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Vegetation characteristics and small mammal traits mediate community response to fire severity

A thesis submitted in partial satisfaction of the

requirements for the degree Master of Arts in Ecology, Evolution and Marine Biology

by

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June 2022

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ABSTRACT

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The frequency of high-severity "mega-fires" has increased in recent decades, with numerous consequences for forest ecosystems. In particular, small mammal communities are not only vulnerable to post-fire shifts in resource availability, but also play a critical role in forest function. Inconsistencies in prior observations of small mammal community response to fire severity underscore the importance of examining mechanisms regulating fire severity effects on post-fire recovery. Here, we compare small mammal abundance, diversity, and community structure among habitats burned at varying fire severity, and use vegetation characteristics and small mammal functional traits to predict community response to fire severity. We captured 544 small mammals at 27 sites in three fire severity categories (unburned, low-moderate severity, and high severity) three years after a mega-fire in the California Sierra Nevada. We measured five vegetation variables known to predict small mammal communities, and determined three small mammal functional traits associated with resource use for the captured species. Using a model-based fourth-corner analysis, we examined how interactions between vegetation variables and small mammal traits regulated post-fire small mammal community structure among fire severity categories. We found that overall small mammal abundance remained similar after fire, although diversity decreased and community structure shifted. Differences between unburned and low/moderate-severity sites were generally minimal while differences between unburned and high-severity sites were large. Three highly correlated fire-dependent vegetation variables (density of live trees, percent litter cover, and percent shrub cover) as well as volume of soft coarse woody debris were most associated with small mammal community structure. Furthermore, we found that interactions between these vegetation variables and three small mammal resource-use traits (feeding guild, primary foraging mode, and primary nesting habit) successfully predicted community structure among fire severity categories. We conclude that resource use is likely important for regulating post-fire small mammal recovery, since vegetation provides necessary resources to small mammals as determined by their functional traits.

- Given the mechanistic nature of our analyses, these results can be applied to other fire-prone forest systems.
- We suggest using these results to inform management decisions about fire severity.

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Introduction

The world is burning at an alarming rate. Across western North America, wildfires in various ecosystems have become larger and more frequent over the past three decades (Abatzoglou & Williams, 2016; Schoennagel et al., 2017; S. L. Stephens et al., 2014; Yue et al., 2013). In California alone, the 2020 wildfire season accounted for five of the largest wildfires on record, often termed “mega-fires” owing to their severity and extent. Yet despite the strong potential for these shifts to affect vertebrate communities, we have limited information on how vertebrate wildlife is affected by changes in forest fire size and severity, much less the mechanisms that drive these effects and how they may vary across functional groups. Recent reviews highlight the need to prioritize research on the mechanisms driving post-fire community shifts in order to tease apart variation across species and fire regimes (Driscoll et al., 2010; Griffiths & Brook, 2014). In particular, determining the effects of fire severity on forest vertebrates is critical both because of needs for their conservation and for the many roles they play in regulating plant communities, forest regeneration, trophic structure, and other ecosystem functions (Morrison et al., 2012). Specifically, studies on high-severity fire effects on mammals are needed; a recent meta-analysis on fire-prone forests of the US found only two studies of high-severity fire impacts on small mammals, despite the roles that small mammals play in forest ecosystems (Fontaine & Kennedy, 2012).

Small mammals are critical for the function of forest ecosystems, including mixed conifer forests. Small mammals can modify the structure of forest vegetation through seed predation and dispersal (Briggs et al., 2009; Schnurr et al., 2004; Vander Wall, 2008), and are key agents for the dispersal of ectomycorrhizal fungi (Pyare & Longland, 2001). In addition, small mammals constitute food for predators, including rare North American species such as the Spotted Owl (*Strix occidentalis*) and Pacific fisher (*Pekania pennanti*) (Carey et al., 1992; Zielinski & Duncan, 2004), and serve as vectors or hosts for multiple pathogens (Ecke et al., 2019; Ostfeld et al., 2018; P. R. Stephens et al., 2016). Given the roles that small mammals play in forests, it is important to delineate the effects of fire severity on their community structure and function (Kirkman et al., 2013).

In general, small mammal community structure shifts after wildfire, although the observed patterns are often inconsistent. Fire can decrease small mammal diversity by favoring generalist species over specialists (Zwolak & Foresman, 2007), but a post-fire decrease in diversity is not always observed (Roberts et al., 2015). Total small mammal abundance tends to be slightly higher in burned habitats (Griffiths & Brook, 2014), but observed abundance patterns are highly variable across systems (Borchert et al., 2014; Converse, Block, et al., 2006; Fisher & Wilkinson, 2005).

Some of these discrepancies may be due to differences in fire severity, which is a measure of the loss of organic material due to fire in a given area. High-severity fire is characterized by a scorched canopy, severe loss of organic matter aboveground and belowground, and a large reduction in plant biomass (Keeley, 2009). Data from birds suggest that high-severity fires often elicit stronger wildlife responses than less severe fires (Fontaine & Kennedy, 2012; Pastro et al., 2014), although responses often depend on time since fire. Bats seem to show greater overall resilience to fire but do some show variation by fire severity, particularly at very large scales (Ancillotto et al., 2020; Law et al., 2018; Steel et al., 2019).

Fires alter forest vegetation according to fire severity both directly and indirectly, thereby changing the availability of vegetation resources for small mammals. As a measure of organic material loss, fire severity correlates with direct vegetation mortality due to fire. Over longer timescales, fire severity also indirectly shapes vegetation structure by regulating light competition, soil nutrients, growth of ruderal species, and accumulation of dead vegetative matter (Webster & Halpern, 2010). High-severity fire often engenders stronger increases in shrub and herbaceous vegetation cover than lower severity fire (Webster & Halpern, 2010), and can influence leaf litter and coarse woody debris inputs through time (Apigian et al., 2006).

In turn, these vegetation shifts influence small mammals by regulating the availability of key resources. Vegetation, downed wood, and litter cover all provide several key resources to small mammals, in the form of protection from predators (Powell & Banks, 2004; Torre & Díaz, 2004), key food resources (Reid, 2006; Whitaker, 1996), nesting sites (Innes et al., 2007; McComb, 2003), and high-quality foraging habitat (Bos & Carthew, 2003; Jia-bing et al., 2005). Indeed, post-fire small mammal recovery may be limited by resource availability and demographic rates more than recolonization (Banks et al., 2011).

Some studies report differences in small mammal response between moderate- and high-severity fire in conifer forests (Kyle & Block, 2000; Roberts et al., 2008), while others show negligible differences (Borchert et al., 2014). Further, vegetation-dependent effects of fire on small mammals appear to be species-specific (Converse, White, et al., 2006; Fontaine & Kennedy, 2012; Kalies et al., 2010; Zwolak, 2009). For example, meta-analyses of small mammal response to fire in North America show that the deer mouse (*Peromyscus maniculatus*) and white-footed mouse (*P. leucopus*) generally increase in abundance after fire, while the southern red-backed vole (*Myodes gapperi*) decreases in abundance after fire (Fontaine & Kennedy, 2012; Zwolak, 2009).

Inter-species variation in small mammal response to fire may be explained by small mammal functional traits, especially those which correspond to resource use. Several small mammal traits are hypothesized to correspond with post-fire shifts in community structure and thereby explain species-specific patterns (Ceradini & Chalfoun, 2017; Kelly et al., 2010; Plavsic, 2014). In particular, traits such as diet, foraging mode, locomotion, and nesting habit are related to resource use and therefore likely to respond to shifts in resource availability after fire (Flynn et al., 2009). Other traits such as reproductive rate, home range size, and longevity have been linked to immediate post-fire responses since they directly influence survival and recolonization ability, but are not as directly linked to resource use (Whelan et al., 2002). Body size has also been correlated with post-fire survival (Griffiths & Brook, 2014), but this may be due in part to its correlation with life history traits directly related to colonization and survival (Hutchings et al., 2012).

The objective of this study was to clarify how interactions between fire severity, vegetation characteristics, and small mammal traits ultimately shape post-fire small mammal community structure. We used a model-based fourth-corner framework to examine these interactions, given that trait-based approaches that incorporate key habitat variables are particularly well-suited for revealing the mechanistic underpinnings of post-fire recovery (Driscoll et al., 2010; McGill et al., 2006). We compared nine sites within each fire severity category, as robust spatial replication is crucial for mechanistic studies in order to account for random habitat variation (Griffiths & Brook, 2014). To our knowledge, this is the first application of fourth-corner techniques to examine drivers of post-fire small mammal communities.

In this study, we examined the drivers of small mammal community structure after the King Fire, a mega-fire in the north-central Sierra Nevada of California. The King Fire burned 39,545 ha in September and October 2014, following a historic California drought (**Fig. 1a**). Over 50% of the total King Fire area burned at a high severity, including one continuous 13,683-ha high-severity patch (G. M. Jones et al., 2016). Within the King Fire perimeter, fire severity ranged from low to high (**Fig. 1b**) with vegetation in high-severity areas shifting drastically from a mixed conifer forest with limited understory before the fire to a homogenous shrub-dominated understory with skeletal trunks after the fire (**Fig. 1d**). The extent of high-severity fires in the north-central Sierra Nevada of California has increased over the past three decades, in part due to timber harvesting practices and past fire suppression (Agee, 1998; Miller et al., 2009). More recently, fire regime shifts are being exacerbated by climate change through a lengthened fire season, warming temperatures, and increased drought frequency (Westerling et al., 2006). As one of the first well-publicized mega-fires in California, the King Fire was a seemingly anomalous event that is quickly becoming the norm.

