should not be built because they are within potential bullfrog dispersal range from existing waters, and areas where new catchments could enhance local water availability and be placed strategically considering existing waters and their invasion history.

Results

Structural connectivity—global metrics

We identified 6214 waters in the *current landscape* scenario, 5378 in the *management reduction* scenario,

and 3558 in the *climate-limited waters* scenario. The difference in numbers between the *climate-limited waters* and the *current landscape* scenarios indicate that a minimum of 43% of the waters in the buffered Sonoran Desert region are rainfall-dependent. This may be a slightly misleading definition however, as many of the remaining waters may also be precipitation-dependent. For example, ephemeral springs or sky island snowpack fed streams are both present in the Sonoran. But these identified 43% are explicitly rainfall dependent based on our methodologies. To achieve coalescence among waters in the *current landscape*, *management reduction*, and *climate-limited waters* scenarios, a distance of 29.1, 47.3, or 31.4 km, respectively, would have to be traveled between any two waters to traverse the network. Therefore, connectivity is predicted to be constrained at a global scale for both native amphibians and bullfrogs in the Sonoran Desert (Table 1), regardless of scenario. However, the scenarios differed in global topology: the average number of links was highest in the *current landscape* scenario and lowest in the *management reduction* scenario. Conversely, graph density was highest in the *management reduction* scenario and lowest in the *current landscape* scenario (Table 2).

Waters that served as the top-ranked stepping stones, hubs, or cutpoints varied by scenario (Online Appendix S5). We identified those waters that were within the top 500 rank as both a hub and as a stepping-stone for all scenarios (Table 3) as candidates for special attention for conservation, as they appear to be important for connectivity across a broad variety of scenarios (Fig. 1).

Across other combinations of the top 500 overlapping waters, we found that 37 of 38 were springs in a comparison of stepping-stone ranks in the *current landscape* scenario and the *climate-limited waters* scenario; 20 of 40 were springs in a comparison of stepping stone ranks in *current landscape* scenario and *management reduction* scenario; 32 of 68 were springs for a comparison of hub ranks in the *current landscape* scenario and *management reduction* scenario; and all 39 hubs in *current landscape* scenario and *climate-limited waters* scenario were springs (Online Appendix S5). The top waters for all scenarios were all springs (Tables S1, S2), making springs appear to be important to connectivity of the greater Sonoran Desert ecoregion, but this could also be an artifact of

Table 2 Global connectivity metrics of the Sonoran Desert’s network of waters for three scenarios based on centroid-to-centroid Euclidean distances: current landscape scenario (n = 6214; all currently known waters in the Sonoran Desert), *management reduction* scenario (n = 5378; only the known natural waters in the Sonoran Desert), and *climate-limited*

waters scenario (n = 3558; only waters that are actively managed or identified as springs, representing waters more likely to persist in the increased temperatures and decreased precipitation forecasted for the Sonoran Desert in the coming decades)

	Current landscape scenario	Management reduction scenario	Climate-limited waters scenario
Number of waters	6214	5378	3558
Graph density	0.029	0.075	0.036
Average # of links	11.8	7.6	9.6
Coalescence distance (km)	29.1	47.3	31.4

Table 3 Node-level connectivity metrics at distances representing a range of dispersal capabilities of Sonoran Desert amphibians for three scenarios based on centroid-to-centroid Euclidean distances: current landscape scenario (n = 6214; all currently known waters in the Sonoran Desert), *management reduction* scenario (n = 5378; only the known natural waters

in the Sonoran Desert), and *climate-limited waters* scenario (n = 3558; only waters that are actively managed or identified as springs, representing waters more likely to persist in the increased temperatures and decreased precipitation forecasted for the Sonoran Desert in the coming decades)

Scenario	Distance (km)	No. clusters	% fragmentation	Mean cluster size	Max cluster size	Network modularity	Diameter
Current landscape	0.5	5328	85.7	1.2	18	−0.0011	1482
	1	4351	70.02	1.4	18	−0.00059	6467
	2	2502	40.3	2.5	88	−0.00034	27,538
	5	572	9.2	10.9	1238	−0.00026	257,111
	10	128	2.1	48.6	4454	−0.00023	700,614
	15	37	0.6	167.9	4796	−0.00022	866,368
Management reduction	0.5	4547	84.5	1.2	18	−0.0012	1482
	1	3643	67.7	1.5	18	−0.00064	5216
	2	1940	36.1	2.8	88	−0.00036	27,538
	5	364	6.8	14.8	1183	−0.00028	261,104
	10	105	2	51.2	3418	−0.00025	592,328
	15	55	1.02	97.8	4174	−0.00025	639,139
Climate-limited waters	0.5	3353	94.2	1.1	5	−0.0032	1188
	1	1948	54.7	1.2	12	−0.0013	5588
	2	1944	54.6	1.8	59	−0.00074	27,691
	5	577	16.2	6.2	680	−0.00051	185,676
	10	147	4.1	24.2	2035	−0.00045	594,767
	15	48	1.3	74.1	2228	−0.00044	611,769

Percent fragmentation may not sum to 100% because of rounding. Units for mean and max cluster size are numbers of waters

excluding anthropogenic waters in the *management reduction* scenario and rain-dependent waters in the *climate-limited waters* scenario.

