



# A range-wide model of contemporary, omnidirectional connectivity for the threatened Mojave desert tortoise

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**Abstract.** As habitat destruction leads to species extinctions globally, conservation planning that accounts for population-level connectivity and gene flow is an urgent priority. Models that only approximate habitat potential are incomplete because areas of high habitat potential may be isolated, whereas intermixed areas of lower habitat potential may still be critical for maintaining connectivity between and among populations. We developed a range-wide, omnidirectional (coreless) connectivity model and map for the threatened Mojave desert tortoise at a high spatial resolution (30 m), based on empirical movement data and a circuit-theoretic approach to estimating connectivity. Specifically, we first estimated habitat potential (i.e., quality) for tortoise movement (as distinct from habitat potential more generally) across its range using hypotheses based on the published literature, linear mixed models, multiple environmental factors derived from remotely sensed data, and recent solar and wind development footprints. The resultant raster output was used to represent landscape conductance in a circuit-theoretic model of connectivity, which relates the flow of electrical current through a circuit to the movement of tortoises through the landscape. We then modeled potential connectivity across the range of the tortoise using *Circuitscape* software and the Julia numerical programming language. Intermediate distances from minor roads, intermediate values of annual average maximum temperature, and increasing density of desert washes were among the strongest predictors of movement habitat quality. There was also strong evidence for increased habitat quality for movement with increasing amounts of vegetation cover. The resulting connectivity model and map was determined to accurately reflect important areas for tortoise movement, but we encourage others to do their own evaluation of the model within local areas of interest and as more data become available. Accordingly, the map can provide an important component to improve management decisions that have the potential to influence the conservation of connected desert tortoise populations throughout the range.

**Key words:** circuit theory; connectivity; conservation; Mojave desert tortoise.

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## INTRODUCTION

Habitat destruction is the leading cause of species extinctions globally, driven at more local levels by patterns of habitat fragmentation that

reduce species persistence and movement (Pimm and Raven 2000, Haddad et al. 2015). Characterizing the potential connectedness of a landscape based on the relevant biology and movement of species can identify areas that facilitate

movement within a fragmented landscape (Rayfield et al. 2011, Kupfer 2012). Restoring or maintaining functional connectivity, in turn, leads to increases in species occurrence or abundance, gene flow, and diversity (Fletcher et al. 2016). It is therefore important to consider the separate contributions of the two major processes of land-use change—habitat loss and fragmentation—on species persistence, in order to identify opportunities where optimizing connectivity could mitigate the negative consequences of habitat alteration (Hadley and Betts 2016).

The Mojave desert tortoise (*Gopherus agassizii*) was listed as threatened under the Endangered Species Act by the U.S. Fish and Wildlife Service (1990) and continues to be negatively impacted by land-use and land cover changes across its range. The vast majority of threats to the species' persistence are associated with both widespread habitat loss or degradation and fragmentation due to human land uses (U.S. Fish and Wildlife Service 2011, Tuma et al. 2016). Moreover, conservation activities are difficult to achieve at a range-wide scale because development continues to occur at local scales and across multiple jurisdictional boundaries (Averill-Murray et al. 2012).

For the Mojave desert tortoise, which occupies a large, heterogeneous range, and yet displays little above-ground movement, it can be challenging to infer landscape-level connectivity from direct observations of movement or dispersal. Rather, indirect methods that infer connectivity from genetic data have been used previously (Hagerty et al. 2011, Sánchez-Ramírez et al. 2018). However, genetic studies might not detect the effects of landscape fragmentation for many generations, which can amount to over a century for this long-lived species (U.S. Fish and Wildlife Service 1994, Landguth et al. 2010). Therefore, although genetic studies can be useful for detecting historical patterns and barriers to landscape connectivity for the tortoise, inferences drawn from these studies cannot account for the recent pace and scale of fragmentation across the species' range.

The Mojave desert tortoise occupies a region impacted by rapid solar energy development and land-use conversion (Lovich and Ennen 2011). Much of this development has occurred in high-quality tortoise habitat, but attention is also on the amount of degraded lands in the Mojave

Desert that are still suitable for development (Cameron et al. 2012, Gibson et al. 2017). Yet, even if new development is proposed in areas with lower regional habitat potential, it is still critical to consider those areas that may have low overall habitat potential but are important for facilitating connectivity.

One approach to manage for connectivity amidst increasing anthropogenic pressures focuses on preserving linkages between habitat cores. For example, focused inter-agency management of Mojave desert tortoise habitat currently occurs within a number of designated tortoise conservation areas (TCAs). Using a resistance surface based on a model of habitat potential, Averill-Murray et al. (2013) delineated least-cost corridors between these TCAs. While this approach provides practical information to help guide the management of discrete habitat areas between TCAs, inferences regarding spatial patterns and degree of connectivity are constrained by the location and extent of these TCAs. A seamless, omnidirectional connectivity map would allow inferences to be made in a range-wide context and would support Mojave desert tortoise management beyond designated TCAs or the least-cost corridors between them.

Given the pace and scale of ongoing development and fragmentation in the Mojave ecoregion, the objectives of our study were to (1) leverage existing, high-resolution telemetry data to develop an empirically based, range-wide model and map of movement habitat potential (i.e., a map of landscape conductance) for the Mojave desert tortoise, and at a resolution relevant to the scale of movement; and (2) use this model to derive a range-wide estimate and map of potential omnidirectional connectivity, and that did not rely on the delineation of discrete habitat or population cores. The principal goal of our work was to provide practical, contemporary information to guide planning and Mojave desert tortoise conservation efforts at local to regional scales.

## STUDY AREA

The range of the Mojave desert tortoise encompasses roughly 13 million ha, with most of this area falling within southern California and Nevada, and some areas in northwestern

Arizona and southwestern Utah (Fig. 1). Vegetation is dominated by a creosote/bursage shrub alliance, with Mojave desert mixed scrub in upland areas and yucca–blackbrush community at higher elevations (Nussear and Tuberville 2014). The northern portion of the range overlaps the Basin and Range geomorphic province, characterized by steep, elongated mountain ranges interspersed by long, flat, dry desert valleys (Randall et al. 2010). The southern portion of the range is characterized by isolated sky-island mountain ranges separated by vast expanses of desert flats and overlaps the Colorado Desert subdivision of the Sonoran Desert in the southern-most extent. Approximately 4.5 million ha of the range has been identified to have some potential habitat value for the desert tortoise, with 94% of this area having above-average habitat potential (Nussear et al. 2009).

## MOVEMENT DATA AND MODELING

To develop an empirical model of movement habitat potential (i.e., quality), we obtained relocation data for individual tortoises and used Brownian bridge movement models (BBMMs) to estimate the probability of an individual moving through a given area between consecutive relocations (Horne et al. 2007, McClure et al. 2017). A central assumption of Brownian bridges is random movement between consecutive locations, which becomes progressively unrealistic as time between locations increases. Therefore, if the time between consecutive locations exceeded 24 h, then a Brownian bridge was not fitted for that location pair. This central assumption limited our dataset to 31 tortoises that were fitted with either very high-frequency (VHF) radio transmitters or global positioning system (GPS) data loggers from 2007 to 2010, and located in the Hidden Valley and the Mormon Mountain foothills, Nevada (Drake et al. 2015, Sah et al. 2016; K. Nussear and T. Esque, *unpublished data*; Fig. 1). Consecutive, daily locations were also screened to be >25 m apart to capture movements that were more likely made beyond (vs. within) clustered burrow networks (Sadoti et al. 2017). By doing so, we assume what's driving these longer distance movements is different than what would drive a movement decision within a more concentrated activity center.

