

The role of fire severity, distance from fire perimeter and vegetation on post-fire recovery of small-mammal communities in chaparral

Jay Diffendorfer^{A,E}, Genie M. Fleming^B, Scott Tremor^B, Wayne Spencer^C
and Jan L. Beyers^D

^ARocky Mountain Geographic Science Center, US Geological Survey, PO Box 25046,
MS 507, Denver, CO 80225, USA.

^BSan Diego Natural History Museum, PO Box 121390, San Diego, CA 92112, USA.

^CConservation Biology Institute, 815 Madison Avenue, San Diego, CA 92116, USA.

^DUSDA Forest Service, Pacific Southwest Research Station, Forest Fire Laboratory,
4955 Canyon Crest Drive, Riverside, CA 92507, USA.

^ECorresponding author. Email: jediffendorfer@usgs.gov

Abstract. Chaparral shrublands in southern California, US, exhibit significant biodiversity but are prone to large, intense wildfires. Debate exists regarding fuel reduction to prevent such fires in wildland areas, but the effects of these fires on fauna are not well understood. We studied whether fire severity and distance from unburned fire perimeter influenced recovery of the small-mammal community from 13 to 39 months after the large (1134.2 km²) Cedar fire in San Diego County. In general, neither factor influenced small-mammal recovery. However, vegetation characteristics, distance to riparian habitat and the prevalence of rocky substrate affected recovery in species-specific patterns. This indicates the effects of fire severity and immigration from outside the fire perimeter, if they occur, do so within 1 year, whereas longer-term recovery is largely driven by previously known relationships between small mammals and habitat structure. Our results, when combined with results from other studies in southern California, suggest where human lives or infrastructure are not at risk, efforts to preserve chaparral biodiversity should focus on maintaining the native plant community. Doing so may require novel management strategies in the face of an increasing human population, ignition sources and the spread of invasive exotic plants.

Additional keywords: coastal sage scrub, fire management, shrubland.

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Introduction

In southern California, the juxtaposition of high biodiversity, a rapidly expanding human population and large, frequent wildfires creates difficult decisions for management agencies. These conditions have also ignited a debate over whether and how to reduce fuel loads in wildland areas. Despite extensive literature on vegetation responses to fire, we do not fully understand the effects of fire on the animal species, diminishing our ability to consider trade-offs between human-modified fire regimes, hazard reduction and effects on native biodiversity in a region with two decades of landscape-scale conservation planning (Babbitt 1999). To reduce this knowledge gap, we studied population and community responses of small mammals following the human-caused Cedar Fire. It began on 25 October 2003 and burned ~113 400 ha of natural and urban areas in southern California.

Previous studies of small-mammal responses to fire vary in time, levels of replication and in particular results. Yet, collectively, these studies suggest a general response to fires.

During fires, species without below-ground burrows likely experience high levels of mortality, though individuals survive in rock crevices and underground burrows where temperatures remain low and air is clear (Chew *et al.* 1959; Quinn 1979; Wirtz 1995). After fires, recovery follows post-fire vegetation dynamics. In California shrub systems, early post-fire sites are utilised by species preferring open habitat, such as the kangaroo rat (*Dipodomys* spp.), pocket mouse (*Chaetodipus* spp.), California vole (*Microtus californicus*), harvest mouse (*Reithrodontomys megalotis*) and deer mouse (*Peromyscus maniculatus*). As shrub density increases and food sources become more varied, shrub-specialising species, such as the woodrat (*Neotoma* spp.), California mouse (*Peromyscus californicus*), brush mouse (*P. boylii*) and cactus mouse (*P. eremicus*) recolonise sites (Cook 1959; Price and Waser 1984; Quinn 1990; Schwilk and Keeley 1998). Similar relationships between post-fire plant succession and small mammals occur in other habitats (Fox 1982; Haim and Izhaki 1994; Torre and Diaz 2004).

Despite this general pattern, several details are not understood. For example, small-mammal responses to fire-related habitat change depend on species-specific life-history strategies (seed caching, winter aestivation, diet, predator avoidance, etc.), but often include changes in abundance and spatial distribution (Price and Waser 1984). These changes may be driven by variation in fire severity (i.e. organic matter consumption as described in Keeley 2009) or in fire size and, hence, distance to unburned perimeters. Fire severity may directly cause small-mammal mortality or indirectly influence post-fire mammal communities through effects on habitat structure and food availability (e.g. Moreno and Oechel 1994; Keeley *et al.* 2008). If species are locally extirpated from a burned area, distance to the burn perimeter and recolonisation sources should affect recolonisation rates. In a grass system, Rosario and Mathias (2007) found greater distances and less vegetation structure inhibited recolonisation of burned areas by the Cabrera vole (*Microtus cabrere*). However, in southern California shrub systems, Schwik and Keeley (1998) found species composition was not consistently related to distance from the unburned perimeter and suggested survival during the fire and rapid migration as potential causes.

We examined how fire severity, distance to the fire perimeter and vegetation influenced patterns of recovery for both individual small-mammal species and community composition relative to unburned control plots. We expected fire severity and distance would affect recovery patterns and interact with post-fire changes in vegetation structure and composition. We expected more severely burned plots to support both fewer individuals and species than less severely burned locations early in the study. These sites might have higher mortality during the fire and higher rates of predation caused by less shrub cover. Furthermore, we anticipated the longer-term effects of burn severity would be mediated by how burn severity affected vegetation recovery.

The size of the Cedar Fire large provided a unique opportunity to explore how recovery varied as a function of distance from the fire perimeter. As fire size increases, animals will generally have to move longer distances to recolonise areas or supplement reduced populations within the burn. Thus, we used distance as a proxy for fire size. We expected areas further from the fire perimeter to show slower post-fire recovery, but anticipated more vagile species tolerating more open habitat conditions would colonise burned areas further from the fire perimeter more rapidly than less vagile species or those preferring closed stands.

Methods

Study context

All wildfires burn heterogeneously and despite mortality, some small mammals survive fires because they take shelter in burrows, areas with large boulders or unburned refugia. Thus, at any site within a burned area, recovery of the small-mammal community will depend on mortality during the fire, species-specific demography after the fire and immigration of new individuals onto the site. Immigration could come from nearby refugia inside the burned area or unburned habitat outside the fire perimeter. Our study design and analyses were based on our

assumption that multiple processes drive small-mammal recovery after a wildfire. We tracked patterns of small-mammal recovery within the burned areas while including covariates related to mortality (fire severity), habitat recovery (vegetation) and immigration (presence of nearby refugia in riparian habitat and distance to the unburned fire edge). Concerning immigration, we were interested in knowing if large-scale recolonisation from the unburned edge of the fire influenced local, ongoing, recovery dynamics. The Cedar fire was one of the largest fires in southern Californian history and represented a unique opportunity to study the influence of colonisation from outside the fire perimeter on post-fire recovery.

Study design

Our experimental design compared 30 burned and 10 unburned plots, spaced >200 m apart, in chaparral vegetation, within the Cleveland National Forest. The four most abundant shrub species included the frequently dominant chamise (*Adenostoma fasciculatum* Hook. & Arn.) and cup-leaf lilac (*Ceanothus greggii* A. Gray), with varying abundances of scrub oak (*Quercus berberidifolia* Liebm.) and the suffrutescent deerweed (*Lotus scoparius* (Nutt.) Ottley).

Burned plots spanned a range of fire severities and distances from the Cedar Fire perimeter. Burned stem diameters on our plots (40 chamise measured per plot with medians 5–27 mm) were similar to those measured by Keeley *et al.* (2008) across 79 locations in the same fire (2–28 mm), indicating we sampled a reasonable range of severity within the burned area. Stem diameters were converted into a fire severity index value developed by Keeley (1998), and the mean index value per plot was used (range = 3.9–7.2, mean = 5.1 ± 0.8 s.d.). Distance was measured as the shortest distance, in kilometres, between the plot centre and the fire perimeter. Burned plots were located <1 to ~8 km inside the perimeter (mean = 3.7 ± 2.8 s.d.) whereas unburned plots were within 2 km of the burned area. Maximum distance to the fire perimeter was lower for unburned plots owing to the location of the existing road network and our attempt to maintain similarity between burned and unburned areas.

