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

extirpated locally. 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; 16% of the gradient). 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.

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2 **warms**
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6 **Authors:** Christy M. McCain[1,2*], Sarah R. B. King[2,3], Tim M. Szewczyk[1,4,5]
7
8 **Authors Affiliation:** [1]Department of Ecology & Evolutionary Biology and [2]CU Museum of
9 Natural History, University of Colorado, Boulder, CO 80309 USA; [3]Natural Resource Ecology
10 Laboratory, Colorado State University, Fort Collins, CO 80523, USA; [4]Department of Natural
11 Resources and the Environment, University of New Hampshire, Durham, NH 03824 USA;
12 [5]Department of Computer Science, University of New Hampshire, Durham, NH 03824 USA
13
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17
18 ***christy.mccain@colorado.edu**
19
20
21 **Abstract:** The largest and tallest mountain range in the contiguous United States, the southern

22 Rocky Mountains, has warmed considerably in the past several decades due to anthropogenic

23 climate change. Herein we examine how elevational ranges of 47 mammal species (42 rodents, 5

24 shrews) have changed from their historical distributions (1886–1979) to their contemporary

25 distributions (post–2005) along 2400 m elevational gradients in the Front Range and San Juan

26 Mountains of Colorado. Historical elevational ranges were based on more than 4580 geo-

27 referenced museum specimen and publication records. Contemporary elevational ranges were

28 based on 7444 records from systematic sampling efforts and museum specimen records. We

29 constructed Bayesian models to estimate the probability a species was present, but undetected,

30 due to undersampling at each 50 m elevational bin for each time period and mountain range.

31 These models leveraged individual-level detection probabilities, the number and patchiness of

32 detections across 50 m bands of elevation, and a decaying likelihood of presence from last

33 known detections. The 95% likelihood elevational ranges were then compared between historical

34   and contemporary time periods to detect directional change. Responses were variable as 23

35   mammals shifted upward, 10 did not change, 10 shifted downward, and 4 were extirpated

36   locally. The average range shift was 122 m upward, while exclusively montane species shifted

37   upward more often (83%) and displayed larger average range shifts (337 m; 16% of the

38   gradient). Changes in upper range limits were best predicted by increases associated with (a)

39   montane species, (b) species with higher maximum latitude in their geographic range, and (c) the

40   study mountain in the southern edge of their geographic range (stepwise multivariate linear

41   regression: $r^2 = 0.4705$, $p < 0.0001$). Thus, mammals in the Southern Rocky Mountains serve as

42   harbingers of more changes to come particularly for montane, cold-adapted species in the

43   southern portion of their ranges.

44

45   **INTRODUCTION**

46   Earth is warming at an unprecedented rate from human-created emissions (Trenberth et

47   al. 2007, USGCRP 2009, Duffy and Tebaldi 2012). Anthropogenic impacts are also affecting

48   precipitation trends as well as increasing the variability and severity of extreme weather events

49   (Trenberth et al. 2007, USGCRP 2009, Duffy and Tebaldi 2012). Essentially the planet and all

50   its inhabitants are in a climate crisis of unknown magnitude. One urgent imperative is tracking

51   the impacts of these climate changes on living organisms to better mitigate the damages and to

52   improve predictions of foreseeable conservation catastrophes. Unfortunately, there are still more

53   publications predicting rather than measuring species' responses (e.g., Dawson et al. 2011,

54   review in McCain and King 2014). Reasons for this disconnect are many-fold, but foremost are

55   the rarity of detailed historical and repeatable surveys across gradients of change (e.g., latitude,

56   elevation, depth), and the significant, long term effort and quantity of data needed to detect

57 organismal responses. As a research community we need to embrace innovative ways to compile

58 historical and contemporary records to robustly track how organisms are currently changing and

59 monitor these changes through time (Dawson et al. 2011, Grytnes et al. 2014).

60   Temperature cools as elevation increases, and species are expected to track temperatures

61 by shifting to higher elevations as average temperatures increase in a region (Fig. 1a; e.g.,

62 McDonald and Brown 1992, Pauli et al. 1996, Inouye et al. 2000). Such tracking could include

63 an upward shift of just the lower or upper end of the species' range, or both range limits

64 depending on the location on the montane gradient and the consistency of the response between

65 the range edges. The published resurveys of historical montane gradients do provide strong

66 evidence that some organisms are shifting their ranges to higher elevations. For example, many

67 small mammals have shifted upwards in the western United States (Moritz et al. 2008, Rowe et

68 al. 2010, Rowe et al. 2015). Many alpine plants in Europe have shifted higher with climate

69 change (Grabherr et al. 1994, Pauli et al. 1996, Lenoir et al. 2008, Engler et al. 2011), moths in

70 the Asian tropics have shifted upwards by an average of 67 m (Chen et al. 2009), and a review of

71 montane shifts detected an 11 m increase in elevational ranges per decade across organisms

72 (Chen et al. 2011). But the upward shifts are not the whole story; one critical element is the

73 variability in responses on these gradients. Overall the shifts are upward, but individual species

74 also demonstrate unexpected responses like downward shifts or no detectable change (Fig. 1b;

75 Lenoir et al. 2010, Crimmins et al. 2011, McCain and King 2014, Rowe et al. 2015). The

76 location of the mountain appears important. For example, American pika on small, isolated sky

77 islands in the western US are experiencing local extirpations linked to higher temperatures,

78 decreased precipitation, and lack of rock ice features (Beever et al. 2003, Beever et al. 2010,

79 Millar and Westfall 2010, Beever et al. 2011). However, the same species in the more expansive,

80   taller, and interconnected southern Rocky Mountains appear to have few, if any, local

81   extirpations (Erb et al. 2011).

82   Other important biogeographic factors mediating responses may include the latitude of

83   the mountain, the location of the mountain in relationship to the species' geographic range, and

84   the size, height and isolation of the mountain (e.g., McCain and King 2014). Traits of the species

85   themselves like body size, activity times, and physiology may also mediate which species

86   respond as predicted to climate change and which do not (e.g., Moritz et al. 2008, Angert et al.

87   2011, McCain and King 2014). So far, such mediating traits are rarely detected in individual

88   montane gradient studies. Despite some initial lack of trait detection in mammals (e.g., Angert et

89   al. 2011), McCain and King (2014) found that the North American mammal species most likely

90   to exhibit expected responses were large, strictly nocturnal or diurnal, or at higher elevations and

91   latitudes. We would expect that if traits were important to mediating responses, we would also

92   detect them on individual mountain gradients or particular regional studies encompassing

93   multiple species as long as sufficient variability in the traits was exhibited among the species.

94   Strong associations between species traits and climate change responses would enable better

95   predictions and improve conservation outcomes for the types of species most at risk from large,

96   detrimental environmental change.

97   Thus, herein, we examine how 47 mammal elevational ranges have changed in response

98   to warming in two regions of the largest, tallest and most interconnected mountains in the

99   contiguous US, the Southern Rocky Mountains. We compile historical elevational ranges for

100   each species based on museum specimens and literature before 1980, and contemporary

101   elevational ranges based on more than a decade of extensive trapping surveys and supplemental

102   museum specimens after 2005. We develop Bayesian undersampling models to accommodate

103 species-, mountain-, and time-period-specific 95% likelihood elevational ranges. Then we assess

104 how elevational ranges have changed, testing for biogeographic and species-trait effects that may

105 mediate which species are and are not moving higher in elevation with increasing temperatures.

106

107 **METHODS**

108 The Rocky Mountains extend from the southwestern USA to western Canada reaching their

109 highest elevations in Colorado, USA. Temperatures in the two mountainous regions studied in

110 the Colorado Rockies (Fig. 2), the San Juan Mountains (1414–4286 m) and the Front Range

111 Mountains (1438–4346 m), have increased since the 1980s (Trenberth et al. 2007, USGCRP

112 2009, McGuire et al. 2012). However, the San Juans are getting increasingly wetter, while the

113 Front Range is becoming increasingly drier (Mote et al. 2005).

114 *Historical Mammal Data—*We amassed specimen data from all museums with Colorado

115 mammal specimens, which included 58,709 specimens from 45 museums (2009–2012; Appendix

116 S1). Nomenclature was updated following Wilson and Reeder (2005), and georeferencing

117 following the MaNis protocols (Wieczorek et al. 2004, Chapman and Wieczorek 2006). For

118 quality assurance, we restricted analyses to rodent and shrew specimens (Fig. 2 circles) with (1)

119 a reliable species-level identification by an expert, re-verified by CMM, or in a robust locality

120 for the species (core elevations in the local distribution); (2) a documented year or time period of

121 collection; (3) an elevation provided by the collector or a locality specific enough to be

122 georeferenced (latitude, longitude, elevation) with a horizontal error <1000 m (designated as

123 usable) or <5000 m (designated as marginal) with the strictest criteria used in the final lowest

124 and highest known sites; and (4) a location within the northeast portion of the Front Range

125 (Boulder and Larimer counties) or the southwestern portion of the San Juans (Dolores, La Plata,

126 Montezuma, San Juan counties). These data were augmented by lowest and highest elevational

127 records in the historical literature, including from the *Colorado Biological Survey* (Cary 1911),

128 *Mammals of Mesa Verde National Park, Colorado* (Anderson 1961), and *Distribution of*

129 *Mammals in Colorado* (Armstrong 1972). The most rigorous vetting focused on the lowest and

130 highest localities for each species, only using records without significant, plausible error in the

131 locality, elevation, or identification.

