Title

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Publication Date

2012-07-01

Public Interest Energy Research (PIER) Program
White Paper

IDENTIFYING VULNERABLE SPECIES AND ADAPTATION STRATEGIES IN THE SOUTHERN SIERRA OF CALIFORNIA USING HISTORICAL RESURVEYS

A White Paper from the California Energy Commission's California Climate Change Center

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JULY 2012
CEC-500-2012-025

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ACKNOWLEDGEMENTS

The Grinnell Resurvey Project: Chris Conroy, James L. Patton, Steven Beissinger, Michelle Koo, Karen Rowe, Kevin Rowe, Adam Smith, Toni Lyn Morelli, Pete Epanchin, Morgan Tingley, Rachel Welsh. Museum of Vertebrate Zoology, University of California Berkeley.

The Wieslander Vegetation Type Mapping Project: Jackie Bjorkman, Thuy-Le Ngoc. Information Center for the Environment, University of California, Davis.

Lorraine Flint and Alan Flint from the United States Geological Survey for the downscaled climate data.

The National Science Foundation, the Yosemite Foundation, and staff from the United States Geological Survey (Les Chow) and National Park Service (many) for support and advice in relation to the Grinnell Resurvey Project.

Four anonymous reviewers that significantly improved the structure, content, and readability of this document; and to Robert Grofe for the English editing.

PREFACE

The California Energy Commission's Public Interest Energy Research (PIER) Program supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

The PIER Program conducts public interest research, development, and demonstration (RD&D) projects to benefit California. The PIER Program strives to conduct the most promising public interest energy research by partnering with RD&D entities, including individuals, businesses, utilities, and public or private research institutions.

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- Transportation

In 2003, the California Energy Commission's PIER Program established the California Climate Change Center to document climate change research relevant to the states. This center is a virtual organization with core research activities at Scripps Institution of Oceanography and the University of California, Berkeley, complemented by efforts at other research institutions.

For more information on the PIER Program, please visit the Energy Commission's website http://www.energy.ca.gov/research/index.html or contract the Energy Commission at (916) 327-1551.

ABSTRACT

Small mammals have shifted their elevation ranges in the Sierra Nevada. We questioned whether this shift can be linked to changes in habitat distribution, whether changes in population abundance match range dynamics, and how the shift affects predictions of future small mammal distribution. We merged data from mammal records of the Grinnell Resurvey Project, vegetation from the Wieslander Vegetation Type Maps and CALVEG and National Park Service, and downscaled PRISM climate data to meet these objectives.

We found that species that expanded their elevational distribution range tracked suitable habitats, and their ecological niche broadened over time. Species whose elevation range has contracted did not track suitable habitats, and their ecological niche remained constant.

Species that tracked their habitat dynamics showed an average decrease in abundance at the leading edge of their distribution range, whereas species that did not track their habitat dynamics showed either no change or increase in abundance at the lagging edge of their distribution range over time.

Life zone (vegetation types across elevation bands as a response to gradients in temperature and precipitation) and climate models performed better than vegetation models when changes over 80 years were analyzed, suggesting that species are responding more rapidly to climate than to vegetation change. Nonetheless, in all of these models, expanding species were harder to model as their ecological niche shifted, whereas contracting species produced more reliable models.

These results imply that modeling future distributions of *sensitive* species will vary according to the direction and magnitude of their sensitivity to both climate and vegetation changes.

The results of this analysis highlight the need to determine these species life history traits, habitat preferences and temporal dynamics, in order to identify which species are *positively* and *negatively sensitive*, and which are relatively insensitive to future climate and land cover change.

Keywords: California, climate, habitat, life zone, models, niche, small mammals, suitability, vegetation

Please use the following citation for this paper:

Santos, Maria J., Craig Moritz, and James H. Thorne (University of California, Berkeley, and University of California, Davis). 2012. ***Identifying Vulnerable Species and Adaptation Strategies in the Southern Sierra of California Using Historical Resurveys.*** California Energy Commission. Publication number: CEC-500-2012-025.

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Section 1: Introduction

Species may change their geographic range over time as a response to changing conditions that define their ecological niche. *Ecological niche* can be defined in two ways: *fundamental* and *realized niche*. Fundamental niche is a theoretical volume of space defined by all the possible environmental conditions a species can potentially occupy, independent of their representation or lack thereof in the natural world. Realized niche is a constrained fundamental niche, where species occurrences are limited to existing environmental conditions and constrained by external factors such as interspecific interactions, disease, and anthropogenic change (Soberon 2007; Soberon and Nakamura 2009). The observed changes in species ranges over time are likely to reflect changes in the realized niche. A species' niche can be considered a hypervolume measured as a function of the environmental conditions in which the species exists (a Grinnellian niche) or of the interactions the species withstands (an Eltonian niche) (Soberon 2007). While environmental factors can be assessed independently (e.g., precipitation, temperature, plant community), often the combination that a given species uses is referred to as *habitat*. Habitat is not a categorical concept; in fact, it is a gradient of suitability defined by the likelihood that species use different environmental combinations that match their ecological preferences. Here we follow the Grinnellian definition of niche (Grinnell 1917; Grinnell 1924) and focus on species' responses to two components of habitat: vegetation and climate.

Species' geographic ranges may exhibit dynamics both in horizontal (latitudinal or longitudinal) and elevational extent (Latimer, Wu et al. 2006; McPherson and Jetz 2007; Morin and Thuiller 2009; Mustin, Benton et al. 2009). In mountain ranges, for example, shifts in climate occur across smaller distances than in flatter areas as a result of the interaction with elevation (Loarie, Duffy et al. 2009; Ackerly, Loarie et al. 2010), and thus are likely to have a stronger effect on species' range dynamics. In theory, species' elevation ranges may contract, expand, shift, or show no change in response to static or changing environmental conditions that delimit their ecological niche. For example, Moritz et al. (2008) showed that small mammal species exhibited expansions, contractions, or no changes in their elevational distribution range over the last 80 years in Yosemite National Park.

While it is well-established that climate and vegetation changes are occurring, the outstanding question is whether and to what extent species are responding to these changes. Recent research has focused on elucidating species' responses to these changes, either by addressing the responses directly or suggesting effects of the following factors:

- Climate (Berry, Dawson et al. 2002; Berry, Dawson et al. 2003; Beaumont, Hughes et al. 2005; Lawler, White et al. 2006; Brooker, Travis et al. 2007; Altwegg, Wheeler et al. 2008; Devictor, Julliard et al. 2008; Kharouba, Algar et al. 2009; Mustin, Benton et al. 2009; Jiguet, Gregory et al. 2010; Lenoir, Gegout et al. 2010; Tingley, Monahan et al. 2010; Dobrowski, Thorne et al. 2011; Morzillo and Alig 2011; Maggini, Lehmann et al. 2011; Rubidge, Monahan et al. 2011; Schippers, Verboom et al. 2011)

- Habitat (Honnay, Verheyen et al. 2002; Berry, Dawson et al. 2003; Franco, Hill et al. 2006; Swihart, Lusk et al. 2006; Ulrich and Hopper 2008; Oliver, Hill et al. 2009; Ashcroft, French et al. 2010; Betts, Nocera et al. 2010; Graham, VanDerWal et al. 2010; Rubidge, Monahan et al. 2011; Stefanescu, Torre et al. 2011)
- Physiological level (Kearney and Porter 2009; Lee, Janion et al. 2009)
- Population level, by measuring abundance (Maurer and Taper 2002; Joseph, Field et al. 2006; Huntley, Barnard et al. 2010)
- Species movements across the landscape (Brooker, Travis et al. 2007; Waltari and Guralnick 2009; Barve, Barve et al. 2011)
- Species traits (Kerbiriou, Viol et al. 2009; Kearney, Simpson et al. 2010; Angert, Crozier et al. 2011; Hof, Levincky et al. 2011)
- Species interactions (Voigt, Perner et al. 2003; Winder and Schindler 2004; Araujo and Luoto 2007; Brooker, Travis et al. 2007; Tylianakis, Didham et al. 2008; Barton and Schimtz 2009; Bascompte and Stouffer 2011; Rubidge, Monahan et al. 2011)
- Potential of extinction (Beever, Ray et al. 2011)

It is now necessary to integrate such empirical and modeled information (for an example of a review of empirical results, see Parmesan 2006; for an example of a review of modeling results and uncertainty, see Wiens, Stralberg et al. 2009). Such an integration helps enable us to understand and be able to predict which components of biodiversity are vulnerable to either climate or vegetation change (Opdam and Wascher 2004), to evaluate impacts on species (Rowland, Davison et al. 2011), and to improve our ability to detect vulnerability (Dawson, Jackson et al. 2011). This can be achieved by connecting geographical distribution with population processes (Maurer and Taper 2002; Mace, Collen et al. 2010) towards the management of biodiversity (Heller and Zavaleta 2009), and the development of adaptation strategies (Lawler 2009). Several approaches to estimate vulnerability have been put forward (for examples see Berry, Dawson et al. 2003; Coops and Waring 2011), such as the NatureServe's Climate Change Vulnerability Index (CCVI; http://www.natureserve.org/prodServices/climatechange/ccvi.jsp) and the National Wildlife Federation's climate change vulnerability assessment guide (www.nwf.org/vulnerabilityguide; Glick, Stein et al. 2011), which have been used by agencies such as the California Department of Fish and Game and the United States Fish and Wildlife Service. These types of assessments allow for an understanding of the trends and the development of predictions for known threatened species and species not yet threatened. While logical, there are few if any direct tests of these prediction frameworks.

However, the identification of vulnerability is not a trivial pursuit. The first limitation is the definition of vulnerability itself. According to the *California Vulnerability and Adaptation Research Project* guidance document (a current Public Interest Energy Research [PIER] Program project), *vulnerability* is "a susceptibility to harm or change; more specifically the degree to which a system is exposed to, susceptible to, and (un)able to cope with and adapt to the adverse effects of climate change, including climate variability and extremes. Vulnerability is a function of the character, magnitude, and rate of climate variation, to which the system is exposed, as well as of non-climatic characteristics of the systems, including its *sensitivity*, and its *coping* and *adaptive capacity*."

Several attempts have been made to predict vulnerability based on climate and vegetation forecasts and species attributes. The outputs, however, are variable and contingent upon existing data, modeling framework, climate change emission scenarios, etc. The challenge is thus to screen the predictions and determine which are more likely and which contain misleading components. One possible avenue by which to achieve this is to link multiple source resurvey data that depicts the direct observation of change over a period of time, in order to establish the trend of the change. This integration further allows for the validating of forecast methods, and assessing whether the vulnerability predictors (in this case climate and vegetation) differ in performance and how they may be linked to species traits.

We devised a series of analyses towards the goal of assessing the direct and the indirect effects of climate, via vegetation change, on small mammal species distribution dynamics (Figure 1). Our analysis starts by quantifying vegetation and climate changes in the study area over the last 80 years, and the observed dynamics of small mammal elevation ranges (boxes labeled vegetation, climate, and mammals in the flow chart). Smaller boxes in the bottom left corner of those boxes indicate the data sets used to assess change: VTM (Vegetation Type Mapping), CalVeg (U.S. Forest Service remotely sensed vegetation map), PRISM+BCM (downscaled climate data produced in the *Climate Vulnerability and Adaptation Study for California*), and GRP (Grinnell Resurvey Project small mammal data). Circles in the bottom right corner of each flow chart component indicate the page in this paper where the detailed information can be found. The starting assumptions are that (1) species are present in their most suitable habitat, and/or (2) species are present in their most suitable climate. In this idealized scenario, the species have a perfect knowledge of the environmental conditions that surround them, and they use it optimally; i.e., by using the most suitable conditions.

To assess whether species are indeed present in their most suitable habitat, we used published Habitat Suitability Index (HSI) values from the California Department of Fish and Game's California Wildlife Habitat Relationships (CWHR; http://www.dfg.ca.gov/biogeodata/cwhr/). First we tested whether the HSI values could be linked to species presence (Box 1 in Figure 1) and found that HSI values can reliably predict the presence of 15 out of 20 species (.

Given these results, we predicted that over time, the observed dynamics in species elevation ranges would be in response to the dynamics of their habitat. To test this hypothesis we assessed whether species are or are not tracking the dynamics of their habitat. We found a 50-50 split between species that track and species that do not track their habitat dynamics. While intuitively this would appear to be a random pattern, it is not, as the species that tracked their habitat dynamics were dominantly those living within low and intermediate elevation that have expanded their elevation range over the last 80 years. Conversely, species that did not track their habitat dynamics occupied higher elevations and have contracted their range over the last 80 years.

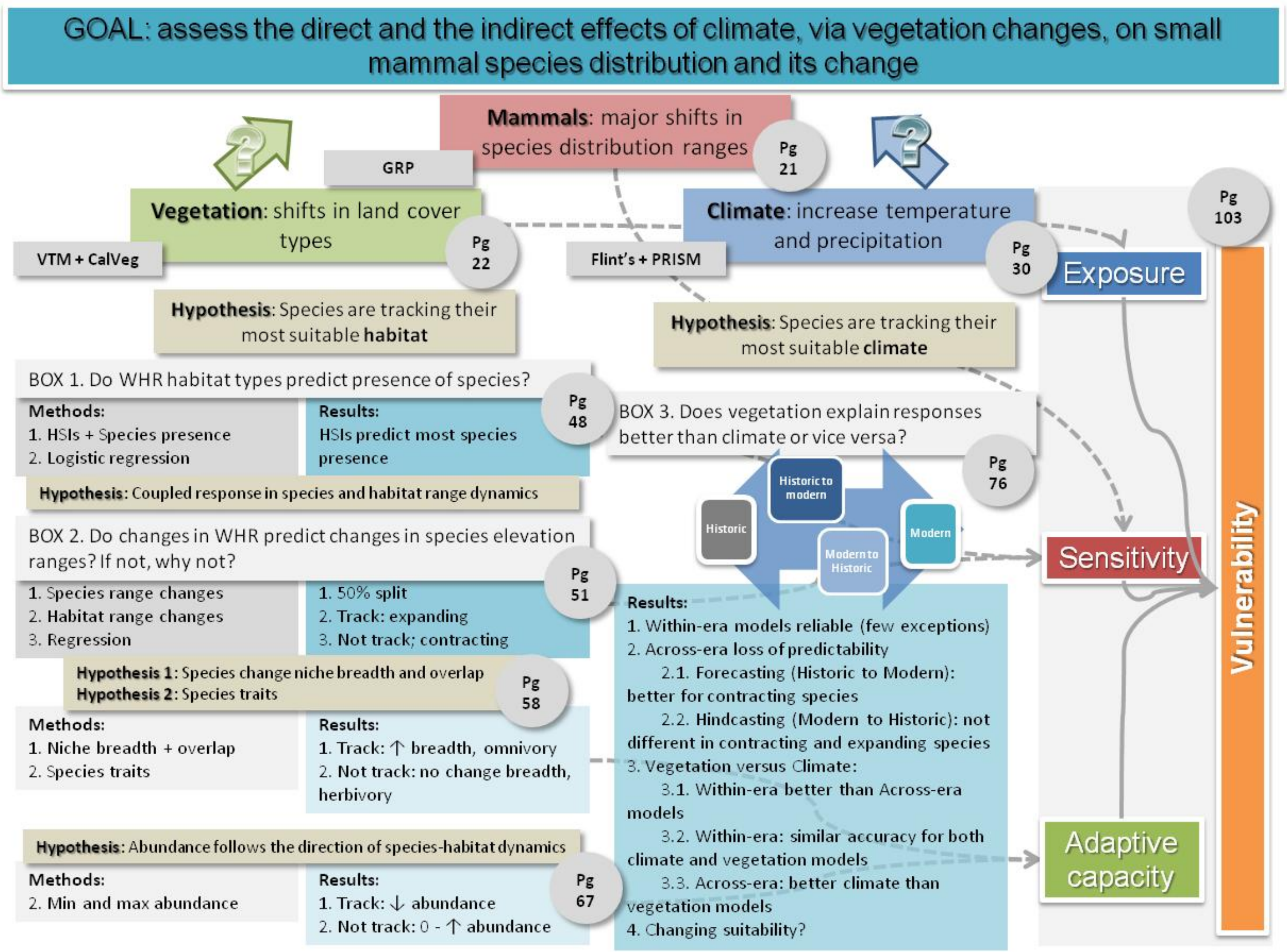
These results suggest that species are not always tracking the most suitable habitat conditions. Species' ability to respond to habitat dynamics is related to the extent to which these dynamics are or are not within their realized niche. If a species' realized niche comprehends all the observed changes in habitat (both vegetation and climate changes), then it is expected that the species will respond to its environmental dynamics; i.e., there will be higher species occupancy in more suitable conditions. However, if dynamics create new environmental spaces that were not previously included in the species' realized niche, two outcomes are possible. Species may experience niche expansion, which would result in increased occupancy in "*perceivably*" less suitable or unforeseen conditions. This could be a case of species occupying environmental spaces outside their realized niche while remaining within their fundamental niche, or it could even be a case of an expansion of the fundamental niche by adaptation. Alternatively, species may experience niche contraction, which would result in decreased occupancy in "*perceivably*" more suitable conditions. This could be a case of change driven deletion of realized niche space, or a reduction in the realized niche by changes in extrinsic factors (such as predator expansion, novel species interactions, and other factors).

To test these hypotheses, we estimated niche breadth and overlap by changing habitat availability, and by changing habitat availability and suitability over time. We found significant differences in niche breadth only when changing both availability and suitability. Species that responded to habitat dynamics showed significantly wider niche breadth, and species that did not respond to habitat dynamics did not significantly change their niche breadth. Further, species traits such as omnivory were more common among habitat-tracking species and herbivory were more common among non-tracking species.

We also questioned whether the dynamics in mammal species abundance would match the observed dynamics in species and habitat ranges, expecting that it would follow the same direction. To do so, we estimated minimum and maximum relative abundance from the capture data and found that non-tracking species either did not change or increased their abundance; whereas, tracking species had lower relative abundance. We also found that historically, tracking species had significantly higher abundance towards the leading edge, while non-tracking species showed a significant increase in abundance at the lagging edge of their modern distribution.

We then used these results to inform our predictions of faunal responses to vegetation and climate (Box 3 in Figure 1), based on the hypothesis that species are likely to be present in their most suitable habitat and climate. We made within-era (historical-to-historical and modern-to-modern) and across-era (historical-to-modern and modern-to-historical) predictions: the first set to assess whether species are modelable; and if so, whether they maintained or changed their habitat and climate associations. The second set were to assess whether models obtained within one era predict accurately across time. We found reliable within-era models, and that species are changing their habitat and climate associations over time. Forecasting produced better models, especially for species that contracted their elevation distribution ranges; whereas, hindcasting did not show differences, except in life zone models and in a trend for vegetation models. Across-era models performed better using climate variables than vegetation. Finally, we used this information to assess species exposure, sensitivity, and adaptive capacity and their vulnerability.

Figure 1. Flowchart of the Analysis and Major Results Presented in This Paper. Circles in the bottom right corner of each of the components indicate the page that contains detailed information on that subject. The smaller boxes in the bottom left corner of the mammal, vegetation, and climate boxes identify the data sets that were used to assess change: VTM (Vegetation Type Mapping); CalVeg (USFS remotely sensed vegetation map); PRISM+BCM (Downscaled climate data produced in the Climate Vulnerability and Adaptation Study for California); GRP(Grinnell Resurvey Project small mammal data); WHR (Wildlife Habitat Relationships classification system), and HSI (Habitat Suitability Index).



GOAL: assess the direct and the indirect effects of climate, via vegetation changes, on small mammal species distribution and its change

Mammals: major shifts in species distribution ranges

Vegetation: shifts in land cover types

Climate: increase temperature and precipitation

Hypothesis: Species are tracking their most suitable **habitat**

Hypothesis: Species are tracking their most suitable **climate**

BOX 1. Do WHR habitat types predict presence of species?

Methods:
1. HSIs + Species presence
2. Logistic regression

Results:
HSIs predict most species presence

Hypothesis: Coupled response in species and habitat range dynamics

BOX 2. Do changes in WHR predict changes in species elevation ranges? If not, why not?

1. Species range changes
2. Habitat range changes
3. Regression

1. 50% split
2. Track: expanding
3. Not track; contracting

Hypothesis 1: Species change niche breadth and overlap
Hypothesis 2: Species traits

Methods:
1. Niche breadth + overlap
2. Species traits

Results:
1. Track: ↑ breadth, omnivory
2. Not track: no change breadth, herbivory

Hypothesis: Abundance follows the direction of species-habitat dynamics

Methods:
2. Min and max abundance

Results:
1. Track: ↓ abundance
2. Not track: 0 - ↑ abundance

BOX 3. Does vegetation explain responses better than climate or vice versa?

Results:
1. Within-era models reliable (few exceptions)
2. Across-era loss of predictability
   2.1. Forecasting (Historic to Modern): better for contracting species
   2.2. Hindcasting (Modern to Historic): not different in contracting and expanding species
3. Vegetation versus Climate:
   3.1. Within-era better than Across-era models
   3.2. Within-era: similar accuracy for both climate and vegetation models
   3.3. Across-era: better climate than vegetation models
4. Changing suitability?

Section 2: Fauna Resurveys: Identifying Sensitive Species

We used the data from the ongoing Grinnell Resurvey Project of the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley (Moritz, Patton et al. 2008), to identify sensitive species. According to the *California Vulnerability and Adaptation Research Project* guidance document, sensitivity is defined as "the degree to which a system is affected, either adversely or beneficially, by climate-related stimuli. The effect may be direct or indirect." Following these guidelines to our specific questions, we considered the species in Table 1 that have or have not significantly changed their elevation range over the last 80 years, including species that contracted and species that expanded their elevation range (contracting species and expanding species, respectively). We defined *contraction* as a significant reduction in the extent of a species' elevation range, which includes upward shifts of lower elevation limits and/or downward shifts of upper elevation limits. We defined *expansion* as a significant increase in the extent of a species' elevation range resulting from downward expansion of lower elevation limits and/or upward shifts of upper elevation limits. These definitions follow those in Moritz, Patton et al. (2008).

Table 1. Species Recorded in the Yosemite Transect, and Observed Elevation Range Dynamics (Moritz, Patton et al. 2008), and Included in this Analysis

Family	Species	Range
Soricidae	*Sorex monticolus*	Expand
Soricidae	*Sorex ornatus*	Expand
Soricidae	*Sorex palustris*	Contract
Soricidae	*Sorex trowbridgii*	No change
Sciuridae	*Otospermophilus beecheyi*	No change
Sciuridae	*Urocitellus beldingi*	Contract
Sciuridae	*Callospermophilus lateralis*	Contract
Sciuridae	*Tamias alpinus*	Contract
Sciuridae	*Tamias quadrimaculatus*	No change
Sciuridae	*Tamias senex*	Contract
Sciuridae	*Tamias speciosus*	No change
Heteromyidae	*Chaetodipus californicus*	Expand
Heteromyidae	*Dipodomys heermanni*	Contract
Cricetidae	*Neotoma cinerea*	Contract
Cricetidae	*Neotoma macrotis*	No change
Cricetidae	*Peromyscus boylii*	No change
Cricetidae	*Peromyscus maniculatus*	No change
Cricetidae	*Peromyscus truei*	Expand
Cricetidae	*Reithrodontomys megalotis*	Expand
Cricetidae	*Microtus californicus*	Expand
Cricetidae	*Microtus longicaudus*	Contract
Cricetidae	*Microtus montanus*	No change
Dipodidae	*Zapus princeps*	Contract

Section 3: Do Observed Shifts in Vegetation Predict Shifts in Fauna?

We considered the small mammal species as potentially affected by climate-related stimuli, and given that the study was conducted in and around a national park where land use change is minimal, we expect that change in distribution and abundance of small mammals will reflect twentieth-century changes in climate and/or vegetation, with the latter being driven by both direct effects of climate change and fire-related dynamics. We assumed this because (1) land cover change in the lower elevation range occurred prior to 1920s with greater logging activities and land use (agriculture and urbanization) transformations occurring circa the turn of the century, (2) Yosemite National Park was established at the turn of the century and park management was responsible for controlling and decreasing land cover change, and (3) management actions included fire suppression policies from 1960–1970s that changed the vegetation density and structure within the park; whereas, later the park reinstated fire to forest management, which resulted in restored plant communities. The changes in vegetation types within the Yosemite transect occurred mostly at middle to higher elevations within the park boundaries (see below for descriptions of vegetation change in the Yosemite transect in the last 80 years). In the subsequent analysis, we assessed the direct and the indirect effects of climate, via vegetation change, on these species' distribution and distribution changes.

Study Area

The study was conducted in the area for which small mammals were historically surveyed by Joseph Grinnell in the early twentieth century and defined in Moritz et al. (2008) as the Yosemite transect (Figure 2). This transect occupies an area of 3,350 square kilometers (km^2), and covers the elevation gradient from the foothills to the higher elevations at Yosemite National Park. Following the gradient in elevation, different plant communities dominate at different elevations: oak woodlands and chaparral dominate at the lower elevations (<1,500 meters [m]); hardwoods, Ponderosa pine, and several other pine species at intermediate elevations (1,000–2,500 m); and lodgepole pine, fir, and hemlock at higher elevations (2,000–3,200 m), with the timberline at about 3,500 m.

Data

Vegetation Data

We used the digital version of the Wieslander and CalVeg land cover maps (Figure 2). The Wieslander data set (http://vtm.berkeley.edu/) corresponds to 1930s Wieslander surveys topographic maps that were georeferenced and hand-digitized on-screen to produce a spatial digital layer of land cover in the 1930s. Given the uncertainty of these assessments from vantage points, this data set was produced at a spatial resolution of 300 m (Thorne, Morgan et al. 2008). Land cover types were subsequently cross-referenced to the California Wildlife Habitat Relationships (CWHR, hereafter WHR) types (http://www.dfg.ca.gov/biogeodata/cwhr/). The original Wieslander data set included a description of the dominant plant species within each patch, which allows for cross-referencing to WHR type.

Wildlife Habitat Relationship types correspond to habitats designed to be used to predict terrestrial vertebrate wildlife species distribution in California. They include 59 habitats (27 tree, 12 shrub, 6 herbaceous, 4 aquatic, 8 agricultural, 1 developed, and 1 non-vegetated), and do not represent a comprehensive classification scheme for the mapping of California's terrestrial vegetation or marine and estuarine habitats. Each habitat is defined by stage (a combination of size and cover class for tree habitats, age and cover for shrub habitats, height and cover for herbaceous habitats, and depth and substrate for aquatic habitats), which is determined by field sampling (http://www.cnps.org/cnps/vegetation/protocol.php). In addition, special habitat elements are also included, such as snags, banks and burrows, aquatic elements, vegetative and animal diet elements, and human-made elements. Each habitat is then described in terms of its structure, composition, and links to other classification schemes, vegetation changes, and duration of stages. Further, each habitat is also described in terms of its biological setting (its position relative to other habitats and wildlife considerations), physical setting (soils, topography, and climate), and geographical distribution in California (http://www.dfg.ca.gov/biogeodata/cwhr/). For each habitat type, there is a comprehensive manual that describes the characteristic criteria; information on classification and mapping the terrestrial vegetation are provided by the Vegetation Classification and Mapping Program (VegCAMP), the Biogeographic Data Branch, and the California Department of Fish and Game (http://www.dfg.ca.gov/biogeodata/vegcamp/).

CalVeg 2000 data were downloaded from the United States Forest Service website (http://www.fs.fed.us/r5/rsl/projects/frdb/layers/ev_mid.html) and corresponds to a semi-automated classification of Landsat imagery data of California onto a vegetation map. The spatial resolution of the original data set was 30 m. Categorical resolution of some land cover classes was relatively low, given the limitations of the classification algorithm to differentiate closely related classes (for example, some conifer classes). These data were fused to available vegetation descriptions for Yosemite National Park and the Sierra and subsequently corrected using field surveys. The finalized map was then upscaled to 300 m and cross-referenced to WHR types (for detailed descriptions see http://www.dfg.ca.gov/biogeodata/cwhr/). The final historical and modern maps correspond to 300 m grids with the categorical resolution that matches the WHR types.

Limitations of the Vegetation Data

Several constraints are associated with evaluating and using time-series land cover data. These include: spatial accuracy, thematic accuracy, cross-referenced thematic accuracy, scale of analysis, and rescaling of data.

The spatial accuracy of the historical vegetation maps was assessed using georegistered historical United States Geological Survey (USGS) topographic quadrangles (used as base maps upon which the historical vegetation patterns were drawn). Geographical information system (GIS) production of the historical vegetation maps registered them onto georeferenced versions of the same-edition USGS topographic quadrangles, using a process that leads to <10 m registration error on 30′ quadrangles (Thorne et al. 2008). The same USGS topographic base maps were then registered to modern topographic maps (Digital Raster Graphics;

http://topomaps.usgs.gov/drg/). Control points were extracted from common locations on both maps (modern and historical USGS topographic quadrangles), and the distance between each location in the historic vegetation map and correspondent historical USGS topographic quadrangles was used to estimate the Root Mean Square Error (RMSE; Lunetta, Congalton et al. 1991), a commonly used metric to assess spatial accuracy. Previous analysis of registration error of the historical USGS topographic quadrangles in relation to modern digital maps produced a registration error of 263 m (Thorne, Morgan et al. 2008), suggesting a final historical map with a minimum mapping unit of 300 m.

In this case, the four primary quadrangles used for this study produced RMS levels of 48 m, 72 m, 83 m, and 161 m. This would have permitted a minimum grid scale of 200 m. However, since a Sierra-wide framework of 300 m had already been produced, we used this level of spatial resolution for the land cover change assessment. Using it produced a more conservative measure of change than using a finer spatial grain would have done.

The modern map spatial accuracy is a part of USGS routine pre-processing levels for Landsat products (http://landsat.usgs.gov/products_productinformation.php). The level of accuracy of the historical map georeferencing (300 m) required the upscaling of the modern map to meet this operational grain size of 300 m and to be deemed reliable for comparisons. Therefore, both historical and modern vegetation maps were rendered to the same 300 m grid. A majority filter was applied to both the historical and the modern vegetation maps to obtain the 300 m final grid-based maps. Although the VTM maps have some polygons smaller than 300 m, this generalization primarily sub-sampled the historical map polygons. The modern vegetation maps have 10 times (or more) polygons per area. For these maps, the 300 m resolution represents a coarsening of the data. However, in each case, the most prevalent vegetation is assigned to each 300 m grid cell. This process had two advantages: it dealt with the spatial uncertainty of in the historic maps, and it provided a common framework, allowing for patterns of change to be analyzed between time periods.

The thematic accuracy of the historical maps is considerably higher than that of the modern vegetation maps. It consists of color-coded polygons hand-drawn on the USGS topographic quadrangles that indicate the vegetation type and are annotated with dominant plant types in rank-order of the percent cover. Every polygon lists at least one, and up to eight species. Plant species combinations for each polygon were concatenated, and labeled as vegetation type using the Manual of California Vegetation (MCV) and then to WHR types (Mayer and Laudenslayer 1988; Thorne, Morgan et al. 2008). These are very commonly used procedures to determine vegetation types and have been verified extensively by plant taxonomists both at the University of California, Davis and the University of California, Berkeley. The historical vegetation maps have considerably more taxonomic detail than the modern vegetation maps, so these historical data are likely more taxonomically accurate than the data for the modern maps.

Thus we considered the thematic accuracy of the historical map reliable. The thematic accuracy of the modern land cover map has two components: the Yosemite Vegetation Map and CalVeg. The Yosemite Vegetation Map contains 220 vegetation types, which can all be reduced to WHR types. It therefore has a high level of thematic accuracy. The CalVeg map thematic accuracy, where reported for Sierran forests, is typically only 50 to 70 percent and can be low for some classes, such as hardwood and mixed hardwood conifer classes. It has been stated by the USFS that the CalVeg product is mainly for regional expansion of plot measurements, and not for detailed spatial modeling. Nonetheless we believe this data set is still usable in our analysis since because (1) we merged it with the Yosemite Vegetation Map, which covers the majority of our area (the Yosemite map extends more than 1 km beyond the edges of the park), and (2) we upscaled the final map to a minimum mapping unit of 300 m, which minimizes certain thematic registration errors.

There were few viable alternatives to consider in representing the vegetation in both time periods. Using the information on the vegetation plots that were conducted by Wieslander and his team, as we expected, would have been questionable because the plots that occur in our Yosemite transect are distant from the locations where the mammals were trapped, and many of them have not been revisited (but see Crimmins, Dobrowski et al. 2011; Dobrowski, Thorne et al. 2011; Dolanc, Thorne et al. in press). We also expected to be able to use the information on habitat from the field notes of Joseph Grinnell and his colleagues, since they were also tasked to delimit life zones (vegetation that corresponds to elevation bands sensu Merriam life zones) in the Yosemite transect. However, the information provided in these notes was non-systematic and spatially restricted, without any relative concise description of the habitat where trapping campaigns were conducted. We therefore eliminated the possibility of using these alternative sources of data to complement our analysis, and decided instead to use the VTM maps compared with the modified CalVeg data. We believe that the rescaling of both maps resulted in comparable spatial and thematic accuracy, which allows for cross-temporal comparisons. This matching of the scales at which vegetation, climate, and mammal data were collected added reliability to the integration of the data sets (see below).

Changes in Vegetation in the Yosemite Transect

In the Yosemite transect there are 33 WHR types. The dominant land cover type in historical time was ponderosa pine (412.7 km^2, 12 percent), followed by lodgepole pine (354.7 km^2, 11 percent), and annual grasslands (336.2 km^2, 10 percent) In contemporary time, Sierran mixed conifer and annual grasslands are co-dominant (SMC: 519.6 km^2; AGS: 517.8 km^2; both 15 percent) (Table 2, Figures 2 and 3). From 1930s to 2000s, the land cover that increased most was Sierra Mixed Conifer (from 17.4 to 519.6 km^2), at the expense of decreases mainly in Ponderosa pine (from 412.7 to 116 km^2) and white fir (from 140.4 to 5.2 km^2; Table 2; Figure 3). Other relevant transitions are the increase in mountain hardwood from 95.8 to 264.3 km^2, and the decrease in chamise-redshank chaparral from 278.1 to 1.5 km^2, blue oak woodlands from 196.7 to 24.6 km^2, and barren areas from 228.6 to 1.6 km^2. The changes in WHR categories add up to 1, and this reflects all the net changes.

Table 2. Area and Percentage Cover of Each WHR Type in the Yosemite Transect in Historical and Modern Time, Ordered by Dominant Land Cover Type

WHR name	WHR	Historical (km^2)	Historical (%)	WHR name	WHR	Modern (km^2)	Modern (%)
Ponderosa Pine	PPN	412.74	12.31	Sierran Mixed Conifer	SMC	519.57	15.49
Lodgepole pine	LPN	354.69	10.58	Annual grassland	AGS	517.77	15.44
Annual grassland	AGS	336.15	10.02	Sub-alpine conifer	SCN	287.55	8.57
Chamise-Redshank chaparral	CRC	278.10	8.29	Montane hardwood	MHW	264.33	7.88
Barren	BAR	228.60	6.82	Douglas fir	DFR	220.77	6.58
Sub-alpine Conifer	SCN	225.63	6.73	Closed-cone pine – Cypress	CPC	208.44	6.21
Blue Oak – Pine	BOP	216.63	6.46	Blue oak – Pine	BOP	205.29	6.12
Blue Oak woodland	BOW	196.74	5.87	Mixed chaparral	MCH	168.12	5.01
Red fir	RFR	151.74	4.52	Lodgepole pine	LPN	161.01	4.80
Jeffrey Pine	JPN	146.43	4.37	Lacustrine	LAC	141.84	4.23
White fir	WFR	140.40	4.19	Red fir	RFR	131.40	3.92
Lacustrine	LAC	126.90	3.78	Ponderosa pine	PPN	116.01	3.46
Montane chaparral	MCP	97.47	2.91	Jeffrey pine	JPN	96.66	2.88
Montane hardwood	MHW	94.77	2.83	Montane hardwood-conifer	MHC	94.68	2.82
Mixed chaparral	MCH	86.49	2.58	Montane chaparral	MCP	48.96	1.46
Agriculture	AGR	68.49	2.04	Agriculture	AGR	34.02	1.01
Wet meadow	WTM	62.28	1.86	Juniper	JUN	27.18	0.81
Douglas fir	DFR	46.53	1.39	Blue Oak woodland	BOW	24.57	0.73
Sierran mixed conifer	SMC	17.37	0.52	Wet meadow	WTM	23.31	0.69
Sage brush	SGB	15.30	0.46	Sage brush	SGB	13.86	0.41
Eastern Pine	EPN	12.15	0.36	Low sage	LSG	11.16	0.33
Juniper	JUN	11.43	0.34	Eastern pine	EPN	8.10	0.24
Closed-cone pine – cypress	CPC	10.53	0.31	Mountain riparian	MRI	6.57	0.20
Mountain riparian	MRI	5.94	0.18	White fir	WFR	5.22	0.16
Aspen	ASP	2.79	0.08	Aspen	ASP	4.86	0.14
Valley riparian	VRI	2.25	0.07	Unknown	UKW	4.77	0.14

Table 2 (cont.). Area and Percentage Cover of Each WHR Type in the Yosemite Transect in Historical and Modern Time, Ordered by Dominant Land Cover Type

WHR name	WHR	Historical (km2)	Historical (%)	WHR name	WHR	Modern (km2)	Modern (%)
Urban	URB	1.53	0.05	Urban	URB	2.07	0.06
Montane hardwood-conifer	MHC	1.44	0.04	Barren	BAR	1.62	0.05
Unknown	UKW	0.72	0.02	Chamise-redshank chaparral	CRC	1.53	0.05
Low sage	LSG	0.63	0.02	Valley riparian	VRI	1.35	0.04
Pinyon-Juniper	PJN	0.45	0.01	Pinyon-Juniper	PJN	0.90	0.03
Valley oak woodland	VOW	0.45	0.01	Freshwater emergent wetland	FEW	0.27	0.01
Freshwater emergent wetland	FEW	0.18	0.01	Valley Oak woodland	VOW	0.18	0.01
	Total	3353.94			Total	3353.94	

Figure 2. Yosemite Transect Land Cover Change. Historical land cover was assessed using the Wieslander land cover maps and Modern land cover was assessed using CalVeg classification results, both crosswalked to WHR types (Wildlife Habitat Relationships type, sensu CDFG). Names correspond to trapping locations.

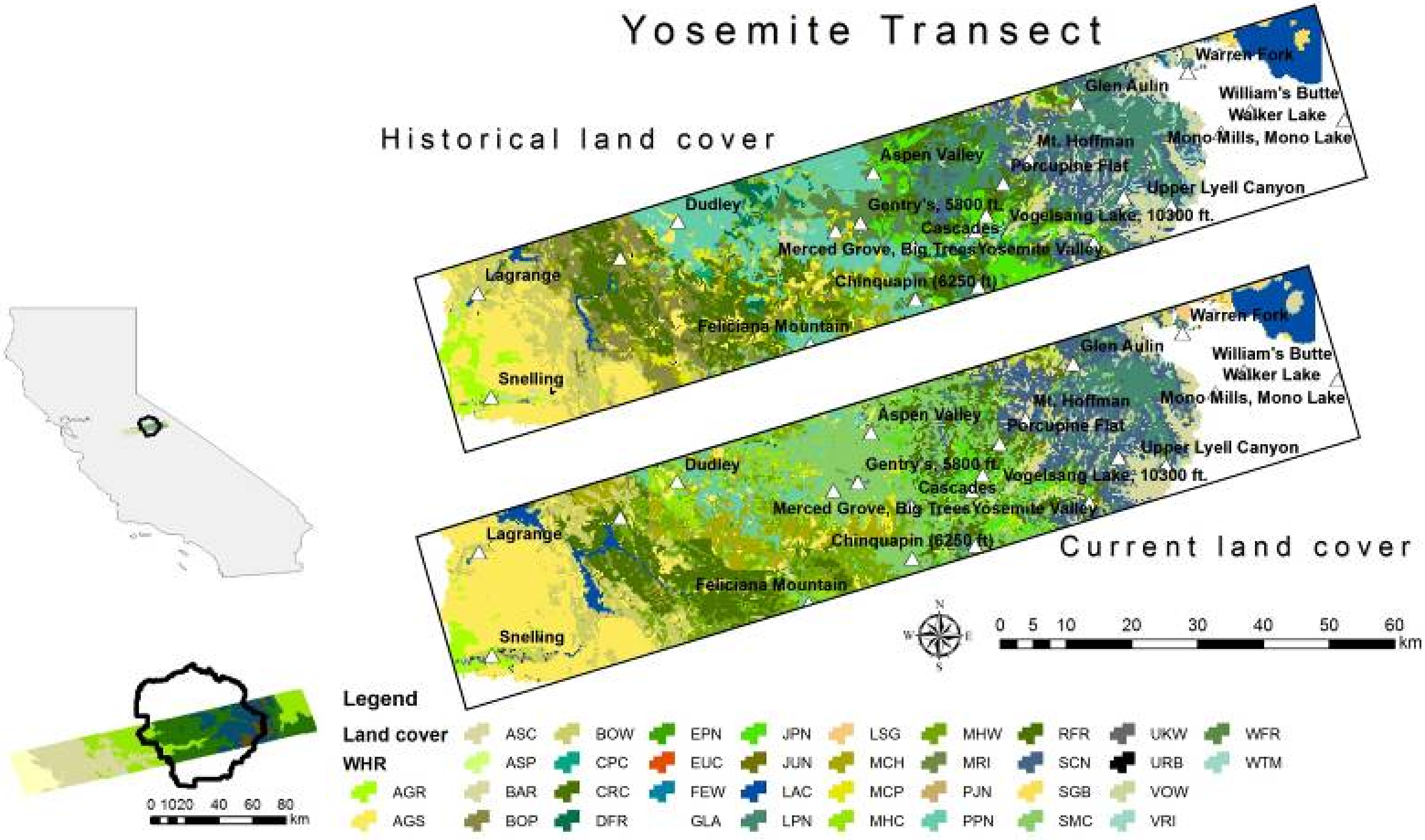
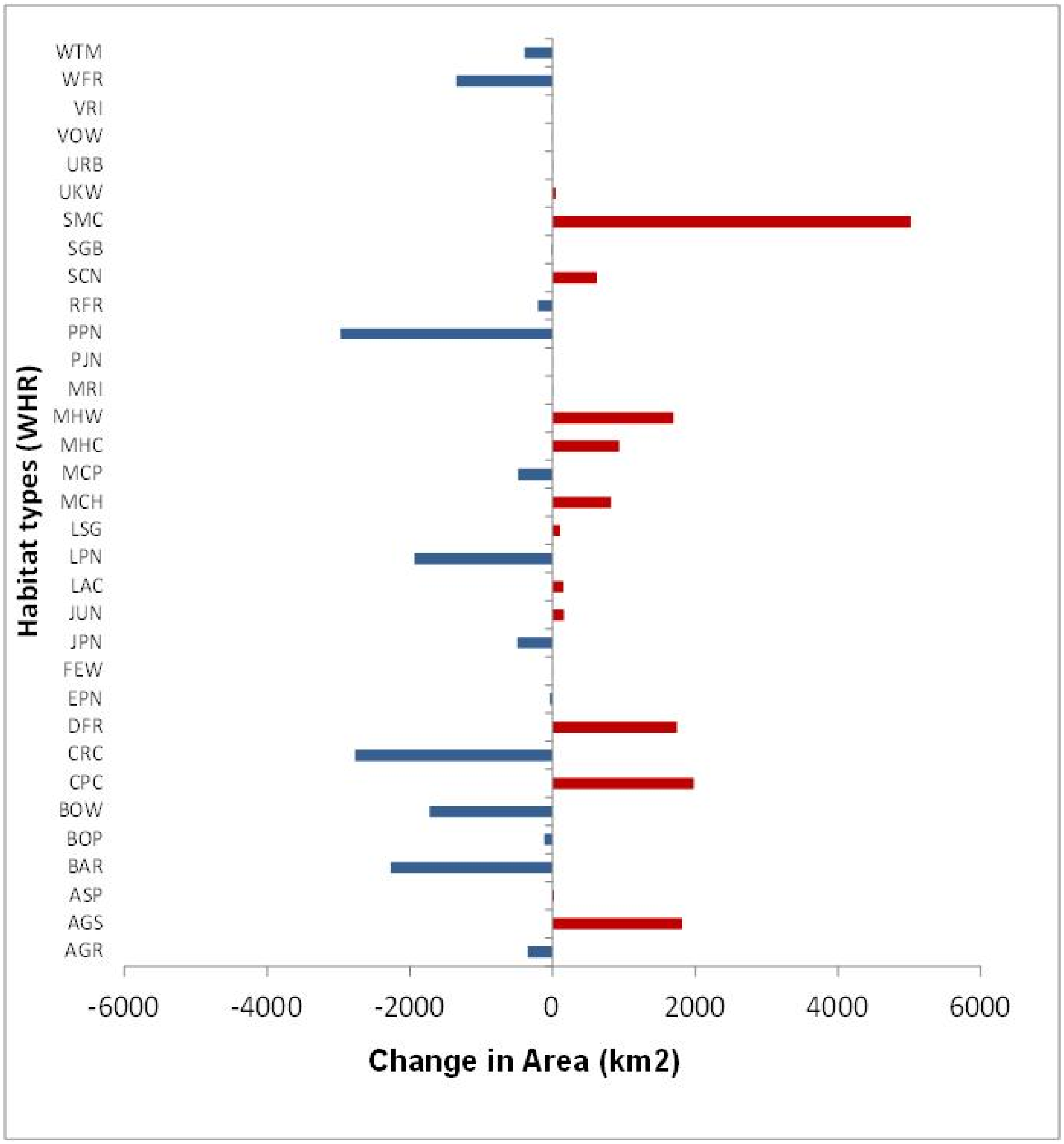
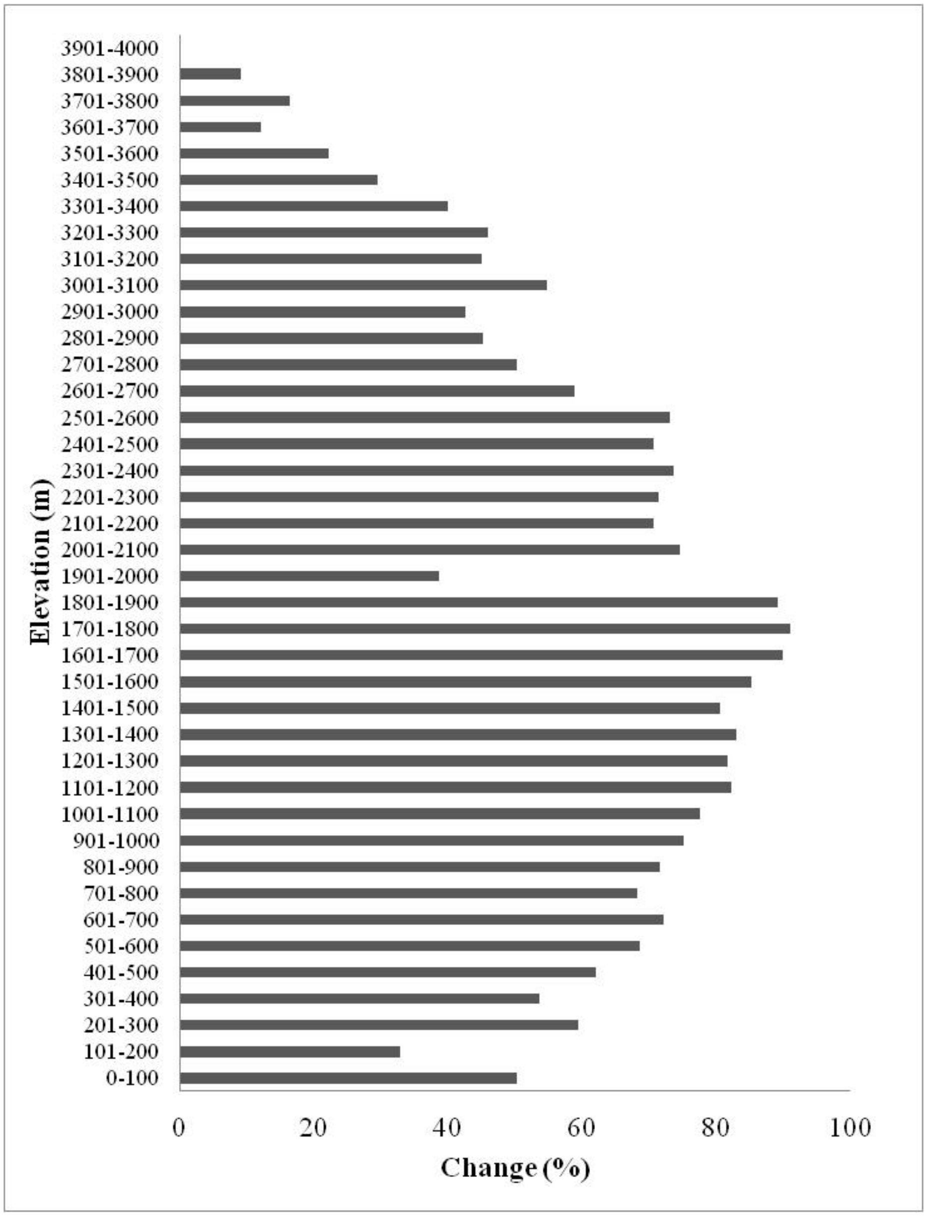


Figure 3. Yosemite Transect Change in Area Covered by Each WHR Land Cover Type. Historical land cover was obtained from the Wieslander land cover maps, and modern land cover was assessed using CalVeg classification results, both crosswalked to WHR types (Wildlife Habitat Relationships type, sensu CDFG). Blue bars represent decreases and red bars represent increases.