Brownian bridge movement models were estimated for each individual per year with at least 25 re-locations in that year (resulting in 1554 total relocations and  $n = 47$  BBMMs), using the BBMM package (Nielson et al. 2015) for R (version 3.5.1; R Development Core Team 2011).

## ENVIRONMENTAL COVARIATES

After estimating BBMMs for individual tortoises, we identified environmental covariates that are known to influence movement by desert tortoises, in order to relate these covariates to BBMM estimates and fit models of movement habitat quality. Because our movement models were estimated in a very small portion of the tortoise's range (Fig. 1), we only identified covariates that showed sufficient variability within the Hidden Valley and the Mormon Mountain foothills, where our relocation data were obtained. Specifically, we focused on covariates describing presence of desert washes, distance to minor roads, amount of available vegetation, and 30-yr average temperatures. Range-wide, spatially explicit data layers representing these covariates were obtained or derived from public data sources, and at 30-m resolution, using bilinear interpolation when appropriate. All values were standardized and rescaled prior to relating them to BBMM estimates (Schielzeth 2010).

Intermittent or ephemeral stream channels, also known as desert washes, are preferred habitat features and foraging corridors used by the Mojave desert tortoise (Jennings and Berry 2015, Nafus et al. 2017). To produce an accurate, range-wide model of washes, we first drew on an existing model of washes derived for the Ivanpah Valley of southern California, in the eastern Mojave Desert (1-m resolution; Farnsworth et al. 2015). This map was derived from USDA National Agricultural Imagery Program (NAIP; U.S. Department of Agriculture Farm Service Agency 2016) imagery using a random forest classification model (Breiman 2001) and had an initial overall accuracy of 88.4% (Farnsworth et al. 2015). We treated this map as training data in a convolutional neural network (CNN) model. Convolutional neural networks are computational models inspired by the way neural networks in the human brain process information. The specific CNN architecture we implemented,

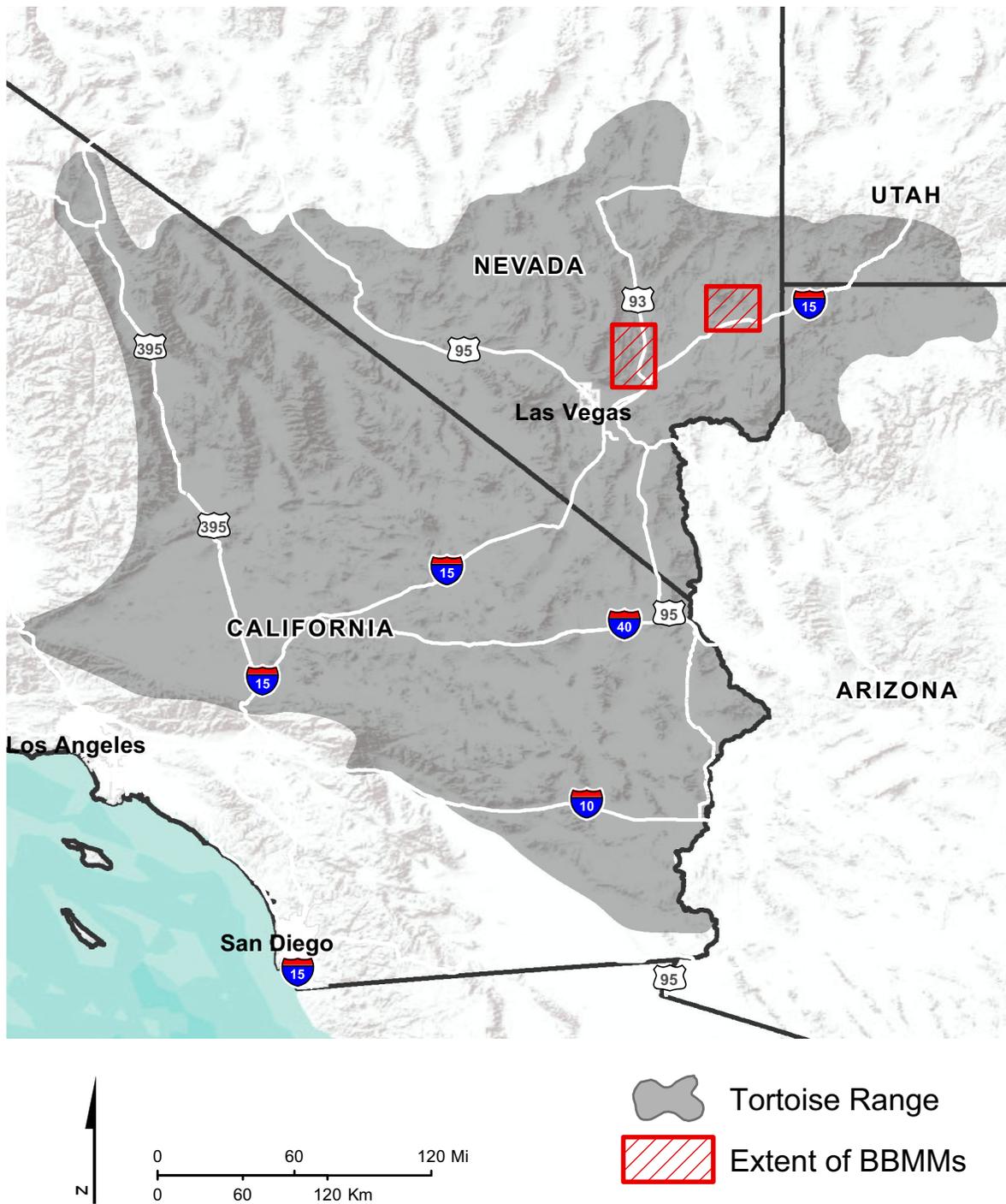


Fig. 1. Range of the Mojave desert tortoise (*Gopherus agassizii*) within the Mojave Desert ecoregion, USA. Tortoise relocation data from 2007 to 2010, collected within the red rectangles, were used to build Brownian bridge movement models (BBMMs) and model movement habitat quality across the range.

called an encoder–decoder, has been successfully applied in a wide variety of image classification studies (Badrinarayanan et al. 2015). In our case, the model was trained to classify each 1-m pixel as the likelihood of it being a wash, based on four-band color-infrared reflectance values of 2016–2017 NAIP imagery across the tortoise’s range. We implemented this model with Keras (<https://keras.io/>), which is a neural network programming interface written in the Python programming language (see also Appendix S1). We then used the 50th percentile of predicted wash values as a cutoff to create a binary map of washes across the tortoise’s range. To capture wash availability for tortoise movement, we calculated mean wash density within a 90-m moving window before resampling to 30 m, assuming tortoises assess conditions within a local use area before making longer distance movements (Sadoti et al. 2017).

We used the same 2016–2017 NAIP imagery described above to derive the Normalized Difference Vegetation Index (NDVI) across the tortoise’s range. NAIP imagery was collected in the early summer of both of these years, when annual plants have typically dried up in the Mojave Desert and there is minimal inter-annual variation in the NDVI profile (Wallace and Thomas 2008). Therefore, the NDVI values can be assumed to primarily capture the variability in perennial vegetation across space, which tortoises rely on for shade and shelter (e.g., shrubs and succulents; Andersen et al. 2000). Similar to washes, we calculated mean NDVI within a 90-m moving window, before resampling to 30 m.

In the Ivanpah Valley, California, tortoises were less likely to move longer distances when they were near minor dirt roads (Sadoti et al. 2017). Therefore, we selected minor road features from the 2016 TIGER/Line products, with the feature class code S1400 or S1500 (U.S. Census Bureau 2016). We calculated distance to the nearest minor road feature at a 30-m resolution.

