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COVER PHOTO: McCain et al. (this issue; Article e03300; doi.org/10.1002/ecy.3300) document how montane mammals are shifting to higher elevations in the Rocky Mountains with warming temperatures. Pictured is a Golden-mantled ground squirrel (*Callospermophilus lateralis*) from Rocky Mountain National Park, which is one of many species that has moved to higher elevations in the Front Range and San Juan Mountains of Colorado, USA with anthropogenic climate change. Photo credit: Christy McCain.

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Unusually large upward shifts in cold-adapted, montane mammals as temperature warms

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Abstract. The largest and tallest mountain range in the contiguous United States, the Southern Rocky Mountains, has warmed considerably in the past several decades due to anthropogenic climate change. Herein we examine how 47 mammal elevational ranges (27 rodent and 4 shrew species) have changed from their historical distributions (1886–1979) to their contemporary distributions (post 2005) along 2,400-m elevational gradients in the Front Range and San Juan Mountains of Colorado. Historical elevational ranges were based on more than 4,580 georeferenced museum specimen and publication records. Contemporary elevational ranges were based on 7,444 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. We compared 95% likelihood elevational ranges between historical and contemporary time periods to detect directional change. Responses were variable as 26 mammal ranges changed upward, 6 did not change, 11 changed downward, and 4 were extirpated locally. The average range shift was 131 m upward, while exclusively montane species shifted upward more often (75%) and displayed larger average range shifts (346 m). The best predictors of upper limit and total directional change were species with higher maximum latitude in their geographic range, montane affiliation, and the study mountain was at the southern edge of their geographic range. 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.

Key words: *climate change; elevation; range contractions; range shifts; rodents; shrews.*

INTRODUCTION

Earth is warming at an unprecedented rate from human-created emissions with related impacts on precipitation trends and extreme weather events (Trenberth et al. 2007, USGCRP 2009, Duffy and Tebaldi 2012). One urgent imperative is tracking the impacts of these climate changes on contemporary organisms to improve our understanding of those species most at risk and improve their conservation outcomes. On mountains, temperature decreases as elevation increases, and species are expected to track favorable temperatures by shifting to higher elevations as average temperatures increase in a region (Fig. 1a; e.g., McDonald and Brown 1992, Pauli et al. 1996, Inouye et al. 2000). 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 and birds have shifted upward in the western United States (Moritz et al. 2008, Rowe et al. 2010, Tingley et al. 2012, Rowe et al. 2015). Many alpine plants in Europe and the United States have shifted higher with climate change (Grabherr et al. 1994, Pauli et al. 1996, Kelly and Goulden 2008, Lenoir et al. 2008, Engler et al. 2011), moths in the Asian tropics have shifted upward 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).

The upward shifts are not the whole story; one critical element is the variability in responses on these gradients. Overall, shifts are upward for most species, but individual species also demonstrate unexpected responses like downward shifts or no detectable change (Fig. 1b; Lenoir et al. 2010, Crimmins et al. 2011, Tingely et al.

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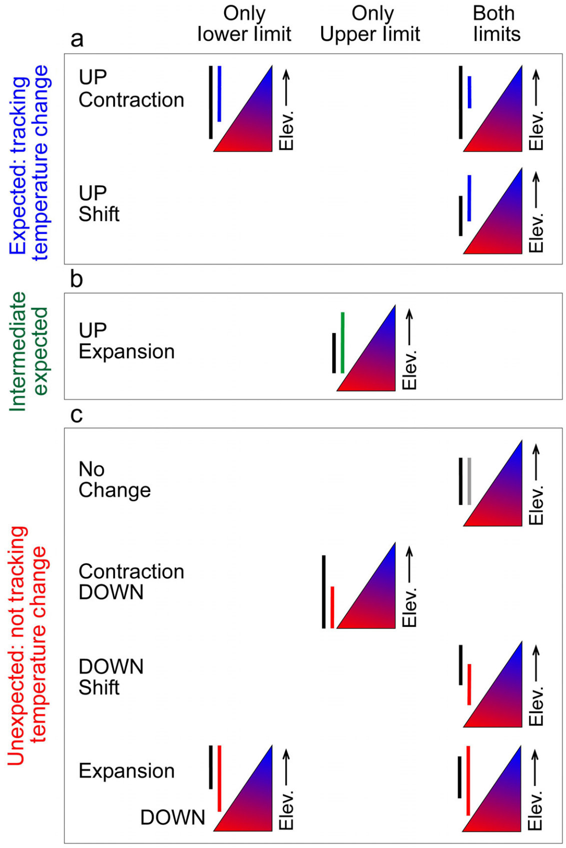

FIG. 1. (a) Expected, (b) intermediate expected, and (c) unexpected responses of small mammals to anthropogenic warming on mountains. (a) Expected: potential upward elevational (Elev.) range contractions and shifts based on changes in the lower range limit or both range limits. (b) Intermediate expected: potential upward elevational range shift in upper range limit but unchanged lower limit. (c) Unexpected: potential lack of change, downward elevational range contractions, and shifts based on changes in one or both range limits, or expansion downward or of both limits. Triangle depicts montane temperature variation from warm (red) to cool (blue). Black lines show historical ranges, blue lines show contemporary upward responses, green lines show contemporary upward expansion, red lines show contemporary downward and/or expansion responses, and gray lines show no contemporary change.

