Title: **Montane mammals moving upward in the Rocky Mountains as temperature warms**

**Short title:** Upward elevational shifts in montane mammals

**Authors:** Christy M. McCain1,2, Sarah R. B. King2,3, Tim M. Szewczyk1,4,5

**Authors Affiliation:** 1Department of Ecology & Evolutionary Biology and 2CU Museum of Natural History, University of Colorado, Boulder, CO 80309 USA; 3Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA; 4Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824 USA; 5Department of Computer Science, University of New Hampshire, Durham, NH 03824 USA

**Corresponding Author:** Christy M. McCain, 265 UCB, University of Colorado, Boulder, CO 80309-0265. Telephone: 303-735-1016; E-mail: christy.mccain@colorado.edu

**Author Contributions:** C.M.M. formulated the ideas, wrote the grant, conducted the fieldwork, mammal identifications, and analyses, and wrote the manuscript. S.R.B.K. aided in collecting and georeferencing the specimen database, fieldwork, and manuscript revisions. T.S. helped with the fieldwork, the statistical models, and manuscript revisions.

**Keywords:** climate change, cold-adapted, Colorado, elevation, latitude, range contractions, range shifts rodents, shrews, trailing edge

**Type of Paper:** Primary Research Article

**Abstract**

The Southern Rocky Mountains, the largest and tallest mountain range in the contiguous United States, have warmed considerably in the past several decades due to anthropogenic climate change. Herein we examine how the elevational ranges of 47 mammal species (42 rodents, 5 shrews) have changed between their historical (pre-1980) and contemporary distributions (post-2005) in the Front Range Mountains and San Juan Mountains of Colorado. Historical elevational ranges were based on more than 4580 geo-referenced museum specimen and publication records. Contemporary elevational ranges were based on 7444 records from systematic sampling efforts and museum specimen records. We constructed Bayesian models to estimate the probability a species was present, but undetected, due to undersampling at each 50 m elevational bin for each time period and mountain range. These models leveraged individual-level detection probabilities, the number and patchiness of detections across 50 m bands of elevation, and a decaying likelihood of presence from last known detections. The 95% likelihood elevational ranges were then compared between historical and contemporary time periods to detect directional change. Responses were variable as 23 mammals shifted upward, 10 did not change, 10 shifted downward, and 4 were locally extirpated. The average range shift was 122 m upward, while exclusively montane species shifted upward more often (83%) and displayed larger average range shifts (337 m). Changes in upper range limits were best predicted by increases associated with (a) montane species, (b) species with higher maximum latitude in their geographic range, and (c) the study mountain in the southern edge of their geographic range (stepwise multivariate linear regression: r2 = 0.4705, p < 0.0001). Thus, mammals in the Southern Rocky Mountains serve as harbingers of more changes to come particularly for montane, cold-adapted species in the southern portion of their ranges.

**Introduction**

Earth is warming at an unprecedented rate from human-created emissions ([Duffy & Tebaldi, 2012](#_ENREF_19), [Trenberth *et al.*, 2007](#_ENREF_55), [USGCRP, 2009](#_ENREF_56)). Anthropogenic impacts are also affecting precipitation trends as well as increasing the variability and severity of extreme weather events ([Duffy & Tebaldi, 2012](#_ENREF_19), [Trenberth *et al.*, 2007](#_ENREF_55), [USGCRP, 2009](#_ENREF_56)). Essentially the planet and all its inhabitants are in a climate crisis of unknown magnitude. One urgent imperative is to track the impacts of these changes on living organisms to better mitigate the damages and to improve predictions of foreseeable conservation catastrophes. Unfortunately, there are still more publications predicting rather than measuring species’ responses ([e.g., Dawson *et al.*, 2011](#_ENREF_18), [review in McCain & King, 2014](#_ENREF_36)). Reasons for this disconnect are many-fold, but foremost are the paucity of detailed historical and repeatable surveys across gradients of change (e.g., latitude, elevation, depth), and the significant and long term effort and quantity of data needed to detect organismal responses. As a research community we need to embrace innovative ways to compile historical and contemporary records to robustly track how organisms are currently changing and monitor these changes through time ([Dawson *et al.*, 2011](#_ENREF_18), [Grytnes *et al.*, 2014](#_ENREF_24)).

Temperature cools at increasing elevations, thus as average temperatures increase in a region, species are expected to track temperatures by shifting to higher elevations (Figure 1: upper panel; e.g., [Inouye *et al.*, 2000](#_ENREF_26), [McDonald & Brown, 1992](#_ENREF_38), [Pauli *et al.*, 1996](#_ENREF_46)). Such upward tracking could include an upward contraction or shift of just the lower or upper end of the species’ range, or both range limits depending on the location on the montane gradient, and the consistency of the response between the range edges. The published resurveys of historical montane gradients do provide strong evidence that some organisms are shifting their ranges to higher elevations. For example, many small mammals have shifted upwards in the western United States ([Moritz *et al.*, 2008](#_ENREF_41), [Rowe *et al.*, 2015](#_ENREF_47), [Rowe *et al.*, 2010](#_ENREF_49)). Many alpine plants in Europe have shifted higher with climate change ([Engler *et al.*, 2011](#_ENREF_20), [Grabherr *et al.*, 1994](#_ENREF_23), [Lenoir *et al.*, 2008](#_ENREF_33), [Pauli *et al.*, 1996](#_ENREF_46)), moths in the Asian tropics have shifted upwards by an average of 67 m ([Chen *et al.*, 2009](#_ENREF_15)), and a review of montane shifts detected an 11 m increase in elevational ranges per decade across organisms ([Chen *et al.*, 2011](#_ENREF_14)). But the upward shifts are not the whole story; one critical element is the variability in responses on these gradients. Overall the shifts are upward, but individual species also demonstrate unexpected responses like downward shifts or no detectable changes (Figure 1: lower panel; [Crimmins *et al.*, 2011](#_ENREF_17), [Lenoir *et al.*, 2010](#_ENREF_32), [McCain & King, 2014](#_ENREF_36), [Rowe *et al.*, 2015](#_ENREF_47)). The location of the mountain appears important. For example, American pika on small, isolated sky islands in the western US are experiencing local extirpations linked to higher temperatures, decreased precipitation, and lack of rock ice features ([Beever *et al.*, 2003](#_ENREF_5), [Beever *et al.*, 2010](#_ENREF_6), [Beever *et al.*, 2011](#_ENREF_7), [Millar & Westfall, 2010](#_ENREF_40)). But the same species in the more expansive, taller, and interconnected southern Rocky Mountains appear to have few, if any, local extirpations ([Erb *et al.*, 2011](#_ENREF_21)). Unfortunately, that is the only multi-site climate change study on mammals in the US Rocky Mountains ([McCain & King, 2014](#_ENREF_36)).

