Landscape effects on gene flow for a climate-sensitive montane species, the American pika

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Abstract

Climate change is arguably the greatest challenge to conservation of our time. Most vulnerability assessments rely on past and current species distributions to predict future persistence but ignore species' abilities to disperse through landscapes, which may be particularly important in fragmented habitats and crucial for long-term persistence in changing environments. Landscape genetic approaches explore the interactions between landscape features and gene flow and can clarify how organisms move among suitable habitats, but have suffered from methodological uncertainties. We used a landscape genetic approach to determine how landscape and climate-related features influence gene flow for American pikas (*Ochotona princeps*) in Crater Lake National Park. Pikas are heat intolerant and restricted to cool microclimates; thus, range contractions have been predicted as climate changes. We evaluated the correlation between landscape variables and genetic distance using partial Mantel tests in a causal modelling framework, and used spatially explicit simulations to evaluate methods of model optimization including a novel approach based on relative support and reciprocal causal modelling. We found that gene flow was primarily restricted by topographic relief, water and west-facing aspects, suggesting that physical restrictions related to small body size and mode of locomotion, as well as exposure to relatively high temperatures, limit pika dispersal in this alpine habitat. Our model optimization successfully identified landscape features influencing resistance in the simulated data for this landscape, but underestimated the magnitude of resistance. This is the first landscape genetic study to address the fundamental question of what limits dispersal and gene flow in the American pika.

Keywords: causal modelling, CDPOP, landscape genetics, Mantel tests

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Introduction

Most climate niche models suggest that many species will shift their ranges poleward or upward in elevation as a result of increases in temperature (Guralnick 2007). According to this hypothesis, high elevation species are particularly at risk because they already exist at or near their upper elevational limits. Such broad-scale projections are useful, but may fail to give accurate predictions when interpreted at a smaller geographical scale, that is, what conditions individuals within a single

population might experience (Ashcroft *et al.* 2009; Suggitt *et al.* 2011). These models rarely take into account the effects of fine-scale topography on microclimate, which are particularly apparent in montane ecosystems (Luoto & Heikkinen 2008; Pepin *et al.* 2011; Suggitt *et al.* 2011). Moreover, they do not consider dispersal and the implications of local habitat fragmentation (Pearson & Dawson 2003; Hampe 2004; Brooker *et al.* 2007), although neither is well understood for many species. The ability of organisms to move among habitat patches, in addition to changes in the distribution of available habitat, has major implications for long-term viability (Fahrig & Merriam 1985; Mönkkönen & Reunanen 1999; Pearson & Dawson

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2003). In consequence, to aid both more realistic modelling of species distribution change and conservation of species in fragmented habitats, dispersal and gene flow should be described and modelled for species identified as potentially vulnerable to climate change.

One species that has gained recent attention because of potential risk from climate change is the American pika (*Ochotona princeps*). American pikas are considered montane specialists, but are found at low elevations in the northern portion of their range (Smith & Weston 1990; Manning & Hagar 2011). American pikas are sensitive to high temperatures when not allowed to behaviourally thermoregulate (Smith 1974b; Smith & Weston 1990), which is reflected in trends in occurrence along elevational and latitudinal gradients (Hafner 1993; Galbreath *et al.* 2009). Broad-scale climate niche models suggest the American pika will experience a substantial range contraction as a result of increased temperatures and decreased precipitation (Galbreath *et al.* 2009). American pikas have already experienced range contractions upward in elevation (Moritz *et al.* 2008) and local extinctions as a result of recent climate change (Beever *et al.* 2003, 2010, 2011; Wilkening *et al.* 2011), but these trends are not consistent across the species' range or even within a particular biogeographical region (Millar & Westfall 2010; Collins & Bauman 2012). A recent study of American pikas in eight National Parks representing a gradient of elevations and habitat types found that pikas' relationship with climate varied from site to site: low pika occupancy was correlated with hot and dry conditions in some parks, but in other parks, with cold and wet conditions (Jeffress *et al.* 2013). That study underscores the importance of replicated fine-scale investigations to avoid missing complex relationships.

However, dispersal, gene flow and the effect of landscape and climate on those processes are still poorly understood for this species. Estimates of maximum dispersal distance range from a few hundred metres (Smith 1974a) to 20 km (Hafner & Sullivan 1995), but many estimates suggest little or no gene flow between populations >10 km apart (Peacock 1997; Henry *et al.* 2012). Previous studies suggest distance, exposure to high temperatures and topography limit dispersal in pikas, as evidenced by direct observation of marked individuals within a single metapopulation (Smith 1974a) and population-based genetic analyses (Henry *et al.* 2012). However, there has been no systematic, individual-based analysis of pika dispersal distance or gene flow over a large landscape.

In this study, we conduct the first fine-scale, individual-based genetic analysis that addresses the effect of landscape and climate on dispersal and gene flow for American pikas. We use a landscape genetics approach to assess the correlation between gene flow and landscape variables for American pikas in Crater Lake National Park (CRLA), Oregon, to identify factors that impede or facilitate dispersal for pikas at fine scales. Landscape genetics provides a framework for evaluating hypotheses relating landscape features to patterns of genetic structure (Storfer *et al.* 2007), including addressing questions about barriers to dispersal, population isolation and ultimately population vulnerability (Manel *et al.* 2003; Balkenhol & Waits 2009; Storfer *et al.* 2010; Manel & Holderegger 2013). While there are many approaches in landscape genetics (Manel *et al.* 2003; Manel & Holderegger 2013), the predominant methodology involves relating matrices of pairwise population or individual genetic distances with cost distances derived from either a least cost path (e.g. Epps *et al.* 2007) or circuit-theoretic approach (McRae 2006; Cushman *et al.* 2013b; Manel & Holderegger 2013). Here, we use partial Mantel tests in a model optimization framework based on the approach proposed by Cushman *et al.* (2006) and as refined by Shirk *et al.* (2010), Wasserman *et al.* (2010) and Cushman *et al.* (2013b).

