

1 **Title:** Differential tracking of habitat range change in elevation by small mammals over the last
2 century

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17 **Abstract:** Over time, both habitat and species' distribution ranges may expand, contract or
18 remain static in elevation. Species *track* habitat dynamics when both habitat and species'
19 [elevation](#) ranges expand or contract synchronously. Conversely, species *do not track* habitat
20 dynamics when habitat and species' [elevation](#) ranges change asynchronously; we equate habitat
21 to vegetation type that is suitable to a species. Tracking habitat [elevation range](#) dynamics [is](#)
22 [likely](#) a function of species' ecological traits. Here we explore if observed changes in habitat
23 [elevation range](#) can explain the observed changes in small mammals' [elevation](#) ranges over the
24 last 80 years in Yosemite National Park. To answer this question we tested for an association
25 between small mammal presence using Grinnell's survey in 1910-1930 and resurveys in 2003-
26 2008, with historical and current maps of habitat suitability. We found about 50% of the species'
27 [elevation ranges](#) tracked their habitat [elevation ranges](#). Most species that tracked their habitat
28 [elevation ranges](#) inhabit low and intermediate elevations and expanded their [elevation](#) range, and
29 those that did not track are high elevation species, whose [elevation](#) range contracted. Habitat
30 [elevation range](#) tracking is mostly linked to the changes in Sierra mixed conifer forests, [likely](#)
31 resulting from fire suppression [and lag effects](#). Adult body mass, diet guild, genus, and neonatal
32 body mass showed significant effects on species' ability to track their habitat [elevation range](#).
33 Omnivores tracked their habitat [elevation range](#) whereas herbivores did not. These results
34 suggest that a broad [diet](#) and higher reproductive rates allowed species to track their habitat
35 [elevation range](#) and expand their [geographical](#) range. Contracting species lack this capacity to
36 track habitat [elevation range](#). Assessing species' ability to track their habitat [elevation range](#) over
37 time is crucial as we use trends in species responses to environmental parameters to identify
38 which species are at risk, and to predict their responses to future conditions.

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45 **Key words:** California Wildlife Habitat Relationships, change detection, habitat suitability,
46 range dynamics, small mammals

47 Introduction

48 Species' geographic range exhibit dynamics in elevation (Gaston 1998). Theoretically, these
49 shifts are a response to changing environmental conditions that delimit species' ecological niche
50 over time (Grinnell 1917b, Soberon and Nakamura 2009). Much related research has been
51 devoted to understanding how species' ranges are shaped by environmental conditions and how
52 they may potentially change over time, termed biogeography, (for example see Elith *et al.* 2010;
53 and references therein). Species range dynamics occur as a function of changes in climate
54 (Lenoir *et al.* 2010, Tingley *et al.* 2010), and habitat (Oliver *et al.* 2009, Graham *et al.* 2010), and
55 can be used to predict changes in species' distributions. Assessing species response to habitat
56 dynamics is complicated because of the lack of historical datasets that comprise both species and
57 habitat data and their change in time. Assessing species' ability to track changes in their habitat
58 range over time could be very informative as it addresses how a species' climatic requirements
59 (as reflected in elevation) and its food/shelter requirements (as presumably captured by the
60 vegetation types) may not shift together as climate changes. In this paper we assess whether
61 small mammals are or are not tracking habitat elevation dynamics over time with the use of two
62 historical datasets from the Yosemite National Park area of California, USA. In our case we
63 focus on elevation range changes.

64 Species track habitat elevation dynamics when both habitat and species' ranges expand or
65 contract synchronously. Conversely, species do not track habitat elevation dynamics when
66 habitat and species' ranges change asynchronously. Here, we equate habitat to vegetation type

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Comment [1]: Rephrase. This sentence is very difficult to follow.

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Comment [2]: Basically, it sounds like you're saying that changes in where you find species "drives" where you find them.

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Comment [3]: You say that "Species track habitat dynamics when both habitat and species range expand, contract or do not change synchronously" - but if they do not change synchronously, then they must change asynchronously, which means they aren't tracking habitat type.

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Comment [4]: Here you say that habitat "drives" range distribution. Since one defines the habitat of a species from where it occurs, this statement ... [2]

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87 that is weighted by its suitability to each species. This is different than a simple metric of
88 vegetation change. Species' life-history traits may also influence how species respond to changes
89 in their environment. However, this link is tenuous (Angert *et al.* 2011) because while traits are
90 associated with species' range dynamics (Broennimann *et al.* 2006, Kearney *et al.* 2010), finding
91 the trait(s) that is(are) responsible for that is challenging. A series of species' traits, such as
92 lifespan (Hanspach *et al.* 2010), number of broods per year and annual fecundity (Jiguet *et al.*
93 2007), habitat specialism (Chen *et al.* 2011), dietary breadth and reproduction habitat (Angert *et*
94 *al.* 2011), and external threats (disease) (Murray *et al.* 2011) may be central to the processes
95 through which species can be changing their distribution range in response to changes in their
96 environment.

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97 Moritz *et al.* (2008) and Rubidge *et al.* (2011) found different small mammal species exhibited
98 primarily upwards expansion in their elevational distribution range over the last 80 years in
99 Yosemite National Park. They suggested these dynamics could potentially be explained by
100 changes in climate and habitat. We set out to test whether elevational changes in habitat could
101 explain observed small mammals' elevational range shifts. We asked two specific questions.

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102 First, can observed changes in species' ranges be explained by shifts in their habitat over time?
103 And second, can species' traits explain the tracking of habitat changes? To answer these
104 questions we tested for an association between small mammal presence in historical and modern
105 times (Grinnell survey in 1911-1917 and resurveys in 2003-2008) and habitat suitability derived
106 from historical and modern assessments of land cover (Wieslander survey 1930-1940 and
107 CalVeg 2000-2006). We then assessed if species' traits could explain species responses to habitat
108 dynamics. We predict that if a species' distribution range is driven by their habitat then species
109 will track the dynamics of habitat elevation ranges. Alternatively species' distribution ranges

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Comment [5]: It might be clearer if this was set up in terms of alternative hypotheses and associated predictions.

may be driven by other factors, such as climate or species interactions, then species will not track habitat elevation range changes. In the first case traits that relate to habitat use (behavior, diet, reproduction, etc) will be linked to species ability to track habitat elevation range dynamics; alternatively, in the second case, traits like physiology, circadian and annual activity, etc will more likely be related with not tracking the habitat elevation range changes.

Methods

Study area – The study covers 3350 km², used an elevational transect that includes the Yosemite National Park, and covers an elevation gradient from 100m to 3500m on the west slope of the California's Sierra Nevada mountains (Figure 1). Different plant communities dominate at different elevations, with oak woodlands and chaparral at the lower elevations (<1500m), hardwoods, Ponderosa pine and other pine species at intermediate elevations (1000-2500m), being replaced by lodgepole pine, fir and hemlock at higher elevations (2000-3200m), and alpine conditions.

Small mammals' data – 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 *et al.* 2008). These data consist of the original data collected by Joseph Grinnell and colleagues while documenting biological diversity in the state (Grinnell 1917a, 1924, Moritz *et al.* 2008). This effort involved the setting up of trapping campaigns across all elevations within the Yosemite transect (and the effort also included the Lassen, Southern Sierras, Central Coast and San Diego transects, but those data were not considered in this analysis), while documenting the Merriam life zones that defined the transect (Figure 1). The

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data were recorded in extensive field note-books, archived at the Museum of Vertebrate Zoology, and subsequently made available digitally through the Museum website (<http://bscit.berkeley.edu/mvz/volumes.html>). It can be argued that these data do not lend themselves readily to comprehensive analyses, as the original Grinnell and colleagues surveys (1910-1920) were not intended to establish a standardized baseline for comparison with repeat samples up to nine decades later. The historical 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. 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. Using that as a foundation, modern analytical tools enabled us to build the details of the survey method into the analytical framework to reduce the effects of the sampling design, allowing for accurate comparisons across time.

