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Multiscale connectivity and graph theory highlight critical areas for conservation under climate change

Thomas E. Dilts,[1,4] Peter J. Weisberg,[1] Philip Leitner,[2] Marjorie D. Matocq,[1] Richard D. Inman,[3]
Kenneth E. Nussear,[3] and Todd C. Esque[3]

[1]*Department of Natural Resources and Environmental Science, University of Nevada Reno,*
1664 N. Virginia Street, Reno, Nevada 89557 USA
[2]*Endangered Species Recovery Program, California State University Stanislaus, One University Circle,*
Turlock, California 95382 USA
[3]*U.S. Geological Survey, Western Ecological Research Center, Las Vegas Field Station, 160 N. Stephanie Street,*
Henderson, Nevada 89074-8829 USA

Abstract. Conservation planning and biodiversity management require information on landscape connectivity across a range of spatial scales from individual home ranges to large regions. Reduction in landscape connectivity due changes in land use or development is expected to act synergistically with alterations to habitat mosaic configuration arising from climate change. We illustrate a multiscale connectivity framework to aid habitat conservation prioritization in the context of changing land use and climate. Our approach, which builds upon the strengths of multiple landscape connectivity methods, including graph theory, circuit theory, and least-cost path analysis, is here applied to the conservation planning requirements of the Mohave ground squirrel. The distribution of this threatened Californian species, as for numerous other desert species, overlaps with the proposed placement of several utility-scale renewable energy developments in the American southwest. Our approach uses information derived at three spatial scales to forecast potential changes in habitat connectivity under various scenarios of energy development and climate change. By disentangling the potential effects of habitat loss and fragmentation across multiple scales, we identify priority conservation areas for both core habitat and critical corridor or stepping stone habitats. This approach is a first step toward applying graph theory to analyze habitat connectivity for species with continuously distributed habitat and should be applicable across a broad range of taxa.

Key words: circuit theory; conservation planning; graph theory; habitat connectivity; habitat network; lattice; least-cost path; Mojave Desert, USA; multiple spatial scales; Xerospermophilus mohavensis.

Introduction

The implications of habitat fragmentation for population viability are widely recognized, leading to a proliferation of studies of landscape connectivity (reviewed in Kool et al. 2013). Several promising quantitative approaches have emerged in recent years including graph theory (Urban and Keitt 2001), circuit theory (McRae et al. 2008), connectivity analysis using individual-based simulation models (Gardner and Gustafson 2004, Lookingbill et al. 2010, Morzillo et al. 2011), causal modeling using landscape genetics data (Cushman 2006), and individual-based metapopulation models to dynamically simulate spatial patterns of gene flow (Landguth et al. 2010). Most seek to derive functional, biological components of landscape connectivity from structural components of habitat (sensu Brooks 2003). However, studies are conducted over a broad range of scales for a wide array of purposes, confounding efforts to find unifying themes and analytical approaches (Table 1).

At the broadest scales, landscape connectivity studies incorporate patterns of distribution, organismal movement, or gene flow across entire species ranges or encompassing major biogeographical divisions within the species distribution. Relevant conservation questions at this scale are often concerned with climate change adaptation, given the expectation that connectivity of suitable habitat for species migration and dispersal is critical for successful adaptation to climate change through shifting species range boundaries (Williams et al. 2005, Vos et al. 2008, McKelvey et al. 2011, Kool et al. 2013). Landscape genetics studies conducted over range-wide scales can be used to delineate major genetic subdivisions within species and to elucidate the landscape and historical factors associated with those groups (Spear et al. 2005, Sork and Smouse 2006, Epps et al. 2007, Pease et al. 2009). Thus, landscape connectivity studies at the broadest scales provide an overall measure of population structure that is integrated over evolutionary time and space and that can, with some strong assumptions, be extrapolated forward within a global change context.

Landscape-scale conservation planning also considers habitat connectivity at the scale of the metapopulation,

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[4]E-mail: tdilts@cabnr.unr.edu

Table 1. Relevant scales for investigations of landscape connectivity, as these relate to conservation objectives and can be quantified using particular analytical approaches.

Level of ecological organization or scale	Relevant conservation questions	Landscape features or biological components	Approach to connectivity analysis
Species range	Climate change adaptation; genetic diversity; development scenario comparisons; change in connectivity/invasion	Population genetic structure; phylogeography; range-wide pattern of connectivity; changes in connectivity	Graph theory; landscape genetics; Circuitscape; dynamic network models
Metapopulation	Landscape conservation planning; genetic diversity; development scenario comparisons; change in connectivity/invasion	Core areas and corridors; source-sink populations; changes in connectivity	Graph theory; metapopulation modeling; individual-based models; Circuitscape; least-cost paths
Local population	Project-level conservation decisions; genetic diversity; development scenario comparisons; change in connectivity/invasion	Pinch points; changes in connectivity	Circuitscape; least-cost path analysis

where management actions influence population dynamics through changing habitat quality, demographic parameters, or dispersal ability. The metapopulation framework facilitates assessment of the conservation importance of particular habitat patches or connections between them (Hanski 1998). Important dispersal corridors can be identified using quantitative approaches integrated within a GIS, such as least-cost path analysis (Beier et al. 2008). Likewise, the importance of particular dispersal corridors for overall metapopulation viability can be assessed through simulation (Jepsen et al. 2005) or using network analysis approaches, such as graph theory (Urban and Keitt 2001). Any of these approaches allows analysis of the potential effects of removal of habitat patches, which may differ depending upon spatial location of the patch and its topological position within the habitat network. Graph theory can also be applied to identify critical patches and connections independently through systematic removal of graph nodes vs. edges (e.g., Lookingbill et al. 2010).

Many conservation applications require fine-scale analysis of how landscape alteration in a relatively localized portion of the range can influence functional connectivity over a range of scales from persistence of local populations in core areas to a broad spatial network of multiple populations (Table 1). For example, many proposed energy development projects in southwestern U.S. deserts have footprints that are much smaller than the entire range of a species. However, the cumulative impacts of many energy projects scattered throughout a species' range combined with rapid climate change may have dramatic effects on movement and gene flow. A major challenge is to integrate our understanding of functional connectivity at biogeographical scales with fine-scale analyses needed to inform management decisions. This includes identification of particular areas as core habitat, connectivity zones, and critical pinch points that may facilitate or restrict movement.

We describe a multiscale analysis of landscape connectivity and demonstrate our approach for Mohave ground squirrel (*Xerospermophilus mohavensis*; hereafter MGS) in the context of solar and wind energy development planned for the Mojave Desert region. Renewable energy offers the potential to reduce the rate of climate change by lowering greenhouse gas emissions, but if energy projects are sited poorly they may negatively impact biodiversity. Inherent differences in habitat needs for different taxa may make a single conservation strategy impractical (Beier et al. 2008, Cushman and Landguth 2012). Previous studies have found that roads have already led to significant decreases in genetic connectivity for desert bighorn sheep (*Ovis canadensis nelsoni*) (Epps et al. 2005) and desert tortoises (*Gopherus agassizii*; Latch et al. 2011), iconic species of the Mojave region, and that proposed energy developments are likely to further exacerbate the problem (Bare et al. 2009). To reduce conflicts between energy development and biodiversity, multiscale approaches are needed to identify sites with a disproportionately large influence on habitat connectivity within a metapopulation framework that further considers potential range shifts in response to climate change (Table 1).

