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Synchronicity in elevation range shifts among small mammal and vegetation over the last century is stronger for omnivores

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In mountain ecosystems, species can be said to respond synchronously to environmental change when the elevation ranges of vegetation types and their associated vertebrates expand or contract in the same direction. Conversely, the response is asynchronous when the elevation ranges of vegetation types and associated vertebrates change in different directions. The capacity of vertebrate species to respond synchronously with change in the elevation ranges of the vegetation that comprises their habitat is likely a function of their ecological traits. Here we combine measures of elevation range shifts in 23 vertebrate species with those of their associated vegetation types across 80 yr, on a large elevation transect in California's Sierra Nevada mountains that encompasses Yosemite National Park. Half the species' shifts were synchronous with vegetation shifts, 1/4 of the species were asynchronous, and the others showed no relationship. Most species that responded synchronously to changes in vegetation elevation ranges expanded their elevation range, and are inhabitants of low and intermediate elevations. In contrast, those species whose range shifts were asynchronous to associated vegetation shifts inhabit high elevations. These species experienced contraction in elevation range even while their associated vegetation types expanded. However, these species were responding synchronously to a subset of their associated vegetation types. Considering trait-based predictors, omnivores were more synchronous than herbivores. Our results on synchronous and asynchronous elevation shifts with vegetation may permit more accurate modeling of future ranges for vertebrates in California's Sierra Nevada. The approach also offers a new method for use in assessment of vertebrate vulnerability in other mountain regions, and can be an important component of assessing their vulnerability to climate change.

Understanding the dynamics of species elevation ranges is crucial for forecasting biotic response to climate and land cover change. Theoretically, these shifts are a response to changing environmental conditions that delimit each species' ecological niche over time including habitat, physiological limits and species interactions (Grinnell 1917a, b, Soberon and Nakamura 2009). Much attention has been given to assessing and modeling the effect of climate change per se on potential distribution of species (Lenoir et al. 2010, Tingley et al. 2010, Smith et al. 2013). By contrast, despite predictions (Burns et al. 2003, Oliver et al. 2009, Graham et al. 2010), there has been limited opportunity to explore how species respond to changes in habitat over a century, a time period relevant for conservation. Assessing species response to habitat dynamics is complicated because of the lack of comparable historic and contemporary datasets that comprise both species and habitat information (but see Roth et al. 2014). Assessing species' ability to track shifts in their habitat can lead to insights about their level of vulnerability to climate change (Moritz and Agudo 2013). In this paper we assess whether changes in elevation ranges of small mammals are or are not synchronous over time with the elevation shifts of associated vegetation types (used as a surrogate of habitat), detected from two historical datasets.

Climate change can affect mammals directly via an animal's physiology. For example, an increase in temperature can have a direct effect on animal thermal regulation and physiological tolerances (Kearney et al. 2009). Further, the interplay of changes in precipitation and temperature can lead species in different directions (Tingley et al. 2012). Climate change, alone or in conjunction with other impacts, can also affect animals indirectly via changes in the habitat they use as, for example, elevation shifts in associated vegetation types. Such vegetation shifts are well reported in the literature, especially for mountain environments. Mountain environments have been identified as having high climatic change sensitivity, but the direction of shift can vary with the vegetation type. For example, previous research has shown both upward (Beckage et al. 2008, Lenoir et al. 2008) and downward shifts (Lenoir et al. 2010, Crimmins et al. 2011) in plant species ranges.

We used a framework in which mammal species and their associated vegetation types may change their elevation range synchronously (when both change in the same direction) or not (when each changes in a different direction). Here, we equate habitat to the vegetation types judged as suitable to each species according to an expert-based classification system (California Wildlife Habitat Relationships system; Mayer and Laudenslayer 1988). Species' life-history traits may also influence how species respond to changes in their environment (Buckley and Kingsolver 2012). However, this link is tenuous (Angert et al. 2011) because while traits are associated with species' range dynamics (Broennimann et al. 2006, Kearney et al. 2010), finding the traits that are responsible is challenging. A series of species' traits, such as lifespan (Hanspach et al. 2010), number of broods per year and annual fecundity (Jiguet et al. 2007), habitat specialism, dietary breadth and reproduction habitat (Angert et al. 2011), may be central to the processes by which species' distribution ranges are determined.

Moritz et al. (2008) and Rubidge et al. (2011) suggested that small mammal range dynamics over the last 80 yr in Yosemite National Park could potentially be explained by changes in both climate and vegetation. We set out to test the contribution of changes in the elevation range of the vegetation types suitable to each species. We asked two specific questions. First, can observed changes in small mammal species' ranges be explained by elevational shifts in vegetation over time? And second, is the ability of small mammals to respond synchronously to changes in vegetation predicted by species' traits? To answer these questions we tested for changes in small mammal presence between historical and modern times (Grinnell survey in 1911–1917 and resurveys in 2003–2008) and changes in vegetation derived from historical and modern maps (Wieslander survey 1930–1940 and CalVeg 2000–2006). We then assessed whether species' traits could explain species responses to vegetation dynamics. We predicted that if a species' distribution range is determined by their vegetation preferences then species will respond synchronously with the dynamics of vegetation, particularly if the species has narrow vegetation preferences (i.e. is a specialist), and will respond asynchronously (or not at all) if the species has broad vegetation preferences (i.e. is a generalist; more detailed predictions from each trait are explained in Supplementary material Appendix 1). Alternatively species' distribution ranges may be controlled by other factors, such as climate, demography, or species interactions. Species ranges would then be asynchronous with vegetation range shifts.

Methods

Study area

The study covers 3350 km^2, and focused on an elevational transect (100–3000 m) that includes the Yosemite National Park on the west slope of the California's Sierra Nevada mountains (Fig. 1). Different vegetation types dominate at different elevations, with oak woodlands (*Quercus* spp.) and chaparral at the lower elevations (< 1500 m), hardwoods, ponderosa pine *Pinus ponderosa* and sierra mixed conifer species (white fir *Abies concolor*, Douglas fir *Pseudotsuga menziesii*, sugar pine *Pinus lambertiana*, incense cedar *Calocedrus decurrens*), and the California black oak *Quercus kellogii* at intermediate elevations (1000–2500 m), being replaced by lodgepole pine *Pinus contorta*, fir *Abies* spp. and hemlock *Tsuga mertensiana* at higher elevations (2000–3200 m), and alpine meadows and rock fields above that.

Small mammal data

The presence and capture history data come from the ongoing Grinnell Resurvey Project of the Museum of Vertebrate Zoology (MVZ), Univ. of California, Berkeley (<mvz.berkeley.edu/Grinnell>; Moritz et al. 2008). These data consist of the original surveys by Joseph Grinnell and colleagues while documenting biological diversity in the state (Grinnell 1917b, 1924). This effort included trapping and identification of all specimens across all elevations within the Yosemite transect to describe species' ecological distributions along Merriam Life Zones (Fig. 1). The data on species captures and descriptions were recorded in extensive field notes, archived at the Museum of Vertebrate Zoology (<http://bscit.berkeley.edu/mvz/volumes.html>).

The historical data collection methods included 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 permitted repetition of the survey design in the modern times, where the same methods were applied, allowing for a comparison between the historic and the modern results. Moritz et al. (2008) conducted a resurvey project that repeated the sampling in approximately the same locations as the historical surveys, to assess whether changes have occurred.

In the historical data there were some uncertainties in the specific geographical 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) following the method in Moritz et al. (2008). The same criteria were applied to the modern data, where traplines within 2 km or 100 m were also aggregated. Species' presence, capture history and trapping effort data were then summarized for the aggregates and used for subsequent analysis.

