Global Change Biology

Montane mammals moving upward in the Rocky Mountains as temperature warms

Journal:	*Global Change Biology*
Manuscript ID	GCB-19-1687
Wiley - Manuscript type:	Primary Research Articles
Date Submitted by the Author:	23-Sep-2019
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Title: **Montane mammals moving upward in the Rocky Mountains as temperature warms**

Short title: Upward elevational shifts in montane mammals

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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.

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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: $r^2 = 0.4705$, $p < 0.0001$). 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, Trenberth *et al.*, 2007, USGCRP, 2009). Anthropogenic impacts are also affecting precipitation trends as well as increasing the variability and severity of extreme weather events (Duffy & Tebaldi, 2012, Trenberth *et al.*, 2007, USGCRP, 2009). Essentially the planet and all its inhabitants are in a climate crisis of unknown magnitude. One urgent imperative is tracking the impacts of these climate 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, review in McCain & King, 2014). 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 detected 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, Grytnes *et al.*, 2014).

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, McDonald & Brown, 1992, Pauli *et al.*, 1996). Such upward tracking could include an upward 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

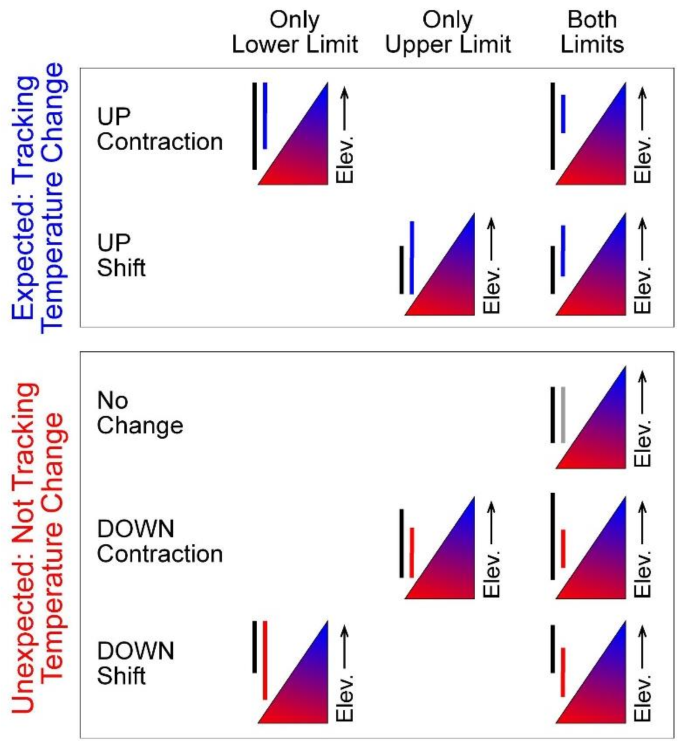

Fig. 1. Expected and unexpected responses to anthropogenic warming on mountains. The upper panel shows expected contemporary responses: potential upward elevational range contractions and shifts based on changes in the lower range limit, the upper range limit or both range limits that are tracking cooler temperatures upslope with anthropogenic warming. The lower panel shows unexpected contemporary responses: 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. The montane color gradient (triangle) depicts 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).

higher elevations. For example, many small mammals have shifted upwards in the western United States (Moritz *et al.*, 2008, Rowe *et al.*, 2015, Rowe *et al.*, 2010). Many alpine plants in Europe have shifted higher with climate change (Engler *et al.*, 2011, Grabherr *et al.*, 1994, Lenoir *et al.*, 2008, Pauli *et al.*, 1996), moths in the Asian tropics have shifted upwards by an average of 67 m (Chen *et al.*, 2009), and a review of montane shifts detected an 11 m increase in elevational ranges per decade across organisms (Chen *et al.*, 2011). 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, Lenoir *et al.*, 2010, McCain & King, 2014, Rowe *et al.*, 2015). 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, Beever *et al.*, 2010, Beever *et al.*, 2011, Millar & Westfall, 2010). 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). Unfortunately, that is the only multi-site climate change study on mammals in the US Rocky Mountains (McCain & King, 2014).

