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# Within-Patch Structures Influence Small Mammal Abundance in Managed Forests of Northern California, USA

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We evaluated how forest type, vegetation structure in trapping webs, and proximate forest types influenced localized (~6.35 hectares) abundances for commonly captured small mammals in northern California, USA. We trapped from May to August of 2011–13 in 69 forest patches that represented: (1) clearcuts (3–5 years postharvest), (2) 10–20 year-old conifer plantations, (3) rotation-aged conifer stands, and (4) Watercourse and Lake Protection Zones. We captured 11 species; four in sufficient numbers for regression modeling. Our average abundance estimates for the study were 4.57 (standard error [SE] = 0.43), 0.32 (SE = 0.11), 0.90 (SE = 0.30), and 0.25 (SE = 0.09) individuals per web location (~0.75 hectares) for *Peromyscus* spp., *Neotoma* spp., California ground squirrels, and Allen's chipmunks. We found that web-level ground cover (shrubs and grass), downed wood, and types of forests containing our trapping webs best described small mammal abundances, whereas proximate forest types were not important. Our results indicated that retaining localized structures in the form of understory shrub cover and downed wood positively influences small mammal abundance in intensively managed forests of northern California.

**Keywords:** California ground squirrel, *Peromyscus* spp., woodrats, clearcut, Klamath Mountains

Small mammals influence distribution and habitat use of predators (Carey et al. 1992), regulate invertebrate populations (Buckner 1966, Carey and Johnson 1995, Elkinton et al. 1996, Carey and Harrington 2001), disperse fungal spores (Maser et al. 1978), and serve as indicators of sustainable forest management (Carey and Harrington 2001). Small mammals are also prey for protected species in the Pacific Northwest (PNW), most notably spotted owls (*Strix occidentalis*), Pacific fisher (*Pekania pennant pacifica*), and marten (*Martes americana caurina* and *M. a. sierrae*). Timber production is a primary land use in PNW (Parks et al. 2005, Oswalt et al. 2014), making the influence of timber management on protected species and their prey a topic of conservation interest. Alternatively, small mammals can also be detrimental to forest regeneration through seed predation and damage to seedlings (Ostfeld et al. 1997, Côté et al. 2003). Understanding how small mammals respond to vegetation patterns that emerge from intensively managed forests can inform management objectives, potentially to benefit small mammal communities and their associated predators (Maser et al. 1978, Aubry et al. 1991, Carey and Johnson 1995, Williams et al. 2014) or reduce damages to regenerating forests from pest populations (Borrecco 1976, Jacob 2008).

Northern California, USA, is an arid environment relative to more northerly forests of PNW. Timber management is a primary land use with approximately 39 percent of forested lands owned by private industry (Christensen et al. 2016). Few studies on small mammals and forestry have occurred in northern California, making this a region that merits further study. We previously demonstrated that small mammal abundance positively correlated with shrub cover and downed wood at small scales in this landscape (i.e., 64 $m^2$; Gray et al. 2016), indicating the importance of localized refugia for conservation of small mammals. Others have documented similar relations in arid forests of the southwestern United States (Ward 2001, Block et al. 2005, 2011, Converse et al. 2006, Kalies et al. 2012).

Riparian zones positively influence small mammals in the PNW (Cross 1985, Doyle 1990, Lehmkuhl et al. 2008) and may effectively

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reduce short-term negative impacts of clearcutting (Cockle and Richardson 2003). One focus of forest practices rules in California is protection of water quality, which is partially accomplished by protecting riparian zones (Watercourse and Lake Protection Zones; WLPZs) during timber harvesting. Hence, WLPZs are an important wildlife feature, as they provide abundant cover, forage, access to water, and cooler microclimates during summer, particularly in arid environments (Hamilton et al. 2015).

Suitable small mammal habitats can vary widely based on forest type, forest age, and management regimes (Hallet et al. 2003). Given that silviculture and timber harvest patterns have direct impacts on many life history requirements of small mammals, proximity and interspersion of forest types likely influence small mammal community composition and abundance. For example, clearcutting results in loss of horizontal and vertical structural diversity in vegetation (Peterken 1996, Lust et al. 1998, Lindenmayer and Franklin 2002, Betts et al. 2005), but some small mammal generalists benefit from this practice (Kirkland 1990, Sullivan et al. 2012). Diverse forest ages in a localized area likely increase small mammal species richness, as older forest classes (ranging from 35 to 730 years) may show few differences in small mammal community assemblages (Aubry et al. 1991).

Forest management in northern California is essential for vibrant rural communities and economic revenue, so understanding the role of forest management in conserving protected species (and their prey) is both relevant and necessary. We used a combination of live-trapping and generalized linear mixed-effect models (GLMM) to explore relations between small mammal abundance and forest conditions resulting from intensive timber management at scales corresponding to the forest patch and proximate areas. Specifically, we (1) documented small mammal communities in four forest types that commonly occur in intensively managed forests, (2) evaluated how proximate forest types influenced localized abundance for the most frequently captured species, and (3) examined effects of forest patch structural features on species abundance. Whereas our previously published work on small mammals in the region focused on a fine scale (64 $m^2$) with relevance to within-patch silviculture or equipment operator decisions (Gray et al. 2016), this study focuses on patch-level configuration and vegetation structure.

# Methods

## Study Area

Our study occurred on timberlands privately owned and managed by Sierra Pacific Industries (SPI). Sampling occurred in the Klamath Mountain ecoregion of northern California, Trinity County, USA. The local climate is Mediterranean, characterized by hot and dry summers (Skinner et al. 2006). Average maximum daily temperatures range from 25 to 34° C, and average monthly precipitation ranges from 3.3 to 0.5 cm from May through August. The coolest and wettest month of the year is May, whereas the driest and hottest months occur in July and August, respectively (Weaverville Ranger Station, US Forest Service, Trinity County). Land use is primarily forestry, agriculture, tourism, and mining (Sleeter and Calzia 2011), with insect and disease outbreaks and wildfires comprising the dominant natural disturbances shaping existing forest structure (Mohr et al. 2000). Vegetation is broadly described as mixed-conifer or Douglas-fir forests (Christensen et al. 2016). Industrial forests owned by SPI are primarily managed for Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), and ponderosa pine (*Pinus ponderosa*). The forests also contain hardwoods not harvested for commercial use, including canyon live oak (*Quercus chrysolepis*), California black oak (*Quercus kelloggii*), and madrone (*Arbutus menziesii*).

## Data Collection

We trapped small mammals from May to August of 2011–13. Our replicate spatial units were forest patches, referring to a relatively homogeneous area of trees harvested at approximately the same time. Small-scale (≤8 hectares) clearcutting is the dominant timber harvest pattern in northern California, followed by site preparation using a combination of chemical, mechanical, and fire-related treatments tailored to enhance survival of planted trees. In our study, managed forest patches (i.e., excluding WLPZs) contained a range of retained structures including riparian buffers, retention patches, downed wood, and occasional single, isolated leave trees. On average, forest patches we trapped were 7–8 hectares and located in areas north and south of Weaverville, California, at elevations ranging from 677 to 1,467 m (Table 1).