Species' capture histories were used to estimate if there were significant changes in species' elevational distribution range in an occupancy modeling framework. Occupancy modeling (MacKenzie and Nichols 2004) is a statistical framework based on a series of probabilistic arguments that allow simultaneous estimation of a species' probability of detection (p) and probability of occupancy (ψ). The outputs of this method allow detecting significant changes in species ranges (Moritz et al. 2008, Tingley et al. 2012). We used the probability of false absence to determine whether a given sampled site corresponded to a true or false absence. We defined true absences as those locations with probability of false absence lower than 0.1. Based on this categorization we then assessed mammal elevation range dynamics (Table 1). Since we were interested in the changes in elevation range and not the entire geographic range, we selected occupancy models over species distribution models (SDMs)

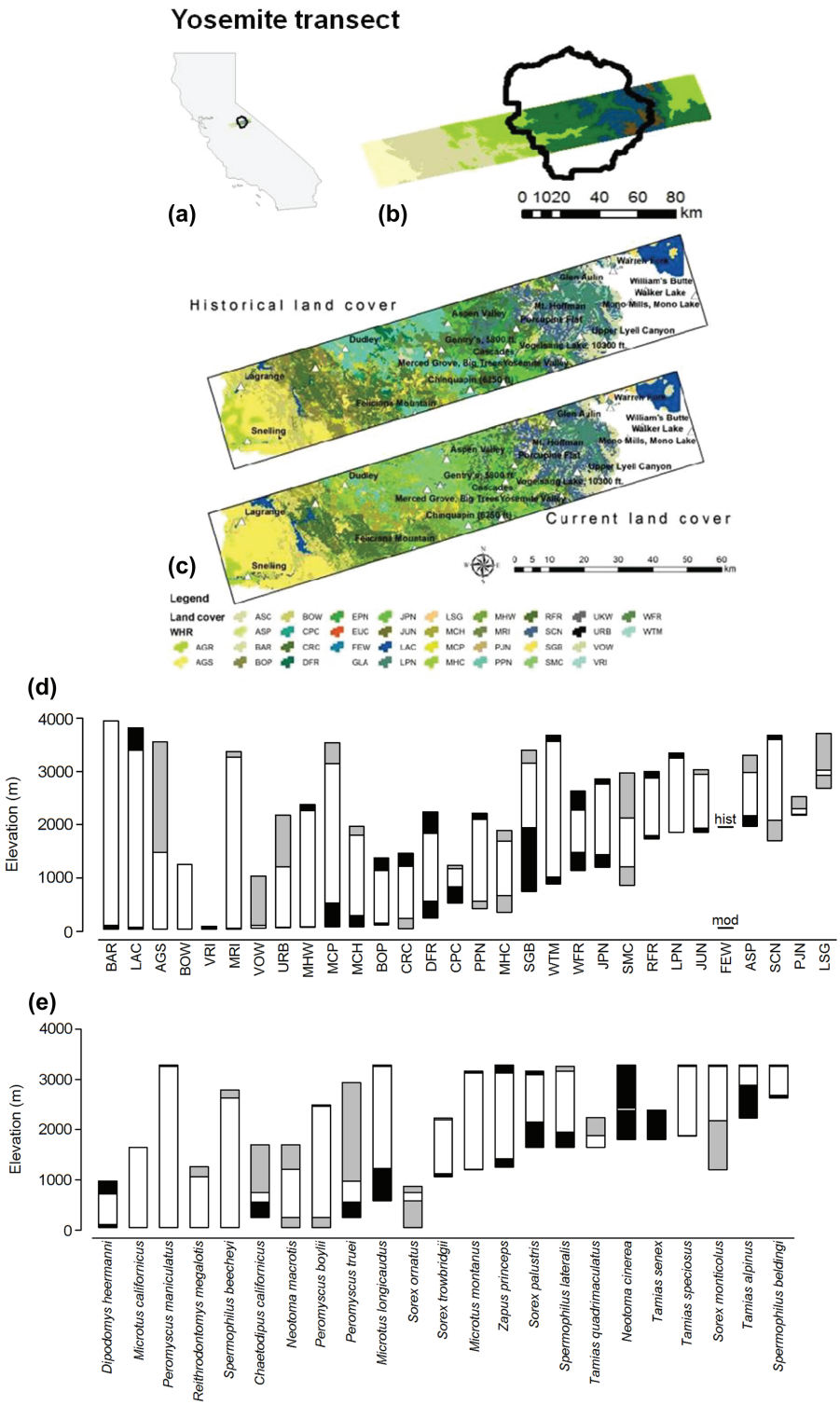

Figure 1. Study area location and changes in WHR vegetation types in the Yosemite transect: (a) location of the Yosemite transect in California and the outline of Yosemite National Park (YNP); (b) Yosemite transect with colors depicting different elevation life zones (sensu Merriam's life zones) and outline of YNP; (c) historical (1930s) and modern (2000s) land cover in the Yosemite transect; (d) historic and modern elevation range of each WHR vegetation type, and (e) historic and modern elevation range of each mammal species (vegetation types: AGR – agriculture, AGS – annual grasslands, ASP – aspen, BAR – barren, BOW – blue oak woodland, BOP – blue oak-foothill pine, CRC – chamise-redshank chaparral, CPC – closed-cone pine-cypress, DFR – Douglas fir, EPN – east side pine, FEW – freshwater emergent wetland, JPN – Jeffrey pine, JUN – juniper, LAC – Lacustrine, LPN – jodgepole pine, MCH – mixed chaparral, MCP – montane chaparral, MHW – montane hardwood, MHC – montane hardwood–conifer, MRI – montane riparian, PJN – pinyon–juniper, PPN – ponderosa pine, RFR – red fir, SMC – sierran mixed-conifer, SCN – sub-alpine conifer, URB – urban, VRI – valley foothill riparian, VOW – valley oak woodland, WTM – wet meadows, WFR – white fir; mammal species codes correspond to the first three letters of each of their names as described in Table 1; black are range contractions and grey are range expansions).

Table 1. Species recorded in the Yosemite transect, observed elevation range dynamics Moritz et al. (2008), and the elevation range they inhabit.

Order	Family	Species	Code	Range	Elevation range
Insectivora	Soricidae	*Sorex monticolus*	SORMON	Expand*	High
Insectivora	Soricidae	*Sorex ornatus*	SORORN	Expand*	Low
Insectivora	Soricidae	*Sorex palustris*	SORPAL	Contract*	High
Insectivora	Soricidae	*Sorex trowbridgii*	SORTRO	No change	Intermediate
Rodentia	Sciuridae	*Otospermophilus beecheyi*	OTOBEE	No change	Intermediate
Rodentia	Sciuridae	*Urocitellus beldingi*	UROBEL	Contract	High
Rodentia	Sciuridae	*Callospermophilus lateralis*	CALLAT	Contract*	High
Rodentia	Sciuridae	*Tamias alpinus*	TAMALP	Contract*	High
Rodentia	Sciuridae	*Tamias quadrimaculatus*	TAMQUA	No change	Intermediate
Rodentia	Sciuridae	*Tamias senex*	TAMSEN	Contract	Intermediate
Rodentia	Sciuridae	*Tamias speciosus*	TAMSPE	No change	High
Rodentia	Heteromyidae	*Chaetodipus californicus*	CHACAL	Expand*	Low
Rodentia	Heteromyidae	*Dipodomys heermanni*	DIPHEE	Contract*	Low
Rodentia	Cricetidae	*Neotoma cinerea*	NEOCIN	Contract*	High
Rodentia	Cricetidae	*Neotoma macrotis*	NEOMAC	No change	Low
Rodentia	Cricetidae	*Peromyscus boylii*	PERBOY	No change	Intermediate
Rodentia	Cricetidae	*Peromyscus maniculatus*	PERMAN	No change	All
Rodentia	Cricetidae	*Peromyscus truei*	PERTRU	Expand*	Low
Rodentia	Cricetidae	*Reithrodontomys megalotis*	REIMEG	Expand	Low
Rodentia	Cricetidae	*Microtus californicus*	MICCAL	Expand	Low
Rodentia	Cricetidae	*Microtus longicaudus*	MICLON	Contract*	High
Rodentia	Cricetidae	*Microtus montanus*	MICMON	No change	High
Rodentia	Dipodidae	*Zapus princeps*	ZAPPRI	Contract	High