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). Traits of the species themselves like body size, activity times, and physiology may also mediate which species respond as predicted to climate change and which do not (e.g., Angert *et al.*, 2011, McCain & King, 2014, Moritz *et al.*, 2008). 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), McCain and King (2014) detected that body size, activity patterns, and locations of latitudinal and elevational ranges were important in explaining which North American mammal species responded to climate change as predicted. We would expect that 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 between species traits and 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, Fitzgerald *et al.*, 1994, McCain *et al.*, 2018). One both gradients, temperature decreases and precipitation increases with increasing elevation (McCain *et al.*, 2018). Climatically, the San Juans in southwestern Colorado are warmer and wetter than the Front Range in the northeastern Colorado Rockies. 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.

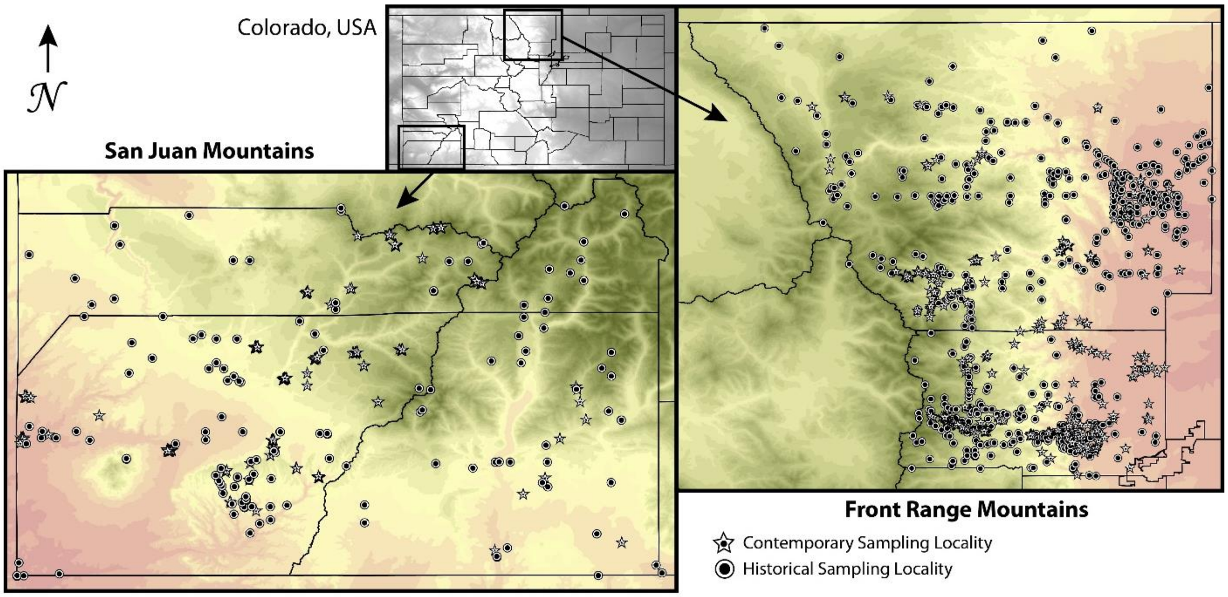

Fig. 2. A map of historical (circles) and contemporary (stars) sampling localities within the two mountainous regions: the Front Range Mountains (right) and San Juan Mountains (left), in Colorado, USA (greyscale inset). The thin black lines denote county boundaries in each region. In the Front Range, 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 of the figure, Montezuma County in the southwest, San Juan County in the northeast and La Plata County in the southeast. Background color gradations depict the elevational change in each region with dark pink as the lowest elevations to dark green as the highest elevations. For the authors' contemporary sampling sites only, see Figure S1.1.

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).

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), and were georeferenced following the MaNis protocols with quantified error estimates (Chapman & Wieczorek, 2006, Wieczorek *et al.*, 2004). 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), *Mammals of Mesa Verde National Park, Colorado* (Anderson, 1961), and *Distribution of Mammals in*

