

RESEARCH ARTICLE

WILDFIRES ALTER RODENT COMMUNITY STRUCTURE ACROSS FOUR VEGETATION TYPES IN SOUTHERN CALIFORNIA, USA

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ABSTRACT

We surveyed burned and unburned plots across four habitat reserves in San Diego County, California, USA, in 2005 and 2006, to assess the effects of the 2003 wildfires on the community structure and relative abundance of rodent species. The reserves each contained multiple vegetation types (coastal sage scrub, chaparral, woodland, and grassland) and spanned from 250 m to 1078 m in elevation. Multivariate analyses revealed a more simplified rodent community structure in all burned habitats in comparison to unburned habitats. Reduction in shrub and tree cover was highly predictive of changes in post-fire rodent community structure in the burned coastal sage scrub and chaparral habitats. Reduction in cover was not predictive for the less substantially burned woodlands and grasslands, for which we hypothesized that interspecific competition played a greater role in post-fire community structure. Across vegetation types, generalists and open habitat specialists typically increased in relative abundance, whereas closed habitat specialists decreased. We documented significant increases in relative abundance of the deer mouse (*Peromyscus maniculatus* Wagner) and Dulzura kangaroo rat (*Dipodomys simulans* Merriam). In contrast, we found significant decreases in relative abundance for the California mouse (*Peromyscus californicus* Gambel), San Diego pocket mouse (*Chaetodipus fallax* Merriam), desert woodrat (*Neotoma lepida* Thomas), and brush mouse (*Peromyscus boylii* Baird). Currently, our research program involves assessment of whether habitat conservation plans (HCPs) in southern California provide long-term protection to HCP covered species, as well as preserve ecosystem function. The scenario of increased wildfires needs to be incorporated into this assessment. We discuss our results in relation to management and conservation planning under a future scenario of larger and more frequent wildfires in southern California.

Keywords: *Chaetodipus*, chaparral, coastal sage scrub, *Dipodomys*, grassland, *Neotoma*, *Peromyscus*, small mammals, wildfire, woodland

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INTRODUCTION

Wildfires have long been a part of the natural and human-altered environments of southern California, USA. However, the frequency and scope of these fires have substantially increased in comparison to historic levels (Wells *et al.* 2004). Keeley *et al.* (2004) related this phenomenon to a combination of fire suppression efforts and an increase in ignition sources associated with human population growth. Although native vegetation communities of southern California evolved various survival strategies to adapt to fire (Hanes 1971, Vogl and Schorr 1972, Keeley and Keeley 1981, Zedler *et al.* 1983, Keeley and Fotheringham 2001), large and repeated fires can drastically and permanently alter the habitat, converting diverse chaparral and coastal sage scrub into simple non-native grasslands (Zedler *et al.* 1983, Keeley 2005). Concomitantly, these fires can have short- and long-term impacts on animal communities in a region already recognized as being one of the most at risk areas for loss of biodiversity (Mittermeier *et al.* 1997).

In October 2003, wildfires burned approximately 300 000 hectares (ha) in southern California. This included approximately 130 000 ha in San Diego County from the Cedar and Otay fires that resulted in the loss of nearly 5000 structures and in 15 human fatalities (CDF 2003). A network of planned reserve habitat and open space totaling almost 80 000 ha, known as the Multiple Species Conservation Plan (MSCP; City of San Diego 1997), was heavily impacted by these two fires. Half of the protected lands within the MSCP were affected by the fires and some protected habitats were entirely burned.

Concern over the recovery of these habitats and the species within them motivated our efforts to conduct this research. As part of a larger long-term study of the effects of wildfires on multiple taxonomic groups (Mendelsohn *et al.* 2008, Rochester *et al.* 2010a, Matsuda *et al.* 2011), we examined the short-term effects of the Cedar and Otay fires on na-

tive rodent communities. Rodents occupy a central position in the food web and perform many ecological functions (Polis *et al.* 1997). As a food source for many predators, they serve as important links between producers and higher level consumers. Rodent burrows provide shelter for many species, serve to aerate the soil, and aid in surface water absorption. Finally, by consuming and distributing seeds, they also affect successional patterns and vegetation characteristics in many habitats (Tevis 1956, Price and Jenkins 1986, Brock and Kelt 2004).

Currently, three rodent species (San Diego pocket mouse [*Chaetodipus fallax fallax* Merriam], Dulzura pocket mouse [*C. californicus femoralis* Allen], and desert woodrat [*Neotoma lepida* Thomas]) in our study are listed as Species of Special Concern by the California Department of Fish and Game (Williams 1986).

Prior to our investigation, studies of fire effects on rodent and small mammal communities have largely been limited to single sites or habitat types without replication over the larger landscape (Cook 1959, Lawrence 1966, Price and Waser 1984, Wirtz *et al.* 1988, Schwilk and Keeley 1998, Converse *et al.* 2006). The size and scope of the 2003 wildfires presented a unique opportunity to sample across four natural reserves within San Diego County. The reserves span low to moderate elevations and each contained a mixture of vegetation types representing the natural landscapes of southern California. Our objectives were: 1) to determine the short-term effects of fire on rodent community structure across four vegetation types (coastal sage scrub, chaparral, grassland, and woodlands), 2) to determine if changes in post-fire community structure were associated with changes in vegetation structure, 3) to determine if individual species responses were predictable based upon habitat preferences and life-history characteristics, and 4) to identify species at risk in consideration of a changing fire regime in southern California.

METHODS

Study Sites

Our study sites were Rancho Jamul Ecological Reserve-Hollenbeck Canyon Wildlife Area (Rancho Jamul), Otay Mountain Wilderness-Little Cedar Ridge (Little Cedar), Santa Ysabel Open Space Preserve (Santa Ysabel), and Elliott Chaparral Reserve (Elliott) in San Diego County, California (Figure 1).

Rancho Jamul is in the lower foothills of southwestern San Diego County, approximately 30 km from the coast. Coastal sage scrub, oak and sycamore woodlands, native and non-native grasslands, and riparian vegetation are the dominant vegetation types. The most common plant species at the site include brome grass (*Bromus* spp. L.), wild oats (*Avena* spp. L.), California buckwheat (*Eriogonum fasciculatum* Benth.), California sage (*Artemisia californica* Less.), coast live oak (*Quercus agrifolia* Née), western sycamore (*Platanus racemosa* Nutt.), laurel sumac (*Malosma laurina* [Nutt.] Nutt. ex Abrams), and San Diego sunflower (*Viguiera laciniata* A. Gray). The property is 2797 ha in size with an average elevation of 250 m. The Otay Fire burned 37% of the southern portion of this site in October 2003.