Other important biogeographic factors mediating responses may include the latitude of the mountain, the location of the mountain in relationship to the species’ geographic range, and the size, height and isolation of the mountain ([e.g., McCain & King, 2014](#_ENREF_36)). Traits of the species themselves like body size, activity times, and physiology may also mediate who responds as predicted to climate change and who does not (e.g., [Angert *et al.*, 2011](#_ENREF_2), [McCain & King, 2014](#_ENREF_36), [Moritz *et al.*, 2008](#_ENREF_41)). So far, such mediating traits are rarely detected in individual montane gradient studies. But for mammals, despite some initial lack of trait detection ([e.g., Angert *et al.*, 2011](#_ENREF_2), [Moritz *et al.*, 2008](#_ENREF_41)), McCain and King ([2014](#_ENREF_36)) detected that body size, activity patterns, and locations of latitudinal and elevational ranges were important in explaining which North American mammal species responded as predicted to climate change. Surely if traits were important to mediating responses, we would also detect them on individual mountain gradients or particular regional studies encompassing multiple species as long as sufficient variability in the traits was exhibited among the species. Strong associations in species traits with climate change responses would enable better predictions and improve conservation outcomes for the types of species most at risk from large, fast, detrimental environmental change.

Thus, herein, we examine how 47 mammal elevational ranges have changed in response to warming in two regions of the largest, tallest and most interconnected mountains in the contiguous US, the Southern Rocky Mountains. We compile historical elevational ranges for each species based on museum specimens and literature before 1980, and contemporary elevational ranges based on more than a decade of extensive trapping surveys and supplemental museum specimens (>2005). We develop Bayesian undersampling models to accommodate species-, mountain-, and time-period-specific 95% likelihood elevational ranges. Then we assess how elevational ranges have changed with climate change, testing for biogeographic and species-trait effects that may mediate which species are and are not moving higher in elevation with increasing temperatures.

**Materials and methods**

The Rocky Mountains extend from northern New Mexico, USA to northwestern, British Columbia, Canada reaching their highest elevations in Colorado, USA. The two mountainous regions studied in the Colorado Rockies, the San Juan Mountains (1414–4286 m) and the Front Range Mountains (1438–4346 m), were chosen for their contrasting climates and geography (Figure 2; [Armstrong *et al.*, 2011](#_ENREF_4), [Fitzgerald *et al.*, 1994](#_ENREF_22), [McCain *et al.*, 2018](#_ENREF_37)). On both gradients, temperature decreases and precipitation increases with elevation ([McCain *et al.*, 2018](#_ENREF_37)). Climatically, the southwestern San Juans are warmer and wetter than the more northeastern Front Range. Both mountains receive precipitation as snow in the winter months, but the San Juans intercept substantial rainfall from summer monsoons predominately at mid- and high-elevations, as the base of the San Juans is semi-arid desert habitat. The Front Range is less arid at the base, characterized by the western-most extension of eastern plains grassland. Temperatures have increased on both mountains since the 1980s, but the San Juans are getting increasingly wetter, while the Front Range is becoming increasingly drier (Mote et al. 2005). Both mountains reside upon a geographically extensive plateau across the western US (Colorado Plateau), thus their base elevations start considerably higher than most mountains in regions nearer to sea level.

Mammal surveys and collecting began in the mid-to-late 1800s in both regions, but the Front Range is more intensively sampled (Figure 2) due to its easier access, the closer proximity of the two largest universities in the state, and the inclusion of Rocky Mountain National Park. We began trapping small mammals in the San Juan Mountains in 2007 and the Front Range Mountains in 2010; thus we have over a decade of mammal surveys and experience in the two ranges (Appendix S1). The two ranges have similar small mammal richness (rodents and shrews) with 35 species in the Front Range and 31 species in the San Juans among which 22 are shared ([McCain *et al.*, 2018](#_ENREF_37)).

*Historical Mammal Data*

We amassed specimen data from all museum collections with mammal specimens from Colorado, USA (Figure 2 circles). We downloaded data from or contacted 75 museums, and received records for 58,709 specimens from 45 of these institutions with Colorado holdings (2009–2012; Appendix S1). These specimen records were updated to current nomenclature following Wilson and Reeder ([2005](#_ENREF_59)), and were georeferenced following the MaNis protocols with quantified error estimates ([Chapman & Wieczorek, 2006](#_ENREF_13), [Wieczorek *et al.*, 2004](#_ENREF_58)). For quality assurance, we restricted analyses to rodent and shrew specimens with (1) a reliable species-level identification by an expert, re-verified by CMM, or in a robust locality for the species (core elevations in the local distribution); (2) a documented year or time period of collection; (3) an elevation provided by the collector or a locality specific enough to be georeferenced (latitude, longitude, elevation) with an horizontal error <1000 m in the latitude-longitude (designated as usable) or <5000 m (designated as marginal) with the strictest criteria used in the final lowest and highest known sites; and (4) a location within the northeast portion of the Front Range (Boulder and Larimer counties) or the southwestern portion of the San Juans (Dolores, La Plata, Montezuma, San Juan counties). Each species’ historical elevational range on each gradient was based on the vetted specimen records dated before 1980. These data were augmented by historical specimens or trapping records in the literature that we did not encounter from the museums, including from the *Colorado Biological Survey* ([Cary, 1911](#_ENREF_12)), *Mammals of Mesa Verde National Park, Colorado* ([Anderson, 1961](#_ENREF_1)), and *Distribution of Mammals in Colorado* ([Armstrong, 1972](#_ENREF_3)) with a particular emphasis on lowest and highest historical records in each mountain region. The most rigorous vetting was implemented for the lowest and highest known localities for each species, in which case records were not used if any significant error was plausible in the locality, the elevation, or the identification.