The Mohave ground squirrel (MGS) is a California state-threatened species with a restricted range that overlaps the focal area for many renewable energy development proposals in the southwestern USA (Inman et al. 2013). Previous studies have estimated that habitat suitability is higher within areas of proposed energy developments compared to elsewhere in its range (Inman et al. 2013), setting the stage for high-stake conflicts between the need for renewable energy development and legislation that protects biodiversity. Climate change also is expected to have a large impact on future habitat availability for MGS, with much of its most suitable habitat predicted to shift northward 200 km based on species distribution models (Inman et al. 2014). Projections of future habitat distribution using correlative species distribution models make several key assumptions, namely that climatic conditions define the limits of climate tolerated by the species (Beale et al. 2008) and that the species has limited ability to adapt to changing climate. Habitat preference for low-elevation, coarse sandy soils may make upslope movement challenging while the rate of expected climate change may require rapid movement through broad valleys in order to keep pace with latitudinal trends in changing temperatures.

We demonstrate a geospatial approach to quantifying landscape connectivity over the entire range of the MGS, but with attention to the requirement of localized decisions for conservation prioritization of key corridor habitat. Our approach utilizes graph theory in combination with habitat suitability models to estimate the overall impacts to habitat connectivity and to identify specific areas of critical connectivity. We use circuit theory for finer-scale analysis of likely movement corridors and the identification of pinch points that may serve as barriers to movement within critical portions of the range,\ or to anticipated range shifts in response to climate change. Our objectives are to (1) quantify changes in habitat connectivity predicted to occur given the projected effects of climate change and proposed land-use change associated with renewable energy development; (2) identify specific areas of high conservation value, such as core habitat and critical pathways for maintaining functionally connected local populations; and (3) identify pinch points that may restrict movement in critical corridors for population persistence and possible climate change adaptation.

While our questions are specific to the study system with which we demonstrate our approach, our analyses provide a novel means through which to investigate multiscale impact of land-use change in any terrestrial species in which overland dispersal occurs between adjacent areas.

Methods

Study area

The 44425-km^2 study area encompasses the known historic range of MGS (Zeiner et al. 1988–1990). The area is situated in the western Mojave Desert in California, USA, and is characterized by basin and range topography in which fault block mountain ranges are separated by broad alluvial valleys. The study area is bounded on the west by the steep eastern escarpment of the Sierra Nevada and on the south by the San Gabriel and San Bernardino mountain ranges. These mountains form a significant orographic barrier and are largely responsible for the region's aridity (with only 100–350 mm of precipitation per year). The preferred habitats of MGS are broad alluvial valleys with moderately coarse sandy soils, precipitation ranging between 90 and 200 mm, and winter climatic water deficit ranging between 20 and 55 mm (Inman et al. 2013). The MGS diet includes many species of herbaceous plants and foliage of shrubs, such as spiny hopsage (*Grayia spinosa*) and winterfat (*Krascheninnikovia lanata*; Harris and Leitner 2005).

Habitat models

Maximum entropy habitat models were fitted using 440 observations based on the California Natural Diversity Database, the Mojave Desert Ecosystem Program, and recent trapping and survey data (P. Leitner, *unpublished data*). Initial modeling examined eight environmental covariates at 1-km^2 cell size, including cumulative winter precipitation, surface texture, surface albedo, winter climatic water deficit, topographic position, probability of three-year drought, maximum summer air temperature, and surface roughness, further described in Inman et al. (2013). The 1-km^2 cell size was determined by the resolution of the predictor variables derived from MODIS satellite imagery (i.e., surface albedo and surface texture) and the spatial precision of occurrence data used in the species distribution model. Maxent software (version 3.3.3e; Phillips et al. 2006) was used to develop a suite of candidate models that were evaluated using Akaike's information criterion for small sample sizes (AIC$_c$). Models containing covariates contributing less than 10% were removed. The final, most parsimonious model selected included cumulative winter precipitation, surface texture, surface albedo, and winter climatic water deficit (Inman et al. 2013).

To accommodate a range of renewable energy development and climate change impacts we created eight habitat models, of which four represented the current climatic conditions and four were developed for 2080. These were based on the downscaled NOAA GFDL CM2.1 global circulation model assuming the A2 emissions scenario (Delworth et al. 2006), using the downscaling procedure described in Flint and Flint (2012). The A2 emissions scenario is among the highest of IPCC CO_2 emissions scenarios predicting increasing CO_2 emissions through the end of the century, and the NOAA GFDL CM2.1 model is among the warmest and driest predictions of the IPCC models for the southwest USA (Cayan et al. 2008). This combination was chosen to represent a worst-case scenario for MGS.

Habitat models were created to represent four land-use scenarios: (1) existing land-use impacts assuming moderate impacts on connectivity, (2) moderate land-use impacts with permitted energy development projects, (3) moderate land-use impacts with Desert Renewable Energy Conservation Plan (DRECP) Alternative 1 scenario (described as the Low Resource Conflict Alternative (DRECP 2012), and (4) moderate land-use impacts with DRECP Alternative 5 scenario (described as the Increased Geographic and Technology Flexibility Alternative [DRECP 2012]). Proposed renewable energy development areas were mapped according to three scenarios resulting in 1367 km^2, 2582 km^2, and 4388 km^2 being impacted by solar and wind energy development representing 3%, 6%, and 10% of the study area. The permitted scenario was represented by areas mapped as suitable for energy development in the Bureau of Land Management Solar Energy Development Programmatic Environmental Impact Statement (BLM 2012) and transmission corridors designated under the California Desert Conservation Area Plan of 1980 (BLM 1980) and the West-wide Designation of Energy Corridors (BLM

