# Title (73, 87 char, limit 90):

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

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# Abstract (WC 147, limit 150):

Resurveys of historical collecting localities across single transects have revealed range shifts, primarily leading edge expansions, which are attributed to overall global warming. However, there have been few spatially replicated community-scale resurveys to tests whether species’ responses are consistent. Here we repeated early 20th century surveys of small mammals along three well separated elevational transects in montane California. Most species’ ranges shifted in at least one region. However, two-thirds of ranges remained stable at one or both elevational limits and few species shifted their elevation limits in the same direction in all regions. When shifts occurred, high elevation species’ lower limits typically contracted upward, whereas low elevation species had heterogeneous responses. Local change in temperature was a better predictor of shift directionality than precipitation. These results emphasise the heterogeneity of species’ responses to recent climate change, but also identify consistent contractions in some high elevation mammals.

# Main Text (WC 1884, limit 3000):

Evidence for the biotic responses to climate change over the last century has continued to accumulate1-5 and is central to the prediction of vulnerability to future change6 (Moritz & Agudo 2013). There is a general trend toward upwards and poleward shifts of elevational and latitudinal boundaries of ranges5,7,8, with “leading edge” expansions detected more often than “lagging edge” contractions9-12. However, there is considerable heterogeneity in the direction and magnitude of species’ responses and ranges of many species have not changed at all13-15. Species respond to local change in climate and habitat rather than global averages, and few studies have accounted for substantial spatial heterogeneity in climate change across the landscape1,15,16. Moreover, there is potential for considerable sampling error because local colonization and extinction cannot be demonstrated convincingly unless detectability (i.e., the probability of “false absence”) is explicitly incorporated into models of state change17. Insights into the dynamics of species’ responses to recent climate change are most likely to come from spatially-replicated resurveys combined with analytical methods that have statistical power to detect both range contractions and expansions.

An unusually detailed historic dataset, combined with contemporary resurveys, allows us to evaluate robustly a century of range responses of birds and mammals to climate change in montane California. Joseph Grinnell’s studies of the elevational distributions of vertebrates of California in the early 1900’s18-20 laid the foundation for the concept of the ecological niche and for understanding the climatic limits of species’ distributions21. Grinnell’s pioneering studies also provided a benchmark for documenting changes in the elevational ranges of species over the last century14,22. Over the past century, mean annual temperature in California has increased by ~0.6 C23. However, the average change masks a large degree of spatial heterogeneity, with regions of local cooling and warming (Fig. 1b) 24,25. Precipitation changes were also spatially heterogeneous, with spatial covariation increasing across the northern part of the state and decreasing across the southern part26,27. Elevational ranges of species in California over this period have shifted heterogeneously, including species moving upslope, downslope or not at all14,15,28. Heterogeneity in movements of species has been partly explained by incorporating local-scale measures of climatic change for both temperature and precipitation15,29; depending on location, increases in the former favour upslope shifts, while increases in the latter favour downslope movements. Local changes in habitat structure due to fire dynamics and grazing pressure are also factors in some areas30,31.

Here we characterized spatial variation in elevational range responses of small mammals in protected areas of montane California by expanding our analysis centred on a single region in central California (Yosemite National Park) 14 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 the present (2003-2010). With data from multiple, geographically-separated regions of montane California that have experienced limited land-use change, we tested four predictions of the influence of climate warming on elevational ranges that emerged from patterns observed in the Yosemite region13 and in birds across montane California15. 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 change 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, respectively15.

*Mammalian Elevational Range Shifts over the Past Century*

Our results suggested strong but locally heterogeneous impacts of recent climate change on the range limits of small mammals.Of the 67 small mammal species we detected in both the historical and modern surveys (Supplementary Table S2, Supplementary Figure S2), we were able to evaluate using robust statistical methods the range shifts of 34 species. 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 analysed (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 (Fig. 2, Supplementary Table S2).

Species’ elevational limits were more than twice as likely to move upslope (69.2%) as downslope (31.8%; one-sided binomial test, *n* = 52, *p* = 0.004; Fig. 3, Supplementary Table S3). Shifts of the upper and lower range limit differed in frequency and directionality between low and high elevation species. High elevation species were significantly more likely to contract their ranges than to expand them (79% contract, *n* = 29, *p* = 0.001), whereas, contrary to our expectation, low elevation species contracted their limits as often as they expanded 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).

Our study highlights that while a coherent pattern of upslope movement was found overall, there was substantial heterogeneity in the response of species, particularly in low elevation species. Heterogeneous range shifts have been demonstrated in a range of taxa5,31, suggesting that species’ responses were influenced by local factors and were context dependent. Tingley et al.14 found even greater heterogeneity in Californian birds sampled across the same transects, wherein only 51% of observed range limit shifts over the last century were upslope.

The vast majority of sites in our study, especially at middle to high elevations, were located in protected reserves or public land with minimal land-use change, although grazing policy, fire regimes and forestry practices may have altered habitat structure32. One might expect low elevation species should have been more likely to experience impacts from land use change at their lower limits in the Central Valley and foothills33,34. However, we detected few contractions at lower limits of low elevation mammals, and shifts were significantly more common at their upper limits where potential land-use impacts are less evident. Greater heterogeneity in responses of low elevation species may reflect stronger biotic influences35,23, such as interspecific competition36, seral dynamics of habitats30, and the spread of invasive species31. Thus, while our findings confirmed some results from an initial study of small mammals from the Yosemite region14 and studies of birds15, butterflies34, and plants27 over the same spatial and temporal scale, they amplify the complex and variable ways that species can respond to climate change.

