

Food and cover resources for small mammals on an industrially logged landscape in the Sierra Nevada of California

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Abstract

The presence and abundance of organisms within an ecosystem often correlate with habitat variables that may have few, or unknown, functional values. Understanding the functional role of these variables is especially important for organisms occupying landscapes managed for timber production and containing diverse habitat patches of different quantities and structures of vegetation. We investigated the strength of associations reported in the literature between small mammal generalists and vegetation. On an industrially logged landscape in northern CA, we used occupancy and mark-recapture analyses across three years to estimate the presence and total numbers for woodrats (*Neotoma fuscipes* Baird, 1858) and deer mice (*Peromyscus maniculatus* (Wagner, 1845)) related to vegetative attributes on coniferous and non-coniferous sites. Abundances of the small mammals correlated positively with shrub cover and hardwoods for woodrats and with shrubs and masting species for deer mice. Indices describing the value of vegetation features for both food and cover, but not these resources independently, described both species' presence and abundances best. We demonstrated that shrubs and non-coniferous trees are particularly important for small mammals and should be of particular focus to forest managers in the Sierras and mountains with similar forest structures.

Key words: cover, food, forest management, functional value, *Neotoma fuscipes*, *Peromyscus maniculatus*

Introduction

Managed landscapes provide roughly replicate environmental conditions on sites with native vegetation. Using such sites, we can test previously hypothesized associations between forest features and the sizes of populations of small mammals. Diverse associations between small mammals and their habitats have been hypothesized to relate to escape routes, shelter, food resources, or a synergy among these functions (Wolff and Hurlbutt 1982; Carey and Johnson 1995; Innes et al. 2007). Often, however, the values of these forest features such as food or cover resources for small mammals were assumed a posteriori rather than as a priori hypotheses tested for their functional significance. Small mammal populations respond consistently to forest elements such as coarse woody debris and canopy cover but, also consistently, the functional explanations for those habitat elements have not been tested as a priori hypotheses (Bowman et al. 2000; Carey and Harrington 2001; Fauteux et al. 2012; Sollmann et al. 2015).

Testing the putative functional roles of forest features for small mammal populations is especially important on managed landscapes where human-caused changes may have severe, cascading, long-term effects (Kelt et al. 2013, 2017). The literature is replete with studies demonstrating how small

mammal species in North America respond uniquely at different sites to specific types of forest management, reflecting the apparent changes in resource availabilities (Morrison et al. 1974; Carey and Johnson 1995; Coppeto et al. 2006; Wilson et al. 2008). Managers may assume incorrectly that managing for one forest element suffices to meet the requirements of multiple small mammal species. Such assumptions, and consequent management actions, rely on studies that may have generalized the functions of specific, individual forest elements without verifying the generality of those functions (Romesburg 1981; Irwin and Wigley 1993). Complementary types of vegetation may meet the same functional requirements to maintain populations within one forest patch, and different suites of vegetation may meet the same functional requirements in other places. Additionally, understanding and testing the hypotheses of functional relationships of specific forest features can also be confounded because vegetation may serve multiple purposes simultaneously. Masting hardwood trees, for example, may provide food, cavities for shelter and reproduction, and escape or refuge from predators. The synergy among these forest elements that contribute to specific functional roles may be more valuable than the sum of each individual forest feature to a specific function.

One potential challenge to testing the putative functional roles of forest features on managed landscapes, however, is the ability to manipulate plots experimentally (Platt 1964; Hayne 1978). Decades of research of the putative functional roles of forest elements for small mammal species abundances and distribution have been cumulated into publicly available databases such as the Fire Effects Information System (FEIS) from the US Forest Service (Zouhar 2015). Resources such as this provide us with the ability to leverage the findings of specific habitat elements for species and test them using quasi-replicated treatments. Moreover, such knowledge allows us to link findings of previous studies to develop nuanced hypotheses of the roles that forest features play in shaping species' presence, absence, and abundances (Bowman et al. 2000; Carey and Harrington 2001; Fauteux et al. 2012; Sollmann et al. 2015).

The requirements of small mammals of specific species should be largely unchanging because their critical resource needs remain consistent, irrespective of forest management, specific vegetation types, and forest structures (Nupp and Swihart 2000; Betts et al. 2014; Sollmann et al. 2015). In different forests, under varying management regimes, some basic needs of small mammals will be met by different forest elements. Alternatively, these requirements may be met by the same forest elements but are categorized differently by humans across locations. Deer mice (*Peromyscus maniculatus* (Wagner, 1845)) and dusky-footed woodrats (*Neotoma fuscipes* Baird, 1858; hereafter "woodrats") are two species that live in diverse habitats and forage selectively for, and cache, seeds and other parts of coniferous and deciduous trees (Carey and Harrington 2001; Hemmes et al. 2002; Lobo and Millar 2013). Deer mice are "generalist" in their habitat associations and appear to depend less than woodrats on forest elements that produce hard mast (Carey and Johnson 1995; Innes et al. 2007). Deer mice depend on their habitats for shelter. Woodrats build their own houses and, therefore, rely on forests for abundant building materials such as small- to medium-sized woody debris in undisturbed stands, as well as for food.

Both deer mice and woodrats can reach relatively high abundances that have correlated in some studies with high canopy closure and dense understory, such as shrubs and woody debris (Coppeto et al. 2006; Innes et al. 2007; Hamm and Diller 2009; Roberts et al. 2015). Canopy closure itself is unlikely to be a requisite of woodrats or deer mice but may correlate with, for example, seed production or with structural complexity on the forest floor that provides shelter and facilitates foraging (Hamm and Diller 2009; Sollman et al. 2015). On managed landscapes, populations of small mammals confront altered forest patches that are simplified through reductions in either overstory, ground layers, or both. In the absence of complexity, altered forest patches could remain viable for small mammals if they provide shrubs and trees for food (fruits and mast) and woody debris for shelter and escape cover.

