# Title

Spatially heterogeneous impact of climate change on small mammals of montane California

# Author List and Affiliations

Kevin C. Rowe1,2\*, Karen M.C. Rowe1,2, Morgan W. Tingley3,5, Michelle S. Koo1, James L. Patton1,4, Chris J. Conroy1, John D. Perrine6, Steven R. Beissinger1,3, Craig Moritz1,7,8.

1Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720-3160, USA

2Present address: Museum Victoria, Sciences Department, GPO Box 666, Melbourne, VIC 3001, AUSTRALIA

3Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3114, USA

4Department of Integrative Biology, University of California, Berkeley, CA 94720-3160, USA

5Woodrow Wilson School, Princeton University, Princeton, NJ 08544, USA

6Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407-0401, USA

7Research School of Biology and Centre for Biodiversity Analysis, The Australian National University, Canberra ACT 0200, AUSTRALIA

8The Commonwealth Scientific and Industrial Research Organization Ecosystem Sciences Division, Canberra ACT 2601, AUSTRALIA

\*Corresponding author: Kevin Rowe, krowe@museum.vic.gov.au

# Abstract

Resurveys of historical collecting localities have revealed range shifts, primarily leading edge expansions, which have been attributed to global warming. However, there have been few spatially replicated community-scale resurveys to test whether species’ responses are spatially consistent. Here we repeated early 20th century surveys of small mammals along elevational gradients in northern, central and southern regions of montane California. Of the 34 species we analysed, 25 shifted their ranges upslope or downslope in at least one region. However, two-thirds of ranges in the three regions remained stable at one or both elevational limits and not one of the 22 species found in all three regions shifted both their upper and lower limits in the same direction in all three regions. When shifts did occur, high elevation species typically contracted their lower limits upslope, whereas low elevation species had heterogeneous responses. For high elevation species, site-specific change in temperature was a better predictor of the direction of shifts than change in precipitation, whereas the direction of shifts by low elevation species was unpredictable by temperature or precipitation. While our results support previous findings of primarily upslope shifts in montane species, they also highlight the degree to which the responses of individual species vary across geographically replicated landscapes.

# Introduction

Evidence for the biotic responses to recent climate change has continued to accumulate [1,2,3,4,5] and is central to the prediction of vulnerability to future change [6]. There is a general trend toward upward and poleward shifts of elevational and latitudinal boundaries of species’ ranges [1,2,3,4,5,7,8], with “leading edge” expansions detected more often than “lagging edge” contractions [9,10,11]. However, there is considerable heterogeneity in the direction and magnitude of species’ responses, and ranges of many species have not changed at all [12,13,14]. Species respond to local change in climate and habitat rather than global averages, and few studies have accounted for substantial spatial heterogeneity in climate change across the landscape [1,14,15]. Moreover, there is potential for considerable sampling error because local colonization and extinction cannot be demonstrated convincingly unless detectability (i.e., the probability of “false absence”) is explicitly incorporated into models of occurrence change [16]. Insights into the dynamics of species’ responses to recent climate change are most likely to come from spatially-replicated resurveys [17, 18] combined with analytical methods that have statistical power to detect both range contractions and expansions.

An unusually detailed historic dataset, combined with contemporary resurveys, allows us to evaluate robustly a century of range responses of mammals to climate change in montane California (Fig. 1a). Joseph Grinnell and colleagues studied the elevational distributions of vertebrates of California in the early 1900’s [19,20, 21]. These data laid the foundation for Grinnell’s concept of the ecological niche and for understanding the climatic limits of species’ distributions [22]. They also provided a benchmark for documenting changes in the elevational ranges of species in California over the last century [11,13,14,23]. Over the past century, mean annual temperature in California has increased by ~0.6 °C [24,25, 26] (Fig. 1b, Supplementary Fig. S1). Precipitation changes were more spatially heterogeneous, with spatial covariation increasing across the northern part of the state and decreasing across the southern part [27,28]. Elevational ranges of species in California over this period have shifted heterogeneously, including species moving upslope, downslope or not at all [13,14,29]. Heterogeneity in movements of species has been partly explained by incorporating local-scale measures of climatic change for both temperature and precipitation [14,30]; increases in the former usually favour upslope shifts, while increases in the latter typically favour downslope movements. Local changes in habitat structure due to fire and grazing are also factors in some areas [31,32].

