Geographically replicated elevation shifts in small mammals of California reveal extent of 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 [eg. land-use, seral dynamics etc.]. 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. While the dominant signature is upwards shifts of range limits leading to range contractions, particularly in high elevation species, patterns across species and regions were heterogeneous. Observed change in minimum temperature was a more reliable predictor of the direction of species’ shifts than other climate variables or an overall model of warming. Among high elevation species, nocturnal, short-lived and large litter size species were more likely to shift their elevation range limits, whereas patterns of shifts in low elevation species were unrelated to life history traits. Additional factors may play a role in the heterogeneous responses across regions, perhaps due to region-specific changes in seral dynamics or interacting effects of local changes in temperature and precipitation. 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, 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, Hill, Morelli et al., 2012 etc.). 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 (REF) and climate change (IPCC 2007) have contributed to a global extinction crisis; 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, 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 between historical and contemporary localities (Tingley et al, 2012).

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 replicates 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). The initial resurvey 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. For example, the pocket mouse (*Chaetodipus californicus*) expanded its range whereas the kangaroo rat (*Dipodomys heermanni*) contracted. 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, (4) differences in species responses show correlative relationships to life history and ecological traits, and (5) 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 (Figure 1): 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 (Figure 1). Yosemite experienced the greatest increase in mean annual temperature with an average increase of XX oC, whereas Sequoia experienced an average increase of XX oC and Lassen experienced almost no change in annual mean temperature, XX oC. Annual mean precipitation increased most in Lassen (+XX mm), less in Yosemite ( +XX mm), and almost not at all in Sequoia (+XX mm). Maximum temperature of the warmest month has remained fairly constant across all three regions (Lassen XX, Yosemite XX, Sequoia XX) whereas minimum temperature of the coldest month has increased in all three regions (Lassen XX, Yosemite XX, Sequoia XX).

*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. 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). 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 because their historical life zone ranges extended from Lower Sonoran to Canadian and above.

*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 (Figure 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. Finally, we analyzed whether the direction (upslope or downslope) of elevation limit shifts of high and low elevation species could be explained by Limit and Zone. Here we examined only significant shifts determined from the *Pfa* analysis above. We used one-sided binomial tests to determine 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). We then compared these results across all three regions to evaluate whether the patterns of range shifts of species from Yosemite were consistent in the other regions (Hypothesis 3).

We also used GLMMs to examine whether species’ traits explained range shifts. We tested eight species’ traits: (1) annual rhythm (obligate hibernator, facultative hibernator, non-hibernator), (2) daily rhythm (diurnal, nocturnal, active anytime), (3) mean litter size, (4) mean litters per year, (5) mean young per year, (6) mean adult mass, (7) mean longevity, and (8) diet (omnivore, herbivore, granivore, insectivore). We also included Limit and Region in these analyses to determine whether species’ traits explained more variation in shifts than models that included Limit and Region (Hypothesis 4). To resolve interactions between Limit and Zone, we analyzed low elevation and high elevation species separately. Each variable was analyzed singly and then in additive models by adding each of the remaining variables to the best model from the previous step. We repeated this procedure in a forward manner until additional variables no longer improved (i.e., lowered) AIC.

*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 on each transect (i.e. upslope or downslope).

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, Figure 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. 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). Twenty-five of the thirty-four species analyzed shifted at least one range limit in one region (Table 1, Figure 2). The nine species with no significant range limit shifts included both 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*).

Region had less of an impact on species range shifts than zone (high or low elevation species) or limit (upper or lower elevation limit). Our overall GLMM analysis revealed the Zone\*Limit interaction model was very strongly supported (AIC wt =1), indicating that the probability of shift differed for each range limit and for high versus low elevation species. Region had little effect on the probability of a range shift, as models containing Region received less support than a Null model (Table 1). The Limit-only model received the greatest support in separate analyses for high and low elevation species. Here, again, Region was poorly supported (Table ?).

*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). In addition, high elevation species were significantly more likely to contract their ranges (79% contract, n = ?, p = ?). However, contrary to our expectation, low elevation species expanded their limits as often as they contracted them (50% contract; one-sided binomial tests, high *n*=29, *p*=0.001; low: *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 heterogeneous patterns in range shifts among regions. Not one of the 22 species found in all regions shifted both upper and lower limits in the same direction in all regions. However, six out of eight high elevation species that exhibited significant upslope shifts at their lowerrange limits in Yosemite also showed these patterns in Lassen and/or Sequoia (Figure 2; *Zapus princeps, Microtus longicaudus, Neotoma cinerea, Sorex palustris, Urocitellus beldingi,* and *Tamias alpinus*). One additional species, *Tamias speciosus,* showed a significant contraction at its lower range limit in Lassen and Sequoia but not in Yosemite. Overall seven out of ten high elevation species with a significant shift at their lower limit showed a similar pattern in at least two regions suggesting limited consistency in individual species’ responses across regions.

