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RESEARCH ARTICLE

# Impacts of fire regime on small mammal communities in California

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## Abstract

Across the world, climate change is contributing to altered fire regimes, including increases in the frequency, area burned, and severity of wildfires. As a result, our understanding of the effects of these changes on ecosystems, biodiversity, and wildlife remains incomplete. The Sierra Nevada region of California supports many important species and includes unique small mammal communities that represent a crucial component of healthy ecosystems. Recently, the Sierra Nevada has experienced increasing impacts of climate change, most notably demonstrated through extreme drought and alterations to the fire regime, such as increases in fire severity, intensity, frequency, and area burned. These factors contribute to changes in vegetation and habitat, to which small mammals are highly sensitive. However, the long-term influence of these changes is poorly understood. This study aims to understand the drivers of small mammal community composition, with a focus on fire regime. We make use of historical survey and resurvey data from the Sierra Nevada, which provide high-quality species occurrence records from several periods over the last century. We examine how small mammal richness and community turnover vary with different components of fire regime, climate, and habitat using single- and multiple-variable linear regression. We found that several fire regime variables explain variation in modern small mammal richness across the Sierra Nevada. Specifically, mean time since last fire had a significant positive relationship with small mammal richness, whereas number of fires, fire return interval, and the standard deviation of time since last fire had significant negative relationships with richness in the multivariate models, in combination with non-fire variables. Additionally, mean time since last fire, standard deviation of time since last fire, and number of fires in a sample area had significant positive relationships with small mammal community turnover. Overall, this work establishes that fire is an essential element that influences small mammal community structure in an era of global change and must be considered alongside climate and habitat.

## Highlights

- Worldwide, global climate change and anthropogenic influences impact natural fire regimes.
- We used multivariate linear models to test the impact of fire regime on small mammal communities (Rodentia, Eulipotyphla) in the California Sierra Nevada mountains.
- Small mammal richness was lower in areas with less time since last fire, longer fire return intervals, and a higher number of fires.
- Small mammal community turnover was higher in areas with more time since last fire and a higher number of fires.

## Keywords

California, community ecology, ecological modeling, Eulipotyphla, richness, Rodentia, Sierra Nevada, spatial distribution, spatiotemporal, turnover

## Introduction

Worldwide, anthropogenic climate change and related changes to other aspects of the environment are substantially influencing wildlife species and biodiversity (Abrahms et al. 2023; Rubenstein et al. 2023; Badr and El-Shazly 2024). One important region is California, which is considered a global biodiversity hotspot due to high species richness and endemism combined with substantial threats from human activities (Myers et al. 2000). Over the last century, the Sierra Nevada region of California has undergone, and continues to experience, significant ecosystem changes as a result of anthropogenic influences, climate change, and related impacts such as drought, reduced snowpack, warming, and vegetation shifts

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(Anderson 2004; Westerling et al. 2011; Stephens et al. 2021). Climate change, in combination with mismanagement of forests in western North America and broad-scale fire suppression, has resulted in increases in the prevalence of severe wildfires (Stephens et al. 2018; Roberts et al. 2019) and an overall change to the historical fire regimes of many regions. Fire regimes are defined by the patterns of fire over time within a region, characterized by fire severity, fire intensity, fire frequency, and area burned (Buechi et al. 2021; Stephens et al. 2021). Changes in the variables that comprise a region's fire regime are likely to impact the biodiversity of the Sierra Nevada, including over 400 species of vertebrates (Graber 1996) and over 3,000 species of vascular plants (Murphy et al. 2004). However, the understanding of how fire regime change has impacted Sierra Nevada ecosystems remains incomplete (Schwartz et al. 2015; Stephens et al. 2021; Buechi et al. 2021).

While the specific variables may differ across elevations and habitat types, historically, much of the Sierra Nevada region has been characterized by a regime of frequent mixed-severity fires, which have maintained the structure and heterogeneity of oak and coniferous forests by clearing understory overgrowth, maintaining meadows, and reducing fuel buildup (Anderson 2004; Westerling et al. 2011; Stephens et al. 2018, 2021; Buechi et al. 2021). Prior to European colonization, forests in California were maintained through the traditional use of controlled low- to moderate-severity burning by Native Americans, as well as natural lightning fires (Adams 2013; Klimaszewski-Patterson and Mensing 2020; Connor et al. 2022). European colonization in the 1800s disrupted Native American forest management, and fire suppression policies in the 20$^{th}$ century disrupted natural ecological processes, leading to a buildup of fuel (Calkin et al. 2015; Stephens et al. 2021; Connor et al. 2022). In conjunction with climate change, which has increased temperatures and decreased effective moisture (Hayhoe et al. 2004; LaDochy and Witiw 2023; Rubenstein et al. 2023), the Sierra Nevada region saw increasing proportions of high-severity fire starting in the 1980s and continuing through the 2000s; future estimates predict further increases in high-severity fire (Calkin et al. 2015; Buechi et al. 2021; Stephens et al. 2021). High-severity fires are generally categorized as "stand-replacing" (Stevens et al. 2017), with 70–90% tree mortality, which is considered a significant change in tree density, canopy cover, and forest type. Low- to moderate-severity fires are characterized by a change in shrub cover and understory brush, with 20–70% basal area tree mortality (Stevens et al. 2017). The shift to a higher proportion of high-severity fire thus resulted in major changes to forest and vegetation structure (Anderson 2004; Dixon et al. 2023). Predictions of the future trajectory of climate and wildfire in the Sierra Nevada (Hayhoe et al. 2004; Westerling et al. 2011) illustrate the need to better understand the combined effects of environmental change—drought, warming, habitat change, and resulting shifts in fire regime—on forest ecosystems, now and into the future.

Small mammals are key components of Sierra Nevada ecosystems, filling many roles such as seed and fungal dispersers, prey, and habitat engineers (Kelt et al. 2013, 2017; Borgmann-Winter et al. 2023; Ayomiposi Ayodele 2025). Thus, changes to small mammal communities will likely have significant impacts on other aspects of forest ecosystems (Hayward and Phillipson 1979; Curtin et al. 2000; Coppeto et al. 2006; Blois et al. 2010; Borgmann-Winter et al. 2023). In addition, small mammals are sensitive to fluctuations in vegetation and climate at both short and long time scales: some mammals have experienced range contractions due to environmental changes such as increases in temperature and drought (Moritz et al. 2008; Rowe et al. 2015; Kelt et al. 2017; Santos et al. 2017), and small mammals are highly dependent on habitat structure, so changes in vegetation have significant consequences for mammal occurrences (Coppeto et al. 2006; Sollmann et al. 2015; Torre et al. 2015). In particular, macrohabitat characteristics such as canopy cover and shrub cover appear to be primary drivers of small mammal community composition (Converse et al. 2006; Coppeto et al. 2006; Sollmann et al. 2015; Culhane et al. 2022). However, preferred vegetation characteristics are not uniform across all species within the small mammal community. For example, meadow voles require open meadow habitat, while water shrews often require dense understory near freshwater sources, and tree squirrels require canopy cover and mature trees (Coppeto et al. 2006; Meyer et al. 2009; Rubidge et al. 2011; Santos et al. 2017). Global change drivers such as fire that influence habitat thus impact small mammal communities in species-specific ways (Block et al. 2016; Ayars et al. 2023).

