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RESEARCH ARTICLE

Characterizing range-wide impacts of anthropogenic barriers on structural landscape connectivity for the Sonoran desert tortoise (*Gopherus morafkai*)

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Abstract

Context Linear anthropogenic barriers may reduce structural landscape connectivity for wildlife.

Objectives Using graph-based connectivity indices, we modeled the potential impacts of linear barriers on structural connectivity and on individual patch importance at different biologically justified dispersal distance thresholds for the Sonoran desert tortoise, a wide-ranging species for which anthropogenic barriers may be reducing structural landscape connectivity.

Methods To characterize the potential impacts of barriers on structural connectivity for the Sonoran desert tortoise, we compared network compartmentalization, individual habitat patch importance, and the spatial distribution of important habitat patches for models of structural connectivity reflecting the landscape prior to the development of linear barriers to models depicting current linear barriers in the landscape at different distance thresholds.

Results Linear barriers fragmented the habitat patch network into a minimum of 239 patch components. Compartmentalization increased little as dispersal distance thresholds exceeded 10 km. In barrier simulations, patch importance mostly decreased and the spatial distribution of important patches shifted south.

Conclusion Barriers are limiting structural connectivity for Sonoran desert tortoises and may prevent dispersal events, rescue effects in the event of localized extinctions, and successful range shift in response to climate change. Management efforts targeted at enhancing connectivity for ecological processes or movements occurring at 5–10 km may enhance the potential for longer-distance movements or generational dispersal occurring at a greater extent. Our methods provide an efficient framework for assessing changes in structural connectivity on a landscape extent that may be applied to addressing different problems or questions related to landscape connectivity.

Keywords Structural connectivity · Graph theory · Dispersal · Sonoran desert tortoise

Introduction

The continued development of linear anthropogenic barriers are altering landscapes and may be reducing landscape connectivity globally (Gurrutxaga et al. 2014 and citations therein). Reduced landscape connectivity may disrupt natural processes like gene flow, dispersal, migration, demographic rescue, and range shift in response to climate change (Taylor et al.

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1993; Tewksbury et al. 2002; Heller and Zavaleta 2009). How linear barriers impact landscape connectivity may differ between taxa (Fahrig and Rytwinski 2009; Beyer et al. 2016) and between different landscapes. For example, connectivity loss may have disproportionately severe impact on species that are poor dispersers, exist in small, isolated populations, or whose resources or populations are widely distributed (Taylor et al. 1993; King and With 2002; Laskey et al. 2011). Reduced landscape connectivity may also have especially pronounced effects in fragmented landscapes (Laksey et al. 2011). Understanding how linear barriers may influence specific landscapes, habitats, or species is becoming increasingly important as networks of these barriers continue to spread.

Intensifying land use change and habitat fragmentation in the Sonoran Desert have drawn attention to the importance of landscape connectivity and the need to examine the impacts of barriers on Sonoran Desert wildlife (Campbell and Kennedy 2010; Flesch et al. 2010). Although previous studies have demonstrated a need to mitigate for the impacts of barriers by protecting or enhancing landscape connectivity (e.g. McRae et al. 2012), there exists no framework for quantifying the impacts of linear barriers or identifying at-risk areas for extents as great as the Sonoran Desert, and the potential impacts of such barriers on many desert species remains understudied.

The Sonoran desert tortoise (*Gopherus morafkai*) is one such species that is threatened by the proliferation of linear barriers throughout its range (USFWS 2021). Sonoran desert tortoises exist in small populations dispersed throughout the Sonoran Desert, where they typically inhabit rocky upland habitat and coalescing alluvial slopes (bajadas; Howland and Rorabaugh 2002; Riedle et al. 2008); occasionally low density populations can be found in valleys that provide important shelter resources (Averill-Murray and Averill-Murray 2005). Although they do not typically inhabit desert valleys, which may isolate upland populations from one another, rare dispersal events through these valleys may occur (Averill-Murray and Klug 2000; Edwards et al. 2004). Indeed, Sonoran desert tortoise populations were historically well-connected, as evidenced by little population genetic structuring throughout their range, suggesting that individuals are capable of making long-distance movements and that, over generations, dispersal between mountain populations has played a critical role in the species' evolutionary history (Edwards et al. 2004), at least in the absence of barriers. Due to the long generation time of the species (approximately 25 years; USFWS 2021), the impacts of barriers to movement among populations take time to manifest and are thus difficult to detect (Landguth et al. 2010). Therefore, our current understanding of gene flow among Sonoran desert tortoise populations reflects landscape connectivity prior to the relatively recent development of linear barriers (Edwards et al. 2004).

Approximately 70% of Sonoran desert tortoise habitat is experiencing some form of nearby urban development (Carter et al. 2020), and urban expansion and associated development of roads is expected to continue in both Arizona and Sonora in the foreseeable future (Gammage et al. 2008; Rosen 2014). High-traffic roads, railroads, canals, and the border wall create barriers to tortoise movement (Latch et al. 2011; Andrews et al. 2015; Dutcher et al. 2020; USFWS 2021), and vary in their permeability to movement. For example, pedestrian fencing along the United States-Mexico border is considered an impermeable barrier to the movement of subadult to adult tortoises (USFWS 2021), irrespective of any adjacent traffic related to border security and border wall construction, degraded habitat, and potential for increased predation along the wall. On the other hand, the permeability of roads may vary greatly along their length, depending on traffic volumes, the presence of culverts designed to facilitate tortoise movement, and more. Despite their permeability, linear barriers have been shown to reduce genetic connectivity between populations (Dutcher et al. 2020) and tortoises may avoid barriers, alter both movement behavior and home range size in proximity to them, and may perish traversing them (Andrews et al. 2015; Peaden et al. 2017). These barriers are likely exacerbating the natural isolation of populations and reducing the chances of recolonization of isolated habitats should they go extinct (Howland and Rorabaugh 2002; Edwards et al. 2004; Rautsaw et al. 2018). Indeed, fragmentation resulting from permanent linear barriers has thus been identified as one of the greatest threats to the persistence of the Sonoran desert tortoise (USFWS 2021). Despite the recognition that connectivity among tortoise populations is important for their long-term persistence, there remains a greater focus on directly protecting core populations than on identifying opportunities to restore connections between them (AIDTT 2000).

Given the proliferation of barriers throughout the species' range, it is hypothesized that the potential for the interpopulation movements that historically linked tortoise populations has been drastically reduced by the development of anthropogenic barriers, so much so that these movements have likely become impossible (Edwards et al. 2004). Indeed, fragmentation resulting from permanent linear barriers has thus been identified as one of the greatest threats to the persistence of the Sonoran desert tortoise (USFWS 2021). Despite the recognition that connectivity among tortoise populations is important for their long-term persistence, there remains a greater focus on directly protecting core populations than on identifying opportunities to maintain or restore connectivity between them (AIDTT 2000). Therefore, addressing the potential impacts of barriers on landscape connectivity may be an important strategy for ensuring the persistence of tortoise populations (Edwards et al. 2004).

Landscape connectivity can be assessed in various ways (Fahrig et al. 2021). The most commonly used approaches can be distinguished by whether their primary aim emphasizes the importance of the structural arrangement of physical features such as habitat patches or barriers on movement, or whether the emphasis is on the importance of the functional movement responses of organisms to heterogeneity of the intervening landscape. Effective conservation of the Sonoran desert tortoise will require an understanding of the extent to which linear barriers may exacerbate isolation of habitat patches and populations. We focused on modeling structural connectivity throughout the range of the Sonoran desert tortoise, with the goals of identifying habitat patches that play an important role in maintaining landscape connectivity, and on estimating the impact of barriers on patch importance and on range-wide structural connectivity.