In the Yosemite transect, land cover changes were variable per elevation band (Figure 4). We extracted the corresponding 300 m cells per each elevation bin (100 m intervals), and their land cover in the historical and modern maps. We then estimated how many cells changed land cover type between the two time periods, and divided this value by the number of cells at that elevation band to obtain a percentage change (Figure 4). It can be observed that most of the change (greater than 70 percent) occurred between 800 m and 1,900 m. These elevations correspond mostly to the lower extent of Yosemite National Park (700 m to 3,900 m), suggesting that most of the land cover change in the Yosemite transect in the last 80 years is linked with park management practices. Further, it shows a much lower rate of land cover change at the lower and highest elevations; the former because land cover change occurred on the turn of the twentieth century with clear-cut, agricultural conversion, and logging, and the latter likely because there is little human influence at these higher elevations.

Figure 4. Percent Change in Land Cover Types in the Yosemite Transect Per Elevation Band. Historical land cover was obtained from the Wieslander land cover maps, and modern land cover was obtained from the CalVeg fused product.



Climate Data

We used the downscaled climate data produced by James Thorne, and Alan and Lorraine Flint (USGS), under the contract for this project and mapped at a spatial resolution of 270 m (Table 3).

The production and validation of these data are presented in another study (Thorne et al. in review) from the overall PIER Vulnerability and Assessment project. The downscaled historical climate data were derived from the PRISM data set (http://www.prism.oregonstate.edu/; Daly, Gibson et al. 2002), which had an original native 4 km^2 grid operational scale, and which provides Tmin, Tmax, and PPT on a yearly and monthly time step. An ecohydrological model, the Basin Characterization Model (BCM) uses these values to produce a series of variables that potentially affect plant response to changing climatic conditions more directly (Table 3; Flint and Flint 2012).

The yearly and monthly weather products were converted into 30-year averages, which reduces the potential bias from weather cycles (for example, the Pacific Decadal Oscillation) and those of extreme weather events. We used these 30-year variables to assess change in climate and hydrological conditions within our study area. This approach using PRISM-based products has been widely used by the scientific community (for example see Ackerly, Loarie et al. 2010). However, to be able to link the climate data to the vegetation and mammal data, it was necessary that the data was at matching scales of collection. Above we presented the scale of analysis (the minimum mapping unit) of the vegetation maps, and how it was restricted by the spatial resolution of the historical maps geo-registration. Likewise, the climate data needed to approximate this scale to exclude the possibility of a scale effect rather than a biologically relevant result. Thus, we used the 270 m grid scale climate data produced under the *Climate Vulnerability and Adaptation Study for California* (Table 3).

These climate variables were created for three past 30 year periods (1911–1940, 1941–1970, and 1971–2000). We used the 1911–1940 climate variables to represent the historical climate conditions because it brackets the periods in which vegetation and mammal data were acquired. We used the 1971–2000 climate variables to represent the modern climate and because this was the 30-year period closest to the modern resurvey period.

Table 3. Downscaled Climate Variables Produced under This Project Using the BCM (Basin Characterization Model); Flint and Flint 2012)

Variable	Code	Creation Method	Units	Equation/Model	Description
Maximum Temperature	Tmax	Downscaled	°C	Model input	The maximum monthly temperature averaged annually
Minimum Temperature	Tmin	Downscaled	°C	Model input	The minimum monthly temperature averaged annually
Precipitation	PPT	Downscaled	mm	Model input	Total monthly precipitation (rain or snow) summed annually
Potential Evapotranspiration	Pet	Modeled/ pre-processing input for BCM	mm	Modeled* on an hourly basis from solar radiation that is modeled using topographic shading, corrected for cloudiness, and partitioned on the basis of vegetation cover to represent bare-soil evaporation and evapotranspiration due to vegetation	Total amount of water that can evaporate from the ground surface or be transpired by plants summed annually
Runoff	Run	BCM	mm	Amount of water that exceeds total soil storage plus rejected recharge	Amount of water that becomes stream flow, summed annually
Recharge	Rch	BCM	mm	Amount of water exceeding field capacity that enters bedrock, occurring at a rate determined by the hydraulic conductivity of the underlying materials; excess water (rejected recharge) is added to runoff	Amount of water that penetrates below the root zone, summed annually
Climatic Water Deficit	Cwd	BCM	mm	Potential evapotranspiration minus Actual evapotranspiration	Annual evaporative demand that exceeds available water, summed annually

Limitations of the Climate Data

There are several limitations of using climate reconstructions based on interpolation of weather data from meteorological stations: these limitations include (1) meteorological station representation over time, (2) weather-recording methods, (3) interpolation methods, (4) validation, and (5) climate norms from weather patterns. Meteorological stations density in California changed substantially over time, with more stations providing more accurate data in the present than in the past; however, more than 2,000 stations were operating since 1895 (not all used in PRISM data), adding credibility to the weather data used (DiLuzio, Johnson et al.

2008). With technological developments, weather-recording devices have changed over time (Daly, Gibson et al. 2007); however, in many cases redundant systems were implemented to allow for continuation of data acquisition and calibration of the new data sets. Interpolation techniques are affected by density of points on which they base the estimation of in-between values. Given the increase in meteorological station density over time in California, it is likely that modern interpolation produces much better results than past interpolation. Nonetheless, cross-validation procedures were implemented into the PRISM algorithm to account for sampling density and better match the accuracy of the interpolations in modern and past time periods (DiLuzio, Johnson et al. 2008). Validation is also conducted simultaneously with the interpolation, where some stations are removed at a time so that the results of the interpolation can be compared with and without the stations. This is an iterative procedure that allows assessing the accuracy of the interpolation (Daly, Gibson et al. 2002).

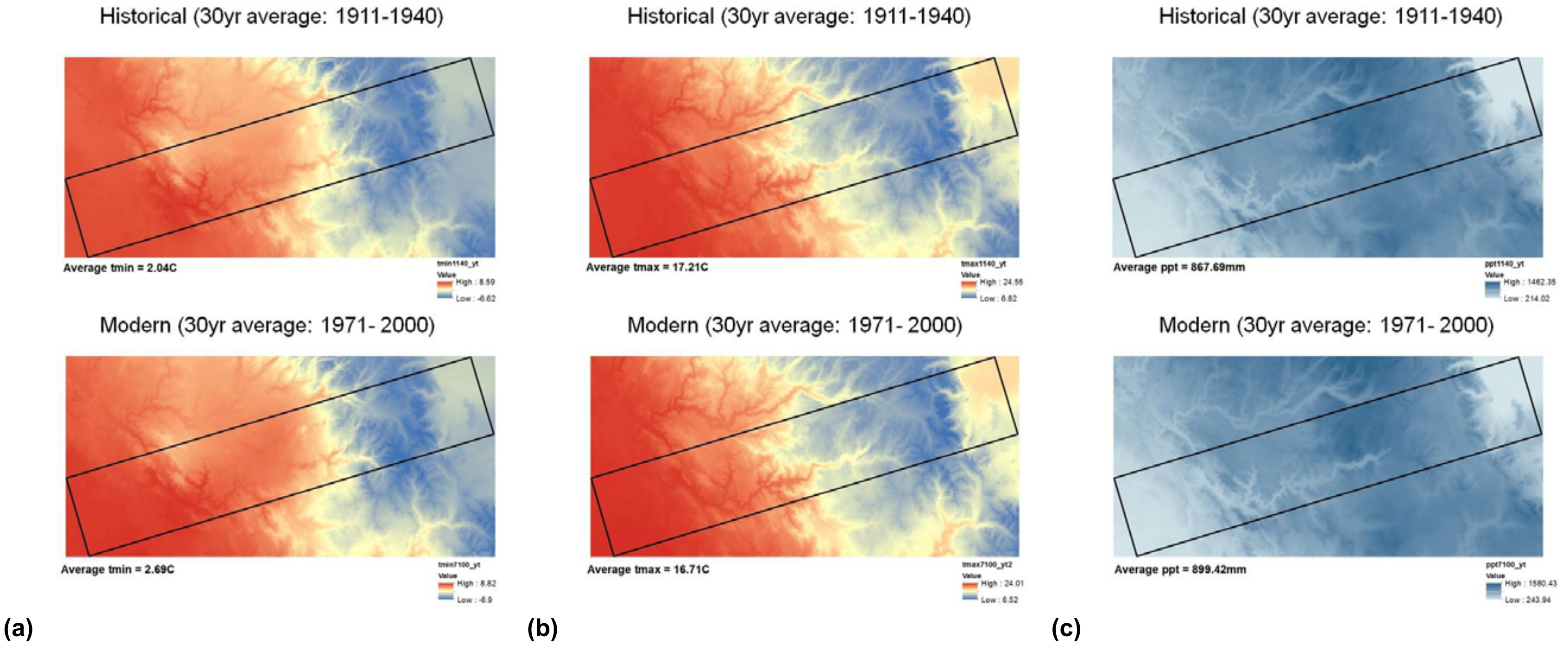
We used historical climate data derived from a PRISM data set with a native 4 km resolution that had already been further downscaled to 270 m grid scale using a modified spatial gradient and inverse distance squared (GIDS) (Flint and Flint 2012). This was the scale at which the BCM was applied. The BCM is an ecohydrological model that uses temperature and precipitation as inputs, in combination with static environmental variables such as soils, geology, and topography to produce maps of a series of variables that are potentially more directly tied to plant response to climate change, such as soil moisture and climatic water deficit (Flint and Flint 2012; Thorne, Boyton et al. 2012). The BCM has the advantage that individual modules in the overall model are explicit, and can be updated as better input data become available. It can also be calibrated by summarizing grid-level predictions of runoff to watersheds to get discharge. Discharge can be calculated for the same pour points where stream gauge data exist, and therefore the accuracy of the model may be assessed and calibrated by adjusting the bedrock permeability.

Given that there are not many alternatives to using these data sets to assess climate changes in the last 80 years in California, and that the BCM results were cross-compared with about 140 streams in California for calibration, we used these data in the subsequent analysis and consider them to be robust and likely to yield biologically informative results.

Climate Changes in the Yosemite Transect

In the Yosemite transect, between 1911–1940 and 1971–2000, there was a change in average annual minimum temperature from 2.04°C to 2.69°C (35.7°F to 36.8°F), in average maximum temperature from 16.71°C to 17.21°C (62.1°F to 62.9°F), and in average precipitation from 867.69 millimeters (mm) to 899.42 mm (Figure 5). These are relatively low changes in precipitation and temperature for 30-year norms. To better depict these changes, we assessed which areas of the Yosemite transect were most affected by changes in minimum temperature (Tmin), maximum temperature (Tmax) and precipitation (PPT). We first calculated the change in Tmin, Tmax, and PPT as the difference between the modern 30-year average (1971–2000) and the historical 30 year average (1911–1940). Then we used principal component analysis to assess the effect of these changes in the different areas of the Yosemite transect.

Figure 5. Yosemite Transect (a) Minimum Temperature (°C), (b) Maximum Temperature (°C), and (c) Precipitation between 1911–1940 and 1971–2000. We used the downscaled climate data produced in this project. Black rectangle indicates the boundaries of the Yosemite transect. Temperature: Red indicates higher values and blue indicates lower values; Precipitation: darker blue indicates high precipitation and lighter blue indicates low precipitation.



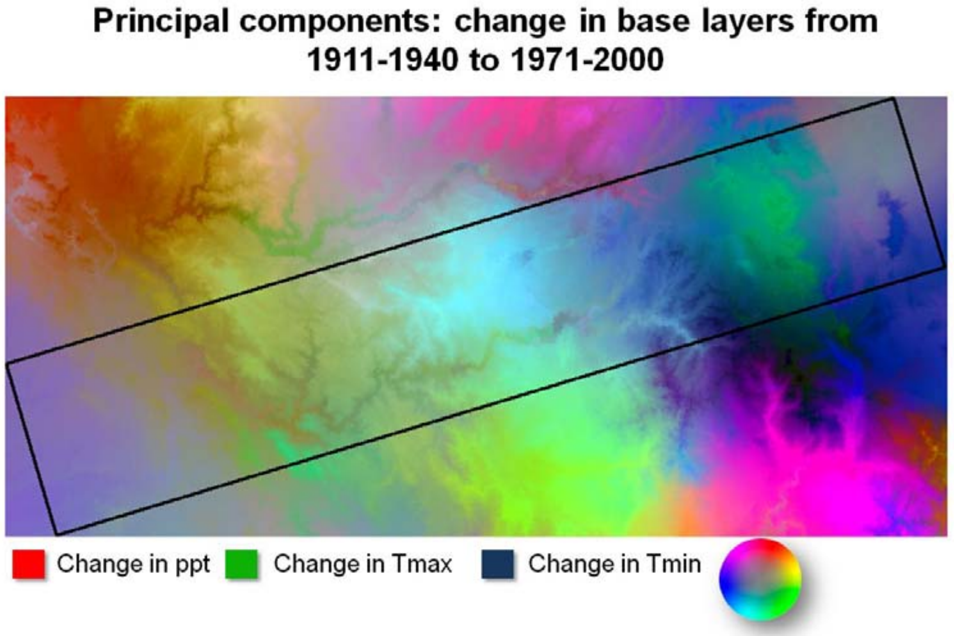
Principal components analysis (PCA) is an ordination technique that allows for determining the composite axis that explains the maximum variance of the data, and then creates orthogonal axes (i.e., perpendicular axes) to that first axis, with the number of orthogonal axes matching the number of input variables. It uses matrix algebra to estimate eigenvectors from the covariance matrix between the variables and their respective eigenvalues. These eigenvectors are then used to create a linear formula that is applied to transform each cell value relative to each of the new axes. In this case, we created a PCA with the change in Tmin, Tmax, and PPT using the covariance matrix. The relative contribution of each variable (or variable loading) to each PCA axis is estimated by the eigenvector associated with that PCA axis, and its magnitude is determined by its eigenvalue (also known as the percentage of variance explained). The three PCA axes can then be used as the three bands (red, green, and blue) in an RGB image to display the contribution of each variable in space.

For the Yosemite transect, each of the three principal component axes were related to a different variable as determined by the eigenvector for each PCA axis. The first axis (PCA1) was mostly associated with change in precipitation, the second axis (PCA2) with the change in maximum temperature, and the third axis (PCA3) with the change in minimum temperature (Table 4). PCA1 has the greatest magnitude with higher percentage of variation explained (99percent), thus being the most significant axis. Nonetheless, because we ran PCA on the covariance matrix, which does not standardize the variables, we represent all the three spatially. This reveals that the three PCA axes are located in very different areas, with a higher contribution of change in precipitation in the northwestern corner (red), a higher contribution of change in minimum temperature in the east (blue), and a change in maximum temperature (green) at the higher elevations (Figure 6).

Table 4. Relative Contribution of the Change in Precipitation (ΔPPT), Change in Maximum Temperature (Δtmax), and Change In Minimum Temperature (Δtmin) to the Principal Component Analysis Axes (PCA1, PCA2, PCA3), and Percentage of Variation Explained by Each Axis

	ΔPPT (mm)	ΔTmax (°C)	ΔTmin (°C)	% variance explained
PCA1	0.99	-0.003	-0.002	99.95
PCA2	-0.003	-0.922	-0.387	0.03
PCA3	0.003	0.387	0.922	0.02

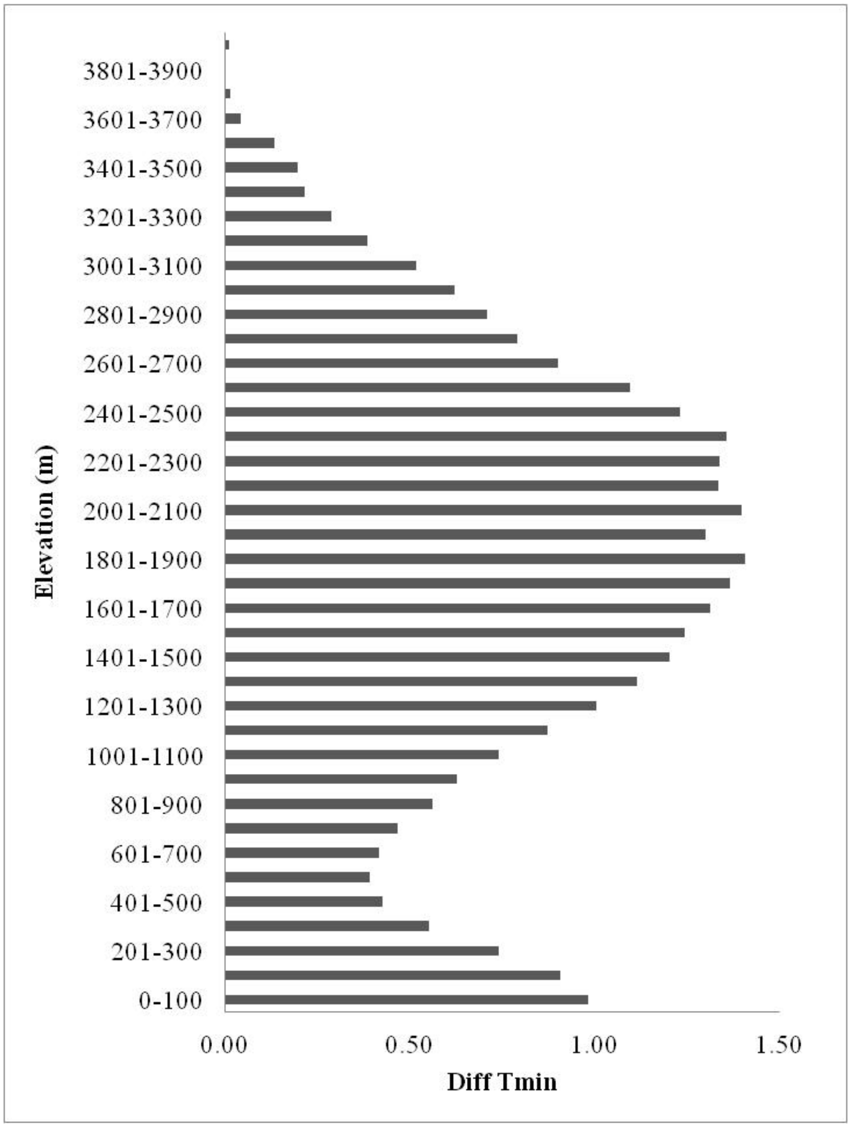
Figure 6. Principal Components Analysis on the Change in Minimum Temperature, Maximum Temperature, and Precipitation Between 1911–1940 and 1971–2000 for the Yosemite Transect Area. Red represents the change in precipitation (PCA1), green represents the change in maximum temperature (PCA2), and blue represents the change in minimum temperature (PCA3). All in-between colors represent a contribution of two or more PCA axes as indicated in the color circle. Low change values in the original variables are depicted as low color saturation values, and high change in the original variables are depicted in higher color saturation values, thus more saturation indicates more change. Positive values (high saturation colors) in the original values indicate an higher value in the variable in the modern time; negative values (low saturation colors) indicate higher values in the historic time.


Principal components: change in base layers from 1911-1940 to 1971-2000

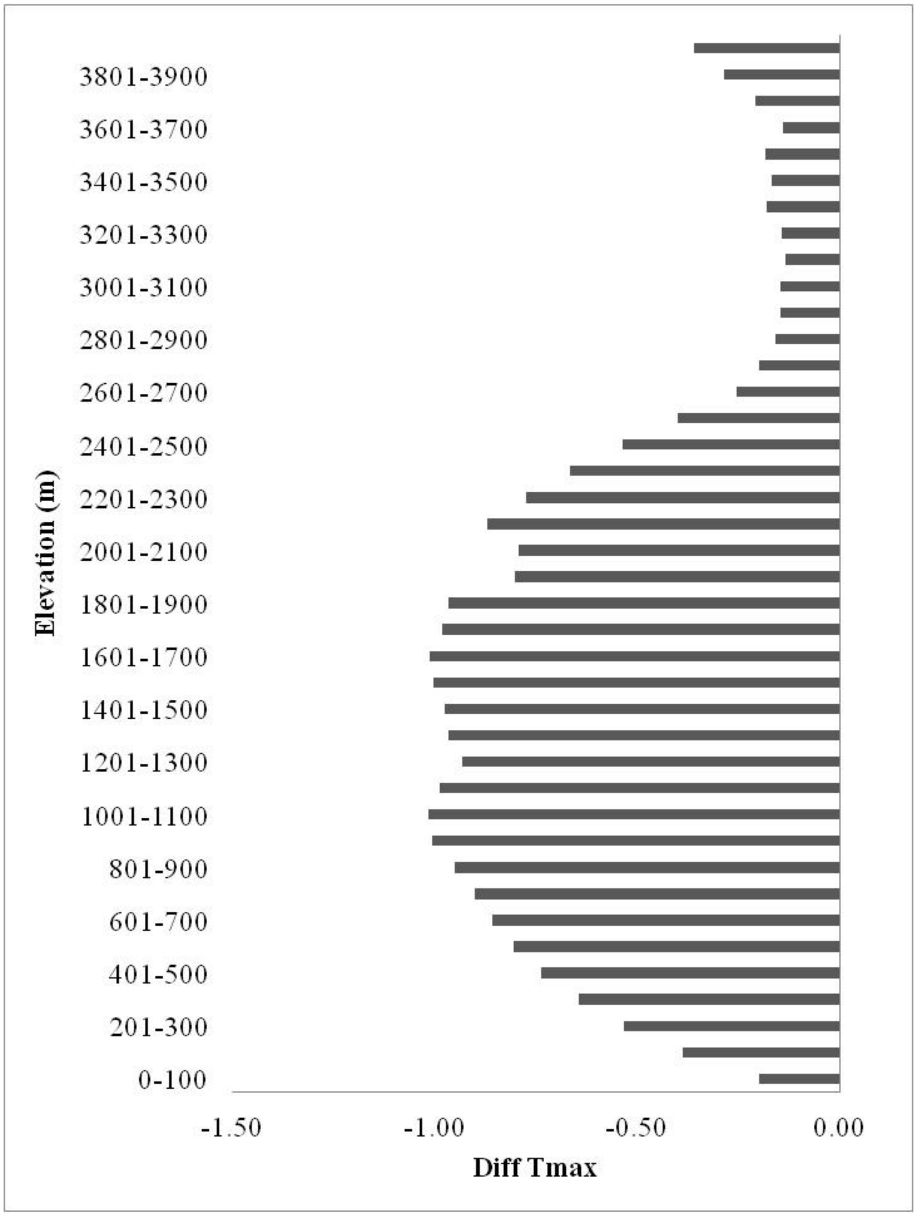
In comparison to Figure 4, we also estimated the percent change in climate variables per elevation band in the Yosemite transect. We extracted the corresponding 300 m cells per each elevation bin (100 m intervals), and their 30 year climate norms (minimum and maximum temperature, precipitation, and climatic water deficit) in the historical and modern periods. We then estimated how many cells changed climate value type between the two time periods, and divided this value by the number of cells at that elevation band, to obtain a percentage change (Figure 7). It can be observed that different climate variables changed at different elevation bands.

Figure 7. Percent Change in Climate Variables in the Yosemite Transect per Elevation Band. Historical climate corresponds to the 1911–1940 average and the modern climate corresponds to the 1971–2000 average. Each figure corresponds to a climate variable: (a) minimum temperature, (b) maximum temperature, (c) precipitation, and (d) climatic water deficit. For formulations on these variables see Table 3.

(a)



(b)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2801-2900
2601-2700
2401-2500
2201-2300
2001-2100
1801-1900
1601-1700
1401-1500
1201-1300
1001-1100
801-900
601-700
401-500
201-300
0-100
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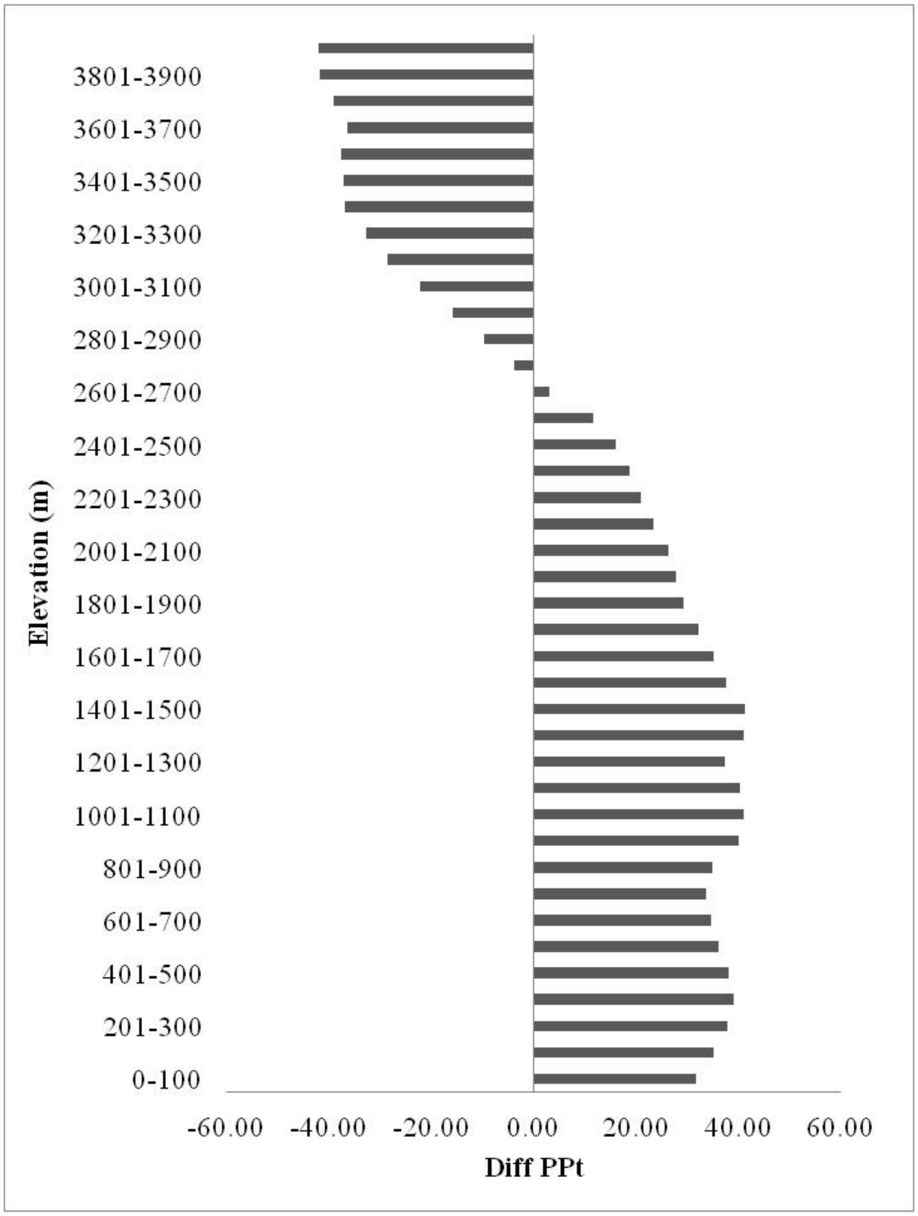
-0.50
0.00
Diff Tmax

(c)


3801-3900
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2601-2700
2401-2500
2201-2300
2001-2100
1801-1900
1601-1700
1401-1500
1201-1300
1001-1100
801-900
601-700
401-500
201-300
0-100
Elevation (m)
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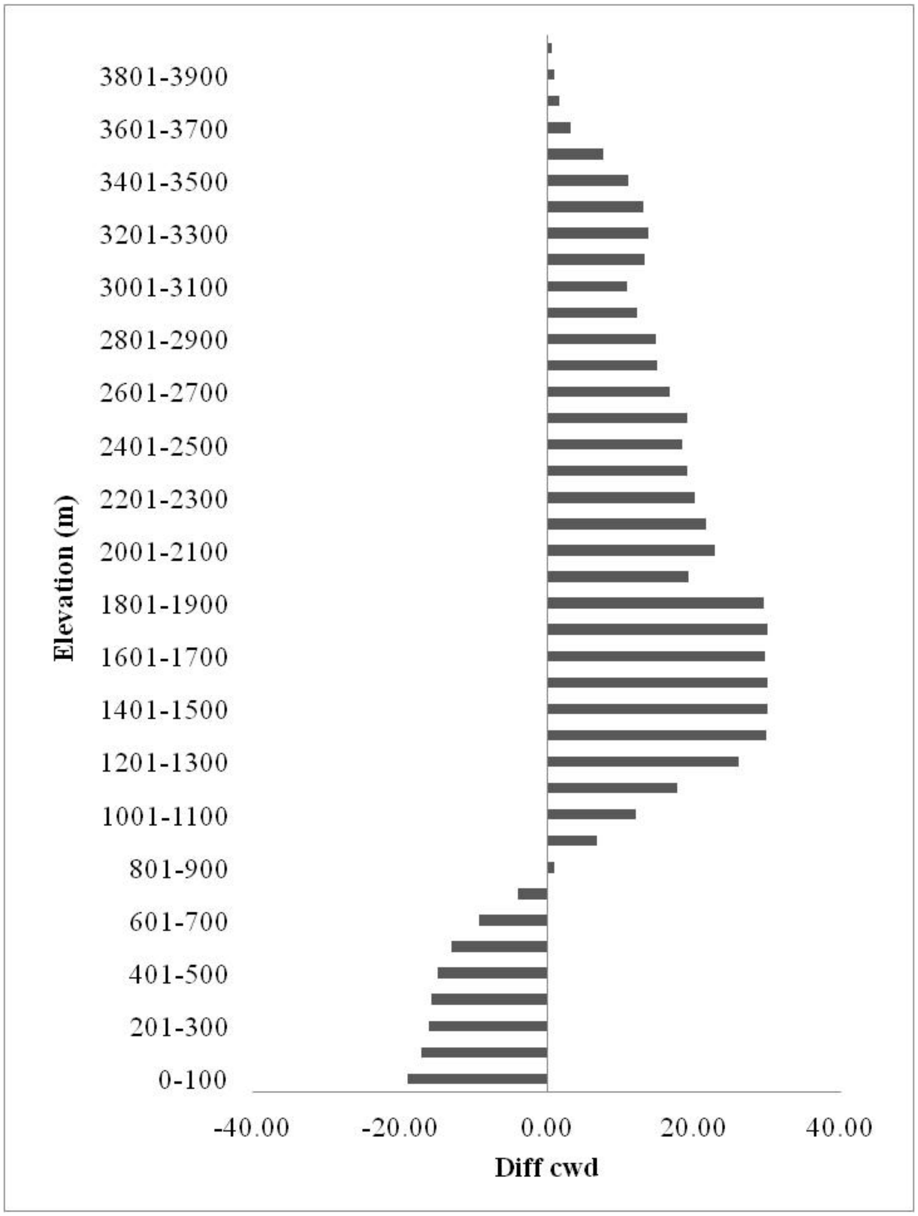
-20.00
0.00
20.00
40.00
60.00
Diff PPt

(d)



3801-3900
3601-3700
3401-3500
3201-3300
3001-3100
2801-2900
2601-2700
2401-2500
2201-2300
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1801-1900
1601-1700
1401-1500
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601-700
401-500
201-300
0-100
Elevation (m)
-40.00
-20.00
0.00
20.00
40.00
Diff cwd

Small Mammal Data

We selected the species in Table 1, and of the 23 analyzed species, 9 contracted, 6 expanded, and 8 showed no changes in their elevation distribution ranges. We used these range dynamics to categorize the species in this analysis.

Mammal species data were from two data sets: (1) presence and capture history data recorded during trapping campaigns throughout the Yosemite Transect (Figure 2 shows trapping locations), and (2) collection of museum records archived in the Mammal Networked Information System - MANIS (http://manisnet.org/) and the Multi-Institution, multi-museum database - Arctos (http://arctos.database.museum/home.cfm).

The presence and capture history data come from the ongoing Grinnell Resurvey Project of the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley (Moritz, Patton et al. 2008). These data consist of the original data collected by Joseph Grinnell and colleagues while documenting biological diversity in the state (Grinnell 1924; Moritz, Patton et al. 2008). This effort involved the setting up of trapping campaigns across all elevations within the Yosemite transect, while documenting the Merriam life zones that defined the Yosemite transect. (The effort also included the Lassen, Southern Sierras, Central Coast and San Diego transect, but those data were not considered in this analysis.) The Yosemite transect data were recorded in extensive field notebooks, archived at the Museum of Vertebrate Zoology, and subsequently made available digitally through the Museum website (http://bscit.berkeley.edu/mvz/volumes.html). Craig Moritz and his colleagues were instrumental in facilitating a resurvey project that aimed at repeating the same sampling in approximately the same locations as the historical surveys to assess whether changes have occurred. It can be argued that these data do not lend themselves readily to comprehensive analyses, as the original Grinnell and colleagues surveys were not intended to establish a standardized baseline for comparison with repeat samples up to nine decades later. Nonetheless, this analysis aims at exploring the potential of these data sets and their integration with the vegetation and climate data sets described above to decipher change patterns and potential correlates within the known limitations of the data. As far as we know, this is one of the few data sets that offer accurate comparisons across time.

The second data set used was a collection of mammal presence data from museum databases (Arctos, http://arctos.database.museum/home.cfm and MANIS, http://manisnet.org/) in historical and modern time in the Yosemite transect. These data sets were used for the modeling exercise in the section of modeling faunal responses to vegetation and climate.

Limitations of the Small Mammal Data

The historical data from Grinnell and colleagues surveys presented several challenges with respect to descriptions of sampling design and limited geographic information. For these reasons, the proposed integration of these data into the current paper created the possibility of a scale effect between the small mammal data and the vegetation and climate data sets.

The historical data set was intended as a survey of the diversity within the State of California. The data collection methods consisted of traplines set at different locations across the Yosemite transect, with a variable number of traps per trapline (averaging about 30) set between three and five nights consecutively. This systematic approach was the basis to justify a comparison with the sampling that Grinnell and his colleagues performed, because the same methods were applicable and the survey design repeated. Using that as a foundation, modern analytical tools enable us to build the details of the survey method into the analytical framework to reduce the effects of the sampling design.

Species capture histories were used to estimate whether there were significant changes in species elevational distribution range in an occupancy modeling platform. Occupancy modeling (MacKenzie, Nichols et al. 2003; Bailey, Simons et al. 2004; MacKenzie and Nichols 2004; Linkie, Dinata et al. 2007; Betts, Rodenhouse et al. 2008; Nichols, Bailey et al. 2008) is a statistical framework based on a series of probabilistic arguments that allow for a simultaneous estimation of a species' probability of detection (p) and its probability of occupancy (ψ). Very few species are likely to be so conspicuous that they will always be detected when present (MacKenzie, Nichols et al. 2003), thus any estimate of species occupancy, colonization, or extinction are likely biased.

To correct for the error associated with the lack of detection of a species when present (i.e., false absence), repeated sampling of the same location is necessary (i.e., a trap set for three or more consecutive nights in a given location) and a survey of multiple locations (for example, the ones represented in Figure 2). The repeated sampling of the same location allows for the creation of a capture history (a series of 0s and 1s; for example, 00111 for five nights of trapping, with no individuals captured in the first two nights and individuals captured in the last three nights of the sampling period) for each location. Each capture history can then be rewritten statistically as a function of the species' probability of detection (p) and its probability of occupancy (ψ) (see MacKenzie, Nichols et al. 2003 for probabilistic arguments details). The survey of multiple locations with respective capture histories provides a basis for estimation of the probability that any given capture history will occur within the study area. Occupancy modeling then uses maximum likelihood estimation to solve for the best approximation of the species parameters: probability of detection (p) and probability of occupancy (ψ), given the data set.

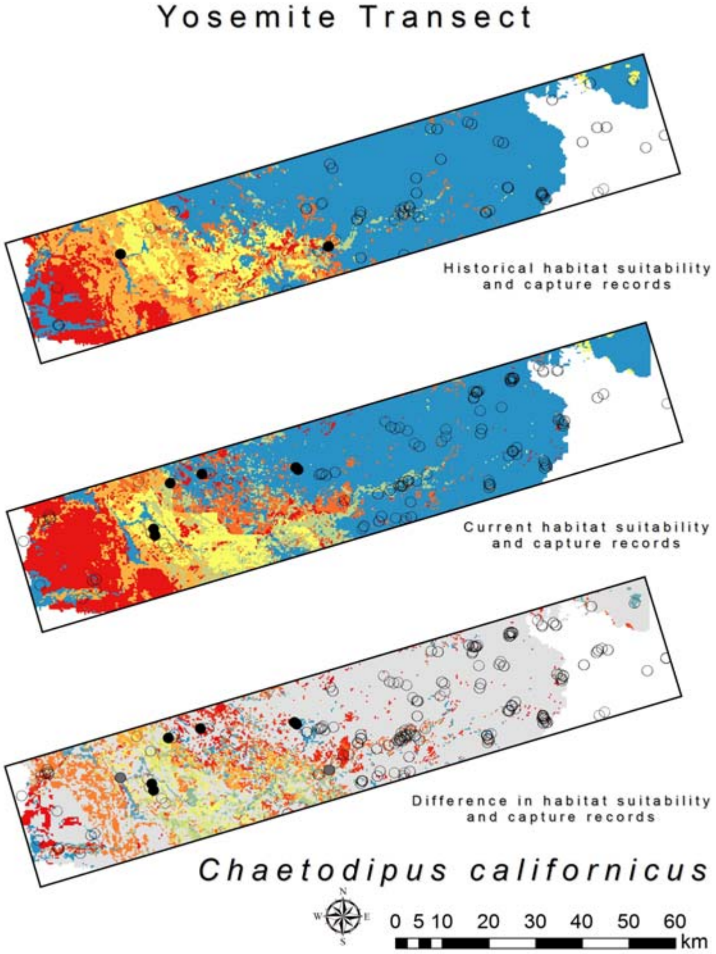
In the historical data there were some uncertainties in the specific location of certain traplines. To reduce uncertainty, we aggregated all traplines known to have been set within a 2 km radius or a 100 m change in elevation of a known location (often a campsite). The same criteria were applied to the modern data, where traplines within 2 km or 100 m were also aggregated. Species presence and capture history data were then summarized for the aggregates and used for subsequent analysis. To account for aggregate data, we unit standard of "trapnights," which calculated the trapping effort (the total number of traps within the aggregate multiplied by the total number of nights traps were sampled).

There is a potential for a scale effect among the small mammal data, the vegetation data, and the climate data. The small mammal data were collected from traplines that generally consisted of 30–40 traps, spaced about 10 m from each other, set in a 300–400 m line. The vegetation maps' minimum mapping unit was set at 300 m and the climate grids' minimum mapping unit set at 270 m. The similarity of these scales of data collection and bolstered confidence in the proposed integration of the data sets. In addition, lack of specificity in the description of the geographic location of the historical traplines created a need for the traplines to be aggregated into a 2 km buffer around the various camp sites. This made the aggregate the minimum unit of analysis, each unit consisting of information from several traplines, while vegetation and climate variables were being collected at similar scales. We feel assured that the alignment of all three collection methods greatly reduces the potential for a scale effect.

