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Responses of Small Mammals to Wildfire in a Mixed Conifer Forest in the San Bernardino Mountains, California

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Abstract.—Wildfires are becoming more prevalent in montane conifer forests of the San Bernardino Mountains of southern California. The effects of fire on stand structure and composition of these forests has been extensively studied but there are far fewer studies on how wildfires affect the fauna. For five years after a wildfire in 2007, we live-trapped small mammals in three burn types: unburned, moderate-severity and high-severity. A primary objective of this study was to document the response of the small mammal community to high-severity fire. Pinyon mice were consistently more abundant in unburned forests and declined by 69–76% between unburned forests and moderate-severity and high-severity burns. In contrast, deer mice responded positively to fire. Their numbers increased by 72%–87% between unburned forests and moderate-severity and high-severity burns. Compared to unburned forests, chipmunk numbers were 43%–64% lower in moderate and high-severity burns. California ground squirrels were unaffected by either severity. Using ordination analysis, we examined the distributions of the four small mammal species in relationship to stand structure and microhabitat variables that changed after fire. When the three burn types were analyzed together, small mammal composition was significantly related to burn type (unburned vs. high-severity), years-after-fire, litter cover and cover of bare ground. When the moderate and high-severity burn types were analyzed without unburned grids, four variables were significant: years-after-fire, rock outcrop cover, bare ground cover, and the combined covers of oak resprouts and shrubs.

Montane yellow pine (*Pinus ponderosa* and *P. jeffreyi*) and mixed conifer forests in the San Bernardino Mountains (SBM) of southern California have undergone significant changes in tree species composition and structure since the advent of fire suppression beginning around 1910 (Minnich et al., 1995). Prior to suppression, frequent surface fires (intervals of 10 to 14 years) cleared the understory of shrubs, coarse woody debris, saplings and pole-sized trees (McBride and Laven, 1976). Stand-replacing fires were uncommon and usually burned small patches totaling no more than 5% of the forested area (Minnich, 2007). This regime of high-frequency, low-intensity fires perpetuated open forests dominated by large-diameter, shade-intolerant conifers such as Jeffrey (*Pinus jeffreyi*) and ponderosa pines (*P. ponderosa*).

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Fire suppression in the SBM contributed to a sharp increase in tree densities, especially in the smaller size classes (Minnich et al., 1995). In some forests the proportions of fire-sensitive, shade-tolerant species such as white fir (*Abies concolor*) and incense cedar (*Libocedrus decurrens*) increased in both the understory and overstory at the expense of the shade-intolerant pines. Overall, the increase in tree density has been accompanied by higher tree mortality and a concomitant accumulation of coarse woody debris (Minnich, 2007).

Despite an overall increase in fuel loading in these forests, fire suppression has continued to be highly effective in extinguishing fires through the 20th century. However, beginning in 2003 there was an abrupt change in both the size and severity of fires in southern California conifer forests (Franklin et al., 2006; Goforth and Minnich, 2008; Keeley et al., 2009). Between 2003 and 2009 approximately 23,500 ha of montane conifer forests burned in the Transverse and Peninsular Ranges; much of the total was in stand-replacing fires (Keeley et al., 2009). Climate-change scenarios suggest that conifer forests of the SBM will continue to experience larger, more severe fires as the regional climate becomes warmer and drier (Westerling and Bryant, 2008; Stephens et al., 2013).

The SBM support the largest island of coniferous forests in the Transverse Ranges or Peninsular Ranges in southern California and yet, while much has been written about fire and vegetation, there are only two studies on the response of vertebrates to wildfires in these forests: carnivores (Borchert, 2012) and California spotted owls (*Strix occidentalis occidentalis*, Lee et al., 2013). Moreover, there are no post-fire small mammal studies in the SBM compared to at least six studies in the Sierra Nevada Mountains. Nevertheless, five of the Sierra Nevada studies focus on the effects of thinning and prescribed burning on small mammals (Meyer et al., 2005; Monroe and Converse, 2006; Meyer et al. 2007; Amacher et al. 2008; Maguire et al., 2008) while only one examines the effects of a wildfire (Roberts et al., 2008).

Because the severity of wildfires in the SBM is expected to increase in the coming decades (Westerling and Bryant, 2008), land managers need to better understand the responses of the fauna to fire, especially high-severity fire (Bond et al., 2012). Therefore, the goals of this study were to (1) to document the response of small mammals to moderate and high-severity fire in a southern California conifer forest and (2) to describe microhabitats favored by small mammals in burned and unburned forests.

Materials and Methods

Study Area

The study was conducted in a 415-ha area approximately 2 km northwest of Fawnskin, California (34°16.51′N, 116°58.18′W) in the SBM. The study area ranges in elevation from 2068–2263 m. Topography is flat to gently undulating (slopes average < 10°) with some parts dissected by the main drainage of Grout Creek and its tributaries. Soils are shallow to moderately deep loamy-coarse sands derived from granite. Jeffrey pine-white fir /California black oak (*Quercus kelloggii*) woodlands and forests dominate the study area. Prominent understory shrubs include mountain whitethorn (*Ceanothus cordulatus*), greenleaf manzanita (*Arctostaphylos patula*), rubber rabbitbrush (*Ericameria nauseosa*) and big sagebrush (*Artemisia tridentata*). Hundreds of mounding rock outcrops are scattered throughout the study area, ranging in size from 500 m^2 to 1.5 ha.