*Contemporary Mammal Data*

All specimens from our Colorado mammal database and contemporary surveys that met the accuracy criteria and were collected or documented after 2005 were included in the contemporary data (Figure 2 stars). The Colorado database was augmented in 2018 using searches on GBIF (Global Biodiversity Information Facility: www.gbif.org) and Arctos (https://arctos.database.museum) for more recent specimens (2006–2018) of just our target species that had been added or collected since our original database construction. These were georeferenced (if not originally) and vetted as were all previous records.

For systematic, contemporary mammal surveys, two elevational transects were established in the southwestern San Juan Mountains and two in the northeastern Front Range ([Figure 2: some stars; Figure S1.1; McCain *et al.*, 2018](#_ENREF_37)). Each transect consisted of eight sites placed every 200−300m in elevation between the base of the range (1400−1700m) and the upper limit of vegetation on the mountain top (3600−3800m) (Figure S1.1). At each of these 32 sites, we conducted small mammal surveys between 2010−2012 using live-trapping, pitfall traps, and visual surveys. We chose sites that reflected the main habitats at that elevation and were anthropogenically undisturbed. Mark and recapture live-trapping was based on 300 Sherman live-traps open for 5 consecutive nights placed across habitat types (1500 trap-nights per site). Additionally, 40 pitfall traps, which better detect shrew species, were sampled across habitats for 90 days (~3600 pitfall trap-nights per site). For diurnal rodents that do not readily enter live-traps, five visual transect surveys were conducted for one hour during each of the trapping days. Visual surveys were stratified by time and location, and each sighted mammal was geo-referenced with a hand-held GPS unit. Trapping data from nine sites in the San Juans in 2007 were also included (Figure S1.1), consisting of 100 live-traps and 10 pitfall traps for 3 consecutive nights per site. Additional strategic trapping and visual surveys were conducted in sites and elevations with critical potential areas of undersampling contemporarily, including Mesa Verde National Park in 2018 with live-trapping at two sites (200 traps for 4 nights per site), pitfall traps at 9 sites (20 traps for 3 weeks per site), and standardized visual surveys at 13 sites (Figure S1.1). We also conducted additional live-trapping (200 traps for 3 nights per site), pitfall trapping (10 pitfall for 3 weeks per site), and visual surveys in three low elevation sites in the Front Range in 2017. Species were identified in hand, based on collected specimens, or with DNA sequences in cases of problematic identifications ([McCain *et al.*, 2018](#_ENREF_37)). Lastly, all mammal sightings while in camps, in transit between sites, scouting sites, or during climate and vegetation data collection were also geo-referenced with elevation recorded.

*Bayesian Undersampling Models*

The documented elevational range of each species was assumed to be between the lowest and highest known localities per time period (i.e., interpolated ranges), as species are not always detected when present ([MacKenzie *et al.*, 2002](#_ENREF_34)). But the sampling along each elevational gradient in each time period was patchily distributed (Figure 2, S1.2). Therefore, to estimate elevations in which each species had a high probability of occurrence beyond the observed range, we developed a Bayesian model. Occupancy models typically rely on repeated surveys and local environmental data to predict a species’ probability of presence when undetected in a particular locality ([Kéry & Royle, 2008](#_ENREF_30), [MacKenzie *et al.*, 2002](#_ENREF_34), [Szewczyk & McCain, 2019](#_ENREF_51)). Such data are unavailable in many cases, including for typical compiled historical datasets. Consequently, we employed a modified conceptual framework for occupancy to evaluate the probability of sampling error rather than directly considering species’ environmental preferences.

Within each time period, mountain range, and elevational bin, we considered the detected individuals as a draw from a multinomial distribution (Fig. S1.2), representing a sample from the community of individuals at those elevations. The number of observed individuals from each species depends on the species’ relative abundance and the probability of detecting a given individual of the species. Thus, for each elevational bin *i*, the number of observed individuals belonging to species 1–*J*, represented as the vector ***yi***, was modeled as:

where ***pj*** is a vector of the probabilities that a random observed individual from elevational bin *i* belongs to each species, *Yi* is the total number of individuals detected across all species in elevational bin *i*, *λij* is the relative abundance of species *j* in elevational bin *i*, *Zij* is a latent binary parameter indicating the true presence (1) or absence (0) of species *j* in elevational bin *i*, and *δj* is the probability of detecting a given individual of species *j*. Note that *pij* is a probability ranging from 0 (species *j* is not present at elevation *i*) to 1 (only species *j* is present at elevation *i*). We used the repeated, mark and recapture survey data in the contemporaneous dataset to calculate the individual-level detection probability, *δj*, for each species. If there were too few recaptures for robust estimation in a particular species, then an average from the clade was used (e.g., *Sorex*).

The unobserved parameter *Zij* is Bernoulli distributed with probability , which is the probability that species *j* was present but unobserved due to sampling error beyond its interpolated range, and is calculated as a function of the elevational distance to the observed elevational limits, the patchiness of the interpolated range (i.e., the proportion of elevational bins without detections within the interpolated range), and their interaction:

where *aj* is the species-specific intercept and *β* are the slopes. The intercepts among species were distributed normally with community-level mean *α* and standard deviation *σ*, while the slopes were community-level with one value for all species.

For each elevational bin beyond each species’ interpolated range, we calculated the probability of occurrence as the posterior probability of *Zij* = 1. A species was assumed absent at an elevation if the probability of occurrence was < 5%, indicating ≥ 95% posterior probability of absence. Based on this dichotomy, we calculated Bayesian interpolated ranges incorporating sampling uncertainty to then use as the elevational range of each species for each mountain in each time period. For the range shift analyses, we only included species with at least 10 historical records per mountain that were also detected in the contemporary sampling.

The model was run with JAGS 4.3.0 in R 3.6.1 using the *rjags* package. For each model, we ran 3 chains for 20,000 iterations, discarding the first 10,000 iterations as burn-in, and then retaining every 10th iteration for the final posterior distributions. We used uninformative prior distributions for *α*, *β*, and *σ*, and a diffuse normal prior distribution constrained to be positive for each *λij* where the mean was the overall abundance of each species (Appendix S1).