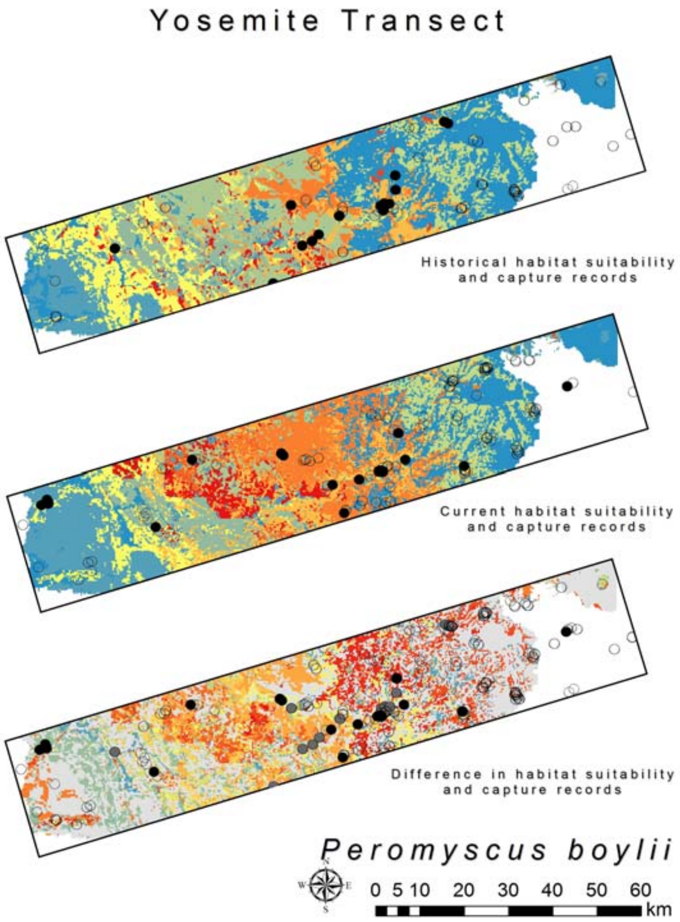
Small Mammal Habitat Suitability

We used the California Wildlife Habitat Relationships (WHR) rankings of species preferences across WHR types (http://www.dfg.ca.gov/biogeodata/cwhr/) to convert historical and modern land cover to habitat suitability values for each of the target species (Table 5). The WHR consists of a relational set of tables that summarize existing knowledge on species-habitat relationships for vertebrates occurring in California. The first step was to create a land cover classification system that classifies vegetation (plant species' composition and structure) into wildlife habitat relationship types (WHR type, as described in Table 2). Then for each vertebrate species, literature was referenced and experts were surveyed to rank the suitability of each WHR type for that specific taxon (http://www.dfg.ca.gov/biogeodata/cwhr/); ranks vary from 0 (not suitable habitat) to 1 (most suitable habitat). The WHR system (the algorithm is provided in a graphical user interface downloadable from the Department of Fish and Game website) then calculates an overall Habitat Suitability Index (HSI) for each WHR type in which the species occurs, as based on either the arithmetic or the geometric mean of the suitability of each stage (a combined metric of seral and structural stages for each WHR type) at which that WHR type occurs in California. In addition, three other Habitat Suitability Indices (cover, food, and reproduction) were calculated. Each HSI value is species- and WHR type- specific and is independent of time periods. For the purposes of our study we used the arithmetic average overall habitat suitability value (not the cover, food, or reproduction specific HSI; Table 5). We used the rankings reported in Table 5 and linked them to the historical and modern land cover maps to calculate the landscape-level habitat suitability per species, at both time periods (Figure 8).

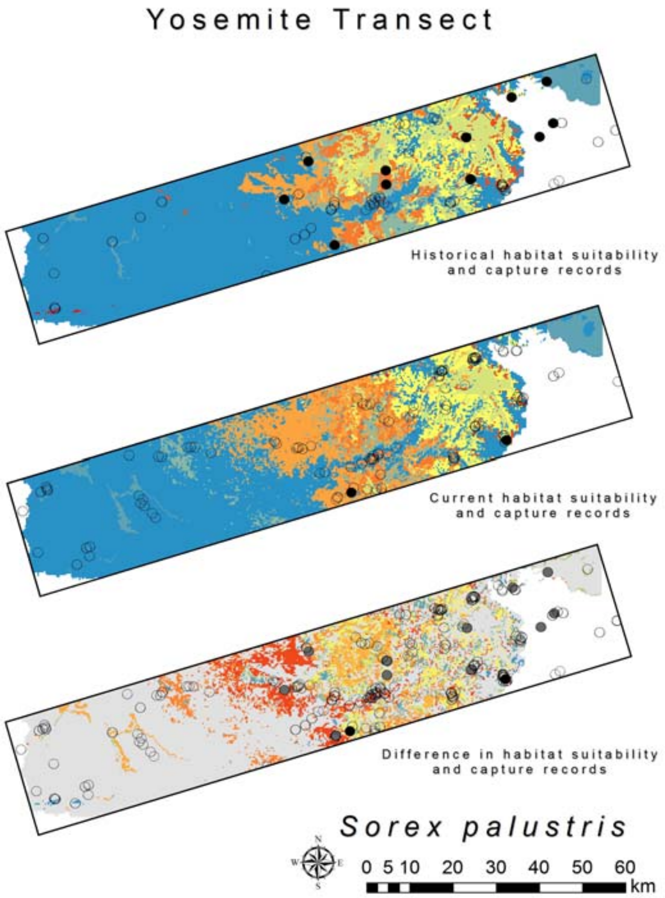
Figure 8. Examples of Change Cross the Yosemite Transect in WHR Ranked Habitat Suitability for Three Species: (a) *Chaetodipus californicus* (California pocket mouse), a low-elevation species that expanded the upper limit of its elevation distribution; (b) *Peromyscus boylii* (brush mouse), an intermediate-elevation species that expanded the lower limit of its elevation distribution; and (c) *Sorex palustris* (water shrew), a high-elevation species that contracted the lower limit of its elevation distribution. Maps represent: upper panel – historical habitat suitability (red to blue gradient, with red representing high suitability and blue low suitability), middle panel – modern habitat suitability (colors as above), and lower panel – difference in habitat suitability (red to blue gradient, with red showing increase in suitability and blue loss of suitability, grey represents no change in suitability).



(a)


Yosemite Transect
Historical habitat suitability and capture records
Current habitat suitability and capture records
Difference in habitat suitability and capture records
Peromyscus boylii
N
W
E
S
0 5 10 20 30 40 50 60
km

(b)


Yosemite Transect
Historical habitat suitability and capture records
Current habitat suitability and capture records
Difference in habitat suitability and capture records
Sorex palustris
N
W
E
S
0 5 10 20 30 40 50 60
km

(c)

Table 5. California Wildlife Habitat Relationships Rankings for the Land Cover Types in the Yosemite Transect and for the Mammal Species Selected for the Analysis

Species	AGR	AGS	ASP	BAR	BOW	BOP	CRC	CPC	DFR	EPN	FEW	JPN	JUN	LAC	LPN	LSG	MCH
Sorex monticolus	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.33	0.00	0.00	0.33	0.00	0.00
Sorex ornatus	0.00	0.50	0.00	0.00	0.41	0.41	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.33
Sorex palustris	0.00	0.00	0.37	0.00	0.00	0.00	0.00	0.00	0.00	0.44	0.00	0.33	0.00	0.20	0.38	0.00	0.00
Sorex trowbridgii	0.00	0.00	0.00	0.00	0.33	0.33	0.00	0.00	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
Otospermophilus beecheyi	1.00	1.00	0.59	0.33	0.60	0.62	0.59	0.54	0.35	0.52	0.00	0.52	0.36	0.00	0.36	0.36	0.56
Urocitellus beldingi	0.77	0.66	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.33	0.00	0.00	0.44	0.77	0.33
Callospermophilus lateralis	0.00	0.11	0.57	0.00	0.00	0.00	0.00	0.00	0.68	0.76	0.00	0.77	0.49	0.00	0.76	0.00	0.67
Tamias alpinus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tamias quadrimaculatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.64
Tamias senex	0.00	0.00	0.48	0.00	0.36	0.36	0.20	0.00	0.45	0.65	0.00	0.65	0.31	0.00	0.49	0.32	0.30
Tamias speciosus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.79	0.00	0.00
Chaetodipus californicus	1.00	1.00	0.00	0.00	0.57	0.57	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.85
Dipodomys heermanni	0.00	0.50	0.00	0.00	0.43	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.58
Neotoma cinerea	0.00	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.57	0.66	0.00	0.83	0.78	0.00	0.66	0.33	0.58
Neotoma macrotis	0.00	0.00	0.00	0.00	0.49	0.66	0.72	0.58	0.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.82
Peromyscus boylii	0.00	0.33	0.00	0.00	0.63	0.63	0.51	0.56	0.62	0.76	0.00	0.71	0.66	0.00	0.00	0.33	0.97
Peromyscus maniculatus	0.66	0.66	0.33	0.33	0.58	0.58	0.56	0.58	0.61	0.86	0.66	0.64	0.84	0.00	0.88	0.43	0.90
Peromyscus truei	0.00	0.55	0.00	0.00	0.00	0.00	0.56	0.00	0.66	0.66	0.00	0.00	0.86	0.00	0.00	0.33	0.72
Reithrodontomys megalotis	0.89	0.92	0.33	0.00	0.43	0.43	0.41	0.52	0.54	0.33	0.66	0.33	0.45	0.00	0.33	0.33	0.51
Microtus californicus	0.77	0.92	0.00	0.00	0.45	0.33	0.00	0.00	0.48	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.33
Microtus longicaudus	0.77	1.00	0.72	0.00	0.00	0.00	0.00	0.00	0.45	0.33	0.66	0.68	0.50	0.00	0.69	0.33	0.33
Microtus montanus	0.66	0.50	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.33	0.43	0.48	0.00	0.46	0.00	0.33
Zapus princeps	0.00	0.33	0.91	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.58	0.00	0.00	0.33	0.00	0.00

Table 5 (cont.). California Wildlife Habitat Relationships Rankings for the Land Cover Types in the Yosemite Transect and for the Mammal Species Selected for the Analysis

Species	MCP	MHW	MHC	MRI	PJN	PPN	RFR	SMC	SCN	URB	VRI	VOW	WTM	WFR
Sorex monticolus	0.00	0.00	0.00	1.00	0.00	0.33	0.33	0.33	0.56	0.00	0.00	0.00	0.66	0.33
Sorex ornatus	0.33	0.00	0.40	0.83	0.00	0.56	0.00	0.40	0.00	0.00	0.82	0.41	0.50	0.00
Sorex palustris	0.00	0.00	0.33	0.96	0.00	0.00	0.58	0.55	0.41	0.00	0.00	0.00	0.62	0.55
Sorex trowbridgii	0.33	0.00	0.63	0.33	0.00	0.60	0.33	0.63	0.00	0.00	0.00	0.33	0.00	0.63
Otospermophilus beecheyi	0.55	0.59	0.56	0.54	0.65	0.54	0.36	0.51	0.38	1.00	0.50	0.60	0.66	0.51
Urocitellus beldingi	0.33	0.00	0.33	0.47	0.33	0.00	0.33	0.33	0.44	0.00	0.00	0.00	1.00	0.33
Callospermophilus lateralis	0.70	0.73	0.73	0.55	0.50	0.73	0.77	0.73	0.76	0.00	0.45	0.00	0.11	0.73
Tamias alpinus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00
Tamias quadrimaculatus	0.00	0.00	0.00	0.00	0.00	0.77	0.00	0.74	0.00	0.00	0.00	0.00	0.00	0.74
Tamias senex	0.30	0.39	0.39	0.48	0.30	0.82	0.65	0.69	0.49	0.00	0.36	0.36	0.00	0.69
Tamias speciosus	0.33	0.00	0.00	0.00	0.00	0.00	0.33	0.52	0.33	0.00	0.00	0.00	0.00	0.52
Chaetodipus californicus	0.85	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.57	0.00	0.00
Dipodomys heermanni	0.53	0.33	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.33	0.00
Neotoma cinerea	0.66	0.62	0.40	0.66	0.66	0.00	0.82	0.57	0.68	0.00	0.60	0.00	0.55	0.57
Neotoma macrotis	0.72	0.72	0.57	0.57	0.00	0.66	0.00	0.63	0.00	0.00	0.58	0.49	0.11	0.63
Peromyscus boylii	0.72	0.71	0.74	0.66	0.76	0.52	0.00	0.73	0.56	0.00	0.66	0.63	0.00	0.73
Peromyscus maniculatus	0.90	0.56	0.83	0.74	0.86	0.66	0.66	0.74	0.66	0.66	0.62	0.58	0.33	0.74
Peromyscus truei	0.77	0.66	0.70	0.58	0.86	0.66	0.00	0.58	0.00	0.00	0.64	0.00	0.33	0.58
Reithrodontomys megalotis	0.61	0.43	0.39	0.74	0.38	0.48	0.33	0.33	0.33	0.00	0.60	0.43	0.50	0.33
Microtus californicus	0.33	0.33	0.41	0.66	0.00	0.33	0.00	0.53	0.00	0.66	0.50	0.45	1.00	0.00
Microtus longicaudus	0.33	0.00	0.42	0.77	0.33	0.52	0.68	0.33	0.68	0.00	0.00	0.00	1.00	0.33
Microtus montanus	0.33	0.00	0.00	0.43	0.00	0.45	0.43	0.33	0.47	0.00	0.00	0.00	0.87	0.33
Zapus princeps	0.00	0.00	0.00	0.81	0.00	0.00	0.58	0.57	0.58	0.00	0.58	0.00	0.87	0.57

Species and Vegetation Relationships

We first assessed whether the WHR rankings were good at predicting species presence over time. To accommodate the uncertainty in the geographical positioning of the historical data, we created a 2 km buffer aggregate around all the traplines linked to that location, and extracted the WHR ranks for each 2 km buffer. We then summed these values and divided them by the number of cells of the habitat map that the buffer included. We called this metric the standardized Habitat Suitability Index (HSI), and these were the values used for the remaining analysis.

To assess whether habitat suitability could explain the presence of small mammal species, we used a multimodel framework using presence and absence data. We tested three models to examine the effect of (1) elevation (measured as the elevation at which the individuals were captured), (2) habitat suitability (measured as HSIs), and (3) their interaction (elevation×HSIs, and the two linear terms). In all the models we added an effect of era to each of the model combinations. We used logistic regression, and for all the models we added an effect of era, as a measure of change from historical to modern time.

Since logistic regression is affected by the correlation between independent variables (Austin 2002), we first calculated the Pearson correlation coefficient between elevation and HSIs at the species presence locations. For those species where there was a significant correlation between the candidate independent variables, we did not conduct the interaction model (elevation×HSIs). We used backward selection logistic regression, using 0.05 as a criterion for inclusion and 0.1 as criterion for exclusion of model parameter.

We tested for spatial autocorrelation of model residuals to meet the assumptions of the logistic regression using Moran's I statistic. We used the difference in Akaike's Information Criteria (ΔAIC) and its weights (w_i) to select the best model. AIC is a metric used for model selection that weights the model fitness (its likelihood) and penalizes over-parameterization. The most parsimonious model of the set has the lowest AIC value and thus ΔAIC of zero, and the other models are compared to it by their ΔAIC value. Values of ΔAIC within <2 indicate that the models are not differentiable in their performance, and values of 4–6 are less competitive models. w_i provides an estimation of how much support a given model has of being the best of the set, and it varies between 0 (no support) to 1 (full support) (Anderson, Burnham et al. 1994).

Eight species showed a significant correlation between elevation and HSIs (*S. ornatus, C. lateralis, T. senex, D. heermanni, N. cinerea,* and *P. boylii*), for which we could not create the interaction model (era×elev×HSIs). Of the twelve species for which we could create the three models, model selection metrics showed stronger support for the full model (era×elev×HSIs; i.e., the change in suitability per elevation per era) for seven species (Table 6). The elevation model was consistently supported for the other five species; however, generally with a lower weight than the full models for the species where this model was the top ranked. This suggests that HSIs may play a minor role in explaining species presence, rather than being totally useless. No support for the HSIs-only model was found for any species (Table 6). There was stronger support for the full model (era×elev×HSIs) for the majority of species that changed their range, except *S. trowbridgii*, *T. speciosus*, *N. macrotis*, all no-change species.

These results show that for 75 percent (15 out of 20) of the species, HSIs was associated with species presence. This program was started by the State agencies as a way to centralize information on habitat suitability for the entire suite of vertebrates that inhabits the state. Since this is a very comprehensive system, it is not surprising that for most species the defined habitat is well-matched with species presence.

Exceptions to the applicability of HSIs to determine species presence (and therefore species' sensitivity to habitat change) include *P. maniculatus, P. truei, S. palustris*, *M. californicus*, and *U. beldingi* (the species that in Table 6 show a stronger support for the model of era×elev). *P. maniculatus* is the species with the most ubiquitous distribution range of the suite of small mammals analyzed in this study, occurring from the low elevations in the foothills to the highest elevations in Yosemite National Park. This species has very broad habitat requirements (Table 5) and can use all the land cover classes complementarily. Thus it is not surprising that this species presence is not related to HSIs values.

P. truei is a low-elevation species dependent on the pinyon-juniper belt and is also found in chaparral (Hoffmeister 1981). This is the only species that showed a shift with both the leading and lagging edge of its distribution shifting upwards in elevation, and thus it did not match the dynamics of its habitat, as juniper remained within the same elevation band (Table 2), and chaparral expanded downwards (Crimmins, Dobrowski et al. 2011). This suggests that perhaps the species has changed its HSIs values over time (since they were assessed based on available literature and professional opinion), which is not reflected in the static use of HSIs values in this analysis. Or it could suggest that other factors, such as species interactions (competition and predation) and climate may be playing a role in explaining the dynamics of this species' presence. *S. palustris,* as the name suggests, is tightly associated with riparian areas (Beneski and Stinson 1987), which are very hard to map with a spatial resolution of 300 m. This is corroborated by the unperceived change in mountain riparian land cover, only covering 0.1 percent (4.9 km^2) of the historical land cover and 0.2 percent (6.6 km^2) of the modern land cover. *M. californicus* (Smolen and Keller 1987) and *U. beldingi* are meadow specialists (Jenkins and Eshelman 1984); this land cover type is very restricted, covering only 2 percent (62.3 km^2) in historical time and 1 percent (23.3 km^2) of the modern land cover. Changes in both these land cover types are likely imperceptible at the spatial resolution of our land cover map, and at the scale of the aggregate where species were trapped.

Table 6. Logistic Regression Model Selection Metrics for Three Candidate Models (era×elev; era×HSIs; era×elev×HSIs): ΔAIC is the metric of model performance in comparison with the other models in the set where values closer to 0 represent the best model; w_i is a metric of model support where values closer to 1 represent more support. These models were only created for species with no significant correlation between elevation and HSIs.

Species	Change	Model	ΔAIC	w_i
Sorex monticolus	E	era×elev	4.61	0.091
		era×HSIs	30.86	0.000
		era×elev×HSIs	**0.00**	**0.909**
Sorex palustris	C	**era×elev**	**0.00**	**0.601**
		era×HSIs	5.92	0.031
		era×elev×HSIs	0.98	0.368
Sorex trowbridgii	NC	era×elev	22.84	0.000
		era×HSIs	2.44	0.228
		era×elev×HSIs	**0.00**	**0.772**
Urocitellus beldingi	C	**era×elev**	**0.00**	**0.635**
		era×HSIs	22.53	0.000
		era×elev×HSIs	1.10	0.365
Tamias alpinus	C	era×elev	0.96	0.382
		era×HSIs	24.99	0.000
		era×elev×HSIs	**0.00**	**0.618**
Tamias speciosus	NC	era×elev	4.42	0.099
		era×HSIs	30.38	0.000
		era×elev×HSIs	**0.00**	**0.901**
Neotoma macrotis	NC	era×elev	18.05	0.000
		era×HSIs	23.11	0.000
		era×elev×HSIs	**0.00**	**1.000**
Peromyscus maniculatus	NC	**era×elev**	**0.00**	**0.610**
		era×HSIs	6.34	0.026
		era×elev×HSIs	1.03	0.365
Peromyscus truei	E	**era×elev**	**0.00**	**0.762**
		era×HSIs	4.92	0.065
		era×elev×HSIs	2.96	0.173
Microtus californicus	E	**era×elev**	**0.00**	**0.602**
		era×HSIs	10.29	0.004
		era×elev×HSIs	0.85	0.394
Microtus longicaudus	C	era×elev	2.67	0.209
		era×HSIs	50.85	0.000
		era×elev×HSIs	**0.00**	**0.791**
Zapus princeps	C	era×elev	1.92	0.276
		era×HSIs	10.82	0.003
		era×elev×HSIs	**0.00**	**0.721**

Dynamics of Change in Species and Vegetation Elevation Ranges

We then assessed whether the dynamics of species ranges were tracking (when both the species' range and its habitat spatially expand or contract synchronously, or do not change) or not tracking (when the habitat and species' range dynamics are asynchronous) the dynamics of habitat range. We opted to include all the species, even those for which the full model was not ranked as significant. This is because there was a consistent lower weight to the model of era×elevation, with some contribution (on average a weight of 0.3) of the full model that included HSIs. This suggests that some part of species presence is explained by the HSIs, and thus we opted to use the HSI-weighted range. This also allows for consistency across the species' input data.

We considered two metrics of the dynamics of the habitat range: elevation and area. The first metric assessed the elevation displacement of habitat, and it was calculated by estimating for each WHR type the difference in elevation range between historical and modern time, weighted by the HSI value for that WHR type, and then averaged across all WHR types known to be suitable to the species. For each mammal species, the overall value in change in elevation range (Δelev) was estimated as:

$$\Delta_{elev} = \left[\sum_{i=1}^{n}\left[\left[(max(elev)_m - min(elev)_m) - (max(elev)_h - min(elev)_h)\right] * HSI\right]_i\right] / N$$

Where *i* corresponds to each of the *N* WHR land cover types suitable to the species, *max(elev)* and *min(elev)* correspond to the maximum and minimum elevation at which a given *i* occurs in either historical (*h*) or modern (*m*) time, and *HSI* corresponds to the Habitat Suitability Index of that given *i* WHR land cover type (Table 3). Maximum and minimum elevations at which each WHR type occurred were estimated as the average of the 95 percent and 5 percent quantiles of the distribution of elevations at which that WHR type occurs. This was calculated for each WHR type. There is a possibility that this equation does not account for shifts in habitat range rather than expansions and contractions. However, we did not observe these changes within our habitat types and thus continued the assessment using this metric.

The second metric assessed the area displacement of habitat, and it was calculated by estimating for each WHR type the difference in area it covered between historical and modern time, weighted by the HSI value for that WHR type, and averaged across all WHR types known to be suitable to the species. For each species, the overall value in change in elevation range (Δarea) was estimated as:

$$\Delta_{area} = \left[\sum_{i=1}^{n}\left[(A_m - A_h) * HSI\right]_i\right] / N$$

Where *i* corresponds to each of the *N* WHR land cover types suitable to the species, *A* is the area of a given WHR in either historical (*h*) or modern (*m*) time, and *HSI* corresponds to the Habitat Suitability Index of that given *i* WHR land cover type (Table 5). We calculated the number of map cells occupied by each WHR type in the historical and the modern maps. This number was then multiplied by the map resolution (300×300 m) to estimate the area covered by each WHR type in historical and modern times.

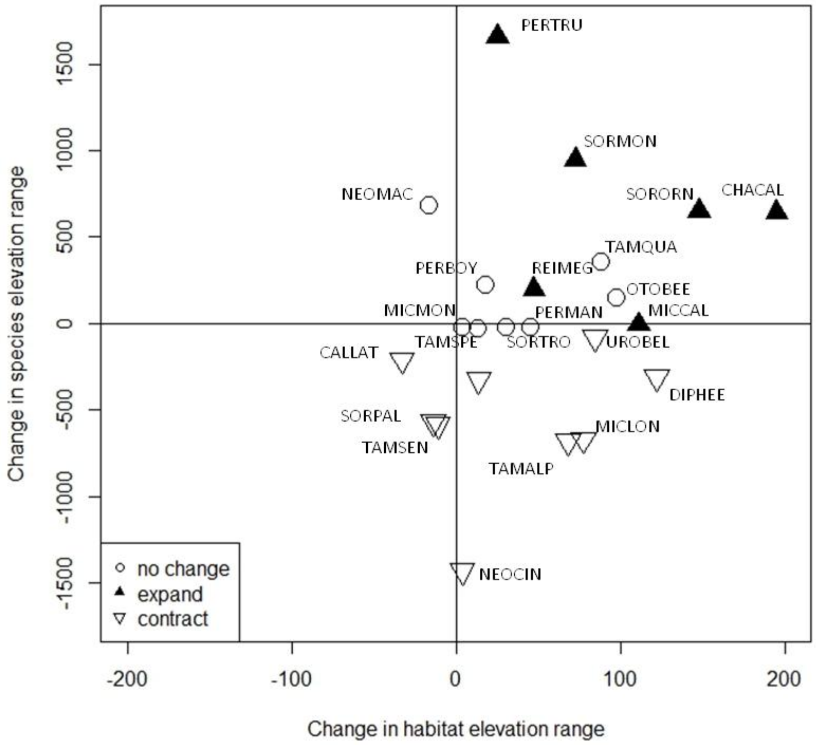
We then plotted these two metrics against the change in the species' distribution range. The change in species distribution range (Δsp_elev) was estimated as the difference in the elevation range where the species occurred from historical to modern time, and was estimated as:

$$\Delta_{sp\_elev} = (max(sp\_elev)_m - min(sp\_elev)_m) - (max(sp\_elev)_h - min(sp\_elev)_h)$$

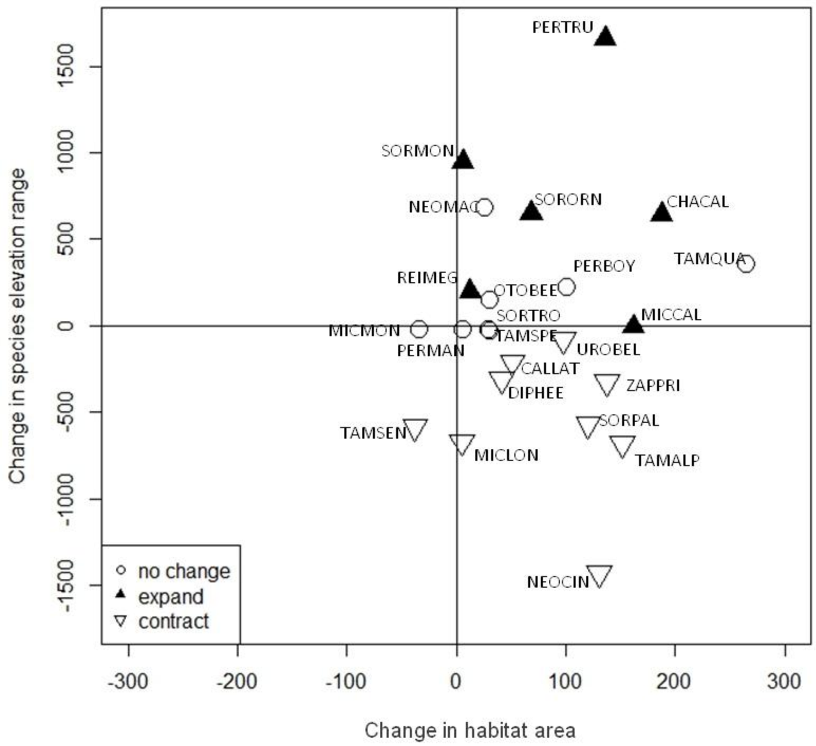
Where *max(sp_elev)* and *min(sp_elev)* correspond to the maximum and minimum elevation at which a species occurs in either historical (*h*) or modern (*m*) time and were estimated as the average, per species, of the 95 percent and 5 percent quantiles of the distribution of elevations at locations where the species was present. In a plot of habitat vertical displacement against species' elevational range, species habitat tracking occurs in the first and third quadrants of this plot; whereas, species not tracking their habitat lie in the second and fourth quadrants; the same applies to a plot of habitat area displacement. This places strong and weak trackers within the same plot, and quadrant placement determines the strength of the tracking.

Eleven of 23 species (48 percent) track the dynamics of their habitat elevation and area (Figure 9), and the other approximately 50 percent do not track the dynamics of their habitat. All species expanding their elevation range are tracking the shifts in elevation and areas of their suitable habitats (the black triangles in Figures 9a and b). Conversely, only three species contracting their elevation range (*C. lateralis*, *S. palustris*, and *T. senex*) are tracking the contraction of their habitat elevation range (third quadrant Figure 9a), and only two species (*T. senex* and *M. montanus*) are tracking the decrease in habitat area (third quadrant Figure 9b). Most contracting species show no tracking of their habitat dynamics.

Figure 9. Changes in Species' Elevation: (a) Habitat Vertical Displacement (elevation) and (b) Habitat Horizontal Displacement (area). The x-axis represents changes in habitat elevation and area ranges (positive values: increase in habitat elevation/area range; negative values: decrease in habitat elevation/area range). The y-axis represents changes in species elevation range (positive values: increase in species elevation range; negative values: decrease in species elevation range). Black triangles indicate species that have significantly expanded their elevation range, white triangles indicate species that have significantly contracted their elevation range, and white circles indicate species that did not change their elevation range. 11 out of 23 species (48 percent) track their habitat in elevation and area. Species are coded to the three first letters of their genus and scientific names, respectively



(a)



(b)

To test the strength of tracking, we categorized species as tracking (species located in the first and third quadrants) and not tracking (species located in the second and fourth quadrants) and used a contingency test for which we excluded species whose range dynamics did not change significantly. We tested the tracking against a random prediction from a binomial distribution. We expected that if tracking was strong, the contingency test would be significant. Next, we used a contingency analysis to test whether tracking was affecting species systematically, by comparing species that occupy high, intermediate, or low elevations; and species that had shown expansion or contraction in their elevation distribution ranges.

We found that habitat tracking was not significantly different from a sample where species were located in quadrants at random ($\chi^2_{\text{elevation}}=0.08$, *P*-value=0.78; $\chi^2_{\text{area}}=0.72$, *P*-value=0.39). Nonetheless, we found that there were significantly more expanding species that tracked, and that more contracting species did not track habitat elevation and area dynamics ($\chi^2_{\text{elevation}}=3.86$, *P*-value=0.04; $\chi^2_{\text{area}}=8.5$, *P*-value=0.004). We found significantly more low-elevation species tracking and more high elevation species not tracking habitat elevation displacement ($\chi^2_{\text{elevation}}=6.52$, *P*-value=0.04); however, we found no significant differences in the area displacement of habitat between species that inhabited low- , intermediate- , and high-elevation ranges ($\chi^2_{\text{area}}=2.5$, *P*-value=0.29).

We found a 50-50 split between species that tracked and those that did not track the dynamics of habitat in elevation and area (11 of 23 species analyzed). Species occupying low and intermediate elevations and those whose elevation range has expanded in the last 80 years tracked their habitat dynamics. Species occupying high elevations and whose range has contracted in the last 80 years did not track their habitat dynamics.

Our results illustrate multiple responses to habitat dynamics within a community. While ecology aims to find generalized responses towards landscape dynamics, the ecological literature has become populated by examples of exceptions. These exceptions are, in a certain way, a corollary of what defines a community per se, as the adaptation of species towards different resource axes and the resulting differentiation of species-specific niches. Given that we analyzed only one of those axes of variation (habitat), it is notably substantial that half of the community is behaving similarly, and shows a concerted response to the variation of habitat over time, especially as it includes species from many different genera (*Sorex*, *Otospermophilus*, *Callospermophilus, Tamias, Chaetodipus, Peromyscus, Reithrodontomys*) and a varied suite of traits. We believe this concerted response is a function of a major change in habitat composition, the increase in Sierran mixed conifer (SMC) which has been documented in the Sierra Nevada over this time period (Thorne, Morgan et al. 2008).

For most of the species that we analyzed, the greatest contribution to the measured changes in habitat elevation and area ranges are due to changes in the availability of SMC (see Appendix A for the relative contribution of each of the land cover types multiplied by HSI for the overall change in habitat elevation range). This explains why in Figures 9a and 9b, most species are located in the positive side of the habitat change axis (*x*-axis). Sierran mixed conifer is an ensemble of five conifers: white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), and the California black oak (*Quercus kellogii*), which have replaced the natural vegetation community at both low and high elevations. At lower elevations, and under regular fire regime, the white fir was prevented from reaching the canopy; however, recent changes in fire regime, with fire suppression in the mid twentieth century and fire restoration in the 1970s (Bill Kuhn personal communication), have allowed the white fir to reach the canopy, frequently replacing Ponderosa pine (Thorne, Morgan et al. 2008; Collins, Everett et al. 2011), leading to vegetation transition to SMC. At higher elevations, the most likely mechanism is the replacement by SMC of red fir (*Abies magnifica*) and lodgepole pine (*Pinus contorta*), just below the sub-Alpine conifer belt (Thorne, Morgan et al. 2008). These dynamics of encroachment of Sierran mixed conifer at lower- and higher-elevation ecotones may then explain why within species that track their habitat dynamics, the relationship is stronger for habitat changes in elevation than area alone, suggesting that a vertical displacement in habitat type is more important than a horizontal displacement of that same habitat type when trying to understand species responses to land cover change.

Most of the small mammal species that inhabit the lower elevations of SMC tracked the dynamics of their habitat (*O. beecheyi*, *T. quadrimaculatus*, *T. senex*, and *P. boylii*). *T. quadrimaculatus* is a conifer habitat specialist, inhabiting denser forests (Clawson, Clawson et al.

1994a), and therefore may be benefiting from the downward expansion of the SMC. For *T. senex,* there was a contraction in both its habitat and distribution ranges; however, this species was only recorded in one location in the modern era. Exceptions to tracking suitable habitat, however, were found for *S. trowbridgii,* which is a species that requires a dense litter layer under the forest canopy (George 1989), likely to be reduced with the prescribed burns in Yosemite National Park. The expansion of the SMC belt at higher elevations may benefit intermediate elevation forest species such as *T. quadrimaculatus* (Clawson, Clawson et al. 1994a) and *P. boylii*. However, this encroachment at higher elevations may have negative effects for species that use open habitats within forests (forest gaps), such as *C. lateralis* (Bartels and Thompson 1993), or *O. beecheyi.* Expansion in SMC may increase forest gaps, but the observed increase in tree density of SMC after the alteration of the fire regime (Collins, Everett et al. 2011) may in fact reduce their extent, or result in a high turnover of available habitat. These potentially divergent effects may also affect species that require heavy debris areas with high herbaceous cover, and fallen logs and shrubs, such as *S. monticolus* (Smith and Belk 1996), or riparian species as *S. palustris* (Beneski and Stinson 1987). The potentially divergent ecotonal dynamics at high elevations may be one of the explanations of why we observed so many species not tracking the dynamics of their habitat ranges.

At least five potential explanations may explain why we found species not tracking the dynamics of their habitat range. The first explanation is that species are not responding to habitat change; instead, they may be responding to other pressures such as direct, physiological effects of climate change, species interactions, etc. However, if this were the case, we would expect to observe this dynamic for all the species that did not track their habitat, and HSI would not be a good predictor of species presence. This was not the case. This pattern was only observed for *P. maniculatus*, a habitat generalist (*P. maniculatus* has an HSI ranking for 30 of the 31 WHR types considered; Table 5). Four species (*N. cinerea*, *D. heermanni*, *M. longicaudus*, and *M. montanus*) showed no significant differences in HSI values in modern locations. The distribution range of *N. cinerea* contracted dramatically such that it was only recorded at three trapping locations in modern sampling. *D. heermanni* and *M. longicaudus* also contracted their distribution range, and *M. montanus* showed no change, all of which were captured in a similar number of locations in both eras.

The second potential explanation is that HSIs are not representing all the possible habitats a species can occur in. We found one situation in which this may be the case. Barren lands (BAR) include the rock talus where *T. alpinus* (Clawson, Clawson et al. 1994b) and *N. cinerea* (Smith 1997) occur. Barren lands reduced substantially in the study area (Table 2), mostly because of the encroachment by the sub-Alpine conifer (SCN) fringe. However, BAR was not listed in the WHR rankings as a suitable habitat for either species, although it is known to be important to *T. alpinus* (Rubidge, Monahan et al. 2011) and to *N. cinerea* (Smith 1997). Such discord with the value of the HSIs would seem to reinforce the importance of a periodic review of these values in light of the newest literature on each species, and, importantly, the possibility that habitat suitability values may change over time.

The third potential explanation is that we were not able to measure the characteristics of the habitat to which the species are responding. Habitat as a component of a species' niche can be measured in a wide variety of ways (Godsoe 2010), and various species will not necessarily respond to the same metrics. In our case, we used a change detection analysis of crosswalked WHR types as our land cover classification system. Change detection of land cover over time may have questionable observer reliability (recall that the historical maps were produced from vantage points), errors in georeferencing, classification (semi-automated classification of satellite imagery may produce classification errors on the modern maps), and crosswalk between the historical and the modern maps.

We believe, however, that these errors are negligible in our analysis, as similar transitions were documented from plot data (Thorne, Morgan et al. 2008; Collins, Everett et al. 2011; Crimmins, Dobrowski et al. 2011), which provide independent validation of the changes measured using the land cover maps. The thematic resolution used in this analysis was selected because it is linked to wildlife habitats; however, some land cover classes may be diluted when represented at a spatial resolution of 300 m. These may include land cover types such as meadows and aspen stands (often small and covering less than 300 × 300 m), or narrow linear features such as riparian areas. This suggests that WHR land cover types such as wet meadows (WTM) and montane riparian (MRI) are under-represented in the land cover maps. For example, WTM only covered 2 percent (62.3 km^2) of our study area in historic time and 1 percent (23.3 km^2) in modern time, and MRI only covered 0.1 percent (4.9 km^2) of the study area in historical times and 0.2 percent (6.6 km^2) in modern time. Changes in both these land cover types are likely imperceptible at the spatial resolution of our land cover map, and at the scale of the aggregate where species were trapped, and may explain why meadow specialists like *U. beldingi* (Jenkins and Eshelman 1984) and *M. montanus* (Sera and Early 2003) showed no tracking. The same rationale can be applied to riparian species such as *Z. princeps* (Hart, Belk et al. 2004). This also explains why we found significantly more species of the genera *Microtus* associated with no tracking, since most of these species are meadow or riparian specialists.

The fourth potential explanation is the potential for divergent effects; on one hand, the encroachment of SMC at higher elevations increases the potential forest gaps, and on the other hand, there is an increase in the tree density of SMC. Acting together, these factors may reduce the availability and extent of open habitats. This could affect species such as *T. alpinus* (Clawson, Clawson et al. 1994b), *M. californicus*, *M. longicaudus* (Smolen and Keller 1987), and *N. cinerea* (Smith 1997).

The fifth potential explanation is that the changes associated with SMC densification (Collins, Everett et al. 2011) are not measured in the WHR categories and thus are not affecting the results for forest species as *S. trowbridgii* (George 1989), or *T. speciosus* (Best, Clawson et al. 1994).

Niche Breadth and Overlap

To understand whether the tracking or not tracking of habitat dynamics was associated with species niche properties, we calculated niche breadth and overlap. Species may change their range to meet their ecological requirements and maintain the same ecological preferences. Alternatively, species may change their ecological preferences and maintain their range by adapting to the changes that occur within it (Oliver, Hill et al. 2009).

We used Smith's measure of niche breadth (FT) (Krebs 1999) as it accounts for the suitability of a given land cover class (as habitat use derived from the proportion of individuals found in a given land cover) and its available area, calculated as:

$$FT = \sum_{i=1}^{n} \sqrt{p_i a_i}$$

where p_i is the proportion of individuals found in or using resource state *i*, a_i is the proportion of resource *i* to the total resources, and *n* is the total number of possible resources. This metric varies between 0 (a narrow niche breadth; i.e., a specialist) and +∞ (a wide niche breadth; i.e., a generalist). Since this metric integrates both habitat suitability and availability, we used a tiered approach to disentangle the effect of changing habitat area, from the combination of changing habitat area and suitability. To test the effect of changing habitat area we held suitability values constant, standardizing by HSI values per species (Table 5). We defined availability of given land cover types as the area occupied by that land cover type in each time frame . To simultaneously test the effect of changing habitat area and suitability, we calculated area as described above, and divided suitability by the total number of individuals of that species in the trapping record.

For each species we calculated the difference in niche breadth from historical to modern time, and using ANOVA, we tested whether these differences were significantly different when the species expanded or contracted their elevation range and when species tracked or did not track their habitat dynamics. For the effect of changing habitat suitability and area on niche breadth, we also estimated the difference in use and availability from historical to modern time, to assess which factor most contributed to the observed changes in niche breadth.

We modified MacArthur's and Levins (Krebs 1999) niche overlap metric (M_{ij}) to allow for measuring the niche overlap between two time periods, rather than two species:

$$M_{ij} = \sum_{i}^{n} p_{ij} p_{ik} \Big/ \sum p_{ij}^{2}$$

Where p_{ij} is the proportion of resource *i* to the total resources that a species uses in time *j*, p_{ik} is the proportion of resource *i* to the total resources that a species uses in time *k*, and *n* is the total of resource states. This metric varies between 0 (no niche overlap) and 1 (full niche overlap), and the reference condition is historical time.

On average, species that tracked habitat dynamics showed a significant increase in niche breadth by changing suitability and availability in comparison to species that did not track habitat dynamics (F = 4.45, *P*-value = 0.04; Table 7), after excluding species that tracked the contraction of their habitat (these species were expected to have decreased their niche breadth). We also found a trend for species that tracked the habitat area changes to increase in niche breadth when changing suitability and availability in comparison to species that did not (F = 3.76, *P*-value = 0.06; Table 7). No other significant differences were found for niche breadth and overlap.

Table 7. Average Values of Niche Breadth (FT) and Overlap (M) When Changing Availability and Suitability and Availability, for the Species That Tracked or Did Not Track the Dynamics of Habitat in Elevation and Area from Historical (h) to Modern (m) Time. Bold values are significant differences (*P*-value<0.05); shaded values are trends (*P*-value<0.1). The changing availability analysis uses FT with standardized HSI values, and the changing suitability and availability analysis uses only FT values.

		Dynamics elevation		Dynamics area	
		Track	Not track	Track	Not track
Changing availability	FT_h	1.812	1.610	1.80	1.62
	FT_m	1.839	1.647	1.81	1.68
	ΔFT	0.027	0.036	0.00	0.06
	M	0.212	0.200	0.21	0.20
Changing suitability and availability	FT_h	1.945	2.018	1.95	2.01
	FT_m	2.090	2.021	2.11	2.00
	ΔFT	**0.144**	**0.002**	0.16	-0.01
	M	0.153	0.177	0.16	0.17

Habitat specificity may change with time and affect species range boundaries (Oliver, Hill et al. 2009); and these changes may act synergistically with, or antagonistically to, changes in climate (Warren, Hill et al. 2001; Brook, Sodhi et al. 2008; Ulrich and Hopper 2008). We tried to determine whether the observed dynamics of species and habitat were a result of a change in species niche breadth resulting from changes in habitat availability alone, or changes in both species habitat use and habitat availability.

We found significant differences in niche breadth only when changing both species' habitat use *and* habitat availability in time and space—a result that is consistent with the conclusion in Oliver, Hill et al. (2009) that species' habitat specificities change both spatially and temporally. We also found that species that tracked the dynamics of their habitat increased their habitat niche breadth. Species that did not track the dynamics of their habitat did not change their elevation habitat niche breadth but showed a decreasing trend in niche breadth when the dynamics of area were analyzed. However we found no significant differences in niche overlap. Thus, these results are in partial agreement with our original hypothesis that species and habitats that expand their range are driven by a widening of their niche breadth.

For species to meet the dynamics of the habitat, they will have to be adaptive and change their responses (Warren, Hill et al. 2001; Swihart, Lusk et al. 2006; Ulrich and Hopper 2008; Oliver, Hill et al. 2009; Graham, VanDerWal et al. 2010). Habitat generalists will likely occupy new habitats as they become available, which will result in an expansion of their range edges (Brooker, Travis et al. 2007; Gaston 2009; Atkins and Travis 2010; Angert, Crozier et al. 2011); conversely, habitat specialists that cannot change their habitat preferences will not be able to meet the spatial and temporal dynamics of their habitat range, likely resulting in a contraction of their geographical ranges. No significant differences were found for niche overlap, probably because the amount of overlap between the two time periods was already relatively low and the difference in M between tracking and non-tracking species is about 10 percent.