We partitioned forest patches ($n$ = 69) into four types based on time since the last timber harvest. Forest types included (a) recent clearcuts (3–5 years old; $n$ = 17), (b) 10- to 20-year-old conifer plantations ($n$ = 16), (c) rotation-aged conifer stands (60–80 years old; $n$ = 19), and (d) WLPZs (restricted harvest; $n$ = 17; Table 1). We used a web-based trapping design (Anderson et al. 1983, Bagne and Finch 2010), with a combination of Sherman (Model LFA, 7.6 × 8.9 × 22.9 cm; H.B. Sherman Traps, Inc., Tallahassee, FL) and Tomahawk (Model 202, 48.3 × 15.2 × 15.2 cm; Tomahawk Live Trap Co., Tomahawk, WI) live traps (Parmenter and MacMahon 1989). We placed a single trapping web in a forest patch and trapped for 3 (2011) and 5 (2012–13) nights.

The trapping web consisted of five spokes that each contained seven nodes, with nodes separated by 7 m (Gray et al. 2016). We placed a Sherman trap at each node (35 Sherman traps per web) and a Tomahawk trap at web center and at the third and fifth nodes of each spoke (11 Tomahawk traps per web). We trapped each forest patch once during our study, and we aimed to trap each

## Management and Policy Implications

We assessed the role of intensively managed forest conditions on small mammal abundances in northern California. For commonly captured species, we found that habitat structures within localized areas (0.75 hectares) were more influential on small mammal abundances than types of adjacent forests or forest type that contained the trapping web, with few exceptions. Our results indicated that relatively low levels of retention within a patch substantially increased small mammal abundance. For example, by increasing localized shrub cover from 0 to 40 percent, managers may potentially increase Allen's chipmunk abundance (i.e., 1.5 additional chipmunks/~6.35 hectares). Our study confirmed benefits of retaining structural elements for conserving small mammal populations during timber harvesting, lending support for using implementation of forest practices rules to conserve wildlife in California. In situations where small mammals are detrimental to forest regeneration, our results indicate that simplifying ground-level structure will correlate to lower abundances.

**Table 1. Number of sites per patch forest type sampled by month, year, and elevation in intensively managed forests of northern California, USA, from 2011 to 2013.**

| Patch forest type[a] | Year | | | | | | | | | | | | Elevation (m) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2011 | | | | 2012 | | | | 2013 | | | | Mean | Range |
| | May | June | July | August | May | June | July | August | May | June | July | August | | |
| 3–5 years | 0 | 4 | 0 | 0 | 1 | 3 | 3 | 1 | 2 | 1 | 1 | 1 | 982 | 716–1,274 |
| 10–20 years | 1 | 1 | 1 | 0 | 0 | 5 | 2 | 1 | 2 | 2 | 0 | 1 | 1,065 | 849–1,467 |
| Rotation | 1 | 4 | 3 | 0 | 0 | 3 | 2 | 1 | 1 | 2 | 2 | 0 | 1,006 | 682–1,309 |
| WLPZ | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 2 | 1 | 8 | 2 | 950 | 677–1,268 |

[a]Patch forest type: 3–5, 3–5 years since clearcut; 10–20, 10–20 years since clearcut; Rotation, rotation-aged type; WLPZ, Watercourse and Lake Protection Zones.

forest type during a sampling period to account for broader seasonal fluctuations in small mammal abundances.

We set traps under or beside ground cover such as logs or heavy foliage, and those traps at risk of exposure to direct sunlight were shaded (Gray et al. 2016). We baited each trap, included polyester fiber as cover, and checked traps daily between dawn and noon (Gray et al. 2016). We individually marked small mammals with a passive integrated transponder (PIT) tag (see Gray et al. 2016) and recorded mass using a 50-g or 1000-g spring scale (Pesola® scales, Präzisionswaagen AG, Switzerland) depending on species. We also recorded whether an individual was reproductively active when females were noticeably pregnant, lactating, or had developed nipples, and if males had descended testes (i.e., scrotal). We tallied mass and reproductive information to better understand the ratio of young to adults in our samples, where adults were defined as the lightest weight of an individual that was reproductively active in each species. Our capture and handling of animals followed California Department of Fish and Game scientific collection permit (SC-11913) and was reviewed by the Institutional Animal Care and Use Committee at Michigan State University (09-27-12).

### Vegetation Sampling

We conducted line-intercept sampling for downed wood along the length of each spoke in a trapping web. For each piece of wood with a large-end diameter ≥11.4 cm that intersected the line, we measured length and large- and small-end diameters. We also noted the location of woody debris along the spoke from the starting position (i.e., web center) to avoid double counting. We then calculated the volume of downed wood per web area (~0.75 hectares). We also calculated the basal area at the center of each web and at the end of each spoke using a 10-BAF prism, ensuring that trees were not double-counted. We calculated an average basal area for the trapping web.

We also collected ground cover data around each trap location. We established a 5-m-diameter plot centered at each trap and used point-line transect surveys in each cardinal direction (i.e., north, south, east, and west). We recorded the type of ground cover (i.e., shrub, forb, grass, and mineral soil) 1.5 m and 2.5 m from the trap, and calculated the proportion of plots by ground cover type. We then averaged these proportions across all trap locations to estimate ground cover composition at the web level. Vegetation sampling was conducted simultaneously with trapping to temporally capture features representative of each trapping period.

### Proximate Forest Types

We obtained ArcGIS (ArcGIS 10.1; Environmental Systems Research Institute, Redlands, CA) data layers on land ownership and forest types from SPI. We also acquired a data layer on forest types that were not part of SPI ownership from the Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG; USDA Forest Service 1981). We first delineated a circular buffer with a radius of 142.2 m (i.e., covering ~6.35 hectares) around the center of each trapping web. This radius corresponds to the maximum straight-line distance moved (i.e., 93.2 m) by any individual small mammal during our study plus length of a web spoke (i.e., 49 m), representing the potential area used by small mammals during trapping. This buffer area exceeded the documented home range sizes for species we captured (i.e., yellow-pine chipmunk [*Tamias amoenus*; a similar species to Allen's chipmunk], ~1.6 hectares [Broadbooks 1970]; dusky-footed woodrat [*Neotoma fuscipes*], ~0.23 hectares [Cranford 1977]; California ground squirrel [*Otospermophilus beecheyi*], ~0.09 hectares [Boellstorff and Owings 1995]; and brush mouse [*Permoyscus boylii*], ~0.12 hectares [Gottesman et al. 2004]), thereby ensuring that multiple home ranges overlapped the trapping web. Within each 6.35-hectare buffer, we calculated the proportional area of each forest type and used these proportions as explanatory variables in abundance models.