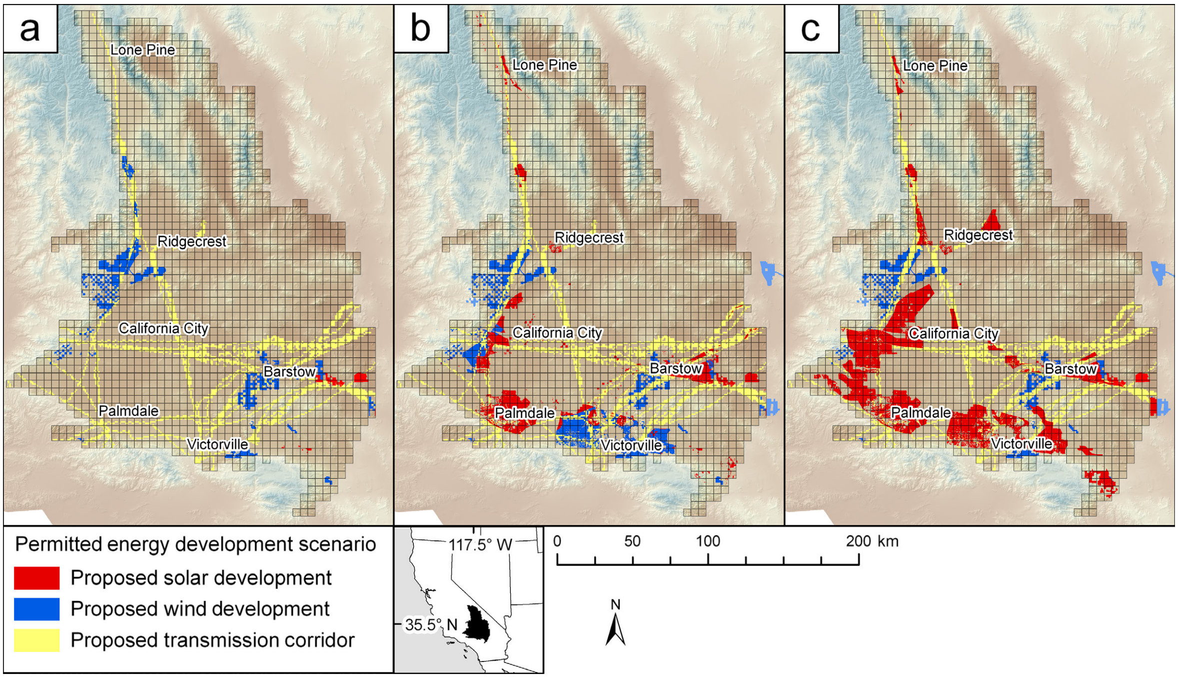

FIG. 1. Renewable energy development scenarios: (a) energy development proposals that are already permitted by the Bureau of Land Management, (b) energy development proposals under the Desert Renewable Energy Conservation Plan Alternative 1, and (c) energy development proposals under the Desert Renewable Energy Conservation Plan Alternative 5.

2009; Fig. 1). The other two scenarios represent more extensive proposed energy development (DRECP 2012). Alternative 1 locates energy developments in previously disturbed lands or other lands that have very few resource conflicts. In contrast, DRECP Alternative 5 opens up large areas to renewable energy development projects. These scenarios are considered illustrative and should not be interpreted as actual build out scenarios in 2080 given that the political and legislative environment concerning renewable energy is experiencing a state of rapid change. The same land use scenarios were applied to the 2080 climate prediction. All land use impacts used in conjunction with climate change models assumed that the footprint of land use will remain the same in 2080 as it is today and that the only new development will be renewable energy development.

Few data exist that estimate the potential impacts of anthropogenic land use on MGS habitat degradation, so we used expert opinion and field observations (P. Leitner, *personal communication*) to calibrate habitat models. The modeled probability of MGS occurrence was reduced by 75% in urban areas and by 25% in former agricultural fields and roads (as in Inman et al. 2013). The modeled probability of MGS occurrence varied by renewable energy development type and was reduced by 100% for solar development, by 50% for wind, and by 10% for transmission lines, based on the degree of vegetation removal expected to result from each development type. Urban areas were derived from the National Land Cover Database (NLCD) 2006 Percent Developed Imperviousness layer and categorized as grid cells with more than 20% of their surface area covered by at least 20% imperviousness. Major roads were identified using U.S. Census Bureau Topologically Integrated Geographic Encoding and Referencing (TIGER) line files and were converted from vector to raster format with a 1-km^2 cell size. Former agricultural fields were digitized from recent aerial photographs based upon evidence of agricultural practices and clearing of natural vegetation. Although others (e.g., Stoms et al. 2013) have characterized agricultural abandonment as a continuum, we chose to treat abandoned agricultural uniformly impacted because agriculture in the western Mohave Desert was usually accompanied by intensive groundwater pumping, and many areas that were abandoned have persisted with very little shrub cover and are noticeably barren despite having 30 years to recover.

Resistance surfaces and least-cost analysis

The influence of heterogeneous landscape structure on functional connectivity for mobile organisms is commonly characterized using resistance surfaces (Adriaensen et al. 2003, Calabrese and Fagan 2004, Beier et al. 2008, Spear et al. 2010). Resistance surfaces describe the difficulty for an organism to move through a pixel in relative terms (Adriaensen et al. 2003). We calculated resistance surfaces as the inverse of habitat suitability, as is commonly done in the absence of detailed empirical data on animal movement probability (Chetkiewicz et al. 2006).

Least-cost analysis offers a computationally efficient and simple method to measure effective distance among habitat patches and has been widely adopted in conservation ecology as a method for assessing potential habitat corridors (Adriaensen et al. 2003, Epps et al. 2007, Cushman et al. 2013). A least-cost path is determined between each pair of possible endpoints by summing the cumulative cost (resistance) that is incurred by moving through all of the cells necessary to connect the two points and then by optimizing the route such that the lowest cumulative cost is achieved (Adriaensen et al. 2003). Typically least-cost paths are used to assess movement among discrete habitat patches through a heterogeneous matrix. MGS habitat was not arranged in discrete patches in that habitat suitability varied continuously rather than abruptly (Inman et al. 2013). Rather than dividing the landscape into binary habitat and non-habitat and assessing connectivity among habitat areas, we adopted the lattice approach of Carroll et al. (2012) in which the entire study area was divided into regular 25-km^2 study blocks. We performed least-cost analysis to estimate the degree of connectivity among neighboring study blocks (queen's case; i.e., all eight neighbors considered) using the 1-km^2 resistance raster derived from inverting the habitat model. To account for an uneven distribution of high quality habitat, locations of study block centroids were weighted by habitat quality using the Mean Center tool in ArcGIS Desktop 10.0 (ESRI 2010). The habitat-weighted centroids, used as endpoints in the least-cost analysis, offered a number of advantages over geometric centroids, including lower sensitivity to changes in habitat availability that might occur in a single 1-km^2 grid cell and the ability to account for heterogeneity in habitat suitability within a study block (Watts et al. 2013, Dilts et al. 2014). We performed least-cost analysis among adjacent habitat-weighted centroids, changing the resistance raster for each land use/climate change scenario. Distance among adjacent study blocks was quantified using cumulative cost rather than least-cost path length as this measure was more highly correlated with genetic distance among MGS (Matocq et al. 2014) and is thought to be the better measure of effective distance in many ecological situations (Etherington and Holland 2013).

Resistance values were calculated as the inverse of habitat suitability and ranged continuously from 0.001 to 1 for all cells with a habitat value greater than 0. For cells with a habitat suitability of zero, a resistance value of five million was assigned to effectively make movement through the cell impossible. All least-cost analyses were conducted using UNICOR software (Landguth et al. 2012).

Connectivity and graph theory

Graph theory has emerged as an effective framework for characterizing connectivity at multiple scales, including the entire network-scale, the scale of individual graph components (nodes and links of the graph that are connected to one another), and the scale of individual nodes and links (Pascual-Hortal and Saura 2006, Rayfield et al. 2011). In ecology, spatial graphs can be constructed to assess the connectivity among habitat patches (represented as nodes) using links. We used the habitat-weighted centroids to represent the 25-km^2 study blocks as nodes (habitat patches) in a graph-theoretic framework, with node weights equivalent to the sum of habitat suitability within the study block. Least-cost paths among adjacent study blocks calculated using the 1-km^2 raster were used as links. We used graph theory to assess overall, network-wide change in habitat availability and connectivity among the different land use and climate change scenarios, as well as changes to special areas of interest (i.e., core habitat areas and connectivity areas; Table 1).