2012, McCain and King 2014, Rapacciuolo et al. 2014, Rowe et al. 2015). Some variability may be due to the geographically heterogeneous nature of the changes in climate with high latitudes warming the most (Trenberth et al. 2007, USGCRP 2009) and some areas experiencing concurrent or discordant temperature and precipitation changes (e.g., Beever et al. 2011, McCain and Colwell 2011, Rapacciuolo et al. 2014). Biogeographic factors potentially mediating responses may include the latitude of the mountain, the location of the mountain in relation to the species' geographic range, and the size, height and isolation of the mountain (e.g., Grabherr et al. 1994, Walther et al. 2002, Parmesan and Yohe 2003, Beever et al. 2011, McCain and King 2014, Smith et al. 2019). Species traits, like body size, reproductive capacity, activity times, niche breadth, and physiology, may also mediate which species respond as predicted to climate change and which do not (e.g., Moritz et al. 2008, Angert et al. 2011, McCain and King 2014, MacLean and Beissinger 2017). So far, such mediating traits are rarely detected in individual montane gradient studies or in meta-analyses (e.g., Angert et al. 2011, MacLean and Beissinger 2017), although McCain and King (2014) found that body size, activity times, elevation, and latitude were important determiners of which among 73 mammal species tested responded negatively to climate change (e.g., range contractions, population declines). Nonetheless, variability in tested trait associations and study methodologies, different types of climate change metrics, and relatively few comprehensive studies limit our understanding whether biogeographic, ecological, or trait relationships more widely mediate responses to climate change. Despite the lack of consistency, at least across clades of organisms so far, 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 environmental change. Thus, more studies are necessary both to elucidate additional species responses to climate change and to examine comprehensive clades for traits mediating heterogeneous responses. Additionally, we need more research in understudied montane regions. For example, most mammal species and populations studied for climate change responses have been conducted in California and Nevada, while only one species has been tested for range shifts in the U.S. Rocky Mountains (McCain and King 2014).

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 United States, 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 after 2005. We develop Bayesian undersampling models to accommodate species-, mountain-, and time-period-specific 95% likelihood elevational ranges, which leverage 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. Then we assess how elevational ranges have changed, testing for biogeographic and species-trait effects that may mediate which species are and are not moving higher in elevation with increasing temperatures.

METHODS

The Rocky Mountains extend from the southwestern United States to western Canada reaching their highest

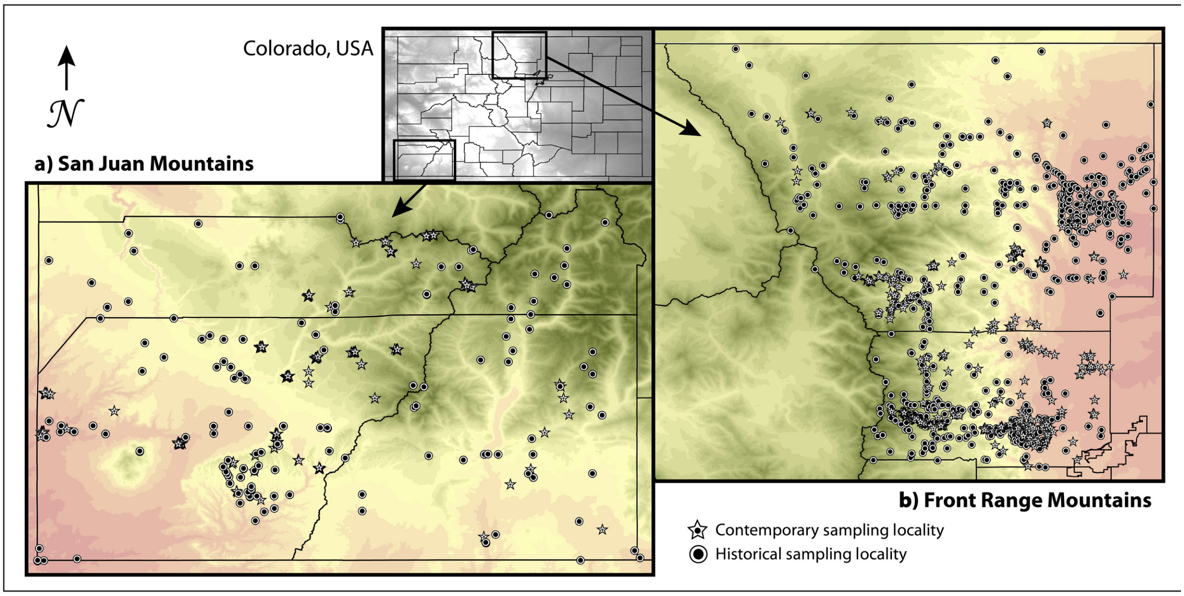

FIG. 2. A map of historical (circles) and contemporary (stars) sampling localities within the two mountainous regions: (a) San Juan Mountains and (b) Front Range Mountains in Colorado, USA (grayscale inset). The thin black lines denote county boundaries in each region. Elevational variation grades from dark pink at the lowest elevations to dark green at the highest elevations. For the authors' contemporary sampling sites only, see Appendix S1: Fig. S1.

elevations in Colorado, USA. Temperatures in the two mountainous regions studied in the Colorado Rockies (Fig. 2), the San Juan Mountains (1,414–4,286 m) and the Front Range Mountains (1,438–4,346 m), have increased since the 1980s (Trenberth et al. 2007, USGCRP 2009, McGuire et al. 2012) with estimates at nearly 2°C warmer for the state as a whole (Frankson et al. 2017). However, the San Juans are getting increasingly wetter, while the Front Range is becoming increasingly drier (Mote et al. 2005). Mid-elevations (2,591–3,048 m) in the Front Range might be warming faster than lower and upper elevations based on trends across five long-term monitoring sites (McGuire et al. 2012), but fine-scale elevational change in temperature and precipitation across both of these mountains has yet to be compiled and robustly analyzed.

