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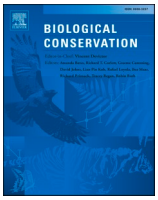

Geographic and taxonomic variation in adaptive capacity among mountain-dwelling small mammals: Implications for conservation status and actions

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ABSTRACT

Contemporary climate change is modifying the distribution, morphology, phenology, physiology, evolution, and interspecific interactions of species. Effects of climate change are mediated not only through the magnitude of change experienced (exposure) and an animal's sensitivity to such changes, but also through the ability of the population or species to adjust to climatic variability and change genetically, behaviorally, or spatially (via its distribution) (i.e., adaptive capacity; AC). Here, we used an attribute-based framework to systematically evaluate and compare the AC of American pikas (*Ochotona princeps*) against four other mountain-dwelling small mammals of North America to determine whether pikas are disproportionately vulnerable to climate change, as has been postulated. Unlike previous analyses, we also compared AC across *O. princeps* lineages and across three taxonomic (and thus, spatial) scales. Our results indicate that pikas have markedly lower adaptive capacity than all compared species except bushy-tailed woodrats (*Neotoma cinerea*), and that our assessments of species generally align with earlier characterizations of climate-change vulnerability based on life-history characteristics. Although AC did not differ dramatically among pika lineages, some attributes are likely constraining AC differently in various parts of the geographic range. Comparisons across taxonomic levels of pikas illustrated that, although AC levels were comparable in pika lineages versus range-wide, AC was assessed as lower in interior-Great-Basin pikas than across the entire *O.p. schisticeps* lineage. We conclude that the comparatively lower AC of pikas results in particularly high susceptibility to anthropogenic climate change, corroborating results from numerous other recent investigations of pikas' climate-responsiveness. Adaptive-capacity evaluations appear useful as a consistent way to identify sentinel species or populations and for conservation prioritization.

1. Introduction

Contemporary climate change is one of the most profound challenges to the conservation and management of biodiversity and ecosystem function, globally. The challenge stems partly from the ubiquity and scope of its effects, the increase in its pace, interactions between climate change and other anthropogenic stressors, and the risk that species' intrinsic adaptive capacity may not accommodate such a rapid pace of change (Quintero and Wiens, 2013; Staudinger et al., 2013; Nolan et al., 2018; Thurman et al., 2020). Observed species- and population-level responses have included altered abundances, distributions, physiologies, morphologies, phenologies, evolutionary responses, and interspecific interactions (e.g., Beever et al., 2013; Rumpf et al., 2019; Stewart et al., 2020; Hamann et al., 2021).

Characterization of species responses to climate change often is conducted via climate-change vulnerability assessments, typically performed at range-wide or region-wide extents. Assessments of vulnerability to climate change are classified as correlative, mechanistic, and trait-based (Pacifici et al., 2015; Foden et al., 2019), depending on the approach and type of data and analyses used (e.g., qualitative or expert-based vs. quantitative). Correlative models can be applied across a wide range of taxa at various spatial scales and are often quick and inexpensive to apply; however, they are less useful in assessments of data-poor (understudied) species and their accuracy can be strongly context-dependent. Mechanistic models, although capable of important insights into underlying eco-evolutionary processes, can be challenging to parameterize accurately over large spatial extents with marked climatic variability (however, see effective parameterizations of Kearney and Porter, 2009, Mathewson et al., 2017). Trait-based approaches allow for rapid assessments of multiple species, and are less data-

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intensive to implement than mechanistic approaches. They are useful for ranking, categorizing, and identifying thresholds based on the suite of characteristics used in the assessment, and can use information derived from both correlative and mechanistic assessments. However, the exact vulnerability thresholds of selected traits and their relative influence may not be known without a mechanistic understanding of species-climate relationships (MacLean and Beissinger, 2017).

Climate-change vulnerability assessments often partition vulnerability into three main components: exposure, sensitivity, and adaptive capacity (AC) (e.g., Dawson et al., 2011; Foden et al., 2019; Thurman et al., 2020). Briefly, **exposure** encompasses the rate and magnitude of change in climatic aspects that a species or population will (or has) experience(d); **sensitivity** refers to how tightly coupled the species' fitness is to such change and is often characterized as the "dose-response" relationship between species and exposure factors; and **AC** represents the ability of the species (or population, subspecies, etc.) to cope with or adjust to such change through genetic, behavioral, or distributional changes (Dawson et al., 2011). Exposure and sensitivity combine to define the potential impact of climate change on a given taxon, whereas AC mediates the translation of that potential impact into actual vulnerability. Although AC is sometimes ignored or assumed to be the inverse of sensitivity, it represents both a research frontier and a powerful pathway for better management and conservation action because AC encompasses many characteristics that can be affected (directly or indirectly) by climate-adaptation actions and management (Beever et al., 2016a; Thurman et al., 2020, 2022; LeDee et al., 2021).

Ecologists have long recognized that numerous phenomena and processes (such as habitat use or competition) depend on the spatial scale in question (e.g., Wiens, 1989). Despite this scale-dependence, many investigations of species-climate relationships and vulnerability make a simplifying but unsupported assumption that those relationships take the same functional form and are governed by the same factor(s) across the species' entire geographic range. However, ecologists are increasingly recognizing that species-climate relationships and species' response to climate change may not occur homogeneously across a species' range, nor across different spatial and temporal scales (e.g., Rapacciuolo et al., 2014). Such context-dependence suggests that predictions of species-climate relationships and species' responses may vary across genetic clades (e.g., Ikeda et al., 2017), geophysical and other environmental factors (Smith et al., 2019), or be tailored to relevant management units (e.g., Jeffress et al., 2013). Given that conservation interventions often are implemented at local scales, identification of particular vulnerabilities, mechanisms of climatic stress, and therefore selection of conservation actions ideally should be informed at local scales, rather than range-wide (e.g., Smith et al., 2019; Fig. S1).

