1   **Title:**

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

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23 **Abstract:**

24 Resurveys of historical collecting localities have revealed range shifts, primarily leading edge

25 expansions, which have been attributed to global warming. However, there have been few

26 spatially replicated community-scale resurveys to test whether species' responses are

27 spatially consistent. Here we repeated early 20th century surveys of small mammals along

28 elevational gradients in northern, central and southern regions of montane California. Most

29 species' ranges shifted upslope or downslope in at least one region. However, two-thirds of

30 ranges remained stable at one or both elevational limits, and few species shifted limits in the

31 same direction in all regions. When shifts did occur, high elevation species typically

32 contracted their lower limits upward, whereas low elevation species had heterogeneous

33 responses. Local change in temperature was a better predictor of shift direction than

34 precipitation, suggesting the heterogeneous responses of small mammals were influenced by

35 local temperature change consistent with 20th century warming.

36

Main Text:

Evidence for the biotic responses to recent climate change has continued to accumulate[1-5] and is central to the prediction of vulnerability to future change[6]. There is a general trend toward upward and poleward shifts of elevational and latitudinal boundaries of species' ranges [1-5,7,8], with "leading edge" expansions detected more often than "lagging edge" contractions[9-12]. However, there is considerable heterogeneity in the direction and magnitude of species' responses, and ranges of many species have not changed at all[13-15]. Species respond to local change in climate and habitat rather than global averages, and few studies have accounted for substantial spatial heterogeneity in climate change across the landscape[1,15,16]. Moreover, there is potential for considerable sampling error because local colonization and extinction cannot be demonstrated convincingly unless detectability (i.e., the probability of "false absence") is explicitly incorporated into models of occurrence change[17]. Insights into the dynamics of species' responses to recent climate change are most likely to come from spatially-replicated resurveys combined with analytical methods that have statistical power to detect both range contractions and expansions.

An unusually detailed historic dataset, combined with contemporary resurveys, allows us to evaluate robustly a century of range responses of birds and mammals to climate change in montane California (Fig. 1a). Joseph Grinnell and colleagues studied the elevational distributions of vertebrates of California in the early 1900's[18-20]. These data laid the foundation for Grinnell's concept of the ecological niche and for understanding the climatic limits of species' distributions[21]. They also provided a benchmark for documenting changes in the elevational ranges of species in California over the last century[12,14,15,22]. Over the past century, mean annual temperature in California has increased by ~0.6 °C[23-25] (Fig. 1b, Supplementary Fig. S1). Precipitation changes were more spatially heterogeneous, with spatial covariation increasing across the northern part of the state and decreasing across the

62 southern part[26,27]. Elevational ranges of species in California over this period have shifted

63 heterogeneously, including species moving upslope, downslope or not at all[14,15,28].

64 Heterogeneity in movements of species has been partly explained by incorporating local-

65 scale measures of climatic change for both temperature and precipitation[15,29]; increases in the

66 former usually favour upslope shifts, while increases in the latter typically favour downslope

67 movements. Local changes in habitat structure due to fire and grazing are also factors in

68 some areas[30,31].

69   Here we characterized spatial variation in elevational range responses of small

70 mammals in protected areas of montane California by expanding our analysis centred on a

71 single region in central California (Yosemite National Park, central Sierra Nevada)[14] to other

72 regions in the north (Lassen Volcanic National Park, southern Cascade Range) and south

73 (Sequoia/Kings Canyon National Parks, southern Sierra Nevada). We control for variation in

74 detectability among species and survey eras to compare elevational limits from the early 20th

75 Century (1911-1934) to the present (2003-2010). With data from multiple, geographically-

76 separated regions of montane California that have experienced limited land-use change, we

77 tested four predictions of the influence of climate warming on elevational ranges that

78 emerged from patterns observed in the Yosemite region[14] and in birds across montane

79 California[15]. If overall climate warming is the predominant driver of elevational range

80 change, then (1) upslope shifts should be the most common change across all regions; and (2)

81 range contractions should be more frequent in high than low elevation species, and range

82 expansions more common in low than high elevation species. If, however, species have

83 responded to the heterogeneous climate change across the landscape and to both temperature

84 and precipitation change, then (3) elevational ranges of species should shift inconsistently

85 across regions; and (4) upslope and downslope shifts should both occur and be associated

86 with local changes in temperature and precipitation, respectively[15].

