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Replicated landscape genetic and network analyses reveal wide variation in functional connectivity for American pikas

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Abstract. Landscape connectivity is essential for maintaining viable populations, particularly for species restricted to fragmented habitats or naturally arrayed in metapopulations and facing rapid climate change. The importance of assessing both structural connectivity (physical distribution of favorable habitat patches) and functional connectivity (how species move among habitat patches) for managing such species is well understood. However, the degree to which functional connectivity for a species varies among landscapes, and the resulting implications for conservation, have rarely been assessed. We used a landscape genetics approach to evaluate resistance to gene flow and, thus, to determine how landscape and climate-related variables influence gene flow for American pikas (*Ochotona princeps*) in eight federally managed sites in the western United States. We used empirically derived, individual-based landscape resistance models in conjunction with predictive occupancy models to generate patch-based network models describing functional landscape connectivity. Metareplication across landscapes enabled identification of limiting factors for dispersal that would not otherwise have been apparent. Despite the cool microclimates characteristic of pika habitat, south-facing aspects consistently represented higher resistance to movement, supporting the previous hypothesis that exposure to relatively high temperatures may limit dispersal in American pikas. We found that other barriers to dispersal included areas with a high degree of topographic relief, such as cliffs and ravines, as well as streams and distances greater than 1–4 km depending on the site. Using the empirically derived network models of habitat patch connectivity, we identified habitat patches that were likely disproportionately important for maintaining functional connectivity, areas in which habitat appeared fragmented, and locations that could be targeted for management actions to improve functional connectivity. We concluded that climate change, besides influencing patch occupancy as predicted by other studies, may alter landscape resistance for pikas, thereby influencing functional connectivity through multiple pathways simultaneously. Spatial autocorrelation among genotypes varied across study sites and was largest where habitat was most dispersed, suggesting that dispersal distances increased with habitat fragmentation, up to a point. This study demonstrates how landscape features linked to climate can affect functional connectivity for species with naturally fragmented distributions, and reinforces the importance of replicating studies across landscapes.

*Key words: American pika (*Ochotona princeps*); climate change; dispersal; functional connectivity; graph theory; landscape genetics; metareplication.*

Introduction

Maintaining landscape connectivity is essential for long-term population persistence (Taylor et al. 1993), especially in the face of rapid climate change (Cobben et al. 2012). Functional connectivity describes how individuals respond to the distribution of resources on the landscape (structural connectivity) as well as their ability to negotiate and disperse through the landscape (Stevens et al. 2006). Climate change has the potential to alter both structural and functional connectivity. Furthermore, complex interactions among multiple factors may produce highly individualistic responses to climate change across species (Rapacciuolo et al. 2014) and regions (Rowe et al. 2015). Predicting how climate change will affect populations, and in turn species persistence, therefore may require understanding the factors influencing both habitat occupancy and functional connectivity, as well as their interactions and the degree to which such factors vary across landscapes (e.g., Shirk et al. 2014). This is particularly true for species that are restricted to naturally fragmented habitats resembling

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metapopulations, such as pond-breeding amphibians (Murphy et al. 2010), and species found primarily on mountaintops (Epps et al. 2004, Walker et al. 2007) where suitable land area is projected to decrease as climates warm, reducing population size and increasing isolation (Guralnick 2007).

Although the importance of functional connectivity for persistence of fragmented populations is well understood (Tischendorf and Fahring 2000), most efforts to forecast impacts of climate on species distributions have focused primarily on climate niche (e.g., Huntley et al. 1995, Kearney and Porter 2004, Calkins et al. 2012). A potential weakness of such species distribution models is that they ignore important ecological processes such as functional connectivity (Pearson and Dawson 2003, Guisan and Thuiller 2005). Effective forecasting will require consideration of the relative importance of climate and connectivity, and the potential interplay between these factors, in shaping a species' distribution. This is particularly true for dispersal-limited species exhibiting a strong relationship between climate and population persistence, such as the American pika (*Ochotona princeps*) (Hafner 1993, Beever et al. 2010, 2013, Erb et al. 2011, Calkins et al. 2012).

For species with naturally fragmented distributions or that exist in metapopulations, predictions of population persistence based on within-patch characteristics alone ignore the possibility that loss of between-patch connectivity could lead to metapopulation collapse and ultimately local extinction. Alternately, a highly interconnected metapopulation could be more resilient to environmental change, particularly in heterogeneous environments (Hanski and Gilpin 1997). Thus, accurate characterization of functional connectivity among patches is needed. In the simplest metapopulation model, the probability a habitat patch is occupied is a function of the rates of patch extinction and colonization, which in turn are a function of patch size as well distance to nearby patches, respectively (Levins 1969). However, in practice, the probability of occupancy is usually patch specific (Fleishman et al. 2002, Prugh et al. 2008). When habitat configuration is considered, distance between habitat patches is often measured as straight-line (Euclidean) distance (e.g., Ficetola and De Bernardi 2004, Franken and Hik 2004); alternatively, patch isolation can be characterized more effectively as a function of landscape resistance, which takes into account how organisms move through heterogeneous landscapes with varying efficiency (McRae 2006). The latter metric may therefore be critical for our understanding of functional connectivity and, in turn, metapopulation persistence in a changing environment. A variety of methods for estimating landscape resistance have been developed (Spear et al. 2015). However, employing such models in conservation may be complicated by variation in landscape resistance among landscapes, although this has rarely been evaluated.

American pikas exemplify the need to assess functional connectivity for conservation planning: they exhibit fine-scale metapopulation dynamics and their distribution is strongly influenced by climate (Hafner 1993, Smith et al. 1997, Moilanen et al. 1998, Smith and Nagy 2015), but in ways that vary among habitats and regions (Jeffress et al. 2013, Schwalm et al. 2016). Their persistence at the patch scale is partly determined by patch size, which affects extinction rates, as well as total habitat area near the focal patch and distance to nearby patches, which affect colonization rates (Beever et al. 2003, 2010, 2011, 2013, Stewart and Wright 2012, Millar et al. 2013, Stewart et al. 2015). The specialized rocky habitats on which American pikas rely provide thermal buffering that enables persistence in seemingly inhospitable regions (Millar et al. 2013). Yet, pika dispersal among habitat patches is poorly understood and likely habitat dependent. Smith (1974*b*) proposed that distances greater than a few hundred meters in hot climates may pose a barrier to dispersal for American pikas, whereas they may be able to traverse multiple kilometers through more hospitable areas. Understanding the degree to which dispersal patterns and behaviors and thus functional connectivity vary among landscapes is likely to be a key component of forecasting influences of environmental change on persistence of pikas as well as for other species with fragmented distributions.

In this study, we used a landscape genetics approach to identify factors influencing functional connectivity for the American pika by characterizing landscape connectivity and gene flow. We employed metareplication (i.e., replicated studies conducted in different locations, seasons, or spatial scales; Johnson 2002) by applying the same study design to eight federally managed study sites across the western United States. Such replication allowed us to evaluate the impact that landscape heterogeneity and configuration could have on limiting factors for dispersal (e.g., Short Bull et al. 2011, Cushman et al. 2011, 2013a) and is critical for broadening the scope of inference (Shirk et al. 2014). We compared the degree of within-site gene flow among the eight study sites by quantifying gene flow threshold, which reflects the distance genetic material can be transported through dispersal and reproduction in successive generations (see *Methods: Network models*). We then used empirically derived landscape resistance models and gene flow threshold estimates to inform a patch-based network analysis using a graph-theoretic approach aimed at determining the current degree of fragmentation within each site as well as identifying patches and linkages with high importance to connectivity at the site level (e.g., Creech et al. 2014). Through these multiple integrated approaches, we identify landscape variables that either promote or inhibit dispersal, test whether dispersal distances vary among landscapes as a function of habitat configuration, assess current fragmentation as a baseline for future

research, and identify locations within study areas that may be important for maintaining functional connectivity.