Small mammals

Rodent populations were sampled twice per year (spring and autumn) during 5-night trapping sessions. Given the timing of the fire relative to the funding cycles at the US Forest Service Joint Fire Science Program, trapping began ~13 months after the fire (November 2004), with additional sessions at 18, 24, 30, 36 and 43 months (May 2007) post-fire. With the year-long delay, our study does not address short-term post-fire effects, but does capture the more sustained effect of fire on small-mammal communities. We used 30 baited Sherman XLK folding traps (HB Sherman traps, Tallahassee, FL, USA) in two lines, 15 m apart, with 7-m intra-line trap spacing. We baited traps before dusk with sunflower seeds (roasted to prevent germination) and checked traps the following morning for five consecutive mornings. Each animal captured was assigned a unique mark, and we recorded date, trap location, species, weight, sex, age and reproductive characteristics.

Small-mammal abundance for each plot, species and trapping session was calculated using Chapman's modified

Lincoln–Petersen estimator (Chapman 1951). Each 5-night session was divided into two sample occasions where nights 1–3 equalled the marking occasion, and nights 4–5 equalled the recapture occasion. This method matches that used by, for example, Menkens and Anderson (1988), who showed population estimates from 5-day trapping periods were close to known values using Monte Carlo simulations.

Precipitation, abiotic factors and vegetation

Southern California is characterised by a Mediterranean-type climate with cool, wet winters and warm, dry summers. We calculated 'precipitation' as the total measured precipitation (in mm) for the 5 months before each trapping session. Precipitation data were from the Descanso, CA, weather station, which was within 10 km of all plots (<http://www.calclim.dri.edu/ccda/rawslist.html>, accessed 3 December 2011).

At each study plot, we measured several abiotic and vegetation variables potentially associated with small mammals. Abiotic variables included presence of a riparian area within 150 m, elevation, slope inclination and azimuth, and soil texture. A total of 10 of 40 plots had small riparian areas nearby. These areas were burned through, but had faster regrowth than non-riparian areas, more standing dead vegetation and running water at some time during the year. We included this variable because we expected these areas provided early post-fire habitat for shrub specialists, and a source of water that could influence post-fire recovery patterns. Inclination (percentage slope) and azimuth (0–360°) were measured in the field using a clinometer and compass. Azimuth was then converted into two variables representing north to south and east to west dimensions of aspect: 'northness' (cosine(azimuth)) and 'eastness' (sine(azimuth)). Northness and eastness variables ranged from –1 to +1, with the positive limit representing north- and east-facing slopes, and the negative limit representing the opposing aspect. Average soil texture (percentages sand, silt and clay) was determined from six soil samples per plot subjected to particle size analysis using a standard hydrometer method.

Vegetation was sampled each spring when plants were at or near their phenological peak. Each plot included two 100 × 1-m belt transects for vegetation sampling, located ~5 m to the outside of each small-mammal trap line. The close proximity of our vegetation transects to the small-mammal traps was designed for two main reasons. First, our previous trapping in similar habitats (Diffendorfer *et al.* 2007) and past studies (Price and Waser 1984) indicated fine-scale vegetation conditions affected small-mammal abundance and community composition. Second, a long vegetation transect captured the fine-scale variation in vegetation around our capture sites while also capturing the broader-scale character of the focal habitat in which the trapping was conducted as study plots were placed within larger areas of generally similar vegetation (see Figs S1–S8 in the Supplementary material for photographs of some study plots). At each sample, we estimated the canopy cover of herbs and woody species (shrubs, subshrubs and suffrutescents) across the plot using a point intercept method. Fifty sample points were spaced at 2-m intervals along each transect starting at 0.5 m. We recorded the identity and maximum height, to the nearest 0.1 m, of each species intercepting each point. Percentage canopy cover of all herbs collectively, all woody species and

individual cover of the four most common woody species (chamise, cup-leaf lilac, scrub oak and deerweed) was calculated as the number of points where a particular type of vegetation was recorded, divided by the total number of sample points.

We also located ten 1-m² quadrats at 10-m intervals along each transect. Quadrats served as the focal point for the fire severity measures described above (two closest burned chamise measured per quadrat), and within each quadrat we measured two finer-scale vegetation properties and two soil surface properties: (1) basal vegetation; (2) visual obscurity; (3) surface rock cover (fragments >5 cm); and (4) surface gravel cover (fragments <5 cm). Basal vegetation was visually estimated as the percentage of the quadrat covered by any vegetation (live, standing dead, litter) within 10 cm of the ground surface. This variable may reflect ease of movement and foraging for some species. Obscurity was visually estimated as the percentage of a vertically oriented metre-stick obscured by vegetation. Separate obscurity estimates were made within three height classes: 0–0.3, 0.3–0.6 and 0.6–1.0 m from the ground surface. Obscurity may, like basal vegetation, affect foraging, but it also may be indicative of cover and, hence, risk of predation. Percentage cover of surface gravel and rock were expected, along with soil texture, to influence burrowing activity. In addition, larger rocks could provide refuge during and after the fire.

Statistical analyses

We employed hierarchical linear modelling (HLM) (Raudenbush and Bryk 2002) in *HLM* 6.02 (Scientific Software International, Lincolnwood, IL, USA) to simultaneously model the combined influences of habitat, fire severity and distance from the perimeter on change through time in (i) individual species' abundances, and (ii) compositional similarity of small-mammal communities between burned and unburned plots. HLM accounts for correlations among multiple observations from individual plots by including random plot effects along with fixed effects of explanatory variables. Though ultimately defined by a single regression equation, with all parameters simultaneously estimated by maximum likelihood techniques, the HLM model can be conceived as a two-level model where data from trapping sessions within plots are modelled at Level 1 as a function of some variable X (e.g. time) and differences among plots are modelled at Level 2 as a function of some variable W (e.g. fire severity):

$$\text{Level 1: } Y = \beta_{0j} + \beta_{1j} \times X + r_{ij}$$

where

$$\text{Level 2: } \beta_{0j} = \gamma_{00} + \gamma_{01} \times W_j + u_{0j}$$

and

$$\beta_{1j} = \gamma_{10} + \gamma_{11} \times W_j + u_{1j}$$

The parameters β_{0j} and β_{1j} are respectively the within-plot intercept (expected Y value when $X=0$) and slope. Thus, the coefficients γ_{01} and γ_{11} give the estimated effect of variable W on the within-plot intercept or slope (it need not, necessarily,

influence both). This effect, though presented in terms of a single variable, is essentially a cross-level interaction effect (e.g. time $\times$ fire severity).

At Level 1, we modelled species abundance within burned plots as a function of time and precipitation and the similarity in species composition on burned v. unburned plots as a function of time. Each plot's intercept and slope over time were treated as random effects, with an estimated variance of u_{qj} . Precipitation was treated as a fixed effect, and values were rescaled around the median 5-month total for the study period (300.9 mm) so the intercept represented expected abundance with median precipitation.

At Level 2, we modelled differences among burned plots in the intercept or slope of abundance through time (pattern of recovery) as a function of abiotic factors, vegetation and fire severity or distance from the burn perimeter. We conducted these analyses in a step-up fashion, where variables were entered into the model one at a time and retained only if the model Akaike's Information Criterion (AIC) was decreased by a value greater than 2 (Burnham and Anderson 2002). Models were built up in this fashion to: (1) preserve statistical power in the face of multiple, and in some cases correlated, explanatory variables; and (2) determine if the effects of fire severity or distance were present after accounting for any important environmental or habitat influences. Thus, the entry order of variables was based on a theoretical 'bottom-up' prioritisation of effects. Abiotic variables were entered first, beginning with broader-scale or 'regional' variables generally affecting an area larger than the plot (e.g. slope aspect) followed by more local variables (e.g. soil texture). Vegetation variables were entered after abiotic factors, again with 'broader', or more general, variables entered first (e.g. general plant-type cover followed specific species cover). Fire severity and distance were entered last. In order to achieve the most parsimonious final model, a variable entered at an early stage could be removed at a later stage. Specifically, if a variable that resulted in early model improvement became non-significant based on univariate t tests ($P > 0.05$) following addition of some new variable, the variable was retained only if the AIC for the new model was at least 2 units lower than a model without the early variable.