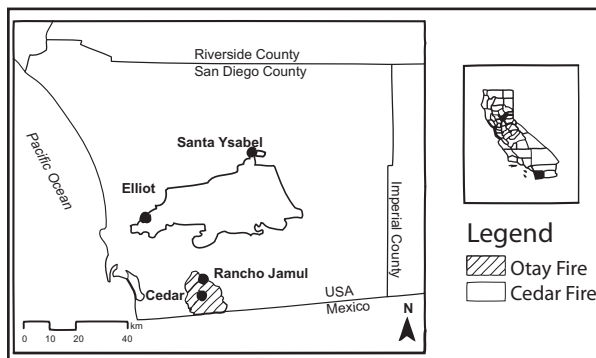


Figure 1. The four study sites in San Diego County, California, USA: Little Cedar Ridge (Little Cedar), Elliott Chaparral Reserve (Elliott), Rancho Jamul Ecological Reserve (Rancho Jamul), and Santa Ysabel Open Space Preserve (Santa Ysabel).

Little Cedar is 6 km south of Rancho Jamul on the northern slopes of Otay Mountain. It is dominated by coastal sage scrub, mixed chaparral, and cypress forest. The most common plant species at the site are chamise (*Adenostoma fasciculatum* Hook. and Arn.), tecate cypress (*Cupressus forbesii* Jeps.), annual non-native grasses, brome grass and wild oats, and California buckwheat (*Eriogonum fasciculatum* Benth.). The property is 6800 ha in size, ranges from 250 m to 1000 m in elevation, and was completely burned in the Otay Fire of 2003. The average elevation of our study plots in the Little Cedar site is 400 m.

Santa Ysabel spans the upper foothills and lower mountains of north-central San Diego County approximately 60 km from the coast and is dominated by oak and pine woodlands, native and non-native grasslands, coastal sage scrub, chaparral, and riparian vegetation. The most common plant species in the various habitats are coast live oak, brome grass, chamise, Engelmann oak (*Quercus engelmannii* Greene), wild oats, and white sage (*Salvia apiana* Jeps.). This property is 2188 ha in size, is split into east and west properties, and has an average elevation of 1078 m. In 2003, 47% of the property was burned in the Cedar Fire.

Elliott is located approximately 25 km from the coast. It is predominately coastal sage scrub and chaparral, with chamise, California buckwheat, and annual non-native brome grass and wild oats. The property, while only covering 43 ha within its boundaries, is bordered by expansive open space in the Marine Corps Air Station Miramar and has an average elevation of 195 m. The entire property was burned in October 2003 by the Cedar Fire.

Rodent Surveys

In the summer of 2001 and fall of 2003, we surveyed rodents at 16 study plots in the coastal sage scrub and grasslands at Rancho Jamul, giving us a limited amount of pre-fire data. In

2005 and 2006, two and three years following the 2003 wildfires, we surveyed for rodents in burned and unburned habitats at 63 study plots across all four sites using the same methods. We sampled each site four times per year, twice in the spring and twice in the fall. All plots were within one of four vegetation types: chaparral, coastal sage scrub, grassland, and woodland (Table 1).

We surveyed all plots using an array of seven pitfall traps, three funnel traps, and 18 Sherman live-traps. For the pitfall trap array, we buried seven 19 L buckets flush with the ground and connected them using shade cloth drift fence. These arrays formed a “Y” shape, with each arm being approximately 15 m long and the buckets buried 7.5 m apart as described by Fisher *et al.* (2008). We placed one funnel trap along each arm between the two outer buckets (Fisher *et al.* 2008). We then placed nine pairs of Sherman live-traps approximately 1 m and 16 m from the center bucket between each arm of the drift fence and approximately 9 m from the center bucket along each arm of the drift fence. Each pair was composed of one Sherman XLK trap (8 cm × 9 cm × 30.5 cm) and one larger Sherman XLF15 trap (10 cm × 11.5 cm × 38 cm). We left pitfall and funnel traps unbaited as passive traps for mam-

mals, and baited Sherman traps with steam-rolled oats. We placed raised bucket lids over the pitfall traps and wood roof tiles over the funnel and Sherman traps to provide daytime shading and cover for captured animals. We placed a baseball sized piece of polyester batting in all of the trap types to insulate captured animals from colder nighttime temperatures. For each session, we sampled traps each morning for four consecutive days. Including all trap types, our sampling effort totaled 168 trap-nights per array before the fire and 336 trap-nights per array after the fire.

We handled and processed all animals in a humane manner as approved by USGS Animal Care and Use Committee and in accordance with ASM guidelines (Sikes and Gannon 2011). We identified all rodents to species and temporarily marked them by hair clipping to identify recaptures within each session.

Vegetation Surveys

We measured the vegetation at each plot before the 2003 wildfires and again in the spring of 2005 and 2006. We recorded species composition, vegetation height, substrate, and leaf litter depth at 0.5 m intervals along a 50 m linear transect for a total of 100 data points per

Table 1. Number of impact and reference plots sampled by study site and vegetation type. Data are presented as number of plots sampled before the fire followed by number of plots sampled after the fire, in brackets. Both the Elliott and Cedar sites burned completely and thus do not contain reference plots. We collected pre-burn data at Rancho Jamul only.

Vegetation	Site						Total
	Cedar	Elliott	Rancho Jamul		Santa Ysabel		
	Impact ^a NR (R) ^c	Impact NR (R)	Reference ^b NR	Impact NR (R)	Reference NR	Impact NR (R)	
CHAP	0 (5)	0 (5)	0 (0)	0 (0)	0 (2)	0 (4)	0 (16)
CSS	0 (4)	0 (5)	4 (4)	4 (4)	0 (2)	0 (2)	8 (21)
GRASS	0 (0)	0 (0)	4 (4)	4 (4)	0 (2)	0 (1)	8 (11)
WOOD	0 (0)	0 (0)	0 (2)	0 (2)	0 (4)	0 (7)	3 (15)
Total	0 (9)	0 (10)	8 (10)	8 (10)	0 (10)	0 (14)	16 (63)

^a Impact refers to all plots burned in the 2003 fires.