*Range changes supported by occupancy models.

because using raw data better describes the elevation range, occupancy models allow incorporating estimates of trapping effort into the estimation of the probabilities of detection and occupancy, and occupancy models do not require the definition of a threshold to create a range limit (except the threshold applied to the occupancy models to decide which probability of false absence corresponds to a 'true' presence). All the species we considered reach an upper and lower range limit within the study extent.

Vegetation data

We compared digital historic (1934) and contemporary (2000) vegetation maps (Fig. 1). The historic Wieslander maps (<http://vtm.berkeley.edu/>) come from a 1930s survey conducted throughout California to define vegetation types and their distribution ranges. Surveyors delineated and color-coded topographic maps to reflect the vegetation types they observed and annotated each map polygon with from one to eight rank-ordered spatially dominant plant species. This sequence of species was used to define the vegetation type assigned to each polygon (described below). The study area maps were georeferenced and digitized to produce a spatial digital layer of vegetation types in the 1930s following methods in Thorne et al. (2008). This approach reproduces the original 1930s maps with < 10 m error. When compared to modern maps, the topographic base maps used to georeference the historic maps have a registration error of 86 ± 32 m. We resampled the historic maps into a 300 m grid, using a majority filter to identify the most extensive vegetation type in each pixel (Thorne et al. 2008).

The contemporary map is a combination of the best available current vegetation maps for our study area: a United States National Park Service (NPS) vegetation map, and a United States Forest Service (USFS) vegetation map for the surrounding areas, CalVeg 2000 (<www.fs.fed.us/r5/rsl/projects/frdb/layers/ev_mid.html>). The NPS map is based on 1 m digital imagery with hand-delineated polygons and a sub-hectare minimum mapping unit while the USFS map is based on Landsat imagery, with an original spatial resolution of 30 m. These two maps were combined to a single contemporary map by the USFS, and the resulting polygons can be portrayed according to several vegetation type classifications, including the one used for this study (description below). We rescaled the contemporary map to the same 300 m pixel frame as the historic map, using the majority sample rule.

Vegetation types from both maps were cross-referenced to the California Wildlife Habitat Relationships (hereafter WHR) types (Mayer and Laudenslayer 1988). The WHR classification is used by California State agencies to delineate the distribution of terrestrial vertebrate species in California based on the vegetation types that are suitable for each species. Each WHR type is defined by plant species composition and stage (a combination of size and cover class for trees, age and cover for shrubs, and height and cover for herbs), which was determined by field sampling (<www.cnps.org/cnps/vegetation/protocol.php>). In addition, special elements are also included, such as snags, banks and burrows, aquatic requirements, animal diet, and human-made structures. Each WHR vegetation type is also described in terms of its links to other classification schemes, and its biological setting (its position relative to other habitats and wildlife considerations), physical setting (soils, topography, and climate), and geographical distribution in California.

Several constraints are associated with evaluating and using time-series vegetation data. These include: spatial accuracy, thematic accuracy, cross-referenced thematic

accuracy, and scale of analysis. The use of a 300 m operational grid accounts for the map and observation records spatial accuracy and sets the scale of map-based analyses. Similar transitions to those we describe, were documented from both vegetation map and concurrent forest plot data (Thorne et al. 2008, Collins et al. 2011, Crimmins et al. 2011), which provide an independent validation of the changes measured using the vegetation maps. The use of the WHR classification system permitted a robust and extensively tested set of vegetation types, specified for suitability to vertebrate species. However, some vegetation types such as meadows and riparian areas may be under-represented at a spatial resolution of 300 m. There is a potential for a scale effect among the small mammal data and the vegetation data. The small mammal data were collected from traplines that consist of 30–40 traps, spaced about 10m from each other, set in a 300–400 m line. The vegetation maps' minimum mapping unit was set at 300 m. The similarity of scales of data collection for both data sets, bolstered confidence in the proposed integration. The 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 unit of analysis, each unit merging information from several traplines, and vegetation data were summarized for these units of analysis. We feel assured that the alignment of the two collection methods and scales of analysis greatly reduces the potential for a scale effect.

Vegetation suitability

To determine historic and modern species-specific vegetation suitability, we used the WHR habitat suitability index (HSI) rankings for each target species. The WHR system consists of a set of relational tables that summarize existing knowledge on species–habitat relationships for California vertebrates, and which are digitally available (CWHR ver. 8.2. from 2008; <www.dfg.ca.gov/biogeodata/cwhr/>). The WHR ranks habitat suitability from 0 (not suitable) to 1 (most suitable). The system provides two types of suitability indices: a global index (average or weighted); and individual suitability values for each vegetation type's suitability for cover, food and reproduction for each vertebrate species. We used the weighted habitat suitability index (Supplementary material Appendix 2). We replaced each vegetation type in our historic and modern vegetation maps by its respective HSI value for each small mammal species. This resulted in an historic habitat suitability map and a modern habitat suitability map for each small mammal species (see Supplementary material Appendix 2 for examples). We then extracted the vegetation map grid cells that corresponded to each trapping aggregate, and calculated the average vegetation suitability per species during both time periods within each 2 km aggregate.

Data analysis

We tested whether vegetation suitability values (HSI) predicted species' presence as observed in the trapping data by using a generalized linear model with a logit link function, and added era (historic vs modern) as a covariate. We used the probability of false absences (p(fA)) to classify aggregates as present or absent for a given species, using a threshold of p(fA) ≤ 0.1 to classify a site as absent. We assessed model predictive ability by regressing observed presence/absence against predicted values. Given that we used the regularly updated expert WHR system to derive these HSI values we expected that vegetation suitability would have a positive effect in predicting species presence. We used era to assess whether the ability of HSI to predict species changed over time. We expected a non-significant effect if there was no change over time, a negative relation if there was a decrease in the ability of HSI to predict species presence from historic to modern time, and a positive relation if there was an increase in the ability of HSI to predict species presence from historic to modern time. We assessed the effect of HSI and era using a z score and its significance. We opted for using aggregate data because we are doing this analysis to confirm that HSIs do a reasonable job at predicting species presence before proceeding with the change analysis.

To answer whether or not there was synchronicity between changes in mammal and vegetation elevation ranges, we had to account for the differential use of vegetation types by each species. We first calculated the change in elevation range of each vegetation type between historical and modern time, and then weighted it by its suitability to each species (HSI value). The final value was calculated as the average across all vegetation types suitable for that species. The overall value of vegetation elevation displacement (Δ_{veg}) was estimated as:

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

where i is each of N vegetation types suitable to the species, $max(elev)$ and $min(elev)$ correspond to the maximum and minimum elevation at which a given vegetation type occurs in either historical (h) or modern (m) times, and HSI is the suitability of a given vegetation type for that species (reported in Supplementary material Appendix 2). Maximum and minimum elevations were calculated as the average of the 95 and 5% quantiles of the distribution of elevations at which a given vegetation type occurs in each time period for the entire study area.