There was a weak, yet significant, Spearman rank correlation between which waters served as hubs and as stepping stones only in the *management reduction*

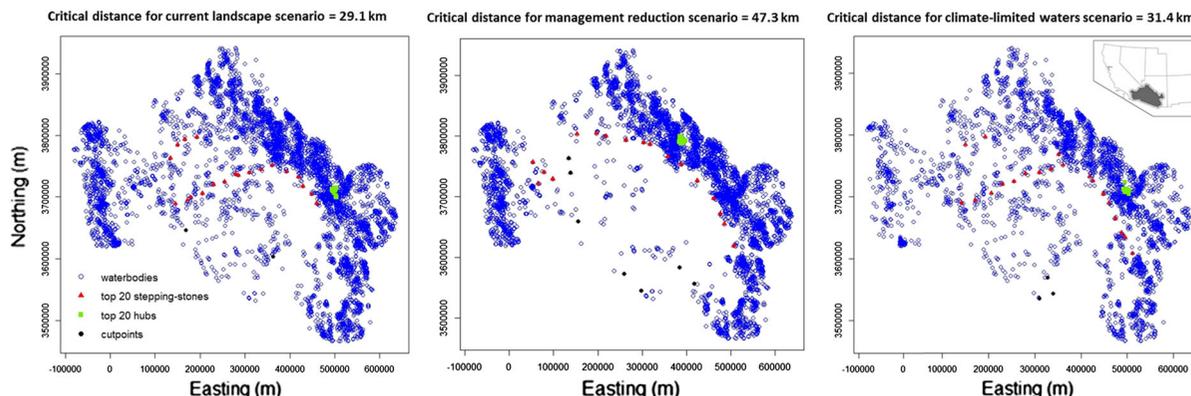


Fig. 1 Graphical representation of the Sonoran Desert waters that represent the top 20 stepping-stones and hubs, along with any waters that acted as cutpoints at the coalescence distance for the *current landscape* scenario ($n = 6214$; all currently known waters in the Sonoran Desert), the *management reduction* scenario ($n = 5378$; only the known natural waters in the Sonoran Desert), and the *climate-limited waters* scenario ($n = 3558$; only waters that are actively managed or identified as springs, representing waters more likely to persist in the

scenario ($\rho = 0.054$, $p < 0.001$), but no correlation was found between metric ranks in the *current landscape* and *climate-limited waters* scenarios ($\rho = 0.0025$, $p = 0.8$; $\rho = 0.025$, $p = 0.1$, respectively). The waters identified as cutpoints varied among scenarios (Online Appendix S5), and each scenario exhibited a different number of waters that acted as cutpoints; two waters were cutpoints in the *current landscape* scenario, seven in the *management reduction* scenario, and three in the *climate-limited waters* scenario.

Structural connectivity—node-level metrics

Coalescence of the system did not occur at any of the dispersal distances tested (up to 15 km) (Fig. S1), meaning that spatially disjunct clusters of waters were present at these finer scales (Fig. 2 shows a representative 5-km scenario). The *current landscape* scenario had the most clusters at the shortest dispersal distance (0.5 km), with clusters merging as dispersal distance increased (Table 3; Fig. S1). The highest (15 km) dispersal distance in this scenario thus exhibited the lowest fragmentation (0.6%; Fig. S1). The *current landscape* scenario had the longest diameter of all the scenarios as well as the largest MCS and largest range of MCS. Mean cluster sizes at lower dispersal distances were very

increased temperatures and decreased precipitation forecasted for the Sonoran Desert in the coming decades). The difference in water site densities between the *management reduction* scenario and the *climate-limited waters* scenario in the south-central portions of the Sonoran Desert provides evidence that artificial catchments are changing the network topology. Highly ranked stepping-stones and hubs are farther south currently because of catchment addition in this portion of the network

low across all scenarios, and network modularity was highest at these low dispersal distances. Overall, at any given dispersal distance, the *climate-limited waters* was the most fragmented based on the number of clusters, fragmentation percentage, MCS, and network modularity. Structural connectivity thus varied with dispersal distance for each of the scenarios, but was compromised more by climate change than by management, relative to current conditions.