^b Reference refers to all plots not burned in the 2003 fires.

^c For multivariate analysis, NR (non-razed) refers to all unburned plots (pre-fire, post-fire reference, pre-fire impact). R (razed) refers to all burned plots (post-fire impact).

plot (Sawyer and Keeler-Wolf 1995, Laakonen *et al.* 2001, Fisher *et al.* 2002). We laid out all vegetation transects in a north-south direction centered at the center bucket of each trapping array. Results from linear vegetation transects have been shown to be comparable to more time-consuming quadrats, especially in chaparral (Bauer 1943).

Data Classification and Reduction

We used a before-after reference-impact approach (BARI) to classify the data for univariate tests (Stewart-Oaten *et al.* 1986, Underwood 1994, Smith 2002). In this process, we classified each sample as either a reference plot or an impact plot. We classified all plots burned during the 2003 wildfires as impact plots and all plots not burned during the wildfires as reference plots. Before-after classification was relevant only to Rancho Jamul because it was the only study area where we sampled before and after the fires (Table 1).

For the multivariate analyses, we pooled the fire classification into two categories: razed and non-razed. This classification allowed for sufficient statistical power to test the significance of fire effects on rodent community structure within each vegetation type. In terms of the BARI classifications described above, non-razed refers to all of the data that we collected in the pre-fire surveys (before reference and before impact) plus the post-fire surveys at the unburned plots (after reference). Razed refers to all of the data that we collected in the impact plots (after impact) after the 2003 wildfires (Table 1). We reviewed the data using nonmetric multidimensional scaling (MDS) to ensure the validity of our pooling of the unburned reference and impact plots (i.e., did not group as separate clusters).

Statistical Analysis

To examine changes to the vegetation, we computed averages and standard errors for the percentages of cover types (grasses, forbs,

shrubs + trees) in reference plots and fire-impacted plots, both before and after the wildfire. Pearson's correlations were also conducted as appropriate to explore relationships between cover types.

For our index of species abundance, we used the minimum number known alive (i.e., number of unique individuals; MNA). We calculated MNA by removing all recaptures within each four-day trapping session at each array. Although MNA can be biased as an abundance estimator, it has been shown to be proportional to population sizes of small mammals and is thus a reasonable index of abundance (Slade and Blair 2000). To reduce variability due to seasonal or other environmental factors, we averaged the MNA for each species across all pre-fire sample sessions and across all post-fire sample sessions. We refer to this average as a capture rate (average number of individuals captured per session). We used the averaged pre-fire and post-fire capture rates with sample plots treated as replicates for the basis for all further analyses.

Before conducting formal significance tests, we initially explored large scale patterns in the data using a combination of approaches. We averaged capture rates by vegetation type and fire condition (razed and non-razed), and created a Bray-Curtis similarity matrix of the data. We used MDS to illustrate similarities among sample plots and fire condition. In an MDS plot, samples that are relatively close together can be interpreted as more similar, while those that are more distant are interpreted as more dissimilar. We used hierarchical agglomerative cluster analysis with group-average linking to examine the degree of similarity between razed rodent communities in comparison to the non-razed communities. We then overlaid vectors on the MDS plot to visualize the relative magnitude and directional response (trajectory) of individual species abundances in relation to razed and non-razed vegetation types (Clarke and Warwick 2001, Clarke and Gorley 2006).

We used a multivariate analysis of variance routine (PERMANOVA; Anderson 2001, McArsle and Anderson 2001) to test whether the factors of burn status (razed or non-razed), site, vegetation type, burn status \times vegetation type, and the percent cover of shrubs and trees predicted any differences in rodent community structure. This was based on a dissimilarity matrix of species abundance data at each sample array. The PERMANOVA routine performs a partitioning of the total sum of squares and calculates a distance-based pseudo-F statistic for each term in the model. We used 999 permutations to calculate *P*-values. We followed up any significant burn status \times vegetation interaction by analyzing each vegetation type independently. For these analyses, to determine how much of the fire-related change in rodent community structure was associated with changes in vegetation structure, we calculated the proportion of variance from the burn status term that was also explained by the cover term (shrub + tree cover). For each vegetation type, we accomplished this by testing two models with ordered terms: 1) burn status then cover, and 2) cover then burn status. The proportion of variance due to fire that was explained by changes in shrub and tree cover was the difference in the component of variation (COV) due to burn status in these two models divided by the total COV due to burn status in the first model.

Finally, we tested for effects of the fire on the relative abundance of individual species within vegetation types in two ways. First, using the post-fire data from each vegetation type, we generated models of relative abundance with site, species, and burn status as fixed factors. We conducted contrast tests to determine whether relative abundance of a species at the impact plots differed from that at the reference plots. For this, we pooled variances across species and sample plots within each vegetation type. Second, for the impact and reference plots where we had both pre-fire and post-fire data (Rancho Jamul: coastal sage

scrub and grassland), we subtracted the pre-fire capture rate from the post-fire capture rate for each species at each plot to produce a “net change after fire” statistic. We then ran a two-way ANOVA with species and burn status (reference vs. impact) as fixed factors. We used the differences of least squares means to test whether the change in rodent abundance at the impact plots differed from the change in abundance at the reference plots.

For all analyses, we set the alpha level at 0.10. We performed all multivariate analyses using Primer-E software (Primer E Ltd. 2006, Plymouth, United Kingdom) and univariate analyses using SAS software (SAS Institute Inc. 2002-2003, Cary, North Carolina, USA).

RESULTS

Vegetation Structure

Coastal sage scrub and chaparral fire-impacted plots had 77% and 46% reduced shrub and tree cover compared to reference plots, respectively. In woodlands, there was less reduction in shrub and tree cover for fire-impacted plots (–26%). Forb cover was an average of 30% greater in coastal sage scrub fire-impacted plots. Over both reference and impact coastal sage scrub plots, increased forb cover was correlated with decreased shrub cover (Pearson’s $r = -0.87$, $P < 0.001$). Forb cover did not differ between reference and impact plots for the other vegetation types. Grass cover did not differ between reference and impact plots in any vegetation type (Table 2). Grasses were composed of predominantly non-native *Bromus* spp. and *Avena* spp. before and after the fires in all vegetation types (Rochester et al. 2010b).