In this study, we tested for relationships between functional roles reported in the literature for common forest elements with the hypothesized cumulative effects of those elements on either or both woodrats and deer mice. On

a landscape managed for sustainable timber production in northern CA, we evaluated whether quantifying forested stands by their a priori hypothesized value, based on the presence of individual forest elements (and vegetative species), explained the variation in both occupancy probability and abundance. Thus, assuming that the general understanding of the values of vegetation has service, we hypothesized (H1) that an index of values, including an index of total value, based on that understanding explains patterns of small mammal occupancy and abundance better than does the presence or absence of specific forest elements. Because this hypothesis is the present dogma, though untested, we take it as our null hypothesis. Alternatively, if the general understanding in the literature about what individual forest elements provide for small mammals is incorrect, then no patterns exist for small mammals relative to these indices of values. Secondly, we tested the hypothesis (H2) that the total value associated with combined food and cover in the same forest elements explains the occupancy and abundance for a species better than do food and cover separately. The literature suggests that both food and cover are important to deer mice and woodrats; therefore, we hypothesized that models incorporating values for both food and cover rank highest. In this study, we assigned a putative functional value of food, cover, or both for small mammals to each forest trait measured per sampling site. From these individual values, we created an index of the cumulative value of each of the forest element on a sampling site. The index included five basic values for each forest trait: ground cover, structure for reproduction, browsing food value, soft mast food value, or hard mast food value. Identifying the habitats containing key forest elements that maintain small mammal communities and populations is critical for enabling forest managers to manage functional, diverse forests.

Methods

Study area

In 2012, 2014, and 2015, we sampled small mammals on Sierra Pacific Industries' (home office in Redding, CA) Stirling Management Area (hereafter Stirling), a 648 km² tract in the northern Sierra Nevada, elevation 424–2400 m, centered approximately 30 km northeast of Chico, CA, USA. From the early 1900s to the 1990s, Stirling was managed mostly using uneven-aged management with selected trees removed from a stand every 15–20 years. Clear cuts were uncommon. Subsequently, Stirling was managed using even-aged management with ~90% of harvested units as clear cuts. For each clear cut, approximately 2% of the stand was left uncut with the goal of retaining structures and diversity in a stand while it regenerated from planted tree seedlings (e.g., Gray et al. 2016). From 2008 through the period of our research, Sierra Pacific Industries logged an average of 6 km² annually on Stirling (Ed Murphy, Sierra Pacific Industries, personal communication). Average clear cut size on Stirling was 8.1 ha.

The climate on Stirling was temperate with >85% of precipitation coming in late fall and winter as rain and snow and with little precipitation occurring in other seasons (Pandey

et al. 1999). The dominant conifer species on Stirling were ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson), sugar pine (*Pinus lambertina* Douglas), incense cedar (*Calocedrus decurrens* (Torr.) Florin), white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.), and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). The most common hard-mast producing trees included California black oak (*Quercus kelloggii* Newberry), tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & Oh), and canyon live oak (*Quercus chrysolepis*, Liebm.; Griffin and Critchfield 1972; Beesley 2007). Prominent shrubs and small trees included deer brush (*Ceanothus integriramus* Hook. & Arn.), manzanita (*Arctostaphylos* spp.), Pacific dogwood (*Cornus nuttallii* Audobon), Himalayan blackberry (*Rubus armeniacus* (Foke)), and shrub forms of both black and tan oaks. The oaks, dogwood, and conifers provided abundant food for small mammals in late summer into winter in years when they had good seed crops. Blackberry provided fruits with seeds in late summer through autumn in most years. The shrubs provided cover when in leaf, and manzanita and dense stands of shrubs provided cover throughout the year (USFS 2020). Most of these species provided both seasonal food and cover.

Small mammal sampling

Both deer mice and woodrats are common throughout the northern Sierra Nevada of northern CA (Coppeto et al. 2006; Kelt et al. 2017). We selected sites in the field for sampling small mammals based on relative site age since being clear cut, on dominant tree types (conifers, hardwoods, and mixed) and on relative canopy cover (<30%, 30%–70%, and >70%). We attempted to sample sites that represented variable combinations of characteristics described above that were representative of the local landscape but varied from adjacent sites. Consequently, although we did not direct the logging to be done on Stirling, we were able to create a set of sampling sites across the landscape that were quasi-replicated treatments that varied continuously along several axes: site age, proportion of canopy in hardwoods, canopy cover, and shrub density. We grouped sites that we sampled at the same time and that had similar ecological, environmental, and forest management conditions into “neighborhoods.” Neighborhoods spanned 2–6 km along their long axes (Fig. 1). We placed individual sites 300–2000 m apart within neighborhoods, depending on the forest conditions, to maximize the capture of variation within each neighborhood.

We entered a new neighborhood each week, established new sampling sites, and sampled over five days (four nights). Within each neighborhood, we established between 8 and 12 sites (Fig. 1), depending on our ability to check them efficiently. Sampling occurred each year from late May through mid-August. We sampled individual sites and neighborhoods within the same two-week window each year to reduce sampling differences among years.

We sampled small mammals on 30 × 30 m sites because they allowed us to sample forest stands while reducing the effects of edges. We used two types of live traps: five Sherman-style, non-folding aluminum traps (8 × 9 × 23 cm) and five wire-mesh box traps (15 × 15 × 40 cm), all baited with peanut