Climate of the study area is Mediterranean which is characterized by cold, wet winters and warm, dry summers. Average annual precipitation recorded at the nearest weather station (Big Bear Lake, CA) is 566 mm, most of which falls as snow from November to

April. Average annual precipitation from the 2008 to August 2012 was 524 mm. Four years of the study were below the long term average precipitation and one year (2010) was almost twice the long term average.

Evidence of late 19th and early 20th century logging in the form of stumps and decaying slash are still present in unburned areas but there are no records of wildfires in the study area in the century before the 2007 Butler 2 Fire which began on 14 September near Butler Peak. Sustained southwest winds of 40 km hour^{-1} enlarged the burn area from 800 ha to 5670 ha in a 12-hour period. As the fire pushed northeast toward the desert, it became a stand-replacing fire although it produced a relatively narrow (0.5–1.0 km) moderate to moderate-high severity zone between unburned forests and those that burned at high-severity.

We selected three burn types for small mammal live-trapping. Four trapping grids were located in a 146-ha unburned area, four in the 100-ha moderate-severity burn and four in a 169-ha high-severity burn. Moderate severity is defined as tree basal area mortality from 40–60% while high-severity basal area mortality is >90% (Fontaine and Kennedy, 2012).

Within each of the three burn types we established four trapping grids. A grid consisted of two parallel transects with 11 traps per transect. Spacing between traps was 20 m and the transects were 20 m apart (Converse et al., 2006a). Thus, there were 4 grids (88 traps total) in each burn type and each covered 0.4 ha. In an attempt to capture the variability in stand structure, we located the grids haphazardly in each type. Rock outcrops were present in all the grids. Grids were located at least 65 m from roads and trails and were spaced a minimum of 300 m (mean 427 m) apart.

Stand Structure and Microhabitat Sampling

Within a 5-m radius (80 m^2) of each trap station we measured the diameter at breast height of all stems >5 cm for each tree species and noted whether they were alive or dead. We recorded overstory cover in the plot with a spherical densiometer but we did not separate live from dead cover (Table 1). Within a radius of 4 m (50.2 m^2) of the station center, we visually estimated cover of the variables listed in Table 1 and placed each estimate into one of seven percent cover classes: 0–1, 2–5, 6–15, 16–25, 26–50, 51–75 and 76–100. Midpoint values of each class were used in the analyses. Stand structure and microhabitat sampling was conducted on each grid at the end of every annual trapping session.

Live-trapping

We placed one extra-large (10.2 cm × 11.4 cm × 38.1 cm) Sherman live trap within 2 m of each station marker under vegetative cover or in close proximity to rocks, tree bases or coarse woody debris. Where natural cover was unavailable, wood shingles were used to shade exposed traps. Cotton batting was placed at the back of each trap for insulation, and a mixture of peanut pieces, walnut pieces and black oil sunflower seeds was provided as bait.

We trapped the 12 grids over a five-week period from late July through August for five years (2008–2012) after the fire. We trapped each grid for four consecutive nights (4 trap-nights). Traps were checked each morning before 10:00 hours. Captured individuals were identified to species, weighed, sexed and marked on the underside of the tail at the base with a permanent marking pen. We applied a different pen color for each capture day so that the capture history of each animal could be discerned from the color sequence. We

Table 1. Microhabitat and stand structure variables.

Variable	Acronym	Description
Rock outcrop cover	Rock	Singular, connected rock mass
Diffuse rock cover	DifRock	Scattered, unconnected individual rocks
Bare ground cover	Bare	Exposed soil
Litter cover	Litter	Dead leaves, pine needles, bark pieces
Forb and grass cover	HerbCv	Herbaceous vegetation and grasses
Live shrub cover	LiveShrb	Green, living shrubs
Dead shrub cover	DeadShrb	Shrubs with no live foliage and dead branches
Black oak resprout cover	OakRsp	Post-fire, green basal resprouts
Canopy cover	Canopy	Overstory, living and dead foliage and branches
Coarse woody debris cover (<10 cm diameter)	CWD ≤10	Twigs and small branches
Coarse woody debris cover (11–30 cm diameter)	CWD 11–30	Larger branches
Coarse woody debris cover (>31 cm diameter)	CWD >30	Logs
Conifer density	ConDen	Conifer stems in 80 m^{-2}
Conifer basal area	ConBA	Conifer m^2 in 80 m^{-2}
Oak stem density	OakDen	Oak stems in 80 m^{-2}
Oak basal area	OakBA	Oak m^2 in 80 m^{-2}
Total basal area	TotBA	m^2 basal area in 80 m^{-2}

identified individual animals using a combination of species, sex, weight, reproductive condition (pregnant or not, testes scrotal etc.) and tail markings (color sequence applied to the tail base).

