

Community occupancy responses of small mammals to restoration treatments in ponderosa pine forests, northern Arizona, USA

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Abstract. In western North American conifer forests, wildfires are increasing in frequency and severity due to heavy fuel loads that have accumulated after a century of fire suppression. Forest restoration treatments (e.g., thinning and/or burning) are being designed and implemented at large spatial and temporal scales in an effort to reduce fire risk and restore forest structure and function. In ponderosa pine (*Pinus ponderosa*) forests, predominantly open forest structure and a frequent, low-severity fire regime constituted the evolutionary environment for wildlife that persisted for thousands of years. Small mammals are important in forest ecosystems as prey and in affecting primary production and decomposition. During 2006–2009, we trapped eight species of small mammals at 294 sites in northern Arizona and used occupancy modeling to determine community responses to thinning and habitat features. The most important covariates in predicting small mammal occupancy were understory vegetation cover, large snags, and treatment. Our analysis identified two generalist species found at relatively high occupancy rates across all sites, four open-forest species that responded positively to treatment, and two dense-forest species that responded negatively to treatment unless specific habitat features were retained. Our results indicate that all eight small mammal species can benefit from restoration treatments, particularly if aspects of their evolutionary environment (e.g., large trees, snags, woody debris) are restored. The occupancy modeling approach we used resulted in precise species-level estimates of occupancy in response to habitat attributes for a greater number of small mammal species than in other comparable studies. We recommend our approach for other studies faced with high variability and broad spatial and temporal scales in assessing impacts of treatments or habitat alteration on wildlife species. Moreover, since forest planning efforts are increasingly focusing on progressively larger treatment implementation, better and more efficiently obtained ecological information is needed to inform these efforts.

Key words: *ecological restoration; evolutionary environment; Microtus mogollonensis; Neotoma mexicana; occupancy modeling; Peromyscus maniculatus; Pinus ponderosa; Sciurus aberti; Spermophilus lateralis; Spermophilus variegates; Tamias cinereicollis; Thomomys bottae.*

INTRODUCTION

Ecological restoration is the process of recovering an ecosystem that has degraded, often due to human pressures and disturbance (Society for Ecological Restoration International Science and Policy Working Group 2004). Restoration projects are among the most extensive conservation efforts worldwide, and are being implemented at increasingly larger scales (Holl et al. 2003) because (1) of the sheer size of degraded areas, such as tropical forests (Lamb et al. 2005); (2) of the complexity and scale of the degrading factors, such as with coral reef loss (Gardner et al. 2003); and (3) many ecological processes occur at the landscape scale, such as migration, dispersal, and hydrologic and nutrient cycles

(Noss 1990, Saunders et al. 1991). Dry conifer forests across western North America have been degrading since at least 1890, when Euro-American settlement introduced multiple ongoing pressures, such as fire suppression, grazing, and logging (Covington and Moore 1994b). These pressures have contributed to forest stands with high densities of small-diameter trees and heavy fuel loads (Taylor and Skinner 1998, Fry and Stephens 2006), in which wildfires are increasing in frequency and severity (Westerling et al. 2006).

To reduce the threat of stand-replacing wildfire, ecological restoration treatments are being implemented in forests that were once fire adapted. The principal objective of these activities is to restore forests to presettlement or “reference” conditions using mechanical thinning and burning treatments (hereafter, treatments), after which the natural fire regime can be reintroduced (Moore et al. 1999, Noss et al. 2006b). The frequent, low-severity fires that used to occur would

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maintain an open forest structure by removing under-story trees, thereby preventing heavy fuel accumulation (Fulé et al. 1997, Everett et al. 2000). These treatments are also an effort to restore overall ecosystem function, by increasing rates of decomposition and nutrient cycling, water availability, carbon storage, plant biodiversity, and populations of native wildlife species (Allen et al. 2002, Finkral and Evans 2008, Boerner et al. 2009, Schwilk et al. 2009). As wildfire risk and associated economic costs escalate (Snider et al. 2006), restoration treatments are being implemented at increasingly larger scales in the western United States. For example, as part of the 2010 Collaborative Forest Landscape Restoration Project (Omnibus Public Land Management Act 2009), nine national forests across the West are planning treatments at scales of tens of thousands of hectares. As the size and pace of treatments increase, scientists and stakeholders need information on the effectiveness of treatments in restoring multiple ecosystem components, including wildlife, at large temporal and spatial scales (Sisk et al. 2006).

Measuring the success of restoration usually involves comparing restored sites to reference conditions. In the absence of data on reference conditions for wildlife populations as a baseline, approximating the evolutionary environment is likely the best approach for restoring wildlife populations (MacMahon and Jordan 1994, Moore et al. 1999). The evolutionary environment is defined as the range of abiotic and biotic conditions that have exerted selection pressure on and are critical to the survival of wildlife populations (Noss and Csuti 1994). Particularly at large scales, restoring the evolutionary environment may be more feasible than trying to meet specific habitat requirements for single or small groups of species (Moore et al. 1999, Lindenmayer et al. 2002). In fire-adapted conifer forests across western North America, wildlife likely was adapted to fire regimes that altered habitat at multiple spatial and temporal scales (Kennedy and Fontaine 2009). The subsequent degradation of these forests has reduced horizontal and structural diversity of habitat, which has had negative consequences for wildlife species dependent on the evolutionary environment (Carey 2003). At the same time, some species have expanded their ranges since presettlement times and are now dependent on dense forests (Battin and Sisk 2003, Chambers and Germaine 2003). For example, Brown and Davis (1998) determined that 34 grassland animal species have experienced extirpation or reduction of their ranges, and 55 forest species have expanded their ranges since 1890 in the American Southwest.