Overall Trapping Results

We captured 16 rodent species across all vegetation types for a total of 4444 captures pre-fire and post-fire. The most common cap-

Table 2. Means and standard errors for the percent cover of forbs, grass, shrubs, and trees over reference and impact plots.

Vegetation type ^a	Cover type	Vegetation cover			
		Post-fire		Pre-fire ^{bc}	
		Reference Non-razed	Impact Razed	Reference Non-razed	Impact Non-razed
CSS	Forb	37.9 (8.1)	69.2 (6.8)	N/A	N/A
	Grass	47.9 (9.5)	54.3 (9.8)	33.0 (7.0)	30.3 (8.6)
	Shrub	59.7 (6.8)	17.3 (6.7)	59.3 (10.1)	72.0 (1.3)
	Tree	0.0 (0.0)	1.2 (1.4)	0.0 (0.0)	0.0 (0.0)
GRASS	Forb	70.1 (6.1)	62.1 (9.7)	N/A	N/A
	Grass	76.8 (8.8)	89.9 (3.4)	79.0 (6.6)	90.4 (2.4)
	Shrub	2.1 (1.3)	2.0 (1.7)	0.8 (0.0)	8.4 (5.6)
	Tree	0.0 (0.0)	0.0 (0.0)	0.2 (0.2)	0.0 (0.0)
CHAP	Forb	48.3 (14.3)	42.9 (5.5)	N/A	N/A
	Grass	37.5 (7.9)	28.2 (6.5)	N/A	N/A
	Shrub	63.3 (3.6)	33.9 (4.8)	N/A	N/A
	Tree	0.0 (0.0)	0.0 (0.0)	N/A	N/A
WOOD	Forb	53.6 (12.3)	55.4 (5.9)	N/A	N/A
	Grass	84.8 (5.7)	67.5 (7.3)	N/A	N/A
	Shrub	9.4 (4.4)	7.1 (2.3)	N/A	N/A
	Tree	36.2 (11.1)	32.7 (3.5)	N/A	N/A

^a CSS = coastal sage scrub, CHAP = chaparral, GRASS = grassland, WOOD = woodland.

^b Rancho Jamul site only.

^c Pre-fire forb cover is not presented because pre-fire vegetation surveys were conducted in the fall when most forbs are dry and disarticulated.

tures included the deer mouse, *Dulzura kangaroo* rat, San Diego pocket mouse, and the harvest mouse (*Reithrodontomys megalotis* Baird). Other species captured were the California pocket mouse, California vole (*Microtus californicus* Peale), desert woodrat, big-eared woodrat (*Neotoma macrotis* Thomas), brush mouse, California mouse, and the cactus mouse (*Peromyscus eremicus* Baird). We also documented the presence of Botta's pocket gopher (*Thomomys bottae* Eydoux and Gervais), house mouse (*Mus musculus* L.), and the California ground squirrel (*Otospermophilus beecheyi* Richardson). We captured these last three species only rarely and therefore did not use them in any analyses.

Post-Fire Multivariate Community Analyses

Multidimensional scaling graphs and hierarchical clustering showed that across vegeta-

tion types, the rodent communities from razed plots more closely resembled each other than the corresponding non-razed rodent communities (Figure 2). Using group-average linking, razed coastal sage scrub, chaparral, grassland, and woodland merged into a single group at a similarity level of 59.2%. This is in contrast to the non-razed communities that merge at a lower similarity level of 38.2% (Figure 2). Vectors of individual species abundance in relation to the razed and non-razed rodent communities showed positive directional responses for both deer mouse and *Dulzura kangaroo* rat to the razed communities, whereas California mouse, brush mouse, San Diego pocket mouse, California pocket mouse, California vole, desert woodrat, and cactus mouse vectors showed positive directional responses to non-razed communities. The harvest mouse response was mixed, with increased abundance along a directional vector toward both

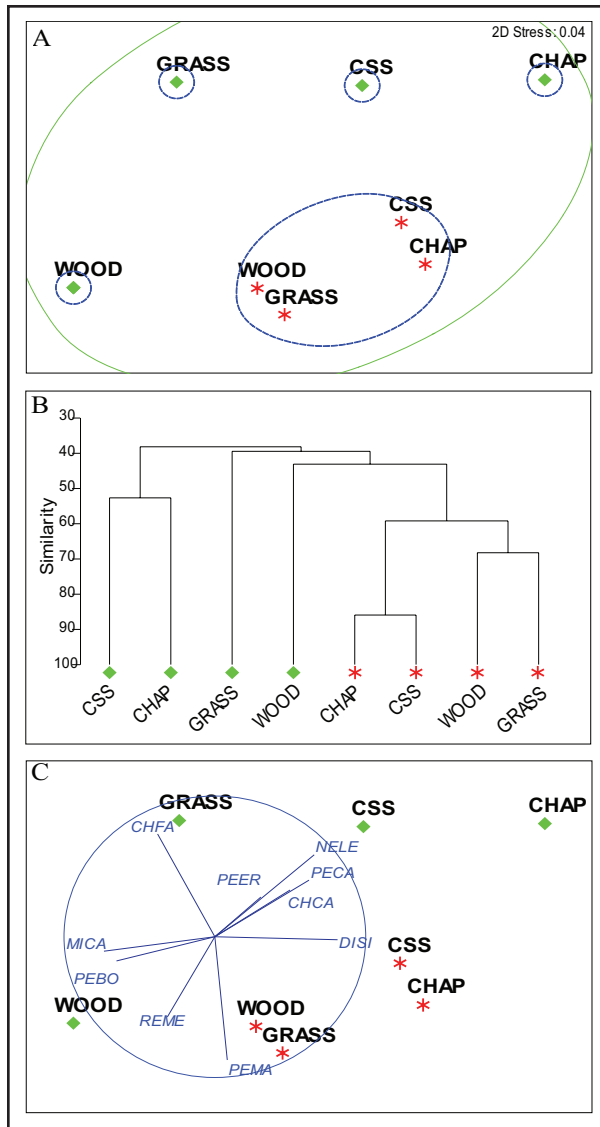


Figure 2. Multivariate Community Analysis. **A:** Nonmetric multi-dimensional scaling (MDS) with **B:** hierarchical clustering showing how the rodent communities in razed plots (R) of coastal sage scrub (CSS), chaparral (CHAP), grassland (GRASS), and woodland (WOOD) shifted away from the communities in the non-razed plots (NR). **C:** Vectors of individual species abundances in relation to the razed (*) and non-razed (◆) communities showed positive responses for both *Peromyscus maniculatus* (PEMA), and *Dipodomys simulans* (DISI) toward the fire-impacted communities, whereas *Peromyscus californicus* (PECA), *Peromyscus boylii* (PEBO), *Chaetodipus fallax* (CHFA), *Microtus californicus* (MICA), *Neotoma lepida* (NELE), *Chaetodipus californicus* (CHCA), and *Peromyscus eremicus* (PEER) showed positive responses toward non-razed communities.

non-razed and razed woodlands and razed grasslands (Figure 2).