Materials and Methods

Study species

American pikas are small lagomorphs (121–176 g) typically found at high elevations within western North America (Smith and Weston 1990). They are restricted to fractured rock habitats, such as talus slopes and lava flows, which provide refuge from predators and thermal buffering (Smith 1974*b*, Smith and Weston 1990, Millar et al. 2014*b*). American pikas are heat sensitive and cannot tolerate prolonged exposure to high temperatures (Smith 1974*d*), but may persist at lower elevations and in hotter climates if there are suitable microclimatic refugia (Millar and Westfall 2010, Rodhouse et al. 2010, Collins and Bauman 2012, Millar et al. 2013, Varner and Dearing 2014). Estimates of their maximum dispersal ability range from a few hundred meters (Smith 1974*d*) to 20 km (Hafner and Sullivan 1995), but most estimates suggest there is little or no gene flow among populations separated by distances greater than 10 km (Peacock and Smith 1997, Henry et al. 2012). American pikas are considered a sentinel of climate warming (Hafner 1993), as there have been numerous apparent recent extirpations reported from relatively hot, dry regions (Beever et al. 2011) and future predictions suggest widespread losses in the species' distribution particularly in, but not limited to, low elevations (Calkins et al. 2012, Stewart et al. 2015).

Study sites

We analyzed data from eight study sites that reflect much of the environmental variation experienced by pikas within the western United States: Crater Lake National Park, Oregon (CRLA); Craters of the Moon National Monument, Idaho (CRMO); Great Sand Dunes National Park, Colorado (GRSA); Grand Teton National Park, Wyoming (GRTE); Lassen Volcanic National Park, California (LAVO); Hart National Antelope Refuge, Oregon (HMAR); Rocky Mountain National Park, Colorado (ROMO); and Sheldon National Wildlife Refuge, Nevada (SHWR; Fig. 1, Appendix S1). Mean elevations within these study areas ranged from ~1700 m (CRMO and HMAR) to ~3150 m (GRSA, Table 1). In addition to differences in elevation range, these sites were selected to represent differences in landform type (Table 1), landscape configuration, amount of potential pika habitat, and dominant vegetation type.

Sampling design

We collected fecal samples for genetic analyses through a combination of random, targeted, and opportunistic sampling methods, with the goal of sampling the greatest extent possible within each site. Random sampling coincided with occupancy surveys conducted under a generalized, random, stratified grid sampling scheme within pika habitat (Stevens and Olsen 2004, Jeffress et al. 2011). For a detailed description of this sampling scheme and identification of potential habitat, see Jeffress et al. (2013). Targeted sampling involved exhaustively searching an occupied area. Opportunistic

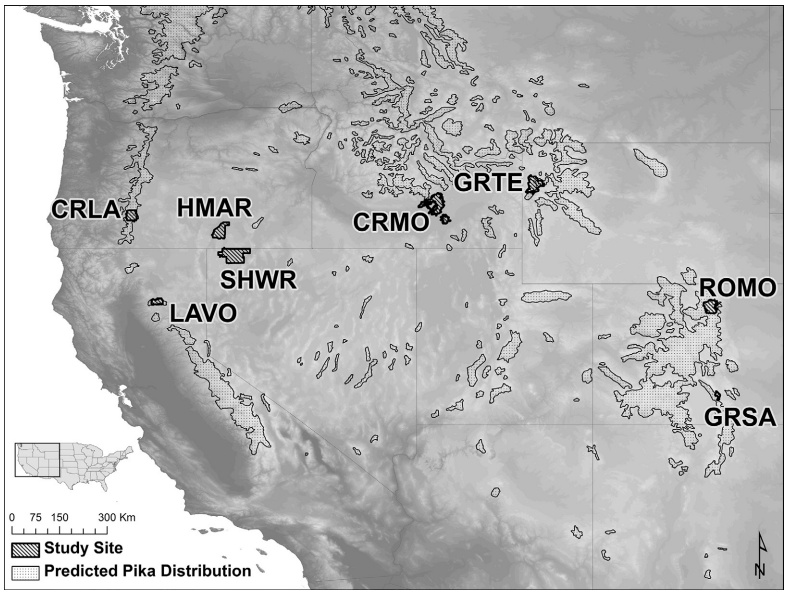

Fig. 1. Map of the western United States showing elevation in grayscale (dark for low elevation, light for high elevation), predicted American pika (*Ochotona princeps*) distribution in gray stippling (redrawn from Hafner and Sullivan 1995), and study sites in thick black outline with hashed shading. See *Materials and Methods: Study sites* for full site names.

TABLE 1. Study site characteristics for each site including biogeographic region, dominant rock landform type of American pika (*Ochotona princeps*) habitat, and elevation ranges for the whole study area as well as only areas characterized as potential pika habitat.

			Elevation (m)				Pika habitat elevation (m)			
Study site	Region	Rock	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD
CRLA	Cascades	1	1119	2722	1792	191	1409	2709	2068	190
CRMO	N Rockies	2	1606	2467	1723	128	1616	1984	1697	47
GRSA	S Rockies	1	2389	4361	3157	417	2627	4080	3421	336
GRTE	N Rockies	1	1872	4201	2427	389	1932	3739	2925	255
HMAR	Great Basin	1, 3	1358	2443	1697	288	1378	2374	1849	223
LAVO	Cascades	1, 2	1340	3187	1948	244	1390	3156	2096	278
ROMO	S Rockies	1	2223	4347	3060	377	2394	4347	3520	215
SHWR	Great Basin	1, 3	1357	2222	1869	101	1659	2221	1916	91

Notes: See *Materials and Methods: Study sites* for full names of sites, see Fig. 1 for map of study sites. Rocky Mountains were divided into northern (N) and southern (S) portions. Rock (landform) types include (1) talus, (2) lava flow, and (3) inselbergs (isolated, rocky exposures).

sampling occurred in transit between survey points. See Castillo et al. (2014) for a detailed description of genetic sampling methods. We collected samples between June and September 2010–2012. We restricted sampling to fresh fecal pellets containing green plant material to ensure they were deposited that year (Nichols 2010) and discrete piles of pellets (i.e., not touching older pellets) to avoid representation of multiple pikas within a genetic sample.

DNA extraction and genotyping

We extracted genomic DNA from fecal samples using a modified AquaGenomic DNA extraction protocol (MultiTarget Pharmaceuticals, Salt Lake City, Utah, USA). We genotyped individuals at 24 microsatellite loci in four multiplex polymerase chain reactions (PCR) using a Qiagen Multiplex PCR kit (Qiagen, Valencia, California, USA). Detailed PCR protocol, primer sequences, and methods for calling and screening microsatellite genotypes are provided in Appendix S3. We screened for duplicate individuals first by using Cervus 3.0 (Kalinowski et al. 2007) to identify matching genotypes, allowing fuzzy matching with up to six mismatching loci. We then used Gimlet (Valiere 2002) to calculate the probability of identity for a full-sibling relationship ($P_{(ID)}$among siblings) (Waits et al. 2001) for each of the matching genotypes identified in Cervus. We identified duplicate individuals if $P_{(ID)}$among siblings $< 10^{-3}$ (Epps et al. 2005) and removed all but one genotype for each of the sets of duplicates. We tested for linkage disequilibrium and significant deviations from expected Hardy-Weinberg genotype frequencies using Genepop (Raymond and Rousset 1995). Finally, we removed individuals with incomplete genotypes from further analysis.

