nature climate change

ARTICLES

https://doi.org/10.1038/s41558-019-0584-8

Alternatives to genetic affinity as a context for within-species response to climate

Adam B. Smith[1], Erik A. Beever[2,3]*, Aimee E. Kessler[1], Aaron N. Johnston[2], Chris Ray[4], Clinton W. Epps[5], Hayley C. Lanier[6], Rob C. Klinger[7], Thomas J. Rodhouse[8], Johanna Varner[9], John D. Perrine[10], Amy Seglund[11], L. Embere Hall[12], Kurt Galbreath[13], Chris MacGlover[14], Peter Billman[15], Gretchen Blatz[16], Jason Brewer[17], Jessica Castillo Vardaro[18], Anna D. Chalfoun[19], Gail Collins[20], April Craighead[21], Chris Curlis[22], Christopher Daly[23], Daniel F. Doak[24], Mitch East[25], Mark Edwards[26], Liesl Erb[27], Kristina A. Ernest[28], Brian Fauver[29], Kerry R. Foresman[30], Ken Goehring[31], Joan Hagar[32], Charles L. Hayes[33], Philippe Henry[34], Kimberly Hersey[35], Shannon L. Hilty[3], Jim Jacobson[36], Mackenzie R. Jeffress[37], Tom Manning[38], Amy Masching[29], Bryce Maxell[39], Rayo McCollough[40], Corrie McFarland[41], Eric Miskow[42], Toni Lyn Morelli[7], Lucas Moyer-Horner[43], Megan Mueller[44], Martin Nugent[45], Beth Pratt[46], Mary Rasmussen-Flores[47], Tom H. Rickman[41], Hillary Robison[48], Arthur Rodriguez[45], Karen Rowe[49], Kevin Rowe[50], Michael A. Russello[51], Vicki Saab[17], Angie Schmidt[52], Joseph A. E. Stewart[53], James N. Stuart[54], Leona K. Svancara[55], Will Thompson[3], Julie Timmins[56], Gregg Treinish[57], Matthew D. Waterhouse[51], Marie L. Westover[58], Jennifer Wilkening[59] and Leah Yandow[60]

Accounting for within-species variability in the relationship between occurrence and climate is essential to forecasting species' responses to climate change. Few climate-vulnerability assessments explicitly consider intraspecific variation, and those that do typically assume that variability is best explained by genetic affinity. Here, we evaluate how well heterogeneity in responses to climate by a cold-adapted mammal, the American pika (*Ochotona princeps*), aligns with subdivisions of the geographic range by phylogenetic lineage, physiography, elevation or ecoregion. We find that variability in climate responses is most consistently explained by an ecoregional subdivision paired with background sites selected from a broad spatial extent indicative of long-term (millennial-scale) responses to climate. Our work challenges the common assumption that intraspecific variation in climate responses aligns with genetic affinity. Accounting for the appropriate context and scale of heterogeneity in species' responses to climate will be critical for informing climate-adaptation management strategies at the local (spatial) extents at which such actions are typically implemented.

An interplay between local adaptation and niche conservatism shapes species' distributions and responses to climate. On the one hand, an increasing body of literature spanning diverse taxa and biomes demonstrates marked intraspecific variation in responses to climate, with differences observed between populations of different genetic affinities (reviewed in ref. [1]). On the other hand, many studies show strongly synchronous responses of conspecific populations separated by hundreds of metres to thousands of kilometres[2–5]. Concurrently, although extreme climate events are occurring more frequently[6], the magnitude and spatial extent of synchrony in climate conditions has increased over the last half-century[7]. Synchronous responses of conspecific populations have been hypothesized[2] and demonstrated[5] to increase extirpation risk in spatially structured populations.

Within a species, heterogeneity in responses to the environment is presumably mediated by the level of genetic adaptation to local environments and thus should be strongly predicted by dividing a species' range into lineages[1,8–10]. Indeed, a growing number of climate-vulnerability assessments demonstrate that subdividing species by genetic lineage yields vastly different outcomes compared with the usual practice of assuming homogeneity across populations[8–13]. Nonetheless, several considerations suggest that variation in climate responses may not be captured exclusively by genetic subdivision. For example, different genetic groups can be parapatric[14] or even sympatric[13,15] in distribution and thus share common environments. Conversely, an individual lineage can occupy broad portions of environmental gradients that lead to local adaptation within the lineage. Finally, the potential for dynamic interplay between genetics (niche conservatism and local adaptation) and ecological context (physiography, geology, hydrology, vegetation and other aspects) suggests that responses to climate might be mediated by more than genetic affinity alone[16]. Further complicating this situation, the current distribution of species can be shaped by factors that vary across a range of temporal scales, from millennial-scale range shifts, contractions and expansions to generation-scale and population- and metapopulation-level dynamics[14,17,18].

A full list of affiliations appears at the end of the paper.

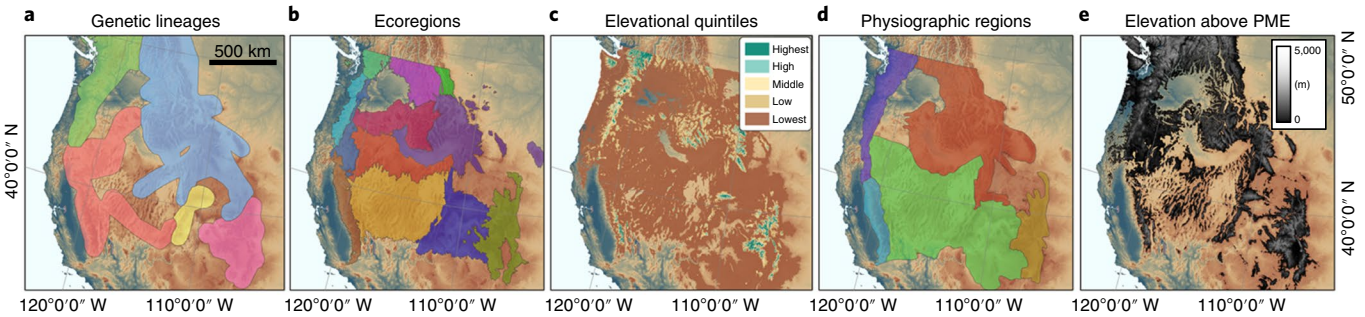

Fig. 1 | Pika minimum elevation (PME) and geographic subdivisions used to explore spatial heterogeneity in responses of the American pika to climate. **a**, Genetic lineages[51] (plus a 47.7 km buffer). **b**, Ecoregions based on US Environmental Protection Agency Level III Ecoregions[31]. Some regions with small sample sizes were combined. **c**, Elevational quintiles relative to locally defined PME. **d**, Physiographic regions[52]. **e**, Elevation above locally defined average PME, below which pikas are rarely found. Projection for all maps: Albers equal-area conic.

Identifying the spatiotemporal scale of responses to climate

Here, we test eight hypotheses about the spatial configuration and temporal dimension of responses to climate of the American pika, *Ochotona princeps*, a lagomorph endemic to western North America that is typically found at higher elevations and has been long studied for its climate sensitivity[18–23]. The pika's vulnerability to climate change broadly reflects the species' poor ability to dissipate heat and a narrow (3 °C) difference between high basal body temperature and upper lethal temperature, among other factors[19]. Since the nineteenth century, researchers have characterized the pika's distribution as a product of climatic patterns[24], rather than species interactions, and the species' distribution has since been shown to correspond to aspects of climate at multiple spatial[18,25,26] and temporal[17] scales (decadal to millennial). More broadly, variation in response to climate may be due to behavioural or adaptive evolution to local conditions[9], a state that is presumably best reflected by subdividing species into genetic lineages (for example, Fig. 1a and Supplementary Fig. 1). Nonetheless, the parapatric distributions and introgression of some pika lineages[15] and the relatively short divergence time between them (a few hundred thousand years, beginning ~1.3 million years ago (Ma)[22]) suggest that evolutionary adaptation to local conditions might play a lesser role in explaining heterogeneous responses to climate. Our hypotheses test whether spatial heterogeneity in species responses most strongly aligns with one of four range-subdivision schemes (that is, divided by genetic lineage, ecoregion, elevation or physiography: Fig. 1a–d and Supplementary Fig. 1; the rationale for each scheme appears in Supplementary Methods and Results), each investigated at two scales. Such a test of division schemes that compares genetic and non-genetic contexts has not previously been attempted, nor has the full array of techniques that we employed to improve model realism.