Weight and pelage color were used to separate *Peromyscus* juveniles from adults and sub-adults; for both species of *Peromyscus* non-reproductive juveniles were < 16 g. We did not distinguish Merriam's chipmunks (*Neotamias merriami*) from obscure chipmunks (*N. obscurus*) so they were combined for the analyses. California ground squirrels (*Otospermophilus beecheyi*) and golden-mantled ground squirrels (*Callospermophilus lateralis*) were weighed in the traps but not handled. We used squirrel weights to identify the number of squirrels on each grid.

Statistical Analyses

During the five year study, we trapped a total 60 grids (3 burn types × 4 replicates per burn type × 5 years). Because the number of individuals captured was not normally distributed for any of the species, we used negative binomial regression (log link function) to determine if the number of individuals captured on the grids were associated with two covariates: burn type and years-after-fire. Negative binomial regression (NBR) was employed because a relatively high proportion of grids had zero individuals resulting in a variance that exceeded the mean (Lindén and Mäntyniemi, 2011). For example, variance-to-mean ratios for the four species ranged from 2.1–9.4.

If abundance was significantly related to burn type in the NBR analysis, we determined which of the types was significant by analyzing pairs of burn types (unburned vs. moderate severity, unburned vs. high severity, and moderate vs. high severity). We compared two types by deleting one of the types and running NBR on the 40 remaining grids. For the analysis we used the function "glm.nb" in the MASS package of R as outlined by Zuur et al. (2009).

We employed canonical correspondence analysis (CCA, ter Braak, 1986; CANOCO software: ter Braak and Šmilauer, 2002) to investigate relationships between rodent species composition and environmental variables in each burn type. This technique has been used to analyze the role of microhabitat variables in small mammal studies in both burned (Simon et al., 2002) and unburned conifer forests (Copetto et al., 2006; Glennon and Porter, 2007; Kelt et al., 2013).

Canonical correspondence analysis is a direct gradient analysis technique that performs an iterative multiple regression between site scores (rodent captures) and environmental variables and identifies significant relationships between the two matrices. It produces eigenvalues that measure how much of the variation in site scores is explained by environmental variables. Canonical correspondence analysis assumes species have normal distributions along environmental gradients but is robust to moderate violations of normality (Palmer, 1993; ter Braak and Šmilauer, 2002).

We utilized captures (not individuals) of the following species for the CCA analysis: pinyon mice, deer mice, Merriam's and obscure chipmunks pooled and California ground squirrels. Three types of variables were analyzed in the CCA: (a) microhabitat, (b) stand structure, (c) years-after-fire and (d) burn type (unburned, moderate severity and high-severity) (Table 1). Burn type was coded as a dummy variable for the analyses and years-after-fire served as the time variable. Captures were log transformed for the analyses. Highly collinear variables identified by CANOCO were removed from the analysis.

Initially, we analyzed species and environmental variables for the three burn types together. Next, we analyzed each burn type separately to elucidate variables unique to each that may have been subsumed in the analysis of all three burn types. We first analyzed the unburned grids and then the burn types. Because significant variables in the analyses of the high- and moderate severity grids were similar, we combined these two types into a single analysis. All together we performed three CCAs: one on the three burn types together, one on the unburned grids and another on the moderate and high-severity grids combined.

We used the forward selection option in CANOCO 4.5 to identify significant ($p < 0.05$) variables. Statistical significance of each environmental variable was tested using a Monte Carlo permutation test (1000 permutations). The importance of each axis in the CCA was interpreted by its eigenvalue, percentage of the variance explained, species-environment correlations and weighted inter-set correlations, i.e. the correlations between the environmental variables and species ordination axes.

We used biplot diagrams to illustrate the relationship between the species and significant variables. In a biplot diagram, species are shown as points and environmental variables are represented by arrows. Species points and arrows jointly represent the species' distributions along each environmental variable (ter Braak, 1986).

Results

Vegetation

In the unburned grids 3% of the tree stems were dead. After the fire, the percentage of dead stems in the moderate-severity grids was 79.2% and in high-severity grids it was 99%. In the unburned grids 7.4% of the basal area was dead while basal area mortality reached 51.1% and 95% in the moderate-severity and high-severity grids, respectively. White fir and California black oaks showed the highest aboveground stem mortality in the burn areas (Table 2). Average stems ha^{-1} of conifers and hardwoods for the unburned, moderate-severity and high severity grids were 97, 57.6 and 72.7, respectively.

Table 2. Changes in forest stand structure after the fire. PIJE is Jeffrey pine, ABCO is white fir, and QUKE is California black oak. Values are means ± 1 SD.