In the Sierra Nevada over the last century, small mammal communities have undergone compositional turnover coincident with climate change (Moritz et al. 2008; Rowe et al. 2015; Santos et al. 2017). In the early- to mid-1900s, Joseph Grinnell and colleagues conducted a series of surveys in the Sierra Nevada, generating a baseline of mammal species occurrences throughout the region (Grinnell 1916; Grinnell and Storer 1924). These sites were resurveyed in the early 2000s by a team affiliated with the University of California, Berkeley, in an effort called the Grinnell Resurvey Project, providing a high-quality dataset of small mammal species-level change and community turnover in the Sierra Nevada (Moritz et al. 2008; Rowe et al. 2015). Across the three regions, 25 of 34 species analyzed shifted their elevational ranges, with a majority of these shifts aligning with the expected species-specific responses to temperature increases and other changes in climate (Moritz et al. 2008; Rowe et al. 2015). These studies observed upward range expansions in low-elevation species such as the pinyon mouse (*Peromyscus truei*), low-end range contractions in mid-elevation species such as the long-tailed vole (*Microtus longicaudus*) and the western jumping mouse (*Zapus princeps*), and overall range contractions in high-elevation specialist species such as the alpine chipmunk (*Neotamias alpinus*) (Moritz et al. 2008; Rowe et al.

2015); overall, there was significant community compositional turnover between the survey and resurvey periods. A subsequent study that focused on a subset of the small mammal species determined that, while climate had the largest influence on small mammal ranges, changes in habitat type and vegetation cover were particularly important for predicting mid-elevation species range shifts (Santos et al. 2017). Several other studies in the Sierra Nevada have demonstrated connections between small mammal communities (i.e., richness and abundance) and habitat components such as canopy cover and canopy height (Coppeto et al. 2006; Kelt et al. 2013; Sollmann et al. 2015).

Compared to the impact of habitat and climate, the long-term impact of wildfire on small mammal communities, especially in the Sierra Nevada, is poorly understood. Some recent studies have explored the connection between fire, habitat changes, and small mammals in the Sierra Nevada but have mostly concentrated on immediate- to short-term responses to fire (Converse et al. 2006; Amacher et al. 2008; Roberts et al. 2008; Borchert et al. 2014; Culhane et al. 2022), with a maximum time since fire of 15 years (Roberts et al. 2015). Additionally, there have been a number of studies conducted on small mammals and prescribed fire regimes in the Sierra Nevada (e.g., Converse et al. 2006; Monroe and Converse 2006; Amacher et al. 2008). Together, these studies provide valuable insight into small mammal responses to fire. Overall, deer mice (*Peromyscus maniculatus*) tend to have a positive association with fire, other generalist species (i.e., chipmunks, ground squirrels) do not have a significant response, and sensitive, specialist species (i.e., shrews, tree squirrels) tend to respond negatively to fire. These studies have provided a strong initial foundation for understanding the impacts of fire on small mammals. However, many of these studies were limited by location and taxon (Zwolak and Foresman 2007; Roberts et al. 2008; Borchert et al. 2014; Culhane et al. 2022; Peyton et al. 2025) and do not capture the full extent of the impacts of fire, especially the impacts of changes to the fire regime on small mammal communities over a longer time scale.

Studies in other parts of the world have identified multiple factors relating to the long-term influence of fire on small mammal communities (Krefting and Ahlgren 1974; Fontaine and Kennedy 2012; Griffiths et al. 2014; Lindenmayer et al. 2016; Rossi and Leiner 2022; Tomassini et al. 2024). In Australia, where frequent fires are also a natural part of the ecosystem, there are multiple studies that incorporate time-series data, a crucial component missing from California datasets (Kelly et al. 2011; Chia et al. 2016; Lindenmayer et al. 2016). In these studies, fire regime variables such as the temporal interval between fires, fire severity, and number of past fires contribute to species occupancy and abundance (Kelly et al. 2011; Lindenmayer et al. 2016). A similar understanding of fire impacts on small mammal communities is needed in the California Sierra Nevada, where fire is an important, prevalent, and increasingly impactful factor within the landscape.

Here, we explore the drivers of small mammal richness and community turnover across a century, focusing on three sets of interrelated variables: fire, habitat and climate. We focus specifically on the influence of fire on small mammal communities because impacts of climate and vegetation are already well-established for mammals (Carey and Wilson 2001; Coppeto et al. 2006; Blois et al. 2010; Rubidge et al. 2011; Kelt et al. 2013, 2017; Sollmann et al. 2015; Santos et al. 2017), though we include all three sets of variables in most of our analyses because of their intertwined nature. First, we confirmed that our processed regional dataset aligned with previously established relationships between small mammal richness and environmental variables by asking: 1) What is the relationship between individual variables and small mammal richness? We anticipate richness will decrease with increased temperatures, and richness will be higher in regions with higher precipitation, elevation, canopy cover and canopy height. (Further expectations and citations are detailed in Suppl. material 1: table S1). Having established that our data processing reproduces known relationships, we ask the following questions: 2) What combination of variables best explains variation in small mammal richness across the Sierra Nevada? 3) Does the inclusion of fire variables improve model fit? We anticipate that a combination of fire, climate and vegetation variables will provide the strongest explanation of small mammal richness. Specifically, we anticipate that an increased number of fires, less time since last fire, and shorter fire return intervals would result in patchier landscapes, and thus higher small mammal richness. Finally, having established the importance of fire for spatial variation in small mammal communities across the region, we examine if fire regime has impacted small mammal community compositional dissimilarity over time (i.e., turnover). We ask: 4) Is there a relationship between turnover and fire variables? 5) Which small mammal species contribute the most to turnover across time? We expect that there will be significant relationships between fire regime variables and community turnover, and that specialist species will contribute the most to turnover.

# Methods

## Overall approach

We relied on data collected by the Grinnell Survey and Resurvey Project, an effort in the early 2000s to document changes in California vertebrate species occurrences through time (Moritz et al. 2008; Rowe et al. 2015). The Grinnell Survey and Resurvey Projects established three elevational transects in the northern, central, and southern regions of the Sierra Nevada and Cascade Mountain ranges in California: the Lassen region (LA; resampled from 2006–2009), the Yosemite region (YO; resampled from 2003–2006), and the Sequoia region (SE; resampled from

2008–2012). Each area was originally sampled by Joseph Grinnell and colleagues from 1904 to the 1940s, who recorded detailed metadata that allowed the resurvey team to approximate the locations of the original trapping sites, making the two datasets comparable. These datasets include high-quality small mammal occurrence data in areas minimally disturbed by direct human impacts. Moreover, the availability of both historic and modern small mammal data allows us to characterize community structure change across a century in California.