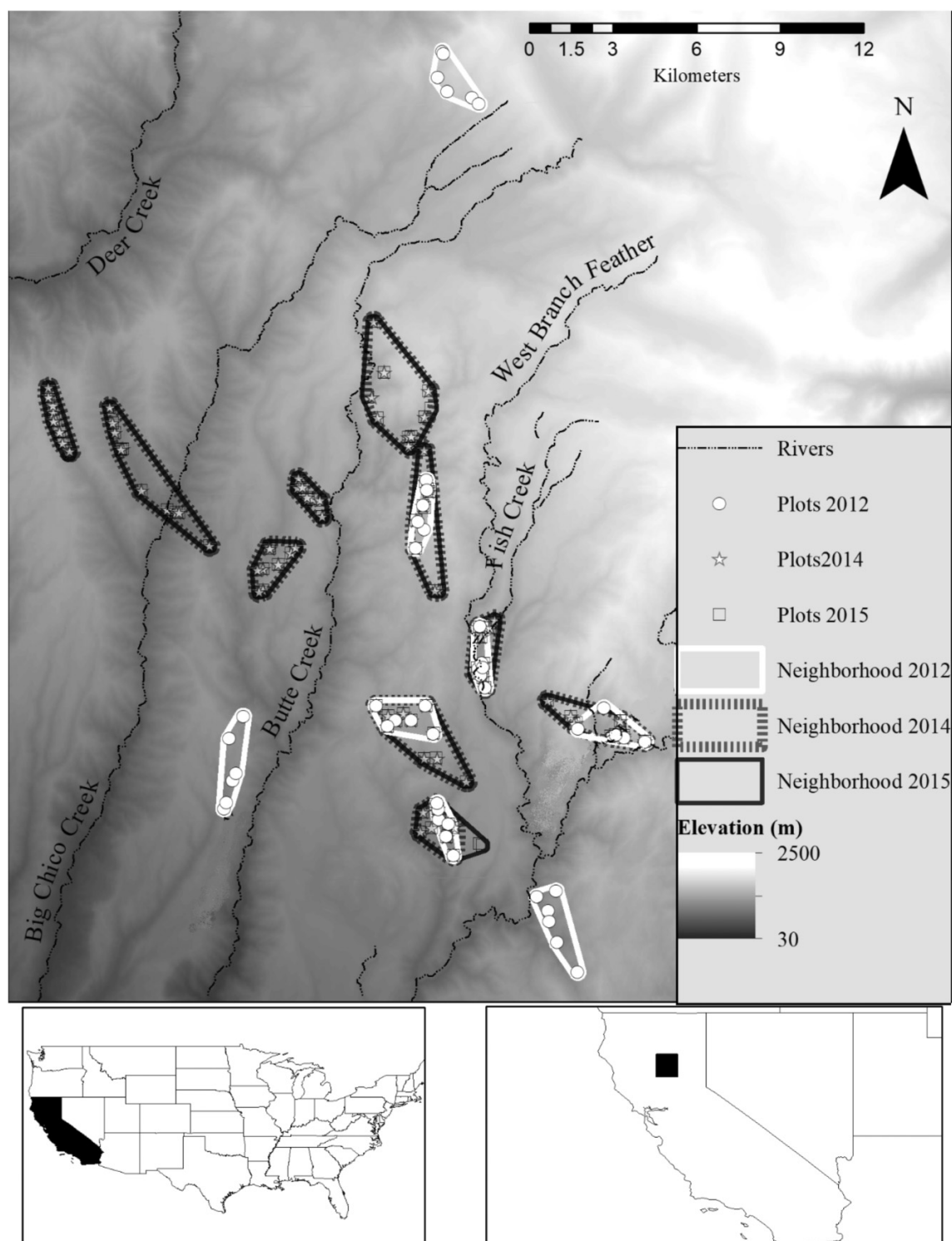
butter and rolled oats. We also placed four additional, extra-large Sherman-style traps (10 × 11 × 38 cm) at random on half of the sites in a neighborhood. We placed all traps in shaded areas beneath trees or shrubs to minimize heat stress for captured mammals. When shade was not available, we placed bark or vegetation on traps. On sites in forested stands with trees of sufficient diameter, one additional wire-mesh box trap was attached to a tree at chest height (~1.5 m) baited with apples for squirrels. If no large tree was present, we placed the squirrel trap on the ground at the center of the site. We checked all traps a minimum of once per day, and traps located on unshaded or warm sites we checked morning and evening.

We processed all small mammals immediately upon finding them in traps. We restrained small mammals in a small handling bag and recorded species, sex, maturity (juvenile or adult), breeding status, relative numbers of ectoparasites, and weight. Individuals that weighed <50 g (e.g., deer mice) were marked with commercial hair dye or colored markers. We marked mammals that weighed >50 g, and that could be restrained safely, with unique passive integrated transponder tags (Biomark, Inc., Boise, ID). Given the average lifespan of less than one year for a wild-caught *Peromyscus* Gloger, 1841 (Baker 1991), we were not concerned with resampling this genus among years. Our methods were consistent with the guidelines of the American Society of Mammalogists for use of wild mammals for research (Sikes et al. 2016) and with the Canadian Council on Animal Care guidelines (Powell and Proulx 2003). We sampled with California State approval under SC-012978.

Vegetation sampling and analyses

On individual sites (our unit of replication), we collected data on woody vegetation using 4 × 15 m transects in each cardinal direction from the center of each site. At the center and at the terminus of each transect, we estimated the canopy cover with a convex spherical densiometer. We identified vegetation to species, measured diameter at breast height for all stems, and counted all logs (down trees and fallen limbs) and snags (dead, standing trees) ≥ 6.35 cm. From these data, we calculated site-level metrics that described the overall amount of timber (individual tree sizes plus total basal area within each site), the composition (e.g., % of trees that were hardwoods), and the structure (mean number of logs and snags) on sites (Supplementary Table S1). We also calculated metrics related to our a priori hypotheses for small mammal populations and food and cover, such as shrub abundance and diversity. Because shrub abundance had affected woodrat numbers elsewhere (Carey et al. 1999), we tested whether the diversity of shrubs (Simpson 1949) influenced the presence or abundance of small mammals better than did total shrubs (quantified as total basal area) on a site. Conceivably, shrub diversity indexed the diversity of foods available or different types or overall abundance of cover (Miller and Getz 1977). Ultimately, we generated 19 variables (including a temporal effect among years and neighborhood effect) that potentially described rodent abundance and distribution (Supplementary Table S1).

Fig. 1. Locations of small mammal sampling sites in 2012, 2014, and 2015 with neighborhood boundaries and elevation in meters (underlying shading) on the Stirling Management District owned by Sierra Pacific Industries in northern CA. This figure was created using ArcMap version 10.2.2 and based on the following data raster and shapefiles: background topographic information from stitched tiles of Digital Elevation Model (GDAL 2020), United States shapefile from the National Atlas of the United States, rivers shapefile (California Natural Resources Agency), all trapping locations (this study), and all bounding polygons or “Neighborhoods” (this study). The map was projected in the WGS 1984 UTM coordinate system.



We assigned a functional value of food, cover, or both for small mammals to each woody species known to be in our study area and other forest traits that we measured using assignments from the FEIS database (USFS 2020). The FEIS database provides a general value of a plant species for wildlife, generally, but also for specific animal types (e.g., rodents) or species where they are known. We also considered other known specific relationships between a plant species and rats and mice where appropriate. We gave an index of 0 or 1 for each of the five basic values for each forest trait: ground cover (shade and protection from predators), structure for reproduction, browsing or grazing food value, soft mast food value, or hard mast food value (Supplemental Table S1). For each measured trait, if the function was provided, it was designated with a 1 and if not, 0. For example, if a woody species provided both sub-categories of cover plus browsing food but provided no soft or hard mast, it would receive a cumulative value of 3. Because we recognized that sizes of individual species could affect their value (e.g., large trees produce more mast), we placed size limitation on species such that trees below a minimum size (13 cm DBH) could not contribute to hard mast. Very small twigs or branches less than 3.3 cm DBH did not count toward cover. We could not account for differences in the actual mast or cover provided by trees or the cover above minimum thresholds. The final index value for a sampling site was the sum of the values for each species times the number of occurrences of that species, accounting for minimum thresholds, on the site. These values provided a cumulative score between 0 and 5 for food, cover, and both for each individual tree, shrub, snag, and log. From these index values, we also estimated the value for a site for cover (1–2), a value for food (1–3), or for both (1–5) and for sub-categories for the type of food or cover they provided.