Longer distance movements by tortoises in the Ivanpah Valley were also limited by the hottest temperatures of their active season (Sadoti et al. 2017). We therefore included a covariate of the average maximum temperature of the warmest month, derived from monthly climate normals across the range. Climate normals for the 30-yr period from 1981 to 2010 were downloaded from

5330 stations in the U.S. Desert Southwest (National Oceanic and Atmospheric Administration National Climatic Data Center; <http://www.ncdc.noaa.gov>) and interpolated at a 30-m resolution using a thin-plate spline regression between the climate value, station locations, and elevation (NatureServe, *unpublished data*).

## SPATIAL PREDICTION OF MOVEMENT HABITAT QUALITY

Following methods of McClure et al. (2017), we used linear mixed models (LMMs) and multi-model inference (Burnham and Anderson 2002) to estimate movement habitat quality, based on the relationship between each BBMM (i.e., the probability of movement) and the environmental covariates described above. The spatial extent of each BBMM was defined to include all areas with  $>0.00001$  probability of movement and was buffered by a distance equal to the greatest step length between daily, consecutive locations observed for each individual (McClure et al. 2017). We then selected a random set of 100 points within each BBMM and extracted the values of covariates at the location of these points (Willems et al. 2009). We assessed covariates for pairwise correlations based on Pearson’s correlation coefficients and for multicollinearity based on variance inflation factors (VIFs). All Pearson’s coefficients were  $<0.5$ , and all VIFs were  $<2$  and so we retained all covariates.

We then fit LMMs to log-transformed BBMM values, using individual as a subject-level random effect, and an exponential spatial covariance structure to account for residual spatial autocorrelation (Dorman et al. 2007). We considered all subsets of a global model that contained linear terms (the fixed effects) for the covariates described above, as well as a quadratic term for all covariates except NDVI, for which we only hypothesized a positive, linear relationship to tortoise movement within the local area where our relocation data were obtained. Maximum likelihood and values of Akaike’s information criterion (AIC; Burnham and Anderson 2002) were used to determine how well the global model approximated the data, compared to a null model that included only a subject-level random effect. A global model with an AIC value  $>10.0$  units lower than the null model was considered

to provide a good approximation of the data (Burnham and Anderson 2002). Subsets of our global model were not used for direct inference. For each environmental covariate (i.e., fixed effect), we derived the model-averaged regression coefficients ( $\beta$ ), unconditional standard errors, and a measure of the weight of evidence in favor of a given covariate ( $w_i$ ; Burnham and Anderson 2002). All analyses were conducted in SAS (v9.3; SAS Institute, Cary, North Carolina, USA) and the R statistical environment (v3.0.3; R Development Core Team 2011).

Range-wide movement habitat quality was mapped continuously at a 30-m resolution using the model-averaged regression coefficients. This map was used to represent landscape conductance ( $C$ ; the reciprocal of landscape resistance, such that higher conductance values denote greater ease of movement) for use in modeling connectivity, after taking two additional steps to account for the effects of terrain (slope) and land cover type (i.e., barren ground, open water, and human disturbance) on landscape conductance. First, since tortoises will typically avoid movement across steeper terrain (Luckenbach 1982), we applied the following penalty to areas with steep slopes:

$$C^{1+(\text{slope}^2 \times 40)}$$

This follows a similar approach taken by Dickson et al. (2017), but also assumes that conductance declines more rapidly with increasing slope, and that tortoises will tend to (but not always) avoid very steep slopes. For average movement habitat quality values, the penalty becomes most severe at approximately 30% slope. Second, to assign lower values of movement habitat quality to human development, water, and barren ground, we used a combination of three public datasets (i.e., the Global Human Settlement Built-Up Grid [GHSL; 38-m resolution; Pesaresi et al. 2015]; the National Land Cover Database 2011 [NLCD; 30-m resolution; Homer et al. 2015]; and TIGER/Line products [U.S. Census Bureau 2016]), and hand-digitized polygons reflecting solar, wind, and golf course developments. Built-up presence represented in the GHSL layer (through 2014), primary and secondary roads in the TIGER dataset (feature class code S1100 or S1200), open water identified in the NLCD, and heads-up digitized

developments were assigned the minimum, non-zero habitat quality value. Barren lands, as well as planted or cultivated cover identified in the NLCD, were assigned the value of the 10th percentile of movement habitat quality. These values were then superimposed on the map of movement habitat quality, and the final map of landscape conductance was compiled in Google Earth Engine (Gorelick et al. 2016) and scaled from 1 to 100 before being exported at 30-m resolution.

## CONNECTIVITY MODEL

We used the map of landscape conductance to model omnidirectional connectivity, which predicts potential connectivity across a landscape without regard to the location of core habitat or population areas (Pelletier et al. 2014). Specifically, we applied a circuit-theoretic model of connectivity, which relates the flow of current through an electrical circuit to the movement of individuals through a landscape and reflects the likelihoods of dispersal and gene flow (McRae and Beier 2007, McRae et al. 2008, Dickson et al. 2018). We first created two pairs of parallel nodes (one-pixel wide) that extended across the approximately eastwest and northsouth edges of the tortoise range, respectively. Using *Circuitscape* software (Bezanson et al. 2017), we calculated current flow at each pixel by injecting 1-amp of current into the node on one side and grounding the node on the other (McRae et al. 2008). Once completed for each pair of nodes, the two models were summed to produce a wall-to-wall map of potential current flow across the desert tortoise range. Resulting values represent the cumulative current flow (or current density) at each pixel and can be interpreted as relative values of potential connectivity.

To demonstrate one application of the connectivity model to Mojave desert tortoise conservation and management, we estimated the current flow centrality (Dickson et al. 2017) of 35 large ( $\geq 50,000$  acres) Areas of Critical Environmental Concern (ACEC). Within the range of the tortoise, a network of ACECs is managed by the Bureau of Land Management to protect assets of cultural, historical, or ecological importance, including habitats for wildlife. Some of these ACECs were established for the preservation of

critical tortoise habitat (U.S. Fish and Wildlife Service 2011). We estimated centrality by calculating the total current flow within each ACEC in this network and dividing by its area. We considered ACECs with relatively high current flow centrality (80th percentile of values) to be those areas more likely to be important for maintaining and facilitating range-wide connectivity across this particular network of ACECs.

Lastly, with limited, high-resolution movement data available to our analyses, we relied foremost on our expert knowledge and personal observations of tortoise habitat use and movement to evaluate the final connectivity model. We inspected specific areas on the landscape that are known to be important areas for tortoise movement or avoidance, including but not limited to: the Ivanpah Valley, California, and the Hidden, Dry Lake, and Eldorado valleys and Mormon Mesa in Nevada. To demonstrate a quantitative, but localized evaluation of the final connectivity model, we used an independent set of tortoise relocations that did not fit the requirements to estimate BBMMs (i.e., independent from those used to build the movement model). These data came from tracking studies in and around the Ivanpah Valley from 2015 to 2018 (K. Nussear and T. Esque, *unpublished data*), where groups of tortoises occurring on 10, 1-km<sup>2</sup> plot-centered study areas were tracked monthly with VHF telemetry, and hourly when equipped with GPS data loggers. The dataset consisted of 102 individual tortoises, and each individual had an average of 18 relocations between 2015 and 2018. We then rescaled the connectivity map to percentiles and determined the percentile value of each cell containing a tortoise relocation (McClure et al. 2016). Across all individuals, we calculated the mean and standard deviation (SD) of percentile values.