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 2km radius or a 100m 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 2km or 100m 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 (see Moritz et al. 2008) and these results were used to select species for the analysis and to describe their elevation range dynamics (Table 1). Since we were interested in the changes in elevation range and not the entire spatial realization of a species geographic range, we believe this method is arguably better than species distribution modeling (SDMs) because (1) it deals with the issue of detectability in a more formalized way than most SDMs, as it incorporates detection probabilities directly into the estimation of species occupancy; (2) it allows incorporating estimates of trapping effort into the estimation of the probabilities of detection and occupancy; (3) tests for changes in occupancy, and therefore similar to SDMs range shifts outputs, which are done on the detectability corrected occupancy estimates; (4) it allows to incorporate effects such as elevation in explaining the significant models; and (5) do not require the definition of a threshold to create a range limit. In a parallel analysis we did compare the results from the species occupancy range changes and that of traditional SDM's outputs and found concordant results for four species (Appendix I; Santos et al. 2012).

Land cover data – We used the digital version of the Wieslander (1934) and CalVeg (2000) land cover maps (Figure 1). The Wieslander data set (<http://vtm.berkeley.edu/>) corresponds to 1930s Wieslander surveys. Surveyors were sent throughout the state to define the vegetation communities. Surveyors color coded topographic maps to reflect the vegetation communities they observed from vantage points; surveyors also annotated the maps to the dominant plant

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species. These maps were then 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 (see description below on accuracy assessment), this data set was produced at a spatial resolution of 300m (Thorne *et al.* 2008).

CalVeg 2000 data were downloaded from the United States Forest Service website (http://www.fs.fed.us/r5/rsi/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 30m. 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 300m to match the spatial resolution of the historical map.

Land cover types were subsequently cross-referenced to the California Wildlife Habitat Relationships (CWHR, hereafter WHR) types (<http://www.dfg.ca.gov/biogeodata/cwhr/>). WHR types correspond to habitats designed to be used to predict terrestrial vertebrate wildlife species' distribution in California. It includes 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. 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/>), 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 300m grids with the categorical resolution that matches the WHR types.

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 USGS topographic quadrangles (used as base maps upon which the historical vegetation patterns were drawn). 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 <10m 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. Previous analysis of registration error of the historical USGS topographic quadrangles in relation to modern digital maps produced a registration error of 263m (Thorne *et al.* 2008), suggesting a final historical map with a minimum mapping unit of 300m. 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 (300m) required the upscaling of the modern map to meet this operational grain size of 300m and to be deemed reliable for comparisons. Therefore both historical and modern vegetation maps were rendered to the same 300m grid. A majority filter was applied to both the historical and the modern vegetation maps to obtain the 300m final grid-based maps. Although the historical maps have some polygons smaller than 300m the generalization primarily sub-sampled the historical map polygons. The modern vegetation maps have 10 times (or more) polygons per area. For these maps, the 300m resolution represents a coarsening of the data. However, in each case, the most prevalent vegetation is assigned to each 300m 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 (Thorne *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.

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 50-70% 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 1km 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 (Crimmins *et al.* 2011, Dobrowski *et al.* 2011). 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 historical 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.

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 generally consisted of 30-40 traps, spaced about 10m from each other, set in a 300-400m line. The vegetation maps' minimum mapping unit was set at 300m. 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 2km 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 variables were being collected at similar scales. We feel assured that the alignment of the two collection methods greatly reduces the potential for a scale effect.

Habitat suitability – We used published California Wildlife Habitat Relationships system rankings of species-habitat suitability to convert historic and modern land cover to habitat suitability values for each target species. This system consists of a set of relational tables that

298 [summarize existing knowledge on species-habitat relationships for California vertebrates. For](#)
299 [each vertebrate species, literature and experts were surveyed to rank the importance of each](#)
300 [WHR type for that specific taxon; ranks varied from 0 \(not suitable\) to 1 \(most suitable\). The](#)
301 [system provides an average or weighted habitat suitability index for each vertebrate species,](#)
302 [calculated from the stage-specific ranks for each WHR type \(low, medium, high\). In addition](#)
303 [three other habitat suitability indexes \(cover, food and reproduction\) are available. We used the](#)
304 [values from the weighted habitat suitability \(Table AII.1.; Appendix II\), and linked them to the](#)
305 [historic and modern land cover maps, and calculated the landscape-level suitability per species](#)
306 [during both time periods.](#)
307 [To accommodate the uncertainty in the geographical positioning of the historical data, we](#)
308 [extracted the WHR ranks for each 2km buffer that represented each aggregate. We then summed](#)
309 [these values and divided them by the number of cells of the habitat map that the buffer included.](#)
310 [We called this metric the standardized Habitat Suitability Index \(HSI\) and used it in the](#)
311 [remaining analyses.](#) ↗

312 ↓↓
313 *Data analysis* – We tested whether HSI values predicted species' presence by using a
314 contingency analysis (χ^2) to see if HSI values were on average significantly higher when a
315 species was present than when it was absent. [Occupancy modeling determined non-detection was](#)
316 [considered as absence.](#) This would indicate whether HSI values could be used to describe
317 species' presence in our study area.

318 To assess whether species and habitat elevation range dynamics were synchronous or not, we
319 estimated habitat displacement [in elevation](#). This metric was calculated as the difference in
320 elevation range of each WHR type between historical and modern time, weighted by its

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Deleted: Mammal species presence data was obtained from Moritz et al. (2008). The results of the occupancy analysis reported in Moritz et al. (2008) were used to select species for the analysis and to describe their elevational range dynamics (Table I).

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Comment [8]: weighted by what?

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Deleted: We used digital versions of the Wieslander (1934) and Calveg (2000) landcover maps (Figure 1). Both maps were resampled 300m spatial resolution to accommodate historic base topographic map location errors (positional error of 48, 72, 83, and 161 m.) (Thorne et al. 2008). We used the California Wildlife Habitat Relationships (WHR) landcover classification scheme (here termed WHR; <http://www.dfg.ca.gov/biogeodata/cwhr/>). The final historical and modern 300m grids were aligned and landcover change measurable on per-grid-cell basis using the WHR classification (for a detailed description of vegetation map production and accuracy assessment see Appendix I). ... [3]

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361 suitability (HSI value) and averaged across all WHR types suitable for each species. The overall
362 value of [habitat elevation](#) displacement ($\Delta_{habitat}$) was estimated as:

363 $\Delta_{habitat} =$
364
$$\left[\sum_{i=1}^N [(max(elev)_m - min(elev)_m) - (max(elev)_h - min(elev)_h)] * HSI_i \right] / N$$
 (Equation
365 1)

366 where i is each of N WHR types suitable to the species, $max(elev)$ and $min(elev)$ correspond to
367 the maximum and minimum elevation at which a given habitat type occurs in either historical (h)
368 or modern (m) times, and HSI for the species comes from Table A1. Maximum and minimum
369 elevations were estimated as the average of the 95% and 5% quantiles of the distribution of
370 elevations at which a given WHR type occurs in each time period. ↓

371 We then plotted the changes of suitable habitat range against the change in species' ranges. The
372 change in species' ranges (Δ_{sp}) was the difference in the species' historical and modern
373 elevational ranges:

374
$$\Delta_{sp} = (max(elev)_m - min(elev)_m) - (max(elev)_h - min(elev)_h) \quad \text{(Equation 2)}$$

375 where $max(elev)$ and $min(elev)$ correspond to the maximum and minimum elevation at which a
376 species occurs in historical (h) or modern (m) times and were estimated as the averages of the
377 95% and 5% quantiles of the distribution of elevations at locations where the species was
378 present. In a plot of changes in habitat ranges against changes in species' ranges, species
379 *tracking habitat* occur in the first and third quadrants of this plot, whereas species *not tracking*
380 *habitat* lie in the second and fourth quadrants (Figure [3](#)).

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Comment [9]: something is wrong with this sentence "There is a possibility that this equation does not account for shifts in habitat range rather than expansions and contractions."

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Comment [10]: What changes? This isn't clear.

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404 We then tested whether the small mammal community showed a non random tracking of habitat
 405 dynamics. We used a contingency test with the counts of species in the 1st and 3rd quadrants –
 406 *tracking species* – against the counts of species in the 2nd and 4th quadrants – *not tracking species*
 407 in Figure 3, against a random prediction from a binomial distribution. We excluded species
 408 whose range dynamics did not change significantly. We expected that if tracking was dominant,
 409 the contingency test would be significant. Next, we used a contingency analysis to test whether
 410 tracking (based on the placement of species in the plot in Figure 3) was affecting species’
 411 systematically; by comparing species that occupy high, intermediate or low elevations; and
 412 species that had shown expansion or contraction in their elevation distribution ranges. We then
 413 tested whether there were range limit specific changes, ie, whether there were different behaviors
 414 at the upper and lower range limits (UL and LL respectively). To do this we modified equations
 415 1 and 2, as in Equations 3 (habitat) and 4 (species) for upper and lower range limits (*L*) in
 416 historic and modern time. We then used a chi-square test to assess whether placement of species
 417 within the plot described in Figure 3 was different from random for both UL and LL.