To reduce the total number of variables and models we tested (Fieberg and Johnson 2015), we conducted a principal components' analysis (PCA) using the R package "PCAmix-data" (Chavent et al. 2014). We selected the variable with the top loading scores from the top seven principal components (PCs) as these explained 84% of the cumulative variation in our environmental data. These seven PCs yielded seven variables that explained the variance in the vegetation data. Five variables were descriptors for food, five for cover, and two for food and cover together (Table 1). Using a Pearson's correlation test, we tested for post hoc correlations among top loading variables to inform downstream analyses. We eliminated variables that were correlated ($\alpha = 0.01$), except for variables that we thought a priori were important to test explicitly, including canopy cover, total basal area of shrubs, and shrub diversity (Table 1). We retained canopy cover and total value in spite of not being top variables in the PCA due to their significance in the literature and in our hypothesis testing framework. Additionally, % hardwood was retained in lieu of % conifer as they mirrored one another; it consistently explained similar patterns of variance in the PCA (Supplemental Table S1) and was not significantly correlated with the other six variables (Supplemental Table S2).

Small mammal presence and population size

We used detection probabilities to parameterize occupancy and abundance models, but detection was not the focus of our analyses. We first used an occupancy approach to estimate probabilities of both detection and occupancy across sites and years. Occupancy was estimated in the R package "unmarked" (Fiske and Chandler 2011). Woodrats and deer mice could have had similar patterns of occupancy and abundance; therefore, we tested for differences between woodrat and deer mouse detection and occupancy before we modeled the species independently. Because detection probabilities for members of a species may be a product of multiple factors besides population density (Parsons et al. 2017), we also modeled detection probabilities with vegetation variables that might describe detection better. We limited these variables to those that we had already identified (Table 1) and included no more than two covariates per species. We first determined the most appropriate model that best described the probability of site detection for each species. We included site-level vegetative variables to account for differences in the availability of woodrats and deer mice on sites due to lack of resources that provided food, cover, or both.

Because we used neighborhoods to account for variability associated with the time of sampling and local conditions, we tested for a neighborhood's effect on occupancy. We thus used these neighborhood variables only if they improved descriptions of site-level probabilities of detection. As we were most interested in the relationships between vegetation types that prescribed specific functions and presence and abundance of woodrats and deer mice, we focused our analyses only on our selected forest elements as additional covariates (Table 1). We then used this detection model to evaluate the abilities of forest elements to describe probabilities of occupancy. Finally, we used these models to estimate occupancy probabilities for each sampling site and year.

To estimate detection probabilities of individual woodrats and deer mice, we constructed daily encounter histories. We had insufficient captures within most sites to obtain precise estimates of the probability of detection per site per year. Therefore, we grouped captures by neighborhood and year to estimate the probability of detection per neighborhood and year. We then tested for patterns of detection associated with vegetation traits within neighborhoods. We used the Huggin's closed capture with the full heterogeneity model in program "MARK" (White and Burnham 1999) to evaluate patterns of capture for both woodrats and deer mice and to produce neighborhood estimates of detection. Our goal was not to estimate population size during this step of the analysis but only to estimate individual detections. Therefore, we used the closed-capture model structures (Otis et al. 1978) to test for both neighborhood and non-neighborhood effects (across all sites) with each of those model types.

We next modeled the local abundances of woodrats and deer mice to account for the probability that animals were present but not detected, and we developed a composite model that incorporated the distribution of site-level probability of occupancy and the individual probabilities of detec-

Table 1. Descriptions of potential explanatory variables used to model the capture rates and abundances of small mammals captured on Stirling Management District of Sierra Pacific Industries in northern CA.

Metric	Abbreviation	Description	Value
Basal area	BA	Total cross-sectional area (m ²) of all trees and shrubs on site	Cover and food
Canopy cover	Canopy	Percentage of the forest floor covered by overstory trees	Cover
Coarse woody debris	CWD	Total basal area of all dead and downed or dead and standing debris that were ≥50 cm at their largest diameter	Cover
Mean downed debris	MeanDD	Mean (across transects) number of dead and downed trees and limbs on the site	Cover
Percent hardwood	PerHard	Percent basal area of all hardwood trees on site	Food
Shrub index	ShrubIndex	Index of shrub diversity on site calculated using Simpson's diversity index	Cover and food
Soft mast	SoftMast	Total basal area of all species that produce soft mast (fruits and berries)	Food
Total shrubs	TotalShrub	Total basal area of all species that were categorized as shrubs	Cover and food
Total value	TotalValue	The total food and cover value for a site as assessed by assigning a value from 0–5 for each individual vegetative or structural item on a site	Cover and food

Note: Abbreviations are used in Table 4.

tion. Where we detected no small mammals, we generated a random variable (with a value of 0 or 1) as

$$\text{True occupancy} \sim \text{binomial}(\text{random.uniform}(a,b))$$

where “a” was the lower 95% confidence limit for occupancy estimate of a site, and “b” was the upper 95% confidence limit for occupancy estimate of a site. We assigned sites a value of 0 when they were unoccupied and undetected and 1 when occupied but undetected.

For sites that were occupied, we estimated their detection-corrected abundance by drawing a random variable from the 95% confidence intervals for detection for a specific neighborhood and year as

$$\text{Detection} \sim \text{random.uniform}(c,d)$$

where “c” was the lower 95% confidence limit, and “d” was the upper 95% confidence limit for detection for a neighborhood and year. We then used this detection probability to adjust the minimum number of small mammals trapped at a site as

$$\text{abundance} = C/\text{detection}$$

where “C” is the number of uniquely identified captured small mammals at that site. In instances where the detection probability for a neighborhood was less than 0.1, we used the 95% confidence intervals for the mean detection observed across all neighborhoods and years. For each site, we replicated this process 1000 times to construct a distribution of population sizes that accounted for the probability of occupancy and individual detection probabilities. We used the mean value from all iterations as the population estimate per site. For sites that we assigned as occupied but had no captures, we used one as the minimum number captured. This model was implemented in Python 3.7.12 using the “NumPy” random package.

General modelling analyses

We used general linear models using the “MuMIn” package in R for our analyses to estimate relationships between our

estimates of abundance for woodrats and deer mice and vegetation. We fit models with an underlying Gamma distribution and log-link function for model testing. We constructed statistical models to evaluate how vegetation attributes of the sites explained differences in local abundances. We ranked competing models using Akaike's information criteria corrected for small sample size (AIC_c; Burnham and Anderson 2002). Most of our models were single-variable models (Table 1) to evaluate which, if any, best described local abundance. Our only multivariate model included canopy cover and the square of canopy cover, the latter to evaluate whether animals reached their highest abundance at moderate levels of canopy cover. Additionally, we included the total shrubs in models with both the proportion of hardwoods and the basal area of masting tree species. We kept our models simple because our goal was to test for the effects of vegetation rather than to describe abundance completely (Fieberg and Johnson 2015). We then calculated the ΔAIC_c and from this the AIC_c weight (w) and AIC likelihood using the formula:

$$\text{AIC}_c = -2(\log - \text{likelihood}) + 2K + (2K(K + 1) / (n - K - 1))$$

where n = sample size and K = number of model parameters. We used the top model to provide parameter estimates for the beta-estimates.