A method that can be used to understand the impact of barriers on structural landscape connectivity is graph theory. Graph theory can be used to quantify structural connectivity at multiple scales and large extents, and it is well-suited to both landscape-scale and patch-level applications in fragmented landscapes (Urban and Keitt 2001; Calabrese and Fagan 2004; Minor and Urban 2007, 2008). In graph theory, the landscape is represented as a spatially explicit graph network of nodes, which may represent habitat patches or populations, and links connecting them. By incorporating a distance threshold, or the maximum distance at which two nodes are considered connected, graph theory can summarize the spatial relationship between resources like habitat patches in a biologically meaningful way (Calabrese and Fagan 2004). Based on species-specific information, this distance threshold may be set to the maximum distance a species can move through the landscape matrix between habitat patches, a distance related to a specific movement strategy (Bodin and Norberg 2007), or different distance thresholds to examine scaling effects on structural connectivity in fragmented landscapes (Keitt et al. 1997). This approach assumes that patches are connected or disconnected solely by the distance between them and disregards the influence of the intervening landscape mosaic on movement. As such, it is appropriate to use when examining connectivity between discrete habitat patches and the role those patches may play in facilitating ecological processes like dispersal or gene flow.

The importance of individual habitat patches based on their contribution to overall network connectivity can be useful in making management decisions to maintain or improve structural connectivity (Urban and Keitt 2001). At the landscape scale, graph theory can be used to calculate the distance at which the habitat patch network coalesces into a completely connected network. At distances below this coalescence threshold, the network is composed of isolated clusters of habitat patches (hereafter, components) whose members are connected to each other but isolated from other such patch clusters. If these distances exceed a species' dispersal capability, ecological and evolutionary processes (e.g. dispersal) are more likely to occur within components than between them (Bodin and Norberg 2007).

Numerous studies have demonstrated innovative applications of graph theory that exploit the ability to examine structural connectivity by adding and removing spatially explicit features to address specific conservation or management actions (Bunn et al. 2000; Drake et al. 2017). In these studies, the features added and removed are individual nodes (e.g. habitat patches) or links between them, and they are iteratively removed to quantify their importance by measuring the relative impact their removal has on overall network connectivity. Our methods differed from these studies by instead identifying and removing specific connections between patches to create new graph networks that simulated barriers to movement where they occur in the landscape. In other words, we modified the traditional node-and-link approach to incorporate the presence of linear anthropogenic barriers. This may allow for a more accurate representation of structural connectivity or, conversely, compartmentalization in a heterogeneous landscape.

To understand the potential impacts of barriers on structural landscape connectivity of Sonoran desert tortoise habitat, we used an approach combining graph theory and GIS that enabled us to quantify the individual and combined impacts of different barrier types on structural connectivity at different spatial scales as measured by network compartmentalization and individual patch importance based on two connectivity indices. We accomplished this by comparing compartmentalization and patch importance between graphs reflecting historic connectivity to graph networks reflecting the modern distribution and extent of linear barriers. Our objectives were to quantify and describe the individual and combined impacts of barriers on structural landscape connectivity between tortoise habitat patches throughout the species range, examine how structural connectivity and the impact of barriers change at different spatial scales, and identify habitat patches that are important for maintaining connectivity in the existing landscape and where local management efforts might enhance connectivity at a greater extent. Although our work addresses the impacts of existing barriers on structural connectivity among Sonoran desert tortoise habitat patches, we demonstrate a framework that may be applied to locating priority areas for potential management actions (such as barrier removal) or future research focused on addressing landscape connectivity, independent of taxon or study system.

Methods

Study area

The study extent covered the entire range of the Sonoran desert tortoise, approximately 18,000 square kilometers (Fig. 1). The species' range is centered on the international border between Arizona, United States and Sonora, Mexico.

Data

As part of the 2021 Species Status Assessment, the United States Fish and Wildlife Service generated 250 m resolution habitat suitability models covering a modern interpretation of the species' range as informed by recent genetic analyses (USFWS 2021). This model was based on 15 environmental variables hypothesized to influence tortoise habitat and classified habitat into three levels of suitability: low, moderate, and high. It is the only model that delineates the current distribution of habitat patches across the range of the species. To generate habitat patches for use in our structural connectivity analyses, we first used ArcGIS Pro 2.9.1 (Esri, Redlands, CA, USA) to combine the moderate and high suitability classes from the USFWS habitat suitability model. We excluded the low suitability class because areas within this class reflect atypical tortoise habitat where, based on extrapolations from long-term population monitoring data, few or no tortoises are expected to live (USFWS 2021). We then modified the combined suitability classes by removing any portions where tortoise habitat overlapped non-habitat areas of urban development, agricultural fields, and standing water, derived from 10 m resolution landcover data (ESA WorldCover, https://esa-worldcover.org/en). We also removed any portions overlapping highways, railroads, canals, or the border wall. Removal of these non-habitat areas divided some patches into separate, smaller ones. Vector data for highways, railroads, and canals were collected from open street maps (OSM; https://www.openstreetmap.org) and data on the border wall were provided by the Wildlands Network (https://wildlandsnetwork.org/). The resulting raster was converted to a polygon feature class for use in an extension (Conefor Inputs Tool for ArcGIS 10, Jenness Enterprises) designed to generate input files for Conefor 2.6 (Saura and Torné 2009). We removed habitat patches on Tiburón Island, Mexico from our analyses under the assumption that tortoises do not move between the island and the mainland. We also removed all patches smaller than 1 square kilometer; most of these patches reflect a potential mapping error (resulting from converting raster data to vector data) or are assumed to be unlikely to be able to