Landscape configuration metrics

We chose landscape configuration metrics that reflected habitat area and fragmentation, which were highly correlated with patch occupancy in previous research (Beever et al. 2003, 2010, 2011, 2013, Stewart and Wright 2012, Millar et al. 2013). We calculated landscape configuration metrics for each study site using Fragstats v. 4.2 (McGarigal et al. 2002). Using a land cover raster modified from the National Land Cover Dataset (NLCD 2006 Land Cover, U.S. Geological Survey) and potential pika habitat maps (e.g., Jeffress et al. 2013), we quantified the percent land cover (PLAND) as well as a modified Simpson's evenness index (MSIEI) using the following cover classes: pika habitat, forested, shrub/scrub, open, and water (lakes and major rivers only). Simpson's evenness index ranges from 0, representing no diversity (i.e., a single large patch) to 1, representing perfectly even distribution of area among patch types. Next we calculated six pika habitat configuration metrics: area-weighted mean patch area (AREA); area-weighted mean radius of gyration (GYRATE), a measure of patch extent where elongated (i.e., linear) patches have a greater radius than round patches of similar area; mean proximity index (PROX), the degree of patch isolation and fragmentation where a value of 0 indicates complete isolation; Euclidean nearest neighbor (ENN), the mean distance between each patch and its nearest neighbor; and patch clumpiness index (CLUMPY), which ranges from −1 for maximally dispersed to 1 for maximally clumped.

Landscape resistance model optimization

We evaluated the hypotheses that exposure to relatively high temperatures, predation risk, and physical limitations (related to body size and locomotion) pose resistance to movement, and therefore gene flow, in American pikas. To accomplish this, we modeled resistance as a function of five landscape variables: elevation and aspect as climate-related variables; topographic complexity and water features as physical impediments; and land cover type as a metric of physical and climate-related

limitations. We created landscape resistance surfaces for a range of model parameters influencing the magnitude of resistance (determined by R_{max}) and shape of the relationship (governed by a function of x, see Appendix S4 for a detailed description) for each landscape variable using ArcGIS 10.0 (ESRI, Redlands, California, USA) for a total of 350+ univariate resistance model hypotheses per study site (Castillo et al. 2014). Each resistance surface raster consisted of ~10-m pixels (1/3 arc second). In addition to the landscape resistance hypotheses, we modeled the isolation by distance (IBD) hypothesis that geographic distance between individuals alone influenced genetic distance, by creating a raster of constant value equal to one. We used Circuitscape v.3.5.4 (McRae 2006) to calculate cumulative resistance between points representing each genotyped individual. This resulted in a matrix of pairwise resistance distances for each landscape resistance hypothesis as well as the IBD hypothesis.

We evaluated landscape resistance hypotheses by assessing the correlation between a genetic distance matrix and resistance distance matrix using partial Mantel tests in a reciprocal causal modeling framework (Shirk et al. 2010, Cushman et al. 2013*b*, Castillo et al. 2014). While the potential for landscape genetics to address questions of functional connectivity is well recognized, the appropriateness of various approaches, particularly the statistical analyses used, is still a topic of debate (Balkenhol et al. 2009). The suitability of Mantel and partial Mantel tests has been questioned (Guillot and Rousset 2011, 2013) and repeatedly evaluated (Cushman et al. 2013*b*, Graves et al. 2013, Castillo et al. 2014). Mantel tests for the correlation between two distance matrices (genetic distance and geographic distance, typically) have been shown to result in high Type I error, particularly in highly similar or correlated landscapes (Cushman et al. 2013*b*). In a previous study (Castillo et al. 2014), we evaluated the use of partial Mantel tests in a reciprocal causal modeling framework proposed by Cushman et al. (2013*b*). In that improved framework, we considered the relative support (see next paragraph) for each model in pairwise competition with every other model in the candidate set, rather than P values as our criterion for support, in addition to stringent causal modeling criteria. Castillo et al. (2014) demonstrated through individual-based, spatially explicit population genetic simulations in CDPOP (Landguth and Cushman 2010) that this method successfully identified the underlying landscape variables influencing gene flow, although accurately identifying the magnitude of resistance for the individual landscape variables was more difficult.

We determined genetic distance among individuals using a principal components analysis to calculate the pairwise genetic distance matrix (Shirk et al. 2010, Castillo et al. 2014) in R 2.13.1 (R Development Core Team 2011). We evaluated each of our univariate landscape resistance hypotheses using the partial Mantel test for correlation between genetic distance (GenD) and resistance distance (RD), after partialling out (i.e., controlling for the effect of) the IBD matrix, with the Ecodist package in R. For each model with a significant correlation, we calculated the relative support (RS; Cushman et al. 2013*b*, Castillo et al. 2014) as compared to each other significant model, for a given landscape variable. Relative support of resistance hypothesis 1 as compared to resistance hypothesis 2 is defined as $RS_{1|2} = (GenD \sim RD_1|RD_2) - (GenD \sim RD_2|RD_1)$, where $(GenD \sim RD_1|RD_2)$ represents the partial Mantel correlation between GenD and RD_1 after partialling out RD_2. We identified the best model hypothesis as the model in which $RS > 0$ for every comparison.

Once we identified the best univariate model for each landscape variable, we built multivariate resistance surfaces by creating rasters equal to the sum of the univariate model rasters for each landscape variable. We started with an additive model representing the sum of the best models for all landscape variables that had a significant correlation with genetic distance after partialling out IBD. We varied the model parameters for one variable, representing a range around the optimum univariate parameters, while holding the other parameters constant. As with the univariate optimization, the best supported multivariate model had positive RS in every comparison. We repeated this optimization process for each landscape variable until the model parameters stabilized (Castillo et al. 2014). In order for a multivariate model to be accepted, it had to pass two reciprocal causal modeling criteria: (1) the partial Mantel test GenD ~ RD|IBD must be significant ($P < 0.05$), and (2) GenD ~ IBD|RD must be nonsignificant ($P > 0.05$). Additionally, the two causal modeling criteria must also be met for the multivariate model and any reduced version of that model (Castillo et al. 2014).

We did not evaluate either panmixia or isolation by barrier hypotheses explicitly in our model selection process. Pikas establish a territory which they defend for their entire lives and mate with their surrounding neighbors (Smith and Weston 1990), therefore panmixia is not a plausible hypothesis at the spatial scale of our analyses (i.e., tens of kilometers). Two additional lines of evidence support rejection of the panmixia hypothesis: (1) IBD was significant in each study site (results not shown), but never performed better than all competing landscape resistance hypotheses, and (2) the observed gene flow thresholds were small (≤4.5 km, see *Results*) compared to the spatial extent of our analyses, suggesting restricted gene flow as opposed to panmixia. We did not identify any likely strong geographic barriers prior to the analysis; rather, we incorporated discrete linear features such as streams and roads, as well as less discrete features such as ridgelines into our landscape resistance hypotheses in order to test whether such features might resist gene flow.

Network models

We constructed network models to compare fragmentation across study sites as well as identify which

portions of the networks are important for maintaining connectivity (Creech et al. 2014, Galpern et al. 2011). We evaluated habitat patch connectivity within each study site using a graph-theoretic approach implemented with the igraph package in R (Csardi and Nepusz 2006). Network models consist of nodes (also called vertices) and edges connecting those nodes. Here, nodes represented a single habitat patch and edges represented distance between patch boundaries, expressed either as resistance distance or Euclidean distance. Initially, networks included all patches (nodes) and all edges. However, so that our model best reflected current conditions, we pruned (i.e., removed from the network) nodes and edges based on site-specific models of occupancy and gene flow, respectively, as follows. Pika habitat maps used in this study included all cover types considered potential pika habitat (e.g., talus and lava), regardless of whether pikas were known to occur there. However, not all rocky habitat is equally suitable for pikas (Jeffress et al. 2013, Millar and Westfall 2010). Therefore, in order to more accurately reflect available pika habitat, we pruned patches that were predicted to have <40% probability of occupancy based on site-specific models developed from occupancy surveys (Jeffress et al. 2013, Schwalm et al. 2016). That threshold was chosen because 99% of occupied sites occurred in patches with >40% probability of occupancy (Schwalm et al. 2016). We did not have predictive occupancy models for HMAR or SHWR. Instead, we pruned the HMAR network based on the observation that no pika sign (fresh or old) was observed on the west-facing slope of the Hart Mountain plateau in any surveys (Collins and Bauman 2012, J. A. Castillo et al., *unpublished data*). We did not prune nodes for SHWR.