The PERMANOVA resulted in a significant burn condition \times vegetation interaction (Pseudo- $F_{5,80} = 1.76$, $P = 0.001$), indicating that the response of the rodent communities to fire varied among vegetation types. Therefore, we did the follow-up analyses of the burn effects for each vegetation type separately. These analyses showed that rodent community structure in razed plots was significantly different than non-razed plots in all four vegetation types; coastal sage scrub (Pseudo- $F_{1,23} = 6.51$, $P = 0.001$, 30.5% of total variation), chaparral (Pseudo- $F_{1,11} = 4.37$, $P = 0.026$, 18.5% of total variation), grassland (Pseudo- $F_{1,15} = 4.53$, $P = 0.004$, 21.6% of total variation), and woodland (Pseudo- $F_{1,13} = 2.73$, $P = 0.016$, 14.0% of total variation). The proportion of variation (POV) of the rodent community structure explained by both burn condition and decreased shrub and tree cover (i.e., shared variation) was high for coastal sage scrub (80%) and chaparral (58%), but relatively low for grassland (12.1%) and woodland (4.6%) habitats.

Differences in Relative Abundance of Species

In coastal sage scrub unburned reference plots, the relative abundance of 11 rodent species was evenly distributed (i.e., all within a factor of four) (Figure 3). However, the distribution was highly skewed in the burned impact plots. Examining the difference in relative abundance of all of our captured species revealed that two rodent species responded positively to fire: the deer mouse (Diff = 2.53, se = 0.92, $t_{209} = 7.49$, $P = 0.006$) and the Dulzura kangaroo rat (Diff = 1.69, $t_{209} = 3.33$, se = 0.92, $P = 0.069$). Conversely, two other species responded negatively to fire, with the California mouse (Diff = -1.61, se = 0.92, $t_{209} = 3.00$, $P = 0.084$) and desert woodrat (Diff = -2.01, se = 0.92, $t_{209} = 4.74$, $P = 0.031$; Figure 3) being less abundant in the impact plots. All other

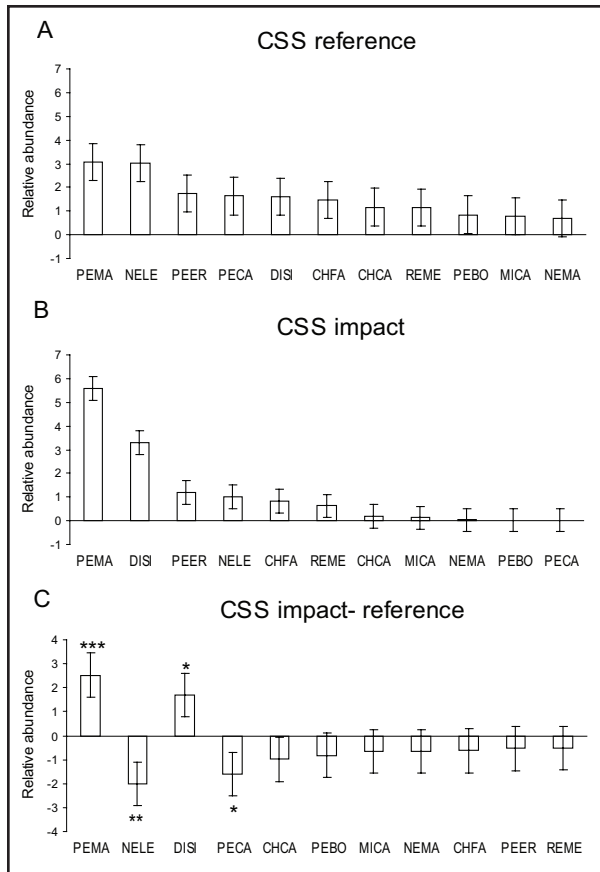


Figure 3. Relative abundance of rodent species from post-fire surveys in reference (A) and impact (B) plots in coastal sage scrub (CSS) communities. Species are ordered from most abundant to least abundant. C) Species differences in relative abundance (impact minus reference) in post-fire CSS communities are presented in the order of greatest change to smallest change. Relative abundance is the minimum number known alive (MNA) per array per sample session. Error bars are ± 1 standard error. Levels of significance are indicated as follows: *** $P < 0.01$, ** $P < 0.05$, * $P < 0.10$. Species codes are as in Figure 2, except for *Reithrodontomys megalotis* (REME).

species were less abundant on average, but not significantly, on plots impacted by the fires. Tests of paired contrasts between the four impact and four reference plots in coastal sage scrub at Rancho Jamul also showed a significant increase in abundance of the Dulzura kangaroo rat (Diff = 3.34, se = 1.914, $t_{41} = 1.75$, $P = 0.088$), but not the deer mouse (Diff = -0.69, se = 1.56, $t_{41} = 0.44$, $P = 0.662$), which also in-

creased at the reference plots in the same sampling year.

In grassland reference plots, the San Diego pocket mouse and deer mouse were the two most abundant species (Figure 4). In grassland burned impact plots, the relative abundance of the San Diego pocket mouse was substantially lower (Diff = -1.83, se = 0.57, $t_{99} = 10.45$, $P = 0.002$). The abundance of the San Diego pocket mouse also decreased at the four impact and four grassland reference plots at Rancho Jamul (San Diego pocket mouse Diff = -5.44, se = 0.98, $t_{19} = 5.54$, $P < 0.001$).