We compiled >14,500 high-quality presence records from museums, state and provincial natural heritage programmes, state and provincial wildlife agencies, and nearly all researchers who have published on the species or were known to have relevant data (Supplementary Table 1). Because distributional changes in pikas are occurring rapidly in some regions (see, for example, ref. [18]), we associated each pika detection with climatic conditions during the 10 years preceding that record (compare Supplementary Table 3), rather than the standard practice of using an invariant (30-year) climate normal for all records. Our approach directly tests whether antecedent climatic conditions influenced occurrence at a given location[27]. To capture variation in patterns of occurrence as a function of climate at different spatiotemporal scales, we contrasted climate at presence locations with climate at background sites selected either from broad extents indicative of long-term processes (for example, range shifts) or narrow extents indicative of short-term habitat selection and metapopulation dynamics. Broad backgrounds covered the entire unit in each division (that is, entire polygons in Fig. 1a–d, representing each of the genetic lineages, ecoregions, elevational bands or physiographic regions), including areas far outside the current species distribution. These broad backgrounds represent potential pika habitat available since the last glaciation[28], especially considering the distribution of fossil pika remains geographically and climatically distant from currently occupied sites[17]. Narrow backgrounds were represented by the portion of each subdivision's unit lying above a locally defined minimum elevation inhabited by pikas (Fig. 1e and Supplementary Fig. 1), and encompassed climatic conditions potentially inhabited over shorter time periods (that is, tens of generations). Minimum inhabited elevation was determined in a multistep procedure (Supplementary Methods and Results) accounting for regional orographic and continental effects and the species-wide latitudinal and longitudinal range. We used spatiotemporal stratification of background sites to correct for spatial, temporal and spatiotemporal sampling bias (Supplementary Fig. 3). Throughout this effort, we employed predictors (Supplementary Table 2) directly relevant to demonstrated or hypothesized (see, for example, refs. [18,23,26]) mechanisms governing occurrence of the species and its particular life-history characteristics, rather than a generic suite of predictor variables.

Identifying the appropriate spatial and temporal scale of climate response is challenging because different methods of subdividing a species' range can yield highly variable results[29], even when subunits do not have a biological basis (for example political units or protected areas[30]). Thus, demonstrating variation in responses to climate across 'populations' is a necessary but insufficient condition for justifying a particular subdivision. Rather, the method of subdivision that best reflects the underlying heterogeneity in climate relationships should display maximum climate 'coherency', achieved when heterogeneity is lowest within units and highest among units (Fig. 2 and Supplementary Figs. 4 and 5). We evaluated coherency in response to individual climate variables while controlling for the effects of other variables. We also examined coherency in response to all climate variables simultaneously. Both tests compared within-unit and among-unit heterogeneity across each combination of spatial subdivision (see the four schemes in Fig. 1a–d) and temporal dimension (reflected by background extent). A third test evaluated the importance of accounting for a subdivision's units when modelling responses to all climate variables together. Where applicable, each analysis controlled for correlations and interactions among variables, non-shared climate space, sample size and geographic distance between training and test regions.

Although we expected genetic lineages to best explain variation in climate relationships across the species' range, we found that subdivision of the range by ecoregions most dependably captured heterogeneity in the pika's responses to climate. For 12 of 20 proximate

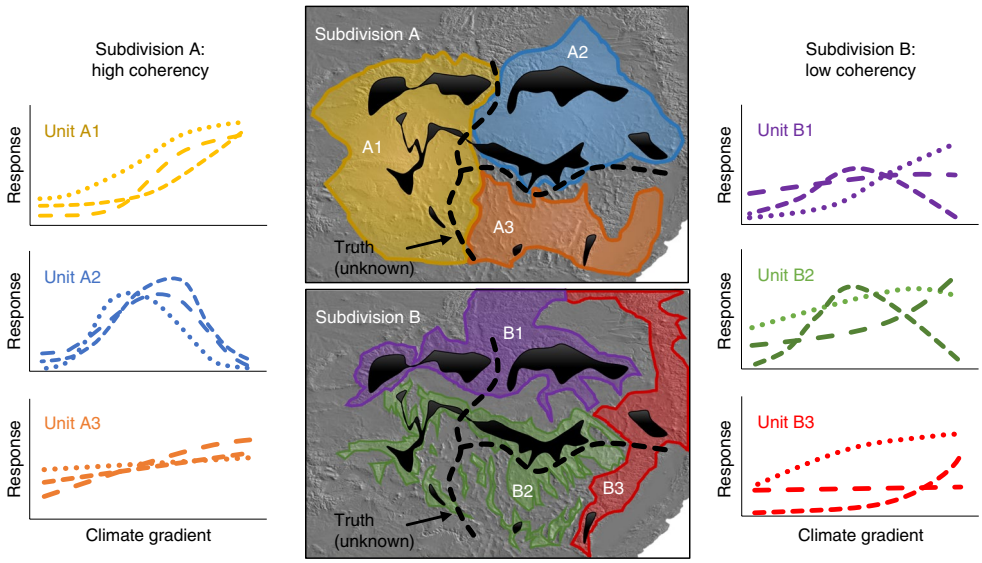

Fig. 2 | Climate coherency. Many species respond heterogeneously to climate across their ranges. Subdividing the range can create a geographic mosaic of units within which responses to climate are more similar than between units, a property termed climate coherency. Many recent studies subdivide ranges on the basis of genetic affinity under the assumption that evolutionary dynamics alone determine intraspecific variation in climate response, other kinds of subdivision can capture processes that may be more relevant to explaining variability in climate response. These include subdivision on the basis of ecological and biological context, topography, hydrology, type and intensity of human impact, areas of past glaciation, primary/secondary vegetation and so on. Competing subdivision schemes thus offer alternative hypotheses about the most relevant factors determining intraspecific variation in responses to climate. The most appropriate subdivision scheme can be identified by comparing climate coherency across methods of subdivision. In this example, the species' range is demarcated with black polygons and the true delineation between units that respond in the same way to climate is indicated by the dashed black line. Two subdivision schemes are compared. Subdivision A has greater climate coherency because within-unit responses are less heterogeneous than among-unit responses, compared with subdivision scheme B, where within-unit response are fairly heterogeneous relative to among-unit responses. Variation in responses within units is indicated by different dotted/dashed lines.

climate variables, the greatest mean coherency in response to individual variables occurred among ecoregions matched with background sites drawn from a broad extent indicative of long-term range dynamics (Fig. 3 and Supplementary Table 5). Responses to an additional four variables were most coherent for ecoregions paired with a narrow background indicative of short-term habitat selection and metapopulation dynamics. For each of the other combinations of subdivision and background, coherency was highest for only one or none of the 20 climate variables considered. Ecoregions matched with background sites drawn from a narrow background indicative of short-term range dynamics had the second-highest coherency for 11 of the 20 variables. Considering all variables simultaneously, ecoregions (matched with broad or narrow backgrounds) were again always among the most coherent subdivisions (Fig. 4 and Supplementary Table 6). This conclusion was further supported by the third analysis, which explicitly accounted for variation in response to multiple climate variables within each subdivision's units. In this case, heterogeneity in responses to climate was best reflected by ecoregions and elevational bands, both with narrow backgrounds (Fig. 5). However, responses varied widely for elevational bands with a narrow background, meaning that even though some bands were more effective at capturing underlying heterogeneity others were far worse. In sum, the underlying heterogeneity in the relationship of pika occurrence to climate was best captured by ecoregional differentiation. Pikas in different ecoregions varied in how they responded to individual climate variables and all variables simultaneously, and responses carried signatures of dynamics transpiring across long and short timescales.

Discussion

Our results demonstrate that landscape context may have as much if not more bearing on intraspecific heterogeneity in responses to climate than phylogenetic affinity; specifically, genetic lineage may not be the most appropriate scheme to capture within-species spatial variation in climate response. Moreover, spatial heterogeneity in environmental responses may reflect temporal differences in range-shaping processes such as habitat selection and metapopulation dynamics and millennial-scale shifts in available habitat arising from climate change. Together, differences in the spatial and temporal scale of response suggest that a spatiotemporal 'mosaic' of context-mediated responses to climate gives rise to the contemporary shape of ranges, such that different portions of the range are determined by diverse processes and factors acting over decades to millennia.

For the American pika, ecoregions best captured intraspecific variation in climate response. As used here, ecoregions are areas with relatively homogeneous geology, landforms, soils, vegetation, hydrology and land use[31,32]. Within and across ecoregions, pika distributions depend heavily on local habitat characteristics that affect microrefugia, physical characteristics of the broken-rock features on which pikas depend, and vegetation (that is, forage) quality or quantity[23,25,26]. For example, cool and moist microrefugial conditions can be associated with labyrinthine lava flows[23], thick moss or dense vegetation canopy[25], gorges and slot canyons[25], subsurface ice[20,23,33] or other conditions that mediate macroclimatic extremes. The suitability of these microclimates also depends on the nature, topographic position and physical characteristics of talus (broken-rock) patches (that is, size and connectivity of interstitial space, presence of subterranean water and cool-air drainage, plus rock colour, porosity, volume and thickness). These characteristics vary across broad landscapes, as do erosional processes that form or infill talus-slope habitat[34]. Together, these characteristics create different opportunities for behavioural thermoregulation, which pikas achieve by moving between surface and subsurface