Colorado (Armstrong, 1972) 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 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; Figure S1.1; McCain *et al.*, 2018). 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 and 2012 using live-trapping, pitfall traps, and visual surveys. We chose sites that reflected the main habitats at that elevation (e.g., meadow, forest, riparian) 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 contemporary undersampling, 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). 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). 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, MacKenzie *et al.*, 2002, Szewczyk & McCain, 2019). 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 $\boldsymbol{y_i}$, was modeled as:

$$\boldsymbol{y_i} \sim Multinomial(\boldsymbol{p_i}, Y_i)$$

$$p_{ij} = \frac{\lambda_{ij} Z_{ij} \delta_j}{\sum_{j=1}^{J} \lambda_{ij} Z_{ij} \delta_j}$$

where $\boldsymbol{p_j}$ is a vector of the probabilities that a random observed individual from elevational bin i belongs to each species, Y_i is the total number of individuals detected across all species in elevational bin i, λ_{ij} is the relative abundance of species j in elevational bin i, Z_{ij} is a latent binary parameter indicating the true presence (1) or absence (0) of species j in elevational bin i, and δ_j is the probability of detecting a given individual of species j. Note that p_{ij} 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, δ_j, 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 Z_{ij} is Bernoulli distributed with probability ψ_{ij}, 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:

$$Z_{ij} \sim Bernoulli(\psi_{ij})$$

$$\psi_{ij} = a_j + \beta_1 * dist_{ij} + \beta_2 * patchiness_j + \beta_3 * dist_{ij} * patchiness_j$$

where a_j 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 $Z_{ij} = 1$. 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 (Plummer, 2017, Plummer, 2019, R Development Core Team, 2019,). For each model, we ran 3 chains for 20,000 iterations, discarding the first 10,000 iterations as burn-in, and then retaining every 10^{th} 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 λ_{ij} 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 was based on the direction of range midpoint shift (Figure 1). In the rare case (i.e., Figure 3: Tqua (*Tamias quadrivittatus*) in San Juans), a large contraction in a contemporary range to just a small portion of the middle elevations of their historical range can result in a slightly lower midpoint. In those rare cases, the overall shift designation is based on the direction of the range limit with the largest shift (i.e., Tqua: lower limit shift upward). 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 accordance with the wide spread in historical lower limits across the gradients. 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 elevations, 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, McCain & King, 2014, Moritz *et al.*, 2008 and references therein), 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, Smith *et al.*, 2003). Daily activity times (obligate diurnal, obligate nocturnal, and flexible) were from the PanTHERIA database (Jones *et al.*, 2009) or species accounts in the journal *Mammalian Species*, and were checked against additional literature sources (Armstrong *et al.*, 2011, Hall, 1981, Nowak, 1991). 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), 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) but modified to only include distributions within North America (Hall, 1981, IUCN, 2011).

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). 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). Because phylogenetic relatedness could impact the robustness of these analyses (e.g., Blomberg & Garland, 2002, Blomberg *et al.*, 2003), 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) pruned to the taxa included in each mountain dataset. Phylogenetic signal was calculated with *phylosignal* (Keck *et al.*, 2016) in *R* (R Development Core Team, 2019) 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 a per-mountain average of 97 specimens historically and 158 specimens contemporarily (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.