Invasive species buffering

Using the clusters identified in the 10- and 15-km dispersal distances from the *current landscape* scenarios, we identified areas where new catchments should avoid being built to limit connectivity for bullfrogs. There were 128 isolated clusters at the 10-km dispersal distance and 37 clusters at 15-km. The total buffer area around these clusters was 115,344 km² for the 10-km dispersal distance and 122,607 km² for 15 km (Fig. 3). We also identified 41,823 and 67,745 km² of land within known clusters for 10 and 15 km scenarios, respectively, that could have new waters built without increasing inter-cluster connectivity (maintaining isolation between clusters) while increasing intra-cluster connectivity (increasing local connectivity).

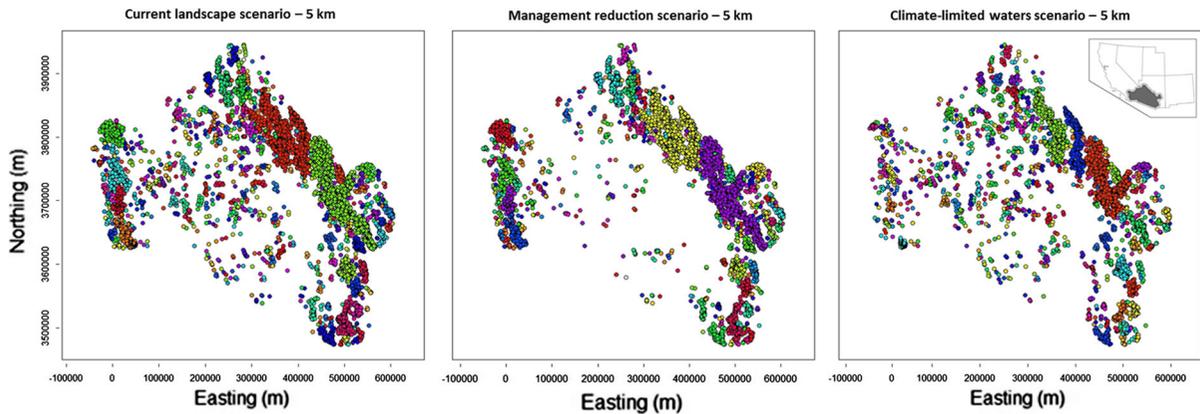


Fig. 2 Graphical representation of the connectivity of Sonoran Desert waters for species that can disperse at least 5 km under the *current landscape* scenario ($n = 6214$; all currently known waters in the Sonoran Desert), the *management reduction* scenario ($n = 5378$; only the known natural waters in the Sonoran Desert), and the *climate-limited waters* scenario ($n = 3558$; only waters that are actively managed or identified as springs, representing waters more likely to persist in the increased temperatures and decreased precipitation forecasted for the Sonoran Desert in the coming decades), showing the

connected waters in clusters that emerge at 5 km. The *colors* represent connected waters in any given cluster: connected waters within 5 km of each other are the *same color*. Colors are randomly chosen and may be used more than once, so multiple clusters may be represented with the *same color* but may not be connected. At the 5 km distance shown, there are 572 clusters in the *current landscape* scenario, 364 in the *management reduction* scenario, and 577 in the *climate-limited waters* scenario

Discussion

The installment of catchments in the Sonoran Desert has increased the structural connectivity of the waters network, evidenced by the lowest coalescence distance, highest average linkages among waters, and lowest graph density for the *current landscape* scenario. This has resulted in a topological shift in network connectivity towards the south, with many highly ranked stepping stones and hubs present in the south; the clusters of waters that ranked as the top 20 hubs shifted approximately 150 km to the northwest when catchments were excluded from the network to reflect natural conditions or a reduction in management (Fig. 1). For an animal to cross the landscape, it would have to be able to travel at least 29.1 km in the *current landscape* scenario, and even farther in the other scenarios (Table 2). Although the *management reduction* scenario had more waters than the *climate-limited* scenario, the *management reduction* scenario's coalescence distance, average number of links between waters, and the graph density were the lowest of all the scenarios. Adding artificial catchments to a water-limited area has thus increased the density and linkages between waters and decreased distances needed to travel among waters (Fig. 1). However,

the structural and possible ecological roles of natural water sources have possibly changed with the addition of artificial catchments. The most important waters in the desert—based on stepping stone, hub, and cutpoint measures—differed by scenario. For example, there was a weak correlation between being a hub and a stepping stone in the *management reduction* scenario, but none for either the *current landscape* or the *climate-limited waters* scenarios.