*Statistical Analyses*

A significant change from the Bayesian historical to the Bayesian contemporary elevational range limits was determined if the change was ≥ 100m. The size of the shift upward or downward was calculated for the (1) lower limit; (2) upper limit; and (3) overall elevational change in range upward or downward based on the direction of range midpoint shift and the combined lower and upper shifts for those species the greatly contract their range (Figure 1). With warming temperatures, species’ elevational ranges are predicted to shift to higher, cooler elevations. This expected trend is most clearly detected in an upward shift of both limits, but is also detectable when only one limit shifts upward and the other remain unchanged, or in cases of an overall range contraction to a smaller area within the historical range with more extreme contraction of the lower limit (Figure 1: upper panel). Unexpected responses to warming temperatures would be no detectable change where both range limits change by less than 100m, or a downward shift in one or both limits such that the contemporary range midpoint is lower (Figure 1: lower panel). Overall, the primary prediction for the small mammal communities on each mountain is that all or most species shift to higher elevations on average, but a secondary prediction is that most range gains occur at mid- to high-elevations thus gains increase with elevation, whereas the losses would be spread across the gradient more or less evenly. In contrast, anthropogenic habitat change declines with elevation on both mountains, but is most pronounced at the base of the Front Range. Thus, if the reduction of available habitat is the predominant factor influencing the elevational distribution of the community, then the prediction would be a concentration of range losses at the lowest portion of the gradients that decreases toward the highest elevations.

To assess whether range losses and range gains were associated with particular areas on the mountains, we calculated the number of species losing or gaining range at their lower and upper limits within each 50m band up each mountain. Because the number of species per elevational band differs (unimodal with highest richness of included species between 1900–2000m), counts of range losses and range gains summed across all species for each 50m elevational band on each mountain gradient is biased towards elevations with more species. Thus, we examined the percentage of range losses and range gains for each 50m elevational band on each mountain gradient by dividing the species counts by the historical number of species present at each band. The net difference between percent gains and losses within each elevational band created an elevational heat-map of the range changes. We used non-parametric Spearman’s rank correlation tests to assess whether the trend in percent range losses decreased with elevation or percent range gains increased with elevation on each mountain gradient.

To assess how species traits influenced the responses to anthropogenic climate change, we examined several traits empirically linked or hypothesized to be important to differential responses to climate change in mammals (e.g., [Angert *et al.*, 2011](#_ENREF_2), [McCain & King, 2014](#_ENREF_36), [Moritz *et al.*, 2008 and references therein](#_ENREF_41)), including body size, activity times, elevational affiliations, high latitude ranges, location of study area within the species biogeographic range (i.e., southern third, middle third or northern third of its range), or whether the study area was near the species’ range edge (e.g., western-most populations of a plains species). Many more traits were possible, but we were limited by our species sample size as well as the similarity or correlation in many other traits considered here (e.g., body size and reproductive traits). Body sizes in grams were taken from the PanTHERIA and MOM databases ([Jones *et al.*, 2009](#_ENREF_28), [Smith *et al.*, 2003](#_ENREF_50)). Daily activity times (obligate diurnal, obligate nocturnal, and flexible) were from the PanTHERIA database ([Jones *et al.*, 2009](#_ENREF_28)) or species accounts in the journal *Mammalian Species*, and were checked against additional literature sources ([Armstrong *et al.*, 2011](#_ENREF_4), [Hall, 1981](#_ENREF_25), [Nowak, 1991](#_ENREF_43)). Each species was denoted as a low elevation species, a montane species, or cosmopolitan (across most habitats and elevations on the mountain) by its known habitat affinities in Colorado ([Armstrong *et al.*, 2011](#_ENREF_4)), but also based on its individual historical distribution on each mountain (all or most of its range below or above the midpoint of the mountain). Latitudinal ranges and study locations within North American geographic ranges were calculated from the PanTHERIA database ([Jones *et al.*, 2009](#_ENREF_28)) but modified to only include distributions within North America ([Hall, 1981](#_ENREF_25), [IUCN, 2011](#_ENREF_27)).

Trends in lower and upper range shifts were analyzed to detect if particular traits were associated with differential increases or decreases using multivariate linear regressions on each mountain. We used stepwise models, the lowest AICc weights, and all variables that were individually significant to detect the best-fit model ([Burnham & Andersen, 2002](#_ENREF_11)). A second set of trait analyses were conducted on expected (upward) and non-expected responses (downward, no change) on each mountain using stepwise multivariate, logistic regressions and the lowest AICc weights to detect the best-fit model as in McCain and King ([2014](#_ENREF_36)). Because phylogenetic relatedness could impact the robustness of these analyses (e.g., [Blomberg & Garland, 2002](#_ENREF_9), [Blomberg *et al.*, 2003](#_ENREF_10)), we estimated a phylogenetic signal in the lower and upper range shifts on each mountain. Phylogenies were from the mammal supertree ([Bininda-Emonds *et al.*, 2007](#_ENREF_8)) pruned to the taxa included in each mountain dataset. Phylogenetic signal was calculated with *phylosignal* ([Keck *et al.*, 2016](#_ENREF_29)) in *R* ([Team, 2019](#_ENREF_52)) using all five significance tests (*Cmean*, *I*, *K*, *K.star*, and *Lambda*). Because no significant phylogenetic signal was detected for the lower or upper elevational range shifts on either mountain (p >> 0.05; Table S1.1), we only used the non-phylogenetically corrected analyses.

**Results**

Our compiled databases for historical and contemporary distributions of small mammals (rodents, shrews) included 35 species in the Front Range Mountains (FR) and 33 species in the San Juan Mountains (SJ). Those species used in the analyses (28 FR, 19 SJ) were well sampled both historically and contemporarily with an average of 97 specimens historically and 158 specimens contemporarily per mountain (Appendix S2). The empirical elevational ranges for each species were based on these data for each mountain and time period (Figure 3: thick bars). Several species were not used in the range shift analyses because they were deemed to be insufficiently detected historically (<10 specimens; 6 FR, 13 SJ) or under-sampled with contemporary trapping methods (3 FR, 1 SJ; see Figure S3.1). The sampling across each elevational gradient in each time period was not uniform (Figure 2; Figure S1.2). This is expected given the historically compiled efforts across multiple generations of researchers. Nonetheless, the number of specimens and localities is quite high both historically (4580 specimen-localities) and contemporarily (7444 specimen-localities) for these two regions. Importantly, the sampling effort is underestimated from these specimen sums. It represents only the successful captures of our target species, but not the captures of non-target mammals, any individuals not saved as specimens, nor the trapping efforts that resulted in no or few specimens. To compensate for the patchy distribution of specimens and sampling across the two mountains and time periods, we constructed Bayesian undersampling models.