### Data Analysis

We portrayed abundance as a count of unique individuals captured at a web. We applied GLMMs with a Poisson probability distribution in program *R* (3.1.2; R Development Core Team 2013) to estimate the effects of independent covariates on small mammal abundance by species. Classical maximum likelihood methods (like GLMM) robustly estimate linear relations between species abundance and environmental correlates, comparable to Bayesian modes of inference (Dorazio 2013). We developed two independent candidate sets of models based on spatial scales of inference. First, we built models that corresponded to the patch level (i.e., 0.75 hectares), which included the forest type containing the trapping web, downed wood volume, and average proportions of various ground cover categories within a web. Next, we built models related to proximate areas (i.e., 6.35 hectares) that included proportions of forest types within the 6.35-hectare buffer as independent variables. We first conducted a two-way ANOVA to check for differences in small mammal species counts among year and forest type that contained the trapping web (including an interaction term between these two factors). For a significant ANOVA ($P \leq .05$), we used a Tukey multiple-comparisons test to identify which years or forest types differed. For nonsignificant ANOVA results, we deemed year and forest type containing the web as unimportant variables for regression modeling. We then used Kendall's tau rank coefficients to

identify combinations of independent variables that were correlated ($P < .05$); correlated variables did not appear in the same candidate model. We combined candidate model sets from both spatial scales in model selection to better elucidate independent variables and scale most influential to small mammal abundance by species. Recognizing that small mammal populations can significantly fluctuate annually (Terman 1966, Smith et al. 1974), we included trapping year as a random effect in all species-specific GLMMs. We used Akaike's Information Criterion for small sample sizes ($AIC_c$) to rank candidate models. We deemed model parameters significant if their 95 percent confidence intervals did not overlap zero (Burnham and Anderson 2002). We considered candidate models within an eighth of the AIC weight of the top-ranked model competing and generated model-averaged predictions (Burnham and Anderson 2002).

## Results

### Vegetation and Proximate Forest Types

Within trapping webs ($n = 69$), we found the average volume of downed wood was highest in WLPZ and rotation-aged types (Table S1). More recently harvested types (i.e., 3–5 and 10–20 years old) had average downed wood volumes of ~0.25 $m^3$/0.75 hectares (Table S1). Generally, downed wood volumes were most variable in older forest types (i.e., rotation-aged and WLPZ), and wood volumes were approximately two to three times higher in older forest types (Table S1). As expected, basal area was also higher in older patches, with rotation-aged patches having the highest basal area on average ($\bar{x}$= 12.38 $m^2$/0.75 hectares, standard error [SE] = 1.02), followed by WLPZ ($\bar{x}$= 10.24 $m^2$/0.75 hectares, SE = 0.87; Table S1). Shrub and forb cover was also highest in WLPZ types, whereas grass and mineral soil cover tended to be higher in younger forest types (Table S1).

Nonforest classes around trapping webs were rare and hence not included in our analyses (Figure S1). Trapping webs located in 3- to 5-year forest types were closer to rotation-aged forests (average >40 percent of the 6.35-hectare buffer) and, to a lesser extent, WLPZs (~>10 percent) than other forest types (Figure S1a). This pattern is consistent with typical spacing of clearcuts and dendritic water systems in northern California. The proportion of different forest types around trapping webs in 10- to 20-year-old forest type was highly variable, with all forest types represented and varying depending on year (Figure S1b). Our trapping webs in rotation-aged type were generally surrounded by other rotation-aged type and, to a lesser extent (<30 percent), other forest types (Figure S1c). Forest types surrounding our webs in WLPZs were also highly variable with all forest types represented (Figure S1d). Collectively these results indicated that our webs in younger forest types tended to occur in a matrix of rotation-aged forests, that webs in rotation-aged forests tended to occur in an older forest matrix, and that webs in 10- to 20-year and WLPZ types were surrounded by highly variable forest conditions.

### Small Mammals

We accumulated 12,503 trap nights, which comprised ~86 percent of the maximum number of trap nights possible. Empty but sprung traps, traps damaged by other wildlife species (e.g., black bear [*Ursus americanus*] and gray fox [*Urocyon cinereoargenteus*]), and malfunctioning traps accounted for most of our lost trap nights. We captured 11 small mammal species: deer mouse (*Peromyscus maniculatus*), brush mouse, California ground squirrel, dusky-footed woodrat, Allen's chipmunk, Trowbridge's shrew (*Sorex trowbridgii*), bushy-tailed woodrat (*N. cinerea*), Douglas squirrel (*Tamiasciurus douglasii*), California vole (*Microtus californicus*), and western harvest mouse (*Reithrodontomys megalotis*). We pooled *Peromyscus* spp. for modeling because field crews could not reliably differentiate juveniles of species belonging to this genus. We also pooled dusky-footed and bushy-tailed woodrats into *Neotoma* spp. because of low captures of bushy-tailed woodrats (~23 percent of *Neotoma* captures; Table S2). Of 434 total captures, *Peromyscus* spp. were most frequently captured (73 percent of all captures; Table S2).

We found that the minimum weights of reproductively active individuals were 10 g and 80 g for *Peromyscus* spp. and *Neotoma* spp., respectively. Our sample included >67 percent adults for *Peromyscus* spp. and 100 percent for *Neotoma* spp. Based on the literature, the minimum weight threshold was 66.80 g for male and 73.00 g for female Allen's chipmunks, and 280 g for California ground squirrels (Hall 1946, Eder and Ross 2005). Our sample included >87 percent adults for Allen's chipmunks and >90 percent adults for California ground squirrels.

The mean number of individuals captured per patch for *Peromyscus* spp. was highest in the WLPZ class, followed by 3- to 5-year, rotation-aged, and 10- to 20-year classes, and we failed to find any forest type and year interaction ($F_{5,58}$ = 1.92, $P$ = .11) but found an almost significant effect of forest type ($F_{3,58}$ = 2.61, $P$ = .06). Our abundance estimates for *Peromyscus* spp. suggest a declining trend across years, regardless of forest type, potentially indicating a broad-scale population response not related to our covariates (Figure 1a). California ground squirrels were more abundant in younger forest types (in 2012), although abundances were low (Figure 1b). We did not find any forest type and year interaction ($F_{5,58}$ = 1.40, $P$ = .24), but the effect of forest type alone was almost significant ($F_{3,58}$ = 2.58, $P$ = .06). We tended to capture *Neotoma* spp. in rotation-aged and WLPZ types, with the exception of two individuals caught in the 10–20 year type (Figure 1c). We did not observe any forest type and year interaction ($F_{5,58}$ = .67, $P$ = .65) but found that forest type was almost significant on woodrat abundance ($F_{3,58}$ = 2.43, $P$ = .07). We rarely captured Allen's chipmunks, with most trapped in rotation-aged forests (Figure 1d), and failed to find any forest type and year interaction ($F_{5,58}$ = 0.56, $P$ = .73) or difference among forest types ($F_{3,58}$ = 0.68, df = 3, $P$ = .57).