As is often the case with relatively young and expanding areas of research, methodologies are constantly being questioned and refined. Recently, there has been controversy over the use of Mantel tests in landscape genetics (Balkenhol *et al.* 2009; Guillot & Rousset 2011, 2013; Graves 2012; Graves *et al.* 2013), but a preferable alternative has yet to be identified that does not also suffer drawbacks. There is no one-size-fits-all approach, and the most appropriate methodology will depend on the research question and landscape under investigation (Balkenhol *et al.* 2009). Cushman *et al.* (2013b) evaluated the performance of causal modelling with Mantel and partial Mantel tests using a series of simulations. They concluded that partial Mantel tests have a very low type II error rate, but high type I error rate especially among highly correlated alternate landscape hypotheses. We use a more robust modelling framework, proposed by Cushman *et al.* (2013b), that is based on the relative support (RS) of each candidate model and includes a reciprocal causal modelling step in our model optimization process. Simultaneously competing alternate models against each other rather than against distance alone reduces the risk of type I error and spurious correlations. We followed with a simulation study to evaluate our framework. The objectives of this study were to (i) identify the relationship between landscape and gene flow for American pikas in CRLA; (ii) assess the ability of our model optimization with partial Mantel tests approach to correctly identify the true underlying landscape model; and (iii) make recommendations for the use of partial Mantel tests in landscape genetics.

Methods

Study area

The study area included approximately 460 km² within CRLA in the Cascade Range of southern Oregon. Potential pika habitat within CRLA is characterized by talus (Smith & Weston 1990), which occurs primarily around the rim of the crater and on mountain peaks and ridges throughout the park (Fig. 1). The crater resulting from the eruption of the Mt. Mazama volcano is the dominant feature on the landscape. The elevation drops approximately 300 m from the rim of the crater to the lake surface. In addition to the crater itself, ridges and ravines represent the most topographically complex areas within the park (Fig. S1, Supporting Information). Streams are also an important feature on the landscape with the majority of the perennial streams located in the southern half of the park (Fig. S2, Supporting Information). The most abundant vegetation type within the park is evergreen forest (Fig. S3, Supporting Information), and elevation ranges from approximately 1200 to 2721 m.

Sample collection

We collected faecal samples for genetic analysis between June 2010 and September 2011 using random, targeted and opportunistic sampling approaches. Random sampling occurred in conjunction with pika occupancy surveys conducted as part of a related study (Jeffress *et al.* 2013). A generalized random tessellation-stratified algorithm (Stevens & Olsen 2004) was used to generate spatially balanced survey sites within potential
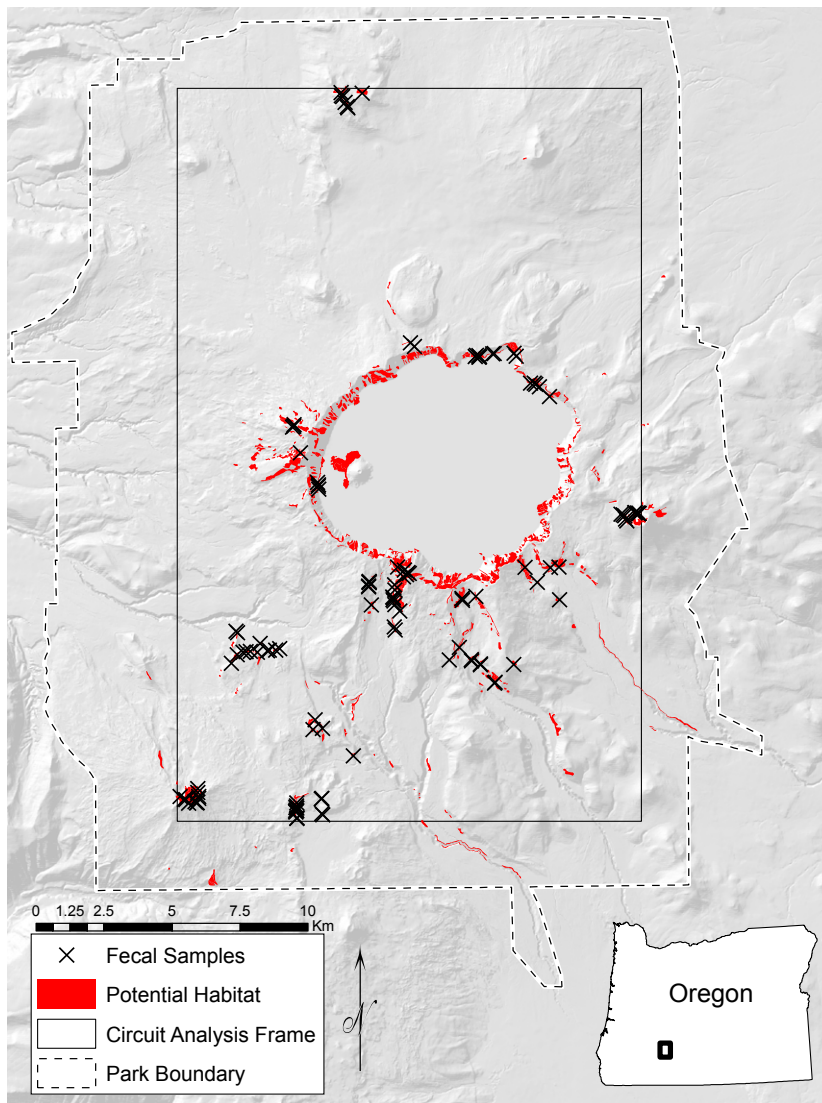

Fig. 1 Map of study area within Crater Lake NP showing sample localities (black X's), potential pika habitat (red) and the circuit analysis frame (black outline).

pika habitat. A more detailed description of the sampling design and potential habitat map is provided in Jeffress *et al.* (2013). Targeted sampling involved exhaustively searching areas identified as potential habitat with the goal of obtaining 10–20 samples within a relatively discreet habitat patch. Pikas are highly territorial, so to avoid sampling individuals multiple times we collected samples at >50 m apart, slightly larger than the average territory size. Opportunistic sampling occurred while in transit between survey sites. To increase genotyping success and reduce risk of contamination between individuals, we attempted to collect samples representing a single defecation event such that they were (i) recently deposited, based on colour and adherence to the substrate; (ii) clumped together and similar in appearance; and (iii) not contacting older faecal pellets.