We pruned edges representing a distance greater than the estimated maximum dispersal distance at each site. Actual dispersal distance is extremely difficult to determine from genetic data alone (Pinsky et al. 2010), therefore a gene flow threshold is sometimes used as a proxy for effective dispersal distance (Waser and Elliott 1991, Shirk and Cushman 2011). However, gene flow threshold reflects the extent of gene flow through multiple generations and therefore is expected to be greater than actual dispersal distance in most cases (Shirk and Cushman 2014). Using a Mantel correlogram approach in the Ecodist package in R, we identified the gene flow threshold in each park as the largest distance interval with a positive, significant correlation with genetic distance that did not follow a distance interval with a negative or nonsignificant correlation (Shirk and Cushman 2011). We calculated this metric for both geographic (Euclidean) distance and resistance distance. We used the estimate for gene flow threshold based on resistance distance between individuals as our initial dispersal distance threshold for considering two patches as connected in each network. Additionally, for all study sites, we pruned edges >4500 m from the network based on (1) observation that long-distance dispersal (>2 km) is rare (Smith 1974*a*, Smith and Ivins 1983, Peacock 1997, Peacock and Smith 1997), and (2) the largest observed gene flow threshold based on geographic distance in this study was 4500 m (see *Results*). We used this threshold to construct the networks based on the reasonable assumption that patches separated by greater distances are extremely unlikely to exchange individuals. However, multiple factors other than distance/resistance contribute to functional connectivity, such as population size and frequency of dispersal between patches. Therefore we assumed that network edges reflect the potential for patches to be connected, rather than the actual degree of connectivity between patches.

From this final network model in each site, we calculated number of clusters (connected components of the graph) and mean percent of connected patches. Mean percent of connected patches (MPCP) was calculated by identifying the number of patches to which a given patch was connected, dividing by the total number of patches in the network, then averaging this value across all patches in the network. These two metrics describe the degree of fragmentation within a site based on whether patches are likely to be connected. We also calculated betweenness for each edge and node. Betweenness represents the number of shortest paths passing through an edge or node, therefore greater betweenness reflects a lack of alternate pathways and likely more importance for maintaining connectivity. Betweenness takes into account the resistance distance between patches, not just whether patches are likely to be connected, when calculating the shortest paths.

For computational efficiency in calculating pairwise patch distances, we combined all potential pika habitat patches within 100 m of each other into a single patch using the aggregate tool in ArcGIS 10.0. For Euclidean distance, we used the "calculate near table" tool in ArcGIS 10.0 to calculate the distance between polygons at their closest point. For resistance distance, we used Circuitscape to estimate cumulative resistance between habitat polygons. Due to computational limitations associated with estimating cumulative resistance among polygons, we reproduced our optimized landscape resistance models at 20 m resolution and ran the analyses in a series of overlapping tiles of ~10 × 10 km. For pairs of patches for which resistance distances were estimated multiple times due to overlapping extent, we used the average resistance distance as our estimate of resistance distance.

Results

DNA extraction and genotyping

After removing samples that failed to amplify at one or more locus, contaminated samples, and multiple samples from a single individual, we obtained complete genotypes for 43–189 individuals per site (Table 2). All 24 loci were initially retained because none exhibited significant linkage disequilibrium within multiple study

TABLE 2. Optimized resistance models for each study site. Value, Mean, and Radius represent the optimum values, x governs the shape of the relationship, and R_{max} determines the magnitude of resistance. See Appendix S4 for model descriptions.

	Aspect			Elevation (m)		Topographic complexity			Water (R_{max})	Land cover			
Site (n)	Value	x	R_{max}	Mean (SD)	R_{max}	Radius	x	R_{max}		x	R_{max}	R_{max}	RS|IBD
CRLA (106)	90°	4	100	–		20	4	500	100	–	–	529	0.22
CRMO (53)			–	1750 (200)	100	10	4	100	–	–	–	136	0.63
GRSA (47)			–	–		–			–	10	10	10†	0.55
GRTE (189)	270°	10	100	–		–			–	10	1000	1100†	0.28
HMAR (43)	90°	0.5	2	–		–			–	–	–	3	0.06
LAVO (81)			–	2250 (300)	2	–			1000	–	–	1003	0.36
ROMO N (61)			–	3500 (300)	10							11	0.41
ROMO S (132)	45°	10	10	–		–			–	–	–	11	0.17
SHWR (47)	0°	1	10	–		–			–	PH = 1	other = 2‡	12	0.36

†Land cover included lakes as a barrier (Resistance = 10000). Maximum resistance (R_{max}) for land cover is presented for the "open" class type and the overall R_{max} excludes lakes.

‡PH = pika habitat. All non-habitat had a resistance of 2. There is no x parameter because this is a binary distinction.

sites. A number of loci were out of Hardy-Weinberg equilibrium (HWE) when calculated at the study site level, but no loci were consistently out of HWE when calculated at a spatial scale reflecting the gene flow threshold (1–4.5 km, see *Network models* below), suggesting deviations from HWE at the site level were the result of population substructure. We removed loci from further analyses if only a single allele was observed or if it failed to amplify consistently within a population, for a total of 17–22 loci per study site (Appendix S3). We observed a particularly large amount of population genetic structure within ROMO and subsequent phylogenetic analysis revealed the presence of individuals from two distinct mitochondrial lineages (concordant with subspecies delineation, Hafner and Smith 2010) within the park boundaries (J. A. Castillo et al., *unpublished manuscript*). Therefore, we partitioned samples from ROMO into northern (ROMO N) and southern (ROMO S) sampling localities and performed analyses on those two data sets separately.

Landscape configuration metrics

Percent cover by land cover classes varied among sites (Fig. 2), with amount of potential pika habitat ranging from 1.9% (HMAR) to 75.5% (CRMO). Indices of habitat continuity (radius of gyration, patch area, clumpiness index, and proximity index) likewise were highest in CRMO (Appendix S2), because the landscape was dominated by a single, large lava flow. Mean Euclidean nearest neighbor distance among patches was greatest in CRLA and GRSA, indicating that patches were most widely separated in those sites, and lowest in SHWR and CRMO (Appendix S2). Land cover class evenness, a measure of habitat heterogeneity measured as a modified Simpson's evenness index, was lowest in SHWR (0.04) and highest in GRTE (0.73, Appendix S2).

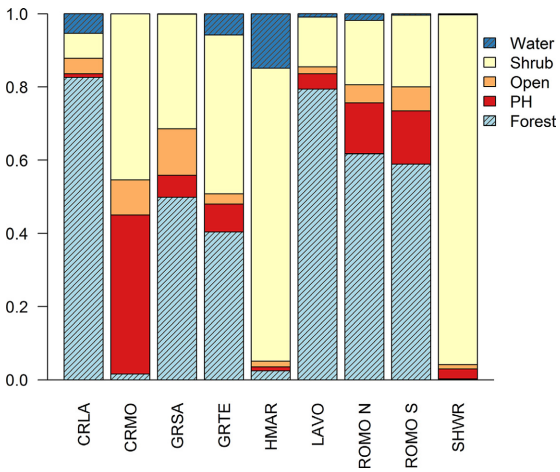

FIG. 2. Proportion of study area characterized by each land cover type for each study site. PH is potential pika habitat.

Model optimization

Across the eight study sites (nine after partitioning ROMO), no two best supported resistance models were identical (Table 2). GRTE and SHWR both included aspect and land cover, but the contrast (difference in resistance values governed by × or standard deviation, see Appendix S4 for details) and magnitude of resistance (R_{max}) for both variables were higher in GRTE. Aspect was included in five of nine models and in all models the aspect with the lowest resistance was >90° and <270°, suggesting south-facing aspects posed more resistance to pika dispersal than north-facing aspects.