To illustrate, 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). These differences may be attributed to region-specific changes in seral dynamics or interacting effects of local changes in temperature and precipitation37. As examples, both the bushy tailed woodrat (*Neotoma cinerea*) and the pinyon mouse (*Peromyscus truei*) showed substantial changes in elevational ranges in Lassen and Yosemite, but not Sequoia and the western gray squirrel (*Sciurus griseus*) contracted strongly in Sequoia, marginally in Yosemite but expanded its range in Lassen. That said, multiple high elevation species showed consistent range reduction – these include Belding’s ground squirrel (*Urocitellus beldingi*), the alpine chipmunk (*Tamias alpinus*) that is endemic to the central-southern montane California, the Pacific jumping mouse (*Zapus princeps*) and the water shrew (*Sorex palutris*). These observations have been confirmed in more extensive analyses of *U. beldingi* and *T. alpinus*12, 36 (, JLP unpublished data). Of note, elevational ranges of the pika (*Ochotona princeps*), which attracted considerable attention because of extirpations and upslope retractions in the Great Basin38,39, were stable across all three regions. This result is consistent with a more extensive study across montane California that found pika thriving across wider geographic and elevation ranges than reported historically40.

*Range Shifts in Relation to Climate*

In previous resurvey studies of birds and plants across the same regions, local changes in precipitation as well as temperature were found to correlate with observed range changes15, 27 (). For small mammals, however, precipitation was a poor predictor of the direction of shifts. Nearest climatic neighbour analyses revealed that both upslope and downslope shifts were predicted by temperature change at range limits (Fig. 1c). For low elevation species, a simple overall warming model (i.e., all upwards shifts) was the best predictor, but this model, as well as each of the climate based predictions, was not significantly better than random (Fig. 4). For high elevation species, change in minimum annual temperature was the best predictor of the direction of range limit shifts, and explained 74.1% of the 52 significant range limit shifts observed. However, change in minimum temperature was only a slight improvement over an overall warming model (72.4% of shifts), local mean annual temperature change (69.2% of shifts), and local maximum annual temperature (72.0% of shifts) and predictions from all four temperature variables were significantly different from random (*p* < 0.05). Mean annual precipitation (40% of shifts) explained fewer shifts than random, although not significantly less (*p* = 0.2122). These results suggested that, at least for high elevation species, changes in local temperature, can explain variability in the direction of species’ responses, highlighting the dynamic nature of species-specific responses to localized climate change.

Climate projections at the global scale suggest that disappearing climates will be an increasing challenge to predicting species’ responses41,42. Nearest climatic neighbour analyses revealed that localized climates at 21 historical sites (all above 1500 m; 3 sites associated with nearest-neighbour analyses) are disappearing from the landscape (Fig. 1c; see definition in Supplementary Information). Minimum annual temperature showed the most significant effect with values in 15% of historical sites disappearing from the modern landscape. Mean annual temperature (1.5% of historical sites), maximum annual temperature (3.7% of historical sites), and mean annual precipitation (0 historical sites) did not decline as dramatically across the landscape.

Our study rigorously identified range shifts of species across multiple transects, revealed a strong overall influence of local change in temperature consistent with response to 20th century climate change2,5, and identified a suite of high elevation mammals undergoing consistent range retraction. However, consistent with other studies24, we also observed substantial heterogeneity in the patterns of elevational range limit shifts within and across regions. The challenge ahead is to understand the proximate causes of the diverse species’ responses to improve predictions of vulnerability6. We need a better understanding of whether species track climatic niches in response to local variation in climate change29, or whether range changes are a response to fire, seral dynamics, or species interactions. Moreover, identifying the life-history traits (e.g., dispersal ability, reproductive rate, and degree of ecological specialization) that best predict persistence or vulnerability10,43 may provide key insights into the mechanisms of species- and region-specific responses to climate change. The diverse responses among closely related taxa that we find here (e.g., among different species of mice, chipmunks, ground squirrels, and woodrats) provide the basis for the detailed comparative studies that are necessary to improve our knowledge of vulnerability.

**Methods (WC 711, limit 800):**

*Survey Regions and 20th Century Climate Change*

Historical surveys occurred between 1911 and 19341718-20 along elevation transects across three regions of montane California (Fig. 1a, Supplementary Table S1): 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”). Each region differed considerably in physiognomy and climate change history (Fig. 1b, Supplementary Figure S1). See Tingley et al.15 for additional details of the sampling regions.

*Survey and Resurvey Data*

We defined localities as an aggregate of concurrent surveys (i.e., traplines) conducted within a 2 km distance and 100 m elevation14. Each locality was georeferenced and elevation was determined using a Digital Elevation Model and verified by ground-truthing or with topographic maps (Supplementary Table S1).

We obtained records from historical surveys conducted at 111 sites. Trapline details such as nightly captures, number of traps set, habitats, location maps and daily records of specimens observed and shot from more than 2,500 pages of field notebooks held in the MVZ Archives (available online at http://bscit.berkeley.edu/mvz/volumes.html). Modern mammal resurveys were conducted at 166 sites between 2003 and 2010 as part of the Grinnell Resurvey Project14,15(Fig. 1a). Of these, 85 of the 111 historical sites were resurveyed. Additional modern sites were selected to maximize elevation coverage and to serve as proxies for otherwise inaccessible historical sites. This resulted in a total of 29,593 records and 14,832 specimens in our data set. See Supplementary Methods for details.

*Species Set*

We present the elevation distribution for 67 species of rodents, shrews, and pika recorded in the historical and modern surveys (Supplementary Table S2). Analyses of range shifts were restricted to 34 species that were detected at >10% of sites for at least one region in both eras. Of these, we were able to model detectability and occupancy for 28 species because they were detected through repeated nights of trapping at sites and where the number of traps set was reported (hereafter “quantitative trapping”). We include an additional six species in our range shift analyses as we made systematic efforts to detect and record these easily observed species. Elevational profiles of species are presented separately for the east and west slope with the exception of localities found within the Yellow Pine (*Pinus ponderosa*) belt on the east slope, which we included as west slope localities (See Supplemental Methods for details).

Species were categorized as low elevation (historical elevation ranges within Lower Sonoran – Transition life zones), high elevation (Transition – Alpine), or widespread14,18-20 (Supplementary Table S4).

*Modelling Changes in Elevational Ranges*

We modelled simultaneously the probability of detection (*p*) and the probability of occupancy (*Ψ*) of each species (*n* = 28) at each locality, to evaluate statistically elevational range shifts using the single-season occupancy model framework implemented in the program MARK v6.043,44. See Supplemental Methods for details on model parameterizations (Supplementary Table S5).