We compared small mammal communities in high-severity, low/moderate-severity, and unburned habitat within one geographic area three years after the King Fire. Specifically, we addressed differences among fire severity categories in relation to the following questions: 1) How do small mammal abundance, diversity, and community structure respond to fires of low/moderate versus high severity? 2) Which vegetation characteristics are associated with fire-related shifts in mammal community structure? 3) Which small mammal traits explain variation in the community response to fire severity?

We hypothesized that the effects of fire severity on small mammal community structure would be mediated by resource use, as shown by significant interactions between vegetation characteristics and small mammal traits. In particular, we expected to see post-fire increases in small mammal abundance, decreases in diversity, and shifts in community structure, consistent with previously reported trends (Griffiths & Brook, 2014; Zwolak & Foresman, 2007), with stronger effects in high-severity vs. low/moderate-severity habitat (Fontaine & Kennedy, 2012; Pastro et al., 2014). We hypothesized that that vegetation shifts in shrub cover, forb and grass cover, litter cover, density of live trees, and amount of well-decayed coarse woody debris would be associated with fire severity and thereby predict post-fire small mammal community structure (Borchert et al., 2014; Bos & Carthew, 2003; Jia-bing et al., 2005; Miklós & Îiak, 2002; Powell & Banks, 2004). We also hypothesized that feeding guild, foraging mode, and nesting habit would explain vegetation-related variation in post-fire small mammal community structure, due to the traits' association with resource use (Flynn et al., 2009; Griffiths & Brook, 2014; Plavsic, 2014).

By using well-controlled methods and replicated study sites, we aimed to clarify the mechanisms driving small mammal community structure after a mega-fire. With the prospect of shifting fire regimes, understanding the mechanisms linking fire severity to changes in small mammal community structure will be crucial for developing informed management plans. General management recommendations:

- This is especially relevant for fire-prone forests, in western North America and globally, that are experiencing more frequent/severe fire
- Our results can guide managers who are planning fire treatments to regulate fire severity with the goal of maximizing small mammal diversity

Methods

Study location

Fieldwork for this study was conducted in Eldorado National Forest (38°45′N 120°20′W), near Placerville, California, within the footprint of the King Fire, which burned 39,545 ha from September to October 2014 (**Fig. 1**). Sampled sites ranged in elevation from 1300-1900 m, and pre-burn vegetation consisted of lower montane mixed conifer forest. Mixed conifer forests are found throughout the Sierra Nevada region and are characterized by a Mediterranean climate with wet winters and dry summers. Common tree species at the study sites included yellow pine (*Pinus ponderosa* and *P. jeffreyi*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), black oak (*Quercus kelloggii*), and red fir (*A. magnifica*). The most common post-fire species were chaparral shrubs such as deer brush (*Ceanothus integerrimus*), mountain whitethorn (*C. cordulatus*), greenleaf manzanita (*Arctostaphylos patula*), and prostrate ceanothus (*C. prostratus*).

Study sites and experimental design

In summer 2017 we established 27 sampling sites across three fire severity categories, with nine unburned control sites (located outside the fire boundary), nine low/moderate-severity sites, and nine high-severity sites (**Fig. 1b**). Site candidates were selected using elevation data and remotely-sensed vegetation classes from the California Wildlife Habitat Relationships program (CWHR) (Mayer & Laudenslayer, 1988), although, as detailed below, burn categories were subsequently validated using both field data and Landsat-derived burn severity imagery.

All sites were established in publicly owned areas with no recent pre-fire logging or post-fire salvage logging and located at least 50 m from the nearest road, stream or dissimilar habitat type, such as a clear-cut. According to Fire and Resource Assessment Program (FRAP) fire perimeter data, none of the sites experienced wildfire or controlled burning within the century before the King Fire (Fire and Resource Assessment Program, 2020). Slopes within all sites did not exceed 30 degrees. Sites were located >100 m from each other (except for two adjacent plots separated by a dirt road), and the average distance from each site to the nearest site was 1.4 km. Sampling took place from late June to early September 2017. To minimize seasonal effects associated with sampling throughout the summer, triplicate unburned, low/moderate-severity, and high-severity sites were sampled simultaneously. All mammal and vegetation surveys at a single site were conducted within 4–5 days. The climate was consistently hot and dry at all sites (15–40ºC), with no precipitation throughout the sampling period.

We established the similarity of vegetation at our sites before the King Fire and compared pre-fire to immediate post-fire conditions using spatial data products from the Landscape Fire and Resource Management Planning Tools program (LANDFIRE) developed in 2012 (LF 1.3.0) and 2014 (LF 1.4.0) (Rollins & Frame, 2006). In particular, we used two metrics from LANDFIRE: Existing Vegetation Cover (EVC), which is a measure of the percent cover of the most dominant lifeform (tree, shrub, or herb) within 30-m cells; and Existing Vegetation Type (EVT), which classifies the dominant terrestrial ecological system within 30-m cells as described by NatureServe (Comer et al., 2003). To compare potential wildlife habitat across sites, we converted the EVT classes into CWHR habitat classes (Comer et al., 2003). Essentially, for each site, we counted the number of cells within each level of vegetation cover (for EVC) or vegetation type (for CWHR, converted from EVT). We included all cells from within each mammal trapping site (90 × 90 m) plus a buffer of 225 m (the diameter of the largest home range of a captured species according to values from the PanTHERIA database, (K. E. Jones et al., 2009), excluding cells from vegetation types that comprised <1% of the area sampled for each time period.

To quantitatively compare EVC among the three fire severity categories for both pre-fire and post-fire periods, we used ordinal ranks for the percent cover of trees based on the categories provided by LANDFIRE, with cell values representing dominant shrubs and herbs lumped into the lowest rank. We compared ranked sums using two Kruskal-Wallis tests with a Bonferroni correction. Effect size was calculated as eta squared using the H-statistic and post hoc pairwise comparisons were conducted using Bonferroni-corrected Dunn's tests. To test differences between pre-fire and post-fire EVC for each of the three fire severity categories, we used three Bonferroni-corrected Wilcoxon ranked sum tests. Wilcoxon effect size was calculated as the r value.

Given the sampling design and the difficulty of using any one metric to describe fire severity, all analyses in this paper were conducted using categorical bins of fire severity (high severity, low/moderate severity, and unburned) rather than a quantitative site-specific severity score. To validate that these bins distinguished meaningfully different fire severity categories, we used both remote sensing and field data. We used remote sensing data from Monitoring Trends in Burn Severity (MTBS) maps, which classify burn severity using Landsat reflectance imagery of pre-fire and post-fire conditions at 30-m resolution

(Eidenshink et al., 2007). MTBS classifies severity into five possible scores (0 = outside the burn boundary; 1 = unburned-low severity within the fire perimeter; 2 = low severity; 3 = moderate severity; 4 = high severity). For each treatment, we determined the mean MTBS pixel value within each mammal trapping site and its home range buffer.

In the field, we also tested for differences in fire-related tree mortality among severity categories based on surveys of trees along two 50-m vegetation transects at each site. For all trees with boles within a 15-m wide band (750 m^2 per transect) and with a diameter at breast height (DBH) greater than 15 cm, we recorded if the tree was alive or dead. We calculated percent tree mortality as the number of dead trees divided by the total. We compared percent tree mortality and average severity pixel value per site between the three fire severity categories using Kruskal-Wallis tests followed by Bonferroni-corrected Dunn's tests.

Vegetation surveys

We used five measures of vegetation to examine relationships between small mammal community structure and environmental conditions: density of live trees (field methods detailed above), litter cover, cover of understory shrubs, cover of understory grass and forbs, and volume of coarse woody debris (CWD). All vegetation data was taken along the same two 50-m transects used for estimating tree mortality at each site. The vegetation transects ran parallel to two sides of the small mammal trapping grid, with either opposite or adjacent placement depending on topography, and were located 10–20 m away from the grid edge. To characterize litter and understory vegetation cover, we estimated percent cover of litter material and live vegetation up to 1 m tall within 1-m^2 quadrats located every 5 m along each transect (10 quadrats per transect, 10 m^2 total). All live understory vegetation was categorized as tree, shrub, grass, or forb, and percent cover was estimated separately for each lifeform.

Coarse woody debris (CWD) was also surveyed along the same vegetation transects, using line-intercept sampling methods (Waddell, 2002). For each piece of CWD (defined as wood longer than 1 m with the diameter at the point of transect intersection >12.5 cm), we recorded the length, smallest diameter, and largest diameter. The volume of CWD per m^2 was determined using Smalian's volume formula and DeVries' formula, which converts line-intercept data into volume per unit area (DeVries, 1973; Waddell, 2002). We also recorded the decay class for each piece of CWD (ranging from 1 = intact sound wood, to 5 = soft powdery wood with no structural integrity, (Maser et al., 1979). Only well-decayed CWD with decay class 3–5 were included in analyses, since this material is more heavily utilized by small mammals than less-decayed wood (Jia-bing et al., 2005).