## RESULTS

The global model of movement habitat quality (including the linear terms of all covariates, and quadratic terms of all covariates except NDVI) had an AIC value 42 units lower (i.e., better) than a null (intercept-only) model, suggesting that it approximated the data well compared to a null model that included only a subject-level random effect. Considering the global model,

intermediate distances from minor roads, intermediate values of annual average maximum temperature, and increasing density of desert washes were among the strongest predictors of movement habitat quality (Table 1). There was also strong evidence for increased habitat quality for movement with increasing amounts of vegetation (i.e., values for NDVI).

Omnidirectional patterns of connectivity across the range showed broad areas of high connectivity associated with less rugged valleys and flats stretching predominantly northwest–southeast across the range (Fig. 2). Low connectivity was associated with prominent mountain ranges (e.g., the Panamint Range in Death Valley National Park), high levels of human modification (e.g., the Las Vegas metropolitan area), and vast expanses of un-vegetated, dry lake beds (e.g., the Cadiz Valley).

At finer scales, tortoise avoidance of very steep slopes was evident in the rugged McCullough mountain range to the east of the Ivanpah Valley, and the Sheep and Las Vegas ranges to the west of Hidden Valley (Fig. 3b, d). These valleys, as well as Mormon Mesa and the Eldorado Valley, accurately depicted distributed current flow in known areas of dispersed movement, surrounded by more constricted movement areas (Fig. 3). These constricted areas of high current

Table 1. Model-averaged regression coefficients ( $\tilde{\beta}$ ), unconditional standard errors (SE), and weights of evidence ( $w_+$ ) for environmental covariates used in the global model of habitat quality for Mojave desert tortoise movement.

Environmental covariate	$\tilde{\beta}$	SE	$w_+$
Intercept	2.95	0.16	
Max temp warmest month <sup>2†</sup>	−0.46	0.12	1.00
Wash density	0.19	0.06	0.99
Distance to minor roads	0.33	0.19	0.98
NDVI	0.08	0.03	0.96
Wash density <sup>2</sup>	−0.06	0.05	0.81
Distance to minor roads <sup>2</sup>	−0.06	0.06	0.76
Max temp warmest month	0.23	0.26	0.67

Notes: NDVI, Normalized Difference Vegetation Index. The global model contained linear terms (the fixed effects) for habitat covariates, as well as a quadratic term for all covariates except NDVI, for which we only hypothesized a positive, linear relationship to tortoise movement within the analysis extent.

<sup>†</sup>30-yr normal of the average annual maximum temperature of the warmest month.

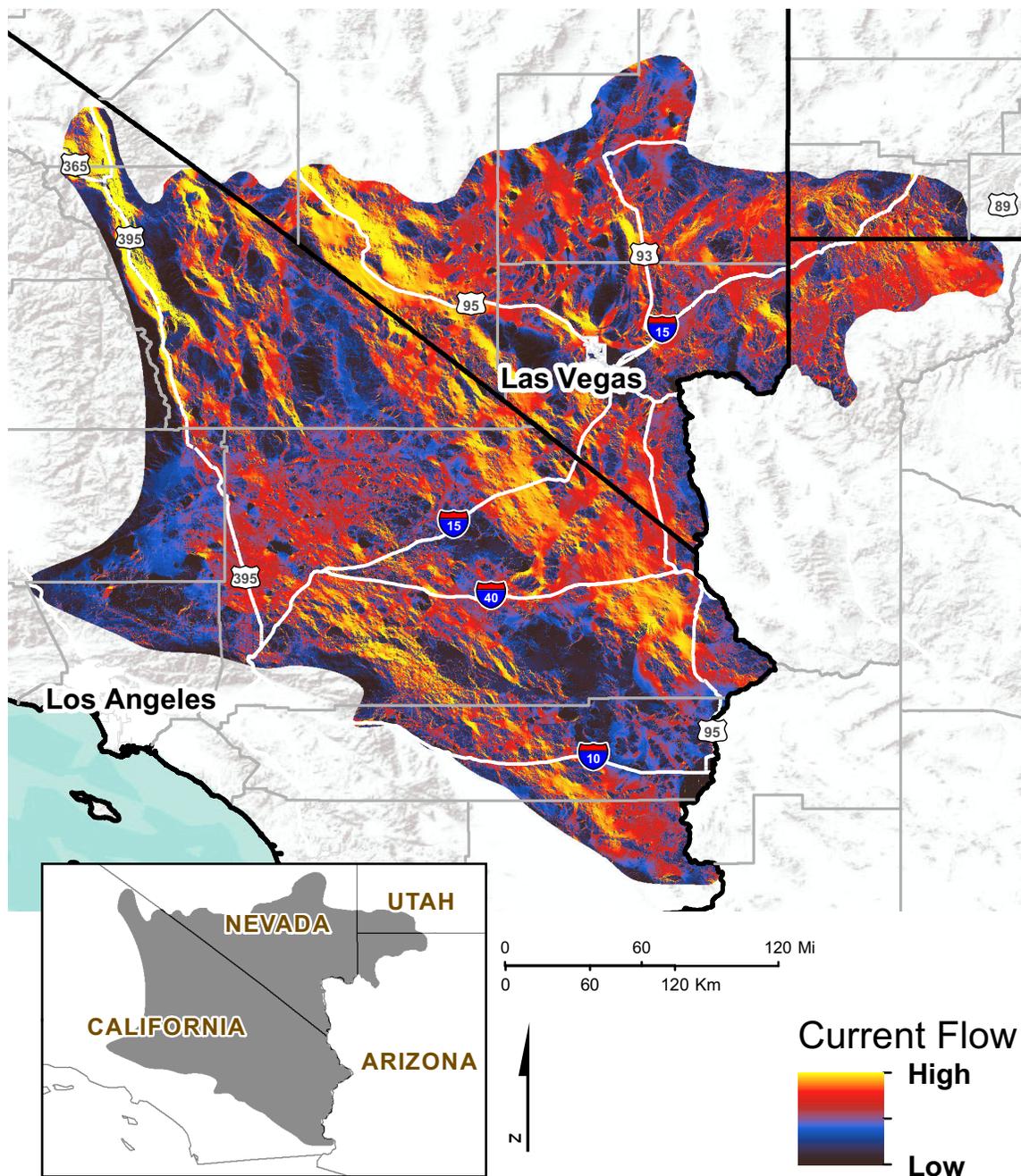


Fig. 2. Map of cumulative current flow used to estimate connectivity for the Mojave desert tortoise across its range. Circuit theory was used to model and map contemporary, omnidirectional connectivity at a 30-m resolution. Map is displayed using a histogram equalize stretch.

density are considered pinch points, where many potential paths converge to pass through a narrow area because few alternative paths are available. Pinch points are the most vulnerable areas

because they would disproportionately impact connectivity if movement through them were impeded (McRae et al. 2008). After reclassifying the connectivity values to percentiles, the