DNA extraction and genotyping

We extracted DNA from faecal samples using a modified AquaGenomic Stool and Soil DNA extraction protocol (MultiTarget Pharmaceuticals LLC). We genotyped individuals at 24 microsatellite loci in four multiplex polymerase chain reactions (PCR) using a Qiagen Multiplex PCR kit (Qiagen) according to the manufacturer's specifications (Table S1, Supporting Information). We visualized PCR products using an ABI 3730 capillary sequencer (Applied Biosystems) and GS500 Liz size standard (Applied Biosystems), then scored genotypes using GENEMAPPER V4.1 (Applied Biosystems). We initially amplified each sample three times for each multiplex PCR. Each allele was considered confirmed if it was typed at least twice in independent amplifications. If an allele was seen only once during the initial three replicates, we repeated PCR up to a total of seven times to construct consensus genotypes. We identified samples with more than two confirmed microsatellite peaks at any locus as contaminated and removed them from further analysis. 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 ($P_{(ID)sib}$) (Waits *et al.* 2001) for each of the matching genotypes identified in CERVUS. We identified duplicate individuals if $P_{(ID)sib} < 10^{-3}$ (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 & Rousset 1995). Finally, we removed individuals with incomplete genotypes from further analysis.

Genetic distance

We calculated pairwise genetic distance among individuals using a principal components analysis (PCA)-based metric (Shirk *et al.* 2010). We constructed a matrix of multilocus genotypes coded such that there is a column for each allele in the population and cells contain the number of occurrences of that allele (0, 1 or 2) for each individual, represented by rows in the matrix. We generated a genetic distance matrix based on the distance between individuals along the first two eigenvectors using the Euclidean distance function in the ECODIST package in R 2.13.1. For comparison, we also calculated Bray–Curtis per cent dissimilarity pairwise distances (Legendre & Legendre 1998) using the ECODIST package (Goslee & Urban 2007) in R 2.13.1 (R Development Core Team 2011). This metric is equal to one minus the proportion of shared alleles, another commonly used metric. The results for the Bray–Curtis per cent dissimilarity were similar to the PCA distance (Table S2, Supporting Information).

Univariate resistance model functions

We evaluated the hypotheses that gene flow in pikas is limited by temperature, exposure to predators and topographical limitations to dispersal. To do so, we modelled landscape resistance as a function of elevation, aspect, land cover, water and topographic complexity (TC). To avoid confounding effects of Crater Lake itself in our analyses, we removed it from the landscape by replacing the corresponding pixels with 'nodata' in the GIS and forced movement paths around the lake. We modelled resistance as a function of elevation, according to the hypothesis that elevation is a proxy for temperature and that there is an optimal elevation around which resistance increases as elevation increases or decreases. To accomplish this, we reclassified a digital elevation model (DEM) according to an inverse Gaussian function (Equation S1, Supporting Information). We evaluated five maximum resistance (R_{max}) values (2, 10, 100, 500 and 1000), seven optimum elevations (E_{opt}) ranging from 1950 to 2550 m in 100-m increments and three standard deviations (E_{SD}) for a total of 105 candidate models.

We modelled resistance as a function of topographical aspect according to the hypothesis that there is an optimal aspect such that increasing or decreasing aspect results in an increase in resistance. McCune and Keon (2002) proposed an index of heat load such that northeast aspects (45°) represent the coolest slope with a value of zero and southwest aspects (225°) represent the warmest slope with a value of 1. To test whether aspect, as a proxy for temperature, influences gene

flow, we modified the heat load index to assess (i) the presence of an optimum aspect and (ii) the range of tolerance about the optimum aspect by including an exponent variable, x (Equation S2, Supporting Information). As the exponent increases so does the contrast (width of tolerance), such that there are fewer pixels with intermediate resistance values. Flat areas, pixels with a value of -1 on the untransformed aspect raster, were reclassified as $R_{max}/2$. We tested aspects in $45°$ increments from 0 to $315°$ with five values of x (0.5, 1, 2, 4 and 10) and the same R_{max} values as for elevation, for a total of 200 candidate models.

We hypothesized that resistance increases as TC increases because of greater energetic expenditure for movement across complex terrain due to the pika's small body size and mode of locomotion. Using the Surface Relief Ratio (SRR) tool in the Geomorphometry and Gradients Metrics toolbox for ARCGIS 10.0 (Evans & Oakleaf 2012), we calculated the SRR for each cell in a DEM. SRR is an index of surface complexity ranging from zero to one calculated within a specified radius. We calculated SRR using three radii (10, 20 and 50) and reclassified the resulting SRR raster according to a power function such that resistance increased towards R_{max} according to a relationship governed by x (Equation S3, Supporting Information). We identified the most appropriate radius, then tested the same values of x and R_{max} as for aspect for a total of 25 candidate models.

We modelled resistance as a function of land cover according to two hypotheses: potential habitat poses less resistance than nonhabitat and forested areas pose less resistance than open areas, but more resistance than potential habitat. These predictions stem from the hypothesis that predation risk and heat exposure increase as cover decreases. Using the potential habitat map described in Jeffress *et al.* (2013), we assigned a resistance value of 1 to potential habitat and tested seven values of R_{max} for nonhabitat (2, 10, 50, 100, 250, 500 and 1000). Next, we reclassified a land cover raster (NLCD 2006 Land Cover, U. S. Geological Survey) into four categories according to cover type: forested, shrub/grassland, open/barren and water. We combined the potential habitat and land cover rasters such that the new raster contained all five land cover categories. We then ranked each cover class according to hypothesized relative resistance with potential habitat: the lowest rank followed by forested, shrub/grassland, open/barren and water as a barrier. We reclassified the resulting categorical rank raster according to the function $R = Rank^x$, rescaled such that $R_{PH} = R_1 = 1$ and $R_4 = R_{max}$. This scaling allows us to hold potential habitat (R_{PH}) and R_{max} values constant while varying the relative resistance of the other two land cover types

according to a relationship governed by x (Fig. S4, Supporting Information). We tested the same five values of x and six values of R_{max} (2, 10, 100, 250, 500 and 1000), for a total of 37 candidate models, including the dichotomous classification scheme.

Finally, we modelled resistance as a function of water features including intermittent streams, perennial streams and lakes. We used two classification schemes. The first was a simple water–land dichotomy where we assigned land a value of 1 and water an R_{max} of 2, 10, 50, 100, 250, 500 or 1000. The second model included the classification of perennial vs. intermittent streams such that intermittent streams received a resistance value of $R_{max}/2$, except in the case of $R_{max} = 2$ where intermittent streams received a value of 1.5.