418
$$\Delta_{habitat_L} = \frac{[\sum_{i=1}^n [(L_m - L_h) * HSI]_i]}{N} \quad \text{(Equation 3)}$$

419
$$\Delta_{sp_L} = (L_m - L_h) \text{(Equation 4)}$$

420 Even if all species track well, some species will likely track habitat changes more closely. To test
 421 this we removed the categorization into tracking and not tracking and created a linear model for
 422 Figure 2. We expected that if tracking was strong, the regression would explain a large proportion of the
 423 deviance, thus have a high R-square, and a significant and positive slope. A significant positive slope
 424 indicates that tracking is more important than not tracking. A slope non-significantly different from zero
 425 suggests equal importance of tracking and not tracking.

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430 Finally, we tested whether species' traits could be related to tracking habitat dynamics using chi-
431 square tests. We assembled information on species' traits from the PanTHERIA database (Jones
432 *et al.* 2009) or from the data published in Moritz *et al.* (2008), which included their relatedness
433 (Genus), behavior (home range size and terrestriality), circadian and annual activity (annual
434 rhythm, activity cycle), physiology (metabolic rate), biometrics (weight, longevity), diet guild,
435 reproduction (litters per year, gestation length, litter size, neonatal weight, young per year).

436 Descriptions of each trait and trait values are detailed in Appendix III. [Because of the number of](#)
437 [comparisons performed we applied a Bonferroni correction to the significance level.](#)

438 **Results**

439 *Land cover changes along the Yosemite Transect*

440 In the Yosemite transect there are 33 land cover types (Figure 1). The dominant land cover type
441 in historical time was ponderosa pine (412.7 km², 12% of the transect area), followed by
442 lodgepole pine (354.7 km², 11%), and annual grasslands (336.2 km², 10%). In contemporary
443 time, Sierran mixed conifer and annual grasslands are co-dominant (SMC: 519.6 km²; AGS:
444 517.8 km²; both 15%). From 1930s to 2000s, the land cover that increased most was Sierra
445 Mixed Conifer (from 17.4 to 519.6 km²; Figure 1c), at the expense of decreases mainly in
446 Ponderosa pine (from 412.7 to 116 km²) and white fir (from 140.4 to 5.2 km²; Figure 1d). Other
447 relevant transitions are the increase in mountain hardwood from 95.8 to 264.3 km², and the
448 decrease in chamise-redshank chaparral from 278.1 to 1.5 km², blue oak woodlands from 196.7
449 to 24.6 km², and barren areas from 228.6 to 1.6 km² (Figure 1d).

450 *Test of HSI for species' presence*

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Comment [11]: If you re-surveyed this right now (or at the same time as the later survey), how much change do you think you would see? In other words, what is the null expectation for changes in these habitat types, if nothing had really changed?

452 For eighteen (out of 23) species, Habitat Suitability Index (HSI) values were significantly higher
453 in locations where the species was present than in locations where the species was absent (Table
454 2). On average, modern HSI values were less different between presence and absence locations
455 (15 out of 23, 61%) than in historical times (18 out of 23, 74%). This suggests the HSI values
456 can be used to assess species' responses to changes in land cover over time.

457 *Tracking habitat changes*

458 Of the 23 species analyzed, 9 contracted, 6 expanded, and 8 showed no changes in their
459 elevational distribution ranges. Eleven out of 23 species (48%) tracked habitat elevation range
460 shifts (Figure 4), and the number of species exhibiting habitat tracking was not significantly
461 different from random ($\chi^2=0.08$, P-value=0.78).

462 All mammal species that significantly expanded their elevation range tracked the expansion of
463 their habitat's elevation range (black triangles in Figure 4a and 5a; $R^2=0.20$, $F_{1,21}=5.15$, P -value-
464 =0.03). Only three (out of 9) species that significantly contracted their elevation range tracked
465 the contraction of their habitat elevation range (third quadrant Figure 4a; *C. lateralis*, *S.*
466 *palustris*, and *T. senex*; for an assessment of potential confounding effects see Appendix III).

467 Range limits showed a similar pattern, with expanding species' lower and upper limit following
468 the limits of the habitat range (Figures 4b and 4c). Contracting species, on the other hand, seem
469 to be at odds with both habitat elevation range limits; where the habitat limit goes down the
470 species limit goes up and vice-versa being this difference more marked for the lower limit
471 (Figures 4b and 4c). These differences were only significant for upper range limits (lower:
472 Figure 5b; $R^2=0.04$, $F_{1,21}=0.78$, P -value=0.39; upper: Figure 5c; $R^2=0.18$, $F_{1,21}=4.48$, P -value=0.04).

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Comment [12]: I don't understand this sentence.

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Deleted:), with the exception of *O. beecheyi*, *T. senex*, and *P. maniculatus*

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Comment [13]: "for simplicity, however, we state tracking or not tracking as referring to elevation dynamics" - please don't do this, but rather be specific in your references. It will significantly help the reader.

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Deleted: Habitat tracking was not significantly different from random ($\chi^2=0.08$, P-value=0.78), excluding species that showed no significant changes in their elevation ranges. However, we found that there were significantly more expanding species that tracked habitat elevation range and that more contracting species did not track habitat elevation range ($\chi^2=3.86$, P-value=0.04).

496 Further, species that inhabited low and intermediate elevations tracked habitat significantly more
497 than species that inhabit high elevations (Figure 6a; $\chi^2=6.52$, $P\text{-value}=0.04$). Tracking only
498 species showed the same pattern (range: Figure 6b; $R^2=0.32$, $F_{2,8}=1.97$, $P\text{-value}=0.05$; lower: Figure
499 6c; $R^2=0.02$, $F_{2,8}=0.08$, $P\text{-value}=0.93$; upper: Figure 6d; $R^2=0.38$, $F_{2,8}=2.44$, $P\text{-value}=0.02$).

500 Tracking habitat changes – tracking closely

501 About 50% of the species tracked well habitat changes; however, species did not track habitat
502 changes closely. The regression explained little variance within the data set ($R^2=0.07$) and slope of
503 the regression was not significantly different from zero ($F_{1,21}=1.586$, $P\text{-value}=0.22$). Regression for the
504 upper and lower limits also (Lower: $R^2=0.02$, $F_{1,21}=1.586$, $P\text{-value}=0.22$; Upper: $R^2=0.06$, $F_{1,21}=1.372$, $P\text{-$
505 value=0.25).

506 Species' traits

507 From the suite of species' traits, only diet guild showed a significant effect on species' ability to
508 track their habitat (Table 3). Species tracking habitat dynamics were omnivorous, whereas
509 species that did not track habitat dynamics were mostly herbivorous. Genus, adult body mass and
510 neonatal body mass traits were only significant prior to the application of the Bonferroni
511 correction.

513 **Discussion**

514 Our main goal was to assess whether changes in habitat elevation range could explain the
515 observed shifts of small mammals' elevational ranges. Our results illustrate multiple responses to
516 habitat dynamics by the assemblage of small mammals in Yosemite National Park. Half of the

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Comment [14]: add results – means and ranges

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Comment [15]: This does not show the size or direction of the effect, or what the differences among the 3 elevational classes were. At least means and ranges would help. This may not be much of an effect. Subtle and drastic effects are measured by effect sizes, not significant differences.

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Comment [16]: Add something about

this MS gets at the issue of how a species' climatic requirements (as reflected in elevation) and its food/shelter requirements (as presumably captured by the vegetation types) may not shift together as climate changes. There can be historical processes (e.g. fire) and lag effects (e.g. long-lived trees) that cause this decoupling. I think that more should be made into more of an explicit theme in the MS.

531 species tracked habitat range changes, where both habitat and species' range expanded or
532 contracted synchronously. The other half of the species did not track habitat range changes,
533 where species and habitat range dynamics were asynchronous. The partition into species that
534 tracked and did not track habitat dynamics differed both by elevation range and by species' range
535 dynamics. Species that tracked habitat tended to occupy low and intermediate elevations and
536 their elevation range significantly expanded in the last 80 years. Conversely, species that did not
537 track habitat dynamics tended to occupy high elevations and their range contracted.

