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Using nested connectivity models to resolve management conflicts of isolated water networks in the Sonoran Desert

JOSEPH C. DRAKE,[1,3] KERRY GRIFFIS-KYLE,[1,]† AND NANCY E. MCINTYRE[2]

[1]*Department of Natural Resources Management, Texas Tech University, Lubbock, Texas 79409 USA*
[2]*Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409 USA*

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Abstract. Connectivity is essential to organisms for dispersal, mate finding, and resource access. Management conflicts may arise if the attempts to maintain connectivity in the face of habitat loss result in opening up dispersal corridors to invasive species and disease vectors to already-threatened native species. Using the mule deer (*Odocoileus hemionus*) and American bullfrog (*Lithobates catesbeianus*) as examples in a network of surface waters in the Sonoran Desert, we illustrate and propose a resolution to these conflicts. We used structural and functional metrics from graph and circuit theory to quantify landscape connectivity within a spatially nested framework under current and future climate-based scenarios at regional and local scales to project structural and functional climate impacts for both species. Results indicated that climate impacts may reduce both structural and functional potential connectivity for each species. Mule deer, however, will be impacted to a lesser degree, and the proposed management mitigation of exclusion areas will have a potential lesser impact on this species. From our results, we propose a method to create exclusion areas and site new waters to help mitigate increasing spread of invasive species like the bullfrog while maintaining resource availability and local connectivity for economically important species like the mule deer. The isolation of local clusters from invasive species may be a successful and useful way to reduce management conflicts in the Sonoran Desert isolated waters network and beyond.

Key words: catchments; circuit theory; climate change impacts; functional connectivity; graph theory; least-cost paths; network theory; springs; structural connectivity; tinajas.

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[3] Present address: Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts 01003 USA.

† **E-mail:** kerry.griffis-kyle@ttu.edu

INTRODUCTION

Connectivity (the interplay between structural topology and functional responses of organisms to structural features) is an essential characteristic of landscapes (Taylor et al. 1993). It facilitates the movement of species among habitat patches for many ecological processes including reproduction, resource access, migration, predator avoidance, and dispersal (Crooks and Sanjayan 2006). Anthropogenic changes to the environment, including habitat fragmentation, habitat loss, and climate change, are altering landscape connectivity. Natural resource managers are increasingly being forced to contend with this issue. For example, much of the regional biodiversity in the Sonoran Desert of North America depends on a network of isolated waters (Souza et al. 2006, Stevens and Meretsky 2008). The Sonoran Desert is expected to become hotter and drier in the coming decades in response to climate change (Seager et al. 2007, IPCC 2014). These changes will cause a decrease in water availability in space and time, leading to changes in landscape connectivity.

One of the main wildlife management tools to mitigate compromised connectivity among waters in desert regions is to augment naturally occurring waters with artificial catchments. Almost 6000 artificial catchments have been built in 11 western states, with over 800 in the Sonoran Desert states (Rosenstock et al. 1999, 2004, Grant et al. 2013). Although costly to install and maintain ($755,000 annually in Arizona alone; Rosenstock et al. 1999), adding waters will likely continue to be used as management option, as there is some evidence it can increase populations of economically important game species like mule deer (*Odocoileus hemionus*; Leslie and Douglas 1979, Hervert and Krausman 1986, Krausman et al. 2006), a species found to be heavily dependent on these anthropogenic catchments (Calvert 2015).

However, such management decisions that change resource availability can also impact connectivity in negative ways. For example, increasing landscape connectivity in general can facilitate the spread of disease among populations (Hess 1994, Cully et al. 2010), contribute to the spread of fire (Brudvig et al. 2012), increase predator activity and decrease reproductive success (Weldon 2006), decrease native biodiversity (Resasco et al. 2014), and increase the rate of dispersal and survival of invasive species (Simberloff and Cox 1987, Puth and Allen 2005, Crooks and Suarez 2006, Resasco et al. 2014). In the isolated waters network of the Sonoran Desert, enhancing connectivity for mule deer may have unintended consequences. American bullfrogs (*Lithobates catesbeianus*) are an invasive species to the Sonoran Desert that can use artificial catchments to reproduce and disperse (Kahrs 2006). They can travel upward of 10 km (Kahrs 2006), much farther than known dispersal distances for native Sonoran Desert amphibians. Hence, the addition of artificial catchments may provide the bullfrog paths to disperse into areas that had formerly been inaccessible. Indeed, bullfrogs have been directly linked to the decline of Sonoran Desert species such as the Chiricahua leopard frog (*Lithobates chiricahuensis*), the Yavapai leopard frog (*Lithobates yavapaiensis*), the Mexican garter snake (*Thamnophis eques*), and possibly the Sonoran mud turtle (*Kinosternon sonoriense*; Schwalbe and Rosen 1988). Furthermore, the bullfrog is an unaffected carrier of *Bactrachochytrium dendrobatidis* (Daszak et al. 2004, Garner et al. 2006) and may be the vector that infected native Arizona frogs with this devastating pathogen (Bradley et al. 2002, Schlaepfer et al. 2007). Additions of suitable habitat for invasives can thus lead to a management conflict where an increase in connectivity is good for some species, but detrimental for others. Managers may be pressured to increase water availability for game species as conditions in the Sonoran Desert become harsher with projected climate change, but doing so by adding artificial catchments increases the density of waters and therefore enhances the connectivity of the isolated waters network (McIntyre et al. 2016). There is thus a clear need to be able to manage connectivity in such a way as to enhance connectivity for at-risk species while simultaneously curtailing spread of invasive species through the same habitat network.

Several methods have been used to describe connectivity, including graph theory (Lookingbill et al. 2010) and resistance methods (Penrod et al. 2008, Sawyer et al. 2011, St-Louis et al. 2014, Bishop-Taylor et al. 2015). Graph theory has commonly been used to quantify structural connectivity, the physical connections of the landscape, whereas resistance methods describe functional connectivity, how an animal perceives connectivity of the landscape. Each method has limitations and advantages, and using them together can compensate for individual deficiencies.

Graph theory has been used in conservation and metapopulation studies (Bunn et al. 2000, Urban and Keitt 2001, Bishop-Taylor et al. 2015). In this approach, habitat patches (such as isolated waters of the Sonoran Desert) can be prioritized on how they contribute to overall connectivity through the network via various metrics (Table 1). The whole network can be addressed when it is completely connected—the coalescence distance —or at shorter distances based on species' dispersal capabilities, which can connect small clusters of wetlands. These clusters are subgraphs, which are a set of waters nested inside the larger graph (network). These clusters can be important conservation elements showing connected patches to protect from invasive species (Drake 2016). We therefore adopted a nested approach to examining connectivity through the isolated waters of the Sonoran Desert, by identifying such clusters and examining them in isolation as well as within the context of the entire network.

Determining at what distance the network coalesces into a single cluster, given the current

Table 1. Important metrics for evaluating connectivity of a landscape and other graph-related terms (adapted from Urban and Keitt 2001, Clauset et al. 2004, Proulx et al. 2005).

Metric	Ecologically relevant definition
Network	Isolated waters of the Sonoran Desert
Node	Isolated water
Link/Edge	Actual or potential dispersal route between wetlands
Stepping stones	Wetlands that facilitate connectivity through the landscape
Cutpoints	Wetlands whose loss results in a disproportionately high degree of network fragmentation
Hubs	Wetlands that are connected to many other wetlands
Coalescence	When the entire landscape can be crossed by an animal moving from wetland to wetland (i.e., wetlands are within the animal's dispersal capacity)
Diameter	The shortest path across the entire network
Modularity	The number of paths between grouped wetlands within and between them; when modularity is high, there are many edges within groups and only a few between them

number and placement of waters, is useful information for managers seeking to determine whether a species of conservation concern would be able to freely disperse through the network. For example, if the coalescence distance is 20 km, an animal would need to disperse at least 20 km to traverse the network, moving from habitat patch (i.e., water) to habitat patch; if that distance is beyond the species' known maximum dispersal capacity, then that species is effectively isolated within clusters of waters that are closer together. This information can then be used to add artificial catchments that would decrease the distance an animal would have to move to traverse the network, or quarantine clusters by not siting catchments near them that could act as stepping stones facilitating spread throughout the network (Table 1).