Maximum dispersal distance can be estimated using genetic data (Epps et al. 2007) by plotting gene flow (Nm, number of migrants contributing alleles per generation) against effective geographic distance and identifying a threshold in which the slope of the relationship between gene flow and distance becomes zero. Although relationships between effective distance and genetic distance were relatively weak for Mohave ground squirrel (Matocq et al. 2014), a threshold of 10000 cost-distance units (approximately 50 km) was identified as an approximate distance at which gene flow reached background levels. This distance effectively connected all occupied habitat blocks indicating that Mohave ground squirrel gene flow historically has been quite high across its range (Matocq et al. 2014). To determine which links exceeded the maximum dispersal cost and therefore were likely to be of very little conservation value, we plotted known MGS occurrences on the graph and connected 95% of known occurrences as a single graph component. The link with the highest cumulative cost was used to estimate the maximum cumulative cost that was likely for MGS. To translate cost distance among study blocks into dispersal probability, a negative exponential decay function was fitted using the maximum cumulative cost to represent 0% probability of dispersal. Connectivity analyses were performed using Conefor 2.6 software (Saura and Torné 2009).

Overall change in the habitat network

We assessed several metrics to describe changes in the overall habitat graph among land use and climate change scenarios (Table 2). Total graph length was calculated as the sum of the length of all links in the graph having a non-zero probability of dispersal. The length of the largest graph component was calculated by summing the length of links that were connected, and the proportion of the largest component was calculated by dividing the length of the largest component by the total graph length. The proportion of the largest component provides a measure of graph fragmentation that is independent of graph size (Fahrig 2003, Ferrari et al. 2007).

Table 2. Habitat area, equivalent connectivity (EC) index, graph link length, and proportion of link length belonging to the largest graph component for each renewable energy development/climate change scenario.

Development/land use scenario	Current land use	Permitted energy	Alt1 scenario†	Alt5 scenario‡
Current climate				
Total graph area	30525	30425	29400	28300
Area of largest component	27825	27725	26450	24900
Proportion largest component	0.91	0.91	0.89	0.88
Weighted habitat area	9534.09	9313.11	8393.09	7850.39
EC index	956.12	887.24	813.04	747.59
Relativized EC	2.20§	3.10	0.85	1.24
Climate change scenario for 2080, GFDL CM2.1 with A2 emissions¶				
Total graph area	17875	17800	17075	16700
Area of largest component	7475	4575	4700	4600
Proportion of largest component	0.42	0.26	0.27	0.27
Weighted habitat area	3245.05	3094.16	2651.90	2523.46
EC index	230.57	214.51	195.10	193.34
Relativized EC	1.15#	1.17	1.12	1.11

Notes: Relativized EC is calculated by dividing the proportional loss of EC from the previous scenario by proportional loss of habitat from the previous scenario. Each habitat scenario represents progressively less habitat for Mohave ground squirrel with DRECP Alternative 5 representing the least habitat. Relativized EC values greater than 1 indicate habitat loss that results in changes in connectivity that are greater than due to random habitat loss.

†The Alt1 scenario is based on the draft Desert Renewable Energy Conservation Plan's alternative 1 disturbed lands/low resource conflict alternative.

‡The Alt5 scenario is based on the draft Desert Renewable Energy Conservation Plan's Alternative 5 increased geographic and technology flexibility alternative (DRECP 2012).

§Based on changes from a historic no land use alternative (Dilts et al. 2014) to the current land use with current climate.

¶GFDL CM2.1 is the Geophysical Fluid Dynamics Laboratory CM2.1 model using the Alternative 2 emissions scenario.

#Based on changes from the current land use scenario with no climate change to current land use with the 2080 GFDL CM2.1 with Alternative 2 emissions.

Weighted habitat area was calculated by summing the habitat suitability values from all of the grid cells within a habitat block. Theoretically values could range from 0 to 25 representing conditions in which no suitable habitat occurred within a block to every cell having the highest habitat suitability of 1. In practice, values ranged from 0.02 to 16.32. To determine whether habitat loss has a disproportionately large impact on the connectivity of the entire habitat graph, as can occur with loss of important key connectivity areas that connect larger areas of habitat, we used the equivalent connectivity index (EC) of Saura et al. (2011). EC, defined as the size of a single theoretically maximally connected habitat patch that would provide the same connectivity value as found in the existing habitat network, was calculated using the following formula (Saura et al. 2011):

$$\mathrm{ECA} = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} (a_i a_j p \times_{ij})},$$

where a_i and a_j correspond to the weighted habitat area associated with nodes i and j (study cells) and $p \times_{ij}$ represents the maximum dispersal probability for all links connecting nodes i and j. The loss of a particular habitat patch may result in a decrease in EC that exceeds the decrease in weighted habitat area A if the lost habitat is vital for maintaining habitat connections of the entire network. In contrast, habitat losses in areas that are well-connected or have redundant habitat may result in decreases in EC that are less than A. Changes in EC were also divided by changes in weighted habitat area to yield what we refer to as the relativized EC. Values greater than 1 indicate that habitat loss results in a connectivity loss greater than random habitat loss, while values less than 1 indicate connectivity losses that are less than random habitat loss. All renewable energy development/land use scenarios are additive, meaning that habitat is only lost with each scenario, never gained. Relativized EC was used to compare the incremental loss of connectivity that occurs between scenarios, while the overall EC index was used to determine the absolute amount of habitat connectivity available for a given scenario.

Mapping core habitat areas

Maintenance of core habitat areas may be critical for persistence of MGS in light of climate change, increasing habitat fragmentation, and land conversion. We mapped and assessed changes in areal extent, habitat suitability, and habitat connectivity of core habitat areas. Areal extent was measured by the number of study blocks mapped as core habitat area. Habitat suitability was measured by summing the habitat suitability values from the 1-km^2 cells within all 25-km^2 study blocks mapped as core habitat. Habitat connectivity was measured using the EC index and the ratio of EC to weighted habitat area.

Core habitat areas were mapped using the PC_{flux} metric of Saura and Rubio (2010), emphasizing not just high quality habitat as the sole criterion for defining core area, but also the centrality of habitat relative to other habitat within the habitat network. PC_{flux} measures how well a patch is connected to other habitat patches and is similar to incidence function model indices (Moilanen and Nieminen 2002). It is the area-weighted dispersal flux from patch k to all connected patches and is defined as (Saura and Rubio 2010)

$$PC_{\text{flux}} = \sum (a_i a_j p \times_{ij}),$$

where a_i and a_j correspond to the weighted habitat area associated with nodes i and j (study blocks) and $p \times_{ij}$ represents the maximum dispersal probability for all links connecting nodes i and j for a particular habitat study block k. In our study, a_i and a_j were calculated as the sum of all habitat suitability grid cells (1 km^2) within the 25-km^2 study block. Study blocks with PC_{flux} values greater than $5e^6$ were mapped as core habitat areas. The value of $5e^6$ was selected because it roughly corresponded with the core areas defined empirically by Leitner (2008).