The Grinnell Resurvey Project based many of its original analyses on life zones (Fig. 1; Moritz et al. 2008), but different life zones encompass different amounts of area, which may affect comparisons of community-level metrics through species-area effects (Rosenzweig 1995). Thus, we defined sample areas as evenly spaced 200 m elevation bands along the approximately 0–3,600 m elevation gradient of the mountain ranges in each region, which should minimize (though not eliminate; Karger et al. 2011; Moradi et al. 2020) this effect. Lassen included data from 0 to 2,600 m in elevation (13 sample areas), Yosemite from 0 to 3,400 m (17 sample areas), and Sequoia from 0 to 3,600 m (18 sample areas), resulting in a total of 48 sample areas across California. This approach captures biologically and environmentally relevant variation across elevation, a dominant gradient in the Sierra Nevada. Additionally, calculating richness in elevation bands buffers small mammal richness against local effects of individual occurrences and short-term sampling, because richness is a variable that emerges at a regional scale over longer time scales (Christensen et al. 2018).

## Small mammal data

We used R (v. 4.5.3) and the packages 'vegan' (Oksanen et al. 2026) and 'tidyverse' (Wickham and RStudio 2023) to calculate modern small mammal richness and compositional turnover from data collected during the Grinnell Survey and Resurvey Projects and described by Moritz et al. (2008) and Rowe et al. (2015). These datasets document mammal species occurrences across 166 sites within the three regions (LA, YO, and SE). At each site, 40–150 traps were placed for 2–4 nights, including both Sherman and Tomahawk traps to capture a range of body sizes, and small mammal species occurrences were recorded. Subsequently, the Grinnell Resurvey Project authors developed occupancy models for each species with enough data to estimate the total elevational range occupied by the species (Rowe et al. 2015).

## Modern richness

Using 'tidyverse' and base R, we calculated modern richness within each sample area by summing the number of species present within each 200 m elevation band (i.e., 1–200 m, 201–400 m), where the presence of a species at an elevation was determined by the modern upper and lower elevation range limits for each species reported in Rowe et al. (2015, Suppl. material 1). We chose this method over summing the observed presences from the trapping data, as the occupancy modeling conducted by Rowe et al. (2015) accounts for sampling bias that may have occurred during surveys and controls for false absences.

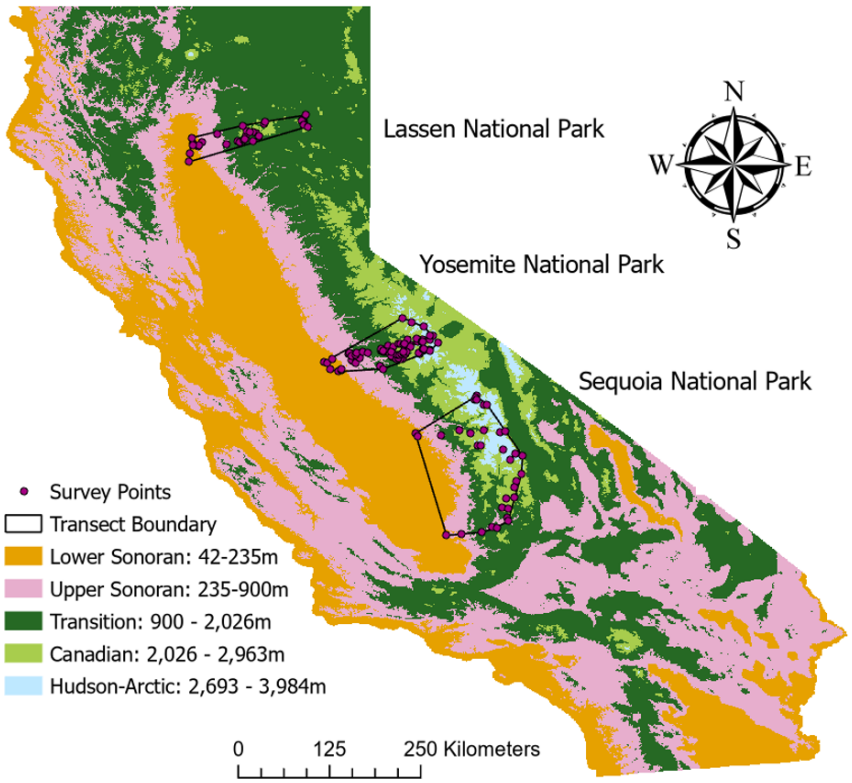


**Figure 1.** Map of California with color-coded elevation life zones. Points represent the survey sites from the Grinnell Resurvey Project (Rowe et al. 2015) in the three focal regions: Lassen National Park (LA), Yosemite National Park (YO), and Sequoia National Park (SE).

## Compositional turnover

We calculated compositional turnover between the historic and modern datasets within each 200 m sample area, using the 'vegdist' function in the R package 'vegan' to calculate Jaccard dissimilarity based on presence/absence data. We again relied on occupancy-modeled elevation range limits for each species in the historic and modern samples. Compositional turnover provides a more in-depth representation of community change compared to richness change, as richness-only measurements can obscure species-specific shifts.

## Environmental data

In ArcGIS Pro v. 3.6 we generated a series of random points at evenly spaced 5 km intervals within each sample area and extracted the environmental values (attributes of fire regime, vegetation, and climate; Table 1) at each point, which we used to characterize the environment for each sample area. We describe each attribute more fully below. Most analyses below were performed using R (v. 4.5.3), except where the use of ArcGIS Pro v. 3.6 is noted.

## Fire regime

We quantified fire regime using a variety of metrics, including time since last fire (TSLF), number of fires occurring across the time frame for each area (Num_Fire), and fire return interval (FRI). To calculate the fire regime variables, we used the California Department of Forestry and Fire Protection: Fire Resource Assessment Program dataset (FRAP), which includes complete fire perimeter data from 1908 to the present (Safford and Water 2014). In ArcGIS Pro v. 3.6, we extracted the year of occurrence for fires with fire perimeters that fell within 1 km of each random point within each region. All fires from the start of the complete dataset in 1908 to the start of the modern small mammal resurvey time periods for each region (YO < 2003, LA < 2006, SE < 2008) were included. This represents the "time frame" for each region.

The number of fires occurring within a specific time frame is a commonly used metric to describe fire regime because this substantially influences vegetation growth and behavior (Safford and Water 2014). Using 'tidyverse' and base R, we calculated number of fires (Num_Fire) as the total number of fires experienced throughout the sample area over the time frame. Similarly, time since last fire (TSLF) relates to the state of the current landscape as a result of the most recent fire (Safford and Water 2014). In addition to the mean time since last fire (mean_TSLF), we also calculated the standard deviation (SD_TSLF) to represent the variance among TSLF within the sample area. Fire return interval (FRI) is generally calculated using the number of fires, representing the amount of time between fires at a site (Safford and Water 2014); thus, we calculated fire return interval as ['number of years' divided by 'number of fires'] +1, in which the number of years corresponds to the amount of time in the fire record (1908 – first surveying year) and 'number of fires' is the 'Num_Fire' variable for the sample area. We explored using fire severity as a variable, but historical data on fire severity are much more limited than fire perimeter data, and we were unable to build a sufficient dataset to compare with small mammal richness and compositional change. All calculations were based on equations described in Safford and Water (2014).

## Vegetation

For vegetation, we used data from the Landscape Fire and Resource Management Planning Tools program LANDFIRE (LANDFIRE 2001). This database was created in 2002 to inform fire management and create publicly available datasets to support habitat and wildfire research. We downloaded the variables 'forest canopy height' and 'forest canopy cover' from the 2001 version of LANDFIRE (LANDFIRE 2001). These data include vegetation data through the year 2001, just prior to when the small mammal surveys were conducted (2003–2012). We extracted vegetation data from LANDFIRE at each of the random points, then we averaged the values within sample areas using 'tidyverse' and base R. The final vegetation variables included mean canopy cover (CC) and mean canopy height (CH).