Estimations of structural connectivity (as in graph theory) often overestimate actual connectivity between habitat patches because they are based on Euclidean distances because the landscape can influence the ability to move or disperse (Pittman et al. 2014, Bishop-Taylor et al. 2015). Although volant species may be assumed to travel more directly than overland dispersers like amphibians or mule deer, the easiest or least costly way for terrestrial dispersers to travel between two habitat patches may not be a straight line. Instead, it may be a circuitous path that is influenced by land cover, disturbance, slope, and other environmental parameters. This functional connectivity is often represented by resistance surfaces—raster grids with assigned values reflecting the cost/resistance to the movement of an organism (Adriaensen et al. 2003, Theobald 2006). Functional connectivity has commonly been assessed using least-cost paths. This method identifies the path of least resistance between two points in the landscape (Theobald 2006). This method has strict limitations, however, identifying a single-cell wide path that some species may not be able to use given the landscape context (Adriaensen et al. 2003). An alternative method using circuit theory was developed to produce multiple alternative paths among habitat patches (McRae et al. 2014). Circuit theory has comparable calculations to random-walk methods, allowing all possible paths to contribute to connectivity (McRae 2006, Cushman et al. 2013), and has been suggested as good method for determining regional connectivity (McRae et al. 2008). Circuit theory-based resistance mapping can complement the least-cost path and Euclidean distance mapping of connectivity (McRae et al. 2008). Using resistance layers to gauge how the landscape influences animal movement provides a more realistic representation of landscape connectivity for a given species (Adriaensen et al. 2003, McRae 2006). Comparing straight-line connectivity (as the most direct assessment of connectivity) with resistance-based assessments allows for the most thorough description of connectivity; furthermore, consensus between methods provides strong evidence for which portions of the landscape are the most influential. Finally, a graph theory-based assessment of connectivity allows for identification of individual waters that play crucial roles in connectivity (as stepping stones, hubs, or cutpoints; Table 1), something that resistance-based assessments do not. Since management actions focus on individual waters (by adding or removing artificial catchments) rather than on landscapes, including a

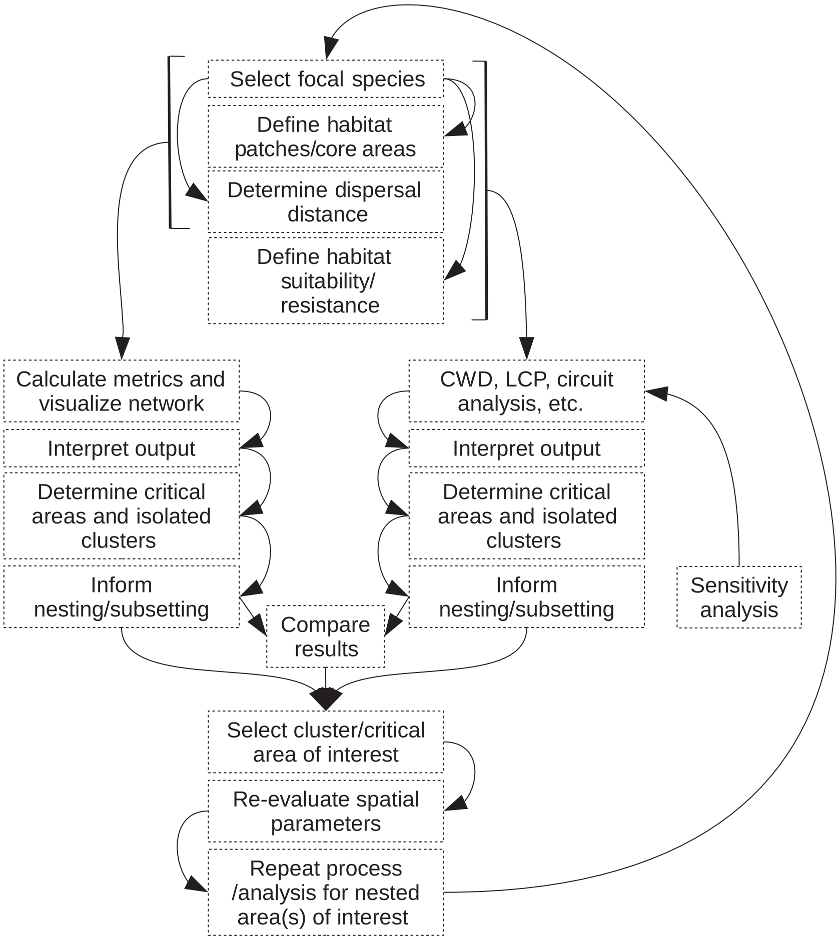


Fig. 1. Flowchart diagramming our connectivity modeling process.

graphical assessment provides additional information that can inform management actions.

Using graph theory in conjunction with circuit theory, we developed a spatially nested analysis that can be used to identify ways to solve management conflicts between connectivity of habitat resources and isolation from invasive species and disease. Spatially nesting the study area by focusing in on specific subsections of the landscape for reanalysis provides more detailed results that may be washed out in the larger extent of the regional analysis. We used graph theory and a combination of resistance-based connectivity models (least-cost path and circuit theory) to (1) quantify and compare structural and functional connectivity in the isolated waters of the Sonoran Desert; (2) show how nesting resistance surface-based analyses can help identify areas most important to connectivity and isolation; (3) describe how the connectivity among Sonoran Desert waters will change under future climate conditions; and (4) examine how these results may be useful in mitigating existing management conflicts. We present a flowchart of this process for clarity (Fig. 1). Although there have been some other comparisons of structural and functional connectivity in other ecosystems on other species (e.g., Susanne et al. 2010, Bishop-Taylor et al. 2015), ours is the first assessment for the isolated waters of the Sonoran Desert, comparing graphical and resistance assessments, for both current and projected future climate conditions.

METHODS

Study area

The United States' portion of the Sonoran Desert is a 140,000-km^2 arid landscape that receives approximately 7.5–38 cm of patchily distributed rainfall annually (Phillips and Comus 2000, Strittholt et al. 2012). To minimize boundary effects within spatial calculations (Koen et al. 2010), we added a 32.2-km buffer around the Sonoran Desert in ArcGIS 10.2.2 (ESRI, Redlands, California, USA) to include waters and raster resistance surfaces immediately outside of the Sonoran Desert boundaries. This buffer distance was twice the maximum dispersal distance of any native amphibian in the region (Drake 2016).

Common Sonoran Desert isolated waters include anthropogenically constructed artificial catchments as well as several types of natural waters (springs, rock pools formed by erosion known as tinajas, and shallow depressions known as charcos). These waters ranged in storage capacity from as little as 5 L to over half a million liters (Drake et al. 2015). The artificial catchments had concrete, steel, or fiberglass tanks and concrete troughs.

We gathered and compiled datasets—some publically available, some by special request of data owner—of the locations of these isolated waters from the Spring Stewardship Institute (Flagstaff, Arizona, USA), Sky Island Alliance (Tucson, Arizona), Arizona Game and Fish Department (AZGFD), Bureau of Land Management (Strittholt et al. 2012), 56th Range Office (Luke Air Force Base, Arizona), and scientists familiar with the area (Appendix S1). There were sometimes duplicate entries of waters between datasets. After merging datasets into a single shapefile, duplicated waters were screened for using two methods. The first method used 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 satellite imagery, and if the water were duplicated, the water with the largest spatial error was removed. We made an effort to include all known isolated waters in the study area, but new isolated waters are still being found on the landscape (Drake et al. 2015). Because many desert waters are naturally ephemeral, our data layer represents a static layer that, if all waters in it were wet simultaneously, would represent a best-case scenario. We therefore also created more realistic scenarios by culling waters from this layer (see *Climate scenarios* section).

Focal species

The mule deer occurs across much of the Sonoran Desert and is dependent on surface water for survival (Calvert 2015). This species is of interest to the public, game managers, and sportsmen and is considered economically and recreationally important to Arizona. Daily movements to water range from 2 to 14 km, but most are below 5 km (Ordway and Krausman 1986, Truett 1987, Rautenstrauch and Krausman 1989).

The American bullfrog is a wetland-dependent invasive species to the Sonoran Desert that was originally introduced to Arizona for sport and forage (Tellman 2002). This generalist predator is very vagile and it has been known to travel 10 km across arid landscapes, although most movements are closer to 3–5 km, and average daily movements are unknown but likely even shorter (Ingram and Raney 1943, Rosen and Schwalbe 1994, Schwalbe and Rosen 1999, Kahrs 2006, Snow and Witmer 2010). Knowing how to avoid placing new dispersal corridors for this harmful invasive species is important ecologically, and there are legal obligations to prevent harm to threatened and endangered species.