Here we characterized spatial variation in elevational range responses of small mammals in protected areas of montane California by expanding our analysis centred on a single region in central California (Yosemite National Park, central Sierra Nevada) [13] to other regions in the north (Lassen Volcanic National Park, southern Cascade Range) and south (Sequoia/Kings Canyon National Parks, southern Sierra Nevada). We controlled for variation in detectability among species and survey eras to compare elevational limits from the early 20th Century (1911-1934) to the present (2003-2010). With data from multiple, geographically-separated regions of montane California that have experienced limited land-use change, we tested four predictions of the influence of climate warming on elevational ranges that emerged from patterns observed in the Yosemite region [13] and in birds across montane California [14]. If overall climate warming is the predominant driver of elevational range change, then (1) upslope shifts should be the most common change across all regions; and (2) range contractions should be more frequent in high than low elevation species, and range expansions more common in low than high elevation species. If, however, species have responded to the heterogeneous climate change across the landscape and to both temperature and precipitation change, then (3) elevational ranges of species should shift inconsistently across regions; and (4) upslope and downslope shifts should both occur and be associated with local changes in temperature and precipitation, respectively [14].

1. **Material and methods**

## *Survey regions and 20th century climate change*

Historical surveys occurred between 1911 and 1934 [16,17,20, 21] along elevation transects across three regions of montane California (Fig. 1a, Supplementary Table S1): a northern region, in the southern Cascade Range, around Lassen Volcanic National Park (“Northern”), a central region, in the central Sierra Nevada, around Yosemite National Park (“Central”), and a southern region, in the southern Sierra Nevada, around Kings Canyon and Sequoia National Parks (“Southern”).

The three regions of montane California differed considerably in climate and physiognomy. The northern region (Lassen) was the coolest and wettest, and had the smallest elevation range and the least topographic complexity. The southern region (Sequoia) was the driest, and had the largest elevation range and greatest topographic complexity. Climate change over the past century differed among the three regions (Fig. 1b). The central region (Yosemite) experienced the greatest and the northern region the least increase in mean annual temperature, whereas precipitation increased in both but not in the southern region. Across all three regions, maximum temperature of the warmest month was constant, whereas minimum temperature of the coldest month increased (Supplementary Figure S1). See Tingley et al. [14] for additional details of the sampling regions.

## *Survey and resurvey data*

We used historical maps, written descriptions in field notes, and modern ground-truthing with historical photographs and hand-held GPS units to georeference historical localities. Modern trapline coordinates were obtained from handheld GPS units, with coordinates recorded at the beginning, middle, and end of each trapline. We defined localities or sampling sites as an aggregate of concurrent surveys (i.e., traplines) conducted within a 2 km distance and 100 m elevation [13]. Each site was georeferenced, and elevation was determined using a Digital Elevation Model derived from the Shuttle Radar Topography Mission (v4) with a resolution of 1 arc second. We verified these values by manual comparison to elevations determined on the ground or on topographic maps (Supplementary Table S1).

Of the 134 historical localities, 34 were in the Northern, 47 were in the Central, and 32 were in the Southern region of montane California (Fig. 1a). Each site was surveyed for 1-16 nights (median = 5) for a total of 681 survey-nights. For most sites, surveys were conducted over consecutive nights. Historical trapping efforts used snap traps, Macabee gopher traps, mole traps, and steel traps that were set in suitable locations in various habitats around a central camp. For each historical site, the average number of traps per night ranged from 6 - 335 (median = 96). Shooting and observations resulted in additional opportunistic records of diurnal mammals, primarily squirrels and pikas. Of the 15,277 historical mammal records used in this study, 8,688 are backed by voucher specimens in the MVZ [1,2,3].These included trapline details such as nightly captures, number of traps set, habitats, location maps and daily records of specimens observed and shot from more than 2,500 pages of field notebooks held in the MVZ Archives (available online at http://bscit.berkeley.edu/mvz/volumes.html).

