Coherent upward contractions of montane small mammals despite spatially heterogeneous impact of climate change across California

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**Abstract**

Resurveys of historical collecting localities, when combined with statistical assessment of detectability, provide strong evidence for range dynamics of species in response to recent climate change. Such studies across single elevational or latitudinal transects have revealed range shifts, primarily in the form of expansions at leading edges, and meta-analyses attribute overall patterns to global warming. However, there have been few detailed community-scale resurveys with spatial replication to control for local effects such as land-use change. Here we expand on resurveys of elevational ranges of small mammals along a single regional transect of montane California (Yosemite National Park) by repeating surveys originally conducted in the early 20th century along elevational transects in regions to the north (Lassen Volcanic National Park) and the south (Sequoia/Kings Canyon National Parks). Two-thirds of elevational ranges remained stable at one or more limits, but ranges of most species (n=34) shifted in at least one region. However, none of the species shifted both their upper and lower limits in the same direction in all three regions. High elevation species exhibited a coherent pattern of upward shifts in their lower range limits, whereas low elevation species had heterogeneous responses at the upper limits. Change in minimum annual temperature was a better predictor of the direction of species’ shifts than change in precipitation change or other temperature variables. These results demonstrate the value of multi-region resurveys and illustrate the complexity of species responses to recent climate change.

**Introduction**

Evidence for the biotic responses to climate change over the last century has continued to accumulate (Walther et al., 2002; Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2006, Chen et al. 2011). There is a general trend towards upwards and poleward shifts of elevational and latitudinal boundaries of ranges (e.g., Thomas and Lennon 1999, Lenoir et al. 2008; Chen et al. 2011), with “leading edge” expansions detected more often than “lagging edge” contractions (Thomas et al. 2004, Angert et al. 2011, Hill et al. 2011, Morelli et al. 2012). However, there is considerable heterogeneity in the direction and magnitude of species’ responses and ranges of many species have not changed at all (Parmesan et al. 1999; Moritz et al. 2008; Tingley et al. 2009, 2012). 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 (Walther 2002, Tingley et al. 2012). 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 modelled (Tingley and Beissinger 2009). 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 our contemporary resurveys, allows us to document a century of range responses of birds and mammals to climate change in California. Joseph Grinnell’s studies of the elevational distributions of vertebrates of California in the early 1900’s (Grinnell and Storer 1924, Grinnell et al. 1930, Sumner and Dixon 1953) laid the foundation for the concept of the ecological niche and for understanding the climatic limits of species’ distributions (Grinnell 1917). Grinnell’s pioneering studies also provided a benchmark for documenting changes in the elevational ranges of species over the last century (Grinnell 1910; Moritz et al. 2008). Over the past century, mean annual temperature in California has increased by ~0.6 C (Bonfils et al. 2008). However, the average change masks a large degree of spatial heterogeneity, with regions of local cooling and warming (Fig. 1B). Precipitation changes were also spatially heterogeneous, with spatial covariation increasing across the northern part of the state and decreasing across the southern part (Kelly and Goulden 2008, Crimmins et al., 2011, and citations within). Elevational ranges of birds and mammals in California over this period have shifted heterogeneously, including species moving upslope, downslope or not at all (Moritz, et al. 2008, Hargrove and Rotenberry 2011, Tingley et al. 2012). Heterogeneity in movements of species has been partly explained by incorporating spatially-specific measures of climatic change for both temperature and precipitation (Tingley et al. 2012); depending on location, increases in the former favor upslope shifts, while increases in the later favor downslope movements.

Here we characterize spatial variation in elevational range responses of small mammals in protected areas of montane California by expanding our analysis centered on a single region in the central Sierra (Yosemite National Park; Moritz et al. 2008) to other regions in the north (Lassen Volcanic National Park) and south (Sequoia/Kings Canyon National Parks). We control for variation in detectability among species and survey eras to compare elevational limits from the early 20th Century (1911-1934) to present (2003-2010). With data from multiple, geographically-separated regions of montane California that have experienced little land-use change, we tested four predictions of the influence of climate warming on elevational ranges that emerged from patterns we observed in the Yosemite region. If overall climate warming is the predominant driver of range change, then (1) upslope shifts should be the most common change across all regions; and (2) range contractions should be more frequent in high than low elevation species, and range expansions more common in low than high elevation species. If, however, species have responded to the heterogeneous climate changed across the landscape and to both temperature and precipitation change, then (3) elevational ranges of species should shift inconsistently across regions; and (4) upslope and downslope shifts should both occur and be associated with local changes in temperature and precipitation, respectively (Tingley et al. 2012).

**Methods**

*Survey regions & climate change*

Between 1911 and 1934, Joseph Grinnell and others from the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley, conducted mammal surveys (Grinnell et al, 1930; Grinnell and Storer, 1924; Sumner and Dixon, 1953) along elevation transects across three regions of montane California (Fig. 1A): a northern region around Lassen Volcanic National Park (“Lassen”), a central region around Yosemite National Park (“Yosemite”), and a southern region around Sequoia and Kings Canyon National Parks (“Sequoia”). See Tingley et al. (2012) for additional details of the sampling regions.

The three regions differed considerably in climate and physiognomy. The northern region, Lassen, is the coolest and wettest, and has the smallest elevation range and the least topographic complexity. The southern region, Sequoia, is the driest, has the largest elevation range and the greatest topographic complexity. Climate change, observed over the last century, differed among the three regions (Fig. 1B). Yosemite experienced the greatest, and Lassen the least, increase in mean annual temperature, whereas precipitation increased in both. Across all three regions, maximum temperature of the warmest month was constant, whereas minimum temperature of the coldest month increased (Fig. S1).

*Survey and Resurvey Data*

Following Moritz et al (2008), we defined a locality or site in this study as an aggregate of surveys (i.e., traplines) conducted within a 2 km geographic distance and 100 m elevation. All surveys within an aggregate were conducted concurrently. Each trapline was georeferenced to a centroid with extent determined by a combination of coordinate uncertainty and trapline extent using the point-radius method (Wieczorek, et al., 2004). Historical traplines were georeferenced from a combination of maps, written descriptions in field notes, and modern ground-truthing with historical photographs and hand-held GPS units. Modern trapline coordinates were obtained from handheld GPS units, with coordinates recorded at the beginning, middle, and end of each trapline. We determined the elevation of each historical and modern trapline using a digital elevation model (DEM) derived from SRTM (v4) with a resolution of 1 arc sec and verified these values by manual comparison to elevations determined on the ground or on topographic maps.

We obtained records from historical surveys conducted at 111 sites including 34 in Lassen, 45 in Yosemite, and 32 in Sequoia (Fig. 1A). Each site was surveyed for 1-16 nights (median = 5) for a total of 681 survey-nights. For most sites, surveys were conducted over consecutive nights. Historical trapping efforts used snap traps, Macabee gopher traps, mole traps, and steel traps that were set in suitable locations in various habitats around a central camp. For each historical locality, the average number of traps per night ranged from 6 - 335 (median = 96). Shooting and observations resulted in additional opportunistic records of diurnal mammals, primarily squirrels and pikas. We extracted key trapline details such as nightly captures records, 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). Of the 15,277 historical mammal records used in this study, 8,688 are backed by voucher specimens in the MVZ (<http://arctos.database.museum/project/historic-grinnell-survey-lassen-transect>; <http://arctos.database.museum/project/historic-grinnell-survey-yosemite-transect>; http://arctos.database.museum/project/historic-grinnell-survey-southern-sierra-nevada-transect).