We then plotted the changes in suitable vegetation elevation against the change in species' elevation. The change in species' ranges (Δ_{sp}) was the difference in the species' historical and modern elevational ranges:

$$\Delta_{sp} = \left(max(elev)_m - min(elev)_m\right) - \left(max(elev)_h - min(elev)_h\right) \quad (2)$$

where $max(elev)$ and $min(elev)$ correspond to the maximum and minimum elevation at which a species occurs in historical (h) or modern (m) times and were estimated as the averages of the 95 and 5% quantiles of the distribution of elevations at locations where the species was present. In a plot of changes in vegetation elevation against changes in species' elevation, synchronous responses occur in the first and third quadrants, whereas asynchronous responses lie in the second and fourth quadrants (Fig. 2a).

We then tested whether small mammals showed more synchronous than asynchronous responses to changes in suitable vegetation. We used a contingency test with the counts of species in the 1st and 3rd quadrants – synchronous

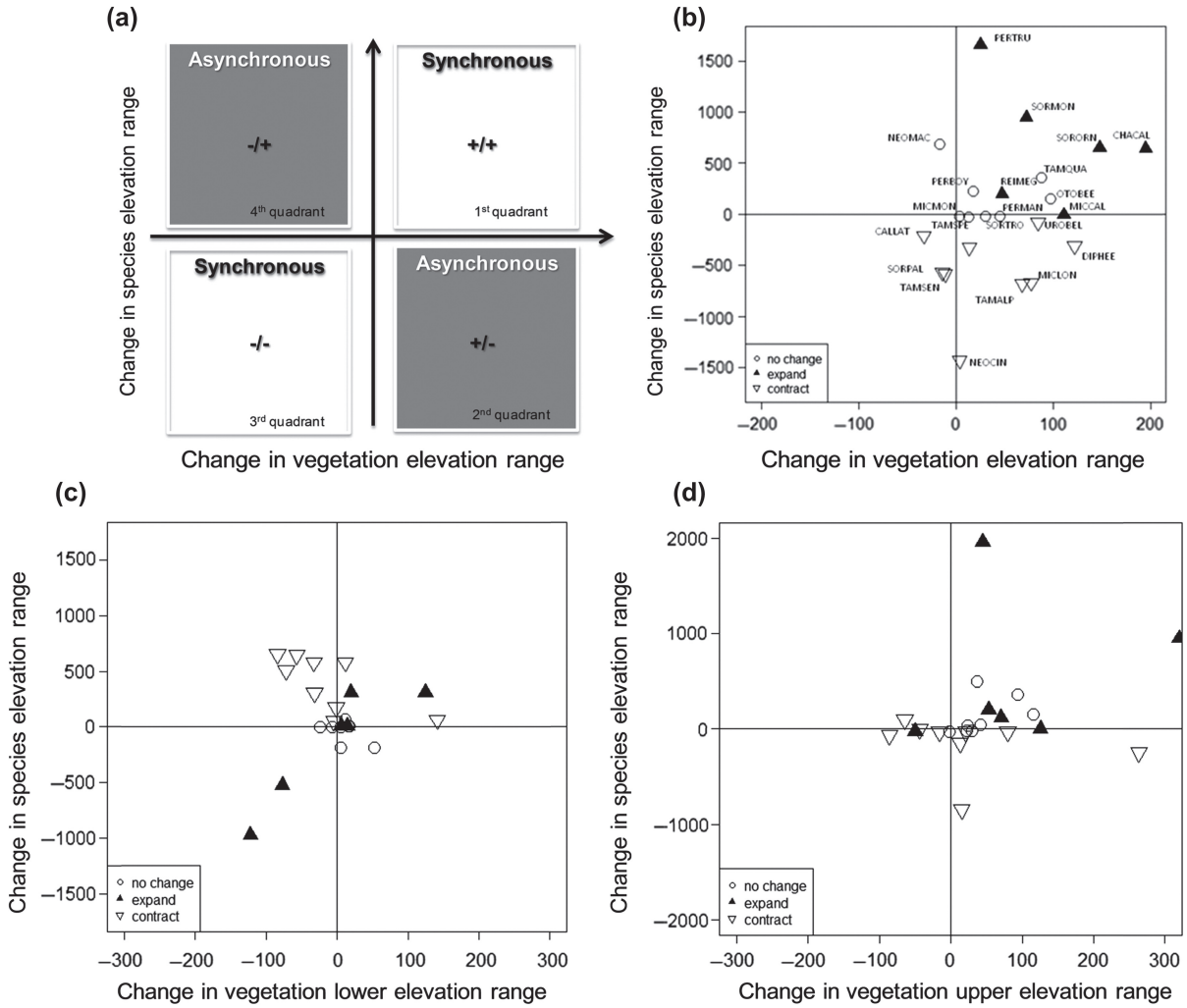

Figure 2. Plot of changes in vegetation elevation range axis (x axis) against the changes in species elevation range (y axis). The x axis represents changes in vegetation elevation ranges (positive values: increase in vegetation elevation range, negative values: decrease in vegetation elevation range), the y axis represents changes in species elevation range (positive values: increase species elevation range; negative values: decrease species elevation range). Synchronicity of change occurs when species are placed in the 1st and 3rd quadrants of this plot, whereas a-synchronous species are placed in the second and fourth quadrants. When a species crosses either of the axes either the mammal species range or the suitable vegetation range did not change; we labeled these cases as having no relationship. (a) Theoretical placement, (b) full range, (c) lower limit, and (d) upper limit. 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 have did not change their elevation range. Note that species that did not significantly change their elevation range may have observed range changes, but they were less than 5% of their historic range extent. Eleven out of 23 species (48%) range shifts are synchronous with those of their suitable vegetation in elevation. Mammal species names are coded to the three first letters of their genus and scientific names (Table 1).

species – and the counts of species in the 2nd and 4th quadrants – asynchronous species – in Fig. 2a, against a random prediction from a binomial distribution. Next, we used a contingency analysis to test whether the prevalence of synchronicity differed between species that inhabit low, medium and high elevations or between contracting versus expanding species. We used the low, medium and high elevation categorization because these elevation ranges are inhabited by different small mammal species, and because the high and low elevation species show different dynamics (Moritz et al. 2008).

We tested whether there were specific changes associated with the upper and lower range limits. To do this we modified Eq. 1 and 2, for Eq. 3 (suitable vegetation) and 4 (species) for upper and lower range limits (L) in historic and modern time. We then used a chi-square test to assess whether placement of species within the plot described in Fig. 2a was different from random for both the upper limit (UL) and the lower limit (LL) of their range.

$$\Delta_{\mathrm{veg}_L} = \left[\sum_{i=1}^{n}\left[\left(L_m - L_h\right)\times HSI\right]_i\right] \Big/ N \tag{3}$$

$$\Delta_{\mathrm{sp}_L} = \left(L_m - L_h\right) \tag{4}$$

Even if all species were synchronous, some species will likely be more closely synchronous. To test this we created a linear regression model of species elevation range change as a dependent variable and average vegetation range change as independent variable. We expected that if synchronicity

was precise, the regression would explain a large proportion of the deviance, thus have a high R-square, and a significant and positive slope. A slope non-significantly different from zero suggests no synchronicity.