These results suggest that niche breadth is a good metric to predict species responses to habitat change, corroborating the results in Swihart et al. (2006). Measuring niche breadth is not a novel task (Colwell and Futuyma 1971; Feinsinger, Spears et al. 1981; Smith 1982), and much of the literature has shown the impact of measuring resource selection without including both a metric of use and a metric of availability. Many studies have measured niche breadth as the number of resources that a species uses (Svensson 1992; Morin and Chuine 2006); however, this may be just part of the question, as the number of resources used is a function of their availability, and the rate of use may change over time, as our results suggest.

A common assumption is that species responses to habitat are constant over time (Guisan and Zimmermann 2000), but this assumption is starting to be questioned (Oliver, Hill et al. 2009). Obtaining temporally calibrated species responses to habitat changes is not an easy task, and not many data sets allow doing so. Our study found that approximately 50 percent of small mammal species are expanding the habitats they use, and that the ones that are expanding have specific characteristics, such as being mostly omnivorous, as shown below. One possible alternative is to find literature that covers a wide temporal span and assess whether major habitat association changes are documented. Further, systems like the WHR may need to start including a temporal component in their habitat rankings.

Species Traits

We also attempted to determine if species traits could predict whether species track change in habitat or not. Species traits may make them better adapted (or in the other extreme, maladapted) to the shifts in their ranges over time. We assembled information about species traits, including their relatedness (Genus), distribution range (range area, mean precipitation, temperature, actual evapotranspiration, and potential evapotranspiration), population density, behavior (home range size and terrestriality), circadian and annual activity (annual rhythm, activity cycle), physiology (metabolic rate), biometrics (weight, longevity), diet guild, reproduction (litters per year, gestation length, litter size, neonatal weight, youngs per year) from the PanTHERIA database (Jones, Bielby et al. 2009) and from the data published in Moritz et al. (2008). Descriptions of each metric are detailed in Table 8, and trait values are presented in Table 9. To test the effect of each trait on species tracking or not tracking their habitat dynamics in elevation and area, we used a multivariate ANOVA comprising whether or not species track habitat dynamics as the dependent variable, and individual traits as independent variables. We used an F-test to assess variable significance in the final model for the continuous variables and a contingency table (with a chi-square test) for the categorical variables.

Table 8. Descriptions of the Species Traits of the Small Mammal Species Analyzed in This Study: (a) PanTHERIA Database, (b) Moritz et al. (2008)

Trait	Description	Metric
Genus	Genera to which each species corresponds; aims at testing the effect of species relatedness on their responses to habitat changes	e.g., *Sorex, Microtus*, etc.
Pop density (a)	Population density as measured by the number of individuals per area	Individuals per km^2
Home range (a)	Individual or social group home range	km^2
Terrestriality (a)	Indicates whether an individual is cursorial or arboreal	1 – Cursorial, 2 – Arboreal
Annual rhythm (b)	Indicates whether or not a species undergoes hibernation	Non-hibernator, facultative hibernator, obligatory hibernator
Activity cycle (b)	Indicates whether a species is diurnal, nocturnal, or both	Diurnal, nocturnal, both
Basal metabolic rate (a)	Indicates the metabolic rate for the species, expressed as volumetric unit of oxygen	mlO_2
Adult mass (b)	Body weight	g
Max longevity (b)	Number of months an individual survives on average	months
Diet (b)	Dietary guild of a species	Omnivore, herbivore, granivore, insectivore
Litters per year (b)	Number of litters per year	Litters
Gestation length (a)	Number of days for gestation	days
Litter size (b)	Number of newborns per litter	Individuals
Neonatal body mass (a)	Body weight at birth	g
Youngs per year (b)	Number of surviving newborns per year	individuals
Range area (a)	Geographical distribution range area	km^2
Mean Precip (a)	Average precipitation in the geographic distribution range	mm
Mean Temp (a)	Average temperature in the geographic distribution range	°F
Mean AET (a)	Average actual evapotranspiration in the geographic distribution range	mm
Mean PET (a)	Average potential evapotranspiration in the geographic distribution range	mm

Table 9. Species Traits, as Described in Table 7 (BMR – Basal metabolic rate, NBM – Neonatal body mass, NH – Non-hibernator, FH – Facultative hibernator, OH – Obligatory hibernator)

	S. monticolus	*S. ornatus*	*S. palustris*	*O. beecheyi*	*C. lateralis*	*T. quadrimaculatus*	*T. senex*	*C. californicus*	*P. boylii*	*P. truei*	*R. megalotis*
Genus	*Sorex*	*Sorex*	*Sorex*	*Otospermophilus*	*Callospermophilus*	*Tamias*	*Tamias*	*Chaetodipus*	*Peromyscus*	*Peromyscus*	*Reithrodontomys*
Pop density (a)	1200.00	11100.00	--	1100.45	--	52.00	--	--	521.08	1419.62	1152.39
Home range (a)	0.0017	--	0.0023	0.0003	--	0.0056	0.0100	--	0.0028	0.0091	0.0010
Terrestriality (a)	1	--	1	1	--	2	2	--	--	--	2
Annual rhythm (b)	NH	NH	NH	OH	OH	FH	FH	NH	NH	NH	NH
Activity cycle (b)	both	both	both	Diurnal	Diurnal	diurnal	diurnal	nocturnal	nocturnal	Nocturnal	nocturnal
BMR (mlO$_2$) (a)	--	52.28	--	317.78	204.67	--	--	21.45	54.28	44.05	22.50
Adult mass (b)	4	4	15	700	250	80	80	25	24	30	10
Max longevity (b)	6	6	6	36	36	24	24	12	12	6	6
Diet (b)	insectivore	insectivore	insectivore	Omnivore	Omnivore	granivore	granivore	granivore	granivore	omnivore	omnivore
Litters/year (b)	2	2	2	1	1	1	1	2	2	2	2
Gestation (a)	--	--	21	28.37	28.42	31.65	--	25.16	23.3	32.37	23.5
Litter size (b)	6	5	6	6	4	4	4	4	3	4	4
NBM (a)	--	0.5	--	9.29	6.09	--	--	1.5	2.19	2.31	1.36
Youngs/year (b)	9	8	12	6	4	4	4	6	6	8	8
Range area (a)	4492367.53	194623.52	6203279.83	459262.56	1705582.39	25579.83	99452.58	116215.94	2628523.09	2131499.23	5125874.07
Mean precip (a)	42.17	35.99	52.33	49.14	33.72	56.96	54.63	34.72	30.57	36.64	40.68
Mean temp (a)	-8.11	127.60	16.95	103.49	56.81	79.65	77.64	117.04	112.74	117.42	112.44
Mean AET (a)	321.61	337.10	392.82	352.34	364.51	379.53	363.14	328.43	426.62	474.31	506.38
Mean PET (a)	521.18	1132.22	559.10	985.35	829.87	1045.01	910.77	1146.70	1021.01	1062.36	964.80

Table 9 (cont.). Species Traits, as Described in Table 7 (BMR – Basal metabolic rate, NBM – Neonatal body mass, NH – Non-hibernator, FH – Facultative hibernator, OH – Obligatory hibernator)

	S. trowbridgii	*U. beldingi*	*T. alpinus*	*T. speciosus*	*D. heermanni*	*N. cinerea*	*N. macrotis*	*P. maniculatus*	*M. californicus*	*M. longicaudus*	*M. montanus*	*Z. princeps*
Genus	*Sorex*	*Urocitellus*	*Tamias*	*Tamias*	*Dipodomys*	*Neotoma*	*Neotoma*	*Peromyscus*	*Microtus*	*Microtus*	*Microtus*	*Zapus*
Pop density (a)	--	2378.64	--	76.48	1160.33	--	--	661.87	13127.21	1200.00	3160.00	292.30
Home range (a)	--	--	--	0.0100	--	0.0300	--	0.0020	0.0001	--	0.0001	0.0019
Terrestriality (a)	1	1	2	2	1	--	--	2	--	--	--	--
Annual rhythm (b)	NH	OH	FH	FH	NH	NH	NH	NH	NH	NH	NH	OH
Activity cycle (b)	both	diurnal	both	diurnal	nocturnal	nocturnal	nocturnal	nocturnal	both	both	both	nocturnal
BMR (mlO$_2$) (a)	--	182.00	--	--	73.17	168.59	--	36.46	68.20	71.82	81.62	--
Adult mass (b)	6	300	35	50	70	450	350	18	60	65	45	30
Max longevity (b)	6	36	24	24	36	36	36	6	6	6	6	24
Diet (b)	insectivore	herbivore	granivore	granivore	granivore	herbivore	herbivore	omnivore	herbivore	herbivore	herbivore	omnivore
Litters/year (b)	2	1	1	1	2	2	1	3	4	3	4	1
Gestation (a)	--	26.19	--	--	30.99	29.69	--	26.68	21.18	--	21.13	18.11
Litter size (b)	4	6	4	4	3	4	3	4	6	4	6	4
NBM (a)	--	6.86	--	--	3.7	14.4	--	1.73	3.28	--	3.89	--
Youngs/year (b)	8	6	4	4	5	8	3	12	24	12	24	4
Range area (a)	377970.17	337927.66	8880.39	67913.09	70348.64	3606599.01	--	13001064.75	307995.54	4018517.85	1453963.15	3361363.77
Mean precip (a)	69.90	30.29	51.65	45.47	40.92	40.78	--	51.30	43.86	43.04	31.01	39.73
Mean temp (a)	83.85	69.70	38.30	87.77	127.75	33.34	--	61.72	111.00	21.49	59.59	32.97
Mean AET (a)	391.84	303.11	333.21	337.35	352.13	356.18	--	486.99	343.33	336.58	353.61	371.16
Mean PET (a)	861.29	853.48	1195.70	1101.98	1144.71	668.38	--	718.81	1058.14	638.89	830.13	648.32

Of the suite of species traits, genus, adult body mass, diet guild, and neonatal body mass showed significant effects on species' ability to track their habitat (Table 10). Species tracking habitat dynamics were significantly more of the genus *Sorex*, tended to have lower adult and neonatal body mass, and tended to be omnivorous; whereas, species that did not track habitat dynamics were significantly more of *Microtus* genus, tended to have higher adult and neonatal body mass, and tended to be herbivorous.

We found significantly more omnivore species tracking their habitat dynamics, and herbivores not tracking habitat dynamics. Being an omnivore ensures a wider variety of food options as the species expands into new habitats. This categorization of dietary guild corresponds to findings on dietary niche breadth in other studies (Angert, Crozier et al. 2011; Hill, Griffiths et al. 2011; Slove and Janz 2011). Further, the wider dietary niche breadth is consistent with the observed widening of the habitat niche breadth in species that tracked their habitat dynamics. As species widen their habitat use, it is likely that those with a less specialized diet will be favored, as they can take advantage of resources provided by the novel habitats. We also found significantly more herbivores in species that did not track habitat dynamics. Since most of these species occupy open areas (*M. californicus*, *M. longicaudus* [Smolen and Keller 1987], and *S. trowbridgii* [George 1989]), meadows (*U. beldingi* [Jenkins and Eshelman 1984]), and *M. montanus* [Sera and Early 2003]), riparian (*Z. princeps* [Hart, Belk et al. 2004]), and talus specialists (*T. alpinus* [Clawson, Clawson et al. 1994b]), it makes sense that a higher number of herbivores is found, as well as the higher number of species of the genera *Microtus*. We also found significantly lower adult and neonatal body mass in species that tracked habitat dynamics. Low adult and neonatal body mass suggests a higher ability to produce offspring and matches the higher proportion of "r-selected" species among those with range expansion reported in Moritz et al. (2008). This also suggests that forest affinity could be used as a predictive trait.

Although not significant, species that tracked habitat dynamics showed on average lower values of home range size (50 percent), and longevity (25 percent) than species that did not. Smaller home range sizes are often linked with more resources, suggesting increasing habitat suitability. Lower longevity suggests that tracking species have a faster population turnover rate, and thus a higher likelihood of adaptation to changing habitat conditions. All of these findings match our measured increase in habitat suitability over time, and the significant increase in niche breadth in species expanding their distribution ranges. Tracking species also had on average higher values for traits like mean temperature, AET, and PET. Since temperature and productivity variables (AET and PET) were higher in expanding-range species, it reinforces the claim that future studies should be aimed at linking habitat and climate in an effort to better understand species range dynamics.

Table 10. Species Traits Effect on Species That Tracked or Did Not Track Their Habitat Dynamics in Elevation and Area (*- F-test if the variable is continuous, Chi-square test if the variable is categorical). Bold values are significant differences (*P*-value<0.05).

	Elevation				Area			
Trait	Track	Not track	Test *	*P*-value	Track	Not track	Test*	*P*-value
Genus	***Sorex***	***Microtus***	**17.96**	**0.05**	*Sorex*	*Microtus*	13.59	0.19
Pop density	3718	3632	0.02	0.90	3718.00	3631.70	0.02	0.90
Home range	0.005	0.014	0.02	0.88	0.005	0.011	0.00	0.99
Terrestriality	1.5	1.33	0.17	0.68	1.67	1.25	1.04	0.31
Annual rhythm	non-hibernator	non-hibernator	0.68	0.71	non-hibernator	non-hibernator	3.55	0.17
Activity cycle	both	Both	0.14	0.93	all	all	0.64	0.72
Basal Metabolic Rate	68.99	112.76	2.45	0.12	**35.07**	**128.10**	**6.55**	**0.01**
Adult mass	**52.30**	**144.29**	**4.12**	**0.04**	**25.5**	**141.67**	**4.77**	**0.03**
Max longevity	12.75	24.00	2.39	0.12	10	23.30	3.11	0.08
Diet	**omnivore**	**herbivore**	**10.68**	**0.01**	all	herbivore	5.28	0.15
Litters per year	1.75	2.00	0.02	0.89	1.83	1.89	0.11	0.74
Gestation length	26.10	25.23	0.01	0.92	27.01	25.08	0.32	0.57
Litter size	4.63	4.43	0.28	0.60	4.5	4.55	0.01	0.95
Neonatal body mass	**2.35**	**7.06**	**3.84**	**0.05**	**1.42**	**6.87**	**6.00**	**0.01**
Youngs per year	7.38	9.00	0.03	0.86	7.17	8.78	0.03	0.86
Range area	2508612.00	1673090.00	0.66	0.42	2026672	2180055.00	0.00	0.99
Mean precipitation	41.36	41.47	0.21	0.64	40.81	41.81	0.22	0.64
Mean temperature	77.22	62.08	0.33	0.56	90.67	56.48	2.00	0.16
Mean AET	386.04	342.24	1.34	0.25	388.49	350.34	0.06	0.81
Mean PET	890.88	886.80	0.01	0.91	956.3	844.10	0.68	0.41

Section 4: Abundance Responses

It is often assumed that species response to environmental change is similar both in presence and abundance, even though it is widely accepted that that is not the case but just a simplification for modeling purposes (Svensson 1992; Brown, Mehlman et al. 1995; Nielsen, Johnson et al. 2005; Royle, Nichols et al. 2005; Gaston, Borges et al. 2006; Ritchie, Martin et al. 2009; Huntley, Barnard et al. 2010). Thus habitat tracking species are predicted to show little to no changes in relative abundance as they use their habitat according to availability, and it would be expected that this would have a cascading effect at the population level. Non-tracking species, on the other hand, are expected to show a decrease in abundance since they do not use their habitat according to its availability, and this mismatch with habitat dynamics would seem likely to have an effect on population abundances. If no changes are observed, then it would seem likely that the species' responses to their habitat (e.g., increased use, change in behavior) have yet to be translated to population level parameters.

We tested whether this was the case by comparing abundance between tracking and non-tracking species. Since we did not have information about recaptures, with which we could have directly estimated abundance, we used two derived measures of estimated relative abundance that we refer to as minimum (mnAb) and maximum (mxAb) relative abundances. We calculated the minimum number of individuals by analyzing the capture history (the number of captures per day at each trapline) for all the traplines within an aggregate (the aggregate being the unit of analysis), and selecting the highest number of individuals captured in a single day, assuming that no recaptures occurred within that day. We calculated the maximum number of individuals by summing all the captures in one aggregate, assuming that no recaptures occurred. These estimates were selected because the percent of individuals removed as specimens varies widely and is hard to estimate from historical records. We then calculated minimum and maximum relative abundance by dividing both the minimum and the maximum number of individuals by the trapping effort (the total number of traps per night multiplied by the number of nights in an aggregate). We plotted the relative abundances at each time period by their elevation bands.

To assess whether abundance varies between species that tracked or did not track their habitat dynamics, we selected the presence-only sites and calculated the mean minimum and maximum relative abundance. We calculated the difference in mean minimum and maximum relative abundance from historical to modern time to assess whether abundance was changing over time and in which direction. We then tested whether there were significant changes using ANOVA.

We also calculated the effect size as the difference between modern and historical average relative abundances standardized by the historical relative abundance and multiplied by 100 ([(MAb-HAb)/HAb] ×100). The effect size allows standardized assessment of the magnitude of the difference. We used a one-way ANOVA to assess whether there were significant changes in the variance of abundance values from historical to modern time.

Of the 18 species analyzed (we omitted three species of ground squirrels and both *T. quadrimaculatus* and *C. californicus* because the historical capture record was mostly from shooting excursions and not from trapping), seven showed an increase in minimum relative abundance and 11 in their maximum relative abundance; 14 species showed consistent increases and decreases in both measurements (Table 11). Seven species decreased their minimum relative abundance, and five their maximum relative abundance. Effect sizes were often an order of magnitude higher for increases in abundance than those observed for decreases in abundance. Two species increased 900–1,100 percent over their historical abundance (Table 11).

Of the nine species that contracted their elevation ranges, six showed increases in relative abundance (Table 11; Figure 10). *M. longicaudus*, *T. alpinus,* and *Z. princeps* were exceptions to this pattern, the first decreasing abundance and the others showing no changes. All the species that expanded their elevation ranges showed a decrease in abundance from historical to modern time, of magnitudes varying from an 8 to 80 percent decrease (Table 11; Figure 10). Species that showed no change in their elevation ranges showed idiosyncratic abundance changes (Table 11; Figure 10). *N. macrotis* increased abundance 900–1,100 percent, whereas the other species mostly decreased their abundance in magnitudes varying from 10 to 86 percent. *T. senex* showed effect sizes of 900 percent and 644 percent; however, the species only had four captures in the modern time, thus this change is not reliable.

On average, we found only barely significant differences in the changes in abundance from historical to modern time for species tracking or not habitat dynamics (mnAb: Track = -0.003, Not track = 0.0001, F = 4.55, *P*-value = 0.05; mxAb: Track = -0.004, Not track = 0.002, F = 3.97, *P*-value = 0.06). There was no effect of the historical abundance (mnAb: Track = 0.005, Not track = 0.0034, F = 0.32, *P*-value = 0.58; mxAb: Track = 0.007, Not track = 0.006, F = 0.18, *P*-value = 0.68), which could have been a confounding effect if species not tracking habitat dynamics had a priori higher abundance. These results were independent of whether the species lived at low, intermediate or high elevation (ΔmnAb: F = 1.42, *P*-value = 0.28; Effect size mnAb: F = 0.37, *P*-value = 0.69; ΔmxAb: F = 0.53, *P*-value = 0.6; Effect size mxAb: F = 0.62, *P*-value = 0.55). These results show that tracking species significantly decreased their minimum and maximum abundances; whereas, non-tracking species either showed no change or increased abundance.

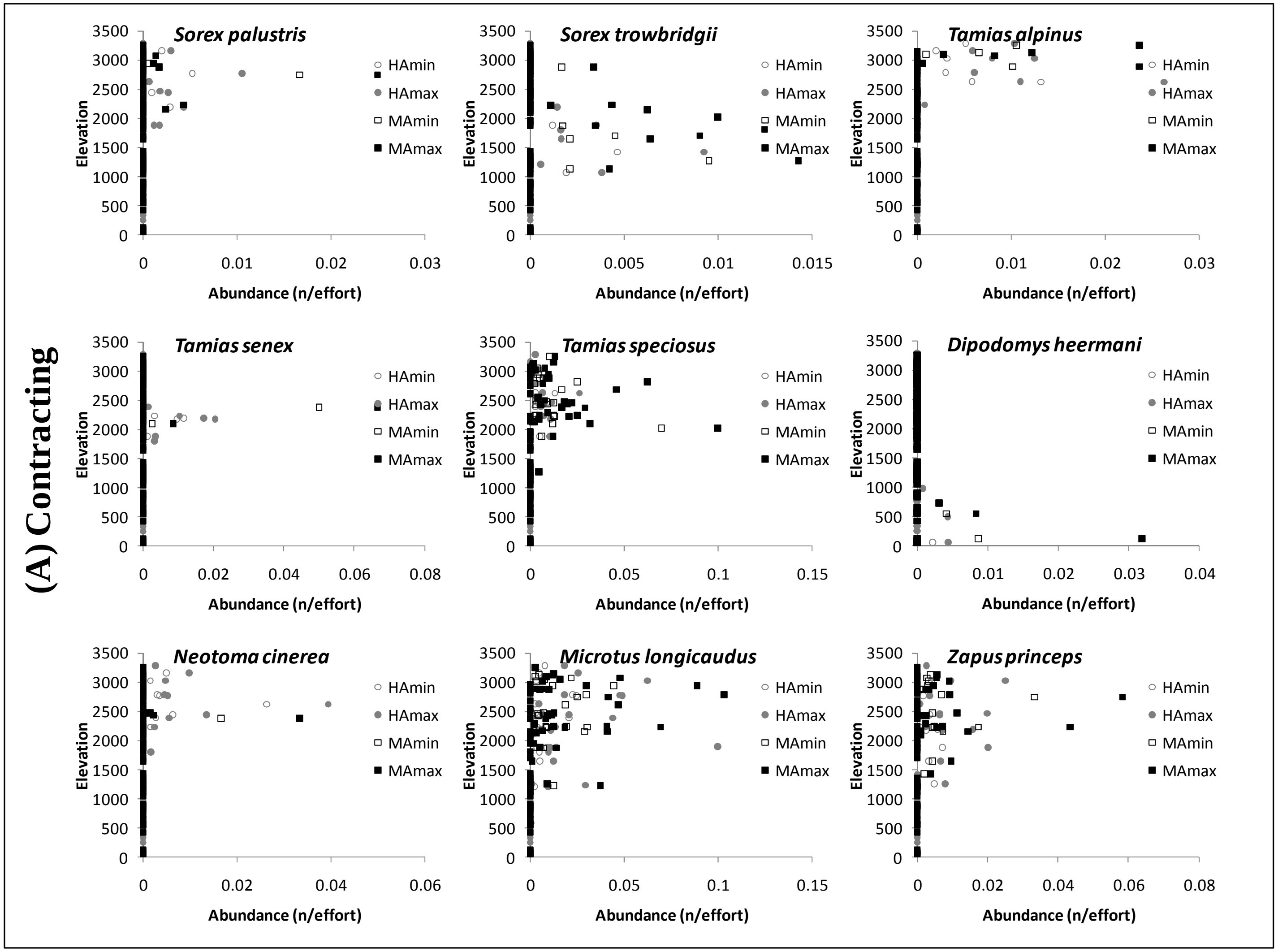
The results suggest that predictions that habitat-tracking species would show an increase in abundance and that non-tracking species would show a decrease in abundance could be questioned. It may be that as species move along with their habitat, their abundance is thinning throughout their distribution range, or it may simply be that the abundance is lower because they are now occupying more area. These possibilities go hand in hand with our previous discussion that tracking species showed lower longevity, suggesting a faster population turnover rate. Further, Moritz et al. (2008) reported a higher proportion of “r-selected” species among those with range expansion, and basic ecological theory would predict these species to expand more rapidly. It is also possible that the population growth rates (even though high) have yet to meet the recruitment rates necessary to occupy the newly available habitat. But the finding that non-tracking species are either not changing (minimum abundance) or increasing (maximum abundance) their abundance is surprising. This suggests that despite failure to match the dynamics of the habitat, population level parameters are already being affected by the changes in species distribution ranges. This may become problematic, as these are the species that showed mostly range contraction, such that more individuals are found in a smaller area.

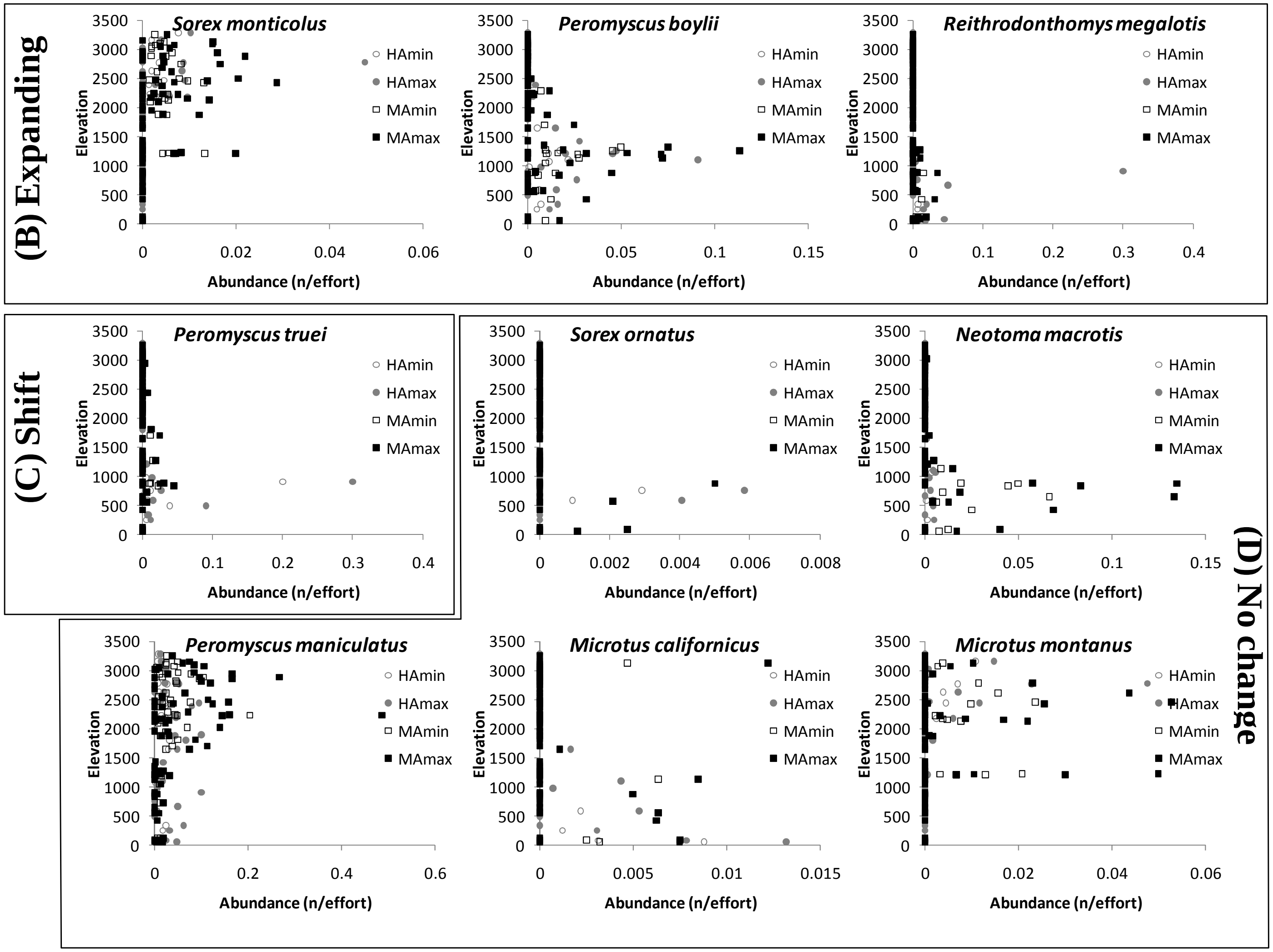
Table 11. Descriptive Statistics of Abundance in Sites Where Mammal Species Were Present in the Yosemite Transect (nH – Number of historical sites where the species was present; nM – Number of modern sites where the species was present; ΔmnAb – Difference in mean minimum relative abundance from historical to modern; ΔmxAb – Difference in mean maximum relative abundance from historical to modern; Effect size – Percentage increase or decrease in abundance from historical to modern time)

Species	nH	nM	ΔmnAb (M-H)	Effect size mnAb (%)	ΔmxAb (M-H)	Effect size mxAb (%)
T. senex	6	1	0.045	900	0.058	644
N. cinerea	11	3	0.002	40	0.004	50
S. palustris	9	7	0.002	100	0.002	67
T. alpinus	8	6	0	0	0.002	20
T. speciosus	12	31	0.005	94	0.009	113
M. longicaudus	23	34	-0.005	-31	-0.001	-4
Z. princeps	13	20	0	0	0	0
S. trowbridgii	7	11	0.003	150	0.004	133
D. heermanni	3	3	0.003	150	0.011	367
P. truei	7	10	-0.029	-74	-0.049	-73
S. ornatus	2	5	0	0	-0.003	-60
N. macrotis	8	16	0.018	900	0.034	1133
M. californicus	8	8	-0.024	-86	0	0
M. montanus	10	19	-0.001	-13	0.006	55
P. maniculatus	31	54	0.006	27	0.028	74
S. monticolus	11	34	-0.002	-29	-0.001	-10
P. boylii	15	24	-0.001	-8	0.003	13
R. megalotis	9	13	-0.037	-84	-0.038	-76

Note: *Tamias senex* had a relatively low number of captures in the modern survey, so its increase is not reliable.

Figure 10. Relative Abundance Indexes of Small Mammal Species Present in the Yosemite Transect at Different Elevations, Grouped by Observed Range Changes: (A) contracting, (B) expanding, (C) shift, (D) no change. Open gray circles – Historical minimum abundance; filled gray circles – Historical maximum abundance; open black squares – Modern minimum abundance; filled black squares – Modern maximum abundance.




(B) Expanding
Sorex monticolus
Peromyscus boylii
Reithrodonthomys megalotis
(C) Shift
Peromyscus truei
(D) No change
Sorex ornatus
Neotoma macrotis
Peromyscus maniculatus
Microtus californicus
Microtus montanus
Elevation
0
500
1000
1500
2000
2500
3000
3500
Abundance (n/effort)
0
0.02
0.04
0.06
0.05
0.1
0.15
0.2
0.3
0.4
0.002
0.004
0.006
0.008
0.6
0.005
0.01
0.015
HAmin
HAmax
MAmin
MAmax

Range dynamics are different at the leading and lagging edge of species ranges (Holt and Keitt 2000; Simmons and Thomas 2004; Fortin, Keitt et al. 2005; Bridle and Vines 2006; Franco, Hill et al. 2006; Oliver, Hill et al. 2009; Tingley and Beissinger 2009; Mace, Collen et al. 2010; Rowe, Finarelli et al. 2010; Angert, Crozier et al. 2011; Hill, Griffiths et al. 2011). This is because the dynamics of the leading edge are a function of colonization and dispersal properties; whereas, the lagging edge reflects extinctions, all of which are potentially confounded by the potential for metapopulation dynamics (Holt and Keitt 2000). Thus it is likely that these dynamics can be measured in terms of population abundance. It can then be predicted that (1) edge abundances are likely to be lower than center of the distribution abundances, (2) the balance of the leading and lagging edge dynamics will result in changes in the abundance distribution over time, (3) species responding to habitat dynamics and expanding their distribution range are more likely to have an abundance distribution skewed to the leading edge, and (4) species not responding to the habitat dynamics and contracting their distribution range are likely to show a abundance distribution skewed towards the lagging edge.

To test these predictions, we used the maximum relative abundance estimates as described above. We first tested whether the abundance distribution was even throughout the species' distribution range by comparing the maximum abundance at the upper and lower limits (that of the aggregates at higher elevations) with the maximum observed abundance within the species' distribution range (the maximum relative abundance of all the aggregates). Significant differences between the upper and lower limits and the maximum abundance values suggest that abundance is uneven within the species distribution range. We also tested whether the elevation at which the maximum abundance was observed was similar or different from the mid-range elevation. Finally we tested for the potential confounding effect of an initially (historical) higher abundance in any of these values that could be biasing the results.

We found significantly higher maximum relative abundance within the elevational range than the abundance at either the lower or upper limits for both species that tracked or did not track habitat dynamics in both historical and modern time (Table 12).

Table 12. Maximum Abundance (units of individuals/trapnight) at the Upper and Lower Limits of Species Distribution Ranges Compared to Maximum Observed Abundance within the Distribution Range for Both Historical and Modern Time in Species Tracking or Not Tracking Their Habitat Dynamics

		Tracking			Not tracking		
		Mean	F	*P*-value	Mean	F	*P*-value
Historic	Upper	0.004	3.36	0.048	0.0059	5.19	0.01
	Lower	0.007			0.008		
	Maximum	0.069			0.03		
Modern	Upper	0.011	0.38	0.0008	0.0096	3.93	0.03
	Lower	0.006			0.016		
	Maximum	0.04			0.088		

We also found that for both tracking and non-tracking species in both historical and modern time, the elevation at which the maximum abundance was observed was significantly higher than the mid-range elevation (estimated as the mean between the upper and lower distribution limits and then extracting the relative abundance value from the aggregate closer to that elevation; Table 13). This shows that abundance is uneven throughout the species distribution range. We found no significant differences between upper and lower and maximum abundance from historical to modern time in both tracking species (UL: F = 1.29, *P*-value = 0.27; LL: F = 0.002, *P*-value = 0.96; Max: F = 0.66, *P*-value = 0.43) and non-tracking species (UL: F = 0.99, *P*-value = 0.33; LL: F = 2.32, *P*-value = 0.14; Max: F = 2.14, *P*-value = 0.16). When removing the widespread *P. maniculatus* from the non-tracking species (since it occurs at all elevation ranges), we found a significant increase in lower limit abundance from historical to modern times (LL: Historic = 0.0046ind/ trapnight, Modern = 0.016ind/trapnight; F = 8.65, *P*-value = 0.008).

Table 13. Maximum Abundance Elevation (m) Versus Mid Range Elevation (m) for Both Historical and Modern Time in Tracking and Non-Tracking Species

		Tracking			Not tracking		
		Mean	F	*P*-value	Mean	F	*P*-value
Historic	Max abundance elevation	1722.8	17.61	0.0004	1889.85	11.39	0.003
	Mid range elevation	510.8			813.81		
Modern	Max abundance elevation	1744.8	16.66	0.0006	2032.1	17.69	0.0004
	Mid range elevation	663.23			726.38		

We then tested whether the leading and lagging edge abundance dynamics would result in changes in the abundance distribution over time. In our case, the leading edge is the upper limit of the species' distribution, and the lagging edge is the lower limit of the species' distribution. We estimated the geographical distance (in meters) from the location with the maximum abundance to the locations that corresponded to the upper and lower limits of the species distributions. We then tested whether there were significant differences in these distances between tracking and non-tracking species. We also tested whether the distance from maximum abundance to the upper and lower limits changed over time.

Historically, tracking species had significantly higher abundance closer to their upper distribution limit (leading edge) than not-tracking species (Table 14). Further, tracking species already showed higher abundance at the leading edge of their distribution before the expansion occurred (Table 15) in historical time. These differences are not observable in modern time.

Table 14. Distance (m) of Maximum Abundance Elevation to the Elevation of the Upper and Lower Limits of Species' Distributions, in Historical and Modern Time and for the Tracking and Non-tracking Species. Bold values represent significant differences.

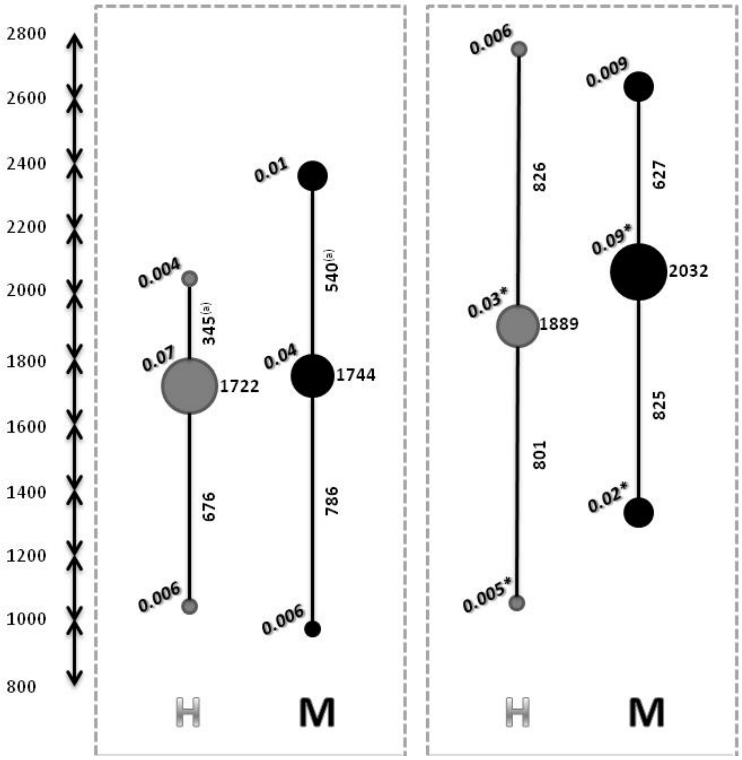
		Distance to Lower Limit			Distance to Upper Limit		
		Mean	F	*P*-value	Mean	F	*P*-value
Historic	Tracking	676.17	0.31	0.58	345.4	**7.41**	**0.01**
	Not tracking	801.51			826.12		
Modern	Tracking	786.27	0.03	0.87	540.19	0.21	0.65
	Not tracking	825.25			627.51		

Table 15. Distance (m) from the Maximum Abundance Elevation to the Elevation of the Upper and Lower Limits of the Species' Distribution for Tracking and Non-tracking Species in Historical and Modern Time. Bold values represent significant differences.

		Track			Not track		
		Mean	F	*P*-value	Mean	F	*P*-value
Historic	Distance to upper limit	**345.41**	**4.27**	**0.05**	826.12	0.01	0.92
	Distance to lower limit	676.17			801.51		
Modern	Distance to upper limit	540.19	1.82	0.19	627.51	0.67	0.42
	Distance to lower limit	786.27			825.25		

These results suggest that tracking species (also expanding species) had historically higher abundances closer to the leading edge of their distribution (the upper limit), a likely source of individuals for the observed range expansion. Also, non-tracking species (except *P. maniculatus*) have significantly increased their abundance in the lagging edge (lower) of their modern distribution (LL: Historical = 0.005ind/trapnight, Modern = 0.02ind/trapnight; F = 8.65, *P*-value = 0.008), likely as a result from the range contraction (Figure 11).

Figure 11. Tracking and Non-tracking Species and the Dynamics of Maximum Relative Abundance and Upper and Lower Range Limits. The left axis represents pseudo-elevation values since it includes averages for tracking and non-tracking species. Bars represent historical (gray) and modern (black) eras for tracking (left panel) and non-tracking (right panel) species. Circles represent maximum relative abundance, and size is matched to abundance values. Abundance values are shown sideways to the circles. Values to the left of the bars and circles represent average elevations for the upper and lower limits, and maximum abundance. Asterisks represent significant differences across time for abundance, and (a) represents significant differences in distance to the upper limit.



Section 5: Modeling Faunal Responses to Vegetation and Climate

Given that differences in niche breadth over time predicts, to some extent, whether or not species and vegetation ranges are having simultaneous dynamics, it can be expected that these same differences will affect modeling of species' responses to habitat and climate. We used maximum entropy (MAXENT) as the modeling platform, this being a widely used, robust species distribution modeling approach (Phillips, Dudik et al. 2004; Araujo and Guisan 2006; Phillips, Anderson et al. 2006; Phillips and Dudik 2008; Elith and Leathwick 2009; Elith, Kearney et al. 2010; Anderson and Gonzalez 2011; Elith, Philips et al. 2011).

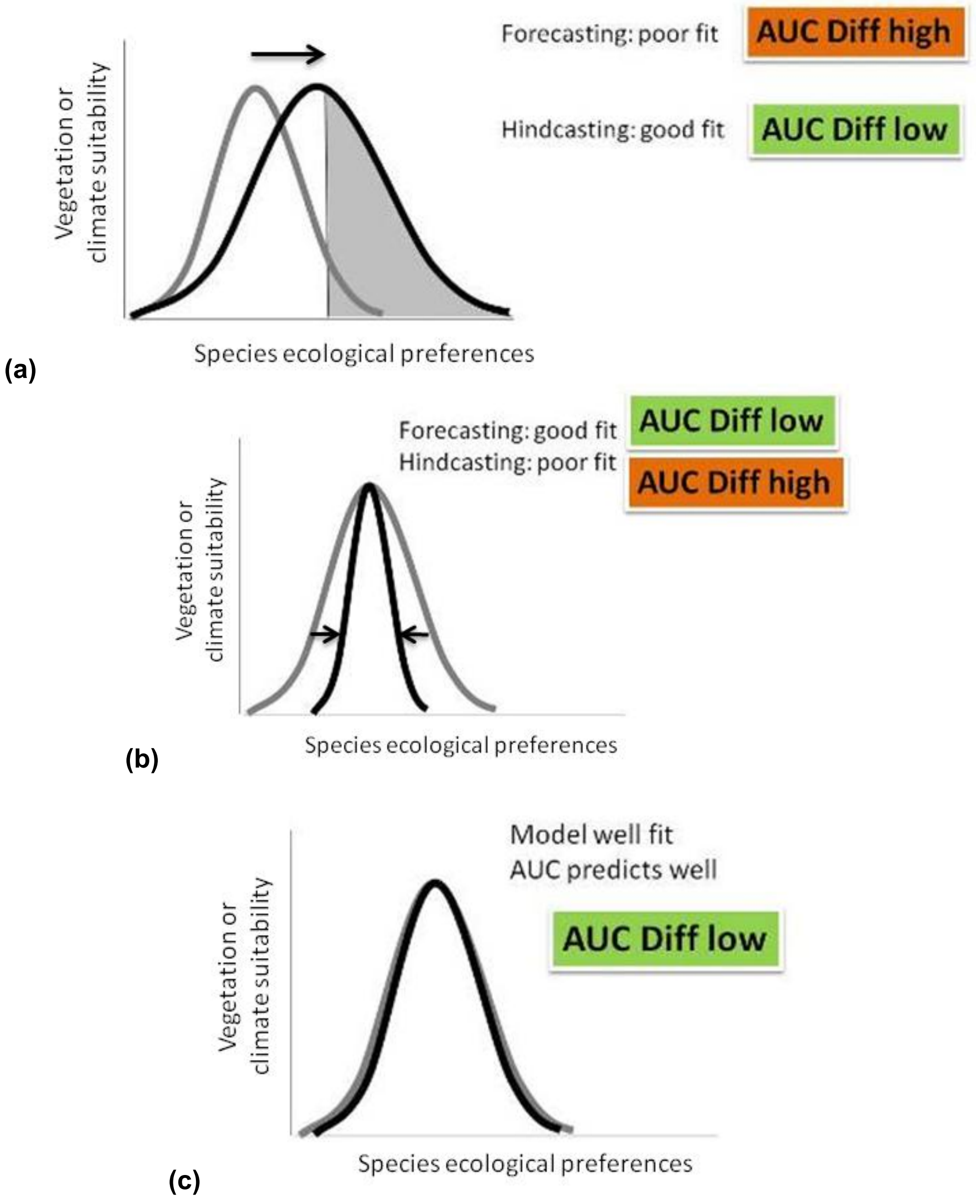
We used museum databases (Arctos, http://arctos.database.museum/home.cfm; and MANIS, http://manisnet.org/) to obtain mammal presence/specimen records for historical and modern time in the Yosemite transect. For each species we subsampled the data set to locations >1 km distant from any other record to avoid potential effects of spatial autocorrelation (Fortin, Keitt et al. 2005) on the modeling results (Guisan and Zimmermann 2000; Elith and Leathwick 2009; Elith, Kearney et al. 2010). For each species, we randomly selected 70 percent of the data for model training and 30 percent of the data for model testing (Guisan and Zimmermann 2000). In addition, we set a few criteria to consider a species "modelable":

1. Enough sample locations (>15) for both historical and modern time periods, an approach taken to maximize the use of information and increase the number of analyzed species at the expense of less conservative models;
2. Sampling occurred through most of the WHR types in the Sierra, to ensure sampling of all the suitable habitats for the species;
3. Data were able to produce a reliable model, with reliability defined as producing a model with AUC > 0.6;
4. Within-era model performance was high (AUC value was more than 0.7).