Mapping connectivity areas

Habitat patches referred to as stepping stones are those that have less value in terms of habitat area but serve to connect larger patches, and so can be critical for maintaining connectivity in fragmented landscapes (Saura and Rubio 2010, Kramer-Schadt et al. 2011, Saura et al. 2013). We define connectivity areas (stepping stones) as areas where the value of facilitating movement among other patches exceeds the value of the weighted habitat area alone. We mapped connectivity areas using the $PC_{\text{connector}}$ index (Saura and Rubio 2010), which measures the contribution of habitat patches in facilitating connections to other (often larger) habitat patches. The $PC_{\text{connector}}$ index is independent of the value of the weighted habitat area of the patch itself and is based mostly on its role within topological network for facilitating movement among other patches. $PC_{\text{connector}}$ is calculated as

$$PC_{\text{connector}} = \sum (a_i a_j p \times_{ij})$$

when $i \neq k$, $j \neq k$, and k is part of the maximum probability path between nodes i and j and $p \times_{ij}$ represents the maximum dispersal probability. Nodes i and j represent two end nodes (study blocks) that are connected by intermediate node k (study block). The loss of k would, by definition, result in decreased connectivity between nodes i and j because k is part of the maximum probability path. The $PC_{\text{connector}}$ index is one component of the probability of connection index (PC) defined by Saura and Pascual-Hortal (2007) and Saura and Rubio (2010),

$$PC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} (a_i a_j p \times_{ij})}{A_L^2},$$

where a_i and a_j correspond to the weighted habitat area associated with nodes i and j (study cells), $p \times_{ij}$ represents the maximum dispersal probability, and A_L^2 represents total habitat as determined by summing all values in the habitat suitability map. We mapped study blocks with a $PC_{\text{connector}}$/PC ratio > 0.5 as key connecting elements and study blocks with a $PC_{\text{connector}}$/PC ratio between 0.25 and 0.5 as important connecting elements.

To assess the effects of renewable energy development on habitat connectivity corridors, we mapped changes in connectivity between scenarios and identified six potential types of changes: key connectivity maintained, key connectivity lost, connectivity maintained, connectivity lost, connectivity role diminished, and connectivity role increased. In some instances, the connectivity role of a study block may increase with habitat loss. This occurs when habitat loss reduces the number of pathways, resulting in an increased role for the remaining pathways. Therefore, it is critical to consider changes in connectivity in conjunction with changes in habitat and overall connectivity of the network.

Movement corridors

Climate change is expected to result in large northward range shifts for MGS but with limited range shifts upward in elevation, due to preference of MGS for flat sandy or gravelly substrates that occur in valley bottoms or lower slopes (Inman et al. 2014). Because of these habitat requirements, the area just north of the current range limit is likely to be critical for the persistence of the species. We used Circuitscape analysis (McRae 2006) to assess movement pathways north of the current range limit and within the northern portion of the current range. Maps produced from Circuitscape analysis are useful for identifying alternative routes of movement as well as critical pinch points that may impede movement (McRae et al. 2008). Circuitscape analysis was performed in pairwise fashion by calculating the cumulative current between pairs of points (Shah and McRae 2008) using the inverse of the current conditions habitat model as a map of resistance. To examine potential for range expansion, a single point near the northern edge of the current MGS range was used as the source point while another point 60 km north of the current range was used as a destination point. To examine potential for movement within the northern portion of MGS range, we selected six evenly spaced source points from high suitability cells in southern areas with numerous MGS occurrences and one destination point at the northern edge of the current MGS range. Least-cost paths were calculated between all source and destination points to represent the single best path. Circuitscape and least-cost path models were developed for both current climate and the year 2080 given the A2 emissions scenario, changing only the cost of movement raster in response to changing climate.

Results

Changes in overall habitat connectivity

Climate change scenarios resulted in a large loss of both habitat area and habitat connectivity compared to renewable energy development under current climate (Table 2). All indicators declined precipitously with climate change (57–97%), while changes due to proposed renewable energy development ranged from 10% to 39%. For current climate conditions, the proportion of the graph within the largest component dropped from 96% to 86% between the permitted energy development scenario and the DRECP Alternative 1 scenario (Table 2). Concurrently, loss of about 10% weighted habitat area occurred between those scenarios. For the future climate, both total graph length and graph length of the largest component decreased by 11% and 24%, respectively, between the permitted energy and DRECP Alternative 1 scenarios.

Absolute changes in the EC were about an order of magnitude larger for the climate change scenarios than for energy development scenarios (change in EC, −725.55 for climate change vs. −68.88 to −208.53 for energy development; Table 2). When relativizing connectivity loss to habitat loss, the largest differences were between the permitted energy development scenario and the current land use scenario (relativized EC, 3.1) indicating that connectivity loss was expected to be three times greater per unit area of habitat loss. In contrast, the difference between the DRECP Alternative 1 and the permitted energy development scenario was less than 1, indicating that connectivity loss is expected to be less per unit area than random habitat loss.

Changes in habitat amount and connectivity within core areas

Habitat extent, amount, and connectivity changed dramatically with renewable energy development and climate change scenarios. Climate change is predicted to result in the complete elimination of core areas within the study region. Under the current climate regime, all renewable energy development scenarios are predicted to lead to a dramatic reduction in the areal extent, habitat availability, and habitat connectivity of core areas. The areal extent of core area was reduced from 2400 km^2 under current conditions to 210 km^2 with the most intensive renewable energy development scenario (Fig. 2, Table 3). Habitat amount within core areas was reduced by 60–76% compared to current conditions.

The greatest incremental losses of habitat amount are predicted to occur between the current land use and permitted energy development scenarios. It is important to note that the core habitat areas delineated in this study share some similarities with, but also differ from, the expert-derived core habitat areas of Leitner (2008). Two core areas identified by Leitner (2008; Coolgardie Mesa-Superior Valley area and the Olancha-Coso Range area) were not shown as core habitat in this study, presumably due to the inclusion of centrality as a criterion for defining core area.

Changing extent and quality of connectivity areas

The impact of land use is expected to have different effects on key connectivity areas depending upon their location in the habitat network. Comparing changes from current conditions to the most extreme energy development scenario shows that key connectivity areas in the eastern portion of the study area remain relatively unaffected, while those in the west are highly impacted (Fig. 3). Diminished connectivity is most pronounced in areas adjacent to major habitat reductions. In some instances, habitat loss appears to increase the relative importance of areas for maintaining connectivity of the network. This is due to a funneling effect in which the loss of multiple movement pathways increases the relative importance of the remaining pathways. However, the number of habitat blocks experiencing connectivity loss appears to be much greater than the relatively small number that saw an increase in relative connectivity importance. Habitat blocks experiencing a relative increase in connectivity, for the most part, did not experience an increase in absolute connectivity as measured by the change in $\mathrm{PC}_{\mathrm{connector}}$.

Identifying pinch points that restrict movement within corridors

Movement corridors constructed using current climate, and extending from the central to the northern portion of the range, identify a handful of alternative movement routes that may facilitate northward movement. However, significant pinch points exist that are associated with human population centers (letters A and B in Fig. 4a). Two alternative pathways (letters D and E in Fig. 4a) do not follow the least-cost path, indicating redundancy in movement pathways. Furthermore, there is more suitable habitat in the central portion of MGS range that may produce greater numbers of emigrants compared to the northern edge of the range where habitat is constricted due to topography. Least-cost path movement corridors projected using 2080 climate shifted to a completely new western corridor in response to changing habitat conditions (letter B in Fig. 4b).

