

CLIMATE CHANGE ECOLOGY

Ecoregion shapes the range response

Within a single species, different populations can show strikingly varied responses to climate – often attributed to genetic differences of geographically separated populations. Now an elegant analysis, weaving together modelling with large-scale empirical data, demonstrates that ecoregion explains spatial variation in climate responses of the American pika.

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As the challenge of predicting, managing and mitigating biogeographic responses of species to climate change intensifies, tackling both the inter- and intraspecific heterogeneity in distributional relationships to climate becomes crucial¹. Variation in the direction and magnitude of range shifts of species in response to changing climatic conditions has been well documented². Underlying this complexity in range shifts is the potential for the relationship and relative importance of climate as a determinant of a species distribution to change across space and time³. Within-species variation in climatic responses has been often attributed to differences in genetic lineages across the distribution of a species⁴. However, populations can also respond to climate in similar ways, exhibiting spatial synchrony or correlated fluctuations across disjunct populations⁵. Writing in *Nature Climate Change*, Adam Smith, Erik Beever and colleagues look beyond the potential for local adaptation to shape species–climate relationships and explore spatial divisions within species distributions (genetic structure, ecoregion, elevational bands and physiography) that may best explain intraspecific heterogeneity in such relationships⁶. Surprisingly, the authors found that the distributional division of ecoregion, not genetic lineages, explained the most spatial heterogeneity in species–climate relationships for the American pika (*Ochotona princeps*).

Ecoregion may act as a modifier for how species experience broad-scale climate conditions. An ecoregion is an area with relatively homogeneous geology, vegetation, hydrology and land use⁷. For animals, ecoregions can represent the types and timing of food availability, an ability to disperse, and frequency of microclimatic conditions, all of which may shape their responses to macroclimate. For plants, ecoregions may lead to very different patterns of seasonal water availability⁸



Fig. 1 | An American pika (*Ochotona princeps*) on its haypile under a large boulder. Credit: Ken Hickman

and exposure to temperature extremes⁹. In this vein, Smith et al. highlight the need to incorporate more biological relevance into the choices made in species distributional modelling.

The American pika is a cold-adapted lagomorph found at high elevations. The species has known physiological links to multiple climate variables, and its survival is highly dependent on local availability of microrefugial topographic and vegetation features of its talus (broken rock) habitat (Fig. 1)¹⁰. This dependence on cool, moist microsites may be in part why ecoregion was found to be the most important driver of spatial heterogeneity for this species–climate relationship. It remains to be seen whether pikas are the exception or the rule for the greater importance of ecoregion relative to

genetic lineages for shaping how species respond to climate.

Identifying the most relevant spatiotemporal division for a species distribution can be difficult. Smith et al. establish an important framework for directly comparing different divisions, including two statistically robust techniques that may be applicable in many other study systems. First, this work introduces and uses a ‘coherency’ metric to test the strength of different divisions for explaining intraspecific variation in species–climate relationships. The climate coherency metric compares within-division heterogeneity to among-division heterogeneity. The division that best explains the underlying heterogeneity in climate relationships is identified as the one with the maximum

climate coherency (where heterogeneity is lowest within units of a division and highest among units of a division). This metric is especially useful as it allows tests of coherency when considering single climate variables as well as combinations of multiple climate variables, which are known to be important for explaining species–climate relationships and climate change responses¹¹.

Second, the coherency component of the work was supplemented by looking at the spatial variation in the relationships at multiple timescales. The authors distinguished between short-term and long-term range dynamics by varying the sites used for species distribution modelling. Short-term dynamics (habitat selection and metapopulation dynamics) were represented by the use of areas currently available to pikas, long-term dynamics (range shifts) by areas available to pikas since the last glaciation. Owing to behavioural and demographic lags driving disequilibrium between a species distribution and current climate^{12,13}, short-term dynamics may cloud long-term species–climate relationships. This distinction is therefore a critical step in disentangling how temporal dynamics may shape the coherency of distributional divisions. Further, the argument for the

importance of ecoregion was strengthened by ecoregion being a consistent predictor of the underlying heterogeneity of the response to climate at both timescales.

The findings of Smith et al.⁶ have important implications for site-specific management and restoration needs for species of concern. Specifically, a management approach that is successful in one area may be irrelevant, or even disastrous, in another. Additionally, the results of this study introduce ecoregion-specific responses to climate as another complicating factor that needs to be considered when examining why shifts are seen in some parts of a species range and not others. In both of these cases, future research needs to identify the mechanisms driving ecoregion differences and how those mechanisms vary for different species. For example, the availability of talus may have a positive impact on the pika's ability to move uphill with a changing climate, but, in contrast, talus being the dominant substrate has been shown to limit the ability of some low-elevation plants to invade the alpine¹⁴. This work⁶ will encourage others to test explicitly for ecoregion effects in their focal systems as well as to further explore the potential mechanism(s) of ecoregion. The extent to which ecoregions can be

used to predict the heterogeneity of species climate relationships generally — from pika to plants to plankton — remains to be seen. □

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