The Bayesian undersampling models utilized the number of observations per 50m elevational band, the estimated probability of detection based on our mark-recapture statistics, the patchiness of the elevational distribution for the species, and a declining probability of undersampling away from the last known detection to estimate a probability of distribution. The changes in the range limits between the empirical data and the Bayesian model varied from 0 to 392 m historically and 60 to 657 m contemporarily. The elevational limits based on the 95% probability for both the lower limit and the upper limit on each species elevational range per mountain per time period was then compared to assess range shifts with climate change (Figure 3: thin bar extensions; Appendix S2). Species that significantly shifted their lower or upper elevational limit contemporarily (≥100m change) included 23 species that shifted upwards and 10 species that shifted downward (Figure 3 blue and red bars, respectively). Another 10 species did not significantly shift either range limits (Figure 3 grey bars), and four species known historically were undetected contemporarily and thus considered locally extirpated (zeros in place of contemporary range bars). In comparison to the expected and unexpected range changes (Figure 1), the majority of upward changes were shifts, while the majority of downward changes were contractions (Figure 3C). The changes indicated by the empirical elevational ranges without the Bayesian model additions were similar, but even more skewed toward upward changes (32 upward, 6 downward, 0 no change), and the percentage of upward contractions was higher (50% versus 30% (the latter in Figure 3C)).

With the Bayesian models, the average elevational range change across all species was upward by 122 m. The Front Range species shifted higher on average (152 m) than did the San Juan species (80 m). These shifts varied across species with both losses and gains in lower limits and upper limits (Figure 3). Elevational heat maps display the non-random distribution of range losses and gains (Figure 4A). The percentage of range gains increased significantly with elevation on both gradients (Figure 4B, C; Spearman’s rank correlations: FR r = 0.42, p = 0.0399; SJ r = 0.53, p = 0.0077). Whereas, the percentage of elevational losses occurred across both elevational gradients rather uniformly (Spearman’s rank correlation FR r = -0.23, p = 0.2827; SJ r = 0.245, p = 0.2485). All four species detected as locally extinct were low elevation rodents with relatively small elevational ranges and all associated with dry desert, grassland or canyon habitats.

A combination of species traits and biogeography influenced the trajectory and magnitude of the range changes, particularly for the shifts in the upper range limits (Figure 5, 6). Montane species shifted higher more often (83%) and with larger upward shifts (337 m) than low elevation (31%, -31 m) or cosmopolitan species (42%, 150 m). The best multivariate linear regression model for the upper range limit shifts based on the lowest AICc weight and all variables individually significant (r2 = 0.4705, p < 0.0001, AICc weight = 605.2) consisted of an increase in upward shifts for montane species (Figure 5A, 6A), for species with high maximum latitude in their geographic range (Figure 6A), and species in which the study mountains were at the southern edge of their geographic range (Figure 6B). The best multivariate linear regression model for the lower range limit shifts was less conclusive (r2 = 0.1025, p < 0.0363, AICc weight 626.9) and only included an increase in upward shifts for species where the study mountain was at the eastern edge of their geographic range (Figure 6C). Lastly, the best multivariate logistic regression model for the expected responses to climate change (upward changes) versus the unexpected responses (downward changes, no responses) detected a greater preponderance of unexpected responses in the low elevation species compared to the montane and cosmopolitan species (Fig. 5B; χ2 = 8.5582, p < 0.0136, AICc weight = 57.4).

**Discussion**

Small mammals are moving to higher elevations in the Colorado Rocky Mountains on average by over 120 m with slightly larger upward shifts in the northwestern Front Range Mountains (180 m) than the southwestern San Juan Mountains (80 m). Since temperatures have warmed across Colorado and within each of these mountains ([McGuire *et al.*, 2012](#_ENREF_39), [Mote *et al.*, 2005](#_ENREF_42), [Trenberth *et al.*, 2007](#_ENREF_55), [USGCRP, 2009](#_ENREF_56)), this confirms the expected response to anthropogenic climate change—species sensitive to temperature will track cooler temperatures at higher elevations as temperatures increase (Figure 1; [Parmesan & Yohe, 2003](#_ENREF_45), [Pauli *et al.*, 1996](#_ENREF_46), [Thomas *et al.*, 2004](#_ENREF_53), [Walther *et al.*, 2005](#_ENREF_57)). This trend is most pronounced in the montane mammals—those with elevational ranges predominately in montane habitats at mid- to high-elevations—who are shifting upward by an average of over 330m (Figure 3, 5A, 6A).

Physiological and biogeographic traits mediate who is responding as expected by shifting higher and which species are not responding as expected by shifting downward or not changing. In particular, the distance shifted upward by small mammals appears to be a function of cold-adaption. This is inferred by the factors associated with increased upper range limits, including species with (a) a montane affiliation, (b) geographic ranges extending to higher maximum latitudes, and (c) the Front Range and San Juan Mountains occurring in their southern, lower geographic limits (Fig. 6A, B; r2 = 0.4705, p < 0.0001). The species least likely to respond as expected were the lower elevation species, which in these areas include mostly semi-arid desert, canyon land, and grassland species adapted to higher temperatures and lower rainfall than their montane counterparts ([Armstrong *et al.*, 2011](#_ENREF_4)) (Fig. 5B; χ2 = 8.5582, p < 0.0136). Changes in lower range limits were more enigmatic and variable across species than upper limits. Species in which the Front Range or the San Juan Mountains were at the eastern edge of their geographic range moved their lower elevational limit higher (Fig. 6C; r2 = 0.1025, p < 0.0363). Again, this may be an indication of montane, cold-adapted species, since most of the species with the southern Rockies as their eastern geographic range edge are species distributed only in the intermountain west or western North America ([Armstrong, 1972](#_ENREF_3), [Armstrong *et al.*, 2011](#_ENREF_4), [Hall, 1981](#_ENREF_25)). For example, some of the eastern edge species that shifted their lower limit upward include Red-back voles (*Myodes gapperi*), Water shrews (*Sorex palustris*), Yellow-bellied marmots (*Marmota flaviventris*), and Golden-mantled ground squirrels (*Callospermophilus lateralis*) (see Appendix S2). Another factor potentially obscuring the lower range edge changes was the contemporary undersampling at the lowest elevations, particularly below 1600m in the Front Range, due to relative lack of remaining intact habitat. The empirical ranges detected many more upward contracting trailing edges (lower limits), than did the Bayesian models that compensated for this low sampling effort. Thus, the results here are a more conservative estimate of lower limit contractions and, consequently, overall range shifts.