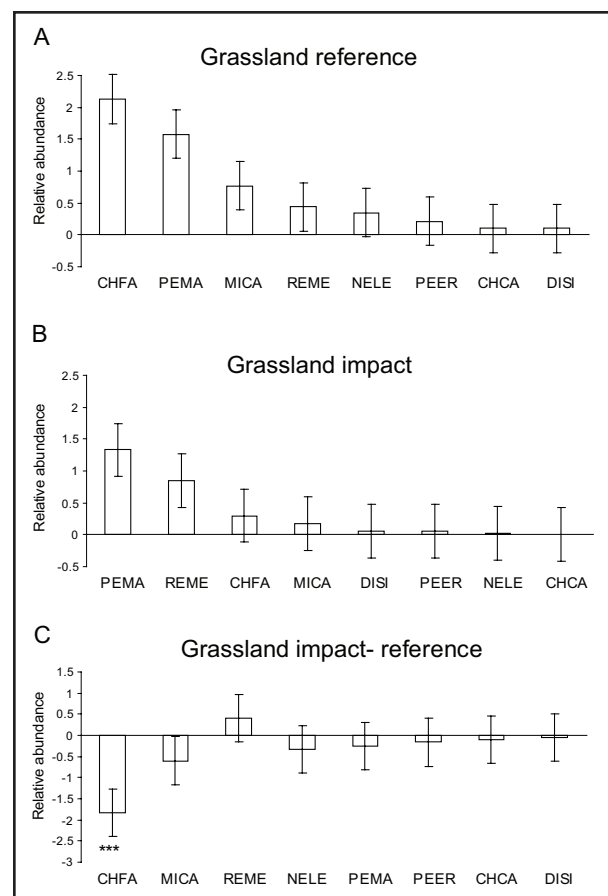


Figure 4. Relative abundance of rodent species from post-fire surveys in reference (A) and impact (B) plots in grassland communities. Species are ordered from most abundant to least abundant. C) Species differences in relative abundance (impact minus reference) in post-fire grassland communities are presented in the order of greatest change to smallest change. Abundance index, error bars, and significance levels are as defined in Figure 2.

In chaparral reference plots, the California mouse and cactus mouse were the two most abundant species (Figure 5), whereas the deer mouse and Dulzura kangaroo rat were both highly abundant in the fire-impacted plots. Results in chaparral were very similar to coastal sage scrub, as the deer mouse (Diff = 5.35, se = 1.23, $t_{154} = 19.04$, $P < 0.001$) and Dulzura kangaroo rat (Diff = 2.76, se = 1.23, $t_{154} = 5.10$, $P = 0.025$) responded positively to fire, whereas the California mouse (Diff = -2.24, se

= 1.228, $t_{154} = 3.32$, $P = 0.07$) responded negatively to fire. Other species showed very little differences in abundance across reference and impact plots (Figure 5).

In the woodland reference plots, the deer mouse and brush mouse were similarly high in their relative abundances. In the fire-impacted plots, however, the relative abundance of the deer mouse was double that of the reference plots (Diff = 2.42, se = 0.63, $t_{143} = 14.50$, $P = 0.002$), and brush mouse abundance was 90% lower than in the reference plots, making it a minor component of the post-fire community (Diff = -1.77, se = 0.63, $t_{143} = 7.68$, $P = 0.006$). Other species showed very little differences in abundance across reference and impact plots (Figure 6).

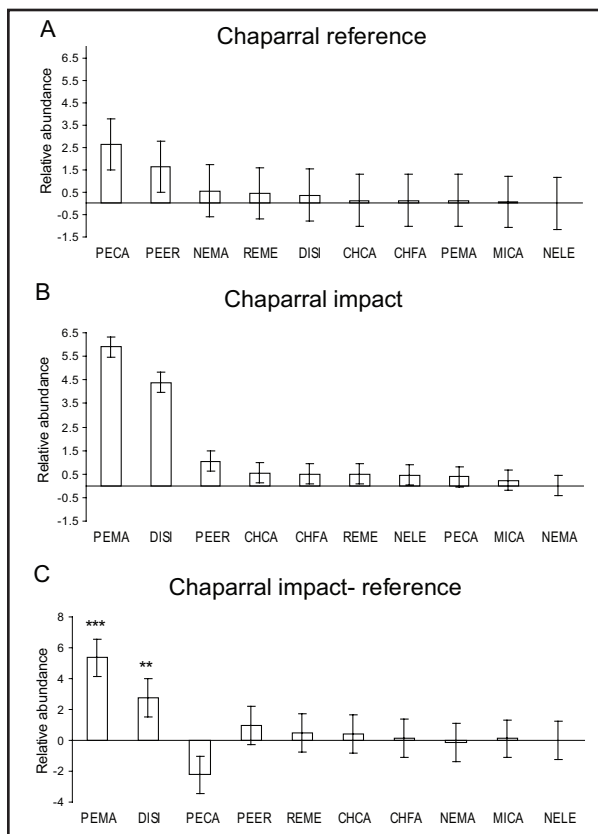


Figure 5. Relative abundance of rodent species from post-fire surveys in reference (A) and impact (B) plots in chaparral communities. Relative abundance is the minimum number known alive (MNA) per array per sample session. Species are ordered from most abundant to least abundant. C) Species differences in relative abundance (impact minus reference) in post-fire chaparral communities are presented in the order of greatest change to smallest change. Error bars are ± 1 standard error. Levels of significance are indicated as follows: *** $P < 0.01$, ** $P < 0.05$, * $P < 0.10$. Species codes are as in Figures 2 and 3.

DISCUSSION

Rodent Community Response to Fire

The results of our study indicate that the coastal southern California rodent community exhibits a strong response to wildfire within the first two to three years after fire. Multivariate tests for the effects of fire on rodent communities showed significant differences in rodent community structure in coastal sage scrub, grassland, chaparral, and woodland vegetation types. Overall, the rodent communities in the burned habitats were much more similar to each other than to rodent communities in the unburned habitats.

This response to fire was consistent across vegetation types in that the generalist deer mouse became the most abundant species in the rodent community at all four vegetation types. Other rodents largely responded in a manner consistent with their microhabitat and food preferences. For instance, the open habitat and seed specialist, Dulzura kangaroo rat, increased in multiple habitats, whereas the closed habitat shrub specialists, California mouse, desert woodrat, and brush mouse, decreased.