Historical mammal data

We amassed specimen data from most, if not all, museums with Colorado mammal specimens, which included 58,709 specimens from 45 museums (specimen data collected 2009–2012; Appendix S1). Nomenclature follows the Handbook of the Mammals of the World (Wilson et al. 2016, 2017, Wilson and Mittermeier 2018), and georeferencing follows the MaNis protocols (Wieczorek et al. 2004, Chapman and Wieczorek 2006). For quality assurance, we restricted analyses to rodent and shrew specimens (Fig. 2 circles) with (1) a reliable species-level identification by an expert, reverified 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 a horizontal error <1,000 m (designated as usable) or <5,000 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, and San Juan counties). These data were augmented by lowest and highest elevational records in the historical literature, 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). The most rigorous vetting focused on the lowest and highest localities for each species, only using records without significant, plausible error in the locality, elevation, or identification.

Contemporary mammal data

Post-2005 specimens that met the accuracy criteria were included in the contemporary data (Fig. 2 stars). In 2018, we augmented the Colorado database to include more recent specimens (2006–2018) using the same vetting protocol of the Global Biodiversity Information Facility data[7]. For systematic, contemporary mammal surveys, we established two elevational transects in the southwestern San Juan Mountains and two in the northeastern Front Range (Fig. 2; Appendix S1:

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[7] https://doi.org/10.15468/dl.fpwafv

Fig. S1; McCain et al. 2018). Each transect consisted of eight sites placed every 200−300 m in elevation between the base of the range (1,400–1,700 m) and the upper limit of vegetation on the mountain top (3,600–3,800 m; Appendix S1: Fig. S1). At each of these 32 relatively undisturbed sites, we conducted small mammal surveys across all habitats between 2010 and 2012 using live-trapping (300 Sherman traps for five consecutive nights), pitfall trapping (40 pitfall traps for 90 consecutive nights), and diurnal visual surveys (five or more 1-h surveys; mostly to detect sciurids and lagomorphs). Thus, trapping was extensive (5,100 trap-nights per site; 163,200 total trap-nights) and equal among sites. Additional mammal survey data for the San Juans included nine sites from a pilot study (2007: three nights per site using 100 Sherman traps and 10 pitfall traps) and 11 sites in Mesa Verde National Park (2018: two sites of live trapping during four nights with 200 Sherman traps; nine sites of 20 pitfall traps for 3 weeks; plus extensive visual surveys) for a total additional 7,550 trap-nights (Appendix S1: Fig. S1). Similarly, for the Front Range (2017), contemporary sampling also included 2,430 trap-nights (3 nights with 250 Sherman traps and 13–21 days with 10 pitfall traps) across three low-elevation sites. All live trapping involved a combination of collapsible Sherman live traps (~80% of 3 × 3.5 × 9 inches [1 inch = 2.54 cm], perforated in hot environments, non-perforated in cold environments, and 20% 3 × 3.75 × 12 inches) half baited with peanut butter and rolled oats and half with a grain–seed mixture. Species were identified in-hand, with specimens, or from DNA sequences (McCain et al. 2018). The University of Colorado Boulder IACUC approved our vertebrate handling protocols (08-07-McC-02; 1103.02; 2548). We do not include medium- to large-sized mammals in these analyses due to their undersampling given contemporary trapping methods (i.e., small-sized traps).

Bayesian undersampling models

The observed elevational ranges likely underestimate the true elevational ranges of species, as species are not always detected even when they are present (MacKenzie et al. 2002), and because the sampling along each elevational gradient in each time period was patchily distributed (Fig. 2; Appendix S2: Fig. S1). 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, often used in resurvey studies, rely on repeated surveys both historically and contemporarily and often use local environmental data to predict a species' probability of presence when undetected in a particular locality (MacKenzie et al. 2002, Kéry and Royle 2008, Tingley and Beissinger 2009, Szewczyk and McCain 2019). Such repeat survey data are unavailable in many cases, including for compiled, historical data sets like the data set used here, which are presence-only data based on all detections within the spatial and temporal study extent. Consequently, we employed a modified conceptual framework for occupancy to evaluate the probability of non-detection based on sampling intensity rather than directly considering species' environmental preferences, aiming to quantify the uncertainty in range boundary estimates in each time period and mountain range.

Within each time period, mountain range, and elevational bin, we considered the detected individuals as a draw from a multinomial distribution (Appendix S2: Fig. S1), representing a sample from the community of individuals living at those elevations across the years included in the time period. For each species within each time period and mountain range, we assume that the number of observed individuals is proportional to the species' relative abundance and that the individual-level detection probability (i.e., the probability that a given individual of that species is detected when present) is consistent across elevations. Thus, for each elevational bin i, the number of observed individuals belonging to species $1 - J$, represented as vector $\mathbf{y}_i$, was modeled as $\mathbf{y}_\mathbf{i} \sim \text{Multinomial}(\mathbf{p}_i, Y_i)$ where $\mathbf{p}_i$ is a vector of the probabilities that a random observed individual from elevational bin i belongs to each species, and Y_i is the total number of individuals detected across all species in elevational bin i. For each species,

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

where 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 (species j is the only species present at elevation i). We used the repeated mark and recapture survey data in the contemporary data set to fit Beta distributions for the individual-level detection probability, δ_j, for each species (Appendix S1), which we used as prior distributions, allowing δ_j to vary across mountain ranges and time periods (Appendix S1: Fig. S2). If there were too few recaptures for robust estimation in a particular species, then we used an average from the clade (e.g., *Sorex*).