We estimated temporal shifts in the lower and upper range limits for each species on each of the three regions following Moritz et al.14. Statistical significance for shifts was determined by estimating locality-specific detection probabilities (*p\**) and the probability of false absence (P*fa*17) 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 and “ecologically relevant” if the movement was both >10% of the species’ historical elevation range and >100 meters in elevation15.

*Testing Predictions of Range Shifts*

We used generalized linear mixed models (GLMM) and one-sided binomial tests to examine how patterns of range shifts were related to region (Lassen, Yosemite, Sequoia), species limit (upper or lower) and the elevational distribution of species (high or low elevation species). We excluded widespread species and those not demonstrating significant limit shifts determined from the *Pfa* analysis. See Supplementary Methods for model details.

*Climatic Nearest Neighbour*

For each species’ limit, we evaluated whether upslope or downslope movement between eras was better predicted based on actual climate data (four BIOCLIM variables) or an overall warming model predicting only upslope movement, using climatic nearest neighbour analysis15 and one-sided binomial tests. See Supplementary Methods for details.

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**Author Contributions**

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

**Competing Financial Interests**

The authors declare no competing financial interest.

# Figure Legends

Figure 1. Climate change and expected elevation shifts across sampling sites. (a) Map of historical survey localities in relation to survey region and life zone; (b) Change in mean annual 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 most similar value of mean annual temperature (red squares) or mean annual precipitation (blue triangles) as historical localities across elevation, based on our climatic nearest neighbour analysis (see Methods); open squares and triangles indicate historical sites where similar climate is underrepresented in the modern era (i.e. disappearing).

Figure 2. Elevation range limit shifts by region of the 34 modelled species, arranged by increasing average elevation range. Species were classified as low elevation (01 – 13), high elevation (16 – 34), or widespread species (14 and 15) 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 (grey) and expansions (white

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 colours of arrows indicate whether the shift resulted in an expansion (yellow) or contraction (red).

Figure 4. Significant range limit shifts in relation to climate predictions. Percent of observed shifts for all species, for 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 upwards) and with nearest neighbour analyses for each of the four BIOCLIM variables. Symbols above bars denote predictions that were significantly better than random (\* = *p* < 0.05).

**Supplementary Information**

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**Supplementary Methods**

*Survey Regions and 20th Century Climate Change*

The three regions, Lassen, Yosemite, and Sequoia 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 (Supplementary Figure S1).

*Survey and Resurvey Data*

We used historical maps, written descriptions in field notes, and modern ground-truthing with historical photographs and hand-held GPS units to georeference historical localities. 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 the Shuttle Radar Topography Mission (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 (Supplementary Table S1).

Of the 134 historical localities, 34 were in Lassen, 47 were in Yosemite, and 32 53 were 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. Of the 15,277 historical mammal records used in this study, 8,688 are backed by voucher specimens in the MVZ1-3.

Modern mammal resurveys were conducted between 2003 and 2010 as part of the Grinnell Resurvey Project4,5; Fig. 1a). We surveyed a total of 166sites, including 85 of the 134 historical sites; 38 were in Lassen, 81 were in Yosemite, and 47 were in Sequoia. 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 in suitable spots. 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. 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 daily. Of the 14,316 modern mammal records obtained from these surveys, 6,144 are backed by voucher specimens in the MVZ6-8.

*Species Set*

Our data set included records for 67 species of small mammals in the modern and/or historical eras (Supplementary Table S2). Our resurvey protocols were not designed to detect carnivores, ungulates, or bats, so these were not included. Following Moritz et al.4, we adjusted the slope cut-off for *Peromyscus truei* to reflect known boundaries between Sierra Nevada and Great Basin subspecies9. We also considered only those west slope species that are characteristic of the Sierra Nevada and Cascade Range. For example, we did not include Mojave Desert species such as *Neotoma lepida* or *Perognathus longimembris*.

*Modelling Changes in Elevational Ranges*

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 v6.010,11). Our single-season model implemented an “unpaired-site” framework12, 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 models13.

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.4 and Tingley et al.5. 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 Supplementary Table S5. Following Moritz et al.4 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 Supplementary Table S5. 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 (Supplementary Table S3). 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 AIC14.

Following Moritz et al.4, 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 (Supplementary 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 models14,4 (Supplementary Figure S3).

*Testing Predictions 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’ package15. Species identity 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). Species widespread across elevations (*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 analysed 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 Neighbour*

We examined spatial heterogeneity in climate change (Prediction 4) by identifying the nearest climatic neighbours of historical localities under modern climate conditions, following the approach described in Tingley et al.5. 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 (PRISM16 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 and the 5% of historical 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 neighbour 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. For each climatic variable at each site, we also identified rare or disappearing climates using climatic thresholds of 1 °C temperature or 10 cm precipitation. We defined rare climates as those that occurred within climatic thresholds at < 2.5% of historical cells. We defined disappearing climates as those that occurred within climatic thresholds at ≥ 5% of historical cells and < 2.5% of modern cells. We excluded this subset of site-specific climate change from nearest neighbour comparisons because they violate an assumption of the method that climatically similar sites are available. 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).

**Supplementary Methods References**

1. <http://arctos.database.museum/project/historic-grinnell-survey-lassen-transect>
2. <http://arctos.database.museum/project/historic-grinnell-survey-yosemite-transect>
3. <http://arctos.database.museum/project/historic-grinnell-survey-southern-sierra-nevada-transect>
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# Supplementary Figure Legends

Supplementary Figure S1.

Supplementary Figure S2.

Supplementary Figure S3. Occupancy curves in the historical and modern eras by region for the 28 occupancy-modelled 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).