Elevation was included in three final models: CRMO, LAVO, and ROMO N (Table 2). For all three of these sites, the optimal elevation closely resembled the mean elevation of pika habitat (Table 1). Pika habitat in

CRMO had the least elevational variation and the lowest maximum elevation of the study sites (Table 1). Topographic complexity was included in two sites: CRLA and CRMO (Table 2). For CRLA, areas of greatest resistance correspond to cliffs and ravines (Castillo et al. 2014). In CRMO, however, there was much less dramatic relief and areas of greatest resistance likely reflected features such as boundaries of lava tubes or areas of greater soil and vegetation development (e.g., flow contact zones and kipukas).

Water was included in CRLA and LAVO, with the relatively high resistance value in LAVO suggesting streams and lakes were significant barriers to gene flow. Land cover was included in the final model for GRSA, GRTE, and SHWR. In GRTE and GRSA, the optimal parameters included high contrast (x = 10), meaning pika habitat, forested, and shrub/grassland cover types had relatively low resistance while open areas had high resistance (Table 2 and Appendix S4). The optimal land cover parameters for SHWR included only pika habitat (resistance = 1) and non-pika habitat (resistance = 2).

Resistance values, such as R_{max}, are difficult to compare between sites because they reflect the relative resistance of particular variables within that location (Castillo et al. 2014); however, we could identify which variables are most influential within and across sites. For example, both R_{max} and RS as compared to the IBD model were low for HMAR (3 and 0.06, respectively), suggesting that geographic distance alone likely explains much of the genetic distance among individuals at that site (Mantel r for GenD~IBD = 0.55, P < 0.001). However, even at HMAR, the aspect model passed all our rigorous causal modeling criteria; therefore, it significantly, although weakly, contributed to genetic distance. In contrast, R_{max} was highest in GRTE and distance alone did not explain much of the genetic distance among individuals (Mantel r for GenD~IBD = 0.1, P < 0.01), suggesting that land cover and aspect strongly influence gene flow. In GRTE, open areas (i.e., bare rock without crevices and roads) posed much greater resistance to gene flow than pika habitat (1000 times greater), forested areas (500 times greater), and shrub/grassland (17.5 times greater).

Network models

Gene flow thresholds based on resistance distance (GFT_{RD}) used to prune each network ranged from 0.8 (GRSA) to 24 (GRTE; Table 3, values not directly comparable between sites). Gene flow thresholds measured as geographic distance (GFT_{GeoD}) ranged from ~1 km (GRSA) to 4.5 km (LAVO), with a mean of 2.8 km (Table 3). Number of distinct clusters ranged from three (CRMO) to 46 (GRTE); but despite the large number of clusters in GRTE, the largest cluster contained nearly all of the nodes (94%, Table 3 and Fig. 3), suggesting a high degree of connectivity overall despite a relatively large number of small, isolated clusters. Likewise, the largest cluster contained >90% of the nodes in HMAR, LAVO, ROMO N, ROMO S, and SHWR (Table 3 and Fig. 3). Mean percentage of connected patches (MPCP, the mean percentage of the network any single node is connected to) ranged from 12% in GRSA to 98% in SHWR. However, SHWR and HMAR are not directly comparable to the other networks because we did not prune the patches based on predicted occupancy. Gene flow threshold was predicted by mean patch area and MPCP, such that sites with smaller patches and greater MPCP had larger gene flow thresholds than sites with larger patches or fewer connected patches (R^2 = 0.69, P = 0.03, df = 2 and 6, Fig. 4).

By visually assessing the network models and quantifying node and edge betweenness, we identified regions that might be at risk of becoming increasingly isolated, regions that are important for maintaining functional

TABLE 3. Network model metrics for each study site of American pikas, including: gene flow threshold estimates in terms of geographic distance (GFT_{GeoD}) and resistance distance (GFT_{RD}); total number of patches (nodes) in the network, not including pruned patches; number of clusters in the pruned network; percentage of nodes in the largest and second largest clusters in the network; and mean percentage of connected patches.

					Percentage of nodes		
Site	GFT_{GeoD} (m)	GFT_{RD}	Patches	Clusters	Largest cluster size	Second-largest cluster size	Mean percentage of connected patches
CRLA	2500	20	126	26	56	19	34
CRMO	1200	7.5	17	3	88	6	73
GRSA	1000	0.8	109	28	47	10	12
GRTE	4000	24	846	46	94	1	88
HMAR	2250	1.8	190	9	95	2	89
LAVO	4500	2.4	567	10	98	0	96
ROMO N	2500	4.5	403	24	94	1	89
ROMO S	2500	4	514	10	98	0.2	96
SHWR	4250	6	1383	16	99	0.1	98

Note: The largest cluster size reflects the proportion of patches that are connected to each other, while the mean percentage of connected patches reflects the average proportion of patches any single patch is connected to.

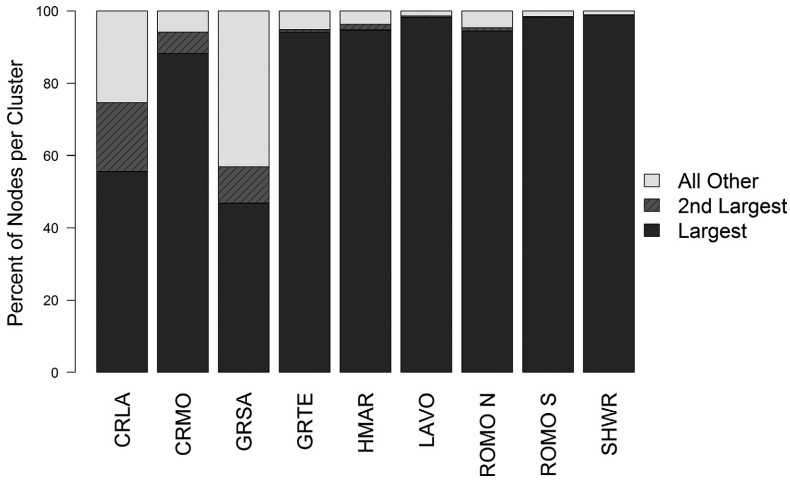

FIG. 3. Distribution of cluster sizes for network models for each site. For all sites, the two largest clusters contained the majority of the nodes in the network. The largest cluster for each of GRTE, HAMR, LAVO, ROMO N, ROMO S, and SHWR contained more than 90% of the nodes. Nodes pruned from the network were not included in the calculation.

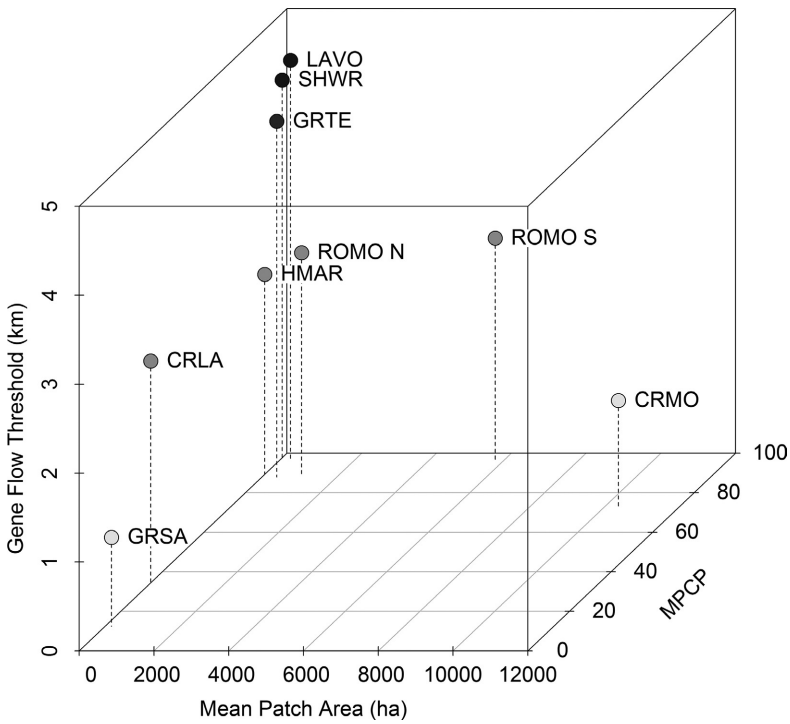

FIG. 4. Relationship between gene flow threshold, mean patch area, and mean percentage connected patches (MPCP). Sites with smaller patches and greater MPCP had larger gene flow thresholds than sites with larger patches or fewer connected patches. Gene flow threshold = 990.65 − 0.19 × patch area + 2847.94 × MPCP.