The *climate-limited waters* scenario illustrates the impact of a reduced water environment on connectivity in the Sonoran Desert. With increased temperatures and decreased precipitation, rain-dependent waters will occur less frequently and persist for shorter periods of time, meaning that overall connectivity will decline. Populations in isolated patches will be more likely to become extinct, and increased isolation will deter recolonization (Hanski 1998; Fagan 2002). For example, bighorn sheep (*Ovis canadensis*) and Sonoran Desert freshwater fishes have both been found to have increased risk of extinction based on increased isolation (Fagan et al. 2002; Epps et al. 2004); the bighorn's persistence in desert mountains was related to precipitation and the location of dependable water sources (Epps et al. 2004). Many species in the Sonoran Desert—like the bighorn—are also likely

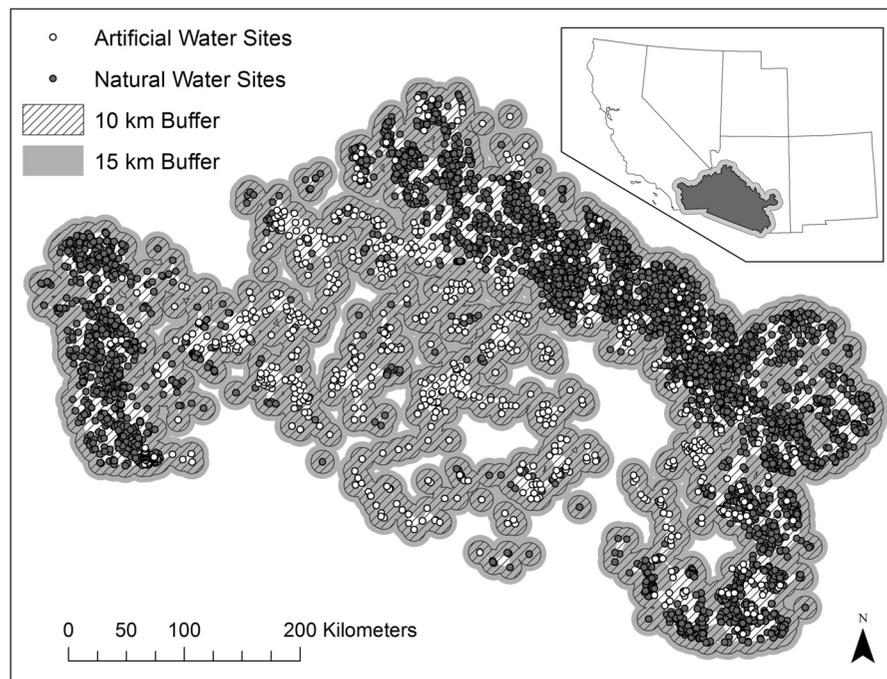


Fig. 3 A network of waters in the Sonoran Desert ($n = 6214$; all currently known waters in the Sonoran Desert), and the buffers identified from clusters formed at dispersal distances of 10 km (known American bullfrog, *Lithobates catesbeianus*, dispersal distance; Kahrs 2006) and at 15 km (a theoretically protective distance 150% farther than known bullfrog movement that isolates clusters of connected waters from each other).

These buffers have identified an area of 115,344 km² for the 10 km dispersal distance and an area of 122,607 km² for the 15 km dispersal distance. Protecting these buffered areas from further development could help prevent the spread of invasive species and accompanying zoonotic diseases to areas that would have been naturally isolated by distance

surviving at their physiological edge; further pressure from increased temperatures and reduced water availability could reduce population numbers and decrease the body condition of remaining individuals (Marshall et al. 2002, 2008; Bleich et al. 2010). Our results suggest that climatic-induced changes to the connectivity of this desert-waters network will challenge the ability of managers to provide reliable water for game animals and other at-risk species. Increasing the number of waters by adding catchments could reduce isolation among disparate groups (Bleich et al. 1990, 2010). Maintaining connectivity is thus important for native species, but the way this is achieved must be done with consideration to dispersal of invasive species as well.

Our study strikes a balanced approach to understanding both regional and local invasion and local and regional connectivity for native species through the use of graph metrics. Stepping-stones are known to help understand regional movement (Saura et al. 2014) for native species. This use of stepping-stone

exploration could easily be extended to invasive species. Here, we identify stepping-stones as nodes that have higher betweenness-centrality ranks relative to those nodes surrounding them. These nodes act as a backbone to the networks that contain the most-shortest paths between nodes in the graph. In our scenarios, these waters may provide ecological thruways for invasions.