Modern mammal resurveys were conducted between 2003 and 2010 as part of the Grinnell Resurvey Project – a multi-year, collaborative effort that seeks to resurvey vertebrate species at historically surveyed localities throughout California and the western U.S. (Moritz et al, 2008; Tingley et al, 2012; Fig. 1A). We surveyed a total of 166sites, including 85 of the 111 historical sites. Additional modern sites were selected to maximize elevation coverage and to serve as proxies for historical sites that were otherwise inaccessible. We surveyed each site for 1-11 nights (median = 6) for a total of 916 survey-nights. As with historical surveys, most modern surveys at a site were conducted over consecutive nights. Using historical locality maps and habitat descriptions recorded in field notebooks, we set traplines to sample historical sites as closely as possible. We used a combination of Sherman traps and Tomahawk traps, with standard traplines containing 40 Sherman traps and 10 Tomahawk traps run for 4 consecutive nights. Pitfall traps, consisting of 32-oz plastic cups placed in the ground, were used to collect shrews and were set at the same time as the Sherman lines. As in the historical era, traps were set in suitable spots to trap small mammals. Pocket gophers were trapped using Macabee gopher traps where gopher mounds were observed. For each modern site, the average number of traps per night ranged from 3-339 (median=65). Additional observational records were recorded on a daily basis. Of the 14,316 modern mammal records obtained from these surveys, 6,144 are backed by voucher specimens in the MVZ (<http://arctos.database.museum/project/grinnell-resurvey-project-lassen-transect>; <http://arctos.database.museum/project/grinnell-resurvey-project-yosemite-transect>; http://arctos.database.museum/project/grinnell-resurvey-project-southern-sierra-nevada-transect).

*Species Set*

We present the elevation distribution for 60 species of rodents, shrews, and pika recorded in the historical and modern surveys (Table S1). Our resurvey protocols were not designed to detect carnivores, ungulates, or bats, so these are not reported. Because two different faunal communities dominate the western and eastern slopes of California’s interior mountains (i.e., Sierra Nevada and southern Cascade Ranges), we divided species elevation profiles into west and east slope. We defined the west slope localities to also include the lower limits of the yellow pine belt on the eastern slope because the species utilizing these elevations are mostly Californian in origin and not from more eastern faunal communities (i.e., Great Basin and Mojave). Following Moritz et al. (2008), we adjusted the slope cut-off for *Peromyscus truei* to reflect known boundaries between Sierra Nevada and Great Basin subspecies (Yang et al. 2011).

Our analyses considered only those west slope species that are characteristic of the Sierra Nevada and Cascade Ranges. For example, we did not include Mojave Desert species such as *Neotoma lepida* or *Perognathus longimembris*. We further constrained our analyses to species that were detected at >10% of sites for at least one region in both eras. This final set included 34 mammal species of which 28 were detected through repeated nights of trapping at sites and where the number of traps set was reported (hereafter “quantitative trapping”). The remaining six species (*Marmota flaviventris*, *Sciurus griseus*, *Tamiasciurus douglasii*, *Ochotona princeps*, *Thomomys bottae*, and *Thomomys monticola*) were readily detected by observations or by specialized trapping methods (e.g., Macabee gopher traps) that rely on detection of species’ sign (i.e., burrows) prior to setting traps. While we were not able to model detection probabilities for these latter six species, systematic efforts were made to detect and record these easily observed species in suitable habitats at all sites, and they are included in range shift analyses.

Following Moritz et al (2008), we categorized species as low elevation, high elevation, or widespread species. Low elevation species had historical elevation ranges that were primarily within the Lower Sonoran - Transition life zones, whereas high elevation species had historical elevation ranges within the Transition - Alpine life zones (Table S2; Grinnell, 1924; Grinnell et al., 1930; Sumner and Dixon, 1953). Two species, *Peromyscus maniculatus* and *Otospermophilus beecheyi,* were widespread elevationally across two or more of the three regions.

*Modeling Changes in Elevational Ranges*

Although the overall survey methodology was comparable between the two eras and among sites within eras, differences in trap types and effort could confound interpretations of absences. To simultaneously estimate the probability of detection (*p*) and the probability of occupancy (*Ψ*) of each species at each locality, we used the single-season occupancy model framework implemented in the program MARK v6.0 (White and Burnham, 1999; Mackenzie et al, 2002). Our single-season model implemented an “unpaired-site” framework (Tingley & Beissinger, 2009), which tests for temporal changes in occupancy by fitting time period (‘era’) as a covariate effect. To fit these models we included the 28 species and 228 sites for which quantitative trapping data were available. We used the package ‘RMark’ v2.0.1 in the R v2.12.2 framework to build design matrices, combine models, and to compare AIC weights among models (Laake, 2013? REFS).

To develop detection-adjusted elevation range profiles for each species in each era and region we parameterized 25 occupancy models (*Ψ*) building on the model set of Moritz et al. (2008) and Tingley et al. (2012). The 25 models included all 2- and 3-way interactions among the following variables: era (categorical: historical or modern), elevation (linear), elevation (quadratic) and region (categorical: Lassen, Yosemite, or Sequoia), as well as a constant model (.). The full model set is listed in Table S3. Following Moritz et al. (2008) we estimated the probability of detection per survey night (*p*) based on 34 competing models with the following variables: era (historical or modern), trend (linear change in detections over sequential nights due to the collection of trapped individuals, trap habituation or to trap-shyness), trap effort (number of traps/100 and the log10 of the number of traps), the interaction between era and trend, and the interactions between era and trap effort variables. We built detection models with all additive combinations of these independent variables, as well as a constant model (.). The full candidate model set is listed in Table S3. We ran this full candidate *p* model set with two parameterizations of *Ψ*: a constant model and a fully parameterized model. From these analyses, we selected the set of *p* models that incorporated the best (lowest AIC) model and all models with ΔAIC < 2 for each species (Table S1). This subset of *p* models (*n* = 16) were then combined with the full set of 25 *Ψ* models for a total of 400 competing models that were run for each species and compared using AIC (Burnham and Anderson, 2002).

Following Moritz et al. (2008), we estimated temporal shifts in the lower and upper range limits for each species on each of the three regions. For elevation distributions, we included all presence data including quantitatively trapped specimens, incidentally collected (shot or salvaged) specimens and observational records (Fig. S2). We plotted all localities in each transect for each era against elevation, and coded each species at a locality as present or undetected. We then calculated the change in elevation of each range limit from the historical to the modern era. To test the significance of these shifts, we estimated locality-specific detection probabilities (*p\**) by model averaging model-specific *p* estimated using AIC weights from our 400 occupancy models (Burnham & Anderson, 2002; Moritz et al, 2008). We calculated the probability of false absence (P*fa*; Tingley & Beissinger, 2009) for each species for sites where the species was undetected in one era and that were located between the lower or upper range limits of the two eras. Range limit shifts with P*fa* ≤ 0.05 were considered statistically significant. We considered a shift to be “ecologically relevant” if the movement was both >10% of the species’ historical elevation range and >100 meters in elevation, the latter being the resolution of our aggregation of traplines into sites. Simulations based on a similar analysis for avian species across the same regions demonstrated that this approach is statistically conservative and robust to violations of closure within era (Tingley et al. 2012), an assumption of the occupancy method (MacKenzie et al. 2006).

*Testing patterns of range shifts*

We used generalized linear mixed models (GLMM) to examine how patterns of range shifts were related to regional variation and the elevational distributions of species. All GLMM models used a logit link and were run in R with the ‘lme4’ package. Species was included as a random effect and model performance was assessed by AIC. We first used GLMMs to evaluate what factors were associated with occurrence of a range shift (as a binary variable). Elevationally widespread species (*P. maniculatus* and *O. beecheyi*) were excluded from this analysis. We defined 12 models comprised of a null model (intercept only) and all additive combinations and one-way interactions between 3 categorical explanatory variables: (1) limit (upper or lower elevation range limit), (2) region (Lassen, Sequoia, Yosemite), and (3) zone (low or high elevation species). Second, to resolve interaction effects associated with zone, we then analyzed low elevation and high elevation species separately, retaining limit and region variables.

We used one-sided binomial tests to evaluate whether upslope shifts were the most common across regions (Prediction 1), whether range contractions were more likely in high elevation species and range expansions were more common in low elevation species (Prediction 2), and to evaluate whether the patterns of range shifts were consistent across regions (Prediction 3). For each of these analyses, we included only those species that exhibited significant shifts determined from the *Pfa* analysis above.