# Supplementary Tables

Supplementary Table S1. Historical and modern locality data for sites included in this study.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Aggregate name | Latitude | Longitude | Era | Slope | Region | Elevation (m) |
| Red Bluff 4 | 40.19033 | -122.22521 | H | W | LA | 83 |
| Red Bluff 5 | 40.21218 | -122.22977 | H | W | LA | 89 |
| Red Bluff 3 | 40.17070 | -122.12540 | H | W | LA | 90 |
| Red Bluff 1 | 40.13390 | -122.20610 | H | W | LA | 92 |
| Battle Creek | 40.37479 | -122.18016 | H | W | LA | 110 |
| Red Bluff 6 | 40.32216 | -122.28557 | H | W | LA | 177 |
| Dales, Payne Creek | 40.31460 | -122.06950 | H | W | LA | 186 |
| Red Bluff 2 | 40.24038 | -122.11096 | H | W | LA | 230 |
| Manton | 40.42544 | -121.88927 | H | W | LA | 564 |
| Lymans | 40.30960 | -121.76780 | H | W | LA | 1051 |
| Turners | 40.30825 | -121.73812 | H | W | LA | 1147 |
| Petes Valley | 40.52927 | -120.46209 | H | E | LA | 1382 |
| Mineral 3 | 40.33776 | -121.59613 | H | W | LA | 1478 |
| Mineral, Summit Creek 1 | 40.34890 | -121.58780 | H | W | LA | 1514 |
| Mineral, Summit Creek 2 | 40.36280 | -121.56630 | H | W | LA | 1550 |
| Eagle Lake 3 | 40.57293 | -120.83802 | H | W | LA | 1562 |
| Eagle Lake 2 | 40.67094 | -120.78958 | H | W | LA | 1564 |
| Eagle Lake 1 | 40.73439 | -120.71964 | H | W | LA | 1583 |
| Kellys 2 | 40.43268 | -121.35207 | H | W | LA | 1607 |
| East Ravendale | 40.79823 | -120.23207 | H | E | LA | 1621 |
| West Red Rock PO | 40.89950 | -120.25399 | H | E | LA | 1623 |
| Grasshopper Valley | 40.85009 | -120.75690 | H | E | LA | 1628 |
| North Observation Peak 1 | 40.86135 | -120.17049 | H | E | LA | 1628 |
| Termo | 40.89150 | -120.45640 | H | E | LA | 1631 |
| Willow Lake | 40.40524 | -121.36573 | H | W | LA | 1654 |
| North Fredonyer Peak | 40.80100 | -120.61175 | H | E | LA | 1711 |
| South West Ravendale | 40.69690 | -120.40900 | H | E | LA | 1717 |
| Hot Spring Valley | 40.44423 | -121.39380 | H | W | LA | 1773 |
| Manzanita Lake | 40.53140 | -121.56480 | H | W | LA | 1790 |
| Butte Lake | 40.56420 | -121.30239 | H | W | LA | 1854 |
| Black Butte | 40.41470 | -121.53190 | H | W | LA | 1979 |
| Warner Creek 1 | 40.45969 | -121.44184 | H | W | LA | 2085 |
| Warner Creek 2 | 40.46351 | -121.47197 | H | W | LA | 2262 |
| Lake Helen | 40.46913 | -121.51850 | H | W | LA | 2476 |
| Sacramento River, Blue Tent Creek | 40.20260 | -122.21628 | M | W | LA | 80 |
| Coyote Creek | 40.09325 | -122.22687 | M | W | LA | 92 |
| Sacramento River, Perry Riffle | 40.29721 | -122.17534 | M | W | LA | 97 |
| Jellys Ferry | 40.31997 | -122.18149 | M | W | LA | 106 |
| Reading Island | 40.38927 | -122.19220 | M | W | LA | 111 |
| Paynes Creek | 40.30254 | -122.10614 | M | W | LA | 168 |
| Dales Lake | 40.33065 | -122.07261 | M | W | LA | 210 |
| Hog Lake | 40.28261 | -122.12289 | M | W | LA | 270 |
| Vasquez Ranch | 40.43653 | -121.87544 | M | W | LA | 597 |
| Lyman Springs | 40.31124 | -121.76428 | M | W | LA | 1047 |
| Petes Valley | 40.52614 | -120.46551 | M | E | LA | 1381 |
| Battle Creek Meadows | 40.33948 | -121.60919 | M | W | LA | 1468 |
| Battle Creek | 40.34945 | -121.63171 | M | W | LA | 1495 |
| Eagle Lake, Merrill Creek | 40.55231 | -120.81467 | M | W | LA | 1559 |
| Eagle Lake Pine Creek | 40.66796 | -120.78612 | M | W | LA | 1568 |
| Eagle Lake, Brockman | 40.59293 | -120.84430 | M | W | LA | 1591 |
| Summit Creek | 40.35804 | -121.55757 | M | W | LA | 1616 |
| Coyote Flat | 40.88974 | -120.26846 | M | E | LA | 1621 |
| Eagle Lake, Papoose Meadow | 40.52582 | -120.76727 | M | W | LA | 1626 |
| Observation Peak 1 | 40.86155 | -120.15990 | M | E | LA | 1631 |
| Observation Peak 2 | 40.84532 | -120.17653 | M | E | LA | 1631 |
| Dodge Ranch | 40.89014 | -120.17355 | M | E | LA | 1632 |
| Horne Ranch | 40.82822 | -120.13889 | M | E | LA | 1647 |
| Willow Lake | 40.40586 | -121.36289 | M | W | LA | 1657 |
| Slate Creek | 40.84260 | -120.76994 | M | E | LA | 1663 |
| Wilson Lake | 40.34412 | -121.43943 | M | W | LA | 1664 |
| Tuledad Road | 40.92563 | -120.13857 | M | E | LA | 1696 |
| Summit Creek North | 40.36890 | -121.53831 | M | W | LA | 1723 |
| Bailey Creek | 40.80572 | -120.61003 | M | E | LA | 1731 |
| Drakesbad | 40.44466 | -121.40850 | M | W | LA | 1750 |
| Dodge Reservoir | 40.96926 | -120.13506 | M | E | LA | 1762 |
| Manzanita Lake | 40.53759 | -121.57018 | M | W | LA | 1791 |
| Pole Spring | 40.58720 | -121.28702 | M | W | LA | 1793 |
| Butte Lake | 40.56241 | -121.29966 | M | W | LA | 1849 |
| Bluff Falls | 40.41220 | -121.53191 | M | W | LA | 1975 |
| Kings Creek Falls | 40.45971 | -121.44478 | M | W | LA | 2100 |