Explanatory variable selection

Because we measured more abiotic and vegetation variables than could reasonably be included in statistical models, we examined bivariate correlations with small-mammal abundance and selected only those variables showing significant ($P < 0.05$) correlations with at least one species in at least two out of three spring trapping sessions or with distance or fire severity. Many of the selected abiotic and vegetation variables were correlated with each other, so we used Principal Components Analysis (PCA) with orthogonal varimax rotation, conducted in *SPSS 12.0* (IBM, New York), to further reduce the number of explanatory variables by creating composite variables reflecting those relationships. Although we measured vegetation change annually on burned plots, our goal was to examine how general, not year-specific, differences in vegetation and abiotic factors influenced mammal patterns over time. Thus, the PCA was executed using data from all years simultaneously to capture

generalised relationships. We then used the coefficients from this PCA and year-specific vegetation values to generate within-year factor scores. As the 2005 factor scores were highly correlated with scores in subsequent years ($r = 0.66\text{--}0.99$), we used them as an index of each plot's vegetation and abiotic structure.

Individual species' abundances

Lincoln–Petersen abundance estimates were started log-transformed ($Y' = \ln[Y + 1]$) for use in analyses. Prior to analysis, we examined scatter plots of abundance v. time or other explanatory variables for evidence of non-linear trends. When detected, both linear ($X - X_{\text{mid}}$) and quadratic ($[X - X_{\text{mid}}]^2$) components for the explanatory variable were used in the HLMs. Rescaling the explanatory variable around its midpoint was performed to remove non-essential collinearity between linear and quadratic components. For consistency of interpretation, we used the same scaling of time in all abundance analyses so the intercept in HLM models represented expected log species abundance at 28 months. Though this is not during a specific trapping session, it represents the midpoint between 13 and 43 months and we use the midpoint of 28 months when reporting results.

Compositional similarity

We used the similarity ratio (Zuur *et al.* 2007) as an index of similarity in small-mammal community composition between burned and unburned plots. We calculated the ratio using the relative Lincoln–Petersen abundance of all species detected during the study. For each trapping session, we calculated similarity between each burned plot and the average of unburned plots (i.e. comparing plot-specific relative abundance for each burned plot with the average relative abundance among unburned plots). Similarity ratios were then square-root transformed to meet distributional assumptions of HLM before use in statistical analyses.

The HLM models investigated changes in similarity between burned and unburned plots through time and factors affecting these changes. Time was scaled so a value of zero represented 13 months since fire, or the start of the study (i.e. time = actual months since fire – 13). This scaling meant the intercept of the HLM equation represented the expected square-root similarity ratio at the start of the study and the time slope represented the estimated incremental change in the ratio per month.

The influence of habitat variables on the rate of monthly change in similarity between burned and unburned plots could be best understood by examining (1) which species contributed most to the similarity measure, and (2) how abundance of these species changed through time on burned plots in relation to habitat variables. We examined which species contributed most to similarity using multiple linear regression separately for each trapping session with the relative abundances of all species included as explanatory variables. Separate analyses were conducted for each session as we expected species' contributions to similarity might change through the recovery process owing to population sizes of different species fluctuating independently through time.

Results

General trends in plot factors, precipitation and vegetation

Plot elevation ranged from 838 to 1256 m on slopes ranging from 7 to 44% inclination. Soils were loams and sandy loams with 7–27% clay. The 2003–04, 2005–06 and 2006–07 water years (October–September) experienced below-average rainfall, whereas precipitation in 2004–05 was 164% of the long-term average for the area. Rainfall in 2006–07 totalled only 46% of average. Herbaceous vegetation cover tracked rainfall patterns, with the highest cover occurring in spring 2005 (~18 months post-fire) and declining thereafter in both burn conditions (Supplementary material, Fig. S9). Woody plant cover remained relatively stable through time on unburned plots but increased on burned plots between 2005 and 2006.

PCA of vegetation and abiotic factors

Preliminary PCA results indicated eastness and clay were unique factors, so they were included in subsequent analyses in their original form. The final PCA (Supplementary material, Table S1) resulted in three factors: (1) shrub composition: a species cover–topographic gradient with low values representing high deerweed cover at lower elevations with more southerly aspects and high values representing high scrub oak and cup-leaf lilac cover at higher elevations with more northerly aspects; (2) growth form abundance: a gradient with low values representing high herbaceous cover and high values representing high woody species cover, especially chamise; and (3) slope inclination: an inclination–surface rock gradient with high values representing steeper slopes with higher surface rock cover in 1 m². Together, the three factors accounted for 71% of the total variance in the set of original variables.

Fire severity was positively correlated with 2005 shrub composition factor values ($r = 0.60$, $P = 0.001$) and negatively correlated with growth form abundance ($r = 0.38$, $P = 0.039$). Distance to the fire perimeter was positively correlated with 2005 growth form abundance ($r = 0.56$, $P = 0.001$) and negatively correlated with eastness ($r = 0.44$, $P = 0.016$). Fire severity and distance to the burn perimeter were not strongly correlated ($r = 0.12$).

Small mammals

General patterns

Over the 30-month study period, we trapped 5613 individuals among 10 rodent species across all 40 study plots. Small-mammal communities on burned v. unburned plots were different at the beginning of the study and remained so despite slowly increasing similarity scores (Fig. 1; average similarity ratio at month 13 = 0.183, s.e. = 0.012 – see γ_{00} in HLM model results for similarity in Supplementary material Table S2; average rate of increase in similarity ratio (γ_{10}) = 0.009, s.e. = 0.001). As expected, shrub-preferring California mice were relatively rare on burned plots but largely dominated unburned plots. Burned plots were initially dominated by species tolerating disturbance or open conditions such as deer mice and kangaroo rats, with kangaroo rat dominance increasing over time. Cactus mice were also relatively abundant on burned plots in many sessions.

Four species, California vole, large-eared woodrat (*Neotoma macrotis*), San Diego pocket mouse (*Chaetodipus fallax*) and harvest mouse (*Reithrodontomys megalotis*) were uncommon (low occupancy or low abundance) on both burned and unburned plots in all trapping sessions, and were excluded from population trend analyses on burned plots. Of the six species modelled, the cactus mouse, Dulzura kangaroo rat (*Dipodomys simulans*) and California pocket mouse (*Chaetodipus californicus*) all declined in abundance with precipitation above the median, though the trend was non-linear for the latter two species (cactus mouse: linear rate of decrease with precipitation (γ_{30}) = -0.0009 , s.e. = 0.0002; kangaroo rat: instantaneous rate of decrease at median precipitation (γ_{30}) = -3.0×10^{-4} , s.e. = 2.0×10^{-4} , deceleration in the rate with increased precipitation (γ_{40}) = 3.0×10^{-6} , s.e. = 1.0×10^{-6} ; pocket mouse: instantaneous rate of decrease at median precipitation (γ_{30}) = -1.0×10^{-3} , s.e. = 2.0×10^{-4} , deceleration in the rate with increased precipitation (γ_{40}) = 3.0×10^{-6} , s.e. = 1.0×10^{-6} ; Supplementary material, Table S2). The California mouse and deer mouse abundances both increased with increasing precipitation whereas the desert woodrat (*Neotoma lepida*) was unaffected by precipitation (California mouse: instantaneous rate of decrease at median precipitation (γ_{30}) = -4.0×10^{-4} , s.e. = 2×10^{-4} , acceleration in the rate with increased precipitation (γ_{40}) = 2.0×10^{-6} , s.e. = 1.0×10^{-6} ; deer mouse: linear rate of decrease with precipitation (γ_{30}) = -0.001 , s.e. = 0.0002; Supplementary material, Table S2).