Small mammal sampling

At each site we sampled small mammal communities within one 90 × 90 m trapping grid, with traps placed 10 m apart (100 traps per grid). Grids were arranged by alternating large (7.5 × 9 × 23 cm) and extra-large (10 × 11.5 × 38 cm) Sherman traps baited with a mixture of oats, peanut butter, bird seed, and molasses. To improve trap success, we allowed animals to acclimate by prebaiting traps while holding them open for three nights. We then sampled each grid for three continuous trap nights (maximum of 300 trap nights per site). Traps were opened between 17:00 and 19:00 and closed between 09:00 and 011:00, with no daytime trapping effort due to heat. Captured small mammals were identified to species using external morphological characteristics and marked with unique ear tags, or for shrews only, clipped fur. We also recorded each mammal's mass and age class, and noted any disturbed traps in order to assess trapping effort. Although traps were primarily open at night, several diurnal species (chipmunks and ground squirrels) were regularly captured; this is probably because traps were consistently open for a few hours after sunrise and before sunset at all sites. Since trapping times were standardized across sites, our sampling scheme allowed a comparison of the relative abundances of all captured species across sites, including diurnal animals.

Small mammal abundance and diversity

From the trapping data, we calculated small mammal abundance as the number of unique individuals captured over each sampling period at each site, representing the minimum number of animals known to be alive (MNKA). To confirm similarity in capture success among treatments, we compared the recapture rate of marked individuals (number of recaptured individuals per number of total captures) among the three fire severity categories using a Kruskal-Wallis test. Due to the capture of five rare species (detailed below), we ran all small mammal abundance, diversity, and community structure analyses twice, with and without rare species included.

Abundance estimates for all analyses were standardized by trapping effort, so that abundance was measured in individuals per trapping grid per trap night (~300 per night, although usually slightly lower when disturbed traps were removed and sprung traps were reduced by half). We calculated the biomass of each species at each site as the product of the species' abundance multiplied by the mean body mass from field measurements of adults. Total small mammal abundance and total biomass, as well as the abundances of individual species, were compared among fire severity categories using Kruskal-Wallis tests followed by Bonferroni-corrected Dunn's tests.

To characterize the diversity of the small mammal community, we calculated species richness and evenness for each site and compared these across fire severity categories using ANOVA with post hoc pairwise comparisons by Tukey HSD. Rarefied species richness was estimated by individual-based rarefaction using the rarefy function in the R package vegan (Oksanen et al., 2018; Thompson et al., 2007; Willott, 2001). We used Pielou's index to calculate species evenness (Pielou, 1966).

Small mammal community structure

We used a combination of model-based and association-based methods for multivariate analysis of the small mammal community. Specifically, we built a multivariate generalized linear model (GLM) to examine differences in small mammal community structure among fire severity treatments and used NMDS ordination for visualization of these patterns. GLMs are ideal for analyzing multivariate abundance data since they can account for key properties of site-species data, namely a strong mean-variance relationship and strong correlation between response variables due to species interactions (Wang et al., 2012; Warton, Foster, et al., 2015).

We built the first multivariate GLM using fire severity category as a predictor variable and small mammal abundances as response variables ($GLM_{severity}$). We standardized across sites by including trapping effort as an offset in the model and assumed a negative binomial distribution of abundance data. We included Principal Components of Neighborhood Matrix (PCNM) distances as a metric of spatial autocorrelation in our models (Dray et al., 2006). The model was created with the function manyglm in R package mvabund, using the approach developed by (Wang et al., 2019). Multivariate test statistics were calculated using the Score statistic since our data included small abundance means due to rare species, and we accounted for correlation between species by shrinking the sample correlation (Warton, 2011). To test model significance, we calculated p-values using the PIT-trap bootstrapping method for resampling of rows with the anova.manyglm function (Warton et al., 2017). We also calculated univariate test statistics and p-values to determine which species were driving patterns.

To visually represent differences in community structure among fire severity categories, we conducted nonmetric multidimensional scaling (NMDS) on the abundance of all captured species across sites using the metaMDS function in the R package vegan (Oksanen et al., 2018). Raw abundance values were standardized using the Hellinger method, which standardizes abundance by site and then applies a square root transformation (Legendre & Gallagher, 2001). We then generated a Bray-Curtis dissimilarity matrix and produced a 3-dimensional ordination. To corroborate the results of $\mathrm{GLM}_{\mathrm{severity}}$, we evaluated the similarity in community structure among fire severity categories using a permutational multivariate analysis of variance of Hellinger-standardized abundance (adonis function in vegan, (Oksanen et al., 2018). Post-hoc pairwise comparisons of categories were conducted using the function pairwise.adonis in R package pairwiseAdonis, followed by Bonferroni corrections (Martinze Arbizu, 2020).

Vegetation drivers

We explored the effect of each of five vegetation variables on small mammal community structure. Variables were selected based on established association with small mammal community composition and included the following metrics: percent shrub cover (Borchert et al., 2014; Torre & Díaz, 2004); percent forb and grass cover (Plavsic, 2014; Powell & Banks, 2004); density of live trees (Lobo, 2014; Miklós & Îiak, 2002); volume of well-decayed coarse woody debris (Fauteux et al., 2012; Jia-bing et al., 2005; McComb, 2003); and percent litter cover (Bos & Carthew, 2003; Greenberg et al., 2007). To visualize how these variables corresponded with small mammal community structure, we plotted vectors for each vegetation variable onto the NMDS plot using the function envfit in vegan (Oksanen et al., 2018).

To determine which of these vegetation characteristics varied with fire severity, we compared among fire severity categories using Kruskal-Wallis tests followed by Bonferroni-corrected Dunn’s tests. We also checked for correlation between the vegetation variables using Spearman’s rank correlation coefficients. For variables with coefficients >0.5, we used principal component analysis (PCA) to collapse the variables into a single metric (the first principal component, PC1) that explained a large portion of variance, which we incorporated into our model.

To determine which vegetation variables predicted most of the variation in small mammal community, we built a second multivariate GLM using PC1 and the remaining vegetation variables as predictors and small mammal abundances as response variables (GLM_{veg}). This GLM also included PCNM distances to account for spatial autocorrelation and was generated using the same methods as above. We used AIC selection to determine which combination of predictors best explained variance in the data, and used the function summary.manyglm with PIT-trap bootstrapping to test the significance of each predictor in the final model.

Small mammal functional traits

We hypothesized that small mammal functional traits related to resource use would correlate with fire-related vegetation changes. Specifically, we explored the following three largely independent resource use traits: feeding guild (Flynn et al., 2009; Plavsic, 2014), primary foraging mode (Flynn et al., 2009), and primary nesting habit (Ceradini & Chalfoun, 2017; Flynn et al., 2009). While other traits might also be important, they are either correlated with these traits (e.g. body size) or poorly known across all species (e.g. dispersal distance and fecundity). To account for variability in the information provided by different literature sources (Fitzsimmons, 2013), trait information was collated from two field guides as well as species accounts from the American Society of Mammalogists (**Appendix S1: Table S1**). Feeding guild was recorded as herbivore, omnivore, or insectivore (**Appendix S1: Table S2**). Primary foraging mode was recorded as ground, scansorial, or arboreal (**Appendix S1: Table S3**). Primary nesting habit was recorded as tree, hollow (aboveground, e.g. rock crevices or brush piles), or burrow (underground) (**Appendix S1: Table S4**).

To investigate interactions between small mammal traits and vegetation variables, we used a model-based fourth-corner approach. Within this framework, three matrices representing site-species data, site-environmental data, and species-trait data are used to calculate a fourth matrix ("fourth corner") that estimates interactions between environmental and trait variables (Brown et al., 2014). We created our fourth-corner model (GLM_{trait}) using the traitglm function in mvabund, which predicts species abundance using environment by trait interactions (Warton, Shipley, et al., 2015). We assumed a negative binomial distribution of abundance data. Since this framework does not yet allow offsets to account for trapping effort, we used site-standardized abundances in our site-species matrix. We only included vegetation variables that were significant in GLM_{veg}. For model selection, we used the LASSO penalty to remove interaction coefficients that did not reduce BIC (Brown et al., 2014). We visualized the model results by creating a heat map of the remaining standardized fourth-corner coefficient estimates. To test for model significance, we calculated a p-value using the PIT-trap bootstrapping method for resampling of rows with the anova.traitglm function (Brown et al., 2014).

All statistical analyses were performed using the program R (R Core Team, 2018). The maps in Fig. 1 were created using QGIS (QGIS Development Team, 2018).

Results

Site classification

Before the King Fire in 2014, vegetation in the 27 sites was consistent across the three fire severity categories, with habitats consisting predominantly of Sierran mixed conifer forest or other conifer forest types in 2012 (**Fig. 2b**). Although pre-fire tree cover was highly variable across sites (range 20–80%), differences were comparatively minimal among the three fire severity categories, with a small effect size (**Fig. 2a**, Kruskal-Wallis $H_2 = 12.3$, $p < 0.01$, effect size = 0.0056).

After the 2014 King Fire, vegetation shifted from mixed conifer forest to montane chaparral, with the most drastic shifts occurring in high-severity sites (**Fig. 2b**). We observed a very large difference between pre-fire and post-fire percent cover of trees in high-severity sites (Wilcoxon W = 3420, $p < 0.001$, effect size = 0.94). In comparison, pre-fire and post-fire tree cover were only moderately different in low/moderate-severity sites (Wilcoxon W = 172929, $p < 0.001$, effect size = 0.33), and indistinguishable in unburned sites (Wilcoxon W = 149933, $p = 0.57$, effect size = 0.039).