Small mammal community composition varies across fire adapted conifer forests, but typically includes tree squirrels (*Sciurus* sp.), ground squirrels (*Spermophilus* sp.), voles (*Microtus* and *Clethrionomys* sp.), gophers (*Thomomys* sp.), chipmunks (*Tamias* sp.), mice (*Peromyscus* sp.), woodrats (*Neotoma* sp.), and shrews (*Sorex* sp.; Kays and Wilson 2002, Converse et al. 2006c,

Zwolak 2009). In forest ecosystems, small mammals are important for recycling nutrients by processing vegetation, dispersing fungal spores and seeds, and aerating and turning soils while digging (Cork and Kenagy 1989, Boal and Mannan 1994). They also provide a substantial part of the prey base for multiple mammalian and avian predators, including federally threatened northern and Mexican spotted owls (*Strix occidentalis caurina* and *S. o. lucida*; Rosenberg et al. 2003, Block et al. 2005). The small body sizes and high reproductive rates of small mammals result in populations that generally respond quickly to disturbance and habitat alteration (MacArthur and Wilson 1967, Brown and Ernest 2002). Thus, small mammals can be indicators of changes to forest structure that result from restoration treatments. For species within a given functional group, we would expect to see both positive and negative responses to treatment (e.g., Dickson et al. 2009, Kalies et al. 2010), since each species necessarily occupies a unique habitat niche (MacArthur and Levins 1967, Converse et al. 2006a). However, the only large-scale small mammal study examining responses to restoration treatments in conifer stands found mostly neutral responses to thinning at the genus and species level (Converse et al. 2006c).

In the Southwest, reference conditions are particularly well understood (Cooper 1960, White 1985, Fulé et al. 1997). In ponderosa pine (*Pinus ponderosa*) forests, which cover >12 million hectares of western North America, the evolutionary environment persisted from about 10 000 years ago, when ponderosa pine trees retreated to the high plateaus and mountains following the last glacial period, up until approximately 1890, which brought Euro-American settlement and associated land management impacts (Covington 2003). This environment included a frequent, low-severity fire regime and open forest structure; additionally, a diversity of habitat components including clumps of Gambel oak (*Quercus gambelii*), snags, and down wood, were probably created and maintained by fire in a patchy distribution (Spies and Turner 1999). We investigated the response of the small mammal community to large-scale forest restoration treatments in ponderosa pine forests in Arizona, and specifically to components of the evolutionary environment. We hypothesized that the occupancy rates for golden-mantled ground squirrels (*Spermophilus lateralis*), Mogollon voles (*Microtus mogollonensis*), and pocket gophers (*Thomomys bottae*) would respond positively to treatment and/or open forest structure; tassel-eared squirrels (*Sciurus aberti*) would respond negatively as dense-forest obligates; and Mexican woodrats (*Neotoma mexicana*), gray-collared chipmunks (*Tamias cinereicollis*), deer mice (*Peromyscus maniculatus*), and rock squirrels (*Spermophilus variegates*) would be tied to other habitat components including down wood, slash, snags, shrubs, oak, and rocks (Table 1). We also hypothesized that no single treatment type would benefit

TABLE 1. Known responses of small mammal species to forest structure, treatment, and other habitat features in southwestern ponderosa pine. The table also reports the source(s) and our hypothesized response to restoration treatments.

Species and habitat relationships	Source(s)	Hypothesized occupancy response to restoration treatments
Golden-mantled ground squirrel		Positive
↑ open forest structure, 0 tree density, 0 vegetation cover	1, 2, 3	
0 (4) or ↑ thinning or thin/burn	4	
0 down wood, 0 shrub cover	3	
Mogollon vole (<i>Microtus</i> sp.)		Positive
↑ open forest structure, herbaceous understory	5, 6	
↑ (2) thinning	7, 8	
Botta's pocket gopher (<i>Thomomys</i> sp.)		Positive
↑ open forest structure, herbaceous understory	9, 10	
↑ thinning	11	
Tassel-eared squirrel		Negative
↑ (5) pine basal area	12, 13, 14, 15, 16	
↑ (3) interlocking canopy trees	14, 15, 17	
↑ quadratic mean diameter, canopy cover	14, 16	
↑ or 0 tree density	12, 13	
↓ (2) selective harvest, ↓ (2) shelterwood, ↓ clearcut	13, 14, 15, 18, 19	
↑ (3) large trees, ↓ saplings, 0 oak	12, 13, 15, 17, 20	
Mexican woodrat (<i>Neotoma</i> sp.)		Neutral
0 tree density	3	
0 (2) thinning	3, 8	
↑ or ↓ down wood, ↑ slash, ↑ or 0 shrubs	3, 11, 21	
0 oak, ↑ rocks, slope	11, 21	
Gray-collared chipmunk (<i>Tamias</i> sp.)		Neutral
↓ tree density, 0 vegetation cover	3	
0 (6) or ↑ (3) or ↓ (2) thinning or thin/burn	4, 7, 8, 22	
0 shrubs, ↑ down wood	3	
Deer mouse		Neutral
↓ tree density, 0 vegetation cover	3	
0 (8) or ↑ (4) or ↓ (2) thinning or thin/burn	4, 7, 8, 23, 24, 25	
↑ large trees, ↑ (3) or 0 down wood, ↑ snags	3, 11, 21, 26	
0 oak, 0 rock, 0 or ↓ shrubs	3, 21	
Rock squirrel		Neutral
↑ oak trees	27	
↑ rocks, slope, bare ground	27	

Notes: An up arrow indicates a positive response, a down arrow negative, 0 neutral; all responses are in terms of density or abundance. A parenthetical number following a response indicates the number of studies that support that response, and no parentheses indicates one study.

Sources: 1, McKeever 1964; 2, Bartels and Thompson 1993; 3, Converse et al. 2006a; 4, Converse et al. 2006c; 5, Chambers and Doucett 2008; 6, Yarborough and Chambers 2007; 7, Wampler et al. 2008; 8, Bagne and Finch 2009; 9, Huntly and Inouye 1988; 10, Hoffmeister 1986; 11, Goodwin and Hungerford 1979; 12, Ratcliff et al. 1975; 13, Patton et al. 1985; 14, Dodd et al. 2003; 15, Dodd et al. 2006; 16, Prather et al. 2006; 17, Patton 1977; 18, A. H. Trowbridge and L. L. Lawson, unpublished manuscript; 19, Pederson et al. 1987; 20, Patton and Green 1970; 21, Block et al. 2005; 22, Lowe et al. 1978; 23, Reading 2001; 24, Roberts 2003; 25, Amacher et al. 2008; 26, Chambers 2002; 27, Ortega 1987.

all species, but the community perspective would reveal tradeoffs (positive and negative responses) among species in response to habitat alteration.