While species may be responding to average elevation changes of all their suitable vegetation types, it is also possible that a given mammal species could track synchronously only one of its many suitable vegetation types (for example, the one that is shifting the most) and show very little-to-no synchronicity with the other suitable vegetation types that change less. To assess this we plotted the elevation range change for each vegetation type weighted by species HSI for each species against that species' elevation range shift. We then calculated how many species were synchronous with each vegetation range displacement, and the upper and lower limit of that vegetation type. We also tested how well species were tracking the vegetation shifts using a regression analysis as described above.

Finally, we tested whether species' traits could be related to synchronicity in species and vegetation range dynamics using chi-square tests. We assembled information on species' traits from the PanTHERIA database (Jones et al. 2009) and from the data published in Moritz et al. (2008), which included their relatedness (Genus), 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, young per year). Descriptions of each trait and trait values are detailed in Supplementary material Appendix 1. Because of the high number of comparisons, we applied a Bonferroni correction to the significance level.

Results

Vegetation change

In the Yosemite transect there are 34 vegetation types, urban areas, and grid cells with unknown cover type in the historic map (Fig. 1). The most extensive historical vegetation type was ponderosa pine (PPN: 412.7 km^2, 12% of the transect area), followed by lodgepole pine (LPN: 354.7 km^2, 11%), and annual grasslands (AGS: 336.2 km^2, 10%). Currently, sierran mixed conifer and annual grasslands are the most extensive (SMC: 519.6 km^2; AGS: 517.8 km^2; both 15%), and SMC also increased the most (from 17.4 to 519.6 km^2), at the expense of ponderosa pine (PPN: from 412.7 to 116 km^2) and white fir (WFR: from 140.4 to 5.2 km^2; Fig. 1c). These changes in vegetation area covered varied with elevation (Fig. 1d). The increases in Sierran mixed conifer and annual grasslands area occurred with an upward expansion of the elevation range of these vegetation types (Fig. 1d). The reductions of ponderosa pine area did not result in a change in the elevation range of this vegetation type, and white fir showed an upward contraction of its lower elevation range and downward contraction of its upper elevation range.

Suitability and species' presence

Presence of twenty (out of 23) species in our trapping data was significantly predicted by HSI, the suitability index (Table 2). On average, species presence/absence records were significantly and positively associated with the HSI values (Table 2, Supplementary material Appendix 3). For four species there was also a significant negative effect of era, showing better prediction for historic values.

Synchronicity between mammal and average suitable vegetation range changes

Of the 23 mammal species analyzed, 11 species were synchronous with suitable vegetation range shifts, six were asynchronous, and six showed no relationship between the change in their elevation range and the changes in suitable vegetation range (Fig. 2b). Synchrony was not related with how many vegetation types the species uses, ranging from species using only 4 vegetation types (*S. monticolus*) to species that can use 22 (*O. beecheyei*) (Supplementary material Appendix 2). Despite many species showing synchrony, the overall relationship was weak to absent. The linear regression of change in species versus vegetation elevation range explained little variance ($R^2 = 0.07$) and the slope of the regression was not significantly different from zero ($F_{1,15} = 1.586$, p-value = 0.22).

Of the fifteen mammal species whose ranges shifted significantly (sensu Moritz et al. 2008), eight were synchronous with suitable vegetation range changes, a proportion (53%) not different from random ($\chi^2 = 0.08$, p-value = 0.78; Fig. 2b). Yet all mammal species that significantly expanded their elevation range did so by tracking the expansion of their suitable vegetation (Fig. 2b; $R^2 = 0.20$, $F_{1,15} = 5.15$, p-value = 0.03). Conversely, vegetation change did not explain species' contractions; only 3/9 species with reduced elevation ranges were observed to track the contraction of their suitable vegetation (third quadrant Fig 2b; *C. lateralis*, *S. palustris*, and *T. senex*; for an assessment of potential confounding effects see Supplementary material Appendix 4). All of the species with upwards expansion in their upper elevation range followed upward expansion of suitable vegetation (Fig. 3c), while the lower range limit shifts showed barely any synchronicity (Fig. 3b).

As a corollary to the above, species that inhabited low elevations were significantly more synchronous with suitable vegetation changes than were species that inhabit high elevations (Fig. 4a; $\chi^2 = 6.52$, p-value = 0.04). Finally, high-elevation species seem to be at odds with both vegetation range limits; where the vegetation edge went down the species range limit went up and vice-versa.

A majority of species showed no relationship with individual upper or lower suitable vegetation range limit shifts (upper: n = 11, lower: n = 10; Fig. 2c, d). Species' lower elevation range limits went upwards (i.e. contracted) for both synchronous and non-synchronous species; while the vegetation upper elevation range limits went upwards (i.e. expanded) for synchronous species and downwards (i.e. contracted) for asynchronous species (lower limit: Fig. 3b; $R^2 = 0.04$, $F_{1,15} = 0.78$, p-value = 0.39; upper limit: Fig. 3c; $R^2 = 0.18$, $F_{1,15} = 4.48$, p-value = 0.04). Again the synchrony was not tight, as the linear regression for the upper and lower limits was also non-significant (lower limit: $R^2 = 0.02$, $F_{1,15} = 1.586$, p-value = 0.22; upper limit: $R^2 = 0.06$, $F_{1,15} = 1.372$, p-value = 0.25).

Table 2. Generalized linear model results for predicting species presence based on HSI values and using era as a covariate. Bold values represent significant effects in predicting species presence.