| Upper Kings Creek Meadow | 40.46521 | -121.47640 | M | W | LA | 2276 |
| Helen, Emerald Lakes | 40.46973 | -121.51398 | M | W | LA | 2499 |
| Minkler | 36.71660 | -119.46410 | H | W | SS | 118 |
| Bakersfield | 35.41984 | -119.00877 | H | W | SS | 139 |
| Dunlap | 36.71710 | -119.13226 | H | W | SS | 636 |
| Bodfish | 35.60013 | -118.49667 | H | W | SS | 721 |
| Mill Creek | 35.53059 | -118.62216 | H | W | SS | 765 |
| Weldon, South | 35.66608 | -118.28948 | H | W | SS | 809 |
| Onyx | 35.68574 | -118.21827 | H | E | SS | 866 |
| Weldon, Fay Creek North | 35.74120 | -118.31000 | H | W | SS | 1261 |
| Walker Pass 05 | 35.68775 | -118.04930 | H | E | SS | 1395 |
| Walker Pass 07, FreemanCanyon | 35.65010 | -118.01090 | H | E | SS | 1481 |
| Walker Pass 06 | 35.66920 | -118.03710 | H | E | SS | 1527 |
| Kings River Canyon | 36.79380 | -118.58100 | H | W | SS | 1533 |
| Hume Lake | 36.78773 | -118.91301 | H | W | SS | 1592 |
| Carroll Creek | 36.50510 | -118.10244 | H | E | SS | 1699 |
| Smith Meadow, Trout Creek | 35.96474 | -118.22947 | H | W | SS | 1860 |
| Jordan Hot Springs | 36.22965 | -118.30169 | H | W | SS | 1984 |
| Hockett Trail 2 | 36.49415 | -118.09586 | H | E | SS | 2000 |
| Kiavah Mountain, Scodie Mountains | 35.68223 | -118.08509 | H | E | SS | 2006 |
| Hockett Trail 5 | 36.49732 | -118.11483 | H | E | SS | 2138 |
| Taylor Meadow | 35.83066 | -118.29175 | H | W | SS | 2147 |
| Cannell Meadow | 35.82508 | -118.36717 | H | W | SS | 2268 |
| Hockett Trail 4 | 36.49577 | -118.11230 | H | E | SS | 2281 |
| Horse Corral Meadow | 36.74744 | -118.75404 | H | W | SS | 2313 |
| Jackass Meadow | 36.09286 | -118.22620 | H | W | SS | 2364 |
| Broder/Monache Meadow | 36.16332 | -118.18188 | H | W | SS | 2424 |
| Hockett Trail 1 | 36.49339 | -118.13676 | H | E | SS | 2610 |
| Dry Meadows | 36.21452 | -118.25257 | H | W | SS | 2624 |
| Redrocks Meadow | 36.27011 | -118.27139 | H | W | SS | 2662 |
| Onion Valley | 36.77438 | -118.33105 | H | W | SS | 2690 |
| Sirretta Meadows | 35.94200 | -118.32800 | H | W | SS | 2758 |
| Little Pete Meadow | 37.10152 | -118.59580 | H | W | SS | 2761 |
| Aster Lake | 36.60014 | -118.67482 | H | W | SS | 2855 |
| Rock Creek | 36.49607 | -118.32648 | H | W | SS | 2954 |
| Whitney Meadow | 36.43413 | -118.26710 | H | W | SS | 2969 |
| Little Cottonwood Creek | 36.47914 | -118.12864 | H | W | SS | 2997 |
| Little Brush Meadow, Olancha Peak | 36.25410 | -118.13000 | H | W | SS | 3005 |
| Hockett Trail 3 | 36.47770 | -118.13728 | H | E | SS | 3036 |
| Bubbs Creek | 36.76389 | -118.40627 | H | W | SS | 3040 |
| Mitchell Peak | 36.73231 | -118.71369 | H | W | SS | 3128 |
| Crabtree Meadow, Whitney Creek | 36.55123 | -118.35854 | H | W | SS | 3147 |
| Flower/Heart Lake | 36.76954 | -118.35611 | H | W | SS | 3175 |
| Moose Lake | 36.60067 | -118.63744 | H | W | SS | 3214 |
| Bullfrog Lake | 36.77297 | -118.40398 | H | W | SS | 3249 |
| Olancha Peak, West Slope | 36.25976 | -118.12327 | H | W | SS | 3287 |
| McClure/Colby Meadows | 37.17130 | -118.70240 | H | W | SS | 3293 |
| Evolution Lake | 37.16860 | -118.69330 | H | W | SS | 3313 |
| Cottonwood Lakes | 36.49815 | -118.22001 | H | W | SS | 3383 |
| Dusy Lake | 37.10230 | -118.55500 | H | W | SS | 3453 |
| Humphreys Basin | 37.26530 | -118.70560 | H | W | SS | 3460 |
| Cirque Peak | 36.46174 | -118.23835 | H | W | SS | 3503 |
| Kearsarge Pass | 36.77250 | -118.37610 | H | E | SS | 3575 |
| Piute Pass, off trapline | 37.23104 | -118.68916 | H | W | SS | 3601 |
| Mt. Gould | 36.78039 | -118.37854 | H | W | SS | 3940 |
| Minkler 01, 02, 03 | 36.75049 | -119.44039 | M | W | SS | 133 |
| Minkler 04, Jesse Morrow Mountain | 36.71289 | -119.41663 | M | W | SS | 135 |
| Bakersfield, Jackrabbit Flat | 35.49501 | -119.05726 | M | W | SS | 238 |
| Bakersfield | 35.51386 | -118.87095 | M | W | SS | 270 |
| Dunlap, Mill Creek | 36.73016 | -119.11864 | M | W | SS | 577 |
| Bodfish 01, 02 | 35.59955 | -118.49673 | M | W | SS | 725 |
| Mill Creek | 35.53533 | -118.61732 | M | W | SS | 741 |
| Weldon 02, 03, 06, 08, South | 35.67853 | -118.29530 | M | W | SS | 810 |
| Kelso Creek Road | 35.63622 | -118.24572 | M | W | SS | 861 |
| Onyx 01, 03, Canebrake Ecological Reserve | 35.72848 | -118.17166 | M | E | SS | 865 |
| Onyx 02, 04, Scodie Canyon | 35.67941 | -118.21441 | M | E | SS | 896 |
| Bodfish 03, Erskine Creek | 35.58777 | -118.44005 | M | W | SS | 932 |
| Bodfish 04, Sandy Flat Campground | 35.58777 | -118.44005 | M | W | SS | 932 |
| Weldon 01, 05, 07, 09, Fay Ranch Road, Fay Creek North | 35.71632 | -118.30522 | M | W | SS | 1041 |
| Olancha Creek | 36.27383 | -118.02917 | M | E | SS | 1221 |