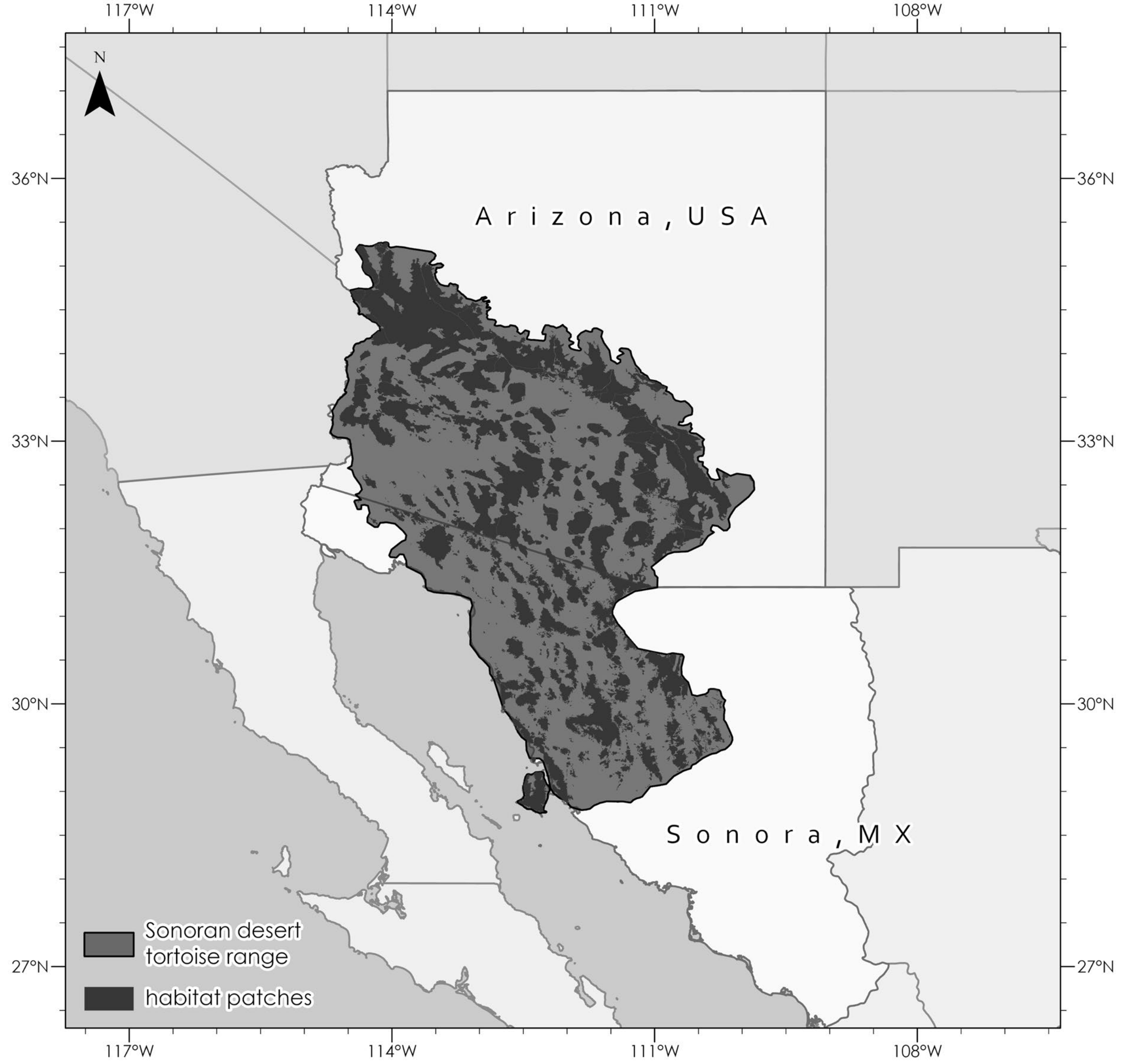


Fig. 1 The range of the Sonoran desert tortoise (dark gray polygon) and distribution of moderate and high suitability habitat classes, i.e., the habitat patches used in our analyses (black polygons within the range)

sustain a Sonoran desert tortoise population and thus unlikely to facilitate gene flow over generations, leaving 962 habitat patches remaining for use in our analyses (Fig. 1). Using ~ 21,000 observations of tortoises from the United States provided by the Arizona Game and Fish Department, we calculated the proportion of observations in patches retained for analysis and patches removed. Of the total number of tortoise observations, approximately 95 percent of observations occurred in patches we retained for analysis, and less than one percent (0.067) were in patches we removed. Although point observations from Mexico were not available, we assume that similar patch associations would be observed in Mexico.

Graph networks

We used Conefor 2.6 to generate graph networks of tortoise habitat patches at different distance thresholds based on the species' dispersal capability. Little is known about how frequently or far North American tortoises move between or disperse from populations (Guyer et al. 2014), and most of what is known about the movement of Sonoran desert tortoises is based on sparse observations or on genetic analyses, the latter of which indicate they historically dispersed between populations and were capable of long-distance movements (Edwards et al. 2004). Movements over 1 km from an individual's home range occasionally occur and are typically considered a dispersal event if the animal does not return to its previously occupied home range (Averill-Murray et al. 2020). The longest recorded movement by a Sonoran desert tortoise was 32 km (Edwards et al. 2004), which is believed to be exceptional and rare. However, this individual was moved by researchers across anthropogenic barriers several times; thus, although tortoises may attempt long-distance movements, movements of this distance are likely impossible in the modern landscape (Edwards et al. 2004). To incorporate the variation in potential movements or dispersal events, we used 1 km as our minimum distance threshold and 35 km as our maximum distance threshold and created graphs within this range at 5 km intervals. These graph networks, based on edge-to-edge geographic distance between habitat patches, reflect how structural landscape connectivity may have existed at each threshold prior to the development of anthropogenic barriers to tortoise movement and served as the baseline for quantifying the potential effects of barriers on structural connectivity.

To examine the effects of linear barriers in the landscape, we modified the previously generated graph networks by using ArcGIS Pro to identify and remove links that intersected major roads and highways (primary and secondary roads and interstate highways), railroads, canals, and segments of United States-Mexico border wall pedestrian fencing. The removal of these links simulates a complete barrier to movement between otherwise connected habitat patches; thus, two patches are not connected if a linear barrier exists between them regardless of the geographic distance between them. This represents the most extreme scenario of constrained connectivity. We constructed graph networks reflecting the loss of structural connectivity caused by each barrier type individually and all barriers combined at each distance threshold from 1 to 35 km, again using Conefor 2.6.

Estimating the impact of barriers on compartmentalization

The number of components in a graph network can be used to describe the degree to which the landscape is connected or, conversely, fragmented (Bunn et al. 2000; Minor and Urban 2008). To determine how linear barriers are impacting structural connectivity among Sonoran desert tortoise habitat patches, we compared the number of habitat patch components for graph networks based on geographic distance to those in graph networks with each barrier type individually and all barrier types combined by calculating the percent change in compartmentalization. We calculated the number of additional patch components created when barriers were simulated in graph networks. This process is summarized in Fig. 2 and allowed us to compare the relative impacts of each barrier type.

Identifying important patches

To quantify the relative importance of individual habitat patches in promoting structural connectivity, we used Conefor 2.6 to calculate two connectivity indices for each patch and at each distance threshold for graph networks excluding barriers and graph networks with barriers present in the landscape. Because Sonoran desert tortoises are believed to disperse generationally, using habitat patches in a stepping stone-like fashion, we calculated Betweenness Centrality (BC; Bodin and Norberg 2007) of each patch. BC quantifies the importance of each patch based on its position in the network and the number of shortest paths through the network that intersect that patch (Bodin and Norberg 2007). Habitat patches with a high BC score are positioned among a relatively greater number of shortest paths through the network than other patches, making BC a useful index for identifying stepping stones, or patches that are important for efficiently traversing the network regardless of their size or quality.

We also calculated the relative integral index of connectivity (dIIC; Pascual-Hortal and Saura 2006). Like BC, dIIC identifies patches that play a disproportionately important role in overall network connectivity, but unlike BC, index values are not based on node topology alone. dIIC incorporates connectivity occurring within and between each patch when quantifying patch importance. For example, dIIC can

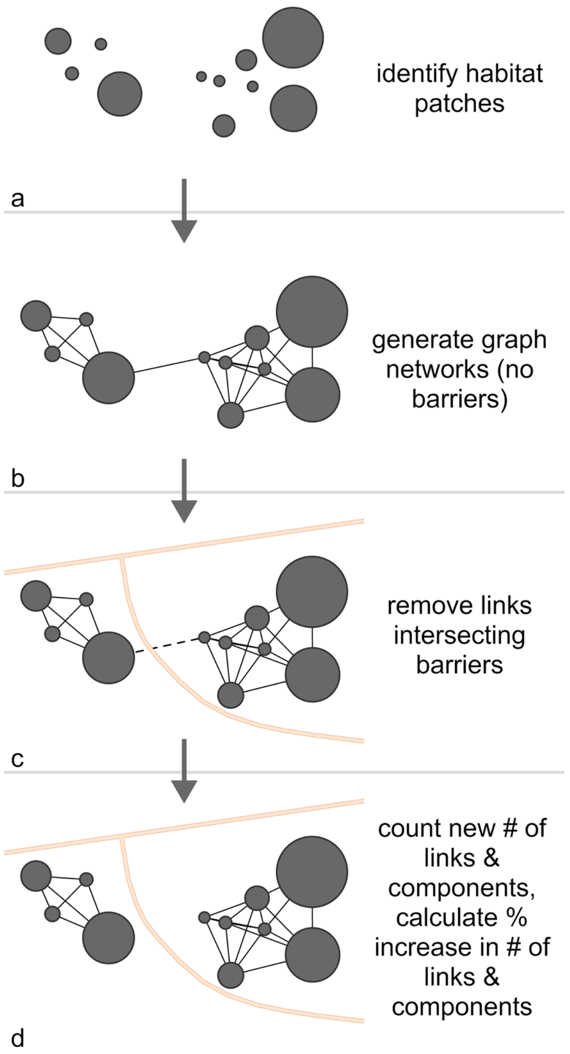
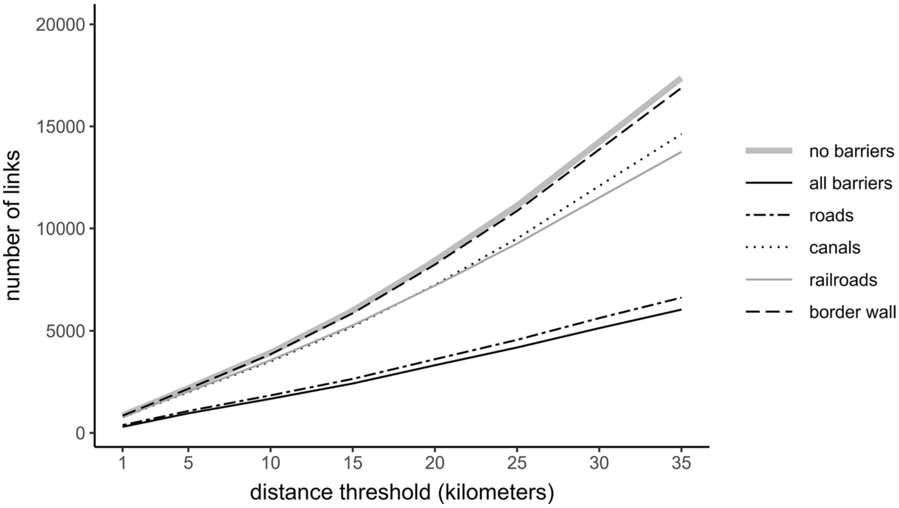