The unobserved parameter Z_{ij} is Bernoulli distributed with probability ψ_{ij}, which is the probability that species j was present at elevation i, and is calculated as a function of the elevational distance from the observed range boundaries, and the patchiness of the interpolated range (i.e., the proportion of elevational bins without detections within the interpolated range) $\psi_{ij} = a_j + \beta_1 \times \text{dist}_{ij} + \beta_2 \times \text{patchiness}_j$ 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 designated as community level with one value for all species. As the probability of non-detected presences should decrease with distance from the interpolated range and increase with patchiness, we constrained β_1 to be negative and β_2 to be positive, with broad truncated normal prior distributions.

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, which we use as the elevational range of each species for each mountain in each time period. For the analyses of range shifts, we only included species with at least 10 historical records per mountain and at least one in the contemporary sampling. We ran the model with JAGS 4.3.0 in R 3.6.1 using the rjags package (Plummer 2017, 2019). For each mountain and time period, we ran three chains for 50,000 iterations, discarding the first 20,000 iterations as burn-in, and then retaining every 50th iteration for the final posterior distributions. We assessed convergence of the MCMC chains by confirming all R values were <1.1. We used lightly informative prior distributions for α, β, and σ corresponding with plausible range extensions of approximately 0–600 m beyond the observed range, 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 S2). We performed sensitivity analyses to evaluate the impact of modeling assumptions as well as elevational bin size and overall sampling effort using simulated data (Appendix S2). See Appendix S2 for Bayesian model code, additional modeling details, and sensitivity analyses.

Statistical analyses

A significant change from the Bayesian historical to the Bayesian contemporary elevational range limits was determined if the overall range change was ≥100 m. We calculated the size of the shift upward or downward for the (1) lower limit, (2) upper limit, and (3) total net change. With warming temperatures, species' ranges are predicted to track to higher, cooler elevations by contracting their lower limit upward, contracting upward to an overall reduced range, or shifting both range limits upward (Fig. 1a). An intermediate predicted response to warming temperatures is a shift upward of the upper range limit, but no current, significant shift in the lower limit (Fig. 1b). Unexpected responses to warming include no change (both range limits change by less than a combined 100 m), a downward contraction in the upper limit, a downward shift in both limits, or an expansion of both range limits or expansion of the lower limit downward (Fig. 1c).

In accordance with regional warming, most range gains should occur at mid-elevation to high elevation and most range losses at low elevation to mid-elevation as species track from unfavorable to more favorable conditions. Anthropogenically developed habitats (developed, cultivated, pastureland) are more pronounced in the Front Range and generally decline with elevation, while the San Juan Mountains are less developed overall and developed land is concentrated at lower mid-elevations (Appendix S1: Fig. S3). Thus, if the reduction of available habitat is the predominant factor influencing the loss in elevational ranges, then we expect correlations between range losses and the distribution of developed land on the two mountains. To assess these trends, we calculated the number of species losing or gaining range at their lower and upper limits within each 100-m band up each mountain. Because the number of species per elevational band differs, we examined the percentage of range losses and range gains for each 100-m elevational band on each mountain gradient by dividing the species counts by the historical number of species present in each band. We tested for elevational trends using Spearman's rank correlations.

To assess how species traits and biogeography influenced the responses to anthropogenic climate change, we examined several factors empirically linked or hypothesized to be important to differential responses to climate change in mammals (e.g., Moritz et al. 2008, Angert et al. 2011, McCain and King 2014). These included body size, activity times, elevational affiliations, high-latitude ranges, and location of study area within the species biogeographic range (e.g., southern edge, eastern edge, middle). Many more traits and biogeographic factors were possible, but we were limited by our species sample size as well as the correlation in traits (e.g., body size and reproductive traits). Trait data were from the PanTHERIA and MOM databases (Smith et al. 2003, Jones et al. 2009), species accounts in the journal *Mammalian Species*, and additional literature sources (e.g., Hall 1981, Nowak 1991, Armstrong et al. 2011, IUCN 2018). Each species was characterized as a low elevation species, a montane species, or cosmopolitan (found 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.

For trait and biogeographic analyses on lower, upper, and total range changes, we used multivariate least squares regression models using JMP Pro 14 (JMP 1994–2020). We assessed correlated quantitative variables using a correlation matrix to detect and remove highly associated factors by including only the stronger factor. We assessed qualitative factors with Wilcoxon Rank Sum tests and all factors with at least a marginally significant relationship ($P < 0.1$) were included in the models. Because phylogenetic relatedness could impact the robustness of these analyses (e.g., Blomberg and Garland 2002, Blomberg et al. 2003), we estimated a phylogenetic signal in the lower, upper, and total range shifts using the mammal supertree (Bininda-Emonds et al. 2007) pruned to the taxa included in each mountain data set. We used phylosignal (Keck et al. 2016) in R to calculate phylogenetic signal by comparing all five significance tests (Cmean, *I*, *K*, K.star, and Lambda). We detected negligible phylogenetic signal, as almost all tests were insignificant (93%; Appendix S1. Table S1); thus, we present non-phylogenetically corrected analyses.