Creating exclusion areas to limit invasive species dispersal

We used R v3.1.3 (R Core Team 2015) and the package *igraph* (Csardi and Nepusz 2006) to calculate structural connectivity metrics for the isolated waters of our study area (see Drake 2016 for methods and reproducible script). We identified clusters of wetlands within 15 km (150% of the longest known travel distance of the American bullfrog; Kahrs 2006) to be relatively well assured of identifying clusters that are isolated from bullfrog invasion. Although using a 15-km distance would make the landscape more connected than would a smaller quarantine distance, this distance was much lower than the coalescence distance (see *Results*). Using ArcGIS, these clusters were converted to polygons using the aggregate points method and buffered using an outside-only condition. This product was merged with a 15-km buffer of single water clusters (Appendix S3: Fig. S1). The final shapefile consisted of a series of spatially referenced polygons that showed areas of the landscape where artificial waters should not be placed—exclusion areas—to prevent new dispersal corridors for the American bullfrog in the Sonoran Desert (Appendix S3: Fig. S2). Intersecting the areas outside the exclusion area buffers and inside the home range/distribution mule deer polygons from the BLM (Strittholt et al. 2012) identified areas for the development of artificial catchments—catchment placement areas (Appendix S3: Fig. S3; for methodological details, see Drake 2016).

Landscape resistance values

To determine the cost of traveling across the landscape, we used up to five different variables to identify costs for different aspects of the landscape that could influence resistance of the landscape to animal movement. These included land use/land cover, elevation, slope, topographic position index, and road density. Land use/land cover data were collected from the National Hydrography Dataset (Smiley and Carswell 2009), National Land Cover Dataset (Jin et al. 2013), USGS EROS Center (Sohl et al. 2014), the BLM's Rapid Ecological Assessment of the Sonoran Desert (Strittholt et al. 2012), and the 56th Range Management Office of Luke Air Force Base (Appendix S1). Several of these layers needed to be converted into a format to be more easily interpreted and biologically relevant as resistance values; out of the original datasets were derived the following environmental data layers for the buffered Sonoran Desert ecoregion:

1. Current land use/land cover: Derived from the National Land Cover Dataset (Jin et al. 2013), this represents land cover (e.g., highly developed, agricultural) and vegetation classes that represent habitat characteristics.
2. Future land use/land cover in climate projection scenarios: Derived from the FORE-SCE land use/land cover projections for the year 2050 under the emissions scenario A1B (Sohl et al. 2014), this represents habitat characteristics projected into the future. The A1B scenario represents a likely future with an increase in energy consumption in both fossil fuels and other energy sources. It also includes rapid economic and population growth by the middle of the 21st century. This climate projection serves as moderate climate scenario among the 2000 Special Report on Emission Scenarios and is considered similar to the 2010 Representative Concentration Pathways scenario 6.0 (Melillo et al. 2014).
3. Elevation: Digital elevation models (DEMs) from the National Elevation Dataset (Gesch et al. 2002, Gesch 2007) stitched together to encompass the entire study area.
4. Slope: This layer was derived from elevation data layer using the slope calculator in ArcMap 10.2.2 (Esri, Redlands, California, USA).
5. Topographic Position Index: This layer was derived from slope and elevation data with the Corridor Design Toolbox (Majka et al. 2007) for ArcMap. Topographic position relates the relative position in the landscape of a specific point (Weiss 2001). Four classes (canyon bottoms, slopes, ridgetops, and flats) were calculated by the Corridor Design Toolbox, which was set based on the predesignated values set for Arizona in the toolbox (Majka et al. 2007) and was verified by comparing to aerial imagery, DEM layers, and author's personal knowledge of the study area.
6. Road density: Road density (kilometers of road per square kilometer) was calculated from the TIGER/Line 2010 Census (U.S.C.B. 2010) and is a known wildlife dispersal barrier (Forman et al. 2002, Shepard et al. 2008).

Based on these data, each grid cell for each layer was assigned a resistance value ranging from 0 to 10, following the protocol in Churko (2016). Resistance values reflect the interpreted cost of traveling through the landscape and can be used to assess how a theoretical individual from the target species would react to the specific landscape factor it was experiencing. Landscape features that represent low resistance to the target species were assigned low values and vice versa. The raster calculator tool in ArcMap 10.2.2 was used to weight resistance values based on all data layers to create a single resistance map for each species. We assigned species-specific resistance using reported values and data when available (Beier et al. 2008) and used expert opinion when there was a lack of quantitative data (Theobald 2006, Spear et al. 2010, Theobald et al. 2012, Zeller et al. 2012). Resistances were assigned for two time periods: current conditions, using the most recent National Land Cover Dataset (Jin et al. 2013), and a potential future scenario based on USGS land cover projections for the year 2050 under emissions scenario A1B (Sohl et al. 2014; see also the *Climate scenarios* section).

We assigned resistances to each of the categories in the environmental data layers listed above (Appendix S2A and S3B), using both published data and expert opinion. Combining multiple sources of information to assign resistance values is one way to supplement a paucity of published data and may be a way of strengthening the inferences drawn (Zeller et al. 2012), particularly since data-informed and expert opinion-informed models appear to biased in opposite directions (Stevenson-Holt et al. 2014). Because some of our environmental data layers were categorical (current or future projected land use/land cover, topographic position), whereas others were continuous (elevation, slope, road density), we converted the continuous data into non-overlapping categories so as to be able to assign discrete resistance values to them. For elevation and slope, 10 equally divided categories were created; for road density, eight categories were used because of the smaller data range following the examples of Penrod et al. (2008) and Beier et al. (2008). Some land use/land cover designations were the same between the current and future scenarios. Some, however, were different; because of the modeling process for the FORE-SCE land cover dataset, the multiple developed land use categories of the National Land Cover Database (NLCD) were collapsed to a single "developed" land cover type. For more discussion of resistance assignment parameters in the context of land use/land cover, see Appendix S2.

Assigning resistance values to different land use/land cover types, elevations, slopes, or topographic positions is one of the primary weaknesses in functional connectivity analyses, as it is subject to lack of data and/or differences in ratings among experts (Johnson and Gillingham 2004, O'Neill et al. 2008, Zeller et al. 2012). Moreover, our resistance assignments are based on our current understanding of animal/habitat relationships, which may change in future climates (O'Neill et al. 2008, Carvalho et al. 2011). However, in many cases, other data or approaches are simply not available (Spear et al. 2010); these limitations should not, however, halt assessments when management needs are present. Instead, uncertainty should be quantified (see *Sensitivity analysis* section) and caution in applications should be advised. Therefore, we acknowledge that limitations are present in our assessments of structural and functional connectivity, particularly when projected to the future, and urge caution in trying to extrapolate our results to other areas, species, or times.

Circuit theory analyses

We used Circuitscape 4.0 for all circuit theory calculations (McRae et al. 2014). One of the most important model parameters to consider is the scale used to calculate resistance value landscapes, that is, the grain of the resistance surface. Spatial layers were kept in native (often 30-m) grid cells during resistance value assignments. However, not all species experience the environment on this scale. It is important to conduct the analyses at the spatial extent that the animals will experience the heterogeneity of the environment lest information is lost to too large a grain (Wiens 1989, Wiens and Bachelet 2010). This need to maintain the smallest grain size necessary also must be weighed against computational limitations (Cushman et al. 2013). Although algorithms are fairly efficient for raster landscapes in circuit theory, there are still computational roadblocks in terms of run time and computer power needed. Circuitscape can calculate all possible combinations of possible pathways but as extent increases, so does the number of calculations needed to be executed. Large patch numbers, small grain size, and large spatial extent are common areas of concern for slower modeling run times and for model failure (McRae et al. 2014), and our system of habitat patches was quite large and many paths had to be calculated between patches, leading to run times of 4–8 weeks on the *Janus* supercomputer at Texas Tech University's High Performance Computing Center. There are several strategies that we used to overcome these roadblocks. We first increased the grain size (following the protocol in McRae et al. 2008) and aggregated resistance layers' grid cells by a factor of five (resulting in grid cells of 150 m) for American bullfrogs and by a factor of eight (resulting in grid cells of 240 m) for mule deer using a maximum aggregation method, using the Spatial Analyst extension in ArcMap and with the Gnarly Landscape Utilities (McRae et al. 2013). Both species were modeled at 250-m grain for the functional climate scenario, as that is the grain size of the FORE-SCE land cover datasets. Even though the bullfrog and mule deer likely perceive landscape structure differently (given their different body sizes and vagilities), 250 m is likely a small enough scale for both of them to readily perceive. In addition, instead of pairwise calculations between focal nodes, we used a cumulative all-to-one calculation method in Circuitscape to find a cumulative current map between many habitat patches for a target species (McRae et al. 2014). In this method, focal nodes are each in turn grounded, while all others are "turned on" to find all possible paths from all waters to each individual water, and a cumulative connectivity of map the landscape is made (McRae et al. 2014). We used Queen's connectivity condition to have calculations connect all eight neighboring cells to a given habitat cell in the grid (McRae et al. 2014).