Large-scale design and implementation of forest restoration treatments necessitates a habitat-focused, multi-species approach to wildlife management and monitoring, due to the time and cost required by single-species approaches (Lambeck 1997, Lindenmayer et al. 2002). We used occupancy modeling, an analytical

technique that allows for a rapid assessment of multiple sites, yielding probabilities of occupancy rather than information on population dynamics, such as survival, reproduction, and population size (MacKenzie et al. 2006). This technique has lesser demands for field data, and may be more appropriate for assessing multiple wildlife responses to habitat alteration at large spatial and temporal scales compared to traditional mark-recapture methods. Our specific objectives were to (1)

quantify the importance of treatment and habitat attributes on occupancy for each individual species and collectively, (2) make inferences from the relationships between key attributes and species occupancy to better inform management decisions, and (3) assess the efficacy of occupancy modeling by determining if treatments and habitat attributes affect species occupancy more than background interannual variation.

METHODS

Study area

One study area was located on the Coconino National Forest, 8 km southwest of Flagstaff, Arizona, in the ponderosa pine-dominated forests of the wildland-urban interface (Fig. 1). Historically, this 18 500-ha area experienced a variety of forest management practices, including selective harvest (100+ years ago), commercial thinning (11–23 years ago, average 17.3), fuels reduction and restoration treatments (1–7 years ago, average 2.9), and no treatment. We established an additional 4800-ha study area on the Kaibab National Forest north of Grand Canyon National Park, Arizona, to capture additional untreated forested areas. Within a geographic information system (GIS; ArcGIS v9.3, ESRI, Redlands, California, USA), we overlaid a 500-m resolution lattice on both study areas to locate prospective sampling points. We eliminated points that fell within private lands and non-forested patches >1 ha, or were located >500 m from a road. From the remaining points, we randomly selected 110 sampling points (100 on the Coconino, 10 on the Kaibab), with approximately half in recent (<10 years) treatments and half with older (>11 years) or no treatments, and then located and permanently marked them in the field using a global positioning system. All treatments consisted of mechanical harvest (not fire) and resulted in a range of forest structure conditions determined by the initial prescriptions and methods of implementation, which varied greatly across the study areas; thus, we focused on time since treatment, density of trees removed, and resulting basal area as the primary metrics to describe treatments.

Data collection

Small mammal sampling.—We used each of the 110 sampling points as the center of a trapping “site.” At each site we centered a 5×5 square trap grid which consisted of 25 Sherman traps (model LNATDG; H. B. Sherman Traps, Tallahassee, Florida, USA) with 20-m spacing, with a 3×3 grid overlaid with nine Tomahawk traps (model 202; Tomahawk Live Trap, Hazelhurst, Wisconsin, USA), one at every other grid intersection. Including a 20-m buffer around the trap grid, total site sampling area was $14\,400\text{ m}^2$ (1.4 ha). We trapped small mammals at each site during the summers of 2006–2009, over a 10-week period between late June and late August. We left both Sherman and Tomahawk traps open overnight, but closed the Sherman traps during the day to prevent animals from overheating. We checked

traps twice daily over a three-day period, which resulted in three nighttime and three daytime trapping sessions. We sampled for Botta’s pocket gopher presence using an open-hole test, disturbing all gopher mounds located at the site with a shovel; we considered the species to be present if a mound was repaired within 24 hours (Smallwood and Erickson 1995). We attempted to assess all terrestrial small mammal species (<3000 g) but were unable to detect lagomorphs or shrews. We determined the number of surveys and relevant habitat and detection covariates at each site using data from our first year (2006).

Vegetation sampling.—We established an 11.3 m radius circular overstory plot (400 m^2) at the site center and measured slope (degrees), total number of stumps, and species and diameter at breast height (dbh) for trees ≥ 1.4 m tall. At the site center, we also established a subplot of 3.6 m radius (40 m^2), within which we assessed species, percent cover, and height class for herbaceous plants, shrubs, and trees <1.4 m. At each subplot and in four additional 40-m^2 plots (located on the trapping grid at each cardinal direction), we measured the relative percent cover of bare ground, stumps and coarse woody debris, litter, and rocks. At the site center, we established a 20-m transect in a random direction and along it recorded the width of each piece of wood >7.5 cm (Brown et al. 1982). Within the entire site, we counted the number of slash piles, and used our observations and state and federal historical records to determine the age of each treatment and the number of years the slash piles were intact before being burned, which always occurred within four years of thinning treatment. All vegetation sampling was conducted in June of each year, immediately prior to small mammal sampling activities.

Data analysis

Habitat and detection covariates.—At each site, we quantified overstory and understory characteristics that we hypothesized could affect occupancy (hereafter, our “habitat covariates”), based on the existing literature and our own field observations. For each site, we calculated slope, pine and oak basal area (m^2/ha), large tree density (>40, >50, and >60 cm dbh classes; number/ha), snag density (all snags and >40, >50, >60 cm dbh classes; number/ha), and the proportion of trees removed by any method of harvesting (Table 1). We also calculated understory plant species richness, percent of vegetation >40 cm in height (i.e., shrub cover), average percent cover of each substrate, and volume of down wood. We determined the number of slash piles/site, the number of years piles were left intact, and the time (years) since treatment. We also calculated treatment size using maps of the treatment areas provided by the implementing federal and state agencies, or by delineating the treatment area using aerial photos and ArcGIS. For each species, we pooled detection histories from all four years of sampling and used “year”