Results

In 2012, we sampled 48 sites in 8 neighborhoods (Fig. 1). In 2014 and 2015, we sampled 185 sites in 10 neighborhoods. We sampled 30 overlapping sites across 5 overlapping neighborhoods in all 3 years. We did not sample in 2013. We retained nine unique vegetative variables for downstream analyses from our process of selection using a priori functional rationale (Table 1) and PCA analyses (Supplementary Table S1). We tested for correlations among these variables post hoc using a Pearson's correlation test (Supplementary Table 2). Canopy cover correlated consistently with other metrics, including basal area, number of soft mast-producing species,

Table 2. Total captures and capture rates (captures per 100 trap-days) in 2012 (3777 trap nights), 2014 (4495 trap nights), and 2015 (4641 trap nights) and across all years for 7 species of small mammals captured: deer mice (*Peromyscus* spp.), woodrats (*Neotoma fuscipes*), California ground squirrels (*Otospermophilus beecheyi* (Richardson, 1829)), chipmunks (*Tamias* spp. (Allen, 1890)), Douglas squirrels (*Tamiasciurus douglasii* (Bachman, 1839)), Trowbridge's shrews (*Sorex trowbridgii* Baird, 1857), and Western gray squirrels (*Sciurus griseus*).

Species	Captures 2012	Captures 2014	Captures 2015	Total Captures	Capture Rate 2012	Capture Rate 2014	Capture Rate 2015	Total Capture Rate
Deer mice	248	345	355	948	6.6	7.7	7.6	7.3
Woodrats	47	137	121	305	1.2	3.0	2.6	2.4
California ground squirrels	9	12	18	39	0.2	0.3	0.4	0.3
Chipmunks	13	0	7	20	0.3	0.0	0.2	0.2
Douglas squirrels	6	2	4	12	0.2	0.0	0.1	0.1
Trowbridge's shrews	4	5	1	10	0.1	0.1	0.0	0.1
Western gray squirrels	2	0	0	2	0.1	0.0	0.0	0.0

Note: Total effort across all three years was 12 913 trap nights.

total value of a site, and total basal area of shrubs. Deer mice and woodrats were the most common small mammals captured among our total of 1336 small mammal captures in 12 913 total trap days (Table 2). Trap effort increased each year of the study from 3777 trap days in 2012 to 4641 in 2015. Deer mice totaled 71% of total captures, while woodrats totaled 23% (Table 2).

Individual detection probabilities

We marked a total of 220 woodrats across all years and sites, but probabilities of recapture were low. We did not recapture individual woodrats between years. We marked 769 deer mice across all years and sites. Because we marked these animals only temporarily, we could not evaluate their recapture rate across subsequent years, but this did not affect our weekly recapture observations.

The site-level vegetation metrics that we modeled to see whether they increased the probability of detection of woodrats on sites were not well supported. The best models of individual detection were supported by the null models for neighborhoods and years followed by a model that incorporated effects from sites and years ($\Delta\text{AIC}_c = 6.04$). Other model structures, including behavior or heterogeneity, were also not well supported across or within neighborhoods ($\Delta\text{AIC}_c > 6.04$). Therefore, we used only pooled or neighborhood-year detection probabilities. Across all neighborhoods, the probability of detection was 0.19 (range = 0.16–0.23). For neighborhoods and years, the highest detection probability was 0.45, whereas the lowest was 0.00065.

Individual detection probabilities for deer mice were best supported by the null models for neighborhood-year combinations (null model across groups $\Delta\text{AIC}_c = 46.1$). As with woodrats, model structures for deer mice, including behavior or heterogeneity, were not well supported across or within neighborhoods ($\Delta\text{AIC}_c > 25$), and we used only pooled or neighborhood-year detection probabilities. Across all neighborhoods, the probability of detection was 0.12 (range = 0.10–0.14). For neighborhoods and years, the highest detection probability was 0.33, whereas the lowest was 0.00006.

Occupancy analysis

We detected woodrats at 26 of 28 (93%) neighborhood-year combinations, demonstrating that woodrats were nearly ubiquitous in the areas we sampled. Deer mice were detected in all neighborhoods and years (Table 3). Capturing or detecting woodrats or deer mice did not differ among the three years.

Mean woodrat detection probabilities across neighborhoods and years was 0.57 (95% CI = 0.50–0.59), with an average occupancy probability for sites of 0.40 (95% CI = 0.34–0.46). The proportion of hardwoods in a site correlated negatively with detection probability (Table 4; $\beta = -0.59 \pm [-0.86 - 0.32]$). Of the models we tested, occupancy was best described by including the effects of the total basal area of shrubs (Fig. 2A; Table 4). Models where we included the total value as an explanatory variable were also highly supported for woodrats ($\Delta\text{AIC}_c = 0.10$). Occupancy probability of woodrats across sites associated positively with the basal area of shrubs ($\beta = 0.0032 \pm [0.00014 - 0.0049]$) and the total value ($\beta = 0.0014 \pm [0.0005 - 0.0023]$). Models that did not include either shrubs or the total value of a site were supported poorly ($\Delta\text{AIC}_c > 14$; Table 4).

Deer mouse detection, 0.63 (95% CI = 0.59–0.66), and occupancy, 0.85 (95% CI = 0.79–0.90), were relatively high across all sites and years. For deer mice, we ultimately included two explanatory variables in the detection model: proportion of the site in hardwoods and the amount of coarse woody debris that was greater than 20 cm in diameter (Fig. 2B; Table 4). We included both terms post hoc because both had support in the detection models and our main goals were not to evaluate the hypotheses surrounding detection probability. Both the proportion of hardwoods ($\beta = 0.66 \pm [0.28 - 1.03]$) and the coarse woody debris ($\beta = 0.16 \pm [0.077 - 0.25]$) correlated positively with the detection probability of deer mice. Probability of occupancy for deer mice was best explained by the total value that occurred on a site and correlated positively (Table 4; $\beta = 0.002 \pm [0.00013 - 0.035]$). Other vegetations had weak support for describing occupancy probabilities (Table 5). Nevertheless, the occupancy probabilities for deer mice were high irrespective of site characteristics, sug-

Table 3. The mean estimated population sizes for both woodrats (*Neotoma fuscipes*) and deer mice (*Peromyscus* spp.), standard deviations of population sizes (SD), and mean minimum number alive (MNA) in each neighborhood and year.