Twenty three species were deemed "*modelable*" under these criteria, and for them we developed: (1) within-era (historical-to-historical and modern-to-modern) models using training and testing data and predictor variables from the same time frame (partitioned in 70 and 30 percent of the data, respectively, for training and testing); (2) forecasting (historical-to-modern) and hindcasting (modern-to-historical) models using training data and predictor variables from time frame 1, projecting the model to the predictor variables in time frame 2, and using time frame 2 data to assess model accuracy. This approach tested model performance (viability for cross-temporal comparisons) across time, and the models are not necessarily independent as this temporal process is inherently dependent (Dobrowski, Thorne et al. 2011). We acknowledge this potential caveat, but as illustrated in the literature, this has proved to be the best way to address range dynamics (Wiens, Stralberg et al. 2009). This approach adds a means to validate model algorithm performance and thus assess the reliability of biological inferences and predictions based on such tools. Because of the observed changes in niche breadth that these species experienced, we expected that within-era models would perform better than across-era models, and that forecast models would be less accurate for species whose range was expanding than for species whose range was contracting; whereas, we expected the reverse for hindcasting models (Figure 12).

We used as a metric of model performance the area under the curve (AUC) metric, derived from the receiver-operating characteristics plots (ROC; Hanley and McNeil 1982). The AUC is calculated by plotting sensitivity (the conditional probability that a positive case is correctly classified) versus one minus specificity (the conditional probability that a negative case is correctly classified). Using this metric, a positive case in this case is the presence of a species, and a negative case indicates its absence. The AUC varies from 0.5 (total randomness in the assignment of classes) to 1 (100 percent correct classification), and values closer to 1 reflect better predictive models. For forecasting and hindcasting models, we calculated the difference in the AUC from time frame 1 to time frame 2. In forecasting, this is the difference between the AUC of the model created with historical data and the AUC of the model projected to modern data; in hindcasting, it is the difference between the AUC of the model created with modern data and the AUC of the model projected to historical data. This difference is a metric that assessed the ability of a model developed with data from one era to predict the distribution range of another era.

Figure 12. Model Expectations: (a) under expanding ecological preferences, (b) under contracting ecological preferences, and (c) under no change in ecological preferences. There is an additional possibility not represented: model expectations when species' ecological preferences shift towards a no-overlap state, which would result in reduced predictive ability both for forecasting and hindcasting models. The gray line represents historical ecological conditions, and the black line represents modern ecological conditions. AUC Diff refers to the difference in performance between a model built using historical data and a model built using modern data, and vice versa. This metric measures the ability of a model developed with data from one era to predict the distribution range of another era, and it helps to assess whether changes in ecological preferences are associated with observed range shifts.



We developed three suites of models, which varied in the predictor variables they used for model development:

- **Life zone models:** These models aim to mimic the elevation dynamics already observed. We used as a predictor variable a description of the life zones, as per Grinnell's descriptions during the historical sampling (from field notes). These models correspond to the application of Merriam's life zones to the California Sierra, and comprise a classification of vegetation types by elevation band. We expected that these models would be the most effective at analyzing the observed species' range dynamics, which are also based on elevational changes.
- **Vegetation models:** These models use vegetation (WHR types) at various time periods to predict species distributions. In these models, we applied the Wieslander and CalVeg data sets described above. When vegetation correlates with species elevation ranges, these models should be well fit to the data set. However, as already shown, species whose habitats are expanding have also broadened their habitat niche breadth, likely affecting the ability of vegetation to predict species ranges.
- **Climate models:** These models included minimum temperature, maximum temperature, precipitation, potential evapotranspiration, runoff, recharge, and climatic water deficit. We included all the climate variables available under the current project (Table 3) as predictor variables of small mammal species distribution. And we used the 1911–1940 averages for the historical time and the 1971–2000 averages for the modern time.

Model performance was tested using the AUC metric, and forecasting and hindcasting ability was assessed using the difference in the metric, as described above.

For each set of models (life zones, vegetation, and climate), we also include a table with the contributions of each predictor variable to the within-era models (historical and modern), to assess whether the relative contributions of each variable changed over time.

Limitations of the Modeling Approach

Several limitations can be associated with the modeling approach, including (1) data sets, (2) spatial autocorrelation, (3) modeling framework, (4) cross-temporal comparisons, (5) model assessment metrics, (6) non-independence of predictor variables, and (7) inference of biological results.

Above, we have described the issues with the small mammal capture data. For this modeling exercise, we used a collection of presence data from two databases of museum records. The reliability of these data is dependent on validation and curating done by museum professionals and experts on the likelihood that any given observation corresponds to a true observation of the species. Often it corresponds to field observations, capture and specimen records by the museum, and researchers that target the specified species. The databases undergo systematic validation and quality control protocols that assess the accuracy of the observations registered. In part, the quality control is limited to the geographic location associated with the observation, including a range of accuracies that depend on the technology available to register the spatial location, observer routine, and the location properties (for example, satellite cover and topographical features). With this in mind, we chose to take a conservative approach by removing all the records within less than 1 km distance, to avoid situations in which the same individual is registered more than once, and to reduce the potential for spatial autocorrelation.

We chose a commonly accepted and robust modeling platform that is well suited to account for positional uncertainty and sample size, thus allowing for the creation of effective models and cross-study and cross-temporal comparisons. Within the framework, we also chose a commonly accepted and best possible model assessment metric that addresses the ability of the model to correctly classify species presence and avoid misclassifications such as incorrectly a location as present. The last concern is about some circularity between vegetation and climate layers, as these are not independent and both are constrained by elevation. To avoid biasing the results due to the interdependence of the factors, we opted not to include vegetation and climate in one model that would assess the relative contribution of each. Given these caveats, we believe that the approach we followed, within the constraints of the input data set, produced reliable models for biological inference and successfully addressed the questions we targeted.

Life Zone Models

Model performance varied between AUC = 0.6 and AUC = 0.89, with *Peromyscus maniculatus* models performing poorly in both eras, likely because this species occurs in all elevation ranges.

Using model coefficients, Tables 16 and 17 show that the Arctic-Alpine life zone (the highest elevation) was not used in the modern models. *Sorex ornatus*, *Urocitellus beldingi, Callospermophilus lateralis, Tamias alpinus, Tamias quadrimaculatus, Tamias speciosus, Reithrodontomys megalotis,* and *Microtus longicaudus* reduced the number of life zones that were relevant for the models; whereas, other species increased the number of relevant life zones from historical to modern time.

Table 16. Historical MAXENT Model Coefficients Measuring the Relevance of the Life Zones as a Predictor Variable: 1. Lower Sonoran, 2. Upper Sonoran, 3. Transition, 4. Canadian, 5. Hudsonian, and 6. Arctic-Alpine. A higher coefficient reflects a greater contribution of that variable towards species presence. Empty rows reflect species for which models were not produced.

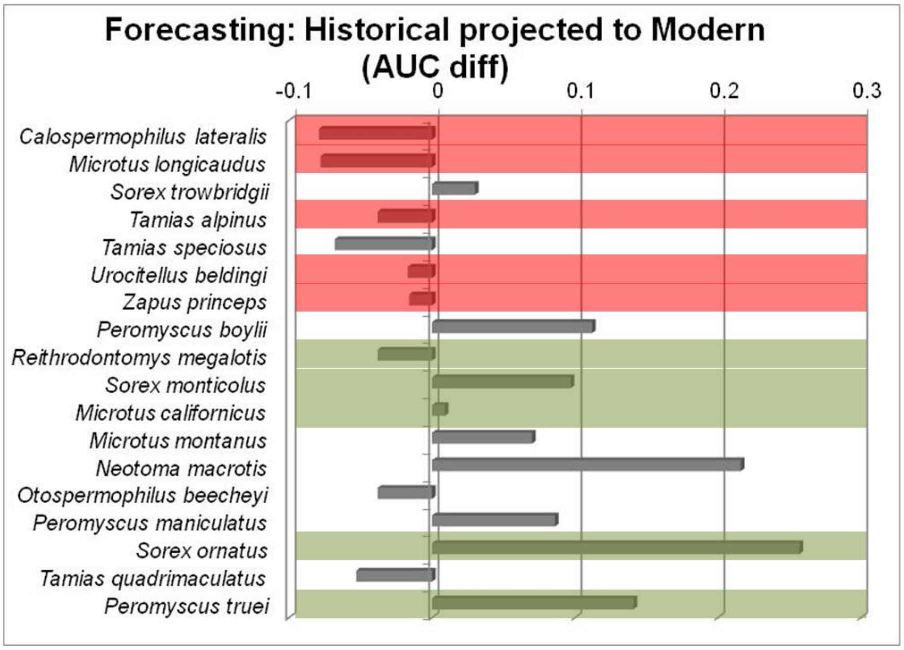
Species	Historic					
	1	2	3	4	5	6
Sorex monticolus				2.294	0.237	1.327
Sorex ornatus		1.569				
Sorex palustris				2.133		
Sorex trowbridgii			1.411	0.772		
Otospermophilus beecheyi		-0.172	0.898	0.178		
Urocitellus beldingi				0.891	2.159	1.085
Callospermophilus lateralis				1.602	1.242	0.927
Tamias alpinus				1.185	3.915	2.904
Tamias quadrimaculatus			1.263	1.539		
Tamias senex				2.722	0.465	
Tamias speciosus				2.429	2.237	2.133
Chaetodipus californicus						
Dipodomys heermanni	2.646					
Neotoma cinerea				1.686	0.069	1.16
Neotoma macrotis			2.464			
Peromyscus boylii			1.286			
Peromyscus maniculatus		-1.494	0.022			
Peromyscus truei		1.396	0.882			
Reithrodontomys megalotis	1.852	0.947				
Microtus californicus	1.308		1.369			
Microtus longicaudus			1.131	1.79	1.673	1.208
Microtus montanus				1.086	0.001	1.092
Zapus princeps				1.602	1.384	

Table 17. Modern MAXENT Model Coefficients Measuring the Relevance of the Life Zones as a Predictor Variable: 1. Lower Sonoran, 2. Upper Sonoran, 3. Transition, 4. Canadian, 5. Hudsonian, and 6. Arctic-Alpine. A higher coefficient reflects a greater contribution of that variable towards species presence. Empty rows reflect species for which models were not produced.

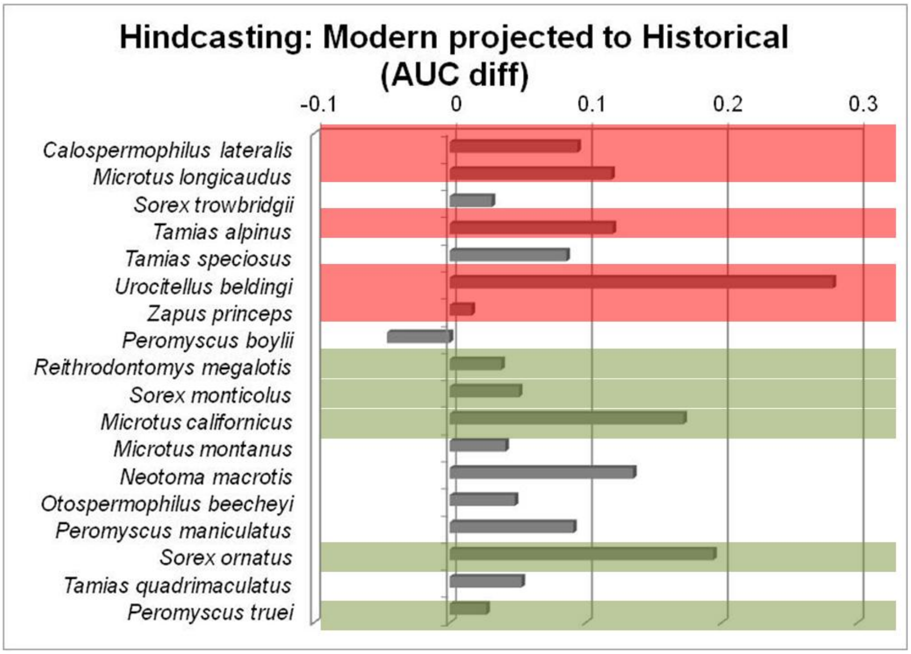
Species	Modern					
	1	2	3	4	5	6
Sorex monticolus			1.039	2.822	1.905	
Sorex ornatus	1.468	0.487				
Sorex palustris						
Sorex trowbridgii			1.592	1.162		
Otospermophilus beecheyi			0.988	1.193		
Urocitellus beldingi					2.626	
Callospermophilus lateralis				3.547	2.081	
Tamias alpinus					3.795	
Tamias quadrimaculatus				2.527		
Tamias senex						
Tamias speciosus				4.187	2.638	
Chaetodipus californicus		3.083				
Dipodomys heermanni	2.167	1.187				
Neotoma cinerea						
Neotoma macrotis	2.294	2.206	0.553			
Peromyscus boylii	1.029	0.362	1.133	0.009		
Peromyscus maniculatus	0.453	-0.522		1.341	0.55	
Peromyscus truei		0.544			0.027	
Reithrodontomys megalotis	2.189	0.577	0.086			
Microtus californicus	2.512	1.532				
Microtus longicaudus			1.132	2.767	2.424	
Microtus montanus			1.596	2.372	1.596	
Zapus princeps			0.601	2.406	1.609	

Model performance across eras was very similar, with AUC difference values on average less than 0.1 AUC point (Figure 13), with two notable exceptions: *N. macrotis* and *S. ornatus*. When comparing AUC differences between species expanding and contracting their elevation ranges, we found significantly better forecasting models for contracting species (lower AUC difference) than expanding species (F = 6.49, *P*-value = 0.03), and no significant differences in hindcasting models (F = 2.81, *P*-value = 0.13). This supports our predictions in Figure 12, because when forecasting the distribution ranges of species that expanded their limits, these species are occurring in new areas not likely to be in the training data set, and thus the model is not expected to perform well. The same explanation could apply to hindcasting contracting species, since the model will project outside the range of conditions that were used to inform the model. However, this will also depend on the rate of change in the use of the life zones that the species experienced, which in this case is of greater importance in the higher life zones (Canadian, Hudsonian and Arctic-Alpine; Tables 16 and 17).

Figure 13. Models of Species' Responses to Life Zone (red are species whose elevation range contracted; green are species whose elevation range expanded): (a) forecasting models (values of AUC diff are calculated as modern minus historical.); (b) hindcasting models (values of AUC diff are calculated as historical minus modern). Positive values indicate improvement of model performance when projecting to modern time; negative values indicate decrease in model performance when projecting to modern time, and vice versa for panel b.



(a)



(b)

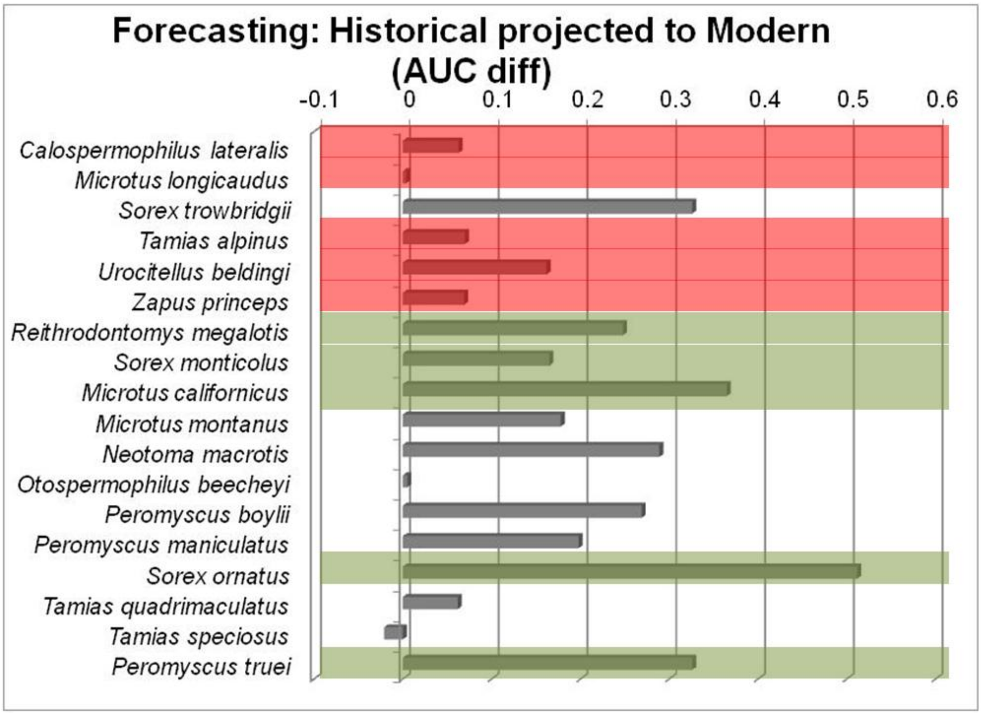
Vegetation Models

Vegetation models produced models with similar reliability to that of the life zones models, with AUC varying between 0.6 and 0.94. Model coefficients (Tables 18 and 19) show that the importance of each WHR type also changed over time, supporting our earlier findings that species that changed their habitat also changed their realized niche breadth. Appendix B shows the predicted range maps for each species in each of the eras and the within-era model accuracy.

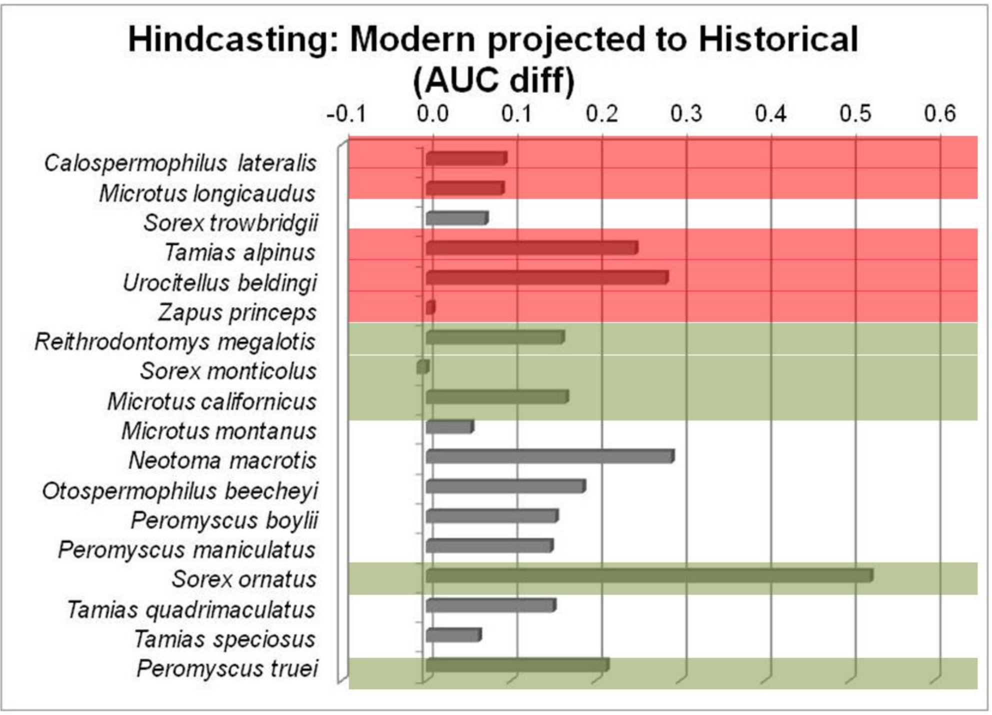
For models based on vegetation (WHR types), AUC differences are larger than those in the life zone models and on average 0.16 to 0.18 AUC points. The AUC difference was above 0.5 for one species *Sorex ornatus* (Figure 14a and b), indicating that using the model based on vegetation from one era to predict another era is potentially unreliable.

This suggests that the most suitable vegetation types across the two eras are shifting importance (Tables 18 and 19). This result coincides with our other analysis results on change in niche breadth for expanding species.

Figure 14. Models of Species' Responses to Vegetation (red are species whose elevation range contracted; green are species whose elevation range expanded): (a) forecasting models (values of AUC diff are calculated as modern minus historical); (b) hindcasting models (values of AUC diff are calculated as historical minus modern). Positive values indicate improvement of model performance when projecting to modern time; negative values indicate decrease in model performance when projecting to modern time, and vice versa for panel b.



(a)



(b)

Table 18. Historical MAXENT Model Coefficients for Vegetation as Predictor Variable. A higher coefficient reflects a greater contribution of that variable towards species presence. Empty rows reflect species for which models were not produced.

	AGR	AGS	BAR	MRI	URB	MHW	MCP	MCH	CRC
Sorex monticolus			0.624						
Sorex ornatus						1.893	3.194		0.847
Sorex palustris			0.489			1.276			
Sorex trowbridgii						1.519			
Otospermophilus beecheyi			0.239		5.627	1.025	1.091		
Urocitellus beldingi			1.497						
Callospermophilus lateralis			0.291			1.077			
Tamias alpinus			3.691						
Tamias quadrimaculatus									
Tamias senex			1.52						
Tamias speciosus			1.632					1.665	
Chaetodipus californicus									
Dipodomys heermanni		1.878			6.445				0.797
Neotoma cinerea			0.752						
Neotoma macrotis			0.451			2.284	2.349		0.19
Peromyscus boylii						2.021	2.604		
Peromyscus maniculatus			1.188		5.784	2.735	1.248		0.136
Peromyscus truei						1.879	3.106		1.994
Reithrodontomys megalotis	1.506		0.357		5.745		2.255		0.097
Microtus californicus	1.462		0.313			1.099	2.212		
Microtus longicaudus			0.339	3.83		1.125			
Microtus montanus									
Zapus princeps			1.087			0.891			

Table 18 (cont.). Historical MAXENT Model Coefficients for Vegetation as Predictor Variable. A higher coefficient reflects a greater contribution of that variable towards species presence. Empty rows reflect species for which models were not produced.

	PPN	WTM	WTF	JPN	LPN	RFR	SCN
Sorex monticolus		1.923		1.056	2.287	1.977	
Sorex ornatus							
Sorex palustris				0.922	1.117	0.862	
Sorex trowbridgii	0.117			2.326		1.106	
Otospermophilus beecheyi	0.604			1.652		1.593	
Urocitellus beldingi		2.795		0.928	1.553		0.492
Callospermophilus lateralis				1.635	1.228	2.068	0.287
Tamias alpinus		4.076			2.863		2.773
Tamias quadrimaculatus	1.942			2.425		2.366	
Tamias senex	0.047		1.099	3.003	1.052	2.365	
Tamias speciosus		3.379	2.069	2.065	2.792	2.007	0.837
Chaetodipus californicus							
Dipodomys heermanni							
Neotoma cinerea		3.098		1.184	1.896		
Neotoma macrotis							
Peromyscus boylii	0.619			0.686			
Peromyscus maniculatus	1.02			2.069		1.561	0.392
Peromyscus truei							
Reithrodontomys megalotis							
Microtus californicus							
Microtus longicaudus		1.638	1.569	2.012	1.113	0.711	1.128
Microtus montanus					3.186	1.939	
Zapus princeps				0.537	1.136	0.478	0.101

Table 19. Modern MAXENT Model Coefficients for Vegetation as a Predictor Variable. A higher coefficient reflects a greater contribution of that variable towards species presence. Empty rows reflect species for which models were not produced.

	AGS	AGR	BOW	MRI	LAC	URB	BAR	CRC	MHW	BOP	MCH	PPN	MHC
Sorex monticolus							0.85						
Sorex ornatus			2.033					0.801				1.465	1.575
Sorex palustris													
Sorex trowbridgii							0.705					1.343	
Otospermophilus beecheyi												3.223	
Urocitellus beldingi				4.407	2.482								
Callospermophilus lateralis					1.41								
Tamias alpinus					2.796		1.082						
Tamias quadrimaculatus													
Tamias senex													
Tamias speciosus					1.246		0.767						
Chaetodipus californicus								3.32			1.818		
Dipodomys heermanni		3.269						3.362					
Neotoma cinerea													
Neotoma macrotis			2.037					2.535			2.234	1.332	
Peromyscus boylii	0.205		0.318					0.247	0.825	2.494	0.516	0.911	
Peromyscus maniculatus	-0.497	0.872	0.056		0.488		0.011	1.173					
Peromyscus truei								2.139		2.643	0.665	1.06	
Reithrodontomys megalotis		1.769	1.661					0.092				0.756	
Microtus californicus			1.584					0.419	0.205			1.083	
Microtus longicaudus	0.243				0.793		0.316						
Microtus montanus	0.097						0.958						
Zapus princeps					1.031								

Table 19 (cont.). Modern MAXENT Model Coefficients for Vegetation as a Predictor Variable. A higher coefficient reflects a greater contribution of that variable towards species presence. Empty rows reflect species for which models were not produced.

	SMC	DFR	MCP	WTM	WTF	SCN	RFR	JPN	LPN	JNP	ADS
Sorex monticolus	2.392		2.276		4.742	1.333	3.137		2.658	2.862	
Sorex ornatus											
Sorex palustris											
Sorex trowbridgii	1.442						2.249				
Otospermophilus beecheyi	2.556						1.584				
Urocitellus beldingi						0.533			1.099		
Callospermophilus lateralis	2.127					1.455		1.655	2.022	4.241	
Tamias alpinus						0.772					
Tamias quadrimaculatus	4.423										
Tamias senex											
Tamias speciosus	2.419		2.193			1.696	2.056		3.173	2.781	
Chaetodipus californicus											
Dipodomys heermanni											
Neotoma cinerea											
Neotoma macrotis	0.653										
Peromyscus boylii	1.193	4.153							1.322		
Peromyscus maniculatus	1.418	2.311	1.434			0.889	1.502		1.457		
Peromyscus truei						1.024			1.591		
Reithrodontomys megalotis		3.206									
Microtus californicus											
Microtus longicaudus	1.962		2.53			1.792	2.359		2.717		
Microtus montanus	2.237					2.201			3.008		4.641
Zapus princeps	0.946		0.976	2.897		1.055	1.861		2.394	2.564	

When comparing AUC differences between species expanding and contracting their elevation ranges, we found a weak trend towards better forecasting models for contracting species (lower AUC difference) than expanding species (F = 3.29, *P*-value = 0.10), and no significant differences in hindcasting models (F = 0.9, *P*-value = 0.77).

To formally test whether there was a relationship between the results of the two separate analyses we regressed the forecasting change in AUC against the change in niche breadth (ΔFT) calculated by changing habitat availability and by changing habitat availability and suitability (see section on niche breadth and overlap; Table 7). We found no significant relationship between the two metrics (Table 20). Both analyses suggest a change in habitat use, and a widening of the niche breadth in expanding species would suggest that models would perform worse in forecasting (higher AUC difference). The former analysis represents a more immediate response to the adjacent habitat changes, whereas this later analysis reflects the changes at larger scales.

Table 20. Regression Analysis of the Relationship Between AUC Difference and ΔFT for Contracting and Expanding Species

		Contracting	Expanding
ΔFT	Changing availability	R^2=0.01, F=0.05, *P*-value=0.84	R^2=0.79, F=3.77, *P*-value=0.3, positive slope
	Changing availability and suitability	R^2=0.36, F=2.25, *P*-value=0.21, positive slope	R^2=0.02, F=0.02, *P*-value=0.91

Climate Models

Climate models had similar AUC values to those of the vegetation models (see Appendix C for climate model maps and AUC values; see Appendix B for comparison with vegetation models), but performed better than did the vegetation models when projected across eras (Figure 14).

Climate variable coefficients (expressed as a percentage of importance to the model) also show that importance of climate variables to each species is temporally dependent (Tables 21 and 22). Whereas in historical models, maximum temperature was important for many species (11 out of 22 species), in the modern models, minimum temperature becomes more important (10 out of 20 species). Precipitation is only important for a few species, except specifically in the form of potential evapotranspiration, runoff and recharge, and climatic water deficit.

Table 21. Climate Models' Variable Importance to the Historical MAXENT Model (Tmin – Minimum temperature, Tmax – Maximum temperature, PPT – Precipitation, PET – Potential evapotranspiration, run – Runoff, and rch - Recharge). A higher coefficient reflects a greater contribution of that variable towards species presence. Empty rows reflect species for which models were not produced.

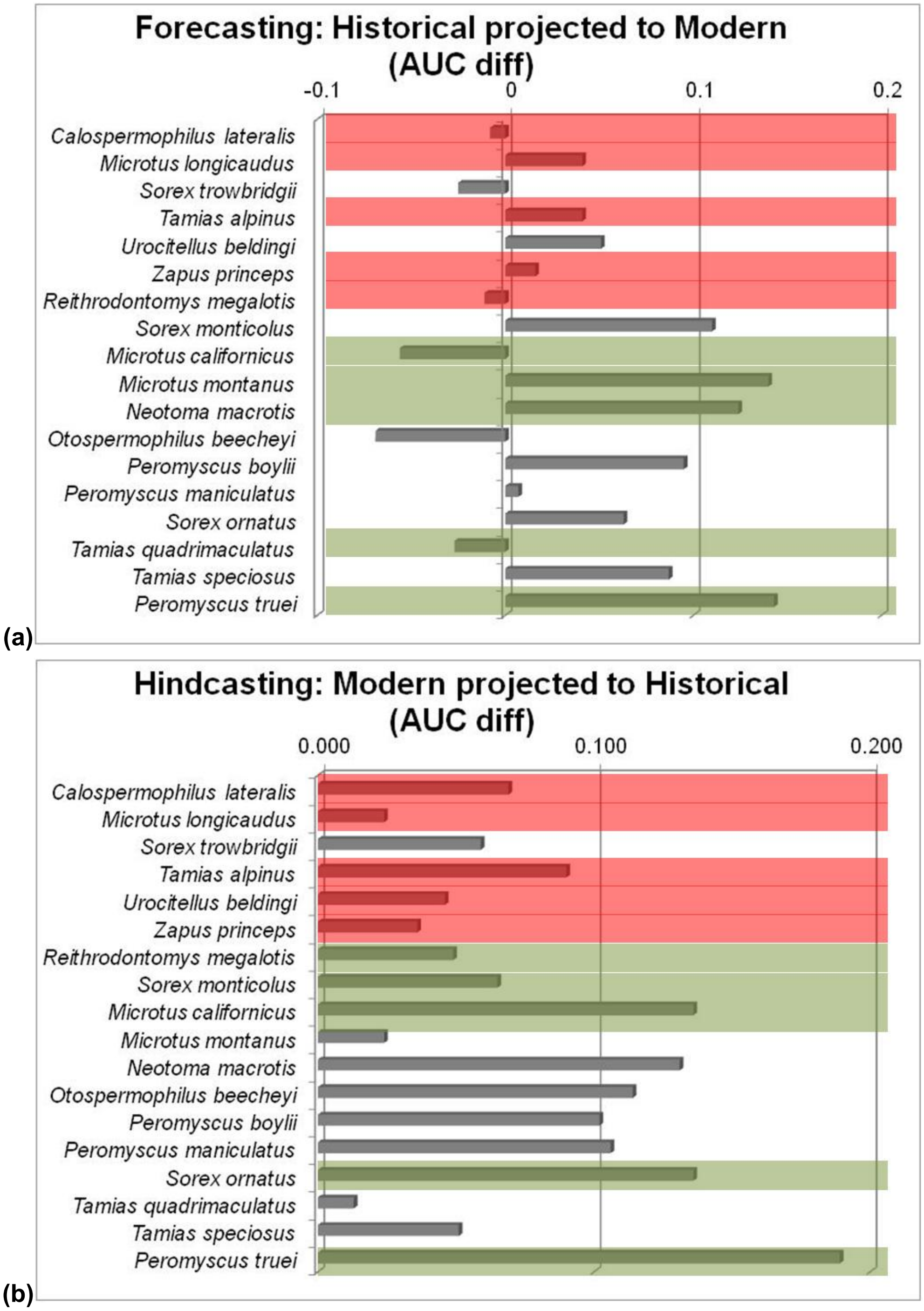
Species	**Historic**					
	Tmin	Tmax	PPT	PET	run	rch
Sorex monticolus	0.40	63.80	31.90	0.00	1.00	2.90
Sorex ornatus	0.00	79.20	12.50	3.10	5.30	0.00
Sorex palustris	0.00	17.00	83.00	0.00	0.00	0.00
Sorex trowbridgii	2.80	0.00	95.70	1.60	0.00	0.00
Otospermophilus beecheyi	90.40	0.70	8.80	0.00	0.00	0.00
Urocitellus beldingi	0.00	77.20	0.00	0.30	21.80	0.70
Callospermophilus lateralis	0.00	92.00	6.70	0.70	0.00	0.50
Tamias alpinus	0.80	74.30	0.10	14.30	0.00	8.20
Tamias quadrimaculatus	41.70	12.40	43.20	0.00	0.00	0.00
Tamias senex	63.70	1.00	24.30	3.80	0.00	7.20
Tamias speciosus	1.00	12.30	1.20	0.00	60.80	23.70
Chaetodipus californicus						
Dipodomys heermanni	1.50	36.30	36.20	0.00	24.00	0.00
Neotoma cinerea	0.00	56.70	0.00	8.20	33.20	1.90
Neotoma macrotis	66.10	0.00	0.80	0.00	33.10	0.00
Peromyscus boylii	38.10	0.00	0.00	37.70	1.40	15.70
Peromyscus maniculatus	7.90	6.80	7.00	14.60	21.40	41.60
Peromyscus truei	0.00	100.00	0.00	0.00	0.00	0.00
Reithrodontomys megalotis	0.00	88.50	0.00	0.00	11.50	0.00
Microtus californicus	0.00	82.20	0.00	0.00	17.80	0.00
Microtus longicaudus	8.20	44.60	3.70	0.60	14.20	18.40
Microtus montanus	0.00	8.80	19.60	0.00	71.20	0.50
Zapus princeps	22.70	44.20	14.50	2.30	9.10	3.00

Table 22. Climate Models' Variable Importance to the Modern MAXENT Model (Tmin – Minimum temperature, Tmax – Maximum temperature, PPT – Precipitation, PET – Potential evapotranspiration, run – Runoff, and rch – Recharge). A higher coefficient reflects a greater contribution of that variable towards species presence. Empty rows reflect species for which models were not produced.

Species	Modern						
	Tmin	Tmax	PPT	PET	run	rch	cwd
Sorex monticolus	10.60	47.80	11.30	2.80	17.00	6.60	3.90
Sorex ornatus	0.00	90.90	0.00	0.00	9.10	0.00	0.00
Sorex palustris							
Sorex trowbridgii	52.10	46.30	0.00	0.00	0.00	0.00	1.60
Otospermophilus beecheyi	50.60	20.00	0.00	5.10	0.00	0.00	24.20
Urocitellus beldingi	99.20	0.00	0.00	0.00	0.00	0.80	0.00
Callospermophilus lateralis	9.50	64.70	6.50	0.00	8.50	7.90	2.90
Tamias alpinus	89.40	2.00	0.00	8.60	0.00	0.00	0.00
Tamias quadrimaculatus	51.60	45.60	2.80	0.00	0.00	0.00	0.00
Tamias senex							
Tamias speciosus	13.60	38.80	0.00	0.00	32.90	12.10	2.70
Chaetodipus californicus	0.00	86.10	13.90	0.00	0.00	0.00	0.00
Dipodomys heermanni	83.30	0.00	0.00	0.00	0.00	16.60	0.10
Neotoma cinerea							
Neotoma macrotis	4.90	57.10	0.00	0.00	3.90	9.40	24.70
Peromyscus boylii	43.80	14.60	2.00	28.00	6.90	4.60	0.00
Peromyscus maniculatus	32.60	37.50	1.90	7.70	14.40	2.50	3.50
Peromyscus truei	96.30	0.00	3.70	0.00	0.00	0.00	0.00
Reithrodontomys megalotis	42.30	36.80	3.60	0.00	0.00	17.30	0.00
Microtus californicus	99.60	0.00	0.00	0.00	0.40	0.00	0.00
Microtus longicaudus	22.90	55.80	8.40	5.50	0.80	2.00	4.50
Microtus montanus	11.90	40.70	0.00	23.00	14.70	9.30	0.50
Zapus princeps	7.20	65.40	16.30	1.70	0.80	6.00	2.40

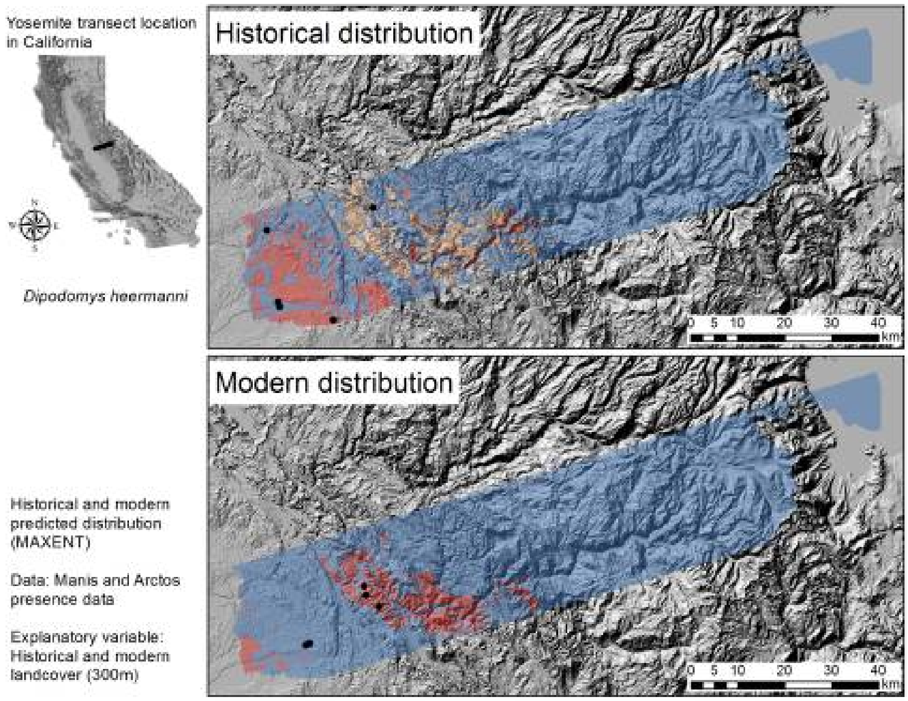
Compared to the life zones and vegetation models, the climate-based models had lower and more consistent difference in AUC. Both forecasting and hindcasting models performed well (AUC differences were between -0.1 and 0.2; Figure 15), and no significant differences were found between forecasting and hindcasting models for contracting or expanding species (forecasting: F = 1.24, *P*-value = 0.3; hindcasting: F = 1.32, *P*-value = 0.28; Figure 15).

Figure 15. Models of Species' Responses to Climate Variables (red are species whose elevation range contracted; green are species whose elevation range expanded): (a) forecasting models (values of AUC diff are calculated as modern minus historical); (b) hindcasting models (values of AUC diff are calculated as historical minus modern). Positive values indicate improvement of model performance when projecting to modern time; negative values indicate decrease in model performance when projecting to modern time, and vice versa for panel b.

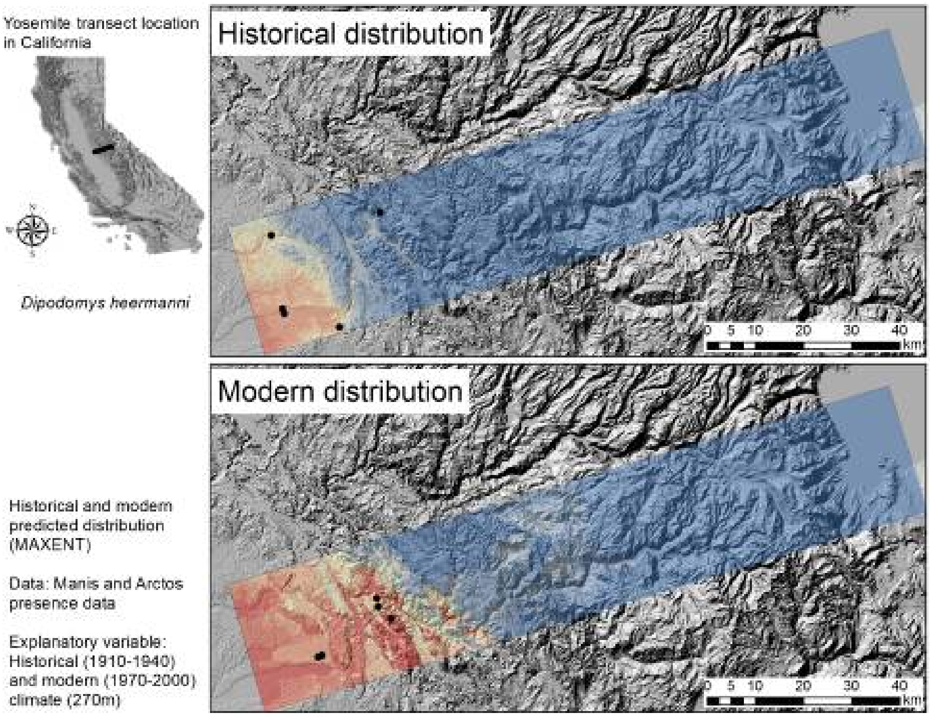


The following figures visually depict the changes in species ranges predicted by our modeling approach. Figures 16a and 16b, respectively, show the vegetation and climate model outputs for a low elevation species (*D. heermanni*). Figures 16c and 16d, respectively, show the vegetation and climate model outputs for a middle elevation species (*T. quadrimaculatus*). Figures 16e and 16f, respectively, show the vegetation and climate model outputs for a high-elevation species (*T. alpinus*). For all models, we use the within-era training and testing data. All species vegetation and climate model outputs are found in Appendix B and C, respectively.