	Unburned		Moderate severity		High severity	
Variable	Live	Dead	Live	Dead	Live	Dead
PIJE density (trees ha^{-1})	111.1 (18.8)	0	8.9 (1.6)	34.9 (11.4)	3.5 (1.9)	127.2 (22.4)
PIJE basal Area (m^2ha^{-1})	4.7 (1.2)	0	7.5 (1.9)	4.7 (1.9)	0.8 (0.4)	10.2 (2.3)
ABCO density (trees ha^{-1})	27.5 (7.5)	4.3 (2.4)	2.4 (1.9)	41.2 (17.7)	0	22.4 (2.4)
ABCO basal area (m^2ha^{-1})	0.8 (0.8)	0.4 (0.4)	0.8 (0.8)	2.4 (1.2)	0	1.2 (0.4)
QUKE density (stems ha^{-1})	232.4 (41.2)	7.1 (0.8)	9.8 (5.5)	92.6 (23.5)	0	128.7 (31.0)
QUKE basal area (m^2ha^{-1})	4.3 (0.8)	1.6 (10.6)	0.8 (0.4)	2.4 (0.8)	0	4.3 (1.2)

Overstory cover of both the moderate and high-severity grids decreased between 2008 and 2012 largely because of dead needle and oak leaf fall (Table 3). Small-diameter dead twigs and branches dropped over time which explains the increase in CWD in the ≤ 10 cm diameter class. Accumulation of CWD >11 cm diameter did not change during the study (Table 3) and, despite high stem mortality in the burn areas, few fire-killed trees had fallen five years post-fire.

Not surprisingly, litter increased and bare ground decreased in the post-fire years (Table 3). Live shrub and black oak resprout cover increased over time in the burn grids. Oak resprout cover increased rapidly in the early post-fire years while shrub cover showed the highest increase in years four and five. The increase in shrub cover was most apparent on the high-intensity grids where the increase averaged 26.2% compared to 11.1% on moderate-severity grids (Table 3). For example, in 2008 mountain whitethorn seedlings were 1-cm high but by 2012 they averaged of 28.3 (SD ± 2.0) cm in the high-severity grids.

Trapping Results

Between 2008 and 2012, 5,280 trap nights yielded a total of 469 individuals of eight rodent species. The two most common species were pinyon mice (193 individuals) and deer mice (161 individuals). We captured 81 chipmunks and, based on animal weights, we

Table 3. Changes in microhabitat variables between 2008 and 2012 in each burn type. Values are means ± 1 SD.

	Unburned		Moderate severity		High severity	
Variable	2008	2012	2008	2012	2008	2012
Overstory	51.3 (33.6)	55.6 (30.6)	56.4 (31.9)	30.0 (24.5)	39.1 (35.5)	18.0 (22.4)
Shrub	11.7 (19.1)	13.7 (22.1)	2.3 (6.4)	13.4 (19.9)	8.8 (12.5)	35.0 (32.1)
Black oak resprouts	0.1 (0.5)	0.2 (0.5)	0.4 (0.9)	1.3 (5.5)	2.3 (7.0)	5.6 (15.9)
Litter	59.3 (26.4)	55.3 (29.4)	36.6 (20.6)	47.3 (26.2)	12.2 (16.6)	17.5 (24.1)
Bare ground	14.2 (15.8)	17.2 (13.8)	47.6 (21.7)	27.4 (24.4)	59.3 (29.4)	34.0 (28.7)
< 10 cm CWD	0.8 (0.9)	0.6 (0.6)	0.8 (0.8)	1.5 (2.9)	1.0 (2.4)	2.4 (4.4)
11–30 cm CWD	0.6 (2.7)	0.8 (2.2)	0.4 (0.7)	0.1 (0.5)	0.2 (0.5)	0.2 (0.5)
>30 cm CWD	0.8 (2.5)	1.0 (2.3)	0.1 (0.4)	0.1 (0.1)	0.1 (0.5)	0.2 (1.2)
Total CWD	2.2 (4.3)	2.4 (6.1)	1.3 (1.3)	1.7 (3.0	1.3 (2.7)	2.7 (4.8)
Rock outcrops	5.7 (14.6)	–	4.8 (17.1)		9.7 (21.0)	–
Diffuse rock	6.6 (15.3)	–	2.2 (4.5)		2.3 (4.9)	–
Total rock	12.3 (21.6)	–	7.0 (17.5)		12.0 (21.0)	–