Year	Neighborhood	Woodrats			Deer Mice		
		Estimate	SD	MNA	Estimate	SD	MNA
2012	30R	3.0	1.7	0.3	30.8	13.8	3.8
	380G	2.0	0.2	0.0	9.7	11.4	1.0
	60B	6.6	4.2	1.5	21.8	12.5	2.7
	A	3.4	3.4	0.3	21.9	15.1	2.7
	Doe Mill	5.6	5.2	1.3	30.9	8.0	3.8
	N	2.2	2.0	0.7	21.2	18.2	2.5
	P	3.8	1.6	0.5	10.5	4.9	3.3
	R	4.8	5.4	0.7	17.4	7.9	2.2
2014	100F	2.4	3.8	0.6	26.1	14.8	3.2
	130G	2.2	1.5	0.6	10.8	8.8	1.2
	250H	2.9	2.5	0.9	7.6	4.8	1.8
	30R	9.9	8.0	1.8	41.8	23.3	5.2
	60B	4.6	4.7	0.6	9.8	11.5	1.0
	70F	11.4	9.1	2.0	24.9	11.0	3.1
	A	1.6	0.2	0.0	14.4	12.4	1.7
	AU	2.0	1.1	0.1	15.5	17.1	1.8
	N	4.5	6.0	0.6	20.4	22.1	2.4
	R	11.6	10.5	2.3	26.0	12.8	5.1
	100F	2.4	3.8	0.5	26.1	14.7	1.9
2015	130G	2.2	1.4	0.2	10.8	8.8	0.5
	250H	2.8	2.4	0.9	7.6	4.6	1.4
	30R	9.9	7.9	1.2	41.8	23.4	5.0
	60B	5.9	6.3	0.7	8.5	10.8	1.0
	70 F	11.4	9.1	0.6	25.0	11.0	2.8
	A	1.6	0.2	0.8	16.1	12.8	3.9
	AU	2.0	1.0	0.2	15.0	15.7	2.3
	N	4.5	6.0	1.1	20.4	22.2	3.9
	R	11.5	10.3	1.8	26.0	12.7	1.9

gesting that they were present in nearly every site and habitat we sampled.

Abundance estimates

Woodrat abundances were high consistently on sites with a large total number of shrubs or with an estimated high total value. From our generalized linear models, our best candidate models for woodrat abundance included effects from the total basal area of shrubs and the total value of food and cover resources on a site (Table 5; Fig. 3A). Models that did not include these effects were not well supported (Table 5). Both effects correlated positively with woodrat numbers in the top two models (Shrubs: $\beta = 0.0012 \pm [0.0002-0.0022]$, Total Value: $\beta = 0.0006 \pm [0.0001-0.0011]$). Other models of abundance had poor support and provided little explanatory power.

Deer mouse abundance was described relatively similarly among five different vegetative covariates (Table 5). The best supported variables were total value and percent hardwoods. Both Total Shrubs and Coarse Woody Debris also had some modest amount of support as descriptors of deer

mouse abundance at sites (Table 5). Total value also related positively to deer mouse abundance ($\beta = 0.00003 \pm [0.0001-0.0006]$; Fig. 3B), as did Total Shrubs and Percent Hardwoods. Finally, Canopy Cover related positively to deer mouse abundance ($\beta = 0.69 \pm [0.28-1.09]$).

Discussion

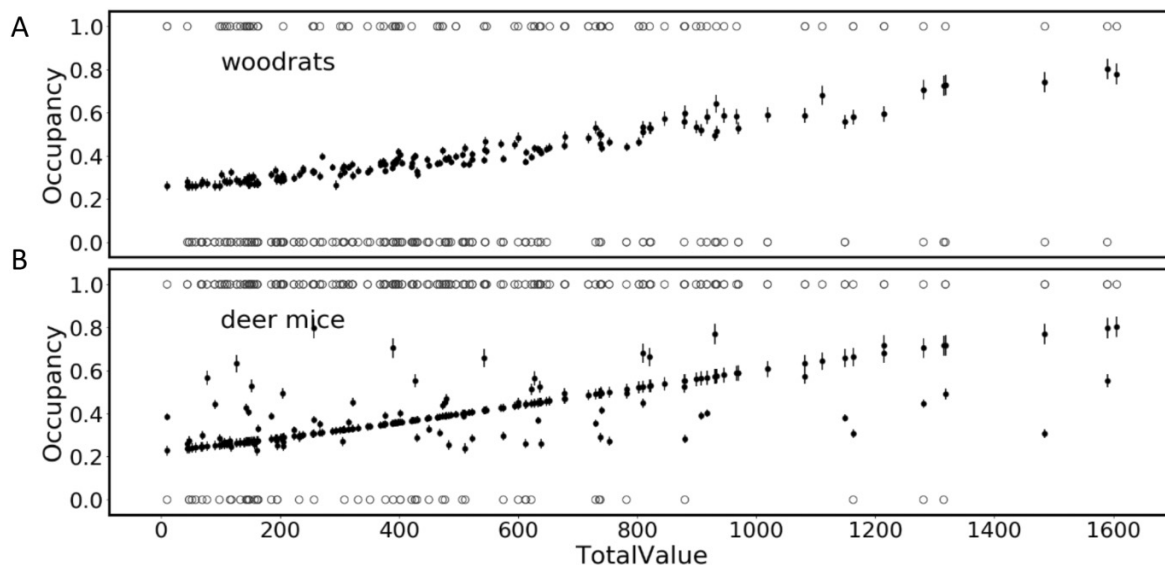
To test our understanding of the functional values of habitat elements for deer mice and woodrats on a landscape managed for timber production in northern CA, we hypothesized that indices summarizing the functional services of forest elements best explained the occupancy and abundance estimates for deer mice and woodrats. Using the results of previous studies cumulated in the FEIS, we summarized the putative values of forest elements for providing food, cover, or both for generalist small mammals. Both deer mice and woodrats occupied a variety of forest types and ages. We captured more deer mice than any other small mammals, followed by woodrats, across all sites in all neighborhoods (aggregations of closely related sam-

Table 4. Occupancy–model selection criteria, including the AIC_c scores, ΔAIC_c comparing the top models to other competing models, the likelihood of each model, the model weight for each competing model (*w*), and the total numbers of parameters (*K*) for the top models from the analyses of occupancy for woodrats.