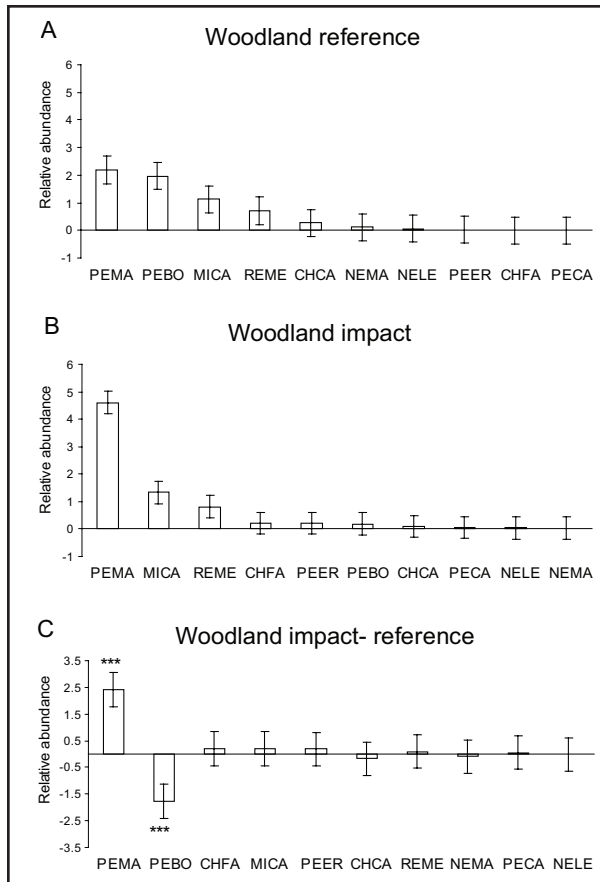


Figure 6. Relative abundance of rodent species from post-fire surveys in reference (A) and impact (B) plots in woodland communities. Species are ordered from most abundant to least abundant. C) Species differences in relative abundance (impact minus reference) in post-fire woodland communities are presented in the order of greatest change to smallest change. Abundance index, error bars, and significance levels are as defined in Figure 2.

Habitat for closed shrub specialists was substantially reduced in the burned coastal sage scrub and chaparral communities, with losses of 77% and 46% shrub and tree cover, respectively. In contrast, the wildfires had less notable impacts on riparian woodlands with an average reduction of 26% shrub and tree cover. The riparian environments contain high levels of moisture, which likely allowed them to maintain more of their pre-fire habitat structure and possibly act as refugia for the animals sheltering within it (Chang 1996). Although

the rodent community in burned grasslands was significantly different than in unburned grasslands, the vegetation structure did not change as measured by shrub, forb, or grass cover. Nor were there significant changes in the proportion of native to non-native grasses (Rochester *et al.* 2010) that may affect the rodent community.

Previous research reported negative relationships between small mammal species richness and loss of vegetation structure in human-degraded coastal sage scrub and chaparral (Bolger *et al.* 1997, Savajout *et al.* 1998, Diefendorfer *et al.* 2007a). In our study, reduction in shrub and tree cover (strongly correlated with increased forb cover) explained most of the variation in fire-altered rodent community structure in coastal sage scrub (80%), but less in chaparral (33%) and woodland communities (5%). Thus, loss of vegetation structure appeared to be a more important driver of fire-related change in rodent community structure in the more heavily burned habitats. We hypothesize that the remaining variation should be largely explained by differences in initial mortality (especially for above-ground nesters), species interactions, and predation pressures, which would appear to be more important drivers in grasslands and in the lesser burned habitats. The major post-fire changes in woodland communities were an increase in deer mouse abundance and a decrease in brush mouse abundance. Similarly, the primary post-fire changes in grassland communities were an increase in deer mouse abundance and a decrease in San Diego pocket mouse abundance. In southern California habitats, this points to potential competitive advantage by the generalist deer mouse in all post-fire environments, even those maintaining a considerable amount of habitat structure.

Individual Species Responses

The deer mouse was the most abundant species in fire-impacted plots across all four

vegetation types. This is in comparison to the reference plots, where the deer mouse was not abundant. This species is a habitat and dietary generalist (Jameson 1952, Cook 1959, M'Closkey 1972, Holbrook 1978) and has been shown to invade post-fire habitats in other studies (Cook 1959, Lawrence 1966, Meserve 1976b, Holbrook 1978, Kaufman *et al.* 1988, Wirtz *et al.* 1988, Schwilk and Keeley 1998, Converse *et al.* 2006). A negative relationship was found between the deer mouse and fire severity in Yosemite National Park; however, sampling ranged from two to 15 years post-fire and may have represented a longer term response (Roberts *et al.* 2008). A combination of reproductive traits such as postpartum estrous and large litter sizes enable the deer mouse to reproduce faster than all other species in this study, except for the similarly fecund harvest mouse (Rood 1966, Richins *et al.* 1974, Jameson and Peeters 2004). In contrast to the harvest mouse, this species occupies all vegetation types. Therefore, the deer mouse is well equipped to respond rapidly to the abundant seed bank resources, new plant growth, and decreased competition from other rodents offered in these southern California post-fire habitats.

There was a significant increase in the relative abundance of the *Dulzura* kangaroo rat in burned coastal sage scrub and chaparral. Post-fire increases of this species have been previously documented in coastal sage scrub (Price and Waser 1984). In both vegetation types, this bipedal heteromyid rodent occupies open habitat on gentle slopes, and its diet is primarily composed of seeds (Meserve 1976a, 1976b; Jameson and Peeters 2004, Kelt *et al.* 2005). By removing dense vegetation and leaf litter and exposing seed resources (Wright and Bailey 1982, Kaufman *et al.* 1988), the fire created more suitable habitat conditions for this species.

The desert woodrat significantly decreased in coastal sage scrub. The woodrat builds large nests above ground in rocks, trees, and shrubs using woody materials and other flammable

debris. The decrease in the relative abundance in burned coastal sage scrub was likely due to direct mortality from the combustion of its above-ground nests as the fires occurred (Wirtz *et al.* 1988). However, some desert woodrats living in rocky outcrops with sufficient retreats may have survived. The populations may be depressed into the near future due to lack of suitable materials with which to build new nests (Wirtz *et al.* 1988). We did not have enough data to evaluate the response of the big-eared woodrat, as it was present in only a few of our sites. Because of its similar life history, we would expect this species to experience similar declines (Bolger *et al.* 1997).