*Climatic nearest neighbor*

We examined spatial heterogeneity in climate change (Prediction 4) by identifying the nearest climatic neighbors of historical localities under modern climate conditions, following the approach described in Tingley et al. (2012). Using four standard BIOCLIM variables (mean annual temperature, B1; maximum temperature of the warmest month, B5; minimum temperature of the coldest month, B6; and mean annual precipitation, B12) from the Parameter-elevation Regressions on Independent Slope Model (PRISM; Daly et al. 2002) at a resolution of 30 arc-second (1 km2), we calculated 20-year averages for the historical (1910-1930) and modern (1989-2009) survey periods. Climatic distances for each of the BIOCLIM variables were calculated between each historical locality and modern era PRISM grid cells within the same region, which was defined by a 20-kilometer buffer around the minimum convex polygon that encompassed all survey sites. For each historical site, we identified the 5% of modern cells that were nearest climatically. This was calculated separately for each climatic variable using the Euclidian distance. We subtracted the elevation of the historical site from the average elevation of the modern nearest climate neighbor cells; positive values indicated upslope movement in climate space. We recorded these values (positive or negative) for the two historical localities defining the upper and lower limits of each species on each transect. These values provided a climate-based prediction for movement of species at their range limits for each region (i.e., upslope or downslope). We compared these climate-data derived models to an “overall warming model” that assumes an increased temperature at all grid cells over the same time period, which always predicted upslope movements.

We used GLMMs to compare the ability of each of the BIOCLIM variables (B1, B5, B6 and B12 discussed above) to predict the direction of significant range shifts. We analyzed 32 models comprised of a null model (intercept only), and all additive combinations of the six variables, except that no more than one temperature variable was included in each model. Because an overall warming model always predicted upslope movement, it could not be compared in a GLMM context. Therefore, we used a one-sided binomial to test if the upslope movement predicted from the overall warming model and predictions from each of the BIOCLIM variables were consistent with the direction of observed shifts (Prediction 4).

**Results**

*General Patterns of Mammalian Elevational Range Shift Over the Past Century*

A total of 57 small mammal species were detected in both the historical and modern surveys (Table S2, Fig. S2). Of these, 22 species occurred in all three regions, 22 species occurred in two regions, and 13 species occurred in a single region. Two species (*Sorex merriami* and *Tamias umbrinus*)were only detected in the historical era and one species (*Sorex tenellus*)was only detected in the modern era.Each of these three species was detected at <10% of sites in a single region in their respective era. *Tamias umbrinus,* however, has been detected in modern surveys outside of this study at other localities in the Sequoia region (J.L. Patton, pers. obs.).Of the 57 species detected, we analyzed range limit shifts for 34 species detected in both the historical and modern eras.

The majority of species’ elevational ranges remained stable at one or more limits, but ranges of most species shifted in at least one region. Across the three regions, we detected 52 significant range limit shifts, representing 31.3% of the 166 region-specific historical range limits across the 34 species analyzed (Fig. 2). We observed no significant range limit shifts in nine species (26.4%), including two gophers (*Thomomys bottae* and *T. monticola*), three chipmunks (*Tamias merriami, T. quadrimaculatus*, and *T. amoenus*), two shrews (*Sorex trowbridgii,* and *S. vagrans*), a widespread deer mouse (*Peromyscus maniculatus*), and pika (*Ochotona princeps*). The remaining 25 species (74.6%) shifted at least one range limit in one or more regions (region (Fig. 2, Table S2).

*Tests of Elevational Range-Shift Predictions*

There was little consistency of patterns in range shifts among regions. None of the 22 species found in all three regions shifted both their upper and lower limits in the same direction in all three regions (Fig. 2). However, some patterns did emerge when examining overall range limit shifts of high and low elevation species.

Shifts of the upper and lower range limit (“limit”) differed in frequency and directionality between low and high elevation species (“zone”). GLMM analysis revealed a strong zone\*limit interaction (AIC wt =1), with region having little effect on the probability of a range shift (Table 1). In separate analyses examining the probability of any shift for high and for low elevation species, the limit-only model again received the greatest support (AIC weight of 0.63 and 0.73, respectively), with little support for differences among regions).

Species’ elevational limits were more than twice as likely to move upslope (69.2%) than downslope (31.8%; one-sided binomial test, *n* = 52, *p* = 0.004; Fig. 3). In addition, high elevation species were significantly more likely to contract their ranges than to expand them (79% contract, *n* = 29, *p* = 0.001). However, contrary to our expectation, low elevation species expanded their limits as often as they contracted them (50% contract, *n*=22, *p*=0.584). These patterns emerged because there were significantly more upslope than downslope shifts of the lower limit of high elevation species (*n =* 21, *p* < 0.001), whereas shifts in the upper limit of low elevation species were heterogeneous with nearly as many downslope shifts as upslope shifts (*n* = 17, *p* = 0.315).

Nearest climatic neighbor analyses revealed that both upslope and downslope shifts were predicted by climate change at range limits (Fig. 1C). Change in minimum annual temperature (Fig. 4) was the best predictor and explained 73.1% of the 52 significant range limit shifts observed. However, it was only a slight improvement over an overall warming model that explained 69% of shifts and mean annual temperature change that accounted for 63.5% of range shifts. Predictions from all three were significantly different from random (*p* < 0.05). Neither the change in maximum temperature (53.8%) nor mean annual precipitation (53.8%) differed significantly from random (*p* = 0.339). Similar patterns were observed for low and high elevation species (Fig. 4), except only change in minimum temperature significantly predicted range limit movements for low elevation species. GLMM analyses of nearest neighbor predictions supported the superior performance of change in minimum temperature in predicting the direction of range shifts (Table 2). The best model was limit + minimum temperature, followed closely by the minimum temperature only model. Thus, minimum temperature was a better predictor of range shift direction than limit, region or other BIOCLIM variables.

**Discussion**

Our results from a multi-region, community-wide analysis of elevational transects across montane California suggested strong but locally heterogeneous impacts of recent climate change on the range limits of small mammals. None of the species shifted both their upper and lower limits in the same direction in all three regions (Fig. 2). There was, however, consistent upslope range contractions in high elevation species, while low elevation species exhibited heterogeneity in the directionality of range limit shifts. While our findings confirmed some results from our initial study of small mammals from the Yosemite region (Moritz et al. 2008) and studies of birds (Tingley et al. 2012), butterflies (Forister et al. 2010), and plants (Crimmins et al. 2011) over the same spatial and temporal scale, they amplify the complex and variable ways that species can respond to climate change.

Despite the predominant pattern in our study of upslope shifts with range contractions at the lagging edge of high elevation species, nearly one-third of shifts overall were downslope, one-fourth of species did not shift elevational range, and shifts by species varied greatly across regions. Tingley et al. (2012) found similar results for Californian birds, where only 51% of observed range limit shifts over the last century were upslope. Heterogeneous range shifts have been demonstrated in a range of taxa (Chen et al. 2011), suggesting that species’ responses were influenced by local factors and were context dependent. The vast majority of sites in our study, especially at middle to high elevations, were located in protected reserves with limited impacts of land conversion, although grazing policy, fire regimes and forestry practices may have changed (REFS, Myers et al. 2000). Low elevation species should have been more likely to experience impacts from habitat conversion at their lower limits (Nogués-Bravo et al. 2008, Forister et al. 2010). However, we detected few contractions at lower limits of low elevation mammals, and shifts were significantly more common at their upper limits. Greater heterogeneity in responses of low elevation species may reflect stronger biotic influences (Brown et al. 1996, Rapacciuolo et al. in review), such as interspecific competition (Rubidge et al. 2011), seral dynamics of habitats (Rowe et al. 2009), and the spread of invasive species (Rowe et al. 2011).