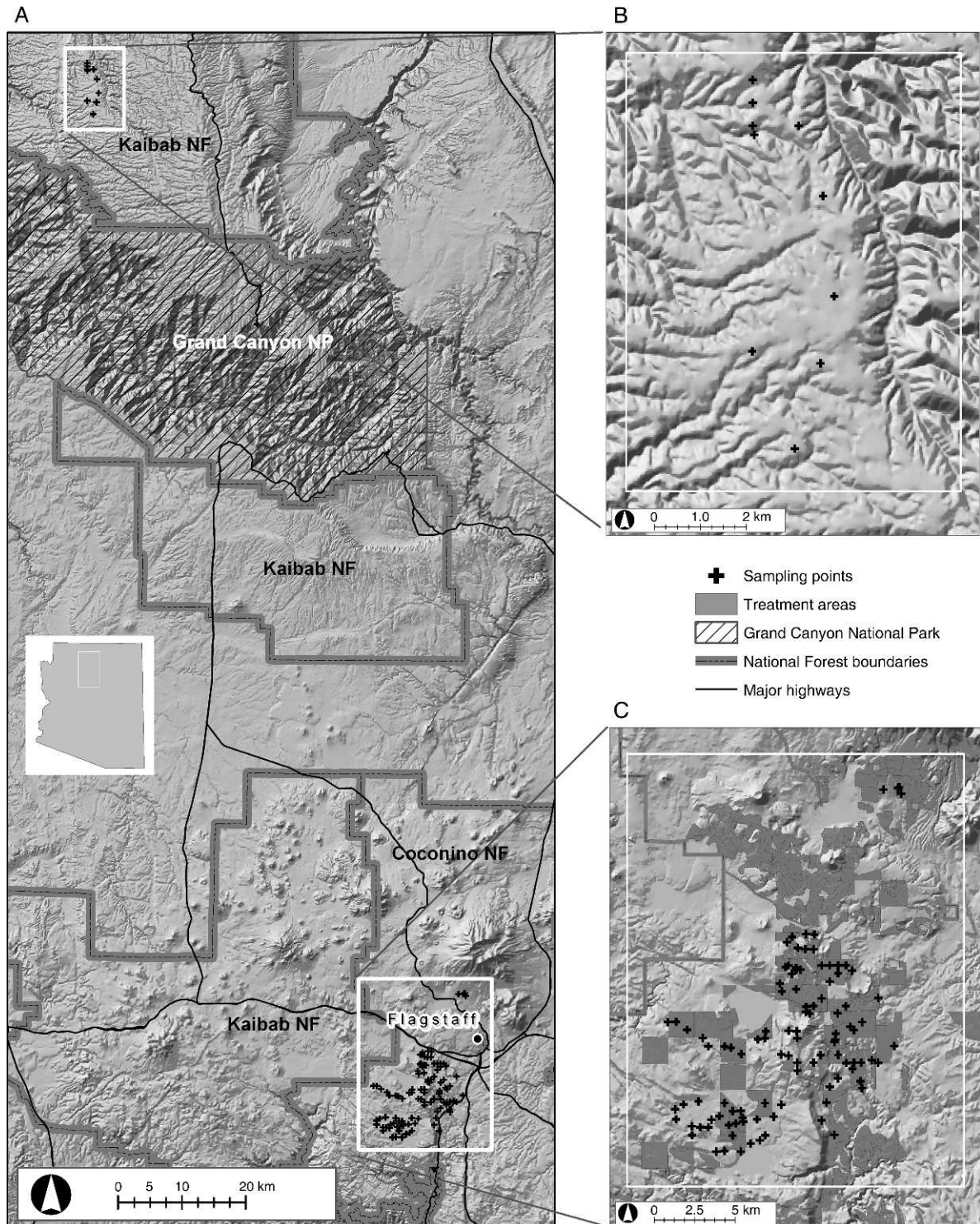


FIG. 1. (A) Location of the two study areas in northern Arizona, USA, with sampling points (sites) indicated by crosses. One study area (B) was on the Kaibab National Forest ($n = 10$ sites) and one (C) on the Coconino National Forest ($n = 98$ sites). Sites were sampled multiple times for a total sample size of $n = 294$ samples over the four-year study.

as a covariate (sensu Rodhouse et al. 2010). We used a binary covariate that discriminated the two study areas (North Kaibab and Coconino).

Covariates that we hypothesized could cause heterogeneity in detection probability (hereafter, our “detection covariates”) included temperature, precipitation, year, week, and survey (defined as which of the three days the site was sampled). Temperature and precipitation can affect activity levels and trapability of animals (Getz 1961). Year and week can capture this variability plus other attributes that are difficult to measure, such as changing resource availability and moon phase. Survey is important because some species will avoid traps after first capture, while others will continue to visit the traps for food and shelter (Getz 1961). We attempted to control for weather-related covariates by timing the trapping session to occur after the beginning of the monsoons; however, we still considered as detection covariates the maximum daily temperature, minimum daily temperature, average daily humidity, and average daily precipitation that was recorded prior to the day or night sampling session. We obtained these data from stations 30–50 km away from each study area.

We standardized all continuous habitat and detection covariates, and diagnosed univariate correlations and multicollinearity using a correlation matrix and variance inflation factors (VIF), respectively. When we observed univariate correlations >0.60 , or VIF >10.0 (Neter et al. 1996), we combined these covariates using a principal components analysis (PCA; implemented in JMP V8.0, SAS Institute Inc., Cary, North Carolina, USA).

Preliminary analyses of covariates.—Using PCA, we combined four covariates into two (Table 1). We created a new covariate “treatment” (eigenvalue = 1.6, explaining 80.0% of the total variance) which represents a range from old treatments that were selectively harvested or thinned at low intensity (in preparation for commercial harvest) with relatively few trees removed per hectare (negative values), to recent fuels reduction or restoration treatments with more trees removed per hectare (positive values). The new covariate “slash” (eigenvalue = 1.5, explaining 74.6% of the total variance) represents a range from no or few slash piles left onsite for a very short period of time (negative values), to many slash piles left on the ground for up to three years (positive values).

We also assessed correlations between detection covariates and found that week, survey, and year were correlated with maximum and minimum temperature, humidity, and precipitation. Since week, survey, and year encompass climatic conditions and other environmental conditions that are difficult to measure, we omitted the climatic covariates from further analysis.

Occupancy modeling and multi-model inference.—Simple, or “naïve,” estimates of occupancy can be calculated for a given site by dividing the total number of detections at that site by the total number of surveys; however, most species are detected imperfectly, so this

method can result in more biased estimates than those that account for detection probability and habitat covariates (MacKenzie et al. 2006). For each small mammal species detected on our sites, we used the single season occupancy modeling framework of MacKenzie et al. (2006) to estimate both detection probability, defined as the probability of detecting the species at a site if it is present, and occupancy, defined as the expected probability that a given site is occupied. We used year as a covariate, and assumed that all sites have the same probability of being occupied regardless of their occupancy state in the previous year.

In order to focus on the covariates that most influenced occupancy for multiple species, and to avoid overparameterizing our models (e.g., see Moore and Swihart 2005), we reduced our list of habitat covariates by building univariate models of each covariate and comparing each model against the null (i.e., intercept-only) model of occupancy for each species using Akaike’s information criterion adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002). We ranked model importance from highest to lowest according to differences (Δ) in their AIC_c values, and retained the covariate from any model that had a lower ΔAIC_c value than the null model for at least three species. We conducted these analyses using Program PRESENCE (version 2.4; Hines 2009).