We observed significant decreases in the relative abundance of the California mouse within burned chaparral and coastal sage scrub communities. This species has strong food preferences for shrub fruits, seeds, and flowers (Meserve 1976a, 1976b). For habitat, this species prefers chaparral and dense coastal sage scrub (M'Closkey 1972) and shelters in burrows and woodrat nests (Grinnell and Orr 1934, Merritt 1974). Mortality from fire and reduced habitat suitability from the thinning of burned chaparral and coastal sage scrub habitats are likely reasons for the significant decreases observed for this species. Post-fire declines in this species have been documented in other studies (Lawrence 1966, Wirtz *et al.* 1988).

There was a significant decrease in the relative abundance of the brush mouse in woodland plots. The brush mouse is arboreal, commonly using trees, logs, and shrub canopies for foraging and nesting (Holbrook 1979, Kalcounis-Rüppell and Millar 2002, Jameson and Peeters 2004). Its post-fire decrease may be due to reduced suitable habitat as it prefers areas with medium to high densities of shrub and tree cover (Holbrook 1979, Quinn 1990, Roberts *et al.* 2008). As discussed, densities may have also been depressed due to increased competition from the deer mouse.

The San Diego pocket mouse decreased in burned grassland. This species is a granivore

with a diet consisting of large amounts of seeds from both annual forbs and grasses (Meserve 1976a). The preferred habitats of the San Diego pocket mouse tend to be sparsely vegetated areas with rocky or sandy soils suitable for digging burrows (Price and Waser 1984, Lackey 1996). Since this species is typically associated with open scrub habitats, we expected an increase in numbers due to an increase in suitable habitat. However, negative relationships of San Diego pocket mouse abundance with fragmentation and fire-related disturbance have been reported (Price and Waser 1984, Bolger *et al.* 1997). We hypothesize that this species requires an intermediate amount of shrub cover and that densities may have been depressed due to a combination of habitat alteration and increased competition from the deer mouse.

In burned coastal sage scrub and grasslands, there were insignificant but marked decreases in the relative abundance of the California vole. In compact clay soils, typical in southern California grasslands, the California vole largely prefers to forage and nest above-ground (Stark 1963). This species also has small home ranges and displays high site fidelity (Stark 1963). Work by Cook (1959) and Pearson (1959) indicate that the California vole requires at least one year's worth of grass growth before cover is suitable. Since our study took place in the second and third years after the fire, when grasses were abundant, we hypothesize that this species was negatively impacted by direct mortality from the fires.

We did not have the power to assess the impact of the fires on some of the less abundant members of the rodent community such as the cactus mouse, harvest mouse, and big-eared woodrat. Results from a concurrent study of both a chaparral and a coastal sage scrub site affected by the 2003 wildfires were consistent with our findings (Diffendorfer *et al.* 2007b)

Implications

Despite suppression efforts and management plans, wildland fires continue to occur from both natural ignition sources and those associated with increasing human population (Keeley *et al.* 2004). Our results indicate that a more frequent and intense fire regime will simplify rodent communities and thus result in a loss of biodiversity for the region and its ecosystems. The result may be rodent communities dominated by generalists and disturbance specialists, such as the deer mouse and the *Dulzura* kangaroo rat.

By understanding the responses of rodent species to fire according to their habitat, nesting, and food preferences, our findings can help managers to identify those species at risk of population decline or extirpation from wildfires, as well as to predict responses of unstudied species. The rodent species at greatest risk from large and intense fires are those associated with mature woodland or shrubland habitats that require some degree of shrub and tree structure for their habitat or dietary needs. In San Diego County, these species include the desert and big-eared woodrats, the California mouse, and the brush mouse. Although data were lacking in this study, we would also expect the California pocket mouse to be at moderate risk for decline. We have found similar patterns with responses of herpetofauna species to these large scale fires, with responses consistent with habitat preferences and life history characteristics (Rochester *et al.* 2010).

The spatial extent and severity of wildfires are important for determining the level of risk to rodent species and populations (Shaffer and Laudenslayer 2006). Smaller, patchy, less severe wildfires may allow more species to survive while also leaving some portions of the vegetation intact. These types of fires, occurring at natural intervals, should allow the persistence of a diverse rodent community. Currently, however, most fires are ignited by human sources during the fall when dry Santa

Ana winds act to spread the flames quickly. These large, intense fires increase mortality and, more drastically, alter wide swaths of habitat. As a consequence, they are more likely to have a greater and more sustained impact on small animal communities. In our study, the fires at Santa Ysabel and Rancho Jamul were patchy, whereas the Elliott and Little Cedar sites experienced intense and complete burns at a much greater distance from unburned refugia. We expect that the communities at these latter two sites will take more time to recover.

In addition to fire severity concerns, fire frequency will be paramount to determining risk and long-term fire impacts to the southern California habitats. Under repeated short-return interval fire events, the potential exists that both the vegetation and animal communities will transition to grassland communities and not rebound to those of intact, unburned chaparral and coastal sage scrub (Zedler *et al.* 1983, Keeley 2005). In our study areas, non-native grasses were present and naturalized in all vegetation types prior to the 2003 wildfires, likely already affecting vegetation fuel properties and thus fire frequency (Brooks *et al.* 2004). In 2007, San Diego County experienced a second series of large scale wildfires that affected most of Rancho Jamul and one array at Santa Ysabel. We are currently re-sampling the vegetation and rodent communities at all four study sites to assess current conditions and states of post-fire recovery.

The scenario of large and more frequent wildfires is also relevant to the Single Large or Several Small (SLOSS) debate about reserve design and the conservation of biodiversity in this region (Diamond 1975, Simberloff and Abele 1976). Although larger reserves should conserve more species and be less affected by habitat fragmentation (i.e., Bolger *et al.* 1997), these reserves are more difficult to defend from wildfires. In contrast, smaller reserves within city boundaries may be more likely to be defended as part of firefighting efforts to defend homes in urban and rural areas. A combination of approaches is likely needed.

Currently, we are trying to assess whether current habitat conservation plans (HCPs) in southern California provide long-term protection to covered species, as well as preserve ecosystem function. Federal and state laws require that HCPs be implemented within an adaptive management framework. This framework represents an iterative approach, where an information feedback loop between monitoring and management improves understanding of species dynamics and ecological systems (Atkinson *et al.* 2004). The future scenario of increased wildfires should be incorporated into this framework (Regan *et al.* 2008). This will likely require creativity in implementing fire minimization measures, creating fire-safe refugia in natural areas, and working with local and state firefighting agencies to include plans for defense of sensitive natural areas.

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