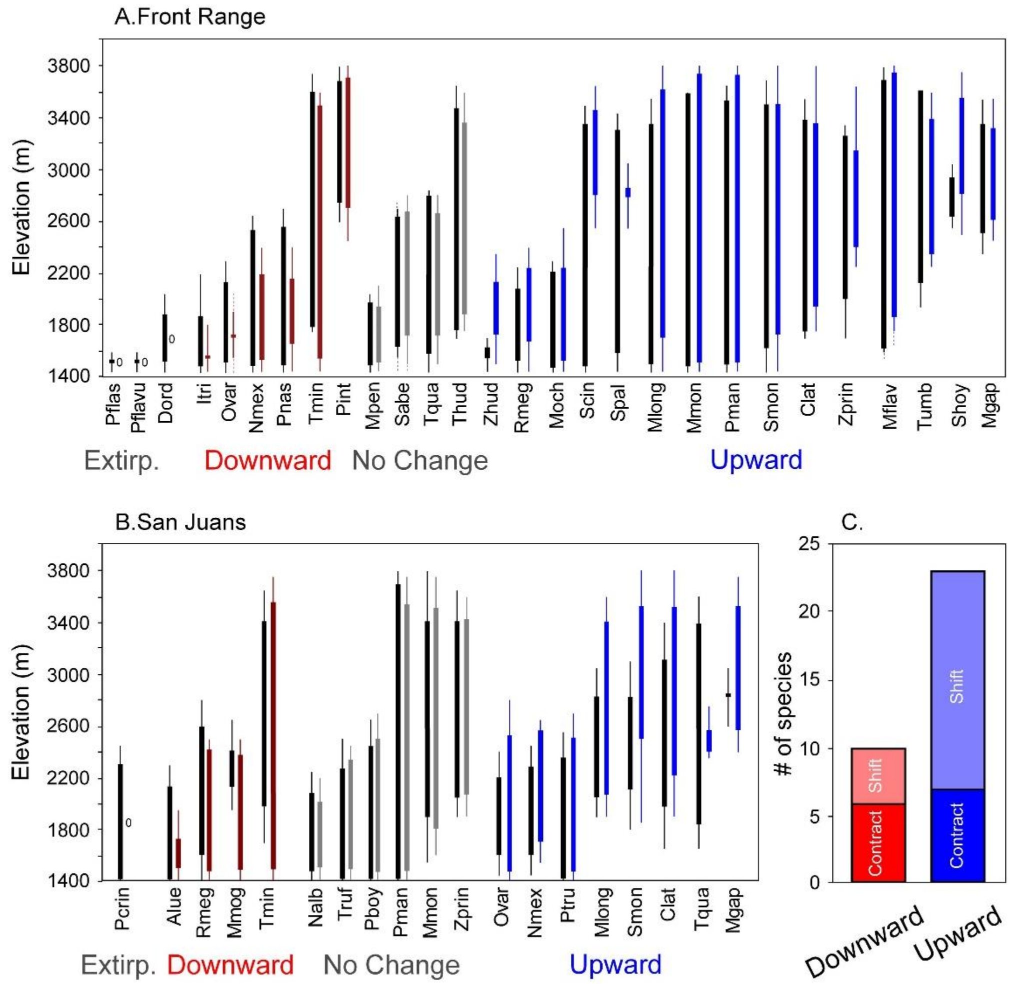

Fig. 3. Paired historical (left bar) and contemporary (right bar) elevational ranges of the included small mammal species on the (A) Front Range Mountains, and the (B) San Juan Mountains. The sum of the range shifts and contractions for upward or downward change is shown in panel C. The species are arrayed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

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 changes with climate change (Figure 3: thin bar extensions; Appendix S2). Species that significantly changed 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 change either range limit (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