Most resurveys designed to detect elevational range shifts take advantage of well-sampled, historical studies of a single set of sites along an elevational gradient (e.g., [Moritz *et al.*, 2008](#_ENREF_41), [Nufio *et al.*, 2010](#_ENREF_44), [Rowe *et al.*, 2010](#_ENREF_49), [Tingley *et al.*, 2012](#_ENREF_54)). Then the contemporary researchers resurvey those particular sites as best as possible to detect changes due to climate change or land use change. But those ideal historical datasets are rare and if we limit ourselves to such studies, we will not proceed in detecting climate change effects much beyond published studies. Herein we used a more expansive methodology by building a dataset of historical elevational distributions for two mountain slopes, the southeastern-facing slope of the San Juan Mountains and the northeastern-facing slope of the Front Range, based on specimens and records of multiple generations of researchers. Then, we compared these historical datasets to contemporarily collected data through an extensive trapping effort augmented by specimens and records of additional researchers. This methodology has advantages as the elevational ranges are based on many more sites, potentially capturing the elevational ranges on a mountain more completely and reducing stochastic effects of the particular time period of sampling ([McCain](#_ENREF_35" \o "McCain, 2016 #3068) *[et al.](#_ENREF_35" \o "McCain, 2016 #3068)*[, 2016](#_ENREF_35" \o "McCain, 2016 #3068)). Further, because the historical ranges are determined by the highest and lowest observations, detecting changes may be a higher statistical bar than detecting changes at single sites. However, there are also disadvantages as the data are not compared at single sites, and the sampling is broader spatially and temporally and thus patchier. Tpotential

We combat these sampling issues in multiple ways. First, the specimens, their identifications, their localities, and elevations were vetted extensively, with particular emphasis on records near the elevational margins for each species since historical and contemporary comparisons are essentially comparisons of the lower and upper maximum records. Difficult to identify species (i.e., shrews, chipmunks, voles, and *Peromyscus*) were dealt with special emphasis on re-identifications, molecular analyses, and quantitative morphological models ([e.g., Chinn, 2018](#_ENREF_16), [King & McCain, 2015](#_ENREF_31), [McCain *et al.*, 2018](#_ENREF_37)). Second, we built Bayesian models to estimate sampling-based uncertainty across each gradient tailored to the species’ detections and detectability as well as the overall distribution of samples. This led to 95% Bayesian limits which were robustly extended beyond the empirical ranges for comparisons between time periods by accounting for the influence of patchy sampling. The maximum contemporary elevation for many species was higher than any historical record for either region (southwest quadrant or northeast quadrant of the state), making it unlikely that the upward shifts were due to historical undersampling of high elevations in each of these two mountains. Similarly, many of the upward shifting species had changes in both their lower and upper limits that were well below the highest elevations on each mountain. The Front Range Mountains were the better sampled of the historical gradients, and showed stronger elevational shifts while detecting similar patterns as the lesser sampled San Juan Mountain species. Thus, the conclusions remain unchanged across both mountain ranges.

Anthropogenic land use change is not absent from these gradients ([Szewczyk & McCain, 2019](#_ENREF_51)), and has been shown to influence other small mammal elevational studies (e.g., [Rowe, 2007](#_ENREF_48), [Rowe *et al.*, 2010](#_ENREF_49)). But along these gradients it is most concentrated at the lowest elevations, particularly at the base of the Front Range Mountains, and declines with elevation. It is likely that the three local extirpations in the Front Range, which were all at the lowest elevations, were predominantly due to direct reduction of their habitat. These three heteromyid species (*Dipodomys ordii, Perognathus flavescens, P. flavus*) were previously detected in areas around the cities of Boulder and Loveland that are now almost completely developed. But despite these localized influences, the effect of land use on the broader gradient appears to be limited. There is no signal of greater numbers of range reductions in the lowest elevations that then decline with elevation on either mountain. In fact, range reductions occur rather evenly across both gradients, while range gains do increase with elevation as expected with climate change (Figure 4B, C).

Other small mammal studies along elevational gradients similarly observed a mixture of species shifting higher and lower as well as those not showing much change ([Moritz *et al.*, 2008](#_ENREF_41), [Rowe *et al.*, 2015](#_ENREF_47), [Rowe *et al.*, 2010](#_ENREF_49)). They each also detected some legacies of land use change. But unlike those studies, we detected species traits that strongly mediated which species shifted upward as expected by climate change and which did not (Fig. 5, 6). This may be due to the larger, more connected, and more diverse mammal community of the southern Rocky Mountains studied here, or potentially the degree of variation in key traits across the included species. When many of those species and their responses from previous studies were analyzed together, upward contractions were supported in montane species, larger bodied mammals, and obligately diurnal species ([McCain & King, 2014](#_ENREF_36)). In this dataset we did not detect an influence of body size, but likely this was an issue of only including smaller sized mammals in our target group, and unlike previous studies, all shrews (the smallest mammals on these mountains) included in our dataset shifted their elevational ranges upward.

These data are clear evidence that small mammals, particularly montane and cold-adapted species, are shifting their ranges to higher elevations as temperatures warm regionally. These data provide a warning that our cold-adapted, high elevation, high latitude species are indeed responding to anthropogenic climate change in general by moving higher. The lower limit shift upward appears to be a less pronounced trend than upper limit extensions. This lag may indicate the temporal variability in climate change conditions year to year allowing some populations to exist despite their low viability long-term, but also may indicate that more sampling is needed at the lowest elevations in existing patches of intact habitat to confirm empirical absences. Clearly, the type of species and where a species is studied within their range are important. Thus, cold-adapted, montane species in the southern edge of their geographic ranges are critical groups of species of conservation concern as temperature continue to warm based on these data an previous analyses ([McCain & King, 2014](#_ENREF_36)). Take heed—it is only going to continue.

**Acknowledgements**

This work was supported by the US National Science Foundation (McCain: DEB 0949601). We thank all researchers and museum collections whose data were used in this study (Appendix S1), and J. Beck and the McCain Mountain Lab for feedback on manuscript drafts.