Our results also suggested that localized climate predictions, particularly change in minimum temperature, could explain variability in the direction of species responses, highlighting the dynamic nature of species-specific responses to localized climate change. Across the same regions, nearest neighbor analyses of bird species found strong support for range-limit shifts, often downwards, associated with site-specific changes in precipitation or temperature (Tingley et al. 2012). Tracking climatic changes in water balance, plant species across montane California also shifted downward over the last century (Crimmins et al. 2011). For small mammals, however, precipitation was a poor predictor of the direction of shifts.

Rising minimum temperatures will have substantial impacts on winter snowpack and the proportion of winter precipitation falling as snow, particularly at mid-elevations where we observed the most consistent upwards range contractions (Johnson 1998, Moser et al. 2009). Snowpack serves an important insulating role for small mammals and increases in snowmelt may increase exposure (Vaughn et al. 2000, Rubidge et al. 2010, Morelli et al. 2012). Snowpack in the Sierra Nevada is especially sensitive to slight changes in minimum temperatures because over 50% of the snow falls at temperatures close to freezing (Bales et al. 2006). Increased minimum temperatures may also increase competition from lower elevation species through community reorganization (Stralberg et al. 2009, Tingley and Beissinger 2013), range expansions of generalist species (Wilson et al. 2007, Davey et al. 2013), and/or shifts in vegetation (Rowe et al. 2009).

A notable finding of this multi-region study was that most high elevation species had heterogeneous responses across regions, perhaps due to region-specific changes in seral dynamics or interacting effects of local changes in temperature and precipitation (e.g., Harrison et al. 2010). The shadow chipmunk (*T. senex*) was an extreme example with almost complete collapse of its elevational range in Yosemite but with no elevational change in Lassen. Similarly, lower limit contractions observed for the golden-mantled ground squirrel (*C. lateralis*) in Yosemite were not replicated in Lassen or Sequoia. On the other hand, consistent patterns emerged for some high elevation species. For example, elevational ranges of the pika (*Ochotona princeps*), which has attracted considerable attention because of extirpations and upslope retractions in the Great Basin (Beever et al. 2003, 2011), were stable across all three regions. This result is consistent with a more extensive study across the Sierra Nevada that found pika thriving across wider geographic and elevation ranges than historically reported (Millar and Westfall 2010). In addition, some high elevation species showed upwards contractions at their lower limits in two of three regions, but lacked evidence for a significant upward contraction in the third. These included Belding’s ground squirrel (*U. beldingi*; Morelli et al. 2012), Bushy-tailed wood rat (*N. cinerea*), Long-tailed vole (*M. longicaudus*), lodgepole chipmunk (*T. speciosus*) and water shrew (*S. palustris*). The Alpine chipmunk (*T. alpinus*; see also Rubidge et al. 2010) and Pacific jumping mouse (*Z. princeps*) exhibited the most consistent elevational range shifts with contractions of their lower limit in each of the regions where they were present. Given the heterogeneity of responses documented here, each of these taxa warrants more intensive study across regions to identify proximate causes of decline.

In conclusion, our study joins the substantial evidence for range shifts of species in response to 20th Century climate change (e.g., Parmesan and Yohe 2003, Chen et al. 2011), but found spatially heterogeneous patterns of elevational range limit shifts across regions. The challenge ahead is to understand the causes of species’ heterogeneous responses to improve predictions of vulnerability. Studies testing whether species track climatic niches and respond to local variation in climate change (e.g., Tingley et al. 2009, 2012), or whether range changes are a response to other local effects, such as fire, seral dynamics, or species interactions are needed. Moreover, identifying the life-history traits (e.g., dispersal ability, reproductive rate, and degree of ecological specialization) that best predict persistence or vulnerability (Angert et al. 2011, Schloss et al. 2012) may provide key insights into the mechanisms of species- and region-specific responses to climate change.

**Acknowledgements**

Funders -

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# Tables

**Table 1. Generalized linear mixed models examining patterns of range limit shifts of 32 montane small mammals of California.**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Elevation Range Metric | Model | Parameters\* | AIC | ΔAIC | AIC Weight |
| All Species | Basic | Zone:Limit | 170.80 | 0.00 | 1.00 |
| Any Shift | - | Null | 189.90 | 19.10 | 0.00 |
|  | - | Zone | 190.50 | 19.70 | 0.00 |
|  | - | Limit | 191.90 | 21.10 | 0.00 |
|  | - | Limit+Zone | 192.50 | 21.70 | 0.00 |
|  | - | Region | 193.60 | 22.80 | 0.00 |
|  | - | Region+Zone | 194.10 | 23.30 | 0.00 |
|  | - | Limit+Region | 195.60 | 24.80 | 0.00 |
|  | - | Limit+Zone+Region | 196.10 | 25.30 | 0.00 |
|  | - | Region:Zone | 196.60 | 25.80 | 0.00 |
|  | - | Region:Limit | 197.60 | 26.80 | 0.00 |
|  |  |  |  |  |  |
|  |  |  |  |  |  |
|  |  |  |  |  |  |
| High Elevation Species | Basic | Limit | 109.50 | 0.00 | 0.63 |
| Any Shift | - | Region:Limit | 111.90 | 2.40 | 0.19 |
|  | - | Region+Limit | 112.20 | 2.70 | 0.16 |
|  | - | Null | 117.70 | 8.20 | 0.01 |
|  | - | Region | 120.80 | 11.30 | 0.00 |
|  |  |  |  |  |  |
| Low Elevation Species | Basic | Limit | 63.19 | 0.00 | 0.73 |
| Any Shift | - | Region+Limit | 65.66 | 2.47 | 0.21 |
|  | - | Region:Limit | 68.53 | 5.34 | 0.05 |
|  | - | Null | 74.46 | 11.27 | 0.00 |
|  | - | Region | 77.44 | 14.25 | 0.00 |
|  |  |  |  |  |  |
| High Elevation Species | Basic | Region+Limit | 35.80 | 0.00 | 0.82 |
| Shift up vs down | - | Limit | 39.98 | 4.18 | 0.10 |
|  | - | Region:Limit | 42.56 | 6.76 | 0.03 |
|  | - | Region | 42.58 | 6.78 | 0.03 |
|  | - | Null | 43.34 | 7.54 | 0.02 |
|  |  |  |  |  |  |
| Low Elevation Species | Basic | Null | 32.84 | 0.00 | 0.52 |
| Shift up vs down | - | Limit | 34.04 | 1.20 | 0.29 |
|  | - | Region | 36.02 | 3.18 | 0.11 |
|  | - | Region+Limit | 37.11 | 4.27 | 0.06 |
|  | - | Region:Limit | 39.09 | 6.25 | 0.02 |

\* Model parameters included: Region (Lassen, Yosemite, Sequoia), Limit (upper elevation limit, lower elevation limit), and Zone (high or low elevation species).