connectivity, as well as areas that might be targets for management actions to maintain and/or improve connectivity. In CRLA, due to a gap along the northeast of the lake, loss of habitat patches along the south and southwest of the lake would result in the single large cluster of patches surrounding the lake breaking into two or more clusters (Fig. 5a). Additionally, improving connectivity between the habitat surrounding the lake with that to the southwest, for instance through artificial talus creation, could lessen the risk of the southwest becoming more isolated or extirpated (Appendix S5). In GRSA, habitat in the south is not suitable for pikas and there are only small habitat patches isolated by areas of high resistance in the north, resulting in a well-connected

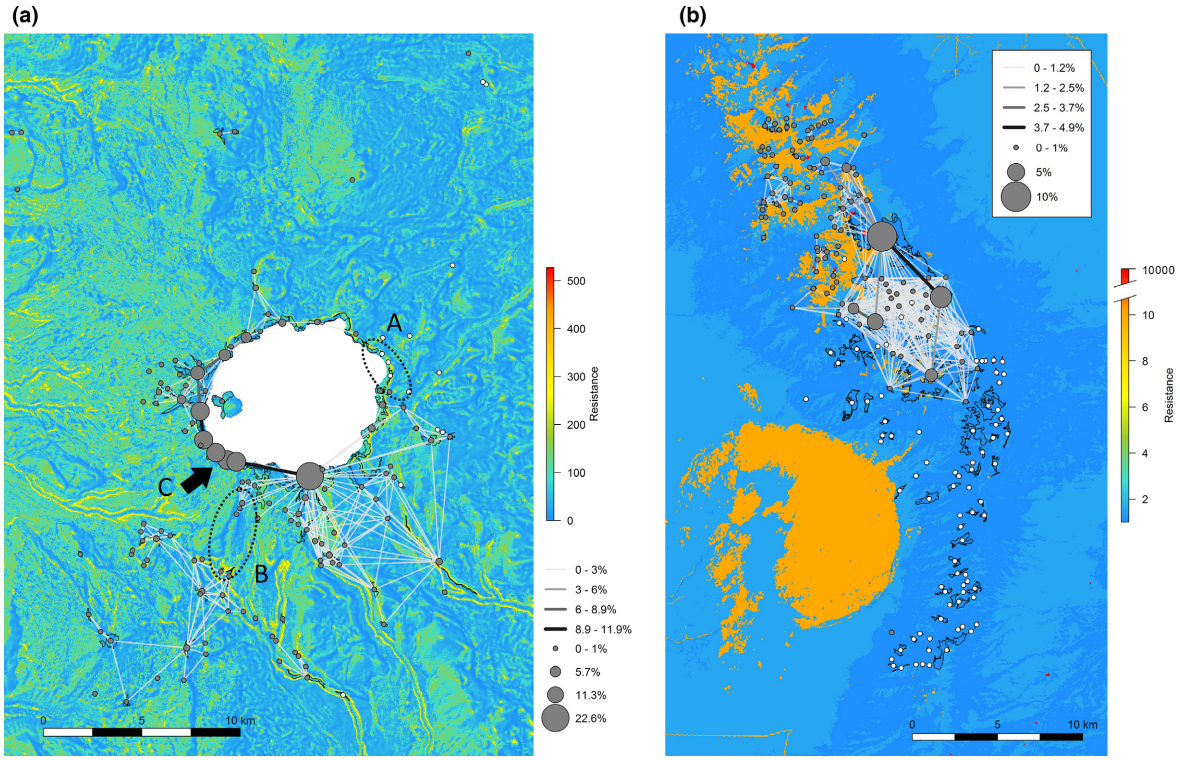

FIG. 5. Maps of the landscape resistance model and network graphs for (a) CRLA and (b) GRSA. The network represents nodes pruned by 40% occupancy probability and edges pruned by a study site-specific resistance distance threshold (see Table 3 for GFT_{RD} estimates for each site) subject to a 4.5 km maximum geographical dispersal distance. Node size is proportional to node betweenness and edge color reflects edge betweenness, such that higher betweenness is darker. Betweenness reflects the number of paths that go through that node or edge, with high betweenness reflecting a lack of alternate pathways. White circles represent pruned (removed) nodes. Node placement on the map corresponds to the patch centroid, therefore, edge length on the map does not reflect actual distance between patches. In (a) CRLA, the dotted outline A shows a current gap in patch connectivity, dotted outline B shows an area of low resistance where a gap in connectivity might be reconnected through construction of artificial habitat, and arrow C points to a region where loss of patch occupancy could result in the network fragmenting into more isolated clusters. Figures for all other study sites are presented in Appendix S5.

region in the center of the park and higher fragmentation in the north, potentially increasing vulnerability to extirpation in that portion of the park (Fig. 5b). Network models revealed a relatively high degree of connectivity for CRMO, GRTE, LAVO, ROMO N, ROMO S, and SHWR (Appendix S5). HMAR was moderate in terms of connectivity with relatively few patches and regions connected by a few key edges (Appendix S5).

DISCUSSION

Our study reinforces a key conclusion from the few studies that have been able to replicate landscape genetic analyses across study sites (e.g., Short Bull et al. 2011): resistance of particular landscape elements vary across space, as do patterns of dispersal, even for a habitat specialist such as the American pika. We also establish three important new insights regarding the vulnerability of this fragmented montane species to climate change. Firstly, we determined that functional connectivity for American pikas is likely influenced by climate-related variables in consistent ways across multiple landscapes, but mediated by strong variation in the relative potential for heat stress in those landscapes, as previously established for pika occupancy on those landscapes (Jeffress et al. 2013). Secondly, based on observed gene flow, we inferred that the potential for functional connectivity remains high in seven of nine study sites on federally protected lands across the western United States, although one of those sites (HMAR) likely is vulnerable due to the small number of occupied patches and isolation at the broader geographic scale. Thirdly, we were able to identify specific habitat patches and linkages of high importance for maintaining or improving connectivity, demonstrating that future management could be targeted to efficiently protect functional connectivity. By establishing relationships between functional connectivity and variables correlated with climate conditions, this study also demonstrates the importance of considering functional connectivity when predicting the consequences of climate change on species with fragmented distributions.

In this study, we used a circuit-theoretic approach and individual-based genetic distances to model resistance to gene flow and identify landscape factors that influence pika dispersal within eight different study sites, compared these factors across study sites to identify general trends, and then applied our landscape resistance models to a patch-based, graph-theoretic analysis of functional connectivity within each site. Many studies have described functional connectivity through resistance-based or network-based approaches. However, few have combined these two approaches (e.g., Creech et al. 2014), despite the many advantages of doing so (Urban et al. 2009, Moilanen 2011, Manel and Holderegger 2013). Landscape resistance surfaces can be derived through a variety of methods including species distribution models (e.g., Laiola and Tella 2006), animal movement data (e.g., Driezen et al. 2007), genetic data (e.g., Shirk et al. 2010), or some combination of these (e.g., genetic and movement data in Epps et al. 2007), each with its benefits and limitations (Spear et al. 2010). In turn, these resistance surfaces have been successfully used to identify movement corridors, barriers to dispersal, and areas of conservation priority. Thus, additional opportunities may exist to integrate network analyses into connectivity models even when the landscape genetic component is not present. One advantage of network-based methods is the ability to quantify the contribution of particular areas to overall connectivity through centrality metrics, as was done with desert bighorn sheep (*Ovis canadensis*) in southern California (Creech et al. 2014) and gray wolves (*Canis lupus*) in western North America (Carroll et al. 2012). In general, such approaches offer the potential to provide more direct guidance for conservation and management than studies that simply develop a resistance model (Keller et al. 2015).