Modern mammal resurveys were conducted between 2003 and 2010 as part of the Grinnell Resurvey Project [13,14]; Fig. 1a). We surveyed a total of 166sites, including 85 of the 134 historical sites; 38 were in the Northern, 81 were in the Central, and 47 were in the Southern region of montane California. Additional modern sites were selected to maximize elevation coverage and to serve as proxies for otherwise inaccessible historical sites. We surveyed each site for 1-11 nights (median = 6) for a total of 916 survey-nights. As with historical surveys, most modern surveys at a site were conducted over consecutive nights. Using historical locality maps and habitat descriptions recorded in field notebooks, we set traplines to sample historical sites as closely as possible. We used a combination of Sherman traps and Tomahawk traps, with standard traplines containing 40 Sherman traps and 10 Tomahawk traps run for 4 consecutive nights in suitable spots. Pitfall traps, consisting of 32-oz plastic cups placed in the ground, were used to collect shrews and were set at the same time as the Sherman lines. Pocket gophers were trapped using Macabee gopher traps where gopher mounds were observed. For each modern site, the average number of traps per night ranged from 3-339 (median=65). Additional observational records were recorded daily. Of the 14,316 modern mammal records obtained from these surveys, 6,144 are backed by voucher specimens in the MVZ [6,7, 8].This resulted in a total of 29,593 records and 14,832 specimens in our data set (data available on Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.[NNNN]).

## *Species set*

We present the elevation distribution for 67 species of rodents, shrews, and pika recorded in the historical and modern surveys (Supplementary Table S2). Our resurvey protocols were not designed to detect carnivores, ungulates, or bats, so these were not included. Following Moritz et al. [13], we adjusted the slope cut-off for *Peromyscus truei* to reflect known boundaries between Sierra Nevada and Great Basin subspecies [33]. We also considered only those west slope species that are characteristic of the Sierra Nevada and Cascade Range. For example, we did not include Mojave Desert species such as *Neotoma lepida* or *Perognathus longimembris*. Analyses of range shifts were restricted to 34 species that were detected at >10% of sites for at least one region in both eras. Of these, we were able to model detectability and occupancy for 28 species because they were detected through repeated nights of trapping at sites and where the number of traps set was reported (hereafter “quantitative trapping”). We include an additional six species in our range shift analyses as we made systematic efforts to detect and record these easily observed species. Elevational profiles of species are presented separately for the east and west slope sites with the exception of sites within the Yellow Pine (*Pinus ponderosa*) belt on the east slope, which we included as west slope sites.

Species were categorized as low elevation (historical elevation ranges within Lower Sonoran – Transition life zones), high elevation (Transition – Alpine), or widespread [13,17,20,21] (Supplementary Table S4). *Thomomys bottae* was classified as low elevation based on its range in the Northern and Central regions, consistent with Moritz et al. [13].

## *Modelling changes in elevational ranges*

To simultaneously estimate the probability of detection (*p*) and the probability of occupancy (*Ψ*) of each species at each locality, we used the single-season occupancy-modelling framework implemented in the program MARK v6.0 [34,35]. Our single-season model implemented an “unpaired-site” framework [16], which tests for temporal changes in occupancy by fitting time period (‘era’) as a covariate effect. To fit these models we included the 28 species and 228 sites for which quantitative trapping data were available. We used the package ‘RMark’ v2.0.1 in the R v2.12.2 framework to build design matrices, combine models, and to compare AIC weights among models [36].

