# Title:

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

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# 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. Most species’ ranges shifted upslope or downslope in at least one region. However, two-thirds of ranges remained stable at one or both elevational limits, and few species shifted limits in the same direction in all regions. When shifts did occur, high elevation species typically contracted their lower limits upward, whereas low elevation species had heterogeneous responses. Local change in temperature was a better predictor of shift direction than precipitation, suggesting the heterogeneous responses of small mammals were influenced by local temperature change consistent with 20th century warming.

# Main Text:

Evidence for the biotic responses to recent climate change has continued to accumulate1-5 and is central to the prediction of vulnerability to future change6. There is a general trend toward upward and poleward shifts of elevational and latitudinal boundaries of species’ ranges 1-5,7,8, with “leading edge” expansions detected more often than “lagging edge” contractions9-12. However, there is considerable heterogeneity in the direction and magnitude of species’ responses, and ranges of many species have not changed at all13-15. 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 landscape1,15,16. 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 change17. Insights into the dynamics of species’ responses to recent climate change are most likely to come from spatially-replicated resurveys 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 birds and 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’s18-20. These data laid the foundation for Grinnell’s concept of the ecological niche and for understanding the climatic limits of species’ distributions21. They also provided a benchmark for documenting changes in the elevational ranges of species in California over the last century12,14,15,22. Over the past century, mean annual temperature in California has increased by ~0.6 °C23-25 (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 part26,27. Elevational ranges of species in California over this period have shifted heterogeneously, including species moving upslope, downslope or not at all14,15,28. Heterogeneity in movements of species has been partly explained by incorporating local-scale measures of climatic change for both temperature and precipitation15,29; 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 areas30,31.

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)14 to other regions in the north (Lassen Volcanic National Park, southern Cascade Range) and south (Sequoia/Kings Canyon National Parks, southern Sierra Nevada). We control 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 region14 and in birds across montane California15. 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, respectively15.

*Mammalian Elevational Range Shifts over the Past Century*

The majority of species’ elevational ranges remained stable at one or more limits, but ranges of most species shifted in at least one region (Fig. 2). 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).

There was little consistency of patterns in range shifts among regions. None 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 but not 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).

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*12,32. Of note, elevational ranges of the pika (*Ochotona princeps*), which attracted considerable attention because of extirpations and upslope retractions in the Great Basin33,34, 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 historically35.

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 structure36. 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 foothills37,38. 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 influences24,30 , such as interspecific competition32, seral dynamics of habitats30, and the spread of invasive species31.

Heterogeneous range shifts have been demonstrated in a range of taxa5,24, suggesting that species’ responses to 20th century climate change were both influenced by local factors and were context dependent. Tingley et al.15 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 California14 and studies of birds15, butterflies38, and plants27 over the similar spatial and temporal scales, they amplify the complex and variable ways that species have changed over the past century in California24. 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.

*Range Shifts in Relation to Climate*

Inconsistent patterns of range shifts among regions may be attributed to region-specific changes or local changes in temperature and precipitation39. In previous resurvey studies of birds and plants across the same regions, local changes in precipitation as well as temperature were related to range changes15, 27. For small mammals, however, precipitation was a poor predictor of the direction of shifts compared to temperature. 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 all four temperature variables were significantly different from random (Fig. 4, *p* < 0.05). Mean annual precipitation (40% of shifts) explained fewer shifts than random, although not significantly less (*p* = 0.21). These results indicate that the ranges of high elevation mammals are likely responding to changes in local temperature, highlighting the dynamic nature of species-specific responses to localized climate change.

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, see Supplementary Information for more details). Twenty-one of the historical sites in our study 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. Consistent with the projected decline of alpine environments, all sites with disappearing climates occur above 1500 m40,41. 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’ responses42,43. 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 taxa24 but that were filtered by the influence of local temperature change consistent with 20th century warming2,5. A suite of high elevation mammals appear to be undergoing range retraction. The challenge ahead is to understand the proximate causes of the diverse species’ responses to improve predictions of vulnerability6. We need a better understanding of whether and how species track climatic niches in response to local variation in climate change29, 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 vulnerability10,44 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.

**Methods:**

*Survey Regions and 20th Century Climate Change*

Historical surveys occurred between 1911 and 193417,18-20 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”). Each region differed considerably in physiognomy and climate change history (Fig. 1b, Supplementary Figure S1). See Tingley et al.15 for additional details of the sampling regions.

*Survey and Resurvey Data*

We defined localities or sampling sites as an aggregate of concurrent surveys (i.e., traplines) conducted within a 2 km distance and 100 m elevation14. Each site was georeferenced, and elevation was determined using a Digital Elevation Model and verified by ground-truthing or with topographic maps (Supplementary Table S1).

We obtained records from historical surveys conducted at 111 sites. 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 at 166 sites between 2003 and 2010 as part of the Grinnell Resurvey Project14,15 (Fig. 1a). Of these, 85 of the 111 historical sites were resurveyed. Additional modern sites were selected to maximize elevation coverage and to serve as proxies for otherwise inaccessible historical sites. 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]). See Supplementary Methods for details.

*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). 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 with the exception of sites within the Yellow Pine (*Pinus ponderosa*) belt on the east slope, which we included as west slope sites (See Supplemental Methods for details).

Species were categorized as low elevation (historical elevation ranges within Lower Sonoran – Transition life zones), high elevation (Transition – Alpine), or widespread14,18-20 (Supplementary Table S4).

*Modelling Changes in Elevational Ranges*

We modelled simultaneously the probability of detection (*p*) and the probability of occupancy (*Ψ*) of each species (*n* = 28) at each site to evaluate elevational range shifts using the single-season occupancy model framework implemented in the program MARK v6.045,46. See Supplemental Methods for details on model parameterizations (Supplementary Table S5).

We estimated temporal shifts in the lower and upper range limits for each species in each region following Moritz et al.14. Statistical significance for shifts was determined by estimating site-specific detection probabilities (*p\**) and the probability of false absence (P*fa*17) 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 elevation15.

*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). We excluded widespread species and those not demonstrating significant limit shifts determined from the *Pfa* analysis. See Supplementary Methods for model details.

*Climatic Nearest Neighbour*

For each species’ limit, we evaluated whether upslope or downslope movement between eras was better predicted based on site-specific climate data (four BIOCLIM variables) or an overall warming model predicting only upslope movement, using climatic nearest neighbour analysis15 and one-sided binomial tests. We excluded predictions from climates identified as either rare (geographically limited in the historical era) or disappearing (geographically limited in the modern era). See Supplementary Methods for details.

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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 (01 – 13), high elevation (16 – 34), or widespread species (14 and 15) based on their range limits in relation to life zone14. 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).

Figure 3. Summary of range shifts of high and low elevation species combined across all regions. Pie charts display proportion of range limits that exhibited significant expansions (yellow), contractions (red), or no significant change (grey). An asterisk next to a pie indicates that significantly more contractions were observed than expansions. Around each pie the width of arrows indicates the proportion of shifts that were in each direction and at each range limit. The colours of arrows indicate whether the shift resulted in an expansion (yellow) or contraction (red).

Figure 4. Significant range limit shifts in relation to climate predictions. Bars represent the percent of observed shifts for low and high elevation species 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. Symbols above bars denote predictions that were significantly better than random (\* = *p* < 0.05).