Figure 16. Models of Species' Responses to Vegetation (red are areas more likely to be occupied in each of the time frames): (a) and (b) low-elevation contracting species (*Dipodomys heermanni*); (c) and (d) mid-elevation stable species (*Tamias quadrimaculatus*); (e) and (f) high-elevation contracting species (*Tamias alpinus*)



(a)



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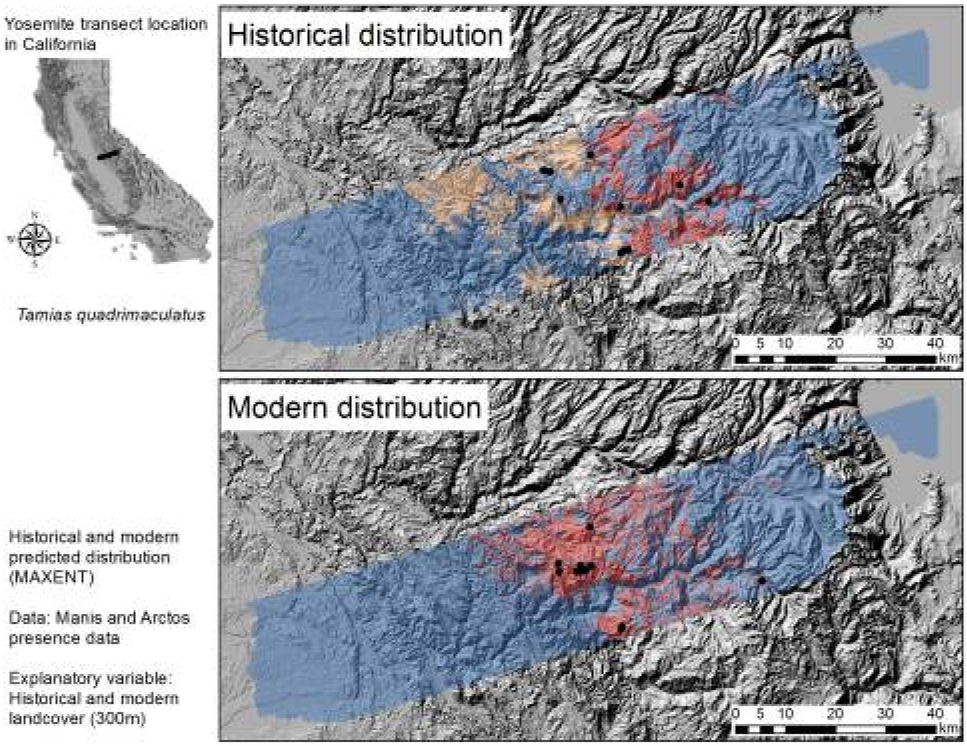
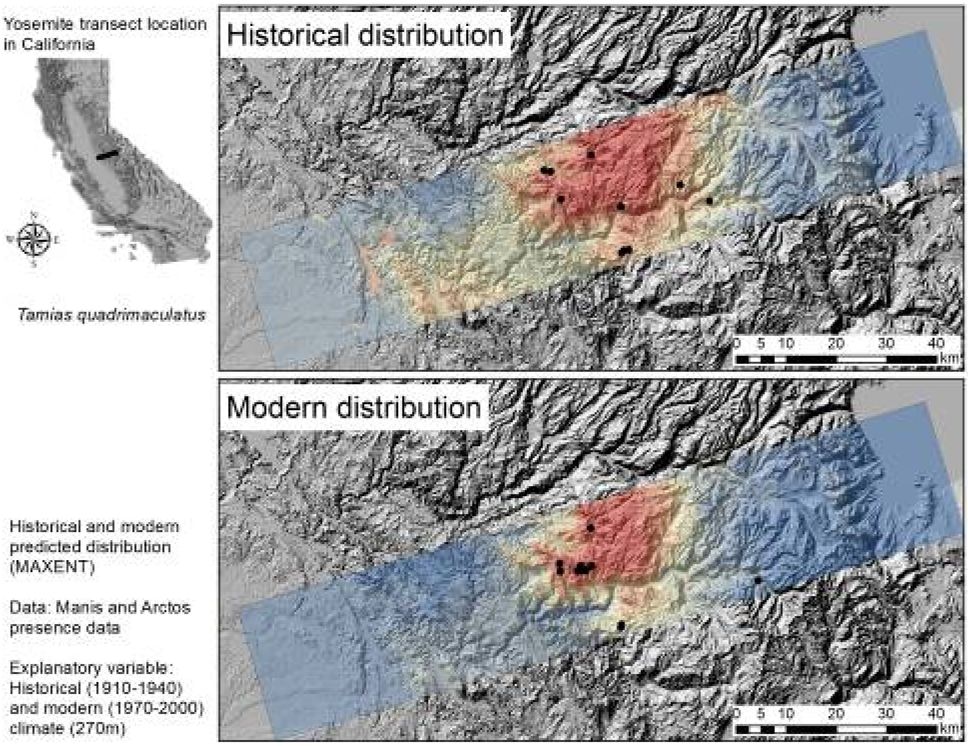
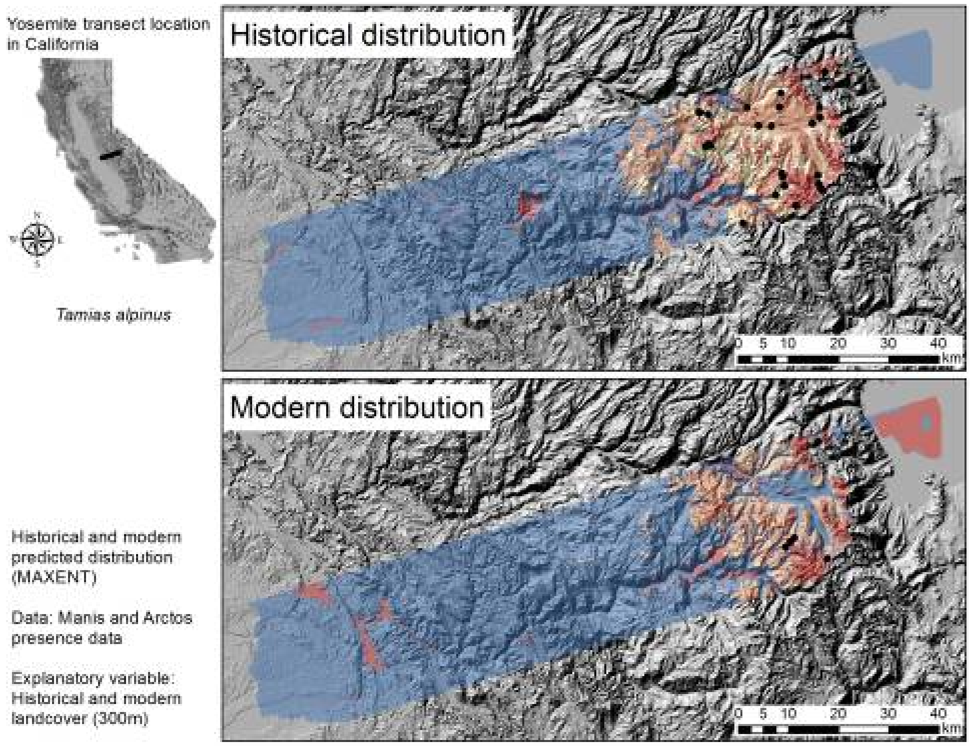

Yosemite transect location in California
N
W
E
S
Tamias quadrimaculatus
Historical distribution
0 5 10 20 30 40 km
Modern distribution
0 5 10 20 30 40 km
Historical and modern predicted distribution (MAXENT)
Data: Manis and Arctos presence data
Explanatory variable: Historical and modern landcover (300m)

(c)


Yosemite transect location in California
N
W
E
S
Tamias quadrimaculatus
Historical distribution
0 5 10 20 30 40 km
Modern distribution
0 5 10 20 30 40 km
Historical and modern predicted distribution (MAXENT)
Data: Manis and Arctos presence data
Explanatory variable: Historical (1910-1940) and modern (1970-2000) climate (270m)

(d)



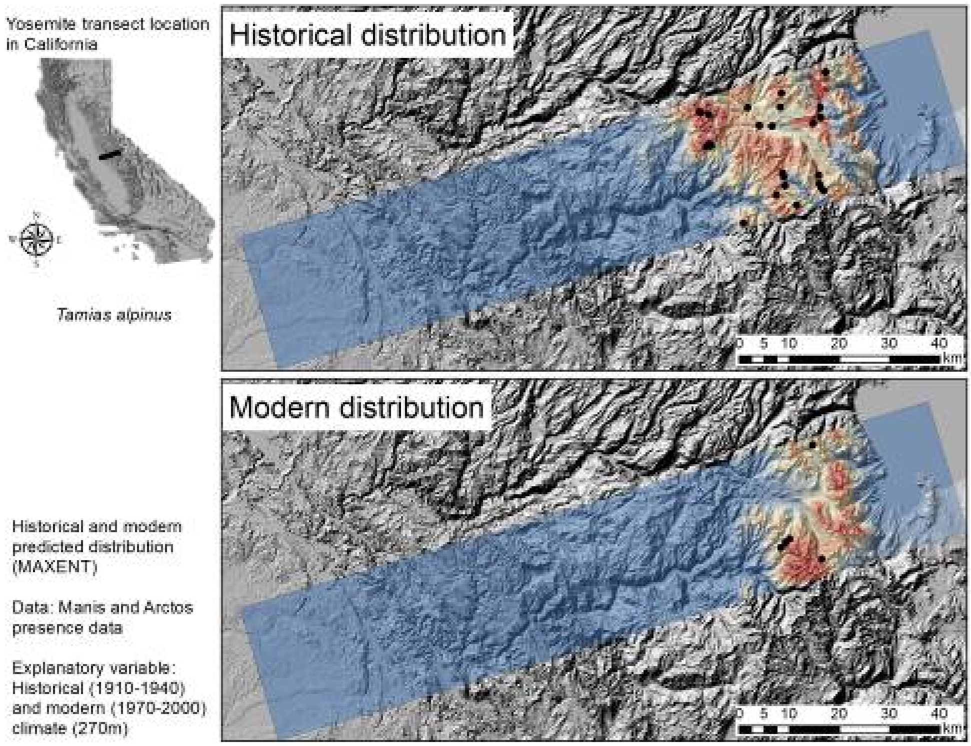
Tamias alpinus

Historical and modern predicted distribution (MAXENT)

Data: Manis and Arctos presence data

Explanatory variable: Historical and modern landcover (300m)

(e)



Tamias alpinus

Historical and modern predicted distribution (MAXENT)

Data: Manis and Arctos presence data

Explanatory variable: Historical (1910-1940) and modern (1970-2000) climate (270m)

(f)

Section 6: Identifying Vulnerable Species: Lessons Learned

This section summarizes the main findings of the analysis detailed in the previous sections. It shows the results per species that were categorized as contracting and expanding, then discusses how these findings relate to species shifting ranges over time, and how they may or may not be related to changes in vegetation and climate.

Contracting and Expanding Species

- Contracting species – Not tracking habitat dynamics:
    - Species presence is linked to their suitability index values in both historical and modern period
    - WHR (vegetation) range dynamics do not match the range dynamics of their habitat, except for three species (*Tamias senex, Sorex palustris,* and *Callospermophilus lateralis*)
    - Issues with thematic representation of the most suitable habitat for these species: meadows, barren land, riparian areas, and open habitats (e.g., forest gaps, dry meadows)
    - Niche breadth and overlap did not change
    - Not tracking habitat dynamics associated with predominance of herbivores, and a trend towards more *Microtus* spp.
    - No significant change in minimum abundance, trends towards increase in maximum abundance over time
    - Abundance is uneven in the species distribution ranges and significantly lower at the range limits, both in historical and modern time
    - Significant increase in abundance at the lagging edge of their distribution from historical to modern time
    - Life zone models perform best as predictors of species presence, followed by climate models, and finally vegetation models.
    - Forecasting models based on life zones perform better because they are still within the historical preferences
    - Models based on vegetation and on climate are not different for contracting and expanding species, suggesting not much change in the ranges for both vegetation and climate that species experienced in historical time

- Expanding species – Tracking habitat dynamics:
    - Species presence is linked to their suitability index values in both the historical and modern period
    - Species elevation range dynamics matches the dynamics of habitat range
    - Species seem to be responding to the increase in Sierran mixed conifer
    - Niche breadth increased significantly, suggesting plasticity in habitat preferences; no changes in niche overlap

- Tracking habitat dynamics associated with predominance of omnivores, and a trend towards more *Sorex* spp.
- Species significantly decreased their minimum and maximum abundances over time
- Abundance is uneven among the species distribution ranges and significantly lower at the range limits, both in historical and modern time
- Significantly higher abundance at the leading edge of their historical distribution, significant expanse of the leading edge
- Life zone models perform better than vegetation and climate models
- Forecasting models were worse than those for contracting species
- Models based on vegetation and on climate are not different for contracting and expanding species, suggesting not much change in the ranges for both vegetation and climate that species experienced in historical time

From this analysis we learned that several factors may be related to shifts in species ranges. Despite the original expectation that vegetation changes were related to species range shifts, this was only verified for half of the species. While apparently a random pattern, it was an elevation-truncated pattern, with high-elevation species showing no response to changes in habitat, and low- and intermediate-elevation species responding to the changes in habitat. This suggests that the pattern is linked to forest affinity. Species that use forested habitats responded to their habitat changes; whereas, species that do not use forested habitats did not respond to shifts in their habitat. This suggests that the presence of a forest layer may be an important predictor to species range shifts, and links the shifts in range with land cover and land use changes.

Further, this also suggests that species that do not respond to habitat changes (by adapting their ecological preferences to meet the dynamics of their habitat) and are not associated with a forest cover are more vulnerable to shifts in climate or other driving factors. This is corroborated by the better performance of climate models, in particular for contracting species. The implication is that these species are shifting their range to stay within their climate preferences rather than adapting to changes.

Expanding species seem to be shifting their ecological preferences in terms of habitat (as indicated by the widening of their niche breadth, and by the lower predictive ability of vegetation models compared with those of contracting species) and to a smaller extent, to their climate (another area where models performed more effectively for contracting species).

Thus the species we analyzed can be split into two categories that relate to the dynamics of their range shifts: expanding and contracting species. Expanding species seem to (1) respond strongly to shifts in habitat, which tended to be forest cover associated with a major shift in Sierran mixed conifer, (2) adapt to these shifts and expand their ranges as a response to the increase in suitable habitats, and (3) be buffered by the forest cover layer from the effects of shifting climate. Contracting species seem to (1) not respond to shifts in habitat, which tended not to be forest cover but could consist, to a smaller extent, of habitat types that may not be fully represented in the vegetation maps used, (2) not adapt to shifts in habitat or the increased extent of some of their suitable habitats, and (3) be (possibly therefore) more sensitive to the effects of climate, as they do not tend to be buffered by forest cover, and are thus shifting their ranges to stay within the most suitable climates.

From the suite of traits that we tested, we found significant effects of genus, adult body mass, diet guild, and neonatal body mass on species' ability to track their habitat. Being an omnivore ensures a wider variety of food options used as the species expands into new habitats. Further, the wider dietary niche breadth is consistent with the observed widening of the habitat niche breadth in species that tracked their habitat dynamics. As species widen their habitat use, it is likely that species with a less specialized diet will be favored, as they can take advantage of resources provided by the novel habitats. Herbivores did not tend to track their habitat dynamics, likely because these species use open areas, which were either not well represented or are decreasing in extent. We also found significantly lower adult and neonatal body mass in species that tracked their habitat dynamics. Low adult and neonatal body mass suggest a higher ability to produce off-spring and reflects the higher proportion of "r-selected" species among those with range expansion reported in Moritz et al. (2008). In addition, our results also suggest that species that expanded and species that contracted geographic ranges have very different abundance distributions historically, with species that underwent range expansion showing higher abundance at the leading edge of their range, perhaps giving them a leading advantage over species whose ranges contracted. Conversely, contracting species showed a significant increase of abundance at the lagging edge of their distribution in modern time, as a result of the contraction.

These results emphasize the need to have a priori knowledge of species range dynamics. Having such knowledge, supported and vetted using multitemporal data sets, allows for a valuable, accurate advance assessment of whether or not a species is adapting to the changes in its habitat and any climate changes affecting its ranges.

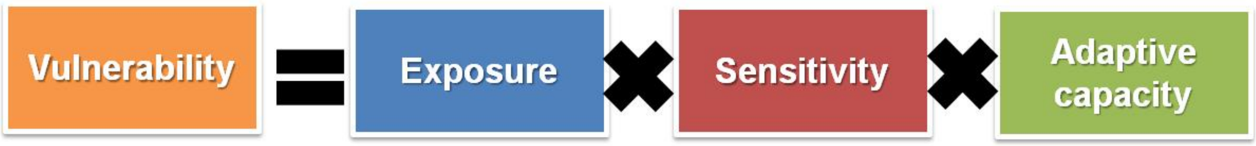
How to Use This Information to Assess Vulnerability

Vulnerability Assessments

Vulnerability assessments often deal with climate change alone, but we propose that they should also include a habitat component. Climate and habitat are two stressors that often go hand-in-hand in research on species' responses to climate change (Martin 2001; Honnay, Verheyen et al. 2002; Berry, Dawson et al. 2003; Iverson, Schwartz et al. 2004; Opdam and Wascher 2004; Franco, Hill et al. 2006; Keith, Akcakaya et al. 2008; Oliver, Hill et al. 2009). In this section we use the information we produced with the previous analysis and the lessons we learned, to assess species vulnerability to habitat changes. To estimate species' vulnerability to habitat changes, we created a ranking system for exposure, sensitivity, and adaptive capacity, and summed the ranks such that highest values indicate higher vulnerability and vice versa.

Climate and habitat changes can act independently, but can also have an interactive effect, which may impact assessments of vulnerability based on climate alone, or even without including other drivers of change. Vulnerability is defined as a function of the interaction between exposure, sensitivity, and adaptive capacity (Figure 17).

Figure 17. The Components of Vulnerability: Exposure, Sensitivity, and Adaptive Capacity



Exposure, sensitivity, and adaptive capacity to both climate and habitat change may be very different in magnitude and direction than a response from only one stressor (Figure 18). For some species, it can be argued that responses to habitat changes are more immediate that those to climate changes (Opdam and Wascher 2004), or may be of different intensity. Conversely, species distribution may change more rapidly than their (presumed) preferred habitats. Using existing knowledge of species' natural history may further our understanding of vulnerability as species-habitat relationships are often better described than species' physiological limitations imposed by climate. In addition, changes in habitat may themselves represent responses to changes in climate, reflected in the dynamics of vegetation and when human-mediated land use change is not a confounding factor.

Figure 18. Potential Outcomes of the Components of Vulnerability to Climate Change When Considering Both Climate and Habitat Changes. Boxes represent the potential outcomes of the interaction between climate and habitat to the three components of vulnerability: exposure, sensitivity, and adaptive capacity. We refer to changes in terms of climate and habitat suitability, as they reflect the availability and species use of each of these environmental factors.

Exposure (degree to which a system is at risk)				
			Habitat	
		Increases suitability	**No change**	**Decreases suitability**
Climate	**Increases suitability**	Low Exposure	Low Exposure	Uncertain Exposure
	No change	Low Exposure	No Exposure	Medium Exposure
	Decreases suitability	Uncertain Exposure	Medium Exposure	High Exposure

Sensitivity (degree to which a system is affected)				
			Habitat	
		Increases suitability	**No change**	**Decreases suitability**
Climate	**Increases suitability**	Positive sensitivity	Positive sensitivity	Uncertain Sensitivity
	No change	Positive sensitivity	Not sensitive	Negative Sensitivity
	Decreases suitability	Uncertain Sensitivity	Negative Sensitivity	Negative Sensitivity

Adaptive capacity (ability of the system to respond)				
			Habitat	
		Increases suitability	**No change**	**Decreases suitability**
Climate	**Increases suitability**	High	Intermediate	Uncertain
	No change	Intermediate	Unnecessary	Intermediate
	Decreases suitability	Uncertain	Intermediate	Low

Exposure

Our results show that small mammal species occurring in the Yosemite transect have been exposed to change over the last 80 years. The downscaled climate layers also show change in climate for the same area (an average increase in minimum temperature from 2.04°C to 2.49°C (35.6°F to 36.5°F), an average decrease in maximum temperature from 16.71°C to 17.21°C (62.1°F to 62.9°F), and an average increase in precipitation from 867.69 mm to 899.42 mm; see Figures 5 and 6). Both fauna and flora species were exposed to these changes in climate (for examples see Guarin and Taylor 2005; Mantgem and Stephenson 2007; Millar, Westfall et al. 2007; Moritz, Patton et al. 2008; Rubidge, Monahan et al. 2011; Rowe, Rowe et al. in prep). Changes in land cover (Vale 1987; Thorne, Morgan et al. 2008), resulting in changes in structure (Lutz, Wagtendonk et al. 2009), and due to fire regime (Collins, Everett et al. 2011), park management (Vale 1987), and climate change (Guarin and Taylor 2005; Mantgem and Stephenson 2007; Millar, Westfall et al. 2007), have been observed in Yosemite National Park.

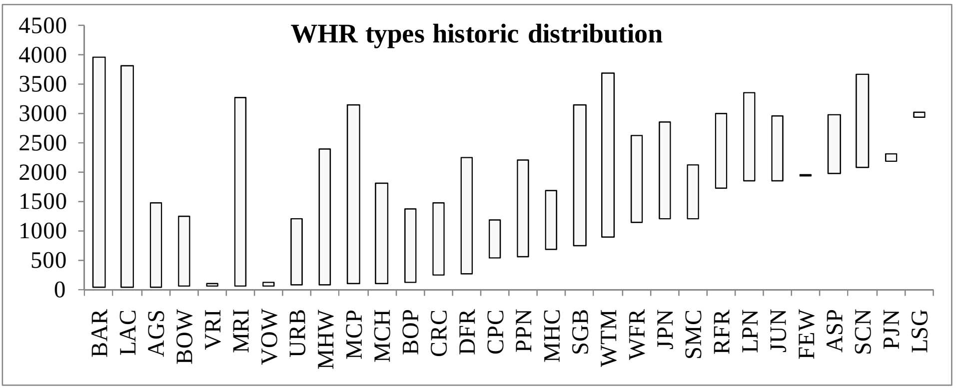
We considered as exposure to habitat change the degree to which the WHR land cover classes changed in our study area. We quantified this change by performing a cell-based change detection to estimate the amount of area that was lost or gained by each WHR type. We also calculated the transition matrix that describes the transitions from each WHR to all the WHR from historical to modern. Finally, we described per elevation band (in 100 m intervals) how much area had changed WHR type and standardized this value by the total area of land that exists at each elevation band. This metric represents the percent change per 100 m elevation intervals.

To create a per-species ranking for exposure, we selected the land cover class that increased the most, and used the inverse of its WHR rankings to rank species' exposure to land cover change. We created three ranks: high (when the suitability for the class that increased the most was low), intermediate (when the suitability for the class that increased the most was intermediate), and low (when the suitability for the class that increased the most was high), to which we attributed the values of 1, 0, and -1, respectively. Thus, high exposure to land cover change was emphasized and low exposure penalized. These types of rankings are similar to those applied in the Climate Change Vulnerability Indexes.

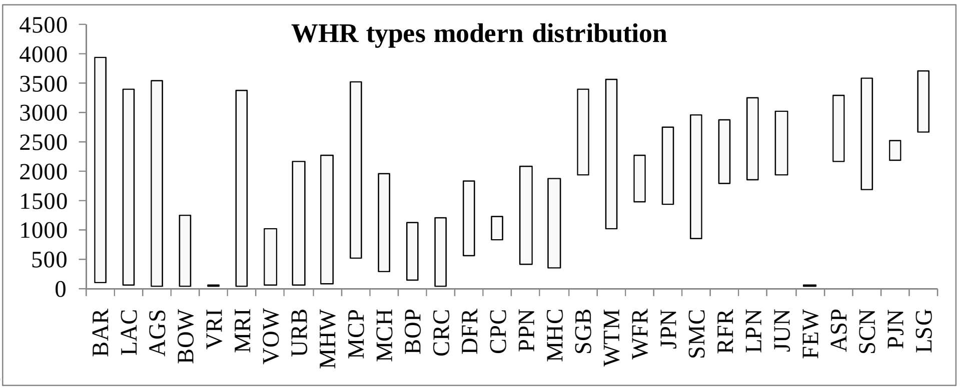
There were considerable changes in land cover from the 1930s to 2000s in the Yosemite transect (Figures 2, 3, and 4). The land cover that increased the most was the Sierran mixed conifer (SMC), at the expense of decreases mainly in Ponderosa pine (PPN) and white fir (WFR) (Table 2; Figures 2 and 3). The transitions between WHR types occurred at most elevations (Figures 4 and 19). The elevation bands where most change occurred were between 1,200 and 1,900 m (Figure 4), with percent changes >80 percent.

Figure 19. WHR types Distribution per Elevation in the Yosemite Transect: (a) historical distribution of WHR types, (b) modern distribution of WHR types

(a)



(b)



Sensitivity

To assess species sensitivity to changes in habitat suitability, we used a two-tiered approach. First we used the results from Table 6 that tested whether HSI values could explain the presence of mammal species. Then, we used the results from the tracking and non-tracking species and habitat area change (Figure 9b).

To create the rankings for sensitivity, we used information on the ability of HSIs to predict species presence and the change in suitable habitat area. We first defined that the ability of HSIs to predict species presence would be an indicator of species' sensitivity to habitat, and the sign of the relationship between species presence and HSIs would dictate whether species were positively or negatively sensitive. Positively sensitive species were ranked -1, negatively sensitive species were ranked 1, and non-sensitive were ranked 0. Next, we ranked species according to the changes in their suitable habitat. Positively sensitive species were those whose suitable habitat area changed in the same direction as the species distribution range (the suitable habitat area increased from historical to modern time and the species distribution range expanded and vice versa), negatively sensitive species were those for which suitable habitat area and the distribution range did not change in the same direction (the habitat expanded and species range contracted or vice versa), and non-sensitive species were those whose habitat or range showed no change. This reflects the results from the occupancy modeling that indicated which species significantly increased or decreased their elevation range over time (Moritz, Patton et al. 2008); i.e., when range shifts were greater than 10 percent of the range. Again, positively sensitive species were ranked -1, negatively sensitive species were ranked 1, and non-sensitive were ranked 0. The final sensitivity rank was the average of both ranks.

Overall, sensitivity to habitat changes ranked ten species as positively sensitive (-1≤sensitivity≤-0.5), three as non-sensitive (rank = 0), and seven as negatively sensitive (0.5≥sensitivity≥1; Table 23).

Table 23. Two Components of Sensitivity: Species Presence Associated with HSIs and Whether the Suitable Habitat Area Changes in the Same Direction as the Species Distribution Ranges (Area)

Species	HSIs	Area	Sensitivity score
Dipodomys heermanni	Non-sensitive (0)	Negative (1)	Negative (0.5)
Sorex palustris	Non-sensitive (0)	Negative (1)	Negative (0.5)
Callospermophilus lateralis	Non-sensitive (0)	Negative (1)	Negative (0.5)
Tamias alpinus	Negative (2)	Negative (1)	Negative (1)
Neotoma cinerea	Positive (-1)	Negative (1)	Non-sensitive (0)
Microtus longicaudus	Positive (-1)	Negative (1)	Non-sensitive (0)
Zapus princeps	Positive (-1)	Negative (1)	Non-sensitive (0)
Urocitellus beldingi	Non-sensitive (0)	Non-sensitive (0)	Non-sensitive (0)
Peromyscus maniculatus	Non-sensitive (0)	Non-sensitive (0)	Non-sensitive (0)
Microtus californicus	Non-sensitive (0)	Non-sensitive (0)	Non-sensitive (0)
Sorex ornatus	Non-sensitive (0)	Positive (-1)	Positive (-0.5)
Sorex trowbridgii	Positive (-1)	Non-sensitive (0)	Positive (-0.5)
Peromyscus truei	Non-sensitive (0)	Positive (-1)	Positive (-0.5)
Microtus montanus	Positive (-1)	Non-sensitive (0)	Positive (-0.5)
Tamias senex	Positive (-1)	Positive (-1)	Positive (-1)
Tamias speciosus	Positive (-1)	Positive (-1)	Positive (-1)
Sorex monticolus	Positive (-1)	Positive (-1)	Positive (-1)
Neotoma macrotis	Positive (-1)	Positive (-1)	Positive (-1)
Peromyscus boylii	Positive (-1)	Positive (-1)	Positive (-1)
Reithrodontomys megalotis	Positive (-1)	Positive (-1)	Positive (-1)

Adaptive Capacity

To assess species adaptive capacity, we examined whether the species elevation range dynamics matched the dynamics of habitat elevation using the information from Figure 9a. The rankings for adaptive capacity were then -1 for habitat tracking species and 1 for non-tracking, penalizing species with adaptive capacity and emphasizing species without it.

Vulnerability

The vulnerability value was the sum of the rankings for exposure, sensitivity, and adaptive capacity. Higher value represents more vulnerable species and lower value represents less vulnerable species. Table 24 represents the ranking system and the values for exposure, sensitivity, and adaptive capacity of small mammals to habitat and the overall vulnerability rank.

Table 24. Habitat Vulnerability Assessment for Mammals in the Yosemite Transect: Exposure (high =1, intermediate = 0, and low = -1), Sensitivity (from Table 24), Adaptive Capacity (tracking = -1, not tracking = 1)

	Change	Exposure	Sensitivity	Adaptive capacity	Vulnerability
Tamias alpinus	C	1	1	1	3
Dipodomys heermanni	C	1	0.5	1	2.5
Microtus longicaudus	C	1	0	1	2
Urocitellus beldingi	C	1	0	1	2
Microtus montanus	NC	1	-0.5	1	1.5
Microtus californicus	E	0	0	1	1
Neotoma cinerea	C	0	0	1	1
Zapus princeps	C	0	0	1	1
Tamias speciosus	NC	0	-1	1	0
Peromyscus maniculatus	NC	-1	0	1	0
Sorex palustris	C	0	0.5	-1	-0.5
Sorex ornatus	E	1	-0.5	-1	-0.5
Sorex trowbridgii	NC	-1	-0.5	1	-0.5
Reithrodontomys megalotis	E	1	-1	-1	-1
Sorex monticolus	E	1	-1	-1	-1
Neotoma macrotis	NC	-1	-1	1	-1
Calospermophilus lateralis	C	-1	0.5	-1	-1.5
Peromyscus truei	E	-1	-0.5	-1	-2.5
Tamias senex	C	-1	-1	-1	-3
Peromyscus boylii	NC	-1	-1	-1	-3

The most vulnerable species to habitat changes were *T. alpinus* and *D. heermanni*, followed by *M. longicaudus*, *U. beldingi,* and *M. montanus*. The least vulnerable species were *P. boylii* and *P. truei*. This is likely because species are exposed to considerable changes in the land-cover types that dominate the Yosemite transect, such as the increase in the Sierran mixed conifer and the decrease in Ponderosa pine and white fir, mostly at elevation bands between 1,200 and 1,900 m. However, the degree of exposure to climate changes is quite different, occurring at different elevation bands than those where vegetation changes occurred (Figure 7). This goes in hand with our discussion point that species that depend on a forest cover may respond differently to land cover and climate changes than species that do not. There were more positively sensitive species to habitat changes (whose suitable habitat area changed in the same direction as the species distribution range) than negatively sensitive species (whose suitable habitat area changed in the opposite direction as the species distribution range). This suggests that a suite of species is able to adapt to the changes in their habitat conditions, and thus have adaptive capacity. The most vulnerable species were species whose distribution range had contracted, of non-forested habitats and lacking the ability to track the changes in their habitat. Conversely, the least vulnerable species were those with the most wide ecological preferences and able to track the changes in their habitat over time, being buffered from habitat and climate changes.

Section 7: Integration with Other Groups

Fire

Because major changes occurred in the Sierran Mixed Conifer Belt, it would be interesting to match the observed responses of vertebrates with the predictions made for fire dynamics in the Sierra.

Plant Modeling

Because major changes occurred in climate, and vertebrates are responding to these changes, the authors of this paper are currently collaborating with UC Santa Barbara to use their predictive models for plant species to create predictions of future WHR in the Sierra and link those to the vertebrate responses.

Other Interest Groups

The authors of this paper have initiated conversations to integrate our results with the ongoing Yosemite National Park Natural Resource Assessment.

The authors of this paper have also initiated conversations with Robert Klinger at the United States Geological Survey for integration of our results to his detailed studies on Alpine mammals.

The authors of this paper have been awarded a grant from the California Landscape Conservation Cooperative to link the results of the occupancy modeling with landscape genetics.

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Glossary

Adaptive capacity	The ability of a system to respond to climate change
California Wildlife Habitat Relationships	Expert-based system that describes vegetation associations based on their role as a habitat for vertebrate species in California, and describes for each vegetation type the suitability of that habitat for each species in the form of a Habitat Suitability Index (HSI).
Distribution range	The geographical range in which a species occurs and is controlled by the environment the species occupies, including biotic and abiotic interactions. Geographical distribution ranges are dynamic, as they reflect the intensity and direction of the controlling factors, and may contract (reduce in extent), expand (increase in extent), or shift (translocate in either direction), and these dynamics can be concurrent between the leading edge (the upper limit) and the lagging edge (the lower limit).
Ecological niche	Defines all the environmental conditions that a species can withstand. It can be defined as the fundamental niche when all possible combinations of environmental conditions are included, or as the realized niche where only the available environmental conditions are depicted, and trimmed by species interactions. Niche breadth corresponds to the width of environmental conditions and resources a species can use, and overlap the degree to which either two species or the same species in two points in time share the same niche properties.
Forecasting and hindcasting	The ability to predict forward and backward, respectively.
Habitat suitability	The degree to which a land cover type is occupied and used by a species. Usually in an index form that varies between 0 and 1, with 0 representing avoidance and 1 representing preference.
Modelable	In this context a species for which a model was produced, given the criteria of: (1) there are enough sample locations for both historical and modern time periods; (2) sampling occurred through most of the WHR types in the Sierra; (3) data were available to produce a reliable model; (4) within-era model performance (AUC value was greater than 0.7) was high.
Relative abundance	An estimated abundance total determined through statistics, such as capture data, measured by the number of individuals.
Sensitivity	"the degree to which a system is affected, either adversely or beneficially, by climate-related stimuli. The effect may be direct or

	indirect." It is calculated with a statistical measure varying in intensity and direction that results in a designation of positively sensitive (when environmental effects are beneficial) and negatively sensitive (when the environmental effects are detrimental), or non-sensitive (when there are no environmental effects).
Vector of change	A depiction of the dynamics of change in multiple parameters simultaneously; for example, in this case we estimated the vector of change for all the habitats deemed suitable for each species concurrently.
Vulnerability	Susceptibility to harm or change.

Glossary of Acronyms

AET	Actual evapotranspiration
AGR	agriculture
AGS	annual grasslands
AIC	Aikake's Information Criterion
ANOVA	analysis of variance
ASP	aspen
AUC	area under the curve of the receiver-operating characteristic plots
BAR	barren
BCM	Basin Characterization Model
BMR	Basal Metabolic Rate
BOW	blue oak woodland
BOP	blue oak-foothill pine
CalVeg	California Vegetation
CCVI	Climate Change Vulnerability Index
CDF	California Department of Fish and Game
CRC	chamise-redshank chaparral
CPC	closed-cone pine-cypress
CWD	climatic water deficit
CWHR	California Wildlife Habitat Relationships (also referred to as WHR)
DFR	Douglas fir

EPN	East side pine
FEW	freshwater emergent wetland
FT	Smith’s measure of niche breadth
GIDS	gradient and inverse distance squared
GIS	Geographic Information Systems
GRP	Grinnell Resurvey Project
HSI	Habitat Suitability Index
JPN	Jeffrey pine
JUN	juniper
LAC	lacustrine
LL	Lower limit
LSG	Low sage
LPN	lodgepole pine
M	niche overlap
MAXENT	Maximum entropy model
MCH	mixed chaparral
MCP	montane chaparral
MCV	Manual of California Vegetation
MHW	montane hardwood
MHC	montane hardwood-conifer
MRI	montane riparian
MVZ	Museum of Vertebrate Zoology
NMB	neonatal body mass
PCA	Principal Component Analysis
PET	potential evapotranspiration
PIER	Public Interest Energy Research
PJN	pinyon-juniper
PPN	Ponderosa pine
PPT	precipitation
PRISM	Parameter-elevation Regressions on Independent Slopes Model

RCH	recharge
RFR	red fir
RMSE	Root Mean Square Error
RUN	runoff
SGB	Sage brush
SMC	Sierran mixed-conifer
SCN	Sub-alpine conifer
Tmax	maximum temperature
Tmin	minimum temperature
UL	upper limit
UNK	unknown
URB	urban
USFS	United States Forest Service
USFWS	United States Fish and Wildlife Service
USGS	United States Geological Survey
VegCAMP	Vegetation Classification and Mapping Program
VRI	valley foothill riparian
VOW	valley oak woodland
VTM	Vegetation Type Mapping
WHR	Wildlife Habitat Relationships
WTM	wet meadow
WFR	white fir
YNP	Yosemite National Park

APPENDIX A:
Contribution of Each Land Cover Type to Niche Breadth Estimation (Removed ASP, CPC, EPN, LSG, MRI, SGB, URB, VOW, VRI)

Table A1. Relative Contribution of Each Land Cover Type to the Calculation of Species Niche Breadth Assuming Constancy Is Species Suitability Values

	AGR	AGS	BAR	BOP	BOW	CRC	DFR	JPN	JUN	LAC
C. californicus	0.000	0.006	0.000	-0.003	0.001	-0.002	0.000	0.000	0.000	0.000
D. heermanni	0.000	0.006	-0.004	-0.002	0.003	0.002	0.000	0.000	0.000	0.002
M. californicus	0.000	0.005	-0.005	-0.001	0.003	0.001	-0.001	-0.002	0.000	0.001
M. longicaudus	0.000	0.004	0.000	0.000	0.000	0.000	0.000	-0.006	0.000	0.000
M. montanus	0.000	0.003	-0.004	0.000	0.000	0.000	0.000	-0.004	0.000	0.000
N. cinerea	0.000	0.000	-0.008	0.000	0.000	0.000	0.000	-0.001	0.001	-0.001
N. macrotis	0.000	0.004	-0.001	-0.002	0.002	0.000	0.000	-0.002	0.000	0.000
P. boylii	0.000	0.002	-0.002	-0.001	0.001	0.000	-0.001	-0.003	0.000	0.000
P. maniculatus	0.000	0.002	0.000	-0.001	0.000	0.000	0.000	-0.004	0.000	0.000
P. truei	-0.001	0.002	0.003	-0.003	0.000	-0.002	0.000	0.001	0.000	0.000
R. megalotis	0.000	0.001	-0.001	-0.002	0.001	-0.001	0.000	0.001	0.000	0.000
S. monticolus	0.000	0.004	-0.005	0.000	0.000	0.000	0.000	-0.005	0.000	0.000
S. ornatus	0.001	0.007	0.000	-0.002	0.006	-0.004	0.000	0.000	0.000	0.001
S. palustris	0.000	0.008	0.003	0.000	0.000	0.000	0.000	-0.007	0.000	0.000
S. trowbridgii	0.000	0.002	-0.001	0.000	0.000	0.001	-0.001	-0.006	0.000	0.000
S. beecheyi	0.000	0.000	0.000	-0.001	0.000	-0.001	0.000	-0.004	0.000	0.000
S. beldingi	0.000	0.005	-0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000
S. lateralis	0.000	0.003	0.000	0.000	0.000	0.000	0.000	-0.006	0.000	0.000
T. alpinus	0.000	**0.007**	-0.002	0.000	0.000	0.000	0.000	-0.004	0.000	0.000
T. quadrimaculatus	0.000	0.005	-0.001	0.000	0.000	0.000	-0.001	-0.007	0.000	0.000
T. senex	0.000	0.000	-0.009	0.000	0.000	0.000	0.000	-0.008	0.002	0.000
T. speciosus	0.000	0.004	-0.003	0.000	0.000	0.000	0.000	-0.007	0.000	0.000
Z. princeps	0.000	0.004	-0.001	0.000	0.000	0.000	0.000	-0.005	0.000	0.000

Table A1 (cont.). Relative Contribution of Each Land Cover Type to the Calculation of Species Niche Breadth Assuming Constancy Is Species Suitability Values

	LPN	MCH	MCP	MHC	MHW	PPN	RFR	SCN	SMC	WFR	WTM
C. californicus	0.000	-0.001	-0.004	0.002	0.007	-0.008	0.000	0.000	**0.015**	0.000	0.000
D. heermanni	0.000	-0.001	-0.003	0.000	0.002	-0.006	0.000	0.000	0.000	0.000	-0.002
M. californicus	0.000	0.001	-0.004	0.001	0.002	-0.012	0.000	0.002	**0.010**	-0.003	-0.001
M. longicaudus	-0.005	0.000	-0.002	0.000	-0.002	-0.008	0.001	0.006	**0.020**	-0.005	-0.002
M. montanus	-0.013	0.000	-0.001	0.000	0.000	-0.005	0.002	0.002	**0.022**	-0.004	-0.003
N. cinerea	-0.007	0.000	-0.001	0.000	-0.001	-0.002	0.006	0.003	**0.030**	-0.001	-0.004
N. macrotis	-0.002	0.001	-0.005	0.001	0.003	-0.013	0.000	0.001	**0.012**	-0.003	-0.001
P. boylii	-0.004	0.000	-0.004	0.001	0.002	-0.011	0.001	0.002	**0.020**	-0.004	-0.002
P. maniculatus	-0.004	-0.001	-0.002	0.000	0.000	-0.007	0.001	0.005	**0.022**	-0.004	-0.002
P. truei	0.003	-0.001	-0.004	0.001	0.002	-0.010	0.001	0.004	**0.016**	0.000	0.000
R. megalotis	0.000	0.000	-0.003	0.001	0.003	-0.009	0.001	0.001	**0.013**	0.000	0.000
S. monticolus	-0.013	0.000	-0.001	0.000	0.002	0.001	0.001	0.000	**0.020**	-0.003	-0.003
S. ornatus	0.000	-0.002	-0.006	0.001	-0.002	**-0.023**	0.000	0.000	0.000	0.000	0.000
S. palustris	-0.005	-0.001	-0.003	0.000	-0.003	**-0.011**	-0.001	0.007	0.009	-0.007	-0.002
S. trowbridgii	-0.004	0.000	-0.003	0.001	-0.002	-0.014	-0.001	0.008	**0.033**	-0.008	-0.001
S. beecheyi	-0.007	0.000	-0.003	0.000	-0.002	-0.013	0.002	0.005	**0.029**	-0.005	-0.001
S. beldingi	**-0.011**	0.000	0.001	0.000	0.000	0.000	0.001	0.000	0.009	0.000	-0.006
S. lateralis	-0.006	0.000	-0.002	0.000	-0.001	-0.006	0.001	0.005	**0.021**	-0.005	-0.002
T. alpinus	**-0.007**	0.000	-0.001	0.000	0.000	0.000	-0.001	0.001	0.005	0.000	-0.003
T. quadrimaculatus	-0.006	0.000	-0.003	0.000	-0.002	-0.018	0.001	0.014	**0.037**	-0.011	0.000
T. senex	0.002	0.000	-0.005	0.000	-0.003	-0.008	0.003	0.012	**0.038**	-0.008	0.000
T. speciosus	-0.008	0.000	-0.002	0.000	0.000	-0.002	0.002	0.003	**0.022**	-0.004	-0.002
Z. princeps	-0.005	0.000	-0.001	0.000	-0.002	-0.006	0.000	0.006	**0.019**	-0.005	-0.003

APPENDIX B: Predicted Distribution Ranges of Small Mammals Based on Vegetation Models

Figure B1. Predicted Historical and Modern Distribution Ranges of *Sorex Monticolus* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}}$ = 0.89; Test $\text{AUC}_{\text{historical}}$ = 0.88; Training $\text{AUC}_{\text{modern}}$ = 0.86; Test $\text{AUC}_{\text{modern}}$ = 0.67).

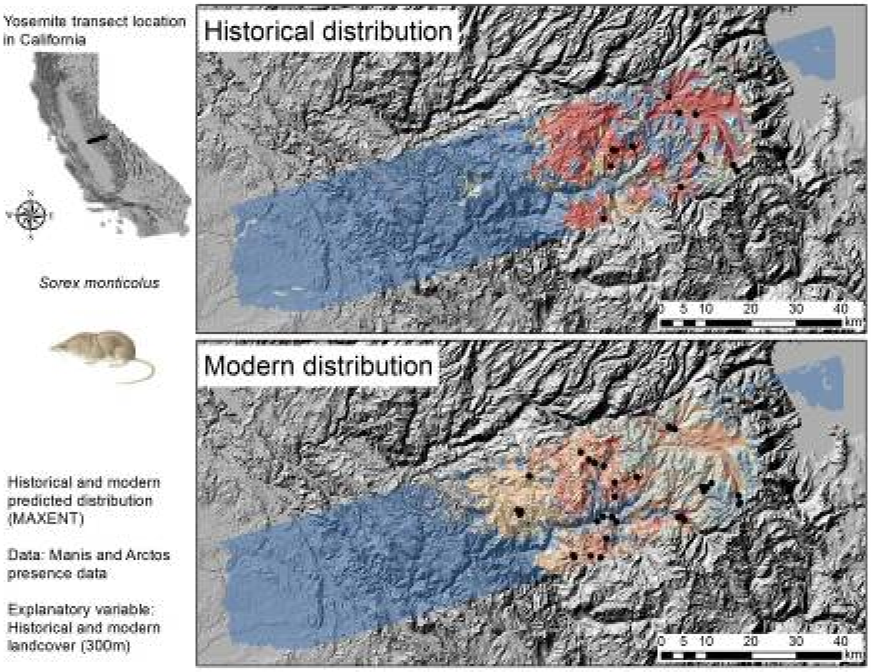


Figure B2. Predicted Historical and Modern Distribution Ranges of *Sorex ornatus* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{historical}$ = 0.96; Test AUC$_{historical}$ = 0.90; Training AUC$_{modern}$ = 0.92; Test AUC$_{modern}$ = 0.93).