The Circuitscape analysis suggests that northward expansion of the MGS range may only be feasible through the relatively narrow Owens River Valley due to the presence of unsuitable habitat to the east and west (Fig. 4c). Along the least-cost path there are two areas where pinch points may impede northward movement (letters A and B in Fig. 4c). Two less suitable routes

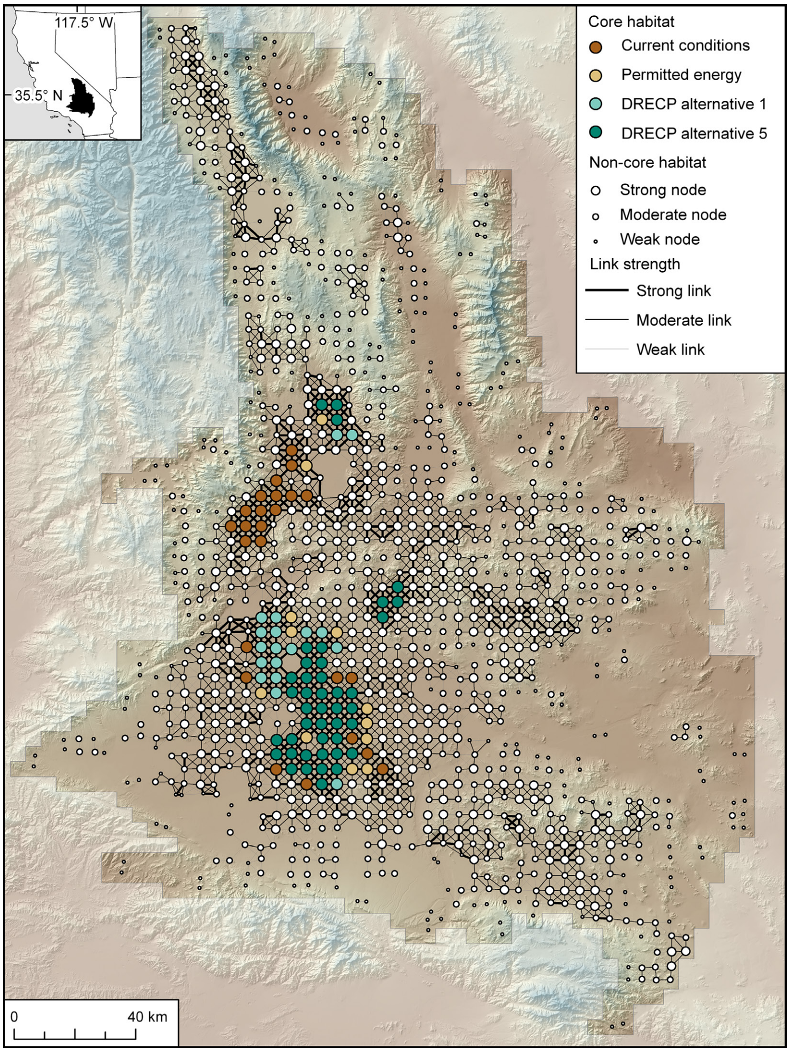

FIG. 2. Core habitat area for five land use/energy development scenarios overlaid on the habitat network. The reduction in core area is cumulative with historic conditions containing the most habitat followed by current conditions (assuming moderate land use), permitted energy projects, DRECP Alternative 1, and DRECP Alternative 5. For example, the core area mapped under the historic condition contains the other four classes. Nodes are weighted by the sum of habitat suitability, and link strength is based on the cost-weighted distance between habitat-weighted centroids.

may also facilitate northward expansion (indicated by letters C and D in Fig. 4c), although they present much higher cumulative resistance.

TABLE 3. Core habitat area, equivalent connectivity (EC) index, and relativized EC for each land use/energy development scenario.

	Current with moderate land use	Current with permitted energy	Current with Alt1 scenario	Current with Alt5 scenario
Habitat area	2503.61	1007.84	818.30	590.58
EC index	72.43	52.33	39.57	27.42
Relativized EC	6.76	0.46	1.30	1.10

Notes: Relativized EC is calculated by dividing the proportional loss of EC from the previous scenario by proportional loss of habitat from the previous scenario. No study cells had high enough connectivity values (PC_{flux}) to be mapped as core area in 2080 using the A2 emissions scenario.

DISCUSSION

Graph theory as a multiscale analysis tool

Our study supports the application of graph theory as a flexible framework particularly suited for addressing conservation problems across multiple scales of investigation including network, neighborhood, and individual habitat elements, such as habitat patches (nodes) and corridors (links; Rayfield et al. 2011) corresponding with the range-wide, metapopulation, and local scales

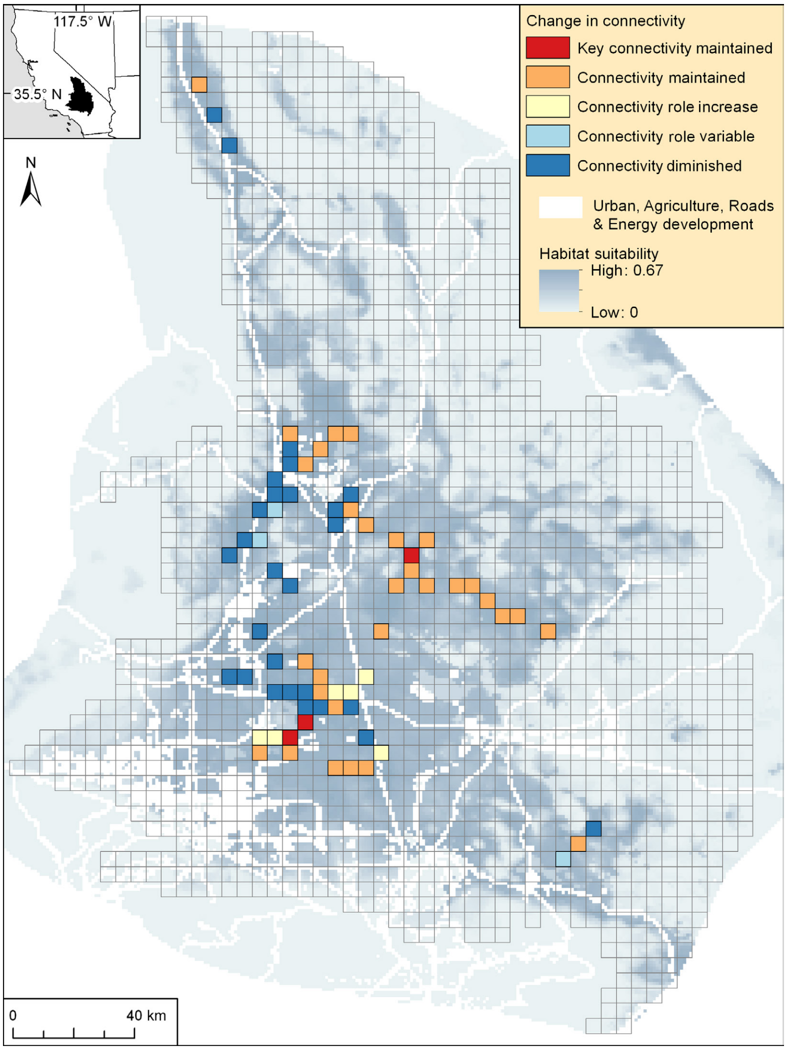

FIG. 3. Change in key connectivity areas between current conditions and the DRECP Alternative 5 endpoints assuming moderate land use summarized across three transitions (current conditions to the permitted scenario, permitted scenario to DRECP Alternative 1, and DRECP Alternative 1 to DRECP Alternative 5). Key connectivity areas were mapped as key connectivity area if $dPC_{connector}/dPC$ exceeds 0.5, important connectivity area if $dPC_{connector}/dPC$ exceeds 0.25, or non-connectivity area. Changes in connectivity were mapped for each scenario. All scenarios assume current climatic conditions. Although habitat is only removed in each scenario (not added), it is possible for the $dPC_{connector}$ to increase because the loss of habitat in neighboring study cells may reduce the redundancy of possible movement pathways.