To address some of these context-dependencies and gain insights into the mechanisms and pathways by which contemporary climate change can affect animals, we sought to characterize the AC of a species with well understood life-history information and whose geographic distribution is relatively broad despite the species having a narrow ecological niche. Our primary goal was to characterize AC of the focal species relative to several sympatric species. We also sought to investigate intraspecific variation in AC of the focal species at two taxonomically finer scales: among geographically distinct lineages, and within a lineage that spans environmentally distinct areas. The American pika (*Ochotona princeps* Richardson; hereafter, "pika") fits these criteria, given the rich history of research on this species and that its distribution spans nearly one-third of a continent and diverse macro-climates yet is typically restricted to patchily distributed, broken-rock habitat (e.g., talus, lava flows, rock quarries). Furthermore, several behavioral and life-history traits of this species (e.g., philopatry, diurnal/crepuscular activity, detectability often >0.90, close relationship to easily mapped habitat) make investigations more tractable and conclusions more robust than those of other mountain-dwelling mammals.

Furthermore, pikas have been used as a model organism to exemplify and explore several areas of ecological theory, including metapopulation and extinction dynamics, island biogeography theory, and stepping-stone and source-sink dynamics (e.g., McDonald and Brown, 1992; Hanski, 1998; Kreuzer and Huntly, 2003). Fundamentally relevant to this study, the persistence of populations, dispersal, occupancy, abundance, diet, indices of physiological stress, and fitness of *O. princeps* are known to be correlated with climate, across much of the species' range, in both paleoecological and contemporary time periods (e.g., Hafner, 1994, Grayson, 2005, Billman et al., 2021; also see Supplemental Information). Whereas the majority of studies on *O. princeps* agree about the species' conservation status and climatic vulnerability (e.g., see citations in adaptive-capacity assessments of pikas in Supplemental Information), some investigations suggest that pikas' behavioral plasticity and characteristics of atypical environments may minimize their range-wide vulnerability to climate-change impacts (e.g., Millar et al., 2018; Smith, 2020). This discrepancy underscores the need for a systematic review of the evidence and life-history pathways by which pikas – and other mountain-dwelling species – are influenced by climate change.

Here, we perform comprehensive assessments of adaptive capacity, following methods of Thurman et al. (2020), for pikas at three spatial scales – range-wide, by genetic lineage, and within the interior hydrographic Great Basin where the most-pronounced climate-driven declines have been documented (e.g., Wilkening et al., 2011; Beever et al., 2016b). Our objective was to assess the vulnerability of pikas to ongoing climate change and to address how such an assessment informs the species' general conservation status. To contextualize the assessment of AC for pikas, we conducted assessments of four other species of small mammals (at the range-wide scale) that often occur sympatrically with pikas and that represent a range of predicted climate-change vulnerabilities (Fig. 1a). Finally, we use the results to consider broader questions about inter- and intra-specific variability in species-climate relationships, and how such assessments can contribute to tractable conservation and management plans.

2. Methods

2.1. Focal species and spatio-taxonomic scales

For the broadest of the three spatial scales, we first evaluated pika adaptive capacity across the entire geographic range (i.e., "range-wide"), and compared it with the AC of four other sympatric species. At the second scale ("lineage"), we compared AC characterizations across all five currently recognized lineages of pikas (Galbreath et al., 2009): *O. p. princeps* (Northern Rocky Mountains), *O. p. fenisex* (Cascade Range), *O. p. saxatilis* (Southern Rocky Mountains), *O. p. uinta* (Central Utah), and *O. p. schisticeps* (Sierra Nevada and Great Basin) (Fig. 1b). For the finest scale, we compared AC characterizations of *O. p. schisticeps* populations from the more-limited interior hydrographic Great Basin against the entire *schisticeps* geographic range. For both comparisons, we predicted that the broader-extent scale would be characterized as having higher AC than the smaller-extent scale, because the former may capture a broader range of variation in—and diversity of—traits and characteristics that support the species' ability to recover from and withstand demographic or stochastic disturbances. The former also promotes greater population redundancy and greater resilience, when population trends are spatio-temporally decoupled ('portfolio effects': e.g., Schindler et al., 2010, Edmunds and Lasker, 2022).

We selected four other species of small mammals that span a range of hypothesized climate change vulnerability (CCV) based on their life-history and distributional characteristics (McCain, 2019). McCain's model of "climate change risk" rates the CCV of mammal species based on traits that show the strongest link to differential responses to climate change such as body size (large mammals respond most negatively to climate change), activity times (mammals with restricted activity times respond most negatively), and spatial distribution (high-latitude and high-elevation mammals respond most negatively). To increase