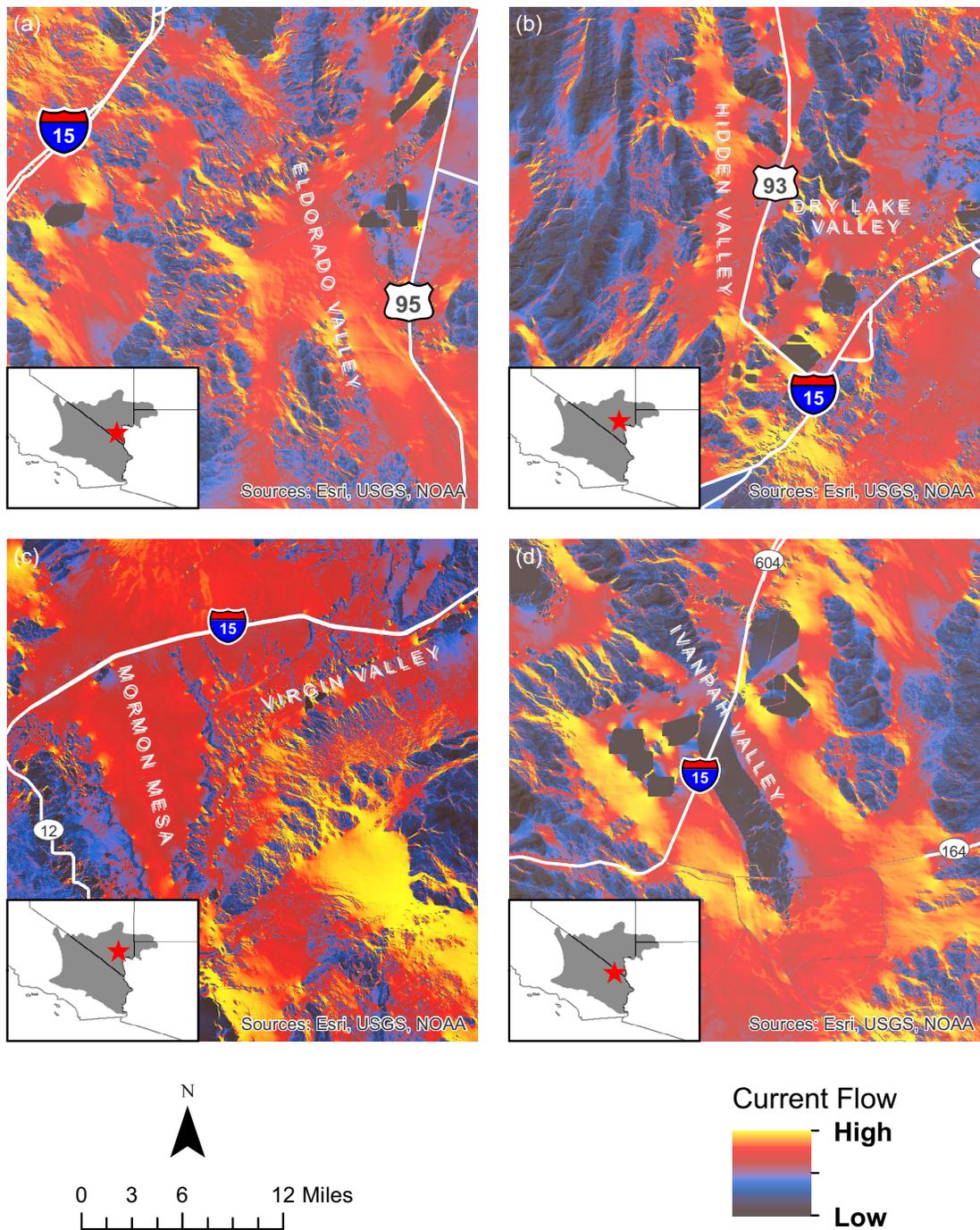


Fig. 3. Circuit theory was used to model and map contemporary, omnidirectional connectivity for the Mojave desert tortoise, and maps of cumulative current flow (i.e., connectivity) are shown here in four areas within its range: (a) the Eldorado Valley, Nevada, (b) Hidden and Dry Lake Valleys, Nevada, (c) Mormon Mesa, Nevada, and (d) the Ivanpah Valley, California. Warmer colors indicate relatively high current flow, and cooler colors indicate relatively low current flow. Highest current flows (yellow) are found at pinch points, where many potential paths condense to pass through a narrow area because few alternative paths are available.

quantitative evaluation of the connectivity model revealed that tortoises on average were relocated in cells with a mean value of 80.01 (SD =  $\pm 12.94$ ; see Fig. 4).

Among the network of ACECs we examined, our centrality analysis identified seven ACECs that appear to be relatively important for maintaining range-wide connectivity: the Beaver Dam ACEC in the northeast, the Shadow Valley and Amargosa North ACECs in the central portion of the range, the Piute-Fenner and Piute-Eldorado ACECs in the east, and the Old Woman Springs and Pipes Canyon ACECs in the south (Fig. 5).

## DISCUSSION

The Mojave desert tortoise Recovery Plan identifies land use and development, and specifically renewable energy development, as the most immediate threats to the species, due to the impacts of habitat fragmentation, isolation of TCAs, and restricted gene flow between these areas (U.S. Fish and Wildlife Service 2011). A number of genetic connectivity studies have shed light on restricted gene flow due to the long-term limiting factors on dispersal (i.e., over multiple generations; Hagerty et al. 2011, Sánchez-Ramírez et al. 2018). Although the model we present here represents a first approximation of potential habitat connectivity for the Mojave desert tortoise, it does account for many of the underlying, contemporary drivers of movement and dispersal that are not reflected in existing models or maps. Therefore, the model has immediate implications for understanding and mitigating the effects of rapid and ongoing habitat fragmentation in the region.

Thanks to the recent proliferation of datasets that track individual tortoise relocations, that is, through VHF or GPS transmitters, and at a high spatial and temporal frequency, it has been possible to draw direct inferences about tortoise movement at multiple sites throughout their range (Drake et al. 2015). In addition to informing how tortoises respond to environmental variability, spatially explicit estimates of movement probability are a direct representation of landscape conductance to movement and provide a more robust way of analyzing potential connectivity than estimates of habitat suitability (Zeller et al. 2012). Basing a resistance surface on habitat

potential alone relies on the assumption that tortoises make movement decisions based on the same preferences they have for selecting core habitat, which may not always be true. For example, tortoises likely make decisions differently when moving within clustered burrow networks, vs. longer distance forays beyond these core activity centers (Sadoti et al. 2017). Therefore, we leveraged available relocation datasets to model the movement of tortoises.

Our results of movement habitat quality are generally consistent with what has been observed in other tracking studies that relate tortoise movements to environmental covariates. For example, in the Ivanpah Valley, tortoises showed lower probability of movement near minor roads (Sadoti et al. 2017). Similarly, we found that tortoises had a higher probability of movement at intermediate distances from minor roads. The berms of these dirt roads may actually provide suitable habitat for burrow site selection (Lovich and Daniels 2000, Nafus et al. 2013). Therefore, tortoises may choose not to stray too far from these habitat features, but to some extent also avoid motor vehicles during longer distance movements.

Similar to our results, Sadoti et al. (2017) reported higher probability of movement with increasing NDVI and lower probability of tortoise movement during the highest monthly maximum temperatures. Maximum temperatures of the warmest months in the Mojave Desert are projected to increase approximately 2–3°C in the 21st century (Bachelet et al. 2016). Although hotter temperatures during these months will likely restrict desert tortoise movements in the future, projected but variable increases in summer precipitation could mitigate the influence of hotter temperatures on such movements, and associated uncertainty in vegetation productivity will also make it difficult to predict how changes in NDVI will restrict or promote movement (Bachelet et al. 2016). Thus, future research should aim to model Mojave desert tortoise connectivity under a range of projected climate and vegetation scenarios.