After statistically accounting for the influence of precipitation, most species on burned plots showed increasing abundance through time, though the deer mouse and desert woodrat showed decreases in abundance during the last half of the study (Fig. 2). Similarity in composition between burned and unburned plots also generally increased through time (Figs. 2–4), but both species-specific abundance and compositional similarity were often influenced by habitat variables. After statistically accounting for habitat, distance to the fire perimeter showed some, but fire severity showed little, influence on species abundance or compositional similarity.

Habitat effects

Slope inclination and aspect (eastness) along with presence of nearby riparian habitat affected several species and, in some cases, compositional similarity. Cactus mice, California pocket mice and, to a lesser extent, desert woodrats had higher abundances on steeper slopes whereas deer mice and kangaroo rats had higher abundances on more gentle slopes (Fig. 2). For example, at 28 months post-fire, expected abundance of cactus mice and pocket mice increased with slope inclination (Fig. 2a, b; cactus mice: influence of inclination on abundance at 28 months (γ_{0n}) = 0.217, s.e. = 0.06; pocket mice: influence of inclination on abundance at 28 months (γ_{0n}) = 0.328, s.e. = 0.093; Supplementary material, Table S2). Cactus mice were also more abundant on more easterly slopes (influence of eastness on abundance at 28 months (γ_{0n}) = 0.269, s.e. = 0.102). Desert woodrats showed slightly lower rates of decline on steeper slopes towards the end of the study period (Fig. 2c; influence of inclination on instantaneous slope of time at 28 months (γ_{1n}) = -0.003 , s.e. = 0.003, influence of

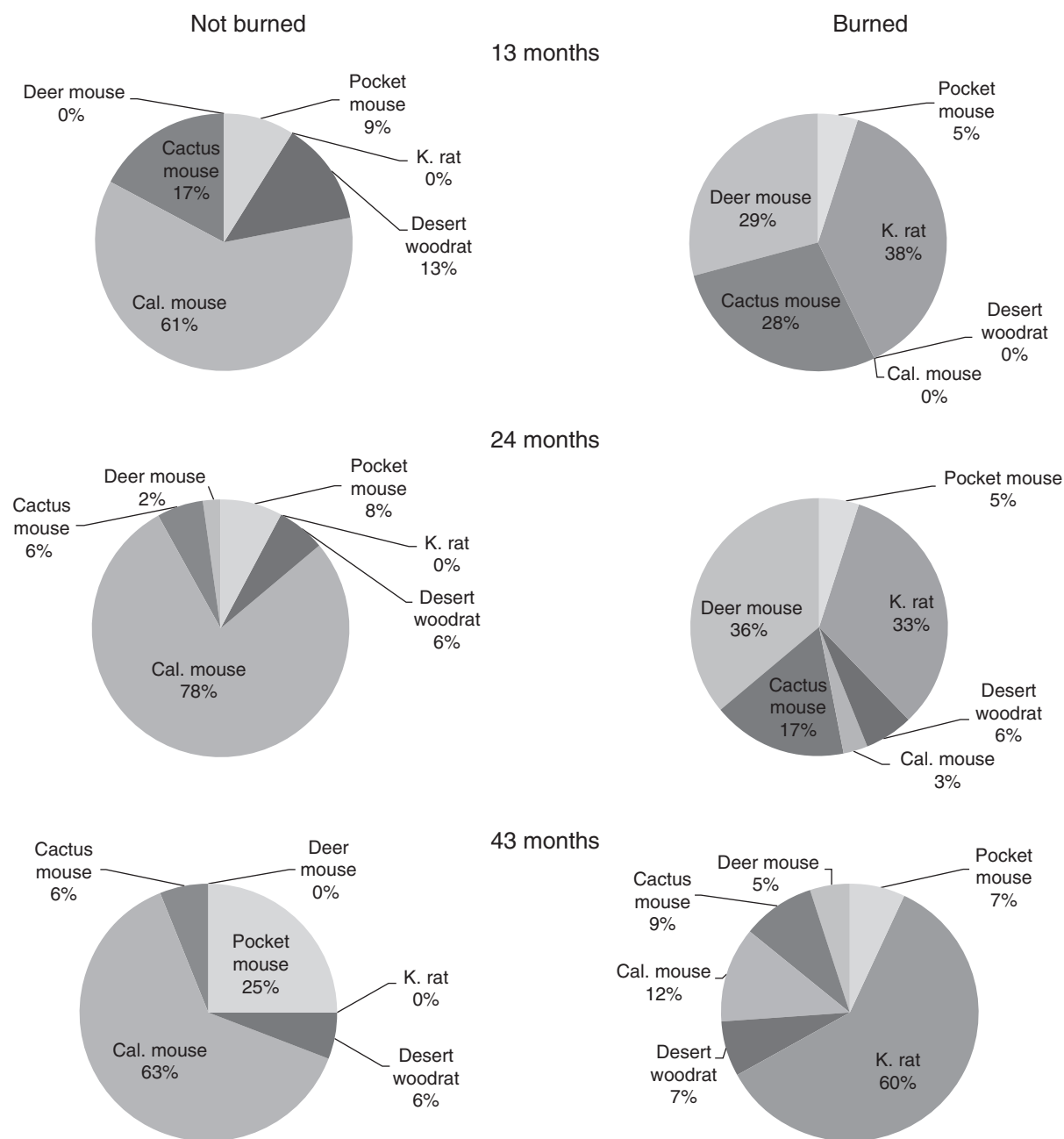


Fig. 1. Relative Lincoln-Petersen abundance for prominent species trapped on unburned (left) and burned (right) plots within Cleveland National Forest between 13 and 43 months following the 2003 Cedar Fire. California pocket mice, large-eared woodrats, western harvest mice, and California voles were excluded given low relative abundances. Trapping sessions at 18, 30 and 36 months post-fire are not shown, but do not differ from the general pattern observed. K. rat, kangaroo rat; Cal. mouse, California mouse.

inclination on acceleration of the slope of time (γ_{2n}) = 0.001, s.e. = 0.002; Supplementary material, Table S2). Because the median abundance of woodrats at month 43 was typically low across plots, differences among plots categorised as low, medium or high inclination in Fig. 2c appear small. However, high-inclination plots showed nearly twice the abundance of medium or low plots. By contrast, expected kangaroo rat abundance at 28 months decreased with slope inclination and on more easterly aspects, whereas the rate of deer mouse

decline towards the end of the study increased with inclination (Fig. 2d, e; kangaroo rats: influence of inclination on abundance at 28 months (γ_{0n}) = -0.322, s.e. = 0.080, influence of eastness on abundance at 28 months (γ_{0n}) = -0.213, s.e. = 0.073; deer mice: influence of inclination on instantaneous slope of time at 28 months (γ_{1n}) = -0.001, s.e. = 0.007; influence of inclination on deceleration in the slope of time (γ_{2n}) = -0.001, s.e. = 0.0003; Supplementary material, Table S2).