We identified 10 competing models for *Peromyscus* spp. (see Table 2 for the top 4). At the level of the trapping web, we found that cover of exposed soil (β = 2.54, SE = 0.72) and downed wood volume (β = 0.28, SE = 0.08) were positively related to *Peromyscus* spp. abundance (Table 3). We also found trapping webs in WLPZs positively influenced *Peromyscus* spp. abundance (β = 0.47, SE = 0.20; Table 3). Abundance of *Peromyscus* spp. showed a nonlinear increase as cover of soil and downed wood volume increased (Figures S2a, b respectively). Abundance increased approximately two to three times across the range of conditions we measured in this study.

We identified eight competing models for *Neotoma* spp. (see Table 2 for the top 4) and found that proportion of grass (β = –20.56, SE = 6.25) and shrub (β = 7.78, SE = 2.19) cover within trapping webs significantly influenced *Neotoma* spp. abundance (Table 3). Increasing proportions of grass cover resulted in rapid declines in

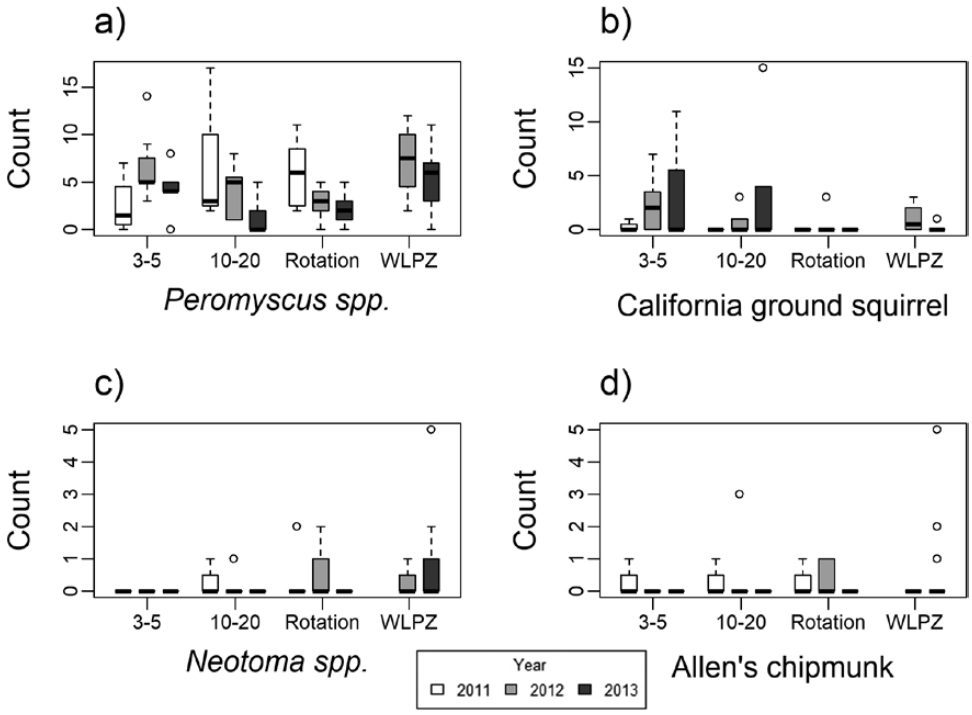


**Figure 1. Count of individual small mammals by forest type, year, and small mammal species in intensively managed forests of northern California, USA from 2011 to 2013. Forest types include 3–5 year-old (3–5), 10–20 year-old (10–20), rotation-aged (Rotation), and Watercourse and Lake Protection Zones (WLPZ).**

**Table 2. Top-ranking generalized linear mixed models for estimating small mammal abundance from trapping web-level attributes (0.75 hectares) and forest types in proximate area (6.35 hectares) in intensively managed forests of northern California, USA, from 2011 to 2013.**

| Species | Model covariates[a] | df | ΔAIC | *w* |
|---|---|---|---|---|
| *Peromyscus* spp. | Soil + Patch Type + Volume ($m^3$) | 7 | 0.00 | 0.23 |
| | Shrub + Soil + Patch Type + Volume ($m^3$) | 8 | 1.44 | 0.11 |
| | Basal + Soil + Patch Type + Volume ($m^3$) | 8 | 1.47 | 0.11 |
| | Forb + Soil + Patch Type + Volume ($m^3$) | 8 | 2.06 | 0.08 |
| *Neotoma* spp. | Grass + Shrub | 4 | 0.00 | 0.23 |
| | Grass + Shrub + Volume ($m^3$) | 5 | 1.18 | 0.13 |
| | Forb + Grass + Shrub | 5 | 2.20 | 0.08 |
| | Grass + Shrub + Soil | 5 | 2.24 | 0.08 |
| Allen's chipmunk | Grass + Shrub + Volume ($m^3$) | 5 | 0.00 | 0.20 |
| | Grass + Shrub | 4 | 0.72 | 0.14 |
| | Basal + Grass + Shrub + Volume ($m^3$) | 6 | 2.17 | 0.07 |
| | Forb + Grass + Shrub + Volume ($m^3$) | 6 | 2.21 | 0.07 |
| California ground squirrel | Basal + Grass + Soil + Patch Type + Volume ($m^3$) | 9 | 0.00 | 0.26 |
| | Basal + Grass + Shrub + Soil + Volume ($m^3$) | 7 | 0.82 | 0.17 |
| | Basal + Grass + Soil + Volume ($m^3$) | 6 | 0.84 | 0.17 |
| | Basal + Forb + Grass + Soil + Patch Type + Volume ($m^3$) | 10 | 2.34 | 0.08 |

[a]Covariates estimated at the web level (0.75 hectares): Forb, Grass, Shrub, and Soil were proportions of each ground cover class; Volume ($m^3$) is the volume of downed wood ≥11 cm diameter; Patch Type: 1 = 3- to 5-year, 2 = 10- to 20-year, 3 = rotation-aged, and 4 = Watercourse and Lake Protection Zones. Covariates estimated for 6.35 hectares surrounding the trapping web: 3–5, 3–5 years since clearcut; 10–20, 10–20 years since clearcut; Rotation, rotation-aged type; WLPZ, Watercourse and Lake Protection Zones.

AIC, Akaike's Information Criterion; df, degrees of freedom.

*Neotoma* spp. abundance, whereas increasing proportions of shrub cover resulted in nonlinear increases in *Neotoma* spp. abundance (Figures S3a, b). We found no significant effects among forest types containing the trapping web or amount of proximate forest types in our GLMMs.

We identified eight competing models for Allen's chipmunks (see Table 2 for the top 4). Proportion of grass (β = –9.83, SE = 4.69) and shrub (β = 9.27, SE = 2.28) ground cover within webs significantly influenced Allen's chipmunk abundance (Table 3). We found that increasing proportions of grass cover nonlinearly reduced abundance of Allen's chipmunks, whereas increasing proportions of shrub cover resulted in a nonlinear increase in abundance (Figure S4a, b).