Climate scenarios

Given the assumption of projected drier and hotter conditions (Seager et al. 2007), we based our analyses on the loss of isolated waters in the system. Scenarios were based on currently known waters (*current waters* scenario) and for a second scenario based on waters that would still exist based on climate change limitations (*climate-limited waters* scenario). Under the *climate-limited waters* scenario, all waters that were not artificial catchments or springs were removed under the assumption that these waters will be the last to dry out in the future, decreasing the number of waters present from 6214 in the *current waters* scenario to 3558 in the *climate-limited waters* scenario (a reduction of 43%). The *climate-limited waters* scenario was based on the facts that although spring flow in arid systems is sometimes linked to rain, springs are some of the most reliable waters in the desert (Unmack and Minckley 2008), and artificial catchments will continue to be managed and filled by state and federal conservation agencies to help supplement waters for game species. The same connectivity methods used for current conditions were used for the climate change scenario.

We ran a nested cluster analysis for both bullfrog and deer structural and functional connectivity analyses for the *current waters* and *climate-limited waters* scenarios. We decided on using a centrally located subgraph component in the Sonoran Desert isolated water network to run the spatially nested analysis. This cluster had a variety of land covers, including roads, agriculture, riparian areas, urban areas, rugged mountain terrain, desert scrub, and sparsely vegetated sands. This cluster was entirely within the predicted mule deer distribution but was also near areas excluded from this range. It was also close to areas with recorded bullfrog sightings. This made it a good candidate to examine in a nested analysis of the Sonoran Desert isolated waters network in the context of conflict mitigation. This subset had 87 waters present in the *current waters* scenario and 81 in the *climate-limited waters* scenario. We reran structural analyses on the subset to understand when the subgraph network coalesced and the influence each known water would have on the subgraph's connectivity. To understand how connectivity of the network behaved below the coalescence distance, we also addressed the connectedness of the graphs at distances between 0.5 and 15 km to better reflect dispersal abilities of different species. We identified the structural components of each subgraph (spatially defined cluster) using mule deer movement distances (i.e., using mule deer dispersal data, we calculated structural connectivity metrics and identified the waters within the subgraph most important for conservation).

After identifying the nested structural analysis, we ran resistance-based functional connectivity analyses on the subset. We used the custom ArcGIS toolbox Linkage Mapper (McRae and Kavanagh 2011) to calculate least-cost paths and cost-weighted distances using the resistance surfaces for both bullfrog and mule deer. To increase computational speed of calculating cost-weighted and least-cost paths, we used a 15-km search window to include only waters within a 15-km diameter of each water in a scenario. This excludes paths that would be longer than the possible dispersal distances for amphibians or farther than likely daily travel distances for mule deer. Using Circuitscape 4.0, we mirrored earlier procedures to analyze all possible routes between focal waters (McRae et al. 2014). We compared output for bullfrog and mule deer to suggest areas most promising to help prevent the spread of invasive species or increase local connectivity for native species, respectively.

To identify subsets, we first interpreted the functional connectivity of the entire landscape using circuit theory. Regional structural connectivity results then revealed a candidate subset to be used to interpret local connectivity. We preferred the structural results to identify subsets because these methods routinely overestimate connectivity and home range measures (Fletcher et al. 2011, Bishop-Taylor et al. 2015, Sutherland et al. 2015), which then provides a very conservative measure of waters connected in terms of an invasive species' dispersal capability. By using the dispersal distance of an invasive species (or a slightly larger distance for good measure), we accounted for connected isolated waters for the focal species. At 15 km, the subgraphs emerged and a local subset was identified so that exclusion areas and artificial catchment placement areas could be estimated. Rerunning structural and functional connectivity analyses within the subset provided direction on where they would be contributing most to isolation and connectivity. The decomposable nature of the subgraphs would allow all networks of waters in the focal area to be analyzed like the full network.

Sensitivity analysis

We quantified uncertainty in our connectivity model outcomes by performing a sensitivity analysis. Because our spatial extent was large and computationally demanding, we conducted this analysis on a ~16,800-km^2 subset of our focal area. Bracketing resistance values has been considered a viable option for evaluating model sensitivity to parameter uncertainty in connectivity corridor studies (Beier et al. 2009). Three alternative scenarios were examined for the current bullfrog resistance output with different landscape variables resistance values being either compressed or extended while keeping the general rank order. The top 10% of overlapping cells were compared between our results and the alternative resistance value scenarios (Beier et al. 2009 & Churko 2016). Sensitivity of model parameters to expert opinion-derived data is important part of the connectivity modeling process (Van der Lee et al. 2006, Fig. 1).

RESULTS

The regional connectivity between waters in all scenarios reduced to various degrees (Fig. 2). Connectivity was measured between the 6214 waters under the current condition model for both bullfrog and mule deer. Finding the least resistant paths between all nodes in each scenario showed that, as expected, the landscape was more resistant at the regional scale to bullfrogs (Fig. 2A) than to mule deer (Fig. 2C). This finding that mule deer likely experience a more permeable landscape in the Sonoran Desert than do bullfrogs, both now and in a projected climate future, is not surprising. What is novel, however, is the identification of specific locations where dispersal will likely be easier for each species in the future, including a rather unexpected role for urban land use. The functional connectivity of Sonoran Desert isolated waters for current conditions and for the projected conditions (2050) for both bullfrog and mule deer (Fig. 2) shows an extremely connected section of the Sonoran Desert to the north and east of the Phoenix, Arizona, metropolitan area. Under current conditions, the mule deer appears to have much less resistance to movement across the Sonoran Desert than the bullfrog (manifested as more "warm" colors representing greater resistance to movement in Fig. 2C compared to A).

The future scenario shows a reduced connectivity between waters across the Sonoran Desert. Although the resolution of Fig. 2 does not allow interpretation of connectivity between individual waters, the dramatic reduction in connectivity across the region for mule deer under future scenarios (if no additional management actions occur) is easily observable and a threat to this species. Under both scenarios, resistance to movement between isolated waters in the network increases as one moves west toward the drier sections of the Sonoran Desert known as El Pinacate y Gran Desierto de Altar Sonora and where the Sonoran Desert meets the Mojave in California. Lowest resistance between isolated waters occurs to the north and east of the Sonoran Desert, with waters acting as islands within a harsh matrix the farther west into the drier reaches of the Sonoran Desert they are. In both species' projected output for the year 2050, the area of medium- to low-resistance cells decreases in size, being generally found in the northeastern section of the graph (Fig. 2B, D). The bullfrog and mule deer both avoid dense urban areas in all scenarios except for the mule deer in the *climate-limited waters* future scenario: The city (particularly the outskirts/suburbs) of Phoenix shows a decrease in resistance to movement. The mule deer retains a larger area of lower resistance in the future scenario (compare