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538 While ecology aims to find a generalized response of communities to habitat dynamics,
539 individual species responses may also play a key role. Our results analyzing only one axis of
540 variation of a species niche (habitat), show a strong signal with half the mammal species
541 responding to changes in habitat, especially as this group includes species from many different
542 genera (*Sorex*, *Otospermophilus*, *Callospermophilus*, *Tamias*, *Chaetodipus*, *Peromyscus*,
543 *Reithrodonthomys*) and a varied suite of traits (Appendix II). This concerted response is a
544 function of a major change in habitat composition, specifically the expansion in Sierra mixed
545 conifer (SMC) which has been documented in the Sierra Nevada over this time period (Thorne *et*
546 *al.* 2008). For most of the species that we analyzed, the greatest contribution to the measured
547 changes in habitat range are due to changes in the availability of SMC (see Appendix II for the
548 HSI per land cover type). This explains why in Figure 4 most species showed positive habitat
549 changes (x axis). These results are consistent when using just the most suitable habitats
550 (HSI>0.5; Appendix III) and no scale effect was observed.

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551 Sierran mixed conifer (SMC) is an ensemble of five conifer species: white fir (*Abies concolor*),
552 Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus*
553 *lambertiana*), incense cedar (*Calocedrus decurrens*), and the California black oak (*Quercus*

571 *kelloggii*). SMC has replaced the adjacent natural vegetation communities at both lower and
572 higher elevations. At lower elevations and under a regular fire regime, the landscape would be
573 dominated by ponderosa pine (PPN), and white fir would be prevented from reaching the
574 canopy; however, fire suppression in mid-20th century and fire restoration in 1970's (Bill Kuhn
575 *personal comment*) have allowed white fir to reach the canopy leading to vegetation transition
576 from PPN to SMC (Thorne et al. 2008, Collins et al. 2011). Most of the small mammal species
577 inhabiting lower elevations tracked the dynamics of their habitat. Specifically, *T.*
578 *quadrifasciatus* is a conifer habitat specialist, inhabiting denser forests (Clawson et al. 1994b);
579 *O. beecheyi* and *P. boylii* are found in a variety of habitats including SMC and therefore may be
580 benefiting from the downward expansion of the SMC. For *T. senex*, there was a contraction in
581 both its habitat and distribution ranges. At higher elevations, tree density of SMC has increased
582 after the alteration of the fire regime (Collins et al. 2011) and encroachment of meadows by trees
583 (Vale 1987). These may reduce open areas and affect species that require heavy debris areas with
584 high herbaceous cover, and fallen logs and shrubs, such as *S. monticolus* (Smith and Belk 1996),
585 or riparian species, such as *S. palustris* (Beneski and Stinson 1987).

586 Species' traits may affect how they respond to their habitat dynamics. From the suite of traits
587 that we tested, we found only significant effects of diet guild on species' ability to track their
588 habitat(s). We found significantly more omnivore species tracking and herbivores not tracking
589 their habitat dynamics. Being an omnivore ensures a wider variety of food options that can be
590 used as the species uses more the current habitats or expands into new ones. This categorization
591 into dietary guild corresponds to other findings of dietary niche breadth (Angert et al. 2011). As
592 habitat patterns change on the landscape, it is likely that species with a less specialized diet will
593 be favored, as they can take advantage of resources provided by the changing habitats. We also

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601 found that herbivores generally did not track habitat dynamics likely because these species use
602 mostly herbaceous dominated habitats, such as open areas [*M. californicus*, *M. longicaudus*
603 (Smolen and Keller 1987), and *S. trowbridgii* (George 1989)], meadows [*U. beldingi* (Jenkins
604 and Eshelman 1984), and *M. montanus* (Sera and Early 2003)], riparian (*Z. princeps* (Hart *et al.*
605 | 2004)), and open talus slopes (*T. alpinus* (Clawson *et al.* 1994a)).

606 Three potential explanations can be advanced for why species did not track habitat range
607 changes. First, species may be responding to other pressures such as direct effects of climate
608 change (Chen *et al.* 2011), altered species interactions (Tylianakis *et al.* 2008), or could show
609 evolutionary adaptation (Atkins and Travis 2010) and exhibit behavioral plasticity (Knowlton
610 | and Graham 2010). However, if species were not responding to habitat, we would expect HSI not
611 to be a good predictor of species presence. This was only the case for *P. maniculatus*, a habitat
612 | generalist species (*P. maniculatus* can use 30 of the 31 WHR types, Appendix II). Two other
613 species, *O. beecheyi* and *T. senex*, showed no significant differences in HSI values in modern
614 absence and presence locations. *O. beecheyi* did not change its distribution range and little
615 changes were observed in its habitat; *T. senex* was only recorded at one trapping location in the
616 modern time. Because only a few species showed no differences in HSI values and presence, and
617 for most of those just in one era, it suggests that species presence is a function of habitat.
618 Secondly, HSI did not represent all of the possible habitats a species could occur in. For
619 example, barren (BAR) lands include the rock talus where *T. alpinus* (Clawson *et al.* 1994a,
620 Rubidge *et al.* 2011) and *N. cinerea* (Smith 1997) occur; however, BAR was not listed in the
621 | WHR rankings for these species and this land cover showed a major decrease in the study area
622 (Figure 1). This does not undermine the value of the HSI, but instead, reinforces the importance
623 of a periodic review of their values in light of the newest literature on each species, and, the

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Deleted: This is also linked to finding a 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 off-spring and matches the higher proportion of "r-selected" species among those with range expansion reported in Moritz *et al.* (2008).

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635 possibility that habitat suitability values may change over time (see below). Thirdly, we were
636 unable to measure the characteristic(s) of the habitat to which species are responding. Habitat as
637 a component of a species' niche can be measured in a wide variety of ways (Godsoe 2010), and
638 not necessarily all species will respond to the same metrics. We used a change detection analysis
639 of habitat (or land cover types) as the predictor for range dynamics of vertebrates. The land cover
640 maps used may have questionable classification accuracy, errors in georeferencing, and the
641 crosswalk between the historical and the modern maps may contain errors. We believe, however,
642 that these errors are negligible in our analysis as similar transitions as those we describe were
643 documented from both vegetation map and concurrent plot data (Thorne et al. 2008, Collins et al.
644 2011, Crimmins et al. 2011), which provide an independent validation of the changes measured
645 using the land cover maps. The thematic resolution (WHR types) used in this analysis was
646 selected because it was linked to wildlife-habitats; however, some land cover classes (meadows,
647 riparian areas, etc.) may be diluted when represented at a spatial resolution of 300m. Changes in
648 both these land cover types known to occur in Yosemite (Vale 1987) are likely imperceptible at
649 the spatial resolution of our land cover map, and at the scale of the aggregates where species
650 were trapped. This may explain why meadow specialists like *U. beldingi* (Jenkins and Eshelman
651 1984) and *M. montanus* (Sera and Early 2003) and riparian species as *Z. princeps* (Hart et al.
652 2004) did not track habitat dynamics. Further, WHR change detection did not measure increase
653 in density in SMC (Collins et al. 2011) and the change in forest structure (Mantgem and
654 Stephenson 2007, Lutz et al. 2009), to which species like *S. trowbridgii* (George 1989) or *T.*
655 *speciosus* (Best et al. 1994) are likely to respond.

656 Assessing species' ability to track changes in their habitat over time is crucial as we use trends in
657 species' responses to environmental parameters to identify which species are at risk, and to

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1)

660 predict their responses to future conditions. Our results show idiosyncratic responses of species
661 in relation to shifts in habitat in the Yosemite transect, however, with a strong pattern by
662 inhabited elevation range and its dynamics. The results presented here suggest the dynamics of
663 species that expanded their range are more easily understood by habitat changes than those that
664 contracted. The next steps should integrate all of these components, and include other factors
665 such as species interactions, diseases, and population dynamics. Only an integrated and holistic
666 assessment of species responses to multiple factors may shed light towards our understanding of
667 range dynamics and improve predictions of future responses.