(Table 1). At the range-wide scale, graph theory is particularly useful for comparing the effects of climate change and land use, as well as the synergistic effects of climate change and land use as demonstrated in this study. Another advantage of using graph theory at the network or range-wide scale is that it can help resolve the question of whether to focus conservation efforts on conserving habitat area or conserving habitat connectivity, which has been a hotly debated issue in conservation biology (Hodgson et al. 2009). Our approach using the habitat relativized equivalent connectivity (EC) index (Saura et al. 2011) quantifies the degree to which habitat loss is expected to result in a greater than random loss of connectivity. This approach avoids the dichotomy between habitat area and habitat connectivity as competing conservation objectives by allowing explicit consideration of habitat connectivity effects above and beyond the primary impacts of habitat loss.

Graph theory proved to be a flexible framework not only because it can address questions at multiple levels of organization, but also because it can accommodate different measures of effective distance. Although we used cost-weighted distance, other distance measures, such as Euclidean distance, least-cost path length, cumulative resistance derived from circuit theory, or simulated dispersal from individual-based models can be used to represent the probability of dispersal between nodes. Broadscale analyses identifying critical areas, such as

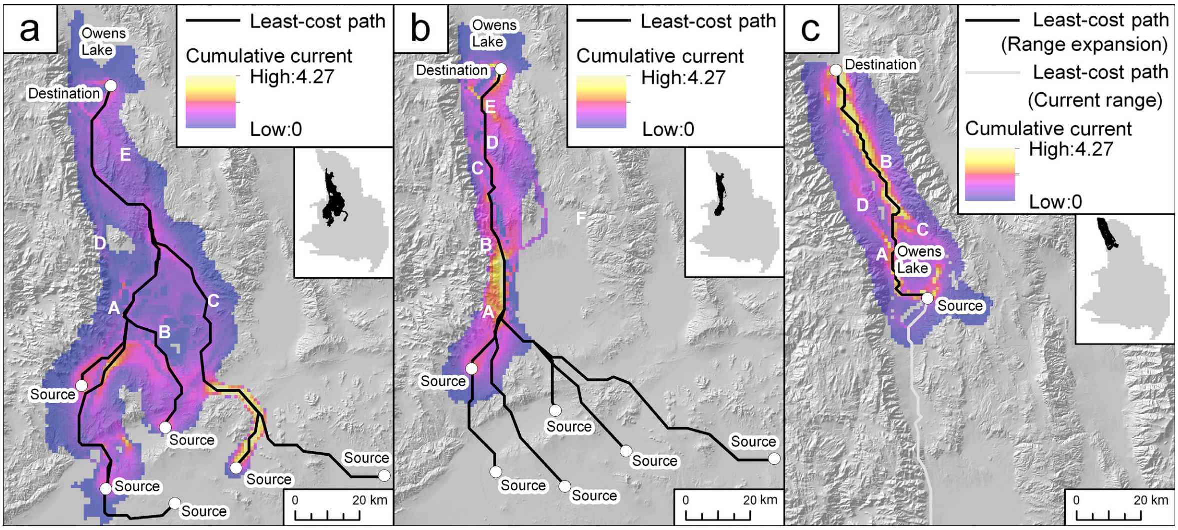

FIG. 4. Least-cost paths and cumulative current for three Mohave ground squirrel movement patterns. (a) Least-cost path and cumulative current for movement between the central and northernmost portions of the range using current climate. A–C indicate pinch points that may serve as obstacles to movement. D and E indicate alternative pathways that do not follow the least-cost path. Source points are located within the central portion of Mohave ground squirrel range (Matocq et al. 2014) and the destination point represents the northernmost known Mohave ground squirrel population. (b) Least-cost path and cumulative current for movement between the central and northernmost portions of the range using 2080 projected climate with the A2 emissions scenario. A–E represent pinch points. F represents an area that was the least-cost path using current climate but is projected to be unsuitable for MGS in 2080. G represents an area where there are no suitable alternatives to the least-cost path. (c) Least-cost path and cumulative current for a range expansion. A and B indicate pinch points that may serve as obstacles to movement. C and D represent alternative pathways that do not follow the least-cost path. The source point is located at the northernmost known population of Mohave ground squirrel. The destination point represents a location that would be well within the future range of Mohave ground squirrel based upon climatic and substrate suitability (Inman et al. 2014).

core areas or stepping stones, can be followed up with more detailed analysis illustrating specific scenarios, such as the range expansion scenario used in this study or specific development or corridor placement scenarios. In this way, broadscale graph analysis can be used to inform the siting of potential developments or corridor placements relative to where they would prevent the largest losses or provide the largest connectivity gains for the overall habitat network. Most existing corridor designs, although they explicitly incorporate information about land ownership and protection status, are opportunistic in nature, meaning that they are built around expanding existing reserve systems. In contrast, approaches that are organism-centered, such as those based on graph theory, highlight areas that are most critical for upholding range-wide habitat connectivity. The approach could be further extended using dynamic network models to address time-sensitive questions, such as changes in distribution in response to climate change (Ferrari and Lookingbill 2009, Ferrari et al. 2014).

Lattice vs. the patch-matrix model

To-date, most habitat applications of graph theory have utilized the patch-matrix model which involves splitting the landscape into habitat and non-habitat and considering movement between patches. This designation can be arbitrary and the selection of particular thresholds may strongly influence the outcome of the analysis (Moilanen 2011). For our MGS study system, we alleviated both of these problems by utilizing a lattice approach (Carroll et al. 2012) in which the landscape was divided into contiguous 25-km^2 study blocks that were treated as nodes in the graph analysis, and connectivity between adjacent nodes was represented using a 1-km cell size resistance raster to generate least-cost paths between habitat-weighted study block centroids. In addition to avoiding the separation of the landscape into binary suitable and non-suitable designations, this approach offers a number of other advantages. In the patch-mosaic model, connectivity can only be considered between patches, not within patches. For species with continuously distributed habitat this can often result in the mega-patch problem, in which one large patch is dominant (Cavanaugh et al. 2014). The lattice approach alleviates this problem by effectively splitting the patch into even-size tiles and considering connectivity among the tiles. The lattice approach may be more realistic compared to the patch-mosaic model in these situations because the removal of an entire mega-patch is unlikely, however the removal of a portion of a mega-patch due to human land use readily occur. By considering portions of patches that are more likely to correspond with actual habitat removal scenarios, the lattice approach may provide more information to conservationists and land managers compared to the patch-mosaic model.