The three fire severity categories also showed strong differences in vegetation and fire severity after the King Fire. Immediately post-fire in 2014, the percent cover of trees among the three fire severity categories differed greatly (**Fig. 2a**, Kruskal-Wallis $H_2 = 1535$, $p < 0.001$, effect size = 0.66, all post hoc $p < 0.001$). In addition, sites in the three fire severity categories showed strong differences in average fire severity, as measured from MTBS pixels (**Fig. 1c**, Kruskal-Wallis $H_2 = 23.4$, $p < 0.001$, effect size = 0.89, all post hoc $p < 0.05$). Three years after the fire, these differences were still distinct, with drastically different tree mortality among treatments according to 2017 field data (**Fig. 1c**, Kruskal-Wallis $H_2 = 25.0$, $p < 0.001$, effect size = 0.96, all post hoc $p < 0.05$).

Small mammal abundance and diversity

We captured 544 individuals of 11 small mammal species over 7810 trap nights. The 11 species captured were the North American deer mouse (*Peromyscus maniculatus*, n = 425), Trowbridge’s shrew (*Sorex trowbridgii*, n = 34), California ground squirrel (*Otospermophilus beecheyi*, n = 23), brush mouse (*P. boylii*, n = 18), long-eared chipmunk (*Neotamias quadrimaculatus*, n = 17), shadow chipmunk (*N. senex*, n = 12), dusky-footed woodrat (*Neotoma fuscipes*, n = 5), yellow-pine chipmunk (*N. amoenus*, n = 4), northern flying squirrel (*Glaucomys sabrinus*, n = 2), pinyon mouse (*P. truei*, n = 2), and western harvest mouse (*Reithrodontomys megalotis*, n = 2). The deer mouse was by far the most frequently captured species, making up 78% of total captures. The results reported here include the five rare species (those with ≤5 captures), since we found no substantial differences upon excluding these species. Species accumulation curves indicate that at the level of fire severity category, trapping effort was sufficient to indicate a species' presence

(**Appendix S1: Fig. S1**). The recapture rate of marked individuals was similar among fire severity categories (Kruskal-Wallis $H_2 = 0.13$, $p = 0.94$)

The relative abundances of different mammal species varied across fire severity categories (**Fig. 4a**). Four species (deer mouse, long-eared chipmunk, California ground squirrel, and brush mouse) were found at sites in all three fire severity categories, although they were trapped more often at sites within the two burned categories. Two species were found in both unburned and low/moderate-severity sites (Trowbridge's shrew and dusky-footed woodrat), but these species were more frequently caught in unburned habitat. Two rare species (northern flying squirrel and western harvest mouse) were caught exclusively at unburned sites, and two chipmunk species (yellow-pine chipmunk and Allen's chipmunk) were caught exclusively at burned sites. The final species was the pinyon mouse, a rare species that was caught once at an unburned site and once at a high-severity site.

Total small mammal abundance did not differ statistically among fire categories, although the median abundance was much higher in high-severity sites (28 individuals) than unburned or low/moderate-severity sites (19 and 16 individuals, respectively) (**Fig. 3a**, Kruskal-Wallis $H_2 = 5.44$, $p = 0.066$, effect size = 0.14). Similarly, differences in total small mammal biomass among treatments were not significant (**Fig. 3a**, Kruskal-Wallis $H_2 = 1.45$, $p = 0.48$, effect size = 0.023). Median deer mouse abundance, however, almost doubled from 13 individuals in unburned sites to 24 individuals in high-severity sites (**Fig. 3b**, Kruskal-Wallis $H_2 = 9.25$, $p < 0.01$, effect size = 0.30, post hoc $p < 0.01$), although there were no differences in deer mouse abundance between unburned and low/moderate-severity sites (post hoc $p = 0.86$). Shrew abundance showed the opposite relationship with fire severity, with median abundance decreasing from unburned sites (4 individuals) to low/moderate-severity and high-severity sites (0 individuals for both) (**Fig. 3b**, Kruskal-Wallis $H_2 = 18.54$, $p < 0.001$, effect size = 0.69, post hoc $p < 0.01$). Differences in shrew abundance between low/moderate-severity and high-severity sites were negligible (post hoc $p = 0.19$). No statistically significant differences in the abundances of other species among burn severity categories were found.

Small mammal diversity as measured by richness and evenness was lower in high-severity sites. Rarefied species richness was much lower in high-severity sites compared to unburned and low/moderate-severity sites (**Fig. 3c**, ANOVA $F_{2,24} = 7.19$, $p < 0.01$, effect size = 0.77, post hoc $p < 0.05$), but differences in rarefied richness between unburned and low/moderate-severity sites were minimal (post hoc $p = 0.36$). Pielou's evenness was also lower in high-severity sites compared to unburned sites (**Fig. 3c**, ANOVA $F_{2,24} = 3.65$, $p = 0.045$, effect size = 0.60, post hoc $p < 0.05$), although evenness in low/moderate-severity sites was statistically similar to both unburned and high-severity sites (post hoc $p = 0.31$, 0.36 respectively).

Small mammal community structure

$GLM_{severity}$ indicated that small mammal community structure differed among fire severity categories ($score_{24,2} = 31.73$, $p < 0.001$). PCNM (accounting for spatial autocorrelation) was not a significant predictor in this model ($score_{23,1} = 12.03$, $p = 0.13$). Species-specific responses showed that the deer mouse ($score_{24,2} = 11.48$, $p < 0.01$) and Trowbridge's shrew ($score_{24,2} = 9.80$, $p < 0.01$) were driving community response to fire severity. NMDS results further demonstrated that community structure varied among fire severity categories (**Fig. 4b**, adonis $F_{2,24} = 4.96$, $R^2 = 0.29$, $p = 0.001$), with post-hoc analysis indicating that community structure in unburned sites was significantly different than both low/moderate-severity and high-severity sites (post hoc $p < 0.01$).

Vegetation drivers

Out of the five vegetation variables that we predicted would affect small mammal community structure, three varied among the fire severity categories. The density of live trees varied most strongly among the fire severity categories, with high-severity sites showing much lower density (**Fig. 5a**, Kruskal-Wallis $H_2 = 22.26$, $p < 0.001$, effect size = 0.84, post hoc $p < 0.05$). Percent litter cover was also lower in high-severity sites (**Fig. 5a**, Kruskal-Wallis $H_2 = 19.06$, $p < 0.001$, effect size = 0.71, post hoc $p < 0.05$), and percent shrub cover was higher in high-severity sites (**Fig. 5a**, Kruskal-Wallis $H_2 = 14.14$, $p < 0.01$, effect size = 0.51, post hoc $p < 0.01$). In addition, live tree density, litter cover, and shrub cover all appeared strongly aligned with the fire severity categories in the NMDS plot (**Fig. 4b**). Unsurprisingly, these three variables were highly correlated (Spearman’s correlation coefficients 0.66–0.74), so we collapsed them into the first principal component for use in GLM_{veg}. The resulting $PC1_{T+S+L}$ accounted for 73.4% of variance in the three variables, and was higher at high-severity sites (**Fig. 5a**, Kruskal-Wallis $H_2 = 21.60$, $p < 0.001$, effect size = 0.82, post hoc $p < 0.05$).

The remaining two vegetation variables, soft CWD and forb/grass cover, did not vary among fire severity categories (**Fig 5b**, Kruskal-Wallis $H_2 = 1.90$, $p = 0.99$ for CWD; $H_2 = 3.33$, $p = 0.95$ for forb/grass cover). Furthermore, soft CWD and forb/grass cover were not strongly correlated with each other or with the other vegetation variables (Spearman’s correlation coefficients <0.4). In the NDMS plot, these variables appear to drive more of the variation within each fire severity category (**Fig. 4b**).

The candidate predictors for GLM_{veg} were $PC1_{T+S+L}$ (vegetation variables that changed with fire), soft CWD, forb/grass cover, and PCNM (controlling for spatial autocorrelation). According to AIC model selection, the best model included $PC1_{T+S+L}$ and soft CWD as predictors (AIC = 583.11, AIC weight = 0.94). No other model received substantial support, although upon re-running analyses without rare species we found that including PCNM in addition to $PC1_{T+S+L}$ and soft CWD marginally improved model fit (with PCNM: AIC = 491.39, AIC weight = 0.33; without PCNM: AIC = 491.61, AIC weight = 0.29). Given the unambiguous AIC results with rare species included as well as the fact that rare species did not affect any other analyses, we excluded PCNM from our final model. The final model displayed good model fit according to Dunn-Smyth residuals and successfully predicted small mammal community structure ($score_{24,2} = 37.57$, $p < 0.01$). $PC1_{T+S+L}$ (vegetation variables that changed with fire) was the strongest predictor of community structure ($score_{24,2} = 27.40$, $p < 0.001$), with volume of soft CWD also having substantial, but much lower, predictive value ($score_{24,2} = 16.72$, $p = 0.028$).

Small mammal functional traits

GLM_{trait} successfully predicted small mammal community structure ($Deviance_{248,12} = 60.89$, $p = 0.02$), indicating that interactions between vegetation variables and small mammal functional traits were important for determining community structure. Specifically, the interaction coefficients of GLM_{trait} showed several correlations between small mammal traits and vegetation variables (**Fig. 6**). $PC1_{T+S+L}$ (representing three vegetation variables that changed with fire: live tree density, shrub cover, and litter cover, **Fig. 5a**), was negatively correlated with insectivory (coefficient = -0.36), but positively correlated with omnivory (coefficient = 0.16). The volume of soft CWD was negatively correlated with nesting in hollows (coefficient = -0.38), but positively correlated with both scansorial foraging (coefficient = 0.37) and nesting in burrows (coefficient = 0.12).