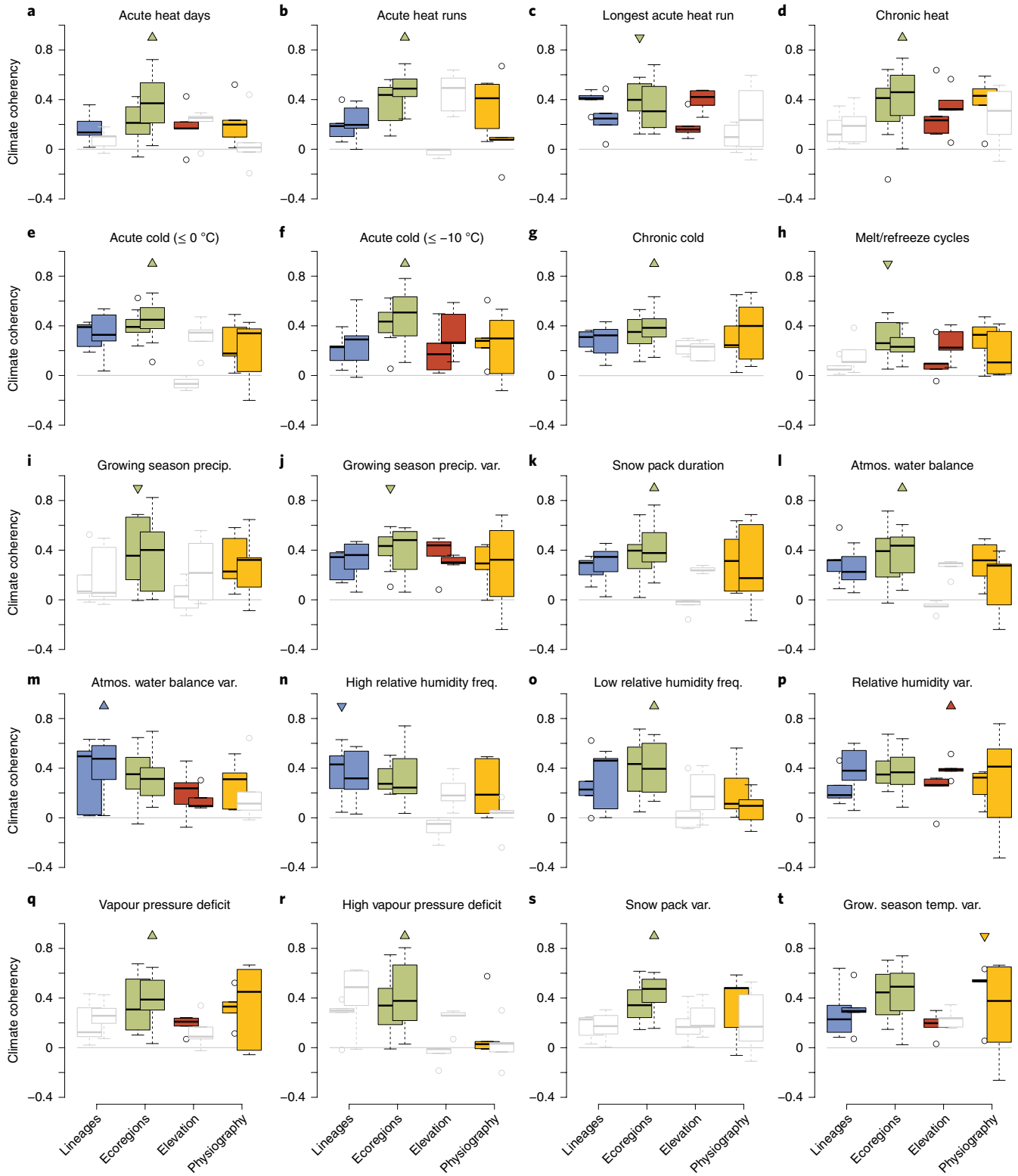

Fig. 3 | Coherency in responses to individual mechanistic climate variables. Each panel pertains to a particular climate variable that indexes one of our hypothesized mechanisms of climatic influence on species occurrence (Supplementary Table 2). The vertical axis represents coherency in response to the given climate variable (among-unit minus within-unit heterogeneity in marginal response curves, across all units in the given subdivision). The potential values of coherency are in the range [−1, 1], with values >0 connoting more coherent responses to the given variable. Each subdivision is represented by two slightly overlapping boxes: coherency using the narrow background (left) or broad background (right). Responses significantly >0 are coloured, and responses non-significantly different from 0 are grey. Triangles indicate which of the significant boxes in a panel represents the greatest mean coherency (down triangles, narrow background; up triangles, broad background). For 12 of 20 variables, ecoregions coupled with a broad background result in the greatest mean coherency. The top and bottom of each box represent the first and third quartiles, respectively, the horizontal line between them the median value, and the whiskers extend to 1.5 times the interquartile range, with values lying outside this range represented as points.

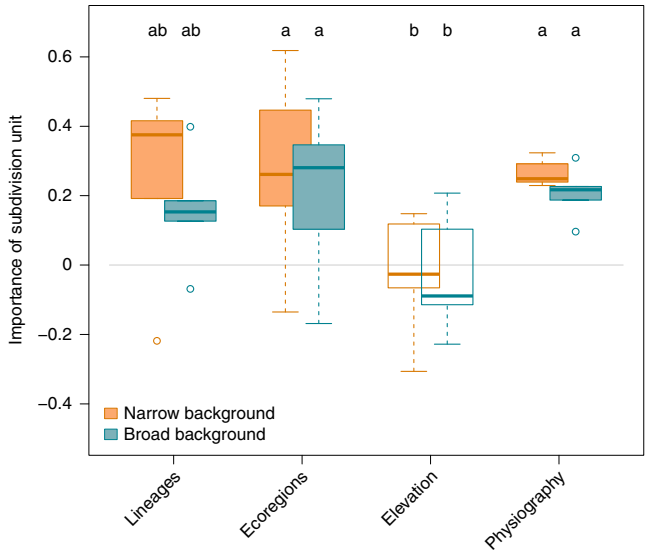

Fig. 4 | Coherency in responses to multivariate aspects of climate across subdivisions and background extents. Boxes represent the performance of a niche model tested against geographically distinct sets of test sites within each unit (within-unit heterogeneity) minus performance of niche models for each unit in a subdivision tested against sites in other units (among-unit heterogeneity). Boxes that have a mean value statistically different from 0 have a solid fill. Significance groups are indicated by letters: combinations of subdivisions and background extent for which climate coherency is statistically indistinguishable have the same letter. The top and bottom of each box represent the first and third quartiles, respectively, the horizontal line between them the median value, and the whiskers extend to 1.5 times the interquartile range, with values lying outside this range represented as points.

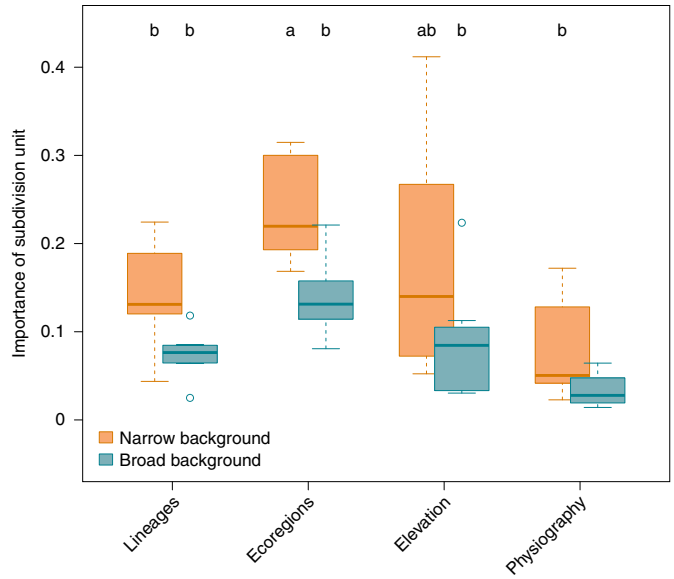

Fig. 5 | Importance of subdivision unit in explaining responses to multivariate aspects of climate. Values on the abscissa are one minus the correlation between predictions of models using data as observed and models using permuted assignment of units to occurrences and background sites within each subdivision. Models allowed (but did not require) responses to climate to vary by unit in each subdivision scheme. Each bar represents the spread of correlations across the units in each subdivision. Higher values indicate that responses to climate depend more on the identity of a subdivision's units. Letters indicate non-significant differences between the cases. For visual clarity, only the significance of the two groups with the highest mean level of importance is shown. Significant differences occurred between other subdivisions but are not shown. The top and bottom of each box represent the first and third quartiles, respectively, the horizontal line between them the median value, and the whiskers extend to 1.5 times the interquartile range, with values lying outside this range represented as points.

microclimates[19]. Additionally, ecoregional differences in vegetation may mediate habitat quality not only by shading[33], but also through diet and winter caching behaviours, which vary regionally[35,36]. Variation in forage species and associated heterogeneity in water content, micronutrients and plant toxin type and concentration could also magnify ecoregional differences in mechanisms of climatic influence on pika populations. Indeed, cover of individual plant species and measures of plant-community characteristics are key predictors of pika occurrence and abundance in multiple regions[23]. Finally, an amalgamation of these factors probably influences pika dispersal distances (for example, via conditions in non-talus matrix habitats), and thus the ability to recolonize talus patches where populations have been extirpated, which differs strongly across ecoregions[26,37]. These factors are likely to have varied in effect across the millennial timescales over which pikas have shifted their ranges in response to glacial cycling[17,21,22]. Such shifts are evidenced by fossil remains of pikas in regions that are now environmentally and geographically remote from contemporary distributions[17].