	Intercept						HSIs						Era						Model performance		
Code	Value	SDE	95% CI		z value	p-value	Value	SDE	95% CI		z value	p-value	Value	SDE	95% CI		z value	p-value	Estimate	z-value	p-value
SORMON	−2.73	0.69	−4.2	−1.46	−3.94	**0.00008**	6.74	2.04	2.96	11.03	3.31	**0.0009**	0.82	0.46	–0.07	1.77	1.76	0.07	4.39	3.5	0.0004
SORORN	−4.25	1.12	−6.9	−2.38	−3.78	**0.0002**	6.04	2.86	0.64	12.21	2.11	**0.03**	0.12	0.89	–1.53	2.13	0.13	0.89	10.34	1.83	0.07
SORPAL	−2.26	0.64	−3.69	−1.11	−3.48	**0.0005**	4.27	1.87	0.82	8.28	2.28	**0.023**	–1.39	0.62	–2.66	–0.21	–2.27	**0.02**	7.95	3.18	0.001
SORTRO	−3.24	0.72	−4.82	−1.97	−4.51	**6E-06**	6.79	1.73	3.66	10.52	3.93	**0.00008**	–0.7	0.61	–1.93	0.51	–1.15	0.25	6.34	4.2	0.00003
OTOBEE	−1.41	1.26	−3.84	1.14	−1.12	0.26	−0.019	2.41	−5.07	4.51	−0.008	0.99	–0.24	0.53	–1.25	0.84	–0.45	0.65	6.87	15.27	0.45
UROBEL	−8.31	2.03	−12.99	−4.93	−4.08	**0.00004**	15.15	4.11	8.08	24.42	3.69	**0.0002**	0.96	0.83	–0.55	2.77	1.16	0.25	5.99	3.82	0.0001
CALLAT	−1.59	0.66	−2.99	−0.36	−2.39	**0.02**	1.86	0.99	0.01	3.97	1.87	0.06	–0.14	0.43	–0.98	0.72	–0.33	0.75	4.69	1.84	0.06
TAMALP	−2.04	0.51	−3.17	−1.13	−3.98	**0.00006**	39.63	9.66	22.88	61.77	4.11	**0.00004**	–2.32	0.9	–4.4	–0.73	–2.58	**0.009**	6.39	4.22	0.00002
TAMQUA	−4.53	1.04	−6.96	−2.79	−4.34	**0.00001**	7.36	1.86	4.11	11.56	3.97	**0.00007**	–0.48	0.79	–2.05	1.13	–0.61	0.55	7.26	4.33	0.000015
TAMSEN	−4.53	1.72	−8.66	−1.72	−2.64	**0.008**	5.84	3	0.6	12.69	1.95	**0.05**	–2.7	1.12	–5.72	–0.87	–2.45	0.01	9.116	3.36	0.0008
TAMSPE	−2.17	0.52	−3.27	−1.21	−4.17	**0.00003**	5.46	1.21	3.2	7.99	4.49	**6E-06**	0.24	0.49	–0.71	1.22	0.49	0.62	4.62	4.53	5.9E-06
CHACAL	−3.38	0.78	−5.17	−2.05	−4.34	**1.4E-05**	4.74	1.42	2.15	7.9	3.34	**0.0008**	–0.89	0.79	–2.5	0.69	–1.13	0.26	7.93	3.28	0.001
DIPHEE	−3.32	0.81	−5.18	−1.92	−4.08	**4.5E-05**	5.96	2.71	0.62	11.72	2.19	**0.028**	–0.91	0.88	–2.74	0.88	–1.03	0.303	12.04	2.34	0.02
NEOCIN	−2.97	1.12	−5.54	−1.04	−2.64	**0.008**	4.46	2.18	0.57	9.32	2.045	**0.04**	–2.99	0.85	–4.97	–1.51	–3.54	**0.0004**	6.94	3.79	0.00015
NEOMAC	−4.12	0.94	−6.28	−2.51	−4.37	**1.2E-05**	6.62	1.58	3.89	10.2	4.19	**0.00003**	–0.12	0.57	–1.24	1.03	–0.21	0.84	6.48	4.66	0.000003
PERBOY	−2.62	0.71	−4.15	−1.33	−3.69	**0.0002**	5.12	1.27	2.78	7.81	4.02	**5.8E-05**	–0.68	0.47	–1.62	0.23	–1.46	0.15	4.78	4.14	0.000036
PERMAN	1.92	1.41	−0.72	4.89	1.36	0.17	−0.78	2.11	−5.18	3.21	−0.37	0.71	–0.47	0.49	–1.49	0.47	–0.95	0.35	5.58	1.04	0.29
PERTRU	−3.03	0.78	−4.77	−1.67	−3.89	**0.0001**	4.33	1.46	1.64	7.46	2.96	**0.003**	–0.59	0.58	–1.73	0.57	–1.03	0.3	6.94	3.24	0.0012
REIMEG	−7.17	1.56	−10.62	−4.46	−4.59	**4E-06**	15.01	3.55	8.82	22.78	4.23	**2.3E-05**	–0.47	0.59	–1.63	0.7	–0.81	0.42	6.37	4.64	3.4E-06
MICCAL	−2.92	0.67	−4.39	−1.71	−4.33	**1.5E-05**	7.07	1.97	3.51	11.38	3.58	**0.00034**	–1.82	0.69	–3.27	–0.52	–2.63	**0.008**	6.05	3.75	0.0002
MICLON	−1.18	0.65	−2.51	0.06	−1.82	0.069	3.48	1.26	1.09	6.09	2.75	**0.006**	–0.51	0.43	–1.35	0.33	–1.19	0.236	4.33	3.06	0.002
MICMON	−3.31	0.96	−5.39	−1.58	−3.4	**0.0006**	5.99	2.4	1.63	11.13	2.49	**0.01**	0.35	0.5	–0.61	1.38	0.7	0.48	5.19	2.37	0.018
ZAPPRI	−2.32	0.61	−3.64	−1.21	−3.77	**0.0002**	5.69	1.53	2.91	8.95	3.74	**0.0002**	–0.81	0.5	–1.82	0.17	–1.62	0.105	4.94	3.72	0.00019

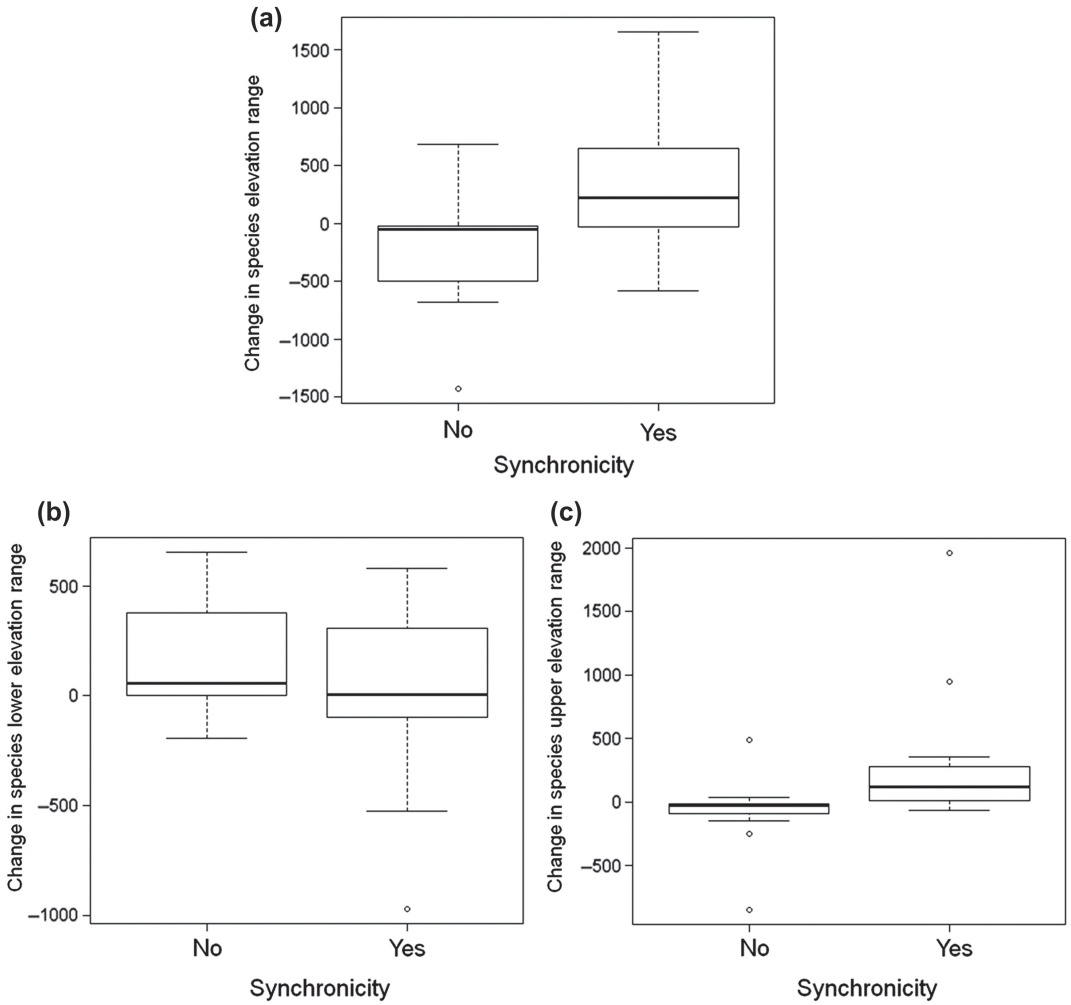

Figure 3. Box plots for synchronous and asynchronous species (a) full range, (b) lower limit, and (c) upper limit.