668

669 **Acknowledgements**

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671 program. We are thankful to the Museum of Vertebrate Zoology at the University of California
672 Berkeley and the Grinnell Resurvey project for the mammal data; to the Information Center for
673 the Environment the University of California Davis for the historical (Wieslander Vegetation
674 Type mapping project) and modern (CalVeg integration with Yosemite National Park vegetation
675 map) land cover maps and crosswalk to Wildlife Habitat Relationship types. Special thanks are
676 due to Adam Smith for his insights in the analysis.

677

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794 | **Figure 1.** Study area location and changes in WHR land cover types in the Yosemite transect: (a)
795 | location of the Yosemite transect in California and the outline of Yosemite National Park (YNP);
796 | (b) Yosemite transect with colors depicting different elevation life zones (*sensu* Merriam's life
797 | zones) and outline of YNP; (c) Historical (1930's) and modern (2000's) land cover in the
798 | Yosemite transect; and (d) change in area (km²) covered by each WHR type from historical to
799 | modern time and blue bars represent loss and red bars increase (AGR –Agriculture, AGS –
800 | Annual Grasslands, ASP – Aspen, BAR – Barren, BOW – Blue oak woodland, BOP – Blue oak-
801 | foothill pine, CRC – Chamise-redshank chaparral, CPC – Closed-cone pine-cypress, DFR –
802 | Douglas fir, EPN – East side pine, FEW – Freshwater emergent wetland, JPN – Jeffrey pine,
803 | JUN – Juniper, LAC – Lacustrine, LPN – Lodgepole pine, MCH – Mixed Chaparral, MCP –
804 | Montane Chaparral, MHW – Montane Hardwood, MHC – Montane hardwood-conifer, MRI –
805 | Montane riparian, PJN – Pinyon-juniper, PPN – Ponderosa pine, RFR – Red fir, SMC – Sierran
806 | Mixed-conifer, SCN – Sub-alpine Conifer, URB – Urban, VRI – Valley Foothill riparian, VOW
807 | – Valley Oak woodland, WTM – Wet meadows, WFR – White fir).

808 | **Figure 2.** [Images of \(a\) Joseph Grinnell's field note books with the annotations of the trapping](#)
809 | [records, \(b\) the hand drawn maps of the trapping locations, and \(c\) Wieslander maps.](#)

810 | **Figure 3.** Plot of changes in habitat elevation range axis (x axis) against the changes in species
811 | elevation range (y axis). Habitat tracking occurs when species are placed in the 1st and 3rd
812 | quadrants of this plot, whereas species that did not track their habitat are placed in the second
813 | and fourth quadrants.

814 | **Figure 4.** Changes in species' and habitat range change: (a) full range, (b) lower limit and (c)
815 | [upper limit](#). The x axis represents changes in habitat elevation ranges (positive values: increase

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818 in habitat elevation range, negative values: decrease in habitat elevation range), the y axis
819 represents changes in species elevation range (positive values: increase species elevation range;
820 negative values: decrease species elevation range). Black triangles indicate species that have
821 significantly expanded their elevation range, white triangles indicate species that have
822 significantly contracted their elevation range, and white circles indicate species that have did not
823 change their elevation range. Eleven out of 23 species (48%) track habitat in elevation. Species
824 names are coded to the three first letters of their genus and scientific names.

825 [Figure 5. Box plots for species tracking and not tracking \(a\) range, \(b\) lower limit, and \(c\) upper](#)
826 [limit.](#)

827 [Figure 6. Species inhabited range and range changes: \(a\) average range change, \(b\) range change](#)
828 [in tracking only species, \(c\) lower limit in tracking only species, and \(d\) upper limit in tracking](#)
829 [only species.](#)

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Yosemite transect

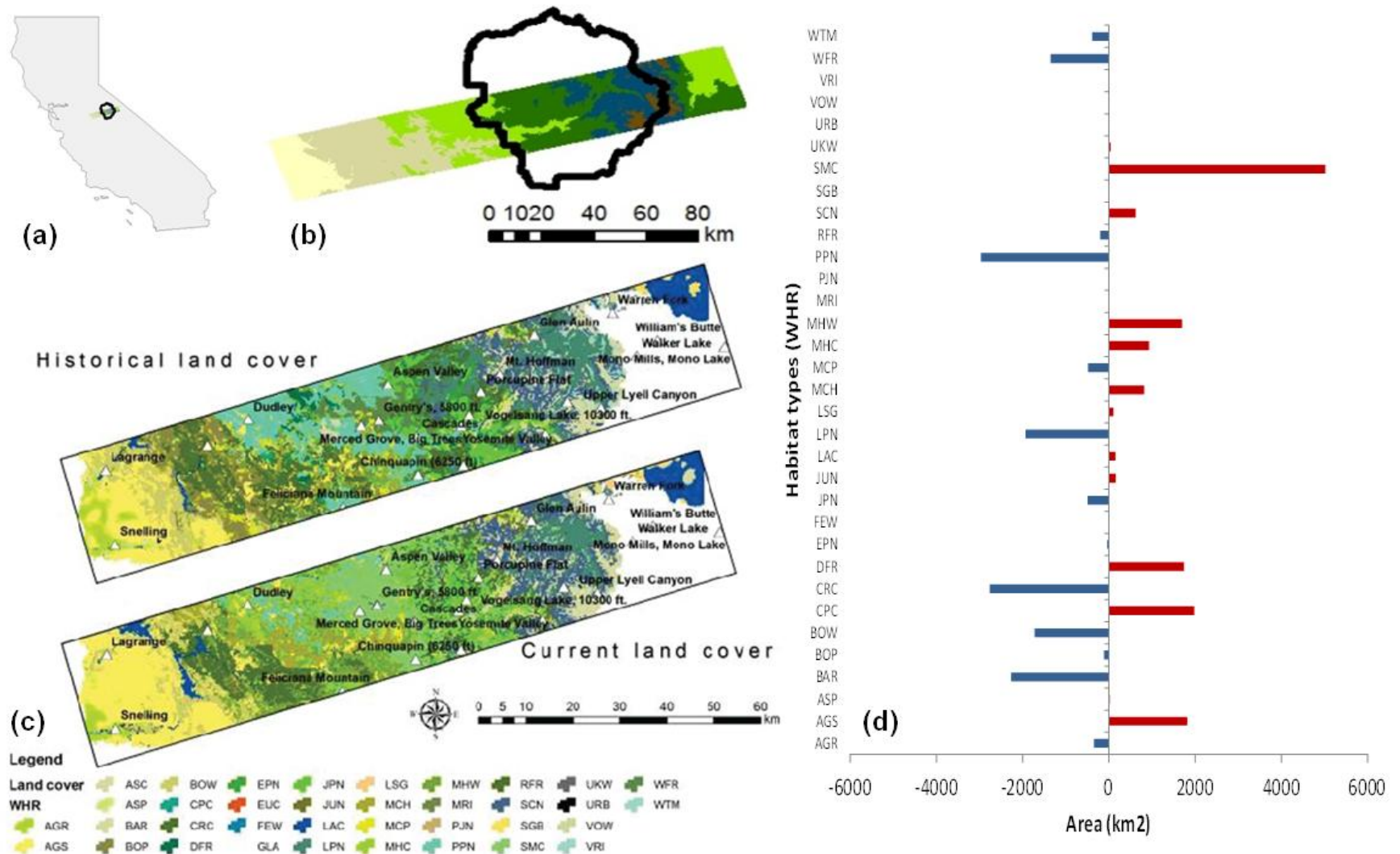


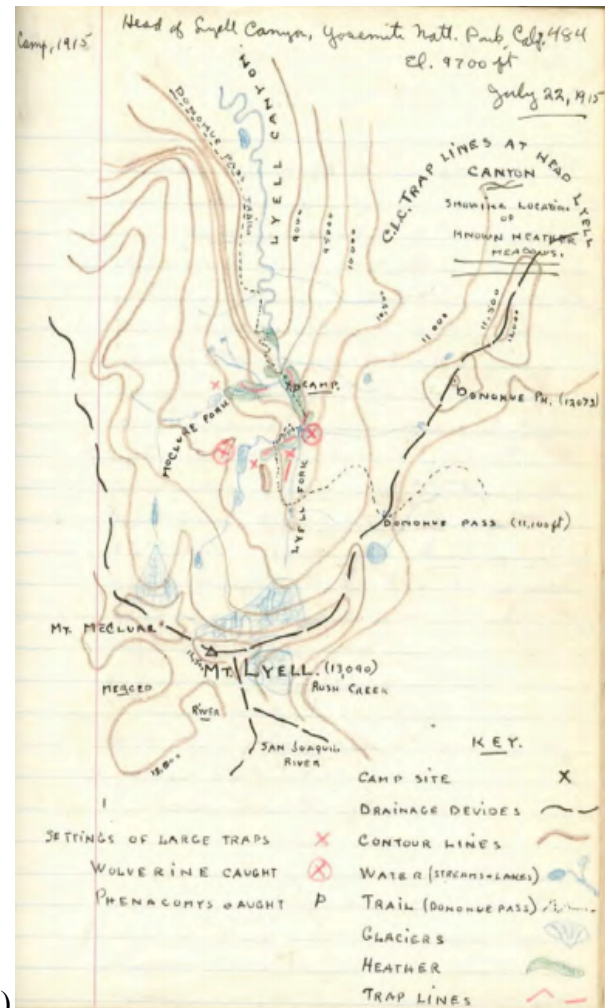
Figure 1.