**References**

Anderson S (1961) Mammals of Mesa Verde National Park, Colorado. University of Kansas Publications, Museum of Natural History*,* **14**, 29–67.

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ (2011) Do species’ traits predict recent shifts at expanding range edges? Ecology Letters*,* **14**, 677-689.

Armstrong DM (1972) Distribution of mammals in Colorado. Monograph of the Museum of Natural History, The University of Kansas*,* **3**, 415.

Armstrong DM, Fitzgerald JP, Meaney CA (2011) *Mammals of Colorado,* Denver, CO.

Beever EA, Brussard PF, Berger J, O'shea T (2003) Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. Journal of Mammalogy*,* **84**, 37-54.

Beever EA, Ray C, Mote PW, Wilkening JL (2010) Testing alternative models of climate-mediated extirpations. Ecological Applications*,* **20**, 164-178.

Beever EA, Ray C, Wilkening JL, Brussard PF, Mote PW (2011) Contemporary climate change alters the pace and drivers of extinction. Global Change Biology*,* **17**, 2054-2070.

Bininda-Emonds ORP, Cardillo M, Jones KE *et al.* (2007) The delayed rise of modern mammals. Nature*,* **444**, 93-96.

Blomberg SP, Garland T (2002) Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. Journal of Evolutionary Biology*,* **15**, 899-910.

Blomberg SP, Garland T, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution*,* **57**, 717-745.

Burnham KP, Andersen DR (2002) *Model selection and multi-model inference: a practical information-theoretic approach,* Heidelberg, Springer-Verlag.

Cary M (1911) A biological survey of Colorado. In: *North American Fauna.* pp Page.

Chapman AD, Wieczorek J (2006) *Guide to best practices for georeferencing,* Copenhagen, Global Biodiversity Information Facility.

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science*,* **333**, 1024-1026.

Chen IC, Shiu HJ, Benedick S *et al.* (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. Proceedings of the National Academy of Sciences of the United States of America*,* **106**, 1479-1483.

Chinn A (2018) Identification error in museum legacy data for Coloradan *Tamias* chipmunk specimens. Unpublished Masters Masters, University of Colorado Boulder, Boulder, Colorado, 47 pp.

Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. Science*,* **331**, 324-327.

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. Science*,* **332**, 53-58.

Duffy PB, Tebaldi C (2012) Increasing prevalence of extreme summer temperatures in the U.S. Climatic Change*,* **111**, 487-495.

Engler R, Randin CF, Thuiller W *et al.* (2011) 21st century climate change threatens mountain flora unequally across Europe. Global Change Biology*,* **17**, 2330-2341.

Erb LP, Ray C, Guralnick R (2011) On the generality of a climate-mediated shift in the distribution of the American pika (Ochotona princeps). Ecology*,* **92**, 1730-1735.

Fitzgerald JP, Meaney CA, Armstrong DM (1994) *Mammals of Colorado,* Boulder, University Press of Colorado.

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. Nature*,* **369**, 448.

Grytnes J-A, Kapfer J, Jurasinski G *et al.* (2014) Identifying the driving factors behind observed elevational range shifts on European mountains. Global Ecology and Biogeography*,* **23**, 876-884.

Hall ER (1981) *Mammals of North America,* New York, John Wiley & Sons.

Inouye DW, Barr B, Armitage KB, Inouye BD (2000) Climate change is affecting altitudinal migrants and hibernating species. Proceedings of the National Academy of Sciences of the United States of America*,* **97**, 1630-1633.

Iucn (2011) IUCN Red List of Threatened Species. Version 2011.2. pp Page, <www.iucnredlist.org>.

Jones KE, Bielby J, Cardillo M *et al.* (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology*,* **90**, 2648-2648.

Keck F, Rimet F, Bouchez A, Franc A (2016) phylosignal: an R package to measure, test, and explore the phylogenetic signal. Ecology and Evolution*,* **6**, 2774-2780.

Kéry M, Royle JA (2008) Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. Journal of Applied Ecology*,* **45**, 589-598.

King SRB, Mccain CM (2015) Robust discrimination of *Reithrodontomys megalotis* and *R. montanus* (Mammalia: Rodentia) from Colorado, using cranial morphology and external characteristics within age classes. Proceedings of the Biological Society of Washington*,* **128**, 1-10.

Lenoir J, Gégout J-C, Guisan A *et al.* (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography*,* **33**, 295-303.

Lenoir J, Gegout JC, Marquet PA, De Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science*,* **320**, 1768-1771.

Mackenzie DI, Nichols JD, Lachman GB, Droege S, Andrew Royle J, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology*,* **83**, 2248-2255.

Mccain C, Szewczyk T, Bracy Knight K (2016) Population variability complicates the accurate detection of climate change responses. Global Change Biology*,* **22**, 2081-2093.

Mccain CM, King SRB (2014) Body size and activity times mediate mammalian responses to climate change. Global Change Biology*,* **20**, 1760–1769.

Mccain CM, King SRB, Szewczyk T, Beck J (2018) Small mammal species richness is directly linked to regional productivity, but decoupled from food resources, abundance, or habitat complexity. Journal of Biogeography*,* **45**, 2533–2545.

Mcdonald KA, Brown JH (1992) Using montane mammals to model extinctions due to global change. Conservation Biology*,* **6**, 409-415.

Mcguire CR, Nufio CR, Bowers MD, Guralnick RP (2012) Elevation-Dependent Temperature Trends in the Rocky Mountain Front Range: Changes over a 56- and 20-Year Record. PLOS ONE*,* **7**, e44370.

Millar CI, Westfall RD (2010) Distribution and climatic relationships of the American pika (*Ochotona princeps*) in the Sierra Nevada and western Great Basin, U.S.A.; periglacial landforms as refugia in warming climates. Arctic, Antarctic, and Alpine Research*,* **42**, 76-88.

Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science*,* **322**, 261-264.

Mote PW, Hamlet AF, Clark MP, Lettenmaier DP (2005) Declining mountain snowpack in western North America. Bulletin of the American Meteorolgical Society*,* **86**, 39-49.

Nowak RM (1991) *Walker's Mammals of the World,* Baltimore & London, The John Hopkins University Press.