87

Mammalian Elevational Range Shifts over the Past Century

89   The majority of species' elevational ranges remained stable at one or more limits, but

90   ranges of most species shifted in at least one region (Fig. 2). Of the 67 small mammal species

91   we detected in either the historical or modern surveys (Supplementary Table S2,

92   Supplementary Fig. S2), we were able to use robust statistical methods to evaluate range

93   shifts of 34 species. Across the three regions, we detected 52 significant range limit shifts,

94   representing 31.3% of the 166 region-specific historical range limits across the 34 species

95   analysed (Fig. 2, Supplementary Fig. S3). We observed no significant range limit shifts in

96   nine species (26.4%), including two gophers (*Thomomys bottae* and *T. monticola*), three

97   chipmunks (*Tamias merriami, T. quadrimaculatus*, and *T. amoenus*), two shrews (*Sorex*

98   *trowbridgii,* and *S. vagrans*), a widespread deer mouse (*Peromyscus maniculatus*), and the

99   pika (*Ochotona princeps*). The remaining 25 species (74.6%) shifted at least one range limit

100   in one or more regions (Fig. 2, Supplementary Table S2).

101   There was little consistency of patterns in range shifts among regions. None of the 22

102   species found in all three regions shifted both their upper and lower limits in the same

103   direction in all three regions (Fig. 2). For example, both the bushy tailed woodrat (*Neotoma*

104   *cinerea*) and the pinyon mouse (*Peromyscus truei*) showed substantial changes in elevational

105   ranges in the northern and central but not the southern Sierra Nevada, while the western gray

106   squirrel (*Sciurus griseus*) contracted strongly in the south and marginally in the central Sierra

107   Nevada, but expanded its range in the north.

108   Nevertheless, some important differences in the frequency and directionality of shifts

109   emerged when examining high and low elevation species that did shift their ranges. Species'

110   elevational limits were more than twice as likely to move upslope (69.2%) as downslope

111   (31.8%; one-sided binomial test, $n = 52$ species' limits, $p = 0.004$; Fig. 3, Supplementary

112   Table S3). High elevation species were significantly more likely to contract their ranges than

113   to expand them (79% contract, $n = 29$ species' limits, $p = 0.001$), whereas, contrary to our

114   expectation, low elevation species contracted their limits as often as they expanded them

115   (50% contract, $n = 22$ species' limits, $p = 0.584$). These patterns emerged because there were

116   significantly more upslope than downslope shifts of the lower limit of high elevation species

117   ($n = 21$ lower limits, $p < 0.001$), whereas shifts in the upper limit of low elevation species

118   were heterogeneous with nearly as many downslope shifts as upslope shifts ($n = 17$ upper

119   limits, $p = 0.315$).

120   High elevation species that showed consistent range reduction included Belding's

121   ground squirrel (*Urocitellus beldingi*), the alpine chipmunk (*Tamias alpinus*) that is endemic

122   to central-southern montane California, the Pacific jumping mouse (*Zapus princeps*) and the

123   water shrew (*Sorex palutris*). These observations have been confirmed in more extensive

124   analyses of *U. beldingi* and *T. alpinus*[12,32]. Of note, elevational ranges of the pika (*Ochotona*

125   *princeps*), which attracted considerable attention because of extirpations and upslope

126   retractions in the Great Basin[33,34], were stable across all three regions. This result is

127   consistent with a more extensive study across montane California that found pika thriving

128   across wider geographic and elevation ranges than reported historically[35].