A spatiotemporal mosaic model of range determination may apply widely and thus be the norm rather than the exception. The 'fingerprint' of cross-temporal processes and their role in determining current distributional boundaries should be evidenced by spatial heterogeneity in responses to environmental drivers. For example, over the past century, ranges of both birds and small mammals in the Sierra Nevada have shifted upslope and downslope heterogeneously within species and across regions[38–40]. Although some of these responses are concordant with predictions based on changes in temperature and precipitation[38–40], others are explained by shifts in habitat[41]. Different aspects of context (subdivision scheme) might become more relevant as climate change accelerates; for example, forage nutrient content may shape responses now, but refugial opportunities may become more important in the future. Thus, climate change may alter the appropriate spatiotemporal mosaic with which responses are best predicted.

Accounting for the mosaic of spatiotemporal factors shaping ranges is critical for understanding responses to past climate change and anticipating responses of species to future change. For example, if ecoregional effects mediate species' responses to climate, how can land managers manage for landscapes that enhance features that favour climate-sensitive species? Depending on the situation, effective management might entail encouraging irrigation to offset drought stress[42], managing for greater forest cover to buffer understory environments from rising temperatures[43] or restricting recreation around climate-buffering landscape features[25]. Similarly, niche theory suggests that species' responses to environmental gradients approximate a bell-shaped curve (akin to a 'Goldilocks effect'[44]). Our results suggest that the position of the optimum value along a climatic gradient can change across ecoregions to such a degree that moving along the gradient can increase the likelihood of occurrence in one region but decrease it in another. In these cases, responses to climate change might be reversed, and appropriate management actions in one area could be contraindicated in another. For example, heavy-snowfall years in high-elevation and high-latitude regions may limit food resources and population connectivity for poorly dispersing resident herbivores, but greater snowfall at lower-elevation areas may reduce drought stress[45]. In this scenario, determining whether the distribution of suitable habitat for individual

populations shifts predictably across years and regions as climate changes poses a pressing challenge, since climate-adaptation management actions should be appropriately tailored to match the spatial extent across which populations respond homogeneously. Finally, although species' responses to contemporary climate change will probably play out over generational timescales, we must also consider how factors that have operated across millennial scales inform appropriate conservation action. For example, over long periods of time, glacial expansion and retreat, shifts in inhabitable climate space, and dynamic hydrogeological features alter habitat connectivity and the probability of founder events that enable colonization of entire regions[46]. In contrast, ecological changes arising from anthropogenic climate change within management-relevant time horizons (that is, within the next 30–100 years) are projected to rival and likely surpass those experienced over the past ~20 millennia[47]. As a result, although management actions operate over 'fast' time cycles compared with glacial–interglacial dynamics, appropriate management action might be just as informed by millennial-scale responses to past climate change.

Similarly to most climate-response studies, ours was conducted in a situation in which the true response of the species to climate is unknown. Behavioural assays[19] and microclimatic data[18] can help us understand the locale-specific responses; however, scaling these results up to regional contexts remains a challenge. Similarly, other aspects of climate for which fine-scale data were not available may differ meaningfully across ecoregions and differentially influence patterns of pika occurrence. Likewise, it is possible that the genetic subdivisions used here may be too coarse to reflect local adaptation[21]. Alternatively, nuclear introgression may occur among units[15,22], 'blurring' lines of local adaptation. Indeed, for all of the subdivisions considered here, common resources, connectivity via dispersal, and gradation of habitat types within and across subdivisions might yield smoother transitions[48] than can be captured by discrete regions (compare Supplementary Table 4). Finally, the temporal and spatial scale of responses to climate are roughly indicated by background extent sampled[28,49], but methodological improvements offer the promise of being able to finely tune estimates of the spatiotemporal scales across the mosaic of processes shaping biogeographic history. Although climate-based factors have accounted for about 75% of the variability in pika occurrence and abundance at some regional and ecoregional scales[18], other species may not display such high degrees of climatic signal. We expect further research to shed light on these issues and our understanding of heterogeneous responses to climate.

Writ large, our results support an increasing effort to account for intraspecific variation in responses to climate[1,8–11,13,29]. At the same time, they challenge the default premise that this variation is best captured by genetic affinity and is thus straightforwardly explained by the balance between local adaptation and niche conservatism across subspecific lineages. Indeed, both niche conservatism and local adaptation can—counter-intuitively—engender patterns of response to climate normally assumed to be indicative of the opposing process[50]. In particular, niche conservatism can interact with changing climatic conditions to split initially homogeneous populations as different subpopulations track aspects of the environment that most closely match the ancestral (and presumably most favourable) aspect of the niche[50], leading to genetic isolation and eventual differentiation. In contrast, plasticity in microhabitat selection and forage requirements can mediate environmental variation across broad regions[33], thus relaxing habitat-level requirements and allowing macroclimatic constraints to remain the same across spatial units. These possibilities draw into question the increasingly common practice of splitting species into subunits on the basis of genetic affinity[8,9,11,13,29], even when they are based on non-neutral markers indicative of selective differences between populations[10]. Our results suggest that geography (that is, ecoregional variation) may be a more relevant template for understanding species' relationships to climate, and that we must consider the interplay between adaptive evolution and landscape variation when predicting responses to climate change.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of code and data availability and associated accession codes are available at https://doi.org/10.1038/s41558-019-0584-8.

Received: 1 October 2018; Accepted: 23 August 2019;
Published online: 23 September 2019

References

1. Smith, A. B., Godsoe, W., Rodríguez-Sánchez, F., Wang, H.-H. & Warren, D. Niche estimation above and below the species level. *Trends Ecol. Evol.* **34**, 260–273 (2019).
2. Walter, J. A. et al. The geography of spatial synchrony. *Ecol. Lett.* **20**, 801–814 (2017).
3. Stephens, R. B., Hocking, D. J., Yamasaki, M. & Rowe, R. J. Synchrony in small mammal community dynamics across a forested landscape. *Ecography* **40**, 1198–1209 (2017).
4. Post, E. & Forchhammer, M. C. Synchronization of animal population dynamics by large-scale climate. *Nature* **420**, 168–171 (2002).
5. Koenig, W. D. Spatial autocorrelation and local disappearances in wintering North American birds. *Ecology* **82**, 2636–2644 (2001).
6. IPCC *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. et al.) (Cambridge Univ. Press, 2013).
7. Koenig, W. D. & Liebhold, A. M. Temporally increasing spatial synchrony of North American temperature and bird populations. *Nat. Clim. Change* **6**, 614 (2016).
8. Hällfors, M. H. et al. Addressing potential local adaptation in species distribution models: implications for conservation under climate change. *Ecol. Appl.* **26**, 1154–1169 (2016).
9. Ikeda, D. H. et al. Genetically informed ecological niche models improve climate change predictions. *Glob. Change Biol.* **23**, 164–176 (2017).
10. Banta, J. A. et al. Climate envelope modelling reveals intraspecific relationships among flowering phenology, niche breadth and potential range size in *Arabidopsis thaliana*. *Ecol. Lett.* **15**, 769–777 (2012).
11. Pearman, P. B., D'Amen, M., Graham, C. H., Thuiller, W. & Zimmermann, N. E. Within-taxon niche structure: niche conservatism, divergence and predicted effects of climate change. *Ecography* **33**, 990–1003 (2010).
12. Maguire, K. C., Shinneman, D. J., Potter, K. M. & Hipkins, V. D. Intraspecific niche models for ponderosa pine (*Pinus ponderosa*) suggest potential variability in population-level response to climate change. *Syst. Biol.* **67**, 965–978 (2018).
13. Prasad, A. M. & Potter, K. M. Macro-scale assessment of demographic and environmental variation within genetically derived evolutionary lineages of eastern hemlock (*Tsuga canadensis*), an imperiled conifer of the eastern United States. *Biodivers. Conserv.* **26**, 2223–2249 (2017).
14. Hotaling, S. et al. Demographic modelling reveals a history of divergence with gene flow for a glacially tied stonefly in a changing post-Pleistocene landscape. *J. Biogeogr.* **45**, 304–317 (2018).
15. Castillo Vardaro, J. A., Epps, C. W., Frable, B. W. & Ray, C. Identification of a contact zone and hybridization for two subspecies of the American pika (*Ochotona princeps*) within a single protected area. *PLoS ONE* **13**, e0199032 (2018).
16. Sexton, J. P., McIntyre, P. J., Angert, A. L. & Rice, K. J. Evolution and ecology of species range limits. *Annu. Rev. Ecol. Evol. Syst.* **40**, 415–436 (2009).
17. Guralnick, R. Differential effects of past climate warming on mountain and flatland species distributions: a multispecies North American mammal assessment. *Glob. Ecol. Biogeogr.* **16**, 14–23 (2007).
18. Beever, E. A., Ray, C., Wilkening, J. L., Brussard, P. F. & Mote, P. W. Contemporary climate change alters the pace and drivers of extinction. *Glob. Change Biol.* **17**, 2054–2070 (2011).
19. MacArthur, R. A. & Wang, L. C. H. Behavioral thermoregulation in the pika, *Ochotona princeps*: a field study using radiotelemetry. *Can. J. Zool.* **52**, 353–358 (1974).
20. Millar, C. I. & Westfall, R. D. Distribution and climatic relationships of the American pika (*Ochotona princeps*) in the Sierra Nevada and western Great Basin, USA: periglacial landforms as refugia in warming climates. *Arct. Antarct. Alp. Res.* **42**, 76–88 (2010).
21. Galbreath, K. E., Hafner, D. J. & Zamudio, K. R. When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, *Ochotona princeps*). *Evolution* **63**, 2848–2863 (2009).