Nufio CR, Mcguire CR, Bowers MD, Guralnick RP (2010) Grasshopper community response to climatic change: variation along an elevational gradient. PLOS ONE*,* **5**, e12977.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature*,* **421**, 37-42.

Pauli H, Gottfried M, Grabherr G (1996) Effects of climate change on mountain ecosystems: upward shifting of mountain plants. World Resource Review*,* **8**, 382-390.

Rowe KC, Rowe KMC, Tingley MW *et al.* (2015) Spatially heterogeneous impact of climate change on small mammals of montane California. Proceedings of the Royal Society B: Biological Sciences*,* **282**.

Rowe RJ (2007) Legacies of land use and recent climatic change: the small mammal fauna in the mountains of Utah. The American Naturalist*,* **170**, 242-257.

Rowe RJ, Finarelli JA, Rickart EA (2010) Range dynamics of small mammals along an elevational gradient over an 80-year interval. Global Change Biology*,* **16**, 2930-2943.

Smith FA, Lyons SK, Ernest SKM *et al.* (2003) Body mass of late Quaternary mammals. Ecology*,* **84**, 3403.

Szewczyk TM, Mccain CM (2019) Disentangling elevational richness: a multi-scale hierarchical Bayesian occupancy model of Colorado ant communities. Ecography*,* **42**, 977-988.

Team RDC (2019) R: A language and environment for statistical computing. pp Page, Vienna, Austria, R Foundation for Statistical Computing.

Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. Nature*,* **427**, 145-148.

Tingley MW, Koo MS, Moritz C, Rush AC, Beissinger SR (2012) The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. Global Change Biology*,* **18**, 3279-3290.

Trenberth KE, Jones PD, Ambenje P *et al.* (2007) Observations: Surface and Atmospheric Climate Change. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* (ed Solomon S, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller) pp Page. Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.

Usgcrp (2009) Global climate change impacts in the United States. (eds Karl TR, Melillo JM, Peterson TC) pp Page, New York, NY, United States Global Change Research Program.

Walther GR, Berger S, Sykes MT (2005) An ecological 'footprint' of climate change. Proceedings of the Royal Society B-Biological Sciences*,* **272**, 1427-1432.

Wieczorek J, Guo Q, Hijmans R (2004) The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. International Journal of Geographical Information Science*,* **18**, 745-767.

Wilson DE, Reeder DM (eds) (2005) *Mammal Species of the World. A Taxonomic and Geographic Reference*, Johns Hopkins University Press.

**Supporting Information Legends**

**Appendix S1. Supplementary Methods: Figure S1.1.** Map of contemporary sampling localities by authors; **Figure S1.2.** Elevational sampling distributions**; Table S1.1.** Phylogenetic signal statistics; R code for Bayesian undersampling model. **Appendix S2.** Dataset of species, traits, samples, range limits and shifts; **Appendix S3**. **Supplementary Results: Figure S3.1.** Range comparison for rare and under-sampled species. **Figure S3.2.** Sums of range gains and losses, and number of historical species across the two mountains.

**Figure Legends**

**Fig. 1.** Expected and unexpected responses to anthropogenic warming on mountains.Potential upward elevational range contractions and shifts based on changes in the lower range limit, the upper range limit or both range limits that are tracking cooler temperatures upslope with anthropogenic warming (upper panel: expected contemporary responses). And potential lack of change or downward elevational range contractions and shifts based on changes in one or both range limits that are not expected if species are tracking a warming climate (lower panel: unexpected contemporary responses). The montane color gradient (triangle) depicts the temperature change with increasing elevation from warm (red) to cool (blue). Historical ranges are shown as black lines and contemporary ranges shown in blue (expected upward responses), red (unexpected downward responses) or grey (no change). Dashed gray lines indicate where range end points occur at equivalent elevations.

**Fig. 2.** A map of the historical (circles) and contemporary (stars) sampling localities within the two mountainous regions, the Front Range Mountains (right) and San Juan Mountains (left), in Colorado, USA (greyscale inset). The thin black lines denote the county boundaries in each region. In the Front Range, the counties are Larimer County in the north and Boulder County in the south. In the San Juans, the counties are Dolores County in the northwest, Montezuma County in the southwest, San Juan County in the northeast of the figure and La Plata County in the southeast of the figure. The background gradations of color depict the elevational change in each region with the dark pink as the lowest elevations and the dark green as the highest elevations. For the author’s contemporary sampling sites only, see Figure S1.1.

**Fig. 3.** Paired historical (left) and contemporary (right) elevational ranges of the included small mammal species on the (A) Front Range Mountains, and the (B) San Juan Mountains. The sum of the range shifts and contractions for upward or downward change (C). The species are arrayed across the x-axis by the contemporary climate change response (local extirpation = zeros, range midpoint shift downward = red, no change = grey, and range midpoint shift upward= blue). The empirical ranges based on the minimum and maximum specimen or literature localities are in thick bars and the Bayesian 95% limits based on the undersampling models are in thin extensions. Species names denoted by first initial of the genus and the first few letters of the specific epithet; for complete taxonomic names, see Appendix S2.

**Fig. 4.** Elevational heat maps of the net change in range limit percentage gains and losses across the studied species (A: San Juans on left, Front Range on right) with greens and blues showing overall net gains (predominantly at high elevations), cream showing no or relatively little change, and yellows to reds showing overall net losses. The percentages of range gains (black bars) and losses (grey bars) based on dividing the sums of range edge changes by the number of historical species (Fig. S3.2) for each elevational band are shown for the San Juans (B) and the Front Range (C) Mountains.

**Fig. 5.** A comparison of the differences in elevational range shifts among low elevation, cosmopolitan and montane species. A. Distribution of mean (circle) and 1 standard deviation (bars) of change in lower (L) and upper (U) range limits for each group. B. The number of species with a predicted (upward shift; dark grey) and non-predicted (downward shift, no change; light grey) response to climate change for each group.

**Fig. 6.** The magnitude of range changes in the upper and lower range limits were a function of species traits. A. The upward shift of upper range limits was larger for species whose geographic ranges extended to higher latitudes and this was particularly pronounced among montane and cosmopolitan species. B. The upward shift of upper range limits was larger for species in which the studied mountain range (Front Range or San Juans) was at the southern edge of their geographic ranges, but not the north, east, or west edges nor the middle (non-edge) of the range. C. The upward shift of the lower range limits was larger for species at the eastern edge of their geographic range.