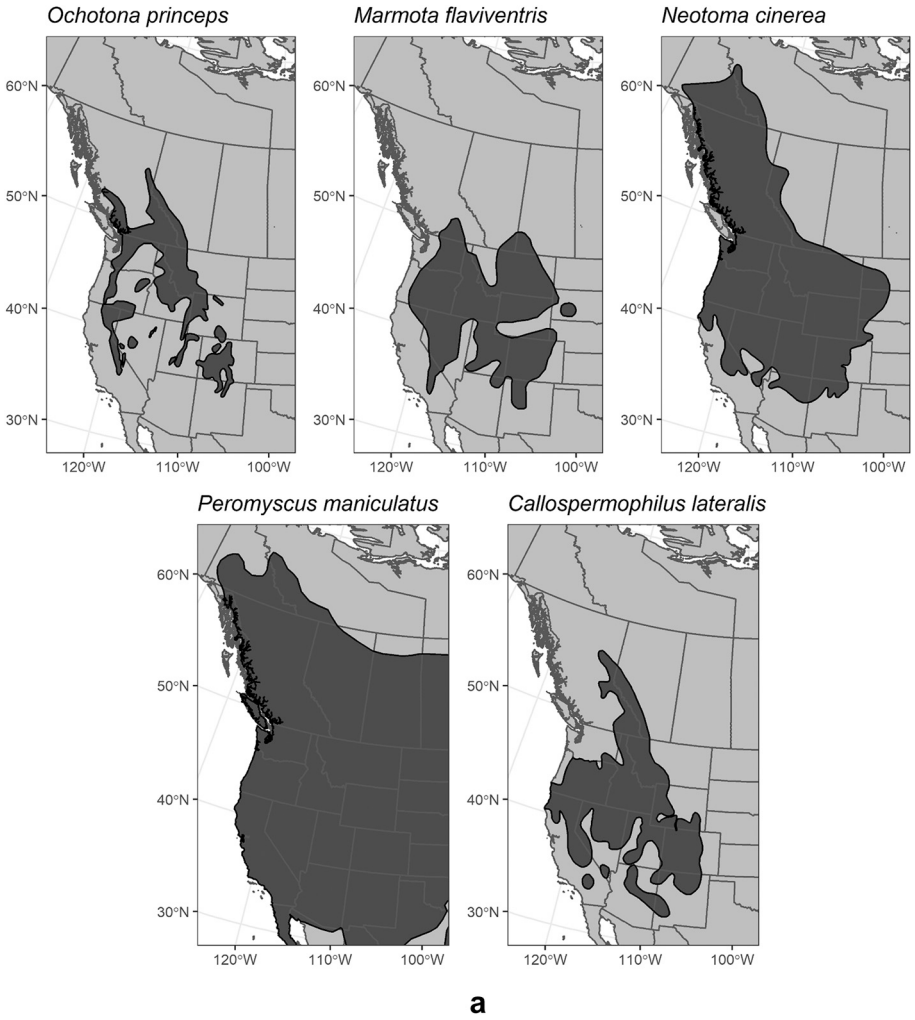

Fig. 1. Range maps of the various a) focal species, and b) infraspecific pika clades listed in Table S1.

comparability and remove the most obvious sources of confounding influence (when assessing CCV), we chose species that, like pikas, are mountain-dwelling (either facultatively or obligately), occur across extensive geographic ranges, and have well understood life histories. These species (with McCain's CCV in parentheses) are the deer mouse, *Peromyscus maniculatus* (5/10); bushy-tailed woodrat, *Neotoma cinerea* (6.5/10); golden-mantled ground squirrel, *Callospermophilus lateralis* (9/10); and yellow-bellied marmot, *Marmota flaviventris* (10/10). Although all occur in talus slopes across some of the range of *O. princeps*, the woodrat and marmot are more strongly associated with rocky habitats than the other two species. For all four species, we evaluated research and information from across each species' entire geographic range.

2.2. Assessments of adaptive capacity

To thoroughly and objectively assess the AC of our five species of interest, we used a recently published framework (Thurman et al., 2020). This framework includes 36 attributes used to systematically assess AC, wherein attributes are grouped into distribution, movement, evolutionary-potential, ecological-role, abiotic-niche, life-history, and demography complexes. For each attribute, species are evaluated on a 5-level scale from Low to High, using criteria to accommodate either quantitative or qualitative assessment. None of these five species is migratory, so we did not consider the four migratory attributes (thus, $N_{total} = 32$ attributes/species). Most trait-based assessments that utilize expert elicitation, like the adaptive-capacity framework used here, support both quantitative and qualitative evaluations and extrapolate information about complex processes from a suite of easily measured characteristics. These approaches thus inherently have some subjectivity, despite reflecting existing literature.

To increase confidence and objectivity in our assessments, two different researchers or teams independently assessed more than half (6 of 11) of the taxonomic groups (species, clades, or ecoregional populations), and consistent criteria were used for selecting levels of AC (also see six additional approaches in the SI that we used to reduce bias). The two assessors for a taxonomic group then compared their assessments, corrected inaccuracies (e.g., noted when a study used was from an area outside the domain of a pika lineage and was for an attribute unlikely to be highly conserved), shared references, and mutually offered critical review. We did not homogenize responses across the two assessors; instances in which final assessments differed are indicated by two levels of AC (separated by a "/") and tallied at one-half weight for each respective level (Figs. 2 and S2, Table S1). To increase transparency and repeatability of our literature search, we used standardized search terms in combination with scientific or common names for each species and attribute. We performed these searches in multiple search engines, and included peer-reviewed articles, technical reports, theses and dissertations, and other relevant resources (see Table S2), with the goal of