## Climate

For climate, we relied on modern PRISM data collected at 4 km resolution (PRISM Group 2024). For each of the region years (YO: 2003–2006, LA: 2006–2008, SE: 2008–2012), we downloaded mean annual temperature and total annual precipitation at the coordinates of each of the randomly generated points using the R package 'prism' (Edmund et al. 2025). Using 'tidyverse' and base R, we averaged the values within sample areas. The final climate variables included mean annual temperature (tmean) and mean total precipitation (ppt).

## Analyses

We examined the relationships between modern small mammal richness and environmental/spatial variables to determine the most significant factors impacting small mammal communities. Additionally, we explored the relationships between community turnover and fire regime variables to examine the effects of fire on small mammals over the last century. Depending on whether variables were numerical or categorical, we used linear regression and ANOVA, respectively. We assessed normality of residuals using the function 'ad.test' from the R 'nortest' package (Gross and Ligges 2015) to run the Anderson-Darling test (Pettitt 1977). All datasets and model residuals conformed to the assumptions underlying linear regression and ANOVA. For

all analyses, we used the R packages 'ggplot2' (Wickham et al. 2026), 'gridextra,' (Auguie and Antonov 2026) and 'broom' (Robinson et al. 2026) to develop graphs and visualizations.

### Drivers of contemporary small mammal richness: individual relationships between richness and environment

We first explored trends in richness across regions and elevation. In base R, we used ANOVA to identify significant differences in richness across regions. Next, we used linear regression to identify the relationship between richness and elevation, and between richness and calculated environmental variables. For the elevation variable, we relied on the midpoint of each elevation band for a sample area. Our goal with the single variable linear regressions was to identify whether the quantification of richness followed expected relationships with environmental variables, such as vegetation and climate (listed in Suppl. material 1: table S1). Additionally, because we anticipated that many of the environmental variables would be collinear (e.g., elevation and temperature), we identified possible collinearity between all environmental variables using absolute Pearson correlation in base R (Suppl. material 1: fig. S1, table S2). We considered variables moderately collinear if the absolute Pearson correlation coefficient fell between 0.3 and 0.5 and strongly collinear if the correlation was above 0.5.

### Drivers of contemporary small mammal richness: multiple variable relationships between richness and environment

Based on the results from the previous section, including collinearity between environmental variables (Suppl. material 1: fig. S1, table S2), the relationships between individual variables and richness (Suppl. material 1: fig. S2), and biological factors likely to most strongly influence small mammal richness (Suppl. material 1: table S1), we developed two sets of multivariate regression models in base R to explore how multiple factors combined to influence richness. First, we performed multivariate analysis with all variables despite collinearity (All-Variables Model), and second, we performed multivariate analysis with PCA-based predictor variables (All-Variables PCA Model).

The All-Variables Model included small mammal richness as the dependent variable and all other variables, including temperature (tmean), precipitation (ppt), canopy cover (CC), canopy height (CH), elevation (elev), mean time since last fire (mean_TSLF), standard deviation of time since last fire (sd_TSLF), number of fires (Num_Fire), and fire return interval (FRI), as predictors. Fire return interval and number of fires contributed to non-normality of the residuals of the final models, so these variables were log-transformed (logNum_Fire, logFRI).

The All-Variables PCA Model used principal component analysis (PCA) to address collinearity and reduce the dimensionality of the predictors. We sought to identify whether a combination of multiple variables better represented richness than any single-variable relationship, even after accounting for collinearity. We used the function 'prcomp' from base R to develop composite, non-collinear variables. We then developed a multivariate model with small mammal richness as the dependent variable and the first four principal component axes as the predictor variables.

For each approach, we used the 'dredge' function from the package 'MuMIn' (Bartoń 2010) to narrow down the initial model to a series of final, best-fit models based on AIC values corrected for sample size (AICc). We excluded region from both sets of multivariate models because it 1) did not explain a significant amount of variation in the univariate models, 2) could not be transformed by PCA, as it is a categorical variable, and (3) contributed to non-normality of the model residuals.

### Relationship between fire regime and small mammal community change

To examine the relationships between fire and community change through time, both univariate and multivariate linear regression models were developed to compare compositional turnover of the small mammal community between the historic and modern sampling periods with each of the fire regime variables. We calculated turnover using the 'vegdist' function from the 'vegan' package (Oksanen et al. 2026), using the Jaccard dissimilarity index. In addition, in base R we calculated individual species contributions to community turnover, with species contribution being equal to the total number of changes (either gains or losses) in presence between historic and modern sampling periods.

## Results

### Drivers of small mammal richness: individual relationships between richness and environmental variables

The univariate models demonstrated that all variables generally behaved as expected (Suppl. material 1: fig. S2A–F), particularly the climate and vegetation variables that have been well studied previously. However, there were no significant univariate relationships between richness and individual fire regime variables (Suppl. material 1: fig. S2G–J).

### Collinearity between environmental variables

Several variables exhibited moderate to strong collinearity with one another, motivating the development of the All-Variables PCA models (Suppl. material 1: fig. S1, table S2).

## Multi-variable relationships between richness and environmental variables: all-variables model

The initial multivariate model included all environmental and spatial variables (except for region, as explained above) (Table 1). After variable selection, three models were within two ΔAICc units of each other (Table 2, All Variables Model). The best model ($F_{(6, 41)}$ = 12.41, adj. $R^2$ = 0.59, $p$ < 0.001, $\Delta AIC_c$ = 0) included all four fire regime variables in addition to canopy height and mean annual temperature. There were significant negative relationships between richness and log-transformed fire return interval, log-transformed number of fires, sd_TSLF, and temperature, and significant positive relationships between richness and mean_TSLF and canopy height (Table 2, Model All-1). The next best model was nearly the same ($F_{(6, 41)}$ = 12.41, adj. $R^2$ = 0.59, $p$ < 0.001, $\Delta AIC_c$ = 0.93), with a significant positive relationship with elevation instead of a negative relationship with temperature (Table 2, Model All-2). The third top model ($F_{(2, 45)}$ = 26.23, adj. $R^2$ = 0.59, $p$ < 0.001, $\Delta AIC_c$ = 1.83) included only two variables, canopy height and mean annual temperature; richness had a significant positive relationship with canopy height and a significant negative relationship with temperature (Table 2, Model All-3).

## All-variables PCA model

The first PCA axis (PC1) explained 40% of the variation, and we interpret it as a climate axis; precipitation and elevation midpoint had the strongest positive loadings and mean annual temperature had a strong negative loading on PC1 (Suppl. material 1: table S3). The second PCA axis (PC2) explained 25% of the variation and primarily represented fire and vegetation, with canopy cover, canopy height, and log number of fires negatively loaded and log fire return interval positively loaded on the axis. The third PCA axis (PC3) explained 15% of the variation, with canopy cover positively loaded and mean_TSLF negatively loaded. Lastly, the fourth PCA axis (PC4) explained 14% of the total variation, with mean_TSLF and sd_TSLF negatively loaded. Together, these four PCA composite axes explained 94% of the variation in environmental variables among sample areas (Suppl. material 1: table S3); we thus used the first four principal components for the All-Variables PCA model.