Synchronicity between range changes of mammal species and each suitable type

Notably, seven of the nine contracting species showed significant tracking of the contraction of Jeffrey pine (JPN), and red fir forest (RFR) elevation ranges (explaining 30 and 50% of the variability in the data, Table 3; Supplementary material Appendix 5). By contrast, expanding species showed no significant tracking of any individual suitable vegetation type (Table 3; Supplementary material Appendix 5); rather they appear to respond in a more general way (Supplementary material Appendix 6).

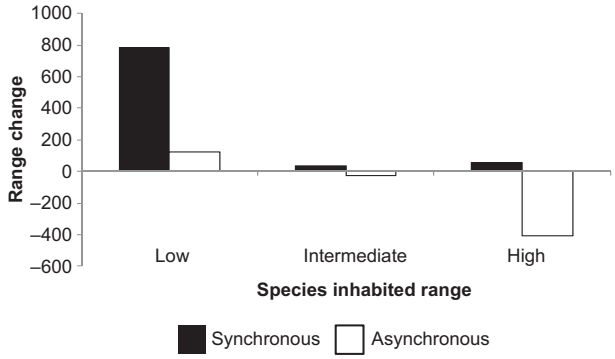

Figure 4. Species inhabited elevation range in meters and average range change. Species inhabited elevation ranges were split into three bins: low, intermediate and high. Species values are color-coded according to synchronicity.

Species' traits

From the suite of species' traits only diet guild showed a significant effect on species' ability to respond synchronously to changes in vegetation ranges (Table 4). Omnivore species were more synchronous than herbivores. Genus, adult body mass and neonatal body mass traits were only significant prior to the application of the Bonferroni correction.

Discussion

Our main goal was to assess the extent to which small mammal species' range dynamics can be explained by vegetation range dynamics. Our results illustrate multiple responses to vegetation dynamics by the assemblage of small mammals in the Sierra Nevada. Half of the species range shifts were synchronous with suitable vegetation range changes, 1/4 of the

Table 3. Synchronicity between mammal species and individual vegetation types range shifts. Codes in the first column correspond to vegetation types (see Fig. 1 for vegetation type names). We counted the number of species for which each vegetation type was suitable and how many times species were tracking the dynamics of the vegetation ranges, whether the mammal species were contracting, no changing or expanding their range, and strength of the association. Graphs for each individual vegetation type are presented in Supplementary material Appendix 5.

	Number of species for which vegetation type is suitable	Number of species tracking	Type of species	R^2	F-value	p-value
AGS	16	7	5 expanding, 2 no change	0.0007	0.009	0.92
ASC	9	0	–	0.011	0.078	0.79
ASP	10	1	1 expanding	0.15	1.38	0.27
BAR	3	0	–	NA	NA	NA
BOP	11	2	2 contracting	0.22	2.59	0.14
BOW	11	0	–	0.13	1.36	0.27
CPC	5	0	–	0.07	0.23	0.66
CRC	8	0	–	0.36	3.35	0.12
DFR	12	4	4 contracting	0.15	1.83	0.21
EPN	14	7	7 contracting	0.02	0.2	0.66
FEW	7	0	–	<0.001	0.0004	0.98
JPN	14	**7**	7 contracting	0.30	5.026	0.04
JUN	10	0	–	0.06	0.55	0.48
LAC	1	–	–	NA	NA	NA
LPN	13	5	5 contracting	0.1	1.27	0.28
LSG	9	4	2 expanding, 2 no change	<0.001	0.0004	0.998
MCH	18	0	–	0.12	2.16	0.16
MCP	18	1	1 contracting	0.1	1.77	0.20
MHC	15	6	3 expanding, 3 no change	0.16	2.54	0.14
MHW	12	3	3 contracting	0.05	0.57	0.47
MRI	19	7	4 expanding, 3 no change	0.008	0.14	0.72
PJN	10	4	2 expanding, 2 no change	0.20	1.97	0.20
PPN	15	0	–	0.01	0.19	0.66
RFR	14	**7**	7 contracting	0.56	15.01	0.002
SCN	15	4	2 expanding, 2 no change	0.02	0.29	0.60
SGB	15	7	7 contracting	0.22	3.72	0.08
SMC	20	8	4 expanding, 4 no change	0.004	0.08	0.79
URB	3	1	1 no change	NA	NA	NA
VOW	11	6	3 expanding, 6 no change	0.13	1.36	0.27
VRI	12	0	–	0.17	2.06	0.18
WFR	18	7	7 contracting	<0.001	0.005	0.94
WTM	16	7	7 contracting	0.09	1.304	0.27
Average		3.4				

species shifted ranges in opposite directions to the changes in their suitable vegetation and the other 1/4 showed no relationship with vegetation changes. Low and intermediate elevation species were more synchronous with vegetation shifts and expanded their range as their suitable vegetation range also expanded. High-elevation species contracted their range even as their overall suitable vegetation ranges expanded.

Table 4. Species traits effect on species tracking or not tracking habitat in elevation. Bold values are significant differences (Bonferroni corrected p-value <0.01).

Trait	Track	Not track	χ^2	p-value
Genus	*Sorex*	*Microtus*	17.96	0.05
Home range	0.005	0.014	0.02	0.88
Terrestriality	1.5	1.33	0.17	0.68
Annual rhythm	non-hibernator	non-hibernator	0.68	0.71
Activity cycle	both	both	0.14	0.93
Basal metabolic rate	68.99	112.76	2.45	0.12
Adult mass	52.30	144.29	4.12	0.04
Max longevity	12.75	24.00	2.39	0.12
Diet	**omnivore**	**herbivore**	**10.68**	**0.01**
Litters per year	1.75	2.00	0.02	0.89
Gestation length	26.10	25.23	0.01	0.92
Litter size	4.63	4.43	0.28	0.60
Neonatal body mass	2.35	7.06	3.84	0.05
Youngs per year	7.38	9.00	0.03	0.86

This study focused on one axis of variation of a species niche – vegetation. The small mammal species that were synchronous with vegetation included species from many different genera (*Otospermophilus*, *Callospermophilus*, *Tamias*, *Chaetodipus*, *Peromyscus*, *Reithrodonthomys*, *Sorex*) and with a varied suite of traits (Supplementary material Appendix 1). *Chaetodipus californicus* and *P. truei* (west slope) expanded upwards following localized conversion of Sierra mixed conifer (SMC) forest to chaparral after fire. *Callospermophilus lateralis* retracted upwards a bit but remained within the SMC. *Tamias senex* retracted upwards considerably still within the SMC forest. There are two species of *Sorex* that expanded ranges, *S. monticolus* and *S. ornatus*, downslope within the range of SMC, but these species use mostly moist meadow or riparian vegetation. Thus, most of the synchronous species elevation range shifts occurred at the elevations occupied by the SMC and its adjacent vegetation types. Sierra mixed conifer is an ensemble of five conifer species: white fir, Douglas fir, ponderosa pine, sugar pine, incense cedar, and the California black oak. The SMC has replaced the adjacent

vegetation communities at both of its elevation range limits. At lower limit and under a regular fire regime, the landscape would be dominated by ponderosa pine (PPN), and white fir would be prevented from reaching the canopy. However, fire suppression in mid-20th century (B. Kuhn pers. comm.) has allowed white fir to reach the canopy leading to vegetation transition from PPN to SMC (Thorne et al. 2008, Collins et al. 2011). At the upper limit, tree density of SMC has increased after suppression of the fire regime (Collins et al. 2011) and encroachment of meadows by trees (Vale 1987, Millar et al. 2004). These changes have reduced open areas and may be affecting species that require moist meadow conditions, including riparian vegetation along streams, such as *S. monticolus* (Smith and Belk 1996), or running water and shallow montane lakes, such as *S. palustris* (Beneski and Stinson 1987). SMC is also the vegetation type that is most suitable for most of the small mammal species that we analyzed (Supplementary material Appendix 2), thus likely explaining the synchronicity between small mammal range changes and average vegetation range changes.

