Geographically replicated elevation shifts in small mammals of California reveal heterogeneous impact of 20th century warming on montane species.

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**Abstract**:

Resurveys of historical collecting localities, when combined with statistical assessment of detectability, provide strong evidence for range dynamics in response to recent climate change. Such studies across single elevational or latitudinal transects have revealed range shifts, primarily expansion at leading edges, and meta-analyses attribute overall patterns to global warming. However, there have been few detailed community-scale analyses in which multiple transects have been resurveyed to control for local effects such as land-use and seral dynamics. Here we expand on resurveys of elevational ranges of small mammals along a single regional transect of montane California (Yosemite) by additional regional surveys to the north (Lassen) and the south (Sequoia), repeating surveys originally conducted in the early 20th century. High elevation species showed a coherent pattern of upward shifts in their lower range limits whereas low elevation species showed heterogeneous responses at the upper limits. While the elevational ranges of some species remained stable across regions, only a few species shifted their elevational range consistently across regions. Observed change in minimum temperature was a more reliable predictor of the direction of species’ shifts than precipitation change or other temperature change variables. Additional factors may play a role in differences between high and low elevation species and in species’ response across regions, perhaps due to changes in seral dynamics or interacting effects of local changes in temperature and precipitation. We identify a suite of high elevation taxa with consistent upwards range contractions and which warrant more detailed analyses of proximate causes of vulnerability. These results demonstrate the value of multi-region resurveys and illustrate the complexity of species responses to recent climate change.

**Introduction**

The evidence for the biotic response 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). Despite a general trend towards upwards shifts of elevational (and latitudinal) boundaries (e.g. Thomas and Lennon 1999, Lenoir et al, 2008; Chen et al. 2011), considerable heterogeneity of species’ responses has occurred with many species exhibiting no shifts (Parmesan et al, 1999, Moritz et al, 2008, Tingley et al, 2009, 2012). Species respond to local trends in climate and habitat change, not global averages, and few studies are able to account for the substantial spatial heterogeneity in climate change across the landscape (Walther, 2002, Tingley et al. 2012).Furthermore, “leading edge” expansions are detected more often than “lagging edge” contractions (Thomas et al. 2004, Angert et al. 2011, Hill et al. 2011, Morelli et al., 2012). While biological factors likely contribute to both observations, there is also potential for sampling and analytical effects, particularly for lagging edges, where local extinction cannot be demonstrated unless detectability (or probability of “false absence”) is incorporated into the analysis (Tingley & Beissinger, 2009). Spatially-explicit resurveys across multiple regional areas, together with statistical power to detect both range contractions and expansions, can be expected to generate more insight into the dynamics of species’ responses to recent climate change.

Joseph Grinnell’s historic studies of the elevational distributions of vertebrates of California (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 that century, both anthropogenic landscape alteration (Myers et al. 2000) and climate change (IPCC 2007) have contributed to a global extinction crisis (Thomas et al. 2004); models of future climate-change and land use scenarios predict increased extinction risks, large range shifts, restructured communities, and the disappearance of unique biomes (Ackerly et al. 2010, Wiens et al. 2011, Stralberg et al. 2009).

During the past century, mean annual temperature in California has increased by ~0.6 C (Bonfils et al. 2008). However, this average change masks a large degree of spatial heterogeneity (Fig. 1B). Precipitation changes are also 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 range shifts of birds and mammals in California over this period have been equally heterogeneous, including upslope shifts, downslope shifts and no change (Moritz, et al, 2008; Hargrove and Rotenberry, 2011; Tingley et al, 2012). Some of the heterogeneity in the upslope and downslope movements of species has been explained by incorporating spatially specific measures of climatic similarity, considering both temperature and precipitation, between historical and contemporary localities (Tingley et al, 2012).

The initial resurvey of small mammals across Yosemite revealed a strong pattern of upward shifts of species’ ranges, especially high elevation species, consistent with rising temperature including the alpine chipmunk (*Tamials alpinus*), Belding’s ground squirrel (*Urocitellus beldingi*), and water shrew (*Sorex palustris*) (Moritz et al. 2008), as well as range collapse in the bushy-tailed woodrat (*Neotoma cinerea*) and shadow chipmunk (*Tamias senex*). The responses of low elevation species were more heterogeneous and differed among even closely related taxa, resulting in substantial changes in local assemblages.

Here we characterize regional variation in elevational range responses of small mammals of montane California by expanding our analysis from a single region in the central Sierra (Yosemite; Moritz et al. 2008), with two other transects to the north (Lassen) and south (Sequoia). We control for variation in detectability among species and survey eras to compare elevational limits from the early 20th C (1911-1934) to the present (2003-2010). With data from multiple, geographically-separated regions of montane California we evaluated the following hypotheses emerging from patterns we observed in the Yosemite region: (1) upslope range shifts are the most common change across all regions, (2) range contractions are more common in high elevation species whereas expansions are more common in low elevation species (3) elevation range shifts of species, particularly those with large movements in Yosemite, show consistency across regions, and (4) predictions of upslope and downslope shifts are improved by identifying whether modern sites that are climatically similar to historical sites are on average upslope or downslope.