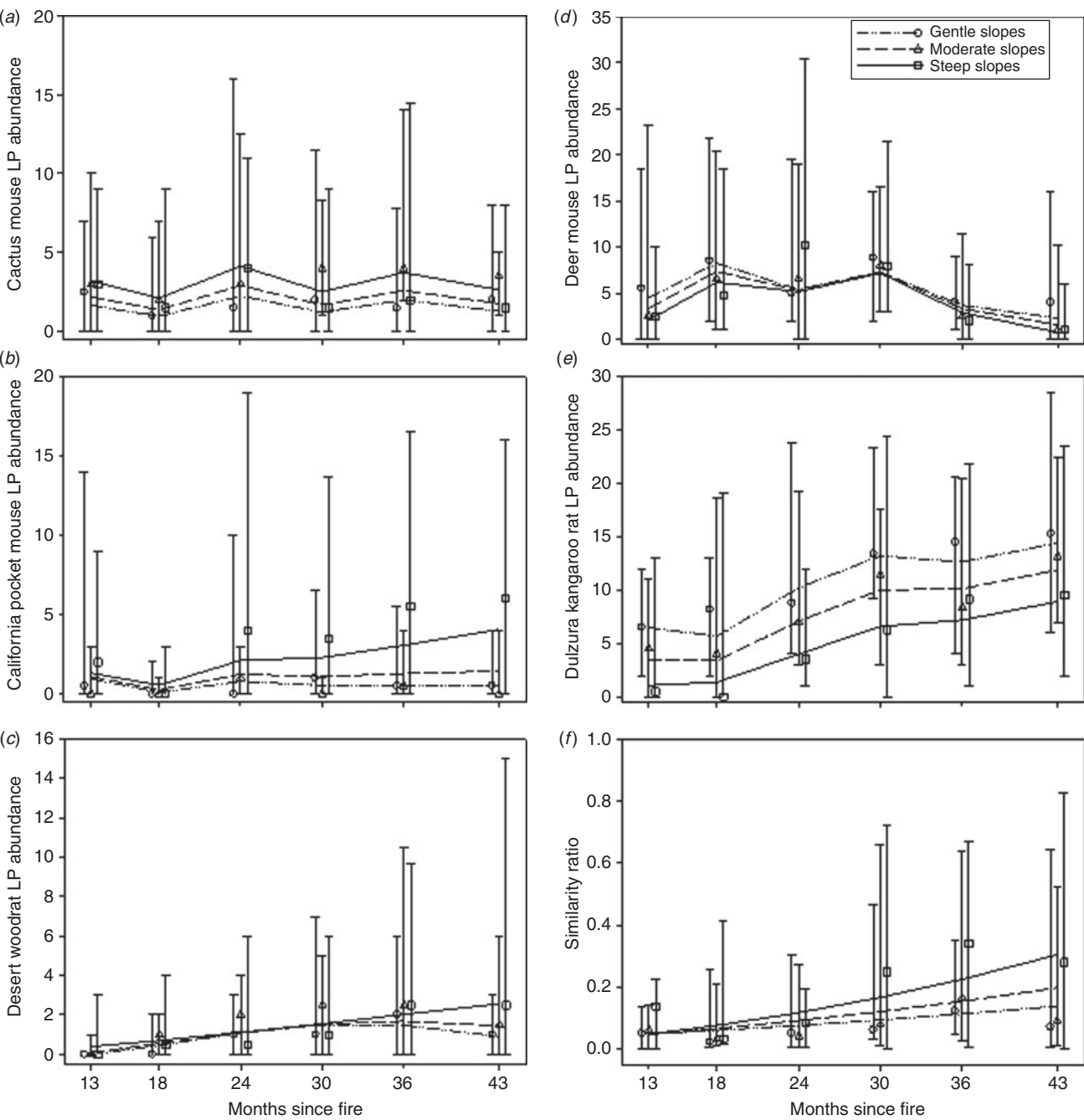


Fig. 2. Changes through time in Lincoln–Petersen (LP) abundance (a–e) and compositional similarity of small-mammal communities on burned v. unburned plots (f) as a function of slope inclination and surface rock cover (a composite factor; see text for details). Lines represent the expected change through time, holding other variables constant at their means, for a plot with an ‘average’ low, medium or high inclination value based on hierarchical linear modelling (HLM) and back-transformation of expected square root or log values. Symbols represent the observed medians for groups of plots categorised (for graphical purposes) as low, medium or high inclination; bars represent minimum and maximum observed values within those categories. Because HLM, like linear regression, tests for change in the dependent variable across the range of the explanatory variable, symbols and bars show the central tendency and range of the data, rather than implying significant differences between groups. All plots were sampled at approximately the same time post-fire, but points have been offset along the time axis for greater clarity.

Compositional similarity also increased at a faster rate on steeper slopes (Fig. 2f, Supplementary material, Table S2; influence of inclination on the linear slope of time (γ_{1n}) = 0.003, s.e. = 0.001). Holding other variables constant, a burned plot on a gentle slope might have had a similarity ratio of 0.05 at 13 months

and 0.14 at 43 months, whereas the similarity ratio on a steep plot would have been comparable at 13 months but increased to 0.31 by 43 months (based on back-transformation of expected square-root values). Abundance patterns of cactus mice and kangaroo rats likely drove this pattern, as the relative abundances

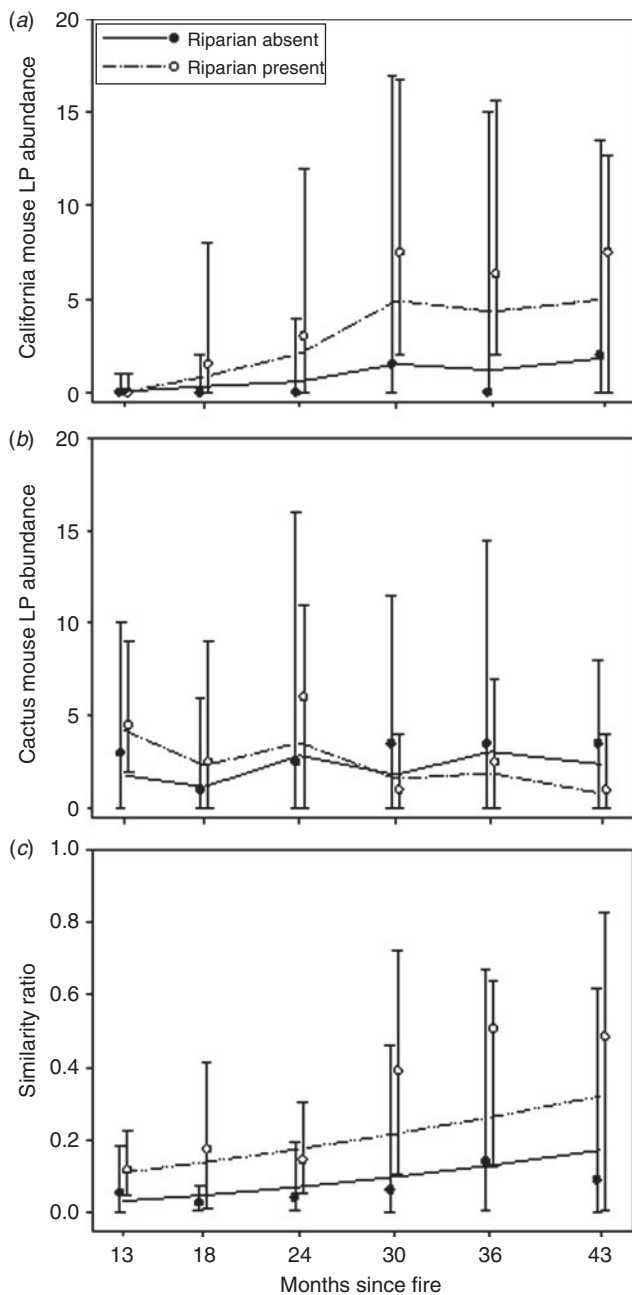


Fig. 3. Changes through time in Lincoln–Petersen (LP) abundance (a, b) or compositional similarity of burned to unburned plots (c) as a function of riparian habitat presence within 150 m. Symbols represent observed medians within presence–absence categories; bars represent minimum and maximum observed values; lines represent the expected change through time based on hierarchical linear modelling (HLM) and holding other variables constant at their means. All plots were sampled at approximately the same time post-fire, but points have been offset along the time axis for greater clarity.

of these species showed statistically significant relationships with similarity in early and late trapping sessions (kangaroo rat: month 13, regression of relative abundance onto community similarity ratio $B = -0.10$, s.e. = 0.004, $P = 0.015$; month 43, $B = 0.030$, s.e. = 0.006, $P < 0.001$. Cactus mouse: month 13, $B = 0.022$,

s.e. = 0.005, $P = 0.001$; month 36, $B = 0.011$, s.e. = 0.003, $P = 0.003$; see Supplementary material, Table S3, for detailed results including the squared semipartial correlation coefficients between species relative abundance and the similarity ratios).

Presence of nearby riparian habitat appeared beneficial to California mice and deleterious for cactus mice, but ultimately contributed to higher similarity of burned to unburned plots. California mouse abundance was very low on all burned plots at the start of the study, but it increased at a faster rate near riparian habitat (Fig. 3a; e.g. increase in instantaneous slope of time at 28 months for riparian present v. absent (γ_{1n}) = 0.027, s.e. = 0.012; Supplementary material, Table S2). By 28 months post-fire, expected California mouse abundance was approximately three times higher near riparian habitat (increase in abundance at 28 months for riparian present v. absent (γ_{0n}) = 0.805, s.e. = 0.235). In contrast, cactus mouse abundance decreased slightly through time on plots near riparian habitat and increased slightly on plots away from riparian habitat (Fig. 3b; decrease in linear slope of time for riparian present v. absent (γ_{1n}) = -0.042, s.e. = 0.011; Supplementary material, Table S2). Although we did not detect significant differences in cactus mouse abundance between plots near or far from riparian habitat in follow-up analyses, the slightly higher abundance of cactus mice on burned plots near riparian habitat at the beginning of the study implied by the HLM model (Fig. 3b) likely contributed to higher compositional similarity to unburned plots early on. Holding other variables constant, the expected similarity ratio between burned and unburned plots was 0.11 for plots near a riparian area compared with a value of 0.03 where riparian was absent (Fig. 3c). Relative abundance of cactus mice was positively related to similarity in early trapping sessions and explained the greatest proportional variation in similarity in the first session (Supplementary material, Table S3). In later sessions, higher California mouse abundance near riparian areas likely contributed to the continued higher compositional similarity to unburned plots (month 36, $B = 0.021$, s.e. = 0.003, $P < 0.001$; month 43, $B = 0.030$, s.e. = 0.006, $P < 0.001$; Fig. 3c).

Vegetation characteristics also influenced species-specific abundance patterns on burned plots and compositional similarity to unburned plots. Contrary to our expectations, cover of shrubs in general (i.e. growth form abundance) showed less influence than the composition of the shrub canopy. Abundances of California mice, California pocket mice and, to some extent, deer mice were positively associated with increasing cover of scrub oak and cup-leafed lilac, whereas cactus mice and, to a lesser extent, kangaroo rats responded negatively to oak and cup-leafed lilac and positively to increasing deerweed cover (Fig. 4). By 28 months post-fire, expected abundance of California mice and pocket mice increased incrementally with cover of scrub oak and cup-leafed lilac, as did the overall rate at which California mice were added to the population (Fig. 4a, b; California mice: influence of shrub composition on abundance at 28 months (γ_{0n}) = 0.442, s.e. = 0.128, influence of inclination on the instantaneous slope of time at 28 months (γ_{1n}) = 0.020, s.e. = 0.008; pocket mice: influence of shrub composition on abundance at 28 months (γ_{0n}) = 0.277, s.e. = 0.084; Supplementary material, Table S2). Rates of decline in deer mouse abundance towards the end of the study were lowest where scrub oak cover was high (influence of

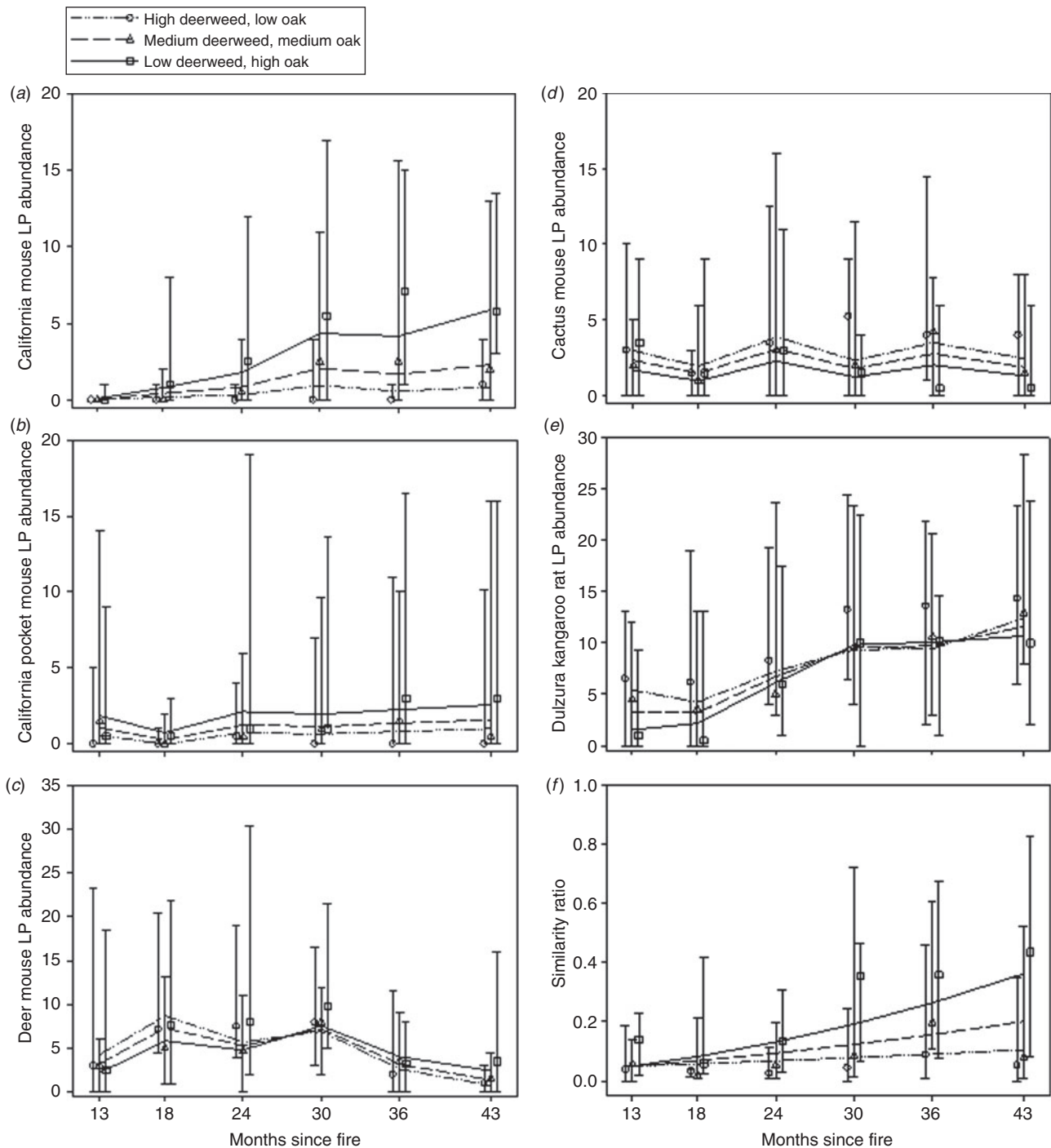


Fig. 4. Changes through time in Lincoln-Petersen abundance (LP) (a–e) or compositional similarity of burned to unburned plots (f) as a function of shrub composition (a composite factor; see text for details). Symbols represent observed medians within shrub composition categories; bars represent minimum and maximum observed values; lines represent the expected change through time based on hierarchical linear modelling (HLM) and holding other variables constant at their means. All plots were sampled at approximately the same time post-fire, but points have been offset along the time axis for greater clarity.

inclination on the instantaneous slope of time at 28 months (γ_{1n}) = 0.018, s.e. = 0.006; influence of inclination on deceleration in the time slope (γ_{2n}) = 0.0002, s.e. = 0.0004, so at 43 months post-fire, deer mouse abundance increased incrementally with scrub oak and cup-leaf lilac cover (Fig. 4c; also supported by follow-up multiple linear regression using data from 43 months

only: $\log \text{abundance} = 1.0 - (0.3 \times \text{inclination}) + (0.4 \times \text{shrub composition})$, $R^2_{adj} = 0.30$, $P_{\text{composition}} = 0.005$). In contrast, expected abundance of cactus mice decreased with cover of scrub oak and cup-leaf lilac, or alternatively, increased with cover of deerweed (Fig. 4d, influence of shrub composition on abundance at 28 months (γ_{0n}) = -0.188, s.e. = 0.081; Supplementary

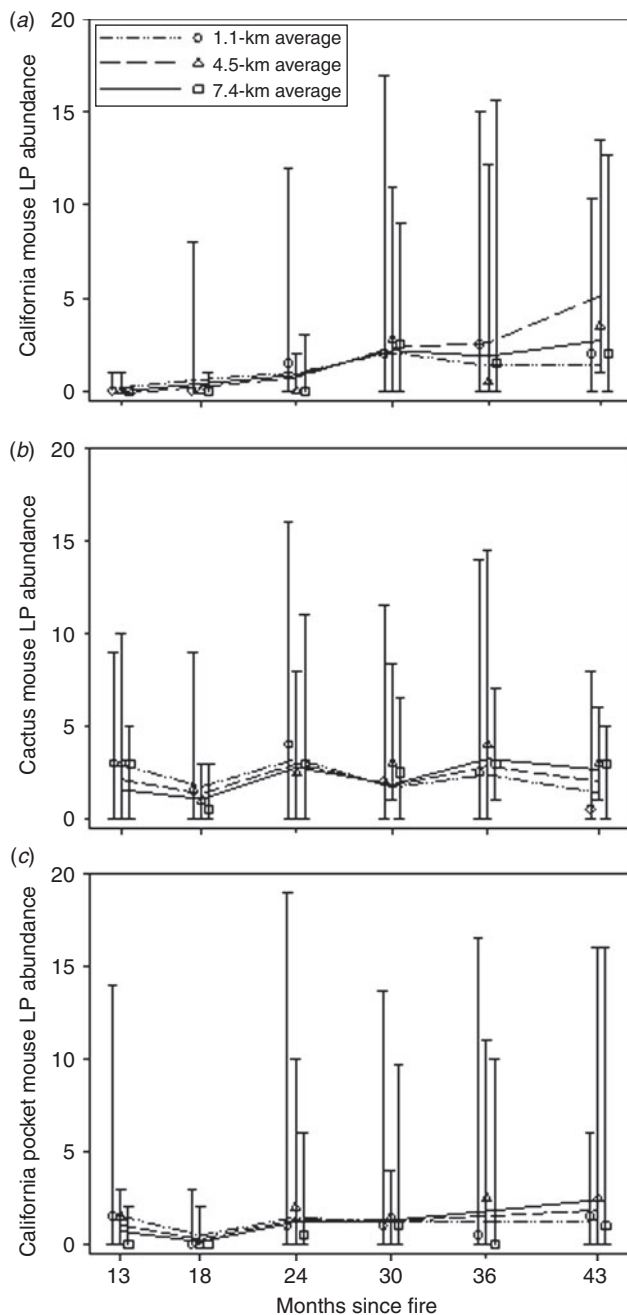


Fig. 5. Changes through time in Lincoln–Petersen (LP) abundance as a function of distance from the fire perimeter. Symbols represent observed medians within distance categories; bars represent minimum and maximum observed values; lines represent the expected change through time based on hierarchical linear modelling (HLM) and holding other variables constant at their means. All plots were sampled at approximately the same time post-fire, but points have been offset along the time axis for greater clarity.

material, Table S2). Kangaroo rat abundance increased with deerweed during early sessions but those same plots had lower rates of population growth, so differences diminished with time (Fig. 4e; multiple linear regression using data from 13 months only: $\log \text{abundance} = 1.8 - (0.5 \times \text{inclination}) + (0.4 \times \text{growth}$

$\text{form abundance}) - (0.4 \times \text{shrub composition})$, $R^2_{adj} = 0.72$, $P_{\text{composition}} < 0.001$; influence of inclination on the instantaneous slope of time at 28 months ($\gamma_{1n} = 0.013$, s.e. = 0.005; influence of inclination on deceleration in the time slope ($\gamma_{2n} = -0.001$, s.e. = 0.0003; Supplementary material, Table S2). Expected kangaroo rat abundance also increased with woody cover, a result somewhat contrary to the usual observation that the species prefers more open conditions (influence of plant growth form abundance on kangaroo rat abundance at 28 months ($\gamma_{1n} = 0.275$, s.e. = 0.065).

Among burned plots, small-mammal compositional similarity to unburned plots increased faster where deerweed cover was low and scrub oak cover was high (Fig. 4f; influence of inclination on the linear slope of time ($\gamma_{1n} = 0.004$, s.e. = 0.001; Supplementary material, Table S2). Greater abundance of California and pocket mice where scrub oak cover was higher likely caused this pattern, because the relative abundance of each of these species contributed positively to similarity during the last half of the study (California mouse: month 43, $B = 0.030$, s.e. = 0.006, $P < 0.001$; pocket mouse, month 43, $B = 0.018$, s.e. = 0.006, $P = 0.006$). Relative abundance of cactus mice and, especially, kangaroo rats also contributed to similarity towards the end of the study. Their importance appeared independent of the influence of shrub composition, as cactus mice contributed positively to similarity at 36 months and as kangaroo rat abundance no longer differed substantially as a function of shrub composition by the study end.

Distance from fire perimeter

After accounting for our measured habitat variables, distance from the fire perimeter had little influence on compositional similarity of burned to unburned plots. Distance did influence population trends of California mice, cactus mice and California pocket mice (Supplementary material, Table S2), but not always in expected directions. For example, we expected faster recovery of shrub-preferring California mice in areas closer to unburned habitat, but found the fastest rates of population increase and highest end-of-study abundance among mid-distance plots (Fig. 5a; polynomial regression at 43 months: $\log \text{abundance} = 1.61 + (0.81 \times \text{riparian}) + (0.54 \times \text{shrub composition}) + (0.10 \times \text{distance}) + (0.07 \times \text{distance}^2)$, $R^2_{adj} = 0.49$, $P_{\text{distance}} \leq 0.04$).

The population growth rates of both California pocket mice and cactus mice were positively related to distance from the fire perimeter, with the farthest plots showing the highest rate of increase (Fig. 5b, c; pocket mice: influence of inclination on the linear slope of time ($\gamma_{1n} = 0.004$, s.e. = 0.002; cactus mice: influence of inclination on the linear slope of time ($\gamma_{1n} = 0.004$, s.e. = 0.002; Supplementary material, Table S2). This might be expected if a species recolonised areas close to the perimeter before the onset of sampling (resulting in slower population growth rates on closer plots over the period examined) but recolonised far areas during the course of sampling (resulting in higher growth rates). California pocket mice appeared to fit this pattern, whereas cactus mice did not. Pocket mouse abundance was lower on the farthest plots at the start of the study, but by 43 months post-fire, differences due to distance were minimal (Fig. 5c; multiple regression

at 13 months: $\log \text{abundance} = 1.24 + 0.16 \times \text{inclination} + 0.06 \times \text{shrub composition} - 0.13 \times \text{distance}$, $R^2_{adj} = 0.13$, $P_{\text{distance}} = 0.03$). By contrast, cactus mouse abundance at 13 months showed little difference based on distance, though 18-month abundance was lower on far plots (multiple regression at 18 months: $\log \text{abundance} = 0.9 + 0.1 \times \text{inclination} + 0.8 \times \text{riparian} - 0.2 \times \text{shrub composition} - 0.1 \times \text{distance}$, $R^2_{adj} = 0.29$, $P_{\text{distance}} = 0.03$). During the final trapping session, differences in abundance based on distance showed only marginal statistical significance after accounting for habitat factors, but suggested that abundances were somewhat higher on far plots (multiple regression at 43 months: $\log \text{abundance} = 0.8 + 0.1 \times \text{inclination} - 0.4 \times \text{riparian} - 0.1 \times \text{shrub composition} + 0.1 \times \text{distance}$, $R^2_{adj} = 0.15$, $P_{\text{distance}} = 0.08$).

Discussion

Our results highlight the dramatic changes in rodent community composition and species abundance caused by fire in chaparral and reinforce the compositional differences shown in previous work. This study also suggests the direct effects of fire severity and distance to unburned perimeter on post-fire rodent populations and communities are minimal and not substantially negative. Instead, habitat heterogeneity and vegetation composition influenced patterns of recovery. Thus, our study indicates the role vegetation communities play in supporting small-mammal communities.

Composition of communities in unburned v. recently burned chaparral

As expected, burned plots were dominated by species favouring disturbed or open habitat, including the deer mouse and the Dulzura kangaroo rat, whereas unburned plots were dominated by species associated with mature chaparral, such as the California mouse. Community composition differed even nearly 4 years after fire though trends in the abundance of individual species suggested continued change towards an unburned state. Pocket mice showed slow increases in abundance to levels approaching those in unburned chaparral. Even woodrats trended towards unburned abundances, though their numbers were generally low on all plots. Some species with high abundances in the early post-fire environment, such as deer mice, declined in abundance towards unburned levels several years following fire. However, kangaroo rats continued to increase in abundance 43 months post-fire.

Fire severity and distance to unburned perimeter

No species were directly affected by fire severity and only one of the six common species studied (California pocket mice) appeared to fit our hypothesised pattern of slower recolonisation and population increase in areas further from unburned sources. Even in this case, the effect mostly disappeared by the middle of the study. Fire severity and distance effects could be strongest immediately post-fire. If so, we may have missed them because the study began, owing to funding cycles relative to burn date, 13 months after the fire. For example, Rosario and Mathias (2007) studied recolonisation of 18 sites 9–1364 m from unburned habitats by the endangered Cabrera vole. No sites were recolonised for 8 months after the fire, but during the next

4 months, 11 of the 18 sites were colonised. However, in the study of Rosario and Mathias, longer-term patterns of occupancy were driven largely by vegetation characteristics.

Some studies suggest fire severity can affect mortality. For example, large numbers of dead woodrats and rabbits have been reported immediately after severe burns (Chew *et al.* 1959; Quinn 1979) whereas Howard *et al.* (1959) reported low mortality during low-intensity prescribed burns. Even if fire severity caused differences in mortality, our results suggest these effects last less than 13 months for most species and are unlikely to have long-term ramifications on small-mammal recovery.

Although the minor distance effects we noted in this study only apply 13 months or later after fire, Schwikl and Keeley (1998) studied distance effects on post-fire rodent numbers in California shrublands ~9–12 months post-fire and also found few correlations between number of captures and proximity to the unburned fire edge. The distances we studied in the unusually large-size Cedar fire were much larger than those generated by the majority of wild or prescribed fires. Consequently, even if distance effects exist in the early post-fire months, they are unlikely to have lasting effects on small-mammal recovery in this system.

It may seem our results support an indirect influence of fire severity on small-mammal recovery because we found influential post-fire vegetation characteristics, such as shrub composition, were correlated with fire severity. However, we reject this interpretation because the positive correlation between fire severity and increasing scrub oak and cup-leafed lilac cover likely reflects the influence of prefire vegetation on fire severity. Keeley *et al.* (2008) found higher prefire cover of cup-leaf lilac contributed to higher local fire severity. In addition, despite greater relative abundance of deerweed on lower-severity sites, it is unlikely post-fire deerweed cover was reduced by high-severity fire as high-severity fires favour seed germination and post-fire cover of this species (Keeley *et al.* 2005).

Habitat effects

Including habitat and vegetation data in our analyses allowed us to show how heterogeneity in vegetation composition, the location of riparian habitat and rocky substrate affected post-fire patterns in small-mammal abundance and community composition. In addition, our construction of variables such as the shrub composition factor reduced a confound that is often present between the amount of plant cover on a plot and the species constituting that cover. This allowed us to show the post-fire influence of chaparral shrubs on small mammals depends, in part, on the composition of plant species and goes beyond the role of vegetation cover facilitating predation escape in a partially denuded landscape.

The influence of shrub composition on small-mammal populations or communities in burned chaparral likely arose from behavioural idiosyncrasies, dietary preferences and interspecific interactions among various species. For example, scrub oak often leaves behind standing and downed large woody stems and is also a strong, evergreen resprouter, and the evergreen *Ceanothus* (lilac) species show high seedling recruitment under high fire severity conditions (Keeley *et al.* 2005). Consequently, burned stands of these species may have abundant and tall

post-fire shrub cover, available nest building materials and perennial green foliage. California mice, which we found in greater abundance among scrub oak and cup-leaf lilac, are arboreal and are known to inhabit aboveground nests built by large-eared woodrats from woody material (Meserve 1976b; Merritt 1978). In addition, Mills (1983) found mammalian herbivores showed a preference for cup-leaf lilac seedlings over chamise in burned chaparral and Meserve (1976a) showed California mice consume shrub foliage.

The positive influence of nearby riparian habitat or increasing rock exposure on steeper slopes on the abundance of many species may reflect how these features serve as refugia during or after fire. It may also reflect microhabitat preferences among the species. For example, Meserve (1974) considered California mice a transient resident of coastal sage scrub habitat with year-round occupation of 'canyons', which may be analogous to our riparian areas. Other studies have shown cactus mice and woodrats exhibit a bias towards rocky microhabitats in burned and unburned shrubland (Thompson 1982; Price and Waser 1984).

In summary, our data suggest three non-exclusive explanations for the influence of habitat on small-mammal abundance after fire: species may: (1) have higher abundances in these preferred habitats before the fire; (2) preferentially recolonise or utilise specific areas after fire; or (3) have lower mortality in certain locations during the fire. Regardless of which of these apply, the habitat variables showing the most influence on post-fire species-specific abundances also influenced community recovery or the compositional similarity of burned to unburned plots. However, our analyses also demonstrate the problematic nature of judging 'recovery' from a management perspective. Because species' population sizes may cycle independently, community composition based on relative abundance is not static in either burned or unburned locations. Consequently, there is no single, time-independent benchmark for evaluating recovery.

Conclusions

Though unexpected, particularly for non-burrowing species, our results largely suggest fire size and severity have no lasting effects on small-mammal abundances or community composition in southern California chaparral, at least over 4 years. This may be welcome news for reserve land managers as our 'negative' results may mean one less issue to concern them when planning responses to large or intense chaparral wildfires. This may equally apply to the use of prescribed fire on reserve land. As long as post-fire vegetation recovery is expected, our results suggest small mammals can be expected to follow suit.

More critically for managers, the close bottom-up relationship between small mammals and the vegetation they utilise increases the need for attention to the interaction between fire, native vegetation structure and invasive exotic plant species. Several studies suggest fire in southern California shrublands occurs more frequently than historic variation and has increased the long-term abundance of exotic plants, decreased native shrub cover and altered overall vegetation composition (Zedler *et al.* 1983; Haidinger and Keeley 1993; Fleming *et al.* 2009). A shift from intact shrublands to open conditions dominated by

exotic herbs will result in a parallel shift in the small-mammal community and in other consumer taxa, primarily from the loss of shrub specialists (Diffendorfer *et al.* 2007). The interplay between fire, intact shrubland communities and the animal species they support suggests reducing fire frequency maybe the singular most important goal for land managers focussed on maintaining functioning ecosystems. Thus, land managers should be highly cognisant of how prescribed burns or any fuel reduction efforts affect the broader shrubland landscape. Along the wildland-urban interface, shrub clearing will occur to assure human safety. But in reserve systems, prescribed fires, given their potential effects on vegetation community and the species it supports, may conflict with other management goals.

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