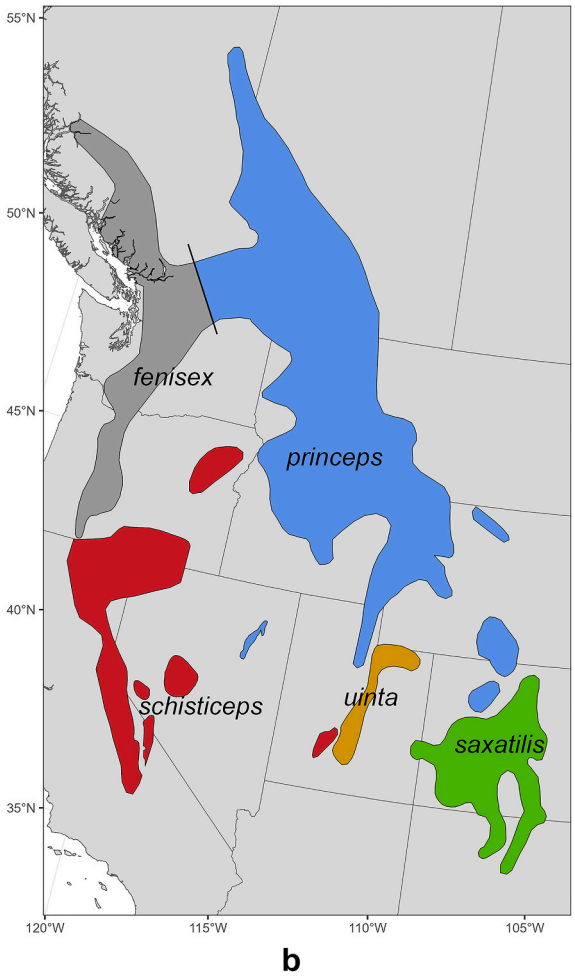

Fig. 1. (*continued*).

achieving the highest possible evidence score (a characterization of certainty with specific criteria; Thurman et al., 2020: WebTable 2) for each attribute and species or clade. We tallied rankings of all attributes with equal weight, regardless of their evidence scores.

We identified three traits (Mating System, Dispersal Phase, Dispersal Syndrome) that we expected *a priori* should be highly conserved across pika clades, but that could be assessed differently based on interpretation of the criteria. We standardized these three traits for pikas, based on a preponderance of evidence for the species (both from the literature and from phylogenetic knowledge), to ensure that diverse interpretations did not falsely create heterogeneity in assessment of a highly conserved attribute. To illustrate, pikas are serially monogamous (having more than one mate in a lifetime but only one mate per season), and extra-pair copulations are relatively infrequent; such a phenomenon does not fit squarely into any of the available, pre-defined options for Mating System: asexual (Low AC), monogamy (Moderately low), polygamy (Moderately High), and promiscuity (High AC). Because serial monogamy has implications for genetic mixing and consequent vulnerability that align more closely with polygamy than strict monogamy, we assessed Mating System for all pika clades as Moderately High AC. When comparing the AC of our five species range-wide, we considered pika AC levels to differ "meaningfully" from other species for any attribute when at least 2 species differed in the same direction (i.e., both higher or both lower) from pikas.

We made statistical comparisons in JMP (SAS 2022), and R (R Core Team 2022) of AC among species and among lineages using both a 1) chi-square goodness-of-fit test to assess whether the distribution of the 32 focal attributes among the five AC categories (i.e., number of attributes in each category, without regard to ranking) differed significantly among clades, and 2) Friedman test (Conover, 1980, NIST 2015; and pairwise comparisons with Wilcoxon signed-rank tests) to compare whether ranked levels of AC differed among clades. For 1), we retained the assessed rankings of AC as ordinal categorical data, assigning order by assuming for each attribute that Low = 0 and High = 1 and all categories are equally spaced (e.g., Moderately Low = 0.33, Moderately High = 0.67) and that mixed-evaluation ranks (when the two assessors assigned different levels of AC to a given attribute) are intermediate between the constituent ranks (e.g., Moderately High/High = 0.833). To ensure robustness of results, we analyzed data with various permutations of assumptions: a) removing Unknown values, or retaining them as Moderate (akin to a Bayesian uninformed prior; a third option is described in the Supplemental Information); and b) retaining cells with mixed ranks as their own categories, or assigning Low/Moderately Low ranks to Moderately Low and Moderate/High and Moderately High/High ranks to Moderately High values (to reduce number of categories). For 2), characterizations of the level of AC were converted to a scale of 1 to 9 (as noted above), and analyzed non-parametrically. We again performed analyses with respect to differing assumptions (a) and (b), above.

3. Results

3.1. Interspecific comparisons

When comparing the range-wide assessments of our five species, pikas were assessed as having meaningfully lower AC for 14 out of 32