To develop detection-adjusted elevation range profiles for each species in each era and region, we parameterized 25 occupancy models (*Ψ*) building on the model set of Moritz et al. [13] and Tingley et al. [14]. The 25 models included all 2- and 3-way interactions among the following variables: era (categorical: historical or modern), elevation (linear), elevation (quadratic) and region (categorical: Northern, Central, or Southern), as well as a constant model (.). The full model set is listed in Supplementary Table S5. Following Moritz et al. [13], we estimated the probability of detection per survey night (*p*) based on 34 competing models with the following variables: era (historical or modern), trend (linear change in detections over sequential nights due to the collection of trapped individuals, trap habituation or to trap-shyness), trap effort (number of traps/100 and the log10 of the number of traps), the interaction between era and trend, and the interactions between era and trap effort variables. We built detection models with all additive combinations of these independent variables, as well as a constant model (.). The full candidate model set is listed in Supplementary Table S5. We ran this full candidate *p* model set with two parameterizations of *Ψ*: a constant model and a fully parameterized model. From these analyses, we selected the set of *p* models that incorporated the best (lowest AIC) model and all models with ΔAIC < 2 for each species (Supplementary Table S3). This subset of *p* models (*n* = 16) were then combined with the full set of 25 *Ψ* models for a total of 400 competing models that were run for each species and compared using AIC [13].

We estimated temporal shifts in the lower and upper range limits for each species in each region following Moritz et al. [13]. For elevation distributions, we used all detection data including quantitatively trapped specimens, incidentally collected (shot or salvaged) specimens, and observational records (Supplementary Figure S2). We plotted all localities in each transect for each era against elevation, and coded each species at a locality as present or undetected. We then calculated the change in elevation of each range limit from the historical to the modern era. Statistical significance for shifts was determined by estimating site-specific detection probabilities (*p\**) by model averaging model-specific *p* estimated using AIC weights from our 400 occupancy models [37,13] (Supplementary Figure S3) and the probability of false absence (P*fa* [16]) for each species at sites where the species was undetected in one era and that were located between the lower or upper range limits of the two eras. Range limit shifts with P*fa* ≤ 0.05 were considered statistically significant and “ecologically relevant” if the movement was both >10% of the species’ historical elevation range and >100 meters in elevation [13].

## *Testing predictions of range shifts*

We used generalized linear mixed models (GLMM) and one-sided binomial tests to examine how patterns of range shifts were related to region (Northern, Central, Southern), species limit (upper or lower) and the elevational distribution of species (high or low elevation species). All GLMM models used a logit link and were run in R with the ‘lme4’ package [39]. Species identity was included as a random effect and model performance was assessed by AIC. We first used GLMMs to evaluate what factors were associated with occurrence of a range shift (as a binary variable). Species widespread across elevations (*P. maniculatus* and *O. beecheyi*) were excluded from this analysis because they could not be categorised into low or high elevation species. We defined 12 models comprised of a null model (intercept only) and all additive combinations and one-way interactions between 3 categorical explanatory variables: (1) limit (upper or lower elevation range limit), (2) region, and (3) zone (low or high elevation species). Second, to resolve interaction effects associated with zone, we then analysed low elevation and high elevation species separately, retaining limit and region variables.

We used one-sided binomial tests to evaluate whether upslope shifts were the most common across regions (Prediction 1), whether range contractions were more likely in high elevation species and range expansions were more common in low elevation species (Prediction 2), and to evaluate whether the patterns of range shifts were consistent across regions (Prediction 3). For each of these analyses, we included only those species that exhibited significant shifts determined from the *Pfa* analysis above.