Hubs, or those nodes highly connected to other nodes may also be more susceptible to invasion, especially if these nodes are closely linked to highly ranked stepping-stones in the network. Managers, by knowing which nodes are most likely to contribute to the graphs connectivity through stepping stones and hubs, can direct monitoring efforts, saving precious time and money for more effective responses to invasion. This may be critical to helping detect invasive species at early phases when they are more easily removed before permanent establishment. If these metrics are used in combination with a historical tracking of the invasion fronts, even more effective

and accurate directional predictions of ongoing invasions can be assessed (Ferrari and Lookingbill 2009; Ferrari et al. 2014). Often, however, this information is not readily available for a manager to make a timely decision for response especially in early states of local invasion. Understanding the structural connectivity of a landscape may give the necessary early stage information to have an edge in responding to invasive species.

The connectivity of the landscape depends in part on the vagility of the species in question: the farther an animal can travel, the more likely it is to access resources (D'Eon et al. 2002). Vagility is relative, however: what is short to one species may be large to another; what is relevant is whether a species' dispersal capacity is above or below the coalescence distance, which will dictate whether global or node-level connectivity metrics are appropriate. Species with very low-vagility (dispersal of 0.5 km or less) would only be able to access on average 1.2 waters or at most 18 waters in the *current landscape* scenario (Table 3). This does not change when artificial waters are removed. With reduced waters based on future conditions, however, average cluster size decreases to 1.1 waters, with a maximum of five waters in a cluster. This is a marked reduction of available habitat and is reflected in the difference in fragmentation across scenarios: 85.7% for *current landscape* scenario and 94.2% for *climate-limited waters* scenario at a 0.5 km dispersal distance.

Compare this to species with higher vagility (dispersal of 5 km), which can access an average of 10.9 waters in the *current landscape* scenario and 6.2 waters in the *climate-limited waters* scenario, and will thus experience much less landscape fragmentation with projected climate change impacts such as loss of resources on the landscape (Table 3). Species with the highest vagilities could access the majority of waters in any of the three scenarios. This is good and bad news for managers. Vagile native species have potential access to many different waters. The highly vagile and invasive bullfrog, however, would also have access to the majority of waters. Isolating waters (especially those with naturally longer hydroperiods, such as springs) from invasives may be necessary as the landscape changes.

Cutpoints in both local regional and local scales may be a way to isolate waters. Since cutpoints effectively subdivide the network and isolate the

resulting subgraphs, this maybe a way to look at preventing the spread of invasive species. This may be most effective on a local scale, however, as a network or dispersal ability grows larger, cutpoints may lose relevancy as connections between nodes emerge. However, iterative removal of nodes in a spatial graph has been used to examine dispersal sensitivity to the landscape structure (Urban et al. 2009), but also could be applied to better understanding invasive species ability to disperse in a network. Instead of this iterative random removal across a graph, managers could direct this exploration using graph theory and explicitly testing specific removals ability to isolate sensitive areas from habitat patches that are already at risk of or are already invaded. With little additional effort the manager would be able to explore the graph at both native species dispersal ability and the invasive species dispersal ability to determine how the removal of habitat patches on local connectivity. Conversely, if a manager was inclined to try and increase connectivity in a system, they could add nodes to the graph and explore how this action changes overall graph metrics. For example, if a manager wanted to understand how a new artificial catchment may contribute to local connectivity for a mule deer while understanding how it may increase local waters susceptibility to invasion by American bullfrogs, they could explore hypothetical catchment placements in graph space before breaking ground in real life (Drake et al. 2017).

We demonstrated a method by which managers can identify and barricade avenues of dispersal for harmful invasive species by using graph theory. A few papers have alluded to the possible value of graph theory for understanding and managing invasive species (Etherington 2012; Bishop-Taylor et al. 2015; Perry et al. 2016). However, there are no studies, to our knowledge, that have created reproducible scripts to be used as tools to assist management methods. The nearest approaches used graph theory to describe connectivity for pests and diseases of various crops in the U.S. (Ferrari and Lookingbill 2009; Margosian et al. 2009).

It should be pointed out that our maps are best viewed as hypotheses to be tested, and that testing them will require empirical data to evaluate how well they actually describe connectivity. Such empirical data could include movement data obtained from marked individuals, or genetic data to evaluate successful dispersal at a population level. And as mentioned in the Methods: Data section, obtaining

such data could allow more detailed and realistic connectivity models to be built. Our use of graph theory may thus be considered a rapid-response approach to identifying the likely maximum potential invasive species risk for an area.