**Table 2. Generalized linear mixed models examining patterns of upslope or downslope range limit shifts of 32 montane small mammals of California in relation to climate.**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Elevation Range Metric | Model\* | Parameters† | AIC | ΔAIC | AIC Weight |
| Shift up vs down | NN | B6+Limit | 60.52 | 0.0 | 0.20 |
|  | - | B6 | 61.02 | 0.5 | 0.16 |
|  | - | B6+B12+Limit | 62.50 | 2.0 | 0.08 |
|  | - | Limit | 62.62 | 2.1 | 0.07 |
|  | - | B6+B12 | 63.09 | 2.6 | 0.06 |
|  | - | B12+Limit | 63.22 | 2.7 | 0.05 |
|  | - | B1+Limit | 63.26 | 2.7 | 0.05 |
|  | - | B5+Limit | 63.35 | 2.8 | 0.05 |
|  | - | B6+Limit+Region | 63.48 | 3.0 | 0.05 |
|  | - | B1+B12+Limit | 64.72 | 4.2 | 0.02 |
|  | - | B5+B12+Limit | 64.81 | 4.3 | 0.02 |
|  | - | B12 | 64.91 | 4.4 | 0.02 |
|  | - | B6+B12+Limit+Region | 65.37 | 4.9 | 0.02 |
|  | - | B6+B12+Region | 65.74 | 5.2 | 0.01 |
|  | - | Null | 65.79 | 5.3 | 0.01 |
|  | - | Limit+Region | 65.93 | 5.4 | 0.01 |
|  | - | B12+Limit+Region | 65.98 | 5.5 | 0.01 |
|  | - | B1 | 66.04 | 5.5 | 0.01 |
|  | - | B1+Limit+Region | 66.21 | 5.7 | 0.01 |
|  | - | B1+B12 | 66.50 | 6.0 | 0.01 |
|  | - | B5+Limit+Region | 66.73 | 6.2 | 0.01 |
|  | - | B5+B12 | 66.91 | 6.4 | 0.01 |
|  | - | B1+B12+Limit+Region | 67.30 | 6.8 | 0.01 |
|  | - | B5 | 67.36 | 6.8 | 0.01 |
|  | - | B5+B12+Limit+Region | 67.77 | 7.2 | 0.01 |
|  | - | B12+Region | 67.78 | 7.3 | 0.01 |
|  | - | B1+Reg | 69.03 | 8.5 | 0.00 |
|  | - | B1+B12+Region | 69.11 | 8.6 | 0.00 |
|  | - | Region | 69.22 | 8.7 | 0.00 |
|  | - | B6+Region | 69.22 | 8.7 | 0.00 |
|  | - | B5+B12+Region | 69.76 | 9.2 | 0.00 |
|  | - | B5+Region | 70.78 | 10.3 | 0.00 |

\*Model is based on the nearest climate neighbor analysis and includes only statistically significant range limit shifts (see Methods for details).

†Parameter included: Region (Lassen, Yosemite, Sequoia), Limit (upper elevation limit, lower elevation limit), B1 (mean annual temperature), B5 (maximum temperature of the warmest month), B6 (minimum temperature of the coldest month), and B12 (mean annual precipitation).

# Supplemental Tables

**Table S1. List of small mammal species examined in this study.**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  | Lassen‡ | | |  | Yosemite | | |  | Sequoia | | |
| Species |  | Detection method§ | Occupancy analysis† |  | Slope | H | M |  | Slope | H | M |  | Slope | H | M |
| *Ammospermophilus leucurus* |  | St | - |  | E | 0 | 1 |  | --- | | |  | E + W | 1 | 1 |
| *Aplodontia rufa* |  | Sp | - |  | W | 0 | 1 |  | E + W | 1 | 1 |  | --- | | |
| *Callospermophilus lateralis* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Chaetodipus californicus* |  | St | Y |  | --- | | |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Clethrionomys californicus* |  | St | - |  | W | 1 | 1 |  | --- | | |  | --- | | |
| *Dipodomys agilis* |  | St | Y |  | --- | | |  | --- | | |  | E + W | 1 | 1 |
| *Dipodomys californicus* |  | St | - |  | E + W | 1 | 1 |  | --- | | |  | --- | | |
| *Dipodomys heermanni* |  | St | Y |  | --- | | |  | E + W | 1 | 1 |  | E + W | 1 | 0 |
| *Dipodomys merriami* |  | St | - |  | --- | | |  | --- | | |  | E + W | 1 | 1 |
| *Dipodomys ordii* |  | St | - |  | E | 1 | 1 |  | --- | | |  | --- | | |
| *Dipodomys panamintinus* |  | St | - |  | --- | | |  | E | 1 | 1 |  | E + W | 1 | 1 |
| *Glaucomys sabrinus* |  | St | - |  | W | 1 | 1 |  | W | 1 | 1 |  | --- | | |
| *Lemmiscus curtatus* |  | St | - |  | E | 1 | 1 |  | E | 1 | 1 |  | --- | | |
| *Marmota flaviventris* |  | Obs | N |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | W | 1 | 1 |
| *Microdipodops megacephalus* |  | St | - |  | E | 1 | 1 |  | E | 1 | 0 |  | --- | | |
| *Microtus californicus* |  | St | Y |  | W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Microtus longicaudus* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Microtus montanus* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Neotoma bryanti* |  | St | - |  | --- | | |  | --- | | |  | E + W | 1 | 1 |
| *Neotoma cinerea* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Neotoma fuscipes* |  | St | Y |  | E + W | 1 | 1 |  | --- | | |  | --- | | |
| *Neotoma lepida* |  | St | - |  | E | 1 | 1 |  | --- | | |  | E + W | 1 | 1 |
| *Neotoma macrotis* |  | St | Y |  | --- | | |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Ochotona princeps* |  | Obs | N |  | E + W | 1 | 1 |  | W | 1 | 1 |  | W | 1 | 1 |
| *Onychomys leucogaster* |  | St | - |  | E | 1 | 1 |  | E | 1 | 1 |  | --- | | |
| *Onychomys torridus* |  | St | - |  | --- | | |  | --- | | |  | E + W | 1 | 1 |
| *Otospermophilus beecheyi* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Perognathus inornatus* |  | St | - |  | --- | | |  | W | 1 | 1 |  | W | 1 | 1 |
| *Perognathus longimembris* |  | St | - |  | --- | | |  | --- | | |  | E + W | 1 | 1 |
| *Perognathus parvus* |  | St | - |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E | 1 | 0 |
| *Peromyscus boylii* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Peromyscus californicus* |  | St | - |  | --- | | |  | W | 1 | 1 |  | W | 1 | 1 |
| *Peromyscus crinitus* |  | St | - |  | E | 1 | 1 |  | --- | | |  | E + W | 1 | 1 |
| *Peromyscus maniculatus* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Peromyscus truei* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Phenacomys intermedius* |  | St | - |  | --- | | |  | W | 1 | 1 |  | W | 1 | 1 |
| *Reithrodontomys megalotis* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Sciurus griseus* |  | Obs | N |  | W | 1 | 1 |  | W | 1 | 1 |  | W | 1 | 1 |
| *Sorex merriami* |  | St | - |  | E | 1 | 0 |  | --- | | |  | --- | | |
| *Sorex monticolus* |  | St | Y |  | --- | | |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Sorex ornatus* |  | St | Y |  | --- | | |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Sorex palustris* |  | St | Y |  | W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Sorex tenellus* |  | St | - |  | --- | | |  | W\* | 0 | 1 |  | W | 0 | 1 |
| *Sorex trowbridgii* |  | St | Y |  | E + W | 1 | 1 |  | W | 1 | 1 |  | W\* | 0 | 1 |
| *Sorex vagrans* |  | St | Y |  | E + W | 1 | 1 |  | --- | | |  | --- | | |
| *Tamias alpinus* |  | St | Y |  | --- | | |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Tamias amoenus* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | --- | | |
| *Tamias merriami* |  | St | Y |  | --- | | |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Tamias minimus* |  | St | - |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | W | 1 | 1 |
| *Tamias panamintinus* |  | St | - |  | --- | | |  | --- | | |  | E + W | 1 | 1 |
| *Tamias quadrimaculatus* |  | St | Y |  | --- | | |  | E + W | 1 | 1 |  | --- | | |
| *Tamias senex* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | --- | | |
| *Tamias speciosus* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Tamias umbrinus* |  | St | - |  | --- | | |  | --- | | |  | E + W | 1 | 0 |
| *Tamiasciurus douglasii* |  | Obs | N |  | E + W | 1 | 1 |  | W | 1 | 1 |  | W | 1 | 1 |
| *Thomomys bottae* |  | Sp | N |  | W | 1 | 1 |  | W | 1 | 1 |  | W | 1 | 1 |
| *Thomomys monticola* |  | Sp | N |  | W | 1 | 1 |  | W | 1 | 1 |  | --- | | |
| *Thomomys talpoides* |  | Sp | - |  | E | 1 | 0 |  | E + W | 1 | 1 |  | --- | | |
| *Urocitellus beldingi* |  | St | Y |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
| *Zapus princeps* |  | St | Y |  | W | 1 | 1 |  | E + W | 1 | 1 |  | E + W | 1 | 1 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| **Total 60** |  | **52** | **34** |  |  | **38** | **38** |  |  | **43** | **43** |  |  | **42** | **41** |

§Detection methods were standardized trapping (St), specialized trapping (Sp), or observation (Obs).