Finally, the lattice approach used in this study uses two spatial scales of information, the 25-km^2 study blocks to represent node strength and 1-km^2 grid cells to represent connectivity among study blocks. The coarser spatial scale approximates the maximum dispersal distance of individual male squirrels as evidenced by fine-scale genetic autocorrelation studies (Matocq et al. 2014) and field observations (Harris and Leitner 2005). The finer spatial scale used for determining node connectivity allows consideration of fine-scale impediments to movement, such as development of energy facilities, roads, or urban expansion.

Assumptions in the modeling framework

The modeling framework employed in this study makes some key assumptions that should be considered carefully. The species distribution model used to predict habitat suitability and landscape resistance used two predictor variables (surface texture and surface albedo) from MODIS satellite imagery, which have relatively coarse spatial resolution (1-km^2 cell size) yet contributed 46.6% and 25.4%, respectively, to the overall habitat model (Inman et al. 2013). Finer scale models have been shown to increase the geographic extent of habitat relative to coarser scale models, because topographic and climatic heterogeneity within a grid cell may result in microclimates being omitted at the coarser spatial resolution (Randin et al. 2009, Ackerly et al. 2010). We expect that our results may overestimate the effects of climate change due to the potential omission of microclimates within a grid cells. We note, however, that there are aspects of microclimate that cannot be modeled simply by using finer scale data, but rather, require process-based models to incorporate phenomena such as cold air drainage (Lundquist et al. 2008). The species distribution model in this study was based on downscaled climate variables from the NOAA GFDL CM2.1 model (Delworth et al. 2006) with the A2 emissions scenario for 2080 that has been commonly used to represent climate change predictions on the hot and dry end of existing GCM scenarios (Cayan et al. 2008, Flint and Flint 2012). Inman et al. (2014) assessed climate change impacts on Mohave ground squirrel habitat for the A2 and B1 emissions scenarios for 2030 and 2080. Although there were noticeable differences in the extent of habitat along the eastern margin of the range between the two emissions scenarios for 2030, both scenarios tended to predict similar habitat extent with strong contractions in the amount of habitat available between 2030 and 2080. Due to the similarity in habitat extent in 2080 between the two emissions scenarios, we employed a single climate scenario and focused our analysis of habitat connectivity on differences between renewable energy development scenarios. We did not incorporate urban expansion scenarios into our modeling framework, although we acknowledge that others, such as Davis et al. (2013), did examine urban expansion scenarios in the Mojave Desert, finding that the bulk of the expansion occurring along the southern and southwestern periphery of Mohave ground squirrel's range.

The modeling approach required decisions regarding several thresholds. One such threshold was the maximum dispersal cost above which graph links were considered unusable by Mohave ground squirrels. Given the relatively short dispersal distance of individual squirrels (0–6230 m; Harris and Leitner 2005), we opted to use genetic distance to select a maximum cost distance above which dispersal could not occur. In the absence of genetic information, it is possible to use individual-based models to estimate intergenerational dispersal (Lookingbill et al. 2010) and use these estimates to inform graph link strength. The use of weighted graphs in which the likelihood of dispersal is described as continuous may minimize some of the error associated with choosing a threshold compared to unweighted graphs that use a binary suitable/unsuitable threshold. We also used a single threshold approach to delineate core areas. Due to uncertainty surrounding this threshold, though, our estimates of habitat loss in core areas should be viewed as relative measure in comparison to habitat loss across the entire habitat network.

Using spatial lattices to model habitat connectivity with graph theory requires several parameter decisions prior to analysis. One decision involves selecting the appropriate size lattice (study block) relative to the cell size of the resistance raster. Larger lattice sizes relative to resolution of the resistance raster would be expected to result in larger node weightings for highly suitable habitat. However, very large lattices relative to the resolution of the resistance raster would result in greater cost-weighted distance between adjacent study blocks, likely reducing the probability of dispersal. In contrast, a very small lattice greatly reduces the number of potential least-cost paths, possibly leading to results that more closely approximate Euclidean distance with a higher probability of dispersal between study blocks. Since PC_{flux}, being the area-weighted flux (Saura and Rubio 2010), is conceptually related to the number of emigrants, it is logical to set the lattice resolution approximately equal to the estimated home range size of the organism.

Applications to conservation

Demand for renewable energy is growing worldwide, and in the California deserts, 33000–290500 hectares are slated for designation as development focus areas for solar, wind, and geothermal energy development so far (DRECP 2012). With such large areas potentially affected, conservation decisions will have long-lasting effects on biodiversity and population viability of threatened species. Our analysis approach supports decision makers by providing information at multiple scales of ecological organization. At the range-wide scale, climate change is expected to have the largest impact on Mohave ground squirrel in terms of both habitat area and habitat connectivity, likely fragmenting the species range into three distinct clusters roughly corresponding with the three genetic groups identified by Bell and Matocq (2011). Although climate change is expected to have a larger impact on Mohave ground squirrel habitat area, losses due to renewable energy development in core areas as identified in this study are expected to be as large as climate change losses range-wide. This is particularly evident for the central population where much of the proposed renewable energy development is planned. In both the current climate scenario and the future climate scenario, the relativized EC index suggested that permitted energy development is likely to have a larger impact on habitat connectivity than the two DRECP scenarios we examined. These results highlight the need to examine habitat change at the range-wide scale to provide context for habitat loss and loss of connectivity for critical areas including core habitat.

Our analysis of potential movement pathways indicates that climate change is likely to result in much of the China Lake Basin (Fig. 4a between A and C) becoming too hot and dry to support Mohave ground squirrel. Under current conditions, we estimate that optimal movement routes for Mohave ground squirrel would include those that skirt the eastern and western portions of that the China Lake Basin, providing redundancy of potential pathways for dispersal. With these areas removed, only a single, narrow best-route exists connecting northern and central populations along the foothills of the Sierra Nevada Mountains. Occurrence data not used in the species distribution model suggest that portions of this route are useable by Mohave ground squirrel (P. Leitner, *personal communication*), although it remains unknown whether the species can move through the pinch point identified in this study. This pinch point consists of a narrow zone of marginally suitable habitat situated between the slopes of the Sierra Nevada and a lava flow. Penrod et al. (2012) propose a conservation corridor in this area, although not strictly designated for Mohave ground squirrel. Despite the critical position and uniqueness of this corridor, the Increased Geographic and Technology Flexibility Alternative of the draft DRECP identifies this corridor as a "Development Focus Area" would, which streamlines environmental permitting and promote development of projects on these sites (DRECP 2012). All other alternatives identified by the DRECP, including the preferred alternative, do not designate this as a Development Focus Area. Fine-scale sampling using cameras traps and radio collaring in the vicinity of the pinch point could help determine the viability of this corridor and determine its potential role in facilitating gene flow and movement-based adaptation to future climate change. While the uniqueness of this corridor has not been explicitly assessed for other species, as one of the only low-pass connections between the Mojave Desert and the broad, low valleys to the north, we expect this corridor represents a particularly critical north-south corridor of climate adaptation for many species currently occupying the Mojave Desert.

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