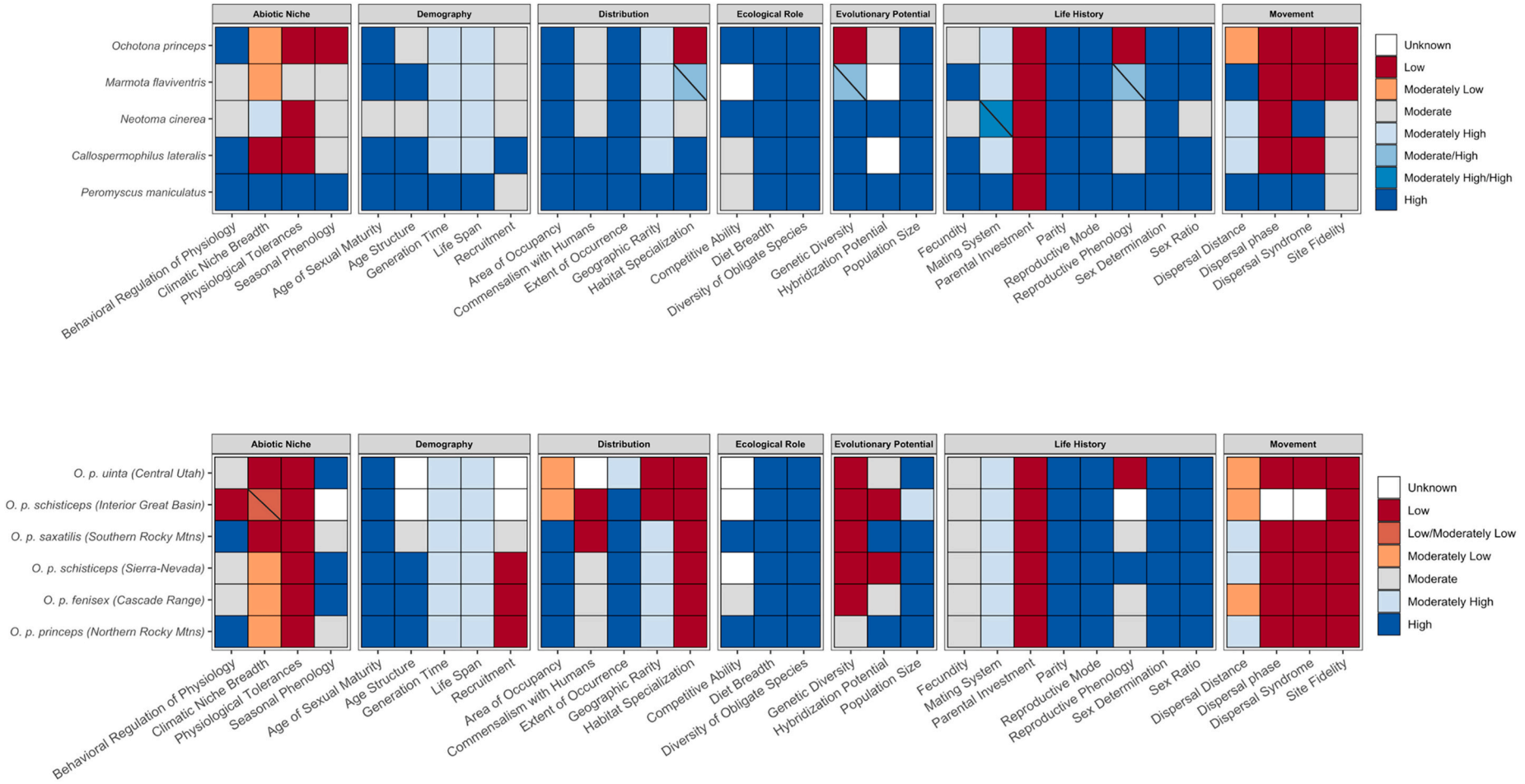

Fig. 2. Depiction of the various levels of adaptive capacity (AC), across a) our 5 focal species, and b) the five lineages of *O. princeps* (American pikas). The "\" (backward slash mark) indicates that assessors differed in their evaluation of AC, for that clade and attribute.

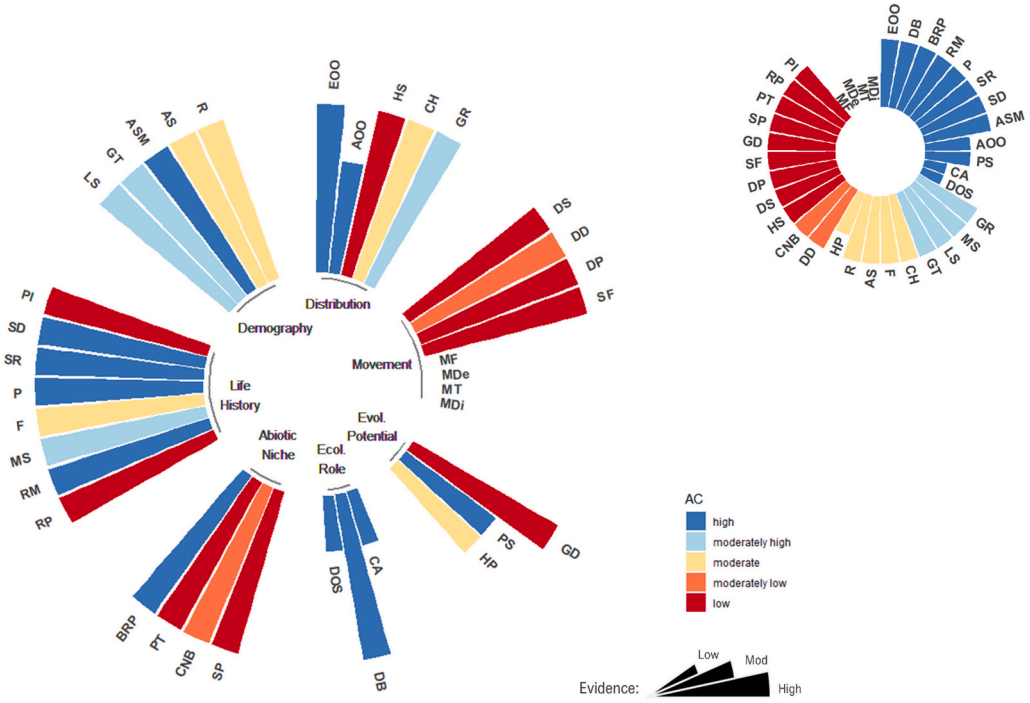

Fig. 3. Levels of adaptive capacity (AC; as well as level of evidence) for each attribute for *Ochotona princeps* at the range-wide level, summarized by attribute complex and by level of AC. Whereas the larger wheel organizes attributes within attribute complexes (as in Figs. 2, S2, S3 and Table S1), the smaller wheel groups attributes by level of AC. Full names corresponding to the abbreviation for each attribute are found in Fig. 2, wherein attributes are also organized into attribute complexes.