Although tortoise site fidelity and selective foraging within desert washes has been shown in previous studies (Nafus et al. 2017), our analysis also showed that tortoises were more likely to make longer distance movements in areas where

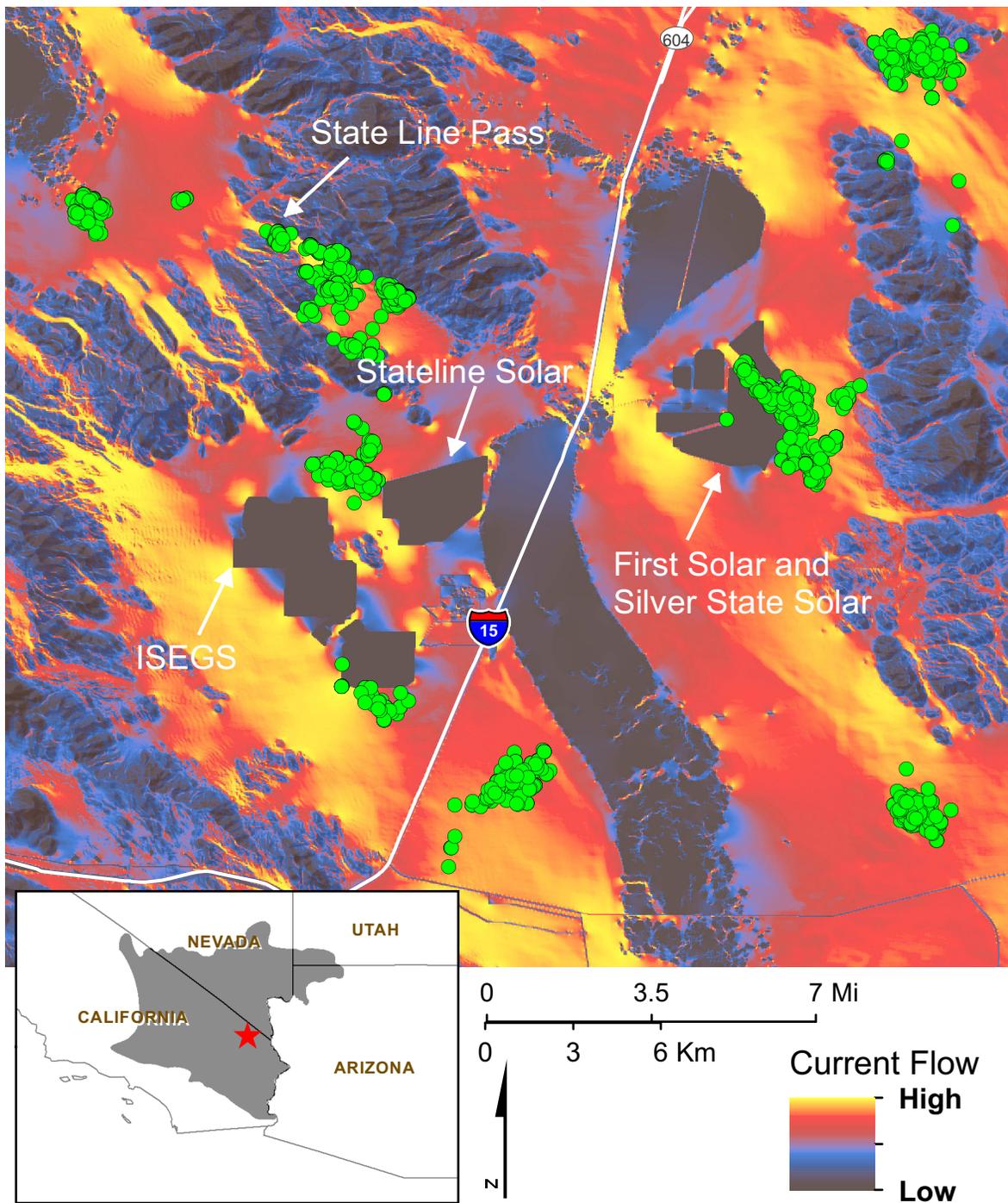


Fig. 4. Tortoise relocation data (green dots) within the Ivanpah Valley, California, were used for a local evaluation of our tortoise connectivity model. Warmer colors indicate relatively high current flow (i.e., connectivity), and cooler colors indicate relatively low current flow. After reclassifying the connectivity values to percentiles, tortoises on average were relocated in cells with a mean connectivity percentile value of 80.01 ( $\pm 12.94$ ).

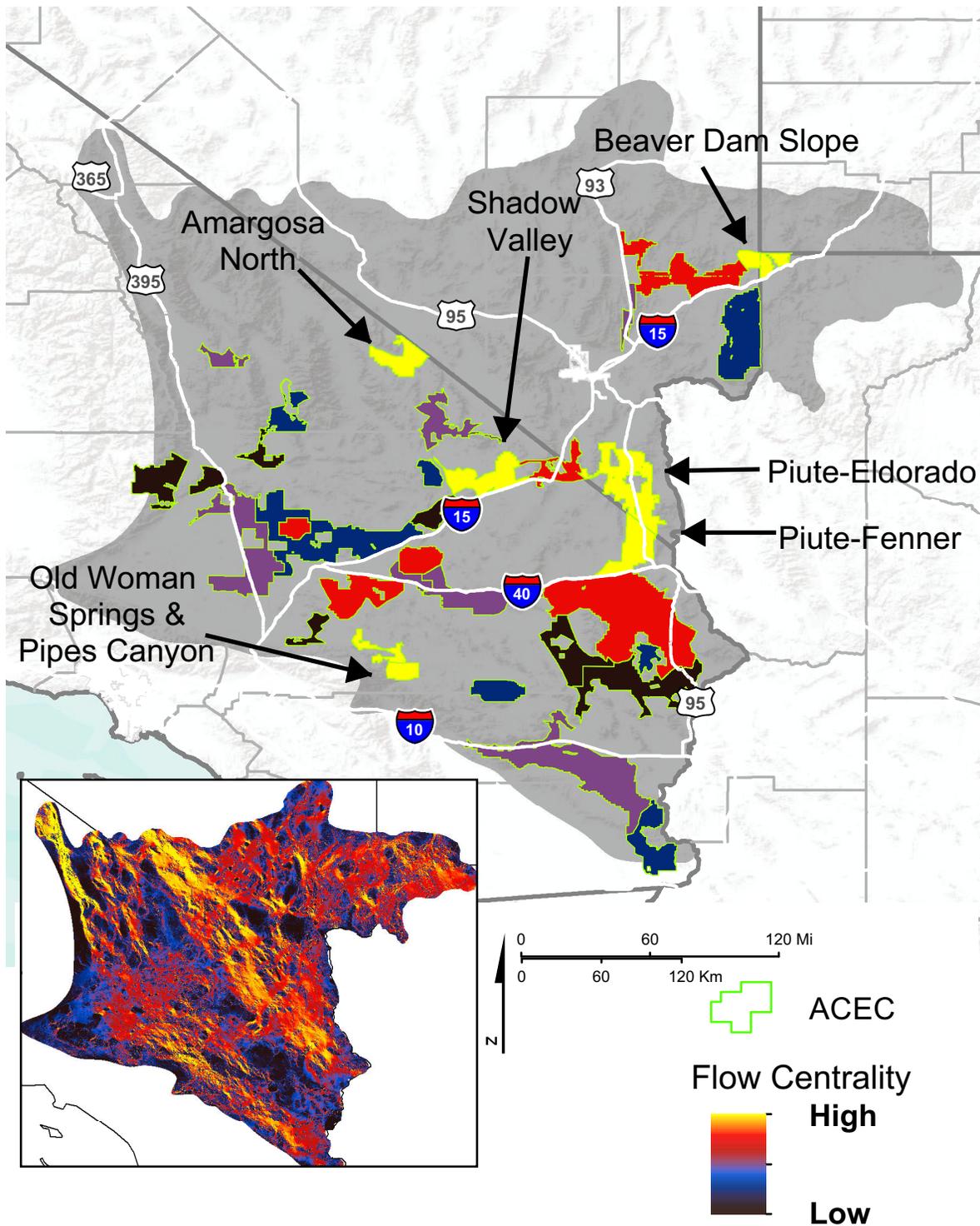


Fig. 5. Circuit theory was used to model and map contemporary, omnidirectional connectivity for the Mojave desert tortoise across its range. Resulting maps of cumulative current flow (i.e., connectivity) were used to estimate area-weighted centrality for 35 large ( $\geq 50,000$  acres) Areas of Critical Environmental Concern (ACEC).