After variable selection, three PCA models were within two $\Delta AIC_c$ units of each other (Table 2, All Variables PCA Model). In the top All-Variables PCA model ($F_{(3, 44)}$ = 15.91, adj. $R^2$ = 0.49, $p$ < 0.001, $\Delta AIC_c$ = 0), richness had a significant positive relationship with PC1 and a significant negative relationship with PC2; there was neither a significant positive nor a significant negative relationship with PC4, though it contributed to the overall model (Table 2, Model PCA-1). In the next best model ($F_{(4, 43)}$ = 12.28, adj. $R^2$ = 0.49, $p$ < 0.001, $\Delta AIC_c$ = 1.31), richness again had a significant positive relationship with PC1 and a significant negative relationship with PC2; there was neither a significant positive nor a significant negative relationship with PC3 or PC4, though both variables contributed to the overall model (Table 2, Model PCA-2). In the final model ($F_{(2, 45)}$ = 12.28, adj. $R^2$ = 0.46, $p$ < 0.001, $\Delta AIC_c$ = 1.35), richness had a significant positive relationship with PC1 and a significant negative relationship with PC2; there was no contribution from PC3 or PC4 (Table 2, Model PCA-3). Overall, PC1 and PC2 were the significant axes explaining variation in richness.

**Table 1.** Environmental variables used in this study, including variables representing fire, vegetation, climate, and space (spatial). For each variable, the acronym used throughout the text and figures is provided. Dataset refers to the underlying dataset for each set of variables.

| Variables | Acronym | Dataset |
|---|---|---|
| **Fire** | | |
| Number of Fires | Num_Fire<br>logNum_Fire | California Department of Forestry and Fire Protection: Fire Resource Assessment Program (1908-present). For some analyses, fire return interval and number of fires were log-transformed (logFRI, logNum_Fire) |
| Fire Return Interval | FRI<br>logFRI | |
| Mean Time Since Last Fire | mean_TSLF | |
| Standard Deviation TSLF | SD_TSLF | |
| **Vegetation** | | |
| Forest Canopy Cover | CC | 2001 LANDFIRE database |
| Forest Canopy Height | CH | |
| **Climate** | | |
| Total Annual Precipitation | ppt | PRISM at 4 km resolution, averaged over resurvey time periods |
| Mean Annual Temperature | tmean | |
| **Spatial** | | |
| Elevation midpoint | elev | Grinnell Resurvey Project dataset |
| Region | region | |

**Table 2.** Multivariate models of variables significantly associated with small mammal (Rodentia, Eulipotyphla) modern richness and community turnover in the California Sierra Nevada mountains, based on *n* = 48 sample areas. Variable acronyms for the 'Modern richness: all variables model' and the 'Community turnover: fire regime variables model' can be found in Table 1. Acronyms for the 'Modern richness: all variables PCA model' refer to numerical PCA components. Adj. $R^2$ = adjusted R-squared. $AIC_c$ = Akaike Information Criterion corrected for sample size. The $AIC_c$ value is reported for each top model, and then $AIC_c$ shows subsequent additions for other models; all models within two $\Delta AIC_c$ units of the top model are shown. Significance codes: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

| **Modern Richness: All Variables Model** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Intercept** | **CH** | **logFRI** | **logNum_ Fire** | **mean_ TSLF** | **elev** | **sd_TSLF** | **tmean** | **adj. $R^2$** | ***p*-value** | **$AIC_c$** |
| All-1 | 101.50** | 0.02*** | −20.31* | −16.85* | 0.06* | | −0.11** | −0.29*** | 0.59 | $p < 0.001$ | 212.50 |
| All-2 | 109.50*** | 0.02** | −23.31** | −19.56* | 0.07* | −0.001*** | −0.11* | | 0.58 | $p < 0.001$ | + 0.93 |
| All-3 | 12.36*** | 0.02*** | | | | | | −0.20** | 0.52 | $p < 0.001$ | + 1.83 |
| **Modern Richness: All Variables PCA Model** | | | | | | | | | | | |
| **Model** | **Intercept** | **PC1** | **PC2** | **PC3** | **PC4** | | | | **adj. $R^2$** | ***p*-value** | **$AIC_c$** |
| PCA-1 | 12.73*** | 0.72*** | −1.07*** | | 0.55 | | | | 0.49 | $p < 0.001$ | 218.70 |
| PCA-2 | 12.73*** | 0.72*** | −1.07*** | −0.30 | 0.55 | | | | 0.49 | $p < 0.001$ | + 1.31 |
| PCA-3 | 12.73*** | 0.72*** | −1.07*** | | | | | | 0.46 | $p < 0.001$ | + 1.35 |
| **Community Turnover: Fire Regime Variables Model** | | | | | | | | | | | |
| **Model** | **Intercept** | **FRI** | **mean_ TSLF** | **Num-Fire** | | | | | **adj. $R^2$** | ***p*-value** | **$AIC_c$** |
| Turn-1 | 0.08*** | | 0.003*** | 0.005** | | | | | 0.30 | $p < 0.001$ | −83.40 |
| Turn-2 | 0.10* | −0.001 | 0.003*** | 0.004* | | | | | 0.29 | $p < 0.001$ | + 1.63 |

## Community turnover: single-variable models

There were significant positive relationships between community turnover and mean_TSLF (Fig. 2A; $F_{(1, 46)} = 7.62$, adj. $R^2 = 0.12$, $p = 0.008$), sd_TSLF (Fig. 2B; $F_{(1, 46)} = 4.25$, adj. $R^2 = 0.06$, $p = 0.04$), and number of fires (Fig. 2C; $F_{(1, 46)} = 5.27$, adj. $R^2 = 0.08$, $p = 0.03$). There was no significant relationship between turnover and fire return interval (Fig. 2D; $F_{(1, 46)} = 0.28$, adj. $R^2 = -0.02$, $p = 0.60$).

## Community turnover: multivariate models

After model selection, two multivariate community turnover models were within two $\Delta AIC_c$ units of each other (Table 2, Community Turnover). In the top multivariate model for community turnover, turnover had significant positive relationships with the number of fires and mean_TSLF (Table 2, Model Turn-1; $F_{(2, 45)} = 10.91$, adj. $R^2 = 0.30$, $p < 0.001$, $\Delta AIC_c = 0$). In the second model (Table 2, Model Turn-2; $F_{(3, 44)} = 7.51$, adj. $R^2 = 0.29$, $p < 0.001$, $\Delta AIC_c = 1.63$), turnover also had significant positive relationships with the number of fires and mean_TSLF; in addition, there was neither a significant positive nor a significant negative relationship with fire return interval, though this variable contributed to the overall model.

## Species-specific turnover

Of the 34 species, 27 demonstrated gains or losses between the two time periods within at least one sample area (Fig. 3, Suppl. material 1: table S4). Five species were the highest contributors to community turnover (>10 total changes across sample areas): long-eared mice (*Peromyscus truei*: total change = 14 sample areas, gains = 8, losses = 6), water shrews (*Sorex palustris*: total change = 12 sample areas, gains = 1, losses = 11), the bushy-tailed woodrat (*Neotoma cinerea*: total change = 11 sample areas, gains = 0, losses = 11), the western gray squirrel (*Sciurus griseus*, total change = 11 sample areas, gains = 3, losses = 8), and the meadow jumping mouse (*Zapus princeps*: total change = 10 sample areas, gains = 3, losses = 7).