We identified seven competing models for California ground squirrels (see Table 2 for top 4). We found that basal area (β = –0.47, SE = 0.08), downed wood volume (β = –0.73, SE = 0.28), and

**Table 3. Model-averaged coefficients (β) and standard errors (SE) from generalized linear mixed models for estimating small mammal abundance from trapping web-level attributes (0.75 hectares), forest type containing the trapping web (Patch Treatment), and proximate area (6.35 hectares) forest types in intensively managed of northern California, USA, from 2011 to 2013.**

| Scale[a] | Covariates[b] | *Peromyscus* spp. | | *Neotoma* spp. | | Allen's chipmunk | | California ground squirrel | |
|---|---|---|---|---|---|---|---|---|---|
| | | β | SE | β | SE | β | SE | β | SE |
| Web | Basal area ($m^2$) | –0.01 | 0.01 | 0.00 | 0.03 | 0.01 | 0.04 | –0.47* | 0.08 |
| | Forb | –0.14 | 0.49 | –0.12 | 1.05 | –0.16 | 1.32 | 0.20 | 0.84 |
| | Grass | 0.01 | 0.22 | –20.56* | 6.25 | –9.83* | 4.69 | –2.79* | 1.05 |
| | Shrub | 0.21 | 0.50 | 7.78* | 2.19 | 9.27* | 2.28 | –0.84 | 1.67 |
| | Soil | 2.54* | 0.72 | 0.08 | 1.10 | –0.14 | 1.48 | –7.01* | 2.70 |
| | Volume ($m^3$) | 0.28* | 0.08 | –0.11 | 0.23 | –0.58 | 0.72 | –0.73* | 0.28 |
| Patch forest type | 10–20 year | –0.11 | 0.18 | – | – | – | – | –0.50* | 0.59 |
| | Rotation | –0.04 | 0.20 | – | – | – | – | –0.37 | 0.62 |
| | WLPZ | 0.47* | 0.20 | – | – | – | – | –0.39 | 0.57 |
| Proximate areas | 3- to 5-year | – | – | – | – | – | – | – | – |
| | 10- to 20-year | – | – | – | – | – | – | – | – |
| | Rotation | – | – | – | – | – | – | – | – |
| | WLPZ | – | – | – | – | – | – | – | – |

*Note:* β, model-averaged coefficient; SE, standard error. *Indicates significance: 95 percent confidence intervals did not overlap zero.

[a]Web, trapping web level (~0.75 hectares); Patch forest type, forest type containing the trapping web; Proximate areas, ~6.35-hectare area surrounding the trapping web.

[b]Forb, Grass, Shrub, and Soil are proportions, and Volume ($m^3$) is volume of downed wood ≥11 cm diameter. Proportions of forest types where 3- to 5-year is 3–5 years after clearcut; 10- to 20-year is 10–20 years after clearcut; Rotation, rotation-aged type; WLPZ, Watercourse and Lake Protection Zones.

[c]Covariate did not appear in competing models.

proportion of grass cover (β = 2.79, SE = 1.05) and bare soil (β = –7.01, SE = 2.70) significantly influenced ground squirrel abundance (Table 3). Abundance of California ground squirrels nonlinearly decreased with increasing basal area, levels of grass bare soil cover, and downed wood volume (Figures S5a–d). Similar to *Peromyscus* spp., we found a significant effect of forest type containing our trapping webs, with California ground squirrel abundance lower in the 10- to 20-year than in the 3- to 5-year forest type (β = –0.50, SE = 0.59; Table 3).

## Discussion

We assessed the influence of patch-level vegetation structure and spatial context on four commonly captured small mammal species in intensively managed forests of northern California. We found that within-patch structures and forest type containing the trapping web more closely correlated with small mammal abundance than proximate forest types surrounding the focal patch. Important within-patch factors varied by species, but represented factors that can be directly manipulated during forest-management activities. For example, shrub cover within a patch positively related to *Neotoma* spp. and Allen's chipmunk abundances. Industrial forest landowners directly control shrub cover amounts in recent timber harvest areas through the use of selective herbicides or fire (Demarais et al. 2017) to decrease competition with newly planted seedlings. Similarly, downed wood volume was an important within-patch correlate of *Peromyscus* spp. and California ground squirrel abundances in our study. Adjustment of downed wood volume can occur during timber harvest operations via implementation of retention guidelines (Demarais et al. 2017).

Our study used a multiscale approach to elucidate influential features in managed forest landscapes that correlated with small mammal abundances. For each commonly captured species, within-patch ground vegetation cover and retention structures were more influential than the surrounding patch mosaic. This finding aligns with other studies that explored habitat relations and small mammals at multiple scales (Bowman et al. 2001, Manning and Edge 2004). Given the relatively small home ranges of our study organisms (i.e., <1 hectares) and that most (except for California ground squirrel) are nonterritorial, the importance of localized factors on small mammal abundances is not surprising. Our results generally imply that if suitable localized structures exist, the small mammal species we commonly captured in intensively managed landscapes of northern California are ubiquitous.

Although we found significant correlates of small mammal abundance, we failed to find any single models with substantial support in the data. This potentially indicates high among-site variation in small mammal–habitat relations, complex habitat relations not consistently portrayed by our simple models, or unquantified sources of variation in small mammal abundance (e.g., influence of year). Increases in shrub cover corresponded to positive responses for *Neotoma* spp. and Allen's chipmunks in our study, aligning with other small mammal studies conducted in arid climates of the southwestern United States (Block et al. 2005, Converse et al. 2006, Block et al. 2011). Shrubs provide thermal refuge (Chappell 1978) and likely provide important food sources to small mammals. Seeds from shrubs are an important dietary component in Allen's chipmunks of northeastern California (Tevis 1953).

Other significant within-patch correlates to small mammal abundance included grass cover, basal area, bare soil, and downed wood volume. The strong negative relation to increasing grass cover by *Neotoma* spp. in our study aligns with research indicating that this species mostly occupies woody thickets and areas featuring dense understory cover (Murray and Barnes 1969, Meserve 1974, Innes et al. 2007). Similarly, for Allen's chipmunk, grass cover negatively influenced abundance, likely relating to this species' affinity for closed canopy forests (Sharples 1983, Waters and Zabel 1998) that generally contained low amounts of grass cover in our study. The negative influence of basal area and grass cover on California ground squirrels corresponds to their use of areas with minimal tree canopy and ground cover (Evans and Holdenried 1943, Fitch

1948, Owings and Borchert 1975, Owings et al. 1977, Ordeñana et al. 2012). The negative effect of bare soil on California ground squirrels may relate to their dependence on herbaceous vegetation during the growing season (Fitch 1948). The positive influence of bare soil on *Peromyscus* spp. in our study likely relates to the ability of this species to thrive in recently disturbed and early successional forest types (Tevis 1956, Gashwiler 1970, Sullivan 1979, Kirkland 1990, Fantz and Renken 2005). Although these findings have implications for small mammal conservation, they also provide insight for managers looking to control overabundant or pest populations through postharvest stand treatments (i.e., fire, herbicide). In our study area, small mammal populations responded negatively to simplified ground-level forest structure. Hence, in areas susceptible to forest regeneration damage from small mammals, prescriptions that simplify ground-level vegetation (e.g., remove shrubs and downed wood) are useful.