129   While a coherent pattern of upslope movement was found for high elevation species,

130   there was substantial heterogeneity in the response of low elevation species. The vast

131   majority of sites in our study, especially at mid to high elevations, were located in protected

132   reserves or public lands with minimal land-use conversion, although grazing, fire regimes

133   and forestry practices may have altered habitat structure[36]. One might expect low elevation

134   species should be more likely to experience impacts from land use change at their lower

135   limits in the Central Valley and foothills[37,38]. However, we detected few contractions at lower

136   limits of low elevation mammals (Fig. 3), and shifts were significantly more common at their

137   upper limits where potential land-use impacts were less evident. Greater heterogeneity in

138   responses of low elevation species may reflect stronger biotic influences[24,30], such as

139   interspecific competition[32], seral dynamics of habitats[30], and the spread of invasive species[31].

140   Heterogeneous range shifts have been demonstrated in a range of taxa[5,24], suggesting

141   that species' responses to 20th century climate change were both influenced by local factors

142   and were context dependent. Tingley et al.[15] found even greater heterogeneity in Californian

143   birds sampled over the last century in the same regions; only half the observed range limit

144   shifts of birds were upslope. Thus, while our findings confirmed some of the results from our

145   initial study of small mammals in central montane California[14] and studies of birds[15],

146   butterflies[38], and plants[27] over the similar spatial and temporal scales, they amplify the

147   complex and variable ways that species have changed over the past century in California[24].

148   Moreover, intra-species heterogeneity in range shifts appears widespread from our data but is

149   probably under-reported in the literature due to the infrequency of studies replicating range

150   shift studies across spatially and ecophysically distinct survey regions.

151

152   *Range Shifts in Relation to Climate*

153   Inconsistent patterns of range shifts among regions may be attributed to region-

154   specific changes or local changes in temperature and precipitation[39]. In previous resurvey

155   studies of birds and plants across the same regions, local changes in precipitation as well as

156   temperature were related to range changes[15, 27]. For small mammals, however, precipitation

157   was a poor predictor of the direction of shifts compared to temperature. Nearest climatic

158   neighbour analyses revealed that both upslope and downslope shifts were predicted by

159   temperature change at range limits (Fig. 1c). For low elevation species, a simple overall

160   warming model (i.e., all upwards shifts) was the best predictor, but this model, as well as

161   each of the climate-based predictions, was not significantly better than random (Fig. 4). For

162   high elevation species, change in minimum annual temperature was the best predictor of the

163   direction of range limit shifts, and explained 74.1% of range limit shifts observed. However,

164   change in minimum temperature was only a slight improvement over an overall warming

165   model (72.4% of shifts), local mean annual temperature change (69.2% of shifts), and local

166   maximum annual temperature (72.0% of shifts). Predictions from all four temperature

167   variables were significantly different from random (Fig. 4, $p < 0.05$). Mean annual

168   precipitation (40% of shifts) explained fewer shifts than random, although not significantly

169   less ($p = 0.21$). These results indicate that the ranges of high elevation mammals are likely

170   responding to changes in local temperature, highlighting the dynamic nature of species-

171   specific responses to localized climate change.

172   Our nearest climatic neighbour analysis also identified climatic conditions that are

173   disappearing from the landscape (i.e., a reduction of their historical geographic representation

174   to less than half in the modern era, see Supplementary Information for more details). Twenty-

175   one of the historical sites in our study had climatic conditions that fit this definition of

176   disappearing climates for at least one climate variable. Minimum annual temperature showed

177   the most substantial effect with values at 15% of historical sites disappearing from the

178   modern landscape. Mean annual temperature (1.5% of historical sites), maximum annual

179   temperature (3.7% of historical sites), and mean annual precipitation (0 historical sites) did

180   not decline as dramatically across the landscape. Consistent with the projected decline of

181   alpine environments, all sites with disappearing climates occur above 1500 m[40,41]. For species

182   inhabiting such sites historically, nearest climatic neighbours (Fig. 1c) provide poor

183   prediction of contemporary range shifts as climatic analogues at nearby elevations are now

184   rare or do not exist. Global climate projections suggest that disappearing climates will be an

185   increasing challenge for predicting future species' responses[42,43]. While no-analogue climates

186   are typically considered when predicting future species' ranges, ours is the first study to

187   examine how such disappearing climates can affect inference and interpretability of observed

188   range shifts.