Metapopulation persistence is a function of both within-patch factors that determine patch occupancy and population density, such as climatic conditions and availability of forage, as well as between-patch factors that influence dispersal ability and colonization rates, such as distance and landscape barriers (Hanski and Gilpin 1997). Our study demonstrates that aspect influences gene flow and thus between-patch movements for American pikas across the majority of our study sites (Table 2). Aspect is a temperature-related variable such that in the northern hemisphere solar insolation is greater at southwest-facing aspects (McCune and Keon 2002). Elevation likewise reflects temperature and was included in models in an additional three sites, such that all but one site, GRSA, included a temperature-related variable. We interpret aspect and elevation as indirect and relative measures of temperature, but they may also reflect differences in vegetation that may contribute to resistance to dispersal. However, we considered vegetation classes (land cover) in our candidate models, with results suggesting that a relationship between temperature and dispersal is the most likely explanation for our results. The effects of aspect and elevation identified here establish a mechanism by which increasing temperatures could reduce dispersal of American pikas, reducing functional connectivity and, in turn, decreasing the resilience of these metapopulation systems to environmental change. Nonetheless, in seven of nine study sites the majority of habitat patches likely remain connected based on observed gene flow (Table 3), assuming that our estimates are still representative of current conditions given the potential time lag in changes in genetic structure after a perturbation (Landguth et al. 2010, Spear and Storfer 2008, Epps and Keyghobadi 2015). This potential connectivity suggests the potential for resilience of pikas in these study sites. Ultimately, our study paves the way for evaluating how environmental change will interact with both structural connectivity (i.e., distribution of suitable habitable patches) and functional connectivity (the relationships described here) for American pikas, and demonstrates a feasible approach for evaluating vulnerability of other species for which local metapopulation dynamics could influence persistence.

Replication across study sites

Our study demonstrates that factors contributing to resistance to gene flow and therefore functional connectivity can vary spatially. Such variation comes from different sources: spatiotemporal variation in environmental conditions leads to local behavioral and genetic adaptations (Holt 2003), whereas differences in landscape composition and configuration result in different factors limiting species' ecological requirements in different parts of their range (Cushman et al. 2013*a*, Shirk et al. 2014). Understanding such variation will be necessary to effectively manage and conserve species over broad scales and diverse landscapes, and can be better achieved through metareplicated studies rather than comparisons among independent studies that may differ in scale, methodologies, and covariates evaluated (Shirk et al. 2014). However, this study and associated studies (Jeffress et al. 2013 and Schwalm et al. 2016) that represent metareplicated species distribution modeling for American pikas also point to the challenges of metareplication in ecological studies. The need for consistency across sites imposes trade-offs: for instance, snow depth, duration of snow cover, and timing of snow melt likely play an important role in pika dispersal, but fine-scale snow data were not available for the majority of our study sites and landscape genetic approaches in general are limited in their ability to deal with temporal variation. Likewise, for comparability we used vegetation data spanning the whole of the continental United States (NLCD 2006) rather than data sets derived from and potentially more appropriate for individual sites.

Landscape resistance

The final landscape resistance models differed across each of our study sites, perhaps not surprisingly given

the dramatic differences in landscape and habitat characteristics among sites, as well as the varying relationships between pika occupancy and environmental variables observed within these and other study sites (Jeffress et al. 2013). However, replication across diverse study sites enabled us to draw some general conclusions as to the effect of landscape and climate related variables on gene flow for American pikas. Among our nine study sites, including ROMO as two separate sites, either aspect or elevation was included in all but one and aspect never had a south-facing optimum. In the northern hemisphere, southwest-facing slopes have a greater heat load than northeast-facing slopes (McCune and Keon 2002). Likewise, temperature tends to decrease with increased elevation (Körner 2007). Thus, we conclude that exposure to relatively high temperatures limits pika dispersal.

GRTE, a cold, wet, high-elevation site, had a west-facing optimal aspect while the other four sites which included aspect in their final model had north- or east-facing optima. Similarly, Jeffress et al. (2013) found a positive trend with pika occupancy and measures of heat stress, suggesting cold stress or other cold related factors may restrict pikas in such cold and wet locations as GRTE. One potential explanation is that snow cover may persist longer on north- and east-facing slopes in GRTE than other sites, which could deter pikas either as a physical barrier or because there is less vegetation readily available for foraging and haying. Elevation was included in the final model for CRMO, LAVO, and ROMO N. For all three of those study sites, the optimum elevation closely matched the distribution of potential pika habitat within the study area (Table 1). Therefore, the inclusion of elevation in those sites may reflect the distribution of pika habitat rather than temperature, as was occasionally observed in simulations of gene flow for CRLA where the underlying resistance model was known (Castillo et al. 2014). However, in CRMO, elevation was previously determined to be an important predictor of pika occupancy based on occupancy surveys throughout the National Monument (Rodhouse et al. 2010), not just the 5 km buffer around our genetic sample localities. Jeffress et al. (2013) also found that elevation explained some of the observed variation in occupancy among all eight national parks investigated. Therefore, we cannot exclude elevation as a potential climate-associated factor in any of those three sites.

Land cover was included in three of nine study areas: GRTE, GRSA, and SHWR. In GRTE and GRSA, landscape heterogeneity was highest and mean patch area and extent were moderate compared to the other study areas (Appendix S2). In those two sites, forested and shrub/grassland cover types were only slightly more resistant to gene flow than pika habitat, while open areas such as bare rock and water posed the greatest resistance. In SHWR, the land cover model component consisted only of pika habitat versus non-habitat. SHWR was the most homogenous landscape in that 96.5% of the landscape was shrub/grassland and vegetation type was not a limiting factor; however, SHWR also had the most habitat patches (>500 more than the next site, GRTE), the second smallest habitat patches on average (after HMAR), and the shortest mean nearest neighbor distance between patches (Appendix S2). Therefore, in SHWR, the inclusion of land cover in the model primarily reflects the influence of pika habitat configuration on gene flow rather than other land cover types acting as a barrier to gene flow (e.g., open areas in GRTE and GRSA, and linear water features in CRLA and LAVO). This suggests that (1) in sites where pika habitat was more contiguous (i.e., large patch size as well as high clumpiness and proximity indices), land cover was not a limiting factor for gene flow (e.g., ROMO and CRMO); (2) in sites where pika habitat was sparse but well distributed (i.e., low clumpiness index) and close in proximity (i.e., low nearest neighbor distance), gene flow was strongly influenced by habitat configuration; and (3) in sites where land cover was only moderately heterogeneous (e.g., LAVO and CRLA), either we could not detect the effects of land cover due to lack of heterogeneity, or other landscape variables such as linear water features were more influential. Finally, when there were only a few, small, isolated habitat patches in a homogenous landscape as in HMAR, geographic distance alone was a good predictor of genetic distance. Cushman et al. (2011) demonstrated that landscape heterogeneity and configuration affect detectability of variables as limiting factors for gene flow. Likewise, a study that similarly modeled resistance to gene flow in black bears (*Ursus americanus*) found that features were supported in resistance models only when they were highly variable (Short Bull et al. 2011), underscoring the importance of metareplication in landscape genetics.

Our study provided additional insight on the effects of habitat configuration on pika dispersal patterns. Interestingly, sites with the most contiguous habitat did not have the largest gene flow threshold (Tables 2 and 4). Gene flow threshold was highest in LAVO and SHWR, where habitat patches were smaller but had a high potential to be connected to other patches throughout the study area (Fig. 4). Thus, pikas likely disperse out of their natal patch more frequently when patches are small and as a result gene flow occurs over a greater spatial extent. This pattern was first described by Peacock and Smith (1997) within manmade habitat patches consisting of mine ore dumps in Bodie, California, and is consistent with observed patterns of natal philopatry, a density-dependent competition-for-resources model of dispersal, and rare long-distance dispersal events for pikas (Smith 1974*a*, Smith and Ivins 1983, Peacock 1997, Peacock and Smith 1997). Our results suggest these patterns are robust to replication across multiple study areas and dispersal abilities as influenced by landscape resistance.