Detection models	Occupancy models	AIC _c	ΔAIC _c	<i>w</i>	<i>K</i>
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (N-TotalShrub, P-TotalValue)	2134.09	0.00	0.45	10
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (TotalValue)	2134.19	0.10	0.43	9
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (TotalShrub)	2137.28	2.57	0.12	9
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (Canopy)	2149.66	14.95	0.00	9
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (PerHard)	2150.33	15.62	0.00	9
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (SoftMast)	2151.07	16.37	0.00	9
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (CWD20)	2152.03	17.31	0.00	9
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (Species)	2152.21	17.50	0.00	7
<i>p</i> (N-BA, P-PerHard + CWD20)	ψ (Species)	2154.23	19.52	0.00	7
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (ShrubIndex)	2154.24	19.52	0.00	9
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (BA)	2155.25	20.54	0.00	9
<i>p</i> (N-PerHard, P-PerHard + CWD20)	ψ (MeanDD)	2155.60	20.70	0.00	9
<i>p</i> (Species)	ψ (Species)	2158.98	24.27	0.00	4

Note: An “N” prefix within a model indicates “Neotoma” (*Neotoma fuscipes*), whereas as a “P” prefix indicates the modeling for “Peromyscus” (*Peromyscus* spp.). For each model the species-specific models are specified by “N-” for *Neotoma* and “P-” for *Peromyscus* followed by the vegetative covariation used for that species. The detection model was tested for each species prior to any evaluation of the “occupancy” portion and was, therefore, held constant in these final sets of reported models. Species-level effects are reported to demonstrate improvements to model-descriptive power when including covariates.

Fig. 2. (A) The estimated woodrat (*Neotoma fuscipes*) occupancy $\pm$ 95% confidence interval rate per individual site. Detection is a function of the % of a site composed of hardwoods, and occupancy is a function of both the total basal area of all shrubs (shown) and the total basal area of masting tree species. (B) The estimated deer mouse (*Peromyscus* spp.) occupancy probability per individual site. Detection is a function of the total canopy cover and occupancy of the proportion of the site composed of hardwood trees. In both panels, open circles show the raw data where species were detected.



pling sites) and forest types (Table 2). Generally, we found high variation in abundances of small mammals among sites within neighborhoods and across neighborhoods (Table 2).

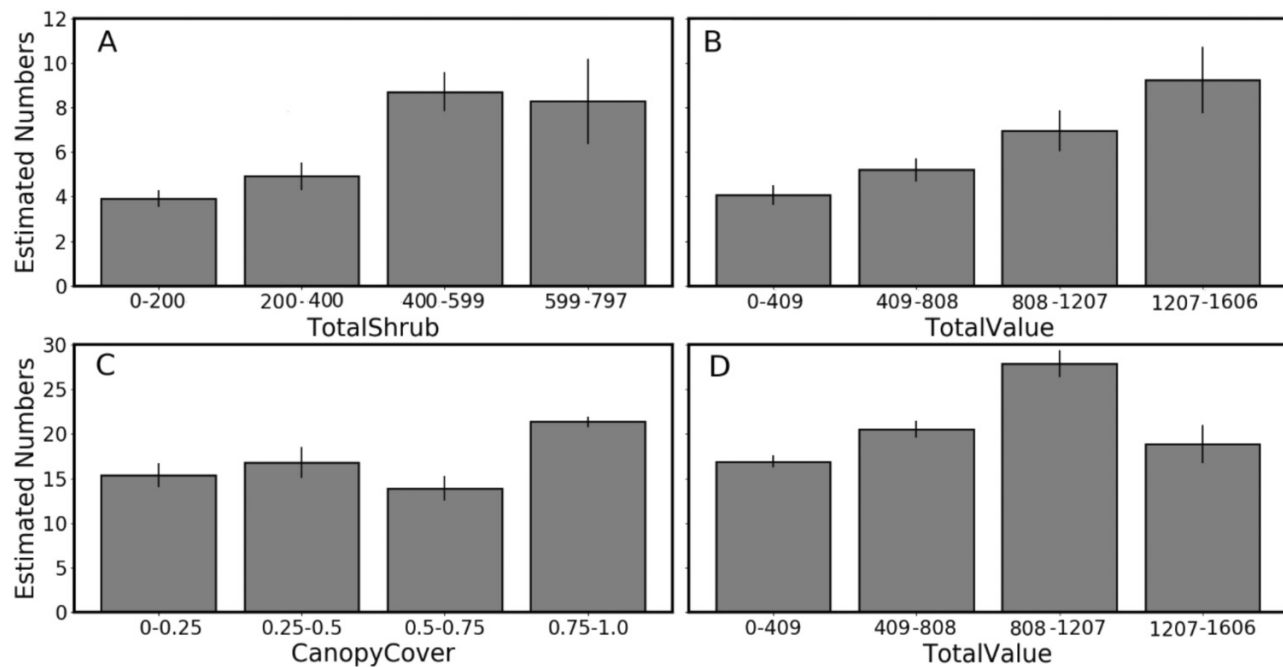
Our results do not allow us to reject either hypothesis—neither that indexes of the functions of forest elements to provide food and cover explain small mammal population dynamics better than the presence of the forest elements them-

selves (H1), nor that resources work synergistically to provide both food and cover (H2). For both woodrats and deer mice, we found best support for the hypothesis that forest elements that provided both food and cover were important (Table 5). Our analyses suggest that our index of total value provided descriptive power for both occupancy and abundance estimates. Yet, our main results indicate that even a basic accounting of functional traits of forest elements, and across

Table 5. Ranking of the 10 competing variables with potential to describe abundances of woodrats (*Neotoma fuscipes*) and deer mice (*Peromyscus* spp.) in 2012, 2014, and 2015, including the AIC_c scores, Δ AIC_c, and the weight for each competing model (*w*).