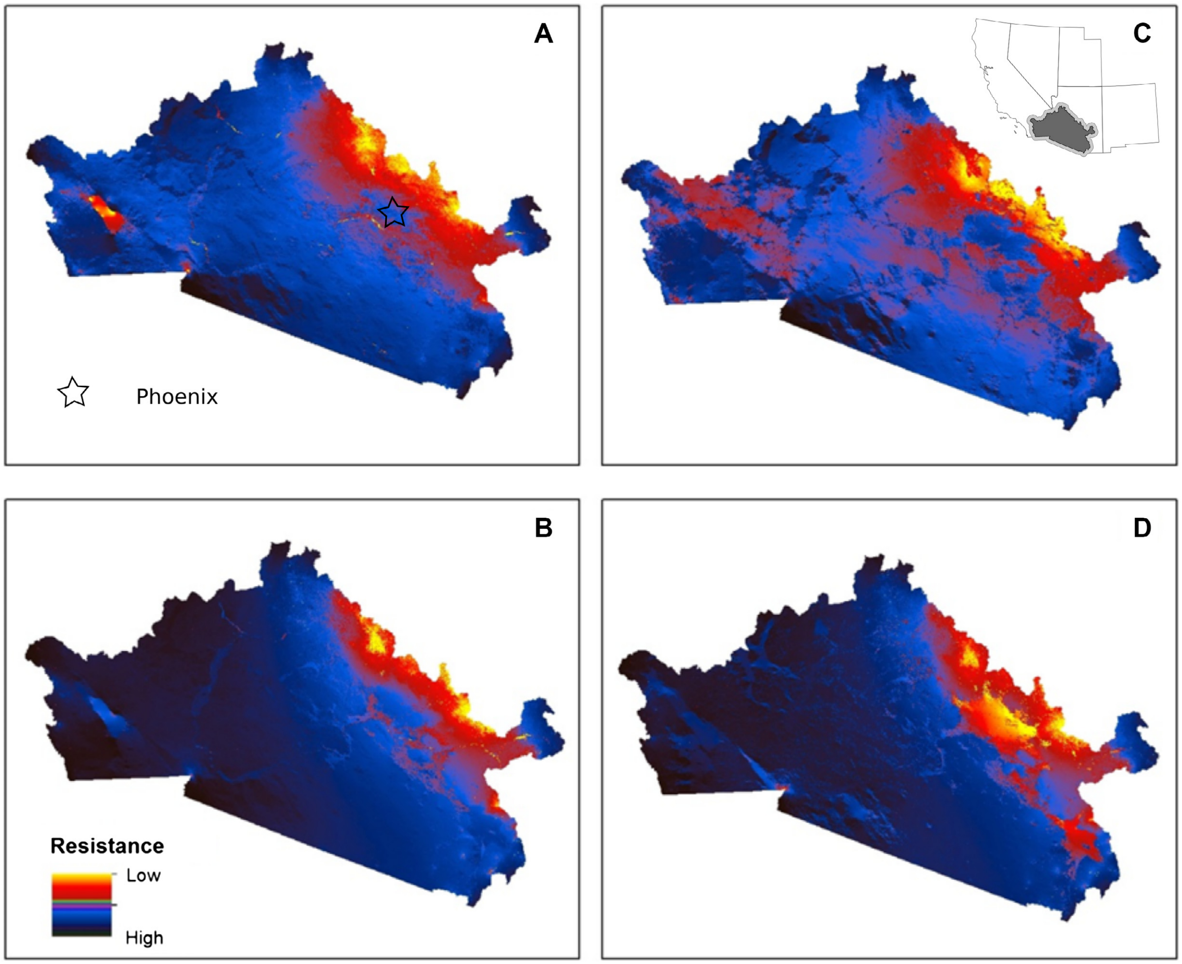


Fig. 2. Circuit theory-based functional connectivity maps for the invasive American bullfrog (A and B) and native mule deer (C and D). The top panels (A and C) represent the *current waters* scenario (n = 6214 isolated waters of the Sonoran Desert) for the resistance surface calculated with the 2011 National Land Cover Dataset (Jin et al. 2013). The bottom panels (B and D) represent the *climate-limited waters* scenario where only perennial springs and managed waters remain on the landscape (n = 3558) and a resistance surface calculated using the USGS FORE-SCE land cover projections for the year 2050 under the emissions scenario A1B (Sohl et al. 2014).

Fig. 2D to B), but overall connectivity is reduced across a greater portion of the desert. Mixed into the high-resistance matrix are the 6214 waters under current conditions and 3558 waters in the 2050 projected scenario. Although many of these were congregated in the low-resistance areas north and east in the graph, many were isolated by >15 km. These waters were often represented by a single pixel in the raster landscape. These waters act as low-resistance islands in an overall harsh matrix.

Considering a dispersal maximum of 15 km, we identified 37 clusters among the 6214 isolated waters known in the Sonoran Desert. These clusters occupied approximately 67,745 km^2 (Appendix S3: Fig. S2). The exclusion area created from buffering 15 km around single points and the aggregated point clusters totaled to 122,606 km^2 of Sonoran Desert that should not have additional waters constructed within them without proper mitigation or monitoring to avoid providing increased dispersal corridors for bullfrogs (Appendix S3: Fig. S3). The areas of the mule deer home range that did not intersect with the exclusion area totaled to 45,361 km^2.

A total of 87 waters existed in the *current waters* scenario in the nested subgraph, and 81 in the *climate-limited waters* scenario. Of these 87, only six were neither managed by the AZGFD nor were springs, meaning that they were rain-dependent. Structural connectivity decreased greatly in the future *climate-limited waters* scenario. The coalescence distance for *current waters* scenario was 13 km, whereas under the *climate-limited waters* scenario, it increased to 24.9 km; both of these distances are beyond the maximum known dispersal of the American bullfrog (Kahrs 2006) as well as typical daily movements for mule deer (Ordway and Krausman 1986, Truett 1987, Rautenstrauch and Krausman 1989), meaning that both of these species are experiencing a fragmented landscape, but one that will be nearly doubly so in the projected future climate scenario.

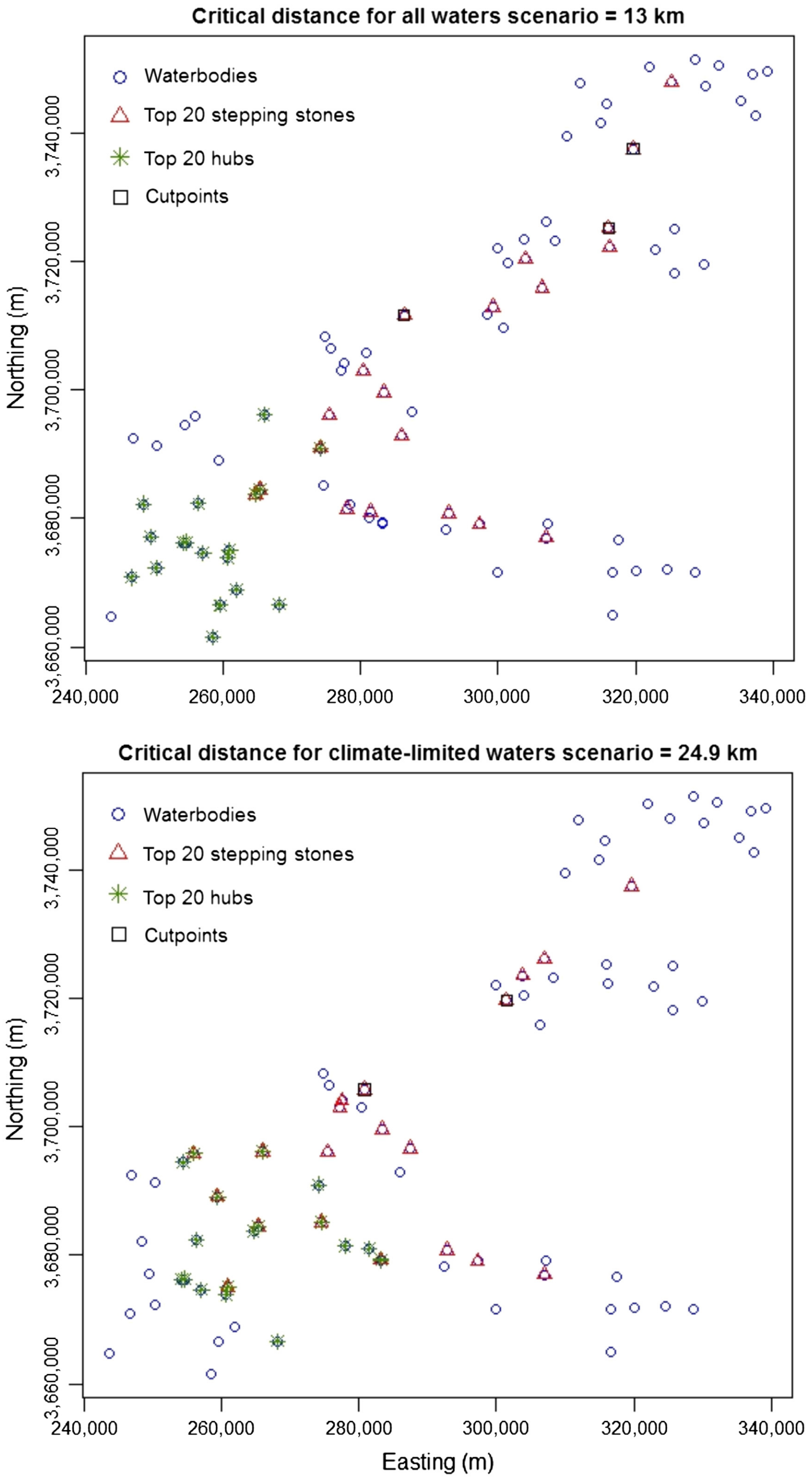
Many of the waters overlapped as highly ranked stepping stones and hubs between scenarios (Fig. 3); in the *current waters* scenario at coalescence distance, three cutpoints emerged, whereas two emerged in the *climate-limited waters* scenario. Many of the top waters in the system overlapped roles between scenarios, particularly with many hubs also being stepping stones. All cutpoints were also stepping stones. Because these waters simultaneously play multiple roles, they are particularly important to consider for connectivity conservation (McIntyre et al. 2016).