Our positive influence of downed wood on *Peromyscus* spp. coincides with other studies in the PNW (Carey and Johnson 1995, Carey and Harrington 2001, Lee 2004). Downed wood provides resting and thermal cover, and serves as substrate for reproduction and foraging (Maser et al. 1978, Amaranthus et al. 1994, Carey and Johnson 1995, McComb 2003). Our negative impact of downed wood on California ground squirrels likely relates to their affinity for areas with long sight distances (Grinnell 1918, Owings and Borchert 1975, Fehmi et al. 2005, Ordeñana et al. 2012). Retention of downed wood can increase abundance of *Peromyscus* spp. while subsequently reducing abundance of California ground squirrels. The benefits of this practice are twofold, given that *Peromyscus* spp. are an important dietary component for spotted owls (Franklin 1997, Smith et al. 1999) and that California ground squirrels are a destructive species (Marsh 1998) capable of hindering forest regeneration.

In addition to within-patch structures, we found the forest type containing our trapping webs significantly influenced *Peromyscus* spp. abundance. We found more *Peromyscus* spp. in WLPZ relative to other forest types. In the Cascade Range of Oregon, more *Peromyscus* spp. were captured, males had greater weights, and more adults were in breeding condition in riparian than in upland areas (Doyle 1990). Similarly in western Oregon, captures of deer mice decreased as distance from stream increased (McComb et al. 1993). In northern California, deer mice were more abundant near larger streams than upland areas, potentially because of greater availability of food (Waters et al. 2001). In arid regions similar to our study area, riparian areas adjacent to early successional and recently harvested patches might serve as important sources of food, water, and microclimate for *Peromyscus* spp. In some instances, retained riparian buffers have been shown to reduce short-term impacts on small mammals following intensive timber harvest (Cockle and Richardson 2003). Our findings with *Peromyscus* spp. potentially support the utility of this riparian retention practice.

We found fewer California ground squirrels in our 10- to 20-year forest type, likely because of the increased amount of herbaceous understory cover in this forest type compared to recently harvested or more mature forest types containing greater amounts of canopy cover. We captured California ground squirrels most often in the 3- to 5-year forest type, as these areas were relatively open and offered conditions favorable for predator detection, a habitat requirement for this species (Grinnell 1918, Owings and Borchert 1975, Fehmi et al. 2005, Ordeñana et al. 2012). This finding further emphasizes how managers seeking to reduce damages caused by California ground squirrels may benefit from allowing development of herbaceous understory.

Our results suggest that relatively low levels of woody debris retention can substantially increase small mammal abundance. For example, an increase from 1 to 3 $m^3$/0.75 hectares (4 $m^3$/hectare) of downed wood may result in a twofold increase in *Peromyscus* spp. abundance at the trapping web level. This amounts to retaining approximately 13 logs 20 cm in diameter and 10 m in length per hectare. Similarly, increasing shrub cover from 0 to 40 percent could potentially result in an additional 1.5 Allen's chipmunks/~6.35 hectares. We acknowledge that retention of shrubs and downed wood incurs operational and opportunity costs (e.g., reduced tree growth because of shrub competition) to landowners, and hence these practices are not feasible as broad prescriptions. However, in locations where small mammal abundance is important for supporting protected predator species (e.g., within a spotted owl foraging area) or managing detrimental impacts from pest populations, our study offers guidance on types and amounts of structure needed to affect different small mammal species.

## Conclusion

Small mammals are essential components of forested ecosystems that provide a variety of necessary functions and services. Understanding how small mammals influence forest function and biodiversity are significant ecological issues that affect conservation (Hallet et al. 2003). Intensively managed forests can support a diverse small mammal community if forest elements such as shrub cover, downed wood, and riparian zones are retained (Gomez and Anthony 1998, Carey and Harrington 2001, Cockle and Richardson 2003, Manning and Edge 2008, Lee 2012, this study). Small mammals generally adapt to perturbations at smaller scales (Middleton and Merriam 1983, VanDruff and Rowse 1986), if both habitat patches and surrounding matrix facilitate movement and stability of small mammal populations (Szacki and Liro 1991). Managers that manipulate localized habitat structures for small mammals within timber harvest areas and provide a mosaic of forest types over relatively small scales will most effectively manage small mammal populations to meet conservation and forest-regeneration goals.

## Supplementary Materials

Supplementary data are available at *Forest Science* online.

## Literature Cited


Amaranthus, M., J.M. Trappe, L. Bednar, and D. Arthur. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. *Can. J. For. Res.* 24:2157–2165.

Anderson, D.R., K.P. Burnham, G.C. White, and D.L. Otis. 1983. Density estimation of small-mammal populations using a trapping web and distance sampling methods. *Ecology* 64:674–680.

Aubry, K.B., M.J. Crites, and S.D. West. 1991. Regional patterns of small mammal abundance and community composition in Oregon and Washington. P. 285–294 in *Wildlife and vegetation of unmanaged Douglas-fir forests.* USDA Forest Service Gen. Tech. Rep. PNW-GTR-285, Pacific Northwest Research Station, Portland, OR.

Bagne, K.E., and D.M. Finch. 2010. Response of small mammal populations to fuel treatment and precipitation in a ponderosa pine forest, New Mexico. *Restor. Ecol.* 18:409–417.

Betts, M.G., A.W. Diamond, G.J. Forbes, K. Frego, J.A. Loo, B. Matson, M.R. Roberts, M. Villard, R. Wissink, and L. Wuest. 2005. Plantations and biodiversity: A comment on the debate in New Brunswick. *Forest. Chron.* 81:265–269.

Block, W.M., J.L. Ganey, P.E. Scott, and R. King. 2005. Prey ecology of Mexican spotted owls in pine–oak forests of northern Arizona. *J. Wildlife Manage.* 69:618–629.

Block, W.M., R.E. Russell, and J.L. Ganey. 2011. Occupancy and habitat associations of four species of sciurids in ponderosa pine–Gambel oak (*Pinus ponderosa–Quercus gambelii*) forests in Northern Arizona. *Southwestern Nat.* 56:193–203.

Boellstorff, D.E., and D.H. Owings. 1995. Home range, population structure, and spatial organization of California ground squirrels. *J. Mammal.* 76:551–561.

Borrecco, J.E. 1976. Controlling damage by forest rodents and lagomorphs through habitat manipulation. In *Proceedings: Seventh Vertebrate Pest Conference*, C.S. Siebe (ed.). March 9–11, Monterey, CA.

Bowman, J., G. Forbes, and T. Dilworth. 2001. Landscape context and small-mammal abundance in a managed forest. *Forest Ecol. Manag.* 140:249–255.