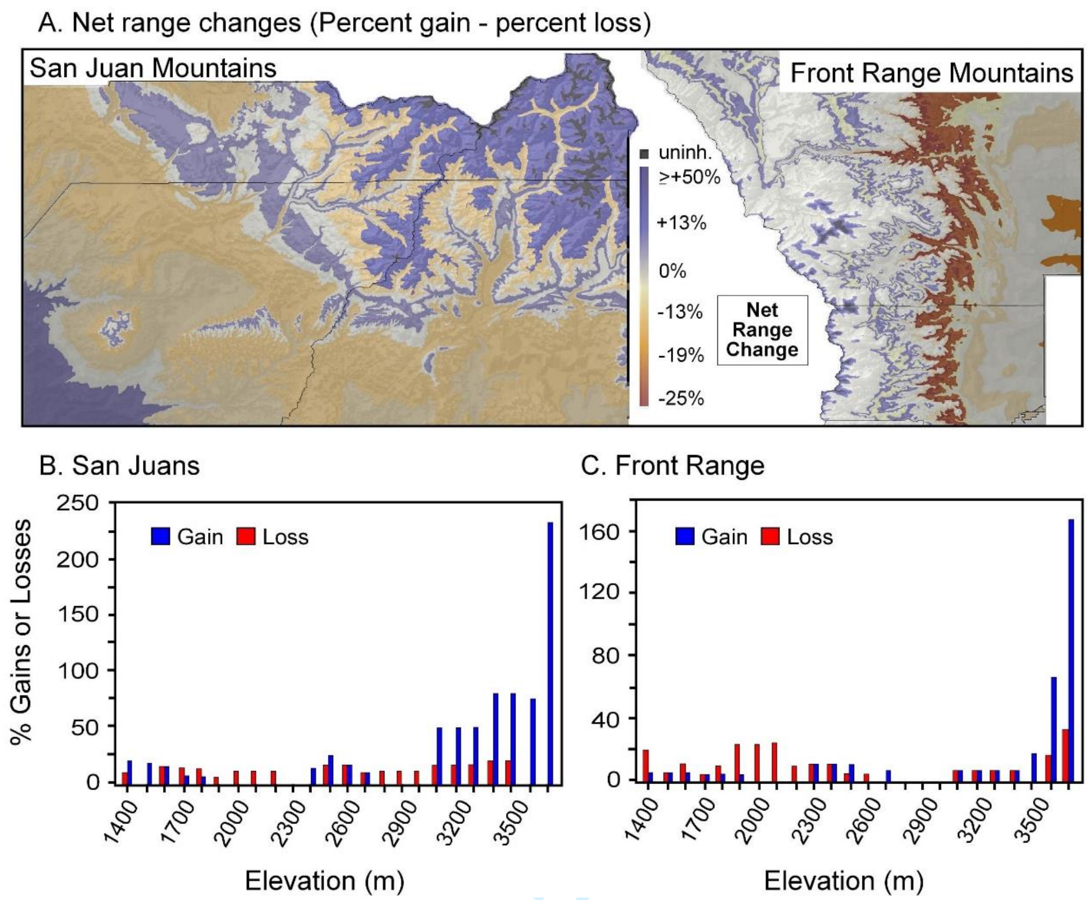

Fig. 4. Elevational heat maps of net change in percentage gains and losses at range limits across the studied species (A: San Juans on left and Front Range on right) with blues showing net gains (predominantly at high elevations), light gray showing no or relatively little change, and yellow to reds showing increasing net losses (see scale legend in figure). The percentages of range gains (blue bars) and losses (red 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.

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 were 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 ($r^2 = 0.4705$, $p < 0.0001$, 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 ($r^2 = 0.1025$, $p < 0.0363$, 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; $\chi^2 = 8.5582$, $p < 0.0136$, AICc weight = 57.4).

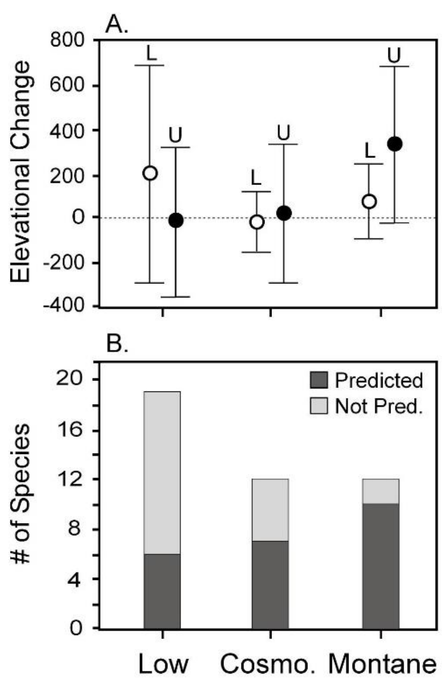

Fig. 5. A comparison of the differences in elevational range shifts among low elevation, cosmopolitan and montane species. A. Distribution of mean (circle) and 1 standard deviation (bars) of change in lower (L) and upper (U) range limits for each group. B. The number of species with a predicted (upward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

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 over the past several decades (McGuire *et al.*, 2012, Mote *et al.*, 2005, Trenberth *et al.*, 2007, USGCRP, 2009), 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, Pauli *et al.*, 1996, Thomas *et al.*, 2004, Walther *et al.*, 2005). 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).