(Fig. 5. *Continued*)

Area-weighted centrality was estimated by calculating the total current flow within each ACEC and dividing by its area. Centrality is symbolized with five percentile classes, with warmer colors indicating relatively high centrality and cooler colors indicating relatively low centrality. Areas of Critical Environmental Concerns with relatively high centrality (80th percentile of values) were considered to be more likely to be important for maintaining range-wide connectivity among this network of ACECs.

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washes were present. The probability of movement declined with the highest values of wash density, which may underlie their preference for smaller stream channels that are 1–2 m wide (Jennings and Berry 2015). Importantly, our high-resolution (1 m) desert wash model provides a novel method and variable for future habitat modeling in arid systems. Desert washes are important landscape features that enhance plant dispersal and provide key habitat for many wildlife species in these systems (Heaton et al. 2006, Gaddis et al. 2016, Kotschwar Logan 2016).

Although we lacked data with which to evaluate our range-wide connectivity model in a comprehensive manner, we demonstrated a localized evaluation using existing relocation data, within and proximate to the Ivanpah Valley. This region represents some of the highest predicted habitat potential for the Mojave desert tortoise (Nussner et al. 2009) and is also the site of one of the largest solar thermal power facilities in the world. Therefore, it was an ideal location in which to evaluate the movement and dispersal of tortoises in response to contemporary development. We used a metric that objectively determined how well the model agreed with the data and found that relocations, on average, were found within the 80th percentile of connectivity values. In addition to providing an interpretable measure of model performance, this metric might also inform conservation applications of the model. For example, areas defined by the 80th percentile of connectivity values may provide a target to delineate future movement corridors and focus habitat mitigation efforts. We encourage others to do their own evaluation of the model within local areas of interest and as more data become available.

Another promising application of this model will be integration into decision-support systems that consider multi-criteria impacts to both core habitat (i.e., increased habitat loss) and impacts to habitat connectivity (i.e., increased

fragmentation). Considering the potential for new development in the Mojave ecoregion, as well as the potential for land acquisitions that may benefit tortoise conservation, it is critical to conserve both intact tortoise habitats and to maintain connections between them (U.S. Fish and Wildlife Service 2011). Inclusion of contemporary connectivity estimates into a structured and cohesive approach to decision support will allow for better-informed, prioritized decisions across jurisdictions and across the tortoise's range (Averill-Murray et al. 2012). We demonstrated one application of how designated ACECs may be further prioritized and managed based on their importance for maintaining and facilitating regional connectivity. The top seven ACECs that emerged from our analysis are each important for the local protection of tortoises and their habitat, but also appear to contribute disproportionately to range-wide connectivity. As new land protections, including ACECs, are considered within the range of the tortoise, our connectivity model could be used to help optimize their location and extent, potentially enhancing the regional effectiveness of such areas.

Numerous empirical studies, across climates and taxa, have found that habitat fragmentation and habitat loss contribute independent effects on species persistence (Hadley and Betts 2016). Similarly, the conservation of habitat area, quality, and connectivity all contribute independently to species persistence and should be considered independently in planning and conservation decision-making (Hodgson et al. 2011). This holistic view of conservation is critical to mitigate the undisputed contributions of habitat alteration more broadly. Specifically, optimizing functional landscape connectivity encourages dispersal between core habitat and leads to increases in occurrence, gene flow, and diversity (Gilbert-Norton et al. 2010, Fletcher et al. 2016). In the midst of ongoing, rapid habitat loss and species extinctions globally, spatially explicit estimates of

contemporary connectivity are a critical tool to be considered alongside estimates of habitat potential.

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## LITERATURE CITED

- Andersen, M. C., J. M. Watts, J. E. Freilich, S. R. Yool, G. I. Wakefield, J. F. McCauley, and P. B. Fahnestock. 2000. Regression-tree modeling of desert tortoise habitat in the central Mojave desert. *Ecological Applications* 10:890–900.
- Averill-Murray, R. C., C. R. Darst, K. J. Field, and L. J. Allison. 2012. A new approach to conservation of the Mojave desert tortoise. *BioScience* 62:893–899.
- Averill-Murray, R. C., C. R. Darst, N. Strout, and M. Wong. 2013. Conserving population linkages for the Mojave desert tortoise (*Gopherus agassizii*). *Herpetological Conservation and Biology* 8:1–15.
- Bachelet, D., K. Ferschweiler, T. Sheehan, and J. Strittholt. 2016. Climate change effects on southern California deserts. *Journal of Arid Environments* 127:17–29.
- Badrinarayanan, V., A. Kendall, and R. Cipolla. 2015. Segnet: a deep convolutional encoder-decoder architecture for image segmentation. *IEEE Transactions on Pattern Analysis and Machine Intelligence* 39:2481–2495.
- Bezanson, J., A. Edelman, S. Karpinski, and V. B. Shah. 2017. Julia: A fresh approach to numerical computing. *SIAM Review* 59:65–98.
- Breiman, L. 2001. Random forests. *Machine Learning* 45:5–32.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Second edition. Springer, New York, New York, USA.
- Cameron, D. R., B. S. Cohen, and S. A. Morrison. 2012. An approach to enhance the conservation-compatibility of solar energy development. *PLOS ONE* 7: e38437.
- Dickson, B. G., C. M. Albano, B. H. McRae, J. J. Anderson, D. M. Theobald, L. J. Zachmann, T. D. Sisk, and M. P. Dombeck. 2017. Informing strategic efforts to expand and connect protected areas using a model of ecological flow, with application to the western United States. *Conservation Letters* 10:564–571.
- Dickson, B. G., et al. 2018. Circuit-theory applications to connectivity science and conservation. *Conservation Biology* 33:239–249.
- Dorman, C. F., J. M. McPherson, M. B. Araujo, and R. Bivand. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628.
- Drake, K. K., T. C. Esque, K. E. Nussear, L. A. Defalco, S. J. Scoles-Sciulla, A. T. Modlin, and P. A. Medica. 2015. Desert tortoise use of burned habitat in the eastern Mojave desert. *Journal of Wildlife Management* 79:618–629.
- Farnsworth, M. L., B. G. Dickson, L. J. Zachmann, E. E. Hegeman, A. R. Cangelosi, T. G. Jackson, and A. F. Scheib. 2015. Short-term space-use patterns of translocated Mojave desert tortoise in southern California. *PLOS ONE* 10:1–18.
- Fletcher, R. J., N. S. Burrell, B. E. Reichert, D. Vasudev, and J. D. Austin. 2016. Divergent perspectives on landscape connectivity reveal consistent effects from genes to communities. *Current Landscape Ecology Reports* 1:67–79.
- Gaddis, K. D., P. G. Thompson, and V. L. Sork. 2016. Dry-washes determine gene flow and genetic diversity in a common desert shrub. *Landscape Ecology* 31:2215–2229.
- Gibson, L., E. N. Wilman, and W. F. Laurance. 2017. How green is “green” energy? *Trends in Ecology and Evolution* 32:922–935.
- Gilbert-Norton, L., R. Wilson, J. R. Stevens, and K. H. Beard. 2010. A meta-analytic review of corridor effectiveness. *Conservation Biology* 24:660–668.
- Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2016. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment* 202:18–27.
- Haddad, N. M., et al. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances* 1:1–10.