†Species included in the analysis of range shifts were both species with (Y) and without (N) sufficient data for occupancy analysis. Of the 60 species we examined, 52 were detected using standardized trapping, 28 were included in the occupancy analyses and an additional 6 species were included in the analysis of range shifts.

‡Species were detected on the east (E) and/or west (W) slopes within each region and detections within each region are listed as detected (0) or not detected (1) in the historical (H) or the modern (M) eras.

\* New species records detected during our surveys.

**Table S2. Model parameterizations of detectability (*p*) and occupancy (*ψ*) run for each species with quantifiable trapping effort data (see Table S1 for list of modeled species).**

|  |
| --- |
| **Detectability models (*p*)** |
| 1. null |
| 2. Era+LogT+Era\*LogT+T100+Time |
| 3. Era+LogT+Era\*LogT+Time+Era\*Time+T100 |
| 4. Era+LogT+Era\*logT+Time+Era\*Time |
| 5. Era+logT+Era\*logT+Time |
| 6. Era+logT+Time |
| 7. Era+T100+Era\*T100+logT+Era\*logT+Time |
| 8. Era+T100+Era\*T100+logT+Time |
| 9. Era+T100+Era\*T100+Time+Era\*Time |
| 10. Era+T100+Era\*T100 |
| 11. Era+Time+Era\*Time+logT |
| 12. Era+Time+Era\*Time+T100+logT |
| 13. T100+logT+Time |
| 14. T100+Time |
| 15. Time |
| 16. Era+T100+Era\*T100+logT+Era\*logT+Time+Era\*Time |
|  |
| **Occupancy models (*ψ*)** |
| 1. null |
| 2. Era |
| 3. Elev |
| 4. Elev+Elev2 |
| 5. Region |
| 6. Era+Elev |
| 7. Era+Elev+Elev2 |
| 8. Era+Elev+Era\*Elev |
| 9. Era+Elev+Elev2+Era\*Elev+Era\*Elev2 |
| 10. Era+Region |
| 11. Era+Region+Era\*Region |
| 12. Elev+Region |
| 13. Elev+Elev2+Region |
| 14. Elev+Region+Elev\*Region |
| 15. Elev+Elev2+Region+Elev\*Region+Elev2\*Region |
| 16. Era+Elev+Region |
| 17. Era+Elev+Elev2+Region |
| 18. Era+Elev+Region+Era\*Elev |
| 19. Era+Elev+Elev2+Region+Era\*Elev+Era\*Elev2 |
| 20. Era+Elev+Region+Elev\*Region |
| 21. Era+Elev+Elev2+Region+Elev\*Region+Elev2\*Region |
| 22. Era+Elev+Region+Era\*Region |
| 23. Era+Elev+Elev2+Region+Era\*Region |
| 24. Era+Elev+Region+Era\*Elev+Era\*Region+Elev\*Region+Era\*Elev\*Region |
| 25. Era+Elev+Elev2+Region+Era\*Elev+Era\*Elev2+Era\*Region+Elev\*Region+Elev2\*Region+Era\*Elev\*Region+Era\*Elev2\*Region |