Fig. 2 A diagram of the process for creating graph networks and calculating the percent increase in fragmentation resulting from the inclusion of barriers in the graph networks. This process was performed for each barrier type individually and all barrier types combined. Habitat patches are represented as gray circles; gray lines are links. **a** Habitat patches are located on the landscape. **b** A distance threshold is applied to create a habitat patch network (graph network) of patches separated by greater than that distance. **c** The effects of barriers on the network can be simulated. Orange lines are barriers; a link intersected by a barrier is indicated by a dashed line. **d** Based on links removed in step c, the change in network connectivity (e.g. the splitting of a network component) can be quantified

integrate the area provided by each patch individually with the habitat area that becomes available through connections with other patches and may thus be considered a habitat availability index (Pascual-Hortal and Saura 2006). By integrating habitat area or quality with interpatch connectivity, dIIC is sensitive to changes to changes within each patch (e.g. from a reduction in patch area or degradation of habitat quality within a patch) and between patches (e.g. from the loss of a patch in the network, or the loss of connections to other patches), making it an ideal index for prioritizing patches for the maintenance of structural landscape connectivity (Pascual-Hortal and Saura 2008). Calculating dIIC involves calculating an overall value for structural connectivity (integral index of connectivity, IIC; Pascual-Hortal and Saura 2006), then iteratively removing each patch and recalculating that overall value to quantify the relative change in the network's connectivity. Patches that create a relatively greater decline in overall structural connectivity when removed receive a high dIIC score and are thus important for maintaining connectivity based on their position in the network and size. We calculated dIIC using patch area (square kilometers) as the additional attribute to identify patches of moderate to high suitability habitat that may serve as a source of dispersing individuals to a relatively high number of neighboring patches, regardless of their topological position. When considering patch area with this metric, high-scoring patches are typically the largest patches, or those that strike a balance between the area they provide and the number of adjacent patches to which they are connected.

To identify patches that played an important role in maintaining structural landscape connectivity prior to the development of barriers and those that are important for maintaining connectivity given the extent of barriers in the modern landscape, we calculated these indices for graph networks that excluded barriers and graph networks that included all barrier types combined. We then ranked all patches within the species' range based on their respective BC and dIIC scores, identified the top 50 highest-scoring patches for both indices at all distance thresholds, and calculated the proportion of those patches that are within the United States, Mexico, or that are shared between the two countries. To quantify the effect of linear barriers on individual patch importance, we computed the difference in these index values per patch for both scenarios to identify patches whose role in maintaining structural connectivity has been diminished by the development of barriers, or patches that have become more important for connectivity in the modern landscape.

Fig. 3 The number of intact links between habitat patches at each distance threshold for graph networks excluding barriers and graph networks including barriers. Graph networks incorporating all linear barriers caused the greatest decrease in links between habitat patches, though only slightly more so than roads



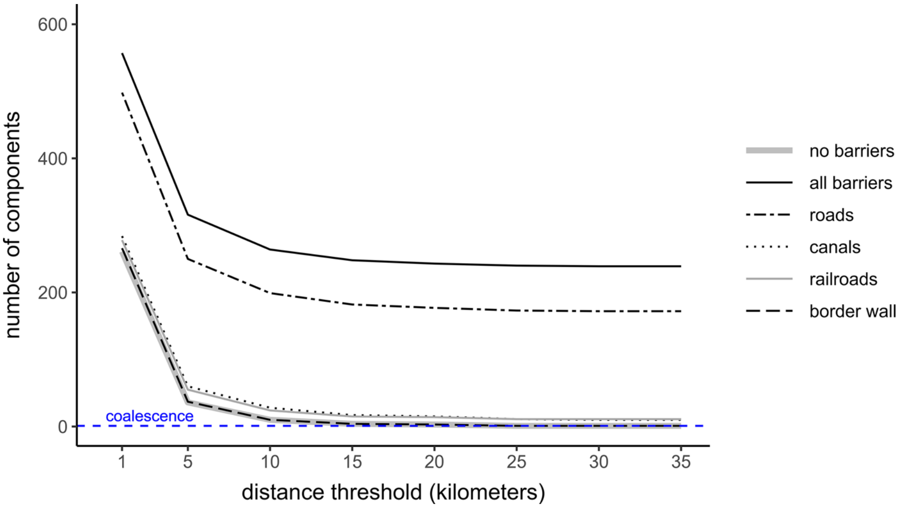
Results

Impacts of barriers on network compartmentalization

For graph networks excluding linear barriers, structural connectivity increased as the distance threshold increased. This was demonstrated by a gradual increase in the number of links between habitat patches (Fig. 3) and a gradual decrease in the number of patch components until all habitat patches coalesced into a single component (Fig. 4). At the 1 km distance threshold, the graph network was composed of 261 separate components, the largest of which comprised nearly a quarter of all habitat patches in the network (232 of the 962 habitat patches). Of these 261 components, 161 represented individual habitat patches with no neighboring patch within 1 km. The network of isolated components began to coalesce as the distance threshold increased, forming a single component (a fully connected network) at the 25 km distance threshold.

For graph networks with barriers in the landscape, the number of links also steadily increased as the distance threshold increased, but the number of links left intact differed for each barrier type (Fig. 3) and coalescence did not always occur. Network compartmentalization was greater for graphs incorporating barriers than those excluding linear barriers at all distance thresholds except for those incorporating only the border wall (Fig. 4). The border wall alone resulted in relatively little increase in compartmentalization at distance thresholds of 1 to 5 km, and there was no

Fig. 4 The number of components (clusters of habitat patches) at each distance threshold for graph networks excluding barriers and graph networks including barriers. Lines that intersect the dashed blue line (coalescence) indicate those barrier types that do not prevent network coalescence. The larger the difference between lines, the greater the effect of the barrier type on connectivity. Lines that intersect the dashed blue line coalesced into a single habitat patch cluster



increase in compartmentalization at distance thresholds greater than 10 km. Ultimately, the coalescence distance of the network remained unchanged when the border wall was included in the analysis.