189   Our rigorous study of elevational range shifts of mammals across montane California

190   revealed heterogeneous responses of species within and among regions that were consistent

191   with studies of other taxa[24] but that were filtered by the influence of local temperature change

192   consistent with 20th century warming[2,5]. A suite of high elevation mammals appear to be

193   undergoing range retraction. The challenge ahead is to understand the proximate causes of

194   the diverse species' responses to improve predictions of vulnerability[6]. We need a better

195   understanding of whether and how species track climatic niches in response to local variation

196   in climate change[29], or whether range changes are a response to ecosystem dynamics or

197   species interactions. Moreover, identifying the life-history traits (e.g., dispersal ability,

198   reproductive rate, and degree of ecological specialization) that best predict persistence or

199   vulnerability[10,44] may provide key insights into the mechanisms of species- and region-

200   specific responses to climate change. The diverse responses among closely related taxa that

201   we find here (e.g., among different species of mice, chipmunks, ground squirrels, and

202   woodrats) provide the basis for the detailed comparative studies that are necessary to improve

203   our knowledge of vulnerability.

Methods:

Survey Regions and 20th Century Climate Change

Historical surveys occurred between 1911 and 1934[17,18-20] along elevation transects across three regions of montane California (Fig. 1a, Supplementary Table S1): a northern region, in the southern Cascade Range, around Lassen Volcanic National Park ("Northern"), a central region, in the central Sierra Nevada, around Yosemite National Park ("Central"), and a southern region, in the southern Sierra Nevada, around Kings Canyon and Sequoia National Parks ("Southern"). Each region differed considerably in physiognomy and climate change history (Fig. 1b, Supplementary Figure S1). See Tingley et al.[15] for additional details of the sampling regions.

Survey and Resurvey Data

We defined localities or sampling sites as an aggregate of concurrent surveys (i.e., traplines) conducted within a 2 km distance and 100 m elevation[14]. Each site was georeferenced, and elevation was determined using a Digital Elevation Model and verified by ground-truthing or with topographic maps (Supplementary Table S1).

We obtained records from historical surveys conducted at 111 sites. Trapline details such as nightly captures, number of traps set, habitats, location maps and daily records of specimens observed and shot from more than 2,500 pages of field notebooks held in the MVZ Archives (available online at http://bscit.berkeley.edu/mvz/volumes.html). Modern mammal resurveys were conducted at 166 sites between 2003 and 2010 as part of the Grinnell Resurvey Project[14,15] (Fig. 1a). Of these, 85 of the 111 historical sites were resurveyed. Additional modern sites were selected to maximize elevation coverage and to serve as proxies for otherwise inaccessible historical sites. This resulted in a total of 29,593

228   records and 14,832 specimens in our data set (data available on Dryad Digital Repository.

229   http://dx.doi.org/10.5061/dryad.[NNNN]). See Supplementary Methods for details.

230

231   *Species Set*

232   We present the elevation distribution for 67 species of rodents, shrews, and pika

233   recorded in the historical and modern surveys (Supplementary Table S2). Analyses of range

234   shifts were restricted to 34 species that were detected at >10% of sites for at least one region

235   in both eras. Of these, we were able to model detectability and occupancy for 28 species

236   because they were detected through repeated nights of trapping at sites and where the number

237   of traps set was reported (hereafter "quantitative trapping"). We include an additional six

238   species in our range shift analyses as we made systematic efforts to detect and record these

239   easily observed species. Elevational profiles of species are presented separately for the east

240   and west slope with the exception of sites within the Yellow Pine (*Pinus ponderosa*) belt on

241   the east slope, which we included as west slope sites (See Supplemental Methods for details).

242   Species were categorized as low elevation (historical elevation ranges within Lower

243   Sonoran – Transition life zones), high elevation (Transition – Alpine), or widespread[14,18-20]

244   (Supplementary Table S4).