- Hadley, A. S., and M. G. Betts. 2016. Refocusing habitat fragmentation research using lessons from the last decade. *Current Landscape Ecology Reports* 1:55–66.
- Hagerty, B. E., K. E. Nussear, T. C. Esque, and C. R. Tracy. 2011. Making molehills out of mountains: landscape genetics of the Mojave desert tortoise. *Landscape Ecology* 26:267–280.
- Heaton, J. S., A. R. Kiestler, and S. M. Meyers. 2006. LizLand: a geomorphic approach to lizard habitat modeling in the Mojave desert. *Journal of Arid Environments* 67:202–225.
- Hodgson, J. A., A. Moilanen, B. A. Wintle, and C. D. Thomas. 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology* 48:148–152.
- Homer, C., et al. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing* 81:345–354.
- Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. *Ecology* 88:2354–2363.
- Jennings, W. B., and K. H. Berry. 2015. Desert tortoises (*Gopherus agassizii*) are selective herbivores that track the flowering phenology of their preferred food plants. *PLOS ONE* 10:e0116716.
- Kotschwar Logan, M. 2016. Assessing site occupancy of Mohave ground squirrels: implications for conservation. *Journal of Wildlife Management* 80:208–220.
- Kupfer, J. A. 2012. Landscape ecology and biogeography: Rethinking landscape metrics in a post-FRAGSTATS landscape. *Progress in Physical Geography* 36:400–420.
- Landguth, E. L., S. A. Cushman, M. K. Schwartz, K. S. McKelvey, M. Murphy, and G. Luikart. 2010. Quantifying the lag time to detect barriers in landscape genetics. *Molecular Ecology* 19:4179–4191.
- Lovich, J. E., and R. Daniels. 2000. Environmental characteristics of desert tortoise (*Gopherus agassizii*) burrow locations in an altered industrial landscape. *Chelonian Conservation and Biology* 3:714–721.
- Lovich, J. E., and J. R. Ennen. 2011. Wildlife conservation and solar energy development in the desert southwest, United States. *BioScience* 61:982–992.
- Luckenbach, R. A. 1982. Ecology and management of the desert tortoise (*Gopherus agassizii*) in California. Pages 1–37 in R. B. Bury, editor. *North American tortoises: conservation and ecology*. Wildlife Research Report 12. U. S. Fish and Wildlife Service, Washington, D. C., USA.
- McClure, M. L., B. G. Dickson, and K. L. Nicholson. 2017. Modeling connectivity to identify current and future anthropogenic barriers to movement of large carnivores: a case study in the American Southwest. *Ecology and Evolution* 7:3762–3772.
- McClure, M. L., A. J. Hansen, and R. M. Inman. 2016. Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. *Landscape Ecology* 31:1419–1432.
- McRae, B. H., and P. Beier. 2007. Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences USA* 104:19885–19890.
- McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89:2712–2724.
- Nafus, M. G., T. C. Esque, R. C. Averill-murray, K. E. Nussear, and R. R. Swaisgood. 2017. Habitat drives dispersal and survival of translocated juvenile desert tortoises. *Journal of Applied Ecology* 54:430–438.
- Nafus, M. G., T. D. Tuberville, K. A. Buhlmann, and B. D. Todd. 2013. Relative abundance and demographic structure of Agassiz's desert tortoise (*Gopherus agassizii*) along roads of varying size and traffic volume. *Biological Conservation* 162:100–106.
- Nielson, R. M., H. Sawyer, and T. L. McDonald. 2015. BBMM: Brownian bridge movement model. R package version 3.0. <https://cran.r-project.org/web/packages/BBMM/BBMM.pdf>
- Nussear, K. E., T. C. Esque, R. D. Inman, L. Gass, K. A. Thomas, C. S. A. Wallace, J. B. Blainey, D. M. Miller, and R. H. Webb. 2009. Modeling habitat of the desert tortoise (*Gopherus agassizii*) in the Mojave and parts of the Sonoran Deserts of California, Nevada, Utah, and Arizona. 1102. U.S. Geological Survey, Reston, Virginia, USA.
- Nussear, K. E., and T. D. Tuberville. 2014. Habitat characteristics of North American tortoises. Pages 77–84 in *Biology and conservation of North American tortoises*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Pelletier, D., M. Clark, M. G. Anderson, B. Rayfield, M. A. Wulder, and J. A. Cardille. 2014. Applying circuit theory for corridor expansion and management at regional scales: tiling, pinch points, and omnidirectional connectivity. *PLOS ONE* 9: e84135.
- Pesaresi, M., D. Ehrlich, A. Florczyk, S. Freire, A. Julea, T. Kemper, P. Soille, and V. Syrris. 2015. GHS built-up grid, derived from Landsat, multitemporal (1975, 1990, 2000, 2014). European Commission Joint Research Centre, Brussels, Belgium.

- Pimm, S. L., and P. Raven. 2000. Extinction by numbers. *Nature* 403:843–845.
- R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Randall, J. M., S. S. Parker, B. Cohen, J. B. Mackenzie, and S. Morrison. 2010. Mojave desert ecoregional assessment. The Nature Conservancy of California, San Francisco, California, USA.
- Rayfield, B., M.-J. Fortin, and A. Fall. 2011. Connectivity for conservation: a framework to classify network measures. *Ecology* 92:847–858.
- Sadoti, G., M. E. Gray, M. L. Farnsworth, and B. G. Dickson. 2017. Discriminating patterns and drivers of multiscale movement in herpetofauna: the dynamic and changing environment of the Mojave desert tortoise. *Ecology and Evolution* 7:7010–7022.
- Sah, P., K. E. Nussear, T. C. Esque, C. M. Aiello, P. J. Hudson, and S. Bansal. 2016. Inferring social structure and its drivers from refuge use in the desert tortoise, a relatively solitary species. *Behavioral Ecology and Sociobiology* 70:1277–1289.
- Sánchez-Ramírez, S., Y. Rico, K. H. Berry, T. Edwards, A. E. Karl, B. T. Henen, and R. W. Murphy. 2018. Landscape limits gene flow and drives population structure in Agassiz's desert tortoise (*Gopherus agassizii*). *Scientific Reports* 8:1–17.
- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103–113.
- Tuma, M. W., C. Millington, N. Schumaker, and P. Burnett. 2016. Modeling Agassiz's desert tortoise population response to anthropogenic stressors. *Journal of Wildlife Management* 80:414–429.
- U.S. Census Bureau. 2016. TIGER/LINE Shapefiles. <https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>
- U.S. Department of Agriculture Farm Service Agency. 2016. NAIP: National Agriculture Imagery Program. <https://www.fsa.usda.gov/programs-and-services/aerial-photography/imagery-programs/naip-imagery/>
- U.S. Fish and Wildlife Service. 1990. Endangered and threatened wildlife and plants; determination of threatened status for the Mojave population of the desert tortoise. *Federal Register* 55:12178–12191.
- U.S. Fish and Wildlife Service. 1994. Desert tortoise (Mojave population) recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- U.S. Fish and Wildlife Service. 2011. Revised recovery plan for the Mojave population of the desert tortoise (*Gopherus agassizii*). U.S. Fish and Wildlife Service, Pacific Southwest Region, Sacramento, California, USA.
- Wallace, C. S. A., and K. A. Thomas. 2008. An annual plant growth proxy in the Mojave desert using MODIS-EVI data. *Sensors* 8:7792–7808.
- Willems, E. P., R. A. Hill, and P. Willems. 2009. Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology* 90:546–555.
- Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. Estimating landscape resistance to movement: a review. *Landscape Ecology* 27:777–797.

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