When other barrier types were included in network graphs, coalescence never occurred, and some components or individual patches were isolated from one another, though to varying degrees of severity (Fig. 4). For example, the presence of canals in the landscape created only 23 additional components at the 1 km distance threshold and 10 additional components at the 35-km distance threshold. The impact of railroads on network compartmentalization was comparable to canals. Highways, on the other hand, severely compartmentalized the network: At the 1 km distance threshold there were nearly twice as many network components as graphs excluding these linear barriers. At the 25 km distance threshold, the distance at which the habitat patch network would coalesce in a barrier-free landscape, the network with roads and highways consisted of 173 isolated components. Unsurprisingly, the inclusion of all linear barrier types combined created the most severe increase in network compartmentalization: The network was fragmented into 239 components, 69% of which were individual habitat patches that were isolated from any other patch by the border wall, a canal, railroad, or major road or highway. For all graph networks, there was relatively little change in network compartmentalization at distances greater than 10 km.

Patch importance

Patch importance for graph networks excluding barriers differed from graph networks simulating linear barriers in the landscape. When comparing the centrality (BC) of individual patches before and after barriers were simulated in the landscape, patch centrality mostly decreased or remained unchanged (Fig. 5). The proportion of patches for which centrality increased, decreased, or did not differ when barriers were incorporated into graph networks changed as the distance threshold increased. Fewer patches remained unchanged by the inclusion of barriers as the distance threshold increased and, consequently, the proportion of patches that experienced a decrease in centrality when barriers were included went up from 30 to 97%. Patches experienced the most severe reduction in centrality when the distance threshold increased from 1 to 5 km. Few patches increased in centrality, and the proportion of patches that did fluctuated between < 1.5% and 4%. The case for the most important patches for maintaining structural connectivity based on dIIC was much different (Fig. 6). At the 1 km distance threshold, the proportion of patches that decreased or increased in importance was nearly equivalent: 46% of patches decreased in importance and 54% of patches increased in importance. However, the proportion of patches that decreased in importance sharply increased to 78% at the 5 km threshold and remained between 73 and 79% with increasing distance. All patches experienced some change in importance at each distance threshold.

The spatial distribution of important patches also changed when barriers were included in graph networks. For graph networks excluding barriers, the top 50 most important stepping stones were distributed throughout the species' range at all distance thresholds except the 1 km threshold, for which 96% of these patches were in the United States (Fig. 7). For graph networks including barriers, most (80–96%) stepping stones were in Mexico for each distance threshold (Fig. 7). The reverse of this pattern was seen when patch importance was based on dIIC. When barriers were excluded from graph networks, most of the highest importance patches were in the United States (66–83%) for all distance thresholds (Fig. 8). However, when barriers were included in the analysis, the proportion of important patches in Mexico and the United States became nearly equivalent for each distance threshold (Fig. 8). When barriers were included, the number of important patches shared between both countries for both indices increased by one or two patches for each distance threshold (Figs. 7, 8).

Discussion

Historically, geographic distance appears to have been the greatest limiting factor in dispersal between Sonoran desert tortoise populations (Edwards et al. 2004). Little genetic structuring throughout their range suggests that gene flow between populations was made possible by long-distance movements that may no longer occur (Edwards et al. 2004). We showed that permanent, linear barriers may be reducing structural connectivity of Sonoran desert tortoise

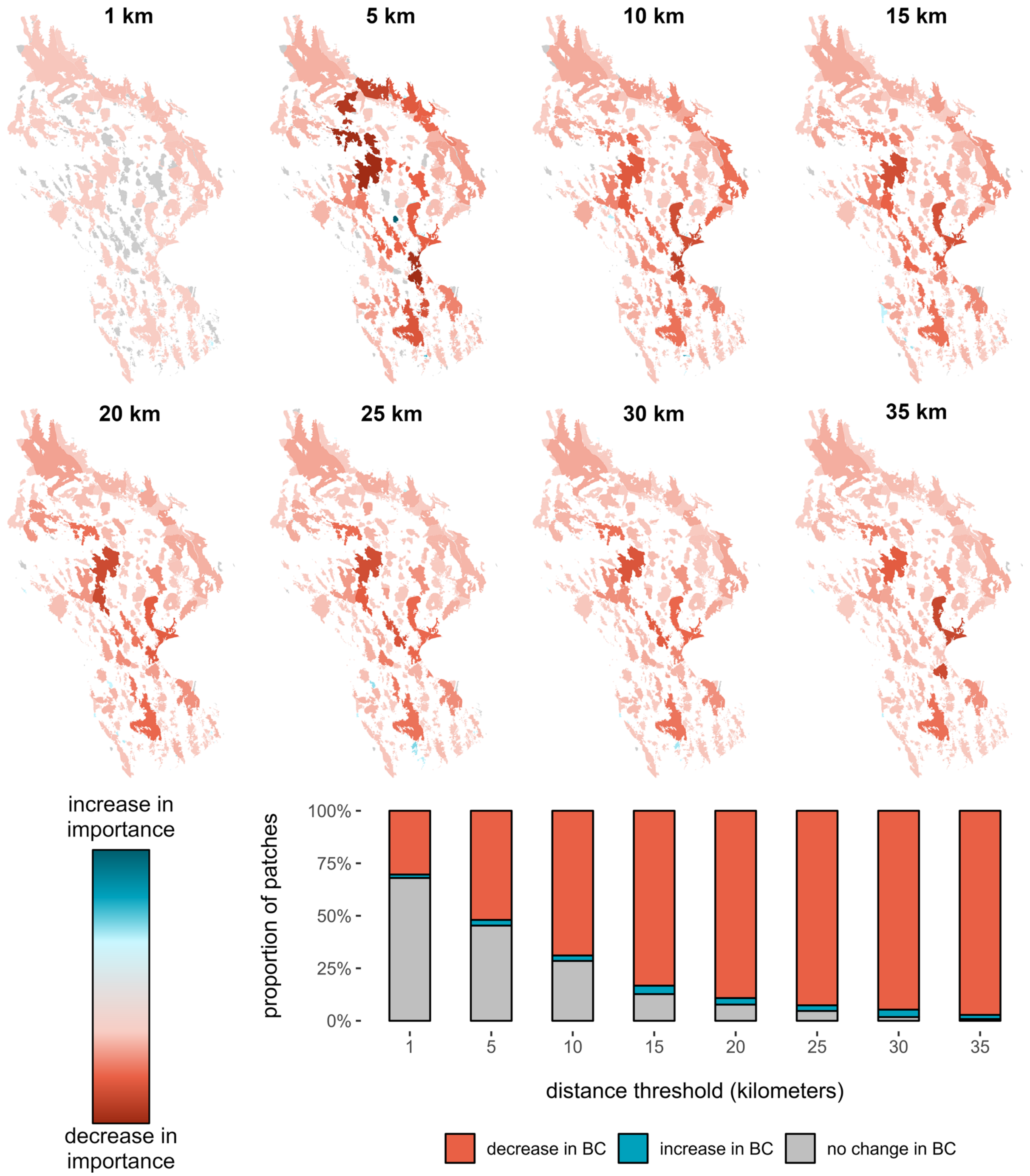


Fig. 5 Changes in patch importance at different distance thresholds (1–35 km) when barriers of all types were included in the landscape. Habitat patches (shaded polygons) that experienced an increase (blue), decrease (red), or no change (gray) in centrality (i.e., importance as a stepping stone patch based on their BC score) are depicted

habitat throughout the species' range, and that this impact is disproportionately seen in the northern half of their range. This decrease in structural connectivity was indicated by increases in network compartmentalization across spatial scales. Canals, railroads, major roads, and highways increased network

