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Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach

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Abstract

Ecological niche theory holds that species distributions are shaped by a large and complex suite of interacting factors. Species distribution models (SDMs) are increasingly used to describe species' niches and predict the effects of future environmental change, including climate change. Currently, SDMs often fail to capture the complexity of species' niches, resulting in predictions that are generally limited to climate-occupancy interactions. Here, we explore the potential impact of climate change on the American pika using a replicated place-based approach that incorporates climate, gene flow, habitat configuration, and microhabitat complexity into SDMs. Using contemporary presence–absence data from occupancy surveys, genetic data to infer connectivity between habitat patches, and 21 environmental niche variables, we built separate SDMs for pika populations inhabiting eight US National Park Service units representing the habitat and climatic breadth of the species across the western United States. We then predicted occurrence probability under current (1981–2010) and three future time periods (out to 2100). Occurrence probabilities and the relative importance of predictor variables varied widely among study areas, revealing important local-scale differences in the realized niche of the American pika. This variation resulted in diverse and – in some cases – highly divergent future potential occupancy patterns for pikas, ranging from complete extirpation in some study areas to stable occupancy patterns in others. Habitat composition and connectivity, which are rarely incorporated in SDM projections, were influential in predicting pika occupancy in all study areas and frequently outranked climate variables. Our findings illustrate the importance of a place-based approach to species distribution modeling that includes fine-scale factors when assessing current and future climate impacts on species' distributions, especially when predictions are intended to manage and conserve species of concern within individual protected areas.

Keywords: American pika, functional connectivity, genetic neighborhood, National Parks, *Ochotona princeps*, Random Forest, realized niche, species distribution modeling

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Introduction

Ecological niche theory provides the basis for explaining patterns of species occurrence (Chase & Leibold, 2003). Concern about climate change impacts on reduced or shifting species distributions has heightened the need to characterize species' niches in comprehensive, ecologically relevant terms to inform conservation action (Peters & Lovejoy, 1994). Although the multidimensionality of the niche makes this a challenging task, a more achievable goal centers on investigating the 'realized' niche of a species constrained by biotic interactions, habitat connectivity, and other limitations (Guisan & Thuiller, 2005). Such investigations have relied primarily on species distribution models (SDMs), widely used to estimate potential future impacts of climate change on species distributions and to assess population vulnerability (Guisan & Thuiller, 2005). In theory, SDMs model a species' niche by investigating the relationship between occupancy and a suite of biotic and abiotic variables, then extrapolating to predict the species' distribution (Soberón & Peterson, 2005). In practice, many SDMs predict distributions based only on climate-occupancy relationships, limiting inference to the climatic dimension of the realized niche (Pearson & Dawson, 2003).

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At broad spatial scales, climate is a dominant factor influencing a species' niche and range (Thomas, 2010), but at finer spatial scales representing populations within a species' range, niche and distribution are shaped spatially and temporally by local factors (Austin & Van Niel, 2011; Stewart-Koster *et al*., 2013). Recent studies have argued that local effects on niche breadth and plasticity are key to climate change forecasting (Quintero & Wiens, 2013; Valladares *et al*., 2014), allowing for novel responses in portions of the species' range. While SDMs provide critical predictions at the scale of a species' range, they may poorly predict site-specific patterns of change (Gillingham *et al*., 2012). Conservation actions, typically implemented at the local scale (Theobald 2005), are best supported by an understanding of the complex relationships that influence species distributions in separate localities. Yet, the incorporation of local-scale, non-climatic predictors in SDMs has lagged (Pearson & Dawson, 2003; Guisan & Thuiller, 2005), as has consideration of the dynamic nature of variables such as habitat configuration. Extending SDMs to include non-climate dynamic variables that more fully describe niche complexity (Guisan & Thuiller, 2005; Franklin, 2010; Barve *et al*., 2011) at appropriate scales for generating conservation solutions (Guisan *et al*., 2013) remains a pressing need.

Functional connectivity (i.e., the extent to which individual movement is facilitated or impeded by the landscape; Taylor *et al*., 1993) is one important example of a dynamic non-climatic factor critical to the formation of the realized niche and species distribution (Soberón & Peterson, 2005; Barve *et al*., 2011). Measures of functional connectivity have been included with increasing frequency in studies of how species may respond to climate change (Bateman *et al*., 2013; Vasudev *et al*., 2015). However, most studies focus on dispersal conduits (Vasudev *et al*., 2015) and employ an 'all or nothing' dispersal assumption (Bateman *et al*., 2013) rather than projecting the dynamics of functional connectivity. A practical approach to projecting functional connectivity is to measure habitat characteristics, such as patch size and configuration, in terms of gene flow. As the identity and relative importance of factors that influence functional connectivity often vary between regions (Short Bull *et al*., 2011), investigating the interplay between functional connectivity and species distributions may best be explored at a local scale.

As an example, the American pika is predicted to experience dramatic range reductions due to climate change (Galbreath *et al*., 2009; Beever *et al*., 2010; Calkins *et al*., 2012; Johnston *et al*., 2012; Stewart *et al*., 2015), given the low heat tolerance exhibited by captured pikas (Smith, 1974) and observed extirpations in some warmer portions of the species' range (Beever *et al*., 2003, 2011). However, the relationship between pika occurrence and climate can be highly variable and even counterintuitive (Erb *et al*., 2011; Jeffress *et al*., 2013; Varner & Dearing, 2014). Pikas persist at low elevations and in warm climates, in places where rocky substrates mediate ambient temperatures at fine scales (Rodhouse *et al*., 2010; Millar *et al*., 2013; Varner & Dearing, 2014). Recent SDMs have investigated the potential impact of climate change on the American pika at broad spatial scales (Galbreath *et al*., 2009; Calkins *et al*., 2012; Johnston *et al*., 2012; Stewart *et al*., 2015), but have been unable to address the influence of fine-scale microclimates on pika occurrence. In addition, habitat configuration was not incorporated in these models (but see Stewart *et al*., 2015), despite its apparent influence on pika occurrence (Beever *et al*., 2003; Millar *et al*., 2013).

How does local variation in the interdependencies between climate, connectivity, and microhabitat shape the American pika's realized niche? Do idiosyncrasies in the pika's realized niche (Jeffress *et al*., 2013) undermine the generality of projected climate change impacts? We investigate these questions for pika populations inhabiting eight landscapes across the western United States in two unique ways: first, we incorporate estimates of functional connectivity, as measured by gene flow, directly into the SDM framework; second, we use a replicated place-based approach to develop SDMs for each spatially disjunct population. Thus, we explore dynamic local variation in the pika's realized niche and evaluate how this variation affects forecasted distributional trajectories for the species at scales relevant to site-based conservation.

Methods

Study areas and occupancy surveys

We assessed contemporary and future pika occupancy patterns in eight US National Park Service units (Fig. 1): Craters of the Moon (CRMO), Crater Lake (CRLA), Grand Teton (GRTE), Great Sand Dunes (GRSA), Lava Beds (LABE), Lassen Volcanic (LAVO), Rocky Mountain (ROMO), and Yellowstone (YELL). These study areas were chosen to represent the majority of habitat types (montane talus, boulder fields, and lava flows) and climatic conditions inhabited by the species. Among study areas, average annual precipitation ranged 33.4–206.4 cm and mean temperatures in the warmest quarter ranged 8.72°–18.0 °C (Fig. 2; PRISM averages, 1981–2010; PRISM Climate Group, 2014). We defined four categories of contemporary temperature-precipitation climate regimes based on mean annual precipitation and summer temperature (Fig. 2): warm-wet, warm-dry, cold-wet, and cold-dry.

Pika presence–absence data were obtained from occupancy surveys described in Jeffress *et al.* (2013; details in Appendix S1). Additional presence-only data were obtained

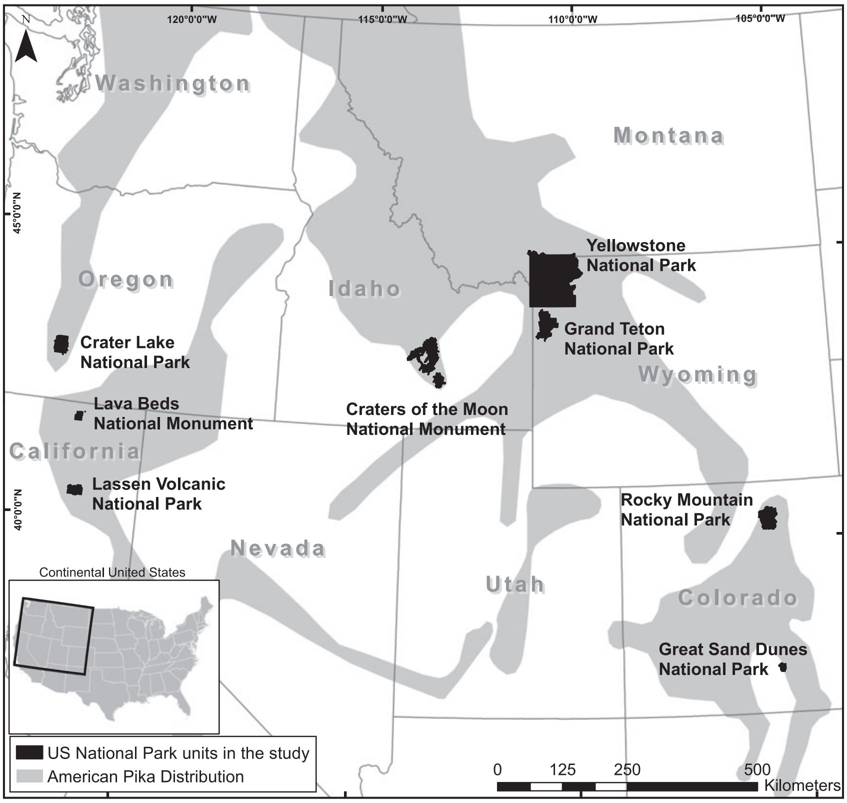

Fig. 1 Geographic location of eight federally managed units used as study areas for pika occupancy modeling. Full property names are followed by their 4-letter designation code (figure reproduced from Jeffress *et al.*, 2013). The current distribution map was provided by The International Union for Conservation of Nature (IUCN).

from targeted genetic sampling locations described in Castillo *et al.* (in prep). To reduce the influence of uneven spatial sampling, which can introduce bias especially in presence only datasets (Phillips *et al.*, 2009), we omitted data from genetic sampling locations within 100 m of occupancy survey areas. The total number of presence and absence records retained per study area ranged from 121 to 329 (Table 1).

Variable selection and calculation

We selected 21 predictor variables based on observed or expected relationships with heat stress (Beever *et al.*, 2010; Wilkening *et al.*, 2011), cold stress (Beever *et al.*, 2010; Erb *et al.*, 2011), growing season (Jeffress *et al.*, 2013) and habitat configuration (Moilanen *et al.*, 1998) (Table 2). Values for each predictor variable were extracted from raster data sets at each record of pika presence or absence using ARCGIS 10.0 (ESRI, Redlands, CA USA) and the point intersect tool in the Geospatial Modelling Environment (available online at spatialecology.com). For each study site, all predictor variables were tested for multicolinearity using QR-matrix decomposition (Murphy *et al.*, 2010). Where correlated variables were observed ($P < 0.05$), a single variable was retained based on published relationships or expert opinion.

Contemporary climate data were obtained from PRISM Climate Group (2014). Future climate projections were obtained from the NASA Earth Exchange (NEX) Downscaled Climate Projections (DCP) for the conterminous US (NEX-DCP30; Thrasher *et al.*, 2013), generated from the Coupled Model Intercomparison Project Phase 5 projections (CMIP5). We calculated 13 climate variables (Table 2) at 800 × 800 m resolution for one contemporary (1981–2010) and three future (2011–2040, 2041–2070 and 2071–2099) intervals. For each future, we evaluated one ensemble and eight global climate models (BCC-CSM1.1, CCSM4, CSIRO-Mk3.6.0, GISS-E2-R, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MIROC5) driven by two Representative Concentration Pathway (RCP) greenhouse gas scenarios, which bracketed climate response under relatively modest (RCP 4.5 W m^{-2}) and high 'business as usual' (RCP 8.5 W m^{-2}) emissions. Pika occupancy is influenced by persistence of the subnivium (*sensu* Pauli *et al.*, 2013), which provides refuge from extreme winter temperatures (Beever *et al.*, 2010; Pauli *et al.*, 2013) and predation. Unfortunately, future estimates of snow depth, density and duration, which drive subnivium conditions, were unavailable from NEX-DCP30. Therefore, we estimated potential snow accumulation using the cumulative precipitation across months with mean temperatures <0 °C. We also derived measures of growing season duration and growing season precipitation. These metrics are traditionally calculated using daily climate data; however, PRISM and NEX-DCP30 are monthly. Therefore, we estimated growing season duration as the total

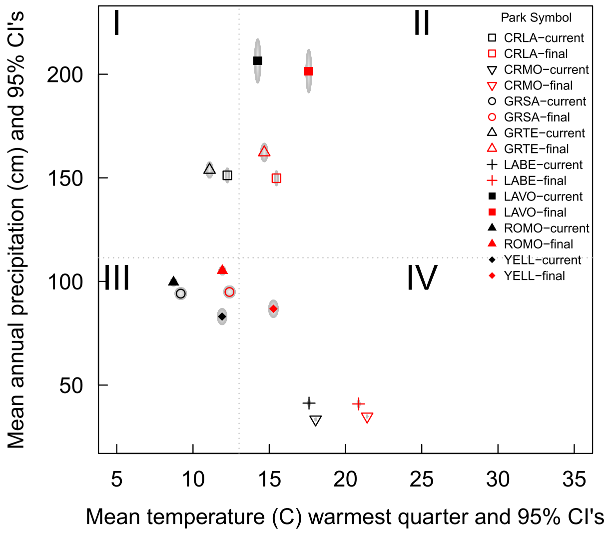

Fig. 2 Contemporary (1981–2010; 'current') and future (2070–2099; 'final') climate regimes, based on mean temperature in the warmest quarter (a measure of chronic heat stress) and annual precipitation (important for both warm season and cold season stressors), for pika survey locations in each of eight study areas. For 2070–2099, the ensemble model at RCP 4.5 is shown. Ellipses represent the 95% CI for each metric; dashed lines represent contemporary temperature and precipitation means across all eight study areas and divide the plot into four temperature-precipitation climate regime quadrants: I = cool-wet, II = warm-wet, III = cool-dry, and IV = warm-dry.

number of months with minimum temperatures >5 °C, while we estimated growing season precipitation as cumulative precipitation for all months with minimum temperatures >5 °C.

We also considered habitat configuration and functional connectivity using an empirically derived measure of connectivity derived from genetic data. We characterized functional connectivity using a measure of genetic neighborhood distance; that is, the distance across which gene flow occurs within a given population. This metric has the advantage of integrating connectivity over time across the study site and population of interest, reflecting the cumulative effects of multiple individual dispersal events. We calculated habitat metrics based on genetic neighborhood distance as follows. First, multilocus microsatellite genotypes were obtained for individual pikas in each study area using scat samples (sample numbers, allelic richness, and heterozygosity provided in Supporting Information Table S1; further details provided in Castillo *et al.*, 2014). Second, we estimated genetic neighborhood distance within each study site using a Mantel correlogram approach in program SPAGeDi (Hardy & Vekemans, 2002). This approach allowed us to assess the correlation between genetic distance (Rousset's â; Rousset, 2000) and Euclidean geographic distance among all individuals segregated into distance intervals. Break points between distance intervals were optimized to equalize the number of individuals among intervals. We repeated this process starting with 10 intervals and increased the number of intervals by 5 until there were fewer than 100 individuals per distance interval, or up to 50 distance classes, whichever came first. We then estimated genetic neighborhood distance as the point at which genetic distance and Euclidean distance were no longer significantly correlated ($P > 0.05$; e.g., Fig. S1). This method was robust to choice of individual genetic distance measure, as an alternate metric (PCA, Castillo *et al.*, 2014) showed nearly identical results (data not shown). Finally, we used FRAGSTATS 4.1 (McGarigal *et al.*, 2012) to calculate habitat configuration metrics parameterized by the genetic neighborhood for each study area. For each habitat metric (Table 2), we used a moving window with a radius equal to the site-specific genetic neighborhood distance to generate continuous surfaces.

To capture changing habitat connectivity and availability in future time periods, we established a threshold value based on occupancy probability (see below). This value (40%) was selected as the lowest occupancy probability value at which >99% of contemporary occupied pika locations were retained. At each future 30-year interval, we first removed all habitats below this threshold in the previous time step and then recalculated FRAGSTATS metrics for use in occupancy prediction, generating shifting habitat metrics for each future time step.

In two study areas where complete 1 m resolution LiDAR data were available (CRLA and GRSA), we also generated two measures of surface complexity to address our hypothesis that

Table 1 Samples sizes and genetic neighborhood distance estimates for American pika localities at each of eight study areas, separated by survey type (i.e., occupancy or genetic) and occupancy record (i.e., presence or absence)

Site ID	Total records	# Occupancy survey records	# Genetic survey records	# Presence records	# Absence records	Genetic neighborhood distance (km)*
CRLA	204	153	51	157	47	2.5
CRMO	201	158	43	70	131	1.2
GRSA	121	80	41	88	33	1.1
GRTE	329	184	145	240	89	4.3
LABE	160	160	0	65	95	3.5
LAVO	122	151	51	109	93	4.5
ROMO	164	106	58	116	48	3.5
YELL	185	185	0	89	96	3.4

*The distance at which gene flow occurs within the focal population.

Table 2 Variable name, description, and ecological justification for inclusion for 21 predictor variables used to assess current and future pika occupancy patterns in eight study areas

Variable	Variable description	Ecological justification
tmax	Ave max temp, July (Bioclim 5)	Acute heat stress
tmin	Ave min temp, January (Bioclim 6)	Acute cold stress
meantwq	Mean temperature warmest quarter (Bioclim 10)	Chronic heat stress
meantcq	Mean temperature coldest quarter (Biolclim 11)	Chronic cold stress
tempseas	Temperature seasonality (Bioclim 4)	Extremity of seasonal differences in temp
precip	Annual precipitation (Bioclim 12)	Multiple influences across seasons
precipwq	Precipitation, warmest quarter (Bioclim 18)	Forage availability and quality
precipcq	Precipitation, coldest quarter (Bioclim 19)	Potential subnivium insulation or rainfall
precseas	Precipitation seasonality (Bioclim 15)	Extremity of seasonal differences in precip
hmr	Heat to moisture ration. Calculated as [Mean temp May –Sep]/[(sum of monthly precip May – Sep)*(1000)]	Relationship with genetic connectivity (Henry *et al.*, 2012)
gs_dur	Duration of growing season; # months with temp >0 C	Available time for vegetation growth and haypile activity
gsp	Summed precipitation for months with mean min temp >0 C	Forage availability and quality
potsnow	Summed monthly precipitation for pixels with mean temp ≤ 0	Potential subnivium insulation
scosa	Potential solar insolation; as in Jeffress *et al.*, 2013	Solar/heat exposure
resid	Pika-adjusted elevation; as in Jeffress *et al.*, 2013	Associated with temperature and precipitation gradients
clumpy*	Measure of habitat aggregation; ranges from 1 (maximum aggregation) to −1(maximum disaggregation) within a site-specific, genetically derived measure of dispersal	Spatial aggregation of habitat influences population persistence and colonization
lpi*	Largest habitat patch within genetic neighborhood distance	Proximity to potential source population
pland*	Percent of the landscape that is pika habitat within genetic neighborhood distance	Influences pop size and habitat connectivity within the dispersal radius
prox*	Size and proximity of habitat patches within genetic neighborhood distance	Size and proximity of habitat on the landscape influences population persistence colonization
srr	Surface relief ratio, calculated for CRLA and GRSA only	In-site shelter; between site traversability
rough	Surface roughness; calculated for CRLA and GRSA only	In-site shelter; between site traversability

*Calculated using a moving window approach based on site (park)-specific estimates of the genetic neighborhood distance as a proxy for dispersal distance.

surface complexity, as a proxy for favorable microclimates, may predict pika site occupancy (Millar & Westfall, 2010). We calculated roughness and the surface relief ratio within a moving window with a 30 m radius using the Geomorphometry and Gradient Metrics toolbox (Evans & Oakleaf, 2012) in ARCGIS 10.0.

Modelling contemporary and future pika distribution and occupancy probability

For an earlier investigation of place-based occupancy-climate relationships in the American pika (Jeffress *et al.*, 2013), we constructed models using Bayesian hierarchical logistic regression (BHLR; Royle & Dorazio, 2008) that provided us flexibility for pooling data across all study sites and making global and park-specific parameter estimates (via hyperparameters). For the present work, we investigated a second modeling approach, Random Forest (Brieman, 2001). In all study sites, we found that Random Forest models outperformed BHLR (as measured by AUC, data not shown); further, the Random Forest approach was much less computationally intensive and produced more stable results. Thus, we chose to use Random Forest as our final modeling approach. We built Random Forest models using the R package randomForest (Liaw & Wiener, 2002; R Core Team 2013). We generated replicated, bootstrapped classification trees, randomly withholding 30% of data in each replicate as an out-of-bag (OOB) sample to measure misclassification error (i.e., the incorrect classification of a presence as an absence or vice versa; lower values indicate higher classification accuracy). The number of replicates for each site was chosen at the point where OOB error stabilized (range = 1000–2500 replicates). As a second measure of model performance, we used the area under the receiver operating characteristic curve (AUC) to measure predictive accuracy and discriminative power. We categorized model discrimination as poor (AUC < 0.70), acceptable (0.70 ≤ AUC < 0.80), excellent (0.80 ≤ AUC < 0.90), or outstanding (AUC ≥ 0.90) (Gogol-Projurat, 2011). We built models using the model improvement ratio (MIR; Murphy *et al.*, 2010), which creates a parsimonious model by selecting, from the full suite of variables, those predictors that decrease OOB error above a pre-defined threshold (0.03 in this instance; the default value).

Finally, we predicted pika occupancy for current and future time steps as a continuous gradient of occurrence probability (as opposed to binary presence/absence; Cushman *et al.*, 2010). We then clipped these prediction surfaces to include only known pika habitat with occupancy probability >40%. This threshold reflects the pattern of occurrence in contemporary habitats: occupancy probability exceeds 40% in 99% of patches in which pikas currently occur. We recorded the range of values along the gradient of occurrence probability in pika habitat (hereafter 'occupancy probability') and calculated the proportion of total habitat with predicted occupancy probability >40% (hereafter 'distribution') for each contemporary and future prediction.

Results

Changing climate regimes

We predicted shifts in temperature-precipitation regimes in all study areas (Fig. 2). Temperature was predicted to increase similarly across all study areas except CRMO, where more pronounced warming was projected. Wet study areas were predicted to become drier while dry study areas were predicted to become wetter, excepting the two most arid areas (CRMO and LABE), which showed little change. Climate models predicted three study areas will transition from cool to warm temperature regimes (CRLA, GRTE, and YELL) and a fourth (GRSA) will approach this shift, while no study areas will transition from warm to cool regimes. No study areas were predicted to transition to a different precipitation regime, although ROMO will approach the shift from dry to wet.

Site-specific model structure and performance

The performance of site-specific SDMs varied widely among study areas (Table 3). We observed acceptable to outstanding model predictive power, based on AUC values (range: 0.70–0.94; Table 3), for all study areas except LABE (AUC = 0.58). We observed varying rates of model classification accuracy based on OOB misclassification error. Classification accuracy was often skewed, usually against absence, but overall accuracy was good to moderate for all study areas (range: 15.69–34.05; Table 3) except LABE (OOB = 42.94). Performance of the LABE model implied low power for predicting pika occupancy, so we did not include LABE in further analyses.

The importance of predictor variables and frequency of their selection varied widely among study areas, although elements of heat stress, cold stress, growing season and habitat configuration were supported in models for almost every study area (Table 3 and Fig. S2). We detected evidence of cold stress driving pika occupancy patterns in two study areas (CRLA and ROMO), heat stress in three study areas (CRMO, GRSA, and YELL), growing season in one

Table 3 Random Forest models predicting occupancy probability of American pikas, with associated measures of model discriminatory power (AUC) and model precision (out-of-bag or OOB error), for each of eight study areas

Site ID	Model variables (ranked most to least important)	OOB overall	OOB presence	OOB absence	AUC
CRLA	*potsnow*, precip, **scosa**, **hmr**, *precipcq*, resid, **tmax**, *tmin*, pland, *meantcq*	15.69	5.73	48.94	0.83
CRMO	**tmax**, lpi, gsp, precip, pland, precipwq, resid, *tmin*, clumpy	21.39	34.80	14.62	0.84
GRSA	resid, precipwq, precseas, **scosa**, clumpy, pland, lpi, precip, *precipcq*, *potsnow*, gsp, srr, prox	16.10	5.81	43.75	0.90
GRTE	pland, resid, prox, **scosa**, lpi, **hmr**, **tmax**, **meantwq**, tempseas, clumpy	23.94	9.92	62.50	0.70
LABE	clumpy, pland, lpi, resid, **hmr**, *tmin*, **meantwq**, tempseas, *meantcq*, precip, *precipcq*, precseas	42.94	48.19	38.30	0.58
LAVO	resid, lpi, clumpy, pland, tempseas, gsp, *tmin*, **meantwq**, **tmax**, **scosa**	31.82	30.19	33.70	0.94
ROMO	prox, *tmin*, *meantcq*, precipwq, *precipcq*, **tmax**, precip, pland, resid, *potsnow*	31.10	15.51	68.75	0.70
YELL	**meantwq**, **hmr**, precipwq, pland, resid, lpi, *meantcq*, *potsnow*	34.05	34.09	34.02	0.72

Model precision (OOB) is shown for records of presence, absence and overall; the lower the value, the higher the precision. Variable names are provided in Table 2. Variable relationship with heat stress, cold stress, and habitat configuration are shown in **bold**, *italicized*, or underlined text, respectively; plain-type text indicates variables with relationships to more than one factor.

site (CRMO), and habitat connectivity in five study areas (CRMO, GRTE, LAVO, ROMO, and YELL). Residual elevation (resid) and proportion of habitat on the landscape (pland) were included in models for all eight study areas (Table 3). Other variables included in over half of the models were: maximum and minimum temperature (tmax and tmin; seven models), annual precipitation (precip; six models), and potential snow accumulation (potsnow; five models). However, the ranks of these variables differed between models (Table 3, Fig. S2).

Contemporary and future pika distributions

We predicted current and future pika distributions in seven study areas (Figs 6, 7, 8, S3, S4, S5, and S6). Overall, contemporary predictions of pika distribution ranged from 28 to 99% of potential habitat (Figs 3 and 4), with three of seven study areas exhibiting nearly complete occupancy of available habitat (CRLA, GRTE, and YELL). Future populations showed an increase in distribution in two study areas (GRTE and LAVO; Fig. 4) and eventual decline in the remaining five study areas. Monotonic decline was predicted for only three study areas (CRLA, ROMO, and YELL). Complete extirpation was predicted in ROMO and YELL (Fig. 4) under some climate model/RCP combinations. Across all study areas, we observed three primary kinds of trends in future pika distributions: consistent monotonic decline (Fig. 6, ROMO), little to no change (i.e., flat trend; Fig. 7, GRTE) and fluctuations over time, but with an overall decline (Fig. 8, GRSA).

Occupancy probability

Although the majority of parks showed a declining trend in mean and maximum occupancy probability, the decrease was not consistent across all populations or, in some instances, within a population over time (Figs 3 and 5). Occupancy probabilities in ROMO and YELL declined consistently but were more variable and generally higher in YELL (Figs 3 and 5). In CRLA, GRTE and LAVO (Fig. 5), occupancy probabilities were consistent across future scenarios but differed considerably from contemporary values (Fig. 3). For CRMO, results were highly variable and model dependent (Fig. 5). Although we observed a decrease in occupancy probability overall (Fig. 3), individual model outcomes ranged widely (56–89%; Fig. 5) and lacked a clear trend.

Discussion

The predicted responses of pika populations to climate change in eight US National Park units were highly

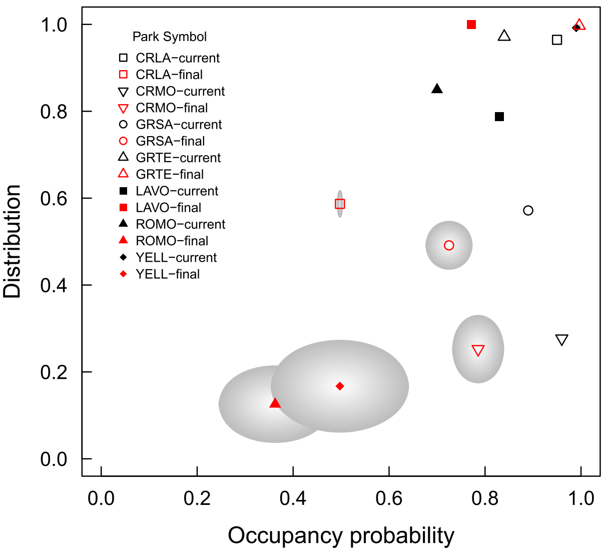

Fig. 3 Changes in occupancy probability (*x* axis) and distribution (*y* axis) for pika populations in each of eight study areas. Distribution represents the proportion of potential pika habitat with an occurrence probability >0.4, while mean occurrence probability is calculated across all potential pika habitat. Contemporary and future periods are defined as in Fig. 2. Ellipses represent the 95% CI across all 16 climate model and RCP combinations.

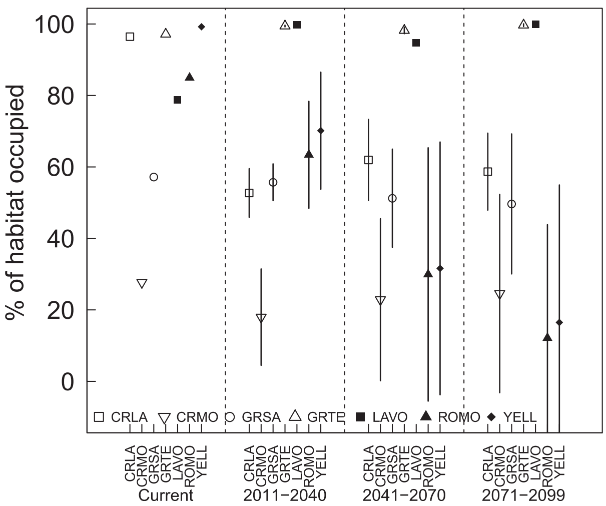

Fig. 4 The proportion of all potential pika habitat within study area boundaries predicted to be occupied with >40% probability currently and in three future periods (2011–2040, 2041–2070, and 2071–2099). Values for future time steps show the range and mean proportion for each site in each period, generated by individual prediction results from 16 unique climate model-RCP combinations.

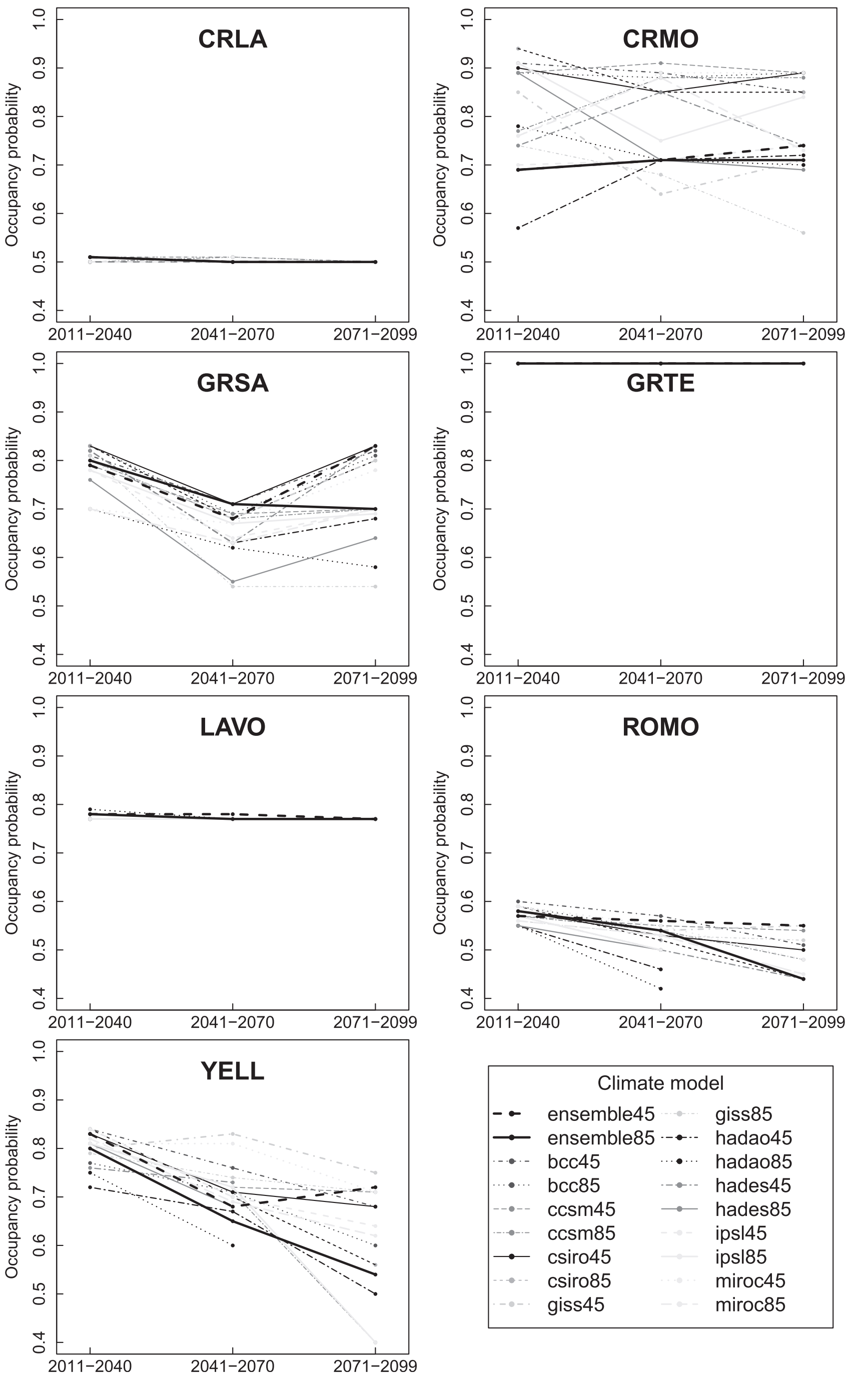

Fig. 5 Maximum predicted pika occupancy probability in each of eight study areas for three future 30-year periods. In each period, occupancy was predicted using eight climate models and one ensemble climate model, each of which was driven by a modest and high carbon forcing scenario (RCP 4.5 and 8.5, respectively). Where points are not shown, maximum occupancy probability is less than 40%, and extirpation is expected.

variable, with outcomes ranging from complete extirpation (e.g., Fig. 6) to stability (e.g., Fig. 7) by the end of the 21st century. Strikingly, climate variables were not consistently the dominant determinant of occupancy; rather, site-specific factors including habitat configuration and connectivity – modified by climate – were critical elements in some study areas (Table 3). Our study demonstrates that local variation in the relationships between changing environmental conditions and biotic response, the so-called 'idiosyncrasies of place'

(Billick & Price, 2010; Jeffress *et al.*, 2013), may result in divergent local population trajectories. To illuminate complex population responses to global climate change, we urge consideration of local variation in a species' realized niche and the causes of that variation. Our study provides a model place-based framework for doing so by replicating large-sample studies across multiple areas or regions.

Local variation in future population trajectories

Warming climate has frequently been predicted to result in partial or complete extirpation of species (Bellard *et al.*, 2012), including the American pika (Beever *et al.*, 2011; Calkins *et al.*, 2012). Our study predicts that local extirpations are possible within the next 90 years but only in the minority of sites we investigated, and it implies that the relationship between changing climate and occupancy of at least some species may not be straightforward. For example, although all of our study areas showed a warming trend, only five of eight exhibited declining distribution and occupancy probability (Figs 3–5). Where they occurred, declines in occupancy and especially distribution varied from dramatic to slight, while some study areas are expected to support stable, robust populations in the future (Figs 6–8, S3–S6).

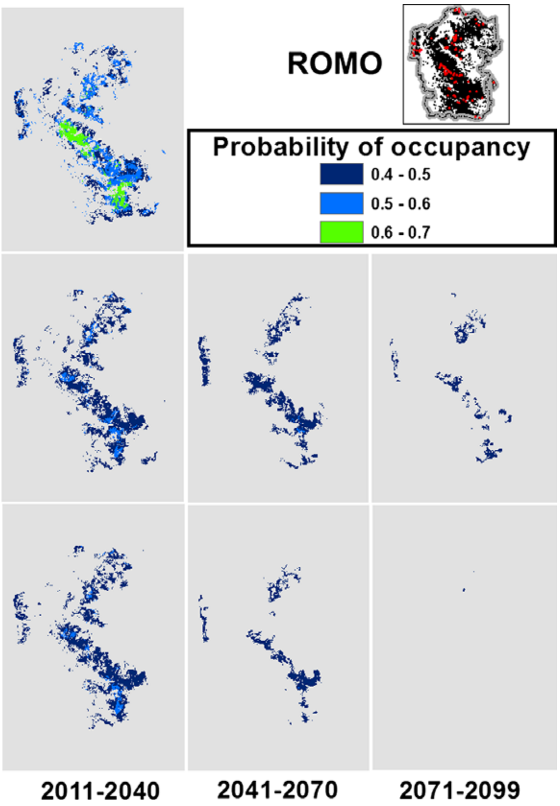

Fig. 6 Example of a pika population predicted to experience a steady decline in suitable habitat throughout this century (ROMO). Shown are total potential habitat (in black) and site boundaries (upper right), predicted current occupancy probability (upper left), and predicted occupancy probability using the ensemble climate model with two carbon forcing (RCP) scenarios (6 lower panels). Individual sampling locations are shown as red dots in the upper right study area map.

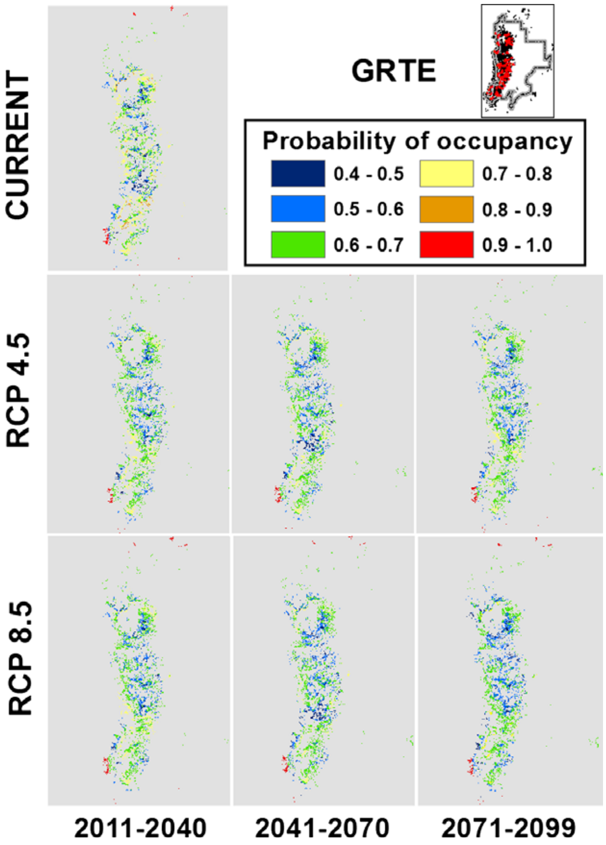

Fig. 7 Example of a pika population predicted to experience no change in suitable habitat throughout this century (GRTE). Panel contents are as defined in Fig. 6.

Furthermore, the relationship between our two measures of pika population persistence (distribution and occupancy probability) was not congruent across study areas. Distribution reflects the typically employed binary characterization of habitat as occupied above some threshold probability (here, >40%), whereas occupancy probability captures the variability within those predictions. In ROMO and YELL, both distribution and occupancy probability declined simultaneously across future time steps, indicating consistently declining persistence. Conversely, distribution remained relatively stable while occupancy probability declined by almost 20% in GRSA, indicating a constant potential distribution but increased volatility in occupancy patterns.

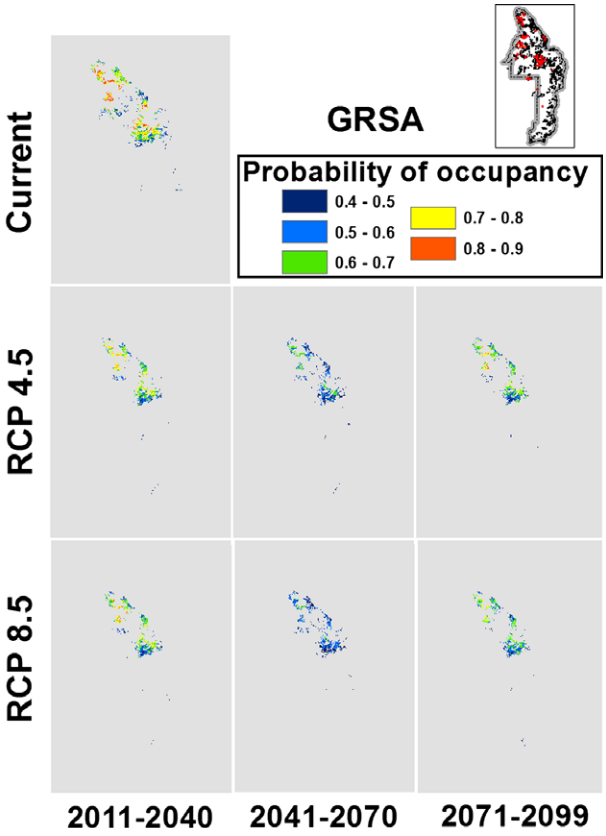

Fig. 8 Example of a pika population predicted to experience fluctuating habitat suitability throughout this century (GRSA). Panel contents are as defined in Fig. 6.

Elsewhere, including GRTE, occupancy probability increased while distribution remained constant near its maximum, indicating a robust population long-term. Taken together, these results illustrate the value of moving beyond binary presence–absence portrayals of future species distributions (Cushman *et al.*, 2010). Interpreting our results solely on arbitrary presence–absence distributional categories would imply negative futures for pika populations in most study areas. For example, using a 50% threshold (e.g., Stewart *et al.*, 2015), parks like CRLA would show substantial loss of pika distribution. By considering a gradient of occupancy probability, we have illustrated that pika persistence is threatened by both declining distribution and declining occupancy probability in many locations, while highlighting stark contrasts in some study areas, where occupancy probabilities imply very different odds of persistence, despite similarly restricted final distributions (e.g., YELL and ROMO vs. CRMO).

Occupancy trajectories for individual study areas varied widely compared to previous range-wide predictions based solely on climate (Galbreath *et al.*, 2009; Calkins *et al.*, 2012). Calkins *et al.* (2012) used a stepped increase in temperature alone to model pika futures, while Galbreath *et al.* (2009) incorporated a suite of climate variables. Adding to these efforts, we incorporated landscape variables and produced local SDMs. Galbreath *et al.* (2009) and Calkins *et al.* (2012) predicted extirpation in regions where we predict stability (LAVO) or limited decline (CRLA). In these study areas, our results suggest that favorable local climates and habitats may persist, thereby sustaining pika populations. Conversely, Calkins *et al.* (2012) predicted larger future pika distributions in ROMO and YELL than our study, suggesting either that our models have underestimated the physiological capacity of pika to respond to climate change or the Calkins *et al.* (2012) model over-predicted occupancy by failing to incorporate functional connectivity. Predictions for GRTE and GRSA were comparable between this study and Calkins *et al.* (2012), but exceeded the range predicted by Galbreath *et al.* (2009). No prediction for CRMO was produced by either Galbreath *et al.* (2009) or Calkins *et al.* (2012), illustrating how unique peripheral populations are sometimes excluded from coarse-grain SDMs. While opposing conclusions may result from different inputs, scales of analysis, and methodologies, our findings highlight the relevance of developing and evaluating SDMs parameterized at local scales, which may better reflect population-level response to climate change (Randin *et al.*, 2009; Tingley *et al.*, 2012).