| Walker Pass 04 | 35.72501 | -118.07559 | M | E | SS | 1226 |
| Walker Pass 01, Freeman Canyon | 35.65561 | -118.01381 | M | E | SS | 1506 |
| Walker Pass 03 | 35.66638 | -118.04098 | M | E | SS | 1512 |
| Kings River Canyon | 36.79111 | -118.60029 | M | W | SS | 1514 |
| Hume Lake | 36.79198 | -118.90404 | M | W | SS | 1586 |
| Walker Pass 02 | 35.66385 | -118.02601 | M | E | SS | 1625 |
| Carroll Creek | 36.51022 | -118.10295 | M | E | SS | 1716 |
| Smith Meadow, Trout Creek | 35.96536 | -118.22669 | M | W | SS | 1856 |
| Taylor Meadow | 35.83000 | -118.29572 | M | W | SS | 2170 |
| Cannell Meadow | 35.83344 | -118.37075 | M | W | SS | 2278 |
| Horse Corral Meadow | 36.74671 | -118.76644 | M | W | SS | 2281 |
| Jackass Meadow | 36.09292 | -118.22693 | M | W | SS | 2361 |
| Broder/Monache Meadow | 36.16605 | -118.19191 | M | W | SS | 2403 |
| Evolution Valley 5 | 37.09910 | -118.59700 | M | W | SS | 2703 |
| Onion Valley | 36.77509 | -118.33419 | M | W | SS | 2755 |
| Sirretta Meadows | 35.94471 | -118.32744 | M | W | SS | 2756 |
| Aster Lake | 36.60162 | -118.67790 | M | W | SS | 2780 |
| Little Cottonwood Creek 01, 02 | 36.47535 | -118.12039 | M | W | SS | 2876 |
| Little Brush Meadow, Olancha Peak | 36.25324 | -118.13418 | M | W | SS | 2922 |
| Whitney Meadow | 36.43149 | -118.27482 | M | W | SS | 2957 |
| Little Cottonwood Creek 03 | 36.47916 | -118.12861 | M | W | SS | 2997 |
| Evolution Valley 2 | 37.17170 | -118.71600 | M | W | SS | 3012 |
| Little Cottonwood Creek, camp | 36.45175 | -118.17046 | M | W | SS | 3072 |
| Crabtree Meadow, Whitney Creek | 36.55265 | -118.35768 | M | W | SS | 3151 |
| Bullfrog Lake | 36.77011 | -118.40407 | M | W | SS | 3237 |
| Moose Lake | 36.60390 | -118.64100 | M | W | SS | 3269 |
| Rocky Basin Lakes | 36.44449 | -118.31813 | M | W | SS | 3292 |
| Evolution Valley 4 | 37.16230 | -118.69100 | M | W | SS | 3310 |
| Cottonwood Lakes | 36.49873 | -118.20772 | M | W | SS | 3398 |
| Evolution Valley 3 | 37.18860 | -118.70200 | M | W | SS | 3441 |
| Evolution Valley 6 | 37.10270 | -118.55600 | M | W | SS | 3453 |
| Evolution Valley 1 | 37.20990 | -118.68900 | M | W | SS | 3640 |
| La Grange 1 | 37.66610 | -120.46986 | H | W | YO | 52 |
| Snelling 1 | 37.52687 | -120.43744 | H | W | YO | 77 |
| Pleasant Valley 1 | 37.65638 | -120.29042 | H | W | YO | 251 |
| Pleasant Valley 2 | 37.64441 | -120.30118 | H | W | YO | 335 |
| Coulterville 1 | 37.71082 | -120.21451 | H | W | YO | 472 |
| El Portal 2 | 37.67373 | -119.79354 | H | W | YO | 587 |
| Mt. Bullion 1 | 37.50822 | -120.04390 | H | W | YO | 661 |
| El Portal 1 | 37.67989 | -119.78318 | H | W | YO | 843 |
| Coulterville 3 | 37.75354 | -120.10580 | H | W | YO | 904 |
| Coulterville 2 | 37.73845 | -120.14187 | H | W | YO | 975 |
| Sweetwater 1 | 37.58897 | -119.88128 | H | W | YO | 1068 |
| Cascade 1 | 37.72577 | -119.71094 | H | W | YO | 1101 |
| El Portal 3 | 37.68819 | -119.76422 | H | W | YO | 1202 |
| Yosemite Valley 2 | 37.73732 | -119.60247 | H | W | YO | 1207 |
| Yosemite Valley 3 | 37.73931 | -119.57204 | H | W | YO | 1213 |
| Yosemite Valley 1 | 37.74985 | -119.59055 | H | W | YO | 1223 |
| Happy Isles 1 | 37.73160 | -119.56100 | H | W | YO | 1230 |
| Yosemite Valley 4 | 37.74580 | -119.60540 | H | W | YO | 1412 |
| Merced Grove 1 | 37.74873 | -119.83866 | H | W | YO | 1626 |
| Cascade Creek 1 | 37.73870 | -119.70290 | H | W | YO | 1817 |
| Chinquapin 1 | 37.65236 | -119.70260 | H | W | YO | 1845 |
| Aspen Valley 1 | 37.82773 | -119.77121 | H | W | YO | 1878 |
| Crane Flat 1 | 37.75559 | -119.79805 | H | W | YO | 1889 |
| Mono PO 1 | 37.99058 | -119.14107 | H | E | YO | 1952 |
| Glen Aulin 2 | 37.92886 | -119.46116 | H | W | YO | 1971 |
| Salmon Ranch 1 | 37.96326 | -118.92360 | H | E | YO | 2001 |
| Dry Creek 1 | 37.93465 | -118.93519 | H | E | YO | 2070 |
| Williams Butte 1 | 37.90891 | -119.10530 | H | E | YO | 2090 |
| Mono Craters 2 | 37.90167 | -118.99140 | H | E | YO | 2167 |
| Indian Canyon 1 | 37.77432 | -119.56902 | H | W | YO | 2195 |
| Mono Meadow 1 | 37.66340 | -119.59227 | H | W | YO | 2216 |
| Merced Lake 1 | 37.72806 | -119.39179 | H | W | YO | 2222 |
| Silver Lake 1 | 37.79923 | -119.12130 | H | E | YO | 2224 |
| Mono Mills 1 | 37.88764 | -118.95987 | H | E | YO | 2241 |
| Glen Aulin 1 | 37.91206 | -119.42135 | H | W | YO | 2386 |
| Walker Lake 1 | 37.87338 | -119.17100 | H | E | YO | 2438 |
| Porcupine Flat 1 | 37.80526 | -119.55632 | H | W | YO | 2464 |
| Tuolumne Meadows 2 | 37.87850 | -119.36650 | H | W | YO | 2622 |
| Tuolumne Meadows 1 | 37.87941 | -119.39498 | H | W | YO | 2632 |
| Ten Lakes 1 | 37.90389 | -119.52552 | H | W | YO | 2727 |