Using the 10 retained covariates plus the study area covariate (for all species detected at both study areas), we constructed models for all subsets of covariates ($n = 1025$ subsets) for each species using Program MARK (White and Burnham 2010). We computed AIC_c values, ΔAIC_c values, and AIC weights (w_{ij} , weight of covariate i for species j ; Burnham and Anderson 2002). We ranked relative covariate importance by summing the AIC weights across all models in which a given covariate occurred, and used cumulative weights to rank relative covariate importance for each species. Since the larger the w_{ij} the more important covariate i is, relative to the other variables (Burnham and Anderson 2002), we considered $w_{ij} \geq 0.50$ indicative of a strong species occupancy response to the covariate (Barbieri and Berger 2004), $0.50 \geq w_{ij} \geq 0.30$ a moderate response, and $w_{ij} \leq 0.30$ a weak response. For each covariate, we averaged w_{ij} across small mammal species to estimate its community-level importance (Dickson et al. 2009). We also calculated model-averaged parameter estimates for each covariate to assess the direction of the response by each species and the community as a whole.

Spatial autocorrelation.—We investigated local-scale spatial autocorrelation in our site-level presence–absence data using logistic regression models for all species, for each year and region. These models included the 10 habitat covariates considered in our occupancy analyses. We used the GLIMMIX and VARIOGRAM procedures in SAS to estimate the residuals in each model, and used a Moran’s I statistic (Z) to determine if statistically significant ($P < 0.05$) spatial structuring was

present in our data. Only three of 30 models resulted in a statistically significant Z value. Thus, we decided that explicitly accounting for spatial autocorrelation in our occupancy models would overly complicate our ability to interpret the estimates and relative importance of our covariates, when little or no residual spatial structure was present in our data.

RESULTS

Small mammal sampling

Due to various logistical issues that occurred each year (e.g., impassable roads, areas closed due to fire risk, excessive heat), sampling effort varied among years. We sampled 19 sites in 2006 (pilot year), 96 in 2007, 96 in 2008, and 83 in 2009 ($n=294$). In each year, we detected the Mogollon vole, Mexican woodrat, deer mouse, tassel-eared squirrel, golden-mantled ground squirrel, rock squirrel, gray-collared chipmunk, and Botta's pocket gopher.

Detection probabilities

Detection probabilities for the eight species of small mammals ranged from 0.3 to 0.9 over four years (Fig. 2), which are considered adequate for occupancy analysis (MacKenzie and Royle 2005). The most parsimonious models of detection probability included the following covariates: survey for the golden-mantled ground squirrel, year for the deer mouse and tassel-eared squirrel, week for the Mogollon vole and Botta's pocket gopher, and none (null models) for the Mexican woodrat, rock squirrel, and gray-collared chipmunk.

Preliminary habitat covariate analyses

Our analysis identified nine covariates that did not perform better than the null model for at least three species, including treatment size, understory vegetation >40 cm high (percent shrub cover), understory vegetation species richness, slope, downed wood volume, two size classes of large trees, and two size classes of snags (Table 2). Thus, we retained 10 habitat covariates: pine basal area (m^2/ha), oak basal area (m^2/ha), understory vegetation (percent cover), rock (percent cover), large tree density (number of trees >50 cm dbh/ha), snag density (number of snags/ha), large snag density (number of snags >40 cm dbh/ha), slash, treatment, and year (Table 2). Pine basal area and understory vegetation were not highly correlated (-0.32) as other factors can affect understory vegetation cover, including livestock grazing which we did not otherwise quantify.

Occupancy probabilities

Forest structure was described in terms of pine basal area, understory vegetation cover, oak basal area, and large trees. Sites with higher pine basal area and lower understory vegetation cover were associated with a positive occupancy response from only tassel-eared squirrels and Mexican woodrats; rock squirrels responded negatively to both pine basal area and understory

vegetation, but positively to oak basal area (Table 3). Golden-mantled ground squirrels, Mogollon voles, Botta's pocket gophers, gray-collared chipmunks, and deer mice responded negatively in terms of occupancy to pine basal area and positively to vegetation cover (i.e., open forest structure; Table 3). All responses were moderate or strong. Three species responded strongly to oak basal area (rock squirrels, positively; Mogollon voles and golden-mantled ground squirrels, negatively), and two moderately (tassel-eared squirrel, positively; deer mouse, negatively; Table 3). Large tree (>50 cm dbh) density elicited the most consistent response across species of all the covariates; all but Mogollon voles responded positively, with all species exhibiting moderate to strong responses (Table 3).

Five species (golden-mantled ground squirrel, Mogollon vole, gray-collared chipmunk, deer mouse, rock squirrel) responded positively in terms of occupancy to treatment, and three responded negatively (Botta's pocket gopher, tassel-eared squirrel, Mexican woodrat); all responses were moderate or strong (Table 3). Only Botta's pocket gopher has a consistent response to both pine basal area and treatment; i.e., it responded positively to open forest structural conditions, but negatively to the treatment that reduces tree basal area and density.

Other habitat covariates assessed included slash, snags, and rock cover. All species but two (gray-collared chipmunk and rock squirrel) responded positively in terms of occupancy to slash quantity and duration, although only tassel-eared squirrels and Mexican woodrats demonstrated a moderate response and golden-mantled ground squirrels a strong response (Table 3). Only one species responded strongly to snag density (gray-collared chipmunks; negatively) and three moderately (Botta's pocket gopher, tassel-eared squirrel, Mexican woodrat; negatively), but five species responded strongly to large snag (>40 cm dbh) density (Mogollon vole, gray-collared chipmunk, deer mouse, positively; golden-mantled ground squirrels and rock squirrels, negatively; Table 3). Two species responded strongly to rock cover (Mogollon voles and deer mice, positively) and four moderately (Mexican woodrat, positively; golden-mantled ground squirrel, Botta's pocket gopher, tassel-eared squirrel, negatively; Table 3).

Golden-mantled ground squirrels and rock squirrels had strong occupancy responses to year, and Mogollon voles, tassel-eared squirrels, gray-collared chipmunks, and deer mice had moderate responses (Table 3). Gray-collared chipmunks had the highest rates of occupancy and Mexican woodrats the lowest across all sites (Fig. 3).