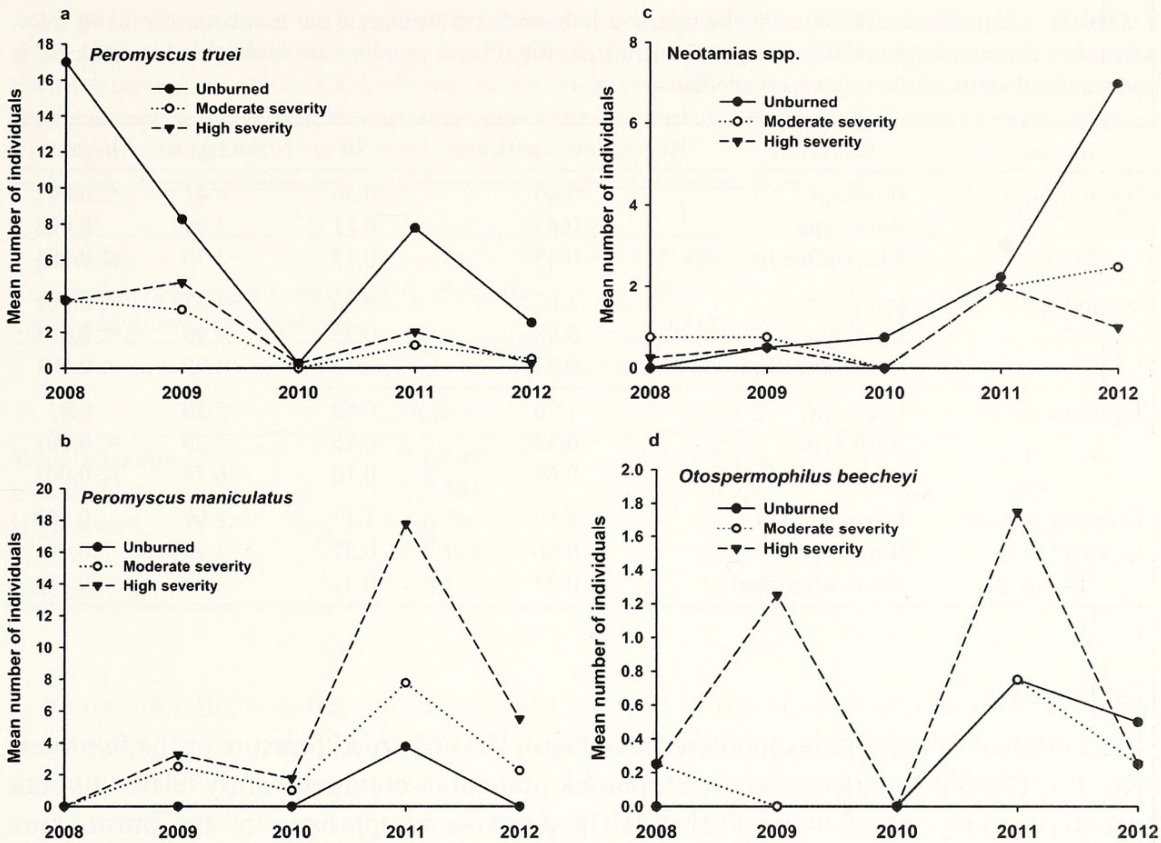

Fig. 1a. Mean number of pinyon mice (*Peromyscus truei*) in the three burn types: unburned, moderate severity and high severity. 1b. Mean number of deer mice (*Peromyscus maniculatus*) in the three burn types: unburned, moderate severity and high severity. 1c. Mean number of chipmunks (*Neotamias merriami* and *N. obscurus*) in the three burn types: unburned, moderate severity and high severity. 1d. Mean number of California ground squirrels (*Otospermophilus beecheyi*) in the three burn types: unburned, moderate severity and high severity.

captured 24 California ground squirrels. In addition, we captured three big-eared woodrats (*Neotoma macrotis*), four golden-mantled ground squirrels, one Pacific kangaroo rat (*Dipodomys agilis*) and one brush mouse (*Peromyscus boylii*).

Pinyon Mice

Pinyon mice were consistently most abundant in unburned forests throughout the study (Fig. 1a), except in 2010 when few mice were captured in any burn type. The NBR analysis showed pinyon mice numbers were significantly related to both burn type and years-after-fire (Table 4). In pairwise comparisons, unburned vs. moderate severity was significant ($p < 0.001$) as was unburned vs. high severity ($p = 0.001$). On the other hand, high and moderate severity types were not significantly different ($p = 0.54$).

Deer Mice

Deer mice were higher in both moderate and high-severity grids than in unburned grids (Fig. 1b). Deer mice numbers were significantly related to both burn type and years-after-fire (Table 4). In pairwise comparisons, unburned vs. moderate severity was significant ($p = 0.01$) as was unburned vs. high severity ($p < 0.001$). High and moderate severity types were not significant ($p = 0.11$). Deer mice first appeared in the burned grids in 2009. They were present in unburned grids in just one year (2011) (Fig 1b).

Table 4. Significant covariates in the negative binomial regressions of the numbers of pinyon mice, deer mice, chipmunks and California ground squirrels. Significant p-values are highlighted in bold. SE is one standard error of the regression coefficient.

Species	Covariate	Regression coefficient	SE	z-statistic	p-value
Pinyon mouse	Intercept	3.60	0.56	6.41	**< 0.001**
	Burn type	−0.65	0.21	−3.09	**0.002**
	Years-after-fire	−0.45	0.12	−3.70	**< 0.001**
Deer mouse	Intercept	−3.67	0.50	−4.57	**< 0.001**
	Burn type	0.98	0.25	3.96	**< 0.001**
	Years-after-fire	0.73	0.15	4.99	**< 0.001**
Chipmunks	Intercept	−1.26	0.50	−2.50	**0.01**
	Burn type	−0.52	0.15	−3.59	**< 0.001**
	Years-after-fire	0.69	0.10	6.74	**< 0.001**
California ground squirrel	Intercept	−3.50	1.17	−2.99	**0.003**
	Burn type	0.66	0.37	1.76	0.08
	Years-after-fire	0.35	0.21	1.64	0.10

Chipmunks

The number of chipmunks increased steadily in the unburned forest over the five years (Fig. 1c). The NBR analysis showed chipmunk numbers were significantly related to both burn type and years-after-fire (Table 4). In pairwise comparisons of the burn types, unburned vs. moderate severity was significant ($p = 0.01$) as was unburned vs. high severity ($p < 0.001$). High severity and moderate severity types were not significantly different ($p = 0.15$). In the first four years post-fire, chipmunk numbers were relatively evenly distributed among the three burn types but in 2012 numbers in the unburned forest exceeded the moderate and high-severity forests by three and seven times, respectively (Fig. 1c).