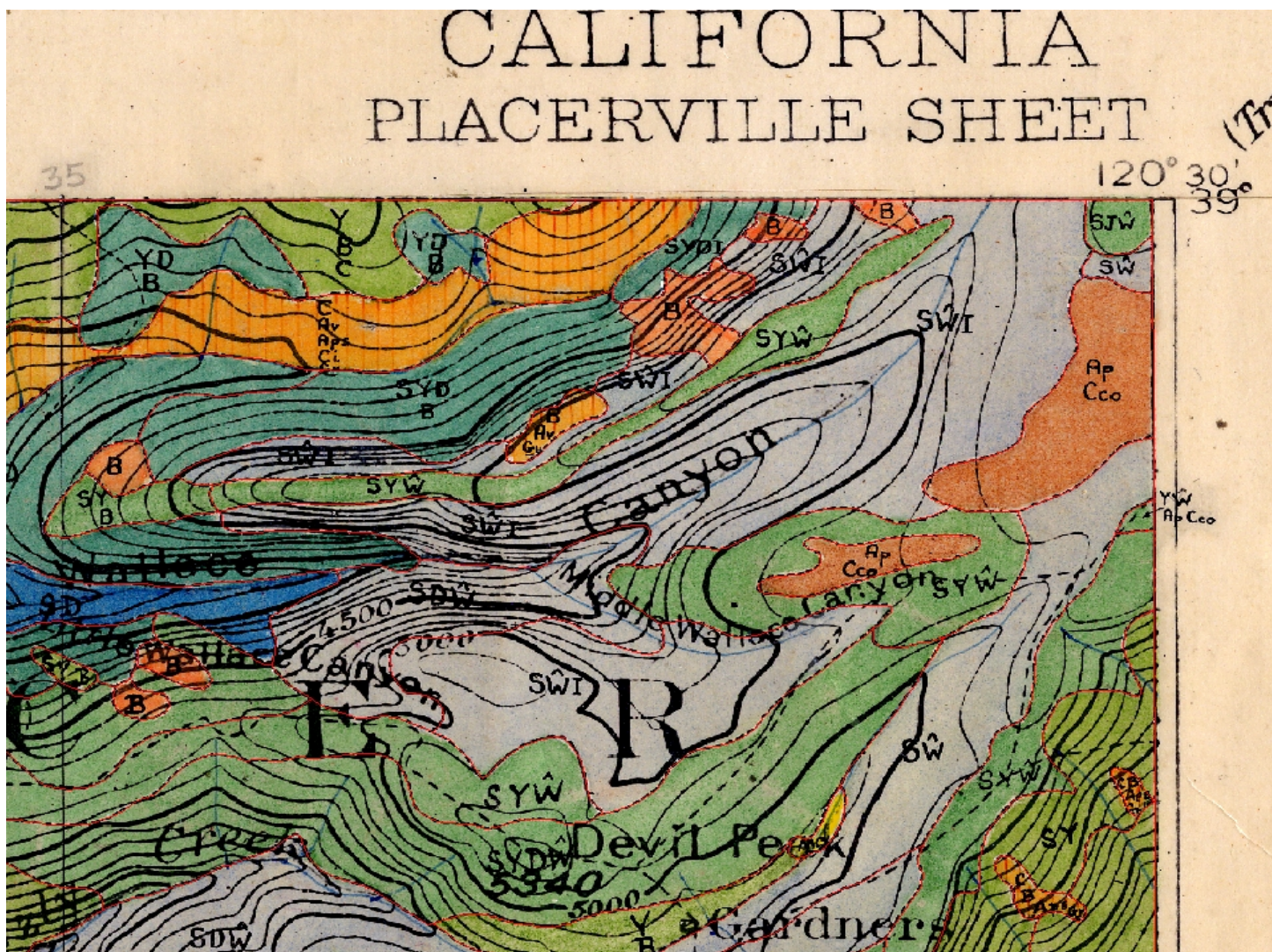
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Yosemite
July 30

3433 *Neotoma f. streatoni* ♀ 378x180x35x26

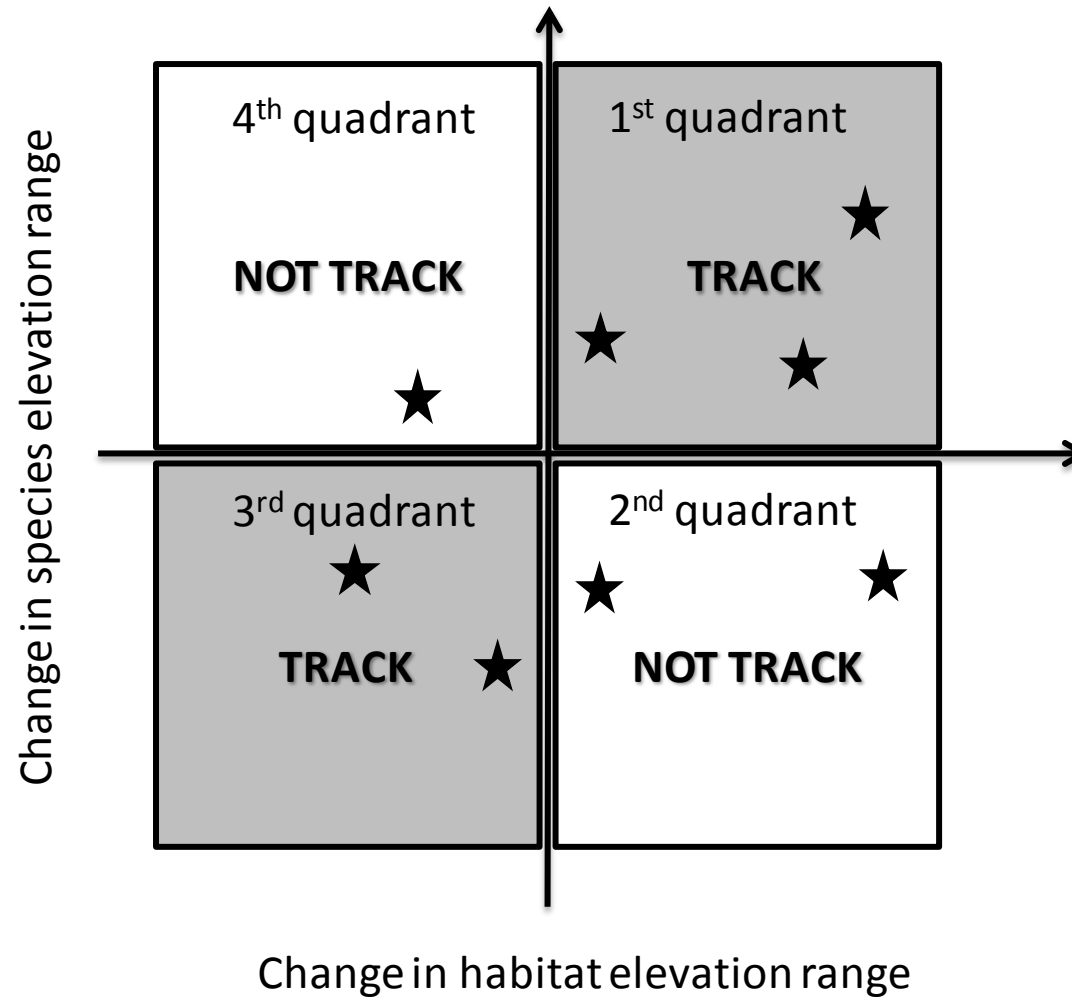
The line of 24 rat traps set up the boulder cone below Rocky Point, primarily for chipmunks as previously described, produced this morning: 1 Wood rat as above; 7 *Peromyscus boylii* 2 ♀♀ 6 ♂♂, all adults, the latter with very large testes, one of the ♀♀ with three embryos. The 24 traps were all in exactly same kind of ground namely steep piles of boulders along