245

246   *Modelling Changes in Elevational Ranges*

247   We modelled simultaneously the probability of detection (p) and the probability of

248   occupancy (Ψ) of each species ($n = 28$) at each site to evaluate elevational range shifts using

249   the single-season occupancy model framework implemented in the program MARK v6.0[45,46].

250   See Supplemental Methods for details on model parameterizations (Supplementary Table

251   S5).

252   We estimated temporal shifts in the lower and upper range limits for each species in

253   each region following Moritz et al.[14]. Statistical significance for shifts was determined by

254   estimating site-specific detection probabilities ($p*$) and the probability of false absence (P_{fa}[17])

255   for each species at sites where the species was undetected in one era and that were located

256   between the lower or upper range limits of the two eras. Range limit shifts with $P_{fa} \leq 0.05$

257   were considered statistically significant and "ecologically relevant" if the movement was

258   both >10% of the species' historical elevation range and >100 meters in elevation[15].

259

260   *Testing Predictions of Range Shifts*

261   We used generalized linear mixed models (GLMM) and one-sided binomial tests to

262   examine how patterns of range shifts were related to region (Northern, Central, Southern),

263   species limit (upper or lower) and the elevational distribution of species (high or low

264   elevation species). We excluded widespread species and those not demonstrating significant

265   limit shifts determined from the P_{fa} analysis. See Supplementary Methods for model details.

266

267   *Climatic Nearest Neighbour*

268   For each species' limit, we evaluated whether upslope or downslope movement

269   between eras was better predicted based on site-specific climate data (four BIOCLIM

270   variables) or an overall warming model predicting only upslope movement, using climatic

271   nearest neighbour analysis[15] and one-sided binomial tests. We excluded predictions from

272   climates identified as either rare (geographically limited in the historical era) or disappearing

273   (geographically limited in the modern era). See Supplementary Methods for details.

274

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Author Contributions

KCR, JLP, JDP, SRB, CM conceived and designed the experiments; KCR, KMCR, JLP, CJC, JDP performed the experiments; KCR, KMCR, MSK, MWT, SRB analysed the data; KCR, MSK, MWT, SRB contributed materials/analysis tools; KCR, KMCR, MWT, SRB, CM wrote the paper. All authors discussed the results and commented on the manuscript.

Competing Financial Interests

The authors declare no competing financial interest.

410   **Figure Legends**

411   Figure 1. Climate change and expected elevation shifts across sampling sites. (a) Map of

412   historical survey localities in relation to survey region and life zone; (b) Change in mean

413   annual temperature (red) and mean annual precipitation (blue) between the historical (base of

414   arrow) and modern (tip of arrow) eras across elevation; (c) average expectation of elevation

415   shift in the modern era to achieve the most similar value of mean annual temperature (red

416   squares) or mean annual precipitation (blue triangles) as historical localities across elevation,

417   based on our climatic nearest neighbour analysis (see Methods); open squares and triangles

418   indicate historical sites where similar climate is underrepresented regionally within the

419   historical era (i.e., rare) or in the modern era (i.e., disappearing).

420

421   Figure 2. Elevation range limit shifts by region of the 34 modelled species, arranged by

422   increasing average elevation range. Species were classified as low elevation (01 – 13), high

423   elevation (16 – 34), or widespread species (14 and 15) based on their range limits in relation

424   to life zone[14]. For each species, statistically significant elevation range contractions (red) and

425   expansions (yellow) between the historical and modern eras are shown, along with non-

426   significant contractions (grey) and expansions (white).

427

428   Figure 3. Summary of range shifts of high and low elevation species combined across all

429   regions. Pie charts display proportion of range limits that exhibited significant expansions

430   (yellow), contractions (red), or no significant change (grey). An asterisk next to a pie

431   indicates that significantly more contractions were observed than expansions. Around each

432   pie the width of arrows indicates the proportion of shifts that were in each direction and at

433   each range limit. The colours of arrows indicate whether the shift resulted in an expansion

434   (yellow) or contraction (red).