132   *Contemporary Mammal Data*—All specimens that met the accuracy criteria and were

133 documented after 2005 were included in the contemporary data (Fig. 2 stars). The Colorado

134 database was augmented in 2018 under the same vetting protocol using a search of the Global

135 Biodiversity Information Facility (www.gbif.org) for more recent specimens (2006–2018). For

136 systematic, contemporary mammal surveys, two elevational transects were established in the

137 southwestern San Juan Mountains and two in the northeastern Front Range (Fig. 2; Fig. S1.1;

138 McCain et al. 2018). Each transect consisted of eight sites placed every 200−300m in elevation

139 between the base of the range (1400−1700m) and the upper limit of vegetation on the mountain

140 top (3600−3800m) (Fig. S1.1). At each of these 32 anthropogenically undisturbed sites, we

141 conducted small mammal surveys between 2010 and 2012 using live-trapping, pitfall trapping

142 and visual surveys across all habitats. Trapping was extensive (5100 trap-nights per site; 163,200

143 total trap-nights) and equal among sites. Additional mammal survey data for the San Juans

144 included seven sites from a pilot study (2007) and 13 sites in Mesa Verde National Park (2018)

145 for a total additional 7,550 trap-nights (Fig. S1.1). Similarly for the Front Range (2017),

146 contemporary sampling also included 2430 trap-nights across three low elevation sites. Species

147 were identified in-hand, with specimens, or DNA sequences (McCain et al. 2018). IACUC

148 vertebrate handling protocols were approved by CU Boulder (08-07-McC-02; 1103.02; 2548).

149 *Bayesian Undersampling Models*—The documented elevational range of each species was

150 assumed to be between the lowest and highest known localities per time period, as species are

151 not always detected when present (MacKenzie et al. 2002). But the sampling along each

152 elevational gradient in each time period was patchily distributed (Fig. 2, S1.2). Therefore, to

153 estimate elevations in which each species had a high probability of occurrence beyond the

154 observed range, we developed a Bayesian model. Occupancy models typically rely on repeated

155 surveys and local environmental data to predict a species' probability of presence when

156 undetected in a particular locality (MacKenzie et al. 2002, Kéry and Royle 2008, Szewczyk and

157 McCain 2019). Such data are unavailable in many cases, including for typical compiled,

158 historical datasets. Consequently, we employed a modified conceptual framework for occupancy

159 to evaluate the probability of sampling error rather than directly considering species'

160 environmental preferences.

161 Within each time period, mountain range, and elevational bin, we considered the detected

162 individuals as a draw from a multinomial distribution (Fig. S1.2), representing a sample from the

163 community of individuals at those elevations. The number of observed individuals from each

164 species depends on the species' relative abundance and the probability of detecting a given

165 individual of the species. Thus, for each elevational bin i, the number of observed individuals

166 belonging to species 1–J, represented as vector $\boldsymbol{y_i}$, was modeled as: $\boldsymbol{y_i} \sim Multinomial(\boldsymbol{p_i}, Y_i)$

167 where $\boldsymbol{p_j}$ is a vector of the probabilities that a random observed individual from elevational bin i

168 belongs to each species, and Y_i is the total number of individuals detected across all species in

169 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

170 in elevational bin i, Z_{ij} is a latent binary parameter indicating the true presence (1) or absence (0)

171 of species j in elevational bin i, and δ_j is the probability of detecting a given individual of species

172   j. Note that p_{ij} is a probability ranging from 0 (species j is not present at elevation i) to 1 (only

173   species j is present at elevation i). We used the repeated, mark and recapture survey data in the

174   contemporaneous dataset to calculate the individual-level detection probability, δ_j, for each

175   species. If there were too few recaptures for robust estimation in a particular species, then we

176   used an average from the clade (e.g., *Sorex*).

177   The unobserved parameter Z_{ij} is Bernoulli distributed with probability ψ_{ij}, which is the

178   probability that species j was present but unobserved due to sampling error beyond its

179   interpolated range, and is calculated as a function of the elevational distance to the observed

180   elevational limits, the patchiness of the interpolated range (i.e., the proportion of elevational bins

181   without detections within the interpolated range), and their interaction: $\psi_{ij} = a_j + \beta_1 * dist_{ij} +$

182   $\beta_2 * patchiness_j + \beta_3 * dist_{ij} * patchiness_j$ where a_j is the species-specific intercept and β are

183   the slopes. The intercepts among species were distributed normally with community-level mean

184   α and standard deviation σ, while the slopes were community-level with one value for all species.

185   For each elevational bin beyond each species' interpolated range, we calculated the

186   probability of occurrence as the posterior probability of $Z_{ij} = 1$. A species was assumed absent at

187   an elevation if the probability of occurrence was < 5%, indicating ≥ 95% posterior probability of

188   absence. Based on this dichotomy, we calculated Bayesian interpolated ranges incorporating

189   sampling uncertainty to then use as the elevational range of each species for each mountain in

190   each time period. For the range shift analyses, we only included species with at least 10 historical

191   records per mountain and detected in the contemporary sampling. The model was run with JAGS

192   4.3.0 in R 3.6.1 using the *rjags* package (Plummer 2017, 2019). For each model, we ran 3 chains

193   for 20,000 iterations, discarding the first 10,000 iterations as burn-in, and then retaining every

194   10th iteration for the final posterior distributions. We used uninformative prior distributions for α,

195 β, and σ, and a diffuse normal prior distribution constrained to be positive for each λ_{ij} where the

196 mean was the overall abundance of each species (Appendix S1).

197   *Statistical Analyses*—A significant change from the Bayesian historical to the Bayesian

198 contemporary elevational range limits was determined if the change was $\geq$ 100m. The size of the

199 shift upward or downward was calculated for the (1) lower limit; (2) upper limit; and (3) overall

200 change based on the range midpoint (Fig. 1). Occasionally (i.e., Fig. 3: Tqua (*Tamias*

201 *quadrivittatus*) in San Juans), a large contraction in a contemporary range to just a small portion

202 of the middle elevations of the historical range can result in a slightly lower midpoint. In those

203 rare cases, the shift direction is the range limit with the largest shift. With warming temperatures,

204 species' ranges are predicted to shift to higher, cooler elevations (Fig. 1a). Unexpected responses

205 to warming would be either no change, where both range limits change by less than 100m, or a

206 downward shift in one or both limits such that the new range midpoint is lower (Fig. 1b).

207   Most range gains will occur at mid- to high-elevations under a scenario of regional

208 warming. Thus, we expect range gains to increase with elevation, whereas range losses would be

209 spread across the gradient more or less evenly in accordance with the wide elevational spread in

210 historical lower limits. contrast, anthropogenic habitat change declines with elevation on both

211 mountains, although most pronounced in the Front Range. Thus, if the reduction of available

212 habitat is the predominant factor influencing the elevational distribution of the community, then

213 the expectation would be a concentration of range losses at the lowest portion of the gradients

214 that decreases toward the highest elevations. To assess these trends, we calculated the number of

215 species losing or gaining range at their lower and upper limits within each 50m band up each

216 mountain. Because the number of species per elevational band differs, we examined the

217 percentage of range losses and range gains for each 50m elevational band on each mountain

218   gradient by dividing the species counts by the historical number of species present in each band.

219   We tested for elevational trends using Spearman's rank correlations.

220   To assess how species traits influenced the responses to anthropogenic climate change,

221   we examined several traits empirically linked or hypothesized to be important to differential

222   responses to climate change in mammals (e.g., Moritz et al. 2008 and references therein, Angert

223   et al. 2011, McCain and King 2014). These included body size, activity times, elevational

224   affiliations, high latitude ranges, location of study area within the species biogeographic range

225   (i.e., southern third, middle third or northern third of its range), or whether the study area was

226   near the species' range edge (e.g., western-most populations of a plains species). Many more

227   traits were possible, but we were limited by our species sample size as well as the correlation in

228   traits (e.g., body size and reproductive traits). Trait data were from the PanTHERIA and MOM

229   databases (Smith et al. 2003, Jones et al. 2009), species accounts in the journal *Mammalian*

230   *Species*, and additional literature sources (e.g., Hall 1981, Nowak 1991, Armstrong et al. 2011,

231   IUCN 2018). Each species was denoted as a low elevation species, a montane species, or

232   cosmopolitan (across most habitats and elevations on the mountain) by its known habitat

233   affinities in Colorado (Armstrong et al. 2011), but also based on its individual historical

234   distribution on each mountain.

235   To detect if particular its were associated with differential increases or decreases of the

236   upper lower range limits on using on each mountain, we used stepwise, multivariate linear

237   regressions models, the lowest AICc weights, and all variables that were individually significant

238   to detect he best-fit model (Burnham and Andersen 2002). Similarly, a second set of trait

239   analyses were conducted on expected (upward) and non-expected responses (downward, no

240   change) on each mountain using logistic regressions. Because phylogenetic relatedness could

241 impact the robustness of these analyses (e.g., Blomberg and Garland 2002, Blomberg et al.

242 2003), we estimated a phylogenetic signal in the lower and upper range shifts using the mammal

243 supertree (Bininda-Emonds et al. 2007) pruned to the taxa included in each mountain dataset.