As the dispersal distance was increased, various connectivity metrics of increased and cluster size decreased (Fig. 4). Of the connectivity metrics examined, graph diameter, maximum cluster sizes, and mean cluster sizes were similar between the *current waters* scenario and the *climate-limited waters* scenario. The *current waters* scenario coalesced at 13 km (Appendix S3: Fig. S4), but the future *climate-limited waters* remained fragmented into isolated clusters at this distance (Appendix S3: Fig. S5). Because of the small difference in the numbers of waters between these two scenarios, the largest difference between cluster numbers was at the lowest dispersal distances (0.5 and 1 km), with 82 clusters and 76 clusters at 0.5 km and 79 and 75 clusters at 1 km for the current and future scenarios, respectively.

There is less functional connectivity of the nested waters for both scenarios for each species according to both circuit theory and cost-weighted conditions compared to Euclidean distance and least-cost path distances, and especially decreased connectivity in the future for both species compared to current conditions (Appendix S3: Fig. S6). Under the *current waters* conditions for the bullfrog, 203 of the 242 least-cost path dispersal routes were <15 km compared to the 450 links found during graph analysis at a 15-km dispersal distance. These 203 links connected all 87 waters in the network. Only 35 of the 242 cost-weighted distance links were <15,000 cost-weighted dis tance units (referred to from here on as units and relational to the map unit used in calculation: meters; McRae and Kavanagh 2011). These 35 links connected 45 waters in 15 clusters (Fig. 5; Appendix S3: Fig. S7A). The cost-weighted distance analysis found 21 paths under 15,000 units. These links connected 33 waters in 13 clusters (Appendix S3: Fig. S7B). Bullfrogs appear likely to use riverine corridors and areas of agricultural land as prime dispersal corridors away from the highly dense areas of springs and waters in the northeastern sections of the desert based on the circuit output showing lower-resistance paths (Fig. 6). This appears to reflect the currently known locations of bullfrog occurrences in the Sonoran Desert (iMapinvasives.org, last accessed July 2015). In *the climate-limited waters* scenario for bullfrogs, 190 of 228 least-cost path links were <15 km; compare this to 397 Euclidean distance links found at a 15-km dispersal distance under the same scenario.

The *current waters* scenario for the mule deer had 202 of the 244 least-cost paths <15 km compared to the 450 found during graph analysis at a 15-km dispersal distance. These 202 links connected all 87 waters in the network. Only 67 of the 244 cost-weighted distance links were <15,000 units. These 67 links connected 71 waters into 19 clusters (Appendix S3: Fig. S7C). In the future *climate-limited waters* scenario for mule deer, 191 of 230 least-cost paths links were <15 km compared to the 397 links at 15 km dispersal distance. The cost-weighted distance analysis found 66 paths under 15,000 units. These links connected 68 waters into 16 clusters (Appendix S3: Fig. S7D).

Upon initial visual inspection, the sensitivity analysis of circuit theory output for alternative



Critical distance for all waters scenario = 13 km

Critical distance for climate-limited waters scenario = 24.9 km

Fig. 3. Waters that contribute most to structural connectivity of the focal subset of the Sonoran Deserts isolated waters network.

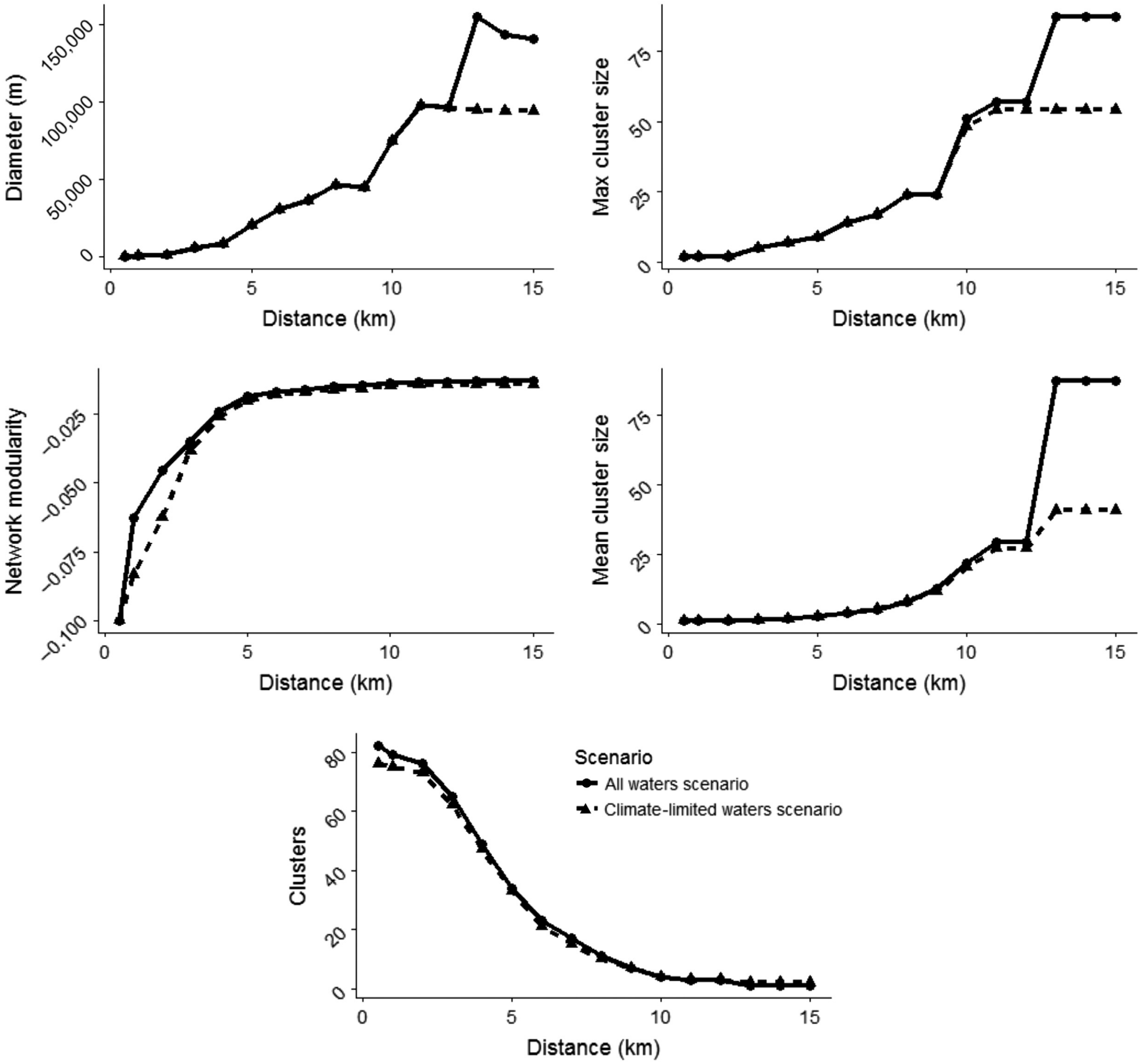


Fig. 4. Graph theory-based connectivity metrics. *All waters* scenario (whole line) represents current conditions (n = 87 waters). The *climate-limited waters* scenario (dashed line) represents a future where only springs and artificial catchments remain (n = 81 waters).

resistance scenarios held stable to our initial results. For the lowest 10th percentile of cells representing resistance pathways produced in the circuit theory analysis output, we saw 92–98% overlap between alternative resistance scenarios and our initial resistance valuation of the landscape. Because the areas around water catchments would be the least resistant to travel because of the bias produced in circuit theory analysis in proximity to source nodes, we also dropped the least resistant cells (below the 5th percentile) to remove the influence of habitat patch nodes in the output (Churko 2016). When these least resistant cells were removed from the overlap, we saw 76–93% overlap of cells in the 5th to 10th percentile of cells on the landscape. These findings indicate that our rank order of environmental factors (such as slope, land cover) was stable to extreme perturbations to the valuation of resistances in our nested study area. Although limited in scope, because of the strong stability in low-resistance corridors in the circuit