**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 historical mammal surveys (Grinnell et al, 1930; Grinnell and Storer, 1924; Sumner and Dixon, 1953). These included surveys 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 National Park (“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 20th century, differed among the three regions (Fig. 1B). Yosemite and Lassen experienced the greatest and least increase in mean annual temperature, respectively, 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 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 SRTMv4 with a resolution of 1 arcsec 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 sciurids 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 2500 pages of field notebooks held at the MVZ (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://mvz.berkeley.edu).

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.

*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 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 S3; 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.

*Elevation Range Models*

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 (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** **S2**. 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 S2**. 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 delta AIC less than two 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 (Tingley et al. 2012), an assumption of the occupancy method (MacKenzie et al. 2006).

*Mixed-model testing of range shifts*

We used generalized linear mixed models (GLMM) to examine how patterns of range shifts were related to regional variation and species’ traits defined below. 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 whether a range shift occurred or not (as a binary variable). Widespread species (*n* = 2) 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.

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

*Climatic nearest neighbor*

We examined spatial heterogeneity in climate change 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 all 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 a naïve “overall warming model” that assumes an increased temperature at all grid cells over the same time period. The overall warming model therefore always predicts upslope movements of species.

We used GLMMs to compare the ability of each of the Bioclim variables (B1, B5, B6 and B12) to predict the direction of significant range shifts. We analyzed 32 models comprised of a null model (intercept only), and all additive combinations of our 6 variables, except no more than one temperature variable was included in each model. Because an overall warming model always predicts upslope movement, it could not be compared in a GLMM context. Therefore, we used a one-sided binomial to test if the predictions from the overall warming model (i.e. upslope) and each of the Bioclim variables were consistent with the direction of observed shifts (Hypothesis 5).

**Results**

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 detected in the historical era only and one species, *Sorex tenellus,* was detected in the modern era only.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 (Patton pers. obs.).From the 57 species detected, we analyzed range limit shifts for 34 species detected in both the historical and modern eras.

Across the three regions, we detected 52 significant range limit shifts representing 31.3% of the 166 region-specific historical range limits in our study (Fig. 2). Thus, the majority of species’ elevational ranges remained stable at one limit at least. Of the thirty-four species analyzed in this study, we observed no significant range limit shifts in nine species. These included the 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 twenty-five species shifted at least one range limit in one region (Table 1, Fig. 2).

Overall, both upper and lower range limit shifts differed in frequency and directionality between low and high elevation species. Our overall GLMM analysis revealed the Zone\*Limit interaction model was very strongly supported (AIC wt =1), with the variable Region having little effect on the probability of a range shift (Table 1). In separate analyses for high and low elevation species, the Limit-only model received the greatest support when looking at the probability of any shift, again with poor support for an effect of Region, whereas the probability of an upslope or a downslope shift received the strongest support from a Region and Limit model for high elevation species, but none of the variables were more predictive than a null model for low elevation species (Table 1)

*General patterns of range shifts (Hypotheses 1 & 2)*

Consistent with patterns observed in Yosemite, species limits were more 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 (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).

*Regional variation in range shifts (Hypothesis 3)*

Despite our prediction that species with strong elevation range shifts in Yosemite would show consistent trends across other regions, we found limited consistency of patterns in range shifts among regions for high or low elevation species. Not one of the 22 species found in all regions shifted both upper and lower limits in the same direction in all regions (Fig. 2). However, when examining range limit shifts of high and low elevation species across regions, there was an overwhelming pattern of significantly more upslope than downslope shifts of the lower limit of high elevation species (*n =* 21, *p* < 0.001; Fig. 3), 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 climate neighbor analysis (Hypothesis 4)*

Our nearest climatic neighbor analyses revealed that both upslope and downslope shifts were predicted by observed climate change at the historical range limits of species (Fig. 1C). Consistent with our hypothesis, we found that nearest minimum temperature was the best predictor and explained 73% of the 52 significant range limit shifts observed in this study. However, this was only a slight improvement over an overall warming model that explained 69% of shifts. Predictions from an overall warming model, minimum temperature, and mean annual temperature were each more consistent than random, but maximum temperature and mean annual precipitation were not (*n*= 52, warming (69.2%), *p*=0.004; mean annual temperature (63.5%): *p*=0.035; maximum temperature (53.8%): *p*=0.339; minimum temperature (73.1%), *p*=0.001; mean annual precipitation (53.8%), *p*=0.339). Similar patterns were observed for low and high elevation species (Fig. 4) except that for low elevation species, only minimum temperature was more consistent than random. GLMM analyses of nearest neighbor predictions supported the superior performance of minimum temperature in predicting the direction of range shifts (Table 3). The best model was the additive Limit and minimum temperature model, 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 California suggested strong but differential impacts of recent climate change on the range limits of small mammal species. Responses differed between high and low elevation species, with consistent upslope range contractions in high elevation species and heterogeneity in the directionality of range limit shifts for low elevation species. These findings confirmed and extended the results from our initial study of small mammals from the Yosemite region (Moritz et al 2008) and were consistent with similar studies in the same region over the same time scale in birds (Tingley et al 2012), butterflies (Forister et al 2010), and plants (Crimmins et al 2011).