244 Phylogenetic signal was calculated with *phylosignal* (Keck et al. 2016) in *R* using all five

245 significance tests (*Cmean*, *I*, *K*, *K.star,* and *Lambda*). No significant phylogenetic signal was

246 detected (p >> 0.05; Table S1.1); thus, we present non-phylogenetically corrected analyses.

247

248 **RESULTS**

249 　　　　Our compiled databases for historical and contemporary distributions of small mammals

250 (rodents, shrews) included 37 species in the Front Range Mountains (FR) and 33 species in the

251 San Juan Mountains (SJ). Species used in the analyses (28 FR, 19 SJ) were well sampled both

252 historically and contemporarily with a per-mountain average of 97 specimens historically and

253 158 specimens contemporarily (Appendix S2). The empirical elevational ranges for each species

254 were based on these data for each mountain and time period (Fig. 3: thick bars). Several species

255 were not used in the range shift analyses because they were deemed to be insufficiently detected

256 historically (<10 specimens; 6 FR, 13 SJ) or under-sampled with contemporary trapping methods

257 (3 FR, 1 SJ; see Fig. S3.1). The sampling across each elevational gradient in each time period

258 was not uniform (Fig. 2; Fig. S1.2). This is expected given the historically compiled efforts

259 across multiple generations of researchers. Nonetheless, the number of specimens and localities

260 is quite high both historically (4580 specimen-localities) and contemporarily (7444 specimen-

261 localities) for these two regions. The changes in the range limits between the empirical data and

262 the Bayesian model varied from 0 to 392 m historically and 60 to 657 m contemporarily. Based

263 on the 95% Bayesian ranges (Fig. 3: thin bar extensions; Appendix S2), species that significantly

264   changed their lower or upper elevational limit contemporarily (≥100m change) included 23

265   species that shifted upwards and 10 species that shifted downward (Fig. 3 blue and red bars,

266   respectively). Another 10 species did not significantly change either range limit (Fig. 3 grey

267   bars), and four species known historically were undetected contemporarily and thus considered

268   locally extirpated (zeros in place of contemporary range bars). In comparison to the expected and

269   unexpected range changes (Fig. 1), the majority of upward changes were shifts, while the

270   majority of downward changes were contractions (Fig. 3c). The changes indicated by the

271   empirical elevational ranges without the Bayesian model additions were similar, but even more

272   skewed toward upward changes (32 upward, 6 downward, 0 no change), and the percentage of

273   upward contractions was higher (50% versus 30% (the latter in Fig. 3c)).

274   With the Bayesian models, the average elevational range change across all species was

275   upward by 122 m (median 88 m). The Front Range species shifted higher on average (152 m)

276   than did the San Juan species (80 m). These shifts varied across species with both losses and

277   gains in lower limits and upper limits (Fig. 3). The percentage of range gains increased

278   significantly with elevation on both gradients (Fig. S3.3; Spearman's rank correlations: FR r =

279   0.42, p = 0.0399; SJ r = 0.53, p = 0.0077); whereas, the percentage of elevational losses occurred

280   across both elevational gradients rather uniformly (Spearman's rank correlation FR r = -0.23, p =

281   0.2827; SJ r = 0.24, p = 0.2485). Thus, on both gradients, net range gains increase with elevation

282   (elevational heat map: Fig. S3.3). All four species detected as locally extinct were low elevation

283   rodents with small elevational ranges and dry desert, grassland or canyon habitat associations.

284   A combination of species traits and biogeography influenced the trajectory and

285   magnitude of the range changes, particularly for the shifts in the upper range limits (Fig. 4).

286   Montane species shifted higher more often (83%) and with larger upward shifts (337 m) than low

287 elevation (31%, -31 m) or cosmopolitan species (42%, 150 m). The best multivariate linear

288 regression model for the upper range limit shifts ($r^2 = 0.4705$, $p < 0.0001$, AICc weight = 605.2)

289 included an increase in upward shifts for montane species (Fig. 4a), for species with high

290 maximum latitude in their geographic range (Fig. 4a), and species in which the study mountains

291 were at the southern edge of their geographic range (Fig. 4b). The best multivariate linear

292 regression model for the lower range limit shifts ($r^2 = 0.1025$, $p < 0.0363$, AICc weight 626.9)

293 only included an increase in upward shifts for species where the study mountain was at the

294 eastern edge of their geographic range (Fig. 4c). Lastly, the best multivariate logistic regression

295 model for the expected responses to climate change (upward changes) versus the unexpected

296 responses (downward changes, no responses) detected a greater preponderance of unexpected

297 responses in the low elevation species compared to the montane and cosmopolitan species ($\chi^2 =$

298 8.5582, $p < 0.0136$, AICc weight = 57.4).

299

300 **DISCUSSION**

301   Small mammals are moving to higher elevations in the Colorado Rocky Mountains on

302 average by over 120 m with slightly larger upward shifts in the northwestern Front Range

303 Mountains (180 m) than the southwestern San Juan Mountains (80 m). Since temperatures have

304 warmed across Colorado and within each of these mountains over the past several decades (Mote

305 et al. 2005, Trenberth et al. 2007, USGCRP 2009, McGuire et al. 2012), this confirms the

306 expected response to anthropogenic climate change—species sensitive to temperature will track

307 cooler temperatures at higher elevations as temperatures increase (Fig. 1; Pauli et al. 1996,

308 Parmesan and Yohe 2003, Thomas et al. 2004, Walther et al. 2005). This trend is most

309 pronounced in the montane mammals—those with elevational ranges predominately at mid- to

310   high-elevations—who are shifting upward by an average of over 330m (Fig. 3, 4). These

311   montane shifts are nearly 8 times the average upward shifts detected in other studies (84 m per

312   decade vs 11 m per decade in a review; Chen et al. 2011).

313   Physiological and biogeographic traits mediate which species are responding as expected

314   by shifting higher and which are not responding as expected by shifting downward or not

315   changing. In particular, the distance shifted upward by small mammals appears to be a function

316   of cold-adaption. This is inferred by the factors associated with increased upper range limits,

317   including species with (a) a montane affiliation, (b) geographic ranges extending to higher

318   maximum latitudes, and (c) the Front Range and San Juan Mountains occurring in their southern,

319   lower geographic limits (Fig. 4a,b; $r^2 = 0.4705$, $p < 0.0001$). The species least likely to respond

320   as expected were the lower elevation species, which in these areas include mostly semi-arid

321   desert, canyonland, and grassland species adapted to higher temperatures and lower rainfall than

322   their montane counterparts (Armstrong et al. 2011) ($\chi^2 = 8.5582$, $p < 0.0136$). Changes in lower

323   range limits were more enigmatic and variable across species than upper limits. Species in which

324   these mountains were at the eastern edge of their geographic range moved their lower elevational

325   limit higher (Fig. 4c; $r^2 = 0.1025$, $p < 0.0363$). Again, this is an indication of montane, cold-

326   adapted species, since most species with the southern Rockies as their eastern geographic range

327   edge are distributed only in the intermountain west or western North America (Armstrong 1972,

328   Hall 1981, Armstrong et al. 2011). For example, some of the eastern edge species that shifted

329   their lower limit upward include Red-backed voles (*Myodes gapperi*), Water shrews (*Sorex

330   palustris*), Yellow-bellied marmots (*Marmota flaviventris*), and Golden-mantled ground squirrels

331   (*Callospermophilus lateralis*) (see Appendix S2). Another factor potentially obscuring the lower

332   range edge changes was contemporary undersampling at the lowest elevations, particularly

333   <1600m in the Front Range, due to lack of remaining intact habitat. The empirical ranges

334   detected many more upward contracting lower limits, than did the Bayesian models that

335   compensated for this low sampling effort. Thus, the results here are a conservative estimate of

336   lower limit contractions, and consequently, overall range contractions.

337   Most resurveys designed to detect elevational range shifts take advantage of well-

338   sampled, historical studies of a single set of sites along an elevational gradient (e.g., Moritz et al.

339   2008, Nufio et al. 2010, Rowe et al. 2010, Tingley et al. 2012). The contemporary researchers

340   resurvey those particular sites as best as possible to detect change. But those ideal historical

341   datasets are rare and if we limit ourselves to such studies, we will not proceed in detecting

342   climate change effects much beyond published work. Herein we used a more regionally

343   expansive methodology by building a dataset of historical elevational distributions for two

344   mountain slopes, based on specimens and records of multiple generations of researchers. Then,

345   we compared these historical datasets to contemporarily collected data through an extensive

346   trapping effort augmented by specimens and records of additional researchers. This methodology

347   has advantages as the elevational ranges are based on many more sites, potentially capturing the

348   elevational ranges on a mountain more completely and reducing stochastic effects of a particular

349   year or two of sampling (McCain et al. 2016). Further, because the historical ranges are

350   determined by the highest and lowest observations across nearly 100 years of sampling, detecting

351   changes may be a higher statistical bar than detecting changes at single sites sampled briefly.

352   However, there are also disadvantages as the comparisons are not at known single sites, and the

353   sampling is broader spatially and temporally, and thus patchier. There is also more potential error

354   in the species identifications and locality information than in a single gradient study.