## *Climatic nearest neighbour*

We examined spatial heterogeneity in climate change (Prediction 4) by identifying the nearest climatic neighbours of historical localities under modern climate conditions, following the approach described in Tingley et al.[14]. Using four standard BIOCLIM variables (mean annual temperature, B1; maximum temperature of the warmest month, B5; minimum temperature of the coldest month, B6; and mean annual precipitation, B12) from the Parameter-elevation Regressions on Independent Slope Model (PRISM [38] at a resolution of 30 arc-second (1 km2), we calculated 20-year averages for the historical (1910-1930) and modern (1989-2009) survey periods. Climatic distances for each of the BIOCLIM variables were calculated between each historical locality and modern era PRISM grid cells within the same region, which was defined by a 20-kilometer buffer around the minimum convex polygon that encompassed all survey sites. For each historical site, we identified the 5% of modern cells that were nearest climatically and the 5% of historical cells that were nearest climatically. This was calculated separately for each climatic variable using the Euclidian distance. We subtracted the elevation of the historical site from the average elevation of the modern nearest climate neighbour cells; positive values indicated upslope movement in climate space. We recorded these values (positive or negative) for the two historical localities defining the upper and lower limits of each species on each transect. These values provided a climate-based prediction for movement of species at their range limits for each region (i.e., upslope or downslope). We compared these climate-data derived models to an “overall warming model” that assumes an increased temperature at all grid cells over the same time period, which always predicted upslope movements. For each climatic variable at each site, we also identified rare or disappearing climates using climatic thresholds of 1 °C temperature or 10 cm precipitation. We defined rare climates as those that occurred within climatic thresholds at < 2.5% of historical cells. We defined disappearing climates as those that occurred within climatic thresholds at ≥ 5% of historical cells and < 2.5% of modern cells. We excluded this subset of site-specific climate change from nearest neighbour comparisons because they violate an assumption of the method that climatically similar sites are available. We used a one-sided binomial to test if the upslope movement predicted from the overall warming model and predictions from each of the BIOCLIM variables were consistent with the direction of observed shifts (Prediction 4).

1. **Results**

## *Mammalian elevational range shifts over the past century*

Of the 67 small mammal species we detected in either the historical or modern surveys (Supplementary Table S2, Supplementary Fig. S2), we were able to use robust statistical methods to evaluate range shifts of 34 species. Across the three regions, we detected 52 significant range limit shifts, representing 31.3% of the 166 region-specific historical range limits across the 34 species analysed (Fig. 2, Supplementary Fig. S3). We observed no significant range limit shifts in nine species (26.4%), including two gophers (*Thomomys bottae* and *T. monticola*), three chipmunks (*Tamias merriami, T. quadrimaculatus*, and *T. amoenus*), two shrews (*Sorex trowbridgii,* and *S. vagrans*), a widespread deer mouse (*Peromyscus maniculatus*), and the pika (*Ochotona princeps*). The remaining 25 species (74.6%) shifted at least one range limit in one or more regions (Fig. 2, Supplementary Table S2).

We observed little consistency in range shifts of individual species among regions. Not one of the 22 species found in all three regions shifted both their upper and lower limits in the same direction in all three regions (Fig. 2). For example, both the bushy tailed woodrat (*Neotoma cinerea*) and the pinyon mouse (*Peromyscus truei*) showed substantial changes in elevational ranges in the northern and central regions but not in the southern Sierra Nevada, while the western gray squirrel (*Sciurus griseus*) contracted strongly in the south and marginally in the central Sierra Nevada, but expanded its range in the north.

Nevertheless, some important differences in the frequency and directionality of shifts emerged when examining high and low elevation species that did shift their ranges. Species’ elevational limits were more than twice as likely to move upslope (69.2%) as downslope (31.8%; one-sided binomial test, *n* = 52 species’ limits, *p* = 0.004; Fig. 3, Supplementary Table S3). High elevation species were significantly more likely to contract their ranges than to expand them (79% contract, *n* = 29 species’ limits, *p* = 0.001), whereas, contrary to our expectation, low elevation species contracted their limits as often as they expanded them (50% contract, *n* = 22 species’ limits, *p* = 0.584). These patterns emerged because there were significantly more upslope than downslope shifts of the lower limit of high elevation species (*n =* 21 lower limits, *p* < 0.001), whereas shifts in the upper limit of low elevation species were heterogeneous with nearly as many downslope shifts as upslope shifts (*n* = 17 upper limits, *p* = 0.315).

## *Range shifts in relation to climate*

Nearest climatic neighbour analyses revealed that both upslope and downslope shifts were predicted by temperature change at range limits (Fig. 1c). For low elevation species, a simple overall warming model (i.e., all upwards shifts) was the best predictor, but this model, as well as each of the climate-based predictions, was not significantly better than random (Fig. 4). For high elevation species, change in minimum annual temperature was the best predictor of the direction of range limit shifts, and explained 74.1% of range limit shifts observed. However, change in minimum temperature was only a slight improvement over an overall warming model (72.4% of shifts), local mean annual temperature change (69.2% of shifts), and local maximum annual temperature (72.0% of shifts). Predictions from the four temperature variables were significantly better than random (Fig. 4, *p* < 0.05). Mean annual precipitation (40% of shifts) explained fewer shifts than random, although not significantly less (*p* = 0.21).