The increasingly complex nature of resource management in the Sonoran Desert means that understanding the implications of management decisions is more important than ever. Catchments may become more necessary to address climate change-driven water scarcity, but their use must be informed to prevent further damage to native ecosystems. To help prevent the spread of invasive species, we illustrate how managers can use structural connectivity data to identify important waters in the network. Our method gives managers a tool to address complicated and sometimes conflicting management goals, which can be used to identify those waters that are important to connectivity for different scenarios and species with different dispersal capabilities, but also to identify areas that may need protection from increased connectivity because of the repercussion of invasive species spread and determine groups of potentially connected resource patches that might be at risk. For example, managers could use a given dispersal distance to identify all the patches in a network that are close enough to a known “infected” patch and then remove cutpoints to limit access of invasive species to the rest of the network, creating buffered areas to isolate healthy habitat for native species. Similarly, they could identify areas where increasing connectivity by adding artificial catchments could be done to enhance resource availability for native species with little risk of facilitating spread of invasive species.

Such an approach could be a useful framework for managers in any patchy ecological network, not just the waters of the Sonoran Desert. Graph theory—which has had an important impact on understanding structural connectivity for local species—could and should be used to help understand the growing problem of invasive species the world over. Graph theory could be used solely for understanding structural connectivity dynamics of an invaded system, but as we have demonstrated, it can also be used to guide management decisions on the mitigation, removal, and monitoring of invasive species.

Acknowledgements Funding was provided by the Desert Landscape Conservation Cooperative through the Bureau of

Reclamation Water SMART program (U.S. Department of the Interior) (Grant No. (FOA) R13AS80009). Several people provided key information, including Jeri Ledbetter and Larry Stevens at the Springs Stewardship Institute; Louise Misztal at the Sky Island Alliance; James Cain III at NMSU; John Arnett and Chris Black at the 56th Range Office of Luke Air Force Base; and Jami Kuzek and Michael Sredl at the Arizona Game and Fish Department. Comments from Jeff Jenness and two anonymous reviewers greatly improved the manuscript.

References

- Adams M (2000) Pond permanence and the effects of exotic vertebrates on anurans. *Ecol Appl* 10:559–568
- AZGFD (2015) Habitat enhancement and wildlife management proposal: Antelope Hills water catchment construction. Arizona Game and Fish Department, Prescott. http://www.azgfd.gov/w_c/documents/15-310AntelopeHillsHPCProposal2015.pdf
- Benard MF, McCauley SJ (2008) Integrating across life-history stages: consequences of natal habitat effects on dispersal. *Am Nat* 171(5):553–567
- Bishop-Taylor R, Tulbure MG, Broich M (2015) Surface water network structure, landscape resistance to movement and flooding vital for maintaining ecological connectivity across Australia’s largest river basin. *Landscape Ecol* 30:2045–2065
- Bleich VC, Marshal JP, Andrew NG (2010) Habitat use by a desert ungulate: predicting effects of water availability on mountain sheep. *J Arid Environ* 74:638–645
- Bleich VC, Wehausen JD, Holl SA (1990) Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. *Conserv Biol* 4:383–390
- Bloom F (2003) Wildlife water development team report 2002. Arizona Game and Fish Department, Phoenix. http://www.azgfd.gov/pdfs/outdoor_recreation/nrm/WDT%20Final%20Report%207.15.03.pdf. Accessed 17 Nov 2016
- Calabrese JM, Fagan WF (2004) A comparison-shopper’s guide to connectivity metrics. *Front Ecol Environ* 2:529–536
- Cromie RL, Lee R, Delahay RDJ, Newth JL, O’Brien MF, Fairlamb HA, Reeves JP, Stroud DA (2012) Ramsar wetland disease manual: guidelines for assessment, monitoring and management of animal disease in wetlands. Ramsar Technical Report No. 7. Ramsar Convention Secretariat, Gland, Switzerland
- Csardi CN, Nepusz T (2006) The igraph software package for complex network research. *Interjournal Complex Syst* 1695:1–9
- 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
- Drake JC, Griffis-Kyle K, McIntyre NE (2017) Nesting connectivity models to resolve management conflicts of isolated water networks in the Sonoran Desert. *Ecosphere* 8(1):e01647. doi:10.1002/ecs2.1652
- Epps CW, McCullough DR, Wehausen JD, Bleich VC, Rechel JL (2004) Effects of climate change on population persistence of desert-dwelling mountain sheep in California. *Conserv Biol* 18:102–113