California Ground Squirrels

Ground squirrel numbers were erratic in all three burn types over the course of the study (Fig. 1d). Ground squirrel numbers were not significantly related to either burn type or years-after-fire (Table 4).

Ordination Analysis

In the CCA of the three burn types pooled for all five years, significant variables were: years-after-fire ($p = 0.002$), unburned ($p = 0.002$), high severity ($p = 0.004$), litter cover ($p = 0.006$), and bare ground ($p = 0.04$) (Table 5). A Monte Carlo permutation test showed the first canonical axis was significantly correlated with species distribution patterns ($p = 0.002$). The first CCA axis was most highly correlated with years-after-fire, and explained 18.7% of the variance in the species data with a species-environment correlation of 0.715. After this variable, the highest inter-set correlation coefficients for CCA 1 are unburned and high-severity burn types. Deer mouse is located on the left side of the biplot (Fig. 2) because it increased in abundance over time on the high-severity grids (Fig. 1b). California ground squirrel is associated with bare ground in the high-severity burns. In contrast, pinyon mice and chipmunks occupy the unburned (undisturbed) end of the gradient where litter cover was high (Fig. 2).

Table 5. Summary of the canonical correspondence analysis for the combined grids (N = 60) of the unburned, moderate-severity and high-severity forests for the five years of the study. Values are given for the first three axes of the CCA. Presented for each axis are eigenvalues, percentage of the variance explained, species-environment correlations and the inter-set correlation coefficients for variables that were significant ($p < 0.05$) in forward selection.

Axis	1	2	3
Eigenvalues	0.459	0.105	0.039
Cumulative percentage variance of species data	18.7	4.2	1.6
Species-environment correlations	0.715	0.351	0.234
	Inter-set correlation coefficients		
	Axis 1	Axis 2	Axis 3
Years-after-fire	−0.599	−0.164	−0.016
Unburned	0.394	−0.236	0.024
High severity	−0.260	0.216	0.059
Litter	0.185	−0.119	0.143
Bare ground	−0.158	0.042	−0.034

Years-after-fire was the only significant variable in the analysis of the unburned grids (no Figure presented). CCA Axis 1 (eigenvalue 0.396) explained 15.1% of the total variation in the small mammal data and had a species-environment correlation of 0.664. A Monte Carlo permutation test showed the first canonical axis was significantly correlated to species distribution patterns ($p = 0.002$). This axis reflects the general decrease in captures of pinyon mice (Fig. 1a) and an increase in chipmunks in the five years (Fig. 1c).

In the CCA of the combined moderate- and high-severity grids four variables were significant: years-after-fire ($p = 0.002$), rock outcrop cover ($p = 0.01$), litter cover ($p = 0.004$), and the combined cover of live shrubs and resprouting black oaks ($p = 0.02$)

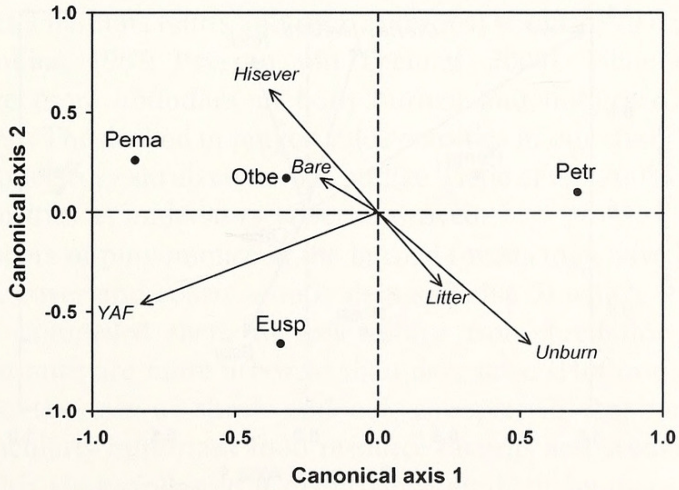

Fig. 2. Biplot of the canonical correspondence analysis of small mammal captures and environmental variables for the grids in the unburned forest and the moderate and high-severity burns. Arrow length indicates the strength of correlation between the variables and the canonical axes. *YAF* is years-after-fire, *Bare* is bare ground cover, *Litter* is litter cover, *Hisever* is high-severity burn grids, *Unburn* is unburned grids. Species acronyms are: Pema = *Peromyscus maniculatus*, Petr = *Peromyscus truei*, Nesp = *Neotamias merriami* and *N. obscurus* combined, and Otbe = *Otospermophilus beecheyi*.

Table 6. Summary of the canonical correspondence analysis for the combined grids (N = 40) of the moderate-severity and high-severity forests for the five years of the study. Values are given for the first three axes of the CCA. Presented for each axis are eigenvalues, percentage of the variance explained, species-environment correlations and the inter-set correlation coefficients for variables that were significant ($p < 0.05$) in forward selection.