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 anywhere, and patterns within species varied across regions. Tingley et al. (2012) found a similar result in California birds where only 51% of observed range limit shifts over the last 100 years were upslope. Heterogeneous range shifts have been demonstrated in a range of taxa (Chen et al. 2011), indicating 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 large-scale land conversion, although impacts such as grazing policy, fire regimes and forestry extraction may have significant effects outside the scope of this study (REFS, Myers et al. 2000). Low elevation species were most 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 their lower limits and shifts were significantly more common at their upper limits. The more heterogeneous responses of low elevation species perhaps reflected stronger biotic influences (Brown et al. 1996, Rapacciuolo et al. In Review), such as species competition (Rubidge et al. 2011), habitat conversion and seral dynamics (Rowe et al. 2009), and the spread of invasive species (Rowe et al. 2011). A detailed analysis of vegetation change coupled with the mammal data from the Yosemite region (Moritz et al, 2008) found that low elevation species were more likely than high elevation species to track habitat and expand their ranges (Santos et al In Prep). Santos et al. XXX)Consistent with their study, we observed far more contractions than expansions in high elevation species and as many expansions as contractions in low elevation species.

Our results also suggested that localized climate predictions, in this case minimum temperature, may help 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 whereas minimum temperature performed as well or better than an overall warming model of upslope movement, suggesting that some downslope movements may actually track local changes in temperature.

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 elevation shifts (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 as over half 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).

Our analyses identified higher elevation taxa that warrant more detailed study including identifying proximate causes of vulnerability. The alpine chipmunk (*T. alpinus*, endemic to the Sierra Nevada) showed a consistent and substantial retraction of its lower limits across both regions within its range. For Yosemite this correlated with an increase in minimum temperature, independent of changes in its congeners (Rubidge et al. 2010) and was associated with decreased overall genetic diversity associated with the population extinctions rather than a contraction of the species’ distribution and increased isolation among now fragmented populations (Rubidge et al., 2012). Belding’s ground squirrel (*U. beldingi*) also showed a consistent pattern of elevation retraction across all three regions. A more extensive analysis of the species across the Sierra Nevada found a similar pattern of local extinction over the 20th century, especially at lower (warmer) elevations (Morrelli et al, 2012). Our results suggested that other high elevation species including the Pacific jumping mouse (*Zapus princeps*), long-tailed vole (*Microtus longicaudus*) and water shrew (*Sorex palustris*) warrant more detailed study, especially of proximate mechanisms underlying range contractions.

Several other high elevation taxa showed more 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). Pika (*Ochotona princeps*), which attracted considerable attention because of extirpations and upslope retractions in the Great Basin (Beever et al, 2003, 2011), were stable across all three regions in this study. This 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).

This study joins the substantial evidence for range shifts of species in response to 20th Century climate change (Parmesan and Yohe 2003, Chen et al. 2011). We showed coherent patterns shifts of elevational range limits even though responses within species were not consistent across regions. The challenge ahead is to understand what underpins the heterogeneity of species’ responses in order to improve predictions of vulnerability. Studies addressing whether species track climatic niches and respond to local variation in climate change (e.g., Tingley et al 2009, 2012) or whether they respond to other local effects such as fire regimes or seral dynamics, as well as those focused on identifying the life-history traits, such as dispersal ability, reproductive rate, and ecological generalization, that best predict persistence or vulnerability (Angert et al. 2011, Schloss et al. 2012) will provide key insight into the mechanisms of species- and region-specific responses to climate change.

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# Tables

# Supplemental Tables

Table S1. List of small mammal species examined in this study. 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. Species were detected on the east (E) and/or west (W) slopes within each region. Detections within each region are listed as detected (0) or not detected (1) in the historical (H) or the modern (M) eras. Asterisks (\*) denote new species records detected during our surveys. 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.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  | 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** |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

# Figure Legends

Figure 1. (A) Map of historical survey localities in relation to region and life zone. (B) Change in (mean annual or 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 (mean annual or 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 species included in this study, 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* and *N. macrotis* (06) found only in XXXX and XXXX, respectively 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 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 indicate that predictions were significantly better than random.

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 regions?) with median (white circle) and upper and lower quartiles (black bar).

Figure S2. Distribution by elevation and region of all 68 species of small mammal examined in this study. Green diamonds and crosses represent species presences recorded through quantifiable (e.g., Sherman live trap) or non-quantifiable (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.