attributes across 6 different complexes, exactly or nearly equivalent level of AC as the other species for 16 attributes, and higher AC for 2 attributes (Table S1, Fig. S2). Pikas' lower-AC attributes were not distributed evenly among attribute complexes. Three complexes each had three attributes with lower pika AC than the other four species (75 % of Movement, 75 % of Abiotic-Niche, and 38 % of Life-History attributes were lower-AC), two complexes had two lower-AC attributes (67 % of Evolutionary-Potential and 40 % of Distribution attributes), Demography had one (20 %), and the Ecological-Role complex had none (Table S1, Figs. 2,3,S2,S3). Overall, pikas had many more attributes ranked as Low AC ($n = 9$ attributes) than the other mountain-dwelling species ($n = 1$ to 5; mean = 3.25). The pika-vs.-other-species gap widened when including attributes ranked as either Low or Moderately Low ($n = 11$ attributes for pikas, vs. 1 to 5 [mean = 3.5] for other species). Similarly, pikas had fewer attributes rated as High or Moderately High AC than all four other species ($n = 16$ for pikas, vs. 18 to 28 [mean=22.0] attributes for other species; Table S1, Figs. 2,3). Goodness-of-fit tests suggested that the distribution of attributes into various assessed levels of AC differed markedly across our five species (Likelihood Ratio chi-square ≥ 40.51, $p \leq 0.011$; Pearson chi-square ≥ 37.20, $p \leq 0.002$). Corroborating these results, Wilcoxon and Friedman tests suggested that: a) pikas had lower AC than the deer mouse, golden-mantled ground squirrel, yellow-bellied marmot (under most assumptions), and, when attributes with any Unknown values were removed from analyses, marginally lower AC ($0.068 \leq p \leq 0.083$) than bushy-tailed woodrats; b) the deer mouse had higher AC than all other species; and c) all other pairs of species had comparable AC.

Two patterns emerged after ordering the non-pika species from greatest to least climate-change vulnerability (CCV). As CCV score increased, more attributes were assessed as High AC and fewer as Low AC (except for one species in each ordering; Table S1).

3.2. Intraspecific comparisons: Pikas range-wide, clades, and interior Great Basin

3.2.1. Comparison of range-wide pika AC vs. AC of individual lineages, and statistical comparisons among pika lineages

Distribution of attributes into various assessed levels of AC did not differ across lineages, regardless of assumption (a) (how to treat Unknowns), and there were no mixed-evaluation assessments among lineages (Likelihood Ratio chi-square ≤ 18.29, $p \geq 0.57$; Pearson chi-square ≤ 18.05, $p \geq 0.58$). However, Wilcoxon comparisons for each pair illustrated that the *O.p. uinta* lineage had lower assessed values of AC than all other lineages if traits with any Unknown values were removed from analyses, and all lineages other than *O.p. fenisex* (nearly different: $p < 0.086$) if Unknown values were converted to Moderate. All other lineages were comparable. Attributes of *uinta* were lower than at least two other lineages especially in the attribute complexes of Distribution (3 of 5 attributes) and Abiotic Niche (2 of 4). A Friedman test detected some (but not statistically significant) heterogeneity in AC ranking among the five pika lineages ($F_{4,\ 108} = 2.81$, $p < 0.07$; four AC attributes were omitted due to "Unknown" values). A least-significant-difference test indicated *O. p. uinta* had lower AC than other lineages ($p = 0.05$), if the full assemblage result is considered significant.

In contrast to our predictions, a qualitative assessment of AC levels did not reveal pikas to have higher AC range-wide as compared to at the lineage level. Levels of AC for pikas range-wide were assessed higher than in pika lineages (using the same criterion of "meaningful" difference) for three attributes. However, range-wide levels of AC were lower than within lineages for twice as many ($n = 6$) attributes.

3.2.2. Non-statistical comparison of O.p. schisticeps-wide AC vs. AC of interior Great Basin pikas

We did not perform statistical comparisons between the AC of pikas in the interior Hydrographic Great Basin versus pikas across the entire *schisticeps* lineage because: 1) there were so few references available for many attributes from the Sierra Nevada portion of the lineage, thus many of the attributes' two assessments reflected information from the

same investigations, and 2) the *schisticeps* lineage entirely encompasses the interior-Great-Basin populations; thus, the two groups' are statistically non-independent. This comparison nonetheless provided a second level of comparison between taxonomic levels: an entire lineage versus a regional subset of that lineage. As has been reported using other lines of evidence (e.g., Smith, 2020; Millar and Westfall, 2010), assessed AC of pikas in the interior Great Basin was lower. Whereas 7 attributes were ranked as having lower AC in the interior Great Basin, zero attributes were ranked as higher AC in the interior Great Basin than lineage-wide.

4. Discussion

Understanding the factors governing responses of species and populations to departures from previously experienced ecological conditions has been a focus of disturbance ecology and conservation biology for decades (reviewed in Beever et al., 2019). Species must cope or adjust to this disturbance—a process often referred to as adaptive capacity—or suffer reduced fitness and risk local extirpation or extinction. Potential coping mechanisms include evolutionary adaptation, phenotypic plasticity (e.g., alter diel activity patterns, use microrefugia), epigenetic changes, and shifts in distribution (Dawson et al., 2011; Nicotra et al., 2015).

Our major finding is that, broadly, American pikas appear to have notably lower adaptive capacity relative to other montane mammal species also considered vulnerable to climate change to varying degrees (e.g., the yellow-bellied marmot, bushy-tailed woodrat, and [projected-less-vulnerable] golden-mantled ground squirrel), and far lower AC than the ubiquitous deer mouse. At the species level, pika AC was equivalent to or lower than at least two of the other four species in all but two of the 32 attributes evaluated. Pikas' lower AC was pervasive (i.e., in $\geq$67 % of traits) in the Movement, Abiotic-Niche, and Evolutionary-Potential attribute complexes, and occurred in three Life-History attributes (Table S1). Additionally, several attributes in the Life-History and Ecological-Role complexes had uniformly high AC across all species, reflecting these five mammal species' similar body mass, broad diet breadth, and *r*-selected reproduction characteristics (e.g., viviparity, iteroparity, altricial young). To be conservative, we did not remove these unvarying attributes; that we found significant differences in levels of AC across species in spite of these homogeneous attributes further underscores the lower AC of *O. princeps* compared to the other sympatric mammal species.