Community-level response

For the community, the habitat covariates from most to least importance (based on average w_{ij}) in predicting occupancy were understory vegetation cover, large snag density (>40cm dbh), treatment, large tree density (>50cm dbh), oak basal area, rock cover, pine basal

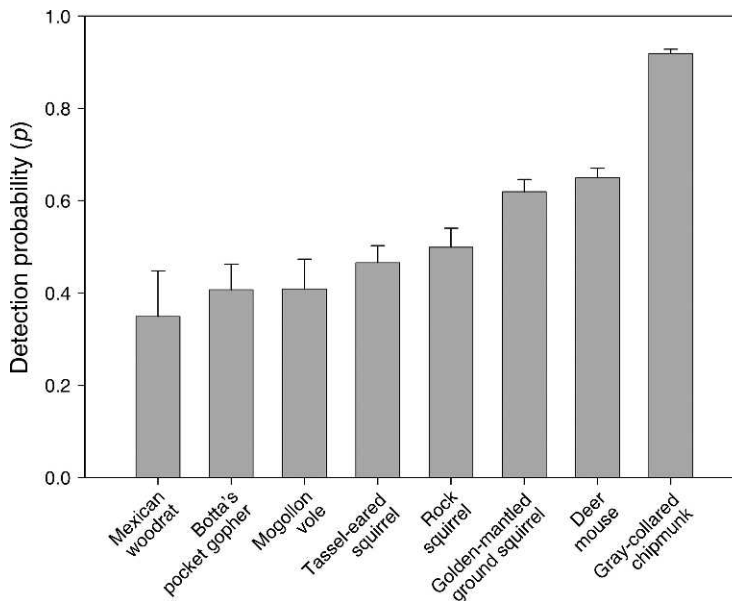


FIG. 2. Detection probabilities (+SE; $n = 294$ samples) for eight species of small mammals over the four years of the study. Each model uses the most parsimonious model of occupancy for each species.

area, year, slash, and snag density (Table 3). Although understory vegetation cover was the most important covariate, we provided occupancy rates in response to pine basal area as this covariate is most easily manipulated by managers, and impacts vegetation cover (Fig. 3).

DISCUSSION AND MANAGEMENT IMPLICATIONS

Managing fire-adapted forests for the small mammal community

Large-scale forest restoration does not afford the luxury of managing wildlife using single species approaches (Carey 2003). Previous studies on fire adapted forests found that most members of the small mammal community exhibited variable and weak responses to treatment and other habitat attributes (as synthesized by Converse et al. 2006c), making it difficult to predict effects at other sites. However, in terms of occupancy, we found that members of the small mammal community were sensitive to treatments and consistent across sites in their responses to habitat covariates. Across the community we examined, the most important predictors of occupancy were understory vegetation, large snags, and treatment, all which can be managed through restoration efforts and the control of livestock grazing. Furthermore, most small mammal species (five of eight; Mogollon vole, deer mouse, golden-mantled ground squirrel, rock squirrel, Botta's pocket gopher) responded strongly and positively to at least one feature typical of open or treated forest, including increased vegetation, decreased basal area, or treatment. One of these species (pocket gophers) responded positively to open forest structure but negatively to treatment, indicating sensi-

tivity to disturbance caused by restoration in the short term. In addition, we identified two forest generalists (deer mice, gray-collared chipmunks) that were common across sites and responded positively to treatments. Past studies have indicated mostly neutral responses to treatments by these genera, likely because certain habitat elements, such as down wood and snags, respond variably to treatment (as synthesized by Converse et al. 2006c). By ranking the relative response of animals to habitat covariates, we found that chipmunks and deer mice responded positively to open forest structure and thinning, but more strongly to rocks, big trees, and large snags, indicating that these features are more important to the species than treatment.

We identified two species that were associated with dense forests (tassel-eared squirrels, Mexican woodrats). In particular, the tassel-eared squirrel (a tree squirrel) has been highlighted as a species that will be negatively impacted by forest treatments (Patton et al. 1985, Dodd et al. 2003, 2006). Tassel-eared squirrels were moderately associated with high basal area and low vegetation cover, but responded strongly positively only to large trees, indicating this was its most important habitat feature. Restoration treatments should promote the growth of both small and large trees in the long term by releasing them from competition (Skov et al. 2005), and thus should eventually ameliorate treatment effects on reduced squirrel density in this and many similar forest systems (Carey 2000, Lehmkühl et al. 2006). Similarly, woodrats were moderately associated with dense forest conditions, and responded strongly negatively to restoration treatments. However, they responded positively to slash piles, which are only found in treated sites. The number and duration of slash piles

TABLE 2. Descriptions and summary statistics for habitat covariates measured at each sampling at each site ($n = 294$ samples) in northern Arizona.

Habitat covariate	Calculation	Range	Median	Average	SD	Final covariate
Treatment size (ha)	calculated from GIS	3–263	54	79	74	omitted from analysis
Pine basal area (m ² /ha)	sum([(dbh/100/2) ²] × 3.14) × 40†	0–109.5	28.6	33.4	20.2	pine basal area
Oak basal area (m ² /ha)	sum([(dbh/100/2) ²] × 3.14) × 40†	0–42	0	1.8	5.0	oak basal area
Understory vegetation (% cover)	average of five plots per site	0–65	19.1	21.4	13.6	understory vegetation
Understory vegetation >40 cm high (% shrub cover)	average of five plots per site	0–43	0	1.0	3.5	omitted from analysis
Understory vegetation species richness (no. species)	total number of species/center plot	1–19	7.3	7.8	3.5	omitted from analysis
Slope (%)	as measured in field	0–30	5.0	6.5	5.7	omitted from analysis
Rock (% cover)	average of five plots per site	0–47	10.2	12.3	9.3	rock
Down wood volume (m ³ /m ²)	9.87 × (sum of widths of wood pieces in plot) ² /8 × 20‡	0–1910.6	3.5	54.5	201.1	omitted from analysis
Density of trees >40 cm dbh (trees/ha)	(trees/plot) × 40	0–240	45.0	68.0	58.1	omitted from analysis
Density of trees >50 cm dbh (trees/ha)	(trees/plot) × 40	0–240	0	25.2	36.6	large tree density
Density of trees >60 cm dbh (trees/ha)	(trees/plot) × 40	0–160	0	10.8	25.7	omitted from analysis
Density of snags (snags/ha)	(snags/plot) × 40	0–1120	0	54.3	124.7	snag density
Density of snags >40 cm dbh (snags/ha)	(snags/plot) × 40	0–40	0	2.6	9.7	large snag density
Density of snags >50 cm dbh (snags/ha)	(snags/plot) × 40	0–40	0	1.4	7.3	omitted from analysis
Density of snags >60 cm dbh (snags/ha)	(snags/plot) × 40	0–40	0	0.75	5.3	omitted from analysis
Slash piles	piles/site	0–38	0	1.4	4.9	slash (combined using PCA)
Time of intact slash piles (yr)	years that piles are present	0–3	0	0.4	0.7	
Proportion of trees removed (%)	(stumps/ha)/([total trees/ha] + [stumps/ha])	0–97.9	37.5	38.5	30.5	treatment (combined using PCA)
Time since treatment (yr)	years	1–109	12	24.3	36.1	
Year	year 1 = 2006, year 2 = 2007, year 3 = 2008, year 4 = 2009					year

† The abbreviation dbh stands for diameter at breast height.