Univariate resistance model optimization

We evaluated our univariate resistance models by assessing the correlation between pairwise genetic distance and pairwise resistance distance between individual sampling localities. We used CIRCUITSCAPE V.3.5.4 (McRae 2006) to model isolation by resistance and construct a pairwise resistance matrix for each landscape resistance surface. We calculated cumulative resistance between point localities for each pair of genotyped individuals using an eight neighbour connection scheme. All resistance models consisted of approximately 10 m by 10 m pixels.

We assessed correlation between matrices using Mantel tests with the ECODIST package in R. We controlled for the effect of distance alone by estimating resistance in CIRCUITSCAPE with a raster of a constant value of 1 and evaluated partial Mantel correlation after 'partialling out' the resulting cumulative resistance matrix (henceforth referred to as model IBD). For each landscape variable, we identified the top candidate model by a unimodal peak of support in partial Mantel r values (Shirk *et al.* 2010). In the cases where there was a plateau rather than a peak of support, we chose the model corresponding to the point at which values began to plateau.

Next, we identified a set of candidate models within a range of parameters similar to the top model described above (e.g. $\pm45°$ for aspect) and evaluated that set of models against each other rather than just against IBD. We quantified the RS of each model as compared to each other model as:

$$RS_{1|2} = (GD \sim RD_1|RD_2) - (GD \sim RD_2|RD_1)$$

where GD is the genetic distance matrix, RD_1 is the resistance distance matrix obtained from model 1, RD_2 is the resistance distance matrix obtained from model 2, and $(GD \sim RD_1|RD_2)$ is the partial Mantel correlation between GD and RD_1 after partialling out RD_2. $RS_{1|2}$ in

the above equation represents the RS of model 1 as compared to model 2. The model with positive RS in every comparison represents the best candidate model (Cushman *et al.* 2013b).

Multivariate resistance model construction and optimization

We built our multivariate resistance surfaces by creating rasters equal to the sum of the univariate model rasters for each landscape variable. We used two methods for our multivariate model optimization. The first is similar to the methods in Shirk *et al.* (2010). We started with the two landscape variables with the highest partial Mantel correlation for GD ~ RD|IBD and then created a series of bivariate models by varying the model parameters for the second variable, while holding the first constant. We repeated the methods used in the univariate model optimization to identify the best supported model parameters for the second variable based on the partial Mantel correlation GD ~ RD|IBD. Next, we identified the optimum parameters for the first landscape variable while holding the second constant. We then added additional landscape variables one at a time. For each additional variable, we held the other variables constant, optimized the new variable and then repeated optimization for the variables previously established in the model. If the best supported parameter value for any previously established variable changed, we reoptimized the remaining variables. We repeated the process until the best supported multivariate model did not change.

The second multivariate model optimization procedure was similar to the first, except we evaluated models by their RS rather than GD ~ RD|IBD. We started with the combination of the best models for those landscape variables that had positive RS when compared to IBD. We varied the model parameters for one variable while holding the others constant. The multivariate model with positive RS in every comparison represented the best candidate model. We repeated this process until the variable parameters stabilized.

In order to be accepted, the multivariate model needed to pass the two causal modelling criteria signifying that it was better than IBD: (i) GD ~ RD|IBD must be significant and (ii) GD ~ IBD|RD must be nonsignificant (Wasserman *et al.* 2010). Additionally, in order for a landscape variable to be included in the final multivariate model, it had to also pass the causal modelling criteria with the reduced model. For example, GD ~ (TC + W + A) | (TC + W) must be significant and GD ~ (TC + W) | (TC + W + A) must be nonsignificant in order for A to be included.

Simulation study

The purpose of the simulation study was to evaluate the ability of the Mantel framework to correctly identify the relationship between genetic distance and landscape variables (e.g. Shirk *et al.* 2012) in this particular landscape and sampling scheme. To accomplish this, we created a multivariate model including TC (high contrast and high R_{max}) and water (low R_{max}) to represent the 'true' landscape resistance model. We simulated gene flow among pikas in CRLA by first creating hypothetical individuals using ARCGIS and then simulating mating and dispersal as a function of landscape resistance using CDPOP (Landguth & Cushman 2010). CDPOP is a spatially explicit, individual-based, landscape genetic model that simulates mating and dispersal as a probabilistic function of movement cost among individual localities and then reports individual genotypes through each specified generation (Cushman *et al.* 2012).

If the Mantel framework is robust, then repeating the model optimization process with the simulated genotypes should result in the best supported model being the same as, or very similar to, the model we used to specify landscape resistance as input for CDPOP. In order to conclude that the partial Mantel framework is effective, we determined that the best supported model must (i) include all the variables included in our simulated landscape (topography and water) and (ii) not include any of the variables not included in our simulated landscape. Additionally, the parameters of the individual landscape variables in the best model should not differ greatly from the simulated landscape.

We included sampling localities for all our genotyped individuals, plus hypothetical individuals spaced approximately 40 m apart within potential pika habitat for a total of 3692 localities. Individual territory size estimates for pikas result in 20–30 m spacing (Smith 1974b; Smith & Weston 1990); however, we were unable to run simulations at that density due to computer memory limitations. We calculated pairwise resistance distance among all simulated individuals in CIRCUITSCAPE using a resistance surface that included TC (high contrast and high R_{max}) and water (low R_{max}). We then simulated mating and dispersal for 500 overlapping generations with input parameters reflecting pika life history: 50% birth mortality, equal sex ratio at birth, 50% juvenile survival and 30% adult survival up to age 5 years. We simulated a larger litter size than reported for pikas (8 instead of 3 or 4) to reduce the number of empty localities resulting from adult mortality. We defined mating probability by a negative exponential function such that mating was much more likely among individuals with low cumulative resistance distance between them. We set a maximum mating distance at

10% of the maximum pairwise resistance distance observed. This corresponds to a mean mating distance of approximately 110 m (SD ≈ 90 m). Pikas typically mate with individuals in neighbouring territories (Smith & Ivins 1983, 1984); therefore, our simulated mating parameters are realistic for pikas. Dispersal probability was the same as mating, except that the maximum dispersal distance was 20% of the maximum pairwise resistance distance observed, corresponding to a mean dispersal distance of approximately 400 m (SD ≈ 675 m). Estimates for pika dispersal distance range from tens of metres to a few kilometres (Smith & Ivins 1983; Smith & Weston 1990; Hafner & Sullivan 1995; Peacock 1997). Previous studies found that almost all juvenile pikas settle within 50 m of their natal home range (Smith & Ivins 1983), long-distance migration (>1 km) is rare (Peacock 1997), and under nonfavourable environmental conditions (i.e. high ambient temperature), distances >300 m may pose a barrier to dispersal (Smith 1974a). Therefore, our simulated dispersal parameters are realistic for pikas. Vacant territories (empty localities) occurred when an individual died and was not replaced by a dispersing juvenile. This could have been the result of demographic stochasticity affecting the sex ratio within an area and/or landscape resistance reducing mating and dispersal ability. Vacant territories could be recolonized at any subsequent generation; therefore, number and location of vacant territories varied across generation and simulation run.

Genotypes for the initial population were generated at random for 21 loci with six alleles per locus. Mutations were allowed at a rate of 0.0005 mutations per generation according to a random mutation model. Individual genotypes were recorded at generations 0, 100, 250 and 500. We repeated the simulation for a total of 10 Monte Carlo (MC) replicates to account for stochasticity. We calculated pairwise genetic distance for each of the 10 MC replicates, using only those genotypes that corresponded to real sampling localities, in the same way as described for our real genetic data.

We evaluated the correlation between simulated genetic distance and each of the univariate landscape resistance models evaluated for our real data set, using the methods described above. For each of the five landscape variables, we ranked the univariate models according to partial Mantel correlation after partialling out the IBD model within each MC replicate, and then according to average rank across all 10 MC replicates. We used the average rank to identify a best supported model, representing a unimodal peak or plateau of support where possible, for each landscape variable. We repeated the univariate optimization and multivariate model construction and optimization based on RS to identify a best

supported model as employed for the real data. However, we ranked models according to the number of positive RS values and identified the best model as the one with highest average rank across all MC replicates.

Results

Sample collection and genotyping

We collected 369 faecal samples for genetic analysis between June 2010 and September 2011 through a combination of random ($n = 116$), targeted ($n = 237$) and opportunistic ($n = 16$) sampling schemes. We extracted DNA from 210 faecal samples chosen for relative freshness and spatial distribution. Four loci were excluded

Table 1 Best univariate models of landscape resistance for pikas in Crater Lake NP, for each of the five variables, based on partial Mantel correlation after partialling out the IBD model. Optimized parameter values, partial Mantel correlation and significance of partial Mantel test are shown

Landscape variable	Optimized parameter values*	Partial Mantel r	P
Topographic complexity	$x = 2$, $R_{max} = 3$	0.15	0.01
Water	Classified, $R_{max} = 10$	0.14	0.03
Aspect	90°, $x = 4$, $R_{max} = 3$	0.13	0.02
Elevation	1950 m, SD = 300, $R_{max} = 3$	0.09	0.09
Land cover	$x = 2$, $R_{max} = 2$	0.08	0.10

*Optimized values include equation parameters for contrast (x or SD; the shape of the relationship) and R_{max} (the magnitude of the relationship); see Equations S1–S3 (Supporting Information).

Table 2 Best univariate models of landscape resistance for pikas in Crater Lake NP, for each of the five variables based on relative support (RS). Only the RS as compared to IBD is shown. A model was supported if it passed the causal modelling criteria with IBD

Landscape variable	Optimized parameter values*	$RS_{i|IBD}$	Supported?
Topographic complexity	$x = 4$, $R_{max} = 1001$	0.21	Yes
Water	Classified, $R_{max} = 100$	0.12	Yes
Aspect	90°, $x = 4$, $R_{max} = 11$	0.10	Yes
Elevation	1950 m, SD = 300, $R_{max} = 3$	0.12	No
Land cover	$x = 2$, $R_{max} = 2$	0.15	No

*Optimized values include equation parameters for contrast (x or SD; the shape of the relationship) and R_{max} (the magnitude of the relationship); see Equations S1–S3 (Supporting Information).

for failure to amplify or lacking variability in this population (P7, OCP03, OCP16 and OCP17, Table S1, Supporting Information). An additional five loci exhibited heterozygote deficit within CRLA, but not consistently in other populations at study sites not included in this study ($n = 8$, Table S1, Supporting Information); therefore, we retained them. Two comparisons of 180 exhibited significant linkage disequilibrium after correction for multiple comparisons. However, no comparisons exhibited significant linkage disequilibrium across multiple study sites. After removing duplicate individuals ($n = 28$), contaminated samples ($n = 39$) and samples that failed to amplify at one or more loci ($n = 37$), we had a total of 106 individuals genotyped at 20 loci (Fig. 1). The average number of alleles per locus was 5.7. A description of the population structure within CRLA is presented in the Fig. S5 (Supporting Information). We did not find significant evidence that our data violated the assumption of linearity when genetic distance was compared to resistance distance.

Univariate model optimization

Topographic complexity had the strongest correlation with genetic distance, after partialling out the IBD model, followed by water, aspect, elevation and land cover (Table 1). The optimum parameter values for contrast (x) were low to medium and the magnitudes of resistance values (R_{max}) were either low or lowest of those evaluated for all landscape variables. The optimum aspect was east facing. The partial Mantel correlation was not significant for either elevation or land cover.

Similarly, the landscape variable with the greatest RS when compared to IBD was TC, followed by land cover, water, elevation and aspect, respectively (Table 2). However, only TC, water and aspect passed the causal modelling criteria with IBD. The R_{max} values were greater for the three supported variables determined using RS than with the optimization based on partial Mantel correlation. Additionally, the degree of contrast was greater for TC.

Multivariate model optimization

The best multivariate model based on optimization with partial Mantel correlation after partialling out the IBD model included only TC and water. This model included the best model from the univariate optimization for TC, but a greater magnitude of resistance for the water component (Table 3, model 1). Equally well supported was a model that included TC, with medium contrast and highest resistance, and water with lowest resistance (Table 3, model 2).

The best multivariate model from the optimization based on RS included TC, water and aspect (Table 3, model 3). Including aspect only slightly improved the RS over the same model without aspect (RS = 0.05). The partial Mantel correlation after partialling out the reduced model was nearly significant ($P = 0.07$), while the converse was nonsignificant ($P = 0.26$), suggesting that including aspect improved the model. When we compared models 1, 2 and 3 against each other and IBD using RS, model 3 performed best (Table 4). The RS for model 3 compared to models 1 and 2 was only slightly greater than zero, but it still passed the causal modelling criteria for significance.

Simulation study

After 500 generations, the number of individuals ranged from 3495 to 3502 for the 10 independent simulations, representing approximately 95% of the original population. The correlation between genetic distance and resistance distance increased rapidly and then began to asymptote around 250 generations, indicating stabilization of the relationship between landscape resistance and genetic structure (Fig. S6, Supporting Information). After partialling out the IBD model, of the top-ranked models for each landscape variable TC had the strongest Mantel correlation with genetic distance, followed by aspect, elevation, water and land cover (Table 5). When we evaluated the RS for the group of top candidate models within each landscape variable against each other and IBD, the top models for TC and water

Table 3 Results of the multivariate model optimization for pikas in Crater Lake NP. Models 1 and 2 are the best models based on partial Mantel correlation after partialling out IBD. Model 3 is the best model from the optimization based on relative support. Optimized model parameters*, partial Mantel correlation and significance of partial Mantel test are shown

Model	Topographic complexity	Water	Aspect	Partial Mantel r	P
(1) T + W	$x = 2$, $R_{max} = 3$	Classified, $R_{max} = 100$	—	0.22	0.00
(2) T + W	$x = 4$, $R_{max} = 1001$	Unclassified, $R_{max} = 2$	—	0.22	0.00
(3) T + W + A	$x = 4$, $R_{max} = 501$	Unclassified, $R_{max} = 100$	90°, $x = 4$, $R_{max} = 100$	0.13	0.02

*Optimized values include equation parameters for contrast (x or SD; the shape of the relationship) and R_{max} (the magnitude of the relationship); see Equations S1–S3 (Supporting Information).

were the only two variables that consistently performed better than distance alone (Table 6). The top model for TC included a higher R_{max} than the top model based on partial Mantel correlation alone. The top model for water was the same as the top model based on partial Mantel correlation alone. The best model for aspect, representing highest contrast and lowest R_{max} and therefore the model most closely resembling IBD, performed better than IBD in four MC replicates only. The top model for elevation, representing mid-elevation with highest contrast (lowest standard deviation) and lowest R_{max}, performed better than IBD 50% of the time. Only those elevation models with lowest resistance and an optimum elevation of 2150 or 2250 m performed better than IBD. The IBD model performed better than land cover 100% of the time.

The optimized multivariate model based on RS included TC and water only. Including elevation in the model produced inconsistent results across MC replicates. Including elevation improved the RS in 90% of MC replicates, but no single model (of the six evaluated) was the best supported model in more than 20% of MC replicates. Likewise, none of the models including elevation passed the causal modelling criteria with the reduced model more than 50% of the time.

Elevation did not consistently improve the model and was therefore not included. The optimum R_{max} for TC was high (501), higher than the best supported univariate model. There was no significant difference between the model with $R_{max} = 2$ and $R_{max} = 10$ for water ($P \geq 0.12$ and RS ≤ 0.09 across all ten MC replicates).

The model used as the input landscape for the simulated population included TC, with highest contrast and highest R_{max}, and water with no stream-type classification and $R_{max} = 10$. The final optimized multivariate model identified by analysing the simulated data included both variables, passed the causal modelling criteria with IBD in 90% of the MC replicates and passed the causal modelling criteria with the reduced model in 100% of the MC replicates. Therefore, we were able to consistently identify the correct landscape variables (Fig. 2). We were also able to identify the correct degree of contrast for TC, but the magnitude of resistance was underestimated. The true parameters for water did not include a classification of stream type, whereas our optimization did, and we were not able to distinguish between $R_{max} = 10$ and $R_{max} = 2$. The optimized multivariate model had higher RS than the true model and passed the causal modelling criteria in 100% of MC replicates.

Discussion

Model optimization and reciprocal causal modelling

The results of the univariate model optimization suggested that TC was the landscape factor most strongly correlated with gene flow for pikas in CRLA, followed by water, aspect, elevation and land cover, with the latter two variables not significantly influencing gene flow. We saw a similar pattern for variable support in the within-variable optimization based on RS, but the magnitude of resistance was greater for all three significant variables in the latter method. This was also the case

Table 4 Matrix of relative support of the model in the row as compared to the model in the column. Model numbers refer to Table 3

Model	1	2	3	IBD
1	—	0.01 (0.13)	−0.06 (0.19)	0.22 (0.02)
2	−0.01 (0.15)	—	−0.08 (0.34)	0.21 (0.01)
3	0.06 (0.03)	0.08 (0.04)	—	0.22 (0.00)
IBD	−0.22 (0.87)	−0.21 (0.88)	−0.22 (0.81)	—

Numbers in parentheses are P-values for the correlation between genetic distance and the model in the row partialling out the model in the column.

Table 5 Best univariate models of landscape resistance for pikas in Crater Lake NP, for each variable from the simulated genotypes, based on average rank across Monte Carlo (MC) replicates for partial Mantel correlation, partialling out IBD. Optimized parameter values and summary statistics for the partial Mantel correlation across all ten MC replicates are shown

Landscape variable	Optimized parameter values*	Partial Mantel r			
		Minimum	Maximum	Mean	SD
Topographic complexity	$x = 10$, $R_{max} = 3$	0.24	0.46	0.39	0.08
Aspect	45°, $x = 10$, $R_{max} = 101$	0.11	0.29	0.23	0.06
Elevation	2250 m, SD = 200, $R_{max} = 1001$	0.13	0.33	0.21	0.07
Water	Classified, $R_{max} = 2$	0.01	0.07	0.03	0.02
Land cover	Habitat vs. nonhabitat, $R_{max} = 250$	−0.22	0.08	−0.09	0.10

*Optimized values include equation parameters for contrast (x or SD; the shape of the relationship) and R_{max} (the magnitude of the relationship); see Equations S1–S3 (Supporting Information).

Table 6 Best univariate models of landscape resistance for pikas in Crater Lake NP, for each variable from the simulated genotypes, based on relative support (RS). The column $RS_{i|IBD}$ is the number of Monte Carlo (MC) replicates of ten where that model had positive RS compared to IBD

Landscape variable	Optimized parameter values*	$RS_{i|IBD}$
Topographic complexity	$x = 10$, $R_{max} = 101$	10
Water	Classified, $R_{max} = 2$	8
Aspect	45°, $x = 10$, $R_{max} = 3$	4
Elevation	2250 m, SD = 100, $R_{max} = 3$	5
Land cover	Habitat vs. nonhabitat, $R_{max} = 2$	0

*Optimized values include equation parameters for contrast (x or SD; the shape of the relationship) and R_{max} (the magnitude of the relationship); see Equations S1–S3 (Supporting Information).

with TC in the simulation study, suggesting that while examining the partial Mantel correlation after partialling out IBD may correctly identify the significant landscape variables, it may underestimate the magnitude of the relationship.

Simultaneously competing models against each other through reciprocal causal modelling also improved our ability to identify the best multivariate model. We demonstrated through the simulation study that (i) we could identify the correct landscape variables influencing gene flow and (ii) evaluating RS resulted in within-variable parameter estimates being closer to truth than when only evaluating the correlation after partialling

out the IBD model. Without reciprocal causal modelling, we would not have identified aspect as an important landscape variable. However, neither model optimization method is effective at differentiating among highly similar models, such as models 1 and 2 (Table 3). In CRLA, TC is often greatest in ravines with streams at the bottom. Therefore, with either model 1 or 2, the relative cost of crossing these features is similar whether resistance is high for topography and low for water, or the converse scenario.

The best supported model suggests that dispersal for pikas in CRLA is limited primarily by physical constraints, with topographically complex areas such as cliffs and ridges posing resistance to movement and streams potentially posing barriers. Aspect also was important, with west-facing slopes posing more resistance to movement than east-facing slopes, but not as influential as either TC or water features.

Simulation study

This simulation study supports the reciprocal causal modelling with partial Mantel tests approach as an effective means to identify the relationship between gene flow and landscape variables. Despite the obvious utility and recognized need for using simulation to validate methods in landscape genetics (Epperson *et al.* 2010; Balkenhol & Landguth 2011; Cushman *et al.* 2013a; Shirk *et al.* 2012), very few studies have combined empirical data with simulated population genetic data to do so. Shirk *et al.* (2012) simulated gene flow through the resistance landscape obtained from the
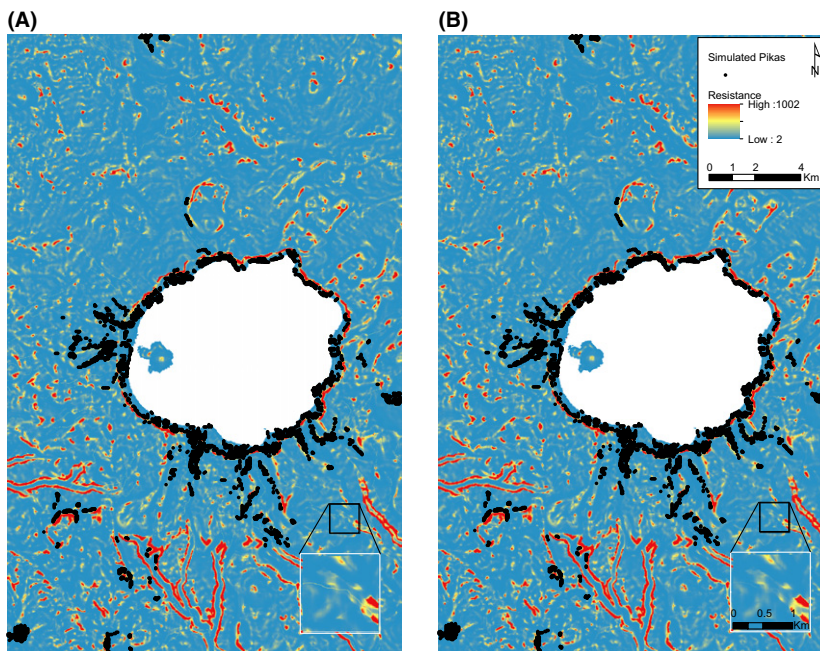

Fig. 2 Map of simulated pikas within Crater Lake NP showing landscape resistance for the 'true' model (A) and the model resulting from the optimization framework (B). Inset boxes show a zoomed-in portion for comparison of streams.

causal modelling with Mantel tests framework. They simulated gene flow under isolation-by-barrier and isolation-by-distance scenarios to evaluate whether the observed pattern of genetic isolation from their empirical data was best explained by the isolation-by-resistance hypothesis. Rather than test whether we could reproduce the observed genetic structure and therefore infer the underlying process, we chose to test whether our methods could identify the correct landscape resistance model in this particular scenario.

The optimized multivariate model from our simulated genotypes was extremely close to the input landscape parameters. The difference in classification for water and inconsistent support for elevation are likely the result of the distribution of individuals on the landscape. The majority of the potential habitat, and therefore simulated pikas, was concentrated around the rim of the crater (Fig. 1). As a result, relatively few pairwise distances involved crossing a stream, and of those, most were perennial streams (Fig. S2, Supporting Information). Furthermore, for the low magnitude of resistance, the difference between perennial and intermittent streams was likely negligible (2 and 1.5, respectively) when compared to an R_{max} of 502. The ability to detect the effect of water at all when the true R_{max} values for water and TC were 10 and 1001, respectively, suggests that this method is highly effective. Likewise, it is not surprising that elevation sometimes performed better than IBD. The only models that sometimes had positive RS compared to IBD had an R_{max} of 3 and an optimum elevation of 2150 or 2250 m. Fifty-four per cent of the simulated pikas were located between 2050 and 2450 m; therefore, most pairwise distances were within this elevation range. Very few comparisons within the mating and dispersal distance involved crossing elevations with resistance values >2.5; therefore, these models are very similar to IBD. If pikas were evenly distributed throughout the landscape rather than restricted to rocky habitat, elevation may not have performed as well against IBD. Spatial distribution of sampling points is known to affect performance and should be carefully considered when interpreting results (Schwartz & McKelvey 2009).

We have demonstrated that model optimization with partial Mantel tests and reciprocal causal modelling is an effective tool for identifying the landscape variables influencing gene flow. Simultaneously competing models against each other rather than just against distance reduces type I error rates and spurious correlations between similar alternate hypotheses. While optimization with reciprocal causal modelling improved model selection over the traditional method, the final model still underestimated the magnitude of resistance. We must therefore be careful in our interpretation of the final model parameters. For example, we can

confidently state that topographically complex areas pose much greater resistance than flat areas and that steep cliffs likely act as barriers to dispersal. However, we cannot conclude with certainty that topographically complex features pose 500 times more resistance than flat areas, despite the utility of such statements for conservation planning (Graves et al. 2013). Additionally, it is important to understand the conditions that affect our ability to detect these relationships and have the potential to confound our results, such as sample distribution and landscape configuration. In addition to false associations, such as was the case occasionally with elevation in this study, it is possible to incorrectly assume landscape variables are not important if we do not detect a significant relationship. Previous studies have addressed these issues (e.g. Cushman et al. 2013a,b; Graves et al. 2013; Prunier et al. 2013). We should continue to evaluate the effectiveness of our methods both in hypothetical situations and in real landscapes to corroborate findings and assess limitations.

Implications for pikas

Topographic complexity and water are the two landscape variables that most strongly limit gene flow for pikas in CRLA, suggesting that pika dispersal is primarily restricted by physical limitations. Slope aspect may also have a significant effect, with west-facing aspects posing greater resistance than east-facing aspects. West-facing aspects typically experience higher temperatures than east-facing aspects, and pikas are known to alter their behaviour and become less active when ambient temperatures are high (Smith 1974a,b; Conner 1983). However, other factors such as vegetation cover also may make east-facing aspects more favourable. Land cover was not strongly correlated with gene flow in CRLA. This is somewhat surprising as land cover could influence both predation risk and exposure to high ambient temperatures. However, the ability of this approach to identify landscape effects on gene flow is affected by the heterogeneity of the landscape variables (Short Bull et al. 2011; Cushman et al. 2013a). More than 80% of the landscape is evergreen forest, and the majority of the heterogeneity occurs around the rim of the crater.

Pikas are considered by some to be a sentinel of climate warming because of their sensitivity to high temperatures (Smith 1974b; Hafner 1993). Our results suggest that if temperatures continue to increase, pika connectivity may be adversely affected within CRLA if the correlation between aspect and gene flow is related to temperature. Pikas were found at all aspects in this and previously documented studies (e.g. Erb et al. 2011), suggesting that talus microclimate and/or behavioural thermoregulation allows them to avoid

high temperatures. Juvenile pikas typically disperse late in their active season (summer to early fall) (Smith 1974b) and rarely during the winter months (Peacock 1997). Therefore, increased temperatures will likely adversely affect population connectivity (i.e. ability to move through nontalus habitats) before it will affect population persistence. However, the two are ultimately interrelated. Streams are not likely to change course dramatically in the near future, but climate change is likely to alter the timing and magnitude of water flow. It is possible that changes in stream flow and/or dispersal timing may be affected by climate change, which could in turn affect whether streams pose a barrier to pika dispersal (Mote 2003; Stewart *et al.* 2005).

We need to be cautious about making generalizations for all pikas from a single study. We cannot yet rule out the potential influence of land cover in other populations, nor can we confidently attribute the observed correlation with aspect to temperature alone. Replicating this study on many diverse landscapes will strengthen our ability to tease apart effects of variables with high correlation in this particular landscape, and determine which variables limit gene flow for pikas in general (Short Bull *et al.* 2011).

Conclusion

American pikas in CRLA appear to be restricted in their dispersal capability by physical limitations and exposure to west-facing aspects. These findings have implications for the long-term persistence of the population in the face of climate change as increased temperatures may result in a decrease in population connectivity. However, investigation of other landscapes is required before ruling out other variables and making generalizations at the regional and/or species range scale. Our study also underscores the utility of combining empirical optimization with simulation in landscape genetics. This simulation study validated our model selection framework for this particular landscape and suggests that it may be inappropriate to discard the Mantel test altogether. We suggest that future studies similarly evaluate the appropriateness of this model selection framework for their particular study areas. Simulation studies also enable us to consider alternative hypotheses that might produce similar genetic structure, as well as how changes to the landscape may affect genetic structure in future. This study is an important step in understanding how landscape affects population connectivity for a species of concern. Finally, because pikas are a high elevation indicator species (Hafner 1993; Beever *et al.* 2003), this study will inform future research on climate change impacts and will have implications for other montane species with similar habitat requirements.

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Data accessibility

Genetic distance matrix and GENEPOP file; XY coordinates for sampling localities; CDPOP input files and output data; and GIS raster data archived on DRYAD entry doi:10.5061/dryad.7c2n8.

Supporting information

Additional supporting information may be found in the online version of this article.

Equation S1 Landscape resistance as a function of elevation; inverse Gaussian function.

Equation S2 Landscape resistance as a function of aspect; modified heat load index.

Equation S3 Landscape resistance as a function of topographic complexity.

Table S1 Details for each microsatellite locus, including original source.

Table S2 Final multivariate models from the optimization with partial Mantel correlation after partialling out the IBD model for (1) PCA and (2) Bray–Curtis per cent dissimilarity genetic distance metrics.

Fig. S1 Map of the analysis frame within Crater Lake National Park showing surface relief ratio, a measure of topographic complexity.

Fig. S2 Map of the analysis frame within Crater Lake National Park showing the location of streams and simulated pikas.

Fig. S3 Map of Crater Lake National Park showing land cover categories from the 2006 National Land Cover Dataset.

Fig. S4 Resistance values for each land cover category ranked according to cover, with lowest rank assigned to land cover types that provide greater cover.

Fig. S5 Population genetic structure of pikas at Crater Lake National Park.

Fig. S6 Correlation between genetic distance and geographical distance (open circle, solid line), resistance distance (solid circle, dotted line) and resistance distance after partialling out geographical distance (solid triangle, dashed line), averaged across all ten MC replicates.