Additional support for the hypothesis that warming temperatures will curtail pika dispersal comes from a 40-year study of a pika metapopulation in Bodie, California. Using data from Bodie, Smith (1974*a*) demonstrated that

pikas can expire when exposed to common surface temperatures (e.g., 28°C) if they are unable to behaviorally thermoregulate (i.e., retreat into talus), and suggested that warmer temperatures should limit dispersal ability in this species (Smith 1974*d*). Since that time, the southern half of the Bodie metapopulation has collapsed in a pattern attributed to climate-mediated reductions in dispersal and recolonization (Smith and Nagy 2015). More generally, we emphasize that incorporating functional connectivity in predicting future species distributions is of critical importance in metapopulation systems (Schwalm et al. 2016). The resistance to gene flow posed by exposure to high temperatures is expected to increase with increased climate warming, further limiting pika dispersal ability, and potentially resulting in a breakdown of metapopulation dynamics prior to that predicted solely by loss of suitable habitat area. However, while our landscape resistance models suggest a relationship between dispersal and climate, precise changes to landscape resistance as a result of climate change are difficult to predict. Changes in ambient temperature, precipitation, and phenology likely have complex interactions with each other as well as aspect, elevation, and land cover.

Patch network

For species with fragmented distributions, natural or otherwise, managing connectivity is an important conservation strategy in the face of other threats (Rudnick et al. 2012). Identifying key linkages can inform management by prioritizing focus on potentially vulnerable areas and/or those that may have the greatest overall impact (Carroll et al. 2012, Creech et al. 2014). Our network models allowed us to describe connectedness of pika habitat, identify key linkages and habitat patches, and identify regions that are likely disconnected or at risk of becoming increasingly isolated (Fig. 5, Appendix S5). For American pikas, management actions may include assisted migration (Wilkening et al. 2015) as well as maintaining, improving, or creating pika habitat (Hobbs et al. 2009). Negative effects of temperature may be mediated through behavioral thermoregulation (Smith 1974*d*), but only if enough potential habitat refugia below some exposure threshold are present on the landscape and accessible to pikas. The rocky habitat used by pikas reduces exposure to extreme temperatures as well as predators (Smith and Weston 1990, Holmes 1991). Therefore, supplementing existing pika habitat may be an important conservation strategy in the face of climate change. Pikas are known to readily colonize artificial rock talus such as those created by road cuts and riprap (Manning and Hagar 2010, Nichols 2010). Network models such as those developed here can be used to test the effects of adding or removing specific habitat patches and/or connections and can be used to evaluate alternate management strategies (Creech et al. 2014), as in the case of proposed road construction, trail maintenance, or other alterations to the landscape, or to explore impacts of climate change. Our findings also illustrate the importance of incorporating habitat configuration, landscape resistance (between-patch), and occupancy (within-patch) in explaining patterns of population connectivity. This is particularly important for understanding metapopulation dynamics and risks to population extinction for species found in naturally fragmented landscapes (Lopez and Pfister 2001, Murphy et al. 2010).

Considerations

Combining multiple methodologies (landscape resistance modeling, habitat-specific occupancy modeling, and graph-theoretic approaches) replicated on multiple landscapes allowed us to systematically describe functional connectivity in American pikas. However, these approaches are not without limitations. Estimating resistance distance for habitat patches (as opposed to point locations) over an entire landscape is computationally impossible with the current version of Circuitscape, and our overlapping tile approach does not allow all possible pathways on the landscape to be considered in the estimation of cumulative resistance. Moreover, Castillo et al. (2014) demonstrated that while the model optimization procedure implemented here was able to correctly identify the variables contributing to landscape resistance, the magnitude of the resistance estimates for those variables were less precise. Although we did not explicitly test for the effects of the magnitude of resistance on the resulting patch network, our network models should be relatively resilient to differences in magnitude of resistance estimates because we used genetic data to estimate gene flow thresholds in terms of resistance distance derived from each resistance model. We are confident that the relative magnitudes of the resistance values for the different variables are robust. However, if our optimization procedure did not correctly identify the relative magnitude, then the connectivity network could be affected and this could potentially alter conclusions about network connections. Given current computational limitations of Circuitscape, sensitivity analysis for large landscapes and metareplicated studies remains a challenge and an opportunity for future research.

The availability of appropriate spatial data also posed some limitations, as commonly encountered in landscape studies. Our potential pika habitat maps included anything that appeared talus-like, and therefore, likely over-predicted potential habitat in most cases and under-predicted habitat in parks with high amounts of forested talus such as GRTE. Functional connectivity was likely overestimated in SHWR and HMAR in particular due to limited information on pika distribution. Precipitation-related metrics (e.g., rainfall, snow depth or duration, duration of the growing season) were not included in our landscape resistance models because comparable data at the relevant scale to pika dispersal

were not available and such metrics that are highly temporally variable (i.e., may vary dramatically from one year to the next) are challenging to address using landscape genetics. Precipitation, particularly as snow, appears to be important in predicting pika occupancy (Jeffress et al. 2013, Schwalm et al. 2016) and persistence (Beever et al. 2010, 2011), and it is likely that precipitation influences dispersal as well, as suggested by our results in GRTE. Moreover, while we considered aspect and elevation as microclimate-related variables, we could not explicitly rule out the possibility that those variables reflect fine-scale vegetation (as opposed to cover class) or some combination of factors. Furthermore, combining slope and aspect might have provided a more accurate measure of heat load than aspect alone (McCune and Keon 2002), although that approach could have confounded resistance estimates based on topography. Despite these limitations, these network models reflect a more realistic representation of functional connectivity for American pikas than previously considered, and this method of inferring maximum effective dispersal based on landscape resistance could improve estimates of functional connectivity within other metapopulation systems.

Conclusions

This study represents the most comprehensive analysis of functional connectivity for American pikas to date and has implications for other species found in similar habitats (e.g., marmots and woodrats), as well as those characterized by metapopulation dynamics or similarly restricted to fragmented habitats in other systems. Through metareplication across landscapes representing much of the environmental variation experienced by pikas, we found that connectivity in American pikas is likely influenced by climate-related variables and habitat configuration, and temperature sensitivity may limit dispersal in pikas. Restricting our investigation to any one study site would not have revealed these insights. Researchers should therefore consider the potential benefits and limitations of replicating landscape genetic studies across multiple study areas, balancing the needs of better understanding broadscale species–habitat relationships and how to best inform specific management actions within a particular management area. We also concluded that potential for functional connectivity is still high for pika populations on most of the landscapes in this study. However, we likewise established that determining whether those landscapes will remain connected as climate changes will necessitate considering both changes in patch occupancy and changes in functional connectivity. Small metapopulations of American pika may be especially vulnerable to collapse in a warming climate (Smith and Nagy 2015), and our results more broadly imply that reduction in functional connectivity may lead to the collapse of even larger metapopulations before habitat patches are predicted to become unsuitable, as described by Schwalm et al. (2016). Populations of American pikas as well as other climate-sensitive montane species are most at risk in low elevation sites with relatively few, isolated habitat patches (Millar et al. 2014a), such as HMAR. Many Great Basin populations follow this description, and, in fact, most local extinctions of American pikas to date have occurred in that region (Beever et al. 2003, 2010, 2011, Wilkening et al. 2011). Conservation and management of this and other species should focus efforts on areas that have potential for maintaining functional connectivity at multiple scales, and combining landscape genetics, graph networks, and ecological niche models of future occupancy can be a powerful approach to accomplish this goal.

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