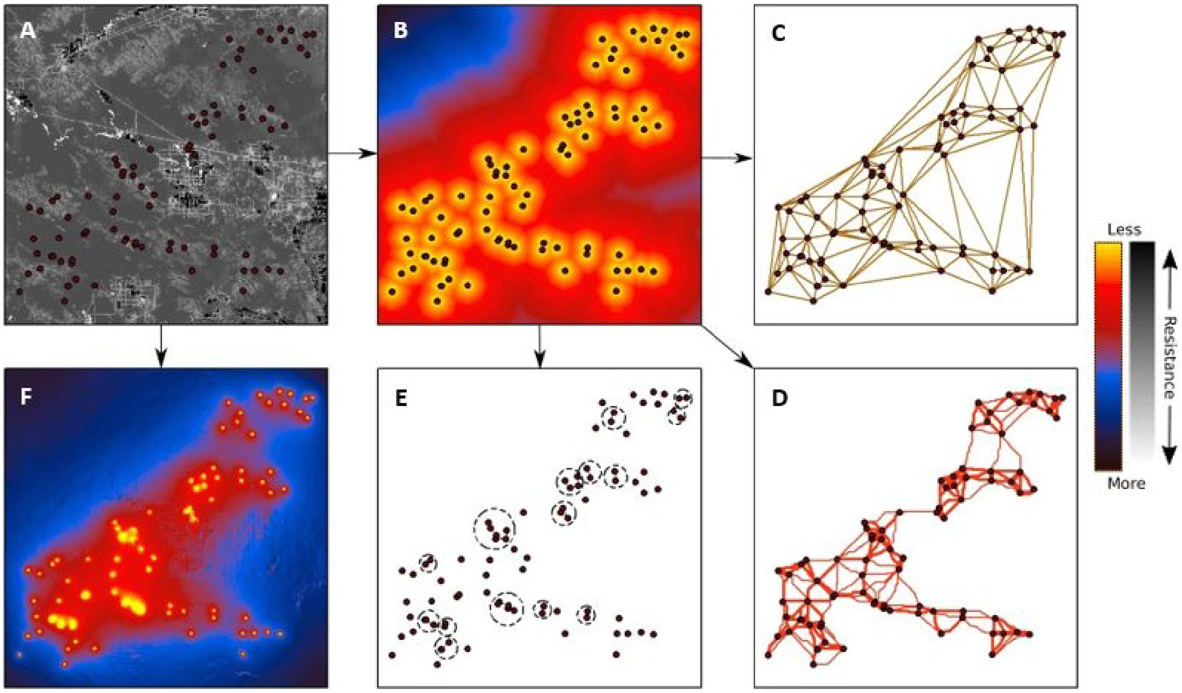


Fig. 5. Connectivity metrics for the American bullfrog compared under current conditions for a subset of the Sonoran Desert. Clockwise from top left: (A) resistance surface and isolated waters based on current conditions in the Sonoran Desert; lighter grays are less resistant to bullfrog movements. (B) Habitat patches and cost-weighted map based on resistance surface; yellow is least resistant and darker colors more resistant. (C) Euclidean distance map of possible connections in the system. (D) Least-cost path map based on resistance map with all paths <15 km. (E) Cost-weighted resistance map; 15 clusters of 45 connected waters are connected via paths that are <15,000 cost-weighted units. (F) Circuit theory analysis of resistance surface showing less connectivity between waters than other methods in A–E.

output among alternative scenarios and the study results, this sensitivity analysis helps reduce uncertainty in our model.

DISCUSSION

We used a multi-scale, multi-analysis approach to examine landscape connectivity of the isolated waters of the Sonoran Desert for two economically and ecologically important species. Our approach of comparing two nested scales gave a deeper insight and wider scope than any single one would have provided, helping illustrate details of local connectivity between individual features (waters) that were masked in regional models (e.g., Fig. 2). There was an overall reduction in structural and functional connectivity between current and future conditions for both the mule deer and the American bullfrog in many areas of the Sonoran Desert. As a consequence, artificial catchments will likely become even more important in supplementing reductions in water in the Sonoran Desert for managed game species such as mule deer. However, artificial catchments have increased the connectivity of waters across the landscape in such a way that makes the region better habitat for invasive species like the bullfrog: The 13-km coalescence distance under the *current waters* scenario is perilously close to the maximum known movement distance of bullfrogs (Kahrs 2006), and adding even more artificial catchments will decrease the coalescence distance even more. This will likely be counterbalanced by the reduction in connectivity that is expected under climate change (a near doubling of the coalescence distance that was seen from the *current waters* to the

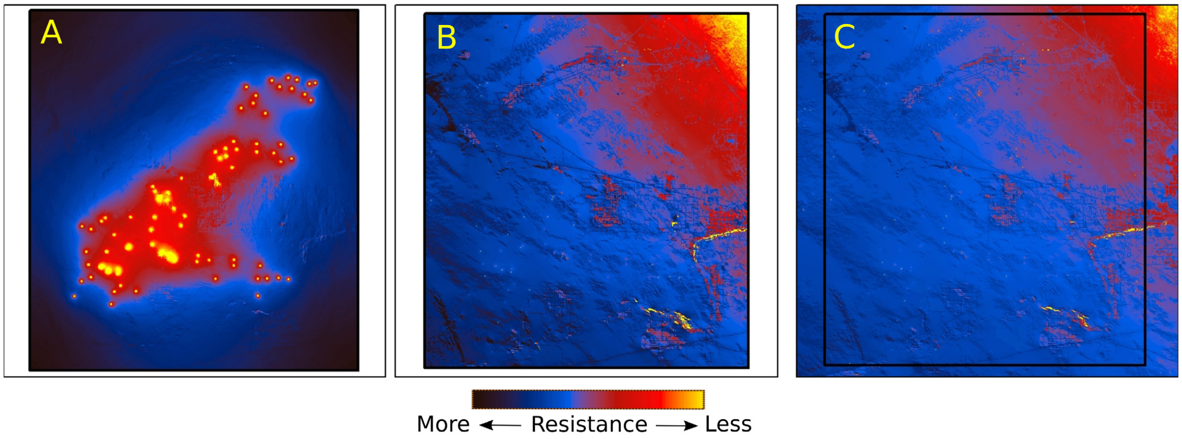


Fig. 6. Comparison of scenarios for American bullfrog circuit theory results for the area of the nested subset in the *current waters* scenario. Panels include the nested subset of waters (A), isolated section of the full area that has been clipped to the nested subset (B), and the full Sonoran Desert bullfrog circuit theory results zoomed into the nested subset area (C). All results are visualized using a color ramp stretched using a percent clip (min: 0.5, max: 0.5). Results of the nested subset (A) used only the waters within the boundaries of the graphical subset calculated at the regional scale at a 15-km dispersal distance.

climate-limited waters scenarios). However, this also means that all species (and not just invasives) will experience constrained connectivity with greater isolation risks (as well as quarantine benefits).

Both of our focal species exhibited an increase in resistance to movement in future scenarios, but bullfrog movement was less changed in the areas with highest densities of springs. The mule deer, however, appeared to retain a larger area of lower resistance compared to the bullfrog in the future. Also, the total area of lower-resistance area loss was greater for the mule deer, suggesting that much of the Sonoran Desert may become difficult to disperse through for even this relatively large, vagile species. Surprisingly, mule deer appear to have very low resistance in suburban and agricultural areas around the Phoenix metropolitan area in the future scenario. Given how reduced rainfall will diminish forage quality in much of the desert based on declining rainfall estimates, species like the mule deer may seek water and forage in settings where it has become artificially available. Much like the white-tailed deer (*Odocoileus virginianus*) nuisance in much of the eastern United States, mule deer have the potential to become pests where natural habitat has been replaced by human activities.