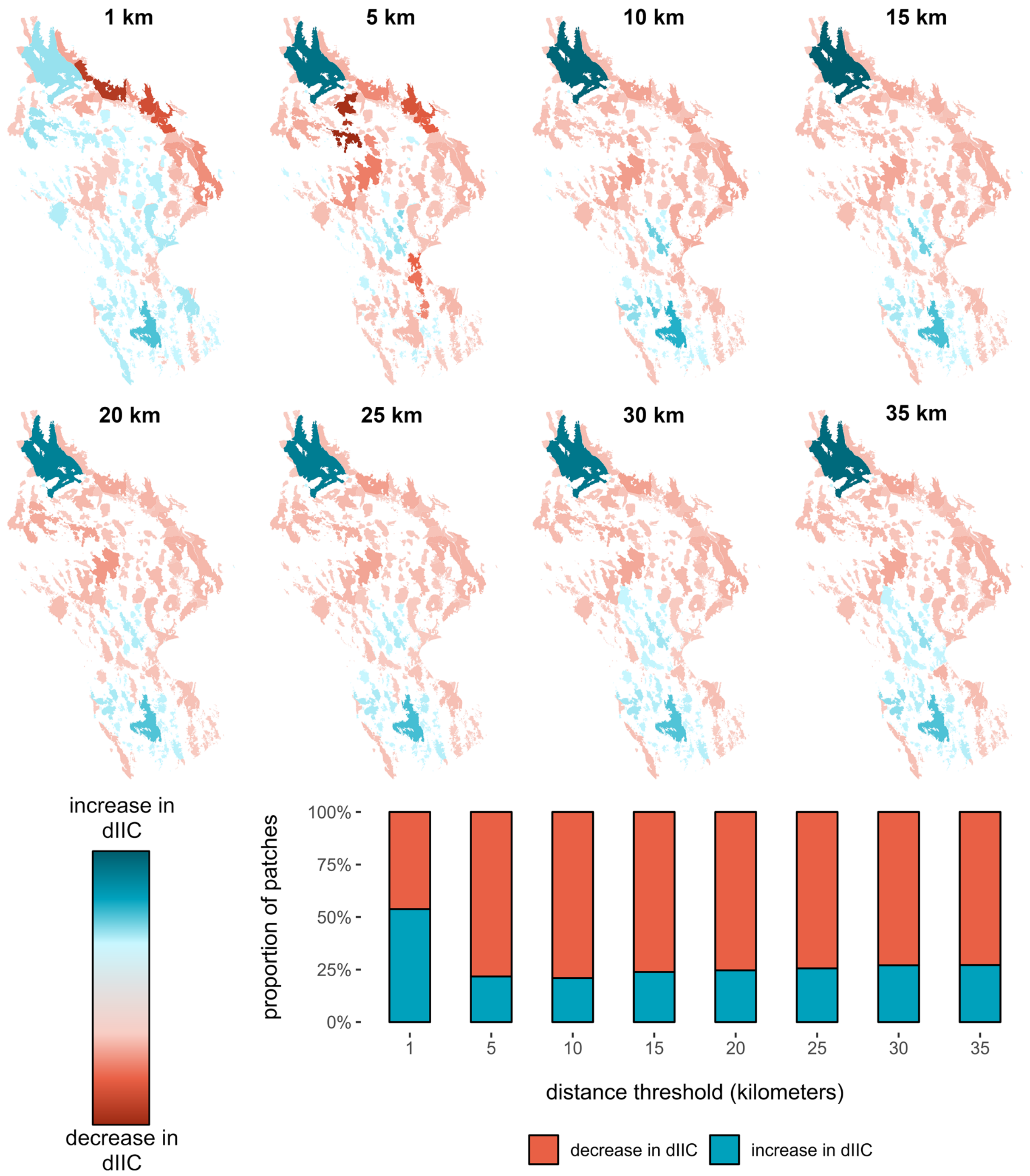


Fig. 6 Changes in patch importance at different distance thresholds (1–35 km) when barriers of all types were included in the landscape. Habitat patches (shaded polygons) that experienced an increase (blue) or decrease (red) based on their dIIC score are depicted

compartmentalization and, with the exception of the border wall, also prevented the network from coalescing at all distance thresholds (Fig. 4). However, the impacts of each barrier individually varied in severity, possibly due to differences in their prevalence on the landscape: canals and railroads were relatively less common than roads and highways. Barriers in the landscape also caused the importance and spatial

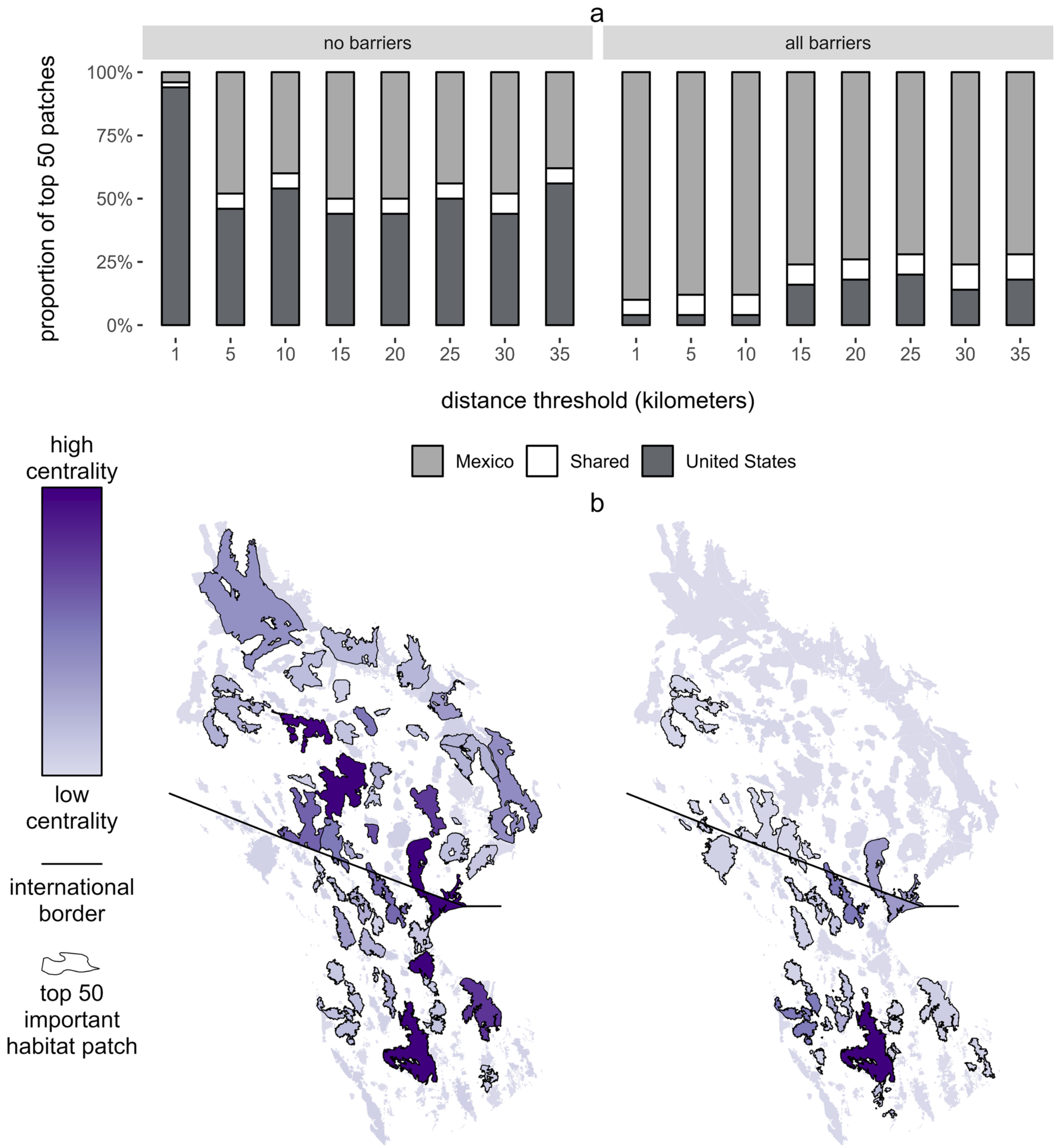


Fig. 7 **a** Changes in the proportions of the top 50 most important stepping stone patches (based on BC score) at different distance thresholds (1–35 km) within the US (dark gray), Mexico (light gray), and common to both countries (white) due to the effect of barriers. **b** Changes in the location of the top 50 most important stepping stone patches at the 35 km distance threshold when barriers of all types were included in the landscape

distribution of habitat patches to change, resulting in fewer important patches in the northern portion of the species' range and more important patches located along and south of the international border (Figs. 7, 8). Although the consequences of these barriers on movement or gene flow (e.g. reduced structural connectivity) may not become detectable until generations have passed (Landguth et al. 2010), our results