**Table S4. Range limits and shifts of the 34 modeled species examined in this study.**

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Species | Region | *p* (H) § | *p* (M) | Historical Elevation Range (m) | Lower Limit Shift | Upper Limit Shift | Pattern | Best Occupancy Model† | AICc Weight | Historical Life Zone¶ |
| 1 | ***Sorex ornatus*** |  |  |  |  |  |  |  | era + elev + elev2 + region | 0.2246 | Upper Sonoran (L) |
|  |  | Lassen | NA | NA | NA | NA | NA | NA |
|  |  | Yosemite | 0.55 | 0.32 | 549-914 | -492 | No Change | Expand -L |
|  |  | Sequoia | 0.31 | 0.49 | 118-180 | No Change | +1362 | Expand +U |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 2 | ***Dipodomys heermanni*** |  |  |  |  |  |  |  | era + elev + region + era\*elev | 0.2148 | Lower-Upper Sonoran (L) |
|  |  | Lassen | NA | NA | NA | NA | NA | NA |
|  |  | Yosemite | 0.35 | 0.61 | 52-975 | No Change | -247 | Contract -U |
|  |  | Sequoia | 0.95 | Undetected | 118-636 | Undected Current | Undected Current | NA |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 3 | ***Microtus californicus*** |  |  |  |  |  |  |  | era + elev + region + elev\*region | 0.0669 | Lower-Upper Sonoran (L) |
|  |  | Lassen | 0.83 | 0.89 | 79-1335 | No Change | No Change | No Change |
|  |  | Yosemite | 0.76 | 0.60 | 52-1647 | No Change | No Change | No Change |
|  |  | Sequoia | 0.96 | 0.90 | 118-1261 | +465 | No Change | Contract +L |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 4 | ***Reithrodontomys megalotis*** |  |  |  |  |  |  |  | elev | 0.1738 | Lower–Upper Sonoran (L) |
|  |  | Lassen | 0.82 | 0.86 | 79-1478 | No Change | -434 | Contract -U |
|  |  | Yosemite | 0.90 | 0.64 | 52-1158 | No Change | +110 | Expand +U |
|  |  | Sequoia | 0.96 | 0.90 | 118-1860 | No Change | -861 | Contract -U |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 5 | ***Chaetodipus californicus*** |  |  |  |  |  |  |  | era + elev + elev2 + region | 0.2355 | Lower-Upper Sonoran (L) |
|  |  | Lassen | NA | NA | NA | NA | NA | NA |
|  |  | Yosemite | 0.37 | 0.75 | 183-914 | No Change | +787 | Expand +U |
|  |  | Sequoia | 0.83 | 0.91 | 118-2147 | +113‡ | +226 | Shift +LU |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 6 | ***Neotoma fuscipes/macrotis*** |  |  |  |  |  |  |  |  |  |  |
|  | ***Neotoma fuscipes*** | Lassen | 0.69 | 0.98 | 79-1051 | +32‡ | +515 | Expand +U | elev + elev2 + region | 0.2508 | Lower Sonoran–Transition (L) |
|  | ***Neotoma macrotis*** | Yosemite | 0.57 | 0.78 | 183-1647 | No Change | No Change | No Change | elev + elev2 + region + elev\*region + elev2\*region | 0.1464 | Lower Sonoran–Transition (L) |
|  | ***Neotoma macrotis*** | Sequoia | 0.59 | 0.91 | 118-2147 | +113‡ | +226 | Shift +LU |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 7 | ***Peromyscus truei*** |  |  |  |  |  |  |  | era + elev + elev2 + region + era\*elev + era\*elev2 + era\*region + elev\*region + elev2\*region + era\*elev\*region + era\*elev2\*region | 0.4677 | Upper Sonoran (L) |
|  |  | Lassen | 0.67 | 0.60 | 79-1051 | +529 | +408 | Shift +LU |
|  |  | Yosemite | 0.85 | 0.74 | 183-975 | +374 | +836 | Shift +LU |
|  |  | Sequoia | 0.82 | 0.74 | 636-3147 | -53‡ | -207 | Contract -U |
|  |  |  |  |  |  |  |  |  |  |  |  |
| \*8 | ***Sciurus griseus*** |  |  |  |  |  |  |  | \*Not subject to occupancy analyses | | Lower–Upper Sonoran (L) |
|  |  | Lassen |  |  | 103-1051 | No Change | +671 | Expand +U |
|  |  | Yosemite |  |  | 183-1951 | No Change | -262 | Contact -U |
|  |  | Sequoia |  |  | 787-2364 | +720 | -750 | Contract +L, -U |
|  |  |  |  |  |  |  |  |  |  |  |  |
| \*9 | ***Dipodomys agilis*** |  |  |  |  |  |  |  | era + elev + elev2 + region | 0.2470 | Lower-Upper Sonoran (L) |
|  |  | Lassen | NA | NA | NA | NA | NA | NA |
|  |  | Yosemite | NA | NA | NA | NA | NA | NA |
|  |  | Sequoia | 0.49 | 0.49 | 721-1860 | +89‡ | +307 | Expand +U |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 10 | ***Tamias merriami*** |  |  |  |  |  |  |  | elev + region | 0.1284 | Lower–Upper Sonoran (L) |
|  |  | Lassen | NA | NA | NA | NA | NA | NA |
|  |  | Yosemite | 0.25 | 0.21 | 488-1524 | No Change | No Change | No Change |
|  |  | Sequoia | 0.43 | 0.59 | 636-2732 | No Change | No Change | No Change |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 11 | ***Peromyscus boylii*** |  |  |  |  |  |  |  | era + elev + elev2 + region + elev\*region + elev2\*region | 0.5811 | Upper Sonoran–Transition (L) |
|  |  | Lassen | 0.85 | 0.99 | 79-1051 | +89‡ | No Change | Contract +L |
|  |  | Yosemite | 0.88 | 0.88 | 183-2464 | -126‡ | No Change | Expand -L |
|  |  | Sequoia | 0.97 | 0.99 | 118-3147 | +20‡ | -865 | Contract -U |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 12 | ***Thomomys bottae*** |  |  |  |  |  |  |  | \*Not subject to occupancy analyses | | Lower Sonoran-Transition (L) |
|  |  | Lassen |  |  | 75-1335 | No Change | No Change | No Change |
|  |  | Yosemite |  |  | 57-1676 | No Change | No Change | No Change |
|  |  | Sequoia |  |  | 118-3384 | No Change | No Change | No Change |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 13 | ***Otospermophilus beecheyi*** |  |  |  |  |  |  |  | era + elev + elev2 + era\*elev + era\*elev2 | 0.1069 | Lower Sonoran–Canadian (W) |
|  |  | Lassen | 0.05 | 0.67 | 79-1051 | No Change | +734 | Expand +U |
|  |  | Yosemite | 0.28 | 0.42 | 61-2632 | No Change | No Change | No Change |
|  |  | Sequoia | 0.07 | 0.82 | 118-2997 | No Change | -57‡ | No Change |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 14 | ***Peromyscus maniculatus*** |  |  |  |  |  |  |  | era + elev + elev2 + region + era\*elev + era\*elev2 + era\*region + elev\*region + elev2\*region + era\*elev\*region + era\*elev2\*region | 0.4195 | Lower Sonoran–Arctic-Alpine (W) |
|  |  | Lassen | 0.94 | 0.99 | 79-2514 | No Change | No Change | No Change |
|  |  | Yosemite | 0.95 | 0.93 | 52-3281 | No Change | No Change | No Change |
|  |  | Sequoia | 0.99 | 0.99 | 118-3384 | No Change | No Change | No Change |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 15 | ***Sorex trowbridgii*** |  |  |  |  |  |  |  | elev + elev2 + region | 0.0988 | Transition–Canadian (H) |
|  |  | Lassen | 0.49 | 0.68 | 1051-2061 | No Change | No Change | No Change |
|  |  | Yosemite | 0.65 | 0.68 | 1068-2286 | No Change | -54‡ | No Change |
|  |  | Sequoia | 0.76 | 0.69 | 1507-2373 (Modern) | Undetected Historical | Undetected Historical | New record Modern |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 16 | ***Tamias quadrimaculatus*** |  |  |  |  |  |  |  | elev + elev2 + region | 0.1681 | Transition–Canadian (H) |
|  |  | Lassen | NA | NA | NA | NA | NA | NA |
|  |  | Yosemite | 0.54 | 0.49 | 1494-2210 | No Change | No Change | No Change |
|  |  | Sequoia | NA | NA | NA | NA | NA | NA |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 17 | ***Sorex vagrans*** |  |  |  |  |  |  |  | elev + region | 0.0963 | Transition–Canadian (H) |
|  |  | Lassen | 0.62 | 0.96 | 1335-2514 | No Change | No Change | No Change |
|  |  | Yosemite | NA | NA | NA | NA | NA | NA |
|  |  | Sequoia | NA | NA | NA | NA | NA | NA |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 18 | ***Tamias senex*** |  |  |  |  |  |  |  | elev + elev2 + region | 0.2866 | Canadian (H) |
|  |  | Lassen | 0.55 | 0.99 | 1478-2462 | No Change | No Change | No Change |
|  |  | Yosemite | 0.87 | 0.49 | 1402-2743 | +981 | -360 | Contract +L-U |
|  |  | Sequoia | NA | NA | NA | NA | NA | NA |
|  |  |  |  |  |  |  |  |  |  |  |  |
| \*19 | ***Tamiasciurus douglasi*** |  |  |  |  |  |  |  | \*Not subject to occupancy analyses | | Transition-Hudsonian (H) |
|  |  | Lassen |  |  | 886-2061 | No Change | +430 | Expand +U |
|  |  | Yosemite |  |  | 1229-3185 | No Change | No Change | No Change |
|  |  | Sequoia |  |  | 1592-3384 | No Change | No Change | No Change |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 20 | ***Zapus princeps*** |  |  |  |  |  |  |  | elev + elev2 + region |  | Transition–Hudsonian (H) |
|  |  | Lassen | 0.78 | 0.87 | 1478-2462 | +138 | No Change | Contract +L | 0.1800 |
|  |  | Yosemite | 0.92 | 0.86 | 1211-3281 | +213 | No Change | Contract +L |
|  |  | Sequoia | 0.92 | 0.85 | 1592-2657 | +821 | +583 | Shift +LU |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 21 | ***Microtus montanus*** |  |  |  |  |  |  |  | elev + elev2 + region + elev\*region + elev2\*region | 0.6766 | Transition-Hudsonian (H) |
|  |  | Lassen | 0.77 | 0.92 | 1335-1784 | +133 | +66‡ | Shift +L |
|  |  | Yosemite | 0.65 | 0.90 | 1211-3161 | No Change | No Change | No Change |
|  |  | Sequoia | 0.95 | 0.89 | 1984-3384 | No Change | No Change | No Change |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 22 | ***Microtus longicaudus*** |  |  |  |  |  |  |  | elev + elev2 | 0.2043 | Transition-Hudsonian (H) |
|  |  | Lassen | 0.95 | 0.84 | 1672-2462 | -204 | No Change | Expansion |
|  |  | Yosemite | 0.94 | 0.81 | 583-3281 | +644 | No Change | Contract +L |
|  |  | Sequoia | 0.99 | 0.88 | 1529-3474 | +638 | No Change | Contract +L |
|  |  |  |  |  |  |  |  |  |  |  |  |
| \*23 | ***Thomomys monticola*** |  |  |  |  |  |  |  | \*Not subject to occupancy analyses | | Canadian–Hudsonian (H) |
|  |  | Lassen |  |  | 1561-2514 | No Change | No Change | No Change |
|  |  | Yosemite |  |  | 1905-3155 | No Change | No Change | No Change |
|  |  | Sequoia |  |  | NA | NA | NA | NA |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 24 | ***Neotoma cinerea*** |  |  |  |  |  |  |  | era + elev + elev2 + region + era\*elev + era\*elev2 + era\*region + elev\*region + elev2\*region + era\*elev\*region + era\*elev2\*region | 0.1123 | Canadian–Arctic-Alpine (H) |
|  |  | Lassen | 0.66 | 0.67 | 1478-2514 | +202 | -729 | Contract +L-U |
|  |  | Yosemite | 0.79 | 0.51 | 1803-3281 | +580 | -807 | Contract +L-U |
|  |  | Sequoia | 0.67 | 0.87 | 1529-3384 | No Change | No Change | No Change |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 25 | ***Tamias speciosus*** |  |  |  |  |  |  |  | era + elev + elev2 + era\*elev + era\*elev2 | 0.4140 | Canadian–Hudsonian (H) |
|  |  | Lassen | 0.78 | 0.98 | 1561-2514 | +222 | No Change | Contract +L |
|  |  | Yosemite | 0.76 | 0.82 | 1768-3281 | +113‡ | No Change | No Change |
|  |  | Sequoia | 0.96 | 0.97 | 1529-3384 | +638 | No Change | Contract +L |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 26 | ***Tamias amoenus*** |  |  |  |  |  |  |  | elev + elev2 + region | 0.0765 | Transition–Hudsonian (H) |
|  |  | Lassen | 0.79 | 0.96 | 1561-2514 | No Change | No Change | No Change |
|  |  | Yosemite | 0.96 | 0.96 | 2438-2865 | +36‡ | -81‡ | No Change |
|  |  | Sequoia | NA | NA | NA | NA | NA | NA |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 27 | ***Sorex palustris*** |  |  |  |  |  |  |  | era + elev + region + era\*elev + era\*region + elev\*region + era\*elev\*region | 0.2046 | Canadian–Hudsonian (H) |
|  |  | Lassen | 0.53 | 0.24 | 1583-2514 | -975 | -1906 | Contract -L,-U |
|  |  | Yosemite | 0.46 | 0.15 | 1647-3161 | +506 | No Change | Contract +L |
|  |  | Sequoia | 0.77 | 0.40 | 2314-3384 | +676 | No Change | Contract +L |
|  |  |  |  |  |  |  |  |  |  |  |  |
| \*28 | ***Marmota flaviventris*** |  |  |  |  |  |  |  | \*Not subject to occupancy analyses | | Canadian–Arctic-Alpine (H) |
|  |  | Lassen |  |  | 1561-1971 | No Change | +520 | Expand +U |
|  |  | Yosemite |  |  | 2469-3353 | No Change | No Change | No Change |
|  |  | Sequoia |  |  | 2268-3503 | No Change | No Change | No Change |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 29 | ***Urocitellus beldingi*** |  |  |  |  |  |  |  | elev + elev2 + region + elev\*region + elev2\*region | 0.1967 | Canadian–Arctic-Alpine (H) |
|  |  | Lassen | 0.71 | 0.88 | 1485-1845 | No Change | -217 | Contract -U |
|  |  | Yosemite | 0.74 | 0.66 | 2286-3281 | +399 | No Change | Contract +L |
|  |  | Sequoia | 0.86 | 0.92 | 2761-3474 | +555 | No Change | Contract +L |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 30 | ***Callospermophilus lateralis*** |  |  |  |  |  |  |  | era + elev + elev2 + region | 0.1752 | Transition-Hudsonian (H) |
|  |  | Lassen | 0.60 | 0.89 | 1561-3124 | No Change | No Change | No Change |
|  |  | Yosemite | 0.61 | 0.69 | 1646-3200 | +305 | No Change | Contract +L |
|  |  | Sequoia | 0.83 | 0.91 | 2147-3474 | +115‡ | No Change | Contract +L |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 31 | ***Sorex monticolus*** |  |  |  |  |  |  |  | era + elev + elev2 + region | 0.1349 | Canadian–Hudsonian (H) |
|  |  | Lassen | 0.59 | 0.67 | NA | NA | NA | NA |
|  |  | Yosemite | 0.74 | 0.68 | 2176-3281 | -971 | No Change | Expand -L |
|  |  | Sequoia | 0.84 | 0.80 | 1529-3474 | No Change | No Change | No Change |
|  |  |  |  |  |  |  |  |  |  |  |  |
| \*32 | ***Ochotona princeps*** |  |  |  |  |  |  |  | \*Not subject to occupancy analyses | | Canadian–Arctic-Alpine (H) |
|  |  | Lassen |  |  | 1478-2514 | No Change | No Change | No Change |
|  |  | Yosemite |  |  | 2377-3871 | No Change | No Change | No Change |
|  |  | Sequoia |  |  | 2732-3384 | No Change | No Change | No Change |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 33 | ***Tamias alpinus*** |  |  |  |  |  |  |  | era + elev + region | 0.0603 | Hudsonian–Arctic-Alpine (H) |
|  |  | Lassen | NA | NA | NA | NA | NA | NA |
|  |  | Yosemite | 0.86 | 0.81 | 2386-3353 | +497 | No Change | Contract +L |
|  |  | Sequoia | 0.92 | 0.86 | 2314-3503 | +471 | No Change | Contract +L |
|  |  |  |  |  |  |  |  |  |  |  |  |