355   We combat these sampling issues in multiple ways. First, the specimens, their

356   identifications, their localities, and elevations were vetted extensively with particular emphasis

357   on records near the elevational margins for each species since historical and contemporary

358   comparisons are essentially comparisons of the range limit samples. Difficult to identify species

359   (i.e., shrews, chipmunks, voles, and *Peromyscus*) received special emphasis on re-identifications,

360   molecular analyses, and quantitative morphological models (e.g., King and McCain 2015, Chinn

361   2018, McCain et al. 2018). Second, we built Bayesian models to estimate sampling-based

362   uncertainty across each gradient tailored to the species' detections and detectability as well as the

363   overall distribution of samples. This led to 95% Bayesian limits that were robustly extended

364   beyond the empirical ranges for comparisons between time periods by accounting for the

365   influence of patchy sampling. The maximum contemporary elevation for many species was

366   higher than any historical record for either region (southwest quadrant or northeast quadrant of

367   Colorado), making it unlikely that the upward shifts were due to historical undersampling of high

368   elevations in each of these two mountains. Similarly, many of the upward shifting species had

369   changes in both their lower and upper limits that were well below the highest elevations on each

370   mountain. The Front Range Mountains were the better sampled of the historical gradients, and

371   showed stronger elevational shifts while detecting similar patterns as the lesser sampled San Juan

372   Mountains.

373   Anthropogenic land use change is not absent from these gradients (Szewczyk and

374   McCain 2019), and has been shown to influence other small mammal elevational studies (e.g.,

375   Rowe 2007, Rowe et al. 2010). But along these gradients it is most concentrated at the lowest

376   elevations, particularly at the base of the Front Range Mountains, and declines with elevation. It

377   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 (Fig. S3.3). 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 (<1600m) in the Front Range than did historically due to

human development, but more sampling is 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. 2010, Rowe et al. 2015). 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. 4). 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 and King 2014). In this dataset we did not detect an influence of body size, but

likely this was because (a) only smaller sized mammals were included, and all shrews (the

smallest terrestrial mammals) in our dataset shifted their elevational ranges upward.

401   These data are clear evidence that small mammals, particularly montane and cold-adapted

402   species, are rapidly and drastically shifting their ranges to higher elevations as temperatures

403   warm regionally. They shifted upward by an average of 337m or 16% of the 2400m gradient in

404   four decades; a trend that if it continues will reduce their available habitat so much they will be

405   at risk of local extinction. The lower limit shift upward appears to be a less pronounced trend

406   than upper limit extensions. This lag may indicate the temporal variability in climate change

407   conditions year to year allowing some populations to exist despite their low viability long-term,

408   but also indicates that more sampling is needed at the lowest elevations in existing patches of

409   intact habitat to confirm empirical absences. Clearly, the type of species and where a species is

410   studied within their range are important. Thus, cold-adapted, montane species in the southern

411   edge of their geographic ranges are consequential species of conservation concern as temperature

412   continues to warm, based on both these data and previous analyses (McCain and King 2014).

413   Take heed—it is only going to continue.

414

415   **ACKNOWLEDGMENTS**

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548

549   **Supporting Information: Appendix S1.** Supplementary Methods; **Appendix S2.** Dataset of

550   species, traits, samples, range limits and shifts; **Appendix S3**. Supplementary Results**.**

551

552   **Figure Legends**

553   **Figure 1.** Expected (a) and unexpected (b) responses to anthropogenic warming on mountains. a.

554   Expected: potential upward elevational range contractions and shifts based on changes in the

555   lower range limit, the upper range limit or both range limits. b. Unexpected: potential lack of

556   change or downward elevational range contractions and shifts based on changes in one or both

557   range limits. Triangle depicts montane temperature variation from warm (red) to cool (blue).

558   Black lines = historical ranges; blue lines = contemporary upward responses; red lines =

559   contemporary downward responses); and grey lines = no contemporary change.

560

561 **Figure 2.** A map of historical (circles) and contemporary (stars) sampling localities within the

562 two mountainous regions: a. San Juan Mountains and b. Front Range Mountains in Colorado,

563 USA (greyscale inset). The thin black lines denote county boundaries in each region. Elevational

564 variation grades from dark pink at the lowest elevations to dark green as the highest elevations.

565 For the authors' contemporary sampling sites only, see Figure S1.1.

566

567 **Figure 3.** Paired historical (left bar) and contemporary (right bar) elevational ranges of the

568 included small mammal species on the (a) Front Range Mountains, and the (b) San Juan

569 Mountains. c. The sum of the range shifts and contractions for upward or downward change is

570 shown in panel C. Thick bars = empirical ranges; thin extensions = Bayesian range limits.

571 Species names are abbreviated; for complete taxonomic names, see Appendix S2.

572

573 **Figure 4.** Species traits and range shifts. Upward change in upper range limits was larger for

574 species (a) whose geographic ranges extended to higher latitudes, particularly for montane and

575 cosmopolitan species; and (b) for which the studied mountain range was at the southern edge of

576 their geographic range. c. Upward change in lower range limits was larger for species at the

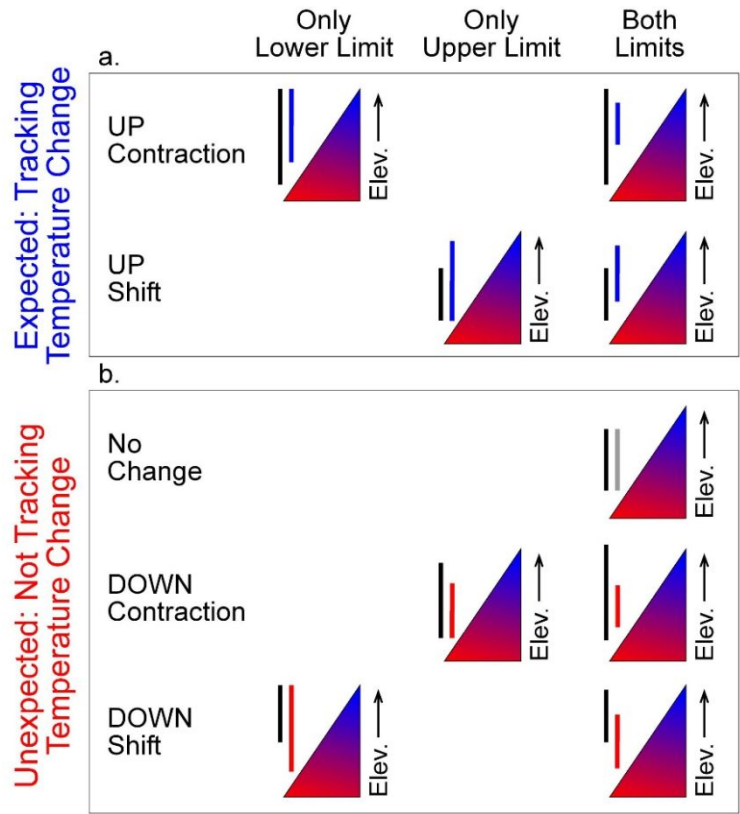577 eastern edge of their geographic range. Non-edge = middle of range.

578

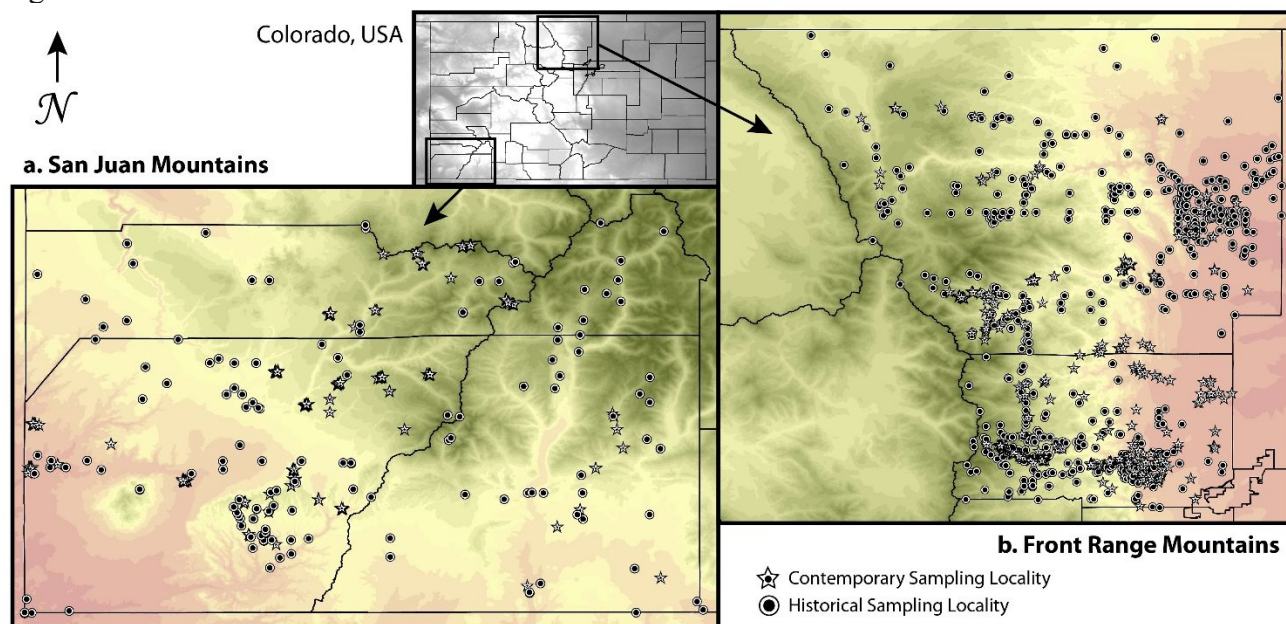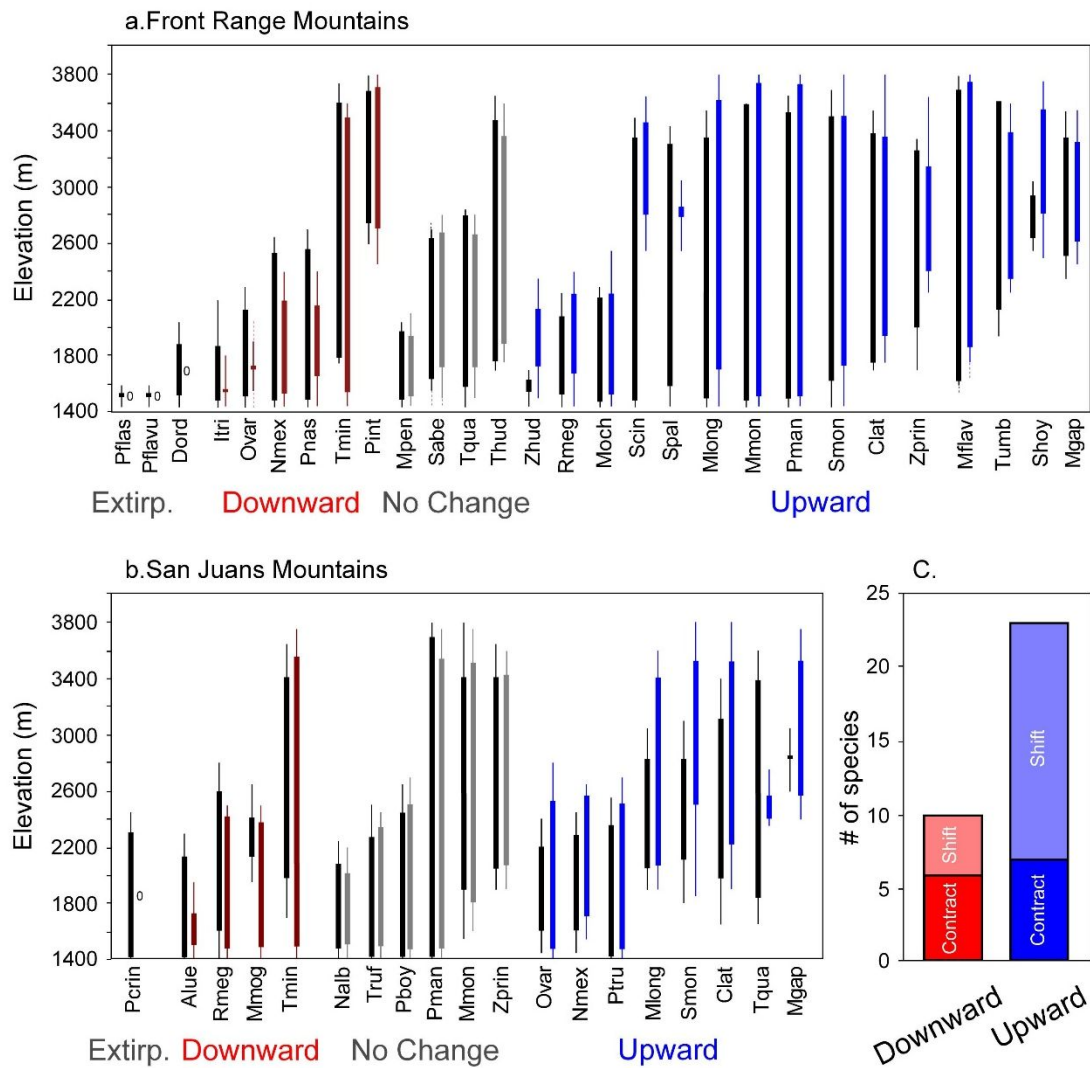579 Figure 1.

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581   Figure 2.

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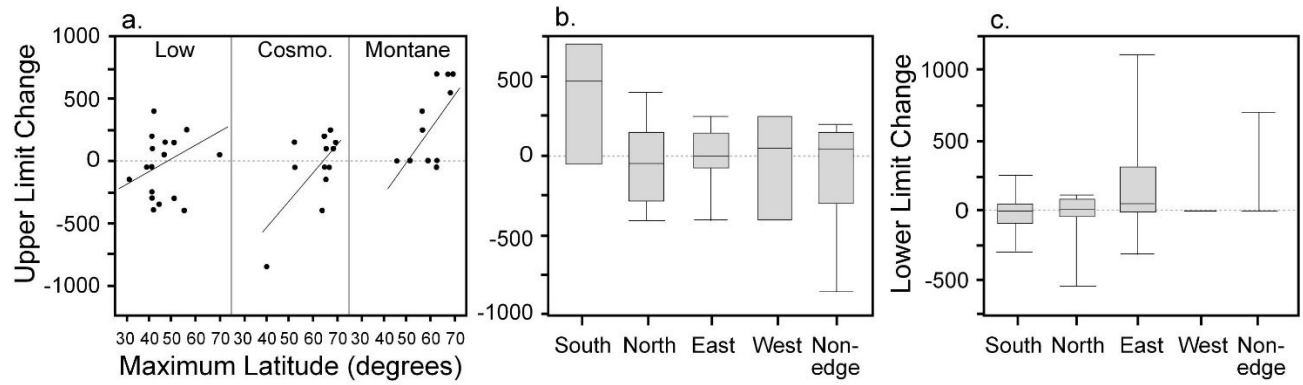
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588   Figure 4.

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Appendix S1. Supplementary Methods

The historical portion and contemporary supplement of the Colorado mammal specimen database was constructed mostly from museum specimen records, and includes records for all mammals in the state from all dates and localities. We received these records by contacting museum personnel or through online data repositories (i.e., GBIF [www.gbif.org], Arctos [https://arctos.database.museum]). The museums from which we received specimen data included: Academy of Natural Sciences of Philadelphia, American Museum of Natural History, Angelo State Natural History Collection, Brigham Young University Monte L. Bean Life Science Museum, California Academy of Science, Carnegie Museum of Natural History, Cornell University Museum of Vertebrates, Denver Museum of Nature and Science, Eastern New Mexico University Natural History Museum, Field Museum, Florida Museum of Natural History, Illinois Natural History Survey, James R. Slater Museum of Puget Sound University, Los Angeles County Museum of Natural History, Louisiana State University Museum of Natural Science, Museum of Comparative Zoology Harvard University, Michigan State University Museum, Museum of Southwestern Biology University of New Mexico, Museum of Texas Tech University, New Mexico Museum of Natural History and Science, North Carolina State Museum of Natural Sciences, Oklahoma State University Collection of Vertebrates, Oregon State University Department of Fisheries and Wildlife Mammal Collection, Royal Ontario Museum, San Diego Natural History Museum, Santa Barbara Museum of Natural History, State Museum of Pennsylvania, Sternberg Museum of Natural History Fort Hays State University, Texas A&M University Texas Cooperative Wildlife Collection, United States National Museum of Natural History, Universidad Nacional Autónoma de México, University of Alaska Museum of the North, University of Arizona Collection of Mammals, University of California Berkeley Museum of Vertebrate Zoology, University of Colorado Museum of Natural History, University of Georgia Museum of Natural History, University of Kansas Museum of Natural History, University of Michigan Museum of Zoology, University of Minnesota James F. Bell Museum of Natural History, University of Nebraska State Museum, University of Oklahoma Sam Noble Oklahoma Museum of Natural History, University of Washington Burke Museum, University of Wisconsin Zoological Museum, Utah Museum of Natural History, Western New Mexico University Museum, and Yale University Peabody Museum. This work would not have been possible without the countless number of people contributing, preserving, and supporting natural history collections; we thank each and every one past, present, and future.

The sites of contemporary sampling by the authors included 32 sites from 2010–2012 (Figure S1.1: white circles) with the lowest three sites in the northern Front Range transect resampled in 2017; pilot study sampling in the San Juans in 2007 (blue circles); additional sampling in Mesa Verde National Park in 2018 (live trapping and pitfall sites: black stars, pitfall sites: black dots). For a detailed discussion of the mammal sampling design and results, see (McCain *et al.*, 2018). Overall, the authors' sampling effort for this comparative study included ~77,030 trap-nights in the Front Range and ~81,550 trap-nights in the San Juans plus all the visual surveys and other sighted mammals. These contemporary data were augmented with all other specimen data from these mountain regions collected or documented by other researchers in the Colorado mammal database in 2006 or later.
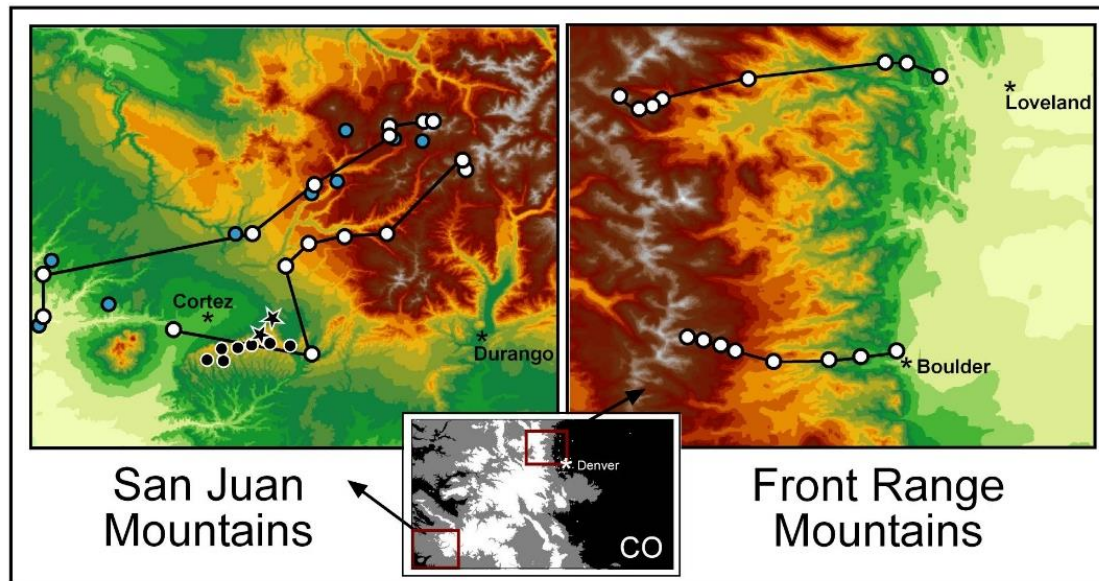
Figure S1.1. The contemporary mammal survey sites in the Colorado Rocky Mountains. The four elevational transects sampled in 2010-2012 in the northeast (Front Range Mountains) and two in the southwest (San Juan Mountains) are shown in white circles connected with black lines. The lower three in the northern Front Range transect were resampled in 2017. The nine sites sampled in the San Juans in 2007 are shown in blue circles, and the sites sampled in Mesa Verde National Park are shown in stars (all survey methods) and black dots (pitfalls & visual surveys).

The Bayesian models:

     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 constructed models using the overall community sampling distribution (Fig. S1.2), each species' abundance distribution, the probability of detecting a given individual of each species, the elevational distance to the observed elevational limits, and the patchiness within the species' interpolated range (i.e., the proportion of elevational bins without detections within the

interpolated range). See the article text for model details and *R* code below using JAGS and the rjag package (Plummer, 2017, Plummer, 2019)).

We included a second set of Bayesian models for the larger small mammal species (e.g., tree squirrels, marmots). These species historically were live trapped, but also hunted with rifles for collection. Contemporarily, they are still caught in live traps but usually just immature individuals in the smaller traps with larger traps needed specifically for adults, and are now more likely just to be sighted in visual surveys. Thus, these species have a lower sampling effort and their sampling may be less associated with the complete sampling effort of other small mammals, particularly contemporarily. Thus, we used the specimen-localities for just the larger species as an estimate of the sampling effort over each gradient per time period to reassess just the larger species Bayesian range limits. The range limits were slightly larger than using the complete sampling effort (Appendix S2). For example, for the four species used in the analyses the differences between the all-sample Bayesian sampling models and the large-only Bayesian sampling models was on average only 32 m per species. Some of these enlarged ranges appeared
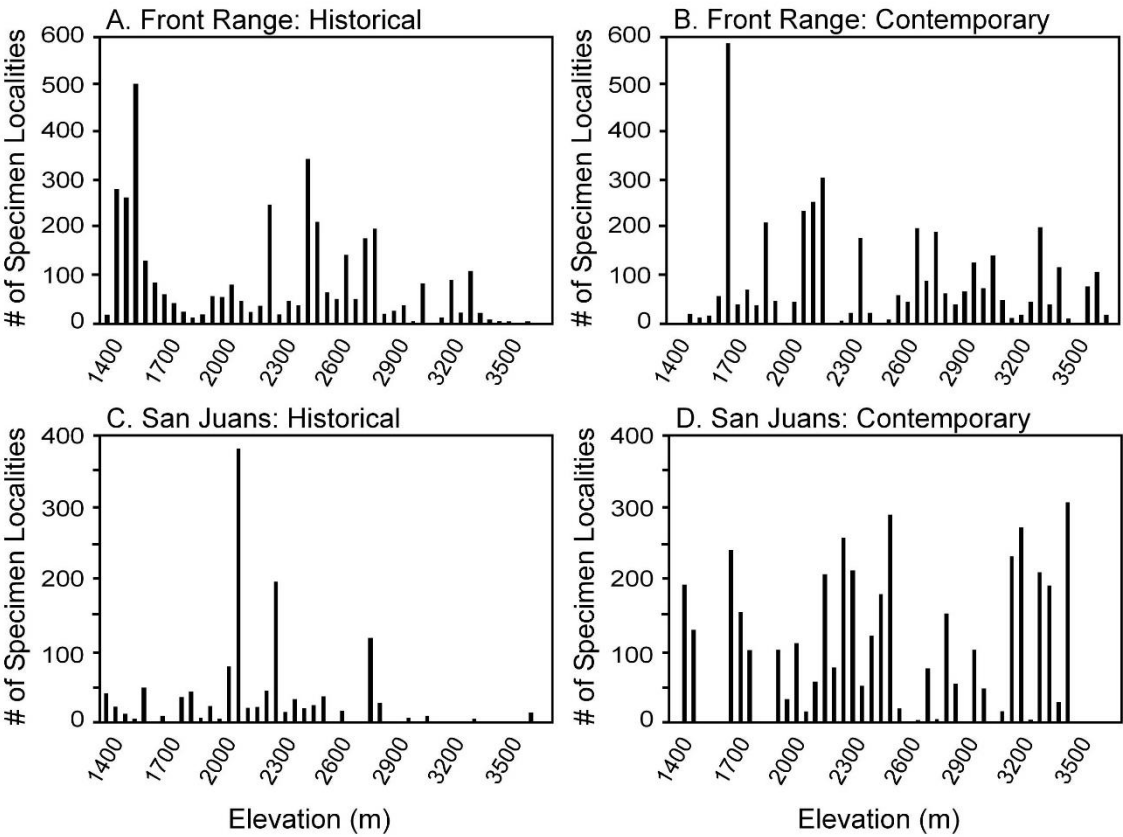
Figure S1.2. The historical and contemporary distribution of mammal specimen-localities along the Front Range (A, B) and San Juan (C, D) elevational gradients. These sums were used in the Bayesian undersampling models and give a minimum indication of the sampling effort on both mountains. This underestimates the sampling effort, since trap-nights per band were not recorded, thus unpreserved captures, specimens on non-target species, and efforts with few or no captures or specimens are not included.

implausible given our knowledge of the species on each mountain, and since they are based on few samples, are less well-supported. Thus, we used the all-sampling effort Bayesian models for the range shift analyses in the text, but the potential range extensions are shown in Figure 2 as dashed lines.

For testing the phylogenetic signal in the lower and upper range shifts, we used 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*). Table S1.1 includes all of the *phylosignal* test values and significances; all of which are non-significant.

Table S1.1. Statistics from phylogenetic signal tests in the upper and lower range shifts (p = p-value).

Range Limit	Cmean	p	I	p	K	p	K.star	p	Lambda	p
FR Lower	0.119	0.073	0.047	0.085	0.279	0.113	0.289	0.147	0.242	0.203
FR Upper	-0.135	0.754	-0.062	0.571	0.178	0.534	0.185	0.534	<0.001	1.000
SJ Lower	-0.107	0.685	-0.087	0.705	0.120	0.936	0.139	0.950	<0.001	1.000
SJ Upper	-0.046	0.416	-0.036	0.368	0.224	0.383	0.229	0.478	<0.001	1.000

R code for Bayesian undersampling model:

```
#-------------------------------------------------
# Model for each mountain range per time period
#-------------------------------------------------
#
# written for JAGS
#
# DATA ------------------------------------------
#  n.el = number of elevational bins
#  J = number of species
#  y[n.el, ] = number of detections of each species
#  Y[n.el] = total number of detections at each elevation
#  delta[J] = pr(detect an individual if present)
#  LAMBDA[J] = total number of detections of each species
#  distAway[n.el,J] = number of meters from bin i to last detection
#     NOTE: 0 if inside interpolated range, positive if outside interpolated range
#  interpPatchy[J] = proportion of bins without detections in interpolated range
#
# NOTE: distAway and interpPatchy were z-transformed to a standard normal
# distribution (mean=0, sd=1) for improved MCMC convergence
#
# PARAMETERS ------------------------------------
# lambda[n.el,J] = true relative abundance of each species (unobserved)
# beta[3] = slopes (all species together)
# a[J] = intercepts (species-specific)
# alpha = average intercept across all species
# sigma = standard deviation in intercept across all species
# Z[n.el,J] = true presence (1) or absence (0) of species
# psi[n.el,J] = pr(Z=1) based on sampling uncertainty
```

```
model{
  # Likelihood
  for(i in 1:n.el) {

    # species pool probabilities
    p[i,1:J] <- lambda[i,1:J]*delta[1:J]*Z[i,1:J]

    # detections from a multinomial distribution
    # with probabilities p (divide by sum(p) to enforce [0,1] & sum = 1)
    y[i,] ~ dmulti(p[i,1:J]/sum(p[i,1:J]), Y[i])

    # occupancy and sampling effects
    for(j in 1:J) {
        Z[i,j] ~ dbern(psi[i,j])
        logit(psi[i,j]) <- a[j] +
          beta[1]*distAway[i,j] +
          beta[2]*interpPatchy[j] +
          beta[3]*distAway[i,j]*interpPatchy[j]
    }
  }

  # Prior distributions
  alpha ~ dnorm(0, 0.01)
  tau <- 1/(sigma*sigma)   # JAGS uses precision = 1/variance
  sigma ~ dnorm(0, 0.01) T(0, )
  beta[1] ~ dnorm(0, 0.01)
  beta[2] ~ dnorm(0, 0.01)
  beta[3] ~ dnorm(0, 0.01)
  for(j in 1:J) {
    a[j] ~ dnorm(alpha, tau)
    # lambda prior for each bin = Normal(mean=total abundance, sd=100)[0,]
    for(i in 1:n.el) {
      lambda[i,j] ~ dnorm(LAMBDA[j], 0.0001) T(0, )
    }
  }
}
```

Supplementary Methods Literature Cited

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Appendix S2. The dataset of small mammal species tested for elevational range changes in the Front Range and San Juan Mountains of Colorado. USA. The taxonomic order, family of rodents, and species name are list for each mountain range. The probability of detection is how likely a single individual of a species is to be detected based on contemporary mark and recapture statistics. Telev. Rng = the location of the species on the mountain: montane, low elevation, or cosmopolitan (across most elevations). Max. Lat. Is the highest latitude in the geographic range of the species in North America. Rng Edge = the location of the study area in relationship to the species geographic edge, if it is not on an edge in the cardinal directions then it is the middle. The empricial number of specimens (Data #), lower elevational limit and upper elevational limit are shown for the hstorical and contemporary time periods as are the Bayseian 95% lower and upper limits in both time periods. The Baeysian models using all the specimen data include "All" in the header whereas those specifically for larger rodents include "Large" in the header. Finally, the elevation change in the lower, upper, and overall combined limits are shown and the type of shift (upward, downward, none, or local extirpation). All elevational values are in meters.

Taxon	Species	Mountain	Probability Detection	Elev. Rng	Max. Lat.	Rng Edge	Empirical: Historical Data #	Lower	Upper	Bayesian: All, Hist. Lower	Upper	Bayes.: Large, Hist Lower	Upper	Empirical: Contemporary Data #	Lower	Upper	Bayesian: All, Cont. Lower	Upper	Bayes.: Large, Cont. Lower	Upper	Lower Change	Upper Change	Overall Change	SHIFT
Rodentia, Sciuridae	Callospermophilus lateralis	Front Range	0.170	Montane	56.4	East	135	1760	3388	1700	3549			100	1939	3356	1750	3799			50	250	300	UP
Rodentia, Heteromyidae	Dipodomys ordii	Front Range	0.220	Low	--	--	29	1524	1890	1438	2049			0	--	--	--	--			--	--	--	EXTIR.
Rodentia, Sciuridae	Ictidomys tridecemlineatus	Front Range	0.241	Low	54.9	West	48	1492	1876	1438	2199			2	1545	1550	1438	1799			0	-400	-400	DOWN
Rodentia, Sciuridae	Marmota flaviventris	Front Range	0.241	Montane	51.1	East	34	1628	3688	1600	3799	1550	3799	34	1863	3737	1750	3799	1650	3799	150	0	150	UP
Rodentia, Cricetidae	Microtus longicaudus	Front Range	0.184	All	68.1	East	97	1506	3353	1438	3549			66	1704	3607	1438	3799			0	250	250	UP
Rodentia, Cricetidae	Microtus montanus	Front Range	0.122	All	52.9	East	129	1506	3528	1438	3649			62	1513	3725	1438	3799			0	150	150	UP
Rodentia, Cricetidae	Microtus ochrogaster	Front Range	0.228	Low	56.0	West	143	1484	2218	1438	2299			31	1532	2242	1438	2549			0	250	250	UP
Rodentia, Cricetidae	Microtus pennsylvanicus	Front Range	0.189	Low	70.3	East	269	1494	1984	1438	2049			9	1519	1942	1438	2099			0	50	50	NONE
Rodentia, Cricetidae	Myodes gapperi	Front Range	0.210	Montane	62.4	East	102	2515	3353	2350	3549			59	2611	3310	2450	3549			100	0	100	UP
Rodentia, Cricetidae	Neotoma mexicana	Front Range	0.289	Low	41.0	North	125	1489	2537	1438	2649			158	1538	2187	1438	2399			0	-250	-250	DOWN
Rodentia, Sciuridae	Otospermophilus variegatus	Front Range	0.241	Low	41.9	North	41	1517	2134	1438	2299	1438	2299	1	1717	1717	1550	1899	1438	2049	112	-400	-288	DOWN
Rodentia, Heteromyidae	Perognathus fasciatus	Front Range	0.220	Low	--	--	10	1524	1524	1438	1599			0	--	--	--	--			--	--	--	EXTIR.
Rodentia, Heteromyidae	Perognathus flavus	Front Range	0.220	Low	--	--	11	1524	1524	1438	1599			0	--	--	--	--			--	--	--	EXTIR.
Rodentia, Cricetidae	Peromyscus maniculatus	Front Range	0.429	All	65.6	Middle	931	1489	3588	1438	3599			1948	1518	3731	1438	3799			0	200	200	UP
Rodentia, Cricetidae	Peromyscus nastutus	Front Range	0.197	Low	41.2	North	167	1494	2560	1438	2699			81	1660	2155	1438	2399			0	-300	-300	DOWN
Rodentia, Cricetidae	Phenacomys intermedius	Front Range	0.175	Montane	58.7	East	19	2742	3673	2600	3799			37	2700	3700	2450	3799			-150	0	-150	DOWN
Rodentia, Cricetidae	Reithrodontomy megalotis	Front Range	0.234	Low	50.6	Middle	53	1531	2084	1438	2249			169	1682	2239	1438	2399			0	150	150	UP
Rodentia, Sciuridae	Sciurus aberti	Front Range	0.241	Low	41.3	North	38	1641	2638	1550	2699	1450	2749	12	1724	2673	1500	2799	1450	2799	-50	100	50	NONE
Soricidae	Sorex cinereus	Front Range	0.200	All	70.3	East	77	1492	3353	1438	3499			63	2798	3452	2550	3649			1112	150	1262	UP
Soricidae	Sorex hoyi	Front Range	0.112	Montane	67.4	South	22	2638	2936	2550	3049			16	2806	3447	2500	3749			-50	700	650	UP
Soricidae	Sorex monticolus	Front Range	0.112	All	69.4	East	103	1628	3505	1450	3699			95	1726	3493	1438	3799			-12	100	88	UP
Soricidae	Sorex palustris	Front Range	0.200	All	65.1	East	61	1591	3307	1450	3449			3	2786	2859	2550	3049			1100	-400	700	UP
Rodentia, Sciuridae	Tamias minimus	Front Range	0.240	All	66.4	East	302	1796	3600	1750	3749			445	1546	3492	1438	3599			-312	-150	-462	DOWN
Rodentia, Sciuridae	Tamias quadrivittatus	Front Range	0.238	Low	41.0	North	49	1585	2795	1438	2849			60	1721	2659	1500	2799			62	-50	12	NONE
Rodentia, Sciuridae	Tamias umbrinus	Front Range	0.325	Montane	45.4	East	77	2134	3414	1950	3599			59	2343	3385	2250	3599			300	0	300	UP
Rodentia, Sciuridae	Tamiasciurus hudsonicus	Front Range	0.241	All	67.8	East	143	1766	3475	1700	3649	1650	3649	126	1882	3356	1750	3599	1550	3599	50	-50	0	NONE
Rodentia, Dipodidae	Zapus hudsonicus preblei	Front Range	0.293	Low	65.0	South	32	1553	1634	1450	1699			6	1726	2130	1500	2349			50	650	700	UP
Rodentia, Dipodidae	Zapus princeps	Front Range	0.293	Montane	62.3	East	109	2006	3259	1900	3349			89	2402	3140	2250	3299			350	-50	300	UP
Rodentia, Sciuridae	Ammospermophilus leucurus	San Juans	0.241	Low	44.1	East	13	1418	2134	1414	2299			6	1506	1735	1414	1949			0	-350	-350	DOWN
Rodentia, Sciuridae	Callospermophilus lateralis	San Juans	0.170	Montane	56.4	South	33	1981	3109	1650	3399			70	2227	3524	1900	3799			250	400	650	UP
Rodentia, Cricetidae	Microtus longicaudus	San Juans	0.184	Montane	68.1	South	59	2050	2827	1900	3049			17	2079	3411	1900	3599			0	550	550	UP
Rodentia, Cricetidae	Microtus mogollonensis	San Juans	0.220	Low	31.3	North	26	2133	2407	1950	2649			21	1494	2384	1414	2499			-536	-150	-686	DOWN
Rodentia, Cricetidae	Microtus montanus	San Juans	0.122	All	52.9	South	57	1895	3407	1550	3799			81	1812	3519	1600	3749			50	-50	0	NONE
Rodentia, Cricetidae	Myodes gapperi	San Juans	0.210	Montane	62.4	South	10	2827	2840	2600	3049			83	2570	3530	2400	3749			-200	700	500	UP
Rodentia, Cricetidae	Neotoma albigula	San Juans	0.257	Low	39.0	North	17	1483	2085	1414	2249			20	1512	2020	1414	2199			0	-50	-50	NONE
Rodentia, Cricetidae	Neotoma mexicana	San Juans	0.289	Low	41.0	North	46	1610	2285	1450	2449			66	1715	2570	1550	2649			100	200	300	UP
Rodentia, Sciuridae	Otospermophilus variegatus	San Juans	0.241	Low	41.9	North	20	1610	2202	1450	2399	1414	2649	25	1482	2530	1414	2799	1414	2849	-36	400	364	UP
Rodentia, Cricetidae	Peromyscus boylii	San Juans	0.434	Low	46.3	Middle	44	1418	2444	1414	2649			96	1482	2510	1414	2699			0	50	50	NONE
Rodentia, Cricetidae	Peromyscus crinitus	San Juans	0.372	Low	--	--	31	1418	2307	1414	2449			0	--	--	--	--			--	--	--	EXTIR.
Rodentia, Cricetidae	Peromyscus maniculatus	San Juans	0.429	All	65.6	Middle	535	1418	3691	1414	3799			1481	1486	3538	1414	3749			0	-50	-50	NONE
Rodentia, Cricetidae	Peromyscus truei	San Juans	0.428	Low	46.7	Middle	76	1418	2354	1414	2549			394	1481	2513	1414	2699			0	150	150	UP
Rodentia, Cricetidae	Reithrodontomy megalotis	San Juans	0.234	Low	50.6	Middle	30	1610	2597	1414	2799			60	1486	2426	1414	2499			0	-300	-300	DOWN
Soricidae	Sorex monticolus	San Juans	0.112	Montane	69.4	South	21	2115	2827	1800	3099			143	2507	3530	1850	3799			50	700	750	UP
Rodentia, Sciuridae	Tamias minimus	San Juans	0.240	All	66.4	South	130	1981	3407	1700	3649			1057	1503	3559	1414	3749			-286	100	-186	DOWN
Rodentia, Sciuridae	Tamias quadrivittatus	San Juans	0.238	All	41.0	Middle	29	1840	3386	1650	3599			13	2410	2570	2350	2749			700	-850	-150	UP
Rodentia, Sciuridae	Tamias rufus	San Juans	0.231	Low	40.8	South	22	1418	2264	1414	2499			50	1503	2348	1414	2449			0	-50	-50	NONE
Rodentia, Dipodidae	Zapus princeps	San Juans	0.293	Montane	62.3	South	25	2050	3407	1900	3649			30	2079	3433	1900	3599			0	-50	-50	NONE

Appendix S3. Supplementary Results

        The dataset of small mammals used in the elevation shift analyses, and their historical and contemporary range limits both for the empirical data and the Bayesian 95% models are in Appendix S2. Six species in the Front Range Mountains (FR) and 13 species in the San Juan Mountains (SJ) were not sampled sufficiently historically (i.e., fewer than 10 specimens) for robust elevational range comparisons. These are presented here for those who may be interested in specific species (Figure S3.1). Four species were detected historically, albeit rarely, that were undetected contemporarily: *Reithrodontomys montanus* (FR), *Xerospermophilus spilosoma* (both), *Perognathus flavescens* (FR), and *Sorex merriami* (SJ). Four species were caught at lower elevations contemporarily: *Peromyscus boylii* (FR), *Notiosorex crawfordi* (SJ), *Sciurus aberti* (SJ), and *Marmota flaviventris* (SJ). Seven species were caught at higher elevations contemporarily: *Chaetodipus hispidus* (FR), *Sorex merriami* (FR), *Perognathus flavus* (SJ), *Dipodomys ordii* (SJ), *Sorex nanus* (SJ), *Tamiasciurus hudsonicus* (SJ), and *Sorex palustris* (SJ). Lastly, a few species of small mammals that are likely under-sampled contemporarily due to differences in sampling methods (e.g., lack of shooting as a collecting method) and/or their patchy and specialized locations (e.g., particular types of montane streams, rocky outcrops), included *Neotoma cinerea* on both transects, and *Urocitellus elegans* and *Sorex palustris* in the Front Range.
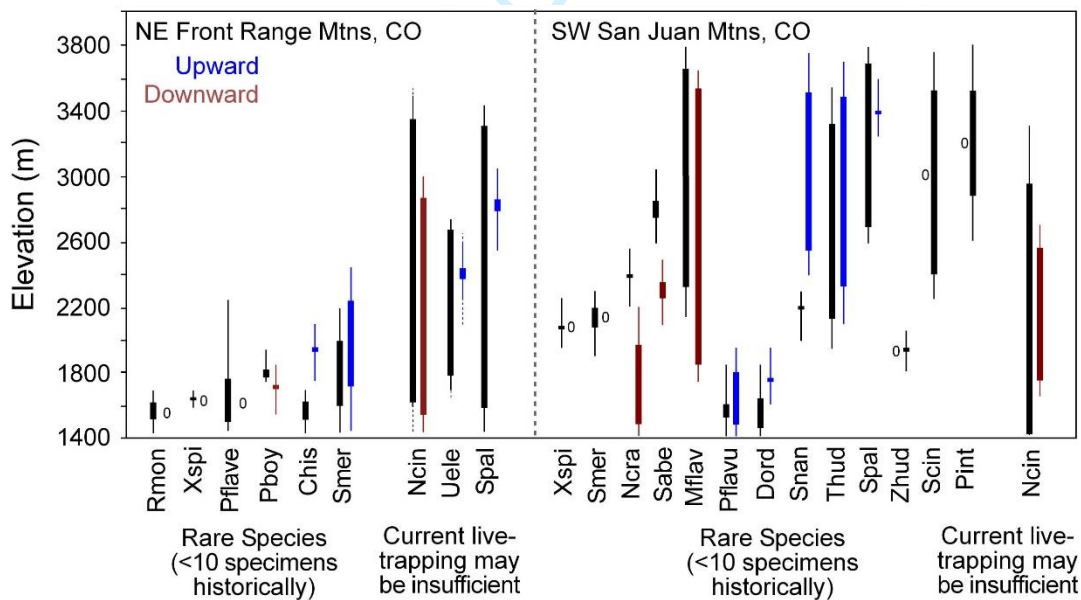

Figure S3.1. Elevational ranges historically and contemporarily for those small mammals that were too rare (<10 specimens historically) to include in the main analyses or potentially too under-sampled contemporarily due to methodological changes.

        To assess whether range losses and range gains at the range edges were associated with particular areas on the mountains across the included species, we calculated the number of species loosing or gaining range at each 50m band up each mountain. Because the number of species per elevational band differs (unimodal with highest richness of included species between
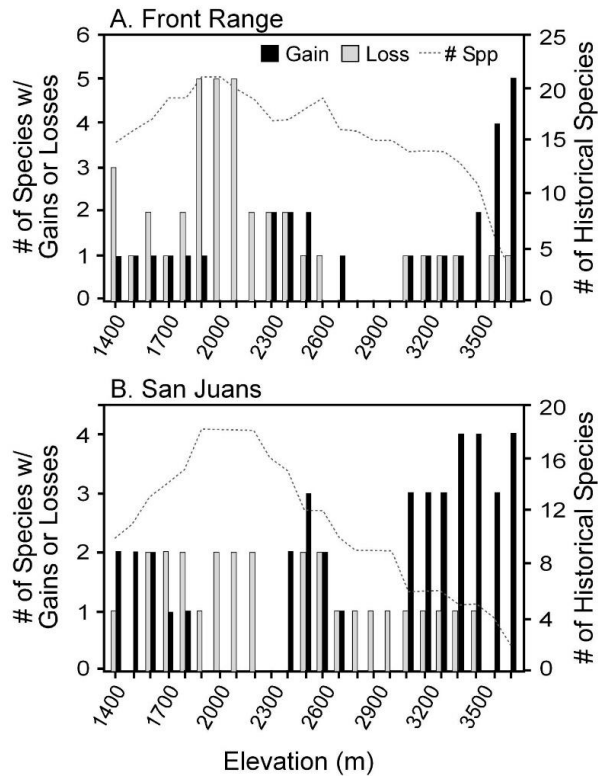
A. Front Range

B. San Juans

Elevation (m)

Figure S3.2. Elevational distribution of the range gains (black bars) and losses (grey bars) for species' range edges summed at each 50m elevational band across the studied species. The summed numbers of gains and losses per band (bars) are shown with the number of species in each band (dotted grey curves) for the Front Range (A) and the San Juans (C).

1900–2000m), counts of range losses and range gains summed across all species for each 50m elevation on each mountain gradient is biased towards elevations with more species (Figure S3.2). Thus, we examined the percentage of range losses and range gains for each 50m elevation on each mountain gradient by dividing the species counts by the historical number of species present at each band and the net value of gains-losses by elevation provides a heat map of the changes (Figure S3.3).

Figure S3.3. Elevational heat maps of net change in percentage gains and losses at range limits across the studied species 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 in figure). Insets show the percentages of range gains (blue) and losses (red).