‡ Calculation from Harmon and Sexton (1996).

TABLE 3. Cumulative Akaike information criterion (AIC) weights (w_{ij}) for assessing the relative importance of habitat covariates used to predict occupancy of eight species of small mammals, and averaged over the community, followed by the direction of the response in parenthesis as indicated by model-averaged parameter estimates.

Species†	Pine basal area	Oak basal area	Rock	Understory vegetation	Density of trees >50 cm dbh	Density of snags
Mogollon vole	0.583 (–)	0.879 (–)	0.611 (+)	0.990 (+)	0.654 (–)	0.268 (–)
Mexican woodrat	0.483 (+)	0.275 (–)	0.350 (+)	0.362 (–)	0.398 (+)	0.486 (–)
Deer mouse	0.342 (–)	0.300 (–)	0.980 (+)	0.386 (+)	0.827 (+)	0.294 (+)
Tassel-eared squirrel	0.425 (+)	0.383 (+)	0.377 (–)	0.401 (–)	0.569 (+)	0.323 (–)
Golden-mantled ground squirrel	0.543 (–)	0.532 (–)	0.316 (–)	0.489 (+)	0.309 (+)	0.270 (–)
Rock squirrel	0.576 (–)	1.000 (+)	0.434 (+)	0.991 (–)	0.340 (+)	0.269 (+)
Gray-collared chipmunk	0.335 (–)	0.277 (–)	0.275 (+)	0.426 (+)	0.373 (+)	0.573 (–)
Botta's pocket gopher	0.350 (–)	0.267 (+)	0.307 (–)	1.000 (+)	0.513 (+)	0.358 (–)
Mean	0.455	0.489	0.456	0.631	0.498	0.355

Notes: Values in boldface type indicate strong evidence for a species response to the habitat covariate ($w_{ij} \geq 0.50$). See Table 2 for complete descriptions of habitat covariates.

† For each species, the most parsimonious model of detection probability was used.

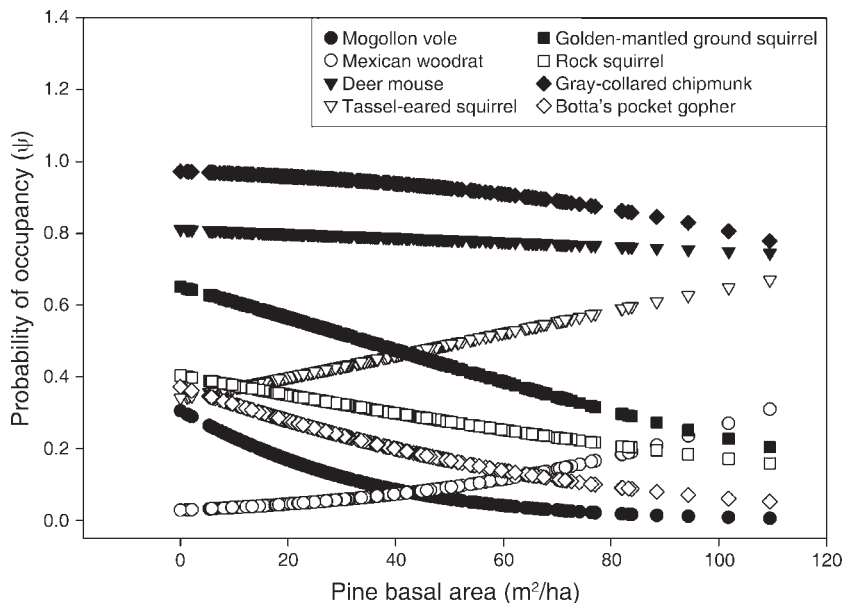


FIG. 3. Probability of occupancy ($n = 294$ samples) for eight species of small mammals in response to pine basal area. Error bars are not shown to increase readability; for each species, average SE across all values of pine basal area is <0.05 (see the Appendix for graph with SEs). Each model uses the most parsimonious model of detection probability for each species.

resulted in a positive occupancy response by most of the small mammal community. This may be because the animals were using the piles as cover, given that recently restored sites are often devoid of woody debris, understory vegetation, and snags in the short term (Chambers and Germaine 2003). Thus, slash piles may serve as surrogate habitat, giving the animals an opportunity to reestablish while the site is otherwise recovering from disturbance, particularly in the absence of down wood. The retention of slash piles on the landscape for several years (piles in our sites were burned after no more than three years) should lead to increased occupancy of most members of the small mammal community. However, because the immediate

removal of these piles can reduce fire hazard, this concern often supersedes opportunities for wildlife habitat enhancement in dry forests.

Although our analysis identified these two species as the “losers” of restoration treatments, their occupancy can be increased by retaining or creating critical habitat features, constituting a reasonable approach to large-scale management. Thus, choosing one species to represent the response of a functional group can be misleading; our finding that each small mammal species increased in occupancy in response to some aspect of restoration treatment demonstrates the benefit of a community perspective on the implications of spatially extensive treatments. In addition, creating a variety of forest structural types on the landscape ensures that the dense-forest obligates are retained, and is likely to lead to higher overall species diversity (Noss et al. 2006a). The occupancy rates we generated in relation to pine basal area can help managers design treatments with varying community compositions, and we would expect similar tradeoffs among these small mammal species or genera in other fire-adapted forest systems (e.g., see Zwolak 2009). Understanding wildlife responses at the community level and across the variability in habitat that results from treatments can thus assist in efforts to design large-scale forest management projects.

Restoring the evolutionary environment

Approximating reference conditions is a successful approach to restoring degraded ecosystems and increasing biodiversity and ecosystem services (Benayas et al. 2009). Since reference conditions for wildlife populations are difficult to reconstruct, recreating the evolu-

TABLE 3. Extended.