Axis	1	2	3
Eigenvalues	0.405	0.074	0.014
Cumulative percentage variance of species data	17.0	3.1	0.6
Species-environment correlations	0.677	0.299	0.147
	Inter-set correlation coefficients		
	Axis 1	Axis 2	Axis 3
Years-after-fire	−0.677	0.021	−0.006
Rock outcrop	0.119	0.199	−0.003
Bare ground	0.134	−0.140	−0.119
Oak resprouts and shrubs	−0.132	0.213	0.002

(Table 6). Once again, Axis 1 was best correlated (−0.68) with years-after-fire which explained 17% of the variance in the small mammal data and was significantly correlated to species distribution patterns ($p = 0.002$). The positions of deer mice and pinyon mice on the first axis (Fig. 3) reflect the general increase in deer mice captures (Fig. 1b) in burned areas and a decrease in pinyon mouse densities in the unburned forests in the years-after-fire (Fig. 1a). Except for years-after-fire, inter-set correlation coefficients for the other four significant variables were low with the highest coefficient of only −0.213 for combined black oak resprout and shrub cover on CCA 2 (Table 6).

The second axis also was significantly correlated to species distribution patterns ($p = 0.01$) and depicts a gradient from relatively high rock outcrop and combined shrub and

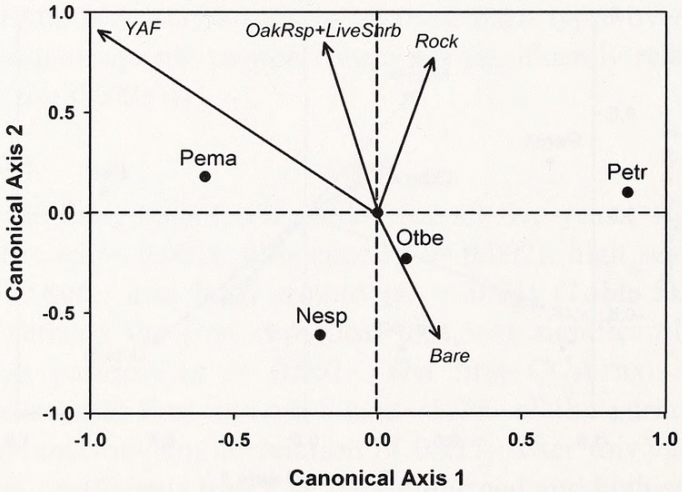

Fig. 3. Biplot of the canonical correspondence analysis of small mammal captures and environmental variables for the grids in the moderate and high-severity burns. Arrow length indicates the strength of correlation between the variables and the canonical axes. *YAF* is years-after-fire, *Rock* is rock outcrop cover, *Bare* is bare ground cover, *OakRsp* is California black oak resprout cover and *LiveShrb* is the cover of living shrubs. Species acronyms are: Pema = *Peromyscus maniculatus*, Petr = *Peromyscus truei*, Nesp = *Neotamias merriami* and *N. obscurus* combined, and Otbe = *Otospermophilus beecheyi*.

oak resprout cover (upper quadrants) to the relative absence of cover in the open represented by bare ground (bottom right quadrant) (Fig. 3). In the burned forests, deer mice show an affinity for the combined cover of oak resprouts and shrubs while pinyon mice favor rock outcrops. Chipmunks and California ground squirrels were captured frequently in the open, away from cover (Fig. 3).

Discussion

Three of the four species in this study showed a response to fire. Pinyon mice declined on the burn areas compared to the unburned forests (Fig 1a) while deer mice increased in the burn areas (Fig. 1b). Chipmunks were equally common in all three burn types for the first four years but increased markedly on unburned grids in the fifth year (Fig. 1c). Statistically, chipmunks responded negatively to fire. California ground squirrels did not appear to be affected by the fire (Fig. 1d). While three species showed a significant change in numbers compared to the unburned grids, comparisons between moderate and high severity burns were not significant for any of the species. Thus, differences in fire severity had no apparent effect on species responses.

This is the first post-fire study of pinyon mice in conifer forests. Pinyon mice were consistently most abundant in unburned forests and decreased, but did not disappear, in burned forests (Fig. 1a). There are three post-fire studies on pinyon mice: two in chaparral (Lawrence, 1966; Borchert and Borchert, 2013) and one in coast live oak (*Quercus agrifolia*)-blue oak (*Q. douglasii*) forests (Tietje et al., 2008). In oak forests pinyon mouse abundance was higher in the burned compared to the unburned area but only in the first fall after a low-intensity prescribed burn (Tietje et al., 2008). In their study pinyon mice became more abundant in the burn areas three and four years post-fire which is the opposite of our results showing pinyon mouse numbers were higher in unburned compared to burned areas four and five years post-fire (Fig. 1a).

In the unburned grids, where densities were highest, pinyon mice were microhabitat generalists, even though rock outcrops were common on all the unburned grids (Table 2). In the burned grids, in contrast, pinyon mice favored rock outcrops especially in the first two years post-fire (Fig. 3). Pinyon mice in desert habitats have shown a consistent preference for rocky habitats (cliffs and rock outcrops) (Geluso, 1971; Hoffmeister, 1981; Llewllyn and Jenkins, 1987; Pearson and Theimer, 2004). Tietje et al. (2008) found pinyon mice were more abundant in both burned and unburned plots where shrub density was highest. The decline in pinyon mice densities in our study also was associated with the loss of understory shrub cover but, unlike Tietje et al. (2008), we did not observe an increase in densities as understory cover improved.