Broadbooks, H.E. 1970. Home ranges and territorial behavior of the yellow-pine chipmunk, *Eutamias amoenus*. *J. Mammal.* 51:310–326.

Buckner, C.H. 1966. Populations and ecological relationships of shrews in tamarack bogs of southeastern Manitoba. *J. Mammal.* 47:181–194.

Burnham, K.P., and D.R. Anderson. 2002. *Model selection and multimodel inference: A practical information-theoretic approach.* Springer Science & Business Media, New York, NY.

Carey, A.B., and C.A. Harrington. 2001. Small mammals in young forests: Implications for management for sustainability. *Forest Ecol. Manag.* 154:289–309.

Carey, A.B., S.P. Horton, and B.L. Biswell. 1992. Northern spotted owls: Influence of prey base and landscape character. *Ecol. Monogr.* 62:223–250.

Carey, A.B., and M.L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecol. Appl.* 5:336–352.

Chappell, M.A. 1978. Behavioral factors in the altitudinal zonation of chipmunks (*Eutamias*). *Ecology* 59:565–579.

Christensen, G.A., K.L. Waddell, S.M. Stanton, and O. Kuegler. 2016. *California's forest resources: Forest inventory and analysis, 2001–2010.* USDA Forest Service Gen. Tech. Rep., PNW-GTR-913, Pacific Northwest Research Station, Portland, OR. 293 p.

Cockle, K.L., and J.S. Richardson. 2003. Do riparian buffer strips mitigate the impacts of clearcutting on small mammals? *Biol. Conserv.* 113:133–140.

Converse, S.J., W.M. Block, and G.C. White. 2006. Small mammal population and habitat responses to forest thinning and prescribed fire. *Forest Ecol. Manag.* 228:263–273.

Côté, M., J. Ferron, and R. Gagnon. 2003. Impact of seed and seedling predation by small rodents on early regeneration establishment of black spruce. *Can. J. Forest. Res.* 33:2362–2371.

Cranford, J.A. 1977. Home range and habitat utilization by *Neotoma fuscipes* as determined by radiotelemetry. *J. Mammal.* 58:165–172.

Cross, S.P. 1985. Responses of small mammals to forest riparian perturbations. P. 269–275 in *Riparian ecosystems and their management: Reconciling conflicting uses*, Johnson, R.R., C.D. Ziebell, D.R. Patten, P.F. Ffolliot, and R.H. Hamre (tech. coords.). USDA Forest Service Gen. Tech. Rep., RM-120.

Demarais, S., J.P. Verschuyl, G.J. Roloff, D.A. Miller, and T.B. Wigley. 2017. Tamm review: Terrestrial vertebrate biodiversity and intensive forest management in the US. *Forest Ecol. Manag.* 385:308–330.

Dorazio, R.M. 2013. Bayes and empirical Bayes estimators of abundance and density from spatial capture–recapture data. *PLoS One* 8:e84017.

Doyle, A. 1990. Use of riparian and upland habitats by small mammals. *J. Mammal.* 71:14–23.

Eder, T., and G. Ross. 2005. *Mammals of California*. Lone Pine Publishing, Auburn, WA.

Elkinton, J.S., W.M. Healy, J.P. Buonaccorsi, G.H. Boettner, A.M. Hazzard, and H.R. Smith. 1996. Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* 77:2332–2342.

Evans, F., and R. Holdenried. 1943. A population study of the Beechey ground squirrel in central California. *J. Mammal.* 24:231–260.

Fantz, D.K., and R.B. Renken. 2005. Short-term landscape-scale effects of forest management on *Peromyscus* spp. mice within Missouri Ozark forests. *Wildlife Soc. B.* 33:293–301.

Fehmi, J.S., S.E. Russo, and J.W. Bartolome. 2005. The effects of livestock on California ground squirrels (*Spermophilus beecheyii*). *Rangeland Ecol. Manag.* 58:352–359.

Fitch, H.S. 1948. Ecology of the California ground squirrel on grazing lands. *Am. Midl. Nat.* 39:513–596.

Franklin, A.B. 1997. *Factors affecting temporal and spatial variation in Northern Spotted Owl populations in northwest California*. Dissertation, Colorado State University, Fort Collins, CO.

Gashwiler, J.S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. *Ecology* 51:1018–1026.

Gomez, D.M., and R.G. Anthony. 1998. Small mammal abundance in riparian and upland areas of five seral stages in western Oregon. *Northwest Sci.* 72:293–302.

Gottesman, A.B., P.R. Krausman, M.L. Morrison, Y. Petryszyn, and L.K. Ammerman. 2004. Movements and home range of brush mice. *Southwestern Nat.* 49:289–294.

Gray, S.M., A.K. Killion, G.J. Roloff, B.P. Dotters, and T.T. Engstrom. 2016. Fine-scale correlates of small mammal abundance in industrial forests of northern California. *Northwest Sci.* 90:301–314.

Grinnell, J. 1918. Natural history of the ground squirrels of California. *Mon. Bull. Calif. State Comm. Hortic.* 7:597–708.

Hall, E.R. 1946. *Mammals of Nevada*. University of California Press, Berkeley, CA.

Hallet, J.G., M.A. O'Connell, and C.C. Maguire. 2003. Ecological relationships of terrestrial small mammals in western coniferous forests. P. 120–156 in *Mammal community dynamics: Management and conservation in the coniferous forests of Western North America*, Zabel, C.J., and R.G. Anthony (eds.). Cambridge University Press, New York, NY.

Hamilton, B.T., B.L. Roeder, K.A. Hatch, D.L. Eggett, and D. Tingey. 2015. Why is small mammal diversity higher in riparian areas than in uplands? *J. Arid Environ.* 119:41–50.

Innes, R.J., D.H. Van Vuren, D.A. Kelt, M.L. Johnson, J.A. Wilson, and P.A. Stine. 2007. Habitat associations of dusky-footed woodrats (*Neotoma fuscipes*) in mixed-conifer forest of the northern Sierra Nevada. *J. Mammal.* 88:1523–1531.

Jacob, J. 2008. Response of small rodents to manipulations of vegetation height in agro-ecosystems. *Integr. Zool.* 3:3–10.

Kalies, E., B.G. Dickson, C.L. Chambers, and W. Covington. 2012. Community occupancy responses of small mammals to restoration treatments in ponderosa pine forests, northern Arizona, USA. *Ecol. Appl.* 22:204–217.

Kirkland, G.L. 1990. Patterns of initial small mammal community change after clearcutting of temperate North American forests. *Oikos* 59:313–320.

Lee, S. 2012. Association between coarse woody debris and small mammals and insectivores in managed forests. *J. Ecol. Environ.* 35:189–194.

Lee, S.D. 2004. Population dynamics and demography of deermice (*Peromyscus maniculatus*) in heterogeneous habitat: Role of coarse woody debris. *Pol. J. Ecol.* 52:55–62.

Lehmkuhl, J.F., R.D. Peffer, and M.A. O'Connell. 2008. Riparian and upland small mammals on the east slope of the Cascade Range, Washington. *Northwest Sci.* 82:94–107.