Density of snags >40 cm dbh	Treatment	Slash	Year
0.951 (+)	0.465 (+)	0.277 (+)	0.472 (-)
0.265 (+)	0.829 (-)	0.495 (+)	0.267 (-)
0.596 (+)	0.304 (+)	0.266 (+)	0.398 (+)
0.264 (+)	0.316 (-)	0.403 (+)	0.476 (-)
0.702 (-)	0.430 (+)	1.000 (+)	0.861 (-)
0.571 (-)	0.810 (+)	0.276 (-)	0.535 (-)
0.851 (+)	0.787 (+)	0.295 (-)	0.331 (-)
0.271 (-)	0.479 (-)	0.281 (+)	0.261 (+)
0.559	0.553	0.412	0.450

tionary environment is often the default (Morrison 2002). In our study area, southwestern ponderosa pine forests had a lower density of trees prior to Euro-American settlement (ca. 1880; Cooper 1960, Moore et al. 1999), and thus forest species were likely adapted to an open stand structure dominated by large-diameter trees and an herbaceous understory (Covington 2003). We found that all but three species were associated with increased vegetation cover. Tassel-eared squirrel and Mexican woodrat occupancy was associated with dense stands, and it is possible that these species were less common on the landscape before Euro-American settlement (Hoffmeister 1986, Brown and Davis 1998). However, the tassel-eared squirrel responded most strongly to the presence of large trees, which were a dominant structural feature of presettlement forests (Cooper 1961). Thus, our results provide evidence that small mammal species are adapted to the evolutionary environment in terms of forest composition and structure.

Similar to Carey and Harrington (2001), we found that fine-scale heterogeneity was more important to small mammals than landscape-scale features, as we detected no response of species to patch size. In ponderosa pine forest, heterogeneity in habitat is consistent with the natural process of low-severity fire, which would burn in a patchy arrangement across the landscape, killing small trees but leaving large ones (Cooper 1961), retaining some snags and down wood while burning others (Spies and Turner 1999), leaving denser stands of trees particularly on north-facing slopes and steep canyons (Noss et al. 2006a), and regulating litter and understory vegetation levels. All but one species (Mogollon vole) responded positively to density of large trees (>50 cm dbh), and our results suggest that this feature was a part of the small mammal community's evolutionary environment. Similarly, only two species responded positively to all snags but five responded positively to snags >40 cm, likely because larger snags provide larger cavities for nesting and cover (Chambers and Mast 2005). Large trees, and in turn, large snags, have decreased in density due to fire suppression and logging (Covington and Moore 1994a, Mast et al. 1999), and thus managers may choose to make efforts to retain them in an effort to restore the evolutionary environment. However, more may not always be better; for example, although Gambel oak is a part of the evolutionary environment, managers in the Southwest retain all oak when implementing fuels reduction or restoration treatments, and this tree species has been increasing in density since presettlement times (Abella and Fulé 2008). Although oak retention may be important for other animals, as has been shown with birds and bats (Rosenstock 1998, Bernardos et al. 2004), we found that higher oak basal area is not a driver of occupancy for most members of the small mammal community. Finally, as most of the small mammal species live underground in burrows (Hoffmeister 1986),

rock cover was an important covariate across most of the community, and a part of the evolutionary environment not affected by changes to forest structure.

Our findings that small mammals are associated with fire-generated habitat features (e.g., patchy overstory distribution, snags, down wood) are consistent with other wildlife studies in fire dependent, dry forests, mostly in the western and southeastern United States (Kennedy and Fontaine 2009). Examples include Bachman's Sparrow's (*Peucaea aestivalis*) dependency on periodically burned herbaceous understory (Tucker et al. 2004), gopher tortoises (*Gopherus polyphemus*) relying on bare ground (Yager et al. 2007), flying squirrel (*Glaucomys sabrinus*) associations with large trees (Lehmkuhl et al. 2006), and Black-backed Woodpecker (*Picoides arcticus*) and Hairy Woodpecker (*Picoides villosus*) use of fire-created snags (Saab et al. 2009). The affinity the small mammal community exhibited to the evolutionary environment in our study indicates that approximating these conditions can be a useful tool for restoring or sustaining native species of wildlife, particularly when single-species approaches are not feasible (Lindenmayer et al. 2002). This result is relevant to restoration projects in other ecosystems with a paucity of data on historical wildlife populations.

Using occupancy approaches to monitor at large scales

We found that the occupancy modeling approach we used was highly effective in evaluating the response of the small mammal community to treatment and other habitat attributes at a broad spatial scale. Wildlife is important to monitor in large-scale perturbations, as animal communities often recover more slowly than plant communities and other ecosystem functions (Jones and Schmitz 2009). Small mammals are often used as indicators of habitat alteration because they are relatively easy to monitor, but these studies are commonly confounded by high year-to-year variability (Brown and Ernest 2002). Species that are *r* selected and have short life spans and high reproductive rates react quickly and dramatically to environmental and climatic changes (MacArthur and Wilson 1967), and particularly in arid regions, many small-mammal population studies end up primarily tracking precipitation patterns (e.g., Amacher et al. 2008, Bagne and Finch 2009). We attempted to account for this variability by including year as a covariate, and showed a lack of a year effect for all but two species. We attribute this to the fact that we estimated occupancy, which may be more robust to yearly changes than density or abundance metrics. In addition, we were able to sample a large number of sites per year because we did not have to uniquely mark each individual animal. Although our study was effort-intensive, we sampled more area than many comparable small mammal studies with similar objectives, which relied on mark-recapture methods for density estimation (Converse et al. 2006a, 2006b, Wampler et al. 2008, Bagne and Finch 2009). We assessed eight species

whereas the maximum in prior studies was four, and were able to sample two species that had not previously been quantitatively assessed (rock squirrel and Botta's pocket gopher). The scope and scale of our study revealed clear patterns of small mammal community response to treatments and habitat attributes, and resulted in reasonably precise species-level estimates of occupancy. We recommend our approach be utilized in other studies that are faced with high variability and broad spatial and temporal scales in assessing impacts of treatments or habitat alteration on wildlife species. Since forest managers are increasingly focusing on the design and implementation of spatially extensive treatments, improved and efficiently obtained ecological information will be necessary to inform these efforts and guide management of the habitats and evolutionary environments on which native wildlife communities depend.

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SUPPLEMENTAL MATERIAL

Appendix

Probability of occupancy for eight species of small mammals in response to pine basal area (Fig. 3) with standard errors (*Ecological Archives* A022-012-A1).