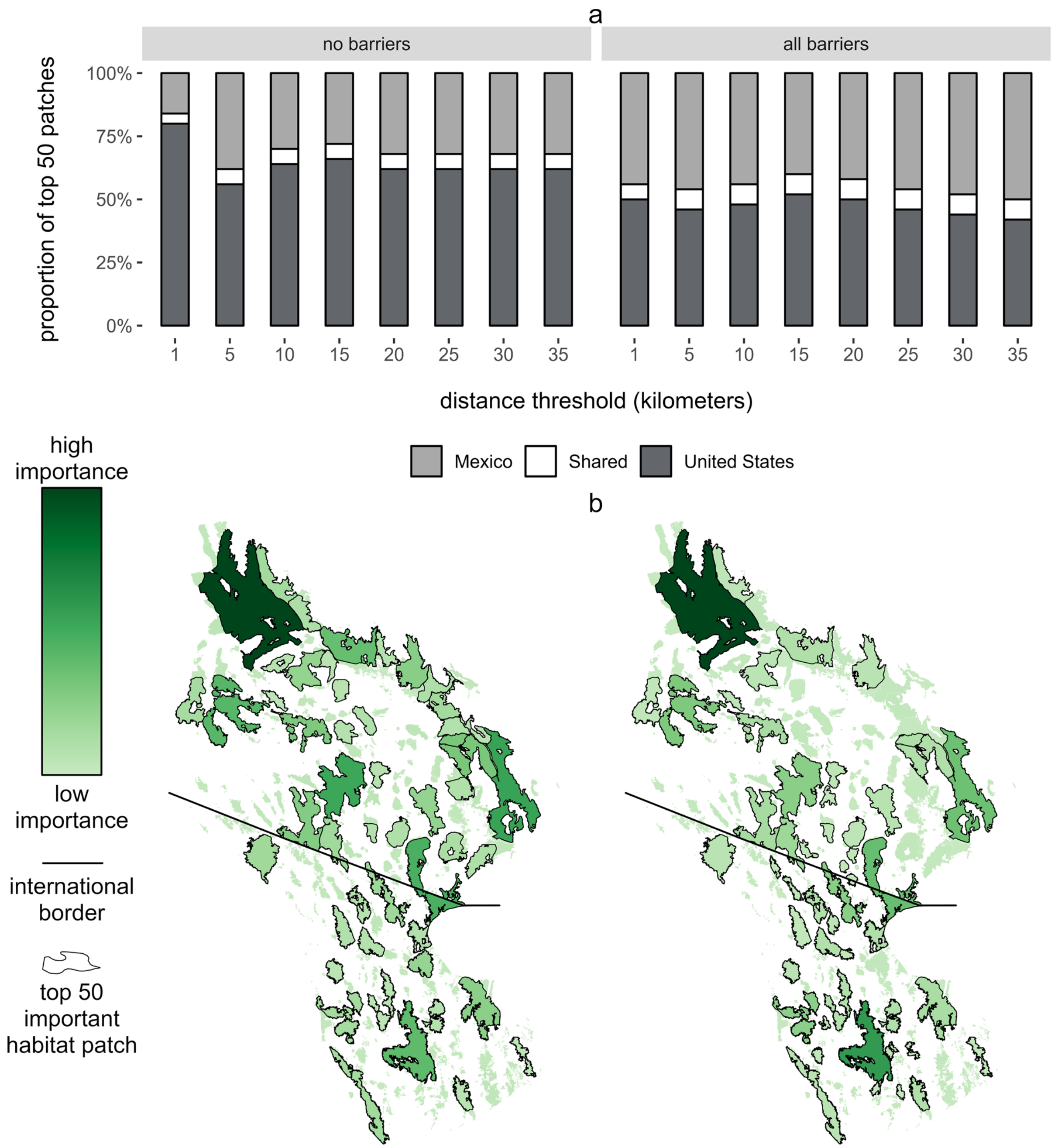


Fig. 8 **a** Changes in the proportions of the top 50 most important patches (based on dIIC score) at different distance thresholds (1–35 km) within the US (dark gray), Mexico (light gray), and common to both countries (white) due to the effect of barriers. **b** Changes in the location of the top 50 most important patches at the 35 km distance threshold when barriers of all types were included in the landscape

support the position that the long-distance movements that once united populations are now likely impossible (Edwards et al. 2004).

In the context of our study, compartmentalization can be interpreted as fragmentation of the habitat patch network that comprises the species' range. Because ecological and evolutionary processes are more likely to occur within than between components (Bodin and Norberg 2007), the increase in the number of network components (i.e., compartmentalization) seen in our results provided evidence that linear barriers are likely reducing the potential for the landscape to facilitate these processes. In doing so, these barriers may be exacerbating the isolation of individual habitat patches and patch clusters that are already isolated by geographic distance and embedded in a harsh desert matrix (e.g. valleys that do not provide tortoise habitat or shelter). Linear barriers created 165 network components that represent individual habitat "islands," which is particularly concerning given that tortoise populations approaching extirpation may heavily rely on immigrants from neighboring habitats (Edwards et al. 2004). An important finding of our analyses was the presence of a critical threshold between 5 and 10 km, at which network compartmentalization resulting from linear barriers only moderately continued to increase with increasing distance. Management actions focused on restoring structural connectivity between habitat patches separated by as little as 5 km are likely to promote connectivity for movements greater than the longest recorded movement of a Sonoran desert tortoise, thus improving the potential for ecological processes, rescue effects, and more that may occur at different spatial and temporal scales.

The changes in individual patch importance that occurred when the impacts of barriers were incorporated in graph networks provided an additional perspective on the consequences of linear barriers. A decrease in importance of a given patch as a stepping stone reflects an increased degree of isolation between habitat patches or patch clusters caused by barriers, which reduces permeability of the landscape. Important linear barriers, namely major roads and highways, are pervasive in the study area; the isolation of even one habitat patch from a cluster it would otherwise be connected to will cause a decrease in centrality and thus a decrease in importance. Patches that saw the greatest reduction in BC score represent patches that may have historically played an important role as stepping stones but, due to the development of linear barriers, now may play a diminished role in facilitating structural landscape connectivity.

Of additional concern is the change in the spatial distribution of important patches (Figs. 7, 8) that occurred when the impacts of barriers were included in analyses. The spatial distribution of stepping stones, once distributed throughout the species' range, became heavily concentrated in the southern part of their range (Fig. 7). The number of important stepping-stones along the international border marginally increased by one to two patches depending on the distance threshold. Stepping stones facilitate long-distance dispersal through the landscape and may facilitate a species' shift in range in response to climate change (Saura et al. 2014). The Sonoran desert tortoise, a species that is considered highly vulnerable to climate change (Griffis-Kyle et al. 2018; USFWS 2021) and that is hypothesized to disperse generationally in a stepping stone-like pattern, may benefit from habitat patches that serve as stepping stones. Under worst-case scenarios projected by the USFWS, high-suitability habitat for the tortoise is expected to shift northward and eastward (USFWS 2021). By causing the most important stepping stone patches to be located in the southern portion of the species' distribution, potential northward range shifts may be impeded by linear barriers and the rapidly changing landscape of the United States-Mexico border region. Although it caused the least effect on network compartmentalization due to its short relative length and limited spatial extent compared to other barriers in our analysis, United States-Mexico border wall pedestrian fencing is an impassable barrier to juvenile and adult tortoises (USFWS 2021) and bisects the heart of the species' range. Additionally, this region experiences intense off-road vehicle use and frequent vehicular traffic related to border security and construction that occurs adjacent to the wall and along the international border. These activities may inhibit or block tortoise movement even where an impassable border wall does not exist, further reducing structural landscape connectivity and thus inhibiting a northward range shift in response to climate change that may occur from populations south of the international border. With the exception of a single habitat patch, the northernmost important BC patches are situated along the international border or within the border region (Hajost 1984), suggesting these patches may be integral to supporting potential range shifts in response to climate change.