§Detectability (*p*) for the historical (H) and modern (M) era is the average detectability of a given species over all sites within that region.

†The best performing occupancy model is given with the corresponding AICc weight.

¶Historical life zone was used to determine whether a species was classified as a low elevation species (L), high elevation species (H) or widespread species (W) following Moritz et al. (2008).

Species not subject to occupancy modeling are designated with an asterisk (\*) and those with a statistically significant, but biologically trivial limit shift (i.e., <10% of the species’ historical elevation range and <100 meters in elevation; see Methods) are represented by a double dagger (‡).

# Figure Legends

Figure 1. (A) Map of historical survey localities in relation to survey region and life zone. (B) Change in minimum temperature (red) and mean annual precipitation (blue) between the historical (base of arrow) and modern (tip of arrow) eras across elevation. (C) Average expectation of elevation shift in the modern era to achieve the same value of minimum temperature (red squares) or mean annual precipitation (blue triangles) as historical localities across elevation, based on our climatic nearest neighbor analysis (see Methods).

Figure 2. Elevation range limit shifts by region of the 34 modeled species, arranged by increasing average elevation range. Species were classified as low elevation (01 – 12), high elevation (15 – 33), or widespread species (13 and 14) based on their range limits in relation to life zone (see Moritz et al. 2008). For each species, statistically significant elevation range contractions (red) and expansions (yellow) between the historical and modern eras are shown, along with non-significant contractions (gray) and expansions (white). Black represents elevations occupied in both eras. *Neotoma fuscipes* (06), found only in Lassen, and *N. macrotis*, found only in Yosemite and Sequoia, are analyzed separately in the occupancy analysis, but are displayed together for convenience.

Figure 3. Summary of range shifts of high and low elevation species combined across all regions. Pie charts display proportion of range limits that exhibited significant expansions (yellow), contractions (red), or no significant change (grey). An asterisk next to a pie indicates that significantly more contractions were observed than expansions. Around each pie the width of arrows indicates the proportion of shifts that were in each direction and at each range limit. The colors of arrows indicate whether the shift resulted in an expansion (yellow) or contraction (red).

Figure 4. Percent of observed significant shifts of elevation limits for all species, low and high elevation species that are consistent (black bar) or inconsistent (grey bar) with the predictions from an overall warming model (i.e., all up) and with nearest neighbor analyses for each of the four BIOCLIM variables. Symbols above bars denote predictions that were significantly better than random (\* = *p* < 0.05, † = *p* 0.10).

# Supplemental Figure Legends

Figure S1. Violin plot of BIOCLIM variables (A) B1 (mean annual temperature), (B) B5 (maximum temperature of the warmest month), (C) B6 (minimum temperature of the coldest month), and (D) B12 (mean annual precipitation) for each region in the historical and modern eras. Each plot represents all cells within 20-kilometer buffer around the minimum convex polygon that encompassed all survey sites. Median and the upper and lower quartiles are represented by the white circle and black bar, respectively.

Figure S2. Distribution by elevation and region of all 68 species of small mammal detected within the study regions over both eras. Green diamonds and crosses represent species presences recorded through quantitative (e.g., Sherman live trap) or non-quantitative (e.g., Shotgun) trapping effort, respectively. Blue crosses represent species presences recorded through observation alone. For species subject to detectability analysis, the size of the open circle represents site-specific detectability. Grey circles represent elevation of surveyed sites for those species not subject to detectability analysis.

Figure S3. Occupancy curves in the historical and modern eras by region for the 28 occupancy-modeled small mammal species. Curves represent the probability of occupancy in the historical (dark blue) and modern (green) eras across elevations with the elevation of sites surveyed in each era given by triangles (historical) and circles (modern).