2 (c)

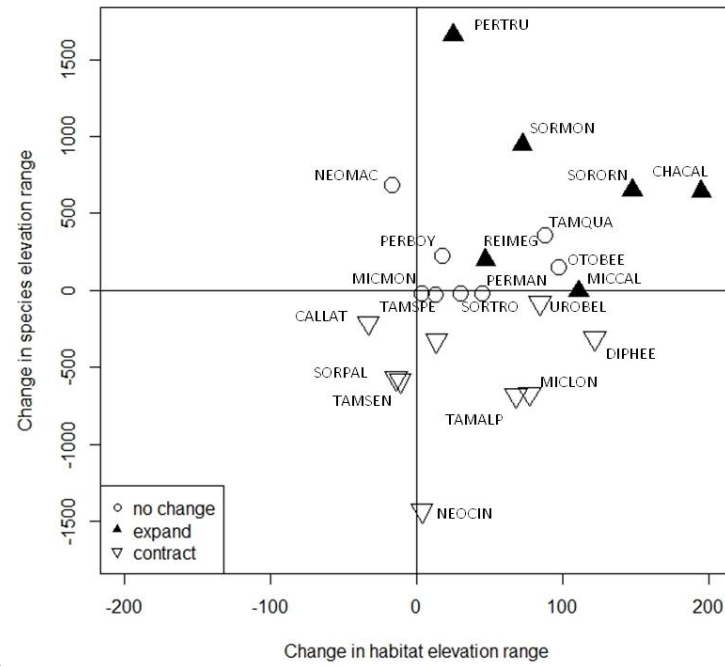
3 Figure 2.



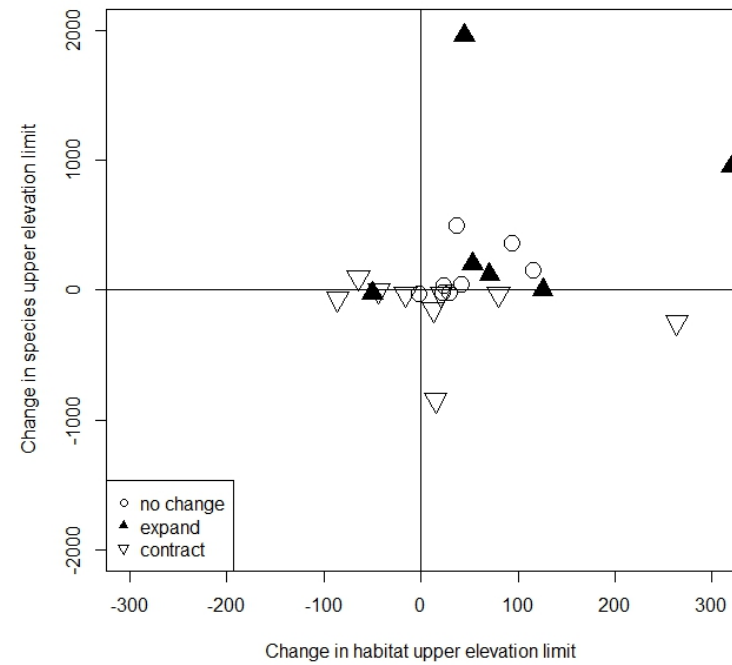
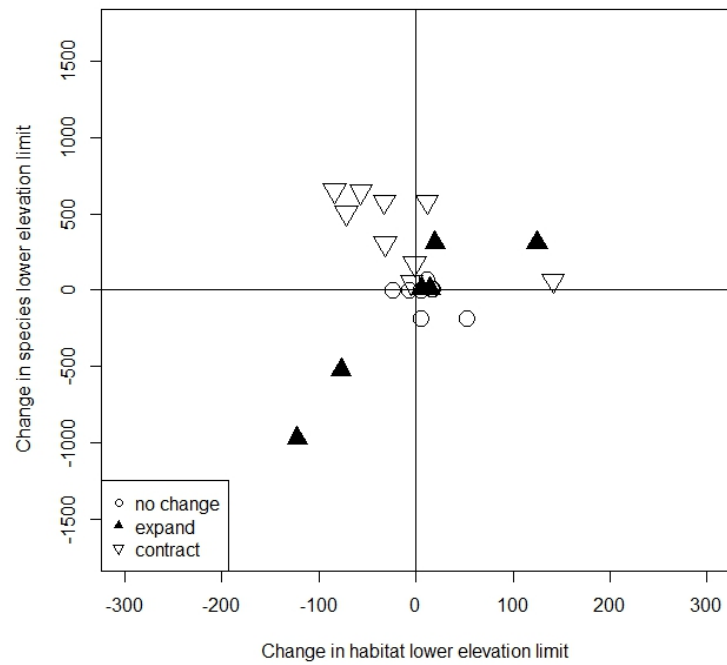
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2 **Figure 3.**

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(a)

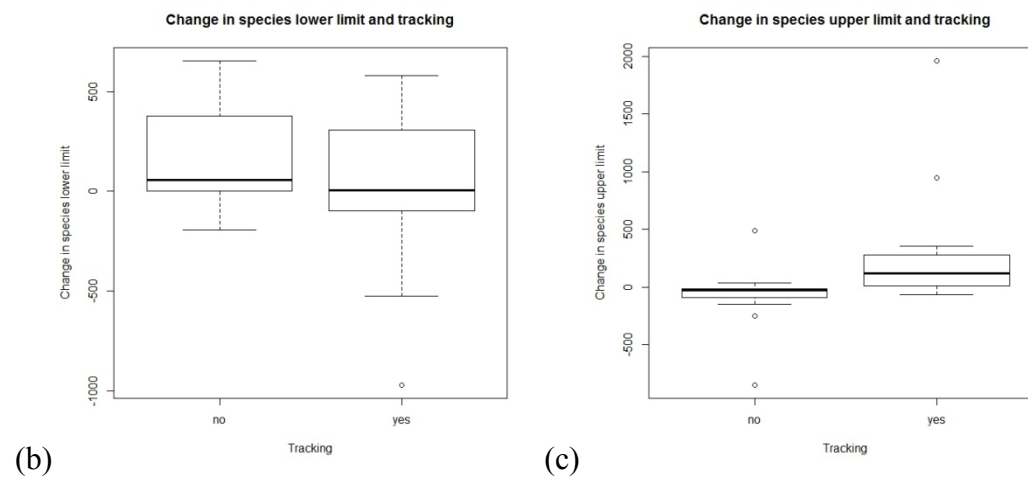
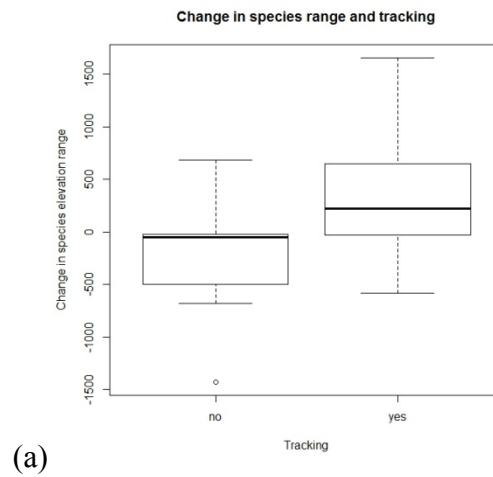


2 (b)