In contrast to the changes in importance and the spatial distribution of stepping stones, not all patches decreased in importance when measured by dIIC, which takes patch area into account. Some patches, especially in the southern portion of the species' range, increased in importance when barriers in the landscape were included in our analyses. Patches that increased in importance were typically those that retained connections to adjacent habitat patches, whereas others became isolated from adjacent patches by the presence of a linear barrier between them. Patches with a relatively high dIIC value were typically the largest patches or ones with intact connections to several adjacent patches. These may be interpreted as potential sources of dispersing individuals or a likely recipient for immigrating individuals. In some instances, smaller patches that had many connections to neighboring patches received a high dIIC score. These may be interpreted as more reachable patches, or patches that are more likely to receive immigrant tortoises than others because of their intact connections with adjacent patches.

In our study, patches with a high dIIC are less likely to experience local extirpation or extinction because they are either large enough to provide habitat for a viable population, or well-connected (less isolated by barriers) enough to receive immigrants and thus rescue effects from other patches (MacArthur and Wilson 1967; Frankel et al. 1981; Lande 1988). Including barriers in the landscape caused a southern shift in the spatial distribution of the most important dIIC patches, though to a much lesser degree than for stepping stones, resulting in an approximately even proportion on either side of the international border (Fig. 8). Because dIIC considers available habitat area to be an important aspect in maintaining overall structural connectivity, many of the largest habitat patches remained within the top 50 important patches because of the amount of habitat they provide, regardless of whether they experienced an increase or decrease in importance when barriers were included in the landscape. For this reason, despite the greater prevalence of important patches in the northern portion of the species' range, the less-severe southern shift in important dIIC patches compared to the dramatic shift in stepping stone patches was unsurprising. Approximately 72% of Sonoran desert tortoise habitat in the United States is on managed, multi-use, or Tribal-owned land (USFWS 2021), so many large and relatively intact habitat patches still exist.

Although canals and the border wall pedestrian fencing are considered impermeable barriers to tortoise movement (USFWS 2021), the permeability of other barriers included in our analysis vary in space and time. For example, although tortoises are highly vulnerable to mortality and population isolation from roads (Andrews et al. 2015), the most dynamic in permeability of the barriers included in our study, they do occasionally cross them. Factors such as speed limit and traffic volume influence the permeability of this barrier to tortoise movement (Nafus et al. 2013), and culverts may provide safe passage from one side of a high-traffic road to the other (Boarman et al. 1997). For this reason, the results of our study best represent a worst-case scenario of barrier hardness, and the clusters of habitat patches resulting from the inclusion of roads in the landscape may be best viewed as groups of habitat patches between which movement, dispersal events, or gene flow are diminished. Furthermore, the results of our analyses should not be interpreted as areas where connectivity should necessarily be enhanced, as there are potentially negative consequences to increasing connectivity without careful consideration. Previous studies have illustrated that increasing connectivity can facilitate the spread of invasive species (Drake et al. 2017) or disease (Burgess et al. 2021), both of which are concerns for desert tortoises (Burgess et al. 2021; USFWS 2021). However, the flexibility in the framework we present provides managers the ability to incorporate information that can help predict and prevent these often unforeseen, negative consequences of enhancing structural connectivity. For example, incorporating spatially explicit information on disease presence may help managers identify strategies that enhance connectivity among tortoise populations while isolating infected populations.

Our results may be useful for identifying areas where restoring connectivity between tortoise habitat patches should be explored as a potential management strategy or for identifying at-risk or priority habitat patches to direct conservation efforts. Our results may also be useful to researchers targeting areas for future studies focused on exploring other aspects of tortoise ecology related to barriers to movement or habitat fragmentation. For example, managers may focus on maintaining landscape connectivity for intact patch clusters by preventing the development of new barriers through them or ensuring the matrix between patches in the cluster does not become degraded by activities that may inhibit tortoise movement (e.g. off-road vehicle use). Conversely, managers may instead focus efforts on patch clusters that became fragmented when barriers were included in our analyses by placing signage or developing road culverts along the barrier to help restore structural connectivity. Managing some barriers (e.g. an interstate highway) or matrix habitat between managed lands may not be an option, though the ranking of individual patch importance based on BC and dIIC may be useful in prioritizing habitat patches to focus conservation efforts. For example, a stepping stone patch that facilitates structural connectivity within a patch cluster, or a large habitat patch with some smaller, connected neighboring patches (high dIIC), may be a prime target for actions seeking to uphold habitat quality to ensure such patches continue to serve their respective roles in maintaining structural landscape connectivity. Researchers may similarly target intact or fragmented clusters, or areas where patches fluctuate in importance. These areas may provide opportunities to further examine aspects of tortoise connectivity or ecology that are beyond the scope of our current analyses, like whether a specific barrier (e.g. a segment of railroad) is reducing gene flow between populations, as has been studied for the desert tortoises in the Mojave Desert (Dutcher et al. 2020).

In this study, we demonstrated how linear barriers to tortoise movement and dispersal are fragmenting landscape connectivity and may be changing the role and spatial distribution of important habitat patches, which may suppress the species' ability to persist in the rapidly changing landscape that is the Sonoran Desert. Our results may best be interpreted as estimates of the extent to which linear barriers may be fragmenting connectivity among habitat patches, or a worst-case scenario should these barriers become less permeable to movement. We recommend using our results to guide future studies using empirical data to test the impacts of barriers on movement or gene flow between Sonoran desert tortoise populations. Additionally, the habitat patches we identified as being important for range-wide connectivity may best be considered potential targets for future studies and investigation, as well as the intervening valleys adjacent to these potentially important patches. Empirical data derived from studies examining space and habitat use (e.g. home range analyses) and movement through the landscape (e.g. tortoise responses to landscape characteristics) may help develop meaningful wildlife corridors (e.g. sufficient width and resources) for desert tortoises (Beier 2019; Hromada et al. 2020) and may help elucidate the impacts of barriers on local scale and range wide.

Our modification of the traditional node-and-link measures of connectivity presents a unique framework that may be applied to other taxa and at different spatial scales to examine the potential impacts of natural or anthropogenic barriers on landscape connectivity. Additionally, our approach may be applied to examining the potential impacts of a future barrier development and may be useful in determining where a barrier (e.g. road, canal) may have the least overall impact on connectivity. Furthermore, by reversing our approach (e.g. remove a barrier, add a link between patches), it would be possible to examine the effects of removing a barrier. We recommend other researchers and managers consider other innovative approaches to examining the impacts of barriers on connectivity, including incorporating empirical data to their approach.

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Author contributions S.W.S. developed the methods, performed all analyses, and drafted the manuscript. N.E.M. and K.G.K. wrote the proposals that funded the work, provided valuable input on the final methods and manuscript, financially supported the research, and edited the manuscript. All authors read and approved the final manuscript.

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Data availability All data produced as part of this study are property of the U.S. Department of the Interior National Park Service Southwest Border Resource Protection Program. Code and example data for reproducing these analyses will be made available upon request to the corresponding author.

Declarations

Competing interest The authors have no relevant financial or non-financial interests to declare.

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