While expanding species were mostly tracking the overall range expansion of all their vegetation types, contracting and typically high elevation species were only tracking a few vegetation types, namely red fir *Abies magnifica* and Jeffrey pine *Pinus jeffreyei* forest. For most contracting species red fir and Jeffrey pine forest are medium-to-highly suitable habitat (see Supplementary material Appendix 2 for the WHR rankings). This is because these forests produce a lot of seeds, which have been related to the reported higher densities of small mammal species in red fir forests than in other Sierra Nevada Mountains conifer forests (Wilson et al. 2008). Further these mammal species also have an important role in seed dispersal of these conifer forests (Briggs et al. 2009), suggesting a more symbiotic process. Only two expanding species (*S. monticolus* and *S. ornatus*) tracked specific vegetation types elevation range shifts, the small downward expansions of the lower range limit of ponderosa pine (PPN) and valley foothill riparian forests (VRI). Again this may be linked to the food availability in ponderosa pine forests and also with habitat specificity in riparian species.

Species' traits are expected to modulate response to vegetation dynamics (Buckley and Kingsolver 2012). From the suite of traits that we tested, we found only a significant effect of diet guild. Omnivore species were more synchronous and herbivores less synchronous with vegetation range shifts. Being an omnivore ensures a wider variety of food options, and thus it would be expected that they would be less tied to vegetation dynamics. However, we found the opposite, with omnivores being the species that were more synchronous with vegetation dynamics. This suggests that omnivores may be tied to some prey items that respond to changes in vegetation rather than tied to vegetation shifts alone. Herbivores may have more flexibility in eating different plant species as they change over time and thus not tracking vegetation changes. This categorization into dietary guild corresponds to other findings that a wider dietary niche breadth was associated with range changes (Angert et al. 2011). We also found that those herbivores generally not synchronous with vegetation dynamics were species that use mostly herbaceous vegetation types, such as 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 et al. 2004)], and rock slab [*T. alpinus* (Clawson et al. 1994)]. Such vegetation types tend not to be as spatially dynamic because they are mostly tied to the local topography and geologic structure.

Several explanations can be advanced for why some species' shifts were not synchronous with their suitable vegetation elevation changes. First, species may respond to direct effects of climate change on physiology (Kearney et al. 2009), rather than a response to vegetation dynamics. Species may also show an indirect response, such as changes in species interactions due to responses in other species to changing conditions (Tylianakis et al. 2008) or changes in atmospheric pollution (for example, nitrogen deposition), and fire frequency or intensity. Species responses may also include behavioral plasticity (Knowlton and Graham 2010), or local adaptation through selection (Davis et al. 2007). However, if species are not responding to vegetation dynamics, or responding in a way unaccounted for in the HSI, we would expect HSI not to be a good predictor of species presence. We found that HSI was not a good predictor of species presence for *O. beecheyi*, *C. lateralis* and *P. maniculatus.* This is potentially because of wide habitat preferences: *P. maniculatus* is a generalist species that can use 30 of the 31 vegetation types found in the study area (Supplementary material Appendix 2 and 3); or because there was no change in either species and vegetation ranges, *O. beecheyi* did not change its distribution range and little change was observed in its suitable vegetation. One additional species, *C. lateralis*, contracted its range and HSI was almost still not significant. This is perhaps because of the low trapping success of this species in the modern era.

A second explanation is that our suitability values did not represent all of the possible vegetation types a species could use. For example, barren (BAR) lands include the rock slabs around which *T. alpinus* lives (Clawson et al. 1994, Rubidge et al. 2011), and the rock talus where *N. cinerea* (Smith 1997) occurs. However, BAR was not listed in the WHR rankings for these species and this vegetation type showed a decrease in the study area (Fig. 1). Presence of some species (*S. palustris*, *T. alpinus*, *N. cinerea* and *M. californicus*) was better predicted for historic times. This could indicate a trend towards asynchronicity because the modern habitat use was not being captured within the known habitat preferences; except for *S. palustris*, the other species were indeed asynchronous. We believe, however, that this does not undermine the value of the suitability index. Instead it suggests that it might be important to periodically update HSI values, in light of the newest literature on each species, and the possibility that suitability values may change over time. Such change in the future might also be indicative of the dissassembly of communities under the rapid pace of climate change (Lomolino and Perault 2000, Sheldon et al. 2011).

A third possibility for why some species did not show synchronous dynamics is that we were unable to measure the fine-scale characteristic(s) of the vegetation to which species are responding, such as seed production, cover, etc. Some vegetation types, such as meadows and riparian areas, are known to have changed in Yosemite (Vale 1987),

but are not likely to have changed spatially as they are tied with hydrologic features of the landscape that are static. In this case, species tied to static vegetation types, could actually be synchronous with the vegetation but were not identified as such by our analysis, as it focused on change. This may explain why meadow specialists like *U. beldingi* (Jenkins and Eshelman 1984) and *M. montanus* (Sera and Early 2003) and riparian species as *Z. princeps* (Hart et al. 2004) were not synchronous to changes in vegetation ranges. Further, WHR vegetation type change detection did not measure increase in density in SMC (Collins et al. 2011) and the change in forest structure (Mantgem and Stephenson 2007, Lutz et al. 2009), to which species like *S. trowbridgii* (George 1989) or *T. speciosus* (Best et al. 1994) are likely to respond.

Finally, it is important to note that most of the species which were not synchronous with their overall vegetation range changes were synchronous with one or two vegetation types. These were mostly species that inhabited high elevations and whose elevation ranges contracted. It could be that climate limitations take precedence over vegetation (Chen et al. 2011). The elevations where these species exist do not have tree canopy, vegetation height is relatively low, and there are many bare areas. This increases species' direct exposure to solar radiation, and its effects on temperature and on the snow/ice cover cycle. Often, these high-elevation species have lower physiological tolerance to increases in temperature, higher exposure to radiation, and because they hibernate they are also sensitive to changes in the snow/ice cover cycle (Rubidge et al. 2011).

Assessing species' ability to respond synchronously to changes in their suitable vegetation over time is crucial to predicting their responses to climate and land cover change, to identify which species are at risk, and to predict their responses to future conditions. Our results show idiosyncratic responses of species in relation to shifts in vegetation in the Sierra Nevada Yosemite transect. Our results suggest that changes in overall vegetation distribution provide a more robust prediction for expanding than contracting mammal species. Thus, predicting the vulnerability of species to combined climate and land cover change will require simultaneous considerations of their physiological limits, species interactions and changes in vegetation (Buckley and Kingsolver 2012). The next steps should integrate all of these components, and include other factors such as disease, and population dynamics.

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Supplementary material (Appendix ECOG-00931 at <www.ecography.org/readers/appendix>). Appendix 1–6.

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