# Discussion

A century of fire suppression in the Sierra Nevada has resulted in changes to fire regimes that will likely have substantial impacts on ecosystems going forward (Calkin et al. 2015; Buechi et al. 2021; Stephens et al. 2021). We sought to better understand how fire impacts small mammal communities, both isolated from and in tandem with vegetation and climate. Metrics of fire regime emerged as important variables in both small mammal richness and community compositional change, explaining variation in community structure above and beyond climate and vegetation alone.

## Impacts of fire, vegetation, and climate on small mammal richness

Fire suppression has negatively impacted Sierra Nevada forests by reducing the heterogeneity of vegetation across the landscape and increasing the total amount of fuel, leading to high-severity and stand-replacing megafires. Given these impacts and the importance of both heterogeneity and canopy cover for small mammals (Coppeto et al. 2006; Borchert et al. 2014; Sollmann et al. 2015), we

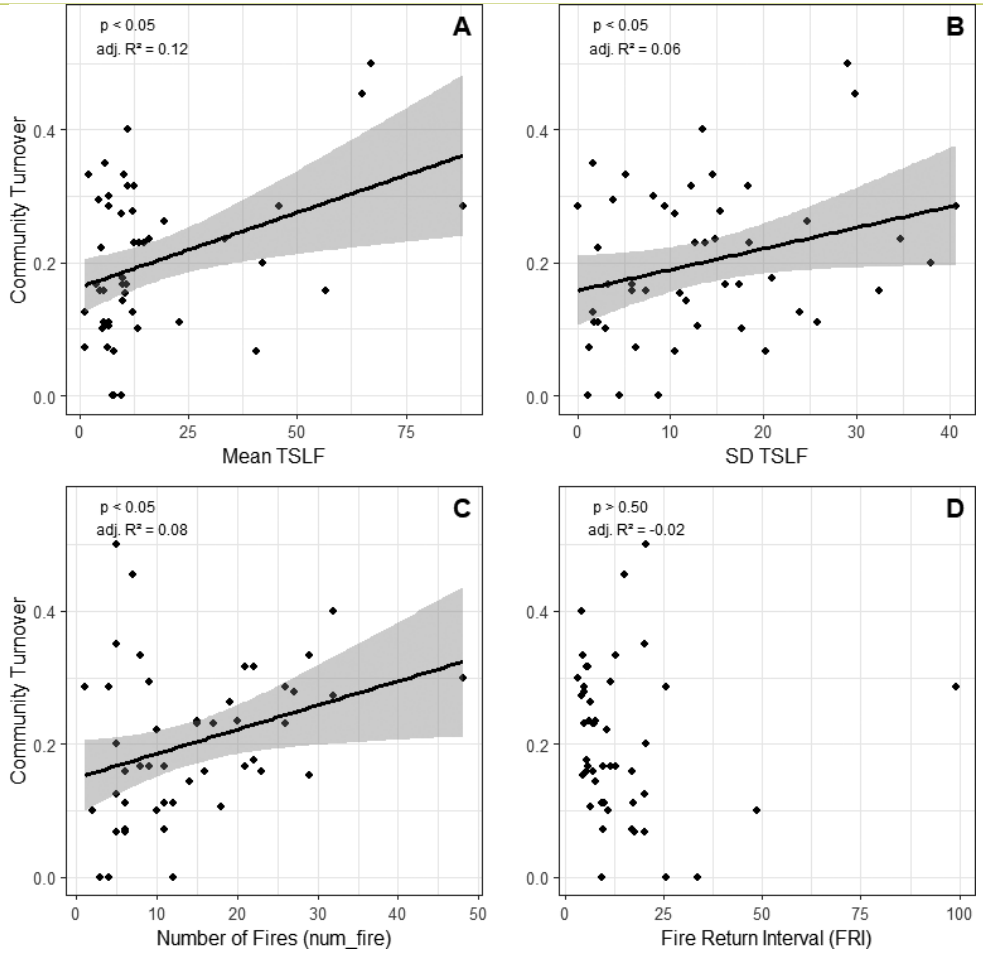


**Figure 2.** Linear regression models comparing small mammal (Rodentia, Eulipotyphla) community turnover in the California Sierra Nevada mountains ($n$ = 48 sample areas) to fire regime variables. **A.** Mean time since last fire (mean_TSLF) ($F_{(1,45)}$ = 7.67, $p$ < 0.01, adj. $R^2$ = 0.13); **B.** Standard deviation of time since last fire (SD TSLF) ($F_{(1,45)}$ = 5.11, $p$ < 0.05, adj. $R^2$ = 0.08); **C.** Number of fires ($F_{(1,45)}$ = 4.29, $p$ < 0.05, adj. $R^2$ = 0.07); and **D.** Fire return interval (FRI) ($F_{(1,45)}$ = 0.28, $p$ = 0.60, adj. $R^2$ = −0.02). Gray shading indicates the 95% confidence interval around the regression line.

expected to see significant relationships between fire regime variables and small mammal richness (Suppl. material 1: table S1). This expectation was supported by the multivariate models, which highlighted that each of the fire regime variables contributed in some way to small mammal richness, either positively or negatively, though not all relationships matched expectations. In addition, the results reaffirm the importance of vegetation and climate as factors influencing small mammal richness, generally conforming to established relationships between richness and vegetation, climate, and elevation in California.

We expected that higher small mammal richness would correspond with a greater number of fires, more recent fires (lower mean TSLF), and a shorter fire return interval (Suppl. material 1: table S1). This expectation was partially met: in the modern richness multivariate models, higher small mammal richness was associated with shorter fire return intervals (a negative relationship between the two variables), in addition to decreased temperatures, greater canopy height, and higher elevations (Table 2). Previous studies in the Sierra Nevada mountains have identified that small mammal species are moving upslope coincident with climatic warming (Moritz et al. 2008; Rowe et al. 2015; Santos et al. 2017; Abercrombie et al. 2026), suggesting that richness would be greater at higher elevations and lower temperatures. In addition, the observed negative relationship between longer fire return intervals and richness makes sense, as a longer overall cycle of fire over the last century is likely associated with areas that experienced strong fire suppression, which led to habitat homogenization and lower richness.