The lower numbers of pinyon mice in the burned forests may have been due to the loss of shrub and oak cover and coarse woody debris (Table 3) which, in the early post-fire years, may have compelled them to seek refuge from predation in rock outcrops. Moreover, pinyon mice are more arboreal than deer mice (Holbrook, 1978; Ribble and Samson, 1987) so the loss of shrub and oak canopies in the burn areas may have eliminated a particularly important food resource (acorns and seeds).

Deer mice in this study followed a disturbance gradient by increasing in abundance from unburned forests to high-severity burns (Fig. 1b). Deer mice are habitat generalists, although they tend to favor open, xeric habitats (Zwolak, 2009). Despite being habitat generalists, deer mice are disturbance specialists (Keftig and Ahlgren, 1974; Martell, 1984; Kyle and Block, 2000; Zwolak and Foresman 2007; Zwolak 2009; Fontaine and Kennedy, 2012 but see Roberts et. al. 2008). More specifically, they increase in

abundance as disturbance intensity increases (Zwolak, 2009). Our results add to the many studies that consistently show deer mice increase after high severity fires.

Although numerous studies have focused on changes in densities of deer mice in response to fire, few have addressed their microhabitat affinities in burned areas. Most microhabitat studies of deer mice have focused on unburned conifer forests (summarized in Converse et al., 2006a). There were too few captures of deer mice in unburned forests to describe microhabitat preferences in this study. In the burned forests, however, deer mice were frequently captured under or near shrub and oak resprout cover (Fig 3). Kyle and Block (2000) also noted a positive relationship between deer mice densities and increasing forb and shrub cover. In burn areas Zwolak et al. (2012) found a positive relationship between deer mice numbers and open areas and coarse woody debris but not shrub cover.

Chipmunk numbers differed significantly among burn types and years. In our study they increased steadily in the unburned grids over the five years (Fig. 1c). Other studies have shown that the responses of chipmunks to prescribed fire and wildfire in conifer forests are highly variable. After prescribed burns, which most closely resemble the moderate-severity burn in this study, chipmunks responded negatively (Converse et al., 2006c; Maguire et al., 2008) or showed no response (Monroe and Converse, 2006; Meyer et al., 2007; Amacher et al., 2008). After wildfire, chipmunks declined in burned compared to unburned areas (Martell, 1984; Kyle and Block, 2000; Roberts et al., 2008) or showed no change (Monroe et al., 2004; Converse et al., 2006b; Zwolak and Foresman, 2007; Converse et al., 2006a). The increase in chipmunks in the unburned forest in our study suggests it may become more prevalent in this type but a longer study is needed to verify this trend.

California ground squirrels numbers were not significantly related to burn type (Table 4). In Yosemite National Park the capture rate for California ground squirrels decreased with increasing fire severity and, unlike this study, squirrels were not captured in high-severity burns (Roberts et al., 2008). In another study of Sierran mixed conifer forests Amacher et al. (2008) failed to find a significant difference in the abundance of California ground squirrels among the following treatments: unburned, low-intensity prescribed burn, mechanical thinning treatments and thinning plus fire.

Results of the ordinations were similar in that relatively little variation in the small mammal distributions were explained by stand structure or microhabitat characteristics. Microhabitat affinities of small mammals that developed in the burned areas were modest at best (Table 6). Even so, a comparison of burned and unburned forests showed that the microhabitats small mammals occupied changed after fire. In unburned forests none of the stand structure or microhabitat variables explained the distributions of the four common species. In contrast, in the burned forests small mammals showed greater microhabitat segregation—the crecitids favored cover elements while chipmunks and California ground squirrels were active in the open (Fig. 3), presumably where herbaceous food resources were more abundant.

Conclusions

High-severity fire in conifer forests has traditionally been viewed as both unnatural and undesirable by land management agencies (Bond et al., 2012). However, as studies accumulate on the response of the fauna to moderate and high-severity fire, it is becoming apparent that early stages of forest succession play a vital role in landscape recovery (Swanson et al. 2011). Many species benefit from this early stage and others are

highly dependent on it (Bond et al., 2012; Hanson et al., 2013; Odion and Hanson, 2013). Still, the number of post-fire studies on different vertebrate groups is uneven at best. Fontaine and Kennedy (2012) carried out a meta-analysis of the response of birds and small mammals to low/moderate and high-severity fire. There were 52 studies of birds but only twelve studies of small mammals, of which only two were in high-severity burns. Moreover, none of the small mammal studies lasted longer than four years. Bats, medium-to-large mammals, amphibians and reptiles studies summed to five.

Research on the effects of fire on vertebrate groups in southern California conifer forests lags well behind what is known about vegetation responses. If high-severity fires increase in southern California conifer forests as the climate becomes drier, it is imperative that greater attention be given to the post-fire responses of the fauna.

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