3 **Figure 4.**

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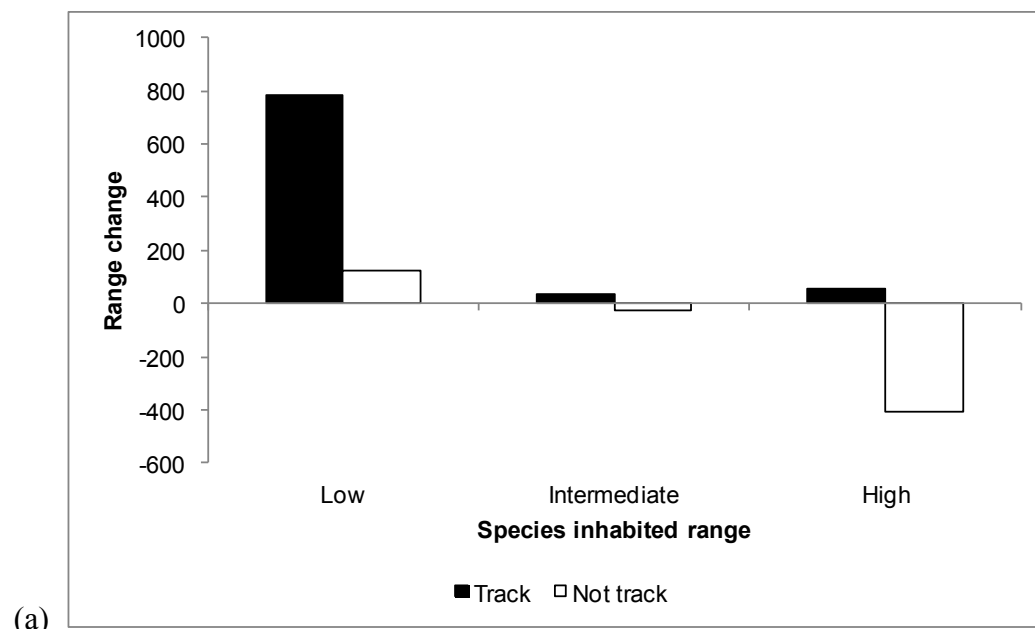


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3 **Figure 5.**

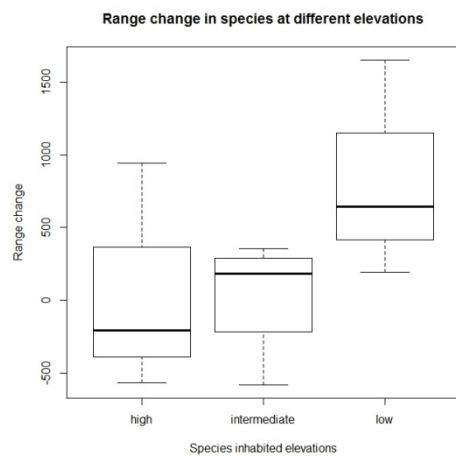
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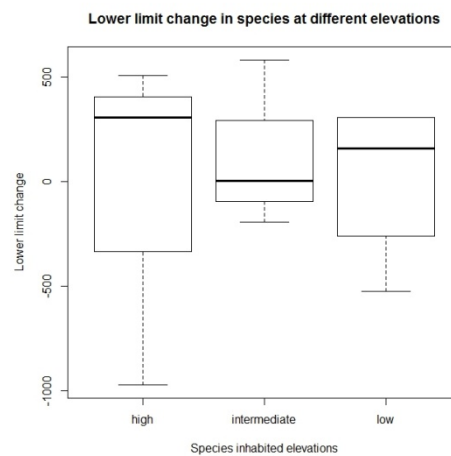


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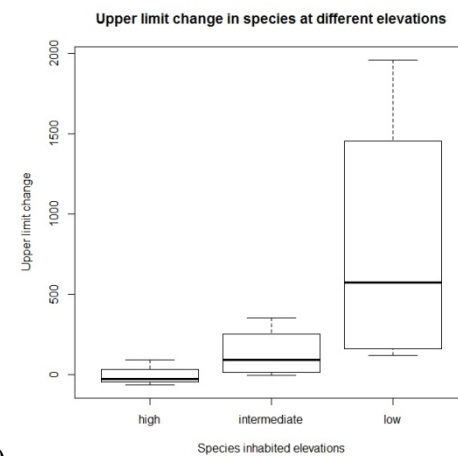
(b)



(c)



(d)



3 **Figure 6.**

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

				Elevation
Order	Family	Species	Range	range
Insectivora	Soricidae	<i>Sorex monticolus</i>	Expand	High
Insectivora	Soricidae	<i>Sorex ornatus</i>	Expand	Low
Insectivora	Soricidae	<i>Sorex palustris</i>	Contract	High
Insectivora	Soricidae	<i>Sorex trowbridgii</i>	No change	Intermediate
		<i>Otospermophilus</i>	No change	Intermediate
Rodentia	Sciuridae	<i>beecheyi</i>		
Rodentia	Sciuridae	<i>Urocitellus beldingi</i>	Contract	High
		<i>Callospermophilus</i>	Contract	High
Rodentia	Sciuridae	<i>lateralis</i>		
Rodentia	Sciuridae	<i>Tamias alpinus</i>	Contract	High
Rodentia	Sciuridae	<i>Tamias quadrimaculatus</i>	No change	Intermediate
Rodentia	Sciuridae	<i>Tamias senex</i>	Contract	Intermediate
Rodentia	Sciuridae	<i>Tamias speciosus</i>	No change	High
Rodentia	Heteromyidae	<i>Chaetodipus californicus</i>	Expand	Low
Rodentia	Heteromyidae	<i>Dipodomys heermanni</i>	Contract	Low
Rodentia	Cricetidae	<i>Neotoma cinerea</i>	Contract	High
Rodentia	Cricetidae	<i>Neotoma macrotis</i>	No change	Low
Rodentia	Cricetidae	<i>Peromyscus boylii</i>	No change	Intermediate
Rodentia	Cricetidae	<i>Peromyscus maniculatus</i>	No change	All

Rodentia	Cricetidae	<i>Peromyscus truei</i>	Expand	Low
		<i>Reithrodontomys</i>	Expand	Low
Rodentia	Cricetidae	<i>megalotis</i>		
Rodentia	Cricetidae	<i>Microtus californicus</i>	Expand	Low
Rodentia	Cricetidae	<i>Microtus longicaudus</i>	Contract	High
Rodentia	Cricetidae	<i>Microtus montanus</i>	No change	High
Rodentia	Dipodidae	<i>Zapus princeps</i>	Contract	High

1 **Table 2.** Contingency test of the effect of HSI values on species presence. Bold values represent
2 significantly higher HSI values in locations where the species was present.

	Historical		Modern	
	χ^2	P-value	χ^2	P-value
<i>Sorex monticolus</i>	9.88	0.002	4.69	0.03
<i>Sorex ornatus</i>	1.72	0.19	3.81	0.05
<i>Sorex palustris</i>	8.4	0.004	0.21	0.65
<i>Sorex trowbridgii</i>	6.25	0.01	10.91	0.001
<i>Uroditellus beldingi</i>	7.08	0.008	13.79	0.0002
<i>Callospermophilus lateralis</i>	4.23	0.04	0.32	0.57
<i>Otospermophilus beecheyi</i>	0.09	0.76	0.08	0.77
<i>Tamias alpinus</i>	25.11	0.0001	13.74	0.0002
<i>Tamias quadrimaculatus</i>	7.47	0.006	10.83	0.001
<i>Tamias senex</i>	3.49	0.06	0.62	0.43
<i>Tamias speciosus</i>	15.48	0.0001	11.3	0.0008
<i>Dipodomys heermanni</i>	4.86	0.028	1.55	0.21
<i>Chaetodipus californicus</i>	8.59	0.0034	4.89	0.03
<i>Neotoma cinerea</i>	4.49	0.03	0.97	0.32
<i>Neotoma macrotis</i>	8.81	0.003	17.23	0.0001
<i>Peromyscus boylii</i>	2.63	0.11	16.26	0.0001
<i>Peromyscus maniculatus</i>	0.032	0.86	0.71	0.39
<i>Peromyscus truei</i>	4.4	0.03	4.97	0.03
<i>Reithrodontomys megalotis</i>	14.02	0.0002	14.6	0.0001

<i>Microtus californicus</i>	8.14	0.004	7.64	0.006
<i>Microtus longicaudus</i>	4.69	0.03	3.77	0.05
<i>Microtus montanus</i>	6.69	0.009	2.1	0.15
<i>Zapus princeps</i>	9.33	0.0023	6.73	0.009

1 **Table 3.** Species traits effect on species tracking or not tracking habitat in elevation. Bold values
2 are significant differences (Bonferroni corrected P -value<0.01).

Trait	Track	Not track	χ^2	P-value
Genus	<i>Sorex</i>	<i>Microtus</i>	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