However, contrary to our expectations, higher small mammal richness corresponded with fewer fires, more time since last fire, and less variation (lower standard deviation) in time since last fire. Because some of these relationships between richness and fire regime variables appear to be contradictory (e.g., shorter fire return interval vs. more time since last fire), teasing out the exact response of the small mammal community to fire can be difficult, as exhibited by multiple previous studies (Krefting and Ahlgren 1974; Kelly et al. 2011; Borchert et al. 2014; Lindenmayer et al. 2016). However, all of the relationships with fire were observed in tandem with climate, elevation, and vegetation variables, as fire regime variables only emerged as significant in the multivariate and PCA models, rather than the univariate models. Thus, when considering all of the variables together,

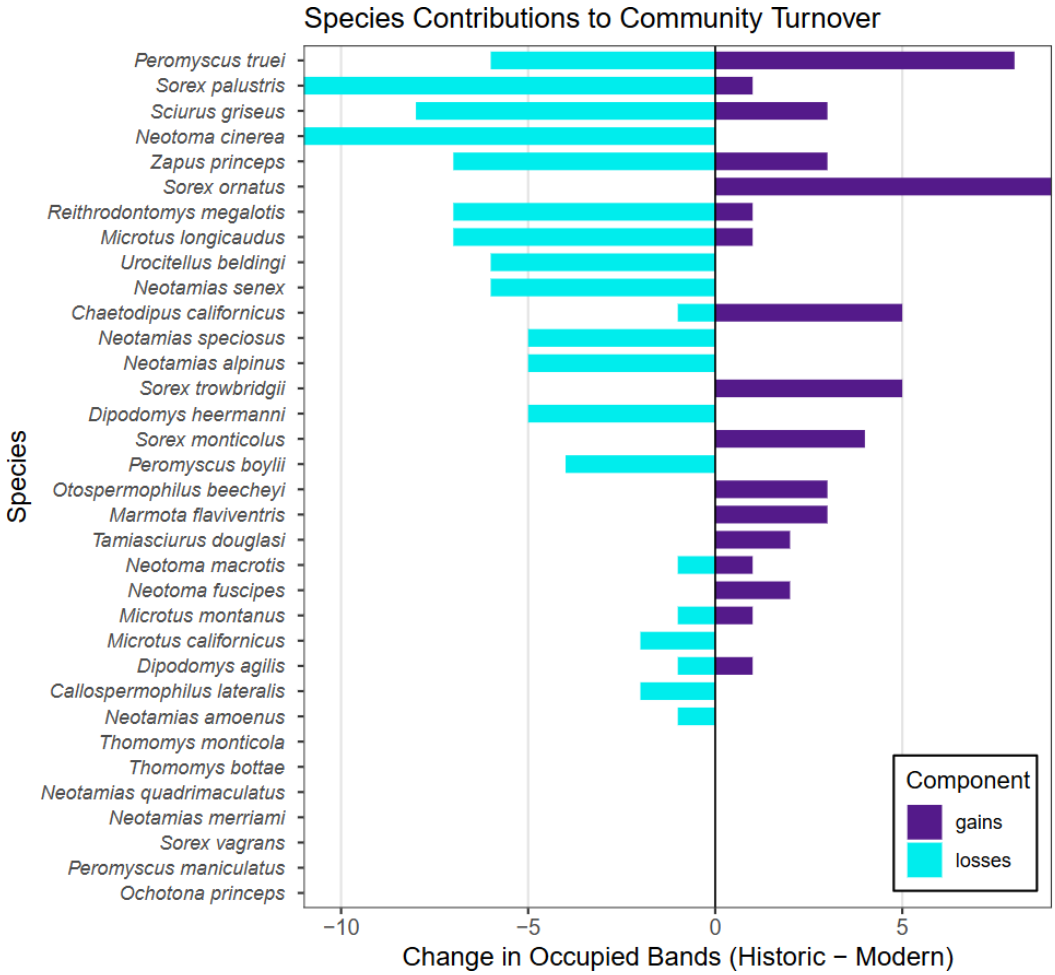


**Figure 3.** Species contributions to small mammal (Rodentia, Eulipotyphla) community turnover in the California Sierra Nevada mountains (*n* = 48 sample areas or occupied bands) between historic and modern sampling periods. The figure is ordered with the species with the highest contribution at the top. Values above 0 (right, dark) indicate the number of sample areas to which a species is added through time (gains). Values below 0 (left, light) indicate species losses or the number of sample areas at which a species disappears through time. Corresponding values are reported in Suppl. material 1: table S4.

including vegetation, as a 'fire regime' rather than simply individual variables, the patterns become clearer. Our data indicate that sample areas with more recent fires have lower small mammal richness, likely because at shorter time scales, fire and its impact on vegetation reduce species richness; the community needs time to fully recover after fire. Additionally, the more recent fires are likely associated with higher fire severity (Miller et al. 2009; Stevens et al. 2017), a variable not captured in the model, which contributes to the strong impacts on vegetation.

These same patterns are also largely seen in the PCA-based models that better account for collinearity between variables. Richness is strongly related to variation in PC1 and PC2. PC1 primarily captures variation in climate and elevation, and the PCA model demonstrates that richness is positively related to precipitation and elevation and negatively related to temperature. PC2 captures variation in vegetation and fire attributes, and the PCA model shows that richness is negatively related to fire return interval (higher richness at shorter FRI) and positively related to the number of fires, canopy cover, and canopy height. This matches the current understanding of the importance of these variables for richness in the Sierra Nevada mountains, though it shows a different relationship between richness and the number of fires than the multivariate model. This difference is not particularly surprising, given that the influence of fire as a whole on small mammal richness seems to be mediated by the interaction between fire and vegetation.

Overall, the impact of climate, vegetation, and fire regime on small mammals has considerable nuance. The extent to which each category of variables impacts small mammal communities varies, with many studies highlighting climate, and often temperature, as the primary indicator of small mammal distributions (Moritz et al. 2008; Knapp et al. 2011; Tingley 2011; Rowe et al. 2015; Roberts et al. 2019). In contrast, our work identified that vegetation, and in particular canopy height, was the most important variable structuring small mammal communities. Other studies exploring habitat characteristics of vegetation show that some small mammal species prefer more open canopies with higher shrub density (Coppeto et al. 2006; Sollmann et al. 2015), while certain specialist species

prefer less open canopies (Meyer et al. 2009; Kelt et al. 2013), in line with variation in individual species' niches. These mixed results on the local impacts of variables among different species (Carey and Wilson 2001; Coppeto et al. 2006; Sollmann et al. 2015) make parsing out a community-wide trend across multiple different regions in the Sierra Nevada difficult. Our study explored richness on a broad, regional scale and demonstrated strong positive relationships with vegetation (canopy cover and height) and negative effects of long fire regimes and the legacy of fire suppression on Sierra Nevada forests.

## Impacts of fire on small mammal turnover across the last century

Community turnover over the last century was explained through a combination of multiple fire variables (Table 2). Small mammal communities experienced higher turnover coincident with a greater amount of time since last fire, as well as a higher number of fires, a result supported by both the univariate and multivariate models. Taken together, this suggests that a recent fire was unlikely to greatly disturb community composition, but that many fires occurring within the same sample area led to a shift in the composition of the community. Given that these variables are somewhat contradictory, we propose that these fire regime variables likely contribute to turnover differently in different regions, rather than occurring within the same sample area. For example, in some places, turnover is driven by the lack of fire (i.e., high mean TSLF), while in other places, turnover is driven by multiple fires occurring within the sample area. Based on this, we would expect to see both gains and losses in areas with more time since last fire, while primarily species losses in areas with a higher number of fires.