4.1. Comparison of AC and climate-change vulnerability, across species

The specific life-history characteristics of pikas provide insights into why they may have generally lower AC for contemporary climate change, yet appear to have greater resiliency and lower vulnerability within certain constrained contexts. *O. princeps* is generally philopatric and a central-place forager, and the species is typically associated with broken-rock features that occur patchily across landscapes, an association that is more obligate than for any other of the species we analyzed. Furthermore, longer-distance movements occur infrequently and dispersal distances are shorter (thereby producing smaller genetic neighborhoods) in warmer, drier climates and locations (Castillo et al., 2016; Schwalm et al., 2016). Consequently, pikas are less likely than other species to quickly and effectively track bioclimatic envelopes that shift across physiographically complex mountains at seasonal, annual, and longer time scales (e.g., Johnston et al., 2019). Although their broken-rock habitats are effectively static over ecological time scales, the climate envelope in mountain landscapes that is pika-suitable is shifting to higher elevations and wetter locations over timescales of years to decades (e.g., Beever et al., 2011, 2016b; Stewart et al., 2015, 2017; Billman et al., 2021). Phenomena such as snow droughts and heavy-snow winters can also produce such shifts inter-annually (e.g., Johnston et al., 2019). Climate-mediated dispersal distance also applies directly to re-colonization; although the species continues to exhibit metapopulation dynamics that include both extinctions and re-colonizations at the patch level, extinctions are often outpacing re-colonizations (and sometimes by several-fold), in numerous trailing-edge (i.e., southern and low-elevation) populations across the species' range (e.g., Nichols et al., 2016; Stewart et al., 2017; Westover, 2019).

Decades of observational, manipulative, longitudinal, and gradient-based investigations on the physiology, energetics, genetics, and other aspects of *O. princeps* provide further clues as to why pikas may have generally lower AC than other sympatric species. For example, due partly to the species' low emissivity of heat from its dense fur and narrow window between the species' average resting and upper-lethal body temperatures (3 °C), experiments strongly suggest that *O. princeps* is physiologically intolerant of elevated temperatures, particularly when no suitable, accessible thermal refugium exists (Smith, 1974; MacArthur and Wang, 1973). Furthermore, the anomalously high mass-specific metabolic rate for *O. princeps* demands that individuals take in large amounts of forage to balance their energy budget. Pikas also have comparatively lower realized fecundity than many other lagomorph species. On the other hand, pikas have AC attributes that help them accommodate chronic and acute climate stresses, including being dietary generalists as a species, the ability to modify surface-active windows within a diel period across space and seasons (e.g., Hall and Chalfoun, 2019), and the ability to modify behavior to take advantage of microrefugia (e.g., preferential use of shade, moss-insulated microsites, subsurface ice [Varner and Dearing, 2014, Beever et al., 2017]).

Our study reinforces the premise that robust prediction of the vulnerability of species and populations to contemporary climate change (and other stressors) hinges on understanding not only the particular mechanisms by which organisms are affected (Beever and Belant, 2011), but also the underlying life history of the focal taxon or taxa. Our systematic, comprehensive AC assessments for the pika lineages and focal species are more informative of clades' conservation status, climate-change vulnerability, and climate-adaptation options than considering solely a subset of the attributes. Analogously, our assessments using literature and our collective fieldwork from across the entirety of each of three spatial extents are more likely to reflect a clade's overall status and vulnerability, compared to drawing broader conclusions from a handful of sites (e.g., Millar and Smith, 2022).

Knowledge gaps hinder full analysis, but also underscore research frontiers for fuller understanding of our compared species' vulnerability (Table S1, Fig. 3). For example, we rated hybridization potential as unknown for two of five species, and competitive ability as unknown for two of five clades in our analyses of pika lineages. Such attributes merit further investigation (e.g., Age Structure and Recruitment for *O.p. uinta*, dispersal and phenology attributes for interior-Great-Basin pikas), to fully inform conservation-status designations, allocation of conservation effort, and selection of climate-adaptation actions. However, based on our experience with AC analysis and the consistency of our results across methodological permutations (i.e., treatment of Unknowns and mixed-evaluation attributes; see Methods), we believe our results will be robust to the inclusion of additional data. Combination of AC assessments and investigations replicated across multiple contexts can inform 'right-sizing' of climate-adaptation actions for species such as mountain-dwelling ones whose geographic ranges can encompass great climatic, physiographic, phenotypic, and genetic diversity.

4.2. Comparison of climate-change vulnerability, below the species level

Although early research on climate-change vulnerability suggested that species may be either 'climate-change winners' or 'losers,' subsequent research has shown not only that populations from different portions of a species' range may fare differently amidst contemporary climate change (e.g., Ikeda et al., 2017), but also that different aspects of climate change may be the dominant stressors in different portions of a species' range (Smith et al., 2019; Fig. S1). Intraspecific variation has been shown to affect phenomena as diverse as community composition,

nutrient cycling, primary productivity, trophic cascades, and effects of predators (Des Roches et al., 2018). Such variation can be produced via numerous pathways, including artificial selection, local adaptation, parental conditions, and phenotypic plasticity, as well as by evolutionary mechanisms of divergent selection and incipient speciation (Violle et al., 2012). Heterogeneous response to climatic stresses across a species' range may be further influenced by spatial variability in geology, forage or prey species, hydrology, and land use, which can collectively influence biotic interactions, availability of microrefugia, nutritional ecology, and conservation-action options, among other factors (Jeffress et al., 2013; Smith et al., 2019). We suspect that across species and among populations, differences may also exist in the ability to cope with and adjust to particular climate stressors (e.g., drought stress, chronic-heat stress, acute-cold stress). Incorporation of context-dependency in conservation-status and vulnerability assessments will likely have to be balanced against analytical feasibility and strength of justification.