435

436   Figure 4. Significant range limit shifts in relation to climate predictions. Bars represent the

437   percent of observed shifts for low and high elevation species that are consistent with the

438   predictions from an overall warming model (i.e., all upwards) and with nearest neighbour

439   analyses for each of the four BIOCLIM variables. Symbols above bars denote predictions

440   that were significantly better than random (* = $p < 0.05$).

441

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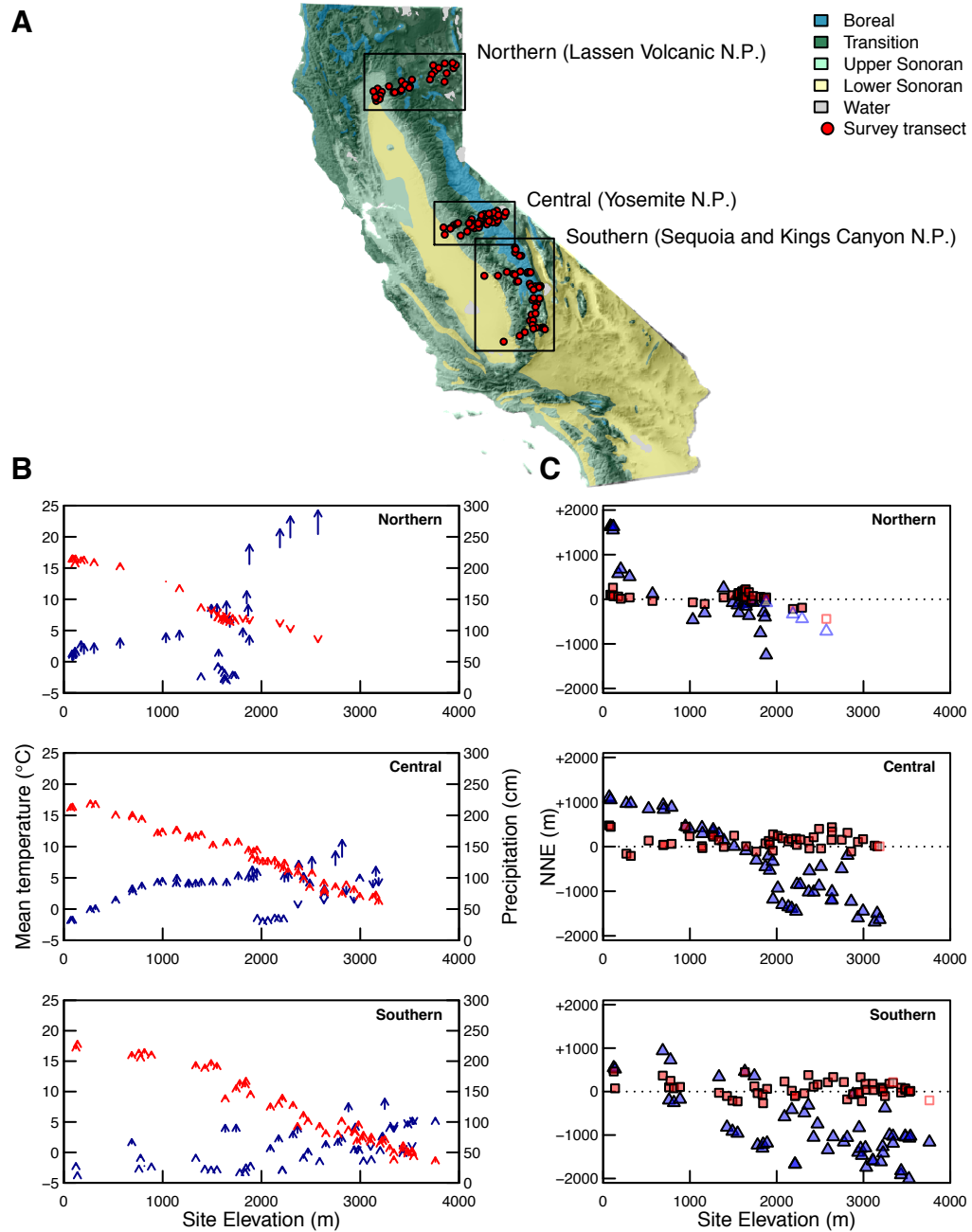