22. Galbreath, K. E., Hafner, D. J., Zamudio, K. R. & Agnew, K. Isolation and introgression in the Intermountain West: contrasting gene genealogies reveal the complex biogeographic history of the American pika (*Ochotona princeps*). *J. Biogeogr.* **37**, 344–362 (2010).
23. Ray, C., Beever, E. A. & Rodhouse, T. J. Distribution of a climate-sensitive species at an interior range margin. *Ecosphere* **7**, e01379 (2016).
24. Merriam, C. H. The geographic distribution of life in North America, with special reference to Mammalia. *Proc. Biol. Soc. Wash.* **7**, 1–64 (1892).
25. Varner, J. & Dearing, M. D. The importance of biologically relevant microclimates in habitat suitability assessments. *PLoS ONE* **9**, e104648 (2014).
26. Schwalm, D. et al. Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. *Glob. Change Biol.* **22**, 1572–1584 (2016).
27. Ryo, M., Yoshimura, C. & Iwasaki, Y. Importance of antecedent environmental conditions in modeling species distributions. *Ecography* **41**, 825–836 (2018).
28. Barve, N. et al. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* **222**, 1810–1819 (2011).
29. Marcer, A., Mendez-Vigo, B., Alonso-Blanco, C. & Pico, F. X. Tackling intraspecific genetic structure in distribution models better reflects species geographical range. *Ecol. Evol.* **6**, 2084–2097 (2016).
30. Raes, N. Partial versus full species distribution models. *Nat. Conserv.* **10**, 127–138 (2012).
31. Omernik, J. M. & Griffith, G. E. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environ. Manag.* **54**, 1249–1266 (2014).
32. *Ecological Regions of North America: Toward a Common Perspective* (Commission for Environmental Cooperation, 1997; map updated 2006).
33. Varner, J., Horns, J. J., Lambert, L. S., Westberg, E., Ruff, J. S., Wolfenberger, K., Beever, E. A. & Dearing, M. D. Plastic pikas: behavioural flexibility in low-elevation pikas (*Ochotona princeps*). *Behav. Process.* **125**, 63–71 (2016).
34. McDonald, K. A. & Brown, J. H. Using montane mammals to model extinctions due to global change. *Conserv. Biol.* **6**, 409–415 (1992).
35. Varner, J. & Dearing, M. D. Dietary plasticity in pikas as a strategy for atypical resource landscapes. *J. Mammal.* **95**, 72–81 (2014).
36. Smith, J. A. & Erb, L. P. Patterns of selective caching behavior of a generalist herbivore, the American pika (*Ochotona princeps*). *Arct. Antarct. Alp. Res.* **45**, 396–403 (2013).
37. Castillo, J. A. et al. Replicated landscape genetic and network analyses reveal wide variation in functional connectivity for American pikas. *Ecol. Appl.* **26**, 1660–1676 (2016).
38. Rowe, K. C. et al. Spatially heterogeneous impact of climate change on small mammals of montane California. *Proc. R. Soc. B* **282**, 20141857 (2015).
39. Moritz, C. et al. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322**, 261–264 (2008).
40. Tingley, M. W., Koo, M. S., Moritz, C., Rush, A. C. & Beissinger, S. R. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Glob. Change Biol.* **18**, 3279–3290 (2012).
41. Santos, M. J., Smith, A. B., Thorne, J. H. & Moritz, C. The relative influence of change in habitat and climate on elevation range limits in small mammals in Yosemite National Park, California, U.S.A. *Clim. Change Responses* **4**, 7 (2017).
42. Morelli, T. L. et al. Anthropogenic refugia ameliorate the severe climate-related decline of a montane mammal along its trailing edge. *Proc. R. Soc. B* **279**, 4279–4286 (2012).
43. De Frenne, P. et al. Microclimate moderates plant responses to macroclimate warming. *Proc. Natl Acad. Sci. USA* **110**, 18561–18565 (2013).
44. Austin, M. P. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol. Model.* **157**, 101–118 (2002).
45. Johnston, A. N. et al. Ecological consequences of anomalies in atmospheric moisture and snowpack. *Ecology* **100**, e02638 (2019).
46. Silva, G. S. C. et al. Transcontinental dispersal, ecological opportunity and origins of an adaptive radiation in the Neotropical catfish genus *Hypostomus* (Siluriformes: Loricariidae). *Mol. Ecol.* **25**, 1511–1529 (2016).
47. Nolan, C. et al. Past and future global transformation of terrestrial ecosystems under climate change. *Science* **361**, 920–923 (2018).
48. Beale, C. M., Brewer, M. J. & Lennon, J. J. A new statistical framework for the quantification of covariate associations with species distributions. *Methods Ecol. Evol.* **5**, 421–432 (2014).
49. VanDerWal, J., Shoo, L. P., Graham, C. & William, S. E. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecol. Model.* **220**, 589–594 (2009).
50. Pyron, R. A., Costa, G. C., Patten, M. A. & Burbrink, F. T. Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. *Biol. Rev.* **90**, 1248–1262 (2015).
51. Breiner, F. T., Guisan, A., Bergamini, A. & Nobis, M. P. Overcoming limitations of modelling rare species by using ensembles of small models. *Methods Ecol. Evol.* **6**, 1210–1218 (2015).
52. Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C. & Guisan, A. Climatic niche shifts are rare among terrestrial plant invaders. *Science* **335**, 1344–1348 (2012).

Acknowledgements

We thank C. Corkran, C. I. Millar, C. Shank, E. Willy, D. Wright, state and provincial Natural Heritage programmes and the Bow Valley Naturalists for contributing data on unequivocal detections of *O. princeps*. We thank M. Forister, J. Walter and C. Jarnevich for critical reviews of drafts of the manuscript. A full list of funding acknowledgements is provided in Supplementary Table 7. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government. The contents, findings and conclusions of this report are solely the responsibility of the authors and do not necessarily represent the views of the US Geological Survey, US Fish and Wildlife Service or US National Park Service.

Author contributions

A.B.S. refined the shared data, revised the list of climatic predictors, performed all of the ecological niche modelling, devised all of the novel improvements to typical modelling norms, produced all tables and figures and cowrote and revised the manuscript. E.A.B. conceived of the idea, coordinated all the authors, contributed the largest number of the retained records, devised an initial list of climatic predictors, cowrote and revised the manuscript and convened the smaller group of analysts. A.E.K. developed the PME model, identified and refined the specific subdivision schemes and their constituent subunits and helped quality-check the pika dataset. A.N.J. helped select specific data sources for predictors, and helped identify mechanisms by which climatic variables may act on *O. princeps*. E.A.B., C.W.E., A.N.J., R.C.K., H.C.L., C.R. and T.J.R. iteratively advised on analytical approaches and research objectives, and edited drafts of the manuscript. C.D. provided (spatially and temporally) high-resolution (PRISM) data on our climatic predictor variables. J.V. and L.E.H. provided comprehensive editing of later drafts. All authors except A.B.S., A.E.K., H.C.L. and C.D. provided data on locations of *O. princeps* detections, provided input to analysis design and reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41558-019-0584-8.

Correspondence and requests for materials should be addressed to E.A.B.

Peer review information *Nature Climate Change* thanks Klaus Hackländer, Masahiro Ryo and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This is a U.S. government work and not under copyright protection in the U.S.; foreign copyright protection may apply 2019

[1]Center for Conservation & Sustainable Development, Missouri Botanical Garden, Saint Louis, MO, USA. [2]Northern Rocky Mountain Science Center, US Geological Survey, Bozeman, MT, USA. [3]Department of Ecology, Montana State University, Bozeman, MT, USA. [4]University of Colorado, Boulder, CO, USA. [5]Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA. [6]Department of Biology and Sam Noble Museum, University of Oklahoma, Norman, OK, USA. [7]Western Ecological Research Center, US Geological Survey, Oakhurst, CA, USA. [8]National Park Service Inventory and Monitoring Program, Bend, OR, USA. [9]Colorado Mesa University, Grand Junction, CO, USA. [10]Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA, USA. [11]Colorado Parks and Wildlife, Montrose, CO, USA. [12]University of Wyoming & Wyoming Game and Fish Department, Laramie, WY, USA. [13]Department of Biology, Northern Michigan University, Marquette, MI, USA. [14]Department of Veterinary Sciences, University of Wyoming, Laramie, WY, USA. [15]Department of Earth Sciences, Montana State University, Bozeman, MT, USA. [16]Wildlife Science Division, Washington Department of Fish & Wildlife, Olympia, WA, USA. [17]Modoc National Forest, US Forest Service, Alturas, CA, USA. [18]Department of Biological Sciences, San José State University, San Jose, CA, USA. [19]Wyoming Cooperative Fish and Wildlife Research Unit, US Geological Survey, Laramie, WY, USA.