Within the range of American pikas, the *uinta* lineage (central Utah) showed a slightly lower AC than other lineages, which may merit further investigation, particularly given that this lineage has the smallest spatial extent and lowest levels of observed heterozygosity (Appendix 1). Pikas have been extirpated from Zion National Park and maintain variable and sometimes tenuous occupancy at Cedar Breaks National Monument (Beever et al., 2016b), but pika monitoring state-wide at higher elevations suggests greater population stability. The interior Great Basin 'population,' which inhabits the driest portion of the species' range, was ranked as having generally lower AC for many attributes compared to across the entire *schisticeps* lineage in which it occurs and to clades in other parts of the species' geographic range. This finding aligns with reports of comparatively rapid and spatially extensive pika distributional change and losses within the (Basin) region in the last century (Beever et al., 2011, 2016b; Jeffress et al., 2017; Wilkening et al., 2019) and since the Last Glacial Maximum (e.g., Grayson, 2005). Contrastingly, pika lineages had twice as many attributes assessed as higher at the lineage level than at the range-wide level, compared to attributes wherein lineages had lower AC assessments. Such variation further supports our determination that adaptive capacity can differ considerably over space and highlights the importance of recognizing and selecting the scales at which modeling, monitoring, and conservation actions should occur.

4.3. Conservation implications

Understanding how species' abilities to cope with or adjust to environmental changes might differ over space and time will be crucial for effective management and conservation moving forward, because conservation actions are typically implemented at local scales (Angeler et al., 2019). For example, identifying climate-adaptation actions to receive greater consideration for implementation will be improved by understanding the factors constraining a species' or population's fitness, mechanisms of climatic influence, and attributes or attribute complexes with lower AC (Thurman et al., 2022). To illustrate using *O. princeps* as an example, actions that can ameliorate the lower AC of pikas in Movement, Abiotic-Niche, Evolutionary-Potential, and some Life-History attributes may be pathways to facilitate persistence and higher fitness, particularly for lineages or regions where the species appears to have lowest AC (Thurman et al., 2022). Although none of these actions have yet been tested for our focal species, possible conservation actions include: preventing further fragmentation of rocky habitats (e.g., due to highways, harvest of boulders from taluses for construction or landscaping), maintaining metapopulation connectivity (related to Movement attributes), and conserving features providing meso- and microrefugial conditions (factors related to Abiotic-Niche attributes, such as rock-ice features, moss and other vegetation [Varner and Dearing, 2014], fine-scale natural temperature-buffering elements [Beever et al., 2017], and shade). Future research would help to evaluate these as feasible and effective climate-adaptation actions. Despite the unknowns discussed above, conservation actions will typically be required prior to all knowledge gaps being filled, to effectively reduce overall extinction risks (Conroy et al., 2011).

5. Conclusions

Our approach constitutes one of several for evaluating climate-change vulnerability. Although our approach is not as unilaterally quantitative as approaches such as bioclimatic-niche modeling and physiological experiments, it is more comprehensive in capturing the spectrum of mechanisms by which weather and climate may affect species. Nicotra et al. (2015) posited that for prioritizing climate-adaptation conservation actions to address particular species' AC, practitioners may be able to assess AC at landscape to ecoregional scales using life-history or functional traits (e.g., Foden et al., 2013). Within a particular community or management unit, however, they posited that practitioners may want to instead assess various species' potential for adaptive phenotypic plasticity and evolutionary response based on trends observed (i.e., a 'triage' approach). Our approach also uses data collected either non-invasively or in compliance with current animal-welfare guidelines. We combine our collective experience with published literature from a large number of sites and regions across our focal species' ranges. Furthermore, more information on relevant information gaps and research frontiers, the importance of refugia, and caveats are also provided in the Supplemental Information. By evaluating species' AC in a consistent, repeatable, comprehensive fashion that is more quantitative than a checklist, conservation practitioners can be provided a range of potential vulnerabilities and pathways to identify and prioritize climate-adaptation actions (*sensu* Thurman et al., 2022). Moreover, such an approach could also indicate how those actions may need to differ across a species' range to enhance adaptive capacity. Long-term forecasts of vulnerability and main pathways leading to such vulnerability may also fit into decision frameworks surrounding ecosystem transformations (e.g., Lynch et al., 2021), a topic that conservation practitioners will increasingly face in the coming years to decades (and that may feed back into population trends).

Our approach using trait-based methods to assess AC can be applied to other species for which basic natural-history information is available as one component of assessing their vulnerability to climate change. We suggest that groups of researchers collaborating on AC assessment for particular species use similar literature-review criteria, including common sets of keywords (e.g., species name, ecological sub-discipline, synonyms for the given attribute) and literature databases. Additionally, for species where AC assessments show discrepancies among populations or regions, more-detailed analysis could help elucidate disproportionately important attributes and more accurately identify specific thresholds at which AC categories shift (e.g., from Moderate to Low). Broadly speaking, our results synthesize dozens of investigations (of genetics, occupancy and distribution, abundance, fitness, physiology, behavior, and indirect effects) indicating comparatively high conservation need in *O. princeps*. By focusing on mechanisms of climatic influence on populations (e.g., cold stress due to declining snowpacks, decreased forage availability due to chronically high heat, dehydration due to greater vapor pressure deficit), conservation practitioners can connect assessments of AC to the identification of potential climate-adaptation conservation actions.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All of the AC assessments are included explicitly in the MS. There are no other data or code.

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