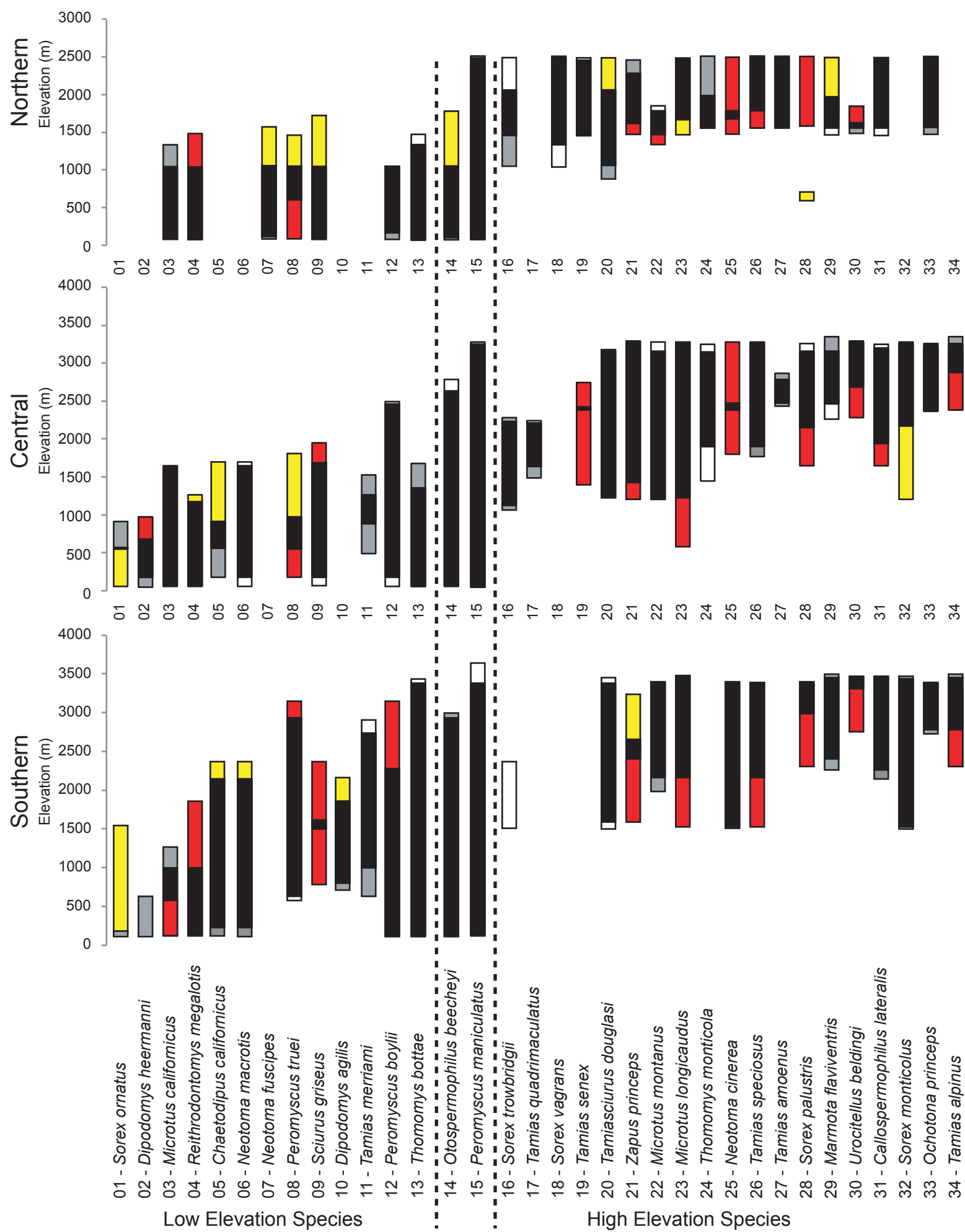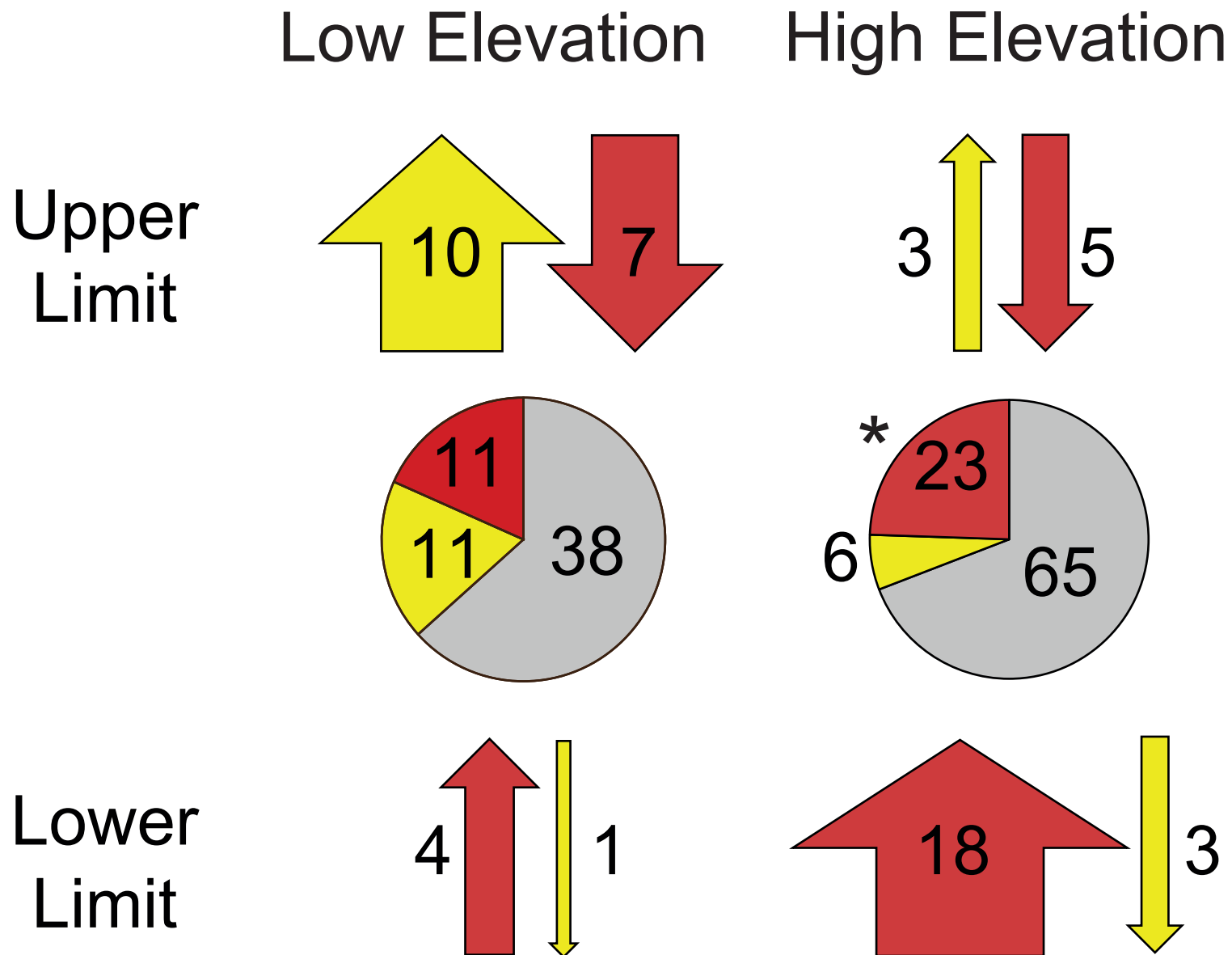California
Figure 1.

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Figure 2.

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Figure 3.

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Figure 4.