[20]Sheldon-Hart Mountain National Wildlife Refuge Complex, US Fish and Wildlife Service, Lakeview, OR, USA. [21]Craighead Institute, Bozeman, MT, USA. [22]California Department of Fish and Wildlife, Rancho Cordova, CA, USA. [23]Department of Chemical, Biological, and Environmental Engineering, Oregon State University, Corvallis, OR, USA. [24]Environmental Studies Program, University of Colorado, Boulder, Boulder, CO, USA. [25]Georgia Department of Natural Resources, Social Circle, GA, USA. [26]Royal Alberta Museum, Edmonton, Alberta, Canada. [27]Biology and Environmental Studies, Warren Wilson College, Swannanoa, NC, USA. [28]Central Washington University, Ellensburg, WA, USA. [29]Denver Zoo, Denver, CO, USA. [30]Division of Biological Sciences, University of Montana, Missoula, MT, USA. [31]College of the Siskiyous, Weed, CA, USA. [32]Forest & Rangeland Ecosystem Science Center, US Geological Survey, Corvallis, OR, USA. [33]Ecological and Environmental Planning Division, New Mexico Department of Game and Fish, Santa Fe, NM, USA. [34]University of Northern British Columbia, Prince George, British Columbia, Canada. [35]Utah Division of Wildlife Resources, Salt Lake City, UT, USA. [36]Unaffiliated: Jim Jacobson. [37]Nevada Department of Wildlife, Elko, NV, USA. [38]Department of Forest Ecosystems & Society, Oregon State University, Corvallis, OR, USA. [39]Montana Natural Heritage Program, Helena, MT, USA. [40]University of New Mexico, Albuquerque, NM, USA. [41]Lassen National Forest, US Forest Service, Susanville, CA, USA. [42]Nevada Natural Heritage Program, Carson City, NV, USA. [43]University of Utah, Salt Lake City, UT, USA. [44]Rocky Mountain Wild, Denver, CO, USA. [45]Oregon Department of Fish and Wildlife, Salem, OR, USA. [46]National Wildlife Federation, Midpines, CA, USA. [47]Modoc National Forest, US Forest Service, Cedarville, CA, USA. [48]Yellowstone Center for Resources, National Park Service, Mammoth Hot Springs, WY, USA. [49]Museums Victoria, Melbourne, Victoria, Australia. [50]Sciences Department, Museums Victoria, Melbourne, Victoria, Australia. [51]Department of Biology, University of British Columbia, Kelowna, British Columbia, Canada. [52]Idaho Department of Fish and Game, Boise, ID, USA. [53]University of California, Santa Cruz, CA, USA. [54]New Mexico Department of Game and Fish, Santa Fe, NM, USA. [55]Idaho Department of Fish and Game, Moscow, ID, USA. [56]Parks Canada, Banff, Alberta, Canada. [57]Adventure Scientists, Bozeman, MT, USA. [58]Department of Biology, University of New Mexico, Albuquerque, NM, USA. [59]US Fish and Wildlife Service, Las Vegas, NV, USA. [60]Bureau of Land Management, Lander, WY, USA. *e-mail: EBeever@usgs.gov

Methods

Our goal was to determine which combination of subdivision and background extent (broad, indicative of long-term range shifts, and narrow, indicative of short-term range dynamics) best captures heterogeneity in pikas' responses to climate. The best subdivision and background set should display the highest coherency, defined here as the difference between heterogeneity (in response to climate) within versus among spatial units (Fig. 2), or equivalently the difference in niche model performance when tested against withheld data in the same unit and model performance when tested against other units. As an example, consider a range subdivided into spatially distinct units. Within a particular unit (for example, the *fenisex* lineage in the northwesternmost part of the range, Fig. 1a and Supplementary Fig. 2), models might show an increasing trend in response to a particular climate variable. In other units, responses might be unimodal in nature, and across others the response might be relatively unchanging (Fig. 2). In this example, there is a relatively high degree of heterogeneity in responses to the same climate gradient across units. If responses of models trained on subsets of the data within each unit are fairly similar (for example, generally always increasing, decreasing or unchanging), then the particular subdivision scheme has a high level of climate coherency and thus serves as a reliable proxy for differences in how the species responds to climate. (Importantly, in each case the response is measured across the range of the climate variable shared across all units—that is, responses are compared only within comparable climate space.) Coherency can also be measured using metrics of niche model performance, which serve as an index of similarity in responses to multivariate aspects of climate. In this case, high coherency is indicated by high performance against withheld test data in the same unit in which the model was trained, coupled with low performance of the same model tested against data from other units (while controlling for confounding effects such as differences in sample size and geographic distance between calibration and evaluation sites).

Species records. We collected records of pika presence from all readily available sources by querying peer-reviewed and grey literature archives, individual researchers, state wildlife agencies (United States; including the Washington Department of Fish and Wildlife's Wildlife Survey Data Management Database version Oct. 15, 2015), natural heritage programs, museums, online databases (BISON, VertNet, iDigBio, GBIF) and citizen-science programs across the species' geographic range (iNaturalist, Adventure Scientists, Bow Valley Naturalists, Front Range Pika Project and Cascades Pika Watch). Contributors reported pikas detected by sight or sound, and the detection of signs uniquely characteristic of pikas including fresh 'haypiles' (food caches that clearly contained chlorophyll to indicate freshness) and faecal pellets (when freshness was unequivocal). Of 38,095 records collected, we retained 14,513 after applying our criteria for data quality and filtering procedures (Supplementary Methods and Results). Of these, 13,338 occurred in the United States and were used in the niche modelling. The remainder occurred in Canada and were included in calculation of PME and for spatiotemporal bias correction.

Environmental data. We calculated 20 variables reflecting demonstrated or hypothesized mechanisms of climate limitation on the distribution of pikas (Supplementary Table 2) that relate directly to exposure to chronic or acute heat, chronic or acute cold, resource availability, and water availability and demand. Some of the variables used thresholds to reflect physiologically limiting conditions conducive to (or inhibitive of) pika presence. For each surveyed presence and background site, environmental variables were summarized for the 10-year window before and including the survey date. We used daily estimates of precipitation and minimum and maximum temperature from the AN81d version of the Parameter Regression of Independent Slopes Model (PRISM[53]), and monthly values of dewpoint temperature and minimum and maximum vapour pressure deficit from the AN81m version of PRISM supplemented with data from other sources for variables not represented by PRISM (Supplementary Table 2). Our primary assumption was that climate is the dominant factor shaping the species' range.

PME. To help delineate background extents and select background sites, we estimated PME, the lowest average elevation expected to be inhabited by pikas in areas across the United States and Canada[54]. PME was estimated from the minimum elevation predicted across an ensemble of models using longitude and latitude as predictors. The response was the mean elevation of the lowest fifth percentile of elevations at occupied sites in a set of 70-km-diameter circular regions selected such that each had an adequate number of occurrences. Areas covered by permanent snow and ice were removed.

Subdivisions. We assessed the ability of four different subdivision schemes (phylogenetic, ecoregional, elevational and physiographic) to capture region-specific responses to climate (Fig. 1a–d). Phylogenetic regions were defined following Galbreath et al.[21,22] and Hafner and Smith[55], who delineated five geographically allopatric subspecies (Fig. 1a) on the basis of nuclear DNA, mitochondrial DNA, allozymes and skull measurements. We added a 47.7 km buffer to the five polygons defined in the shapefile to also include 95% of the 466 presence records in our dataset (3.2% of the total) that fell outside the original polygons. Ecoregions were adopted from the EPA Level III ecoregionalizations[32,56,57] with a modification by Sarr et al.[58] (Fig. 1b). Elevational divisions were defined relative to PME (Fig. 1c). After subtracting PME from the observed elevation at each presence site, we classified the differences into five quintiles (for example, the highest band encompassed the ~20% of records that were highest relative to their locally defined PME). Physiographic regions (Fig. 1d) were adapted from the 'provinces' and 'divisions' of Fenneman and Johnson[59]. Fenneman delineated physiographic regions by geological origin of the base material and the type and stage along primary erosional processes.

Background sites. We used narrow and broad definitions of the background environment available to pikas to explore the effects of spatial extent and, indirectly, the temporal time frame of habitat selection. The narrow background encompassed areas that could be colonized by dispersing pikas over ~1–2 generations and thus indicates habitat selection occurring across short time frames. To define the narrow background for a given focal unit (for example, a specific lineage within the genetic subdivision), we intersected areas above PME with each unit (for example, the intersection of any given polygon in any of Fig. 1a–d with the area above PME shown in Fig. 1e) then added a 3 km buffer to expand the region to areas that could be at least 'sampled' through dispersal. Areas covered by permanent snow and ice were removed after applying the buffer. For all units combined, the narrow background mask was defined by intersecting the areas above PME (plus the 3 km buffer with areas of ice and snow removed) with the entire set of polygons with recorded presences of pikas for the given division scheme (that is, the intersection of all polygons in any of Fig. 1a–d with the area above PME in Fig. 1e). The broad background was defined by using the entire unit polygon (or all unit polygons combined if the entire range was being considered). Narrowly defined and broadly defined background sites were drawn from the area delineated by the respective masks.