Discussion

With fire regimes changing across western North America and the risk of large high-severity wildfires increasing, the 2014 King Fire provides an important opportunity to examine wildlife response to “mega-fires.” We used this system to investigate the mechanisms driving small mammal community structure three years post-burn. We were able to successfully predict small mammal community structure using vegetation characteristics of the sites and traits of the captured small mammals, indicating that resource use is likely an important component of post-fire small mammal recovery.

Fire effects on small mammals

Contrary to our expectation that small mammal abundance would increase at burned sites owing to the proliferation of deer mice, we did not find significant differences in overall abundance or biomass among sites in different fire severity categories; however, there were marginally significant increases (**Fig. 3a**, $p < 0.07$). Most of this effect was driven by deer mouse abundance, which was much higher at high-severity than unburned sites, although abundance was similar between low/moderate-severity and unburned sites (**Fig. 3b**). Because deer mice accounted for 78% of total captures, the non-significant patterns in total mammal abundance were largely a reflection of deer mouse abundance.

In general, omnivores such as the deer mouse, long-eared chipmunk, California ground squirrel, yellow-pine chipmunk, and shadow chipmunk were more frequently found in burned sites (**Fig. 4a**), although only the deer mouse showed statistically significant differences in median abundance between fire severities (**Fig. 3b**). Similarly, GLM_{trait} showed an interaction between omnivory and fire-related changes in vegetation, indicating that generalists tend to fare better in post-fire habitats (**Fig. 6**). The patterns in deer mouse abundance match those found in the literature, with abundance consistently increasing with fire severity (Fontaine & Kennedy, 2012; Krefting & Ahlgren, 1974; Zwolak, 2009). As generalist consumers, deer mice often invade disturbed habitats such as burned areas, clear-cuts, mine waste piles, and the blast zones of volcanic eruptions (Andersen & MacMahon, 1985; Kirkland, 1976; Sullivan & Krebs, 1981).

In contrast, the abundance of Trowbridge's shrew was much greater in unburned than both low/moderate- and high-severity sites (**Fig. 3b**). Unlike deer mice, shrews tend to decrease in abundance after fire, especially high-severity fire (Greenberg et al., 2007; Zwolak & Foresman, 2007). Previous work has shown that shrews are much more likely to decline after high-severity disturbances that remove leaf litter rather than after disturbances that leave litter intact (Greenberg et al., 2007). Consistent with this pattern, we found a large decrease of litter cover in high-severity sites; however, litter cover was similar between unburned and low/moderate-severity sites (**Fig. 5a**). Given the mismatch between high litter cover and low shrew abundance in low/moderate-severity sites, another habitat variable seems to be driving shrew abundance in these habitats. A plausible driver is soft CWD, which serves as habitat for invertebrates, a staple of the shrew diet (Jia-bing et al., 2005). However, our data do not show any strong differences in soft CWD among fire severity categories (**Fig. 5b**), and in fact GLM_{trait} showed a slight negative correlation between insectivory and soft CWD (**Fig. 6**). This indicates that an additional variable that we did not measure might be important.

Several uncommonly captured species were also exclusively or disproportionately captured in unburned habitats. For example, the dusky-footed woodrat and the northern flying squirrel were only captured in unburned habitats. While this is likely a real effect given that these species are negatively affected by fire given their ecology (dependency on high tree density and use of wood pile dens), the sampling design of this study was not adequate to capture abundance effects of these species. As in many community-scale studies, it is difficult to detect effects on rare species, and thus we would strongly caution against interpreting lack of significant response in uncommonly detected species as evidence of lack of effect.

Small mammal richness and evenness were lower in high-severity compared to unburned sites, consistent with our initial hypotheses and literature findings (**Fig. 3c**, (Fisher & Wilkinson, 2005; Zwolak & Foresman, 2007). We did not find differences in richness and evenness between low/moderate-severity and unburned sites, however. In addition, we found that there were no statistically significant differences between low/moderate-severity and unburned sites in the vegetation variables that changed with fire (**Fig. 5a**), in part due to substantial variation among sites within the same fire severity category. Some fire effects in low/moderate-severity sites may also have dissipated in the three years between burning and sampling. The effects of high-severity fire are likely more long-lasting than effects of low/moderate-severity fire; previous studies have shown that small mammal responses to low-severity fire can be limited to <2 years (Horncastle et al., 2019). Notably, these results are limited by the fact that our analyses are all based on the minimum number of animals known to be alive (MNKA), considering the low sample size of many species. This method does not account for differences in detectability, which may bias evenness metrics. However, given that our evenness results are consistent with richness responses (not limited by MNKA) we believe that this result is robust.

Despite statistical insignificance, small mammal richness and evenness appeared qualitatively lower in low/moderate-severity sites versus unburned sites, as did live tree density and litter cover (**Fig. 3c, Fig. 5a**). This validates previous studies showing that higher severity fires elicit stronger wildlife responses (Fontaine & Kennedy, 2012; Pastro et al., 2014). Interestingly, the results of our permutational multivariate analysis of variance contradicted our richness and evenness findings and indicated that overall small mammal community structure was more similar between low/moderate-severity and high-severity sites and differed in unburned sites (**Fig. 4b**). This pattern may have been driven largely by the Trowbridge's shrew, the second most frequently trapped mammal, which was virtually absent in all burned sites.

Mechanisms

In general, small mammal community structure is highly correlated with vegetation characteristics, perhaps more so than with other spatial characteristics (Schmid-Holmes & Drickamer, 2001). Vegetation provides several key resources to small mammals; in particular, understory vegetation cover serves as protection from predators (Powell & Banks, 2004; Torre & Díaz, 2004), as well as providing key food resources such as seeds, fruits, and vegetative matter, which are especially important to rodents (Reid, 2006; Whitaker, 1996). In mixed conifer forests, live trees are another major seed food source, even for ground-dwelling species (Lobo, 2014). Semi-arboreal mammals such as woodrats and flying squirrels are even more dependent on live trees for nesting and food storage (Innes et al., 2007; Smith, 2007). Dead trees provide additional resources to small mammals through coarse woody debris and other types of litter material. Well-decayed coarse woody debris hosts a variety of mammal food items such as fungi and insects (Jia-bing et al., 2005), as well as providing cover and nesting space for small mammals (Fauteux et al., 2012; McComb, 2003). Leaf litter provides similarly high-quality foraging opportunities (Bos & Carthew, 2003), especially for shrews (Greenberg et al., 2007; MacCracken et al., 1985).

Since post-fire changes in live tree density, shrub cover, and litter cover were highly correlated in our sites, we could not reliably tease apart their effects on small mammals. However, in combination, these three variables appear to be strong drivers of small mammal community structure (**Fig. 4b**). Based on previous studies, shrub cover may be primarily responsible for these patterns. Post-fire shrub cover is often associated with shifts in small mammal community structure, in part since it provides protection from predators (Borchert et al., 2014; Converse, Block, et al., 2006; Torre & Díaz, 2004). Shifts in shrub cover, as well as shifts in litter cover, were likely directly linked to decreases in tree density, since post-fire reduction of trees increases light availability and decreases leaf litter inputs. Trees are also important for partially arboreal species such as the northern flying squirrel and dusky-footed woodrat, which were mostly absent from burned sites (**Fig. 4a**). Similarly, $\mathrm{GLM}_{\mathrm{trait}}$ showed a slight negative correlation between arboreal foraging and tree-nesting and fire-related changes in vegetation ($\mathrm{PC}_{\mathrm{T+S+L}}$ in **Fig. 6**). While sample size was relatively small for some of these species, these results are consistent with other findings (e.g. flying squirrels avoiding disturbed forest sites, (Sollmann et al., 2016).

Soft CWD also predicted small mammal community structure in our sites (significant predictor in GLM_{veg}, p = 028; **Fig. 4b**), although we did not find differences among fire severity categories (**Fig. 5b**). In contrast, previous studies have found that forest fires usually decrease coarse woody debris (Converse, Block, et al., 2006; Knapp et al., 2005). However, this discrepancy may be due to the timing of our study, which took place three years after fire. Volume of CWD can quickly rebound after fire as burned trees fall over (Bassett et al., 2015).

Similarly, we did not observe any differences in forb/grass cover between fire severity categories. Forb/grass cover was low (<15%) in the majority of sites, likely due to the dominance of other vegetation lifeforms, mainly trees in unburned sites, shrubs in high-severity sites, and both trees and shrubs in low/moderate-severity sites. As indicated by previous studies, differences in forb and grass cover were likely more apparent soon after the fire (Converse, Block, et al., 2006), before shrubs had time to grow and shade out forbs and grass. These results underscore the importance of considering relative timescales of different vegetation recovery processes when analyzing habitat (and wildlife) recovery post-fire.

Conclusions

Three vegetation variables (density of live trees, shrub cover, and litter cover) were different in high-severity sites compared to other sites; furthermore, these variables were significant predictors of small mammal community structure when combined (**Fig. 5**). In turn, these vegetation characteristics influenced community structure by interacting with three small mammal traits related to resource use: feeding guild, foraging mode, and nesting habit (**Fig. 6**). Because small mammals are a key component of the structure and function of forests, delineating their interactions with post-fire habitat is particularly important (Kirkman et al., 2013). As emphasized by recent reviews, studies on the mechanisms driving post-fire shifts in small mammal community structure are especially needed (Driscoll et al., 2010; Griffiths & Brook, 2014). Here, we used GLMs within a fourth-corner framework to determine that post-fire small mammal community structure was driven in part between habitat-mammal resource use interactions; extending this framework to additional systems and across longer timescales is a logical next step.