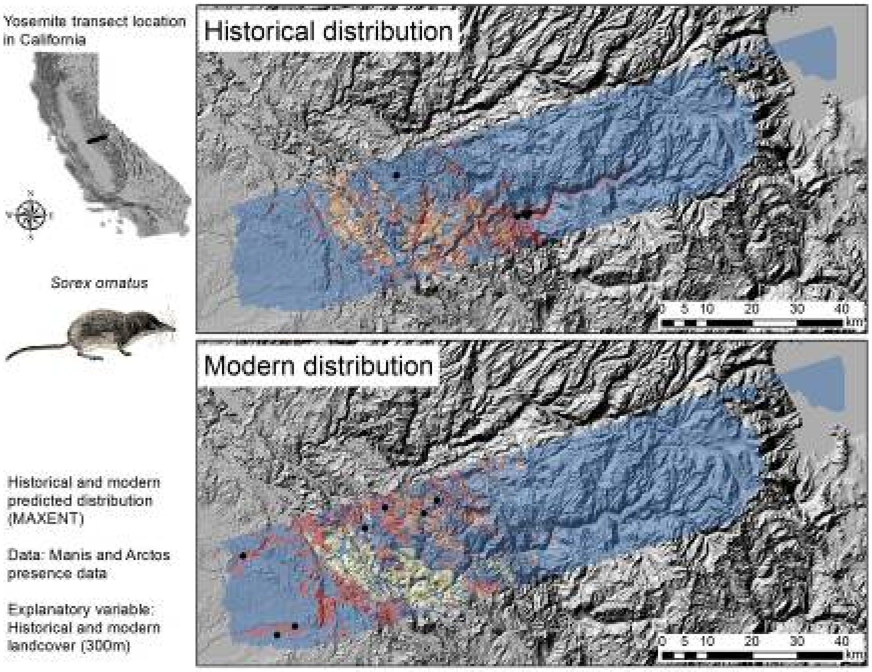


Figure B3. Predicted Historical and Modern Distribution Ranges of *Sorex palustris* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{historical}$ = 0.87; Test AUC$_{historical}$ = 0.58; no modern era model).

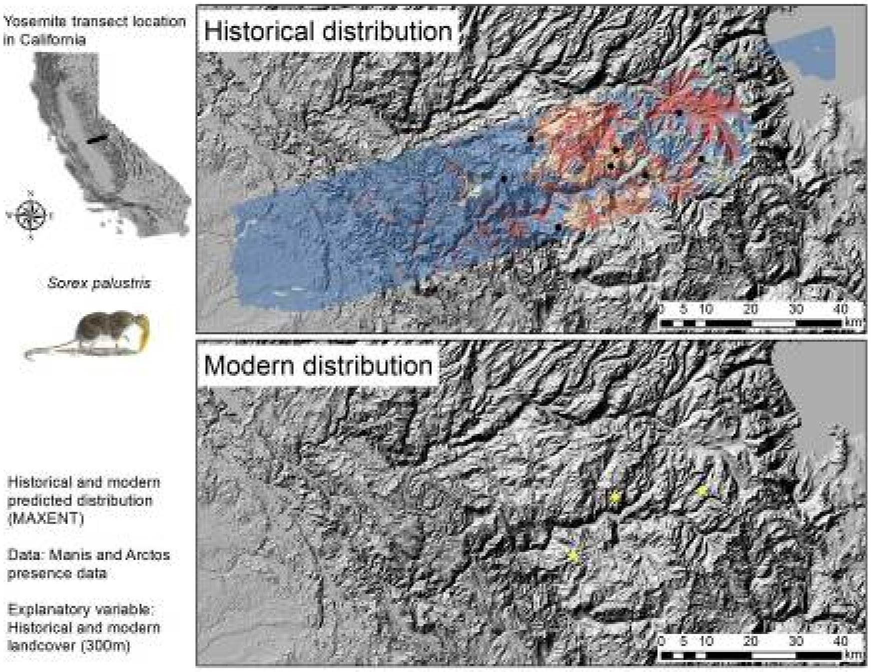


Figure B4. Predicted Historical and Modern Distribution Ranges of *Sorex trowbridgii* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{historical}$ = 0.93; Test AUC$_{historical}$ = 0.90; Training AUC$_{modern}$ = 0.88; Test AUC$_{modern}$ = 0.89).

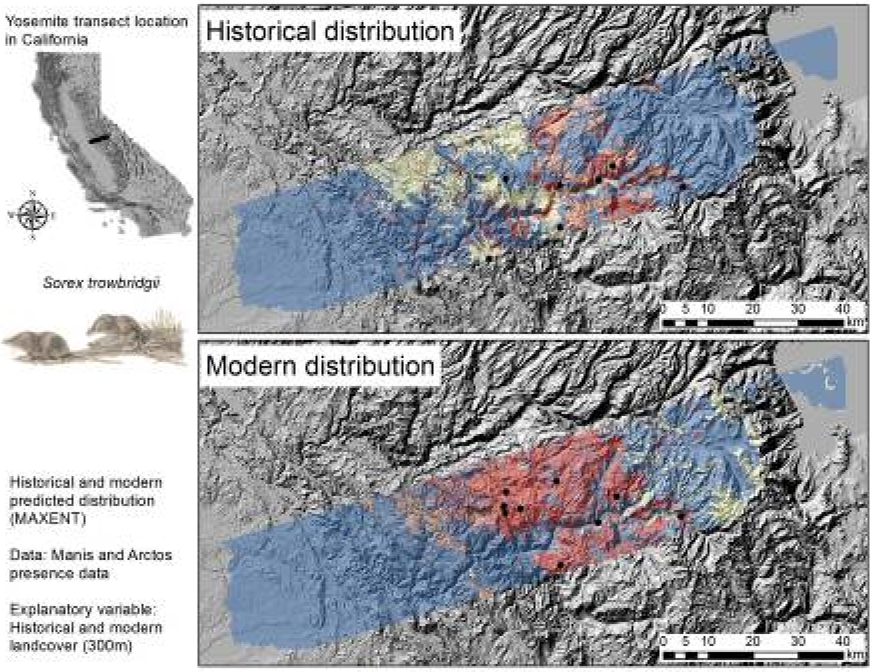


Figure B5. Predicted Historical and Modern Distribution Ranges of *Otospermophilus beecheyi* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{historical}$ = 0.89; Test AUC$_{historical}$ = 0.55; Training AUC$_{modern}$ = 0.91; Test AUC$_{modern}$ = 0.72).

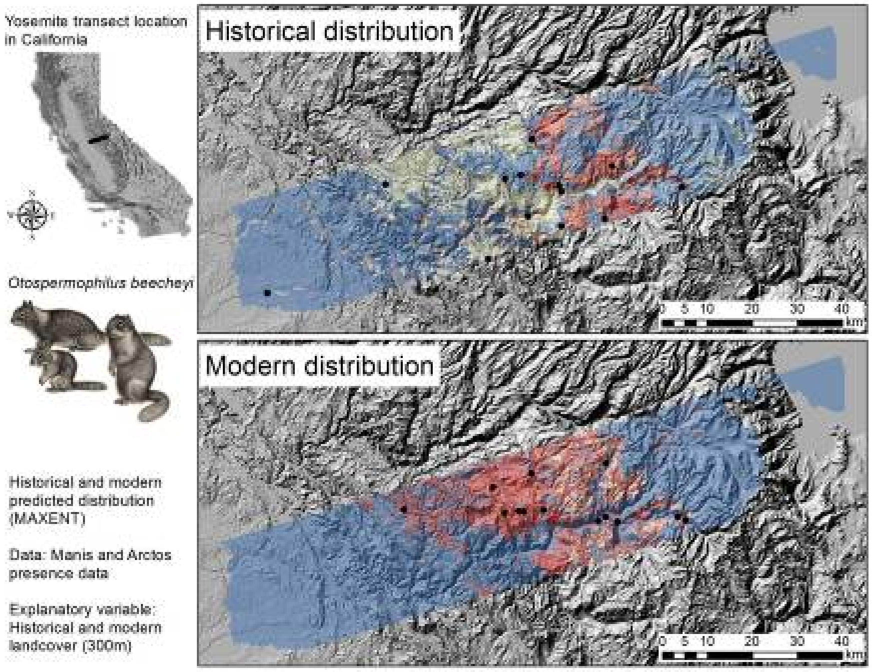


Figure B6. Predicted Historical and Modern Distribution Ranges of *Urocitellus beldingi* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{\text{historical}}$ = 0.89; Test AUC$_{\text{historical}}$ = 0.87; Training AUC$_{\text{modern}}$ = 0.95; Test AUC$_{\text{modern}}$ = 0.87).

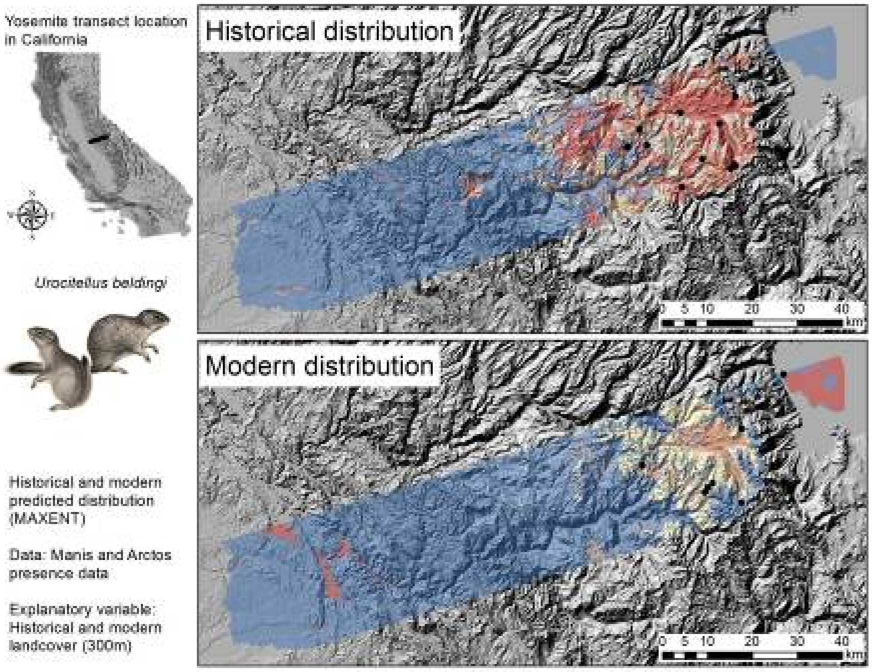


Figure B7. Predicted Historical and Modern Distribution Ranges of *Callospermophilus lateralis* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{\text{historical}}$ = 0.83; Test AUC$_{\text{historical}}$ = 0.79; Training AUC$_{\text{modern}}$ = 0.86; Test AUC$_{\text{modern}}$ = 0.73).

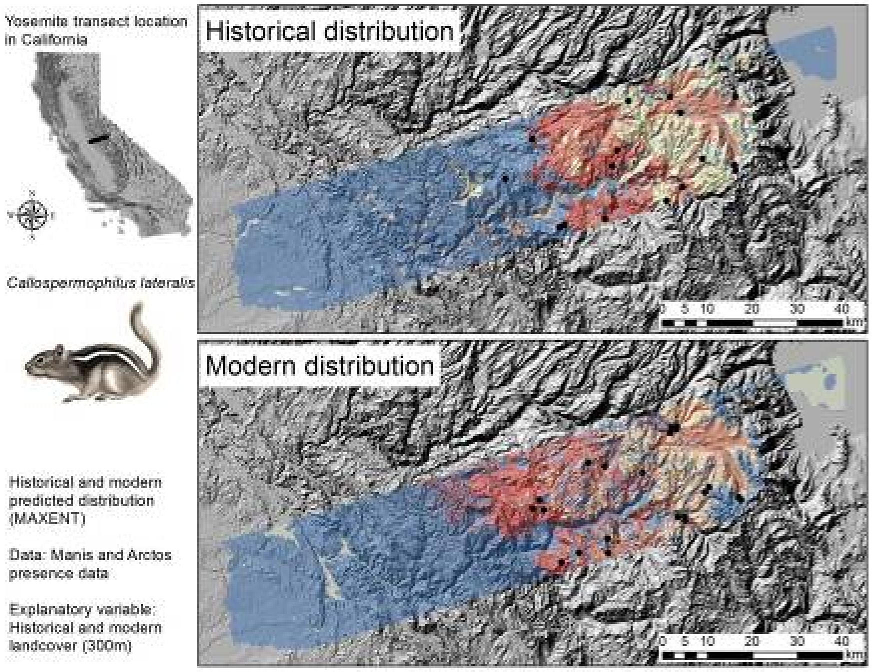


Figure B8. Predicted Historical and Modern Distribution Ranges of *Tamias alpinus* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.90$; Test $\text{AUC}_{\text{historical}} = 0.79$; Training $\text{AUC}_{\text{modern}} = 0.94$; Test $\text{AUC}_{\text{modern}} = 0.85$).

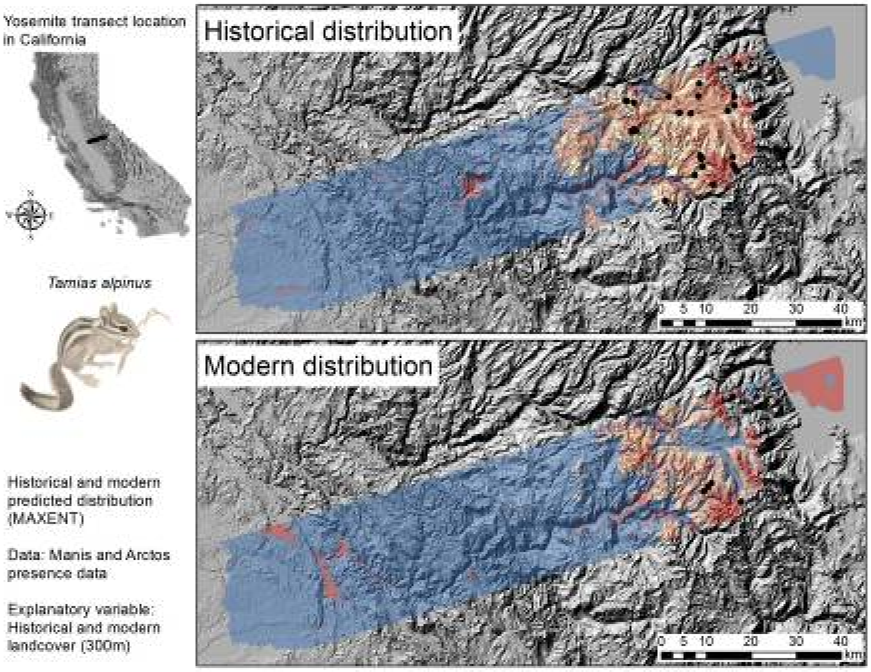


Figure B9. Predicted Historical and Modern Distribution Ranges of *Tamias quadrimaculatus* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.91$; Test $\text{AUC}_{\text{historical}} = 0.55$; Training $\text{AUC}_{\text{modern}} = 0.92$; Test $\text{AUC}_{\text{modern}} = 0.92$).

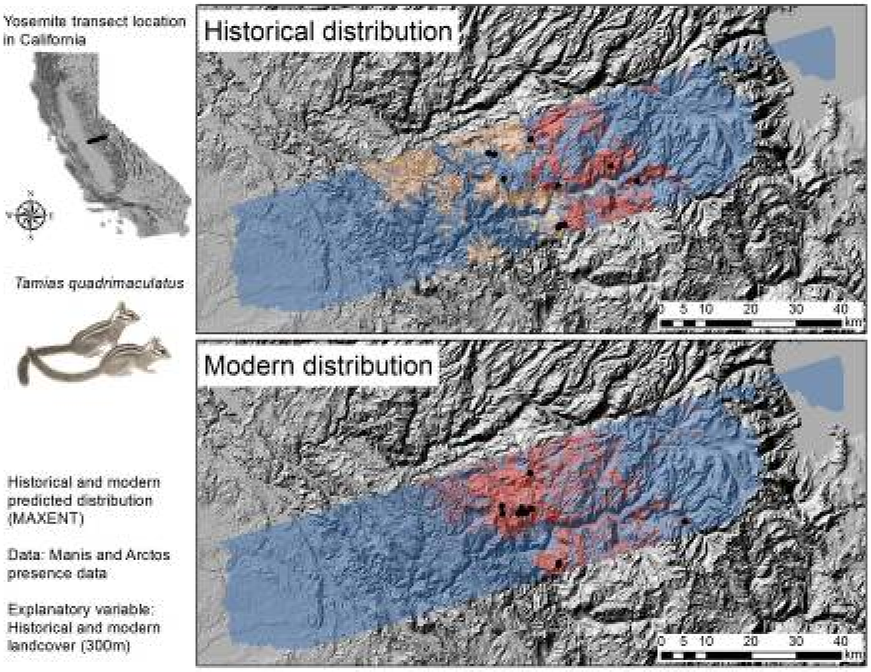


Figure B10. Predicted Historical and Modern Distribution Ranges of *Tamias Senex* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{\text{historical}}$ = 0.89; Test AUC$_{\text{historical}}$ = 0.74; no modern era model).

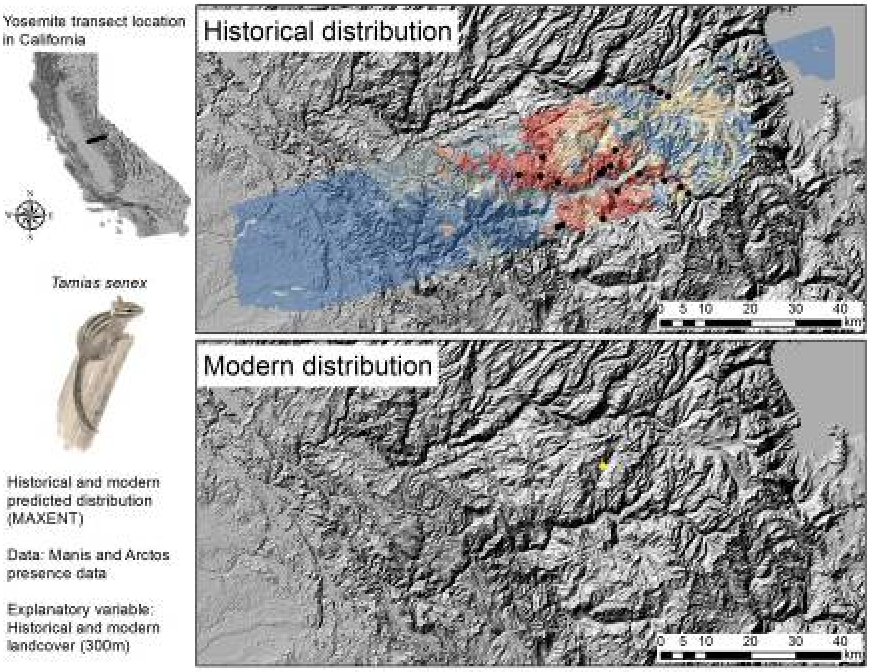


Figure B11. Predicted Historical and Modern Distribution Ranges of *Tamias Speciosus* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{\text{historical}}$ = 0.86; Test AUC$_{\text{historical}}$ = 0.68; Training AUC$_{\text{modern}}$ = 0.85; Test AUC$_{\text{modern}}$ = 0.74).

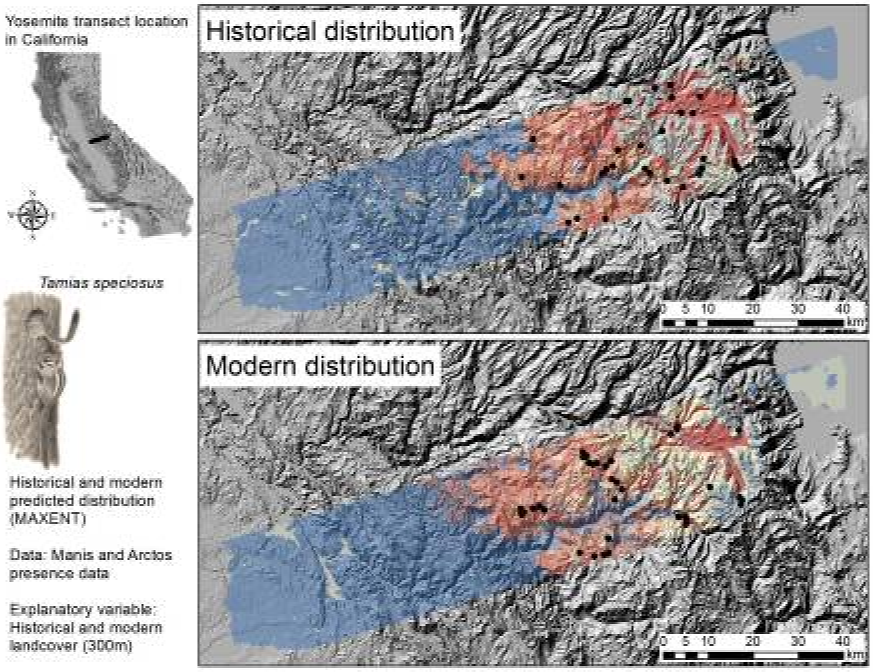


Figure B12. Predicted Historical and Modern Distribution Ranges of *Dipodomys Heermanni* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical}$ = 0.94; Test $AUC_{historical}$ = 0.41; Training AUC_{modern} = 0.96; Test AUC_{modern} = 0.46).

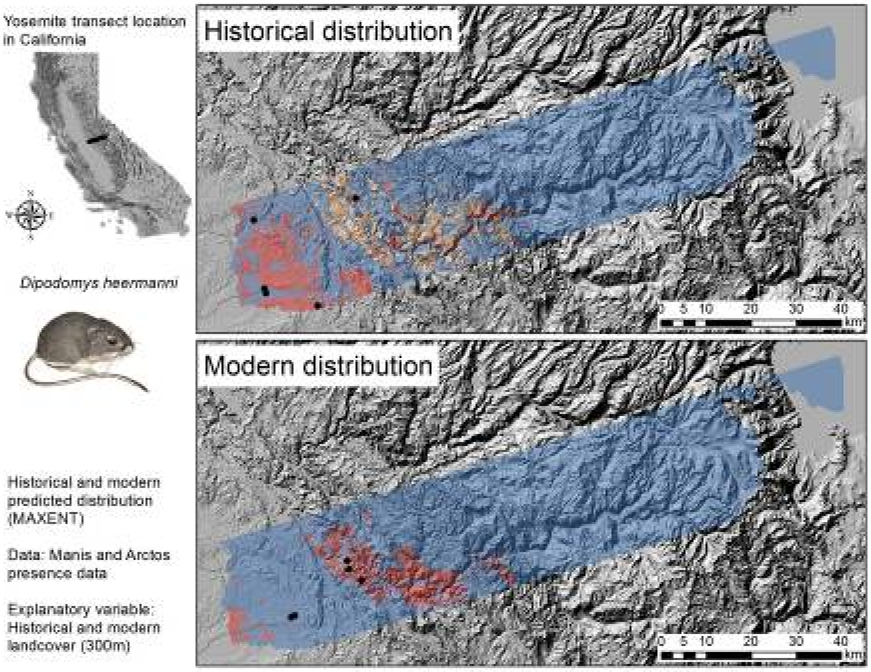


Figure B13. Predicted Historical and Modern Distribution Ranges of *Neotoma Cinerea* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical}$ = 0.92; Test $AUC_{historical}$ = 0.39; no modern era model).

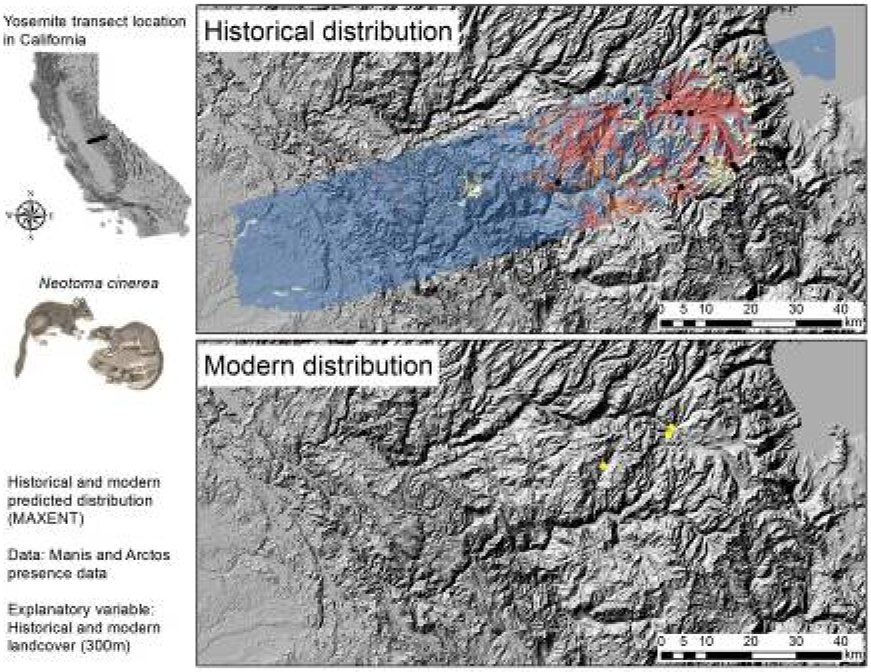


Figure B14. Predicted Historical and Modern Distribution Ranges of *Neotoma Macrotis* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical}$ = 0.86; Test $AUC_{historical}$ = 0.68; Training AUC_{modern} = 0.85; Test AUC_{modern} = 0.74).

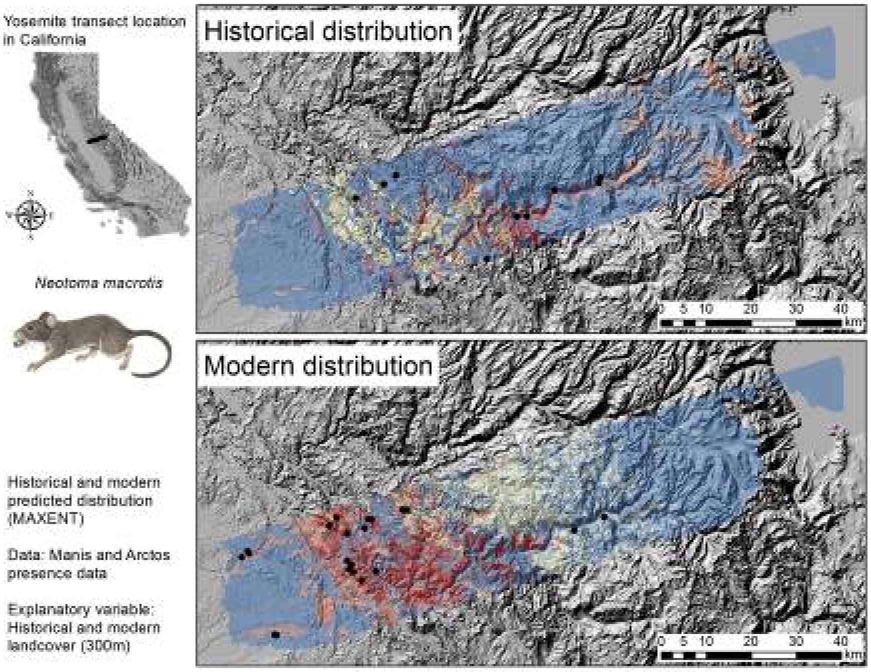


Figure B15. Predicted Historical and Modern Distribution Ranges of *Peromyscus Boylii* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical}$ = 0.83; Test $AUC_{historical}$ = 0.67; Training AUC_{modern} = 0.78; Test AUC_{modern} = 0.71).

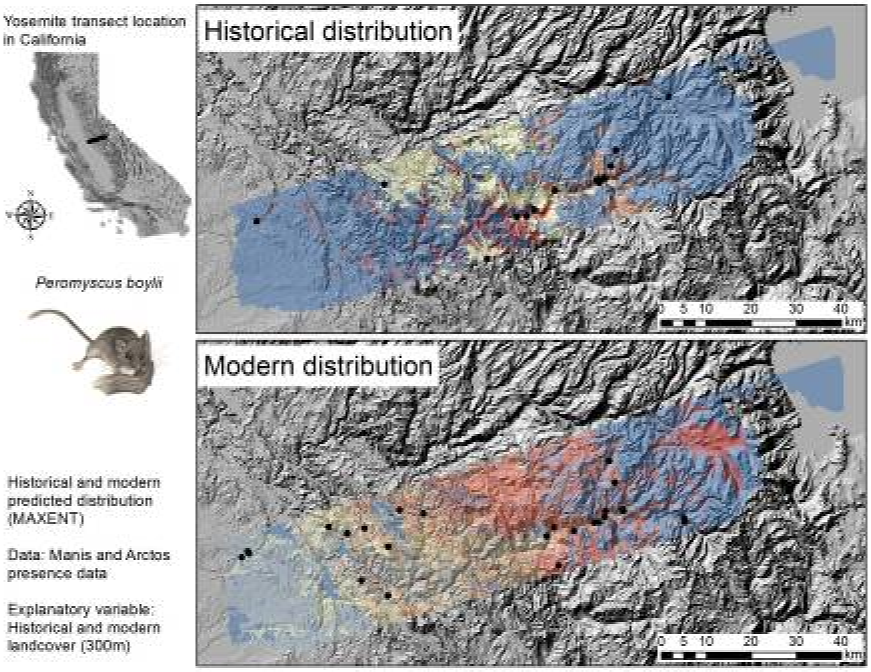


Figure B16. Predicted Historical and Modern Distribution Ranges of *Peromyscus Maniculatus* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{\text{historical}}$ = 0.83; Test AUC$_{\text{historical}}$ = 0.49; Training AUC$_{\text{modern}}$ = 0.73; Test AUC$_{\text{modern}}$ = 0.72).

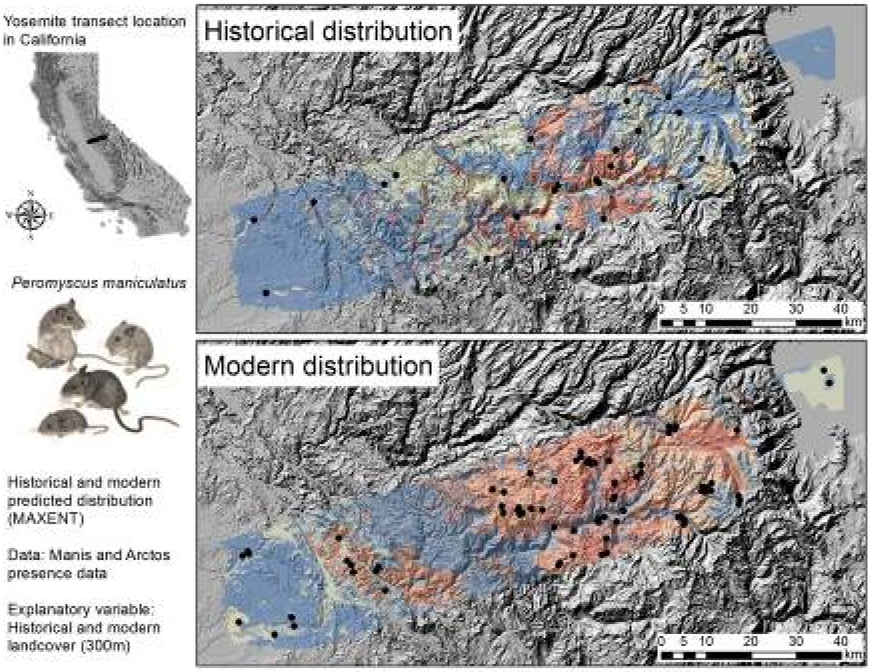


Figure B17. Predicted Historical and Modern Distribution Ranges of *Peromyscus Truei* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{\text{historical}}$ = 0.94; Test AUC$_{\text{historical}}$ = 0.68; Training AUC$_{\text{modern}}$ = 0.85; Test AUC$_{\text{modern}}$ = 0.72).

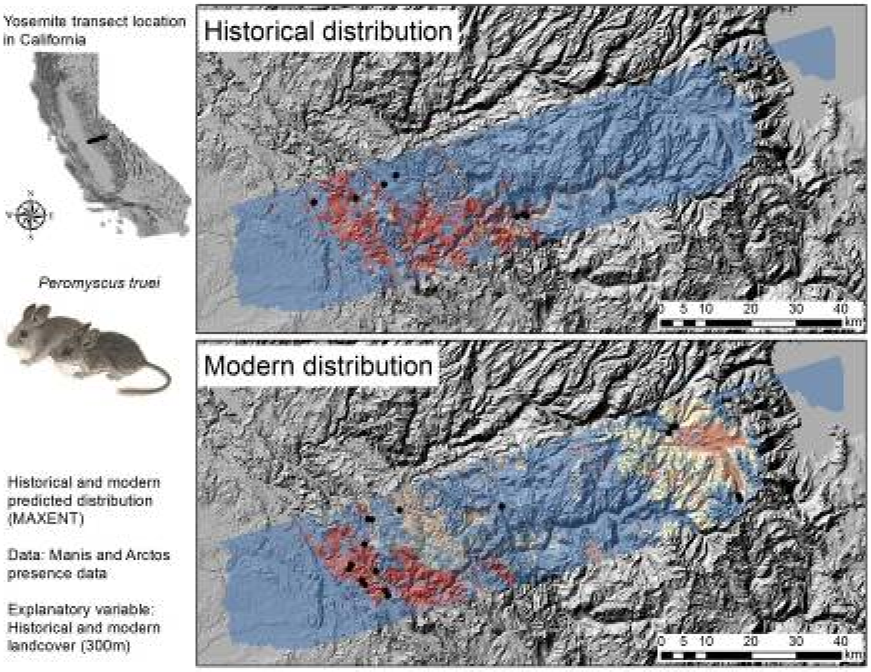


Figure B18. Predicted Historical and Modern Distribution Ranges of *Reithrodontomys Megalotis* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}}$ = 0.87; Test $\text{AUC}_{\text{historical}}$ = 0.62; Training $\text{AUC}_{\text{modern}}$ = 0.79; Test $\text{AUC}_{\text{modern}}$ = 0.74).

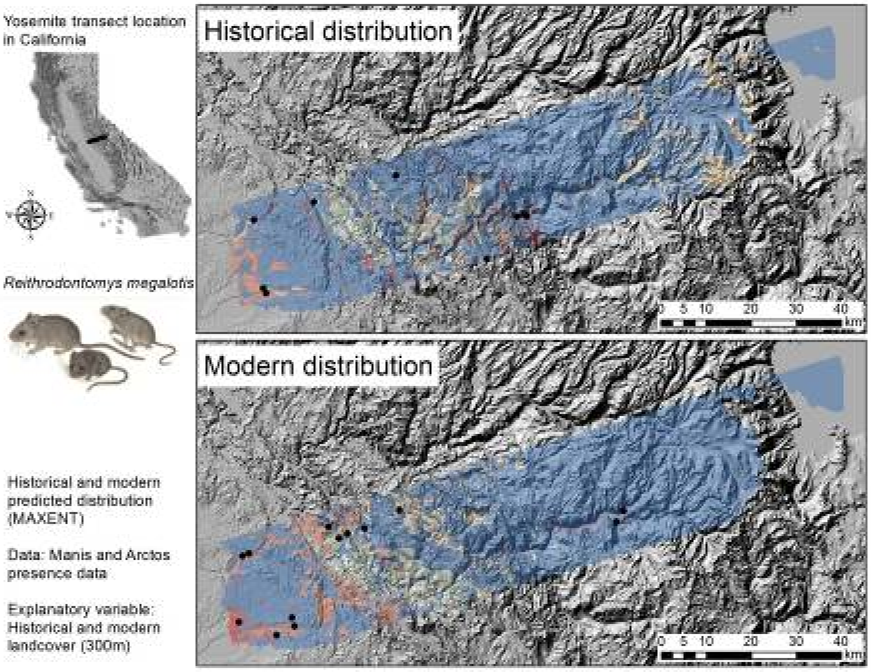


Figure B19. Predicted Historical and Modern Distribution Ranges of *Microtus Californicus* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}}$ = 0.80; Test $\text{AUC}_{\text{historical}}$ = 0.68; Training $\text{AUC}_{\text{modern}}$ = 0.82; Test $\text{AUC}_{\text{modern}}$ = 0.97).

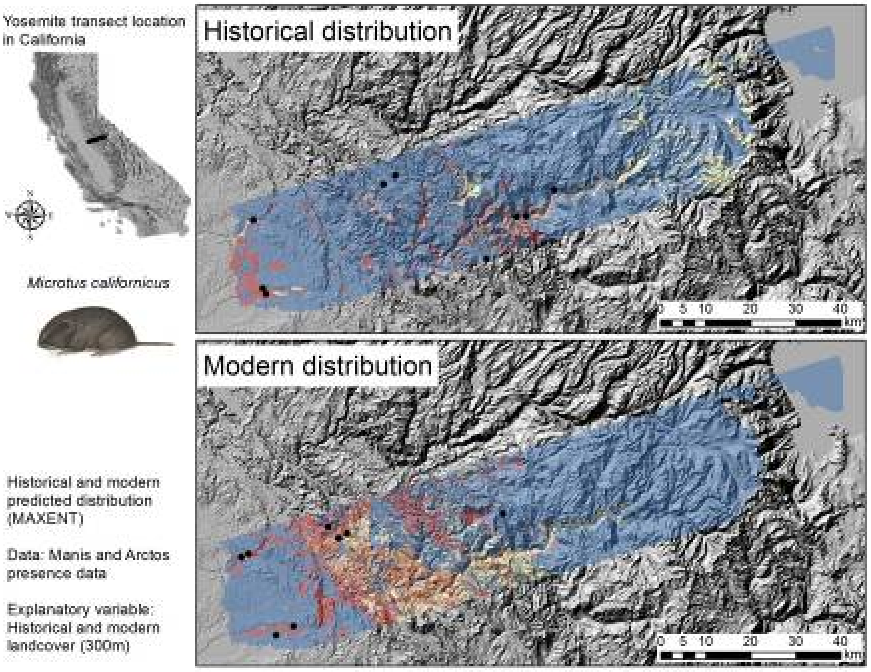


Figure B20. Predicted Historical and Modern Distribution Ranges of *Microtus Longicaudus* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.79$; Test $\text{AUC}_{\text{historical}} = 0.59$; Training $\text{AUC}_{\text{modern}} = 0.82$; Test $\text{AUC}_{\text{modern}} = 0.64$).

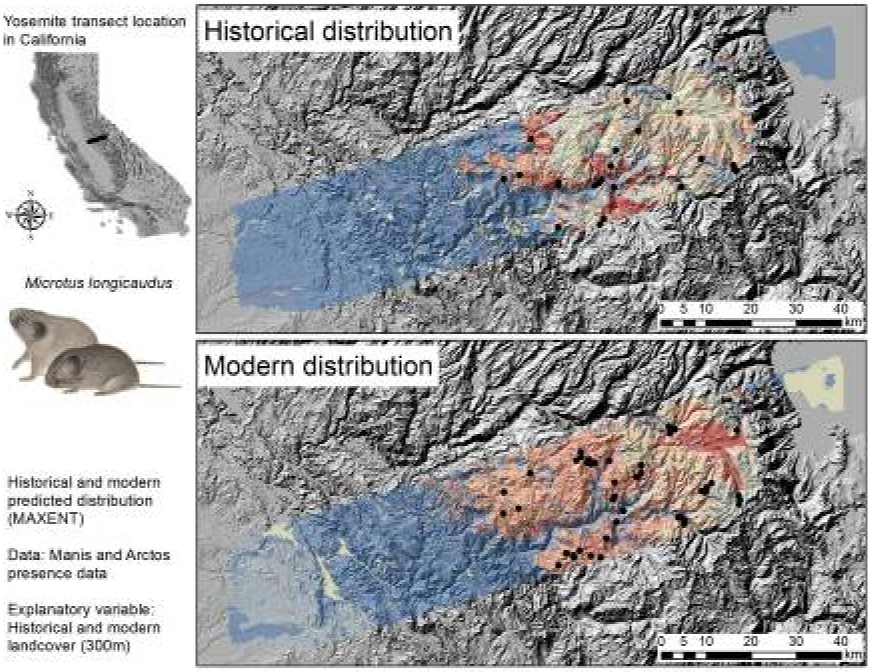


Figure B21. Predicted Historical and Modern Distribution Ranges of *Microtus Montanus* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.93$; Test $\text{AUC}_{\text{historical}} = 0.43$; Training $\text{AUC}_{\text{modern}} = 0.86$; Test $\text{AUC}_{\text{modern}} = 0.71$).

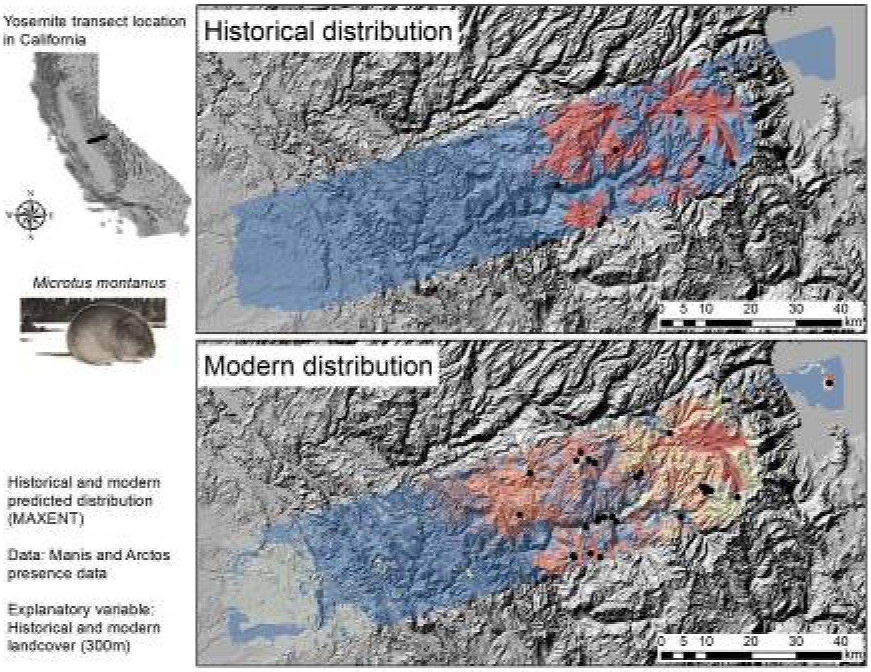
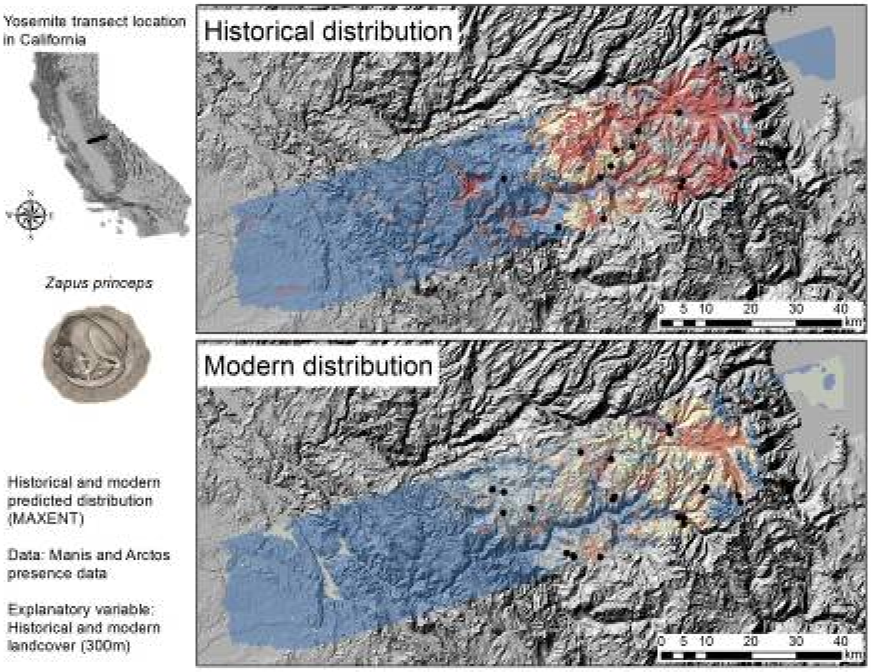


Figure B22. Predicted Historical and Modern Distribution Ranges of *Zapus Princeps* Based on Historical and Modern Vegetation. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{historical}$ = 0.79; Test AUC$_{historical}$ = 0.88; Training AUC$_{modern}$ = 0.84; Test AUC$_{modern}$ = 0.62).



APPENDIX C:
Predicted Distribution Ranges of Small Mammals Based on Climate Models

Figure C1. Predicted Historical and Modern Distribution Ranges of *Sorex Monticolus* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.89$; Test $\text{AUC}_{\text{historical}} = 0.87$; Training $\text{AUC}_{\text{modern}} = 0.94$; Test $\text{AUC}_{\text{modern}} = 0.89$).