RESULTS

Our compiled databases for historical and contemporary distributions of small mammal species (27 rodents, 4 shrews) included 37 elevational ranges in the Front Range Mountains (FR) and 33 elevational ranges in the San Juan Mountains (SJ). Elevational ranges 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 (~10–16 times the minimum criterion of 10; Appendix S3). We used these data to delineate the empirical elevational ranges for each species per mountain and time period (Fig. 3: thick black bars). We eliminated several species from the range shift analyses because of insufficient detections (<10 specimens) historically (7 FR, 13 SJ) or undersampling with

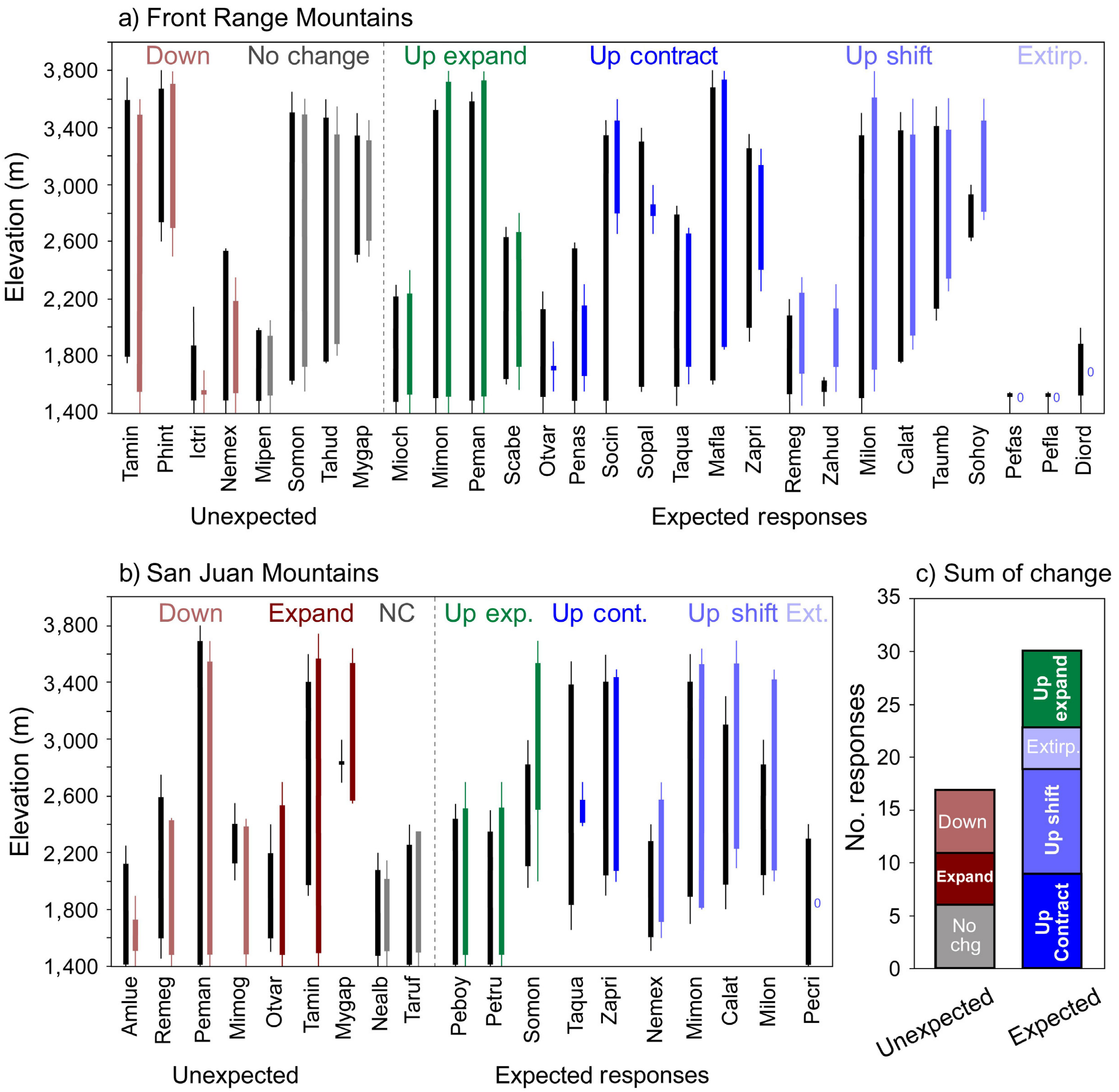

FIG. 3. Paired historical (left bar) and contemporary (right bar) elevational ranges of the included small mammal species on (a) the Front Range Mountains and (b) the San Juan Mountains. (c) The sum of expected or non-expected change: down, downshift or contraction; expand, downward expansion or expansion of both limits; NC/no chg, no change; ext./extirp., extirpation. Thick bars, empirical ranges; thin extensions, Bayesian range limits. Species names are abbreviated; for complete taxonomic names, see Appendix S3.

contemporary trapping methods (2 FR, 1 SJ; see Appendix S4: Fig. S1). As expected, sampling across each elevational gradient in each time period was not uniform (Fig. 2; Appendix S2: Fig. S1) due to the historically compiled efforts across multiple generations of researchers. Nonetheless, the number of specimens and localities is quite high both historically (4,580 specimen-localities) and contemporarily (7,444 specimen-localities) for these two regions. The overall range limit differences (range size) between the empirical data and the Bayesian model varied from 101 to 387 m historically and 75 to 676 m contemporarily. Based on the 95% Bayesian ranges (Fig. 3: thin black bar extensions; Appendix S3), species that significantly changed their lower or upper elevational limit contemporarily (≥100 m total change) included 26 species that shifted upward (9 contracted up, 10 shifted up, and 7 expanded upward) and 11 species that shifted downward (5 contracted down, 1 shifted down, 2 expanded down, and 3 expanded both limits; Fig. 3). Another 6 species did not significantly change either range limit (Fig. 3), and 4 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 (Fig. 1), the majority were upward changes (64%) with the Front Range species shifting upward more often than the San Juan species (Fig. 3c). The differences in empirical elevational ranges without the Bayesian model range extensions were similar (66% expected; 34% unexpected). Despite the substantial ecological differences in the two mountains, 50% of the shared species responded similarly (upward, downward, or no change) in their range shifts. This was particularly true for shared montane and cosmopolitan species of which 67% responded similarly (Appendix S3).

With the Bayesian models, the average elevational range change across all species was upward by 131 m (median 100 m). The Front Range species shifted higher on average (162 m) than did the San Juan species (89 m). Elevational range changes varied among species with both losses and gains in lower limits and upper limits (Figs. 3, 4), but with overall net gains in ranges at high elevations and net losses at low elevations (Fig. 4a). Elevational species richness compared historically and contemporarily also clearly display these changes (Appendix S4: Fig. S2). Correcting for historical richness differences, the percentage of range gains increased with elevation on both gradients, while the percentage of range losses generally decreased with elevation on both gradients but with some large losses toward the highest elevations as well (Fig. 4b, c). Overall, net range change was significantly positively correlated with elevation in accordance with the predictions of climate change (Spearman's ρ: FR = 0.83, $P < 0.0001$, df = 22; SJ = 0.55, $P = 0.0053$, df = 22). The distribution of anthropogenic development (Appendix S1: Fig. S3) defined as the percentage of developed, cultivated, and pastureland per elevation was positively correlated with range losses in the Front Range (Spearman's $\rho = 0.64$, $P = 0.0007$, df = 22), although unrelated to range losses in the San Juans (Spearman's $\rho = -0.13$, $P = 0.5587$, df = 22). All four species detected as locally extinct were low elevation rodents with small elevational ranges and dry desert, grassland or canyon habitat associations.

A combination of species traits and biogeography influenced the trajectory and magnitude of the range changes (Fig. 5). Montane species shifted higher more often (75%) and with larger upward shifts on average (346 m) than low elevation (53%, −21 m) or cosmopolitan species (58%, 158 m; total change, ANOVA $F_{2,40} = 3.47$, $P = 0.0409$; upper limit: $F_{2,40} = 3.26$, $P = 0.0487$; lower limit NS; Fig. 5a). Activity times (diurnal, nocturnal, flexible) were unrelated to range changes (Wilcoxon Rank Sums test, upper $\chi^2 = 2.62$, $P = 0.2697$; lower $\chi^2 = 0.98$, $P = 0.6143$; total $\chi^2 = 0.83$, $P = 0.6589$). Due to a correlation between body size and maximum latitude, we included only latitude, which had the stronger relationship with range changes, in the model (Appendix S4: Table S1). The remaining variables (elevational affiliation, maximum latitude in the species' geographic range, location of study area within its geographic range) were consistently supported and positively related to both upper and overall elevational range shifts in multivariate least squares regression models (upper, $r^2 = 0.50$, $P = 0.0006$; total $r^2 = 0.30$, $P = 0.0194$). Species with higher maximum latitude in their geographic range displayed significantly larger increases in upward elevational shifts of their upper range limit as well as the overall elevational range change in the models (e.g., Fig. 5b). Montane species (Fig. 5a) and species studied in the southern edge of their geographic range (Fig. 5c) also shifted higher in both models (significant individually only in the upper limit model). In contrast, there were no significant factors detected for the change in lower range limits.

DISCUSSION

Small mammals are moving to higher elevations in the Colorado Rocky Mountains on average by over 131 m with slightly larger upward shifts in the northwestern Front Range Mountains (162 m) than the southwestern San Juan Mountains (89 m). Since temperatures have warmed by at least 2°C across Colorado and within each of these mountains over the past several decades (Mote et al. 2005, Trenberth et al. 2007, USGCRP 2009, McGuire et al. 2012), this result confirms the expected response to anthropogenic climate change: species sensitive to temperature will track cooler temperatures at higher elevations as temperatures increase (Fig. 1; Pauli et al. 1996, Parmesan and Yohe 2003, Thomas et al. 2004, Walther et al. 2005). This trend is most pronounced in the montane mammals, those with elevational ranges predominately at mid-elevation to high elevation, who are shifting upward by an average of over 346 m, or 86.5 m per decade (Figs. 3, 5). These montane

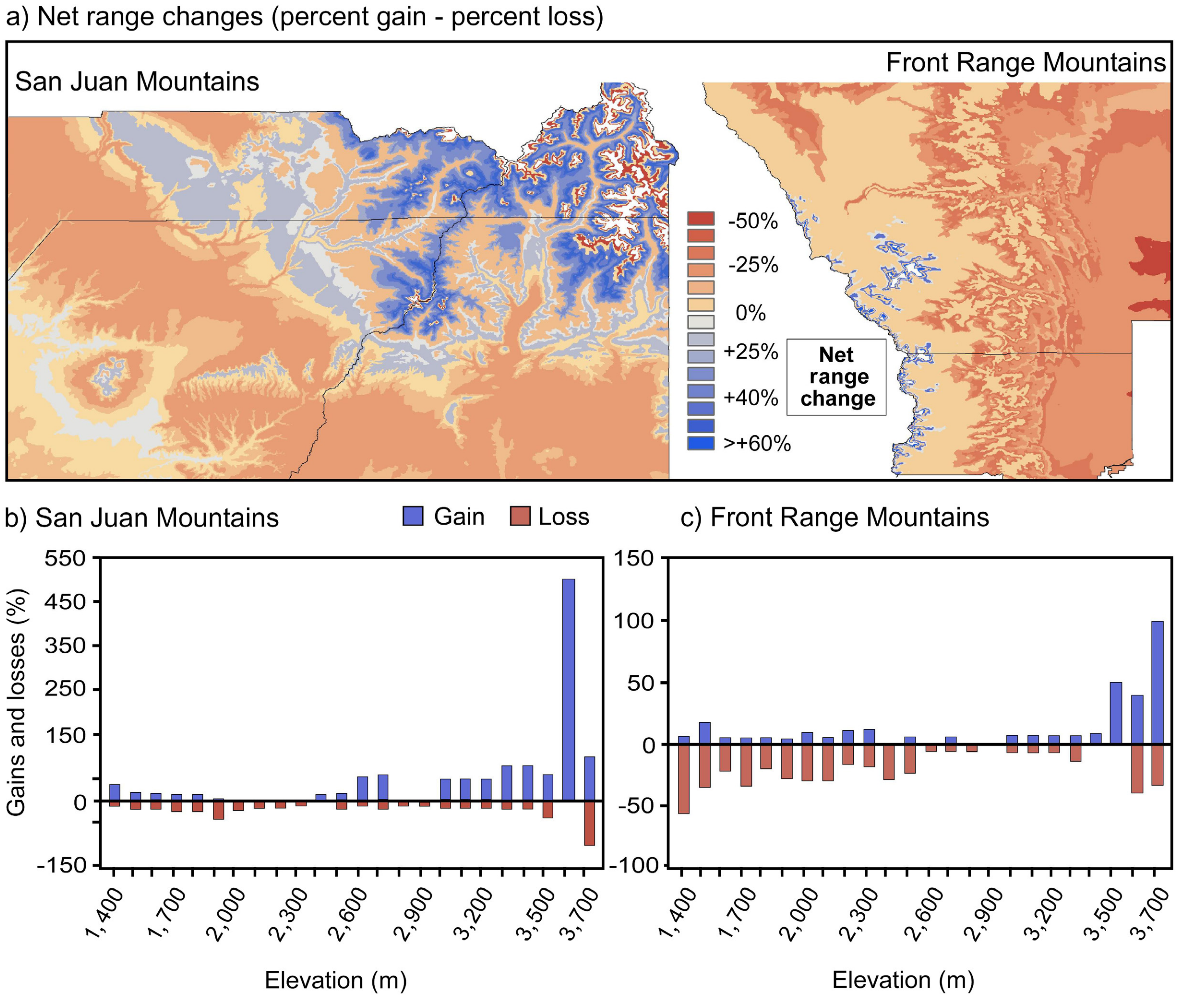

FIG. 4. (a) Elevational heat maps for the San Juan and Front Range Mountains showing change in percentage gains and losses at range limits with blues showing net gains predominantly at high elevation, light gray showing no or relatively little change, and yellow to reds showing increasing net losses (see scale legend). (b and c) Elevational distribution of the percentage range gains (blue bars) and losses (red bars) across all elevational range edges for the San Juans (b) and Front Range (c).

shifts are much larger than the average upward shifts detected in other studies (11 m per decade in a review; Chen et al. 2011).

Species traits and biogeography mediate which species are responding as expected by shifting their ranges 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 factors associated with increased upward change overall and upper range limits, including species with (1) a montane affiliation, (2) geographic ranges extending to higher maximum latitudes, and (3) the Front Range and San Juan Mountains occurring in their southern, lower geographic limits (Fig. 5). Changes in lower range limits were more enigmatic and variable across species than upper limits.

Most resurveys designed to detect elevational range shifts take advantage of repeatedly sampled, historical studies of a single set of sites along an elevational gradient (e.g., Moritz et al. 2008, Tingley and Beissinger 2009, Nufio et al. 2010, Rowe et al. 2010, Tingley et al. 2012). Contemporary researchers use repeat resurveys of those particular sites to detect change, and often use occupancy models to test for significant shifts (Appendix S2). However, historical data sets of repeat sampling both historically and contemporarily are relatively rare. If we limit ourselves to such studies, we will not proceed in detecting climate change effects much beyond published work unless we can more widely leverage presence-only historical data sets commonly preserved in natural history collections. Herein we used a more regionally expansive methodology by building a data set of historical elevational distributions for two mountain ranges, based on presence-only specimens and records from multiple generations of researchers. Then, we compared these historical data sets to contemporarily

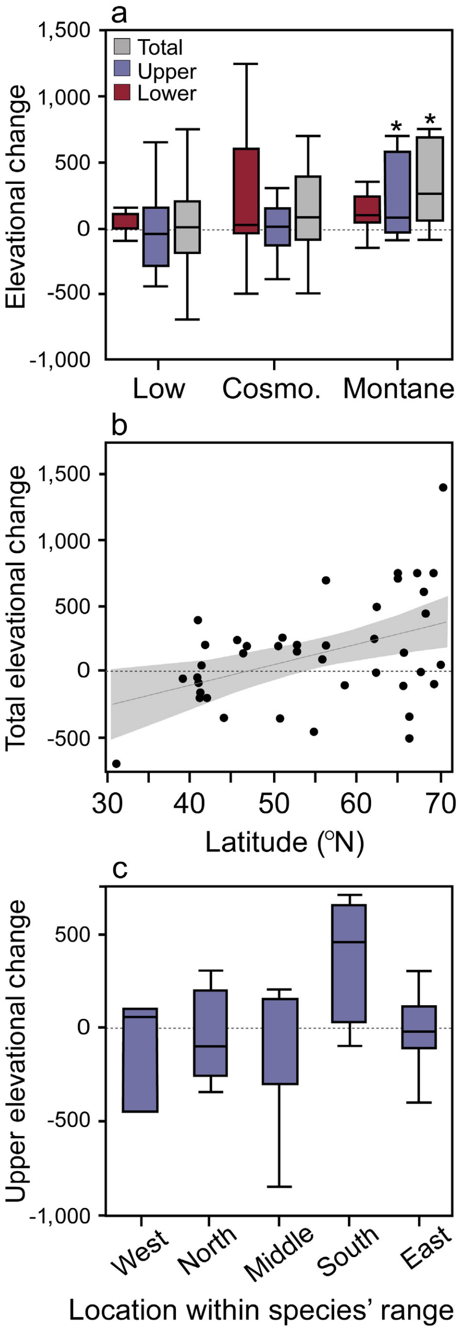

FIG. 5. Distributions of range shifts, including the three factors consistently, positively, and significantly associated with upper range limit and total range changes. (a) Elevational affiliation: a comparison of the lower limit, upper limit, and total change for low elevation, cosmopolitan (i.e., found across a wide range of elevations), and montane species. Box plot components are mid line, median value; box edges, 1st & 3rd quartile; whiskers, upper & lower values (not including outliers). Asterisks significant at $P < 0.05$. (b) Maximum latitude in a species' geographic range: species with higher latitude ranges had larger, upward shifts. (c) Location of study area within geographic range: species in which the studied mountain range was at the southern edge of their geographic range displayed larger, upward range shifts (Middle, = middle of range, or non-edge).

collected data through an extensive, repeat sampling 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 effects of stochastic, interannual variability in population sizes and detection compared to a particular year or two of sampling (McCain et al. 2016). Further, because we determined the historical ranges based on the highest and lowest observations across nearly 100 years of sampling, detecting changes may be a higher statistical bar than detecting changes at single sites sampled briefly. However, there are also disadvantages as the comparisons are not from known single sites, without repeat sampling for occupancy and detection probabilities, 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 (Tingley and Beissinger 2009). Presence-only historical data may be biased to overpredict historical ranges through inclusion of false positives or biased to underpredict due to lack of true absence data, but these data are likely the most commonly available for resurvey studies; alternative statistical methods are necessary for their broader utilization (Tingley and Beissinger 2009).

We combat these sampling issues in multiple ways. First, we vetted the specimens, their identifications, localities, and elevations extensively. Our efforts emphasized records near the elevational margins for each species since historical and contemporary comparisons are essentially comparisons of the range limit samples. 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., King and McCain 2015, Chinn 2018, 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 robustly estimated 95% Bayesian limits, which accounted for the influence of patchy sampling for each time period and mountain. The maximum contemporary elevation for many species was higher than any historical record for either region (southwest quadrant or northeast quadrant of Colorado), broadening the historical sampling evidence at high elevations, and making it less likely 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 Mountains.

Anthropogenic land-use change exists on these gradients (Appendix S1: Fig. S3; Szewczyk and McCain 2019), and has been shown to influence elevational ranges in other small mammal studies (e.g., Rowe 2007, Rowe et al. 2010). However, along these gradients anthropogenic activity is most concentrated at the lower elevations, particularly at the base of the Front Range Mountains, and declines with elevation. The losses in lower limits were positively correlated with land-use change in the Front Range, but not in the San Juans (Fig. 4). 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*) lived in areas around the cities of Boulder and Loveland that are now almost completely developed. Thus, land-use change may be exacerbating climate change effects, particularly at the base of the Front Range, but it is not solely responsible for the changes since it cannot explain the upward shifts at middle and high elevations nor the range changes in the San Juans at lower or higher elevations.

Other small mammal studies along elevational gradients similarly observed a mixture of species contracting, shifting and expanding their ranges as well as those not showing much change (Moritz et al. 2008, Rowe et al. 2010, 2015). They each also detected some legacies of land-use change. Herein, we detected species traits and biogeographic factors that strongly mediated which species shifted upward as expected by climate change and which did not (Fig. 5). 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. In a previous mammal meta-analysis, montane species, larger bodied mammals, and obligately diurnal species were more likely to shift upward as expected due to climate change (McCain and King 2014). In this data set, we did not detect a positive influence of body size, but likely this was because only smaller sized mammals were included, and most shrews (the smallest terrestrial mammals) in our data set shifted their elevational ranges upward.

These data provide clear evidence that small mammals, particularly montane and cold-adapted species, are rapidly and drastically shifting their ranges to higher elevations as temperatures warm regionally. They shifted upward by an average of 346 m in four decades; a trend that, if it continues, will reduce their available habitat so much they will be at risk of local extinction. For example, land area on a mountain decreases linearly above the 2,400-m contour, such that only about 5% of land area occurs at or over 3,400 m. The amount of land that is uninhabitable (rock and ice) also increases dramatically at these highest elevations, such that the amount of habitable land at or above 3,400 m is only 1–2% of habitable land area on the mountain as a whole. Thus, even if mammals and other organisms can track higher, the amount of habitable land at the highest elevations is minimal, which is evident in Fig. 4, particularly in the Front Range. Clearly, variation in species' responses is large, and the type of species and the study location within their geographic range are important (Lenoir et al. 2010, Tingely et al. 2012, McCain and King 2014, Rapacciuolo 2014, Smith et al 2019). Thus, cold-adapted, montane species in the southern edge of their geographic ranges are consequential species of conservation concern as temperature continues to warm, based on both these data and previous analyses (McCain and King 2014). Importantly, these trends match what physiological models and climate change scientists predicted early on: montane species would be bellwethers for climate change responses (e.g., McDonald and Brown 1992, Grabherr et al. 1994, Inouye et al. 2000, Beever et al. 2003, Parmesan and Yohe 2003).

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DATA AVAILABILITY STATEMENT

Additional code for the simulation and sensitivity analysis is available on Zenodo: http://doi.org/10.5281/zenodo.4305815