| Gem Lake 1 | 37.75857 | -119.15940 | H | E | YO | 2773 |
| Warren Fork 1 | 37.95505 | -119.22830 | H | E | YO | 2773 |
| Lyell Canyon 1 | 37.77390 | -119.26088 | H | W | YO | 2989 |
| Mt. Hoffman 1 | 37.84461 | -119.50018 | H | W | YO | 3026 |
| Young Lakes 1 | 37.93780 | -119.34063 | H | W | YO | 3047 |
| Vogelsang 1 | 37.79090 | -119.34256 | H | W | YO | 3246 |
| Lyell Canyon 2 | 37.76409 | -119.25208 | H | W | YO | 3282 |
| LG3 | 37.66747 | -120.46795 | M | W | YO | 62 |
| LG2 | 37.62181 | -120.52589 | M | W | YO | 63 |
| LG1 | 37.62480 | -120.56688 | M | W | YO | 76 |
| S2 | 37.53619 | -120.48598 | M | W | YO | 89 |
| S1 | 37.51121 | -120.38391 | M | W | YO | 90 |
| S3 | 37.52907 | -120.35093 | M | W | YO | 115 |
| S4 | 37.54692 | -120.35495 | M | W | YO | 124 |
| CPV6 | 37.70881 | -120.22121 | M | W | YO | 420 |
| CPV2 | 37.65594 | -120.22132 | M | W | YO | 545 |
| CPV4 | 37.72381 | -120.26375 | M | W | YO | 552 |
| CPV8 | 37.71951 | -120.17941 | M | W | YO | 569 |
| CPV5 | 37.73883 | -120.24826 | M | W | YO | 691 |
| CPV1 | 37.64055 | -120.21173 | M | W | YO | 724 |
| MD2 | 37.74401 | -120.03202 | M | W | YO | 726 |
| CPV3 | 37.61422 | -120.18232 | M | W | YO | 855 |
| MD1 | 37.75542 | -120.08468 | M | W | YO | 868 |
| CPV9 | 37.73636 | -120.16646 | M | W | YO | 894 |
| CPV7 | 37.68405 | -120.12141 | M | W | YO | 899 |
| Ca1 | 37.72315 | -119.71200 | M | W | YO | 1044 |
| Ch1 | 37.68599 | -119.72439 | M | W | YO | 1096 |
| FM3 | 37.54498 | -119.83822 | M | W | YO | 1122 |
| FM2 | 37.57904 | -119.88213 | M | W | YO | 1154 |
| YV1 | 37.71515 | -119.66500 | M | W | YO | 1191 |
| YV2 | 37.72193 | -119.63632 | M | W | YO | 1205 |
| YV3 | 37.73242 | -119.60770 | M | W | YO | 1207 |
| YV4 | 37.74276 | -119.58765 | M | W | YO | 1209 |
| YV5 | 37.74053 | -119.57217 | M | W | YO | 1209 |
| YV6 | 37.73267 | -119.55807 | M | W | YO | 1227 |
| YV7 | 37.75337 | -119.54557 | M | W | YO | 1256 |
| FM1 | 37.56624 | -119.86851 | M | W | YO | 1268 |
| YV8 | 37.75236 | -119.58723 | M | W | YO | 1321 |
| F1 | 37.70369 | -119.74008 | M | W | YO | 1341 |
| HM1 | 37.79611 | -119.86781 | M | W | YO | 1424 |
| MG1 | 37.74826 | -119.83938 | M | W | YO | 1644 |
| HG1 | 37.76525 | -119.86233 | M | W | YO | 1684 |
| MG2 | 37.76208 | -119.84264 | M | W | YO | 1811 |
| AV1 | 37.82534 | -119.77221 | M | W | YO | 1872 |
| CF2 | 37.75288 | -119.79769 | M | W | YO | 1879 |
| CF1 | 37.75331 | -119.80890 | M | W | YO | 1956 |
| TF1 | 37.75456 | -119.74298 | M | W | YO | 2015 |
| CF3 | 37.75775 | -119.76990 | M | W | YO | 2096 |
| MMe3 | 37.66780 | -119.62319 | M | W | YO | 2123 |
| TC1 | 37.81096 | -119.71286 | M | W | YO | 2143 |
| WB1 | 37.90766 | -119.12214 | M | E | YO | 2157 |
| MMe2 | 37.66672 | -119.59444 | M | W | YO | 2198 |
| BC1 | 37.90028 | -119.12977 | M | E | YO | 2199 |
| ML1 | 37.72964 | -119.39286 | M | W | YO | 2221 |
| ML2 | 37.73971 | -119.40517 | M | W | YO | 2221 |
| IC1 | 37.77716 | -119.56675 | M | W | YO | 2223 |
| WC1 | 37.89667 | -119.13013 | M | E | YO | 2227 |
| MoMe1 | 37.66637 | -119.67211 | M | W | YO | 2237 |
| MMi1 | 37.88811 | -118.96021 | M | E | YO | 2239 |
| SM1 | 37.67357 | -119.65432 | M | W | YO | 2247 |
| YC1 | 37.85038 | -119.57637 | M | W | YO | 2279 |
| GA1 | 37.91170 | -119.42495 | M | W | YO | 2372 |
| MMe1 | 37.69924 | -119.58647 | M | W | YO | 2372 |
| WW3 | 37.83879 | -119.59254 | M | W | YO | 2383 |
| WW1 | 37.85844 | -119.65120 | M | W | YO | 2444 |
| WL1 | 37.87307 | -119.16297 | M | W | YO | 2445 |
| PF1 | 37.80894 | -119.56863 | M | W | YO | 2480 |
| WW2 | 37.84907 | -119.62282 | M | W | YO | 2531 |
| FD1 | 37.87649 | -119.41609 | M | W | YO | 2554 |
| SN1 | 37.82200 | -119.50471 | M | W | YO | 2587 |
| JR1 | 37.88358 | -119.36340 | M | W | YO | 2685 |
| GM1 | 38.16254 | -119.60461 | M | W | YO | 2745 |
| WF1 | 37.95404 | -119.22714 | M | W | YO | 2772 |
| LM1 | 37.88270 | -119.34655 | M | W | YO | 2815 |
| DL1 | 38.17297 | -119.59475 | M | W | YO | 2864 |
| TL1 | 37.90404 | -119.53357 | M | W | YO | 2865 |
| DeM1 | 37.89922 | -119.34770 | M | W | YO | 2866 |
| KM1 | 38.12201 | -119.48195 | M | W | YO | 2867 |
| LC1 | 37.77909 | -119.26102 | M | W | YO | 2935 |
| MF1 | 37.84097 | -119.49964 | M | W | YO | 2938 |
| DD1 | 37.90828 | -119.34750 | M | W | YO | 2961 |
| RC1 | 38.06129 | -119.33899 | M | W | YO | 3014 |
| WF2 | 37.95899 | -119.26701 | M | W | YO | 3040 |
| V1 | 37.79249 | -119.34852 | M | W | YO | 3054 |
| LC2 | 37.76913 | -119.25686 | M | W | YO | 3094 |
| TP1 | 37.90811 | -119.26396 | M | W | YO | 3148 |
| V2 | 37.79766 | -119.33513 | M | W | YO | 3179 |
| LC3 | 37.76164 | -119.25687 | M | W | YO | 3208 |