Mechanistic understanding of ecological response to wildfire severity is critical for the conservation and management of fire-prone systems (Freeman et al., 2017). Stand-replacing forest fires have become more frequent in the Sierra Nevada of California over the past three decades (Miller, Safford, Crimmins, & Thode, 2009). More broadly, scientists have predicted continued increases in the number and size of wildfires both in western North America (Schoennagel et al., 2017; Yue et al., 2013) and at middle to high latitudes globally (Moritz et al., 2012).

- Our results show substantial differences between the effects of low/moderate-severity and high-severity fires, both in habitat structure and small mammal community response.
- This has implications for anyone trying to maximize diversity while managing for different fire severity regimes.

Figures

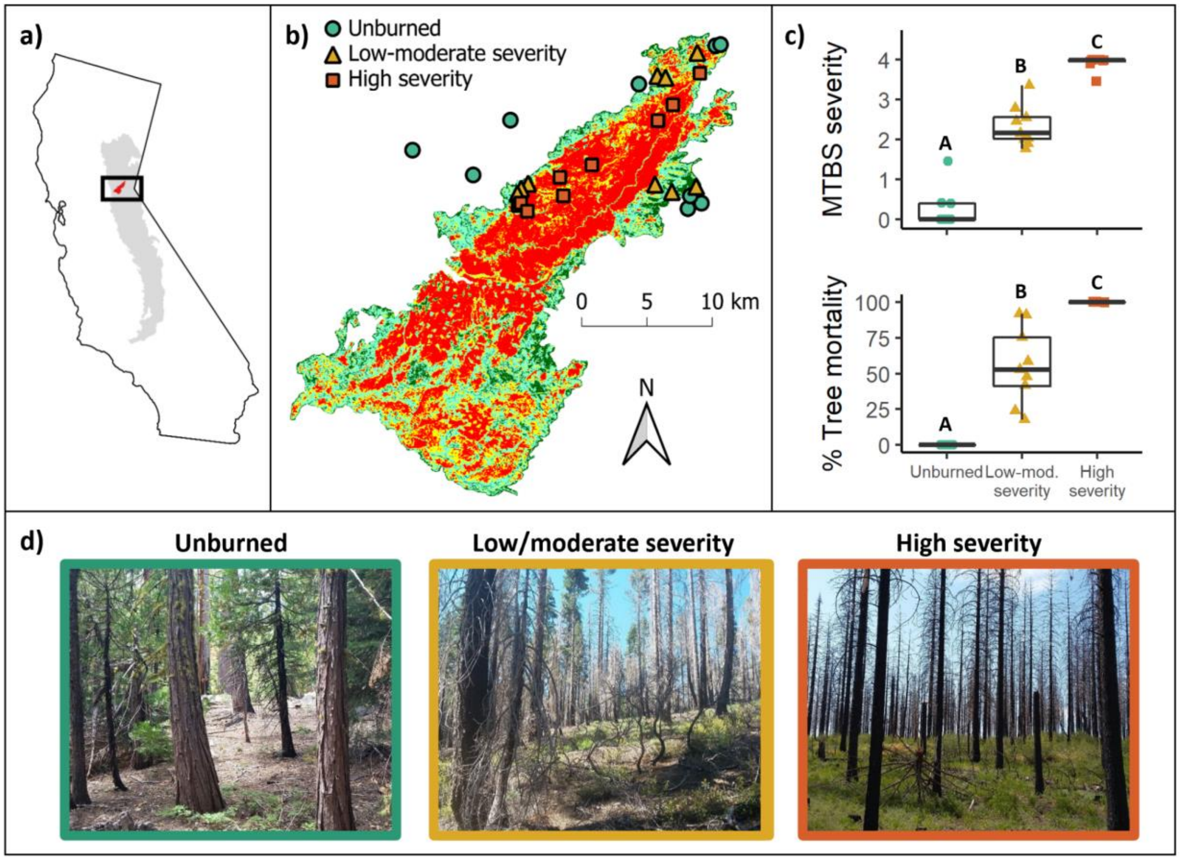

***Fig. 1.* Sites across a fire severity gradient. (a)** The area of the 2014 King Fire is shown in red and the Sierra Nevada ecoregion within California is shown in light gray. **(b)** Sites were categorized by three fire severity levels (unburned, low/moderate severity, and high severity). **(c)** Treatment categories were determined using fire severity data from Monitoring Trends in Burn Severity (Eidenshink et al., 2007) and validated with field measurements of fire-related tree mortality along two 50-m transects per site, three years post-fire. MTBS severity and % tree mortality were different among treatments (Kruskal-Wallis $H_2 = 23.4$, $p < 0.001$, $\eta^2 = 0.89$; $H_2 = 25.0$, $p < 0.001$, $\eta^2 = 0.96$ respectively). Box plots show the median and upper/lower quartiles ($n = 9$ sites in each category). Fire severity categories with the same letter are not significantly different ($p > 0.05$). **(d)** Sites shifted from a mixed yellow-

pine forest to a shrub-dominated understory across the severity categories. Map created using QGIS (QGIS Development Team, 2018).

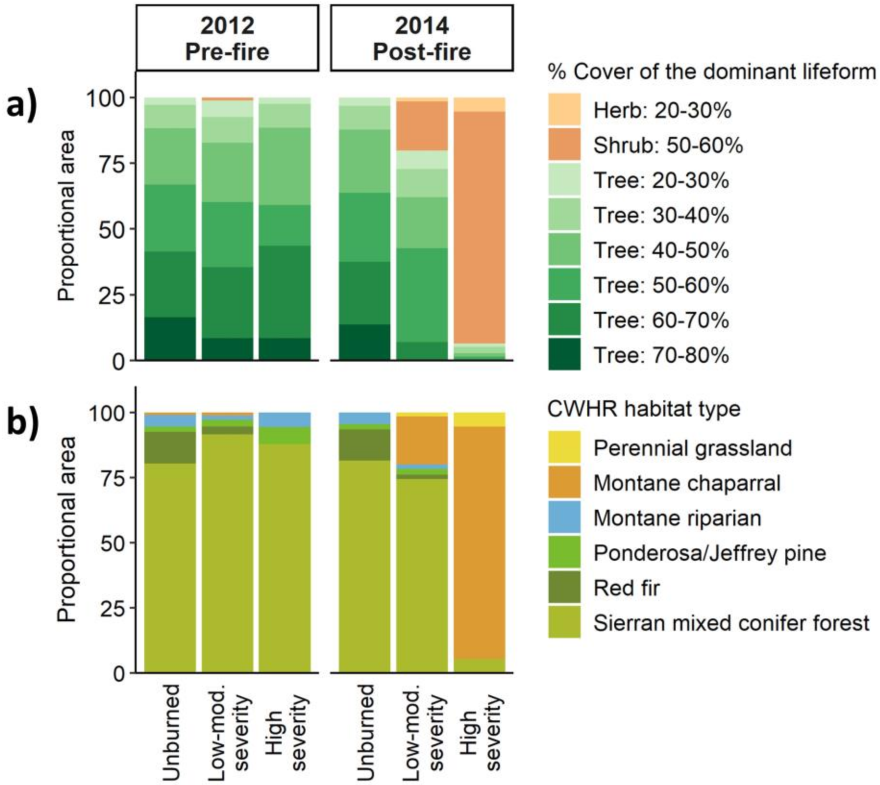

Fig. 2. **Vegetation characteristics were similar across fire severity categories pre-fire (2012) but differed greatly post-fire (2014).** For each fire severity category, stacked bars show the percentage of 30-m cells across nine sites by **(a)** percent cover classes of the dominant lifeform and **(b)** habitat type. There was little difference in % cover of trees among the three fire severity categories (Kruskal-Wallis $H_2 = 12.3$, $p < 0.01$, $\eta^2 = 0.0056$), whereas post-fire differences were large ($H_2 = 1535$, $p < 0.001$, $\eta^2 = 0.66$). Data are from LANDFIRE spatial data products for Existing Vegetation Type (converted into California Wildlife Habitat Relationships classes) and Existing Vegetation Cover (Rollins & Frame, 2006).