Our nearest climatic neighbour analysis also identified climatic conditions that are disappearing from the landscape (i.e., a reduction of their historical geographic representation to less than half in the modern era). Twenty-one of the 134 historical sites in our study (15.7%) had climatic conditions that fit this definition of disappearing climates for at least one climate variable. Minimum annual temperature showed the most substantial effect with values at 15% of historical sites disappearing from the modern landscape. Mean annual temperature (1.5% of historical sites), maximum annual temperature (3.7% of historical sites), and mean annual precipitation (0 historical sites) did not decline as dramatically across the landscape.

1. **Discussion**

Our results from a multi-region, community-wide analysis of elevational transects across montane California suggested strong but locally heterogeneous impacts of recent climate change on the range limits of small mammals. Not one of the species shifted both their upper and lower limits in the same direction in all three regions (Fig. 2). There were, however, consistent and climatically predictable upslope range contractions in high elevation species, while low elevation species exhibited heterogeneous and climatically unpredictable directionality of range limit shifts. High elevation species that showed consistent range reduction included Belding’s ground squirrel (Urocitellus beldingi), the alpine chipmunk (Tamias alpinus) that is endemic to central-southern montane California, the Pacific jumping mouse (Zapus princeps), and the water shrew (Sorex palutris). These observations have been confirmed in more extensive analyses of U. beldingi and T. alpinus [11,40]. Of note, elevational ranges of the pika (Ochotona princeps), which attracted considerable attention because of extirpations and upslope retractions in the Great Basin [41,42], were stable across all three regions. This result is consistent with a more extensive study across montane California that found pika thriving across wider geographic and elevation ranges than reported historically [43].

While a coherent pattern of upslope movement was found for high elevation species, there was substantial heterogeneity in the response of low elevation species. The vast majority of sites in our study, especially at mid to high elevations, were located in protected reserves or public lands with minimal land-use conversion, although grazing, fire regimes and forestry practices may have altered habitat structure [44]. One might expect low elevation species should be more likely to experience impacts from land use change at their lower limits in the Central Valley and foothills [45,46]. However, we detected few contractions at lower limits of low elevation mammals (Fig. 3), and shifts were significantly more common at their upper limits where potential land-use impacts were less evident. Greater heterogeneity in responses of low elevation species may reflect stronger biotic influences [25,31], such as interspecific competition [33], seral dynamics of habitats [31], and the spread of invasive species [32].

Heterogeneous range shifts have been demonstrated in a range of taxa [5,25], suggesting that species’ responses to 20th century climate change were both influenced by local factors and were context dependent. Tingley et al.[14] found even greater heterogeneity in Californian birds sampled over the last century in the same regions; only half the observed range limit shifts of birds were upslope. Thus, while our findings confirmed some of the results from our initial study of small mammals in central montane California [13] and studies of birds [14], butterflies [46], and plants [28] over the similar spatial and temporal scales, they amplify the complex and variable ways that species have changed over the past century in California [25]. Moreover, intra-species heterogeneity in range shifts appears widespread from our data but is probably under-reported in the literature due to the infrequency of studies replicating range shift studies across spatially and ecophysically distinct survey regions.

Inconsistent patterns of range shifts among regions may be attributed to region-specific changes or local changes in temperature and precipitation [47]. In previous resurvey studies of birds and plants across the same regions, local changes in precipitation as well as temperature were related to range changes [14, 28]. For small mammals, however, precipitation was a poor predictor of the direction of shifts compared to temperature. These results indicate that the ranges of high elevation mammals are likely responding to changes in local temperature.