We selected background sites in such a manner as to negate non-random sampling effort and create an unbiased estimate of environmental suitability[60]. Specifically, increasing the ratio of background-to-presence sites within a region of environmental space that has been overly sampled can reduce or eliminate bias due to overrepresentation of that environmental space[61]. This ratio can be altered by either (a) thinning presence records to have some minimum pairwise distance[62], or (b) increasing the number of background sites with environmental values similar to the presence records[60]. We chose the second option, because thinning can markedly reduce sample size and requires decisions about minimum allowable pairwise distance[62,63]. To correct for spatiotemporal sampling bias within a given focal unit and background extent (broad or narrow), we trained an annual kernel density estimator on all presences collected in each year. The kernel density estimator model was then projected back to the given broad or narrow background mask for the focal unit within a given subdivision (Supplementary Fig. 3). For each presence record in a given year, we selected background sites with the per-cell probability of placement proportional to the estimate of the kernel density estimator. For the purposes of calculating associated climate variables, background sites were assigned the same date as the presence sites to which they were matched. The total number of background sites selected within a year was proportional to the number of presence sites in that year, scaled so that the total number of background sites sampled across all years for a given subdivision and background extent was ~10,000.

Overview of modelling and statistical analysis. We employed correlative ecological niche models (sometimes also called species distribution models) to compare patterns of occurrence within shared and unshared environmental space. For each combination of subdivision and background extent, we modelled the species' niche across the entire range and across units and subunits in a spatially nested design (Supplementary Fig. 4). Specifically, for a given unit within subdivision s and background b, we split the presence records into eight geographically distinct subunits to increase the independence between training and test data sets to ensure a more robust estimate of model performance[62] and predictor importance[52,64]. Background sites were assigned to the subunit of the geographically closest presence record. 'Subunit' models were trained on data from seven subunits, then tested on the withheld data, then repeated for a total of eight models trained per subunit. We also trained 'unit' models on all presences within a unit. Finally, we trained a 'composite' model on all data from across the entire range. Our modelling design creates a nested hierarchy of models for each subdivision scheme: subunit models are trained on a subset of the data used in unit models, which in turn are trained on a subset of the data used in a range-wide composite model. We used the contrast between the subunit models of a unit and the unit model as a measure of within-unit heterogeneity or model performance. We used the contrast between the unit models and the composite models as our measure of among-unit heterogeneity or model performance.

Coherency in responses to individual climate variables. To explore responses to individual climate variables (Supplementary Table 2), we employed least-angle generalized linear regression[65] with the degree of regularization (L_1 'lasso' versus L_2 'ridge') penalty tuned using an elastic net[66]. Least-angle generalized linear

regression has several key advantages over traditional, non-regularized techniques, including robustness to collinearity between variables and the tendency to result in 'sparse' models in which only key variables have coefficients that are different from 0 (ref. [65]). Separate models were trained on occurrences from (1) each of the eight subunits in each unit, (2) the entire unit and (3) across the entire US range.

We compared within- versus among-unit heterogeneity in the species' response to each of 20 climate variables while controlling for the effects of the other variables (Supplementary Fig. 5). For a given variable, unit, subdivision and background, the observed within-unit heterogeneity was calculated as the average difference between the response curve predicted by the unit model and each of the k subunit models. We used the marginal prediction for each variable to capture the response to the focal variable independent of other variables, except in cases where there were interactions with the focal variable, in which case the appropriate interaction terms were included. We limited the comparison to the environmental gradient encompassed by 2.5th and 97.5th quantiles taken across all presence sites for the focal unit or subunit. Along this range we selected $N=100$ values, indexed by n, of the focal variable at which we predicted the suitability of the k subunit models (p_{ukn}), the unit model (p_{un}) and the composite models (p_n). We calculated within-unit heterogeneity for a given unit u as

$$w_u = \frac{1}{8N} R^{(u)} \sum_{k}^{8} \sum_{n}^{N} (p_{un} - p_{ukn})^2 \quad (1)$$

$R^{(u)}$ is a scaling factor to reflect the fact that pikas did not respond equally to all climate variables, and is defined as the difference between the maximum and minimum predicted values across all selected presence sites by the unit model ($R^{(u)}$ thus has a range of [0, 1]; Supplementary Fig. 5). Including a scaling factor allows comparison of the values of w across units, subdivisions and climate variables, because the overall level of within- versus among-unit heterogeneity in response to a variable is scaled by the absolute difference in suitability to the focal variable. Consequently, w_u represents the scaled mean squared deviation of the difference between the response curves predicted for the entire unit and subsets of the unit (Supplementary Fig. 5), so higher values correspond to greater within-unit heterogeneity.

We calculated among-unit heterogeneity a_u for a given unit in a similar manner:

$$a_u = \frac{1}{N} R^{(C)} \sum_{n}^{N} (p_{un} - p_n)^2 \quad (2)$$

where $R^{(C)}$ is the difference between the maximum and minimum predicted values across the selected presence sites from the composite model ($R^{(C)}$ thus has a range of [0, 1]). Consequently, a_u represents the scaled mean squared deviation of the difference between responses of a unit and the entire species (Supplementary Fig. 5), so higher values correspond to greater among-unit heterogeneity. Since p_n, p_{un}, p_{ukn}, $R^{(u)}$ and $R^{(C)}$ all have the range [0, 1], the ranges of w_u and a_u are also [0, 1]. Our measure of climate coherency for a given unit in a subdivision scheme was the difference between among- and within-unit heterogeneity in response for that unit ($a_u - w_u$). We used Monte Carlo permutation tests to assess whether the mean coherency within a combination of subdivision and background was >0 (Fig. 3 and Supplementary Table 6).

Coherency in response to multiple climate variables. We also examined the relationship between pika occurrence and climate in 'multivariate' climatic space. To control for collinearity, we first constructed a common principal component model of the derived climate variables for 10,000 randomly selected sites. The first six axes collectively represented >87.5% of the total variation in the derived climate variables, and were used in the subsequent analyses (see factor loadings in Supplementary Table 2). We then applied the principal component rotations to each set of presence and background records used in the subsequent analyses. For each subunit, unit and set of all units in a subdivision we trained five types of correlative ecological niche model (generalized additive models, generalized linear models, Maxent, boosted regression trees and random forests). We then used the mean ensemble prediction for further analyses[67].

We evaluated the model performance using the continuous Boyce index (CBI[68,69]). The CBI represents the correlation between the model predictions and the true probability of presence. It has a range of [−1, 1], with values >0 indicating more accurate models, values ~0 indicating models performing similarly to random expectation and values <0 indicating performance worse than random. Compared with other metrics of performance, CBI is a sensitive metric of model performance[51,52]. Also, unlike the area under the receiver operator curve, it does not have an unknown upper limit when calculated with background sites in place of true absences[70].

We calculated coherency in response to climate as the difference between performance (CBI) of subunit models tested against withheld test presences from the same unit and against presences and background sites in each of the other units for a given subdivision and background. This difference should be ~0 if responses to multivariate climate are similar within and between units, but >0 if there is more heterogeneity among units than within units. We initially attempted to statistically control for potentially confounding factors (for example, distance between test and training sites, number of test and training sites), but the overall explanatory power of these covariates was very low ($R^2 < 0.05$), so we did not correct for these factors. We assessed whether the observed coherency was >0 using Monte Carlo permutation tests that accounted for the non-independence between models for each cross-validation fold of a unit arising from overlapping presence and background data across subunits (Fig. 4).

Variation in responses to climate among units in subdivisions. To corroborate the previous analysis we conducted a second multivariate analysis. This analysis also assessed variation in responses to climate across units in each subdivision. We used the same principal component axes as in the previous analysis to establish a common climate space across all combinations of schemes and extents. Again, ecological niche models were trained using the first six axes of this principal component analysis as predictors, except that in this analysis the unit of the respective scheme was included as a seventh (categorical) covariate, which allowed climate responses to vary across units. As before, we used the ensemble (mean) prediction across five algorithms (Supplementary Methods and Results). For this analysis, we only trained composite k-fold models (that is, models using all data across the entire range except for a portion that was withheld for testing; the withheld portions were geographically distinct from the training data and comprised records from all units in the scheme).

The subdivision and background extent that best captured spatial heterogeneity in responses to climate should have the greatest sensitivity to unit in the model. To measure sensitivity, we applied a permutation test for each combination of subdivision and background. Specifically, we randomly swapped the value of the unit variable across the test data for a given subdivision and background, then calculated the correlation between (a) the predictions at the withheld test sites with data as observed and (b) predictions at the same sites using the permuted data[71]. If unit is an influential predictor, the correlation will be low because the predictions will be different between permuted and as-observed data. In particular, the correlation should be lowest for the subdivision and background extent in which unit best captures differences in responses to climate. We repeated the permutations and calculation of the correlation 1,000 times for each combination of subdivision, background and unit. To visualize the difference, we subtracted the mean of the correlation coefficients from 1, so that higher values connote greater unit importance (Fig. 5). We then applied permutation tests on the correlation coefficients to assess the statistical significance of differences between cases.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The raw PRISM weather variables that support the findings of this study are available from the PRISM Climate Group, but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. These data are available from the authors on reasonable request and with permission of author C. Daly.