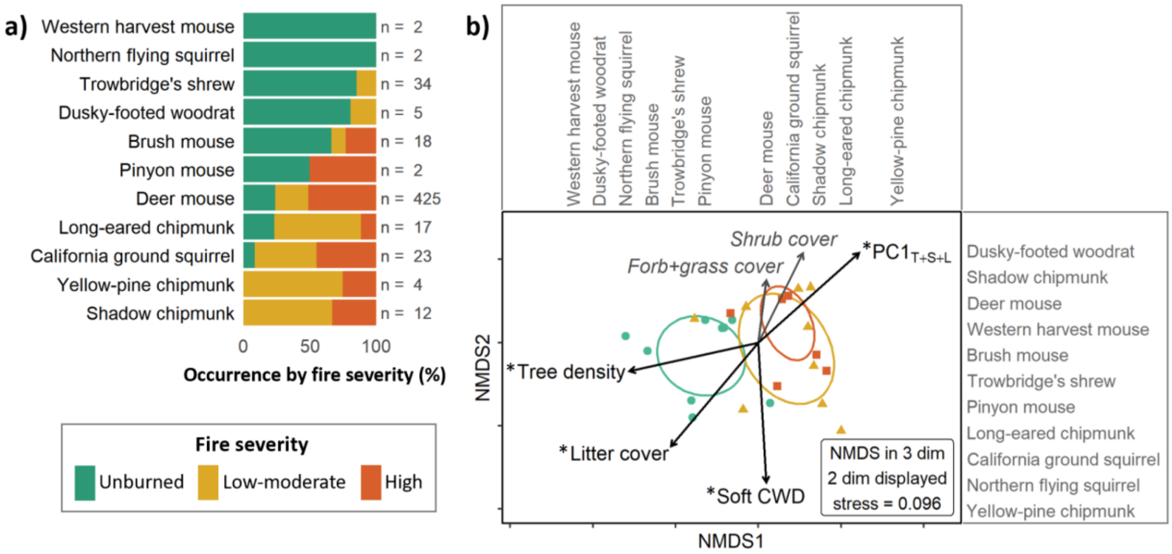

***Fig. 3.* Small mammal community structure and habitat preferences across fire severity categories. (a)** Bar plot showing the percentage of unique individuals trapped in each of the three fire severity categories for each of the 11 species captured, with the number of total captures denoted by *n*. **(b)** NMDS plot showing variation in the small mammal community structure across sites. Each point represents a site, with color-coded ellipses encompassing ±1 standard deviation from the centroid for each category ($n = 9$ sites for each category). Arrows represent vectors for vegetation variables scaled by the *r*-value, with significant correlations ($p < 0.05$) denoted by asterisks. The vegetation variables are soft coarse woody debris (CWD, m^3/ha), shrub cover (% cover), forb/grass cover (% cover), litter cover (% cover), tree density (trees/hectare), and PC1$_{T+S+L}$ (representing the PC1 of the three variables that changed with fire: live tree density, shrub cover, and litter cover). The 11 small mammal species are displayed along each NMDS axis according to their relative association with each axis.

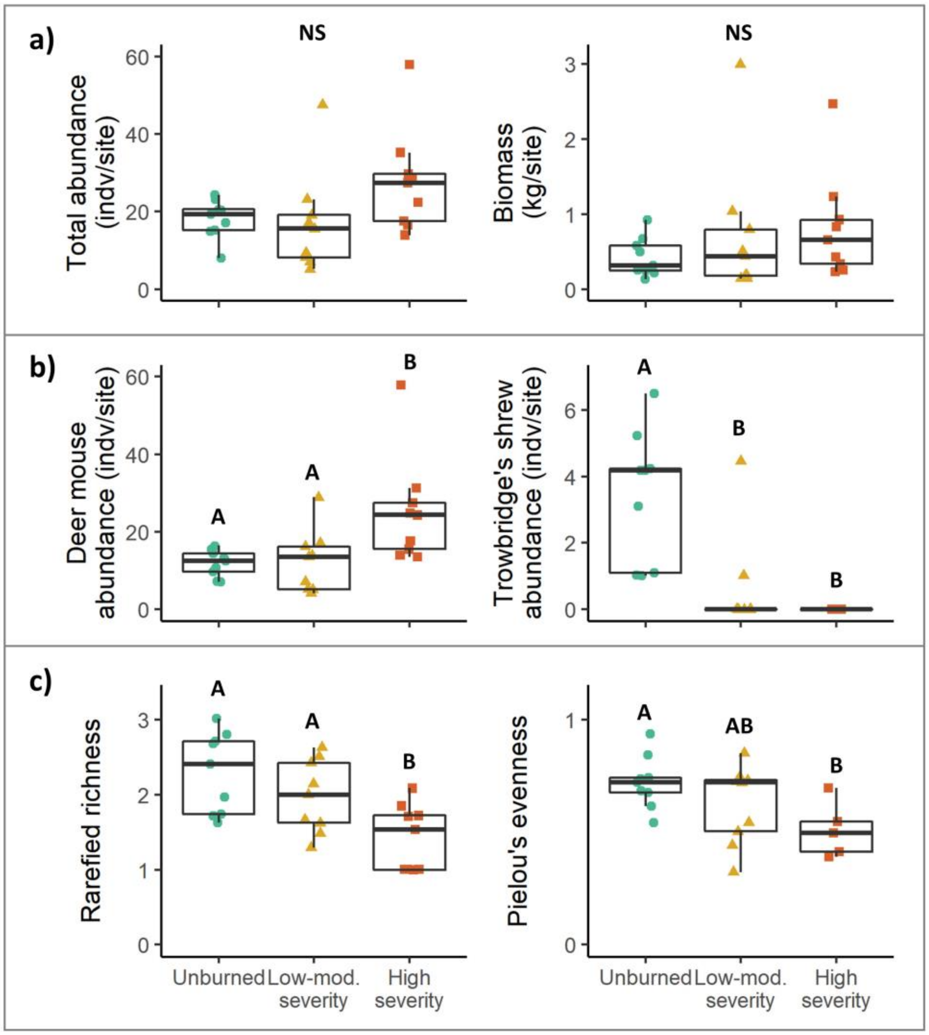

Fig. 4. **Abundance and diversity metrics across fire severity categories.** Box plots show median and upper/lower quartiles (*n* = 9 for each fire severity category). Categories in each plot with the same overlying letter are not significantly different; NS signifies no significant differences among categories. **(a)** Total small mammal abundance, calculated as the number of unique individuals captured over a 3-day sampling period at each site, and total small mammal biomass did not differ among fire severity treatments (Kruskal-Wallis $H_2 = 5.44$, $p = 0.066$, $\eta^2 = 0.14$; $H_2 = 1.45$, $p = 0.48$, $\eta^2 = 0.023$ respectively). **(b)** Individual species showed different responses to fire severity categories: Deer mice were more abundant at

high severity than other sites (H_2 = 9.25, $p < 0.01$, $\eta^2 = 0.30$), whereas Trowbridge's shrews were more abundant at unburned than other sites (H_2 = 18.54, $p < 0.001$, $\eta^2 = 0.69$). **(c)** Small mammal diversity, quantified as rarefied species richness (number of species per five individuals) and Pielou's index for species evenness, were lower at high severity sites than unburned sites (ANOVA $F_{2,24}$ = 7.19, $p < 0.01$, $\eta^2 = 0.77$; $F_{2,24}$ = 3.65, $p = 0.045$, $\eta^2 = 0.60$ respectively).

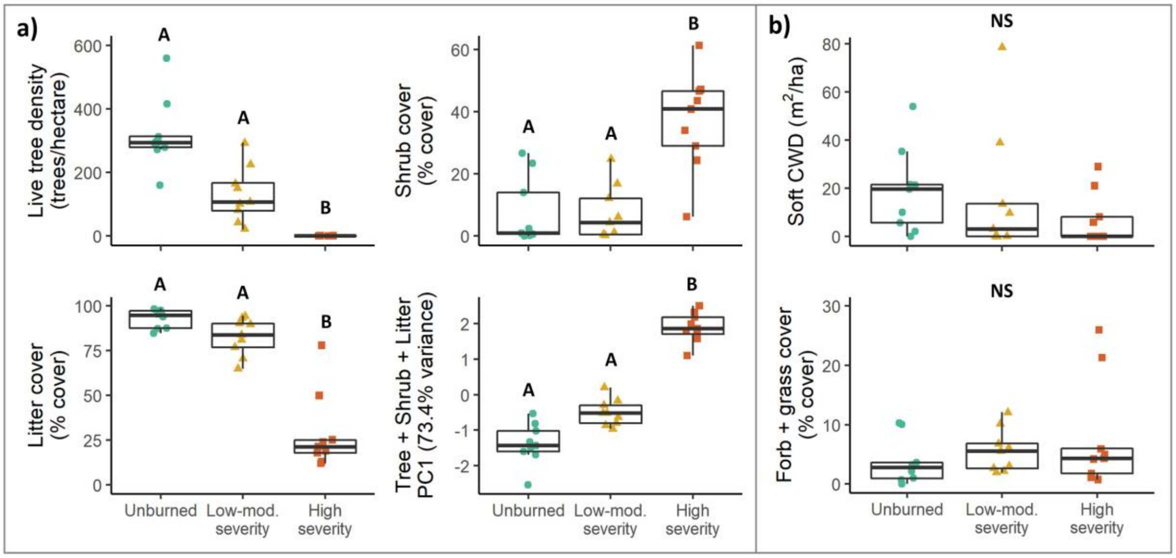

Fig. 5. **Differences in vegetation characteristics among fire severity categories.** Box plots show median and upper/lower quartiles (*n* = 9 for each). Significant differences designated as in Fig. 3. **(a)** Live tree density and litter cover where lower at high-severity sites than other sites (Kruskal-Wallis $H_2 = 22.26$, $p < 0.001$, $\eta^2 = 0.84$; $H_2 = 19.06$, $p < 0.001$, $\eta^2 = 0.71$ respectively), whereas shrub cover was higher at high-severity sites ($H_2 = 14.14$, $p < 0.01$, $\eta^2 = 0.51$). The first principal component ($PC1_{T+S+L}$) of live tree density, shrub cover, and litter cover explained 73.4% of variance in these three variables and was higher at high-severity than other sites ($H_2 = 21.60$, $p < 0.001$, $\eta^2 = 0.82$). **(b)** Volume of soft coarse woody debris (CWD) and forb/grass cover were not different among fire severity categories ($H_2 = 1.90$, $p = 0.99$; $H_2 = 3.33$, $p = 0.95$ respectively).