Locally varying factors shape occupancy

Occupancy was not determined by the same factors across the eight populations we studied. While factors related to heat stress were dominant predictors in previous studies of pika dynamics (Beever *et al.*, 2010, 2011; Wilkening *et al.*, 2011), such factors played a principal role in only three of the seven study areas we were able to model (CRLA, GRSA, and YELL; Table 3). Factors related to cold stress, especially cold-season precipitation, were fundamental in explaining occupancy patterns in two of seven populations (CRLA and ROMO), adding to mounting evidence that the pika's climatic envelope can be influenced by snowpack persistence (Beever *et al.*, 2010; Erb *et al.*, 2011). Precipitation metrics were included in six of seven models, although these varied in seasonality. These results correspond with observations that the interplay between temperature and precipitation can produce heterogeneous, locally varying responses to climate change (Tingley *et al.*, 2012).

Notably, pika occupancy in four of seven study areas was strongly influenced by habitat availability and connectivity (Table 3). Given the species' strong association with habitats that provide unique microclimates (Millar & Westfall, 2010; Rodhouse *et al.*, 2010; Varner & Dearing, 2014), as well as high annual patch extirpation and recolonization rates (Smith, 1980; Jeffress *et al.*, 2013), the importance of habitat metrics in shaping pika occupancy is not surprising. In several instances, the influence of habitat-derived variables surpassed that of the climate variables more traditionally used to predict occupancy for this species, suggesting that climate change impacts on pika populations may be partially mediated where functional connectivity persists. Conversely, where declining habitat suitability subsequently reduces functional connectivity, the impact on pika occupancy may be exacerbated (e.g., ROMO), underlining the importance of considering the interaction between climate change and connectivity for species with metapopulation-like dynamics. Dynamic methods for investigating such interactions (Franklin, 2010; Doerr *et al.*, 2011; Lurgi *et al.*, 2015) offer considerable promise for exploring this complex relationship.

The importance of habitat configuration has received little attention in previous studies predicting future pika-climate interactions. In one noteworthy exception (Stewart *et al.*, 2015), habitat area within a 1-km radius was one of two top predictors of pika persistence in California. Contrary to our findings, however, Stewart *et al.* (2015) projected extirpation in the LAVO area. This contrasting outcome likely reflects differences in scale, study design, and scope of inference. Stewart *et al.* (2015) used a finer scale (270 m rather than 800 m) but focused only on changes in occurrence in historic sites in California without a positive feedback loop on habitat configuration (i.e., habitat configuration was static throughout the forecast period), and used a 50% presence–absence threshold. Our study revealed that the dynamic habitat metrics were important to pika occupancy over time in LAVO. Furthermore, our study demonstrated that habitat connectivity occurs within a 4 km (not 1 km) radius in LAVO, and suggested that a 40% threshold is more appropriate for capturing pika occupancy.

The importance of fine-scale data in species distribution modeling

Accurately, modeling the fine spatial scale at which ecological factors shape occupancy patterns is a persistent challenge for understanding climate change impacts on many species (Potter *et al.*, 2013). Correspondence between the resolution of environmental data and the spatial scale at which organisms interact with their environment is of critical import to species distribution modeling (Seo *et al.*, 2009), in particular for dispersal-limited organisms (Guisan & Thuiller, 2005). Pikas are sensitive to the availability of habitat-mediated microclimates (Millar & Westfall, 2010) and forage availability (Jeffress *et al.*, 2013) within their territories, while climate data is available only at larger scales. In the case of the American pika, our limited ability to predict microclimate influences is likely to underestimate the mediating effects of these factors in the future (Sears *et al.*, 2011; Varner & Dearing, 2014). This may explain the poor explanatory power (LABE) and high inter-model variability (CRMO and YELL) observed in some cases. We reiterate the call for improved availability of high-resolution climate data, which better reflect the scale at which organisms interact with the environment (Halvorsen, 2012; Potter *et al.*, 2013). For example, using data loggers to generate high-resolution (25–30 m) contemporary climate layers exhibits greater potential for investigating microclimate-occupancy associations across geographical regions comparable in size to National Parks and other conserved lands (Fridley, 2009; Ashcroft & Gollan, 2012).

Conclusion

Our study demonstrates that response to climate change is unlikely to be uniform across a species' range. We predicted local variation in the American pika's realized niche, indicating that site-specific SDMs may generate outcomes more applicable to conservation efforts undertaken locally. When species occur across environmentally disjunct regions, local variation in the realized niche is a reasonable expectation (McPherson *et al.*, 2004; Pearman *et al.*, 2010). Thus, when species exhibit fine-scale variation in responses to climate, such as those observed in this study, predictions that generalize across the species' distribution may lead to erroneous expectations for response to climate change at local scales (Randin *et al.*, 2009; Halvorsen, 2012). Moreover, we have shown that functional connectivity can strongly influence how a species occupying fragmented habitat will respond to climate change, and that habitat configuration may stabilize or destabilize occupancy trends in opposition of climate-only models (e.g., Austin & Van Niel, 2011; Bertrand *et al.*, 2012). While range-wide models are still an important tool for inference, incorporating non-climatic variables (Soberón & Peterson, 2005; Bertrand *et al.*, 2012; Halvorsen, 2012) and deriving place-based assessments and conservation strategies that reflect the unique local relationship between climate, landscape, and occupancy (Halvorsen, 2012) also are necessary steps for the understanding and mediation of climate change impacts on diverse biota.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Pika occupancy survey methods.
Figure. S1. Example of a Mantel correlogram.
Figure. S2. Model improvement ratio plots for occupancy models.
Figure. S3. Predicted pika distributions in CRLA.
Figure. S4. Predicted pika distributions in CRMO.
Figure. S5. Predicted pika distributions in LAVO.
Figure. S6. Predicted pika distributions in YELL.