- Etherington TR (2012) Mapping organism spread potential by integrating dispersal and transportation processes using graph theory and catchment areas. *Int J Geogr Info Sci* 26:541–556
- Ewert M (1969) Seasonal movements of the toads *Bufo americanus* and *B. cognatus* in northwestern Minnesota. Dissertation, University of Minnesota, Minneapolis
- Fagan WF (2002) Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* 83:3243–3249
- Fagan WF, Unmack PJ, Burgess C, Minckley WL (2002) Rarity, fragmentation, and extinction risk in desert fishes. *Ecology* 83:3250–3256
- Ferrari JR, Lookingbill TR (2009) Initial conditions and their effect on invasion velocity across heterogeneous landscapes. *Biol Invasions* 11(6):1247–1258
- Ferrari JR, Preisser EL, Fitzpatrick MC (2014) Modeling the spread of invasive species using dynamic network models. *Biol Invasions* 16(4):949–960
- Fletcher RJ, Acevedo MA, Reichert BE, Pias KE, Kitchens WM (2011) Social network models predict movement and connectivity in ecological landscapes. *Proc Natl Acad Sci* 108:19282–19287
- Galpern P (2012) Modelling landscape connectivity for highly-mobile terrestrial animals: a continuous and scalable approach. Dissertation, University of Manitoba, Winnipeg
- Garner TWJ, Garner TW, Perkins MW, Govindarajulu P, Seglie D, Walker S, Cunningham AA, Fisher MC (2006) The emerging amphibian pathogen *Batrachochytrium dendrobatidis* globally infects introduced populations of the North American bullfrog, *Rana catesbeiana*. *Biol Lett* 2:455–459
- Giovanelli JGR, Haddad CFB, Alexandrino J (2008) Predicting the potential distribution of the alien invasive American bullfrog (*Lithobates catesbeianus*) in Brazil. *Biol Invasion* 10:585–590
- Griffis-Kyle KL, Kovatch JJ, Bradatan C (2014) Water quality: a hidden danger in anthropogenic desert catchments. *Wildl Soc Bull* 38:148–151
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49
- Hendrickson D, Minckley W (1985) Cienegas: vanishing climax communities of the American Southwest. *Desert Plants* 6:130–176
- IPCC (2014) North America. In: Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach KJ, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL (eds) *Climate change 2014: impacts, adaptation, and vulnerability, part B: regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p 688
- Kahrs D (2006) American bullfrog eradication in Sycamore Canyon, Arizona, a natural open aquatic system. *Sonoran Herpetol* 19:74–77
- Karl T, Melillo J, Peterson T (eds) (2009) *Global climate change impacts in the United States*. Cambridge University Press, Cambridge. <https://nca2009.globalchange.gov/>. Accessed 17 Nov 2016
- Keitt T, Urban D, Milne B (1997) Detecting critical scales in fragmented landscapes. *Conserv Ecol* 1(1):4
- Koen EL, Koen EL, Garroway CJ, Wilson PJ, Bowman J (2010) The effect of map boundary on estimates of landscape resistance to animal movement. *PLoS ONE* 5(7):e11785
- Landreth H, Christensen M (1971) Orientation of the plains spadefoot toad, *Scaphiopus bombifrons*, to solar cues. *Herpetologica* 27:454–461
- Letnic M, Webb JK, Jessop TS, Florance D, Dempster T (2014) Artificial water points facilitate the spread of an invasive vertebrate in arid Australia. *J Appl Ecol* 51:795–803
- Longshore KM, Lowery C, Thompson DB (2009) Compensating for diminishing natural water: predicting the impacts of water development on summer habitat of desert bighorn sheep. *J Arid Environ* 73:280–286
- Lookingbill T, Gardner RH, Ferrari JR, Keller CE (2010) Combining a dispersal model with network theory to assess habitat connectivity. *Ecol Appl* 20:427–441
- Maret TJ, Snyder JD, Collins JP (2006) Altered drying regime controls distribution of endangered salamanders and introduced predators. *Biol Conserv* 12:129–138
- Margosian ML, Garrett KA, Hutchinson JM (2009) Connectivity of the American agricultural landscape: assessing the national risk of crop pest and disease spread. *BioScience* 59:141–151
- Marshal JP, Krausman PR, Bleich VC (2008) Body condition of mule deer in the Sonoran Desert is related to rainfall. *Southwest Nat* 53:311–318
- Marshal JP, Krausman PR, Bleich VC, Ballard WB, McKeever JS (2002) Rainfall, El Niño, and dynamics of mule deer in the Sonoran Desert, California. *J Wildl Manage* 66:1283–1289
- McIntyre NE, Drake JC, Griffis-Kyle KL (2016) A connectivity and wildlife management conflict in isolated desert waters. *J Wildl Manage* 80:655–666
- 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 RA (1988) Adaptive plasticity in development of *Scaphiopus couchii* tadpoles in desert ponds. *Evolution* 42:774–783
- Newman M, Girvan M (2004) Finding and evaluating community structure in networks. *Phys Rev E* 69:1–16
- Perry GLW, Moloney KA, Etherington TR (2016) Using network connectivity to prioritise sites for the control of invasive species. *J Appl Ecol*. doi:10.1111/1365-2664.12827
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econ* 52:273–288
- R Core Team (2015) R: a language and environment for statistical computing. <http://www.r-project.org/>. Accessed 17 Nov 2016
- Román J (2014) Artificial water points for wildlife management facilitate the spread of red swamp crayfish (*Procambarus clarkii*). *Manage Biol Invasion* 5:341–348
- Rosen PC, Schwalbe C (1994) Introduced aquatic vertebrates in the Chiricahua region: effects of declining native ranid frogs. *RM-GTR-264: biodiversity and management of the*

- Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico, pp 251–261
- Rosenstock SS, Ballard WB, Devos JC (1999) Viewpoint: benefits and impacts of water developments. *J Range Manage* 52:302–311
- Ruiz L, Parikh N, Heintzman LJ, Collins SD, Starr SM, Wright CK, Henebry GM, van Gestel N, McIntyre NE (2014) Dynamic connectivity of temporary wetlands in the southern Great Plains. *Landscape Ecol* 29:507–516
- Saura S, Bodin Ö, Fortin M-J (2014) Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *J Appl Ecol* 51:171–182
- Schlaepfer MA, Sredl MJ, Rosen PC, Ryan MJ (2007) High prevalence of *Batrachochytrium dendrobatidis* in wild populations of Lowland Leopard Frogs *Rana yavapaiensis* in Arizona. *EcoHealth* 4:421–427
- Schwalbe C, Rosen PC (1988) Preliminary report on effect of bullfrogs on wetland herpetofaunas in southeastern Arizona. RM-GTR-166. In: Proceedings of the symposium of management of amphibians, reptiles, and small mammals in North America, pp 166–173
- Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang HP, Harnik N, Leetmaa A, Lau NC, Li C (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316:1181–1184
- Smith MA, Green DM (2005) Dispersal and the metapopulation paradigm in amphibian ecology: are all amphibian conservation populations metapopulations? *Ecography* 28:110–128
- Souza V, Espinosa-Asuar L, Escalante AE, Eguiarte LE, Farmer J, Forney L, Lloret L, Rodríguez-Martínez JM, Soberón X, Dirzo R, Elser JJ (2006) An endangered oasis of aquatic microbial biodiversity in the Chihuahuan desert. *Proc Natl Acad Sci USA* 103:6565–6570
- Sredl M, Jennings R (2005) *Rana chiricahuensis*: Platz and Mecham, 1979, Chiricahua leopard frogs. In: Lannoo M (ed) Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, pp 546–549
- Stevens LE, Meretsky VJ (2008) Spring ecosystem ecology and conservation. In: Stevens LE, Meretsky VJ (eds) Aridland springs in North America. University of Arizona Press, Tucson, pp 3–10
- Strittholt JR, Bryce SA, Ward BC, Bachelet DM (2012). Sonoran Desert rapid ecoregional assessment report, Denver. http://www.blm.gov/wo/st/en/prog/more/Landscape_Approach/reas/sonoran.html#memo. Accessed 17 Nov 2016
- Sullivan BK (2005) Southwestern desert bufonids. In: Lannoo M (ed) Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, pp 237–243
- Tellman B (2002) Human introduction of exotic species in the Sonoran region. In: Tellman B (ed) Invasive exotic species in the Sonoran region. University of Arizona Press, Tucson, pp 25–46
- Tischendorf L, Fahrig L (2000a) How should we measure landscape connectivity? *Landscape Ecol* 15:633–641
- Tischendorf L, Fahrig L (2000b) On the usage and measurement of landscape connectivity. *Oikos* 90:7–19
- Urban D, Keitt T (2001) Landscape connectivity: a graph-theoretic perspective. *Ecology* 82:1205–1218
- Urban D, Minor E, Treml E, Schick R (2009) Graph models of habitat mosaics. *Ecol Letters* 12:260–273
- Weintraub J (1974) Movement patterns of the red-spotted toad, *Bufo punctatus*. *Herpetologica* 30:212–215
- With KA (2002) The landscape ecology of invasive spread. *Conserv Biol* 16:1192–1203
- With KA (2004) Assessing the risk of invasive spread in fragmented landscapes. *Risk Anal* 24:803–815
- Wright JT (1959) Desert wildlife. Wildlife Bulletin No. 6, Arizona Game and Fish Department, Phoenix