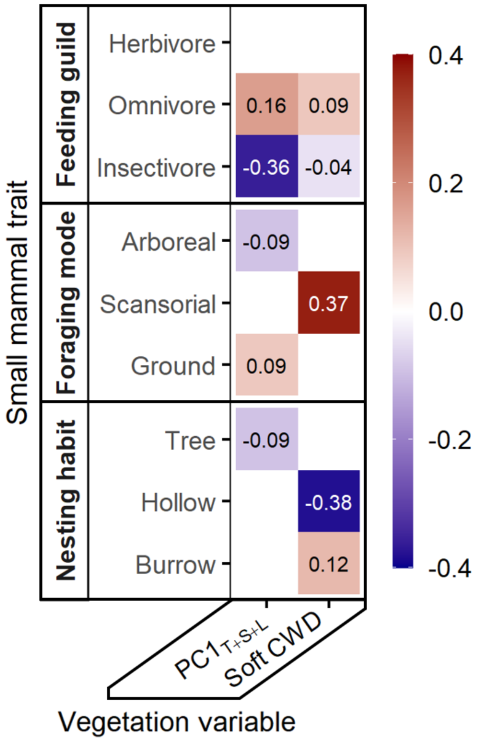

Fig. 6. **Interaction coefficients between small mammal traits and vegetation variables.** The heat map shows standardized interaction coefficient estimates from our fourth-corner model (GLM$_{\text{trait}}$) after variable selection using the LASSO penalty. Red (positive) and blue (negative) shading intensity represents the interaction strength between small mammal traits and vegetation variables. Small mammal traits (feeding guild, foraging mode, and nesting habit) are categorical with three levels each, as designated on the y-axis. The two vegetation variables are soft CWD (soft coarse woody debris, m^3/ha) and veg PC1$_{\text{T+S+L}}$ (representing three vegetation variables that changed with fire: live tree density, shrub cover, and litter cover).

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Appendix S1

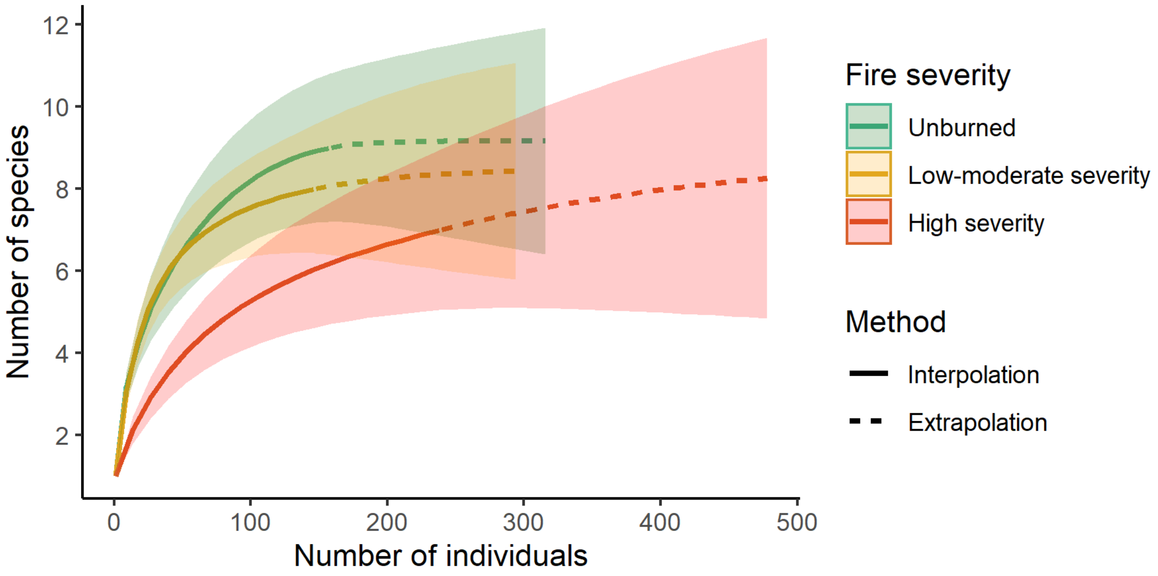

***Fig. S1.* Rarefaction curves estimating small mammal species richness for sites in three fire severity categories.** Rarefied curves indicate the average number of species detected for each additional captured individual, with observations pooled by fire severity category (n = 9 sites per category). Shaded areas represent unconstrained 95% confidence intervals. Rarefaction was conducted via interpolation and extrapolation using the R package iNEXT (Hseih et al. 2020). Study sites were in mixed-conifer habitats of the Sierra Nevada affected by the September-October 2014 King Fire in Eldorado National Forest, California. Mammals were trapped three years post-fire in summer 2017, using one grid of 100 baited Sherman traps per site, open for three consecutive trap nights. We calculated the number of individuals as the minimum number of individuals known to be alive (MNKA) from mark-recapture estimates. In total, 11 small mammal species were captured.

***Table S1.* Trait designations and corresponding literature references for three small mammal functional traits.** For each of the 11 captured small mammal species, we used species accounts to determine designations for three functional traits associated with resource use: feeding guild, primary foraging mode, and primary nesting habit (criteria for trait designations defined in **Table S2**). These traits were hypothesized to correlate with fire-related vegetation changes and thereby predict small mammal community response to fire severity. Small mammal trait designations along with site vegetation characteristics were used as predictor variables in a fourth-corner model ($\mathrm{GLM}_{\mathrm{trait}}$) to predict small mammal species abundances using environment by trait relationships.

Species	Trait	Designation	Reference(s)
Glaucomys sabrinus (northern flying squirrel)	Feeding guild	Omnivore	(Wells-Gosling and Heaney 1984,
	Foraging mode	Arboreal	
	Nesting habit	Tree	

			Whitaker 1996, Reid 2006)
Neotamias amoenus (yellow-pine chipmunk)	Feeding guild	Omnivore	(Sutton 1992, Whitaker 1996, Reid 2006)
	Foraging mode	Scansorial	
	Nesting habit	Burrow	
Neotamias quadrimaculatus (long-eared chipmunk)	Feeding guild	Omnivore	(Clawson et al. 1994, Whitaker 1996, Reid 2006)
	Foraging mode	Scansorial	
	Nesting habit	Tree	
Neotamias senex (shadow chipmunk)	Feeding guild	Omnivore	(Gannon and Forbes 1995, Whitaker 1996, Reid 2006)
	Foraging mode	Ground	
	Nesting habit	Tree	
Neotoma fuscipes (dusky-footed woodrat)	Feeding guild	Herbivore	(Carraway and Verts 1991, Whitaker 1996, Reid 2006)
	Foraging mode	Arboreal	
	Nesting habit	Tree	
Otospermophilus beecheyi (California ground squirrel)	Feeding guild	Omnivore	(Whitaker 1996, Reid 2006, Smith et al. 2016)
	Foraging mode	Ground	
	Nesting habit	Burrow	
Peromyscus boylii (brush mouse)	Feeding guild	Omnivore	(Whitaker 1996, Reid 2006, Kalcounis-Rueppell and Spoon 2009)
	Foraging mode	Scansorial	
	Nesting habit	Hollow	
Peromyscus maniculatus (deer mouse)	Feeding guild	Omnivore	(Whitaker 1996, Reid 2006)
	Foraging mode	Scansorial	
	Nesting habit	Hollow	
Peromyscus truei (pinyon mouse)	Feeding guild	Herbivore	(Hoffmeister 1981, Whitaker 1996, Reid 2006)
	Foraging mode	Scansorial	
	Nesting habit	Hollow	
Reithrodontomys megalotis (western harvest mouse)	Feeding guild	Herbivore	(Webster and Jones 1982, Whitaker 1996, Reid 2006)
	Foraging mode	Scansorial	
	Nesting habit	Hollow	
Sorex trowbridgii (Trowbridge's shrew)	Feeding guild	Insectivore	(George 1989, Whitaker 1996, Reid 2006)
	Foraging mode	Ground	
	Nesting habit	Burrow	

Table S2. **Criteria for small mammal functional trait designations.** We defined three levels for each of three functional trait variables associated with resource use: feeding guild, primary foraging mode, and primary nesting habit. These criteria were used to determine trait designations for each of 11 captured small mammal species according to published species accounts (**Table S1**).

Trait	**Designation**	**Criteria and examples**
Feeding guild	Herbivore	Diet consists of >80% vegetation (foliage, seedlings, stems, twigs, bark, roots, tubers, buds, flowers), seeds (nuts, grains, conifer seeds, acorns, grass seeds), and fruits (fleshy fruits, drupes)
	Omnivore	Diet split between vegetation, invertebrates, vertebrates (bird eggs, fledglings, or adults, mammals, reptiles, amphibians), and fungi (subterranean fungi, fruiting bodies, lichens)
	Insectivore	Diet consists of >80% invertebrates (ground insects, insect larvae, worms, orthopterans, flying insects, centipedes, spiders)
Foraging mode	Arboreal	Primarily forages in trees
	Scansorial	Forages on the ground and by climbing in shrubs or trees
	Ground	Primarily forages on the ground
Nesting habit	Tree	Tree branches, tree cavities, hollow trees or snags
	Hollow	Rock crevices, under fallen trees or vegetation, brush piles, hollow stumps
	Burrow	Underground burrows or tunnels, burrows in leaf mould

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