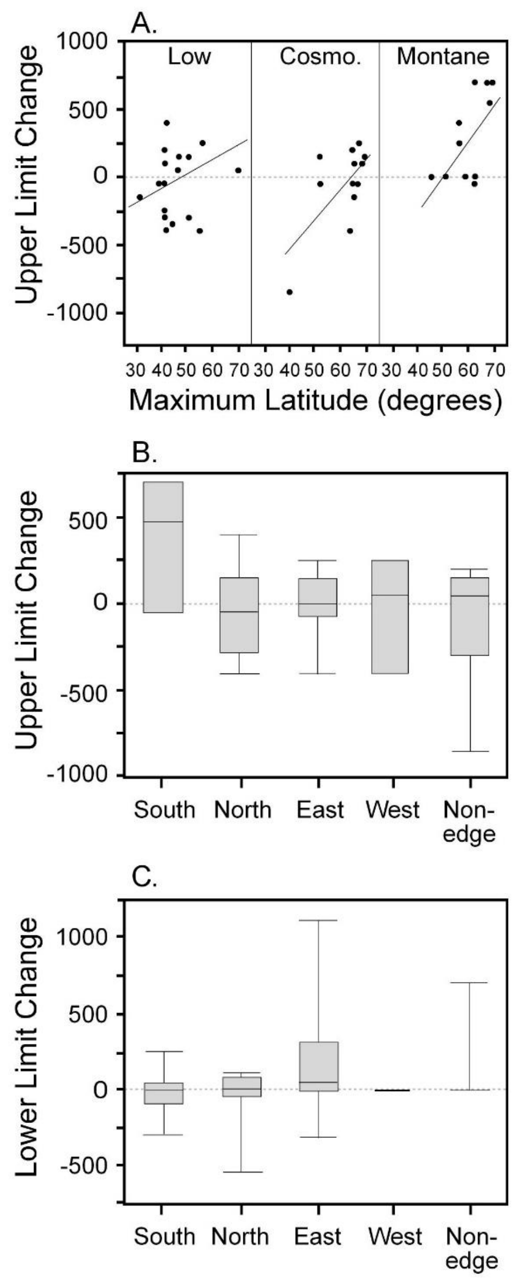

Fig. 6. The magnitude of range changes in the upper and lower range limits were a function of species traits. A. The upward shift of upper range limits was larger for species whose geographic ranges extended to higher latitudes, which was particularly pronounced among montane and cosmopolitan species. 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.

Physiological and biogeographic traits mediate which species are responding as expected by shifting higher and which 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; $r^2 = 0.4705$, $p < 0.0001$). The species least likely to respond as expected were the lower elevation species, which in these areas include mostly semi-arid desert, canyonland, and grassland species adapted to higher temperatures and lower rainfall than their montane counterparts (Armstrong *et al.*, 2011) (Fig. 5B; $\chi^2 = 8.5582$, $p < 0.0136$). 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; $r^2 = 0.1025$, $p < 0.0363$). 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, Armstrong *et al.*, 2011, Hall, 1981). 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 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 conservative estimate of lower limit contractions, and consequently, overall range contractions.

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, Nufio *et al.*, 2010, Rowe *et al.*, 2010, Tingley *et al.*, 2012). 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 work. 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 a particular time period of sampling (McCain *et al.*, 2016). 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. There is also more potential error in the species identifications and locality information than in a single gradient study.

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*) received special emphasis on re-identifications, molecular analyses, and quantitative morphological models (e.g., Chinn, 2018, King & McCain, 2015, McCain *et al.*, 2018). 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 Colorado), 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. Even if you remove all the San Juan analyses, the conclusions remain unchanged.

Anthropogenic land use change is not absent from these gradients (Szewczyk & McCain, 2019), and has been shown to influence other small mammal elevational studies (e.g., Rowe, 2007, Rowe *et al.*, 2010). 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). But, as stated earlier, some low elevation contraction due to habitat reduction is compensated for in the Bayesian undersampling models. And likely, fewer small mammals now reside in the lowest elevations (1400-1599m) in the Front Range than did historically due to human development, but more sampling in needed in remaining habitat patches.

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, Rowe *et al.*, 2015, Rowe *et al.*, 2010). 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 span 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). 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 continues to warm, based on both these data and previous analyses (McCain & King, 2014). Take heed—it is only going to continue.

Acknowledgements

This work was supported by the US National Science Foundation (McCain: DEB 0949601) and the CU Museum of Natural History. We thank all researchers and museum collections whose data were used in this study (Appendix S1), and J. Beck feedback on manuscript drafts. The data collection involved many extraordinary field and lab assistants, including multiple years of assistance from Emily Braker, Holly D'Oench, Hayden Gardner, John Hackemer, Jake Harris, Angela Knerl, Kevin Bracy Knight, Richard Parkhill, Daniella Ramos, Emma Shubin, and Grant Vagle. Approved IACUC vertebrate handling protocols from CU Boulder (08-07-McC-02;

1103.02; Protocol 2548), and permits and permissions for mammal sampling included Rocky Mountain National Park, Sylvan Dale Guest Ranch, City of Boulder Open Space and Mountain Parks, Boulder County Open Space, Roosevelt and Arapaho National Forest, The CU Mountain Research Station and Niwot Ridge LTER, Mesa Verde National Park, San Juans BLM and National Forest Service, and Lizardhead Wilderness.

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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.