Of the species that contributed most to community turnover, there did not seem to be a clear pattern as to whether specialists or generalists were more influential or whether turnover was characterized primarily by gains or losses (Fig. 3). The species that contributed the most to turnover (through both gains and losses) was the pinyon mouse (*Peromyscus truei*), which, as shown in previous studies with the Grinnell dataset, has expanded its range upward between the historic and modern periods, likely due to the impacts of climate (Moritz et al. 2008; Rowe et al. 2015; Abercrombie et al. 2026). Similarly, the long-tailed vole (*Microtus longicaudus*) and the western jumping mouse (*Zapus princeps*), which both greatly contributed to community turnover through losses within sample areas, were recorded in previous studies as experiencing lower-limit range contractions, again attributed primarily to climate (Moritz et al. 2008; Rowe et al. 2015; Abercrombie et al. 2026). Our research suggests that climate was not the only driving force behind these range shifts, as the amount of time since the last fire and the number of fires were significant factors influencing community turnover. Species that contributed the most to turnover through loss in a sample area may have been less able to tolerate multiple fires or the habitat generated by multiple fires in a row, leading to range shifts. Additionally, many of these species prefer shrubs and heterogeneous landscapes and historically come from frequent-fire forests. If a fire occurred more recently, the forest likely became more similar to what it looked like in the early 1900s, before fire suppression efforts.

Here, fire regime variables have been recorded from 1908 to the present, making it possible to see the influence of fire across the last century. In contrast, vegetation change is difficult to measure over the time frames of this study, given the lack of concrete historical data, so changes in vegetation variables through time have not been included in many previous papers or in this study. Since we demonstrated that contemporary vegetation had a strong influence on variation in contemporary richness across space in the previous section, and fire and vegetation were closely linked variables, we expect that fire regime likely represents at least a partial proxy for vegetation change over the last century.

These findings are supported by previous studies conducted in frequent-fire forests that have demonstrated that time since last fire and the number of fires at a site impact the presence of terrestrial small mammal species, though species presence after fire tends to be highly selective based on the habitat associations of these species (Kelly et al. 2011; Borchert et al. 2014; Lindenmayer et al. 2016). Generally, too-frequent fire can reduce the availability of habitat variables such as coarse woody debris and thus reduce species richness, but without the presence of any fire, habitat quality also tends to degrade (Converse et al. 2006; Moritz et al. 2008; Connor et al. 2022). Given this context, semi-frequent low- to medium-severity fire is most likely to generate habitats that support diverse small mammal communities (Roberts et al. 2008, 2015; Connor et al. 2022; Culhane et al. 2022).

## Caveats

We focused on characterizing the overall community richness of mammals to capture an important metric that has been underexplored. In many studies observing the effects of wildfire on small mammals, especially in California, the focus is on the abundance of particular species rather than richness, as demonstrated by a meta-analysis summarizing the impacts of fire on small mammals (Griffiths et al. 2014). However, focusing on abundance or species distributions tends to exclude rare, often more specialist species (e.g., Roberts et al. 2008; Borchert et al. 2014; Chia et al. 2016). While richness is a blunt tool, it captures a broader cross-section of the community. Even so, due to our reliance on occupancy-modeled elevation ranges, which are themselves affected by rarity, we likely still did not capture the full richness of the small mammal community. We sought to dampen site-level sampling effects by compressing data into elevation bands to capture richness across the landscape, but this makes deciphering dynamics within any one sample area difficult.

In addition, many of the environmental variables were significantly collinear, likely contributing to the larger adjusted $R^2$ values observed in the multivariate models compared to the PCA models. However, after accounting for collinearity through principal component analysis, multivariate PCA-based models still outperformed all of the univariate models comparing richness with individual variables (in terms of the total amount of explained variation), and the PCA loadings demonstrate that each of the environmental variables contributed substantially to the final models.

As our focus was on the importance of fire, we did not explore the full scope of climate and vegetation variables. We instead relied primarily on mean annual temperature and mean total precipitation to capture climate differences among sample areas, while other studies have included variables such as precipitation of the wettest month, annual temperature range, and temperature seasonality (Rubidge et al. 2011). In addition, we were unable to model the effects of fire severity due to the limitations in available data and we chose not to use habitat type as a vegetation characteristic due to the difficulty of averaging this categorical value across sites. However, across studies, the climate and vegetation metrics we included have been found to strongly influence small mammals (Rowe et al. 2015; Sollmann et al. 2015; Santos et al. 2017), so our reliance on mean annual temperature and mean total precipitation for climate and canopy height and cover for vegetation likely captures the dominant features explaining variation in small mammal richness at a macro scale.

## Conclusion

Fire is an increasingly dominant force within the Sierra Nevada and elsewhere, and so this study is a first step in better understanding the intertwined impacts of fire, climate, and vegetation on small mammal communities. We document an important relationship between fire and small mammal communities, supporting hypotheses that small mammals prefer frequent-fire, heterogeneous landscapes (Kelt et al. 2013, 2017; Roberts et al. 2015). Though our research suggests that longer fire return intervals result in less rich small mammal communities, and thus shorter fire return intervals support richer small mammal communities, this is tied to the assumption that a frequent fire regime would create the patchy, irregular landscapes preferred by small mammals through low- to mixed-severity fires. With the increase in high-severity stand-replacing megafires, many landscapes are experiencing complete loss rather than healthy turnover (Williams et al. 2022). Recent research has started to demonstrate when, how, and if areas with high-severity wildfires will recover (Zwolak and Foresman 2007; Culhane et al. 2022; Green et al. 2024; Peyton et al. 2025), but more is needed to completely understand the effects of high-severity fire on small mammal species and communities. Furthermore, our research supports the hypothesis that disruption of fire regime will likely have lasting consequences going forward, given that high-severity fires will negatively impact important vegetation attributes such as canopy cover and canopy height, and small mammal richness also had negative associations with recent fire.

A century of fire suppression in the Sierra Nevada has resulted in changes to fire regimes that will likely have substantial impacts on ecosystems going forward (Calkin et al. 2015; Buechi et al. 2021; Stephens et al. 2021). We sought to better understand how fire impacts small mammal communities, both isolated from, and in tandem with, vegetation and climate. Our results are consistent with previous research that identified both climate and vegetation as important factors driving small mammal richness in the Sierra Nevada (Rubidge et al. 2011; Kelt et al. 2017; Santos et al. 2017), as well as studies that have shown the importance of fire in structuring small mammal communities (Zwolak and Foresman 2007; Roberts et al. 2008, 2015). Overall, fire emerged as an important factor in determining small mammal richness and community turnover in almost every analysis we completed. However, fire is also inextricably linked with climate and vegetation, and future research should endeavor to include fire when attempting to understand small mammal community drivers over space and time.

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## Additional information

### Conflict of interest
The authors have declared that no competing interests exist.

### Ethical statement
No ethical statement was reported.

### Artificial Intelligence (AI) use
The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
Regarding the use of AI in the preparation of this manuscript, the authors declare the following: GPT
Used for: Data analysis
We utilized GPT for assistance in development and streamlining of code produced for R and RStudio.

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### Author contributions
RW and JLB designed the project. RW collected and analyzed the data and developed the initial interpretations and draft of the manuscript. JLB provided feedback and edits on data, analyses, interpretations, and text. Both authors revised the manuscript and responded to reviewer comments.

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### Data availability
Data and code are publicly available in the bloispaleolab GitHub repository at: https://github.com/bloispaleolab/Frontiers_Impacts-Fire-SmMammals-California.

## Supplementary materials

## Supplementary material 1

### Additional information (.pdf)
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