Species	Model	AIC _c	Δ AIC _c	<i>w</i>	<i>K</i>	Value
Woodrat	Total Value	1193	0.00	0.58	2	Food and cover
	Total Shrub	1194	0.63	0.42	2	Food and cover
	Canopy	1211	17.62	0.00	2	
	Coarse Woody Debris	1213	20.26	0.00	2	
	BA	1213	20.43	0.00	2	
	Percent_Hardwood	1215	22.17	0.00	2	
	Mean_Downed Debris	1215	22.22	0.00	2	
	Soft Mast	1216	22.47	0.00	2	
	Shrub_Index	1216	22.62	0.00	2	
Deer mice	Canopy	1978	0.00	0.33	2	Cover
	Total Value	1978	0.65	0.24	2	Food and cover
	Percent_Hardwood	1979	1.08	0.19	2	Food
	Total Shrub	1980	2.31	0.10	2	
	Coarse Woody Debris	1981	2.87	0.08	2	
	Soft Mast	1983	5.64	0.02	2	
	Mean_Downed Debris	1984	5.76	0.02	2	
	Shrub_Index	1984	6.07	0.02	2	
	Basal Area	1984	6.19	0.01	2	

Fig. 3. The mean numbers of woodrats (A, B) and deer mice (C, D) $\pm$ 95% confidence intervals estimated on 250 sites in the northern Sierra Nevada in 2012, 2014, and 2015. Numbers of woodrats (*Neotoma fuscipes*) plotted against the total basal area of all shrubs located on a sampling site (A) and against the total value of food and cover resources on a sampling site. Numbers of deer mice (*Peromyscus* spp.) plotted against the mean canopy cover on a site (C) and against the total value of food and cover resources (D). Covariates' values are grouped into quantiles for display only.



stands, has explanatory power for how the populations of two small mammal species responded. More importantly, these evaluations of forested stands are not constrained to these two mammal species or even to the types of forests where we conducted our research. Such an approach should be robust

across species and to any forest type where functional values have been well studied. Our findings allowed us to reject the hypotheses that forest stands are easily described as simply providing only food or only cover independently for woodrats or deer mice. The total amount of resources appeared more

important than the presence of habitat elements that provided only food or only cover.

All of our metrics indicated that deer mice were more abundant than woodrats, consistent with the results of [Kelt et al. \(2017\)](#) elsewhere in the Sierra Nevada. They found that woodrats and deer mice were most abundant in forest stands that contained combinations of mast-producing trees and shrubs and other food resources. Though they found woodrats less abundant than deer mice, woodrats composed a larger proportion of the small mammal community on their study site compared to woodrats elsewhere in CA ([Kelt et al. 2017](#)). Our result that shrub abundance is important for woodrats is consistent with the results of [Carey et al. \(1999\)](#). Shrubs provide food, cover, and materials for woodrat nests.

[Innes and colleagues \(2007\)](#), working at higher elevations than at our site, attributed the association between woodrats and black oaks to be related to food ([Innes et al. 2007](#)). We hypothesize that high biomass of shrubs at our study site explains the high abundance of woodrats in our study sites compared to elsewhere throughout their CA range. The combination of abundant mast-producing trees and shrubs at our site suggests that these elements addressed diverse functional needs: multiple types of covers and multiple types of food. Or, as we have stated, the forested stands that provide food or cover (or other value) are often stands that provide other types of values. Such an observation provides an understanding of why “diverse,” or old forests often have higher diversities or abundances of species (e.g., [Carey and Johnson 1995](#)). We expect that stands and their concurrent resources were valuable for other small mammals that we could not sample effectively, including gray squirrels (*Sciurus griseus* Ord, 1818).

In our analyses, detection was best explained by the presence of hardwoods for woodrats and presence of hardwoods plus coarse woody debris for deer mice. [Townsend \(2019\)](#) demonstrated differences in relative abundances of small mammals, including gray squirrels, based on stand composition that favored mast-producing hardwoods. Our results do not determine explicitly how important hardwoods and shrubs are for cover from predators or how important they are for producing mast and other foods. Additionally, our study assumes strict roles of each habitat variable in providing food, cover, or both resources synergistically across the landscape across species. Nevertheless, if food or cover were driving the probabilities of occupancy or abundance independently in our two species, we would have documented association with forest stands that produced one but not the other ([Wolff and Hurblutt 1982](#)). Therefore, hardwoods and shrubs likely provide both food and cover and should be valued over stands that have just woody debris without forest elements that provide food.

In contrast to findings from previous studies examining the role of forest features on rodent abundance and diversity ([Carey and Johnson 1995](#); [Coppeto et al. 2006](#); [Roberts et al. 2015](#); [Sollmann et al. 2015](#)), we found that both hardwoods and shrubs were important for generating structural complexity and seasonal food resources for deer mice and woodrats. Although locations with high shrub or hardwood abundances are not mutually exclusive of areas with high

canopy or tree size ([Wilson and Carey 2000](#); [Innes et al. 2007](#)), canopy and tree size did not correlate with abundance or occupancy of deer mice and woodrats in our analyses. We hypothesize that areas with large trees and high canopy cover may lack high diversity of vegetation that adds structural diversity, food resources, and cover from predators ([Ishii et al. 2004](#); [Swanson et al. 2011](#)). We did, however, find that canopy cover correlated with a suite of other variables, including the total value of a stand, basal area, abundance of hardwoods, and stand characteristics, and explained abundances of deer mice and woodrats to some degree. Canopy cover, thus, appears to be a surrogate for other more influential metrics while appearing to have little functional value in and of itself. We do not suggest that canopy offers no value (for example, it does offer thermoregulatory refuge) but, of itself, produces few resources that animals consume or need directly. For deer mice and woodrats, small mammal generalists, access to resources in managed forests appears to be important regardless of the forest age.

We have demonstrated in this study that consideration for shrubs and non-coniferous trees is important for forest managers and in the Sierras and probably across mountains with similar forest structure. Many places with diverse forest conditions are likely to have deer mice ([Sollman et al. 2015](#); [Kelt et al. 2017](#)). Woodrats are unlikely to be present and abundant under as many conditions ([Carey and Johnson 1995](#); [Innes et al. 2007](#)). We found that diverse stands with both high and low canopy cover had woodrats so long as shrubs and hardwoods were at least moderately abundant. Such stands may be mature, young and regenerating, or recently burned. Yet, as managers replant, thin, and regenerate stands, they should be cognizant of maintaining shrubs and some mast-producing hardwoods if they wish to maintain relatively high abundances of woodrats. Additionally, such practices will have commensurate positive effects on deer mice and other species by providing structure as well as food resources ([Linden and Roloff 2013](#); [Gray et al. 2016](#)). Furthermore, we tested hypotheses of the functional value of different forest elements’ roles in food, cover, or both harnessing previous work (USFS 2020) in their role for explaining each generalist species’ detection, abundance, and occupancy across sites. The inclusion of habitat elements with a priori, prescribed functions in occupancy and abundance modeling allowed us to quantify the role of multiple resource-producing vegetation types and structures, including mast-producing shrubs and hardwoods, for woodrats and deer mice. This allowed us to discern the functional importance and total value of combinations of forest elements, rather than individual elements, to small mammal abundance. Future work could manipulate groups of vegetative variables on sampling sites to quantify the precise functional values they have for the abundances of these generalist small mammals.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Investigation: AKF, ANF, RAP

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Competing interests

We have no competing interests to declare.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjz-2022-0154>.

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