Lindenmayer, D.B., and J.F. Franklin. 2002. *Conserving forest biodiversity: A comprehensive multiscaled approach*. Island Press, Washington DC.

Lust, N., B. Muys, and L. Nachtergale. 1998. Increase of biodiversity in homogeneous Scots pine stands by an ecologically diversified management. *Biodivers. Conserv.* 7:249–260.

Manning, J.A., and W.D. Edge. 2004. Small mammal survival and downed wood at multiple scales in managed forests. *J. Mammal.* 85:87–96.

Manning, J.A., and W.D. Edge. 2008. Small mammal responses to fine woody debris and forest fuel reduction in southwest Oregon. *J. Wildlife Manage.* 72:625–632.

Marsh, R.E. 1998. Historical review of ground squirrel crop damage in California. *Int. Biodeter. Biodegr.* 42:93–99.

Maser, C., J.M. Trappe, and R.A. Nussbaum. 1978. Fungal–small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* 59:799–809.

McComb, W.C. 2003. Ecology of coarse woody debris and its role as habitat for mammals. P. 374–404 in *Mammal community dynamics: Management and conservation in the coniferous forests of western North America*, Zabel, C.J., and R.G. Anthony (eds.). Cambridge University Press, New York, NY.

McComb, W.C., K. McGarigal, and R.G. Anthony. 1993. Small mammal and amphibian abundance in streamside and upslope habitats of mature Douglas-fir stands, western Oregon. *Northwest Sci.* 67:7–15.

Meserve, P.L. 1974. Ecological relationships of two sympatric woodrats in a California coastal sage scrub community. *J. Mammal.* 55:442–447.

Middleton, J., and G. Merriam. 1983. Distribution of woodland species in farmland woods. *J. Appl. Ecol.* 20:625–644.

Mohr, J.A., C. Whitlock, and C.N. Skinner. 2000. Postglacial vegetation and fire history, eastern Klamath Mountains, California, USA. *Holocene* 10:587–601.

Murray, K.F., and A.M. Barnes. 1969. Distribution and habitat of the woodrat, *Neotoma fuscipes*, in northeastern California. *J. Mammal.* 50:43–48.

Ordeñana, M.A., D.H. Van Vuren, and J.P. Draper. 2012. Habitat associations of California ground squirrels and Botta's pocket gophers on levees in California. *J. Wildlife Manage.* 76:1712–1717.

Ostfeld, R.S., R.H. Manson, and C.D. Canham. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78:1531–1542.

Oswalt, S.N., W.B. Smith, P.D. Miles, and S.A. Pugh. 2014. *Forest resources of the United States, 2012: A technical document supporting the Forest Service 2015 update of the RPA Assessment.* USDA Forest Service Gen. Tech. Rep. WO-91, USDA Forest Service, Washington Office, Washington, DC.

Owings, D.H., and M. Borchert. 1975. Correlates of burrow location in Beechey ground squirrels. *Great Basin Nat.* 35:402–404.

Owings, D.H., M. Borchert, and R. Virginia. 1977. The behaviour of California ground squirrels. *Anim. Behav.* 25:221–230.

Parks, C.G., S.R. Radosevich, B.A. Endress, B.J. Naylor, D. Anzinger, L.J. Rew, B.D. Maxwell, and K.A. Dwire. 2005. Natural and land-use history of the Northwest mountain ecoregions (USA) in relation to patterns of plant invasions. *Perspect. Plant Ecol.* 7:137–158.

Parmenter, R.R., and J.A. MacMahon. 1989. Animal density estimation using a trapping web design: Field validation experiments. *Ecology* 70:169–179.

Peterken, G.F. 1996. *Natural woodland ecology and conservation in northern temperate regions.* Cambridge University Press, Cambridge, UK.

R Development Core Team. 2013. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna.

Sharples, F.E. 1983. Habitat use by sympatric species of *Eutamias*. *J. Mammal.* 64:572–579.

Skinner, C.N., A.H. Taylor, and J.K. Agee. 2006. Klamath Mountains bioregion. P. 170–194 in *Fire in California's ecosystems*, Sugihara, N.G., J.W. van Wagtendonk, J. Fites-Kaufmann, K.E. Shaffer, and A.E. Thode (eds.). University of California Press, Berkeley, CA.

Sleeter, B.M., and J.P. Calzia. 2011. *Klamath mountains ecoregion.* Available online at https://pubs.usgs.gov/pp/1794/a/chapters/pp1794a_chapter13.pdf; last accessed April 14, 2017.

Smith, M.H., J.B. Gentry, and J. Pinder. 1974. Annual fluctuations in small mammal population in an eastern hardwood forest. *J. Mammal.* 55:231–234.

Smith, R.B., M.Z. Peery, R.J. Gutiérrez, and W.S. Lahaye. 1999. The relationship between spotted owl diet and reproductive success in the San Bernardino Mountains, California. *Wilson Bull.* 111:22–29.

Sullivan, T.P. 1979. Demography of populations of deer mice in coastal forest and clear-cut (logged) habitats. *Can. J. Zool.* 57:1636–1648.

Sullivan, T.P., D.S. Sullivan, P.M. Lindgren, and D.B. Ransome. 2012. If we build habitat, will they come? Woody debris structures and conservation of forest mammals. *J. Mammal.* 93:1456–1468.

Szacki, J., and A. Liro. 1991. Movements of small mammals in the heterogeneous landscape. *Landsc. Ecol.* 5:219–224.

Terman, C.R. 1966. Population fluctuations of *Peromyscus maniculatus* and other small mammals as revealed by the North American census of small mammals. *Am. Midl. Nat.* 76:419–426.

Tevis Jr., L. 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. *J. Mammal.* 34:316–324.

Tevis Jr., L. 1956. Responses of small mammal populations to logging of Douglas-fir. *J. Mammal.* 37:189–196.

USDA Forest Service. 1981. *CALVEG: A classification of California vegetation.* USDA Forest Service, California Region, San Francisco, CA.

VanDruff, L.W., and R.N. Rowse. 1986. Habitat association of mammals in Syracuse, New York. *Urban Ecol.* 9:413–434.

Ward, J.P.J. 2001. *Ecological responses by Mexican spotted owls to environmental variation in the Sacramento Mountains, New Mexico*. Dissertation, Colorado State University, Fort Collins, CO.

Waters, J.R., and C.J. Zabel. 1998. Abundances of small mammals in fir forests in northeastern California. *J. Mammal.* 79:1244–1253.

Waters, J.R., C.J. Zabel, K.S. McKelvey, and H.H. Welsh Jr. 2001. Vegetation patterns and abundances of amphibians and small mammals along small streams in a northwestern California watershed. *Northwest Sci.* 75:37–52.

Williams, P.J., S.A. Whitmore, and R. Gutiérrez. 2014. Use of private lands for foraging by California spotted owls in the central Sierra Nevada. *Wildlife Soc. B.* 38:705–709.