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  | 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 |
| *Ammospermophilus nelsoni* |  | St | - |  | --- | | |  | --- | | |  | W | 1 | 0 |
| *Aplodontia rufa* |  | Sp | - |  | W | 0 | 1 |  | E + W | 1 | 1 |  | --- | | |
| *Brachylagus idahoensis* |  | Obs | - |  | E | 1 | 0 |  | --- | | |  | --- | | |
| *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 nitratoides* |  | St | - |  | --- | | |  | --- | | |  | W | 1 | 0 |
| *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 |
| *Scapanus latimanus* |  | Sp | - |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | W | 1 | 0 |
| *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 |  | --- | | |  | --- | | |
| *Sylvilagus audubonii* |  | Obs | - |  | W | 1 | 0 |  | W | 1 | 1 |  | E + W | 1 | 1 |
| *Sylvilagus bachmani* |  | Obs | - |  | W | 1 | 0 |  | W | 1 | 1 |  | W | 1 | 0 |
| *Sylvilagus nuttallii* |  | Obs | - |  | E + W | 1 | 1 |  | E | 1 | 1 |  | W | 0 | 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 67** |  | **54** | **34** |  |  | **45** | **45** |  |  | **48** | **48** |  |  | **50** | **50** |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

**§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 67 species we examined, 54 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.**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | |  |  |  |  | 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 |
| *Ammospermophilus nelsoni* | |  | St | - |  | --- | | |  | --- | | |  | W | 1 | 0 |
| *Aplodontia rufa* | |  | Sp | - |  | W | 0 | 1 |  | E + W | 1 | 1 |  | --- | | |
| *Brachylagus idahoensis* | |  | Obs | - |  | E | 1 | 0 |  | --- | | |  | --- | | |
| *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 nitratoides* | |  | St | - |  | --- | | |  | --- | | |  | W | 1 | 0 |
| *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 |
| *Scapanus latimanus* | |  | Sp | - |  | E + W | 1 | 1 |  | E + W | 1 | 1 |  | W | 1 | 0 |
| *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 |  | --- | | |  | --- | | |
| *Sylvilagus audubonii* | |  | Obs | - |  | W | 1 | 0 |  | W | 1 | 1 |  | E + W | 1 | 1 |
| *Sylvilagus bachmani* | |  | Obs | - |  | W | 1 | 0 |  | W | 1 | 1 |  | W | 1 | 0 |
| *Sylvilagus nuttallii* | |  | Obs | - |  | E + W | 1 | 1 |  | E | 1 | 1 |  | W | 0 | 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 |
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| **Total 67** | |  | **54** | **34** |  |  | **45** | **45** |  |  | **48** | **48** |  |  | **50** | **50** |
| §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 67 species we examined, 54 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. | | | | | | | | |

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**Supplementary Table S3. 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 |
|  |  |  |  |  |  |
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| 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).

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**Supplementary Table S4. Range limits and shifts of the 34 modelled 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 | Undetected Current | Undetected 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 modelling 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 (‡).

**Supplementary Table S5. Model parameterizations of detectability (*p*) and occupancy (*ψ*) run for each species with quantifiable trapping effort data (see Table S1 for list of modelled 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 |