Code availability

The computer code (https://github.com/adamlilith/pika_climateCoherency) and some occurrence datasets analysed during the current study (https://doi.org/10.5066/P9LV1XCF) are available online.

References

53. Daly, C., Gibson, W. P., Taylor, G. H., Johnson, G. L. & Pasteris, P. A knowledge-based approach to the statistical mapping of climate. *Clim. Res.* **22**, 99–113 (2002).
54. Hafner, D. J. North American pika (*Ochotona princeps*) as a late Quaternary biogeographic indicator species. *Quat. Res.* **39**, 373–380 (1993).
55. Hafner, D. J. & Smith, A. T. Revision of the subspecies of the American pika, *Ochotona princeps* (Lagomorpha: Ochotonidae). *J. Mammal.* **91**, 401–417 (2010).
56. Omernik, J. M. Ecoregions of the conterminous United States. Map (scale 1:7,500,000). *Ann. Assoc. Am. Geogr.* **77**, 118–125 (1987).
57. Omernik, J. M. in *Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making* (eds Davis, W. S. & Simon, T. P.) 49–62 (Lewis, 1995).
58. Sarr, D. A., Duff, A., Dinger, E. C., Shafer, S. L., Wing, M., Seavy, N. E. & Alexander, J. D. Comparing ecoregional classifications for natural areas management in the Klamath Region, USA. *Nat. Areas J.* **35**, 360–377 (2015).
59. Fenneman, N. M. & Johnson, D. W. *Physical Divisions of the United States* (US Geological Survey, 1946).
60. Phillips, S. J. et al. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* **19**, 181–197 (2009).
61. Merow, C., Smith, M. J. & Silander, J. A. Jr. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* **36**, 1058–1058 (2013).

62. Boria, R. A., Olson, L. E., Goodman, S. M. & Anderson, R. P. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol. Model.* **275**, 73–77 (2014).
63. Fourcade, Y., Engler, J. O., Rödder, D. & Secondi, J. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. *PLoS ONE* **9**, e97122 (2014).
64. Fourcade, Y., Besnard, A. G. & Secondi, J. Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Glob. Ecol. Biogeogr.* **27**, 245–256 (2018).
65. Efron, B., Hastie, T., Johnstone, I. & Tibshirani, R. Least angle regression. *Ann. Stat.* **32**, 407–499 (2004).
66. Zou, H. & Hastie, T. Regularization and variable selection via the elastic net. *J. R. Stat. Soc. B* **67**, 301–320 (2005).
67. Araujo, M. B. & New, M. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**, 42–47 (2007).
68. Boyce, M. S., Vernier, P. R., Nielsen, S. E. & Schmiegelow, F. K. A. Evaluating resource selection functions. *Ecol. Model.* **157**, 281–300 (2002).
69. Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Model.* **199**, 142–152 (2006).
70. Smith, A. B. On evaluating species distribution models with random background sites in place of absences when test presences disproportionately sample suitable habitat. *Divers. Distrib.* **19**, 867–872 (2013).
71. Breiman, L. Random forests. *Mach. Learn.* **45**, 5–32 (2001).

nature research

Corresponding author(s): Erik A. Beever

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see Authors & Referees and the Editorial Policy Checklist.

Statistical parameters

When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistics including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated
☐	☒	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	N/A
Data analysis	We performed the analysis in Microsoft R Open Version 3.3.3 2017-03-06 using packages compiled as of 2017-05-15 (obtained with the checkpoint library; Microsoft 2016). Analyses relied primarily on the dismo (Hijmans et al. 2017), raster (Hijmans 2016), geosphere (Hijmans 2016), rgeos (Bivand & Rundel 2017), and enmSdm (Smith 2017) packages. All package dependencies are listed in the code and either available on the CRAN repository or GitHub (https://github.com/adamlilith).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The computer code and occurrence datasets analyzed during the current study are available in the Dryad repository, https://datadryad.org [to be deposited upon acceptance of the manuscript or upon request of the editors or reviewers]. The raw PRISM weather variables that support the findings of this study are available from the PRISM climate group but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. These data are available from the authors upon reasonable request and with permission of author C. Daly.

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We examined within-versus-among group responses of subdivisions of the American pika (Ochotona princeps) to mechanistic weather variables using three tests. The first examines responses to each of 20 variables while controlling for the effects of others using least-angle regression (LARS) regularized using an elastic net. Within/among differences were assessed using a null-model randomization procedure comparing the difference between each subgroup's response across the shared range of the focal variable to the group response by swapping the labels on response curves (subgroup or group). The second test compared within/among group differences in response to all climate variables simultaneously (after rotation using principal component analysis). The difference in the performance of an ensemble niche model of subgroups and groups was assessed using null model analysis that swapped measured values among groups being compared. The third test estimated the relative importance of using the "group" label as a factor in an ensemble of niche models. We used a permutation test to swap the subgroup labels and compared the predictions from this scrambled set with predictions of the models using all data as observed. We then applied a null model test which swapped the panel of interest (background extent or group labels).
Research sample	The primary data analyzed in this study comprised 14,513 presence records of the North American pika (Ochotona princeps) collected across its known range between 1990 and 2015. We also used daily- and monthly-scale interpolations of raw weather/ climate variables (min/max/mean temperature, precipitation, min/max relative humidity, and dew point temperature) from the PRISM climate data set for the coterminous United States.
Sampling strategy	We collected records of pika presence from all readily available sources by querying peer-reviewed and grey literature archives, individual researchers, state wildlife agencies (USA; including the Washington Department of Fish and Wildlife's Wildlife Survey Data Management Database version Oct. 15, 2015), natural heritage programs, museums, and several on-line databases (BISON, VertNet, iDigBio, GBIF). We also collected records from citizen-science programs across the species' geographic range (iNaturalist, Adventurers and Scientists in Conservation, Bow Valley Naturalists, Front Range Pika Project, and Cascades Pika Watch).
Data collection	All contributors were asked to supply, at a minimum, data fields indicating detection or non-detection of pikas, longitude and latitude, method used for geolocation and associated error, coordinate reference system, elevation, date of observation, plus pertinent notes on the survey process and site-level observations. As evidence of presence, contributors reported pikas detected by sight or sound, and the detection of signs uniquely characteristic of pikas including fresh "haypiles" (food caches that clearly contained chlorophyll to indicate freshness) and fecal pellets (when freshness was unequivocal).
Timing and spatial scale	Occurrence records were obtained from across the specie's range across the time period extending from 1990 to 2015. PRISM weather data was from 1981-2015.
Data exclusions	We excluded occurrences that were recorded before 1990 because we could not match them with weather data from a 10-yr window prior to their recording (daily PRISM data is available only starting in 1981). For climate-related analyses we removed all records in Canada since they are not covered by the PRISM GIS layers, although these records were used for calculation of sample intensity and pika minimum elevation. We removed all occurrences that could not be confidently located to <200 m of the stated coordinates.
Reproducibility	The computer code was written in Microsoft Open R with a checkpoint date of 2017-05-15. Using our code and data anyone should be able use the same packages versions to recreate the results.
Randomization	We divided pika occurrences using four subdivisions each of which comprised several subunits. These subdivisions were obtained from the literature on pika biology, ecoregions, physiography, or generated by dividing occurrences into elevational bands. To increase independence between model training and test sets we further divided occurrences into eight geographically distinct,

mutually exclusive groups. Membership in a group was assigned based on its spatial proximity to eight centroids located using partitioning around mediods (PAM), a deterministic and reproducible method for clustering when the number of groups is per-ordained. To control for potentially confounding variables we employed 1) comparisons of units only across shared environmental space; and 2) null model randomization within hierarchical structures to ensure comparable unit labels were swapped along with respective subunit labels. For the multivariate analysis in which we tested for differences in niche model performance within/among groups we attempted a post hoc correction using beta regression with niche model performance as a response and potentially confounding covariates as predictors including geographic and temporal distance between training and test sites, training and test sample size, and all two-way interactions of these variables. The best model explained just <5% of the variation so we elected not to correct for the factors in the final analysis.

Blinding	The occurrence data was collected over the course of 25 yr by >80 collaborators and partners. As a result of their experience in the field some of the collaborators may have suspected the existence of spatially-varying controls on pika persistence, but almost no field studies were conducted with the intent of identifying these factors. Those that were comprise a small set of occurrences and were spatially stratified across geographic domains.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Collections occurred any time of the year but were primarily guided by accessibility (e.g., lack of dangerous conditions, passable snow cover). Pikas are active and apparent throughout the year, so the timing of collection will not bias detection.
Location	Sampling occurred throughout western North America (from 35.7 to 54.1 degrees latitude and from -104.9 to -126.9 degrees longitude).
Access and import/export	No new data was collected for the current analysis; the constituent analyses complied with all relevant state, tribal, and national laws.
Disturbance	The original field collections mainly comprised sightings of pikas at sites accessed by trails or otherwise on foot. We supplemented these records from data obtained from publicly accessible online databases (GBIF, iDigBio, BISON) which may or may not comprise physical specimen data (typically skins, skeletons, or other physical remains). These data were originally collected under protocols and procedures specified by the original data providers.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging