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Effects of fire on small mammal communities in frequent-fire forests in California

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Fire is a natural, dynamic process that is integral to maintaining ecosystem function. The reintroduction of fire (e.g., prescribed fire, managed wildfire) is a critical management tool for protecting many frequent-fire forests against stand-replacing fires while restoring an essential ecological process. Understanding the effects of fire on forests and wildlife communities is important in natural resource planning efforts. Small mammals are key components of forest food webs and essential to ecosystem function. To investigate the relationship of fire to small mammal assemblages, we live trapped small mammals in 10 burned and 10 unburned forests over 2 years in the central Sierra Nevada, California. Small mammal abundance was higher in unburned forests, largely reflecting the greater proportion of closed-canopy species such as *Glaucomys sabrinus* in unburned forests. The most abundant species across the entire study area was the highly adaptable generalist species, *Peromyscus maniculatus*. Species diversity was similar between burned and unburned forests, but burned forests were characterized by greater habitat heterogeneity and higher small mammal species evenness. The use and reintroduction of fire to maintain a matrix of burn severities, including large patches of unburned refugia, creates a heterogeneous and resilient landscape that allows for fire-sensitive species to proliferate and, as such, may help maintain key ecological functions and diverse small mammal assemblages.

Key words: fire effects, frequent-fire forests, nonparametric multiplicative modeling, reintroduced fire, small mammal community, species diversity

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Fire is a dynamic ecological process influencing vegetation distribution, community structure, and ecosystem function in diverse landscapes across the globe (Wright and Bailey 1982; Sugihara et al. 2006; Gill et al. 2013). In forested ecosystems, fire directly influences vegetation structure and composition by combustion of biomass and differential mortality of plant species (Scholl and Taylor 2010). However, fire rarely affects vegetation uniformly across forest landscapes, owing to variation in topography, fuels, and local fire weather conditions (van Wagtendonk and Lutz 2007; van Wagtendonk et al. 2012). Consequently, fires within many forest ecosystems commonly burn at variable intensities (i.e., rate of heat energy released per unit of fire front) and resultant severities (i.e., magnitude of fire effects on habitat, such as tree mortality), leading to a mosaic of burn severity patches (Miller and Thode 2007).

Decades of fire suppression activities have altered the function, structure, and composition of many forest ecosystems, especially in the frequent-fire forests of western North America (e.g., Parsons and Debenedetti 1979; Scholl and Taylor 2010; Collins et al. 2011). The reintroduction of fire (e.g., prescribed fire, managed wildfire) may restore some of these critical ecological features in these ecosystems, including habitat heterogeneity that supports a diverse assemblage of wildlife species (Roberts et al. 2008; Fontaine and Kennedy 2012). Yet, very few landscapes in North America have successfully reintroduced fire across large geographic areas for the benefit of wildlife communities or other resource objectives (Fontaine and Kennedy 2012).

The response of animal communities to fire is influenced by the historic fire regime of forest ecosystems, including patterns

of fire frequency and severity (Huff and Smith 2000). In boreal forests of North America, small mammals (excluding arboreal sciurids and bats) generally are most abundant and diverse immediately following stand-replacing (i.e., high severity) fire (Fisher and Wilkinson 2005), which is characteristic of the natural fire regime of these ecosystems (Brown and Smith 2000). In contrast to boreal forests, natural, frequent-fire regimes in interior dry forests of western North America (and some eastern North American forests) typically result in a mixture of severity classes (i.e., primarily low and moderate severity with smaller proportions of high-severity patches) that may increase the diversity of habitat types for wildlife (Brown and Smith 2000; Lyon et al. 2000a; van Wagtendonk and Lutz 2007; Thode et al. 2011). These frequent-fire forests are a matrix of large patches of forest containing variable tree and snag abundances, structure, and canopy densities interspersed with much smaller patches of open habitat with variable tree and shrub abundances (Kane et al. 2013). Fires that are reintroduced into these ecosystems that burn within their natural range of variation (including unburned patches) may increase the diversity of species dependent on these variable habitat types, including small mammals (Lyon et al. 2000a; Fontaine and Kennedy 2012). Conversely, large areas where fire has been suppressed or excluded, or large contiguous patches of stand-replacing fires, atypical of historic frequent-fire regimes, may be of poorer habitat quality for many native species not adapted to these homogenized landscapes (Fontaine and Kennedy 2012), thereby reducing the species diversity of small mammal communities in these ecosystems (Zwolak 2009). However, while the effects of stand-replacing fire are relatively well studied (e.g., Fisher and Wilkinson 2005; Zwolak 2009), the effects of the reintroduction of fire in frequent-fire forest ecosystems of North America have received little attention.

The reintroduction of fire can affect the abundance and distribution of small mammal populations and consequently the composition of communities (e.g., Zwolak 2009; Fontaine and Kennedy 2012). Fire can be especially influential in structuring small mammal communities in forest ecosystems through the differential modification of available habitat structures (e.g., trees, snags, logs), thermal cover (e.g., tree canopy cover), or food availability and quality (e.g., understory plants, tree seeds, invertebrates—Lyon et al. 2000b; Fisher and Wilkinson 2005). In forests of western North America, unburned and low-severity burned habitats may retain critical features for forest-dependent small mammal species, including but not limited to species such as *Glaucomys sabrinus*, *Tamiasciurus douglasii*, and *Sciurus griseus*; these arboreal species often require large habitat structures (i.e., trees, snags, logs) and intact forest canopies for survival and reproduction (Buchanan et al. 1990; Smith 2007). *G. sabrinus*, in particular, is generally associated with old forests characterized by a complex structure of multilayer canopies, large-diameter trees and snags, and large decayed logs (Waters and Zabel 1995; Lehmkuhl et al. 2006; Smith 2007); these features are often associated with fire exclusion in frequent-fire forest ecosystems. In contrast, many ground-dwelling squirrels, such as *Otospermophilus beecheyi* and *Callospermophilus lateralis*, occur primarily in open habitats and may select moderate- to high-severity burned patches that contain open canopies and may be dominated by herbaceous plants and shrubs (Converse et al. 2006a). At the landscape and forest stand scales, patches of these structural features are often associated with forests with an active fire regime (Kane et al. 2013). Habitat generalists, such as *Peromyscus maniculatus* and many species of *Neotamias*, are capable of using a variety of habitat conditions (Lawlor 2003), including those produced by a range of burn severities (e.g., Roberts et al. 2008), indicative of both active fire regime and fire exclusion landscapes.

To assess the effects of a reintroduced fire regime on small mammal communities, we capitalized on the well-documented fire regime in Yosemite National Park, California. Our objectives were to characterize how the reintroduction of fire affected mammalian communities across a gradient in fire frequencies and histories characteristic of a natural fire regime for this ecosystem. We predicted that: 1) small mammal species diversity (richness and evenness) would be greater in areas where fire has been reintroduced (presumably reflecting spatial heterogeneity in habitat structure) and 2) based on changes in a fire severity index (unchanged, low, moderate, high) and post-fire habitat variables (e.g., tree canopy cover), individual species responses to reintroduced fire could be predicted a priori by their known association with either closed-canopy forests (e.g., arboreal species, associated with unburned or low-severity patches), open-canopy habitats (e.g., ground squirrels, associated with moderate- to high-severity patches), or multiple habitat types (e.g., generalist taxa such as *P. maniculatus* and *Neotamias*, associated with all fire severity classes including unburned).

Materials and Methods

Study area.—Yosemite National Park encompasses over 302,600 ha in the central Sierra Nevada, California, approximately 224,700 ha of which comprises pristine lower and upper montane mixed-conifer forest. White fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), California black oak (*Quercus kelloggii*), incense-cedar (*Calocedrus decurrens*), and sugar pine (*P. lambertiana*) dominate the lower montane forests. The dominant species in the upper montane forests are red fir (*A. magnifica*), lodgepole pine (*P. contorta* var. *murrayana*), and Jeffrey pine (*P. jeffreyi*). The shrub understory is dominated by manzanita (*Arctostaphylos patula* and *A. viscida*), whitethorn (*Ceanothus cordulatus*), deer brush (*C. integerrimus*), chinquapin (*Chrysolepis sempervirens*), or huckleberry oak (*Quercus vacciniifolia*). Beginning in the early 1970s, Yosemite managers developed a prescribed burning and managed wildfire program to reduce fuels and lower the risk of stand-replacing fires while conserving the selection pressures historically imposed on these ecosystems by fire (van Wagtendonk et al. 2002). This ongoing management activity resulted in the gradual reintroduction of fire into many of Yosemite's forest ecosystems that had previously experienced decades of fire exclusion. Scientists mapped and digitized all fires (prescribed fires, managed wildfires, and suppressed wildfires) that occurred within Yosemite

since 1930. We used ArcGIS (ESRI 2009) to delineate all fires that burned in the upper and lower montane forests of Yosemite since 1989. Because forest succession is dynamic, we restricted our study to areas that had burned fairly recently (e.g., 1989–2004). This 15-year interval falls within the range of historic fire return interval (2–20 years) for these forest types (van Wagtendonk et al. 2002). The area burned by individual fires in this study ranged from 90 to 24,000 ha. We generated 125 random points each in burned and unburned forests and selected 20 of these sampling areas (10 burned and 10 unburned sites) that were at least 1.5 km apart for sampling small mammal assemblages (Fig. 1). At these random points, we characterized small mammal assemblages in a 64-ha trapping area. For the burned areas, the entire trapping grid was contained within the boundary of a fire. Our site locations represented a random, independent sampling of these habitats and were minimally constrained by logistical factors (e.g., accessibility and crew safety); most notably, we limited our trapping efforts to sites < 6 km from a road because of difficulties in transporting hundreds of traps and other equipment long distances and over rugged terrain.

Vegetation quantification.—Forest stand-level characteristics have a greater influence on small mammal community composition than microhabitat characteristics in Sierra Nevada montane forests (Coppeto et al. 2006). Therefore, we estimated overstory canopy cover (%), oak tree canopy cover (%), and shrub cover (%) at the stand level for each trapping area, using a digital vegetation map with 20-m^2 resolution (Keeler-Wolf et al. 2012). The dominant shrub genera were *Arctostaphylos*, *Ceanothus*, and *Chrysolepis*. We singled out oak tree cover data because acorns are a rich food resource for many small mammals (Jameson 1952; Tevis 1953). To develop the digital vegetation map, observers used aerial photographs in combination with substantial ground-truthing to draw and classify polygons of dominant overstory and understory vegetation types and assigned a cover class to each polygon. Using ArcMap, we superimposed the mammal trapping areas onto the vegetation map and determined the area of each vegetation type polygon contained within each 64-ha trapping area.

We estimated overstory canopy cover for each mammal trapping area by overlaying the vegetation map onto a map of the trapping areas and calculated a weighted mean for each cover class within the trapping area. We followed the same procedure for calculating understory (shrubs and seedlings) and oak tree cover, with 1 exception. Although it was an extremely rare occurrence, when the map did not provide a cover class, we used a default cover of 7.5% because the cover had to be

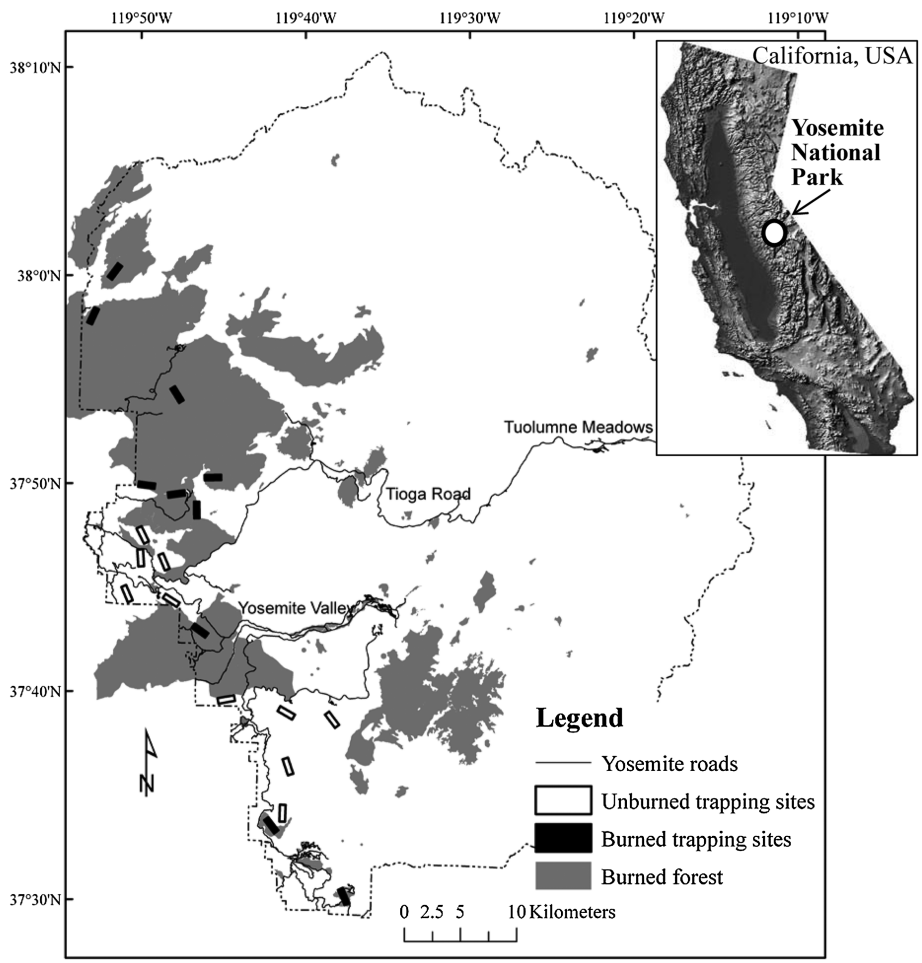

Fig. 1.—Locations of 10 burned and 10 unburned small mammal trapping sites (April to July, 2004 and 2005) in Yosemite National Park, California. Burned trapping areas were completely within the boundary of either wildfire or prescribed fire between 1990 and 2004.

5–10% for the photo interpreter to list it as part of the vegetation type for that polygon (Keeler-Wolf et al. 2012).

Small mammal sampling.—Because our objectives were to compare mammalian assemblage composition and obtain reliable indices of population sizes between treatments, we emphasized increased spatial coverage at the expense of replicate sampling. We conducted a 2-month pilot study to assess the efficacy of trapping grids in this habitat, but due to low site-specific trap success, we opted instead for a series of 4 offset, parallel trap lines to maximize trap success (Pearson and Ruggiero 2003). Thus, we surveyed all sites (10 burned and 10 unburned) with four 750-m long trap lines separated by 100 m. Each trap line included 15 Tomahawk live traps (13 × 13 × 41 cm) at 50-m intervals and 48 Sherman traps (8 × 9 × 23 cm) at 10-m intervals for a total of 63 traps per line and 252 traps per site (Roberts et al. 2008). Starting with the 2nd Tomahawk and ending at the 14th, we placed 4 Sherman traps between each Tomahawk (i.e., the 1st and 15th Tomahawks had no Sherman traps between them). We placed all traps on the ground, covered each with bark, and provided polyester batting for protection from inclement weather. We baited and set all traps every evening around sunset, processed, and released all trapped individuals at sunrise and closed all Sherman traps for the day while rebaiting and resetting all Tomahawk traps. At mid-morning, we checked and then closed all Tomahawk traps until the evening. Our pilot study indicated that the number of new captures of common species dropped to 1–2 individuals after 5 nights of trapping; we observed a similar pattern with new species captures. Therefore, we set our trapping efforts to 5 consecutive days and nights. Each census comprised 1,260 trap-days (on a 24-h clock) of effort (300 with Tomahawk traps, 960 with Sherman traps).

We sampled in the spring and early summer (April through July in 2004 and 2005) to ensure we could distinguish juveniles from adults and control for high temporal variation of juvenile emergence. To further minimize temporal variation in capture rates, we paired (burned, unburned) all small mammal censuses by week throughout the study and conducted our analyses on adults only (based on individual weights). We identified most captured animals to species, recorded their weights, uniquely marked all individuals with numbered ear tags (National Band and Tag Co., Newport, Kentucky), and released all animals at the point of capture. We did not attempt to distinguish among *Sorex* because they were not a target species and were rarely captured (4 individuals). The University of California, Davis, Institutional Animal Care and Use Committee approved all of our procedures and we processed our captured animals according to the guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011, 2012).

Data analyses.—We used available satellite imagery to characterize the effects of fire severity on small mammal capture rates. Miller and Thode (2007) used Landsat Thematic Mapper (TM) imagery to map the severity of fires in the Sierra Nevada between 1984 and 2005 using the Normalized Burn Ratio (NBR), a measure of the amount of change in the green vegetation before versus 1 year after a fire. We used the relative differenced NBR (RdNBR) to account for heterogeneity of prefire vegetation among fires mapped with TM imagery (Miller and Thode 2007). We calculated total fire severity index for each trapping area by multiplying the RdNBR levels (1 = no post-fire change detected, 2 = low severity, 3 = moderate severity, and 4 = high severity) by the proportion of the area each fire severity patch type encompassed and summing the products (Roberts et al. 2008). For areas that burned, total fire severity index was a continuous variable ranging from 1, representing an area entirely inside the boundary of a fire, but for which there was no detected change in vegetation cover after the fire, to 4, representing an area entirely burned at high severity. To distinguish no detectable vegetative change within a fire from unburned sites, we assigned a value of 0 for a fire severity index for each of the unburned trapping areas.

We applied nonmetric multidimensional scaling (NMS) to illustrate patterns in habitat structure (overstory, oak tree, and shrub cover) and responses of small mammals to key environmental variables at burned and unburned sites (McCune and Grace 2002). The "stress" of the ordination quantifies the dissimilarity between the distribution of the data points in the original data space and the ordination space; values < 15 are good representations (McCune and Grace 2002). We used Pearson's correlation coefficient (r) to quantify the magnitude of the relationship between each variable and the composite axes. We used the coefficient of determination (R^2) to describe the correlations between the ordination space and the original data space.

As noted above, we examined 4 habitat variables: overstory canopy cover (%), understory shrub cover (%), oak tree cover (%), and fire severity (index value 0–4). However, to visualize the effects of fire severity on our habitat variables, we only included the vegetation cover metrics in our habitat NMS. For the mammal and habitat NMS, we included all habitat variables and mean trapping site elevation (m) because elevation is strongly associated with the distribution of small mammal species in the Sierra Nevada (Chappell 1978; Moritz et al. 2008). We aggregated the mammal capture data matrix and the environmental/habitat data matrix and used NMS to assess the mammal community and individual species' responses to the habitat variables. Due to low numbers of recaptures at some trapping areas, we used capture rate as an index for abundance. To standardize across all trapping areas, we calculated capture rate (C) for each trapping area as the number of individuals per 1,000 trap-nights (Nelson and Clark 1973): $C = \{(I \times 1{,}000) / [T - (Sp \div 2)]\}$, where I = number of unique individuals captured, T = number of traps, and Sp = number of traps sprung, but empty for unknown reasons. We used the nocturnal effort to calculate the abundance index for the nocturnal species, the diurnal effort for the diurnal species, and time of day of capture (morning or evening) for species that can be either (e.g., *Microtus*).

We initially used program MARK v5.1 (White and Burnham 1999) to model abundance for the 4 most frequently captured species in our study. However, we chose not to use MARK in our analysis because this approach was unable to: 1) estimate

abundance for species that do not have very high capture rates, which often includes only the most abundant species in a community, and 2) incorporate covariates when modeling abundance for closed population studies as found in our study.

In contrast, our approach using nonparametric methods allowed us to model a greater number of species in our study and address our hypotheses without violating key assumptions. Although our analytical methods could compensate for our relatively low capture rates, this approach does not account for nondetections and has the potential to produce biased inferences. Additionally, we modeled the effects of multiple covariates on capture rates for species with relatively low captures, which may produce spurious results. Due to these limitations, our results for small mammal capture rates should be interpreted with caution, especially for those species with relatively few captures.

To minimize skew, we applied an arcsine-square root transformation to our vegetation cover data and a square-root transformation to mammal abundances. Because we measured our habitat variables in different units, we applied general relativation based on 1 for all habitat variables (McCune and Grace 2002). To reduce the noise in the data matrix, we excluded rare species (< 3 individuals captured and < 3 sites of capture) from all analyses except for species richness and evenness estimates (Legendre and Legendre 1983). We used this dataset for the NMS ordination only.

To examine differences in small mammal abundances between the 2 years of trapping (2004 and 2005), we conducted a multiresponse permutation procedure (MRPP), a nonparametric multivariate test analogous to multivariate analysis of variance (Mielke and Berry 2001); MRPP estimates the chance-corrected within-group agreement or effect size and the likelihood a difference is observed due to chance (A and P, respectively—McCune and Grace 2002). To avoid spurious results, we only included species with > 10 captures (n = 7 species) in the individual species analyses (MRPP and subsequent indicator species analysis [ISA] described below). Preliminary analyses revealed no effect of time since fire on capture rates within the 15-year interval for burned sites (MRPP test: $A = -0.06$, $P = 0.82$), and we removed this variable from final models to avoid over-parameterization. In the absence of a year effect, we used MRPP to examine differences in small mammal abundances and species diversity indices in burned and unburned forests across both years. As a complementary analysis to MRPP, we applied ISA to yield an "indicator value" (IV) that is the product of a relative frequency and relative abundance of each species in each group (in this case, burned and unburned forest). This metric ranges from 0 to 100, with IV = 100 representing a "perfect" indicator species for a particular treatment group (e.g., occurring only in 1 treatment type). We evaluated the statistical significance of each IV using 5,000 iterations of a Monte Carlo resampling approach (Dufrêne and Legendre 1997).

To examine the effect of fire on mammal community diversity, we calculated the Shannon–Wiener diversity index (H') and species evenness (E') based on H' (Pielou 1969); for these indices, we included all individuals of all species captured. The latter metric controls for the number of species observed in a community and is more amenable to comparisons across different communities. We tested the effect of fire (grouping sites according to fire history, burned or unburned) on these diversity indices using MRPP. We used PC-ORD (McCune and Mefford 2011) to calculate NMS, MRPP, and ISA according to guidelines outlined by McCune and Grace (2002) and set our alpha value at 0.10 for all statistical tests.

To explore small mammal species responses to habitat characteristics, we used nonparametric multiplicative regression (NPMR—McCune and Mefford 2004). NPMR treats predictor variables (habitat and environmental) as multiplicative, has increased flexibility in the type of effect each variable can have on another variable (e.g., linear, exponential, or unimodal), and does not require normally distributed data. We based our models on the minimum average neighborhood size of 1 (5% of the sample size—McCune and Mefford 2004). We tested our exploratory models with HyperNiche v. 1 (McCune and Mefford 2004), which employs NPMR with kernel functions for curve smoothing and cross-validation model selection. We based our regressions on a local mean estimator and used a kernel weighting function as recommended by McCune and Mefford (2004). We selected the best model for each species by maximizing the cross-validated coefficient of determination (xR^2) which protects against overfitting the model and can yield negative values. This ensured that we selected the model that best optimized the SD ("tolerance" in the case of NPMR) of the kernel function. For exploratory purposes only and to illustrate the modeled effect of each environmental variable on the abundance index of each mammal species, we fitted the modeled curve to the raw data. Therefore, values on the graphs are not intended to suggest definitive thresholds or maximum values for any of the habitat variables.

Results

The dominant tree species in our study area were either Jeffery or ponderosa pine, with a smaller proportion of white fir. The habitat NMS ordination fit well with the data (stress = 6.4) and the first 2 axes represented 96% of the variation (R^2 = 58% and 38%, respectively; Fig. 2). Axis 1 represented a gradient of a composite of overstory canopy cover and oak tree cover ($r = -0.90$ and 0.82, respectively), while axis 2 represented a gradient of variation in shrub cover ($r = 0.85$). In this NMS ordination space, there were few differences in habitat between our burned and unburned sites. However, the greater spread of points indicated greater variation in vegetation structure in burned sites, which is further supported by the larger standard error (Table 1), suggesting greater heterogeneity relative to unburned sites. Further supporting this, habitat structure differed between burned and unburned sites (MRPP: $A = 0.47$, $P < 0.001$). The mean fire severity index for all burned sites was 2.4, which represents a low to moderate fire severity level (Table 1).

From April to July 2004 and 2005, we completed 30,597 trap-nights of effort, yielding 1,053 individuals of 17 species, including 14 at burned sites and 15 at unburned sites. We captured 11 of these species at ≥ 3 sites (Table 2). Although we detected 3 species (*P. truei*, *Thomomys monticola*, and *Zapus princeps*) unique to unburned sites and 2 species (*Chaetodipus californicus* and *Neotoma macrotis*) unique to burned sites, we captured ≤ 2 individuals of each of these; we included these species in analyses of diversity but excluded them otherwise. Small mammal capture rates did not vary annually (MRPP: $A = -0.01$, $P = 0.52$), so we combined capture data across years for the remaining analyses. NMS produced a 2-dimensional ordination of the combined mammal and environmental data that represented 86% of the variation in the raw data ($R^2 = 0.09$ for axis 1 and 0.77 for axis 2) and had low stress (13.1), suggesting a good relationship between the ordination and the raw data (Fig. 3). Sites (points) in close proximity in multidimensional space had similar mammalian assemblages, and mammalian species grouped together presumably had similar environmental preferences. The fire severity index was negatively associated with axis 1 and was the most strongly associated habitat variable on this axis ($r = -0.41$). Variation in oak tree cover was positively associated with axis 2 and was the most influential variable for that axis ($r = 0.51$). The low r values associated with habitat features in this ordination indicate that the distribution of small mammals is not strongly influenced by these metrics; as with the NMS based solely on habitat features (Fig. 2), sites segregated poorly according to treatment type (burned or unburned), and there was no clumping, which indicated variation among the environmental variables. The abundance of the most common small mammal species in our study area, *P. maniculatus* ($r = -0.88$), had the strongest influence on site placement in ordination space. Nearly all mammal species in the analysis (except *P. boylii*) were associated with lower oak tree cover (Fig. 3). Axis 1 represented a gradient influenced by fire severity. *G. sabrinus* showed the greatest sensitivity to fire (i.e., located far to the right along axis 1) and *P. maniculatus* and *T. douglasii* also showed a high sensitivity to fire severity and were located closely together on the ordination. Three species (*N. speciosus*, *O. beecheyi*, and *N. quadrimaculatus*) showed the lowest sensitivity to fire, but only at moderate severity levels.

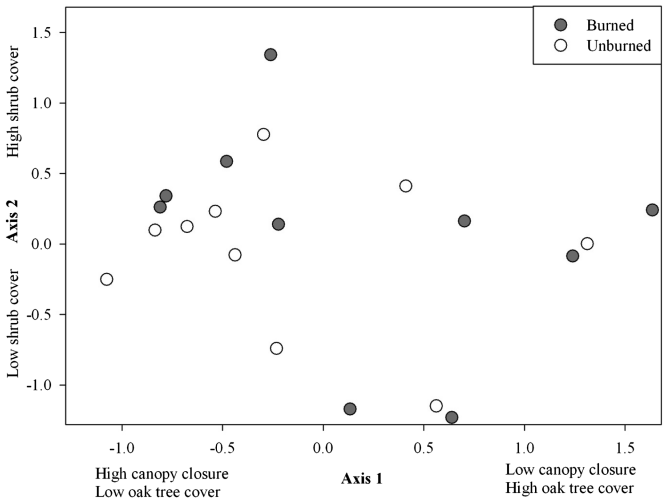

Fig. 2.—Nonmetric multidimensional scaling ordination results for overstory cover (%), oak tree cover (%), and shrub cover (%) at 10 burned and 10 unburned small mammal trapping sites in Yosemite National Park, California, 2004 and 2005. Only the variables with a Pearson correlation coefficient (r) ≥ 0.7 are listed on each axis with overstory canopy and oak tree cover on axis 1 ($r = -0.90$ and 0.82, respectively) and shrub cover ($r = 0.85$) on axis 2. The R^2 was 0.58 and 0.38 for axis 1 and 2, respectively, for a cumulative total of 0.96.

Mammalian community assemblages differed between burned and unburned forests (MRPP: $A = 0.06$, $P = 0.05$). The ISA (using the 7 species with > 10 captures) showed this difference was due to significantly fewer *G. sabrinus* ($P = 0.01$), and a trend toward fewer *T. douglasii* ($P = 0.11$), in burned forests (Table 3).

Assemblage evenness (E') was marginally lower in unburned sites (MRPP test; $A = 0.04$, $P = 0.10$; Table 2). However, there was no difference in species diversity (H'; $A = -0.01$, $P = 0.46$).

NPMR modeling produced models with reasonable fit ($xR^2 > 0.3$) for 5 of the 7 species we tested. For each species, we present only the best model (highest xR^2) and we list the environmental variables in order of descending tolerance (Table 4). Fire severity was the most influential variable for all 7 species and for those species with modest to large xR^2 values, the

Table 1.—Vegetation characteristics (mean and *SE*) and site elevation for 2 forest treatments (10 burned and 10 unburned sites) in Yosemite National Park, California.

Environmental variables	Burned			Unburned		
	Range	$\overline{X}$	*SE*	Range	$\overline{X}$	*SE*
Elevation (m)	1,390–2,047	1715.8	65.0	1,471–2,223	1811.9	81.2
Overstory canopy cover (%)[a]	36–80	62.1	5.1	46–80	70.8	3.5
Shrub cover (%)[a]	0–26	5.8	2.4	0–9	3.1	1.2
Oak tree species cover (%)[a]	0–9	2.5	0.9	0–6	2.1	0.8
Fire severity index[b]	1.5–3.5	2.4	0.2	0.0	0.0	0.0

[a] Vegetation characteristics estimated using aerial photograph interpretation (Keeler-Wolf et al. 2012) and ArcMap (ESRI 2009).
[b] Fire severity index = proportion of area within the boundary of a fire × that area's RdNBR (relative differenced normalized burn ratio) value (Miller and Thode 2007) and summed across fire severity types (0 = unburned, 1 = unchanged, 2 = low severity, 3 = moderate severity, and 4 = high severity).

Table 2.—Number of all small mammal individuals live trapped April to July 2004 and 2005 in montane mixed-conifer forest in Yosemite National Park, California. The years are combined due to no difference in capture rates between years.

Scientific name	Common name	Individuals/forest type			Capture rate[a]			
					Unburned		Burned	
		Unburned	Burned	Total	$\overline{X}$	*SE*	$\overline{X}$	*SE*
Callospermophilus lateralis	Golden-mantled ground squirrel	4	2	6	0.26	0.17	0.13	0.13
Chaetodipus californicus	California pocket mouse	0	1	1			0.11	0.11
Glaucomys sabrinus	Northern flying squirrel	11	1	12	3.89	1.33	0.34	0.34
Microtus longicaudus	Long-tailed vole	1	1	2	0.10	0.10	0.11	0.11
M. montanus	Mountain vole	5	1	6	0.53	0.43	0.11	0.11
Neotoma macrotis	Large-eared woodrat	0	2	2			0.68	0.68
Neotamias quadrimaculatus	Long-eared chipmunk	71	102	173	4.68	1.43	6.68	2.39
N. speciosus	Lodgepole chipmunk	11	49	60	0.72	0.37	3.26	1.65
Otospermophilus beecheyi	California ground squirrel	4	27	31	0.68	0.38	4.81	2.78
Peromyscus boylii	Brush mouse	13	30	43	1.36	0.80	3.16	1.87
P. maniculatus	Deer mouse	436	246	682	45.86	11.02	26.16	5.81
P. truei	Pinyon mouse	2	0	2	0.21	0.14		
Sciurus griseus	Western gray squirrel	2	1	3	0.35	0.23	0.17	0.17
Sorex	Unidentified shrew species	2	2	4	0.21	0.14	0.21	0.14
Tamiasciurus douglasii	Douglas squirrel	24	5	29	1.58	0.94	0.32	0.22
Thomomys monticola	Montane pocket gopher	1	0	1	0.10	0.10		
Zapus princeps	Western jumping mouse	2	0	2	0.21	0.21		
Total individuals (across all species)		585	468	1,053	3.79	4.39	2.89	2.66
Total species richness		15	14	17	5.60	0.52	4.20	0.53
Species evenness					0.54	0.07	0.71	0.04
Species diversity (Shannon–Weiner index)					0.91	0.13	0.95	0.07

[a] Capture rate = I × 1,000 / [T − (Sp ÷ 2)] (Nelson and Clark 1973); I = number of individuals captured, T = number of traps multiplied by number of night traps were open, and Sp = number of traps sprung by all causes (or frozen open due to weather).

tolerance (i.e., *SD* of the kernel function) for this variable was 4–33 times larger than that for any other environmental variable. Three species represented by > 10 individuals (Table 2) yielded models with good fit ($xR^2 > 0.4$). *N. quadrimaculatus* had the best fitting model ($xR^2 = 0.56$) and was strongly and unimodally influenced by fire severity (Fig. 4). In addition, overstory tree canopy cover and trap site elevation had positive, linear effects, while shrub cover showed a positive, exponential effect. In contrast, oak tree cover showed a monotonically negative association with this species, possibly covarying with elevation since oak trees are more abundant at lower elevations in the Sierra Nevada. The best model for *G. sabrinus* included fire severity, shrub cover, and oak tree cover ($xR^2 = 0.54$). Fire severity had a strong negative effect on *G. sabrinus*, whereas shrub and oak tree cover had unimodal and bimodal effects, respectively (Fig. 5). Finally, *N. speciosus* ($xR^2 = 0.44$) was best explained with a model including fire severity and trap site elevation, both of which yielded unimodal effects (Fig. 6). The single most abundant species, *P. maniculatus* (65% of individuals captured), yielded only modest model fit, likely reflecting the generalist nature of this species which may allow it to occupy all habitats in this study.

Discussion

Our results indicated that small mammal communities are significantly influenced by reintroduced fire in frequent-fire forests of the Sierra Nevada. Further, although NMS ordination did not reveal a strong role of fire severity, the NPMR modeling of each species suggested that fire severity had a much stronger influence than any other habitat variables we measured (Table 4). Models that incorporated a strong fire severity effect were best at predicting the abundances of all 7 species tested. In agreement with our predictions, ISA showed that species associated with closed canopies (e.g., *G. sabrinus*, a weaker trend for *T. douglasii*) were most strongly and negatively influenced by fire, even in landscapes with a heterogeneous mixture of fire severities where large patches of closed canopy existed within the boundary of a burn. Species associated with more open habitats (esp. *O. beecheyi*) tended to be captured more frequently in burned areas (Table 2) with lower oak tree cover than in other habitat types (Fig. 3). While the ISA was not significant, *O. beecheyi* was a reliable indicator that a site was burned (Table 3). However, we did not find *O. beecheyi* or any other small mammal species in our study to be strictly fire dependent, which is consistent with previous studies of small mammals in western North America (Zwolak and Foresman 2007; Fontaine and Kennedy 2012). Also consistent with our predictions, generalist species such as *P. maniculatus*, *N. quadrimaculatus*, and *N. speciosus* were frequently captured in both burned and unburned areas. However, these species showed a trend towards greater captures in unburned (*P. maniculatus*) or burned (*Neotamias*) forests, respectively (Table 2; Fig. 3). Both *Neotamias* species showed lower sensitivity to reintroduced fire compared to other species, but *N. speciosus* had the lowest sensitivity overall (Fig. 3). The NPMR modeling indicated that fire severity was the most influential habitat variable for small mammal assemblages in frequent-fire forests of the

Sierra Nevada (Table 4). Hence, while these analyses clearly document an impact of fire on small mammal communities, the similarities in abundances of the generalist species (e.g., *P. maniculatus* and *Neotamias*) between burned and unburned forests indicate these species are resilient to reintroduced fire.

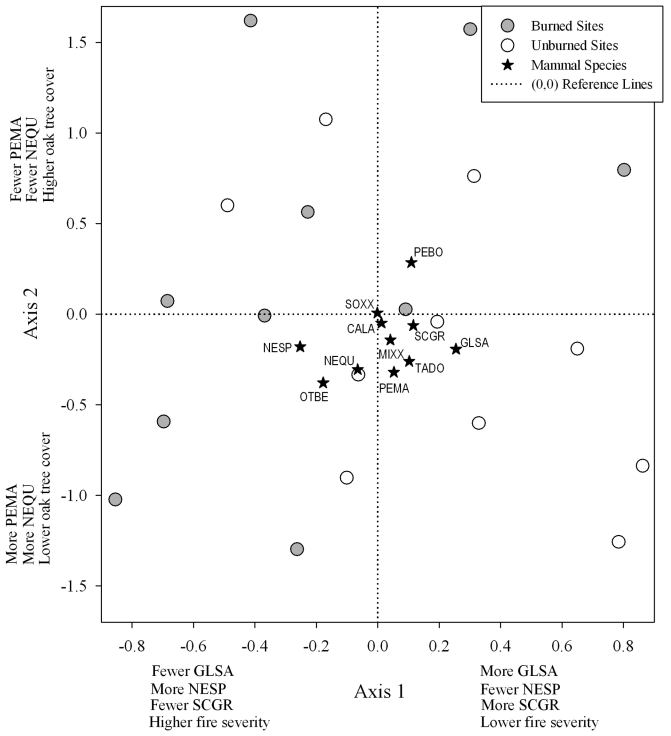

Fig. 3.—Nonmetric multidimensional scaling ordination for the 4 habitat variables (overstory cover, oak tree cover, shrub cover, and fire severity index) and elevation and the 11 most commonly captured mammal species in 10 burned and 10 unburned sites from April to July 2004 and 2005 in Yosemite National Park, California. Only variables with a $r \geq 0.7$ or the environmental variable with the highest r for that axis (i.e., fire severity $r = -0.41$ and oak tree cover $r = 0.51$) are listed on each axis. The R^2 was 0.09 and 0.77 for axis 1 and 2, respectively, for a cumulative total of 0.86. The mammal species codes represent the following: CALA, *Callospermophilus lateralis*; GLSA, *Glaucomys sabrinus* ($r = 0.73$ on axis 1); MIXX, *Microtus* sp.; NEQU, *Neotamias quadrimaculatus* ($r = -0.71$ on axis 2); NESP, *N. speciosus* ($r = -0.67$ on axis 1); OTBE, *Otospermophilus beecheyi*; PEBO, *Peromyscus boylii*; PEMA; *P. maniculatus* ($r = -0.88$ on axis 2); SCGR, *Sciurus griseus* ($r = 0.68$ on axis 1); SOXX, *Sorex* sp.; TADO, *Tamiasciurus douglasii*.

Fire has a spatially dynamic effect on forests, creating a matrix of variable burn severities that include unburned patches and a gradient of post-fire overstory canopy cover within burned areas, especially in these frequent-fire forests of the west (van Wagtendonk and Lutz 2007). If fire creates significant canopy gaps, we would expect an increase in such open-habitat species as *C. lateralis* as well as a decrease in *G. sabrinus* and possibly *T. douglasii* (Waters and Zabel 1998). We also expected a possible increase in *P. maniculatus* and *Neotamias* in recently burned forests due to their generalist diet and ability to capitalize on a more heterogeneous, post-fire habitat (Sharples 1983; Converse et al. 2006b). Although we observed a decrease in *G. sabrinus*, a declining trend in *T. douglasii*, and an increasing trend in *N. speciosus*, we saw none of the expected increases in *Peromyscus* or *C. lateralis*. The latter results contrast with observations from forests characterized by stand-replacing fire regimes (e.g., Zwolak and Foresman 2007) and may reflect more low to moderate intensities of reintroduced fire in frequent-fire forests. Moreover, in our study, spatial heterogeneity in fire behavior and post-fire vegetation structure (e.g., van Wagtendonk and Lutz 2007) and small mammal population dynamics (e.g., Converse et al. 2006a; Amacher et al. 2008)

Table 3.—The results from an indicator analysis on the 7 most common species for 10 burned and 10 unburned trapping sites, April to July 2004 and 2005, Yosemite National Park, California. Statistically significant *P*-value is given in boldface type.

Scientific name	Indicator value (%)[a]		P[b]
	Burned	Unburned	
Glaucomys sabrinus	31	69	**0.01**
Neotamias quadrimaculatus	53	47	0.66
N. speciosus	60	40	0.23
Otospermophilus beecheyi	64	36	0.20
Peromyscus boylii	56	44	0.50
P. maniculatus	43	57	0.17
Tamiasciurus douglasii	41	59	0.11

[a] Indicator value is the product of relative frequency and relative abundance of small mammal capture rates.
[b] *P* refers to the probability of receiving, by chance, an indicator value equal to or greater than the one calculated by the analysis.

Table 4.—Nonparametric multiplicative regression model results for the 7 most common small mammal species captured in Yosemite National Park, California, from April to July 2004 and 2005.

Species	Cross-validated R^2	C[a]	Predictor variable 1	T_1[b]	Predictor variable 2	T_2[b]	Predictor variable 3	T_3[b]	Predictor variable 4	T_4[b]
Glaucomys sabrinus	0.54	1.1	Fire severity	1.02	Shrub cover	0.28	Oak cover	0.02		
Neotamias quadrimaculatus[c]	0.56	1.0	Fire severity	1.93	Canopy cover	0.35	Elevation	0.24	Shrub cover	0.09
N. speciosus	0.44	1.2	Fire severity	1.26	Elevation	0.05				
Otospermophilus beecheyi	0.11	2.0	Fire severity	0.70	Shrub cover	0.05				
Peromyscus boylii	0.35	1.6	Fire severity	2.63	Elevation	0.08	Canopy cover	0.07		
P. maniculatus	0.31	1.4	Fire severity	1.23	Oak cover	0.17	Canopy cover	0.02		
Tamiasciurus douglasii	0.21	1.0	Fire severity	0.53	Shrub cover	0.29	Elevation	0.08		

[a] *C* refers to the average data neighborhood size.
[b] *T* refers to the tolerance (*SD* of the kernel function) for the preceding predictor variable.
[c] The best model for *N. quadrimaculatus* includes a 5th predictor variable, Oak cover, with $T_5^b = 0.05$.

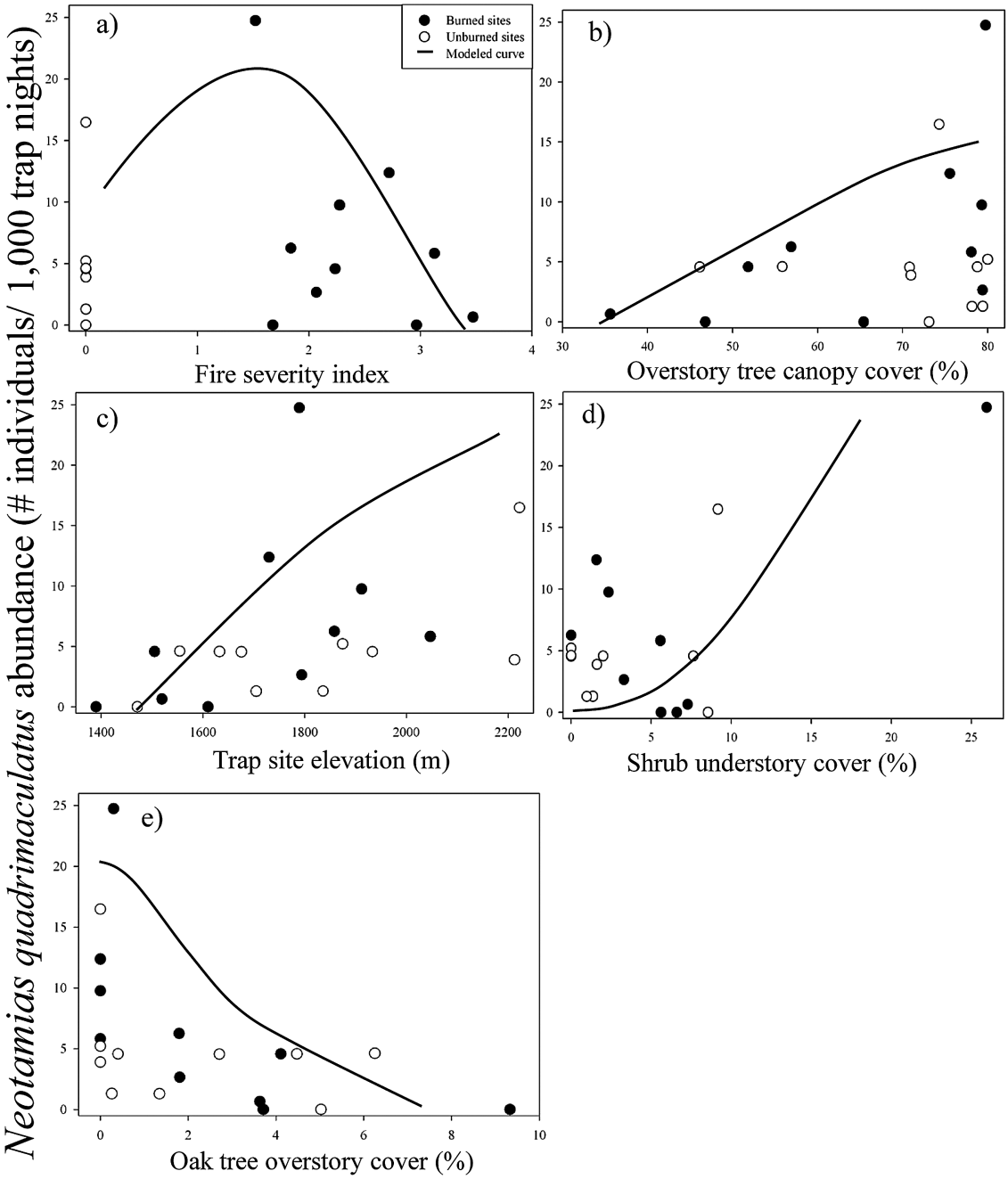

Fig. 4.—Nonparametric multiplicative regression response curves (estimated by kernel functions) for the best model (highest cross-validated xR^2) describing *Neotamias quadrimaculatus* abundance given the habitat characteristics at 20 trapping sites in Yosemite National Park, California (2004–2005). The best model was the full model. The values on the graph are not intended to suggest definitive thresholds or maximum values for any of the habitat variables (see "Materials and Methods").

may mask abundance trends in species, especially those with low capture rates (e.g., *C. lateralis*).

An ecologically important species in the frequent-fire forests of California and western North America (Smith 2007; Carey 2009) is *G. sabrinus*, the occurrence and abundance of which was unequivocally associated with unburned areas. *G. sabrinus* forages extensively on truffles (fruiting bodies of hypogeous fungi—Waters and Zabel 1995), and the abundance, biomass, and frequency of truffles are significantly lower in recently burned than unburned stands in Sierra Nevada frequent-fire forests (Meyer et al. 2005, 2008). Elsewhere on the western slope of the Sierra Nevada, capture rates for *G. sabrinus* were consistently higher in forest patches with high canopy closure (≥ 75%—Waters and Zabel 1995; Meyer et al. 2007a), adequate litter depth (≥ 2 cm—Meyer et al. 2007a), and availability of truffles (Pyare and Longland 2002). Fires that burn large patches with sufficient intensity to remove overstory canopy or litter below a threshold suitable for foraging movements (< 55% canopy cover—Lehmkuhl et al. 2006) and truffle production (≤ 3 cm—Meyer et al. 2008) may reduce habitat suitability for *G. sabrinus*.

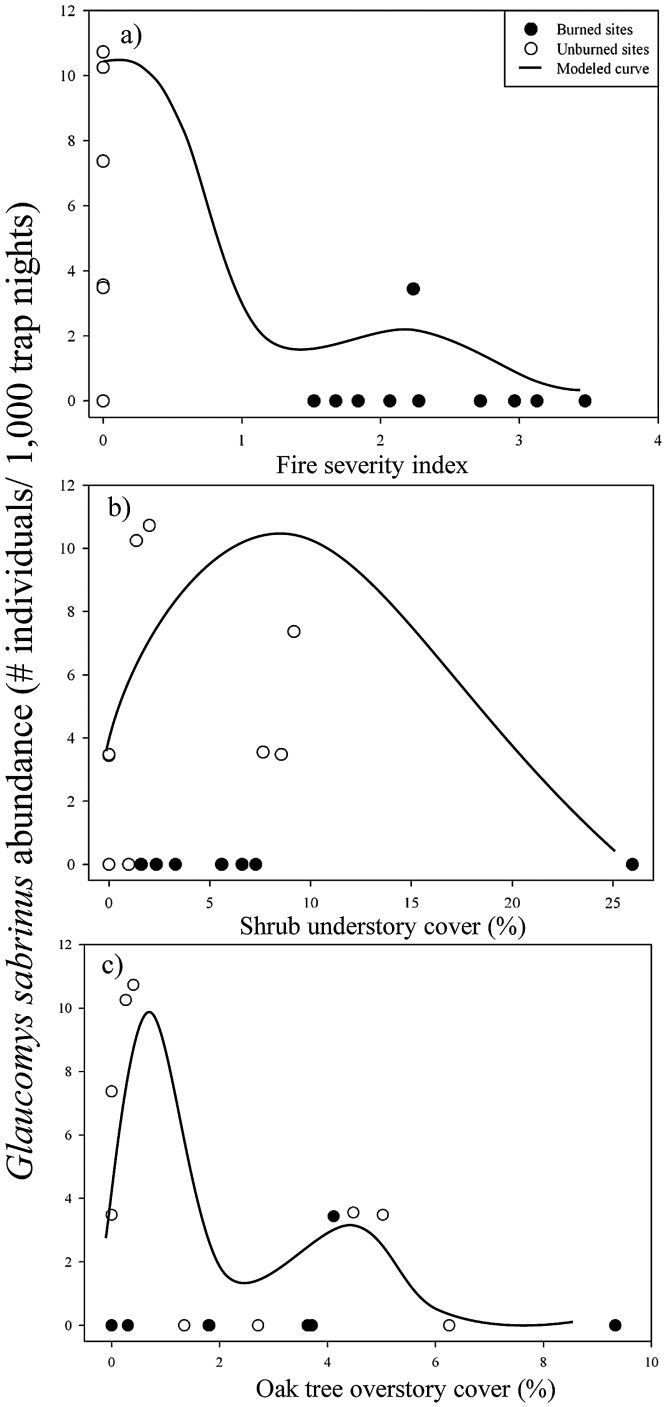

Fig. 5.—Nonparametric multiplicative regression response curves (estimated by kernel functions) for the best model (highest cross-validated xR^2) for describing *Glaucomys sabrinus* abundance given the habitat characteristics at 20 trapping sites in Yosemite National Park, California (2004–2005). The best model included a combination of fire severity (index), shrub species understory cover (%), and oak tree overstory cover (%). The values on the graph are not intended to suggest definitive thresholds or maximum values for any of the habitat variables (see "Materials and Methods").

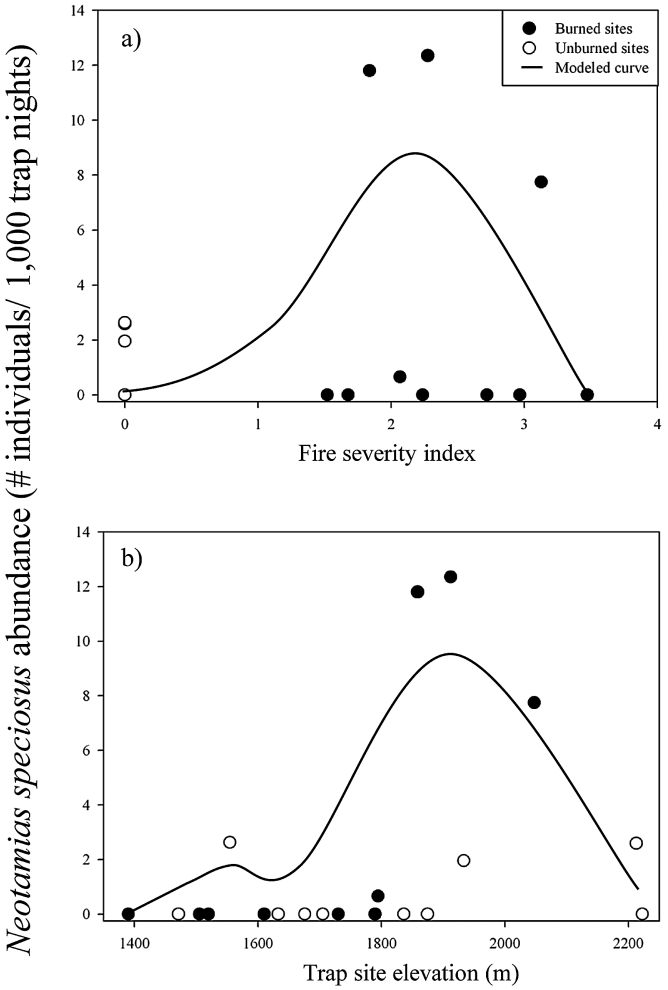

Fig. 6.—Nonparametric multiplicative regression response curves (estimated by kernel functions) for the best model (highest cross-validated xR^2) describing *Neotamias speciosus* abundance given the habitat characteristics at 20 trapping sites in Yosemite National Park, California (2004–2005). The best model included a combination of fire severity (index) and elevation (m). The values on the graph are not intended to suggest definitive thresholds or maximum values for any of the habitat variables (see "Materials and Methods").

The NPMR modeling indicated that fire severity from reintroduced fire had a strong influence on the abundance of *G. sabrinus*, a pattern reinforced by our inability to detect this species in sites burned at moderate or high severity (Fig. 5a). Although less influential, factors associated with vegetation structure and composition demonstrated nonlinear relationships with *G. sabrinus* abundance. The unimodal (Gaussian) effect of shrub cover on *G. sabrinus* abundance (Fig. 5b) indicated that this species may require sufficient understory cover for foraging or concealment from predators (Pyare and Longland 2002). However, excessive shrub or understory cover may be negatively associated with *G. sabrinus* (Manning et al. 2012) and may impede mobility of this volant species during foraging or predator evasion (Hackett and Pagels 2003). Although oak tree cover is never high in these frequent-fire forests, *G. sabrinus* seemed to favor limited cover by oak trees (Fig. 5c); we speculate that this may reflect increased truffle diversity in forests with a hardwood component because many ectomycorrhizal fungi are host specific (Smith et al. 2009).

The NPMR modeling indicated that fire severity had a unimodal effect on both species of *Neotamias*, with NMS ordination suggesting *N. speciosus* may be less sensitive to fire (Figs. 3, 4a, and 6a). These results are consistent with our understanding of these species; *N. quadrimaculatus* (Fig. 4b) tends to inhabit denser forests (Clawson et al. 1994), whereas *N. speciosus* is relatively unaffected by the level of canopy removal (Meyer et al. 2007b). Trap site elevation was an important environmental variable for *N. speciosus* and the unimodal effect described by the NPMR model (Fig. 6b) may reflect the narrow ambient temperature tolerances of this species (Chappell 1978). It is not surprising that our models failed to reflect the mid-elevation preferences of *N. quadrimaculatus* (< 2,270 m—Moritz et al. 2008; Fig. 4c) because none of our trap sites exceeded 2,223 m (Table 1). Although the positive association of shrub cover on *N. quadrimaculatus* abundance may have been strongly influenced by a single site (Fig. 4d), this species may be attracted to understory shrub patches because they provide both protective cover and food, especially *Arctostaphylos* and *Ceanothus* (Tevis 1953, 1955). Abundance of *N. quadrimaculatus* may be negatively associated with oak tree cover (Fig. 4e) because of the potential greater reliance of this genus on conifer seeds rather than acorns in the spring and summer, when we conducted our trapping (Vander Wall 1993).

Species diversity (H') did not differ between burned (i.e., reintroduced fire) and unburned (i.e., mostly fire-suppressed) forests (Table 2). This result contrasts with our predictions, which assumed that fire creates a more heterogeneous landscape with a greater diversity of forage and shelter (e.g., more shrub patches, higher understory diversity) and that greater habitat diversity would support greater small mammal diversity. One reason for this could be that H' is influenced by relative abundances and any potential differences in H' in these 2 forest types were overpowered by the large abundance of generalists species (e.g., *P. maniculatus* and *N. quadrimaculatus*), which were similar in burned and unburned forests. In contrast to diversity, species evenness was higher in burned than unburned forests (MRPP; see Table 2), indicating that species' relative abundances were more similar in assemblages within burned forests. These results are consistent with previous studies demonstrating greater evenness in communities exposed to fire compared to long-unburned forests (Shafi and Yarranton 1973; Crowder et al. 2012). In the Sierra Nevada, as in many frequent-fire montane forests of western North America, small mammal assemblages are dominated by a few abundant species while most other coexisting species are uncommon to rare (Lawlor 2003; Kelt et al. 2013). The greater evenness of small mammal communities in burned forests may promote increased stability and resilience, owing to the relatively lower proportion of rare species and reduced probability of local extinctions (Frank and McNaughton 1991), or increased opportunities for synergistic interspecific interactions (Hillebrand et al. 2008). Further work on the demographic responses of focal small mammal species (especially arboreal sciurids) to different fire regimes would be helpful to understand the ecology of these species and the role of fire in montane forest ecosystems.

The reintroduction of fire has a critical role in the management of wildlife communities throughout western North America. By reducing the potential for large, stand-replacing wildfires, the strategic use of fire can be an effective habitat management tool for select small mammal species (e.g., *G. sabrinus* and *T. douglasii*) that depend on closed-canopied forests and other key habitat features (e.g., large trees or snags, sufficient litter cover) in frequent-fire forests. This is especially crucial for forest management because these species are important prey for some mesocarnivores and raptors of conservation concern (e.g., *Pekania pennanti*, *Strix occidentalis*). Additionally, reintroduced fire can promote landscape biodiversity by creating a heterogeneous matrix of burn severities, primarily consisting of low- and moderate-severity fire patches, but also including patches of high-severity fire consistent with an active fire regime landscape in many western forests (e.g., van Wagtendonk and Lutz 2007). Maintaining forests within their natural fire regime across the landscape, including asynchronous burning across forest stands and reburning previously burned areas, can be important in promoting spatial and temporal habitat heterogeneity (Lydersen et al. 2013). However, paramount to this strategy is the integration of refugia, consisting of both burned and unburned late-successional, closed-canopy forests for species dependent on these conditions. Resource management that promotes the use and reintroduction of fire to create a heterogeneous mixture of fire severities while maintaining connected patches of unburned coniferous forest may have lasting positive effects on small mammal assemblages within these landscapes.

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