Using graph theory to identify subgraphs that could then be analyzed via circuit theory helped create a nested, multi-methodology approach that identified locally important waters that could be the focus of conservation (e.g., monitoring, quarantine, water supplementation, or other activities). Analyzing the subgraph area's functional connectivity also showed how landscapes can influence connectivity between habitat patches such as isolated waters. Using this information in conjunction with buffered exclusion areas, we identified safe locations to add new waters and identified waters that could be removed to reduce the risk of invasion without negatively affecting mule deer access to water across the landscape. Local connectivity, using subsets of data from the regional analysis, provided a different perspective on spatial associations. As the study area was scaled down, visualized results changed because of the loss of influence of the larger resistance context and increased numbers of waters. Circuit theory interpretations of the regional landscape gave important context to the connectivity between all waters (Fig. 2). Individual paths between waters, however, appear to be lost at the larger landscape context (Fig. 6B and C compared to A). The nested subset (Fig. 6A) has a very different result from the full analysis of the Sonoran Desert landscape (Fig. 6C). Even clipped to the same extent (Fig. 6B) as the nested area, however, the results differ because of the influence of calculating all possible paths between all focal habitat patches in the study area. The difference in outcome is due in part to the change in number of focal nodes. It is also due to the reduced number of cells that influence the random-walk calculations. This combination of factors may result in local paths becoming washed out at the regional context. Nesting the graphs within a subset focal area may reduce the scope of the analysis to allow individual paths between waters to become more discernable. In doing so, we identified areas that improved landscape connectivity for mule deer without increasing dispersal corridors to invasive species like bullfrogs. Such analyses can guide local placement of waters to increase local connectivity while maintaining isolation from the regional context of invasive species, because the nested subset increases the resolution of the results (habitat patches can be analyzed to find locally important waters that act as hubs, stepping stones, and cutpoints at this scale). We found that many of the waters that are currently important to connectivity stayed important in future scenarios (Fig. 4); many of these waters also played multiple connectivity roles. These waters should be especially important for managers. For example, a centrally located water acted as both stepping stone and cutpoint. This site maintained connectivity between two large clusters (Appendix S3: Fig. S5).

These structural results at the local scale appear to have overestimated connectivity in the subset compared to the functional analyses using least-cost paths and circuit theory, where the landscape matrix between waters influenced connectivity (i.e., method matters). Least-cost paths did reveal an entirely connected landscape for both species, but cost-weighted paths and circuit theory showed few connections. Bullfrogs experienced a reduction in connectivity from a single cluster at the 15-km scale least-cost path to 45 of 87 waters connected in 15 clusters using cost-weighted paths, and the rest of the waters remained isolated to themselves. The circuit theory interpretation of the resistance surface showed further reduced connectivity, with more waters isolated and fewer cluster forming with low-resistance corridors between them (Fig. 5). The mule deer under current conditions also showed a single least-cost path cluster. The landscape was more connected based on cost-weighted resistance scenarios for the mule deer, with 71 waters connected in 19 clusters. Future scenarios for the mule deer showed two distinct clusters emerging for least-cost path analysis when paths are limited to 15 km dispersal distances. In contrast, the cost-weighted analysis found 68 waters in 16 clusters. This 4% change in the number of waters connected is small compared to the reduction in connected waters in the bullfrog future scenario to 33 waters (approximately a 27% reduction in functional connectivity from current conditions to the projected future scenario for this species).

Differences in sensitivity to connectivity, such as the bullfrog needing a more connected landscape than the mule deer, can be used to isolate infested areas, protect important connectivity areas, and improve connectivity of at-risk regions. By removing artificial waters or temporarily removing natural waters (Maret et al. 2006) to increase boundaries between clean and infected waters, managers can improve their efficiency and effectiveness at managing bullfrog invasions. Reducing overall water on the landscape will likely be politically contentious—and possibly ecologically and economically irresponsible—but removing artificial waters from an area to increase the buffer distance and adding waters in new areas to help support under-connected areas will create benefits. In the nested subset we analyzed, a single water acts as a connection between two large clusters and is at risk to impacts of climate change. New artificial catchments could be placed near the constriction of the graph to support critical waters such as this cutpoint and increase path redundancy and overall connectivity in that area. Removing the outermost artificial waters from the northern section of the graph (Appendix S3: Fig. S8) would not reduce mule deer connectivity to the rest of the subgraph, but could increase the buffer from known bullfrog occurrences. By using the multiple structural and functional analysis approach, areas can be found that could have waters placed inside the catchment placement area to increase local connectivity without jeopardizing isolation in other subgraphs.

Because functional connectivity analyses rely on resistance surfaces built in part from expert opinion-based sources, results may be different than if based on an empirically derived resistance surface using values developed from genetic or telemetry-based methods (Zeller et al. 2012). Like other studies that have used resistance surfaces based on expert opinion, our results should be viewed as "potential" functional connectivity rather than "actual" functional connectivity (Bishop-Taylor et al. 2015). Although an important start to understanding the connectivity of the Sonoran Desert, we suggest that genetic or resource selection-based connectivity studies use a nested multi-analysis strategy and compare multiple species with multiple dispersal potentials at multiple scales to better understand how wildlife waters or other resources can influence landscape resistance and connectivity of habitat patches at regional and local scales.

The data limitations and resolution of our study incorporate a layer of uncertainty that has been attempted to be rectified, although some uncertainty always remains. We have tried to be as thorough as possible, but complete uncertainty analyses are not always feasible or within the scope of a project (Van der Lee et al. 2006). Certain features that may influence connectivity or habitat quality, such as agricultural canals, swimming pools, or urban ponds, could have been missed at the scale of our raster data (30–250 meter cells). It would be pertinent to test more species and climate-based scenarios to understand the full connectivity landscape of the Sonoran Desert. We used two mobile generalist species of interest to land managers in the Sonoran Desert. Choosing others based on low vagility or habitat specificity might reveal other patterns important for land managers. Land use changes and climate data were also based only on one future scenario from the FORE-SCE land cover dataset for SRES scenario A1B in the year 2050 (Sohl et al. 2014). This could be extended to other climate scenarios or years. We were also conservative in estimating that all springs will continue to flow and provide possible habitat, resources, and connectivity for species in the future. As spring flow can be stochastic, the future scenario we used is a "best-case" scenario. In reality, it may become much worse, especially for low-vagility species trying to move between dwindling waters.

CONCLUSIONS

The use of artificially created waters for wildlife will likely remain a common management solution to increasing water limitation due to climate change in the Sonoran Desert (Seager et al. 2007, IPCC 2014) and in other arid regions across the world. In addition to reduced rainfall, groundwater mining and river water diversion are reducing water available to desert soils and may be responsible for reduced spring flow (Patten et al. 2008). The land is also being converted to urban and agricultural uses. These factors will make surface water increasingly scarce. Wildlife managers have known that artificial catchments can provide a limiting resource to bolster local populations of game species (O'Brien et al. 2006). The use of such artificial catchments is likely to continue and become even more necessary. Given reliance by many animals on open water sources (Krausman and Etchberger 1995, Krausman et al. 2006, Calvert 2015), managers may continue to install these artificial features, so it is crucial to understand the potentially negative aspects of artificial catchments and develop ways—like our study's methodology—to mitigate for them. Conservation funds for habitat restoration and resource management are becoming scarcer, which mirror changes in habitat availability: Waters will disappear under climate change and the landscape will become harder to move through. Placing waters on the landscape needs to be informed when improperly placed waters can have negative consequences (Halloran and Deming 1985, Krausman et al. 2006, Calvert 2015). Understanding connectivity will be instrumental in deciding appropriate placement areas for the costly management technique of waters with minimal side effects to non-target species. Our nested strategy helps identify local connectivity within a larger regional context that can provide insight into areas that are structurally and functionally limited on connectivity and areas that are most important for connectivity. This technique is not limited to being useful in the Sonoran Desert isolated waters network. Analyses like ours could also be used on any other patchy-style habitat, such as vernal pools of the northeastern United States or caves, to isolate chytrid fungus or the fungus causing white-nose syndrome in bats (Blehert et al. 2008, Lorch et al. 2011), respectively.

Our study presents a useful new approach to connectivity-based analyses. The use of a multi-scale (Dilts et al. 2016) and nested approach helps to understand the landscape and how organisms respond to it. The Sonoran Desert's isolated waters network will likely be impacted by climate change. Mitigating these impacts can have unforeseen consequences, but by careful analysis of the network topology and landscape, functional response of different species may be considered. Isolation of habitat from invasive species and disease can be accomplished without detrimental impacts to local connectivity. This study increases the understanding of connectivity between limiting resources in the Sonoran Desert, the use of multiple connectivity analysis methods, and the use of nested structures; doing so has created a methodology that could be used to address conflicting management goals.

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