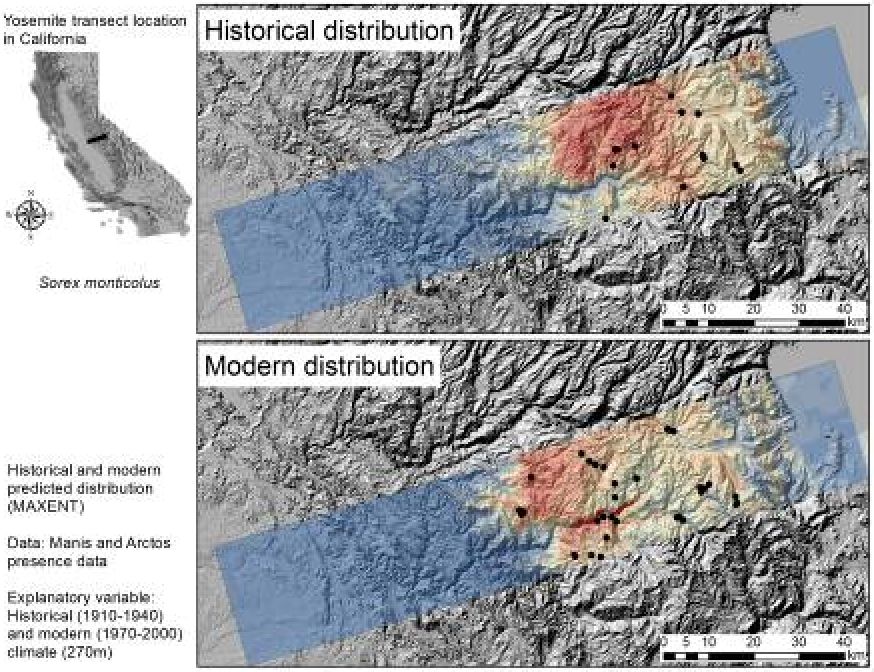


Figure C2. Predicted Historical and Modern Distribution Ranges of *Sorex Ornatus* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.88$; Test $\text{AUC}_{\text{historical}} = 0.75$; Training $\text{AUC}_{\text{modern}} = 0.84$; Test $\text{AUC}_{\text{modern}} = 0.83$).

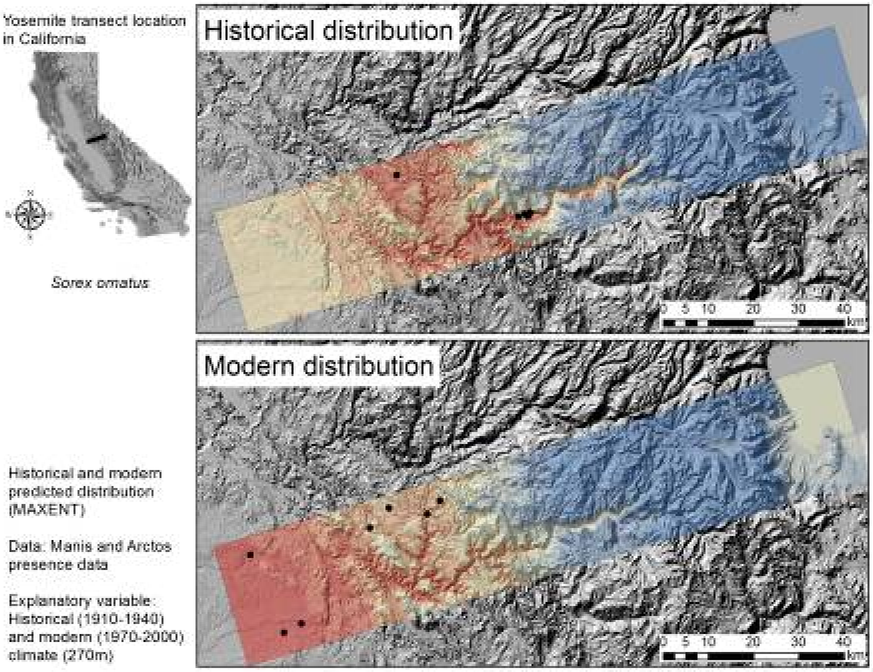


Figure C3. Predicted Historical and Modern Distribution Ranges of *Sorex Palustris* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.77$; Test $\text{AUC}_{\text{historical}} = 0.88$; no modern era model).

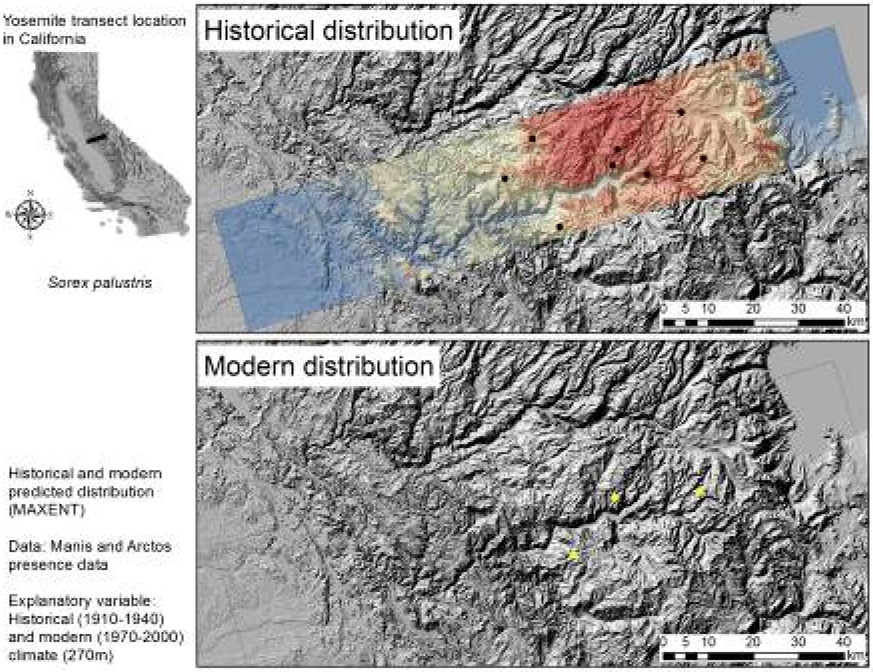


Figure C4. Predicted Historical and Modern Distribution Ranges of *Sorex Trowbridgii* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.79$; Test $\text{AUC}_{\text{historical}} = 0.69$; Training $\text{AUC}_{\text{modern}} = 0.94$; Test $\text{AUC}_{\text{modern}} = 0.93$).

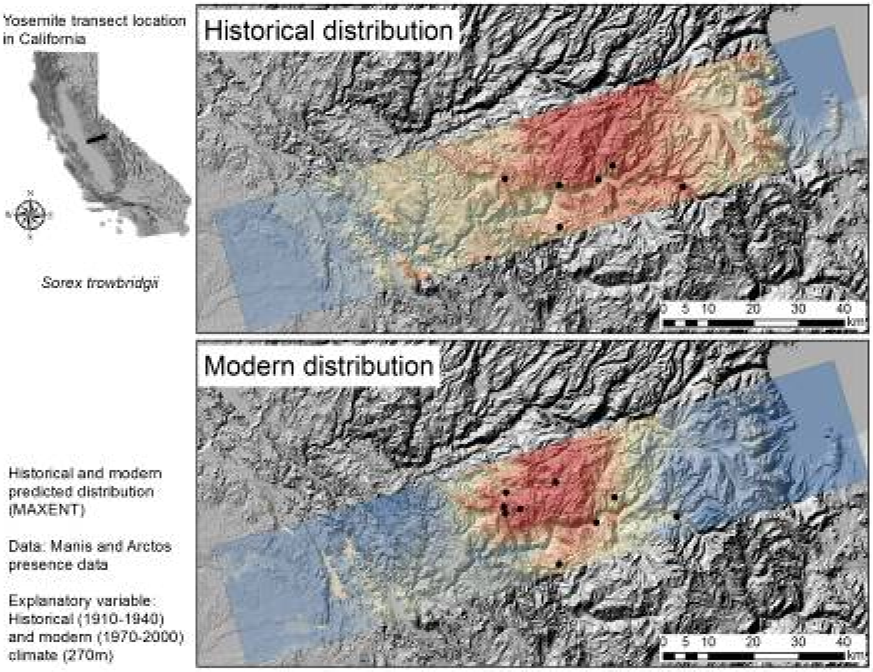


Figure C5. Predicted Historical and Modern Distribution Ranges of *Otospermophilus Beecheyi* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.79$; Test $\text{AUC}_{\text{historical}} = 0.75$; Training $\text{AUC}_{\text{modern}} = 0.89$; Test $\text{AUC}_{\text{modern}} = 0.95$).

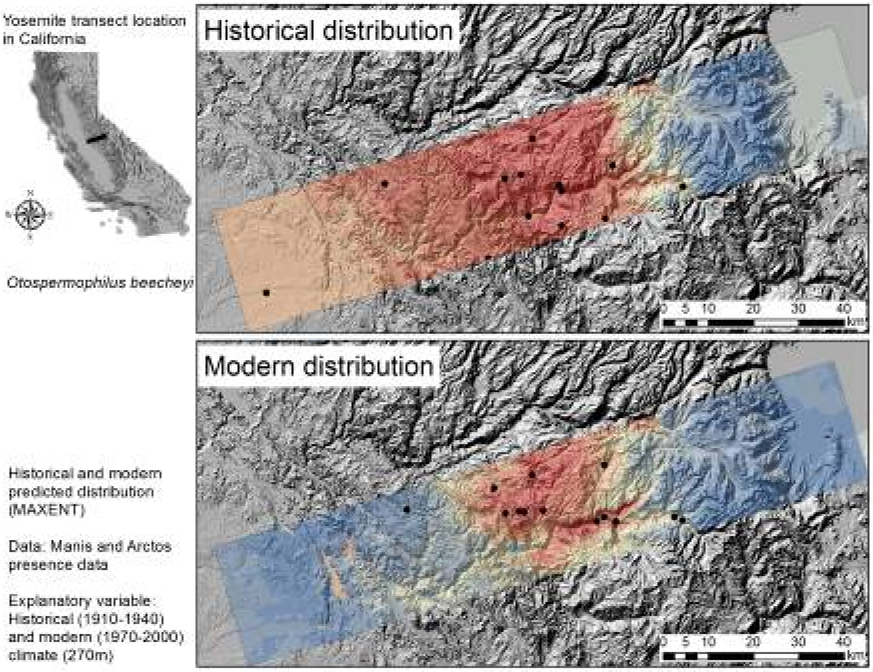


Figure C6. Predicted Historical and Modern Distribution Ranges of *Urocitellus Beldingi* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.88$; Test $\text{AUC}_{\text{historical}} = 0.91$; Training $\text{AUC}_{\text{modern}} = 0.88$; Test $\text{AUC}_{\text{modern}} = 0.97$).

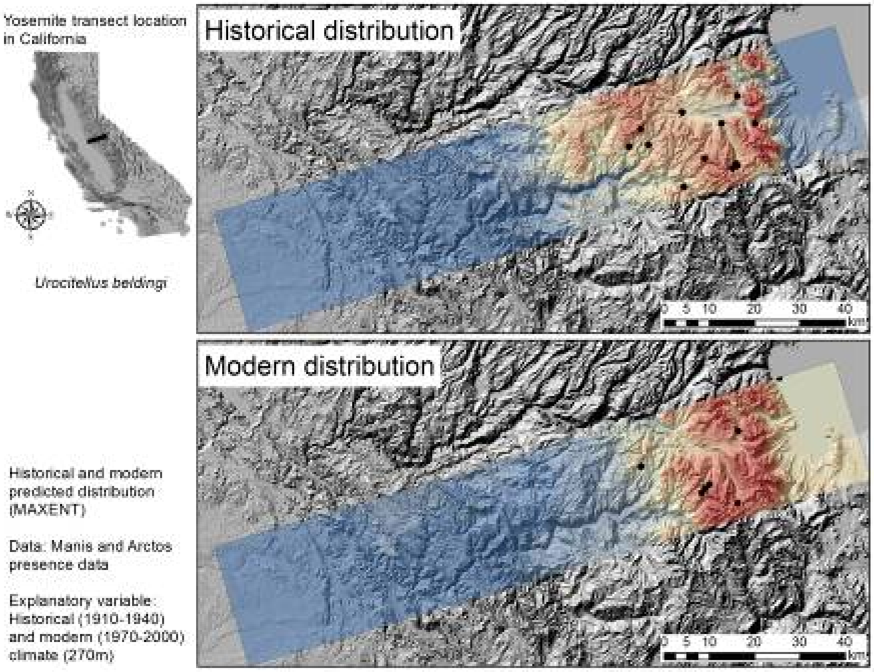


Figure C7. Predicted Historical and Modern Distribution Ranges of *Callospermophilus Lateralis* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.81$; Test $\text{AUC}_{\text{historical}} = 0.77$; Training $\text{AUC}_{\text{modern}} = 0.93$; Test $\text{AUC}_{\text{modern}} = 0.86$).

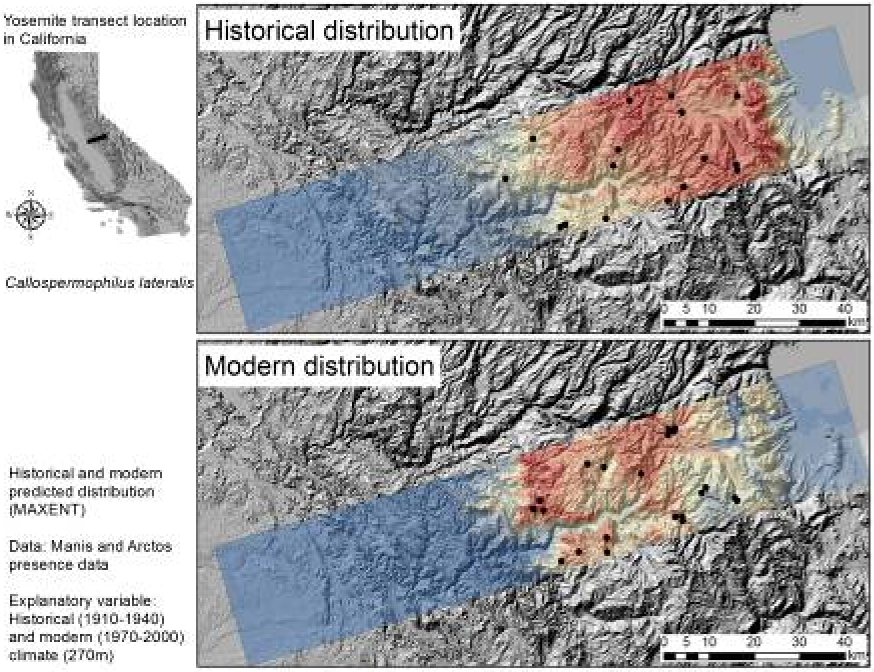


Figure C8. Predicted Historical and Modern Distribution Ranges of *Tamias Alpinus* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical}$ = 0.96; Test $AUC_{historical}$ = 0.94; Training AUC_{modern} = 0.98; Test AUC_{modern} = 0.93).

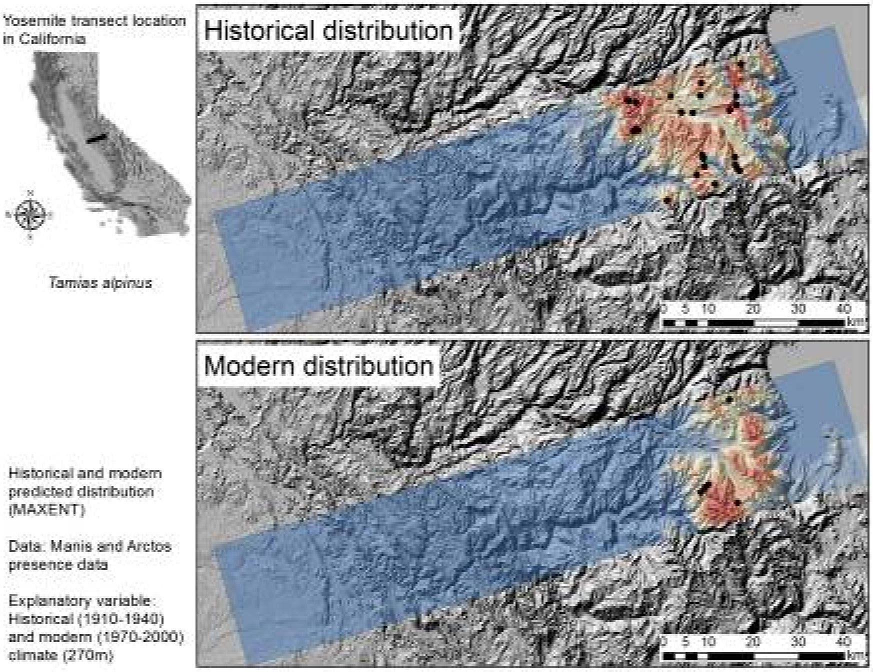


Figure C9. Predicted Historical and Modern Distribution Ranges of *Tamias Quadrimaculatus* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical}$ = 0.92; Test $AUC_{historical}$ = 0.87; Training AUC_{modern} = 0.95; Test AUC_{modern} = 0.96).

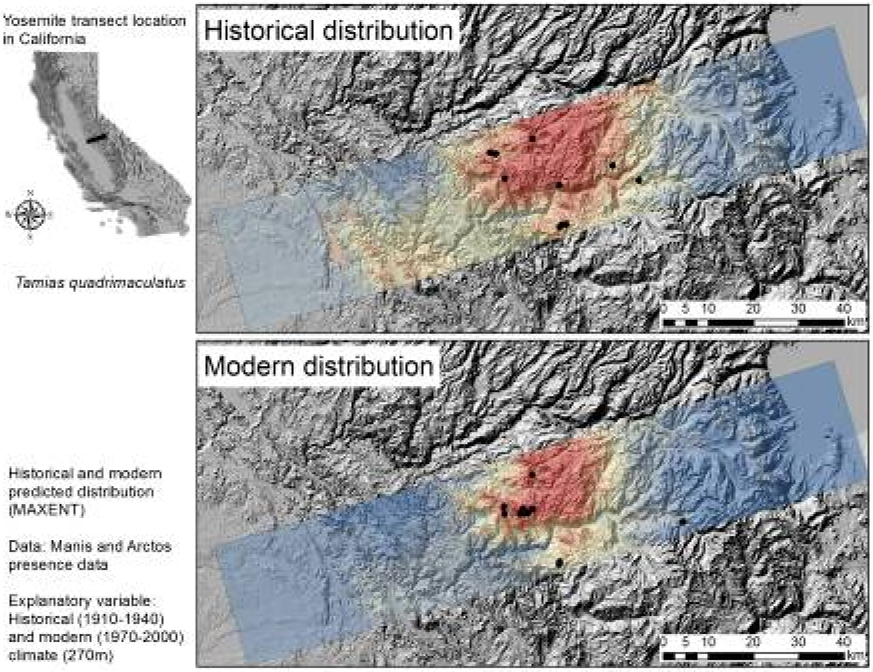


Figure C10. Predicted Historical and Modern Distribution Ranges of *Tamias Senex* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{historical}$ = 0.93; Test AUC$_{historical}$ = 0.90; no modern era model).

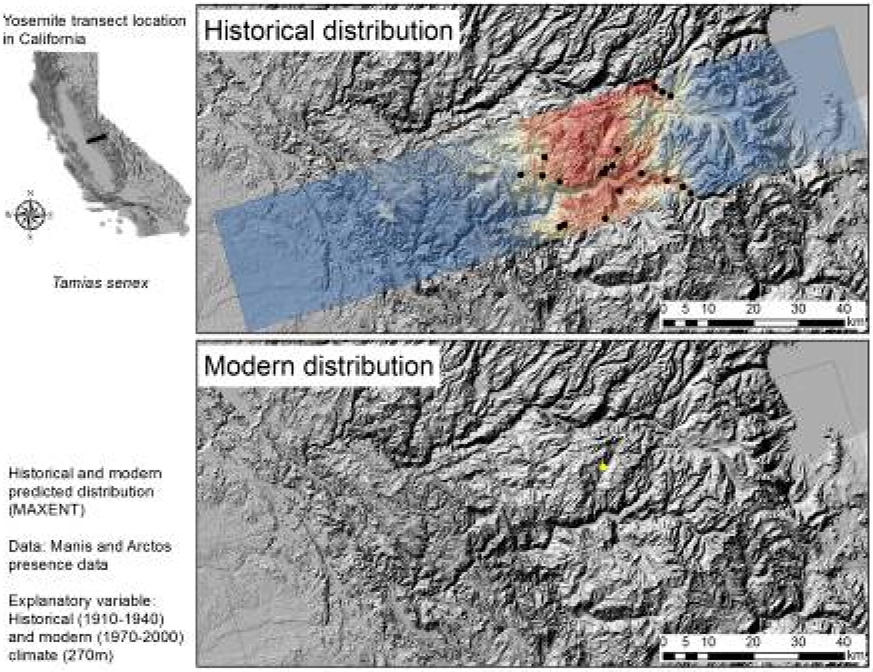


Figure C11. Predicted Historical and Modern Distribution Ranges of *Tamias Speciosus* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training AUC$_{historical}$ = 0.91; Test AUC$_{historical}$ = 0.91; Training AUC$_{modern}$ = 0.94; Test AUC$_{modern}$ = 0.82).

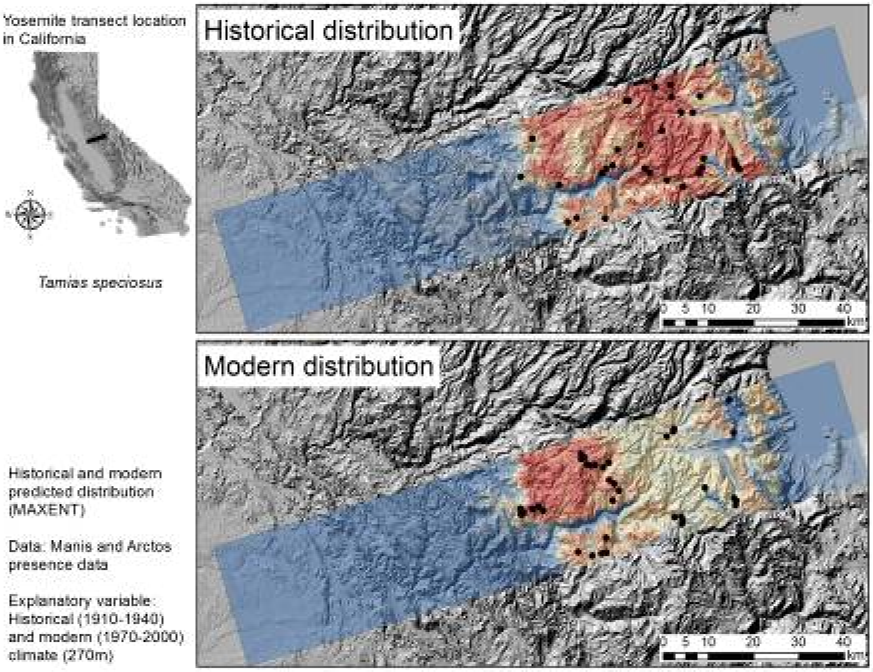


Figure C12. Predicted Historical and Modern Distribution Ranges of *Dipodomys Heermanni* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical}$ = 0.97; Test $AUC_{historical}$ = 0.81; Training AUC_{modern} = 0.95; Test AUC_{modern} = 0.89).

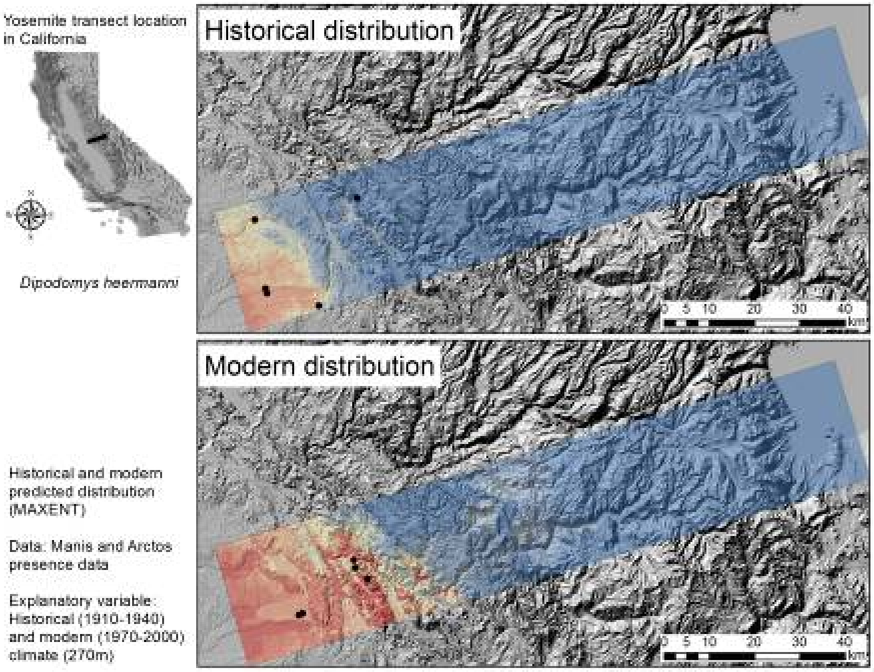


Figure C13. Predicted Historical and Modern Distribution Ranges of *Neotoma Cinerea* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical}$ = 0.88; Test $AUC_{historical}$ = 0.88; no modern era model).

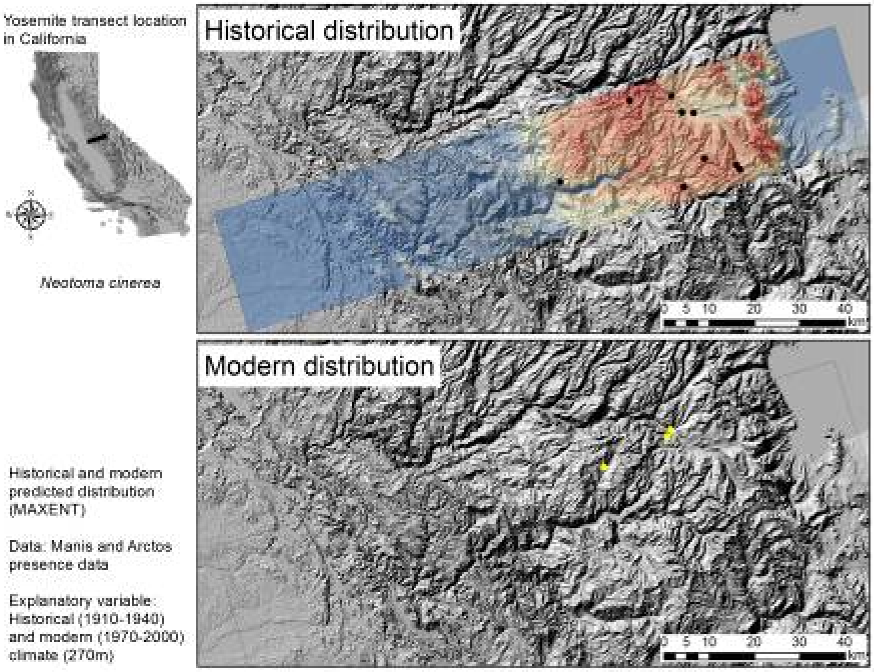


Figure C14. Predicted Historical and Modern Distribution Ranges of *Neotoma Macrotis* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.70$; Test $\text{AUC}_{\text{historical}} = 0.69$; Training $\text{AUC}_{\text{modern}} = 0.87$; Test $\text{AUC}_{\text{modern}} = 0.81$).

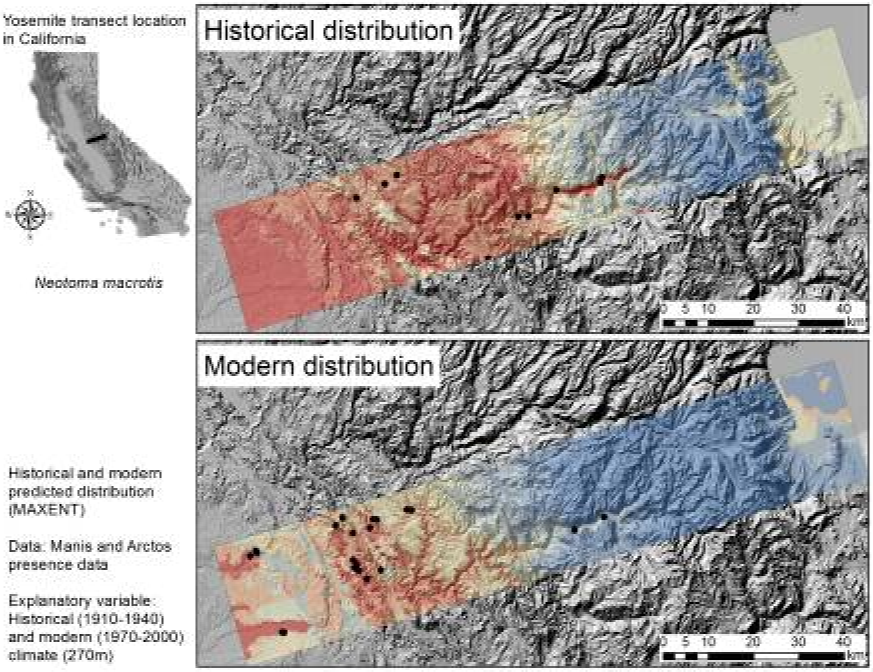


Figure C15. Predicted Historical and Modern Distribution Ranges of *Peromyscus Boylii* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.84$; Test $\text{AUC}_{\text{historical}} = 0.60$; Training $\text{AUC}_{\text{modern}} = 0.89$; Test $\text{AUC}_{\text{modern}} = 0.62$).

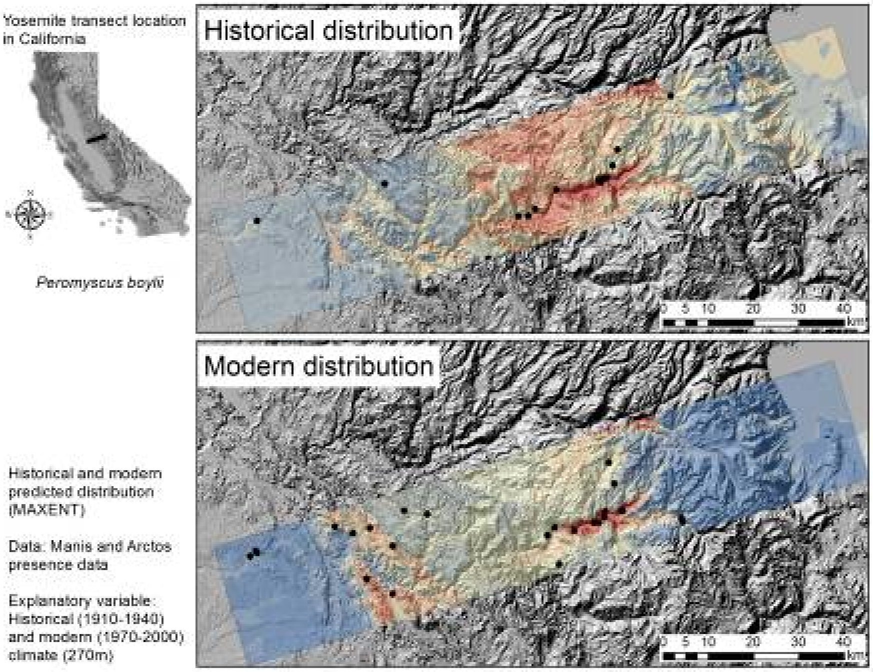


Figure C16. Predicted Historical and Modern Distribution Ranges of *Peromyscus Maniculatus* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical} = 0.81$; Test $AUC_{historical} = 0.55$; Training $AUC_{modern} = 0.86$; Test $AUC_{modern} = 0.82$).

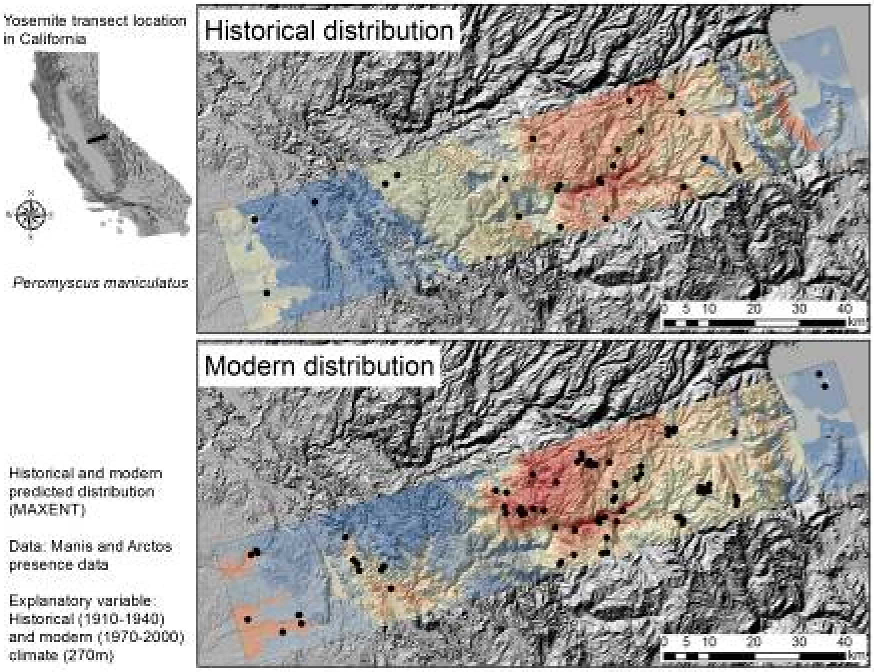


Figure C17. Predicted Historical and Modern Distribution Ranges of *Peromyscus Truei* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical} = 0.75$; Test $AUC_{historical} = 0.67$; Training $AUC_{modern} = 0.62$; Test $AUC_{modern} = 0.77$).

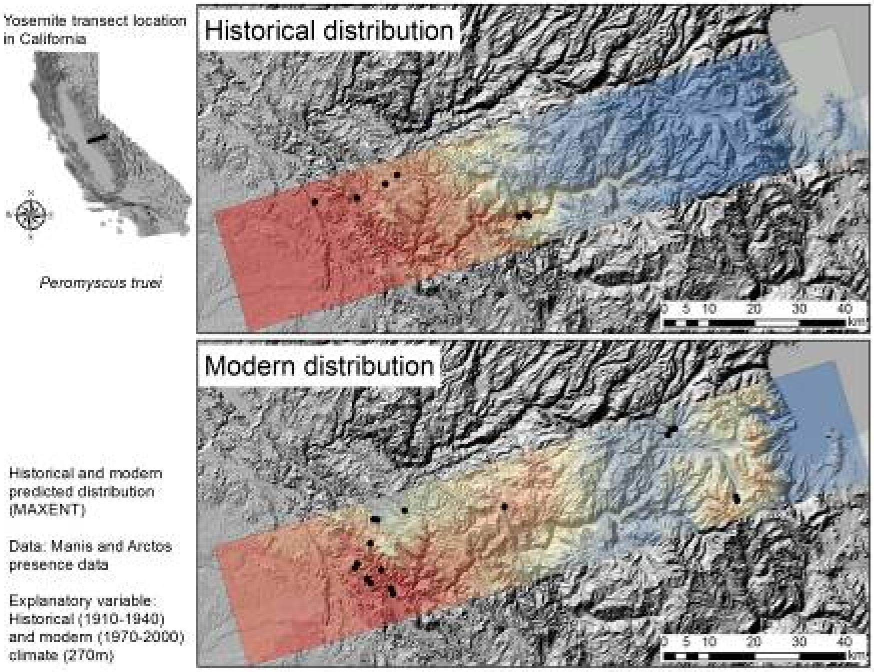


Figure C18. Predicted Historical and Modern Distribution Ranges of *Reithrodontomys Megalotis* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical}$ = 0.84; Test $AUC_{historical}$ = 0.70; Training AUC_{modern} = 0.89; Test AUC_{modern} = 0.70).

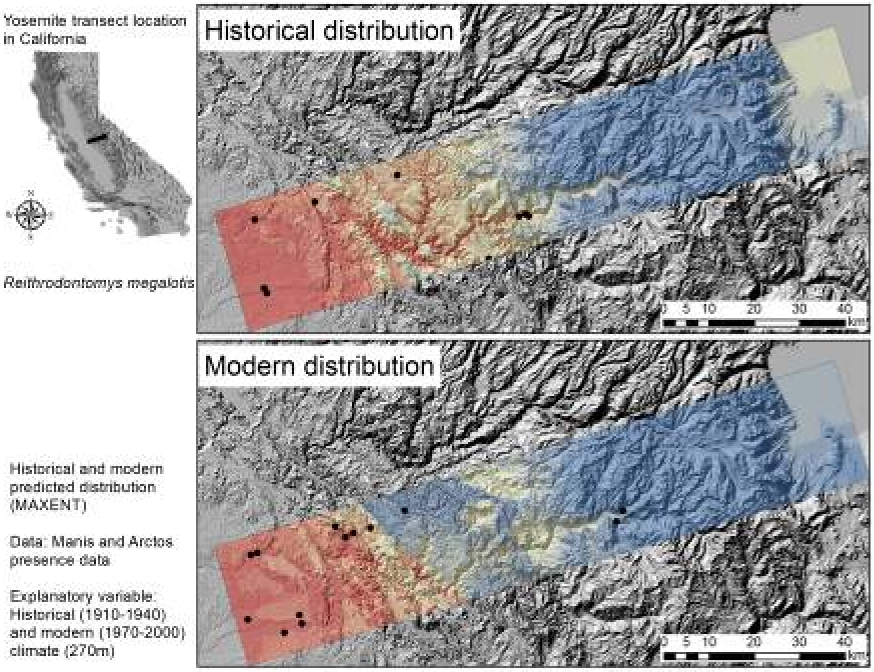


Figure C19. Predicted Historical and Modern Distribution Ranges of *Microtus Californicus* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical}$ = 0.76; Test $AUC_{historical}$ = 0.84; Training AUC_{modern} = 0.90; Test AUC_{modern} = 0.86).

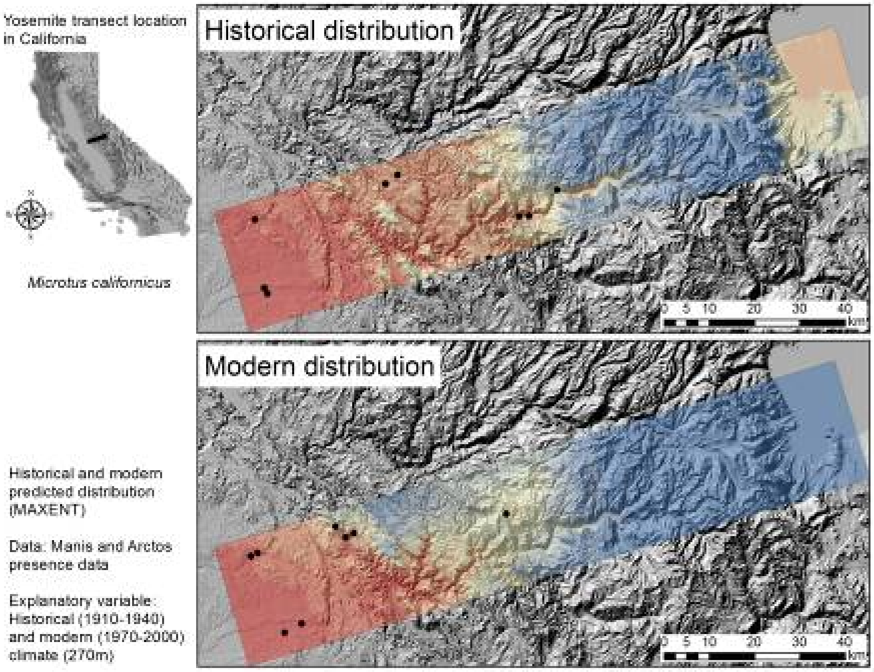


Figure C20. Predicted Historical and Modern Distribution Ranges of *Microtus Longicaudus* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.91$; Test $\text{AUC}_{\text{historical}} = 0.85$; Training $\text{AUC}_{\text{modern}} = 0.92$; Test $\text{AUC}_{\text{modern}} = 0.84$).

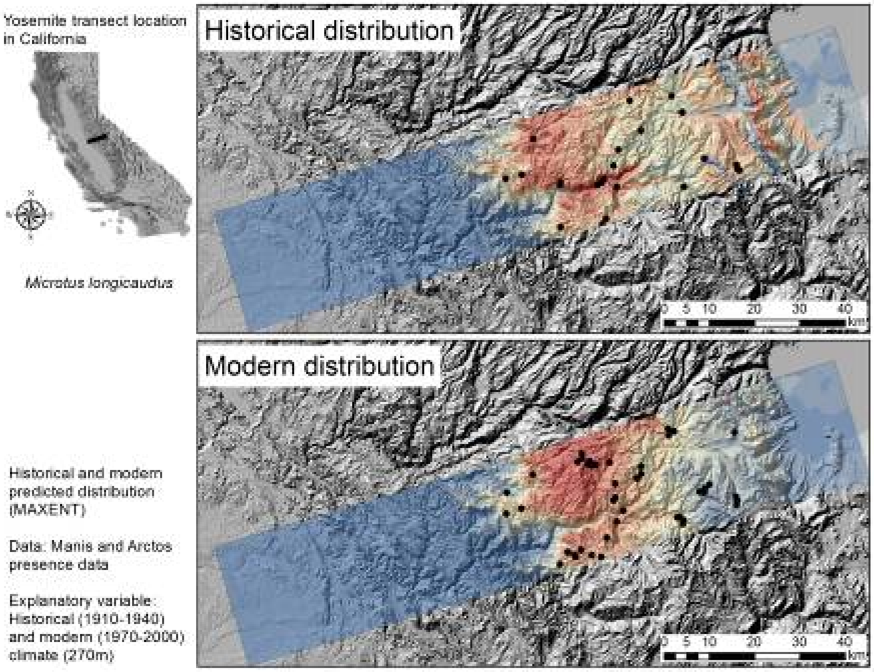


Figure C21. Predicted Historical and Modern Distribution Ranges of *Microtus Montanus* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $\text{AUC}_{\text{historical}} = 0.80$; Test $\text{AUC}_{\text{historical}} = 0.78$; Training $\text{AUC}_{\text{modern}} = 0.91$; Test $\text{AUC}_{\text{modern}} = 0.89$).

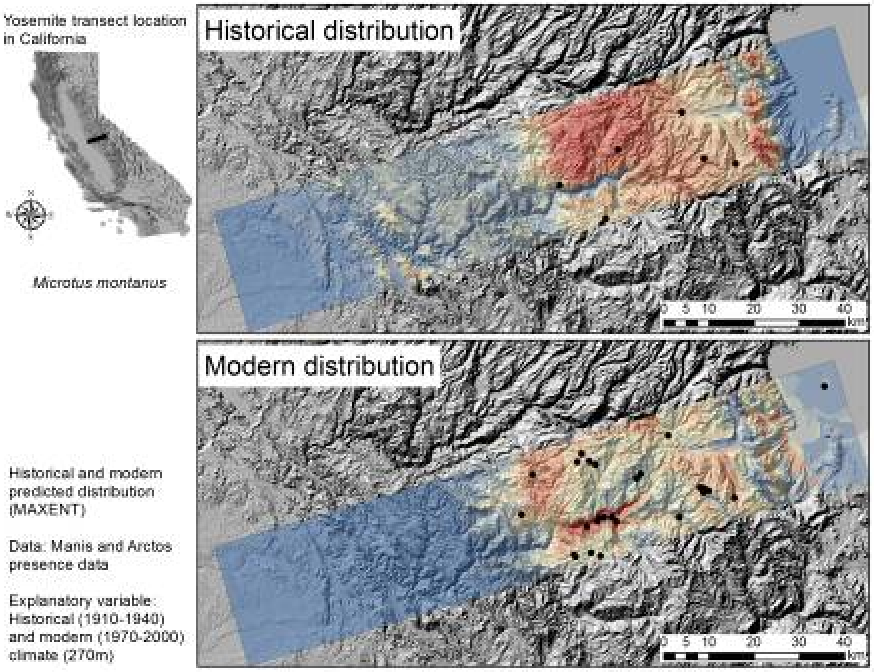


Figure C22. Predicted Historical and Modern Distribution Ranges of *Zapus Princeps* Based on Historical and Modern Climate. Red indicates higher suitability and blue indicates lower suitability. Black dots represent species locations from Manis and Arctos data bases (Training $AUC_{historical} = 0.86$; Test $AUC_{historical} = 0.75$; Training $AUC_{modern} = 0.88$; Test $AUC_{modern} = 0.93$).