Consistent with the projected decline of alpine environments, all sites with disappearing climates occur above 1500 m [48,49]. For species inhabiting such sites historically, nearest climatic neighbours (Fig. 1c) provide poor prediction of contemporary range shifts as climatic analogues at nearby elevations are now rare or do not exist. Global climate projections suggest that disappearing climates will be an increasing challenge for predicting future species’ responses [50,51]. While no-analogue climates are typically considered when predicting future species’ ranges, ours is the first study to examine how such disappearing climates can affect inference and interpretability of observed range shifts.

Our rigorous study of elevational range shifts of mammals across montane California revealed heterogeneous responses of species within and among regions that were consistent with studies of other taxa [25] but that were filtered by the influence of local temperature change consistent with 20th century warming [2,5]. A suite of high elevation mammals appears to be undergoing range contraction. The challenge ahead is to understand the proximate causes of the diverse species’ responses to improve predictions of vulnerability [6]. We need a better understanding of whether and how species track climatic niches in response to local variation in climate change [30], or whether range changes are a response to ecosystem dynamics or species interactions. Moreover, identifying the life-history traits (e.g., dispersal ability, reproductive rate, and degree of ecological specialization) that best predict persistence or vulnerability [9,52,53] may provide key insights into the mechanisms of species- and region-specific responses to climate change. The diverse responses among closely related taxa that we find here (e.g., among different species of mice, chipmunks, ground squirrels, and woodrats) provide the basis for the detailed comparative studies that are necessary to improve our knowledge of vulnerability.

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**Author Contributions**

KCR, JLP, JDP, SRB, CM conceived and designed the experiments; KCR, KMCR, JLP, CJC, JDP performed the experiments; KCR, KMCR, MSK, MWT, SRB analysed the data; KCR, MSK, MWT, SRB contributed materials/analysis tools; KCR, KMCR, MWT, SRB, CM wrote the paper. All authors discussed the results and commented on the manuscript.

**Competing Financial Interests**

The authors declare no competing financial interest.

# Figure Legends

Figure 1. Climate change and expected elevation shifts across sampling sites. (a) Map of historical survey localities in relation to survey region and life zone; (b) Change in mean annual temperature (red) and mean annual precipitation (blue) between the historical (base of arrow) and modern (tip of arrow) eras across elevation; (c) average expectation of elevation shift in the modern era to achieve the most similar value of mean annual temperature (red squares) or mean annual precipitation (blue triangles) as historical localities across elevation, based on our climatic nearest neighbour analysis (see Methods); open squares and triangles indicate historical sites where similar climate is underrepresented regionally within the historical era (i.e., rare) or in the modern era (i.e., disappearing).

Figure 2. Elevation range limit shifts by region of the 34 modelled species, arranged by increasing average elevation range. Species were classified as low elevation, high elevation, or widespread based on their range limits in relation to life zone, following [13]: low elevation (historical elevation ranges within Lower Sonoran – Transition life zones; 01 – 13), high elevation (Transition – Alpine; 16 – 34), and widespread species (14 and 15). For each species, statistically significant elevation range contractions (red) and expansions (yellow) between the historical and modern eras are shown, along with non-significant contractions (grey) and expansions (white). Lack of a bar indicates that species is not found in that region.

Figure 3. Number and proportion of upper and lower range shifts of high and low elevation species across all regions. Pie charts display the proportion of range limits that exhibited significant expansions (yellow), contractions (red), or no significant change (grey). Numbers represent the number of individual shifts observed in each category. An asterisk next to a pie indicates that significantly more contractions were observed than expansions. For each elevation and limit category, the arrows above and below each pie indicate the direction (up or down) and the number of shifts observed in each direction at each range limit, with the width of the arrow indicating the relative proportion observed within each category. The colours of arrows indicate whether the shift resulted in an expansion (yellow) or contraction (red).

Figure 4. Significant range limit shifts of high and low elevation species in relation to climate predictions. Bars represent the percent of observed limit shifts that are consistent with the predictions from an overall warming model (i.e., all upwards) and with nearest neighbour analyses for each of the four BIOCLIM variables. Sample sizes indicate the number of range limit shifts within high and low elevation species that were significant from the *Pfa* analysis. Symbols above bars denote predictions that were significantly better than random (\* = *p* < 0.05).