The patterns for low elevation species were similar. Three out of five low elevation species that exhibited significant shifts at their upper limits in Yosemite showed similar patterns in Lassen and/or Sequoia (*Chaetodipus californicus, Peromyscus truei,* and *Sciurus griseus*). Two species *Reithrodontomys megalotis* and *Neotoma fuscipes/macrotis* showed significant shifts at their upper range limits in Lassen and Sequoia but not in Yosemite. Overall, only five out of eight low elevation species with a significant shift at their upper limit showed a similar pattern in at least two regions.

*Life history traits (Hypothesis 4)*

Our analysis of species life history traits in conjunction with range shifts revealed that the limit of the species’ range (lower or upper) was a stronger predictor of range shifts than any of the eight life history variables we included (Table 2). Region provided little additional information and was not included in any of the top models. For high elevation species significant shifts were more likely to be detected in nocturnal species, species with larger litter sizes and species with shorter lifespans (Table 2). Limit was the most informative single variable followed distantly by Daily Rhythm; these two models were the only univariate models that were more informative than the Null model. For low elevation species, Limit was the best model with little additional information provided by species’ traits. In both high and low elevation species, models containing species’ traits were more informative than models containing Region.

*Nearest climate neighbor analysis (Hypothesis 5)*

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. 1x). 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, whereas an overall warming model 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 (binomial tests, *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 (Figure 3) 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 4). 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 multiple regional elevation transects across California confirm and extend the results from our initial study of small mammals from the Yosemite region (Moritz et al 2008). Even with our conservative statistical approach (Tingley et al. 2012), we found strong evidence for significant and consistent 20th century elevation shifts in small mammals. While other recent studies of birds (Tingley et 2012), invertebrates (Forister et al 2010), and plants (Crimmins et al 2011) in the region found substantial elevation shifts over similar time periods, our data provide the clearest pattern of upslope movements, with range contraction at the lagging edge of high elevation species the most common outcome. These patterns were most pronounced in Yosemite and Sequoia with strong upward contractions of high elevation species. These two regions also experienced greater warming relative to Lassen. The overall patterns from this multi-region and community-wide analysis demonstrate a widespread effect acting across species and regions.

Despite the predominant patterns in our study, nearly one-third of shifts were downslope, one-fourth of species did not shift, and patterns within species often varied across regions. These patterns indicate 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). Low elevation species were likely to experience impacts from habitat conversion at their lower limits (Bravo et al, 2008; Forister, et al, 2010); however, shifts of low elevation species were much more common at their upper limits. The more heterogeneous responses of low elevation species perhaps reflect stronger biotic influences (Brown et al, 1996). A detailed analysis of vegetation change coupled with the mammal data from the Yosemite transect (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). 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 nearest neighbor analyses of site-specific expectations for the direction of elevation shifts suggested that local climate change also explains some of the variation in species’ responses. Across the same regions, nearest neighbor analyses of bird species found strong support for range-limit shifts, often downwards, associated with changes in precipitation (Tingley et al., 2009, 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 model of upslope movement, suggesting that some downslope movements may actually track changes in minimum temperature. Mean annual temperature and maximum temperature were less informative, with maximum temperature being no better than random. Increased minimum temperature was the most consistent change in climate across all three transects. Consistent with the evidence for the importance of minimum temperature, our analysis of life history variables found a higher sensitivity of nocturnal species to elevation 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 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).

Our analyses identify higher elevation taxa that warrant more detailed study including eco-physiological analyses to identify 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 and increasing 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 an overwhelming pattern of local extinction over the 20th century, especially at lower (warmer) elevations (Morrelli et al, 2012). Our results suggest 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. Pika (*Ochotona princeps*), which have 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 et al. 2010).

This study joins the substantial evidence for range shifts of species in response to 20th Century climate change (Parmesan et al. 2003, Chen et al. 2011). We show that consistent patterns can emerge even when responses within species are not consistent across regions. The challenge ahead is to understand what underpins the heterogeneity of species’ responses in order to improve predictions of vulnerability. Are species tracking climatic niches and responding to local variation in climate change (Tingley et al 2009, 2012) or are species responding to other local effects such as fire regimes or seral dynamics?